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

3

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12

13 **Keywords:** demographics; tropical storms; hurricanes; cyclones; bleaching; climate
14 change; global warming; coral growth; recruitment, Discovery Bay

1 **Abstract**

2 Coral reefs throughout the world are under severe challenges from many
3 environmental factors. This paper quantifies the size-structure of populations and the
4 growth rates of corals from 2000-2008 to test whether the Discovery Bay coral
5 colonies showed resilience in the face of multiple acute stressors of hurricanes and
6 bleaching. There was a reduction in numbers of colonies in the smallest size class for
7 all the species at all the sites in 2006, after the mass bleaching of 2005, with
8 subsequent increases for all species at all sites in 2007 and 2008. Radial growth rates
9 (mm/yr) of non-branching corals and linear extension rates (mm/yr) of branching
10 corals calculated on an annual basis from 2000-2008 showed few significant
11 differences either spatially or temporally. At Dairy Bull reef, live coral cover
12 increased from $13 \pm 5\%$ in 2006 to $20 \pm 9\%$ in 2007 and $31 \pm 7\%$ in 2008, while live
13 *Acropora* species increased from $2 \pm 2\%$ in 2006 to $10 \pm 4\%$ in 2007 and $22 \pm 7\%$ in
14 2008. These studies indicate good levels of coral resilience on the fringing reefs
15 around Discovery Bay in Jamaica.

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1 **1. Introduction**

2 Coral reefs throughout the world are under severe challenges from a variety of
3 environmental factors including overfishing, destructive fishing practices, coral
4 bleaching, ocean acidification, sea-level rise, algal blooms, agricultural run-off,
5 coastal and resort development, marine pollution, increasing coral diseases, invasive
6 species, and hurricane/cyclone damage, (Gardner et al., 2003; Bellwood et al., 2004;
7 Crabbe et al., 2009). The fringing reefs around Discovery Bay in Jamaica constitute
8 one of the best documented areas of reef decline in the Caribbean, where loss of
9 corals and macroalgal domination has been due to hurricanes (Woodley et al., 1981,
10 Crabbe et al., 2002), overfishing (Jackson, 1997; Hawkins and Roberts, 2004), die-off
11 of the long-spined sea urchin *Diadema antillarum* in 1983-84 (Hughes, 1994), and
12 coral disease (Aronson and Precht, 2001). Nutrient enrichment does not appear to
13 have been a causal factor in the development of the reef macroalgal communities
14 (Greenaway and Gordon-Smith, 2006).

15 Maintaining coral reef populations in the face of large scale
16 degradation and phase-shifts on reefs depends critically on recruitment (Hughes and
17 Tanner, 2000; Coles and Brown, 2007), maintenance of grazing fish and urchin
18 populations (Mumby et al., 2007), clade of symbiotic zooxanthellae (Stat et al., 2008)
19 and management of human activities related to agricultural land use and coastal
20 development (Mora, 2008). To manage coral reefs it is important to have an
21 understanding of coral population demography – structure and dynamics (Soong,
22 1993, Meesters et al., 2001; Smith et al., 2005). Ideally, this involves the
23 quantification of numbers of individual colonies of different size classes – the
24 population structure- through time, in addition to quantifying coral growth rates,
25 recruitment and survival. The fringing reefs around Discovery Bay have seen a

1 number of climate-related challenges in recent years, notably several hurricanes as
2 well as a mass bleaching event in the Caribbean in 2005 (Jones et al., 2004; 2008).
3 Despite all these negative factors, there is evidence that prior to 2005 some Discovery
4 Bay reefs were recovering (Idjadi et al., 2008), although a study subsequent to the
5 2005 bleaching event is not so positive (Quinn and Kojis, 2008). Healthy reefs have a
6 high proportion of small size-classes that include new recruits and juveniles (Meesters
7 et al., 2001), and the smallest size class of corals can be a good indicator of reef
8 resilience (Loya, 1976; Connell, 1978). This study set out to quantify the size-
9 structure of populations and the growth rates of a number of corals over time in order
10 to test whether the Discovery Bay coral colonies were exhibiting resilience in the face
11 of multiple acute stressors of hurricanes and bleaching. I take the definition of
12 resilience as the ability of the system to recover from disturbance and change, while
13 maintaining its function (Carpenter et al, 2001; Grimsditch and Salm, 2006); for
14 example a coral reef's ability to recover from a bleaching event. Resilience is a multi-
15 faceted concept (Nyström et al., 2008), and factors that can improve coral reef
16 resilience to a mass bleaching event include good species and functional diversity,
17 good connectivity to larval sources, appropriate substrates for larval settlement and
18 protection from other anthropogenic impacts.

19

20 **2. Methods**

21 *2.1. Data on storms, hurricanes and bleaching events impacting Discovery*

22 *Bay*

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

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

4

5 2.2. Sites and Sampling

6 Four haphazardly located transects, each 15 m long and separated by at least 5m, were
7 laid at between 5-8.5 m depth at each of five sites [Rio Bueno (18° 28.805' N; 77°
8 21.625' W), M1 (18° 28.337' N; 77° 24.525' W), Dancing Ladies (18° 28.369' N; 77°
9 24.802' W), Dairy Bull (18° 28.083' N; 77° 23.302' W) and Pear Tree Bottom (18°
10 27.829' N; 77° 21.403' W)] along the fringing reefs surrounding Discovery Bay,
11 Jamaica (Fig. 1). GPS coordinates were determined using a hand-held GPS receiver
12 (Garmin Ltd.). Corals 2m either side of the transect lines were photographed for
13 archive information, and surface areas measured with flexible tape as described
14 previously using SCUBA (Crabbe et al., 2002; Crabbe and Smith 2005; Crabbe et al.,
15 2008). For non-branching corals, this was done by measuring the widest diameter of
16 the coral and the diameter at 90° to that. For branching corals (*Acropora palmata* and
17 *Acropora cervicornis*), linear extension rates were measured using digital
18 photography and image analysis, validated by measurements with flexible tape
19 (Crabbe et al., 2002; Crabbe and Smith, 2005). Depth of samples was between 5-8.5
20 m, to minimise variation in growth rates due to depth (Huston, 1985). To increase
21 accuracy, surface areas rather than diameters of live non-branching corals were
22 measured (Crabbe et al., 2002; Crabbe and Smith, 2005). Sampling was over as wide
23 a range of sizes as possible. Colonies that were close together (<50 mm) or touching
24 were avoided to minimise age discontinuities through fission and altered growth rates
25 (Hughes and Jackson, 1980; Foster et al., 2007; Elahi and Edmunds, 2007).

1 In this study we ignored *Montastrea annularis* colonies, because their surface
2 area does not reflect their age (Hughes and Jackson 1980), and because hurricanes can
3 increase their asexual reproduction through physical damage (Foster et al., 2007).

4 Radial growth rates of non-branching corals and linear extension rates of
5 branching corals were calculated for each year from 2000-2008 as described
6 previously (Crabbe et al., 2002; Crabbe and Smith, 2005). Overall, over 8,000
7 measurements were made on over 1,500 coral colonies, equally distributed between
8 the sites for species and numbers of colonies.

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

14 Computer digital image analysis for coral linear extension rates was
15 undertaken using the UTHSCSA (University of Texas Health Science Center, San
16 Antonio, Texas, USA) Image Tool software (Crabbe and Smith, 2005). One or two-
17 factor ANOVA was used to compare coral data among sites; \pm error values represent
18 standard errors of the data. The skewness coefficient (sk) (Zar, 1999) was used to
19 quantify the relationship between the number of large and small corals within each
20 population. The skewness for a normal distribution about the mean is zero, and any
21 symmetric data should have a skewness near zero. Negative values for the skewness
22 indicate data that are skewed left (more small colonies than in a normal distribution)
23 and positive values for the skewness indicate data that are skewed right (more large
24 colonies than in a normal distribution). Water quality measurements at the sites have
25 been reported previously (D'Elia et al., 1981; Greenaway and Gordon-Smith, 2006).

1

2

3 **3. RESULTS**4 *3.1. Environmental climate stressors- tropical storms and bleaching events*

5 Hurricanes that had the potential to impact the reef sites during the study
6 period are shown in Fig. 2, with their paths of travel. Only one of these storms
7 resulted in any significant damage on the reefs, Ivan in 2004, a category 4 hurricane
8 as it passed south of the island. Visually, the damage was minimal as far as reef
9 destruction was concerned, with some *A. palmata* colonies being fragmented and
10 overturned, notably at Pear Tree Bottom (personal observation). Although hurricane
11 Emily in 2005 was also a category 4 hurricane, the eye passed sufficiently south of the
12 island so that the impact involved sediment transfer owing to the high winds and rain
13 (Crabbe and Carlin 2007). Tropical storms Iris (category 1 hurricane, 2001), Lili
14 (tropical storm, 2002), Bonnie (tropical wave, 2004), Charley (category 1 hurricane,
15 2004), Dennis (category 3 hurricane, 2005), Olga (tropical storm, 2007) and Dean
16 (hurricane category 4, 2007) did not result in significant damage to the reef sites.

