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Recovery of the long-spine sea urchin, *Diadema antillarum*, in Discovery Bay, Jamaica, 27 years after its mass mortality

Jessica Keller

Abstract

The long-spined sea urchin, *Diadema antillarum*, is a well-studied keystone herbivore on Caribbean coral reefs. The sea urchin controls benthic algae populations by grazing on macroalgae. Destruction caused by Hurricane Allen in 1980, along with the mass mortality of this urchin in 1983, greatly impacted Caribbean reef systems. In Discovery Bay, Jamaica, *Diadema* densities have been heavily studied over the years, allowing a review of their recovery and a prediction of their future. In Discovery Bay, densities were recorded to be up to 9.3 and $13.9 \pm 2.8 \text{ m}^{-2}$ at 5 m depth on the forereef before the mass mortality. After this event, values were found to be zero, or nearly zero, at multiple depths up until the mid 1990s. *Diadema* have shown a recovery in numbers as densities in the late 2000s ranged between 3.94 ± 0.68 and $4.39 \pm 0.4 \text{ m}^{-2}$ at 4 – 6 m depth. In most of the wider Caribbean, recovery has been absent with values in many locations still nearly zero, with the exception of St. Croix and Dominica. We predict that *Diadema* densities will continue to increase in the future, but the rate will be slower than that recorded over the past 27 years.

Introduction

Diadema antillarum

The long-spined sea urchin, *Diadema antillarum*, is a well-studied keystone herbivore on Caribbean coral reefs. *Diadema* have venomous, needle-sharp spines which can reach up to a foot in length. The spines are dark in color in adults while juveniles often have checkered spines with alternating bands of white and dark purple. The urchins are often found sheltering in crevices during the day and the juveniles are especially prone to hide, commonly taking shelter in the spines of adults (Randall et al. 1964).

Diadema feed on algae that may compete with or harm corals while their spines shelter other organisms, including juvenile reef fish and juvenile spiny lobsters (Miller et al. 2007). Fish predators of *Diadema* include members of Balistidae (triggerfishes), Carangidae (jacks), Diodontidae (porcupinefishes), Labridae (wrasses), and Pomadasyidae (grunts) (Randall et al. 1964).

***Diadema antillarum* and Macroalgae**

Macroalgae slow the growth of coral by blocking sunlight and encroaching over live coral tissue, causing abrasions (River and Edmunds 2001). Macroalgae also limit recruitment of coral by releasing chemicals that can inhibit the settlement of coral larvae (Miller et al. 2009). *Diadema* control benthic algae populations by grazing on this macroalgae (Liddell and Ohlhorst 1986). *Diadema* are an important grazer of macroalgae as urchins are estimated to be responsible for 40% of the grazing that occurs on a reef (Mumby et al. 2006).

Diadema facilitate coral recruitment and colonization by opening up bare substrate and reducing the direct competition with macroalgae for settlement sites (McCook et al. 2001, Idjadi 2010, Edmunds and Carpenter 2001, Crabbe 2010). *Diadema* have a foraging range of ~0.5-4 m², with the area re-grazed every 3-6 days, making them a more intense grazer than herbivorous fish (Carpenter 1984, Carpenter 1986). Simple algae removal is not the only result of *Diadema* grazing, for the algal composition also changes. When *Diadema* are absent, turf algae are replaced by macroalgae, which are less productive, less palatable to herbivores, and more likely to be exported off the reef as detritus, resulting in a net loss of energy of the reef (Carpenter 1986).

Nugues (2004) demonstrated that physical contact between *Montastrea faveolata*, mountainous star coral, and *Halimeda opuntia*, watercress alga, triggered white plague II in the coral. While the mechanism of the transmission of the disease is unclear, this transfer shows macroalgae as an influence on coral epizootics. Jordan-Garza et al. 2008 noted that *Diadema* were located in patches of healthy *Montastraea annularis*, lobed star coral, while patches of this coral in areas lacking *Diadema* were affected by yellow band and white plague diseases, suggesting *Diadema* as a source of coral health. Macroalgae have obvious negative effects on aspects of coral life while evidence continues to be discovered on how *Diadema* play a positive role.

