

Coral reef encruster communities and carbonate production in cryptic and exposed coral reef habitats along a gradient of terrestrial disturbance

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Received: 17 February 2007 / Accepted: 27 May 2007
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Abstract Encrusting calcareous organisms such as bryozoans, crustose coralline algae (CCA), foraminiferans, and serpulid worms are integral components of tropical framework-building reefs. They can contribute calcium carbonate to the reef framework, stabilise the substrate, and promote larval recruitment of other framework-building species (e.g. coral recruits). The percentage cover of encrusting organisms and their rates of carbonate production ($\text{g m}^{-2} \text{ year}^{-1}$) were assessed at four sites within a coastal embayment, along a gradient of riverine influence (high-low). As the orientation and type of substrate is thought to influence recruitment of encrusting organisms, organisms recruiting to both natural (the underside of platy corals) and experimental substrates were assessed. The effect of substrate exposure under different levels of riverine influence was assessed by orientating experimental substrates to mimic cryptic and exposed reef habitats (downwards-facing vs upwards-facing tiles) at each site. Cryptic experimental tiles supported similar encruster assemblages to those recruiting to the underneath (cryptic side) of platy corals, suggesting that tiles can be used as an experimental substrate to assess encruster recruitment in reef systems.

Encruster cover, in particular CCA, and carbonate production was significantly higher at low-impact (clear water), high wave energy sites when compared to highly riverine impacted (turbid water), low wave energy sites. Cryptically orientated substrates supported a greater diversity of encrusting organisms, in particular serpulid worms and bryozoans. The inverse relationships observed between riverine inputs and encrusters (total encruster cover and carbonate production) have implications for both the current and future rates and styles of reefal framework production.

Keywords Recruitment · Coral reef framework · Experimental tiles · Sedimentation · River runoff · Encrusters

Introduction

Calcareous encrusting organisms, from hereon referred to as encrusters, include bryozoans, crustose coralline algae (CCA), serpulid worms, foraminifera, and bivalves. They form important components of tropical coral reef framework and can fulfil a number of functional roles. Morphologically, they are low in profile, with their basal surface being cemented to the reef substrate. As they grow, they contribute calcium carbonate to the reef framework, reinforce the underlying skeletal structure of coral substrates, infill cracks in the framework, stabilise the substrate, and maintain topographic complexity (Scoffin and Garrett 1974; Martindale 1976; Taylor 1990; Scoffin 1992; Perry 1999; Mallela and Perry 2007). CCA may also induce larval settlement of other types of reef benthos, including some hard and soft corals (Morse et al. 1988; Fabricius and De'ath 2001).

Communicated by Geology Editor B. Riegl.

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The distribution and growth of encrusting communities is influenced by a range of factors, which include habitat type (e.g. exposed or cryptic), light, sediment, wave energy, and substrate stability (Choi and Ginsburg 1983; Martindale 1992; Gischler and Ginsburg 1996; Fabricius and De'ath 2001). Cryptic reef habitats include cavities, crevices, boreholes, and the underside of reef substrates (e.g. rubble, coral colonies, under-hangs). Whilst this makes them hard to observe in situ, for example during routine diver surveys, their function on the reef should not be underestimated. The surface area, and in some case the biomass, of cryptic reef habitats, is thought to exceed that of the exposed reef surface (Buss and Jackson 1979; Gischler and Ginsburg 1996). Cryptic habitats are also characterised by reduced levels of predation and physical disturbance compared to exposed reef habitats.

A number of studies document encruster development on various substrates and under different environmental settings: patterns of coelobite recruitment to the underside of rubble have been described in Florida (Choi and Ginsburg 1983; Gischler 1997), Belize (Gischler and Ginsburg 1996), and Curacao and Bonaire (Meesters et al. 1991); Perry (1999) detailed the role of encrusters in reef framework preservation; whilst Rasser and Riegl (2002) reviewed their role as binding agents of rubble. The ecology of encrusters recruiting to cryptic experimental and natural coral substrates has also been described at various depths in Jamaica (Jackson and Winston 1982) and other studies documented competitive interactions for space on cryptic substrates (Osman 1977; Buss and Jackson 1979). Shifts in encruster development following hurricane and storm generated disturbances in Jamaica and Barbados have also been detailed (Scoffin and Hendry 1984; Perry 2001). Only a limited number of studies have documented variation in encruster development along environmental gradients, or in relation to different habitat types. Fabricius and De'ath (2001) showed an inverse relationship between sediment inputs and CCA recruiting to natural substrates on the Great Barrier Reef, whilst Martindale (1992) detailed encruster zonation, growth rates, and morphology in relation to levels of incident light and water turbulence in Barbados. Martindale (1992) also highlighted how encrusting calcareous communities can be used as palaeoecological tools to interpret environmental conditions such as sea level rise and other catastrophic events.

Interestingly, the majority of encruster studies rely on visual estimates of encruster cover (%) or growth rate measurements (e.g. vertical accretion and lateral extension, mm year^{-1}) in order to determine the relative importance of encruster assemblages with regards to reefal framework production or substrate stabilisation (Jackson and Winston 1982; Davies and Hutchings 1983). Studies of coral calcification highlight how such data should be treated with

caution. Enhanced growth rates in carbonate-producing organisms may not always result in enhanced rates of calcification as skeletal density can vary under different environmental regimes (Hughes 1987; Edinger et al. 2000). Relatively few studies have quantified encruster carbonate production ($\text{g m}^{-2} \text{year}^{-1}$). Of those that have, reef wide averages for CCA are typically given (Stearn et al. 1977) whilst other encrusting organisms have generally been overlooked (but see Harney and Fletcher 2003).