17 The only bleaching event that significantly impacted the reef sites during the
18 study period was the mass Caribbean bleaching event of 2005. Analysis of satellite
19 data showed that there were 6 degree heating weeks (dhw) for sea surface
20 temperatures in September and October 2005 near Discovery Bay, data which was
21 mirrored by data loggers on the reefs (Quinn and Kojis, 2008). Six dhw are
22 equivalent to six weeks of sea surface temperatures (SSTs) one degree Celsius greater
23 than the expected summer maximum.

24

25 *3.2. Coral colony size-frequency distributions and growth rates*

1 Fig 3 a-h compares the size-frequency distribution of the corals *Sidastrea*
2 *siderea*, *Diploria labyrinthiformis*, *Porites astreoides*, and *Colpophyllia natans* at the
3 fringing reef sites Rio Bueno , M1, Dancing Ladies, Dairy Bull, and Pear Tree Bottom
4 in 2002 and 2008. These dates covered the major bleaching event and hurricane Ivan.
5 Size-frequency distributions were also determined for the corals *Diploria strigosa*
6 *Meandrina meandrites*, and *Agaricia* species, and the results discussed below. All the
7 sites showed some similarities in distribution of the size classes for the species studied
8 between 2002 and 2008. However, there were differences between the different sites,
9 and between the different species studied at the sites. Skewness values (sk) were used
10 to compare the distribution of the data between 2002 and 2008. For *S. siderea*, all sk
11 values were positive (skewed to the left, with more large colonies than in a normal
12 distribution) for 02 and 08, with little change between the dates (all sk values between
13 0.5 and 1.6). With *D. labyrinthiformis* colonies, there was a change from negative
14 skewness in 2002 at Dairy Bull and Pear Tree Bottom (skewed to the right, with more
15 small colonies than in a normal distribution) (sk values -0.25 and -0.006 respectively)
16 to more larger colonies than in a normal distribution in 2008 (sk values of 0.20 and
17 0.97 respectively). There were no significant changes from 2002-2008 at the other
18 sites, with positive sk values from 0.1 to 0.89. *M. meandrites* colonies at Rio Bueno
19 and Dairy Bull showed a relative decrease in the distribution of smaller colonies from
20 2002 to 2008, with changes in sk values from -0.03 in 02 to 0.78 in 08, and from -0.05
21 to 0.03 respectively; the other sites all exhibited slightly positive sk values in both
22 years from between 0.1 to 0.5. For *Agaricia* species, there was very little change
23 between the years at all the sites, with sk values from between 0.4 to 1.6. For *P.*
24 *astreoides*, all values were positive for both years, with an increase in skewness at Rio
25 Bueno from 0.2 to 2.6, showing a marked change in distribution towards the larger

1 colony sizes. At the other sites there were only small increases in sk values from 2002
2 to 2008, with Pear tree Bottom showing a decrease in skewness from 0.9 to 0.6. *D.*
3 *strigosa* colonies showed similar results to *P. astreoides*, all sk values being positive
4 for 2002 and 2008, with an increase at Rio Bueno from 0.2 to 2.2 and at Pear Tree
5 Bottom from 0.4 to 2.4; other sites showed similar sk values for 2002 and 2008 from
6 0.6 to 1.6. *C. natans* skewness changed from -0.07 to 0.68 at Rio Bueno from 2002
7 to 2008 (a decrease in smaller colonies relative to a normal distribution), and at
8 Dancing Ladies from -0.31 to 0.38. Other sites showed similar skewness in 2002 and
9 2008 (sk values between 0.5-0.6), except Pear Tree Bottom, which exhibited near
10 normal distribution of colonies about the mean for both 2002 and 2008 (sk values
11 <0.01). There was no correlation between coral size-frequency distributions and
12 water quality, (taken from Greenaway and Gordon-Smith, 2006).

13 As by far the major disturbance to the reef sites was the mass bleaching event
14 of 2005, the mean size class for all the species at all the reef sites were compared for
15 2002, 2006 (after the bleaching event) and 2008, with examples shown in Fig. 4a-d.
16 For *S. siderea* colonies mean size class was lower in 2006 than in 2002 at all sites
17 ($F>1.5$, $p<0.01$) except at Dancing Ladies where there was no significant difference.
18 Mean size class was raised from 2006 to 2008 at all sites ($f>5$, $p<0.001$) except at Rio
19 Bueno (no significant difference) and at Pear Tree Bottom (lower mean size class,
20 $F>2$, $p<0.02$). There were no significant differences in mean size class between 2002
21 and 2008 except at Rio Bueno, where it was lower ($F>1.5$, $p<0.02$). For *D.*
22 *labyrinthiformis* colonies, there were significant reductions in mean size class from
23 2002 to 2006 at Dairy Bull and Pear Tree Bottom (both $F>2$, $p<0.03$) and reductions
24 at M1 and Pear Tree Bottom from 2002 to 2008 ($F>3$, $p<0.01$ and $F>1.5$, $p<0.05$
25 respectively). There were no significant increases in size class from 2006 to 2008.

1 This was also the case for *M. meandrites* colonies, where there were no significant
2 changes in mean size class between the years. In contrast, there were significant
3 reductions in mean size class of *Agaricia* species mean size class at all sites from
4 2002 to 2006 ($F>4$, $p<0.01$), and mean size class was significantly higher from 2006
5 to 2008 at all sites ($F>2$, $p<0.03$ for Rio Bueno, $F>6$, $p<0.008$ for other sites). Mean
6 size class was only significantly lower in 2008 than in 2002 at Dairy Bull ($F>2$,
7 $p<0.01$). Mean class size of *P. astreoides* colonies had reduced significantly from
8 2002 to 2006 only at Dancing Ladies and Dairy Bull ($F>2$, $p<0.01$ for both), and
9 reduced significantly from 2006 to 2008 at Rio Bueno ($F>2$, $p<0.03$). All sites had
10 reduced significantly from 2002 to 2008 ($F>4$, $p<0.01$) except Pear Tree Bottom (not
11 significant). For *D. strigosa*, mean size class had reduced from 2002 to 2006 at
12 Dancing Ladies, Dairy Bull and Pear Tree Bottom (all $F>1.5$, $p<0.04$), and had
13 reduced again in 2008 at Rio Bueno, Dairy Bull and Pear Tree Bottom (all $F>5$,
14 $p<0.002$); mean size class was lower at all sites in 2008 than in 2002 ($F>4$, $p<0.005$)
15 for this species. For *C. natans*, mean size class fell significantly ($F>4$, $p<0.01$) at all
16 sites except at Rio Bueno (no significant difference) from 2002 to 2006. From 2006 to
17 2008, mean size class was raised at Dairy Bull and at Pear Tree Bottom (both $F>5$,
18 $p<0.01$) but fell at Rio Bueno and M1 ($F>3$, $p<0.02$); there was no significant
19 difference at Dancing Ladies. At Rio Bueno, M1 and Dancing Ladies only, mean size
20 had fallen significantly overall between 2002 and 2008 ($F>2$, $p<0.05$).

21 As the viability of small coral colonies over time can indicate reef resilience
22 (Loya, 1976; Connell, 1978), the annual changes in the colony numbers of the
23 smallest size class (0-250 mm² surface area) each year from 2002-2008 was plotted
24 for all the non-branching species studied at the fringing reef sites, with examples
25 shown in Fig. 5 for *Sidastrea siderea*, *Diploria labyrinthiformis*, *Porites astreoides*,

1 and *Colpophyllia natans*. There was a reduction in the smallest size class for all the
2 species at all the sites in 2006, with subsequent increases for all species at all sites in
3 2007 and 2008. Until 2006, there had been modest increases – or least no decreases -
4 in the numbers of the smallest size classes, with the exception of *D. labyrinthiformis*
5 at Rio Bueno, *P. astreoides* at Dancing Ladies, where the trends had decreased
6 slightly. Interestingly, in 2005, the year after hurricane Ivan, the most severe storm to
7 impact the reef sites over the study period, there was a slight reduction in the numbers
8 of the smallest size classes, particularly notable at Dairy Bull.

9 Dairy Bull reef was the site where studies resulted in the suggestion that there
10 had been a rapid phase-shift reversal on Jamaican reefs (Idjadi et al., 2006), and which
11 suffered a major loss of *A. cervicornis* in 2006 (Quinn and Kojis, 2008). Table 1
12 shows mean percentage cover of live coral, macroalgae and live *Acropora* species
13 along transects at Dairy Bull reef in 2005 (pre-bleaching), 2006, 2007 and 2008.
14 Cover of live coral, macroalgae and cover and live *Acropora* for 2005 and 2006 are
15 similar to figures reported by Quinn and Kojis (2008). While macroalgal cover
16 remained essentially unchanged in 2007 and 2008, there were increases in live coral
17 cover and live *Acropora* species in both 2007 and 2008. The majority of the increase
18 in coral is represented by increases in live *A. cervicornis*. This is illustrated in Fig. 6,
19 which shows complete bleaching of an *A. cervicornis* colony typical of Dairy Bull
20 reef after the mass bleaching event of 2005 and a large live colony of *A. cervicornis*
21 typical of Dairy Bull reef in 2008.

