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| 1 | Encrusters maintain stable carbonate production despite temperature | | | | | |
| 2 | anomalies among two inshore island reefs of the Pilbara, Western | | | | | |
| 3 | Australia | | | | | |
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| 14 | Highlights | | | | | |
| 15 | - Higher CCA cover (%) and carbonate production (g cm ⁻² yr ⁻¹) were recorded in | | | | | |
| 16 | topographically complex sites with greater coral cover, rather than sandy lagoon sites | | | | | |
| 17 | with higher macroalgae coverage | | | | | |
| 18 | - We recorded a decline in lateral CCA cover during the tropical wet season, when reefs | | | | | |

- 19 experienced SSTA of up to $3.6 \,^{\circ}\text{C}$
- Constant carbonate production (g cm⁻² yr⁻¹) was maintained seasonally, even with a
 decline in lateral CCA cover, suggesting vertical growth is favoured during hotter
 months.

23 Abstract

Encrusting reef organisms such as crustose coralline algae (CCA), serpulid worms, bivalves, 24 25 bryozoans, and foraminifera (collectively termed encrusters) provide essential ecosystem services and are a critical part of the reef framework. Globally, research into in situ growth and 26 carbonate production of encrusters has focused on clear water fore-reef settings in the Pacific 27 28 and Caribbean, with limited studies being conducted on marginal reef systems or within the 29 Indian Ocean. Here we examined spatial and temporal variation in CCA coverage (%) and total encruster carbonate production rates (g cm⁻² yr⁻¹) across two inshore turbid island reefs of 30 31 northern Western Australia. We recorded average carbonate production rates of 0.039 ± 0.002 g cm⁻² yr⁻¹, which are comparable to healthy reef sites globally. Our results show variation in 32 lateral CCA cover over small spatial scales, with a strong seasonal signature, while constant 33 average carbonate production rates were maintained. Additionally, we recorded in situ water 34 temperatures above predicted coral bleaching threshold of 29°C for four weeks and found 35 annual patterns of sea surface temperature anomalies (SSTA) of 2°C or more being a regular 36 occurrence over the hotter months. Encrusters on these reefs are considered to have a vital 37 contribution to the reef carbonate budgets, and if they maintain stable carbonate production 38 through periods of SSTA, they may support net positive reef carbonate budgets. 39

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41 Keywords: Marine Encrusters, Crustose Coralline Algae, Carbonate production, Inshore reefs,
42 Carbonate budget

44 **1. Introduction**

From the equator to the poles, crustose coralline algae (CCA) and other calcifying encrusting 45 46 taxa such as serpulid worms, bivalves, bryozoans, and foraminifera (hereon referred to as encrusters), play a critical role in tropical and temperate reef ecosystems (Steneck 1986). These 47 organisms contribute to the construction and stabilisation of reef frameworks (Fabricius and 48 49 De'ath 2001; Rasser and Riegl 2002), bind sedimentary particles (Rasser and Riegl 2002), and 50 add to reef systems' carbonate sediments (Perry 2005; Yamano et al. 2005; Gischler 2006). In 51 particular, CCA provide additional ecosystem services through the provision of settlement 52 substrate for invertebrates such as coral larvae (Heyward and Negri 1999; Fabricius and De'ath 2001; Mason et al. 2011; Gómez-Lemos et al. 2018). As such, CCA contribute to the reef 53 carbonate budget directly, and also indirectly through enhanced coral recruitment, thereby 54 facilitating both reef accretion and reef consolidation (Chisholm 2003; Mason et al. 2011). 55 However, like corals, CCA (and other encrusters) are vulnerable to impacts of climate change 56 57 (Anthony et al. 2008; Kuffner et al. 2008; Martin and Gattuso 2009; Diaz-Pulido et al. 2012), with declines in CCA expected to reduce coral larval recruitment rates (Webster et al. 2011; 58 Doropoulos et al. 2012), and therefore, reef accretion. 59

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Over the past three decades, in situ studies of CCA have covered a diverse range of topics 61 including growth rates (Potin et al. 1990; Martin et al. 2006; Roik et al. 2016), carbonate 62 production (Mallela 2007; Mallela 2013; Morgan and Kench 2014; 2017; Chisholm 2000), 63 patterns of succession and accretion (Matsuda 1989; Mariath et al. 2013), cover and dispersal 64 65 across environmental gradients (Fabricius and De'ath 2001; Dean et al. 2015), community structure (Lei et al. 2018), and competition (Belliveau and Paul 2002; Steneck 2011; Vermeij 66 et al. 2011). These studies have primarily focused on clear water, shallow (<10 m) fore-reef 67 environments of the Great Barrier Reef, the Caribbean, or the Mediterranean. In contrast, only 68

three *in situ* studies have been undertaken within the Indian Ocean, with two based in the 69 Maldives (Morgan and Kench 2014; 2017) and one from temperate Western Australia (Short 70 et al. 2015). These Indian Ocean based studies investigated carbonate production rates by 71 encruster (predominantly CCA) growth on artificial substrates, quantified by weight and/or 72 extension rates. Morgan and Kench (2014, 2017) studied tropical CCA growth and carbonate 73 production on a clear-water reef over a year but did not assess the impacts of seasonality or 74 75 environmental parameters on CCA. In contrast, Short (2015) assessed seasonal differences in temperate CCA carbonate production on a clear water reef following the 2010/2011 marine 76 77 heatwave along the Western Australian coast and found CCA mortality due to thermal stress, but no seasonality in calcification rates. Short's findings contradict a multitude of studies that 78 have recorded increased calcification with seasonal increases in water temperatures (Blake and 79 Maggs 2003; Martin et al. 2006; Kamenos and Law 2010). Such contradictions show a paucity 80 of knowledge on CCA responses to environmental fluctuations within a range of environmental 81 settings (e.g. marginal reefs) where key influences of CCA growth may vary. 82