Whilst encruster assemblages are thought to be associated with clear marine waters and sediment free substrates, relatively little is known about how terrestrial inputs (e.g. riverine sediment) influence encruster distribution and carbonate production in different reef habitats. There has also been some debate as to whether or not experimental (artificial) substrates can be used as an alternative to natural substrates (Glasby and Connell 2001). This study assessed: (1) if encruster cover varied between artificial substrates and natural coral substrates; (2) if substrate orientation (i.e. cryptic vs exposed) influenced encruster recruitment and carbonate production; and (3) if riverine inputs influenced encruster recruitment and carbonate production in cryptic and exposed habitats.

Materials and methods

Study sites

Four marine study sites were selected along a gradient of riverine influence within the Rio Bueno embayment, north Jamaica (Fig. 1). Site names, locations and field seasons detailed here are identical to those in Mallela et al (2004). Riverine influence was characterised according to a series of in situ environmental measurements which assessed: (1) terrestrial sediment inputs (sedimentation rates, carbonate:clastic ratios, total suspended sediment, turbidity and light attenuation); (2) salinity; and (3) water temperature. All environmental measurements were taken regularly (weekly, weather permitting) during two field seasons: April–September 2001 and June–August 2002. Detailed descriptions of environmental and water quality parameters, zones of riverine disturbance, monitoring methods, and coral communities at each study site are given in Mallela et al (2004). Mallela et al (2004) identified sites 3 and 6 as sheltered (average Beaufort scale over two field seasons: <2), turbid water reef sites. This was directly attributed to their close proximity to the river mouth (straight line distance: 550 and 700 m respectively). Sites 3 and 6 were subsequently classed as being within the medium to high-impact zone of disturbance within the embayment, from hereon referred to as “high-impact” sites. In contrast, sites 2 and 8 were located further from the river mouth (950 and 1,450 m

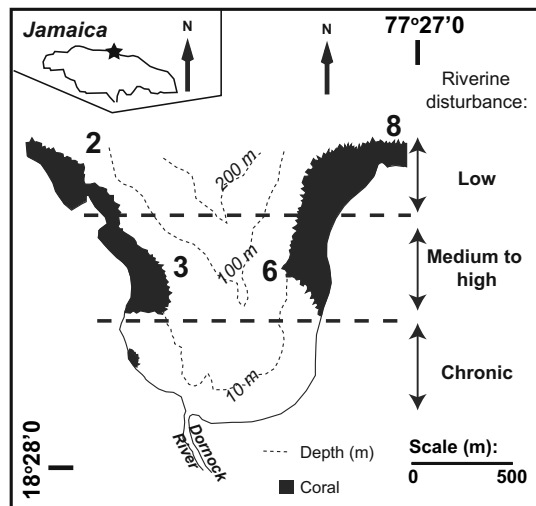


Fig. 1 The Rio Bueno embayment, north Jamaica, and the four study sites: 2, 3, 6, and 8. Riverine disturbance influencing study sites is also summarised

respectively) and analyses of environmental data identified them as “low-impact” (clear water) reef sites, these sites were also positioned in areas of high to moderate wave energy (Beaufort scale: ≥ 2). A summary of key water quality parameters at these study sites is given in Table 1. During this study, reduced salinities were only recorded at shallow depths in the water column (<2 m, Mallela et al. 2004). Consequently, salinity was not considered an important variable in this study, which was conducted at a depth of 10 m.

Experimental design

Ceramic settlement tiles (15.5 cm \times 15.5 cm) were preconditioned in running seawater tanks for 2 weeks. Tiles were then deployed at the four sites at a depth of 10 m, ca. 30 cm above the substrate. At each site 72 tiles were positioned horizontally. Pairs of tiles were placed one on top of the other so that 36 tile surfaces were orientated upwards simulating exposed (e) substrate; and 36 orientated downwards in order to mimic cryptic (c) habitats. Tiles were attached to wire mesh racks using cable ties (zip tie). Settlement tiles were retrieved after exposure for 12 months (August 2001–August 2002).

Approximately 73% of tiles were successfully retrieved, the remainder having been dislodged or broken whilst in situ. Community composition was analysed at each site using 15 c and 15 e randomly selected tiles. Community composition was analysed by superimposing a computer generated 200 point grid over each tile. A 1-cm border around the perimeter of each tile was not sampled in order to avoid edge effects. Encruster cover was recorded under every point to species level, if this level of taxonomic reso-

lution was not possible, encrusters were identified to genus or family, with the exception of cheilostome bryozoans (which were grouped by order). If this was not possible, encrusters were identified by taxa (e.g. serpulid worm, bryozoan, CCA). Encrusting bivalves were grouped, as were coral recruits (<4 mm in diameter) and thin colonies of CCA (<1 mm thick). Areas of uncolonised substrate (bare) and unidentified encrusters (unknown) were also noted.

