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The Great *Diadema antillarum* Die-Off: 30 Years Later*

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Annu. Rev. Mar. Sci. 2016. 8:267–83

First published online as a Review in Advance on June 5, 2015

The *Annual Review of Marine Science* is online at marine.annualreviews.org

This article's doi:

10.1146/annurev-marine-122414-033857

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Keywords

coral reef, algae, recruitment, mortality, population recovery

Abstract

In 1983–1984, the sea urchin *Diadema antillarum* suffered mass mortality throughout the Caribbean, Florida, and Bermuda. The demise of this herbivore contributed to a phase shift of Caribbean reefs from coral-dominated to alga-dominated communities. A compilation of published data of *D. antillarum* population densities shows that there has been moderate recovery since 1983, with the highest rates on islands of the eastern Caribbean. On the average the current population densities are approximately 12% of those before the die-off, apparently because of recruitment limitation, but the exact factors that are constraining the recovery are unclear. Scattered *D. antillarum* cohorts in some localities and aggregation of settled individuals in shallow water have created zones of higher herbivory in which juvenile coral recruitment, survivorship, and growth are higher than they are in alga-dominated areas. Unlike other stressors on Caribbean coral reefs, recent changes in *D. antillarum* populations progress toward aiding the recovery of coral cover.

INTRODUCTION

The last half century has witnessed an alarming number of collapses of marine populations caused by overfishing (Dulvy et al. 2003, Jackson et al. 2001), habitat loss (Jackson et al. 2001), disease (Harvell et al. 1999, 2004; Lafferty et al. 2004, 2015), temperature changes (Glynn 1984), waterborne (Zea 1998) or atmospheric (Shinn et al. 2000, 2003) pollution, or combinations of these factors (Burge et al. 2014; Gardner et al. 2003; Harvell et al. 1999, 2002, 2004; Hoegh-Guldberg et al. 2007; Hughes & Connell 1999; Jackson 2008). Among these collapses, the 1983–1984 mass mortality of the long-spined black sea urchin *Diadema antillarum* in the western Atlantic stands out for its sudden onset, intensity, geographic extent, and impact of the loss of a single species on entire ecological communities.

D. antillarum is a large, highly mobile sea urchin formerly represented by dense populations on coral reefs, rocky bottoms, *Thalassia* beds, and sand banks (Carpenter 1981, 1986; Hay & Taylor 1985; Ogden 1976; Ogden et al. 1973; Sammarco 1982a,b). It ranged in the tropical and subtropical west Atlantic from Florida to Bahia, Brazil. It was previously thought to also occur in the eastern Atlantic, but on the basis of mitochondrial DNA (Lessios 2001, Lessios et al. 2001b) and morphological differences, populations off the coast of Africa have been recently assigned to a separate species, *Diadema africanum* (Rodríguez et al. 2013). The dense premortality populations of *D. antillarum* exerted intense grazing pressure on hard bottoms (Carpenter 1986, 1997; Hay 1984; Sammarco 1982a,b) and removed more calcium carbonate from coral reefs than any other bioeroder (Hunter 1977, Scoffin et al. 1980). The high abundances of this species had been a feature of Caribbean coral reefs for a long time (Jackson 1997, Levitan 1992), possibly for hundreds of thousands of years (Donovan 2005, Lessios et al. 2001a). Removal of its competitors and predators may have further increased its population densities in overfished areas (Hay 1984).

In January 1983, this species of sea urchin (but no others) began dying at the Atlantic entrance of the Panama Canal (Lessios et al. 1984a,b). Over the next 13 months, the mortality spread northward along the coast of Central America all the way to Bermuda, as well as to Jamaica; at the same time, it advanced eastward to Venezuela, Barbados, and the Lesser Antilles. From Florida, it spread to the Bahamas, Puerto Rico, Hispaniola, and the Virgin Islands (Lessios et al. 1984b). Within two weeks of the first appearance of symptoms on each reef, 93–100% of individuals were dead (Bak et al. 1984, Hughes et al. 1985, Hunte et al. 1986, Lessios 1988a, Lessios et al. 1984a). The cause was never identified, but the progress of the die-offs, which moved in the direction of prevailing currents over long distances and haphazardly over proximate ones, suggested a waterborne pathogen, as did the mortality of live sea urchins held in indoor aquaria fed by seawater (Lessios et al. 1984b). No *D. antillarum* population is known to have escaped this mass mortality. *D. africanum* was not affected in 1983–1984 (Entrambasaguas et al. 2008, Hernández et al. 2008), but populations at Madeira and the Canary Islands were reduced by 65% in 2009–2010 by an infestation of *Vibrio alginolyticus* (Clemente et al. 2014).