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It is well established that temperature is a key driver of spatial and temporal growth and 84 calcification of encrusters, particularly CCA (Adey and McKibbin 1970; Kuffner et al. 2008; 85 Hetzinger et al. 2013; Dean et al. 2015). Investigations of CCA physiology with changing 86 temperatures (*in situ* and laboratory) have found higher growth rates during the warmer months 87 (King and Schramm 1982; Potin et al. 1990; Blake and Maggs 2003; Martin and Gattuso 2009). 88 This is expected as warmer waters are more suitable for increased respiration rates (Martin et 89 al. 2007) and photosynthesis (Vásquez-Elizondo and Enríquez 2016; Vogel et al. 2016). 90 91 However, exposure to temperatures outside of thermal limits are likely to reduce CCA growth rates and carbonate production (King and Schramm 1982; Short et al. 2015; Roik et al. 2016; 92 Cornwall et al. 2019, Anton et al. 2020), but at present CCA thresholds to rising temperatures 93

remain ambiguous or largely unknown. This is further compounded by the fact that thermal
thresholds may vary spatially and among species, adding further challenges to understanding
the effects of thermal stress and temperature sensitivity on CCA and other encrusters'.

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Despite the recent increase in attention on the responses of CCA to environmental stressors 98 over the last few decades, the number of studies is considerably less than that for corals. A 99 meta-analysis of laboratory based CCA studies (Cornwall et al. 2019) found only 78 research 100 papers on impacts of ocean acidification (OA) and 14 research papers on rising sea surface 101 102 temperature (SST) effects (or interactions with OA) on CCA calcification. These studies have shown that OA tends to decrease CCA carbonate production rates (Cornwall et al. 2018; 103 Anthony et al. 2008; Kuffner et al. 2008), however, the response varies alongside synergistic 104 interactions with other environmental variables (e.g. temperature, light, nutrients; Hofmann et 105 al. 2014; Ordoñez et al. 2017; Celis-Plá et al. 2015; Comeau et al. 2019). Furthermore, as most 106 107 previous research into the impacts of environmental stress on CCA growth and carbonate production have been conducted in a laboratory setting (e.g. Anthony et al. 2008; Martin and 108 Gattuso 2009; Cornwall et al. 2018), a better understanding of in situ response of CCA to 109 changing environments is required. Doing so will facilitate the identification of CCA (and 110 encruster) environmental thresholds and enable more accurate predictions of future reef 111 stability and development. 112

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Given there is currently little to no knowledge on *in situ* carbonate production rates and thermal thresholds of encrusters within the subtropical Eastern Indian Ocean, this study aimed to quantify rates of CCA carbonate production (g cm⁻² yr⁻¹) and additional encrusting taxa for two inshore marginal island reefs of the Pilbara, Western Australia. Specifically, we: 1) provide the first encruster carbonate production rates for subtropical Western Australia and the Eastern Indian Ocean, 2) assess *in situ* spatial and temporal variations in CCA and encrusting community growth and carbonate production, and 3) identify key environmental and habitat characteristics associated with encruster cover and carbonate production. Finally, we discuss the level of importance encrusters play in the carbonate budgets of these marginal reef systems.

124 **2.** Materials and Methods

125 2.1 Study site

126 The Pilbara coast of north Western Australia hosts a high number of well-developed inshore reef systems that are subject to frequent turbidity events (Baird et al. 2011; Ridgway et al. 127 2016; Moustaka et al. 2018). These reefs are dominated by macroalgae, but also support diverse 128 assemblages of hard corals and invertebrate species (Rosser 2012; Evans et al. 2020). This 129 study was carried out across two inshore island reefs (Eva and Fly) located in Exmouth Gulf, 130 131 which is situated at the southern end of the Pilbara coast (Fig. 1). Eva reef (-21.918454°, 114.433502°), and Fly reef (-21.804829°, 114.554003°) have similar fringing reef morphology, 132 coral cover (8-10 %) and diversity (Shannon-Weiner index 0.73 and 0.76 respectively), and 133 134 wave exposures (high exposure at northern reef sites, with less wave energy experienced at southern sites; Cuttler et al. 2020; Dee et al. 2020). 135

The Pilbara has a dry arid climate, characterised by two main seasons: hot and humid summer, and mild winter (Leighton 2004). Temperatures in the summer average between 36-37°C from November to April, with winter temperatures averaging 28-29°C from May to October. Rainfall is variable annually and is greatest during the summer and early autumn months due to tropical cyclones and storms (Leighton 2004). In this study we focus on these two dominant seasons, and refer to the hot summer months between November and April as the "wet season", and cooler months between May and September as the "dry season".



Figure 1. a) Location of Eva and Fly islands relative to each other with white triangles
depicting where water quality was measured monthly; *b*) and the geomorphology of
surrounding reefs, with white circles indicating the location of experimental tiles and in situ
data loggers for light and temperature.