In order to compare findings on experimental substrates with natural coral substrate, nine recently dead, platy coral samples (*Agaricia* spp. and *Leptoseris cucullata*) were collected between 5 and 15 m at sites 2 and 3. Corals were considered recently dead if they did not show evidence of algal recruitment (i.e. turf algae) to the dead skeleton. The encruster assemblages growing on the underside of colonies were then recorded as an example of encruster assemblages growing on natural substrates in a cryptic environment. Platy coral species can grow rapidly. Radial growth rates of platy corals in Rio Bueno were recorded by Hughes and Jackson (1985): at a depth of 10 m growth rates of *A. agaricites* peaked at 2.4 cm year⁻¹, at 20 m growth rates of *A. lamarcki* peaked at 1.4 cm year⁻¹. Whilst no linear growth rates are given for *L. cucullata*, it was noted for being the fastest growing of all species they sampled. In order to account for the age of the coral substrate, encruster samples were only sampled from the region of recent growth (maximum radial distance from colony perimeter sampled: 5 cm). As with tiles, extreme edges of samples were not assessed in order to avoid edge effects. High resolution, macro digital images of coral colonies were taken and analysed using Coral Point Count (CPCe) software (Kohler and Gill 2006). As the coral colonies sampled were not uniform in size or shape, areas of approximately 49 cm⁻² were selected manually using CPCe and a 100-point grid was superimposed. Encruster cover was recorded as detailed above for encruster tiles.

Carbonate production on tiles was estimated using 10 c and 10 e tiles randomly selected from each site. Tiles were soaked for 24 h in a 5% solution of domestic bleach, rinsed in distilled water, and air dried to a constant weight. Soft organisms (e.g. macroalgae) were removed using a soft brush, and care was taken not to dislodge encrusting organisms. Tiles were weighed (w1), then placed in a bath of 10% hydrochloric acid to remove encrusting organisms. Tiles were rinsed in distilled water, oven dried, air cooled, and reweighed to constant weight (w2). Control tests were also run on broken tiles that had been manually cleared of all encrusting communities. No weight loss was observed on the control tiles. Encruster carbonate production (g year⁻¹) was calculated for each tile (ET) as: $ET = w1 - w2$.

Statistical analysis

In order to compare encruster communities on experimental tiles, each site (2, 3, 6, 8) and habitat type (c or e) were considered to be different treatments ($n = 8$). Encruster assemblages growing on the underside of coral colonies at sites 2 and 3 were included as two separate treatments. Percentage cover of encrusting organisms was assessed using ANOVA with Bonferroni post-hoc comparisons (SPSS 11.5). Community composition was assessed using non-parametric multivariate analysis (PRIMER 6). Multivariate data were square root transformed, and Bray–Curtis similarity matrices were calculated. Data were presented graphically using multi-dimensional scaling (MDS) ordinations, where 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 2D picture but should be interpreted with caution, whilst stress values of <0.1 (as in Fig. 2) indicate good clear ordinations with a minimal likelihood of misinterpretation (Clarke and Gorley 2006). One-way analysis of similarities (ANOSIM) and multiple pair-wise comparisons examined differences in c and e assemblages within sites, and for differences in similar habitat types between sites (Clarke and Gorley 2006). The significance level for pair-wise tests was adjusted to account for multiple comparisons (e.g. from $\alpha = 0.05$ to $\alpha = 0.003$ for 16 multiple comparisons, i.e. 0.05/16; Bonferroni correlation). ANOSIM R -values indicate the degree of overlap in encruster assemblages between 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. Carbonate production between c and

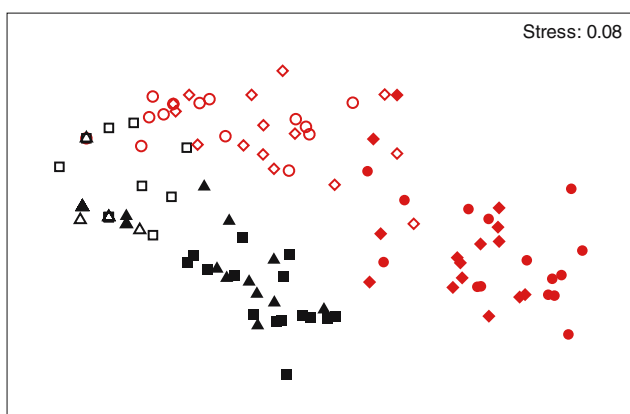


Fig. 2 Multi-dimensional scaling plot of assemblages on cryptic (filled markers) and exposed (open markers) tiles at low-impact (red markers) and high-impact sites (black markers) in Rio Bueno: Site 2 (filled diamond, open diamond); Site 3 (filled square, open square); Site 6 (filled triangle, open triangle); Site 8 (filled circle, open circle). Note the separation of cryptic and exposed tiles and high and low-impact sites

e tiles within sites was compared using two tailed t -tests. Mann–Whitney U tests were used to test non-normally distributed data.

Results

Comparison of encruster cover between different tile orientations and coral substrate

Within sites 2 and 3, ANOVA with Bonferroni post-hoc tests were used to compare encruster cover on coral colonies with different orientations of experimental tiles. At site 2 significant differences existed between groups ($F = 10.081$, $p < 0.001$). Post-hoc tests indicated that encruster cover on exposed tiles was significantly lower than that recorded on both cryptic tiles ($p < 0.001$, Fig. 3) and coral colonies ($p < 0.05$). There was no significant difference between encruster cover on cryptic tiles and coral colonies. Similarly, at site 3 significant differences were observed between treatments ($F = 10.151$, $p < 0.001$). Post-hoc comparisons revealed no significant difference between encruster cover on coral substrate and cryptic tiles. Again, total encruster cover on exposed tiles was significantly lower than that observed on both cryptic tiles ($p < 0.05$) and coral colonies ($p < 0.01$).

