

1 **Population Growth and Distribution of *Diadema antillarum* at Discovery Bay, Jamaica**

2
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8
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11

12 **Abstract**

13 The urchin *Diadema antillarum* Philippi (Echinodermata: Echinoidea) was extremely rare to absent from reefs
14 throughout Jamaica during much of the 1980s and part of the 1990s following a Caribbean wide mortality event.
15 This survey was conducted in 2007 to assess their distribution on the western forereef of Discovery Bay,
16 Jamaica. Mean urchin densities of $3.93 \pm 3.4 \text{ m}^{-2}$ (mean \pm SD) are the highest that have been recorded in
17 Discovery Bay since the mortality event. The increases in *D. antillarum* numbers of the past decade have been
18 accompanied by reductions in macroalgal cover. This study found a strong inverse correlation (Pearson
19 product-moment correlation = -0.597, $p < 0.000$) between macroalgal cover and *Diadema* density, indicating that
20 the urchins are exerting a strong top-down control on macroalgae. Any future increases in urchin densities will
21 most likely result in further reductions of macroalgal cover.

22

23 **Introduction**

24 Over the past thirty years Caribbean coral reefs have undergone a shift in dominance of primary producers,
25 possibly caused by the marked decrease in the population of *Diadema antillarum* Philippi (Echinodermata:
26 Echinoidea) [1]. A seminal study in Jamaica by Goreau [2] documented lush coral communities with densities
27 comparable to those seen on the Great Barrier Reef. When Goreau's survey was conducted, huge tree-like
28 colonies of *Acropora palmata* were common throughout the reef. More than 90 % of the available surface of
29 the buttress (mixed zone) was covered by living coral, and rich beds of *A. cervicornis* were found on the
30 uppermost region of the seaward slope of the reef. In stark contrast to this, studies conducted during the 1990s
31 on the west forereef at Discovery Bay, Jamaica showed percent coverage by coral had declined to $\leq 5\%$ [3].
32 This coral decline was accompanied by dramatic increases in macroalgal cover (44 -79 %) at the surveyed
33 depths.

34 Disturbances which may have also contributed to coral community change include coral bleaching [4],
35 overfishing of large herbivorous fish, and hurricanes Allen and Gilbert in the 1980s [5]. However a mass
36 mortality of *D. antillarum* has been considered by many authors as one of the most significant causes for this
37 phase shift [4-8].

38 Between 1983 and 1984 populations of *D. antillarum* suffered a catastrophic mortality event which affected
39 the entire Caribbean basin except Barbados [1]. Before 1983, the mean populations of sea urchins at locations
40 in Discovery Bay, Jamaica, were as high as 71 urchins m^{-2} [9], 10 urchins m^{-2} in the shallow buttress zone (8 m)
41 and 4 urchins m^{-2} at 15 m [10]. Population densities of this urchin declined sharply to nearly 0 m^{-2} at depths of
42 5-10 m in the forereef by 1983 [7]. By 1998, populations along the northern coast of the island had only
43 recovered to 5-10% of their original densities [10]. To date, reports [11, 12] have documented partial recovery,
44 but urchin densities remain low, especially at mid-depths in the forereef.

45 *Diadema* are a major grazer on macroalgae throughout the Caribbean, and the distribution of their food
46 sources depends on their abundance on the reefs of the region. Previous studies on the feeding habits of the
47 urchin [13, 14] have shown that they are attracted to fleshier species of macroalgae (*e.g. Lobophora variegata*).
48 The urchins have shown low feeding preference to species containing metabolites which repel grazers (*e.g.*
49 *Sargassum* sp., *Dictyota* sp.) and those species with highly calcified tissues (*e.g. Halimeda* sp. and *Galaxaura*
50 sp.), although Sammarco [14] notes that *Diadema* grazing appeared to be most strongly related to proportional
51 abundance of macroalgal community members and that food preference was not a major determinant of algal
52 community structure.

53 The aim of this study was to describe the distribution of *D. antillarum* in comparison to past studies
54 conducted in Discovery Bay, Jamaica, and to determine if urchin populations were continuing to increase, as has
55 been reported by other researchers at Discovery Bay [1, 7, 11, 12, 15, 16]. This study also compared the density
56 of *D. antillarum* to macroalgal cover on the foreereef.