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149 2.2 Encruster composition and carbonate production

To obtain encruster population characteristics and carbonate production rates, encruster growth 150 tiles were deployed at four sites (two northern and two southern) at each of the two island reefs 151 (Fig. 1). Encruster tiles were made of PVC (10 cm x 10 cm) as this material has previously 152 been shown to produce consistent estimates of carbonate production and abundance 153 representative of communities among adjacent reef substrate (Kennedy et al. 2017). Tiles were 154 lightly sanded and weighed (to within 0.001 g) before deployment and fixed using a screw and 155 stainless-steel plate onto limestone blocks, with the tile placed approximately 4 cm above the 156 substrate. A total of 32 tiles per island were deployed in April 2019, with eight tiles at each of 157 the four sites. Four tiles at each site were removed after the six-month dry season and replaced 158

with four clean tiles to capture growth over the wet season. The remaining four tiles remained*in situ* for 12 months to provide annual encruster cover and carbonate production rates.

Once collected, tiles were placed into individually labelled sealable plastic bags and rinsed with 161 distilled water in the laboratory to remove silt or debris. Tiles were then dried for 24 hours at 162 50° C before both sides were photographed. Community composition was determined by 163 overlaying 200 random points across each image using the Coral Point Count software (CPCe; 164 Kohler and Gill 2006). A 1 cm border was placed around the tile perimeter to discount any 165 edge effect (Mallela 2007), and encrusting organisms (CCA, serpulids, bryozoan, coral, 166 bivalve, foraminifera) under each point were identified to the lowest taxonomic group possible 167 168 (Mallela 2007, 2013; Browne et al. 2013).

169

170 Carbonate production rates by encrusting species were calculated by measuring the weight of calcium carbonate deposited on the tiles over the experimental period. Tiles were treated with 171 a 5% solution of sodium hypochlorite (NaClO) for 24 hours to remove organic tissue, leaving 172 carbonate deposits intact. After rinsing in distilled water, tiles were dried at 50 °C for 24 hrs. 173 Each tile was weighed and then placed in a dilute (10 %) solution of hydrochloric acid (HCl) 174 to dissolve all calcium carbonate. Tiles were again rinsed, dried and reweighed. Carbonate 175 production (g cm⁻² yr⁻¹) was calculated as the total mass (g) of carbonate accretion (initial 176 weight minus end weight), divided by the deployment duration (days) and surface area of the 177 178 tile (cm), then multiplied by 365 days to provide annual rates (Mallela 2007). Calcification rates by encrusters across Eva and Fly reefs were calculated based on net rates of carbonate 179 production, and the proportion of reef area (m^2) available for encruster growth derived from 180 181 census based benthic surveys (see Dee et al. 2020).

183 2.3 Environment and water quality

Monthly water quality data (chlorophyll-a, conductivity, salinity, pH, turbidity) was also 184 collected offshore of each reef (Fig. 1) during neap tides between February 2019 and February 185 2020 (12 months). In situ sampling was undertaken using a vertical profiling method with a 186 multi-parameter EXO Sonde 2 (YSI Inc./Xylem Inc.). The Sonde was set to continuous mode, 187 with data logging at 1 Hz. Profiles were obtained by manually lowering the instrument from 188 189 the surface to the bottom of the water column, and the average value through the profile (minus the top and bottom meter to capture the mid-water column) was used for each water quality 190 191 parameter.

192 During periods of tile deployment, temperature loggers (°C; Hobo Pendant UA-001-64) and photosynthetic active radiation (PAR) loggers (μ mol photons m⁻² s⁻¹; Odyssey submersible 193 PAR logger) were deployed at each site with logging intervals of 60 minutes for benthic 194 temperature and 10 minutes for PAR loggers. Sea surface temperature (SST) and anomaly 195 (SSTA) data were obtained from the NOAA Coral Reef Watch (CRW) daily global 5 km 196 197 satellite coral bleaching heat stress monitoring product suite Version 3.1 (https://coralreefwatch.noaa.gov/product/5km/, Liu et al. 2014) to provide insight into long 198 term SST conditions across the study sites (where SSTA data was established from long term 199 SST averages from 1984-2012). Reef benthic habitat data used in this study was collected using 200 line intercept transects across both reefs in September 2018 (method details are described in 201 Dee et al. 2020). 202

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204 2.4 Statistical analysis

Prior to statistical analysis, carbonate production rate data was square-root transformed to meet
assumptions of normal distribution (Shapiro-wilks test) and equality of variance (Levene test).
Unfortunately, CCA cover could not be transformed to meet parametric assumptions and were

analysed using non-parametric methods. Analysis was then conducted using encrusting
carbonate production rates and lateral CCA cover data, as CCA dominated the encrusting
community. We performed Spearman's correlation analysis (confidence level = 0.95) between
carbonate production rates and lateral CCA cover to determine if the lateral cover of CCA was
the primary contributor to carbonate production rates.