***Diadema* in the Caribbean**

In 1983, *Diadema* populations in the Caribbean dramatically dropped when a water-borne pathogen caused a mass mortality of this urchin (Lessios et al. 1984). This unidentified disease started at the mouth of the Panama Canal, and spread by surface currents until the entire Caribbean was affected (Lessios 1988). Within weeks of the *Diadema* die-off, the macroalgal cover in affected areas increased on shallow hard bottoms (Bechtel et al. 2006). After this event many reefs in Jamaica had less than 5% coral cover and over 90% macroalgal cover (Hughes 1994). Three years earlier, in 1980, Hurricane Allen swept through the Caribbean destroying much of the framework coral, including *Acropora palmata* and *Acropora cervicornis*. This had significant effects as these corals provide structure for the reef as well as habitats for other reef organisms, including *Diadema antillarum*.

The combination of the coral loss from Hurricane Allen and the mass mortality of *Diadema* caused many reef systems in the area to shift from coral-dominated to algal-

dominated (Hughes 1994). A benthic algae bloom started in 1983, which began with small ephemeral species, but later these were replaced with longer lived taxa such as *Sargassum*, *Dictyota*, and *Halimeda* (Hughes 1994). There is a known negative relationship between this macroalgae cover and *Diadema* density, but there is recent debate about whether the increase in macroalgae had a larger effect than first thought, representing a change in alternative stable states.

In an alternative stable state, dominance of algae or coral would limit the existence of the other at that particular location. Replacement of one species by the other could only occur if the current dominant species was removed by a disturbance, or if a critical threshold was passed. Once the dominant species changed, it would be very difficult to reverse the process. If coral and macroalgae-dominated reefs are alternative stable states then changes in the environment to favor coral cover may not switch the environment back to coral dominated (Petraitis and Dudgeon 2004).

However, recent studies have found that Jamaican reef communities are not alternative stable states. Instead the reefs have simple, phase-shift responses determined by environmental conditions, like *Diadema* abundance, with reversals in reef dominance possible (Petraitis and Dudgeon 2004, Idjadi 2010). Bruno et al. 2009, surveyed coral reefs around the world and found that few of the reefs are macroalgal-dominated, having over fifty percent macroalgal cover. Only 25 of the 1851 reefs surveyed could be classified as having undergone a complete coral to algal shift; however, all these reefs except for one were located in the Caribbean. As the mass mortality of *Diadema* was limited to the Caribbean, recovery of this urchin can help shift Caribbean reefs back toward a coral-dominated reef system.

***Diadema* Populations in Jamaica**

Discovery Bay, Jamaica, has been a focus of intensive research and *Diadema antillarum* populations have been consistently monitored there in the years since its mass mortality. Prior to the epizootic, *Diadema* populations on the forereef at Discovery Bay were found to be up to 16.2 urchins m⁻² at 15 m depth (Sammarco and William 1982) and 13.3 m⁻² to 13.9 m⁻² between 4 – 6 m (Woodley et al. 1981, Liddell and Ohlhorst 1986). Soon after the epizootic, many studies found densities of zero, or close to zero (Hughes 1987, Liddell and Ohlhorst 1986, Edmunds and Bruno 1996 Aronson and Precht 2000).

In recent years, areas of high *Diadema* numbers have been observed, but these zones of high densities are limited in depth, generally around 3 - 7m. In Jamaica, these areas of high densities, called “urchin zones” or “*Diadema* zones” (Edmunds and Carpenter 2001), appear to be decreasing macroalgae cover and increasing crustose coralline algae (CCA), which induce the growth, survivorship, and recruitment of scleractinian corals (Sellers et al. 2009 and Idjadi et al. 2010). *Diadema*'s limited grazing range does not allow them to move far outside their established zones, but their current location may be linked to rugosity.

Rugosity is a measure of topographic complexity that has been positively correlated with diversity and total abundance of fish assemblages on coral reefs (Luckhurst and Luckhurst 1978). At Discovery Bay, Jamaica, multiple surveys have found that *Diadema* prefer complex habitat structures (Bechtel et al. 2006). *Diadema* in an area of high substrate complexity have crevices available to shelter in during the day as well as cover for juveniles. Field experiments have shown that adding physical structures, and thus enhancing spatial complexity, results in a decrease of algal cover and

an increase in the proportion of urchins (Lee 2006). Macia et al. (2007) transplanted *Diadema* from buttresses with high urchin densities to those with low urchin densities, and the urchins not only decreased the macroalgae cover on the transplant buttresses, but they also aggregated to rugose areas on those buttresses. The high density of *Diadema* between 3 - 5 m, and the lack below 9 m, may be tied to the spatial complexity, or rugosity, of the forereef at those depths.

