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Scleractinian coral population size structures and growth rates indicate coral resilience on the fringing reefs of North Jamaica

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ABSTRACT

Coral reefs throughout the world are under severe challenges from many environmental factors. This paper quantifies the size structure of populations and the growth rates of corals from 2000 to 2008 to test whether the Discovery Bay coral colonies showed resilience in the face of multiple acute stressors of hurricanes and bleaching. There was a reduction in numbers of colonies in the smallest size class for all the species at all the sites in 2006, after the mass bleaching of 2005, with subsequent increases for all species at all sites in 2007 and 2008. Radial growth rates (mm yr^{-1}) of non-branching corals and linear extension rates (mm yr^{-1}) of branching corals calculated on an annual basis from 2000–2008 showed few significant differences either spatially or temporally. At Dairy Bull reef, live coral cover increased from $13 \pm 5\%$ in 2006 to $20 \pm 9\%$ in 2007 and $31 \pm 7\%$ in 2008, while live *Acropora* species increased from $2 \pm 2\%$ in 2006 to $10 \pm 4\%$ in 2007 and $22 \pm 7\%$ in 2008. These studies indicate good levels of coral resilience on the fringing reefs around Discovery Bay in Jamaica.

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1. Introduction

Coral reefs throughout the world are under severe challenges from a variety of environmental factors including overfishing, destructive fishing practices, coral bleaching, ocean acidification, sea-level rise, algal blooms, agricultural run-off, coastal and resort development, marine pollution, increasing coral diseases, invasive species, and hurricane/cyclone damage, (Gardner et al., 2003; Bellwood et al., 2004; Crabbe et al., in press). The fringing reefs around Discovery Bay in Jamaica constitute one of the best documented areas of reef decline in the Caribbean, where loss of corals and macroalgal domination 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). Nutrient enrichment does not appear to have been a causal factor in the development of the reef macroalgal communities (Greenaway and Gordon-Smith, 2006).

Maintaining coral reef populations in the face of large scale degradation and phase-shifts on reefs depends critically on recruitment (Hughes and Tanner, 2000; Coles and Brown, 2007), maintenance of grazing fish and urchin populations (Mumby

et al., 2007), clade of symbiotic zooxanthellae (Stat et al., 2008) and management of human activities related to agricultural land use and coastal development (Mora, 2008). To manage coral reefs it is important to have an understanding of coral population demography – structure and dynamics (Soong, 1993; Meesters et al., 2001; Smith et al., 2005). Ideally, this involves the quantification of numbers of individual colonies of different size classes – the population structure-through time, in addition to quantifying coral growth rates, recruitment and survival. The fringing reefs around Discovery Bay have seen a number of climate-related challenges in recent years, notably several hurricanes as well as a mass bleaching event in the Caribbean in 2005 (Jones et al., 2004; 2008). Despite all these negative factors, there is evidence that prior to 2005 some Discovery Bay reefs were recovering (Idjadi et al., 2006), although a study subsequent to the 2005 bleaching event is not so positive (Quinn and Kojis, 2008). Healthy reefs have a high proportion of small size-classes that include new recruits and juveniles (Meesters et al., 2001), and the smallest size class of corals can be a good indicator of reef resilience (Loya, 1976; Connell, 1978). This study set out to quantify the size structure of populations and the growth rates of a number of corals over time in order to test whether the Discovery Bay coral colonies were exhibiting resilience in the face of multiple acute stressors of hurricanes and bleaching. I take the definition of resilience as the ability of the system to recover from disturbance and change, while main-

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taining its function (Carpenter et al., 2001; Grimsditch and Salm, 2006); for example a coral reef's ability to recover from a bleaching event. Resilience is a multi-faceted concept (Nyström et al., 2008), and factors that can improve coral reef resilience to a mass bleaching event include good species and functional diversity, good connectivity to larval sources, appropriate substrates for larval settlement and protection from other anthropogenic impacts.

2. Methods

2.1. Data on storms, hurricanes and bleaching events impacting Discovery Bay

Data on storm severity as it impacted the Discovery Bay sites was obtained from UNISYS (<http://weather.unisys.com/hurricane/atlantic/>) and the NOAA hurricane site (<http://www.nhc.noaa.gov/pastall.shtml>).

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

2.2. Sites and sampling

Four haphazardly located transects, each 15 m long and separated by at least 5 m, were laid at between 5–8.5 m depth at each of five sites [Rio Bueno (18° 28.805' N; 77° 27.625' W), M1 (18° 28.337' N; 77° 24.525' W), Dancing Ladies (18° 28.369' N; 77° 24.802' W), Dairy Bull (18° 28.083' N; 77° 23.302' W) and Pear Tree Bottom (18° 27.829' N; 77° 21.403' W)] along the fringing reefs surrounding Discovery Bay, Jamaica (Fig. 1). GPS coordinates were determined using a hand-held GPS receiver (Garmin Ltd.). Corals 2 m either side of the transect lines were photographed for archive information, and surface areas measured with flexible tape as described previously using SCUBA (Crabbe et al., 2002; Crabbe and Smith, 2005; Crabbe et al., 2008). For non-branching corals, this was done by measuring the widest diameter of the coral and the diameter at 90° to that. For branching corals (*Acropora palmata* and *Acropora cervicornis*), linear extension rates were measured using digital photography and image analysis, validated by measurements with flexible tape (Crabbe et al., 2002; Crabbe and Smith, 2005; Crabbe, 2007). Depth of samples was between 5–8.5 m, to minimise variation in growth rates due to depth (Huston,

1985). To increase accuracy, surface areas rather than diameters of live non-branching corals were measured (Crabbe et al., 2002; Crabbe and Smith, 2005). Sampling was over as wide a range of sizes as possible. Colonies that were close together (<50 mm) 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).