Multivariate analysis

As not all organisms were identified to species or family level, subsequent analyses of encruster cover were assessed

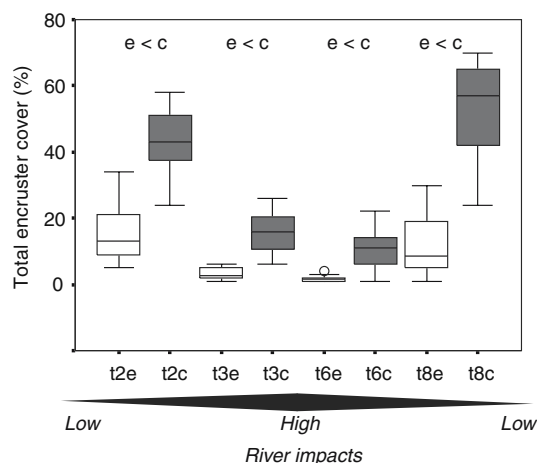


Fig. 3 Box whisker plots detailing total percentage encruster cover on cryptic and exposed tiles (t) at each site. Unfilled boxes indicate exposed tiles (e); dark grey boxes indicate cryptic tiles (c). t -Test results for significant tile orientation differences (cryptic vs exposed tiles site⁻¹) are detailed above box whisker plots ($p < 0.05$). Note significant differences occur at each site ($c > e$). Annotations above the box whisker plots: o = outliers. Riverine inputs are indicated by the relative thickness of the black wedge under the graph

by taxonomic group (e.g. serpulid, bryozoan, foraminifera, CCA, coral recruit). Multivariate analyses were used to compare the percentage cover of taxonomic groups and uncolonised space on tiles. MDS ordinations indicated differences in encruster assemblages between the two habitat types (c and e), and the two zones of river influence (low and high, Fig. 2). Assemblages from low-impact sites 2 and 8 (Fig. 2: red symbols), were distinct from turbid water assemblages from sites 3 and 6 (Fig. 2: black symbols) in the MDS plot. In addition, assemblages on cryptic tiles (Fig. 2: filled symbols) were generally distinct from those on exposed tiles (Fig. 2: unfilled symbols), the MDS stress value (<0.1) indicating good separation between samples.

Analysis of similarities pair-wise comparisons indicated that the composition of encrusters on tiles differed significantly between cryptic and exposed tiles within each site. When similarly orientated tiles (c or e) were compared within zones of disturbances (low- or high-impact) encruster assemblages were similar (e.g. site 2 cryptic tiles had similar assemblages to site 8 cryptic tiles). In contrast, when similar tile orientations were compared between high- and low-impact sites (e.g. tiles 2e vs 3e) encruster

assemblages proved to be significantly different (all p values detailed in Table 2).

Encruster community composition on experimental tiles

The mean (\pm SD) encruster cover on all tiles (sites 2, 3, 6, and 8: cryptic and exposed) was $21 \pm 20\%$, with serpulid worms dominating, followed by CCA > bryozoans > foraminifera. At each of the four sites, total encruster cover was consistently greater on cryptic tiles than exposed tiles (Fig. 3). Within sites, encruster cover by bryozoans and serpulid worms was also consistently greater on cryptic tiles (Fig. 4). CCA was recorded at all sites and habitats (c and e) within Rio Bueno (Fig. 4). Both cryptic and exposed tiles were characterised by significantly higher cover of CCA at low-impact sites (2 and 8) compared to high-impact sites (3 and 6; Mann–Whitney U test: cryptic tiles median_{low-impact} = 7%, median_{high-impact} = 1%, $U = 17.5$, $p < 0.001$; exposed tiles median_{low-impact} = 7%, median_{high-impact} = 1%, $U = 12.5$, $p < 0.001$). Serpulid cover, the dominant category at all sites, also proved to have the greatest coverage at the low-impact sites (Mann–Whitney U test: cryptic tiles

Table 1 Mean (\pm SD) water quality parameters at sites 2, 3, 6, and 8

River influence	Low	Medium–high	Medium–high	Low
Site	Site 2	Site 3	Site 6	Site 8
Surface temperature ($^{\circ}$ C)	28.3 (0.7)	28.2 (0.7)	28.2 (1.0)	28.3 (0.7)
Temperature at 10 m ($^{\circ}$ C)	28.1 (0.7)	28.2 (0.7)	28.1 (0.7)	28.2 (0.7)
Surface salinity	33.7 (3.0)	30.3 (6.8)	30.3 (8.7)	35.0 (1.0)
Salinity at 10 m	35.4 (1.0)	35.5 (1.0)	35.5 (1.0)	35.4 (1.0)
Light attenuation (%)	20.4 (12.4)	14.1 (8.8)	16.9 (10.8)	22.5 (4.3)
Secchi (m)	17.7 (11.2)	9.1 (9.0)	11.5 (7.6)	19.7 (8.4)
Sedimentation ($\text{mg cm}^{-2} \text{ day}^{-1}$)	7.1 (2.4)	13.8 (4.7)	15.7 (14.1)	5.3 (3.6)

Surface seawater temperature (0.15 m, $^{\circ}$ C), seawater temperature ($^{\circ}$ C) at 10 m, surface salinity (0.15 m), salinity at 10 m, light attenuation (% surface light) at 10 m, water clarity (Secchi depth m), and sedimentation rates ($\text{mg cm}^{-2} \text{ day}^{-1}$) at 10 m. Data summarised from Mallela et al. (2004)

Table 2 Analysis of similarities pair-wise comparisons of encruster assemblages on exposed (e) and cryptic (c) tiles at high-impact (sites 3 and 6) and low-impact (sites 2 and 8) sites