This Study

Location

This study was conducted in May 2010 at Discovery Bay Marine Laboratory, located on the north coast of Jamaica. The study area included three sites along the west forereef at Discovery Bay; Dancing Lady, LTS (18 28.388'N, 77 24.833'W), and M1 (18 28.342'N, 77 24.560'W).

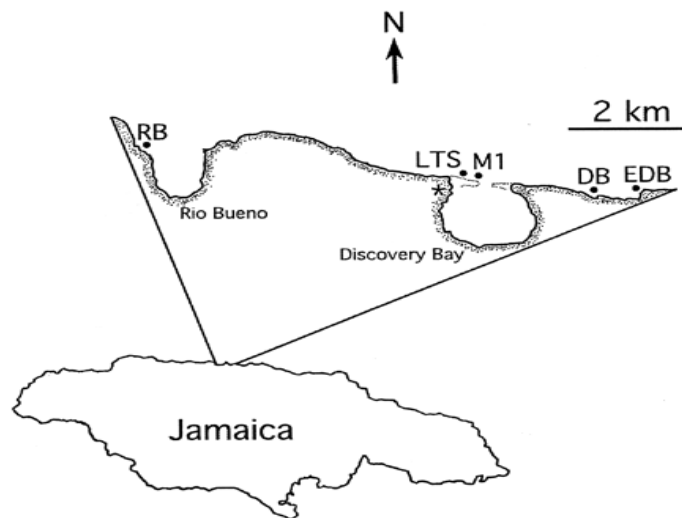


Figure 1. A map of Jamaica showing the area of Discovery Bay and the dive sites in this study (Edmunds and Carpenter 2001).

Data collection

Five belt transects, each 100 ft long (~30 m) and 2 m wide, were run perpendicular to the shore. Two perpendicular transects were run at Dancing Lady and Mooring 1 (M1), while one transect was run at Long Term Study (LTS). Six belt transects were then run parallel to the shore with two transects at each site. Perpendicular transects were run directly north to south, while the parallel transects were run directly west to east. Perpendicular transects were run to determine if *Diadema* were expanding outside of their known zone while parallel transects were ran to obtain better data within the “*Diadema* zone”, with some transects run above, below, and within this zone.

For each belt transect, which covered approximately 61 m², *Diadema* were counted and a *Diadema* density was calculated. Macroalgae cover and composition were recorded using random quadrat sampling along the belt transect. Depths were measured using a VEO 100 dive computer.

The rugosity, or complexity of the reef substrate, was determined using a ~4.6 m chain link line. The chain was laid along the transect line following the benthic contours of the substrate. A Rugosity Index was established by dividing the length of the chain-link line, 4.6m, by the distance between the two ends of the chain (McClanahan and Shafir 1990). A substrate that had no contours at all, such as a sandy bottom, would have a rugosity index of 1 (4.6 m chain / 4.6 m covered along a transect), whereas a substrate with multiple coral heads would have a higher rugosity index (4.6 m / 4 m covered along a transect).

Results

Diadema densities ranged between 0.52 m^{-2} (at 6 m depth) and 6.8 m^{-2} (at 5 m depth) on the forereef with a mean density of $2.77 \pm 2.02 \text{ m}^{-2}$ (mean density \pm standard deviation). The highest rugosity index was 1.92 while the lowest index was 1.09. Both of these indices were found on the same perpendicular transect, which had the lowest average *Diadema* density of 0.52 m^{-2} . The densities of *Diadema* increased as macroalgae cover decreased in both perpendicular and parallel transects and a weak positive relationship was found between density of *Diadema* and rugosity for both perpendicular and parallel transects.