In this study we ignored *Montastrea annularis* colonies for demographic analyses, because 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) although we included this species in growth rate measurements.

Radial growth rates of non-branching corals and linear extension rates of branching corals were calculated for each year from 2000–2008 as described previously (Crabbe et al., 2002; Crabbe and Smith, 2005). Overall, over 8000 measurements were made on over 1500 coral colonies, equally distributed between the sites for species and numbers of colonies.

This work was conducted at Discovery Bay during July 15–31 and December 19–30 in 2000, March 26–April 19 in 2002, March 18–April 10 in 2003, July 23–August 21 in 2004, July 18–August 13 in 2005, April 11–18 in 2006, December 30 in 2006–January 6 in 2007, and July 30–August 16 in 2008. Surveys were made at the same locations at the same sites each year.

Computer digital image analysis for coral linear extension rates 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; \pm error values represent standard errors of the data. The skewness coefficient (sk) (Zar, 1999) was used to quantify the relationship between the number of large and small corals within each population. The skewness for a normal distribution about the mean is zero, and any symmetric data should have skewness near zero. Negative values for the skewness indicate data that are skewed left (more small colonies than in a normal distribution) and positive values for the skewness indicate data that are skewed right (more large colonies than in a normal distribution). Water quality measurements at the sites have been reported previously (D'Elia et al., 1981; Greenaway and Gordon-Smith, 2006).

3. Results

3.1. Environmental climate stressors-tropical storms and bleaching events

Hurricanes that had the potential to impact the reef sites during the study period are shown in Fig. 2, with their paths of travel. Only one of these storms resulted in any significant damage on the reefs, Ivan in 2004, a category 4 hurricane as it passed south of the island. Visually, the damage was minimal as far as reef destruction was concerned, with some *A. palmata* colonies being fragmented and overturned, notably at Pear Tree Bottom (personal observation). Although hurricane Emily in 2005 was also a category 4 hurricane, the eye passed sufficiently south of the island so that the impact involved sediment transfer owing to the high winds and rain (Crabbe and Carlin, 2007). Tropical storms Iris (category 1 hurricane, 2001), Lili (tropical storm, 2002), Bonnie (tropical wave, 2004), Charley (category 1 hurricane, 2004), Dennis (category 3 hurricane, 2005), Olga (tropical storm, 2007) and Dean (hurricane category 4, 2007) did not result in significant damage to the reef sites.

The only bleaching event that significantly impacted the reef sites during the study period was the mass Caribbean bleaching

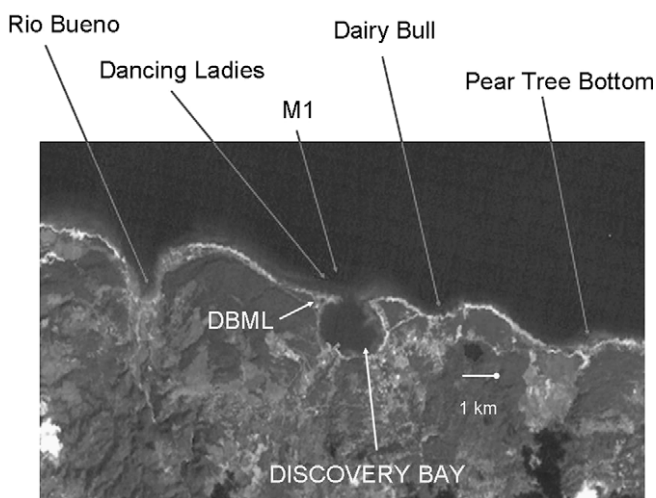


Fig. 1. Satellite image showing the location of fringing reef sites in this study (Rio Bueno, M1, Dancing Ladies, Dairy Bull and Pear Tree Bottom) around Discovery Bay, Jamaica. DBML, Discovery Bay Marine Laboratory. The horizontal line shows 1 km distance. See text for GPS coordinates.