57

58 **Materials and methods**

59 **Study sites and geographic data**

60 Surveys were conducted in May 2007 within the western foreereef of Discovery Bay, Jamaica. Discovery Bay is
61 a semienclosed embayment located on the Jamaican north shore. It is protected from the ocean by a fringing
62 reef which is swept by a slow east to west current. Jamaica usually experiences a mixed tidal range, with
63 primarily diurnal spring tides, and low amplitude diurnal neaps. The tidal range recorded at the Discovery Bay
64 Marine Lab ranged between 16-60 cm [17]. A boat channel which connects the bay to the ocean divides the reef
65 into eastern and western sections. The bay has an areal extent of ~1.4 km² [17-19]. The town of Discovery
66 Bay, a bauxite-processing plant and loading dock and the University of the West Indies, Discovery Bay Marine
67 Lab, are located around the bay. The drainage basin is composed of porous limestone, while the bay itself has
68 springs which are an input of fresher groundwaters [19], and these are thought to be significant sources of
69 nitrates [20, 21].

70

71 **Data collection**

72 Twelve 60 m parallel line transects were laid perpendicular to the reef crest along coral spur heads. Transects
73 began at a mean water depth of 3.81 ± 1.25 m (mean \pm SD) and extended to a mean depth of 6.68 ± 0.93 m
74 (mean \pm SD), with the deepest sample point at a depth of 8.23 m and the shallowest at 1.52 m. Deeper locations
75 were not surveyed as preliminary dives in the area indicated that *Diadema antillarum* were rare to absent below
76 approximately 8 m (personal observations). The twelve transects were oriented along the upper surface of coral
77 spurs ranging from the western edge of the channel entrance to Discovery Bay to 0.5 km to the west. Sites
78 roughly corresponded to historic sampling locations from other studies [10, 11, 22], including Mooring 1 (M1),
79 Dancing Lady, Long-term Study (LTS), and Caribbean Coastal Marine Productivity Program (CARICOMP).
80 Observations were recorded every 6 meters along the transect line. At each sampling site a 1 m² PVC pipe
81 quadrat was placed randomly to the left or right in relation to the line as dictated by values from a random
82 number generator. In sites where no individuals were observed within the quadrat, yet a few individuals were

83 seen near the edges, the sampling area was expanded to 2 m² to obtain values of less than one *Diadema* m⁻².
 84 The depth of the sampling site was recorded using an Aladin Smart Z nitrox dive computer (Scubapro Uwatec
 85 USA and Latin America, El Cajon, CA). *Diadema* density, per cent macroalgal cover, and macroalgae
 86 taxonomic composition within the quadrat (n = 130) were estimated at each site.

87 Mean and standard deviations of abundance of *D. antillarum* were determined by grouping by depth or by
 88 transect. Regression analysis was conducted in SigmaStat 3.11 (Systat Software, Inc., Chicago, IL) where $p \leq$
 89 0.05 was considered significant, and the results graphically displayed using SigmaPlot 9.0 (Systat Software,
 90 Inc., Chicago, IL). Historical comparisons used the data of Liddell and Ohlhorst [7], Morrison [22], Cho and
 91 Woodley [23], Haley and Solandt [11], Moses and Bonem [10], and the present study.

