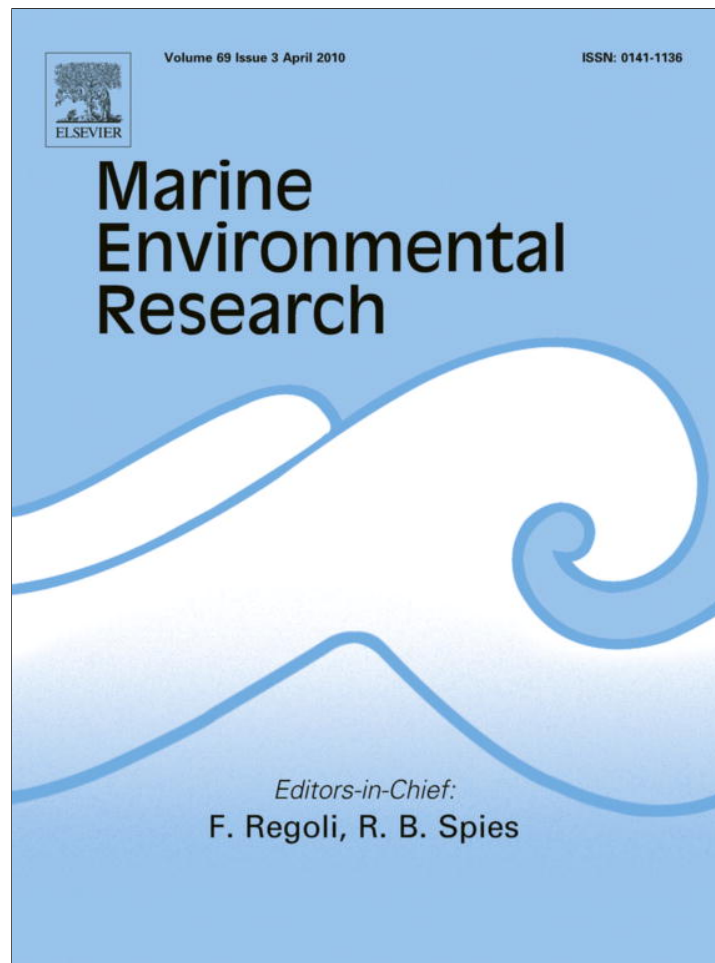


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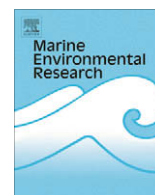
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# Topography and spatial arrangement of reef-building corals on the fringing reefs of North Jamaica may influence their response to disturbance from bleaching

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## ABSTRACT

Knowledge of factors that are important in reef resilience helps us understand how reefs react following major environmental disturbances such as hurricanes and bleaching. Here we test factors that might have influenced Jamaican reef resilience to, and subsequent recovery from, the 2005 bleaching event, and which might help inform management policy for reefs in the future: reef rugosity and contact of corals with macroalgae. In addition, we test in the field, on Dairy Bull reef, whether aggregated *Porites astreoides* colonies exhibit enhanced growth when exposed to superior competition from *Acropora palmata*, as has been found by experiment with the Indo-Pacific corals *Porites lobata* and the superior competitor *Porites rus* [Idjadi, J.A., Karlson, R.H., 2007. Spatial arrangement of competitors influences coexistence of reef-building corals. *Ecology* 88, 2449–2454].

There were significant linear relationships between rugosity and the increase in smallest size classes for *Sidastrea siderea*, *Colpophyllia natans*, *P. astreoides* and *Agaricia* species, and between rugosity and cover of the branching coral *Acropora cervicornis*. Linear extension rates of *A. cervicornis* and radial growth rates of *P. astreoides* were significantly lower ( $p < 0.025$ ;  $F > 6$ ) when in contact with macroalgae. Aggregated colonies of *P. astreoides* in contact with one another, one of which was in contact with the faster growing competitor *A. palmata* showed significantly greater growth rates than with just two aggregated *P. astreoides* colonies alone. These findings suggest that three dimensional topography and complexity is important for reef resilience and viability in the face of environmental stressors such as bleaching. Our findings also support the idea that aggregated spatial arrangements of corals can influence the outcome of interspecific competition and promote species coexistence, important in times of reef recovery after disturbance.