Exposed vs exposed	R -values	Cryptic vs cryptic	R -values	Cryptic vs exposed	R -values
2 e \times 3 e**	0.508	8 c \times 3 c**	0.931	2 c \times 2 e**	0.727
2 e \times 6 e**	0.750	6 c \times 2 c**	0.885	6 c \times 6 e**	0.466
3 e \times 8 e**	0.423	3 c \times 2 c**	0.894	8 c \times 8 e**	0.923
6 e \times 8 e**	0.618	8 c \times 6 c**	0.918	3 c \times 3 e**	0.837
2 e \times 8 e ^{ns}	0.013	8 c \times 2 c ^{ns}	0.036		
3 e \times 6 e ^{ns}	0.189	6 c \times 3 c ^{ns}	0.147		

All comparisons significantly different ($p < 0.003$), except those marked ns ($p > 0.003$). R -values indicate the degree of assemblage overlap between sites. Note how tiles at different sites in the same disturbance zone and with similar orientations are not significantly different and have a high degree of overlap

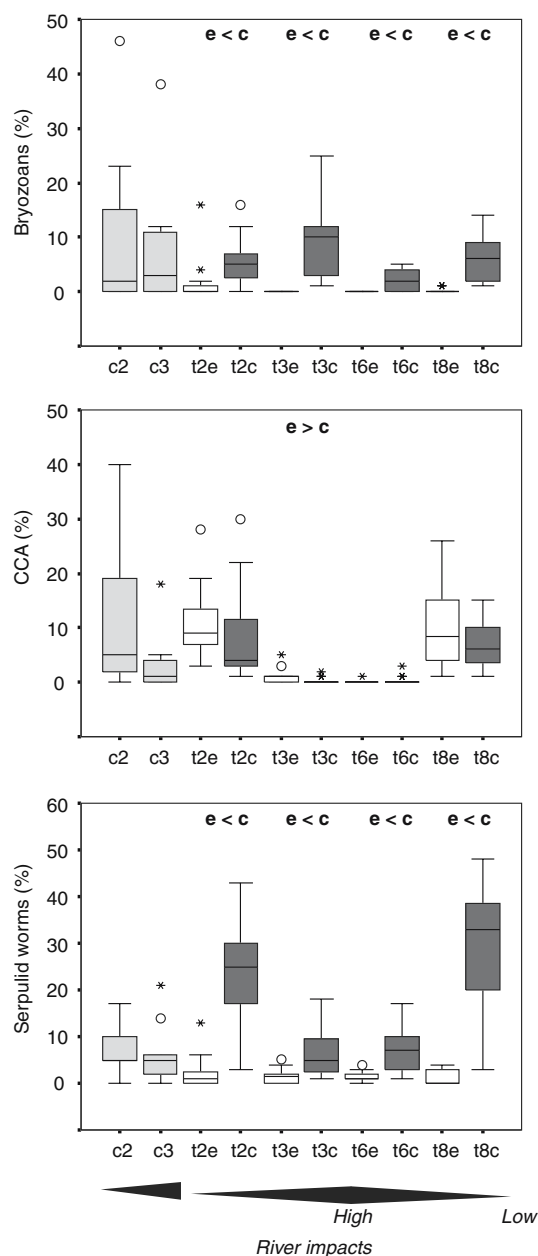


Fig. 4 Boxplots detailing the percentage cover of bryozoans, crustose coralline algae (CCA) and serpulids on cryptic coral substrate at sites 2 and 3, and cryptic tiles and exposed tiles at sites 2, 3, 6, and 8. Light grey boxes indicate coral substrate (c); unfilled boxes indicate exposed tiles (e); dark grey boxes indicate cryptic tiles (c). Significant Mann-Whitney U test results for tile orientation interactions (cryptic vs exposed tiles site⁻¹) are detailed above box whisker plots ($p < 0.05$). Note significant differences occur within each site $c > e$ for bryozoans and serpulid worms. Annotations above the box whisker plots: o = outliers; asterisk = extreme data points. Riverine inputs are indicated by the relative thickness of the black wedge under the graph

median_{low-impact} = 13%, median_{high-impact} = 5%, $U = 77$, $p < 0.001$).

Variations in species composition were also observed between different tile orientations and riverine impacted

zones. At low-impact sites 2 and 8, the only species observed on c and e tiles were *Salmacina* spp. The exposed tiles at low-impact sites 2 and 8 were dominated primarily by CCA, with serpulids, bryozoans, and foraminifera playing a secondary role (see Fig. 4 and Table 3). Whilst serpulid worms were dominated by *Salmacina* spp., other species such as *Pseudovermilia* spp., *Sclerostyla ctenactis* and *Vermiliopsis* spp. were also present. In addition to the cheilostomata, rare occurrences of *Disporella fimbriata* were noted among bryozoan assemblages (Table 3). The foraminifera *Homotrema rubrum* occurred on exposed tiles at both low-impact sites, whilst *Carpenteria utricularis* only recruited to site 2e.

Cryptic tiles at low-impact sites were characterised by greater species richness than exposed tiles (Table 3). Whilst dominated by *Salmacina* spp. other common species included *Pseudovermilia fuscostriata* and other *P.* spp. As with exposed tiles, the bryozoan community was dominated by Cheilostomes, however, *D. fimbriata* was noted at both sites and *Probuscina robusta* only observed at 8c.