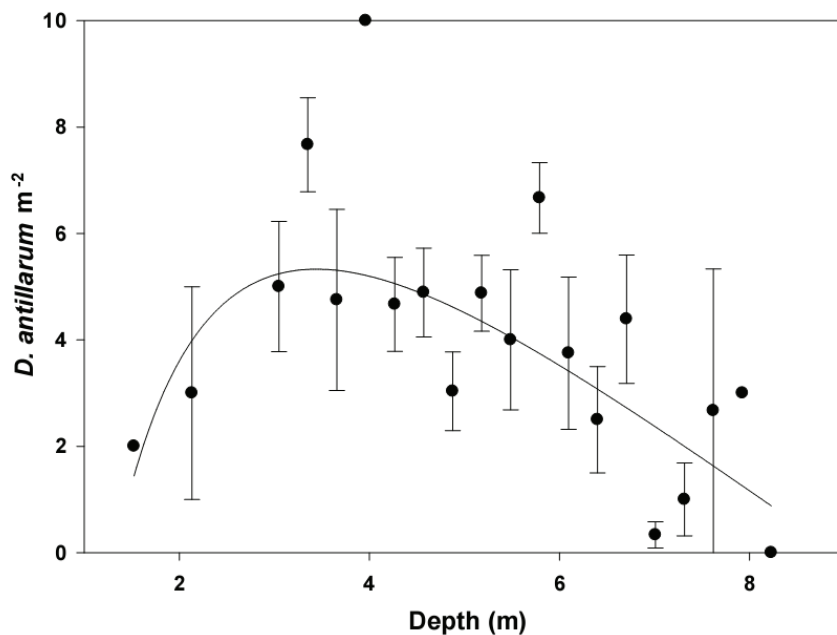
92

93 **Results**

94 ***Diadema antillarum* densities and abundance**

95 Among the 12 transects surveyed throughout the western forereef, the population densities of *Diadema*
 96 *antillarum* at all depths ranged from 0-15 m⁻² with a mean density of 3.93 ± 3.4 m⁻² (mean \pm SD). The
 97 population densities by depth best fit a non-linear curve, although linear analysis revealed significant negative
 98 correlation between density and depth, as well (Pearson product-moment correlation = -0.260, $p=0.003$).

99 Densities were very low in waters less than 2 m and increased rapidly to a peak from 3-5 m. A rapid decrease in
 100 population density occurred after this depth (Figure 1).



101

102 **Figure 1** Distribution of *Diadema antillarum* by depth. Closed circles represent urchin density as mean
 103 individuals m⁻² ± standard error. Non linear regression ($p=0.0034$) indicates a statistically significant
 104 relationship between urchin density and depth.

105

106 The highest mean *D. antillarum* densities were found at a depth of 3 m, while the lowest mean densities were
 107 found at 7 m (Table 1).

108

Table 1 Descriptive statistics for the distribution of *Diadema antillarum*, and macroalgal cover by depth.

Depth (m)	<i>D. antillarum</i> density (mean ± SD)	Max. density	Min. density	% Macroalgal cover (mean ± SD)	Max. % cover	Min. % cover	n =
2	2.67 ± 2.08	5	1	17.33 ± 28.29	50	1	3
3	5.64 ± 2.73	9	2	7.55 ± 17.58	60	0	12
4	4.29 ± 3.27	12	0	10.75 ± 18.33	80	0	40
5	4.77 ± 3.39	11	0	21.27 ± 27.18	99	1	33
6	3.59 ± 3.72	15	0	29.63 ± 27.87	99	1	26
7	1.07 ± 2.23	8	0	61.87 ± 31.27	99	1	14
8	1.50 ± 2.12	3	0	30 ± 0	30	30	2

∑ n = 130

Densities are given in individuals m⁻² with maximum and minimum densities indicated. Macroalgal cover is given in per cent of hard substrate covered by macroalgae with maximum and minimum relative cover of replicate quadrats. Depth bins and their statistics are the result of combining all data collected between that depth and the next deeper depth bin (*i.e.*: data for 3 m includes densities and % macroalgal cover between 3.00 and 3.99 m). The depth bin for 2 m includes data collected at 1.52 m.