The effects on other species in Caribbean coral reef communities were immediate. Macroalgae began covering reefs and reached densities that actually killed adult coral colonies (Carpenter 1988, Hughes 1994, Hughes et al. 1987, Levitan 1988a, Liddel & Ohlhorst 1986). Surviving *D. antillarum* sea urchins grew to large sizes but were unable to keep up with algal production (Levitan 1988a). The long-term effects of the virtual disappearance of this herbivore, especially in areas where herbivorous fishes were removed, have lingered and—in combination with other reef stressors (Hughes et al. 2003)—have led to pronounced reductions of live coral cover and its replacement by algae (Andres & Witman 1995, Aronson & Precht 2000, Carpenter 1985, Hughes et al. 2010).

The 1983–1984 mass mortality of *D. antillarum* and its immediate consequences have been reviewed (Lessios 1988a). More than 30 years have now passed since the first die-offs were noted

at the Atlantic entrance of the Panama Canal. In this article, I summarize the fate of populations of this species during the subsequent three decades, the possible reasons for the shape of its recovery trajectory, and the long-term effects of its demise on coral reef communities.

THE FATE OF *DIADEMA ANTILLARUM* POPULATIONS SINCE 1983

Population Density Since the Mass Mortality

Hughes et al. (2010) presented a graph summarizing the available information on *D. antillarum* population density before and after the mass mortality. They calculated that 25 years after the die-off, aggregate Caribbean populations were 25 times less dense than those before mass mortality. This is a general trend, but to what extent has each population changed? **Table 1** presents information on the extent of population reduction immediately after the mortality event and on changes in population densities as of the most recent date for which they are available. The dates on which mortality occurred at each location are based on the study by Lessios et al. (1984b) except for those for Honduras, Cuba, and Dominica, which were inferred from the progression of the mortality front. No information is available on whether *D. antillarum* mass mortalities took place on the coast of Brazil; in 1995 populations in shallow water at Bahia were quite dense, and they actually increased after the 1997–1998 El Niño event (Attrill & Kelmo 2007, Attrill et al. 2004).

The population densities from different censuses presented in **Table 1** are not strictly comparable either between years or between localities. In most cases, postmortality densities were not measured in exactly the same place or with exactly the same methods as those in 1983–1984. Because *D. antillarum* sea urchins tend to aggregate in shallow water (Lewis & Wainwright 1985; Weil et al. 1984, 2005) and the composition of benthic reef fauna can vary within small distances (Edmunds & Bruno 1996), the placement of transects and quadrats on the reefs and the areas they include can produce large variation between measurements. In the estimation of densities of patchily distributed organisms, there is always the dilemma of how much of the area in which individuals do not occur should be included in the census (Lessios 1996). Researchers with no memories of *D. antillarum* at a particular location before 1983 may exclude a large area where the species is now absent, thus biasing postmortality density measurements upward.

The bias arising from different sampling locations and from preferential placement of sampling is most obvious in **Table 1** for the data from Belize, in which a comparison of densities determined by Carpenter & Edmunds (2006) at Turneffe Atoll in 2004 with densities determined by Lewis & Wainwright (1985) at Carrie Bow Cay before and immediately after the mortality creates the appearance that the density of sea urchins has more than tripled. This density difference comes in part from the distance between these reefs (26 km) but mainly from the method of measurement. Lewis & Wainwright averaged data over the entire reef, whereas Carpenter & Edmunds—being interested in the effects of herbivory—intentionally selected sites at depths of <6 m in which *D. antillarum* was present. Other studies in Belize have reported much lower postmortality *D. antillarum* population densities: The density at Glover’s Reef, 30 km from Turneffe, was 0.001 individuals per square meter in 1997 (McClanahan & Muthiga 1998) and <0.01 at Ambergris Caye, 48 km away, in the same year (Williams & Polunin 2001). The 2004 data from Belize are included in **Table 1** because they are the most recent density measurements from the area, but I do not include them in any of the analyses. A similar artifact does not exist for the north coast of Jamaica, where, using different methods, Haley & Solandt (2001) determined in 2000 that the average number of individuals per square meter at the shallow fore-reef was 3, Edmunds & Carpenter (2001) determined in the same year that it was 4.9, Carpenter & Edmunds (2006) determined in 2004 that it was 3.2, and Sellers et al. (2009) determined in 2005 that it was 3.9.