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## 1. Introduction

Loss of corals and macroalgal domination on the fringing reefs of North Jamaica has been due to hurricanes (Woodley et al., 1981; Crabbe et al., 2002), overfishing (Jackson, 1997; Hawkins and Roberts, 2004), die-off of the long-spined sea urchin *Diadema antillarum* in 1983–84 (Hughes, 1994), and coral disease (Aronson and Precht, 2001). However, increased macroalgal cover by itself does not always lead to reef decline, and the Jamaican example may be an anomaly compared to reefs in other parts of the world (Bruno et al., 2009; Liu et al., 2009). The major acute disturbance in recent years was the Caribbean-wide bleaching event of 2005 (Wilkinson and Souter, 2008; Quinn and Kojis, 2008; Crabbe, 2009). This event was due primarily to high sea surface temperature (SST) hot-spots in the region (Abrego et al., 2008; Donner et al., 2007; Morgan et al., 2008), and thermal stress during this event exceeded any seen in the previous 20 years of satellite data

from the Caribbean, while monthly temperatures were the warmest in over 150 years. The North Jamaican fringing reefs, unlike elsewhere in Caribbean, for example the reefs of Tobago (Mallela and Crabbe, 2009), have shown resilience to acute disturbances from hurricanes and bleaching, in addition to the recurring chronic stressors of overfishing and land development (Idjadi et al., 2006; Crabbe, 2009).

Factors that can improve coral reef resilience include species and functional diversity, connectivity to larval sources, appropriate substrates for larval settlement, and protection from other anthropogenic effects (Nyström et al., 2008; Halford and Caley, 2009). Here we wished to test three other factors that might have influenced Jamaican reef resilience to, and subsequent recovery from, the 2005 bleaching event, and which might help inform management policy for reefs in the future: reef rugosity, contact of corals with macroalgae, and aggregation and competition between corals.

Rugosity has been linked to reef resilience in the South Central Pacific (Adjeroud et al., 2009). Viability of small coral colonies over time was used as a measure of reef resilience, as has been suggested (Loya, 1976; Connell, 1978).

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Most reefs are open non-equilibrium systems, (Connell, 1978) with diversity maintained by disturbance and recruitment (Rogers, 1993). Interspecific competition (Stoll and Prati, 2001; Hartley and Shorrock, 2002) as well as aggregation is pervasive among coral communities, and is important in maintaining their viability (Karlson, 1999; Karlson et al., 2007). Heterospecific competition of corals with algae reduces coral growth and survivorship (Lirman, 2001; Box and Mumby, 2007; Crabbe, 2008). In corals, spatial arrangement, orientation and aggregation may be a key mechanism contributing to species coexistence on coral reefs (Idjadi and Karlson, 2007).

*Porites astreoides* is one of the most abundant corals of the fringing reefs around Discovery Bay (Crabbe, 2009). However, it can be effectively overgrown by the faster growing branching coral *Acropora palmata*. Here we test in the field, on Dairy Bull reef, whether aggregated *P. astreoides* colonies exhibit enhanced growth when exposed to superior competition from *A. palmata*, as has been found by experiment with the Indo-Pacific corals *Porites lobata* and the superior competitor *Porites rus* (Idjadi and Karlson, 2007).

## 2. Methods

### 2.1. Sites and sampling

Studies were conducted using SCUBA at six sites [Rio Bueno (18° 28.805'N; 77° 27.625'W), CREWS (Coral Reef Early Warning Station) (18° 28.375'N; 77° 24.921'W), Dancing Ladies (18° 28.369'N; 77° 24.802'W), M1 (18° 28.337'N; 77° 24.525'W), Dairy Bull (18° 28.083'N; 77° 23.302'W), and Pear Tree Bottom (18° 27.829'N; 77° 21.403'W)] over a three year period (2006–2009) along the fringing reefs surrounding Discovery Bay, Jamaica. In addition, *Acropora cervicornis* growth was studied in 2009 at a new site (New reef) between Dancing Ladies and M1, where *A. cervicornis* cover was comparable to that at Dairy Bull reef. GPS coordinates were determined using a hand-held GPS receiver (Garmin Ltd.). For all sites except CREWS and New reef, four haphazardly located transects, each 15 m long and separated by at least 5 m, were laid at between 5 and 8.5 m depth, to minimise variation in growth rates due to depth (Huston, 1985). Linear extension rates of *A. palmata* and *A. cervicornis* were measured by image analysis, verified by flexible tape, as described previously (Crabbe and Smith, 2005; Crabbe et al., 2008). Non-branching corals 2 m either side of the transect lines were photographed and surface areas measured with flexible vinyl tape; the largest diameter of each colony was measured using a vinyl tape measure, and also the diameter at 90° to that (Crabbe et al., 2002; Crabbe and Smith, 2005). To increase accuracy, surface areas rather than diameters of live non-branching corals were measured. For this study, sampling only included smaller size classes of corals, up to 250 mm<sup>2</sup> surface area (Crabbe, 2009). Radial growth rates of non-branching corals and linear extension rates of branching corals were calculated over the post-2005 bleaching period from 2006 to 2009. Except where colony aggregation was investigated, colonies that were close together (<5 cm) or touching were avoided to minimise age discontinuities through fission and altered growth rates (Hughes and Jackson, 1980; Foster et al., 2007; Elahi and Edmunds, 2007). *Montastrea annularis* colonies were not measured in this study, as their surface area does not reflect their age (Hughes and Jackson, 1980), and because hurricanes can increase their asexual reproduction through physical damage (Foster et al., 2007).