22 Coral growth rates are part of a demographic approach to monitoring coral
23 reef health (Smith et al., 2005), and Table 2 presents radial growth rates (mm yr^{-1}) of
24 non-branching corals and linear extension rates (mm yr^{-1}) of branching corals

1 calculated on an annual basis and tabled from 2000-2003, 2003-2005, and 2005-2008
2 at all the sites studied. The growth rates are similar to those reported by Huston
3 (1985). There were few significant differences between the sites for each species
4 studied, or across the time period of the study. Where growth rates were higher, they
5 tended to be higher at Dairy Bull reef, but the differences were not significant. With
6 the increase of *D. antillarum* at Rio Bueno in recent years, clearing the macroalgae,
7 healthy *A. palmata* and *A. cervicornis* colonies have appeared at the Rio Bueno site
8 from 2006. At Dancing Ladies, a site with much macroalgal cover, *A. cervicornis*
9 colonies which were measurable from 2003-2005 had disappeared in 2006, possibly
10 as a result of the mass bleaching event, while at M1, a site with even greater
11 macroalgal cover, *A. cervicornis* colonies appeared which were measurable in 2008.
12

1 4. DISCUSSION

2 Surveys of size-frequency distribution of corals are important in evaluating the
3 condition of and changes in coral populations (Bak and Meesters, 1998; Meesters et
4 al., 2001; Oigman-Pszczol and Creed, 2004). Here we have used a number of
5 demographic tools to demonstrate the resilience of the fringing reefs around
6 Discovery Bay, Jamaica, to a number of environmental stressors, in particular
7 hurricanes and the mass bleaching event of 2005.

8 Hurricanes and tropical storms cause major damage and delayed mortality to
9 corals (Knowlton et al., 1981; Done, 1999), as happened with hurricane Allen in 1980
10 to the fringing reefs in this study (Woodley et al., 1981). Alteration of substratum by
11 storms reduces recruitment rates, as does the pre-emption of space by other corals or
12 macroalgae (Connell, 1997; Connell et al., 1997). Storms have reduced the
13 recruitment of non-branching corals both on these reefs (Crabbe et al., 2002) and on
14 the Meso-American Barrier Reef off the coast of Belize (Crabbe et al., 2008), and it is
15 interesting that in this study the numbers of colonies in the smallest size class of
16 corals was lower after hurricane Ivan in 2004, although the reduction was
17 insignificant relative to the reduction after the bleaching event of 2005. Bleaching of
18 *Acropora* colonies generally led to mortality, with predation by the coral snail
19 *Coralliophila abbreviata* and the bearded fire worm *Hermodice carunculata* (Quinn
20 and Kojis, 2008); this was often followed by invasion of filamentous algae.

21 It is the synergistic effect of multiple stressors that is damaging to reefs
22 (Hughes and Connell, 1999; Mumby 1999; Gardner et al., 2003). The Jamaican reefs
23 are subject to a number of both acute and chronic stressors, the last including
24 overfishing and continuing coastal development, including the much-publicised
25 development on land adjacent to Pear Tree Bottom reef and the resurfacing of the

1 North Jamaican coastal highway (Westfield et al., 2008). On top of these came
2 tropical storms and the mass bleaching event during the study period. Fortunately,
3 there was little damage after the tropical storms, although in the year following
4 hurricane Ivan, which produced the highest winds in the area of the reef sites during
5 the study period, there was a reduction in the smallest size classes of the majority of
6 the non-branching corals studied, suggesting that the hurricane might have influenced
7 coral recruitment. Storms and hurricanes can influence sedimentation and turbidity,
8 which themselves have significant effects on coral growth (Gimour, 1999; Crabbe and
9 Carlin, 2007). While occasional storms can increase the survivorship of *A. palmata*
10 colonies (Lirman, 2003), increased freshwater inputs from storms reduces salinity,
11 and influences nutrient concentrations (Greenaway and Gordon-Smith, 2006; Mallela
12 and Perry, 2007) which in turn increase pre- and post-settlement mortality, changed
13 larval behaviour and substrate choice upon settlement (Vermeij et al., 2006).

14 Despite the multiple influences on the reef sites over the study period, the size
15 classes of the corals studied showed resilience to change. Interestingly, there were
16 differences between the sites, and between the species of corals. Dairy Bull, Rio
17 Bueno and Pear Tree Bottom showed a decrease in the numbers of smaller colonies
18 relative to a normal distribution for most species from 2002 to 2008. The reef sites
19 which had the most macroalgal cover, Dancing Ladies and M1, showed fewer
20 changes in size class distribution through the study period, possibly because these
21 sites show large macroalgal cover (Crabbe, 2008). There were no significant
22 differences in fishing pressure between the sites. This study concentrates on size-
23 classes and growth rates; coral recruitment or survival (Smith et al., 2005) has not
24 been measured, although we have modelled coral recruitment at these sites (Crabbe et
25 al., 2002) and it has been measured in other studies (Quinn and Kojis, 2008). In this

1 study we have not considered reef connectivities, relative colonisation rates or socio-
2 economic variables in reef resilience (Nyström et al., 2008).

3

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

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

18 Dairy Bull reef has for several years been the fringing reef with the most coral
19 cover, with a benthic community similar to that of the 1970s (Huston ,1985), and it
20 was the subject of the study which suggested a rapid phase-shift reversal (Idjadi et al.,
21 2006). After the 2005 bleaching event there was a major loss of live coral cover,
22 particularly of *A. cervicornis* (Quinn and Kojis, 2008; this study), and it is
23 encouraging that both coral cover and the rapidly growing *A. cervicornis* colonies
24 have returned to the reef at levels approaching pre-bleaching values. The influence of
25 *M. annularis* colonies on the reef, acting as structural refugia (Idjadi et al., 2006), may

1 have facilitated this recovery. Interestingly, we found a variety of clades of
2 zooxanthellae, including clade C, in corals at Dairy Bull reef (Crabbe and Carlin,
3 2007), and that may be a factor in their recovery (Stat et al., 2008).

4 Dairy Bull reef behaves somewhat like a successional niche (Pacala and Rees,
5 1998; Kinzig and Pacala, 2001), as late successional species are not the strongest
6 competitors, and the high population of *D. antillarum* at the site keep the macroalgae
7 in check. Despite continued overfishing (Hawkins and Roberts, 2004), there is a good
8 diversity of fish species, including herbivores such as Scaridae and Acanthuridae,
9 although fish sizes are small (usually <100 mm) (personal observation). Even at M1,
10 with one of the highest covers of macroalgae and no *D. antillarum*, we have seen that
11 *A. cervicornis* can form colonies after the major disturbance of the mass bleaching
12 event in 2005. Most reefs are open non-equilibrium systems, (Connell, 1978) with
13 diversity maintained by disturbance and recruitment. While that may be true at the
14 macro- or landscape level, Dairy Bull reef, after the mass bleaching event, is
15 exhibiting some properties of niche diversification (Jackson, 1991; Pacala and Rees,
16 1998; Kinzig and Pacala, 2001).

17 What is apparent from this study is that despite the chronic and acute
18 disturbances between 2002 and 2008, demographic studies indicate good levels of
19 coral resilience on the fringing reefs around Discovery Bay in Jamaica. The bleaching
20 event of 2005 resulted in mass bleaching but relatively low levels of mortality (Quinn
21 and Kojis, 2008), unlike corals in the US Virgin islands where there was extensive
22 mortality (Miller et al., 2006; Whelen et al. 2007), possibly because of their greater
23 degree heating week values. The Jamaican reefs have suffered from long term
24 human-induced chronic stressors, such as overfishing and land development (Adger et
25 al., 2005; Jdalumbi et al., 2008; Mora, 2008; Mumby and Hasting, 2008).

1 Unfortunately, previously successful efforts to engage the local fisherman in
2 controlling catches around Discovery Bay (Sary et al., 1997) have not been
3 maintained, and it may be that the development of a Discovery Bay Marine Park is the
4 only solution.

5

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13 Bay Marine Laboratory.

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1 **Legends to Figures**

2 Fig. 1. Satellite image showing the location of fringing reef sites in this study (Rio
3 Bueno, M1, Dancing Ladies, Dairy Bull and Pear Tree Bottom) around Discovery
4 Bay, Jamaica. DBML, Discovery Bay Marine Laboratory. The horizontal line shows
5 1 km distance. See text for GPS coordinates.