Table 1 Mean population densities of *Diadema antillarum* before and after the 1983–1984 mass mortality, percent change relative to premortality census densities, and change per year since the first postmortality census

Locality	Date of mortality	Density at last premortality census (N/m ²) (year)	Density at first post-mortality census (N/m ²) (year)	Percent of premortality census density (%)	Density at most recent census (N/m ²) (year)	Percent of premortality census density (%)	Change per year since first postmortality census {[N/(m ² ·year)]·100}	Reference(s)
Northward progression								
Galeta Island, Panama	January 1983	1.38 (1982)	<0.01 (1983)	0.72	0.06 (2015)	4.35	0.16	Lessios et al. 1984a; H.A. Lessios, unpublished observations
Cahuita, Costa Rica	June 1983	4.33 (1980)	0.10 (1983)	2.31	0.53 (2004)	12.24	2.05	Fonseca et al. 2006, Murillo & Cortés 1984
Manzanillo, Costa Rica	June 1983	NA	0.10 (2000)	NA	0.20 (2004)	NA	2.50	Fonseca 2003, Myhre & Acevedo-Gutiérrez 2006
Jamaica (north coast)	July 1983	7.32 (1983)	0.03 (1983)	0.41	3.93 (2007)	53.69	16.25	Hughes et al. 1985, 1987; Sellers et al. 2009
Cayos Cochinos, Honduras	July 1983*	NA	0.19 (1995)	NA	0.53 (2009)	NA	2.43	Bologna et al. 2012, Lessios 1998
Belize	July 1983	0.76 (1982)	<0.01 (1983)	1.32	2.55 (2004)	335.53	12.10	Carpenter & Edmunds 2006, Lewis & Wainwright 1985
Cuba	July 1983*	NA	0.02 (2004)	NA	0.01 (2005)	NA	<0.01	Martin-Blanco et al. 2010
Florida Keys	July 1983	1.7 (1970–1978)	<0.01 (1990–1991)	0.59	0.02 (2011)	1.18	<0.01	Bauer 1980, Chiappone et al. 2013, Forcucci 1994
Bahamas	August 1983	2.9 (1978)	<0.01 (1999)	0.34	0.02 (2007)	0.69	<0.01	Bauer 1980, Harborne et al. 2009, Kramer 2003

(Continued)

Table 1 (Continued)

Locality	Date of mortality	Density at last premortality census (N/m ²) (year)	Density at first post-mortality census (N/m ²) (year)	Percent of premortality census density (%)	Density at most recent census (N/m ²) (year)	Percent of premortality census density (%)	Change per year since first postmortality census {[N/(m ² ·year)]·100}	Reference(s)
St. John, Virgin Islands	December 1983	14.38 (1983)	0.08 (1984)	0.56	0.23 (2011)	1.60	0.56	Levitan 1988a, Levitan et al. 2014
Puerto Rico (north coast)	January 1984	13.8 (1977)	NA	NA	0.95 (2013)	6.88	NA	Bauer 1980, Rodriguez-Barreras et al. 2014
Puerto Rico (south coast)	January 1984	6.1 (NA)	0.01 (1995)	0.16	1.43 (2009)	23.44	10.14	McGehee 2008, Soto-Santiago & Irizarry-Soto 2013, Williams et al. 2013
St. Croix, Virgin Islands	February 1984	5.9 (1983)	0.10 (1983)	1.69	0.20 (2001)	3.39	0.56	Carpenter 1990, Miller et al. 2003
Eastward progression								
San Blas Islands, Panama	April–May 1983	3.63 (1982)	0.24 (1983)	6.61	0.03 (2015)	0.83	−0.66	Lessios et al. 1984a; H.A. Lessios, unpublished observations
Colombia	August 1983	NA	NA	NA	0.91 (2009)	NA	NA	González-Gaviria & García-Urueña 2011
Barbados	September 1983	9.26 (1983)	0.72 (1984)	7.78	1.42 (2003)	15.33	3.68	Carpenter & Edmunds 2006, Hunte et al. 1986
Curaçao	October 1983	2.58 (1983)	0.02 (1983)	0.78	0.16 (2002)	6.20	0.74	Bak et al. 1984, Debrot & Nagelkerken 2006
Venezuela	November 1983	1.84 (1980–1981)	0.48 (1997–1998)	26.09	0.39 (2003)	21.20	−1.50	Nortega et al. 2006
Dominica	December 1983*	NA	0.5 (1985)	NA	2.00 (2004)	NA	0.08	Hunte & Younglao 1988, Steiner & Williams 2006
Bahia, Brazil	NA	NA	4.00 (1995)	NA	8.00 (2001)	NA	0.67	Atrill & Kelmo 2007

The table is arranged according to the progression of the mass mortality northward and eastward (Lessios et al. 1984b). Dates of mortality marked with an asterisk are based on inferences from this progress rather than actual documentation of die-off. Abbreviation: NA, data not available.

The agreement among these values suggests that *D. antillarum* population densities on the north coast of Jamaica are, indeed, on the order of 4 individuals per square meter.