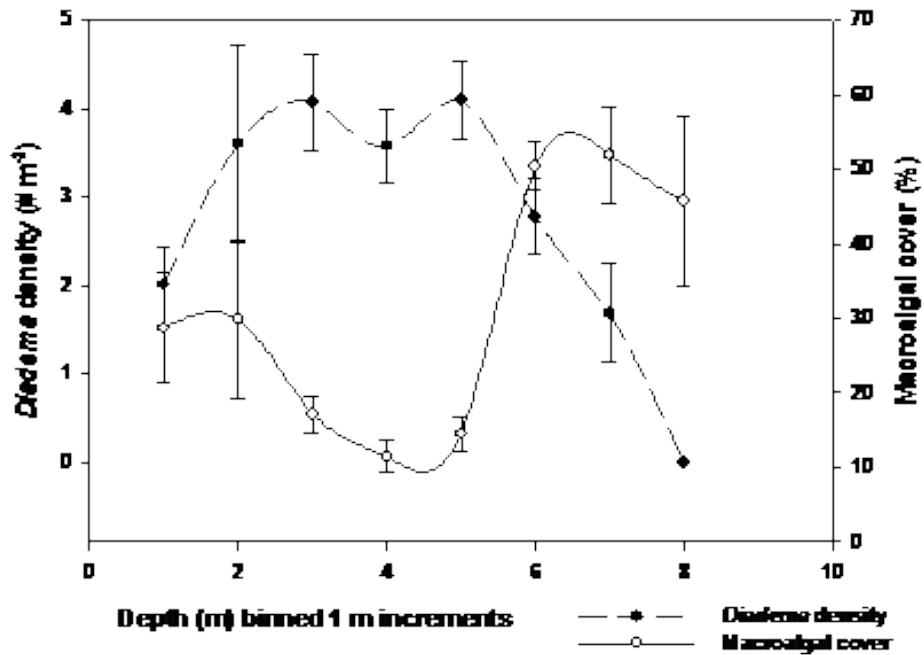


Figure 2. Mean *Diadema* density and macroalgae cover from 2007-2010 (unpubl. data) were binned by depth in 1 m increments and show the inverse relationship between the two factors.

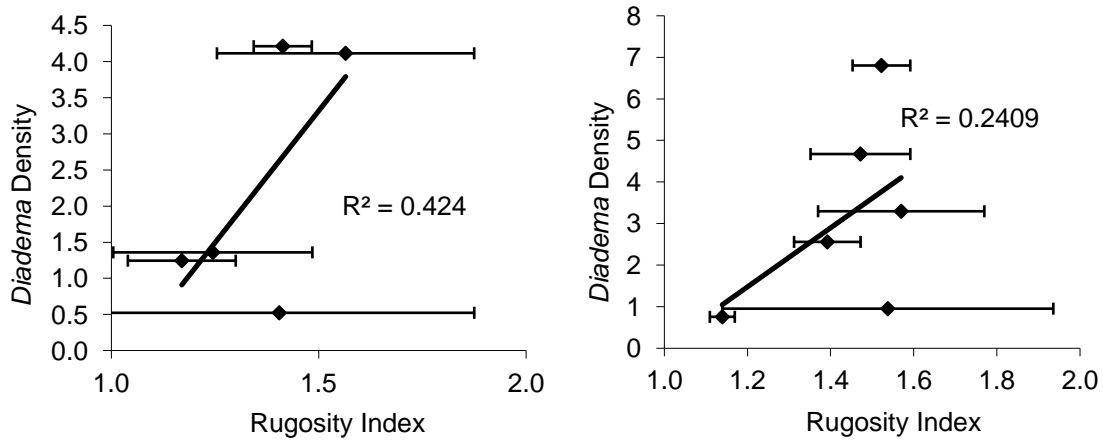


Figure 3. Density of *Diadema* increased as Rugosity increased in both perpendicular (left) and parallel (right) transects.

***Diadema* Recovery in Jamaica**

Diadema densities have been making a healthy recovery at Discovery Bay, Jamaica. By 1997, densities were recorded to be $1.54 \pm 1.5 \text{ m}^{-2}$ and 2.2 m^{-2} (Cho and Woodley 2000, Haley and Solandt 2001) at 5 m on the forereef. By 2000, densities of urchins reached nearly 3 m^{-2} and had increased to 4.1 m^{-2} by 2002 (Haley and Solandt 2001, Idjadi et al. 2010). Data from the past four years show densities varying between $2.26 \text{ m}^{-2} \pm 0.59$ (mean density \pm SE) and $4.39 \text{ m}^{-2} \pm 0.4$ between 4 - 6 m (Zourdos and Trimper unpub. 2008, Casey and Sellers unpub. 2007). *Diadema* zones were previously recorded to be 5 – 7 m, but more recent data indicated that areas of highest *Diadema* and lowest macroalgae are located between 4 – 6 m (Figure 2)

In 2010, the mean density was found to be $3.94 \text{ m}^{-2} \pm 0.68$ in this depth range (Keller and Podmore unpub. 2010). This is significant as Sammarco (1980) observed that the highest experimental coral spat density was in a treatment with a *Diadema* density of 4 m^{-2} .