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For each reef, data from the two southern deployment sites were pooled to represent the 214 "southern zone" of the reef, and the same was done for the two northern sites. This resulted in 215 216 a two layer nested design where zone (north or south) was nested within the factor of reef (Eva or Fly). Annual carbonate production rates and lateral CCA cover from tiles deployed over 12 217 months were used to assess spatial variability among reef zones, with tiles deployed over wet 218 and dry seasons used to assess temporal variability. Three-way analysis of variance (ANOVA) 219 was used to test the effects of season, reef, and zone on carbonate production rates. Non-220 221 parametric Kruskal-Wallis (KW) test was employed to test for variation in lateral CCA cover between spatial levels (reef, zone) and seasons, with a multiple-comparisons Bonferroni 222 correction of $p \le 0.0167$ to control for multiple tests. Any significant results of KW test for 223 factors with more than two levels were followed by a post-hoc Dunn's test to investigate the 224 source of variance. 225

226

Principal Component Analysis (PCA) was used to identify key environmental variables and
reef habitat data (spatial only) that were associated with sites depending on the reef (Eva, Fly),
or the reef zone (north, south). In addition, we carried out Distance Based Linear Modelling
(DistLM, PERMANOVA) to identify key environmental and habitat variables related to both
spatial and temporal variations in CCA cover and carbonate production rates. CCA cover and
encrusting carbonate production rates were square-root transformed, and resemblance matrices

were calculated using the Bray Curtis similarity index. Water quality and habitat data were
normalised and DistLM models were determined using the 'Best' procedure and Akaike
information criterion (AIC) selection criterion with 9999 permutations. DistLM analysis was
implemented in Primer7 software (ver. 7.0.13), with all other analyses performed in RStudio
(version 1.1.463) using the vegan (Oksanen et al. 2019), ggplot2 (Wickham 2011), and Dunn's
test (Dinno 2017) packages.

239

3. Results

241 3.1 Carbonate production rates and encruster cover

On average, encrusters covered 77 \pm 4.9 % and 64 \pm 5.0 % of the PVC tile surface area at Eva 242 and Fly reefs, respectively. Across both reefs, CCA was the dominant encrusting organism 243 with cover ranging from 37 to 95 % (of encrusting cover; 72 % mean) of the tile surface. Other 244 encrusters found on the tiles, but in smaller quantities included bryozoans (mean cover = 1.2245 %), serpulids (mean cover = 0.9 %) and coral recruits (mean cover = 0.8 %). CCA cover and 246 247 carbonate production rates were positively correlated across all deployment periods, with more than 50 % of the variation in CCA cover correlated to carbonate production rates (Dry season: 248 R = 0.53, p = 0.005; Wet season: R = 0.50, p = 0.018; Annual: R = 0.61, p = 0.002; Fig. 2). The 249 data also revealed variability between these two parameters, whereby high CCA cover does 250 not always equate to higher carbonate production. 251



Figure 2. Spearman rank correlation between CCA tile coverage (%) and encruster carbonate
 production rates (g cm⁻¹yr⁻¹) from a) dry season deployment, b) wet season deployment, and c) Annual
 deployment periods. All results are significant at confidence interval 95 %

Table 1. Three-way analysis of variance (ANOVA) to test for effects of season, reef, and zone on rates 258 of carbonate production (g cm⁻¹yr⁻¹) from encrusting taxa on settlement tiles. Significant values

highlighted in bold.

| | df | ms | F value | p value |
|--------------------|----|-------|---------|-----------|
| Season | 1 | 0.000 | 0.021 | 0.885 |
| Reef | 1 | 0.007 | 4.350 | 0.040 |
| Zone | 1 | 0.032 | 18.743 | 4.51 e-05 |
| Season: Reef | 1 | 0.001 | 0.427 | 0.515 |
| Season: Zone | 1 | 0.000 | 0.126 | 0.724 |
| Reef: Zone | 1 | 0.019 | 10.969 | 0.001 |
| Season: Reef: Zone | 1 | 0.009 | 5.058 | 0.027 |
| Residuals | 76 | 0.002 | | |

| 262 | Table 2. a) non-parametric Kruskal-Wallis test show variation in CCA lateral cover(%) between reefs, |
|-----|---|
| 263 | zones, and seasons with a multiple-comparisons Bonferroni correction of 0.0167 applied. Post-hoc |
| 264 | Dunn's test (Bonferroni method) was carried out to investigate variation among b) reef specific zones |
| 265 | and c) seasons. |

| <i>a</i>) | | | | |
|------------|---------------|---------------|---------------|--|
| | Chi-square | | p-value | |
| Reef | 3.533 | 1 | 0.060 | |
| Zone | 24.585 | 1 | 8.32e-07 | |
| Season | 9.25 | 2 | 0.010 | |
| b) | | | | |
| | Eva S - Eva N | Eva S - Fly S | Eva N - Fly S | |
| Ζ | -4.079 | 1.361 | 5.117 | |
| p-value | <0.001 | 0.521 | <0.001 | |
| | Eva S - Fly N | Eva N - Fly N | Fly S - Fly N | |
| Ζ | -2.066 | 2.147 | -3.275 | |
| p-value | 0.117 | 0.096 | 0.003 | |
| <i>c</i>) | | | | |
| | Dry-Wet | Dry- Annual | Wet- Annual | |
| Ζ | 3.745 | 2.459 | -1.322 | |
| p-value | <0.001 | 0.021 | 0.279 | |