Where colony aggregates were studied, fission or fusion did not occur in the three years of this study.

Rugosity ( $R$ ) was determined according to the formula:

$$R = Sr/Sg$$

where  $Sr$  = real surface distance between two points, and  $Sg$  = straight line geometric distance between two points. This was

calculated over a 20 m distance, performed in triplicate, at each site, using photographic image analysis verified by the chain method (Crabbe and Smith, 2002). Rugosity measurements were similar to those used on reefs by Klumpp and McKinnon (1992), Sanchez et al. (1997), McClanahan (1998), and Chapman and Kramer (1999).

Overall, over 2000 measurements were made on over 600 coral colonies, equally distributed between the sites for species and numbers of colonies.

This work was conducted at Discovery Bay during April 11–18 in 2006, December 30 in 2006 – January 6 in 2007, July 30 – August 16 in 2008 and July 27 – August 8 in 2009.

Computer digital image analysis was undertaken using the UTHSCSA (University of Texas Health Science Center, San Antonio, Texas, USA) Image Tool software (Crabbe and Smith, 2005). One or two-factor ANOVA was used to compare coral data among sites; error values represent standard errors of the data. Water quality measurements at the sites have been reported previously (D'Elia et al., 1981; Greenaway and Gordon-Smith, 2006).

### 2.2. Data on bleaching events impacting Discovery Bay

Information on bleaching was obtained from the NOAA coral reef watch site: ([http://coralreefwatch.noaa.gov/satellite/current/sst\\_series\\_24reefs.html](http://coralreefwatch.noaa.gov/satellite/current/sst_series_24reefs.html)) and from Jones et al. (2008).

## 3. Results

Rugosities were calculated for each site as follows: Rio Bueno:  $1.05 \pm 0.15$ , CREWS:  $1.38 \pm 0.2$ , Dancing Ladies:  $1.3 \pm 0.15$ , New reef:  $1.7 \pm 0.14$ , M1:  $1.17 \pm 0.12$ , Dairy Bull:  $2.3 \pm 0.16$ , and Pear Tree Bottom:  $1.23 \pm 0.11$ .

Linear extension rates of *A. cervicornis* were significantly lower ( $p < 0.025$ ;  $F > 6$ ) at M1 and CREWS sites, where they were in contact with *Dictyota* species macroalgae, than at the other sites; there were no significant differences in linear extension rates of *A. palmata* between any site (Table 1). Neither species was found along the belt transects at Dancing Ladies during the period of study. *A. palmata* colonies were >100 mm from any interaction with macroalgae at all sites measured.

There were significant relationships between mean rugosity value and the increase in smallest size classes for *Sidastrea siderea*, *Colpophyllia natans*, *P. astreoides* and *Agaricia* species for five sites on the fringing reefs near Discovery Bay (Fig. 1). In all cases the best-fit linear regression fits are shown;  $R^2$  values for regression were: *S. siderea*, 0.86; *C. natans*, 0.71; *P. astreoides*, 0.41 and *Agaricia* species 0.98.

There was also a significant linear relationship between percentage coral cover of *A. cervicornis* colonies with rugosity values

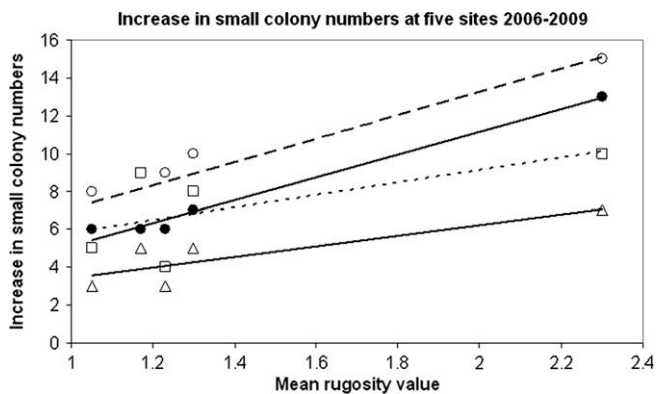
**Table 1**

Linear extension rates (mm yr<sup>-1</sup>) of branching corals *Acropora cervicornis* and *Acropora palmata* at Rio Bueno (RB), CREWS, M1, Dairy Bull reef (DB) and Pear Tree Bottom (PT). Neither species was found along the belt transects at Dancing Ladies during the period of study.