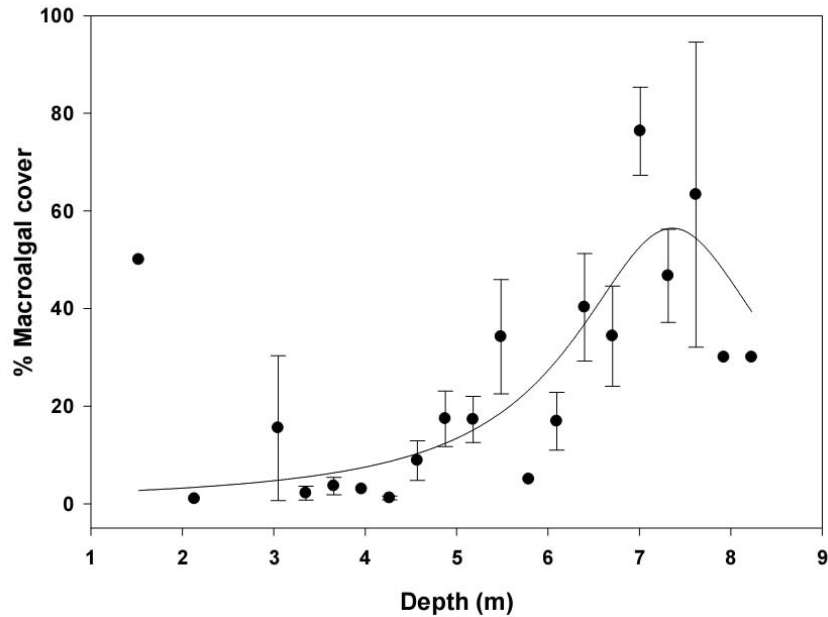
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110 There was a visibly apparent depth contour interval between 3 and 5 m in which *Diadema* were nearly always
 111 present. Urchins were rare to absent at depths less than or greater than this region.

112

113 **Macroalgal cover and distribution**

114 Macroalgal cover was strongly dependent on depth (Pearson product-moment correlation = 0.455, $p<0.000$); as
 115 the depth increased so did macroalgal cover (Figure 2).



116

117 **Figure 2:** Macroalgal cover over the substrate sampled by depth. Closed circles represent % macroalgal cover
 118 mean \pm standard error. Non linear regression ($p < 0.001$) indicates a statistically significant positive relationship
 119 between % macroalgal coverage and increasing depth.

120

121 The lowest macroalgal cover values were consistently recorded in the shallowest regions of the reef, near the
 122 reef crest. The lowest mean percent cover was found at a depth of 3 m, while the highest mean was found at 7 m
 123 (Table 1). Macroalgal dominance was strongest in the deeper sample areas (6-8 m) where mean macroalgal
 124 cover ranged between 29% and 60% of the hard substrate sampled (Table 1). As described for urchin
 125 abundances, a clearly demarcated depth region of high *Diadema*-low algae substrate was noted at all transects
 126 locations on the forereef.

127 This contrast in macroalgal cover between the shallow and deep sample points could be easily observed
 128 during the surveys. At a depth of approximately 5 m a marked boundary existed where on the shallow side
 129 cover was very low, while on the deeper side macroalgae covered a majority of the substrate sampled. The
 130 mean macroalgal percent cover did not exceed 65% for any depth, although certain sampling points reached
 131 values near 100% (Table 1).

132 Some depth dependent variation in the macroalgal species composition was observed. *Sargassum* sp. was
 133 one of the dominant species in the shallower areas (2-4 m) of the reef, but as depth increased other species
 134 became more common, including *Lobophora* sp., which was not seen at depths shallower than 5 m, and
 135 *Cladophora* sp., which was not found at depths shallower than 6 m.