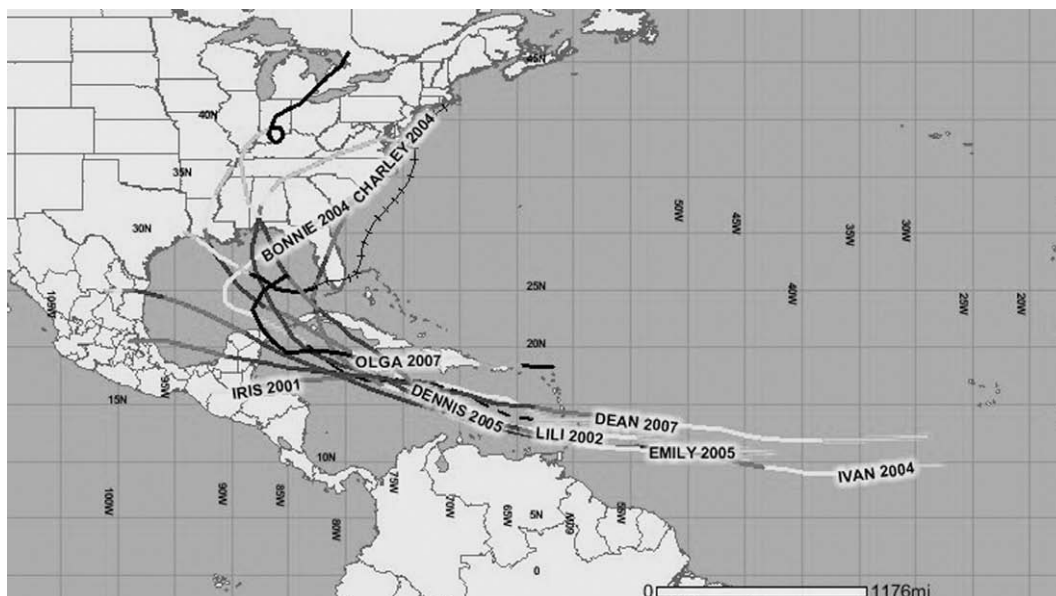


Fig. 2. Hurricane tracks impacting the Jamaican fringing reefs around Discovery Bay.

event of 2005. Analysis of satellite data showed that there were 6° heating weeks (dhw) for sea surface temperatures in September and October 2005 near Discovery Bay, data which were mirrored by data loggers on the reefs (Quinn and Kojis, 2008). Six dhw are equivalent to six weeks of sea surface temperatures (SSTs) 1 °C greater than the expected summer maximum.

3.2. Coral colony size-frequency distributions and growth rates

Fig 3 a–h compares the size-frequency distribution of the corals *Sidastrea siderea*, *Diploria labyrinthiformis*, *Porites astreoides*, and *Colpophyllia natans* at the fringing reef sites Rio Bueno, M1, Dancing Ladies, Dairy Bull, and Pear Tree Bottom in 2002 and 2008. These dates covered the major bleaching event and hurricane Ivan. Size-frequency distributions were also determined for the corals *Diploria strigosa*, *Meandrina meandrites*, and *Agaricia* species, and the results discussed below. All the sites showed some similarities in distribution of the size classes for the species studied between 2002 and 2008. However, there were differences between the different sites, and between the different species studied at the sites. Skewness values (sk) were used to compare the distribution of the data between 2002 and 2008. For *S. siderea*, all sk values were positive (skewed to the left, with more large colonies than in a normal distribution) for 02 and 08, with little change between the dates (all sk values between 0.5 and 1.6). With *D. labyrinthiformis* colonies, there was a change from negative skewness in 2002 at Dairy Bull and Pear Tree Bottom (skewed to the right, with more small colonies than in a normal distribution) (sk values -0.25 and -0.006 respectively) to more large colonies than in a normal distribution in 2008 (sk values of 0.20 and 0.97, respectively). There were no significant changes from 2002–2008 at the other sites, with positive sk values from 0.1 to 0.89. *M. meandrites* colonies at Rio Bueno and Dairy Bull showed a relative decrease in the distribution of smaller colonies from 2002 to 2008, with changes in sk values from -0.03 in 02 to 0.78 in 08, and from -0.05 to 0.03, respectively; the other sites all exhibited slightly positive sk values in both years from between 0.1 and 0.5. For *Agaricia* species, there was very little change between the years at all the sites, with sk values from between 0.4 and 1.6. For *P. astreoides*, all values were positive for both years, with an increase in skewness at Rio Bueno

from 0.2 to 2.6, showing a marked change in distribution towards the larger colony sizes. At the other sites there were only small increases in sk values from 2002 to 2008, with Pear tree Bottom showing a decrease in skewness from 0.9 to 0.6. *D. strigosa* colonies showed similar results to *P. astreoides*, all sk values being positive for 2002 and 2008, with an increase at Rio Bueno from 0.2 to 2.2 and at Pear Tree Bottom from 0.4 to 2.4; other sites showed similar sk values from 2002 to 2008 from 0.6 to 1.6. *C. natans* skewness changed from -0.07 to 0.68 at Rio Bueno from 2002 to 2008 (a decrease in smaller colonies relative to a normal distribution), and at Dancing Ladies from -0.31 to 0.38. Other sites showed similar skewness in 2002 and 2008 (sk values between 0.5–0.6), except Pear Tree Bottom, which exhibited near normal distribution of colonies about the mean for both 2002 and 2008 (sk values < 0.01). There was no correlation between coral size-frequency distributions and water quality (taken from Greenaway and Gordon-Smith, 2006).