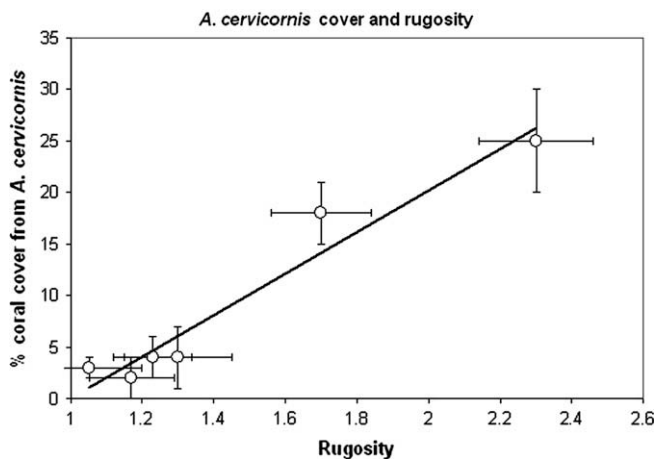
Species	Site RB	CREWS	M1	DB	PT
<i>Acropora cervicornis</i>	110 ± 15	90 ± 10*	85 ± 15*	146 ± 20	125 ± 20
<i>Acropora palmata</i>	55 ± 20	60 ± 20	nm	80 ± 20	65 ± 15

Values represent growth rates ± standard errors;  $n = 4$  for each species. nm, not measurable in sufficient numbers (4).

\* Indicates colonies of *A. cervicornis* were in contact with *Dictyota* species macroalgae at M1 and CREWS sites only. *A. palmata* colonies were >100 mm from any conspecific or heterospecific interaction at all sites measured. Linear extension rates of *A. cervicornis* were significantly lower ( $p < 0.025$ ;  $F > 6$ ) at M1 and CREWS sites, where they were in contact with macroalgae, than at the other sites; there were no significant differences in linear extension rates of *A. palmata* between any sites.



**Fig. 1.** Increase in colony numbers from 2006 to 2009 of smallest size class (0–250 mm<sup>2</sup>) since the bleaching event of 2005 of *Sidastrea siderea*, ○; *Colpophyllia natans*, △; *Porites astreoides*, □; and *Agaricia* species, ●; against mean rugosity values for Dairy Bull reef (2.3), M1 (1.17), Dancing Ladies (1.3), Rio Bueno (1.05) and Pear Tree Bottom (1.23). Standard errors for rugosities have been omitted for clarity.



**Fig. 2.** Percentage coral cover  $\pm 1$  standard error of *A. cervicornis* colonies against rugosity values  $\pm 1$  standard error, for Dairy Bull reef (2.3), M1 (1.17), New reef (1.7), Dancing Ladies (1.3), Rio Bueno (1.05) and Pear Tree Bottom (1.23). Mean rugosity values are in brackets. The line is a best-fit linear regression, with  $R^2 = 0.94$ .

for Dairy Bull reef, M1, New reef, Dancing Ladies, Rio Bueno and Pear Tree Bottom (Fig. 2). The line is a best-fit linear regression, with  $R^2 = 0.94$ . The two reefs with the highest rugosity values, Dairy Bull reef and New reef, exhibited the highest cover of the urchin *D. antillarum* (measured at  $0.4 \pm 0.1$  *Diadema* m<sup>-2</sup> for both reefs), and no macroalgal cover in the vicinity of *A. cervicornis* colonies. In contrast, the other reefs with lower rugosities exhibited extensive macroalgal cover and no *D. antillarum*.

Radial growth rates of *P. astreoides* varied significantly dependent on whether they were single or aggregated colonies, and whether they were in contact with macroalgae or with competitor coral species (Fig. 3). Single colonies of *P. astreoides* at Dairy Bull reef ( $n = 4$ ) not in contact with macroalgal *Dictyota* species had significantly ( $p < 0.002$ ,  $F > 15$ ) greater radial growth rates than single colonies in contact with *Dictyota* at M1 or at Rio Bueno. Two aggregated colonies of *P. astreoides* in contact with one another ( $n = 3$ ) at Dairy Bull reef had significantly lower radial growth rates than single colonies at the same reef ( $p < 0.01$ ,  $F > 7$ ). Two aggregated colonies of *P. astreoides* in contact with one another at Dairy Bull reef, one of which was in contact with the faster growing competitor *A. palmata* ( $n = 3$ ) showed significantly greater radial growth rates than with just two aggregated *P. astreoides* colonies alone

( $p < 0.05$ ,  $F > 5$ ). At Dairy Bull reef there was no significant difference in radial growth rates for *P. astreoides* colonies whether they were in contact with single colonies of the same species, or with single colonies of *S. siderea*, which has similar radial growth rates to *P. astreoides*.