6

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

8

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

14

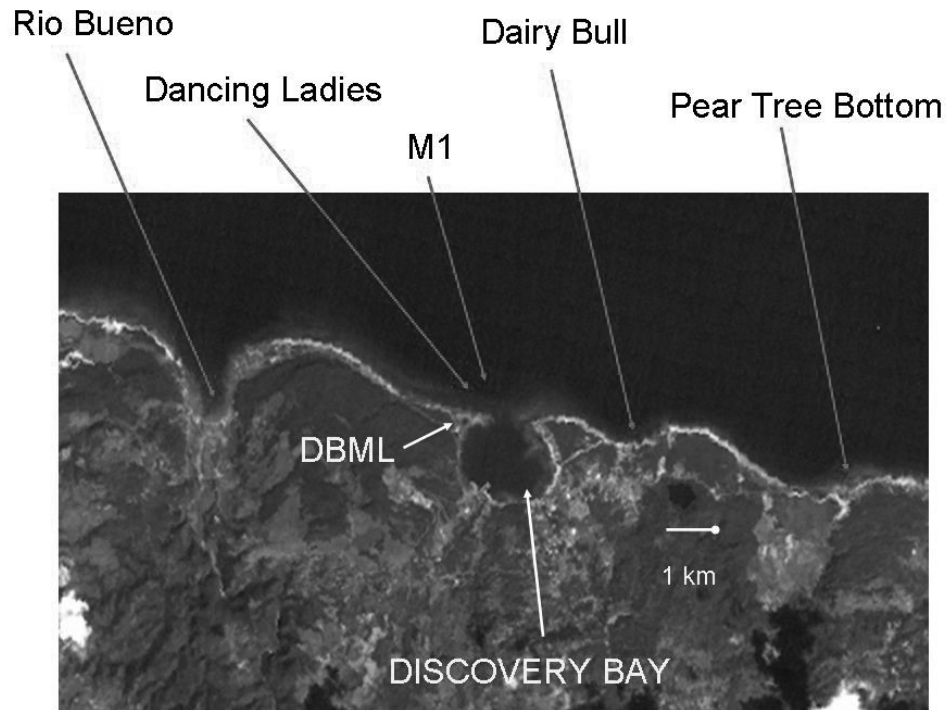
15 Fig. 4. Mean size classes in 2002, in 2006 and in 2008 of: *Sidastrea siderea* (a);
16 *Diploria labyrinthiformis* (b); *Porites astreoides* (c); and *Colpophyllia natans* (d) at
17 Rio Bueno (RB), M1 (M1), Dancing Ladies (DL), Dairy Bull (DB), and Pear Tree
18 Bottom (PTB). Bar lines represent standard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

20

21 Fig. 5. Graphs of annual changes in the colony numbers of the smallest size class (0-
22 250 mm² surface area) from 2000-2008 for: *Sidastrea siderea* (a); *Diploria*
23 *labyrinthiformis* (b); *Porites astreoides* (c); and *Colpophyllia natans* (d) at Rio Bueno
24 (RB), M1 (M1), Dancing Ladies (DL), Dairy Bull (DB), and Pear Tree Bottom (PTB).