As by far the major disturbance to the reef sites was the mass bleaching event of 2005, the mean size class for all the species at all the reef sites were compared for 2002, 2006 (after the bleaching event) and 2008, with examples shown in Fig. 4a–d. For *S. siderea* colonies mean size class was lower in 2006 than in 2002 at all sites ($F > 1.5$, $p < 0.01$) except at Dancing Ladies where there was no significant difference. Mean size class was raised from 2006 to 2008 at all sites ($F > 5$, $p < 0.001$) except at Rio Bueno (no significant difference) and at Pear Tree Bottom (lower mean size class, $F > 2$, $p < 0.02$). There were no significant differences in mean size class between 2002 and 2008 except at Rio Bueno, where it was lower ($F > 1.5$, $p < 0.02$). For *D. labyrinthiformis* colonies, there were significant reductions in mean size class from 2002 to 2006 at Dairy Bull and Pear Tree Bottom (both $F > 2$, $p < 0.03$) and reductions at M1 and Pear Tree Bottom from 2002 to 2008 ($F > 3$, $p < 0.01$ and $F > 1.5$, $p < 0.05$, respectively). There were no significant increases in size class from 2006 to 2008. This was also the case for *M. meandrites* colonies, where there were no significant changes in mean size class between the years. In contrast, there were significant reductions in mean size class of *Agaricia* species mean size class at all sites from 2002 to 2006 ($F > 4$, $p < 0.01$), and mean size class was significantly higher from 2006 to 2008 at all sites ($F > 2$, $p < 0.03$ for Rio Bueno, $F > 6$, $p < 0.008$ for other sites). Mean size

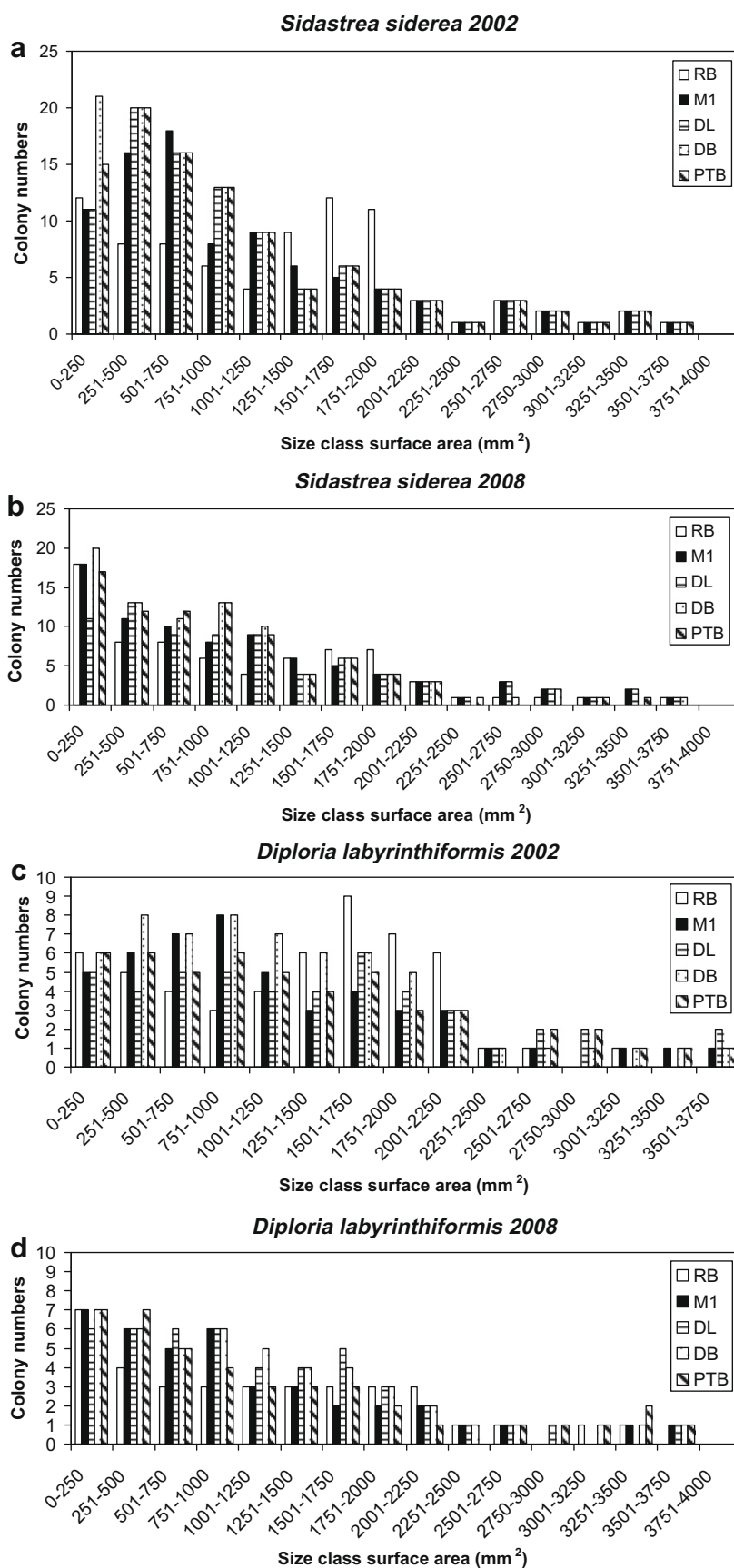


Fig. 3. Size-frequency distribution of colonies in 2002 (a, c, e and g) and in 2008 (b, d, f and h) of: *Sidastrea siderea* (a,b); *Diploria labyrinthiformis* (c,d); *Porites astreoides* (e, f); and *Colpophyllia natans* (g,h) at Rio Bueno (RB), M1 (M1), Dancing Ladies (DL), Dairy Bull (DB) and Pear Tree Bottom (PTB). Skewness (sk) values are discussed in the text.