High-impact sites 3 and 6 exhibited greater species richness on cryptically orientated tiles (Table 3). Serpulid worms dominated turbid water sites, but *Salmacina* spp. and *Pseudovermilia* spp. were the only species found on both cryptic and exposed tiles at these sites (no other species were observed on high-impact, exposed tiles). Cryptic habitats at high-impact sites were dominated by *Salmacina* spp., however other serpulid species included *P. multispinosa*, the smaller *P. fuscostriata*, *S. ctenactis*, and *Vermiliopsis annulata*. Bryozoans were not observed on the exposed tiles in turbid water (3e and 6e). In contrast, Cheilostomes dominated the bryozoan community on cryptic tiles, with *D. fimbriata* found at both sites and *P. robusta* observed only at 6c. *Planorbulina* sp. was observed at site 3e and 3c, whilst *C. utricularis* was only observed at 3e. It is interesting to note the absence of *H. rubrum* and the scarcity of *Carpenteria* spp., at high-impact sites. Whilst they are considered to be an insignificant component of reef framework due to their small size, they are often considered as ubiquitous species on modern day reefs (Martindale 1992; Perry 2001).

Carbonate production

Carbonate production by encrusting organisms in both orientations was consistently greater at low-impact sites than at high-impact sites (two tailed t -test cryptic habitats: $t = 6.53$, $df = 38$, $p < 0.001$; exposed habitats: $t = 8.66$, $df = 38$, $p < 0.001$). At low-impact sites, mean (\pm SD) carbonate production by encrusting organisms ranged from 69.4 ± 6.0 g m⁻² year⁻¹ at site 2 c to 159.0 ± 22.4 g m⁻² year⁻¹ at site 8 e. At high-impact sites, carbonate production ranged from 2.7 ± 2.0 g m⁻² year⁻¹ at site 6 c

Table 3 Summary table detailing the abundance, and species richness of encrusting organisms recruiting to different tile orientations (cryptic and exposed) at each site

	Exposed habitat				Cryptic habitat			
	Site: 2	3	6	8	2	3	6	8
Crustose Coralline algae	●
Bryozoans
<i>Disporella fimbriata</i>
<i>Probuscina robusta</i>
<i>Cheilosomata</i>	○	●	●	○	●
Foraminifera
<i>Carpenteria utricularis</i>
<i>Gypsina plana</i>
<i>Homotrema rubrum</i>
branched	○	●
globose	○
low relief	○
<i>Planorbulina</i> spp.
unidentified
Serpulids
<i>Salmacina</i> spp.	○	●	●	●	●
<i>Pseudovermilia multispinosa</i>	○
<i>Pseudovermilia fuscostriata</i>	●
<i>Pseudovermilia</i> sp.	○	●
<i>Sclerostyla ctenactis</i>	○
<i>Serpula loblancoi</i>
<i>Spirobranchus</i> spp.
<i>Vermiliopsis annulata</i>
<i>Vermiliopsis</i> spp.	○
unidentified
Sabellidae
<i>Calcisabella</i> spp.
Bivalves
Hard coral recruits (< 4mm)
Unidentified	○

..... < 1% rare ○ 1 - 5% occasional ● 6 - 15% common ● 16 - 25% abundant

Rare: dotted lines (<1%), occasional: open circle (1–5%); common: small filled circle (6–15%); abundant: big filled circle 16–25%)

to $29.6 \pm 4.0 \text{ g m}^{-2} \text{ year}^{-1}$ at 3 c (Fig. 5). Within sites, there were significant differences in carbonate production between cryptic and exposed tile orientations at sites 2, 3, and 6, however, results were inconsistent (Fig. 5).

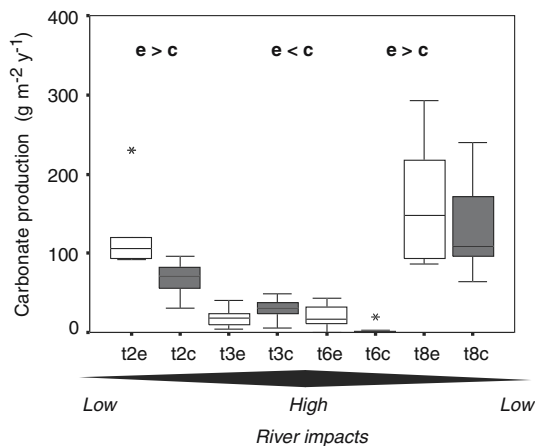


Fig. 5 Box whisker plots detailing carbonate production ($\text{g m}^{-2} \text{ year}^{-1}$) on cryptic and exposed tiles (*t*) at each site. Unfilled boxes indicate exposed tiles (*e*); dark grey boxes indicate cryptic tiles (*c*). *t*-Test results for significant tile orientation differences (cryptic vs exposed tiles site⁻¹) are detailed above box whisker plots ($p < 0.05$). Annotations above the box whisker plots: asterisk = extreme data points. Riverine inputs are indicated by the relative thickness of the black wedge under the graph

Discussion

This study revealed that elevated riverine inputs and reduced wave energy were associated with reduced encruster cover and carbonate production on both cryptic and exposed substrate orientations. It also provides support for the use of experimental ceramic tiles as a proxy for natural coral substrates in reef systems. It should be noted that no attempt has been made to distinguish among the effects of turbidity, light attenuation, sedimentation, and nutrient inputs all of which are positively correlated with increased proximity to the river mouth (Mallela et al. 2004). As such, all these variables are considered together as riverine inputs.

