Coral Reefs (2015) 34:1011–1021
DOI 10.1007/s00338-015-1329-4

REPORT

Using an isolated population boom to explore barriers to recovery in the keystone Caribbean coral reef herbivore *Diadema antillarum*

Max D. V. Bodmer[1,2] · **Alex D. Rogers**[2] · **Martin R. Speight**[2] · **Natalie Lubbock**[1,3] · **Dan A. Exton**[1]

Received: 15 December 2014 / Accepted: 16 July 2015 / Published online: 2 August 2015

Abstract Recovery of the keystone herbivore *Diadema antillarum* after the 1983–1984 mass mortality event poses one of the greatest challenges to Caribbean coral reef conservation, yet our understanding of the problem remains severely limited. Whilst some recovery has been observed, this has been restricted to the shallows ($\leq$5 m). We report a newly discovered, isolated population recovery on Banco Capiro, Honduras, representing the largest recorded post-mortality densities beyond the shallowest environments (0.74–2.27 individuals m^{-2} at depths $\geq$10 m) alongside an unusually high mean percentage scleractinian coral cover of 49–62 %, likely no coincidence. On the nearby island of Utila, we report *D. antillarum* densities of 0.003–0.012 individuals m^{-2} and scleractinian coral cover of 12 % at depths $\geq$10 m, "typical" for a contemporary Caribbean coral reef. The three order of magnitude disparity in population density between sites separated by <60 km presents a unique opportunity to investigate barriers preventing their region-wide recovery by simultaneously addressing a range of previously proposed hypotheses. Despite concerns over the impacts of asynchronous spawning in low-density populations, we find that recruitment is occurring on Utila. This suggests that, whilst Allee effects are likely to be a contributing factor, the major barriers suppressing recovery are instead impacting juvenile survival into adulthood. Similarly, variations in heterospecific echinoids, interspecific competitors, and nutrient availability fail to account for population differences. Instead, we highlight a lack of structural complexity on contemporary Caribbean reefs as the most likely explanation for the limited recovery through a lack of provision of juvenile predation refugia, representing a further consequence of the recent ubiquitous phase shifts throughout the region. Using these findings, we propose future management strategies to stimulate recovery and, consequently, reef health throughout the Caribbean.

Keywords *Diadema antillarum* · Caribbean · Coral reef · Herbivory · Urchin · Phase shift

Introduction

The long-spined sea urchin, *Diadema antillarum*, is a prolific macroalgal grazer (Ogden and Lobel 1978) and as such is a keystone species for the maintenance of Caribbean coral reef health. In the early 1980s, an unknown water-borne pathogen led to an average region-wide population reduction in 95–99 % (Bak et al. 1984; Hughes et al. 1985; Lessios 1988; Levitan 1988a; Carpenter 1990; Betchel et al. 2006), and the devastating ecological consequences of this mass die-off are still apparent today. At high densities, *D. antillarum* consumes the entire daily net primary productivity of the reef through grazing on non-crustose macroalgal recruits (Carpenter 1984). This biases the outcome of space competition in favour of scleractinian corals (Liddell and Ohlhorst 1986; Macia et al. 2007), which in turn provide valuable ecospace through the

---

Communicated by Biology Editor Prof. Brian Helmuth

✉ Dan A. Exton
dan.exton@opwall.com

[1] Operation Wallacea, Wallace House, Old Bolingbroke, Spilsby, Lincolnshire PE23 4EX, UK

[2] Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

[3] Department of Applied Science, University of South Wales, Glyntaff Campus, Pontypridd, Rhondda Cynon Taff CF37 4BE, Wales, UK

creation of highly structured 3-D environments (Hoegh-Guldberg et al. 2007).

The *Diadema* pathogen was first detected in Panama in mid-January 1983, spreading on prevailing currents to infect the entire Caribbean within 12 months (Lessios et al. 1984). Within 4 months of disease outbreak in Discovery Bay, Jamaica, percentage cover of non-crustose macroalgae increased from 30.7 to 72.3 %, at the expense of scleractinian cover (Liddell and Ohlhorst 1986). Removal experiments conducted prior to disease outbreak had already demonstrated macroalgal biomass increases of up to 20 %, and a 37 % net decrease in total ecosystem primary productivity, within just 5 d of *D. antillarum* loss (Ogden and Lobel 1978). These impacts diminish net energy availability in the ecosystem and reduce biodiversity and ecosystem function and are congruent with Carpenter's (1988) finding that urchin-grazed reefs support a higher total species richness than those grazed by fish alone. Studies have subsequently shown that urchin-grazed reefs have up to 10.3 times as many juvenile coral recruits as those where urchins are absent (Carpenter and Edmunds 2006). It is therefore widely believed that the mass mortality event has been a key driver of the ubiquitous phase shifts that currently plague Caribbean reefs (Macia et al. 2007).