266

Annual average carbonate production rates ranged from 0.024 to 0.062 g cm⁻² yr⁻¹ (mean = 267 0.039 ± 0.002 g cm⁻² yr⁻¹) and varied between reefs (Eva = 0.042 ± 0.003 g cm⁻² yr⁻¹, Fly = 268 0.035 ± 0.003 g cm⁻² yr⁻¹, F = 4.350 p = 0.040, Fig 3a). This equates to annual carbonate 269 production rates of 0.436 \pm 0.029 and 0.329 \pm 0.044 kg m⁻² yr⁻² at Eva and Fly reefs, 270 respectively. There was a significant interaction effect between factors reef and zone (F =271 10.969, p=0.001, Table 1) on encruster carbonate production, with the highest carbonate 272 production rates in the northern zone of Eva reef (average = 0.056 ± 0.003 g cm⁻² yr⁻¹). 273 274 Although annual CCA cover was more than 10% higher at Eva reef (Eva = 77%, Fly 64%) there was no statistically significant variation in CCA cover between reefs (H = 3.533, p= 275 0.060, Table 2 Fig 3b). There was, however, a significant variation in CCA coverage between 276 277 zones (H = 24.585, p = 8.32e-07), with post-hoc tests identifying significantly higher CCA coverage at the northern zones at both reefs (Fig 3; Table 2b). 278

Patterns in seasonal encruster carbonate production were not consistent both between reefs, 280 and zone (F = 5.058, p = 0.027; Table 1). For example, highest rates were recorded on annual 281 tiles at Eva north, whereas highest rates during the dry season were recorded on tiles at Eva 282 south, and wet season tiles at Fly south (Fig. 3a). In contrast, lateral cover of CCA was 283 284 consistently higher in the dry season compared to the wet season across all locations (Dunn's test $p = \langle 0.001, Table 2c, Fig.3b \rangle$. Given annual tiles were deployed for twice as long as 285 seasonal tiles, it was interesting to see the average cover of CCA on annual tiles (total average 286 $= 72 \pm 3.7$ %) was only 6 % greater than that of wet season tiles (total average = 65 ± 3.1 %), 287 and 16 % lower than dry season tiles (total average = 81.1 ± 2.7 %, Dunn's test p = 0.021). 288

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290

Figure 3. a) Carbonate production rates (g cm⁻² yr⁻¹) across the four zones (Eva north, Eva south, Fly north, Fly south) between the two reefs (Eva and Fly) during the dry season (April-September), the wet season (October-March) and annually. b) Lateral coverage of CCA across each of the four zones during the dry and wet seasons, as well as annual coverage.

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| AIC | R^2 | RSS | No.Vars | Selections | |
|------------|-------|------|---------|--|--|
| 121.44 | 0.61 | 2294 | 5 | Light, Coral, Macroalgae, Turfing Algae, Sand | |
| 121.74 | 0.61 | 2323 | 6 | Temp, Chlorophyll-a, Turbidity, Salinity, Coral, Sand | |
| 122.10 | 0.56 | 2563 | 4 | Temperature, Light, Salinity, Sand | |
| b) | | | | | |
| AIC | R^2 | RSS | No.Vars | Selections | |
| 89.10 | 0.43 | 648 | 4 | Temp, Light, Salinity, Sand | |
| 89.12 | 0.43 | 649 | 4 | Temp, Salinity, Turfing Algae, Sand | |
| 90.39 | 0.45 | 629 | 5 | Light, Coral, Macroalgae, Turfing Algae, Sand | |

297 *Table 3.* Distance based linear modelling (DistLM) of spatial environmental and habitat data 298 considering a) carbonate production rates (g cm⁻² yr⁻¹) and b) lateral CCA cover (%) on experimental 299 tiles. The model with the lowest AIC values was selected (in bold).

300

a)

301 3.2 Environmental influence on spatial variation of carbonate production and lateral CCA cover302

Annual averages in environmental and habitat data at each of the four zones were used to 303 identify key environmental parameters that were associated with spatial differences in 304 carbonate production rates and lateral CCA cover. Average water temperatures taken at the 305 benthos were comparable between reefs (Fly 24.9 \pm 0.02 °C; Eva 24.8 \pm 0.02 °C), as was 306 salinity (Fly mean = 38.16 ± 0.42 psu; Eva mean = 38.34 ± 0.46 psu), and conductivity (Fly 307 mean = 57149 \pm 982 μ S/cm; Eva mean = 57150 \pm 965 μ S/cm; Table S2). However, Fly reef 308 experienced nearly 50 % higher turbidity levels (Fly mean = 2.27 ± 0.36 FNU; Eva mean = 309 1.48 \pm 0.33 FNU), as well as slightly higher chlorophyll-a (Fly mean = 0.49 \pm 0.05 ug. L⁻¹; Eva 310 mean = 0.38 ± 0.05 ug. L⁻¹) and pH (Fly mean = 8.19 ± 0.03 ; Eva mean = 8.17 ± 0.01 ; Fig. 4a, 311 Table S2), whereas Eva was exposed to higher levels of light (Fly mean = $177.52 \pm 1.73 \mu$ mol 312 photons m⁻² s⁻¹; Eva mean = $228.06 \pm 2.38 \mu$ mol photons m⁻² s⁻¹; Fig. 4a, Fig. 5). In addition, 313

benthic temperatures were comparable between reef zones (north = $24.95 \pm 0.02^{\circ}$ C, south = $24.92 \pm 0.02^{\circ}$ C), whereas light was typically higher in the southern zones (north = $124.63 \pm 1.59 \,\mu$ mol photons m⁻² s⁻¹, south = $220.95 \pm 2.50 \,\mu$ mol photons m⁻² s⁻¹; Fig. 4b and Fig. 5).