1 Fig.1

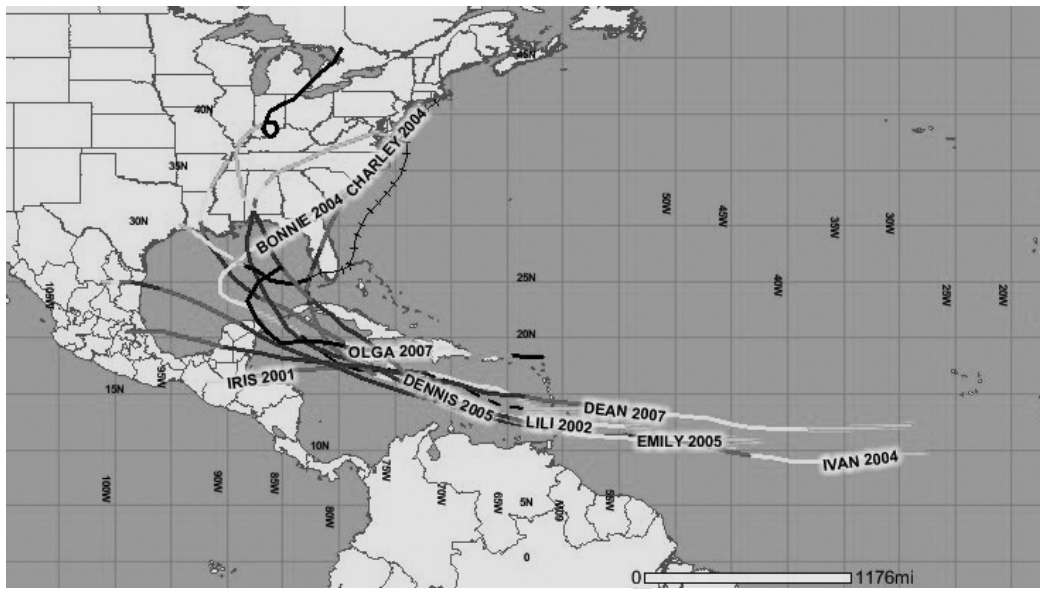
2



3

1 Fig.2

2

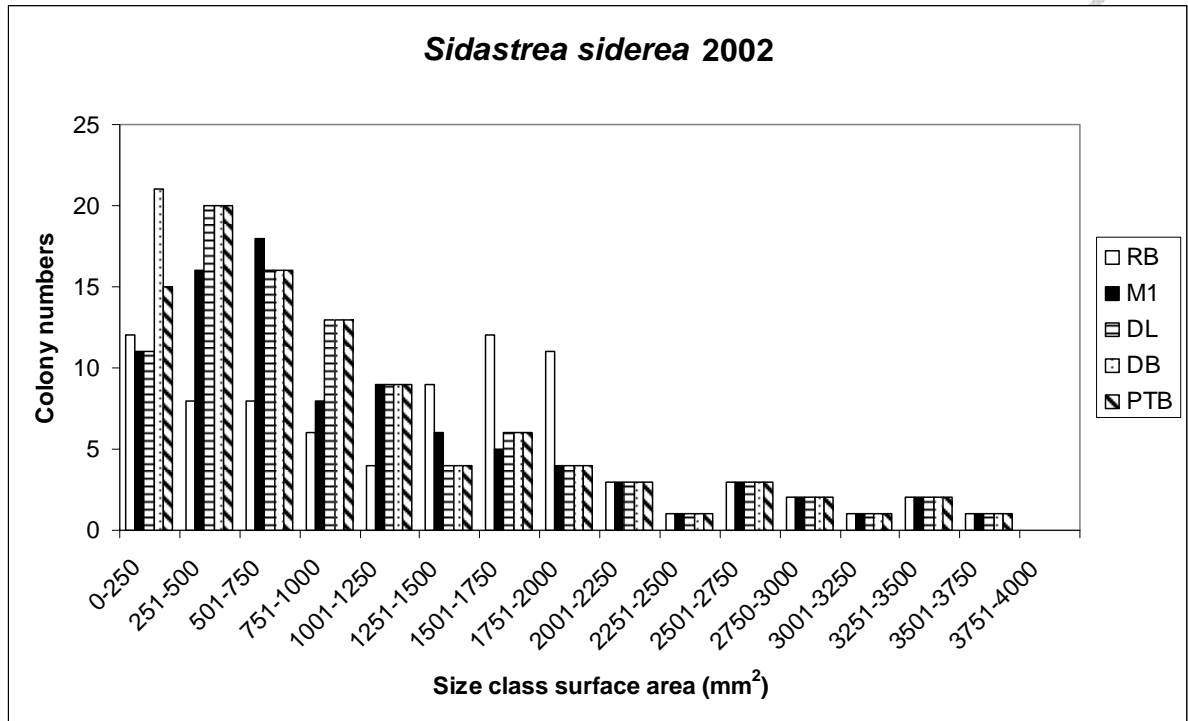


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1 Fig.3

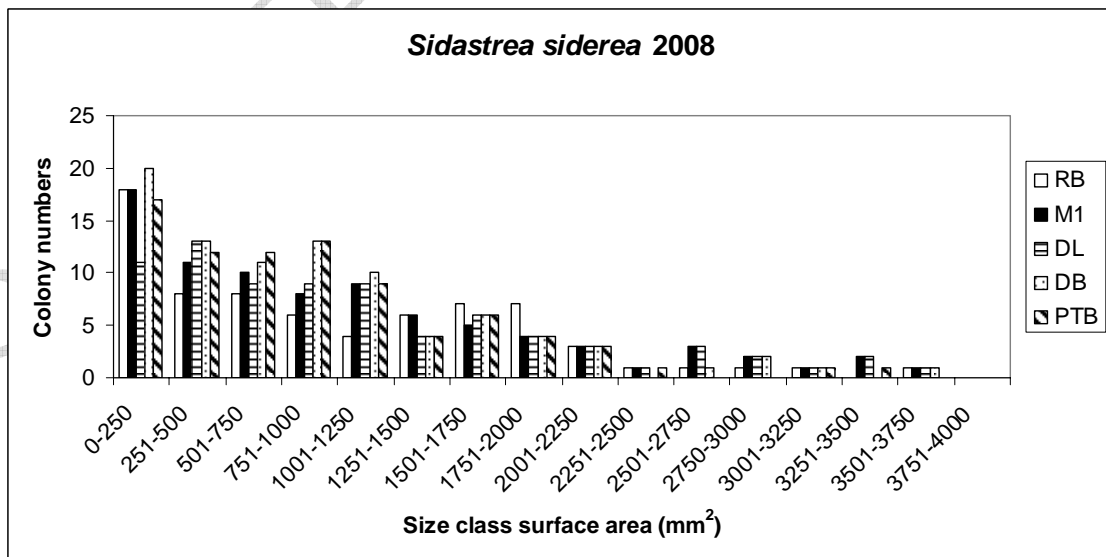
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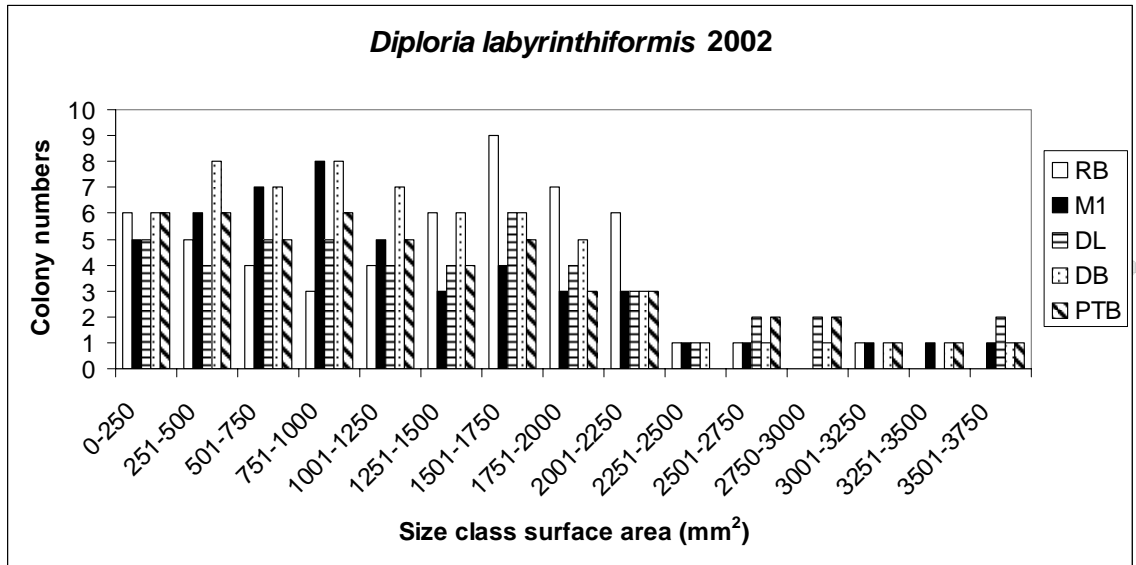
5 Fig. 3a.



6

7

8 Fig 3b.

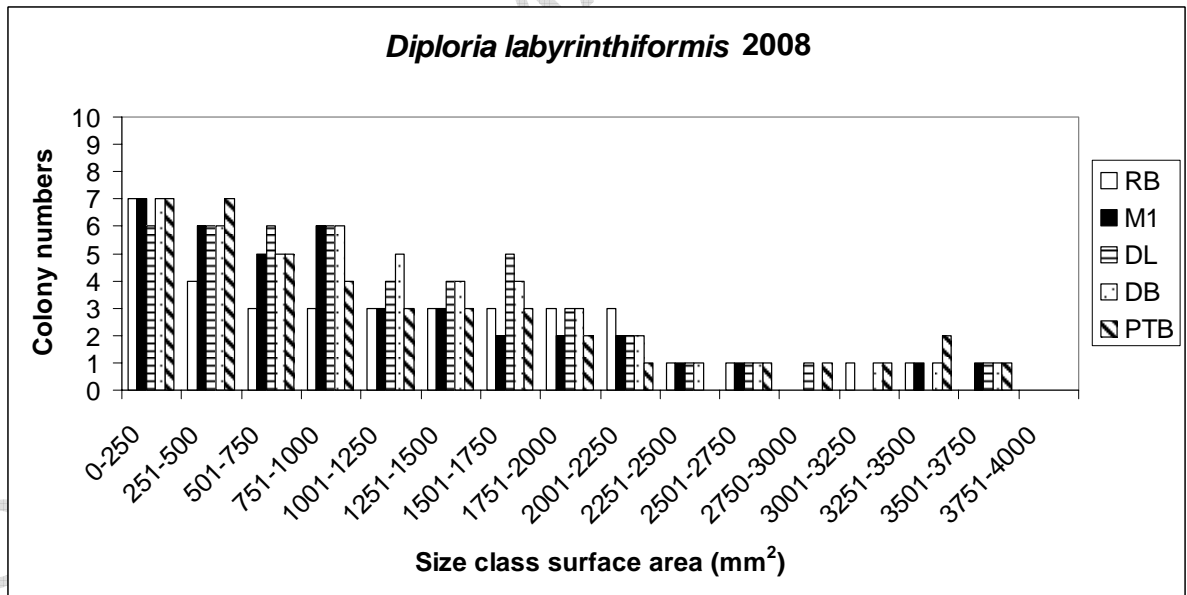


1

2

3 Fig. 3c.

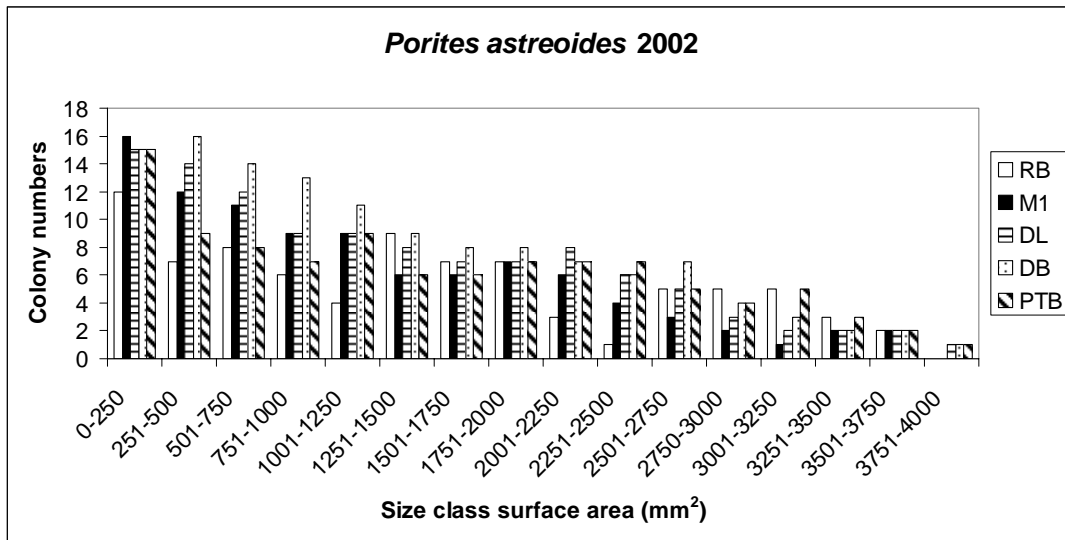
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7 Fig. 3d.

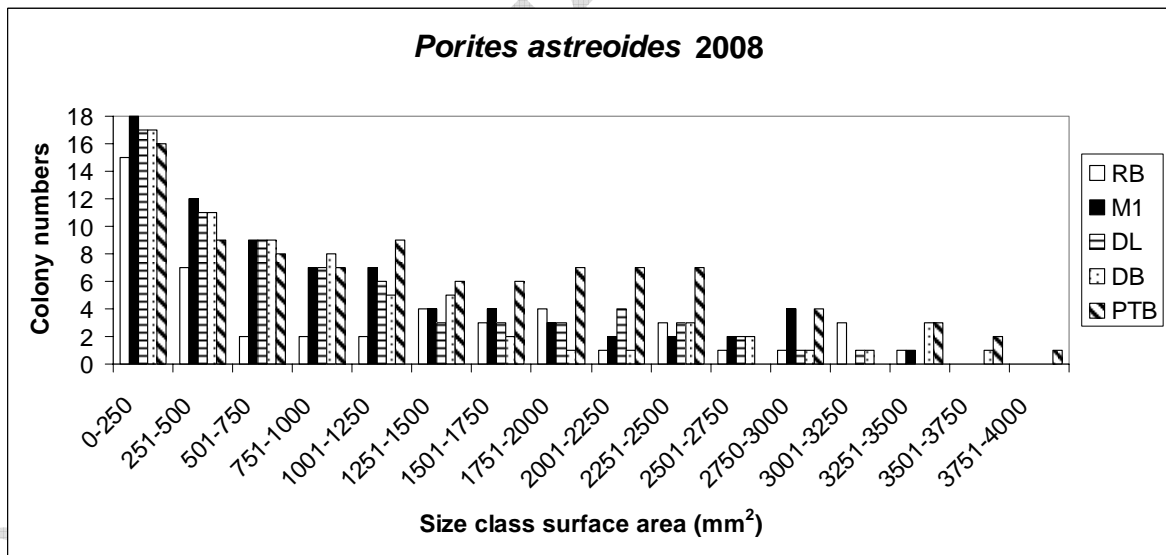


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3 Fig. 3e.