To date, recovery from the 1983 to 1984 mass mortality has been extremely poor. Although some instances of recovery are reported, population densities remain low relative to pre-mortality levels, and these examples of recovery represent a small return on such large-scale loss. Most studies showing "recovered" populations have at least an order of magnitude lower density than prior to the mortality event (Chiappone et al. 2001; Edmunds and Carpenter 2001; Weil et al. 2005; Debrot and Nagelkerken 2006; Bologna et al. 2012). The most significantly recovered populations have maximum densities of 1.7–8.9 m^{-2} (Carpenter and Edmunds 2006) and 16 m^{-2} (Lacey et al. 2013), but these studies only survey shallow reefs (<6 m) and report absolute maximum values rather than local averages. To the authors' knowledge, there have been no reports of significant *D. antillarum* population recovery occurring beyond the shallows consistently across a reef system.

Researchers have proposed numerous mechanisms that could account for the lack of *D. antillarum* population recovery, but we are still far from having a holistic understanding of the problem. The most recent modelling study highlights the need for a shift in the balance between mortality and recruitment, estimating that either a 25 times increase in recruitment or a two order of magnitude decrease in mortality is required to achieve pre-mortality densities across a large spatial scale (Levitan et al. 2014). However, barriers preventing this necessary shift from occurring are not understood, and we are instead restricted to a handful of independent hypotheses, in particular (1) suppressed recruitment resulting from natural asynchronous spawning behaviour, (2) increased competition from vertebrate reef herbivores, (3) predation pressure driving high mortality, (4) ecological interactions with heterospecific echinoids, and (5) loss of structural complexity removing microhabitat provision.

The asynchronous spawning behaviour of *D. antillarum* (Levitan 1988b, 1991; Levitan et al. 2014) means that only 5 % of a population will release their gametes at any one time (Iliffe and Pearse 1982). Naturally high population densities ensure fertilisation success, but mass mortality not only has reduced the density of individuals, and thus the probability of multiple individuals spawning simultaneously, but also has increased average nearest-neighbour distances, meaning that ejaculates are diluted in the water column and fertilisation success is significantly reduced (depensation; Pennington 1985).

It has been suggested that a post-mortality increase in herbivorous fish has increased interspecific competition with *D. antillarum* (Robertson 1991). This hypothesis is supported by data from Panama, where populations of herbivorous surgeonfish species increased by 0–250 % after mass mortality (Robertson 1991). It is important to note that, whilst herbivorous fishes and *D. antillarum* remove similar amounts of macroalgae, fish maintain a much higher level of standing algal biomass (Carpenter 2005), suggesting that *D. antillarum* ecosystem services are irreplaceable. It has also been suggested that the adoption of more generalist feeding strategies by predators of *D. antillarum* as a response to the mass mortality event could have maintained predator abundances at levels that now suppress recovery (Carpenter 1984; Robertson 1987; Miller et al. 2007).

The echinoid, *Tripneustes ventricosus,* removes unpalatable mature macroalgae and clears substrata for the recruitment of juvenile macroalgae, which is the preferred food source of *D. antillarum* (Haley and Solandt 2001; Betchel et al. 2006). Another hypothesis therefore proposes that the increase in mature macroalgae since the *D. antillarum* mortality event exceeds the grazing ability of *T. ventricosus* that in turn suppresses their abundance and subsequently reduces nutrient availability for *D. antillarum* (Liddell and Ohlhorst 1986; Carpenter 2005; Macia et al. 2007).

Diadema antillarum and *Echinometra viridis*, another echinoid species, behave aggressively towards one another (Shulman 1990), and, as such, their population sizes have been found to be negatively correlated (Williams 1981). It is therefore possible that competitive release following the mass mortality of *D. antillarum* facilitated increases in *E. viridis* populations that now act to suppress their competitors. However, it appears that there was no increase in *E. viridis* populations after the *D. antillarum* mass die-off (McClanahan 1999), and Lessios (1995) even found evidence to suggest that *E. viridis* actually facilitates *D. antillarum* recruitment because, similarly to *T. ventricosus*, they remove macroalgae and provide suitable larval settlement surfaces.