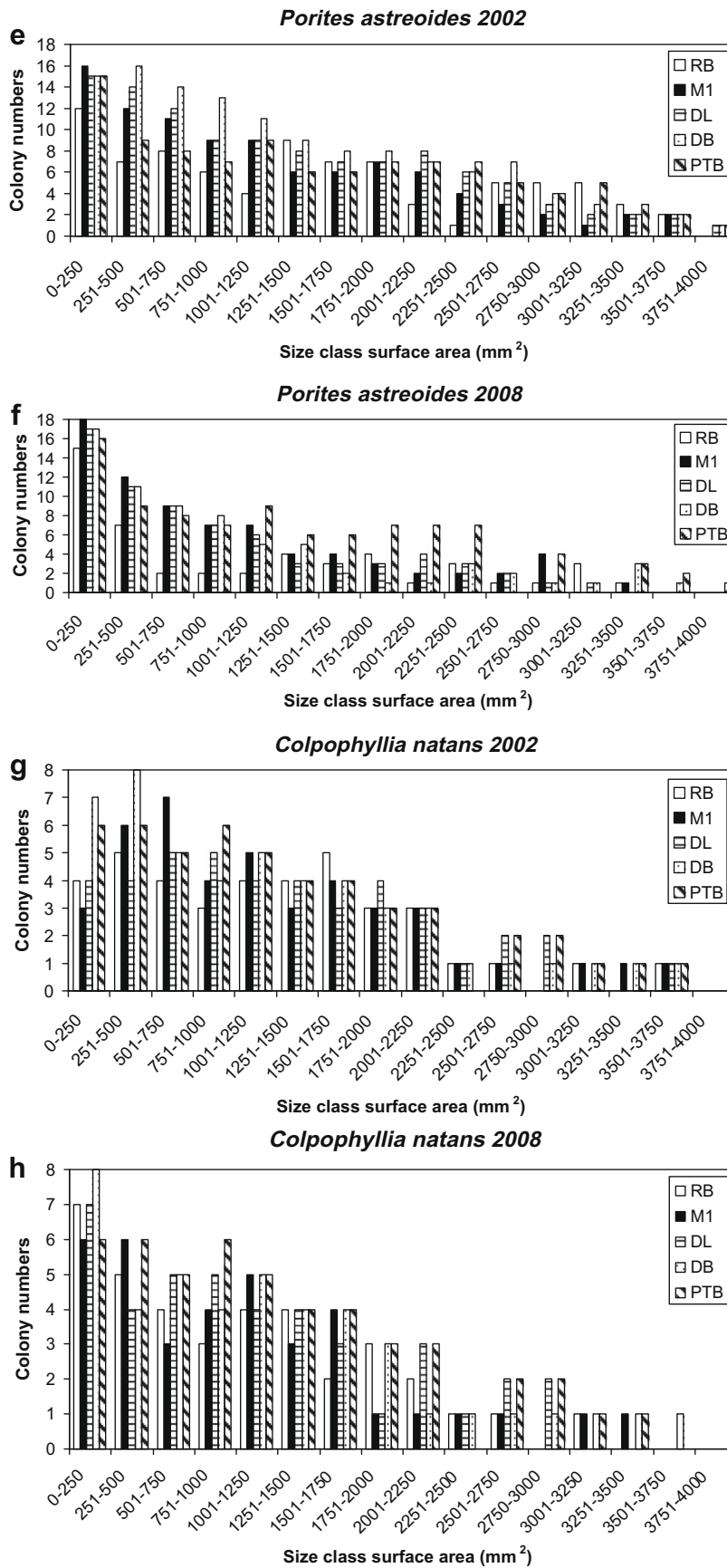


Fig. 3 (continued)