318 Figure 4. Principle component analysis (PCA) of environmental and habitat variables between reefs

- (a), and between reef zones (b). The *x*-axis is the first principal component, and the *y*-axis is the second
- $320 \qquad \text{principal component. MA} = \text{Macroalgae, TA} = \text{turfing algae}$





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Figure 5. Light levels collected by photosynthetic active radiation (PAR) loggers at the benthos during
 encruster growth at north and southern sites at each reef between April 2019 - April 2020. Loggers were
 changed out in early October 2019 at the beginning of the wet season, which is shaded in orange.

Benthic cover was comparable between reefs with similar coral cover (8 % at Fly, 10 % at Eva) 327 and fleshy algal cover dominating the benthos (macro-algae = 35 % at Fly, 56 % at Eva; turfing 328 algae = 15 % at Fly and 16 % at Eva; Dee et al. 2020). However, there were distinct differences 329 in benthic cover between south and north reef zones (Fig. 4b, Table S1). Southern zones were 330 characterised by higher macroalgae cover (52-67 % for Fly and Eva respectively) and 331 exceptionally low coral cover (1-2 %). Whereas northern zones displayed lower macroalgae 332 cover (0-28 %) and higher coral cover (29-37 %), and high cover of turfing algae (16-35 %) 333 with the latter growing predominantly on dead coral substrate. 334

Environmental and habitat data explained 61 % and 43 % of the spatial variation (using annual 335 tiles) in carbonate production rates and lateral CCA cover, respectively (Table 3). Carbonate 336 production rates were found to be predominantly associated with benthic cover (coral, 337 macroalgae, turfing algae) and light, whereas CCA cover was influenced by environmental 338 factors including temperature, light, salinity, and sand cover (Table 3). Marginal tests found 339 temperature and coral cover to have the strongest influence explaining 18 % and 19 % of the 340 variation in lateral CCA cover, respectively (Table S3). In contrast, macroalgal cover was the 341 only significant factor associated with carbonate production rates, explaining 18 % of the 342 spatial variation (Table S3). 343

344

345 3.3 Environmental influence on temporal variation of carbonate production and lateral CCA
346 cover

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The wet season was characterised by more than double light levels (WS = $224.78 \pm 2.04 \mu mol$ photons m⁻² s⁻¹; DS = $105.72 \pm 1.50 \mu mol$ photons m⁻² s⁻¹; Fig 5, Fig. 6); higher conductivity (WS = $59109.25 \pm 1010.74 \mu S/cm$; DS = $55550.29 \pm 754.80 \mu S/cm$) and higher salinity (WS = 39.22 ± 0.13 psu; DS = 37.41 ± 0.54 psu; Fig. 6, supp. Table 2). The wet season also

352 experienced higher benthic temperatures (WS = 29.0 ± 0.4 °C, DS = 24.3 ± 0.6 °C, measured with *in situ* loggers) as well as sea surface temperatures (WS = $25.7^{\circ}C \pm 0.8$, DS = 23.4 ± 0.9 353 °C). During the wet season, specifically between December 2019 to January 2020, SST 354 anomalies (SSTA) ranged from 1 to 3.2 °C (Fig. 7). This level of SSTA is not uncommon for 355 Exmouth Gulf, as SSTA of 2 °C or more have occurred annually during December and January 356 (excluding 2018) since 2003 (Fig 7c). Dry season SST for the duration of this study were 357 comparable to historic temperatures, with the exception of June and July 2019 that experienced 358 average SSTA of -1.8 °C and -1.5 °C (Fig. 7d). Further, the dry seasons experienced higher 359 levels of chlorophyll-a (0.54 ug. L⁻¹ \pm 0.04, WS 0.33 ug. L⁻¹ \pm 0.05) and turbidity (2.03 FNU \pm 360 0.38, WS 1.61 FNU ± 0.13, Fig 6) 361

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Figure 6. Principle component analysis of environmental variables driving seasonal variation between dry (April-September), and wet (October-April) seasons 2019-2020.

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Figure 7. Temperature patterns within the Exmouth Gulf showing a) SSTA recorded over the wet 368 369 (summer) season 2019-2020 for the Exmouth Gulf and Ningaloo coast, b) monthly average sea surface temperatures (SST) recorded between 2003 and 2020, c) monthly average sea surface temperature 370 anomaly (SSTA) recorded between 2003 and 2020, d) daily SST and SSTA recordings from January 371 2019 to April 2020. All data obtained from by NOAA Coral Reef Watch (CRW) daily global 5 km 372 satellite 373 coral bleaching heat stress monitoring product suite Version 3.1 (https://coralreefwatch.noaa.gov/product/5km/.) 374

Table 4. Distance based linear modelling results for seasonal mean environmental and water quality
measures explanation for a) carbonate production rates and b) lateral CCA cover %. The model with
the lowest AIC values was selected (in bold).

| AIC | R^2 | RSS | No.Vars | Selections |
|------------|-------|---------|---------|--|
| 240.76 | 0.11 | 6126.30 | 3 | Temperature, Conductivity, Chlorophyll- a |
| 240.80 | 0.07 | 6392.6 | 2 | Light, Turbidity |
| 240.88 | 0.07 | 6403.0 | 2 | Conductivity, Chlorophyll-a |
| 241.1 | 0.07 | 6437.9 | 2 | Salinity, Conductivity |
| b) | | | | |
| AIC | R^2 | RSS | No.Vars | Selections |
| 158.84 | 0.31 | 1111.80 | 3 | pH, Salinity, Conductivity |
| 158.84 | 0.31 | 1111.80 | 4 | pH, Salinity, Conductivity, Chlorophyll-a |
| 158.84 | 0.31 | 1111.80 | 4 | pH, Salinity, Chlorophyll-a, Turbidity |

a)