#### 4. Discussion

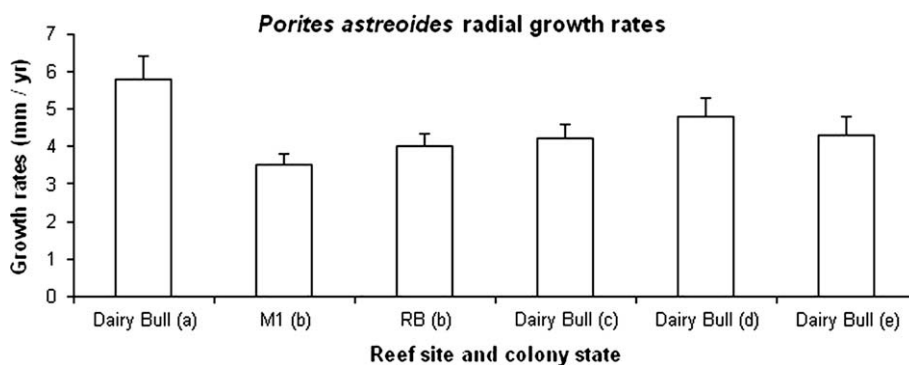
Decline in architectural complexity of Caribbean reefs has been apparent since the 1980s, and coincides with key events in recent Caribbean ecological history (Alvarez-Filip et al., 2009). Rugosity has been selected as a bioindicator for use in monitoring programmes linking changes in water quality to changes in the condition of coral reef ecosystems (Cooper et al., 2009). Reef rugosity correlates well with rocky reef fish community structure in Brazil (Chaves and Monteiro-Neto, 2009), Hawaii (Howard et al., 2009), the Great Barrier Reef (Emslie et al., 2008), Barbados (Chapman and Kramer, 1999), the Seychelles (Wilson et al., 2007), and the Gulf of Mexico (Rooker et al., 1997). Rugose locations aid aggregation of *D. antillarum* urchins, important to keep macroalgae in check (Macia et al., 2007).

The continued presence of small coral colonies over time can indicate reef resilience (Loya, 1976; Connell, 1978), and here we demonstrate that increases in colony numbers of the smallest size class for *S. siderea*, *C. natans*, *P. astreoides* and *Agaricia* species since the mass bleaching event of 2005 is significantly correlated with reef rugosity at all the sites studied. Water quality is not a factor in differences between the reef sites (D'Elia et al., 1981; Greenaway and Gordon-Smith, 2006).

In addition, we show that rugosity positively correlates with coral cover of *A. cervicornis* colonies. Increase in *A. cervicornis* cover was one of the main reasons for suggesting a phase-shift reversal at Dairy Bull reef (Idjadi et al., 2006). It is interesting that New reef, at about 8 m depth between M1 and Dancing Ladies, has similar rugosity and *A. cervicornis* cover to that of Dairy Bull reef. These findings suggest that the three dimensional topography and complexity is important for reef resilience and viability in the face of environmental stressors such as bleaching. Interestingly, rugosity also correlates well with fish abundance on other reefs, for example with parrotfish (Scarid) abundance on reefs of Oahu, Hawaii (Howard et al., 2009), and rugosity has been used in regional modelling of coral habitats for marine conservation (Dunn and Halpin, 2009).

This study shows that absence of macroalgal cover allows increased growth rates of *A. cervicornis*, as has been found with *Montastrea annularis*, *P. astreoides*, and *Sidastrea siderea* (Crabbe, 2008; this study). Macroalgal competition has been found to reduce the survivorship and growth of corals in forereefs in Roatan, Honduras (Box and Mumby, 2007) and in Florida (Lirman, 2001). It is possible that *A. palmata*, consisting generally of taller colonies, is not limited by macroalgal contact or shading in the same way as *A. cervicornis*.

It has been suggested that the spatial dispersion of competitors within habitat patches can determine the outcome of interspecific interactions (Stoll and Prati, 2001; Hartley and Shorrocks, 2002). Experimental studies have found that aggregated spatial arrangements can influence the outcome of interspecific competition and promote species coexistence (Idjadi and Karlson, 2007). This would be important in maintaining species biodiversity during reef recovery from environmental stressors such as bleaching. This field study showed that while aggregated *P. astreoides* colonies exhibited significantly lower growth than single colonies, interaction with the stronger competitor *A. palmata* resulted in a small but significant increase in *P. astreoides* growth rate. The survival of slow growing colonies is important to maintain coral diversity, so a small increase in growth rate could potentially confer a significant advantage on a densely settled substratum (Vollmer and Edmunds,



**Fig. 3.** Radial growth rates ( $\text{mm yr}^{-1}$ ; mean  $\pm$  1 standard error) for *Porites astreoides* colonies at Dairy Bull reef, M1 and Rio Bueno, from 2006 to 2009.  $n = 4$  for all single colony data (a and b);  $n = 3$  for all other data (c–e). (a) Single isolated colonies; (b) single colonies in contact with *Dictyota* sp. macroalgae; (c) two aggregated colonies in contact with one another; (d) two aggregated colonies in contact with one another, one of which was in contact with a colony of the faster growing competitor *A. palmata*; (e) single colony of *P. astreoides* in contact with a colony of *Sidastrea siderea* (which has similar radial growth rates to *P. astreoides*).