My averaging of data that were not necessarily randomly collected or normally distributed has also caused artifacts in the values presented in **Table 1**. Additionally, the elapsed time between premortality density determinations and the first census after the die-offs varied between localities. This is most obvious for data from Venezuela by Noriega et al. (2006), in which the reduction in population density appears to be less than that in other localities because the first postmortality census was conducted 14 years after die-offs occurred on these shores. The table contains data from only a few relatively recent censuses, with most being at least a decade old, but this is the state of the literature as of March 2015. Thus, the mean densities of *D. antillarum* presented in **Table 1** suffer from many of the problems that plague meta-analyses of coral reef communities (Hughes et al. 2010), and the values are probably accurate only within an order of magnitude.

Despite the deficiencies of the data in **Table 1**, the emerging picture is clear: In the decades since the die-offs, many *D. antillarum* populations around the Caribbean have recovered from the extremely low initial postmortality densities, but this recovery has been modest. Before the mass mortality, the densities in 14 locations ranged from 0.76 to 14.38 individuals per square meter; soon after the die-offs, they ranged from <0.01 to 0.72 per square meter (not including Venezuela). On average, the mass mortality removed 98.06% of *D. antillarum* sea urchins. The most recent censuses in 19 locations in the Caribbean (not including Belize), conducted between 18 and 32 years after the die-offs, found densities ranging from 0.01 to 3.93 per square meter (an average of 11.62% of their premortality density), at a population growth rate that ranged from <0.0001 to 0.16 individuals per square meter per year (not counting two populations that have actually declined). In other words, when the change in each locality is calculated separately, the “current” populations of *D. antillarum* are 8.5 times less dense than they were before they die-offs, a less depressing estimate than the 25-fold reduction estimated by Hughes et al. (2010), which presumably came from combining all available pre- and postmortality measurements. Recent populations are densest in the eastern Caribbean at Jamaica, Barbados, Dominica, and Puerto Rico, while either remaining virtually stable at low values or showing small increases on the coast of Central America and in Cuba, Florida, the Bahamas, the Virgin Islands, and Curaçao. The highest rate of increase has been on the north coast of Jamaica, and the lowest in Florida, Cuba, and the Bahamas. Two populations, in Venezuela and the San Blas Islands, Panama, have actually continued to decline with time.

Shape of the Recovery Curve and Rate of Recruitment

Table 1 lists only the end-point values of the first and last postmortality density measurements, but the shape of the recovery curve is also of interest, because it can shed light on the causes of the slow rate of recovery (see below). Studies that followed *D. antillarum* populations at regular intervals for a minimum of five years with the same techniques were conducted at 11 reefs from 1983 to 2015 (with an 11-year hiatus) in the San Blas Islands (Lessios 1988b, 1995, 2005; Lessios et al. 1984a); at 7 sites from 1984 to 2011 (with a 17-year hiatus) in St. John, Virgin Islands (Levitan et al. 2014); at 1,321 sites from 1999 to 2010 in the Florida Keys (Chiappone et al. 2013); and at 14 sites from 1984 to 1993 in Jamaica (Hughes 1994) as well as 3 sites from 1995 to 2000 in a different study on the same island (Haley & Solandt 2001). In all cases, recovery has not been monotonic. Population densities stayed near zero in most Panamanian and Floridean reefs, with sporadic signs of modest increases resulting from the settling of cohorts that disappeared by the next census and were not replaced. Density values also fluctuated widely between censuses in St. John and Jamaica. The most likely explanation (beyond measurement error) is that there were

episodic low-level recruitment events of individuals that subsequently succumbed to mortality and were not replaced. The same conclusion can be drawn (with less certainty) from a combination of studies on the south coast of Puerto Rico in which multiple measurements were made in the same area. Weil et al. (2005) reported a mean density of 1.17 individuals per square meter in 2001, but this dropped to approximately 0.2 per square meter in 2003 (Ruiz-Ramos et al. 2011), fell further to 0.08 per square meter in 2004 (Lugo 2004, as cited in Williams et al. 2013), and then rose to 0.18 per square meter in 2005 (McGehee 2008) and 1.43 per square meter in 2009 (Soto-Santiago & Irizarry-Soto 2013). On the north shore of the same island and two sites on the island of Culebra, southwest of Puerto Rico, populations remained fairly stable, with mean densities of 1.15 per square meter in 2011 and 0.95 per square meter in 2013 (Rodríguez-Barreras et al. 2014). That recruitment has been variable and episodic is also evident in most locations, where a number of reefs had no *D. antillarum* whatsoever between 1984 and 2015 (Beck et al. 2014; Chiappone et al. 2013; Lessios 1995, 2005; Martin-Blanco et al. 2010; Miller et al. 2003; Williams & Polunin 2001).