Findings from this study suggest that clear water sites (low-impact) in high-energy settings were characterised by greater levels of encruster cover and carbonate production on both cryptic and exposed substrates compared to turbid water (high-impact), sheltered sites (3 and 6). Encruster communities from cryptic habitats were typically dominated by serpulid worms, in particular *Salmacina* spp. and cheilostome bryozoans. Exposed tiles were dominated by CCA at low-impact sites, but exposed high-impact sites had very limited CCA cover on all tiles. Turbid water studies in the Great Barrier Reef have suggested that the combined effects of turbidity and frequent physical disturbance limit the occurrence of CCA, and subsequent framework binding

(Smithers and Larcombe 2003). Furthermore, Martindale (1992) noted that bryozoans were absent in areas of high sediment input in Barbados. In contrast, bryozoans in Rio Bueno occurred at high (sediment) impacted sites as well as low-impact sites, however, recruitment was apparently limited on exposed tiles at all sites. Fabricius and De'ath (2001) also noted reductions in CCA in association with elevated sediment inputs. CCA in Rio Bueno was also found to be negatively correlated with increased proximity to the river mouth (i.e. elevated riverine inputs and reduced wave energy), however, substrate orientation did not prove to be a significant variable influencing CCA cover. Serpulid worms are known to be associated with cryptic or semi-cryptic habitats (Martindale 1992) whilst spirorbids typically recruit in greater numbers to unshaded surfaces independent of orientation (Saunders and Connell 2001). In Rio Bueno, serpulids were consistently observed in greater numbers on cryptically orientated substrates, whilst their cover was also found to be negatively correlated with riverine impacts. Interestingly, Jackson and Winston (1982) report values for % cover of CCA and cheilostome on exposed experimental tiles in Rio Bueno at the same site, orientation, and depth as site 2 in this study (Table 4). Observed CCA and bryozoan cover in this study (site 2, exposed tiles) were clearly lower than that reported in the earlier study. Although in the Jackson and Winston (1982) study, tiles were exposed to colonisation for 15 months, it seems unlikely that an additional 3 months would result in a marked increase in percentage encruster cover (1982 CCA: 53, cheilostomes: 6 and 2002 CCA: 11; bryozoan: 2). Such a reduction in encruster cover may have implications for secondary framework production (e.g. reductions in secondary framework production and framework binding). Whilst the decline of primary framework builders (scleractinian corals) on Jamaican reefs has been widely documented (Liddell and Ohlhorst 1993; Hughes 1994), to the author's knowledge no-one has reported a reduction in secondary framework production. Clearly, these tentative findings warrant further attention, as reductions in secondary carbonate production may have implications for framework stability and settlement of coral larvae (Morse et al. 1988; Fabricius and De'ath 2001).

Whilst the use of experimental substrates to examine natural levels of recruitment is commonplace (Davies and Hutchings 1983; Martindale 1992; Glasby 1999; Hibino and van Woosik 2000), relatively few studies provide experimental evidence to suggest that such findings are comparable with natural substrates. Recent studies have also indicated that organisms recruiting to man-made structures (e.g. pontoons) do not reflect those observed recruiting to natural substrates (Glasby and Connell 2001). Within sites 2 and 3, encruster assemblages recruiting to recent cryptic coral substrates were not found to be significantly

different to assemblages recruiting to cryptic experimental tiles, suggesting, at least in this study, that experimental tiles provide a useful proxy for cryptic coral substrate. It was assumed that this was also the case for exposed habitats; however this is yet to be experimentally assessed as this study did not assess any naturally exposed substrate. Based on this assumption results from experimental tiles are discussed in relation to variations in wave energy and riverine inputs.

Total carbonate production by encrusting organisms was reduced with increased proximity to the river mouth, where sites were characterised by high riverine inputs and reduced wave energy. Interestingly, there was no consistent pattern with regards to substrate orientation (cryptic vs exposed). However, as carbonate production is the combined product of (1) benthic cover, (2) growth rates, and (3) skeletal density this is perhaps not surprising. As encrusters can modify these three variables in response to local environmental conditions encruster cover may not be proportional to the rate of calcification. Other studies have reported phenotypic variation in encrusters (CCA and foraminifera) which has been linked to wave energy and turbidity (Martindale 1992). Studies of coral extension, skeletal density, and calcification have reported differences under varying levels of light, salinity, sediment, and nutrient input (Buddemeier 1974; Dustan 1975; Atkinson et al. 1995; Edinger et al. 2000). Consequently, carbonate production in Rio Bueno was probably influenced by wave energy and the simultaneous and synergistic effects of various riverine inputs. As this study only assessed total encruster carbonate production, no conclusions can be drawn with regards to carbonate production by different taxa. It would however be useful to determine which encrusting organisms contribute most calcium carbonate to the reef framework under different environmental regimes. It is difficult to compare figures of carbonate production with other studies, as most do not report carbonate production, and those that do typically only note CCA production. However, as already noted, the total encruster production in Rio Bueno reported in the current study appears to be substantially lower than that reported for CCA in other studies (Table 4).

Prior studies indicate that substrate stability and the period of exposure can influence the development of encruster communities (Osman 1977; Sousa 1979). These variables were not considered here as all tiles were exposed for the same period of time and were attached securely to the substrate. Other factors that could influence the findings of this study include competition for space, predation/grazing, larval behaviour, and water flow (Jackson and Buss 1975; Steneck and Adey 1976; Steneck 1983; Martindale 1992; Gischler and Ginsburg 1996). Space is unlikely to influence these results as all experimental tiles represented bare substrate at the beginning of this study, and at the end of this

Table 4 A summary of studies reporting encruster carbonate production ($\text{g m}^{-2} \text{ year}^{-1}$) and total encruster cover (%) on experimental and natural substrates