2000), such as at Dairy Bull reef. Such a heterospecific interaction growth effect may act in concert with other colonization/competition trade-offs (Cadotte et al., 2006), and would also be important after a major disturbance such as a hurricane or a bleaching event. Although this study does not have the sample numbers or the control of the experimental setup of Idjadi and Karlson, it does suggest that a similar mechanism can operate in the field to promote species coexistence.

Reefs are under stress from a variety of insults that act in synergy (Anthony et al., 2008). It may be that under conditions of low coral cover, low reef rugosity and low biodiversity, a major disturbance such as the 2005 bleaching event crosses a 'threshold' which then induces a cascade to induce the crossing of other thresholds, leading to a stable but less desirable alternative state (Kinzig et al., 2006). An example where this has happened may be the reefs of Tobago (Mallela and Crabbe, 2009). On the reefs of North Jamaica, there is a variable response and resilience, strongest in the case of Dairy Bull reef, which exhibits relatively high rugosity, coral cover and biodiversity with no significant macroalgal cover (Crabbe, 2009; this work). Whether the niche diversification and multiple symbiont clades in corals at Dairy Bull reef (see Crabbe, 2009) is sufficient to allow for adaptive radiation (Brockhurst et al., 2007) in a period of intense climate change and ocean acidification is yet to be resolved.

Reef rugosity, contact of corals with macroalgae, and aggregation and competition between corals could influence reef resilience together with species and functional diversity, connectivity to larval sources, appropriate substrates for larval settlement, and protection from other anthropogenic effects (Nyström et al., 2008; Halford and Caley, 2009). As reefs become increasingly subjected to high sea surface temperatures and thermal stress (Loya et al., 2001; Thompson and van Woeseik, 2009), all these factors will be important to ensure coral resilience to continued environmental stressors.

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### References

Abrego, D., Ulstrup, K.E., Willis, B.L., van Oppen, M.J.H., 2008. Species-specific interactions between algal endosymbionts and coral hosts define their

- bleaching response to heat and light stress. *Proceedings of the Royal Society B* 275, 2273–2282.
- Adjerdou, M., Michonneau, F., Edmunds, P.J., Chancerelle, Y., de Loma, T.L., Penin, L., Thibaut, L., Vidal-Dupiol, J., Salvat, B., Galzin, R., 2009. Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a South Central Pacific reef. *Coral Reefs* 28, 775–780.
- Alvarez-Filip, L., Dulvy, N.K., Gill, J.A., Côté, I.M., Watkinson, A.R., 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B* 276, 3019–3025.
- Anthony, K.R.N., Kline, D.L., Diaz-Pulido, G., Dove, S., Hoegh-Guldberg, O., 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences USA* 105, 17442–17446.
- Aronson, R.B., Precht, W.F., 2001. Evolutionary paleoecology of Caribbean coral reefs. In: Allmon, W.D., Bottjer, D.J. (Eds.), *Evolutionary Paleocology: The Ecological Context of Macroevolutionary Change*. Columbia University Press, New York, USA, pp. 171–233.
- Box, S.J., Mumby, P.J., 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. *Marine Ecology – Progress Series* 342, 139–149.
- Brockhurst, M.A., Colegrave, N., Hodgson, D.J., Buckling, A., 2007. Niche occupation limits adaptive radiation in experimental microcosms. *PLOS One* 2, e193. doi:10.1371/journal.pone.0000193.
- Bruno, J.F., Sweatman, H., Precht, W.F., Selig, E.R., Schutte, V.G.W., 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90, 1478–1484.
- Cadotte, M.W., Mai, D.V., Jantz, S., Collins, M.D., Keele, M., Drake, J.A., 2006. On testing the competition–colonization trade-off in a multi-species assemblage. *American Naturalist* 168, 704–709.
- Chapman, M.R., Kramer, D.L., 1999. Gradients in coral reef fish density and size across the Barbados Marine reserve boundary: effects of reserve protection and habitat characteristics. *Marine Ecology – Progress Series* 181, 81–96.
- Chaves, L.D.T., Monteiro-Neto, C., 2009. Comparative analysis of rocky reef fish community structure in coastal islands of south-eastern Brazil. *Journal of Marine Biological Association of the UK* 89, 609–619.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Cooper, T.F., Gilmour, J.P., Fabricius, K.E., 2009. Bioindicators of changes in water quality on coral reefs: review and recommendations for monitoring programmes. *Coral Reefs* 28, 589–606.
- Crabbe, M.J.C., 2008. Influence of macroalgal cover on coral colony growth rates on fringing reefs of Discovery Bay, Jamaica. *Open Marine Biology Journal* 2, 1–6.
- Crabbe, M.J.C., 2009. Scleractinian coral population size structures and growth rates indicate coral resilience on the fringing reefs of North Jamaica. *Marine Environmental Research* 67, 189–198.
- Crabbe, M.J.C., Smith, D.J., 2002. Comparison of two reef sites in the Wakatobi Marine National Park (SE Sulawesi, Indonesia) using digital image analysis. *Coral Reefs* 21, 242–244.
- Crabbe, M.J.C., Smith, D.J., 2005. Sediment impacts on growth rates of *Acropora* and *Porites* corals from fringing reefs of Sulawesi, Indonesia. *Coral Reefs* 24, 437–441.
- Crabbe, M.J.C., Mendes, J.M., Warner, G.F., 2002. Lack of recruitment of non-branching corals in Discovery Bay is linked to severe storms. *Bulletin of Marine Science* 70, 939–945.
- Crabbe, M.J.C., Martinez, E., Garcia, C., Chub, J., Castro, L., Guy, J., 2008. Growth modelling indicates hurricanes and severe storms are linked to low coral recruitment in the Caribbean. *Marine Environmental Research* 65, 364–368.
- D'Elia, C.F., Webb, K.L., Porter, J.W., 1981. Nitrate-rich groundwater inputs to Discovery Bay, Jamaica: a significant source of N to local reefs? *Bulletin of Marine Science* 31, 903–910.
- Donner, S.D., Knutson, T.R., Oppenheimer, M., 2007. Model-based assessment of the role of human-induced climate change in the 2005 Caribbean coral bleaching event. *Proceedings of the National Academy of Sciences USA* 104, 5483–5488.