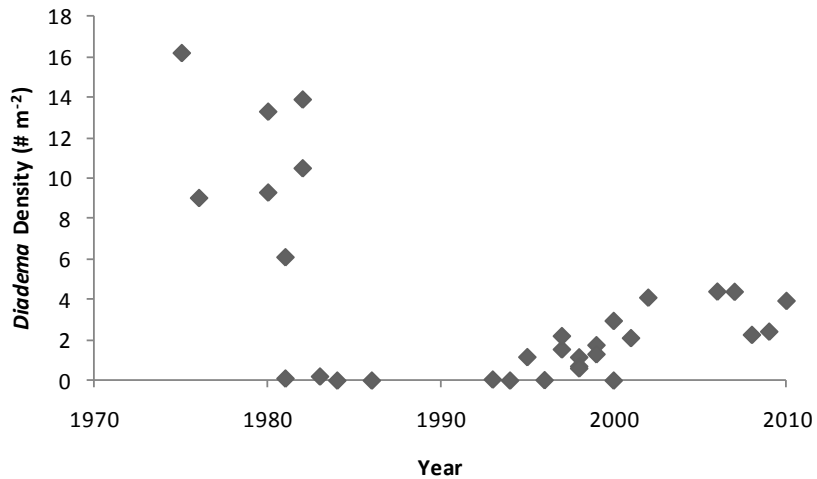


Figure 4. *Diadema* density (# m⁻²) by year in Discovery Bay, Jamaica. See Table 1.

Jamaica is one of the few places in the Caribbean with where *Diadema* are noticeably recovering (Edmunds and Carpenter 2001, Haley and Solandt 2001, Idjadi 2010). This may be partly the result of overfishing of Jamaican reefs as the large, predatory species of fish, such as sharks, groupers, and triggerfish, have disappeared from Discovery Bay, leaving only small, herbivorous fish (Hughes 1994). *Diadema* released from the pressure of predators may result in more time available for feeding and thus the abandonment of homing (Carpenter 1984). *Diadema* able to roam farther graze more substrate, opening new area for coral settlement. Hay (1984) studied reefs throughout the Caribbean and found echinoid densities were indeed much higher on overfished reefs than on pristine reefs. One area of very low *Diadema* density is in the Florida Keys, which has high fish population.

Table 1. *Diadema* densities in Jamaica by location and year.