Calcium carbonate skeletons laid down by reef building scleractinian corals are essential for provision of 3-D complexity and living space (Alvarez-Filip et al. 2009). *D. antillarum* facilitate stony coral domination and therefore promote habitat structure (Lee 2006; Myhre and Acevedo-Gutierrez 2007; Ruiz-Ramos et al. 2011), which in turn provides juvenile urchins with predation refugia. It is therefore possible that the reduction in scleractinian coral cover that accompanied the loss of *D. antillarum* has created a negative feedback loop that is hampering urchin recovery (Lacey et al. 2013).

After a 30-yr period of relative stasis, *D. antillarum* populations throughout the Caribbean are still struggling to recover. A summary of contemporary population densities (Fig. 1), based on a combination of data from this study and Atlantic and Gulf Rapid Reef Assessment (AGRRA) surveys (www.agrra.org), clearly demonstrates not only continued regional suppression, but highlights an isolated population boom that was previously unknown. We use this newly discovered reef system of Banco Capiro, off the north coast of Honduras, as a model "recovered"

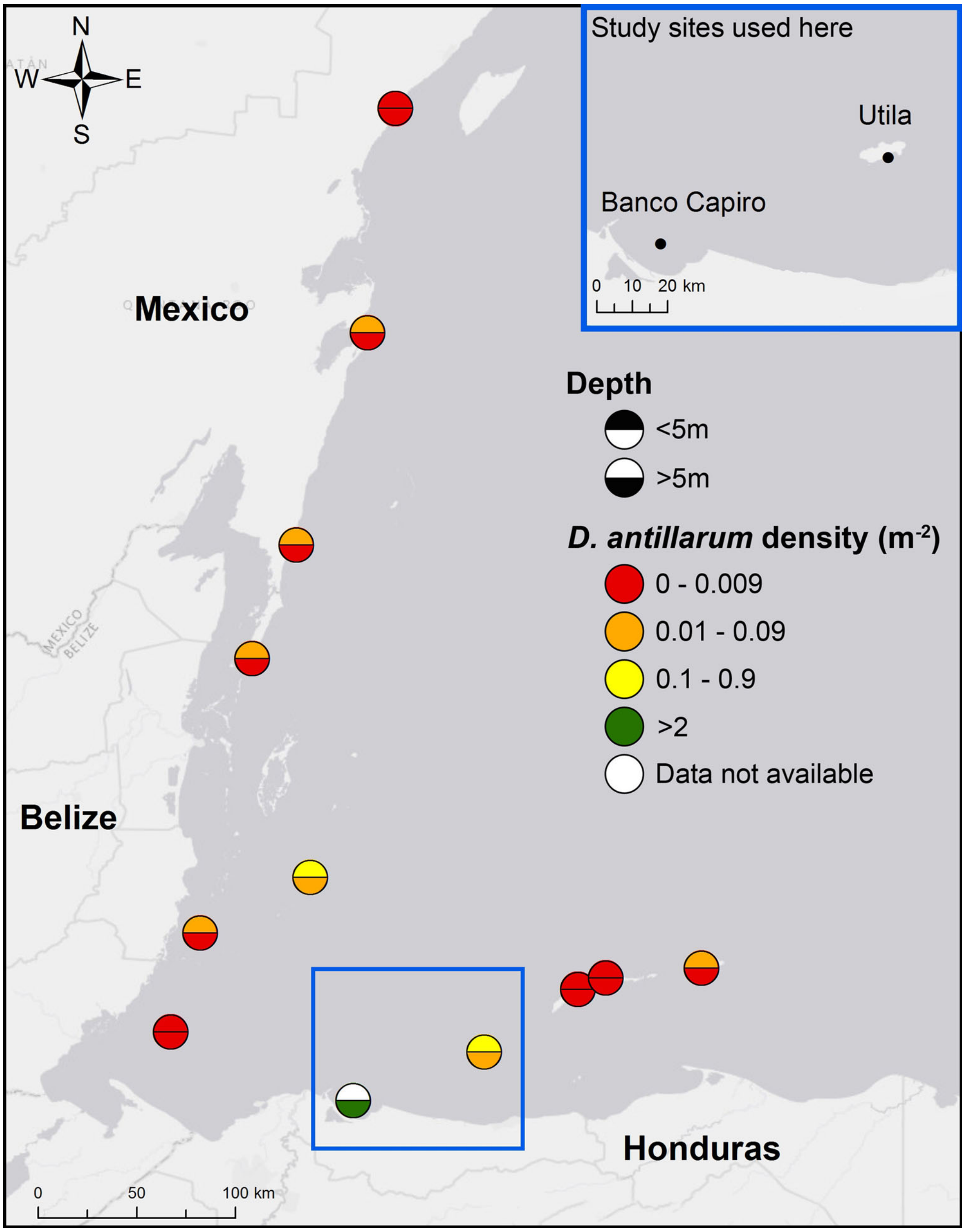

Fig. 1 Status of *Diadema antillarum* population densities throughout the Mesoamerican Barrier Reef system in shallow (<5 m) and deep (>5 m) coral reef environments. Data for Banco Capiro and Utila (Honduras 2014) and Akumal (Mexico 2013) were collected as part of this study. All other data shown are open access sourced from Atlantic and Gulf Rapid Reef Assessment (AGRRA, http://agrra.org) surveys conducted by Healthy Reefs Initiative (HRI, http://healthyreefs.org), using randomly placed 10-m × 1-m belt transects ($n = 6$ per depth and site) completed by SCUBA divers. *Note* that shallow data are not available for Banco Capiro due to the deep offshore topography of the site. *Insert* shows the location of study sites used in this study to address barriers to *D. antillarum* recovery

population to explore the barriers preventing large-scale recovery of *D. antillarum*. We compare Banco Capiro to a "typical" Caribbean reef system on the nearby island of Utila, where *D. antillarum* densities and scleractinian coral cover are in line with expectations for a contemporary Caribbean reef. Large disparities between these two populations, only 60 km apart, suggest that fundamental differences exist between the systems, and we use this unique comparison to explore previously proposed barriers to *D. antillarum* recovery. A combination of assessment techniques is used to explore echinoid population dynamics, biotic and abiotic benthic variables, and a quantification of predation and competition, and to systematically address the mechanisms behind the continued widespread suppression of *D. antillarum* populations. Our findings are used to suggest potential conservation management strategies that may help focus restoration efforts throughout the Caribbean.