- Dunn, D.C., Halpin, P.N., 2009. Rugosity-based regional modelling of hard bottom habitat. *Marine Ecology – Progress Series* 377, 1–11.
- Elahi, R., Edmunds, P.J., 2007. Consequences of fission in the coral *Siderastrea siderea*: growth rates of small colonies and clonal input to population structure. *Coral Reefs* 26, 271–276.
- Emslie, M.J., Cheal, A.J., Sweatman, H., Delean, S., 2008. Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. *Marine Ecology – Progress Series* 371, 177–190.
- Foster, N.L., Baums, I.B., Mumby, P.J., 2007. Sexual vs. asexual reproduction in an ecosystem engineer: the massive coral *Montastrea annularis*. *Journal of Animal Ecology* 76, 384–391.
- Greenaway, A.M., Gordon-Smith, D.-A., 2006. The effects of rainfall on the distribution of inorganic nitrogen and phosphorus in Discovery Bay, Jamaica. *Limnology and Oceanography* 51, 2206–2220.
- Halford, A.R., Caley, M.J., 2009. Towards an understanding of resilience in isolated coral reefs. *Global Change Biology*. doi:10.1111/j.1365-2486.2009.01972.
- Hawkins, J.P., Roberts, C.M., 2004. Effects of artisanal fishing on Caribbean coral reefs. *Conservation Biology* 18, 215–226.
- Howard, K.G., Schumacher, B.D., Parrish, J.D., 2009. Community structure and habitat associations of parrotfishes on Oahu, Hawaii. *Environmental Biology of Fishes* 85, 175–186.
- Hartley, S., Shorrocks, B., 2002. A general framework for the aggregation model of coexistence. *Journal of Animal Ecology* 71, 651–662.
- Hughes, T.P., 1994. Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551.
- Hughes, T.P., Jackson, J.B.C., 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. *Science* 209, 713–715.
- Huston, M., 1985. Variation in coral growth rates with depth at Discovery Bay, Jamaica. *Coral Reefs* 4, 19–25.
- Idjadi, J.A., Karlson, R.H., 2007. Spatial arrangement of competitors influences coexistence of reef-building corals. *Ecology* 88, 2449–2454.
- Idjadi, J.A., Lee, S.C., Bruno, J.F., Preecht, W.F., Allen-Requa, L., Edmunds, P.J., 2006. Rapid phase-shift reversal on a Jamaican coral reef. *Coral Reefs* 25, 209–211.
- Jackson, J.B.C., 1997. Reefs since Columbus. In: *Proceedings of the Eighth International Coral Reef Symposium*, vol. 1, pp. 97–106.
- Jones, L., Alcolado, P.M., Cala, Y., Cobián, D., Coelho, V., Hernández, A., Jones, R., Mallela, J., Manfrino, C., 2008. The effects of coral bleaching in the northern Caribbean and western Atlantic. In: *Status of Caribbean Coral Reefs after Bleaching and Hurricanes in 2005*. Global Coral Reef Monitoring Network. Reef and Rainforest Research Centre, Townsville, Australia, pp. 73–83.
- Karlson, R.H., 1999. *Dynamics of Coral Communities*. Kluwer Academic Publishers, Dordrecht, The Netherlands. 250pp.
- Karlson, R.H., Cornell, H.V., Hughes, T.P., 2007. Aggregation influences coral species richness at multiple spatial scales. *Ecology* 88, 170–177.
- Kinzig, A. P., Ryan, P., Etienne, M., Allison, H., Elmqvist, T., Walker, B. H., 2006. Resilience and regime shifts: Assessing cascading effects. *Ecology and Society* 11. Article no. 20.
- Klumpp, D.W., McKinnon, A.D., 1992. Community structure, biomass and productivity of epilithic algal communities on the great barrier reef-dynamics at different spatial scales. *Marine Ecology – Progress Series* 86, 77–89.
- Lirman, D., 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19, 392–399.