Location	Reef location	Year	Density	Depth	Source
Discovery Bay	Dancing Lady	1975	16.2	15	Sammarco and Williams 1982
Discovery Bay	Backreef	1976	9.03 ± 0.22 *		Williams 1980
Discovery Bay	East Forereef	1980	9.3	5	Woodley et al. 1981
Discovery Bay	West Forereef	1980	13.3	8	Woodley et al. 1981
Discovery Bay	East Forereef	1981	0.1	5	Woodley et al. 1981
Discovery Bay	West Forereef	1981	6.1	8	Woodley et al. 1981
Discovery Bay	West Forereef	1982	13.9 ± 2.8 ^	5	Liddell and Ohlhorst 1986
Discovery Bay	Dancing Lady	1982	10.5 ± 7.2 ^	8	Hughes et al. 1987
Discovery Bay	West Forereef	1983	0.2 ± 0.4 ^	5	Liddell and Ohlhorst 1986
Discovery Bay	West Forereef	1984	0	5	Liddell and Ohlhorst 1986
Discovery Bay	Dancing Lady	1986	0	3-15m	Hughes et al. 1987
Discovery Bay	LTS	1993	0.05	4-6m	Aronson and Precht 2000 (est. from figure)
Discovery Bay	M1	1994	0	10	Edmunds and Bruno 1996
Discovery Bay	West Forereef	1995	1.16	5	Haley and Solandt 2001
Discovery Bay	LTS	1996	0.02	4-6m	Aronson and Precht 2000 (est. from figure)
Discovery Bay	West Forereef	1997	1.54 ± 1.5 ^	5	Cho and Woodley 2000
Discovery Bay	West Forereef	1997	2.2	5	Haley and Solandt 2001
Discovery Bay	LTS	1998	1.15 ± 0.28 ^	5	Moses and Bonem 2001
Discovery Bay	West Forereef	1998	0.7	5	Haley and Solandt 2001
Discovery Bay	LTS	1998	0.6	4-6m	Aronson and Precht 2000 (est. from figure)
Discovery Bay	West Forereef	1999	1.75	5	Haley and Solandt 2001
Discovery Bay	LTS	1999	1.3	4-6m	Aronson and Precht 2000 (est. from figure)
Discovery Bay	LTS	2000	~5	4.5-8.5m	Edmunds and Carpenter 2001
Discovery Bay	West Forereef	2000	2.95	5	Haley and Solandt 2001
Discovery Bay	LTS/M1/DBL	2001	2.1 ± 0.2 *	4-7m	Idjadi et. al 2010
Discovery Bay	LTS/M1/DBL	2002	4.1 ± 0.5 *	4-7m	Idjadi et. al 2010
Discovery Bay	LTS/M1	2006	4.4 ± 5.28 *	3-7m	Raines and Amato 2006
Discovery Bay	West Forereef	2007	4.39 ± 0.4 *	4-6m	Casey and Sellers (unpub)
Discovery Bay	West Forereef	2008	2.26 ± 0.59 *	4-6m	Zourdos and Trimper (unpub)
Discovery Bay	West Forereef	2009	2.42 ± 0.74 *	4-6m	Ehert and Keck (unpub)
Discovery Bay	West Forereef	2010	3.94 ± 0.68 *	4-6m	Keller and Podmore (unpub)
Rio Bueno	W Rio Bueno Wall	1980	6.3	10	Woodley et al. 1981
Rio Bueno	W Rio Bueno Wall	1981	3.8	10	Woodley et al. 1981
Dairy Bull	Blowing Rocks	1994	2.1 ± 0.6 *	10	Edmunds and Bruno 1996
Dairy Bull	DBL	1994	1.6 ± 0.3 *	10	Edmunds and Bruno 1996
Dairy Bull	DBL	1994	6.5	6	Cochran unpub.
Dairy Bull	DBL	1994	2.2	8	Cochran unpub.
Negril	El punto negrilo	2003	0.875	3	Reef Check
Negril	El punto negrilo	2003	2	10	Reef Check
Negril	Ireland pen	2003	0.14	3	Reef Check
Negril	Ireland pen	2003	0.423	10	Reef Check
Negril	Bloody bay	2003	0.59	3	Reef Check
Negril	Bloody bay	2003	0.973	10	Reef Check
Dairy Bull	DBL	2008	2.0 ± 0.35 *	9	Burge unpub.
Dairy Bull	DBL	2009	2 ± 0.47 *	9	Burge unpub.
Dairy Bull	DBL	2010	2.16 ± 0.43 *	9	Burge unpub.

^ represents values with standard deviations

*represents values with standard errors

LTS = Long Term Study

DL = Dancing Lady

M1 = Mooring 1

***Diadema* Populations throughout the Caribbean**

Signs of recovery throughout the Caribbean have appeared in other locations, but densities remain well below historic highs, and lag those currently seen on the north coast of Jamaica. In St. Croix, *Diadema* densities were 9-16 urchins m^{-2} in 2 - 5 m of water before the die-off (Hay 1984), and while values dropped dramatically, there has been evidence of recovery, with increases from 0.368 m^{-2} in 2001 (Miller et al. 2003) to a density of 3.17 m^{-2} at monitored reefs (Miller et al. 2007).

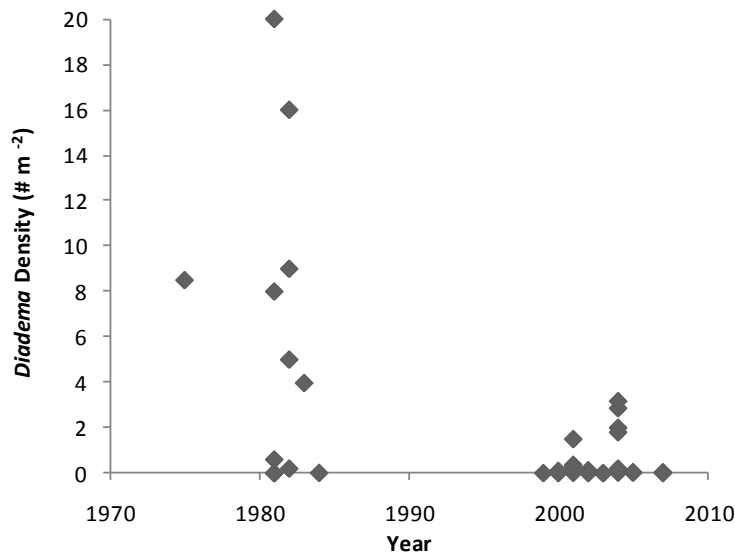


Figure 5. *Diadema* density (# m^{-2}) by year in the wider Caribbean.