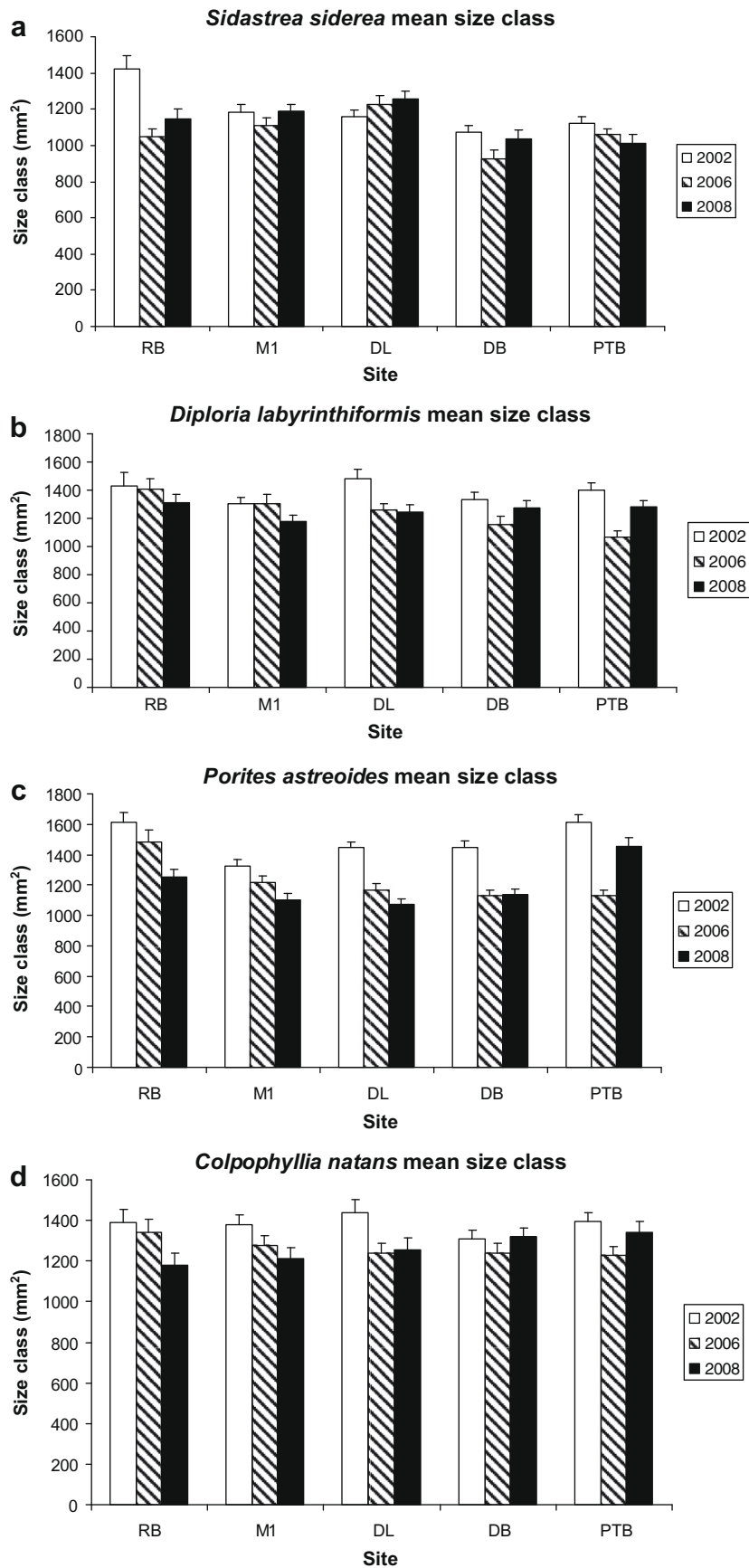


Fig. 4. Mean size classes in 2002, in 2006 and in 2008 of: *Sidastrea siderea* (a); *Diploria labyrinthiformis* (b); *Porites astreoides* (c); and *Colpophyllia natans* (d) at Rio Bueno (RB), M1 (M1), Dancing Ladies (DL), Dairy Bull (DB) and Pear Tree Bottom (PTB). Bar lines represent standard errors; probability values are discussed in the text.

class was only significantly lower in 2008 than in 2002 at Dairy Bull ($F > 2$, $p < 0.01$). Mean class size of *P. astreoides* colonies had reduced significantly from 2002 to 2006 only at Dancing Ladies and Dairy Bull ($F > 2$, $p < 0.01$ for both), and reduced significantly from 2006 to 2008 at Rio Bueno ($F > 2$, $p < 0.03$). All sites had reduced significantly from 2002 to 2008 ($F > 4$, $p < 0.01$) except Pear Tree Bottom (not significant). For *D. strigosa*, mean size class had reduced from 2002 to 2006 at Dancing Ladies, Dairy Bull and Pear Tree Bottom (all $F > 1.5$, $p < 0.04$), and had reduced again in 2008 at Rio Bueno, Dairy Bull and Pear Tree Bottom (all $F > 5$, $p < 0.002$); mean size class was lower at all sites in 2008 than in 2002 ($F > 4$, $p < 0.005$) for this species. For *C. natans*, mean size class fell significantly ($F > 4$, $p < 0.01$) at all sites except at Rio Bueno (no significant difference) from 2002 to 2006. From 2006 to 2008, mean size class was raised at Dairy Bull and at Pear Tree Bottom (both $F > 5$, $p < 0.01$) but fell at Rio Bueno and M1 ($F > 3$, $p < 0.02$); there was no significant difference at Dancing Ladies. At Rio Bueno, M1 and Dancing Ladies only, mean size had fallen significantly overall between 2002 and 2008 ($F > 2$, $p < 0.05$).