Materials and methods

Study sites

Data were collected at Banco Capiro and Utila, Honduras, which are located at the southern end of the Mesoamerican Barrier Reef (MABR). Banco Capiro is a newly discovered reef system located approximately 8 km offshore in the mainland bay of Tela. Initial observations reported that both scleractinian coral cover and *D. antillarum* population densities are unusually high for a contemporary Caribbean reef. Three sub-sites were selected within this previously unstudied system to represent as large a geographical range as possible: Kisci's Garden (15°51′55.48″N 87°30′0.68″W), Pinnacle (15°51′50.90″N 87°30′21.02″W), and The Fingers (15°51′48.71″N 87°29′42.90″W).

Utila was chosen to represent a "typical" modern Caribbean coral reef (Fig. 1) as preliminary observations indicated relatively poor ecosystem health and low *D. antillarum* density, whilst its close proximity to Banco Capiro (ca. 60 km) minimised geographical factors affecting the accuracy of comparisons. Three sub-sites were selected along Utila's more accessible southern shore; Sturch Bank (16°05′19.00″N 86°53′46.46″W), Coral View (16°05′17.96″N 86°54′38.27″W), and Black Coral Wall (16°04′58.35″N 86°55′02.34″W) (Fig. 1).

In situ ecological surveys

All data were collected over two nine-week field seasons (June–August 2013 and 2014) using SCUBA along 50-m transects. The distribution of *D. antillarum* is known to vary with depth (Lessios 1988; Debrot and Nagelkerken 2006), so survey transects were carried out in triplicate at two depths, 10 and 15 m. Additional study depths of 2 and 5 m were surveyed on Utila, but not on Banco Capiro due to the site's naturally deep offshore topography. A haphazardly selected compass bearing was followed for 20 m from the base of the fixed mooring lines. The start of the transect line was then haphazardly placed on the reef whilst avoiding unnecessary damage to the substratum. This protocol was used to avoid pseudoreplication and to ensure that, within our logistical constraints, the largest possible area of each sub-site was surveyed to mitigate any bias associated with the aggregating behaviour of *D. antillarum*.

Echinoid population status and D. antillarum morphometrics

In both 2013 and 2014, belt transects of 2-m width were used, and all *D. antillarum* found within the survey area were recorded and life stage noted; juveniles have a test diameter of <20 mm (Levitan et al. 2014) and white bands on their spines (Randall et al. 1964). The abundances of *Echinometra viridis* (reef urchin) and *T. ventricosus* (West-Indian sea-egg) were also recorded.