- Liu, P.-J., Shao, K.-T., Jan, R.-Q., Fan, T.-Y., Wong, S.-L., Hwang, J.-S., Chen, J.-P., Chen, C.-C., Lin, H.-J., 2009. A trophic model of fringing coral reefs in Nanwan Bay, southern Taiwan suggest overfishing. *Marine Environmental Research* 68, 106–117.
- Loya, Y., 1976. Effects of turbidity and sedimentation on the community structure of Puerto Rican Corals. *Bulletin of Marine Science* 26, 450–466.
- Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., van Woesik, R., 2001. Coral bleaching: the winners and the losers. *Ecology Letters* 4, 122–131.
- Macia, S., Robinson, M.P., Nalevanko, A., 2007. Experimental dispersal of recovering *Diadema antillarum* increases grazing intensity and reduces macroalgal abundance on a coral reef. *Marine Ecology – Progress Series* 348, 173–182.
- Mallela, J., Crabbe, M.J.C., 2009. Hurricanes and coral bleaching linked to changes in coral recruitment in Tobago. *Marine Environmental Research* 68, 158–162.
- McClanahan, T.R., 1998. Predation and the distribution and abundance of tropical sea urchin populations. *Journal of Experimental Marine Biology and Ecology* 221, 231–255.
- Morgan, J., Heron, S., Eakin, M., 2008. The 2005 bleaching event: coral-list log. In: *Status of Caribbean Coral Reefs after Bleaching and Hurricanes in 2005*. Global Coral Reef Monitoring Network. Reef and Rainforest Research Centre, Townsville, Australia, pp. 37–44.
- Nyström, M., Graham, N.A.J., Lokrantz, J., Norström, A.V., 2008. Capturing the cornerstones of coral reef resilience: linking theory to practice. *Coral Reefs* 27, 795–809.
- Quinn, N.J., Kojis, B.L., 2008. The recent collapse of a rapid phase-shift reversal on a Jamaican north coast reef after the 2005 bleaching event. *International Journal of Tropical Biology* 56 (Suppl. 1), 149–159.
- Rogers, C.S., 1993. Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited. *Coral Reefs* 12, 127–137.
- Rooker, J.R., Dokken, Q.R., Pattengill, C.V., Holt, G.J., 1997. Fish assemblages on artificial and natural reefs in the Flower Garden Banks National Marine Sanctuary, USA. *Coral Reefs* 16, 83–92.
- Sanchez, J.A., Diaz, J.M., Zea, S., 1997. Gorgonian communities in two contrasting environments on oceanic atolls of the southwestern Caribbean. *Bulletin of Marine Science* 61, 453–465.
- Stoll, P., Prati, D., 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology* 82, 319–327.
- Thompson, D.M., van Woesik, R., 2009. Corals escape bleaching in regions that recently and historically experienced frequent thermal stress. *Proceedings of the Royal Society B*. doi:10.1098/rspb.2009.0591.
- Vollmer, S.V., Edmunds, P.J., 2000. Allometric scaling in small colonies of the scleractinian coral *Siderastrea siderea* (Ellis and Solander). *Biological Bulletin* 199, 21–28.
- Wilkinson, C., Souter, D., 2008. Status of Caribbean Coral Reefs after Bleaching and Hurricanes in 2005. *Global Coral Reef Monitoring Network*. Reef and Rainforest Research Centre, Townsville, Australia.
- Wilson, S.K., Graham, N.A.J., Polunin, N.V.C., 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology* 151, 1069–1076.
- Woodley, J.D., Chornesky, E.A., Clifford, P.A., Jackson, J.B.C., Kaufman, L.S., Knowlton, N., Lang, J.C., Pearson, M.P., Porter, J.W., Rooney, M.C., Rylaarsdam, K.W., Tunnicliffe, V.J., Wahle, C.M., Wulff, J.L., Curtis, A.S.G., Dallmeyer, M.D., Jupp, B.P., Koehl, M.A.R., Neigel, J., Sides, E.M., 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science* 214, 749–755.