Direct observations of *D. antillarum* larval settlement suggest that recruitment in postmortality populations has been persistently limited for decades, but that the larval supply may be slowly increasing. Larvae of this species take 36 (Eckert 1998) to 90 (Carpenter 1997) days to reach metamorphosis in the laboratory. Plastic plates monitored by Bak (1985) at Curaçao received as many as 13 juveniles per square meter per day before adult populations were decimated at this island in October 1983. Settling continued until April 1984 but stopped five months after major mortality reached upstream areas at Barbados and Venezuela. Between March 1994 and October 1996, I monitored settling plates identical to those of Bak (1985) on two reefs in the San Blas Islands. I examined these plates every two weeks and replaced them with new ones that had been pre-seasoned underwater for a minimum of one week. The maximum recruitment rate on these panels was 0.1 recruits per square meter per day, but this happened during only one of the observation intervals. In the entire 31-month monitoring period, a total of 17 *D. antillarum* individuals were found on the plates, an overall recruitment rate of 0.003 per square meter per day.

Miller et al. (2009) also used plates similar to those deployed by Bak (1985) to study *D. antillarum* settlement at two sites in the upper Florida Keys in 2005 and 2006. These plates attracted a maximum of <0.07 individuals per square meter per day. Settlement was higher in southwest Puerto Rico. At two sites during the same time period, the maximum recruitment rate on similar plates was approximately 0.53 juveniles per square meter per day (Miller et al. 2009). Moored pieces of artificial turf employed by Williams et al. (2011) for two three-month periods in 2008 at the shelf edge in La Parguera received 3.1 recruits per square meter per day from a supply of larvae, which plankton tows had shown to be present in the water column (Williams et al. 2009). Bak's (1985) observations of settlement at Curaçao in 1983–1984 were repeated in 2005 by Vermeij et al. (2010), who monitored settling plates on seven reefs over five months. Recruitment rates were 2.2 times lower than those found by Bak (1985) before the mass mortality but 56.5 times higher than those in the months after the cessation of settlement immediately following the 1983 die-off. Despite this increase in settlement on plastic plates, a much slower rate of increase in the density of populations on the reefs (Debrot & Nagelkerken 2006) led Vermeij et al. (2010) to conclude that an unknown factor of post-settlement mortality also plays a role in preventing population recovery. Although the data come from different locations, there appears to be a trend of increased settlement in the years since the mass mortality.

What is the origin of the larvae that reestablished *D. antillarum* populations at the observed postmortality levels? The mass mortality was density independent, so locations with higher initial population densities were left with more individuals (Lessios 1988a). Dense populations at

Barbados were decimated by 93% in September 1983, but two years later they had recovered to 37% of their premortality levels (Hunte & Younglao 1988). This initial increase does not appear to have held over the long term (**Table 1**). Speculations that larvae from this island might help reseed the rest of the Caribbean (Lessios 1988a) were not confirmed. The pattern of recovery in areas within the Caribbean (**Table 1**) does not show any trend of earlier increases with distance from Barbados, nor does it follow the direction of flow of major currents downstream of that island. It may be that populations not studied before or after the die-offs contained sufficient numbers of survivors to start the observed modest increases. Mitochondrial DNA data indicate that larvae are sufficiently long lived and mixed in the water column to make local Caribbean populations of *D. antillarum* parts of an essentially single panmictic unit (Lessios et al. 2001b), which is still large enough to maintain approximately 35 times more genetic variability than *Diadema africanum* populations in the eastern Atlantic and *Diadema mexicanum* populations in the eastern Pacific (Lessios et al. 2001a). It is certain that Brazilian populations of *D. antillarum* did not contribute any propagules to the Caribbean, because collections made after the mass mortality showed that DNA of individuals from Brazil belongs to a distinct clade that is also present in individuals from Ascension and St. Helena but not present in individuals from the Caribbean (Lessios et al. 2001b).

Why Has Recovery Been So Slow?

Given that *D. antillarum* produces approximately a million eggs per spawning (Levitan 1988b) and generally spawns every new moon (Lessios 1984, 1991) throughout the year (Lessios 1981), and given that reproductive cycles were not disrupted by the mass mortality event (Lessios 1988b), one would have expected that population recovery would be rapid, or at least that it would not be limited by recruitment. Why this did not happen is an open question. Four hypotheses can be formulated; there is evidence both in favor and against each one.