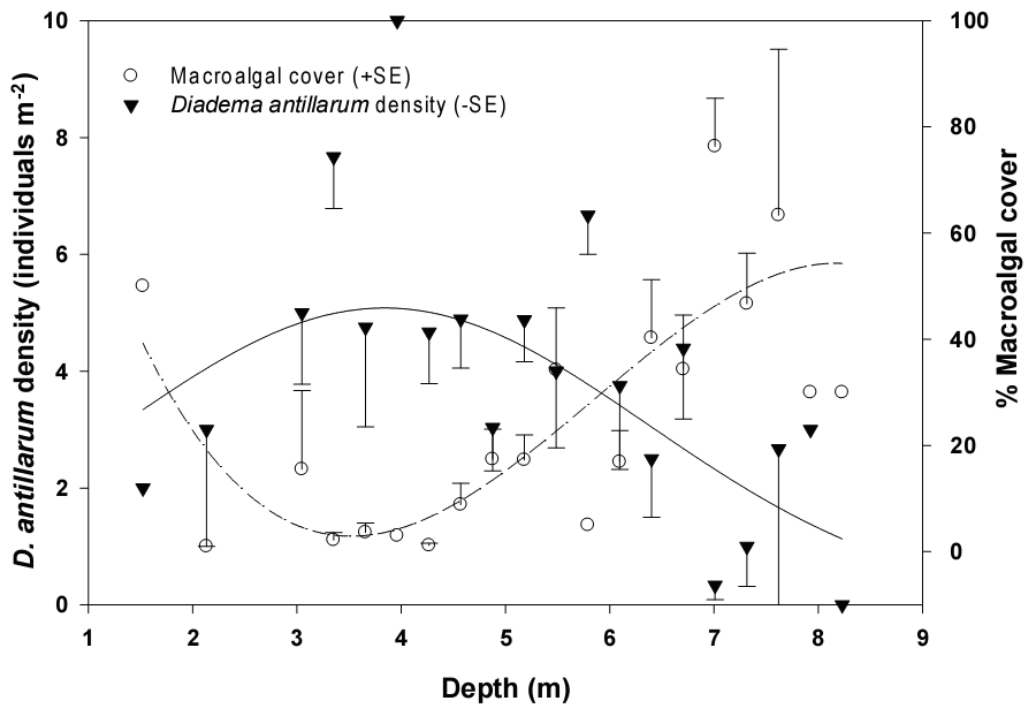
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137 **Algal cover and distribution in relation with *D. antillarum* densities**

138 A significant inverse relationship between the distribution of *D. antillarum* and macroalgal cover was observed

139 (Pearson product-moment correlation = -0.597, $p < 0.000$). *Diadema* densities and macroalgal cover had a

140 negative relationship, as urchin densities increased macroalgal cover decreased (Figure 3).



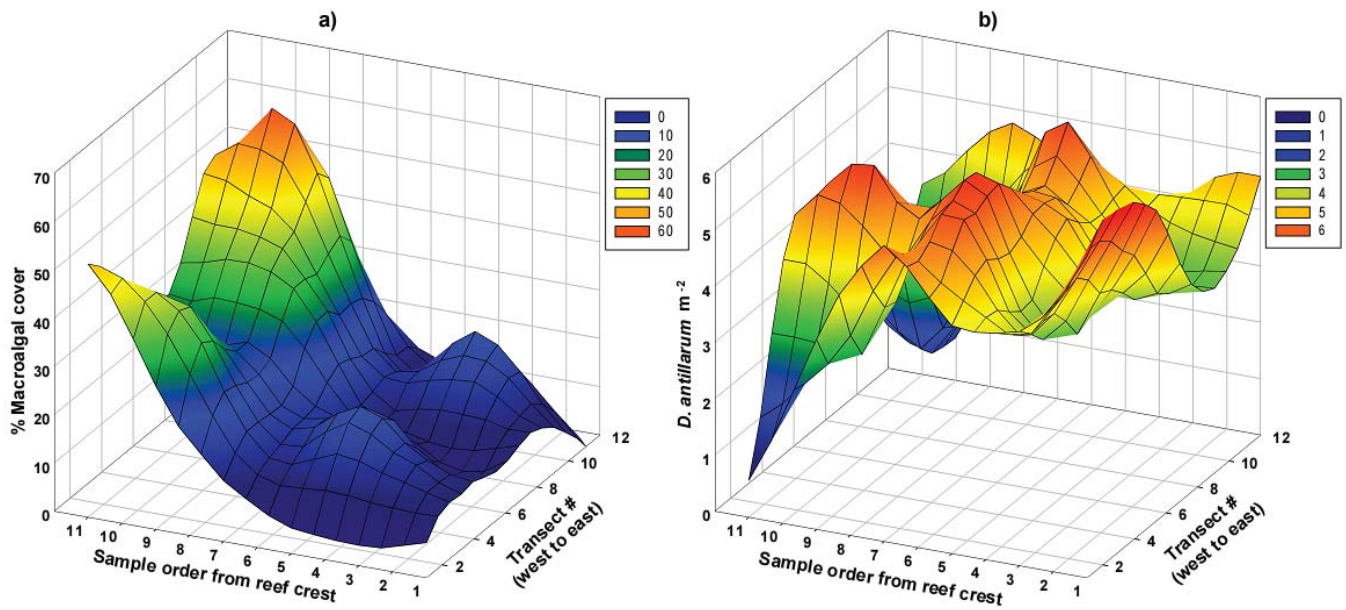
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142 **Figure 3:** Macroalgal cover as a function of *Diadema antillarum* population density. Macroalgal cover (open
 143 circles \circ + SE; dotted line) as percentage of the substrate surveyed covered by macroalgae. Population densities
 144 (closed circles \bullet - SE; solid line) are given as individuals m^{-2} .