Environmental data explained 11 % and 31 % of the temporal variation in carbonate production 379 and lateral CCA cover, respectively (Table 4). Lateral coverage of CCA between seasons were 380 associated with shifts in pH, salinity, and conductivity (AIC = 158.84, $R^2 0.31$), while marginal 381 tests also found benthic temperature to be a significant influencing factor (Pseudo-F = 13.18, 382 p = 0.001, Prop = 0.223, Table S4). CCA cover was significantly lower in the wet season when 383 temperatures, salinity and conductivity were all relatively high. Temperature, together with 384 conductivity and chlorophyll-a were also found to be related to changes in carbonate production 385 rates (Table 4b). However, DistLM marginal tests found no significant association of 386 environmental variables when modelled individually with carbonate production rates (Table 387 S4). This is most likely due to a lack of constant variation in carbonate production rates between 388 389 seasons.

390

391 **4 Discussion**

392 This study provides the first carbonate production rates of encrusters for inshore subtropical reefs within the Eastern Indian Ocean and Western Australia. Annual carbonate production 393 rates of encrusting organisms at Eva and Fly reefs varied from 0.024 to 0.062 g cm⁻² yr⁻¹ (mean 394 = 0.039 ± 0.002 g cm⁻² yr⁻¹), which are comparable to rates recorded in the tropical Indian 395 Ocean, subtropical Atlantic, and from inshore reefs in the Pacific. For example, clear water 396 reefs in the Maldives had mean carbonate production rates at the upper range of our study at 397 0.056 ± 0.029 g cm⁻² yr⁻¹ (Morgan and Kench 2017), with similar rates recorded in a different 398 ocean basin (e.g Florida Keys at 0.054 g cm⁻² yr⁻¹; Kuffner et al. 2013). In the Pacific, inshore 399 sites of the Great Barrier Reef returned highly variable rates of between 0.009 ± 0.001 to 0.058400 \pm 0.012 g cm⁻² yr⁻¹ (Browne et al. 2013), and inshore sites from Tahiti and Moorea recorded 401 higher rates of 0.020 ± 0.019 and 0.065 ± 0.042 g cm⁻² yr⁻¹, respectively (Pari et al. 1998). 402

Among all these sites, CCA was the dominant encrusting taxa (45-99 % of encruster cover), which was also found across sites within this study (77 ± 4.9 % and 64 ± 5.0 % at Eva and Fly reefs, respectively).

406

407 Although we found a mild relationship between lateral CCA cover and carbonate production rates, measuring lateral CCA cover on reef substrate may not be an appropriate proxy for 408 carbonate production. At some sites high CCA cover did not produce higher carbonate 409 production rates, a disconnect that occurred between reefs and seasons. Specifically, annual 410 411 settlement tiles from Eva reef and tiles deployed during the dry season (at both reefs), displayed significantly higher CCA cover than annual tiles at Fly reef and tiles deployed over the wet 412 413 season, respectively. Yet mean carbonate production rates were approximately equal at Eva and Fly and across seasons. This disconnect between lateral CCA cover and carbonate 414 production could potentially be due to different CCA growth morphologies and differences in 415 416 environmental conditions (e.g. light, temperature, salinity) over small spatial scales that may 417 favour CCA taking on different growth strategies over time. We know that early successional CCA species with thin thalli (crust) opportunistically recruit (within two weeks) on to bare 418 419 substrate and then spread laterally (Adey and Vassar 1975; Mariath et al. 2013). These crusts have very little biomass (g) and, therefore, do not provide a substantial contribution to final 420 carbonate production rates, as opposed to successor species that develop thicker crusts 421 (Matsuda 1989; Mariath et al. 2013). The development of thicker crusts by successor species 422 often results in lower lateral growth (Steneck 1986) because of the energetic trade-off between 423 424 lateral growth and maintaining nonphotosynthetic tissue within the crust (Mccoy and Kamenos 2015). This nonphotosynthetic tissue produces seasonal growth banding, whereby warmer 425 426 summer temperatures result in wider bands (see Kamenos and Law 2010). Therefore, if CCA 427 cover on reef substrate is surveyed during warmer months where taxa are prioritising vertical growth, it is suggested that employing lateral cover of CCA as a proxy for carbonate productionmay lead to underestimating production rates.