Location	Substrate type and habitat	Encruster	CaCO ₃ production ($\text{g m}^{-2} \text{ year}^{-1}$)	Total cover (%)	Age of community	Depth (m)	Reference
Rio Bueno, central site 3, Jamaica	Tiles—cryptic	All ^a	29.6 (± 4.0 SE)	16.0 (± 1.7 SE)	12 months	10	This study
	Tiles—exposed	All ^a	18.1 (± 3.4 SE)	3.0 (± 0.6 SE)	12 months	10	
	Coral substrate	All ^a		18.7 (± 4.7 SE)	~2–3 years	<16	
Rio Bueno, central site 6, Jamaica	Tiles—cryptic	All ^a	2.7 (± 2.0 SE)	10.3 (± 1.6 SE)	12 months	10	This study
	Tiles—exposed	All ^a	19.2 (± 4.4 SE)	1.8 (± 0.3 SE)	12 months	10	
Rio Bueno, outer site 2, Jamaica	Tiles—cryptic	All ^a	69.4 (± 6.0 SE)	42.7 (± 2.8 SE)	12 months	10	This study
	Tiles—exposed	All ^a	128.3 (± 17.2 SE)	16.0 (± 2.5 SE)	12 months	10	
	Coral substrate	All ^a		30.8 (± 8.1 SE)	~2–3 years	<16	
Rio Bueno, outer site 8, Jamaica	Tiles—cryptic	All ^a	135.4 (± 20.0 SE)	51.6 (± 4.3 SE)	12 months	10	This study
	Tiles—exposed	All ^a	159.0 (± 22.4 SE)	11.14 (± 2.3 SE)	12 months	10	
Rio Bueno, wall, Jamaica	Tiles—exposed	CCA		52.5	15 months	10	(Jackson and Winston 1982)
		Cheilostomes		6.3	15 months	10	
		CCA		13.4–18.6	Mature	10	
		Cheilostomes		11.9–25.9	Mature	10	
		CCA ^b			3–18 months	1–50	
Bellaire, Barbados	Tiles	CCA ^b	5,125				(Martindale 1976; Stearn et al. 1977)
Oahu, Hawaii	Natural substrate	<i>Porolithon onkodes</i>	2,600				(cited in Harney and Fletcher 2003)
GBR, Australia	Coral blocks—exposed	All ^a		75.0	12 months	12	(Davies and Hutchings 1983)
Rkyu Islands, Japan	Coral blocks—exposed	All ^a		14.5	3 months	1–5	(Hibino and van Woessik 2000)

^a Carbonate-producing encrusting organisms (e.g. bryozoans, crustose coralline algae, coral recruits, foraminifera, serpulids)

^b Four species referred to *Porolithon*, *Neogoniolithon*, *Lithophyllum*, and *Mesophyllum*

study there were still substantial areas of uncolonised substrate on tiles. Predators, in particular grazing fish and urchins, may also have influenced encruster recruitment, growth and abundance. Parallel studies conducted at these sites have noted the limited occurrence of bioeroding urchins, in particular *Diadema antillarum*, and the low abundance of grazing fish species, in particular large bodied species capable of carbonate bioerosion (Mallela and Perry 2007; Mallela et al. 2007). Crabs, a potential source of grazing pressure (Sammarco et al. 1986) were not assessed in this study, however, they were not noted on tiles when observed in situ by divers. Whilst it seems unlikely that sessile grazing organisms significantly influenced encruster abundances in this study, their influence can not be entirely ruled out. It was also assumed that larval supply was uniform as all sites were in close proximity to each other. Studies of coral larvae (Gilmour 1999) have linked high levels of total suspended sediment with increased mortality, reduced fertilisation, limited settlement, and consequently reduced larval recruitment. It is possible that such factors may also influence larval encruster recruitment and, again, this is an area which warrants further attention.

Hydrodynamic energy is also known to influence encruster communities (Steneck and Adey 1976; Gischler and Ginsburg 1996). Previous studies have noted how CCA and vermetid worms are typically abundant in areas of high wave energy, whilst CCA crusts in areas of high hydrodynamic energy were found to be less porous (Martindale 1992; Gherardi and Bosence 2001). Low-impact sites (2 and 8) were subjected to high to moderate wave action, whilst high-impact sites were relatively sheltered from prevailing winds due to their location within the embayment (J. Mallela, personal observation). It therefore seems likely that the direct and indirect effects of riverine inputs in combination with wave energy influenced the distribution of encruster communities within this study.

This study demonstrated that reduced levels of encruster carbonate production and benthic cover were associated with elevated riverine inputs and reductions in wave energy. However, the term riverine inputs here includes a range of disturbances that are intercorrelated, e.g. sedimentation, turbidity, shading, reduced light penetration, and nutrient inputs, the interactive effects of which could not be distinguished. Such inputs typically act simultaneously and often synergistically. Elevated levels of internal bioerosion have also been linked to deteriorating water quality (e.g. Holmes et al. 2000). Given the increased level of terrestrial inputs into near shore coastal zones and the resulting negative implications for framework-building communities, we need to further understand how these processes interact in order to mitigate against future reef deterioration. Clearly, more research is required in order to understand how these different variables interact and influence growth and devel-

opment of primary and secondary framework-building communities.

Acknowledgements JM was funded by an MMU Postgraduate student bursary, additional funding for fieldwork was provided by the Royal Geographic Society, UK—Slawson Award. R. Bastida-Zavala and H.A. ten Hove are thanked for kind help with serpulid worm identification. Numerous staff and students of Discovery Bay Marine Lab (DBML) are thanked for their kind help as are numerous dive buddies. Special thanks to C. Perry, M. Haley, A. Greenway, R. Stephenson, C. Harrod, D. Smilie, C. Roberts, P. Gayle, E. Brown, N. Earle, and K. Taylor. Constructive reviews greatly improved this manuscript. This is DBML publication number 726.

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