Other locations within the Caribbean basin do not appear to have had increases in *Diadema* populations. For example, in Curaçao, *Diadema* densities were found to be 8.5 m^{-2} before the die-off (Bak and van Eys 1975), but values have not made a strong comeback, with recent estimates recording 0.13 m^{-2} at 1 - 3m depth. (Debrot and Nagelkerkon 2006). In Costa Rica, values were found to be only 0.1-0.2 m^{-2} in 1-7 m of

water (Myhre and Acevedo-Gutierrez 2007) while Cuba had densities of about 0.043 m⁻² at 2-3m depth (Blanco et al. 2009). The Florida Keys also have very low densities. Chiappone et al (2005) found densities of 0-0.003 m⁻², but more recently, a density at Bahia Honda State Park was 1.8 m⁻² at 2m depth (Furman and Heck 2009).

Table 2. *Diadema* densities throughout the Caribbean with location and year.

Location	Reef Description	Year	Diadema Density	Depth	Source
Curacao	N/A	1975	8.5		Bak and van Eys 1975
Bahamas	patch reef	1981	<1	2-3m	Hay, 1984
Belize	Forereef	1981	<1	2-3m	Hay, 1984
Belize	patch reef	1981	8	1	Hay, 1984
Belize	halo	1981	0	2-3m	Hay, 1984
Haiti	Forereef	1981	20	3-10m	Hay, 1984
Honduras	forereef	1981	<1	2-3m	Hay, 1984
Honduras	Forereef	1981	0.6	2	Hay, 1984
St. Croix	patch reef	1982	9	2-4m	Hay, 1984
St. Croix	Forereef	1982	0.2	10	Hay, 1984
St.Ccroix	Forereef	1982	16	2-5m	Hay, 1984
St. Thomas	Forereef	1982	5	3	Hay, 1984
Curacao	reef terrace	1983	3.97	3	Bak et al. 1984
Curacao	reef terrace	1984	0.01	3	Bak et al. 1984
Florida Keys	Forereef	1999	0.003 ± 0.007 *	4-7m	Chiappone et al. 2005
Costa Rica	fringing reef	2000	0.1 ± 0.22 ^	1-7m	Myhre and Acevedo-Gutiérrez 2007
Florida Keys	Forereef	2000	0 ± 0 *	4-7m	Chiappone et al. 2005
Dominica	N/A	2001	1.5 ± 0.12 ^		Steiner and Williams 2006
St. Croix	Backreef	2001	0.368 ± 0.54 ^		Miller et al. 2003
St. Croix	patch reef	2001	0.278		Miller et al. 2003
St. Coix	backreef	2001	0.011 ± 0.47 ^		Miller et al. 2003
Curacao	shallow reef	2002	0.13 ± 2.26 ^	1-3m	Debrot and Nagelkerken 2006
Curacao	exposed reef	2002	0 ± 0.01 ^		Debrot and Nagelkerken 2006
Puerto Rico	fringing reef	2003	0-0.9	<4	Ruiz-Ramos et al. 2011
Puerto Rico	fringing reef	2003	0.82-1.55	0->10m	Weil et al. 2005
Costa Rica	fringing reef	2004	0.2 ± 0.2 ^	1-7m	Myhre and Acevedo-Gutiérrez 2007
Dominica	N/A	2004	2 ± 0.05 ^		Steiner and Williams 2006
Forida Keys	N/A	2004	1.8	2m	Furman and Heck, 2009
St. Croix	backreef	2004	3.17 ± 0.8 *	2-3m	Miller et al. 2007
St. Croix	forereef	2004	2.86 ± 0.6 *	2-3m	Miller et al. 2007
St. Croix	backreef	2004	0.02 ± 0.01 *	2-3m	Miller et al. 2007
Cuba	reef slope	2005	0.02 ± 0.012 *	12-15m	Blanco et al. 2009
Cuba	reef crest	2005	0.043 ± 0.012 *	2-3m	Blanco et al. 2009
Bahamas	forereefs	2007	0.04	9-15m	Harborne et al. 2009
Bahamas	forereefs	2007	0	9-15m	Harborne et al. 2009