145

146 In the shallower regions (3-5 m) where urchin densities were highest, macroalgal cover was reduced. As depth
 147 increased, densities of the echinoderm decreased and more substrate was dominated by macroalgae (Figure 4).

148 Comparisons between this 'urchin zone' at 3-5 m and the 'algal zone' (2-3 m and 6-8 m) revealed a significant
 149 difference in estimated macroalgal cover ($p < 0.001$).



150

151 **Figure 4:** a) Macroalgal percent cover as least squares regression estimated values by sample point. Surveys
 152 were taken every 6 m. b) *Diadema antillarum* density means by sample point at 6 m intervals.

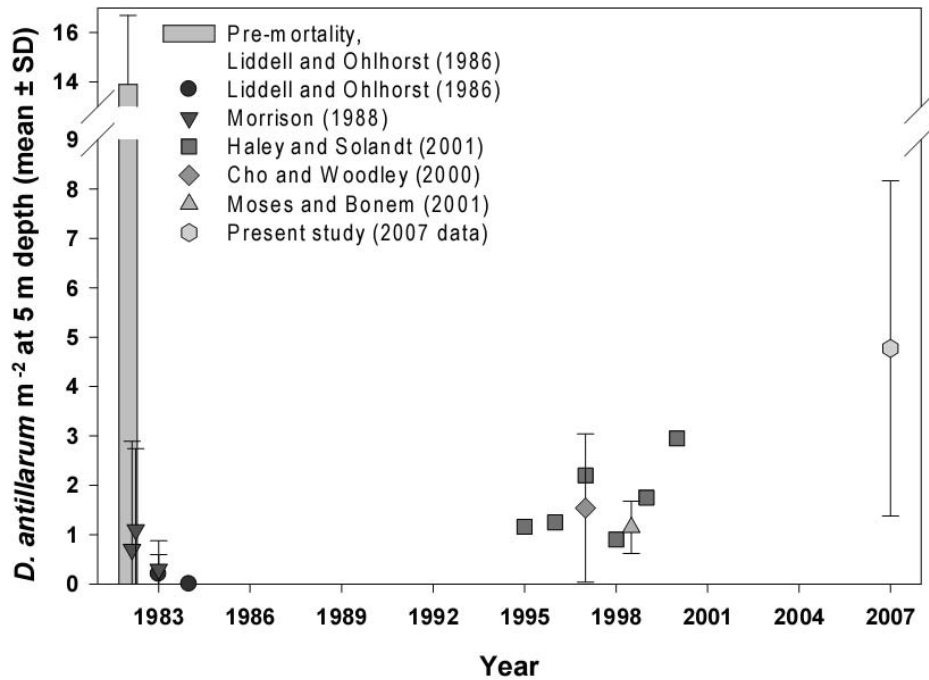
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154 At sites where the population density of *D. antillarum* was high, the macroalgal cover was reduced. These
 155 associations occurred along both shore normal and perpendicular orientations. *Diadema* densities and
 156 macroalgal percent cover are depicted as least squares regression estimated values, and do not show depth or
 157 actual distance from the reef crest. There was a significant correlation ($p < 0.001$, $R^2 = 0.55$) between sample order
 158 from the transect origin and depth.

159

160 **Historical *D. antillarum* densities and slow recovery of the population**

161 Comparisons of historical data on *Diadema* densities from the western forereef of Discovery Bay and the
 162 present study from those same locations indicates that *D. antillarum* densities are increasing, but are not close to
 163 their pre-1983 numbers (Figure 5).