As the viability of small coral colonies over time can indicate reef resilience (Loya, 1976; Connell, 1978), the annual changes in the colony numbers of the smallest size class (0–250 mm² surface area) each year from 2002–2008 was plotted for all the non-branching species studied at the fringing reef sites, with examples shown in Fig. 5 for *Sidastrea siderea*, *Diploria labyrinthiformis*, *Porites astreoides*, and *Colpophyllia natans*. There was a reduction in the smallest size class for all the species at all the sites in 2006, with subsequent increases for all species at all sites in 2007 and 2008. Until 2006, there had been modest increases – or least no decreases – in the numbers of the smallest size classes, with the exception of *D. labyrinthiformis* at Rio Bueno, *P. astreoides* at Dancing Ladies, where the trends had decreased slightly. Interestingly, in 2005, the year after hurricane Ivan, the most severe storm to impact the reef sites over the study period, there was a slight reduction in the numbers of the smallest size classes, particularly notable at Dairy Bull.

Dairy Bull reef was the site where studies resulted in the suggestion that there had been a rapid phase-shift reversal on Jamaican reefs (Idjadi et al., 2006), and which suffered a major loss of *A. cervicornis* in 2006 (Quinn and Kojis, 2008). Table 1 shows mean percentage cover of live coral, macroalgae and live *Acropora* species along transects at Dairy Bull reef in 2005 (pre-bleaching), 2006, 2007 and 2008. Cover of live coral, macroalgae and live *Acropora* for 2005 and 2006 are similar to figures reported by Quinn and Kojis (2008). While macroalgal cover remained essentially unchanged in 2007 and 2008, there were increases in live coral cover and live *Acropora* species in both 2007 and 2008. The majority of the increase in coral is represented by increases in live *A. cervicornis*.

Coral growth rates are part of a demographic approach to monitoring coral reef health (Smith et al., 2005), and Table 2 presents radial growth rates (mm yr⁻¹) of non-branching corals and linear extension rates (mm yr⁻¹) of branching corals calculated on an annual basis and tabled from 2000–2003, 2003–2005, and 2005–2008 at all the sites studied. The growth rates are similar to those reported by Huston (1985). There were few significant differences between the sites for each species studied, or across the time period of the study. Where growth rates were higher, they tended to be higher at Dairy Bull reef, but the differences were not significant. With the increase of *D. antillarum* at Rio Bueno in recent years, clearing the macroalgae, healthy *A. palmata* and *A. cervicornis* colonies have appeared at the Rio Bueno site from 2006. At Dancing Ladies, a site with much macroalgal cover, *A. cervicornis* colonies which were measurable from 2003–2005 had disappeared in 2006, possibly as a result of the mass bleaching event, while at M1, a site with even greater macroalgal cover, *A. cervicornis* colonies appeared which were measurable in 2008.