^represents values with standard deviations

*represents values with standard errors

Further Recovery

While *Diadema* densities have been increasing in Jamaica, certain factors can halt or even reverse this urchin's recovery. Nutrient input onto the reef will affect algae composition as an increase in phosphate decreases the growth of CCA (Björk et al. 1995). Crustose coralline algae plays a role in determining which way a coral-algae shift will occur as some species of CCA contain chemical cues that facilitate both the settlement and metamorphosis of coral planulae (Morse and Morse 1996). A cause for concern is a rise in coastal development, like that in Jamaica, will increase nutrients in the water (Mumby et al. 2006). Low abundance of herbivores including *Diadema* and grazing fishes, along with an influx of nutrients from anthropogenic sources, will produce both top-down and bottom-up controls that allow macroalgae to bloom (Hughes 1994).

Past studies have found that reefs in the Caribbean are becoming flatter and more structurally homogenous, with the proportion of reefs having a rugosity index greater than 2 having declined from 45% to 2% in the past four decades (Alvarez-Filip et al. 2006). If a decline in reef rugosity does exist, there would be severe consequences as many reef fish and invertebrates, including *Diadema*, live in niches provided by the reef. A loss in shelter would slow and perhaps limit the recovery of this urchin in the Caribbean. In this study, no rugosity values found above 2 on any of the three sites studied on the forereef of Discovery Bay. However, the substrate is not homogenous, the forereef has spurs and grooves, and even along a 30 m transect, there was great variation in rugosity indices. Along the transect with the highest rugosity index, 1.92, there were also rugosity values of 1.56 and 1.13. Because of the spur and groove structure, the

substrate at the start of a transect may be coral-dominated, rugose substrate, but the transect may cross a sand channel with very low rugosity. Averaging rugosity values along the belt transect limited the statistical relationship found between *Diadema* density and substrate complexity. Surveys by divers reveal that *Diadema* populations are densest in areas with complex, algae-barren substrates, but sampling methods along with the patchiness of the *Diadema* made measuring this occurrence difficult.

Density measurement methods have varied between studies throughout the years, from random quadrat sampling to block transects or belt transects. The patchiness of *Diadema* makes them difficult organisms to accurately determine a density, but the same method should be used to limit to variability in comparisons by year or location. Block transects (~5 m x 2 m) appear to work best as they provide a broader area to find *Diadema*, but a small enough area that a single Rugosity measurement could be used to represent the substrate complexity.

Humans can aid in the recovery of *Diadema* through aquaculture. However, there are few reports of successful spawning and survivorship of aquacultured *Diadema*. Increasing the density of the broodstock may help as Randall 1964 witnessed spawning occurring in such tightly packed groups that individual urchins were lifted above the substrate on the interlocking spines of the others. There have been restoration attempts in which spawning and production of larvae is successful, but metamorphosis was not witnessed, which could be due to escapement of larvae through filtration systems, or a factor, like certain bacteria, which blocks the metamorphosis (Leber et al. 2008).

In the Florida Keys, there have been multiple attempts at *Diadema* restoration, one of which was thwarted by high mortality of juveniles placed on the reef (Nature

Conservancy, 2003). Juveniles need the spines of the adults as shelter; if adult specimen spread out on the reef, densities may be too low to provide adequate protection for the juveniles.

Monitoring of *Diadema* populations should continue both in Jamaica and throughout the Caribbean. If the densities continue to level off, *Diadema* will likely be able limit the macroalgal growth in certain areas and particular depths, but they will not be able to disperse widely enough across the forereef to significantly lower total algal cover. If a disturbance on the reef occurs, like another hurricane, the stress on *Diadema* as well as the combination of added nutrients and lack of big herbivorous fish could provide another opportunity for algae to bloom. If the population at Discovery Bay continues to increase, *Diadema* will be seen to move outside of their highly aggregated areas and expand their depth range while grazing new areas of the forereef. We predict that *Diadema* will indeed continue to recover in Jamaica, just at a slower rate than that previously recorded.

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