164

165 **Figure 5:** Pre- and post-mortality density estimates of *Diadema antillarum* at 5 m on the west foreereef at
 166 Discovery Bay, Jamaica. Actual sites vary between the studies but all sites were within 0.5 km of each other
 167 and located between the CARICOMP and Mooring 1 (M1) dive sites for all studies. Error bars are given when
 168 standard deviations (SD) were noted by the various authors. Morrison [22] measured *Diadema* densities
 169 immediately (1.5 and 3 mo) after the population collapse at Discovery Bay. Error bars from this study were
 170 calculated from the given standard error (SE) and sample sizes (n) as $(SE = SD (\sqrt{n})^{-1})$. Values for 1996, 1997,
 171 and 1998 were estimated from Figure 1a of Haley and Solandt [11]; values for 1999 and 2000 are given in the
 172 text. Error bars from Moses and Bonem [10] represent the calculated SD as $\sqrt{(\text{variance})}$, from data presented in
 173 the text. Regression of all post-mortality data (1983-2007) indicates a significant population increase in *D.*
 174 *antillarum* ($p=0.0012$; $R^2=0.707$; $y=0.1637x-325.091$).

175

176 A historic time line of the urchin mortality and consequent return to the foreereef at Discovery Bay was plotted
 177 by comparing densities reported by past studies to the values obtained in this survey. Linear regression of all
 178 post-mortality data (1983-2007) indicates a significant population increase in *D. antillarum* ($p=0.0012$;
 179 $R^2=0.707$; $y=0.1637x-325.091$).

180

181 **Discussion**

182 More than 25 years have passed since the catastrophic regional population collapse of *Diadema antillarum* [24].

183 This study supports others that have documented a partial recovery in the past two decades [15, 16], but these

184 new data suggest that the rate of increase in population density has slowed in recent years. *Diadema* is

185 considered a keystone herbivore on Caribbean coral reefs and adjacent habitats [1], and the impacts of the

186 functional removal of this grazer are still particularly evident on the reefs of the north coast of Jamaica. In this

187 study, we documented a highly significant relationship between slowly recovering *Diadema* densities and low

188 macroalgal cover at Discovery Bay, Jamaica.

189 Trends in macroalgal cover and *D. antillarum* abundance (Table 2) show that increases in urchin density

190 over the past decades have been coupled with a reduction in macroalgae [3, 7].

Table 2. Historic timeline of *Diadema antillarum* densities and macroalgal cover at 5 m on the western foreereef of Discovery Bay, Jamaica.

	1982	1983	1984	1992	2007
% Macroalgal cover (mean ± SD)	17.6 ± 6.5	55.4 ± 6.6	72.7 ± 10.0	70.0 ± 2.9	21.3 ± 18.2
<i>D. antillarum</i> m ⁻² (mean ± SD)	13.9 ± 2.8	0.2 ± 0.4	0	unknown	4.8 ± 3.4

Values from 1982, 1983, and 1984 were obtained from Liddell and Ohlhorst [7]. Values from 1992 were obtained from Andres and Witman [3]. The data for 2007 was provided by this study.

191

192 Results from the present survey reveal that a strong correlation between macroalgal cover and *D. antillarum*

193 distribution still exists. Just as reported in Edmunds and Carpenter [16], a high urchin density zone was

194 observed during this survey. This high grazing zone formed a continuous contour at 3 m in which algal cover

195 was noticeably low and high densities of *D. antillarum* were observed (Figures 3 and 4). Edmunds and

196 Carpenter [16] found this zone to be at depths between 5 m and 8 m in 2000. The present study found that the

197 zone has shifted to shallower depths in the foreereef (3-5 m), although it is not known whether the location of the

198 band is temporary or whether it fluctuates within a narrow range of depths. This zone of relatively high urchin

199 abundance is in marked contrast to historical depth distributions from the north coast of Jamaica. Prior to the

200 mass mortality, Liddell and Ohlhorst [7] reported high densities of *Diadema* ($6.6 \text{ m}^{-2} \pm 1.9 \text{ SD}$) extending to at

201 least 15 m depth, and individuals were still common at 22 m ($2.5 \text{ m}^{-2} \pm 0.7 \text{ SD}$).