One possibility is that the presumed waterborne pathogen that caused the mass mortality is still present and continues to kill *D. antillarum* sea urchins. Indeed, two outbreaks causing the same symptoms that were observed during the 1983–1984 die-offs (but with much lower mortality) were noted in Panama in 1985 (Lessios 1988b) and in Florida in 1991 (Forcucci 1994). Similar symptoms have not been reported on any other occasion or at any other locality in more than 30 years of increasingly intense scrutiny, leading both Lessios (1988b) and Levitan et al. (2014) to reject this hypothesis. Nevertheless, it is not entirely impossible that, if newly settled sea urchins succumb to disease, they perish before the symptoms are observed.

Beck et al. (2008, 2014) tested coelomocytes of various species of Caribbean sea urchins collected after the mass mortality for humoral responses to immune reaction stimulators and found that those of *D. antillarum*, in contrast to those of other species, did not respond to lipopolysaccharide, a component of the cell walls of gram-negative bacteria. They suggested that the immune system of *D. antillarum* may be compromised. According to Beck and colleagues, this could explain why *D. antillarum* alone was affected, and why it has not made a strong recovery. However, because the postmortality individuals are all descendants of individuals that survived the mass mortality, one would expect them to have inherited genes resistant to the pathogen. Beck and coworkers suggested that there may not have been such selection, either because the survivors were among the minority that randomly escapes mortality during an epidemic, or because they came from larvae that were in the water column while the adults were dying. It is not clear, however, how random survival or escape of individuals at one life history stage would explain the persistence of immunocompromised genotypes over generations and thus account for the slow recovery. A pathogen continuously present since 1984, if it inflicted mortality that prevented populations from increasing, would also be constantly selecting against susceptible genotypes.

The second hypothesis is that, despite high fecundity, not many zygotes are being produced, because the population density on most reefs is so low that individuals do not come close enough to each other for fertilization to succeed. Because of sperm dilution, *D. antillarum* eggs released more than 3 m away from sperm have a very low probability of being fertilized (Levitan 1991). The fertilization rate would thus be positively correlated with population density, and if mortality in the plankton has remained constant before and after mass mortality, then the number of settling juveniles per parent would be reduced, a classical Allee effect (Courchamp et al. 1999).

Levitan (1991) has shown experimentally and Levitan & McGovern (2005) have argued that the recruitment rate in *D. antillarum* is density independent, because the effect of low population density (and the resultant increasing distance between individuals) is counterbalanced by higher per-capita gamete production owing to the sea urchins' larger body size. In their opinion, the combination of one positively density-dependent factor and one negatively density-dependent factor results in density independence (Levitan & McGovern 2005). It is true that premortality *D. antillarum* populations exhibited an inverse relationship between population density and average body size (Levitan 1988c, 1989) and that *D. antillarum* survivors grew to larger sizes after the die-off (Levitan 1988a), but the same form of compensation for reduced population density by larger body size cannot hold for both the high and the extremely low postmortality density values. Levitan et al. (2014) supported the lack of dependence of recruitment rate on population density with empirical data from St. John, but given the potential dispersal distances of larvae, the rate of zygote production on a single island would not necessarily influence recruitment on the same island. Thus, the hypothesis that recruitment limitation is caused by a reduction of the rate at which *D. antillarum* eggs are fertilized after mass mortality could partly explain why the population recovery has been so slow.

The third possibility is that pervasive algal turfs that developed after 1983, particularly in areas where fishing kept populations of herbivorous fishes at low levels, have been preventing larval settlement. Caribbean reefs became overgrown with algae when *D. antillarum* disappeared (Carpenter 1988, 1990; de Ruyter van Steveninck & Bak 1986; Hughes et al. 1987; Liddel & Ohlhorst 1986; Shulman & Robertson 1996). Before the mass mortality, *D. antillarum* larvae recruited at high numbers onto slightly fouled plastic plates but not onto plates heavily covered by filamentous algae (Bak 1985), perhaps because of larval preferences or because of micropredators among the algae. Because *D. antillarum* adults on the reef efficiently removed algae before the mass mortality (Carpenter 1986; Sammarco 1982a,b), the absence of adults after the die-off would depress the number of juveniles that enter alga-covered reefs, and a positive relationship between resident adults and recruits would be expected. This aspect of density dependence does not appear to hold. On a local scale, the postmortality algal standing crop within the home range (Carpenter 1984) of *D. antillarum* individuals at St. John remained at premortality levels, yet there was no spatial association between juveniles and adults (Levitan et al. 2014). On a regional scale, the islands that showed the highest rates of *D. antillarum* population increase [Jamaica, Puerto Rico, Barbados, and Dominica (Table 1)] are also areas of heavy fishing pressure, whereas locations with moderate fishing pressure (such as Panama) showed little *D. antillarum* recovery, despite an increase in the density of at least one species of herbivorous fish in Panama after the mass mortality (Robertson 1991). It is therefore unclear to what degree the slow rate of *D. antillarum* recovery is due to the accumulation of algae after the die-off. However, grazing of turf algae may not be unrelated to rates of *D. antillarum* recruitment. Lessios (1995) maintained four shallow patch reefs with areas of 408–1,800 m², one with only *D. antillarum* at premortality densities, one with *D. antillarum* plus *Echinometra viridis*, one with only *E. viridis*, and one with no sea urchins. I monitored recruitment at monthly intervals from 1983 to 1992, and reversed the treatments between reefs halfway through the experiment to control for reef effects.