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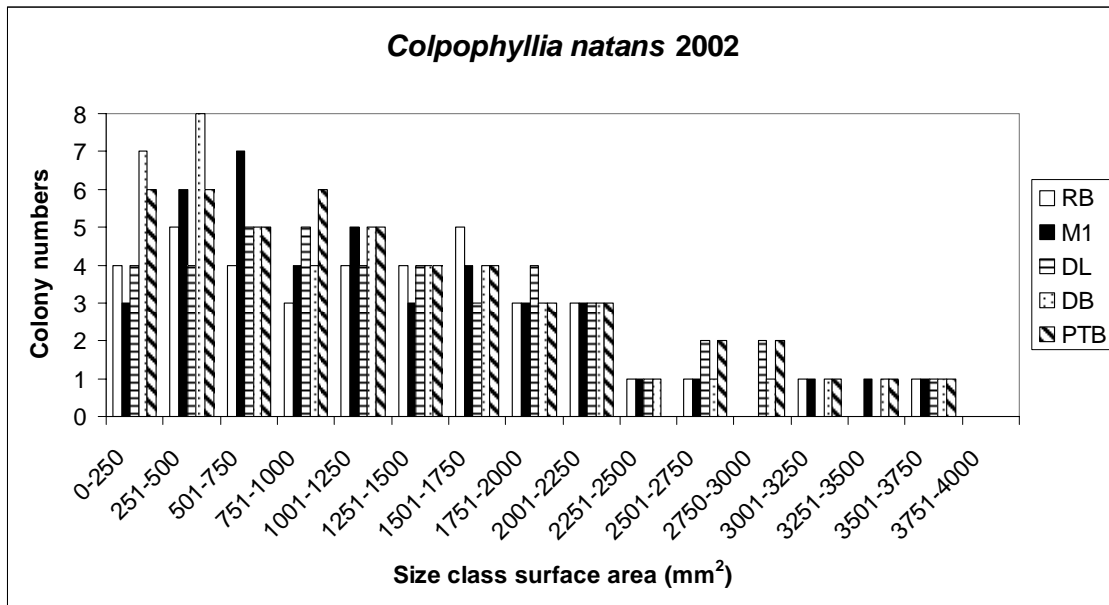


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7 Fig. 3f.

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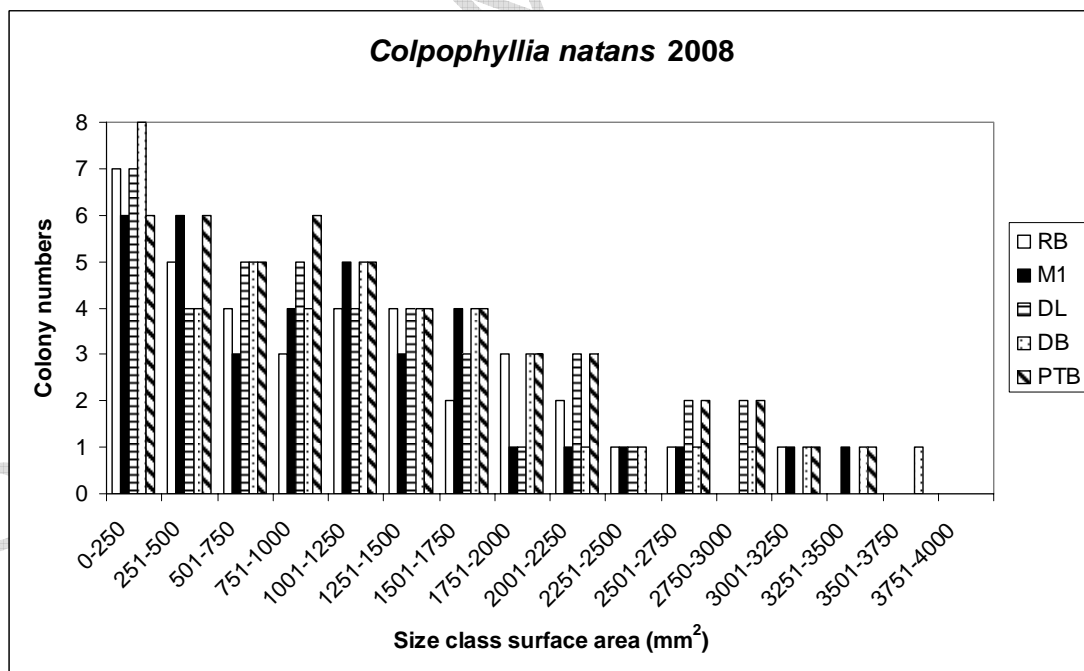


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2

3 Fig. 3g.

4



5

6

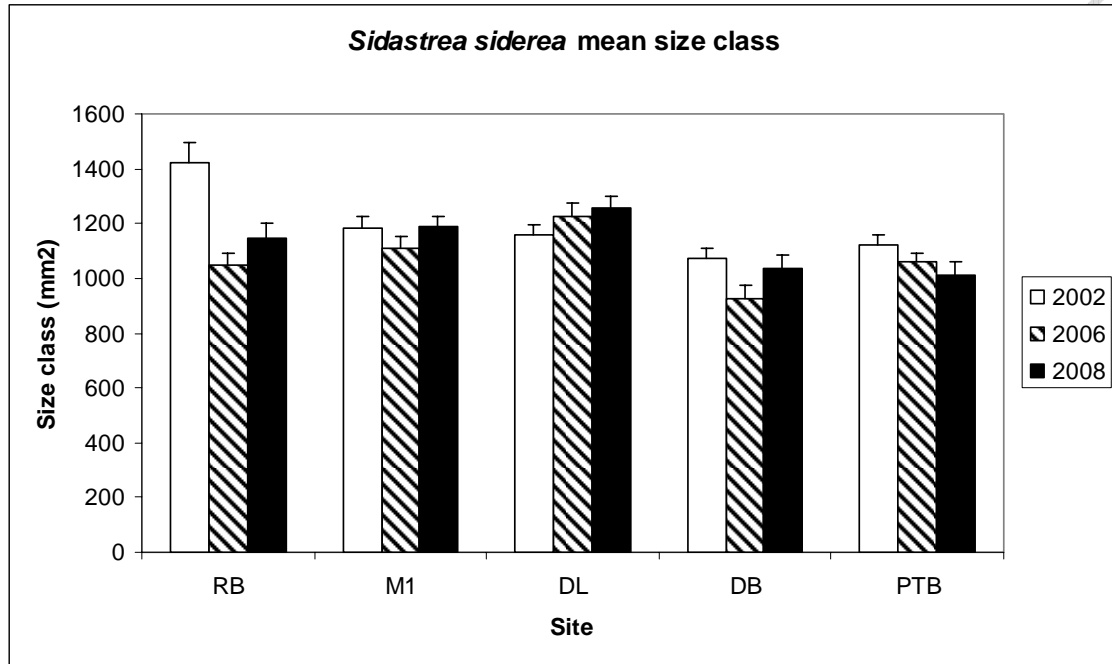
7 Fig. 3h.

8

1 Fig.4

2

3



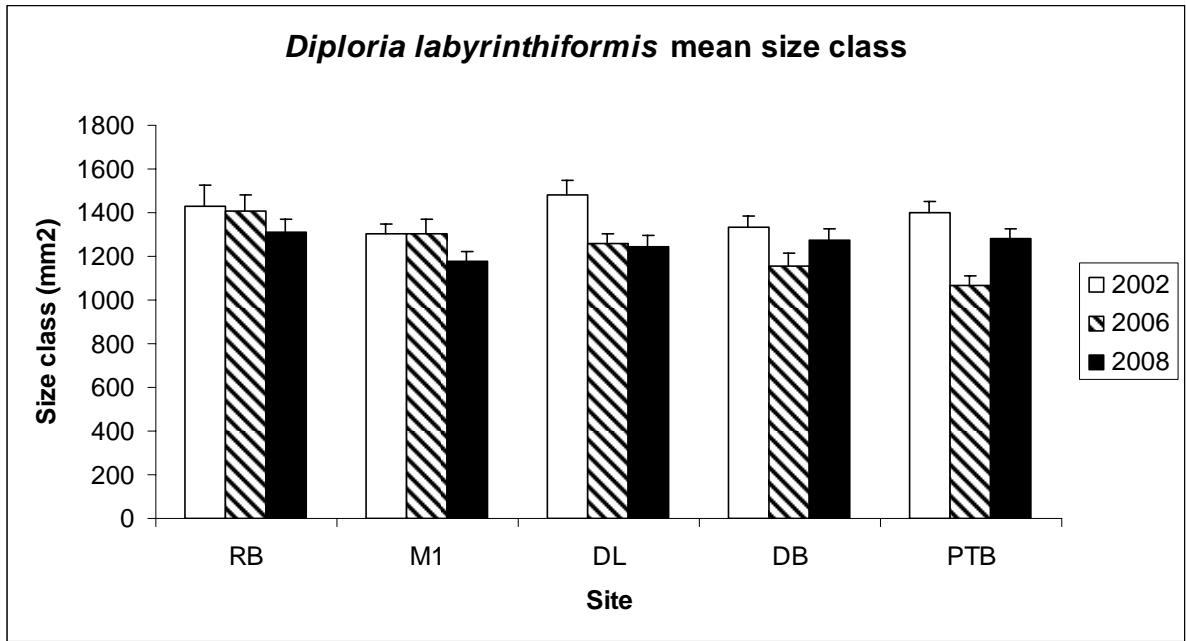
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6 Fig. 4a.