202 Although these new data clearly indicate that *D. antillarum* densities are increasing, their recovery on the

203 foreereef of Discovery Bay may be slowing and appears to be confined to shallower depths than the species has

204 historically occupied (personal observations). Mean population density doubled between 1995 and 2000 in the
205 forereef [11]. In contrast, mean *Diadema* densities only increased by 0.98 m⁻² in the seven years since the work
206 of Haley and Solandt [11] and urchin densities observed within the *Diadema* zone during the present survey are
207 very similar to those found by Edmunds and Carpenter [16]. The apparent decrease in the rate of recovery may
208 very well be a sign that the urchin population may plateau in the coming years. Results of the 2007 study
209 presented here suggested that the *Diadema* population on the forereef was very patchily distributed within
210 preferred habitat. This is likely due to a combination of the patchy distribution of *D. antillarum* associated with
211 daytime refugia [25] and their rapid decrease in population density with depth. As noted the high urchin density
212 zone observed during this survey occurred primarily between 3-5 m, but the overall density calculated ($3.93 \pm$
213 3.4 m^{-2}) encompassed depths from 2-8 m, thereby increasing the overall observed variation in the density
214 estimate. Large standard deviations for *Diadema* density at 5 m in this study (Figure 5) are likely the result of
215 variations between transects where in some cases 5 m was within the high density urchin zone, and in others it
216 was just outside this area.

217 Increases in density have been observed in other areas of the Caribbean as well. By 1985, just two years
218 after the initial die-off took place, the densities of *D. antillarum* on reefs of Barbados had returned to values up
219 to 57 % of their pre-1983 populations [26]. Increases were also reported during the 1990s in Puerto Rico [27],
220 and in Curacao [28]. Some increases have been more dramatic than others, but to this day populations have not
221 yet made a full basin-wide recovery.

222 Other areas of the region have not seen any significant increase in *Diadema* populations that would indicate
223 a recovery is taking place. In Panama, where the mortality was first observed and the population of *Diadema*
224 has had more time to recover, their numbers still remained below 6.5 % of their pre-mortality densities 20 years
225 after the die-off event [29]. Similarly in the Florida Keys densities still have not experienced a recovery; in
226 1999, only 16 individuals were observed in an area spanning 200 km [30].

227 The variability in the population dynamics of *D. antillarum* throughout the Caribbean suggests that
228 conditions that may encourage their recovery in some sites are not found in the sites where densities remain low.
229 One possible explanation for the long-term depression of *D. antillarum* populations could be habitat loss.
230 *Diadema* retreat into crevices during the day presumably to seek shelter from predation [11]. Before 1980
231 *Acropora cervicornis* and *A. palmata* dominated most of the forereef in Discovery Bay, and provided
232 appropriate cover for the urchins to hide [31, 32]. However, much of this coral cover was destroyed by
233 hurricanes Allen and Gilbert in 1980 and 1988 respectively [5, 17] leaving little shelter for the urchins.

234 Reductions in coral cover resulted in a homogeneous environment dominated by macroalgae. Habitat
235 complexity has been shown to attract *D. antillarum*, experimental studies showed that urchin presence and
236 grazing on macroalgae increased in areas of the reef with higher habitat complexity [25]. In general acroporids
237 across the Caribbean have been in retreat for many years [33]. This reduction in coral cover may have hindered
238 the recovery of the urchins across the region.

239 In summary, although this study documented continuing growth in *Diadema antillarum* densities on the
240 western forereef at Discovery Bay, Jamaica, the rate of this recovery seems to have slowed. This research, and
241 that of others [16], documents a small spatial region of relatively high abundance for *D. antillarum* (3-5 m depth
242 in the case of this survey), although these urchins have not yet returned in appreciable numbers to deeper waters.
243 Within their zone of high abundance, *Diadema* continue to be an important grazer on macroalgae, and have
244 important impacts on benthic community structure. Several questions arise from the observations made during
245 this survey and highlight the need for research to address ongoing population dynamics of *Diadema* and the
246 potential for alternate phase shifts between coral and macroalgae dominated systems.

247

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