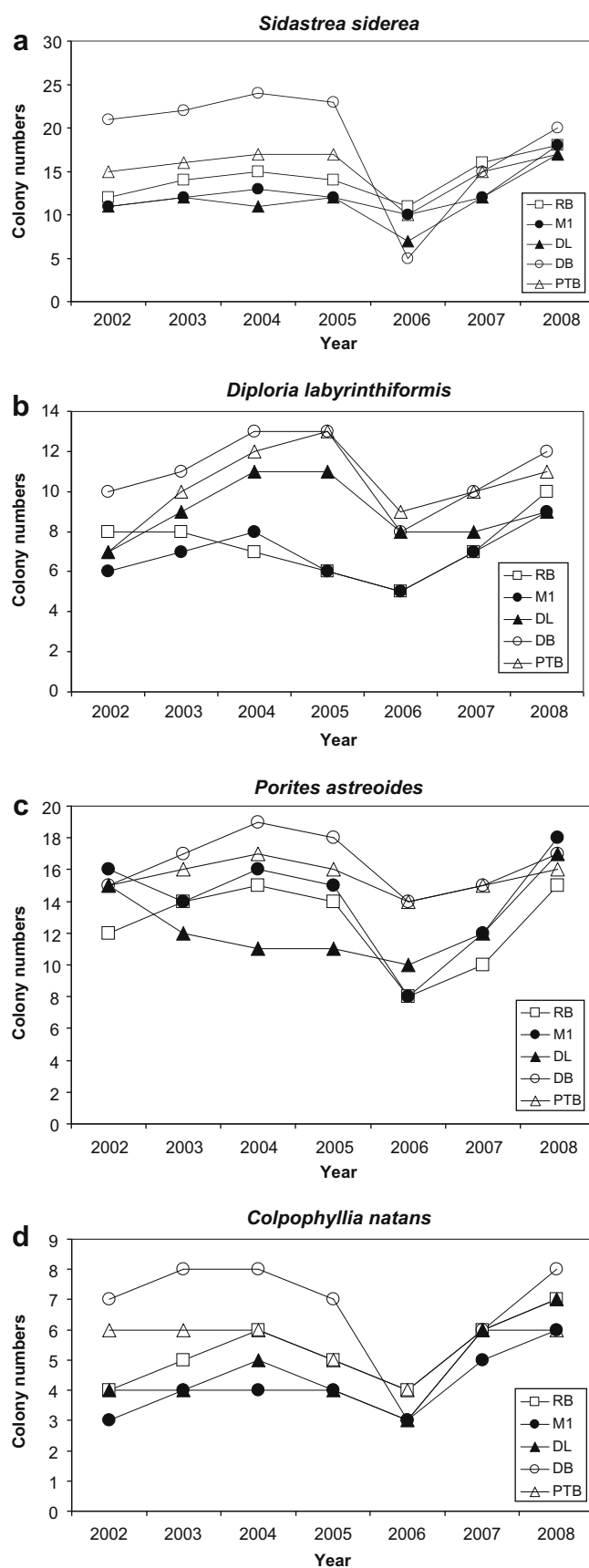


Fig. 5. Graphs of annual changes in the colony numbers of the smallest size class (0–250 mm² surface area) from 2000–2008 for: *Sidastrea siderea* (a); *Diploria labyrinthiformis* (b); *Porites astreoides* (c); and *Colpophyllia natans* (d) at Rio Bueno (RB), M1 (M1), Dancing Ladies (DL), Dairy Bull (DB), and Pear Tree Bottom (PTB).

2008. The reef sites which had the most macroalgal cover, Dancing Ladies and M1, showed fewer changes in size class distribution through the study period, possibly because these sites show large macroalgal cover (Crabbe, 2008). There were no significant differences in fishing pressure between the sites. This study concentrates on size-classes and growth rates; coral recruitment or survival (Smith et al., 2005) has not been measured, although we have modelled coral recruitment at these sites (Crabbe et al., 2002) and it has been measured in other studies (Quinn and Kojis, 2008). In this study we have not considered reef connectivities, relative colonisation rates or socio-economic variables in reef resilience (Nyström et al., 2008).

By far the major acute influence on the reef sites was the mass bleaching event of late 2005. Mean size classes of most of the corals studied at the reef sites were reduced in 2006, and while there was considerable recovery by 2008 in mean size class of some species studied, there was no significant recovery to 2002 levels in mean size class for *C. natans*, *D. labyrinthiformis*, or *D. strigosa* colonies at most sites between 2006 and 2008, and in general mean size class was lower for these corals than in 2002. While there was a considerable drop in the smallest size class of all corals at all sites after the 2005 bleaching event, by 2008 numbers of colonies at all the sites had recovered considerably. In the coming years, if there are no major new catastrophic disturbances, these smaller colonies may result in increases in the mean size class to pre-2006 levels.

Interestingly, growth rates of both branching and non-branching corals showed similar values throughout the study period, with trends, not significant, for slightly higher values at Dairy Bull reef.

Diary Bull reef has for several years been the fringing reef with the most coral cover, with a benthic community similar to that of the 1970s (Huston, 1985), and it was the subject of the study which suggested a rapid phase-shift reversal (Idjadi et al., 2006). After the 2005 bleaching event there was a major loss of live coral cover, particularly of *A. cervicornis* (Quinn and Kojis, 2008; this study), and it is encouraging that both coral cover and the rapidly growing *A. cervicornis* colonies have returned to the reef at levels approaching pre-bleaching values. The influence of *M. annularis* colonies on the reef, acting as structural refugia (Idjadi et al., 2006), may have facilitated this recovery. Interestingly, we found a variety of clades of zooxanthellae, including clade C, in corals at Dairy Bull reef (Crabbe and Carlin, 2007), and the potential for symbiont shuffling, as we have found in 111 colonies of *Acropora* species from the Ningaloo reef, Australia (Crabbe and Carlin, 2009), may be a factor in their recovery (Stat et al., 2008).

Dairy Bull reef behaves somewhat like a successional niche (Pacala and Rees, 1998; Kinzig and Pacala, 2001), as late successional species are not the strongest competitors, and the high population of *D. antillarum* at the site keep the macroalgae in check. Despite continued overfishing (Hawkins and Roberts, 2004), there is a good diversity of fish species, including herbivores such as Scaridae and Acanthuridae, although fish sizes are small (usually < 100 mm) (personal observation). Even at M1, with one of the highest covers of macroalgae and no *D. antillarum*, we have seen that *A. cervicornis* can form colonies after the major disturbance of the mass bleaching event in 2005. Most reefs are open non-equilibrium systems, (Connell, 1978) with diversity maintained by disturbance and recruitment. While that may be true at the macro- or landscape level, Dairy Bull reef, after the mass bleaching event, is exhibiting some properties of niche diversification (Jackson, 1991; Pacala and Rees, 1998; Kinzig and Pacala, 2001).

What is apparent from this study is that despite the chronic and acute disturbances between 2002 and 2008, demographic studies indicate good levels of coral resilience on the fringing reefs around Discovery Bay in Jamaica. The bleaching event of 2005 resulted in mass bleaching but relatively low levels of mortality (Quinn and

Kojis, 2008), unlike corals in the US Virgin islands where there was extensive mortality (Miller et al., 2006; Whelan et al., 2007), possibly because of their greater degree heating week values. The Jamaican reefs have suffered from long term human-induced chronic stressors, such as overfishing and land development (Adger et al., 2005; Jdalumbi et al., 2008; Mora, 2008; Mumby and Hastings, 2008). Unfortunately, previously successful efforts to engage the local fisherman in controlling catches around Discovery Bay (Sary et al., 1997) have not been maintained, and it may be that the development of a Discovery Bay Marine Park is the only solution.

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