The number of *D. antillarum* juveniles did not significantly differ between reefs with and without *D. antillarum*, so there was no relationship between adult densities and recruitment. However, there was a significant difference in *D. antillarum* recruitment between reefs with and without *E. viridis*. Apparently, grazing by the more numerous *E. viridis* facilitated recruitment to a larger extent than grazing by *D. antillarum*. Thus, *D. antillarum* larval settlement may not be dependent on the presence of conspecific adults but could still be dependent on grazing rates by other echinoids.

The fourth hypothesis about the slow rate of *D. antillarum* recovery is that predators with a predilection for this species are exerting heavier pressure on the remaining populations than they did when their preferred prey was plentiful. That the sea urchins spread on the reef at night to feed and return to shelter during the day (Carpenter 1984) suggests that visually oriented predators have exerted selection pressures on their behavior at some point in their history. Areas protected from fishing in the Bahamas, which contain higher numbers of *D. antillarum* potential predators, harbor fewer *D. antillarum* sea urchins than unprotected areas (Harborne et al. 2009). This is not due to lower algal cover where herbivorous fishes are protected, suggesting the importance of predation upon *D. antillarum*.

There is, however, no evidence that the rate of predation on *D. antillarum* increased after the mass mortality. Examination of the stomach contents of fishes that were previously eating *D. antillarum* showed that after the die-off, the predators switched to other prey (Reinthal et al. 1984, Robertson 1987). The abundance of predatory fishes has been declining since 1983 (Paddock et al. 2009), so it is hard to imagine that predation pressure on *D. antillarum* has increased since then. However, the rate of predation on juvenile sea urchins may be affected indirectly by the absence of adults. Miller et al. (2007) reported that *D. antillarum* juveniles (<2 cm in diameter) placed on 1-m² artificial reefs constructed of cinder blocks were more likely to be relocated if surrounded by a high, rather than low, density of adults. They also found a significantly positive association between the number of naturally occurring adult and juvenile *D. antillarum* sea urchins. By contrast, Levitan et al. (2014) found no evidence of a correlation between adult density and rate of recruitment or rate of mortality. The problem with studying the role of predation in regulating *D. antillarum* populations is that most of the predation pressure is probably exerted on very young individuals, which are difficult to observe and contribute little to fish stomach contents. Tethering experiments are of no value in addressing this question because they prevent escape responses, such as the cryptic behavior of *D. antillarum* juveniles (Aronson et al. 2001).

The explanation for the low rates of *D. antillarum* recovery may be a combination of the factors mentioned above. As long as recruitment rates remain low, experiments testing the importance of each factor will not be conclusive, both because they need to last for a long time to produce statistically significant results, and because the stochasticity associated with larval recruitment would require extensive replication on a regional scale. Even if per-capita larval production and mortality rates have not changed since the die-offs, the rates of larval settlement and juvenile survivorship have probably always resulted from a combination of low probabilities subject to the vagaries of water circulation, availability of settling sites during the time of larval competence, and proximity of predators during phases of maximum vulnerability. As the apparently haphazard settlement of cohorts on some reefs indicate, various environmental factors need to combine to produce a successful recruitment event, and it may take many such events to cause a measurable population increase. The diminished postmortality larval supply resulting from adult rarity, whether density dependent or not, may have simply caused these stochastic events to become rare, leading to only scattered and modest population increases. A model based on observed recruitment rates and mortality densities of *D. antillarum* at St. John predicted that its postmortality populations are at equilibrium under current values for these parameters (Levitan et al. 2014). An earlier version

of this model (Karlson & Levitan 1990) also predicted that *D. antillarum* populations were not likely to increase, which has proven correct for populations at St. John but not for those at Jamaica, Puerto Rico, and Barbados (Table 1). According to the model of Levitan et al. (2014), recruitment would need to become 25 times higher or mortality 710 times lower than their present values at St. John to restore *D. antillarum* populations to their premortality levels.