430

Within this study, carbonate production and lateral CCA cover of encrusters was greater among 431 432 northern reef sites that were more characteristic of "healthy" reef systems. High coral cover (29-37%) found in northern zones of Eva and Fly reef, provide hard substrate and greater 433 topographic complexity for encruster settlement and offers some protection from grazing 434 predators (Graham and Nash 2013). In contrast, southern zones were characteristic of lagoonal 435 habitats with higher coverage of macroalgae, which compete with CCA for space and 436 irradiance (Dethier 1994; Marcia et al. 1996). Furthermore, it is known that CCA species with 437 thin crust, such as *Mesophyllum spp.*, are predominantly found under macroalgal canopies 438 (Figueiredo and Steneck 2000). Although southern zones were moderately shallow and 439 exposed to high levels of light, inadequate substrate (soft sand and patchy macroalgae) meant 440 441 there are less established CCA with thick crusts to provide recruits to settlement tiles. This spatial variation in habitat demonstrates a limited potential for substantial carbonate production 442 in habitats characterised by high levels of macroalgae and minimal hard substratum. 443

Seasonally, carbonate production rates varied inconsistently, maintaining stable average 444 seasonal production rates across all zones. Meanwhile, lateral CCA cover showed consistent 445 seasonal fluctuations. Annual tiles were expected to have the greatest lateral coverage of CCA 446 since they were deployed for twice as long as seasonal tiles, however, tiles deployed over the 447 six month dry season had the highest lateral CCA cover. This suggests that established CCA 448 on the annual tiles may have died off or been physically removed during the wet season. We 449 450 propose multiple theories to explain these findings. Firstly, there may have been an increase in predation by grazers of thin crusts (e.g. urchins and fish; Padilla 1984; Steneck 1986) on tiles 451 during the wet season. Secondly, partial or total mortality of dry season recruits during the wet 452

453 season, with replacement by recruits employing different growth strategies (vertical rather than
454 lateral growth). We propose the later theory is more likely considering the relationship between
455 warmer waters and crust thickness discussed above, as well as high SST recorded during the
456 wet season that were potentially above thermal thresholds of some CCA.

457

Sea surface temperatures above 29°C and SSTA over 2°C have caused significant thermal 458 stress on encrusters globally as well as among temperate West Australian reefs. For example, 459 SST's from 25-29°C (SSTA 1-4°C) affected the health and survival of CCA and bryozoan 460 species in the Mediterranean (Martin and Gattuso 2009; Pagès-Escolà et al. 2018), while SST's 461 between 26 and 33°C reduced carbonate production rates of CCA in the Red Sea (Roik et al. 462 2016), and SST's from 28 to31°C (SSTA 2-4°C) reduced calcification and survival of CCA 463 from the Great Barrier Reef, Australia (Webster et al. 2011; Diaz-Pulido et al. 2012). Short et 464 al. (2015) recorded thermal stress and mortality of CCA off temperate Western Australia due 465 to consecutive summer periods (2012 and 2013) with SSTA of 2°C during a major marine 466 heatwave event along the West Australian coast (Feng et al. 2013; Lafratta et al. 2017). Given 467 these findings, as well as a decline in lateral CCA cover, we expected a decline in carbonate 468 production rates on tiles deployed over the wet season in response to substantial SSTA 469 experienced at Eva and Fly reefs. But carbonate production only declined among the southern 470 zone of Eva reef, while all other zones displayed constant rates across seasonal deployment 471 periods. A comparison with historical SSTA confirms that over the last eight years, the inshore 472 reefs of Exmouth Gulf are regularly exposed to prolonged SSTA of 2°C during the wet season. 473 474 As a decline in carbonate production was not observed in this study, we hypothesise that CCA and encrusting taxa inhabiting these reefs may be tolerant to these annual conditions. 475

Encrusters play an important role in the consolidation and stabilisation of reef framework, 477 therefore consistent carbonate production by encrusters is vital to a reef's carbonate budget. 478 Calcification rates by encrusters across Eva and Fly reefs were estimated based on net rates of 479 production, and the proportion of reef area (m²) available for encruster growth to be 0.436 \pm 480 0.029 and 0.329 \pm 0.044 kg m⁻² yr⁻². These calcification rates are approximately 11.4% of the 481 rates produced by corals across both reef sites (see Dee et al. 2020). This contribution to the 482 483 overall carbonate budget is a magnitude higher than that of inshore reefs of the Great Barrier Reef, where encrusters contributed 0.94 - 4.27 % of the calcification rates produced by corals 484 485 (Browne et al. 2013). Similarly, calcification rates of encrusters from an inshore site of Jamaica contributed 2.61% of that produced by corals (Mallela and Perry 2007). The rates recorded for 486 Eva and Fly show that encrusters (particularly CCA) make up a vital portion of the carbonate 487 budgets of these inshore reefs, and if they have the potential to maintain stable carbonate 488 production with rising ocean temperatures, could result in net positive carbonate budgets in 489 periods where carbonate production by corals is impeded. 490

491

We have documented the maintenance of stable carbonate production by CCA through a period 492 of high SSTA. However, we stress that we are not able to confirm long-term encruster 493 community adaptations or shifts in CCA growth morphologies from this study due to data being 494 collected over one annual cycle. In order to fully understand the effects of thermal stress and 495 temperature sensitivity of CCA (and other encrusters), future works should be conducted over 496 multiple years and include seasonal, reef scale experiments. Species identification to determine 497 498 population and morphology shifts that occur seasonally, as well as in situ measurements of CCA physiology on temporal and spatial scales, would bring greater understanding of how 499 500 CCA are responding to ocean change within their reef settings. This knowledge will be valuable 501 for carbonate budget and reef growth estimates given that expected climate change scenarios

502 (RCP 8.5) are predicted to lead to declines in coral cover and reef health (van Woesik and 503 Cacciapaglia 2018). As CCA is a preferred settlement substrate for coral larvae, a better 504 understanding of how CCA respond to climate stressors *in situ* would give more confidence to 505 predictions of reef recovery after a disturbance.

506

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