7

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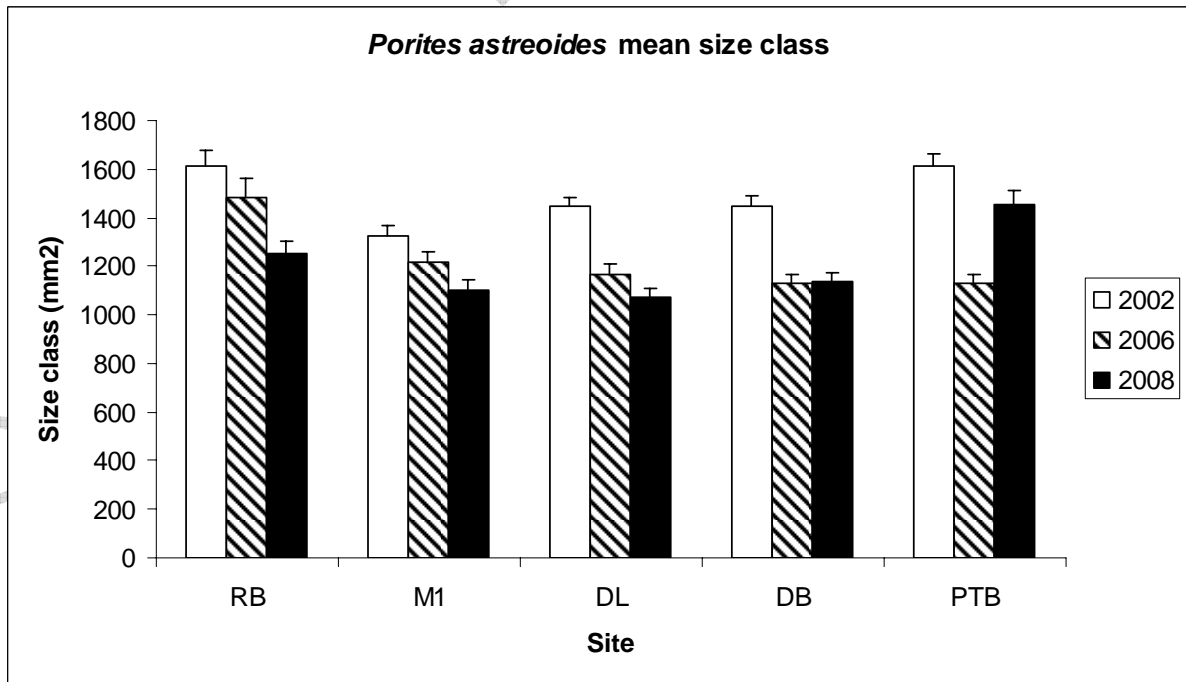


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3 Fig. 4b.

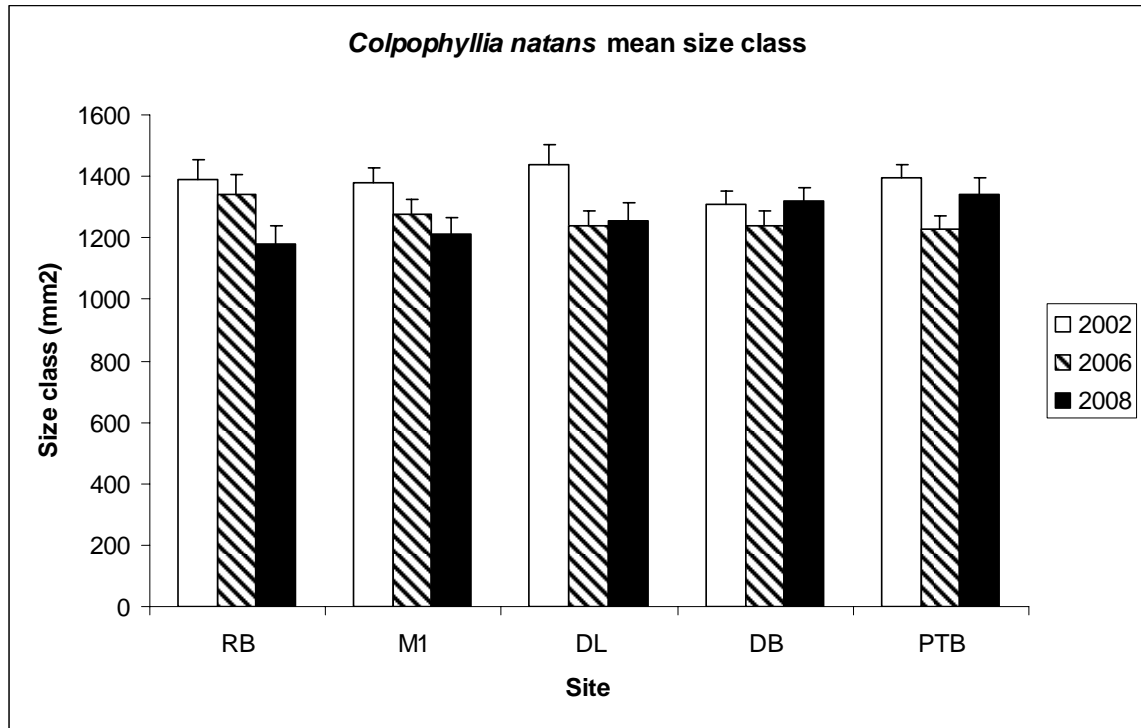
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5

6 Fig. 4c.

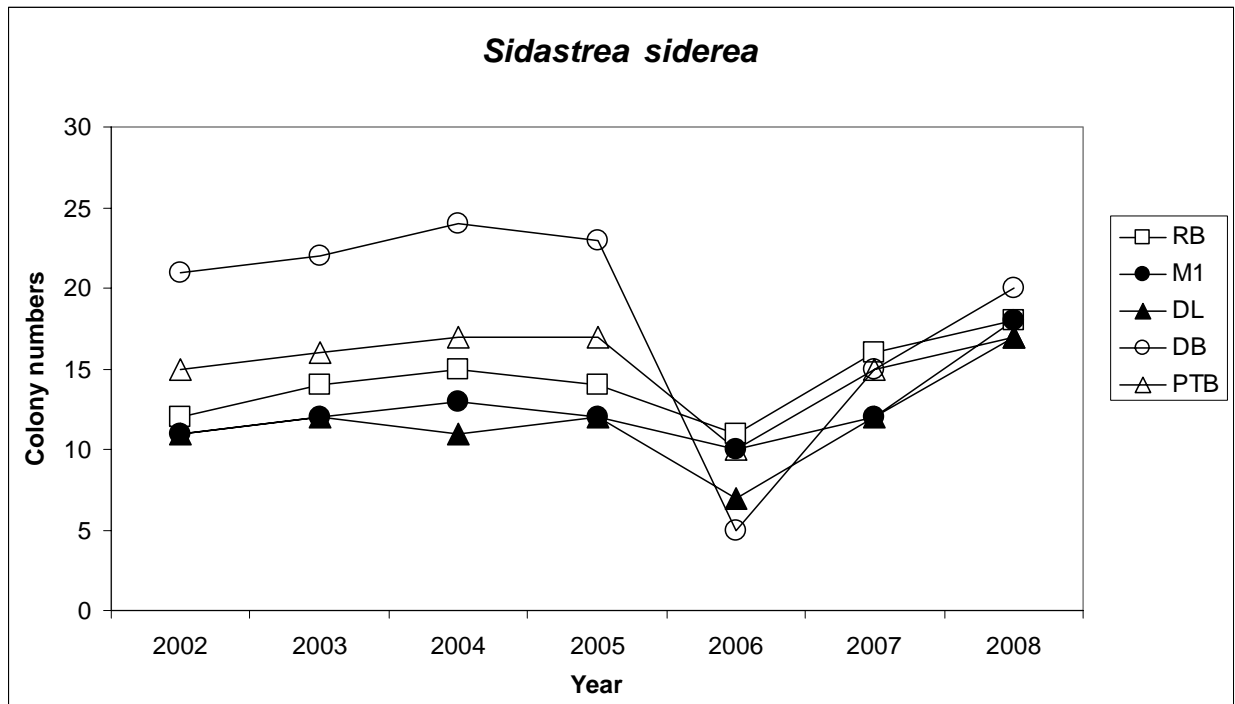
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1