CHANGES IN REEF COMMUNITIES IN THE ABSENCE OF *DIADEMA ANTILLARUM*

As has been recently reviewed (Hughes et al. 2010), the demise of *D. antillarum*—along with coral disease and overfishing—has led to phase shifts in Caribbean reefs from coral-dominated to alga-dominated communities. The metadata on algal and coral cover suffer from many of the same problems mentioned above with respect to *D. antillarum* density (Cote et al. 2013, Hughes et al. 2010), but the signal is so strong that it overwhelms the noise. Caribbean-wide coral cover had begun declining and algal cover had begun increasing before the *D. antillarum* die off, with the highest rates occurring in 1980–1981, when white band disease began to infect *Acropora palmata* and *Acropora cervicornis* (Schutte et al. 2010). Over the next two to three years, *D. antillarum* apparently removed a significant portion of the algae, thus reducing competition with adult coral colonies and permitting the recruitment of coral spat. After the *D. antillarum* die-off, standing crops of macroalgae underwent dramatic local increases (Carpenter 1990, de Ruyter van Steveninck & Bak 1986, Hughes 1994, Hughes et al. 1987, Levitan 1988a, Liddel & Ohlhorst 1986). Algal cover peaked in 1986, then declined and remained stable until 2006 (Schutte et al. 2010). That the algal cover suddenly increased when herbivory was reduced while nutrient loading remained steady suggests that algae had been controlled by herbivores (Aronson & Precht 2000, Hughes et al. 1999) rather than by nutrients (Lapointe 1997).

What caused the decline in algal cover after 1986 is not clear, because Caribbean-wide *D. antillarum* population density had not increased by that year (Hughes et al. 2010). Although one species of surgeonfish dramatically increased in density after the *D. antillarum* die-offs in the San Blas Islands (Robertson 1991), herbivorous fishes around the Caribbean have been declining (Paddack et al. 2009). A temporary invasion of Jamaican reefs by the sea urchin *Tripneustes ventricosus* was quickly reversed (Haley & Solandt 2001, Moses & Bonem 2001, Woodley et al. 1999), and other species of sea urchins showed no numerical response (Lessios 1988b, Lessios et al. 1984a). A model by Mumby et al. (2007) designed to determine the degree to which algal cover is resilient or transient showed that parrotfishes became the dominant herbivore after the *D. antillarum* die-off, and that Caribbean reefs are likely to remain covered with algae as long as the combined grazing by sea urchins and parrotfish removes algae from less than 42% of the reef surface every six months.

As *D. antillarum* populations have begun to recover in some areas, patches of bare substrate have formed in an area extending a few meters around its aggregations, where the sea urchins spread during the night to feed. Several Caribbean reefs now have “*Diadema* zones” and “algal zones,” with distinct lines of separation between the two (Carpenter & Edmunds 2006, Edmunds & Carpenter 2001, Furman & Heck 2009, Idjadi et al. 2010). Publications by Idjadi et al. (2010) and Macintyre et al. (2005) include photographs depicting the striking difference between the two areas. More juvenile coral colonies can be found in the *Diadema* zones (Carpenter & Edmunds 2006, Edmunds & Carpenter 2001, Furman & Heck 2009, Myhre & Acevedo-Gutierrez 2006). These colonies have higher survivorship and higher growth rates than colonies in algal zones (Idjadi et al. 2010). If this trend continues and *D. antillarum* densities increase, there is hope of at least a partial recovery of coral cover in Caribbean reefs.

CONCLUSIONS

Although studies conducted before the *D. antillarum* mass mortality attested to its capacity to remove algae and its importance where herbivorous fish were under anthropogenic pressure, full appreciation of the ecological role of this single species of sea urchin developed only after its demise. Even those of us who had worked extensively with *D. antillarum* did not expect that its recovery would be so slow or that its absence would contribute so dramatically to changes in complex ecological communities such as coral reefs. We saw the mass mortality as a grand (although uncontrolled) natural experiment that was more likely to provide ecological information than to cause irreversible changes (see Lessios 1988a,b). To be sure, if Caribbean reefs were pristine, free of coral disease, and not overfished, the absence of *D. antillarum* may have not caused the observed shift from coral to algal domination. Given that the frequency of coral disease will probably increase with global warming and that overfishing can be prevented only in protected areas (which cannot expand indefinitely if people continue obtaining their protein from the sea), the best hope for Caribbean reefs is that *D. antillarum* will recover. We do not yet understand what factors are limiting the expansion of *D. antillarum* populations, and as long as recruitment remains low, it will be difficult to obtain definitive answers. Thus far, the recovery has been slow, but there has been recovery. Increased sea urchin populations have helped coral spat to recruit and survive. This is the only hopeful ray in the gloomy prospects for Caribbean reefs.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

I thank R. Carpenter and P. Edmunds for information on the dates on which they performed their measurements around the Caribbean, and L. Geyer and A. Hiller for comments on the manuscript.

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Errata

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