2 Fig. 4d.

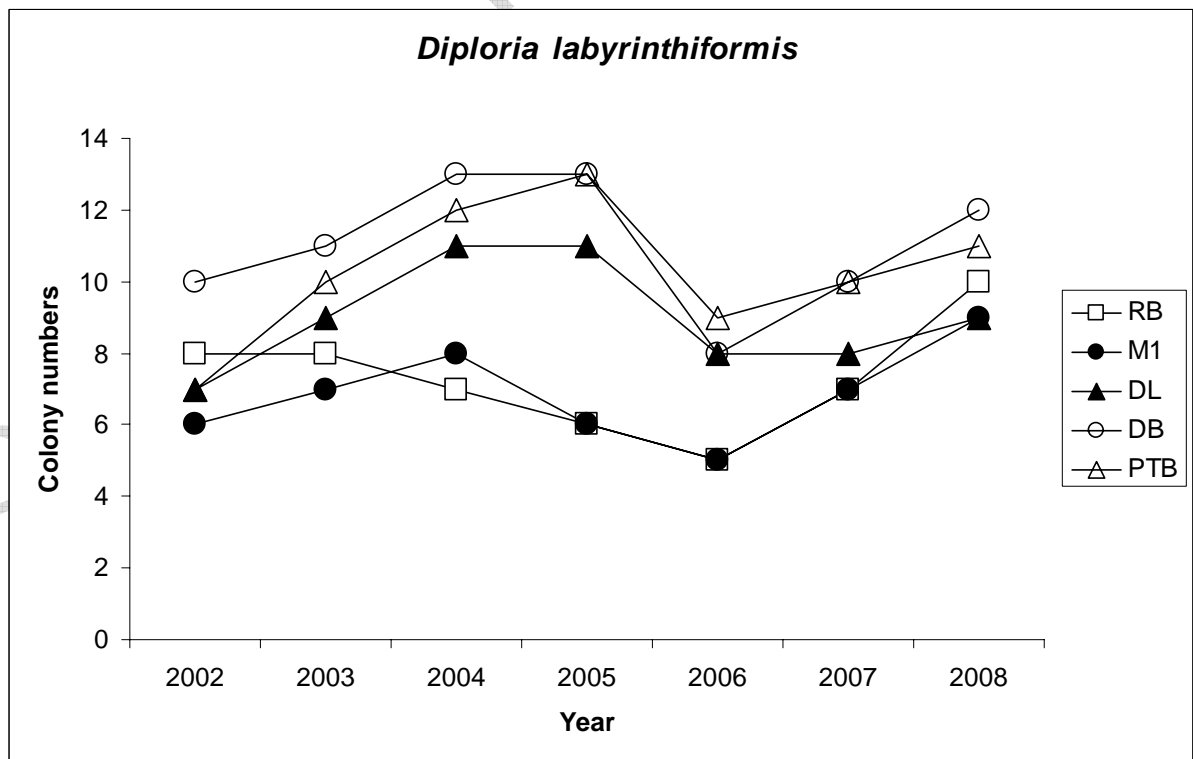
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2

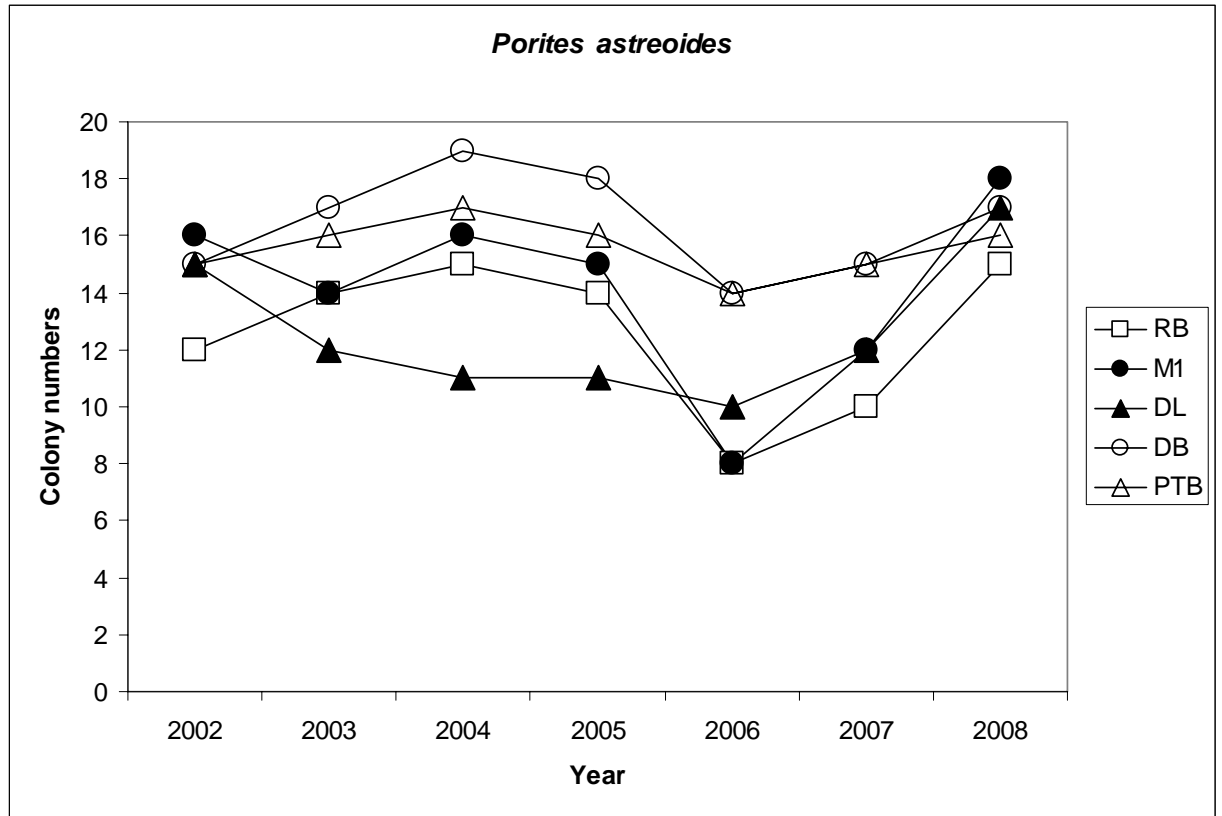
3 Fig. 5a.



4

5 Fig. 5b.

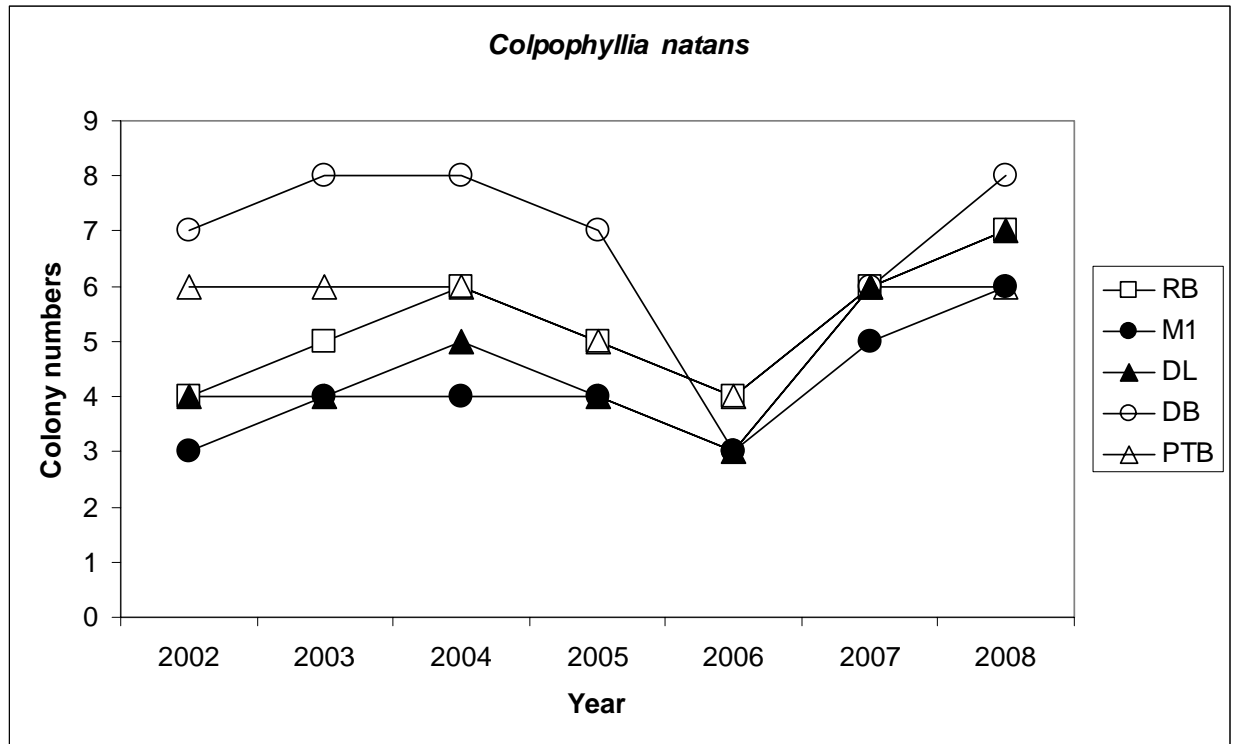
1



2

3 Fig. 5c.

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1

2 Fig. 5d.

ACCEPTED MANUSCRIPT

1 Table 1. Mean percentage cover of live coral, macroalgae and live *Acropora* species
2 along transects at Dairy Bull, in 2005 (pre-bleaching), 2006, 2007 and 2008. Values
3 are \pm standard errors.

4	5 Year	6 Live coral (%)	7 Macroalgae (%)	8 <i>Acropora</i> species (%)
9	2005	46 \pm 8	8 \pm 3	33 \pm 5
10	2006	13 \pm 5	6 \pm 3	2 \pm 2
11	2007	20 \pm 9	6 \pm 3	10 \pm 4
12	2008	31 \pm 7	5 \pm 2	22 \pm 7

13

14

15

16