Benthic community assessment

Benthic communities were assessed using the line-point-intercept method via underwater videography (GoPro Hero 3, 1080 HD, 60 frames s^{-1}) with data points taken at 25-cm intervals. These data were used to determine (1) percentage cover of live scleractinian coral as a proxy for reef health and (2) percentage cover of mature macroalgae. Habitat assessment scores (HAS) were also recorded four times along each transect following the protocol of Gratwicke and Speight (2005). In addition, abundances of juvenile coral recruits were noted along the 2-m-wide belt transects described earlier for echinoid surveys. A coral recruit is defined as a colony <4 cm across its longest dimension (Edmunds and Carpenter 2001).

Population abundance of selected fish families

To investigate the impact of predation and competitive herbivory on population recovery, the abundances of key fish families known to interact with *D. antillarum* were recorded using 5-m × 5-m underwater visual census (UVC) belt transects (Samoilys and Carlos 2000). Specifically, abundance data were collected for known *D. antillarum* predators; Ballistidae, Haemulidae, and Labridae, and interspecific competitors; Acanthuridae, Scaridae, Chaetodontidae, and Pomacentridae. Chaetodontidae is considered as a competitor of *D. antillarum* because both are corallivores (Bak and van Eys 1975).

Statistical analyses

Preliminary analysis of within-site variation indicated no significant differences in any variable measured, thus allowing sub-site data to be pooled leaving $n = 9$ for each depth. All data pertaining to the ecological variables of interest (echinoid abundances, predation, competition, nutrient limitation, and HAS) were non-normally distributed; therefore, a series of Kruskal–Wallis tests were conducted to investigate the differences in all factors between sites and depths, as well as between years. Data could not be transformed to normality and so relationships between each variable and *D. antillarum* population size were tested using generalised linear models (GLMs) that accounted for site and depth as potentially confounding variables. GLMs were performed using Poisson ANCOVA, with *D. antillarum* as the continuous response variable, ecological variables of interest as continuous explanatory variables, and site/depth as discrete explanatory variables. Poisson ANCOVAs were also used to investigate the relationship between *D. antillarum* population size and three proxies of their ecological functions (juvenile coral recruitment, scleractinian coral cover, and macroalgal cover) to confirm that they provide the same key services on these reefs as is documented elsewhere in the literature.

Results

Diadema antillarum population structure

Diadema antillarum population densities on Banco Capiro in 2014 were 225.67 ± 26.06 100 m^{-2} (mean ± 1 SE) and 73.56 ± 19.11 100 m^{-2} at 10 m and 15 m, respectively. This was up to three orders of magnitude higher than on Utila, where densities were 1.22 ± 0.43 and 0.33 ± 0.17 100 m^{-2} at the same depths (10 m: $H_1 = 12.95$, $p < 0.001$; 15 m: $H_1 = 13.340$, $p < 0.001$). At 10 m on Banco Capiro, *D. antillarum* population density increased by >50 % between 2013 (146.89 ± 16.96 100 m^{-2}) and 2014 ($H_1 = 4.31$, $p < 0.05$), whilst all other depths and sites showed no significant change between years. Mean *D. antillarum* densities were 17.00 ± 8.09 and 3.33 ± 0.55 at 2 and 5 m, respectively, on Utila (Fig. 2).

Our reports of observed high population densities on Banco Capiro are supported by surveys conducted by the Atlantic Gulf Rapid Reef Assessment (AGRRA) in May 2011 (unpublished), which recorded mean *D. antillarum* densities ($n = 7$) of 156 ± 82 individuals 100 m^{-2}. To further confirm our assumption that high *D. antillarum* population densities are a homogeneous characteristic across the Banco Capiro reef system, both temporally and spatially, we conducted surveys at two additional sub-sites in 2014 (Mushroom Mountain: 15°86′49.70″N 87°49′73.10″W; Rotonda: 15°86′56.10″N 87°50′68.00″W), recording mean densities of 178.00 ± 38.74 and 224 ± 25.54 individuals 100 m^{-2}, respectively, at 10 m depth. By demonstrating similarly high densities in three different survey years (2011, 2013, and 2014), two different seasons (spring and summer), and across the geographical extent of Banco Capiro, we are confident that our results represent the true status of *D. antillarum* populations and are not simply a temporary phenomenon or an artefact of survey technique.

With all study depths combined (due to low sample size availability on Utila), the proportion of juveniles within *D. antillarum* populations was 22-fold higher on Utila than Banco Capiro ($H_1 = 16.37$, $p < 0.001$). On Utila, 71.87 ± 5.77 % of all surveyed *D. antillarum* were juvenile ($n = 197$), compared to just 3.35 ± 0.90 % on Banco Capiro ($n = 4541$). The proportion of juveniles did not significantly differ between depths. However, the number

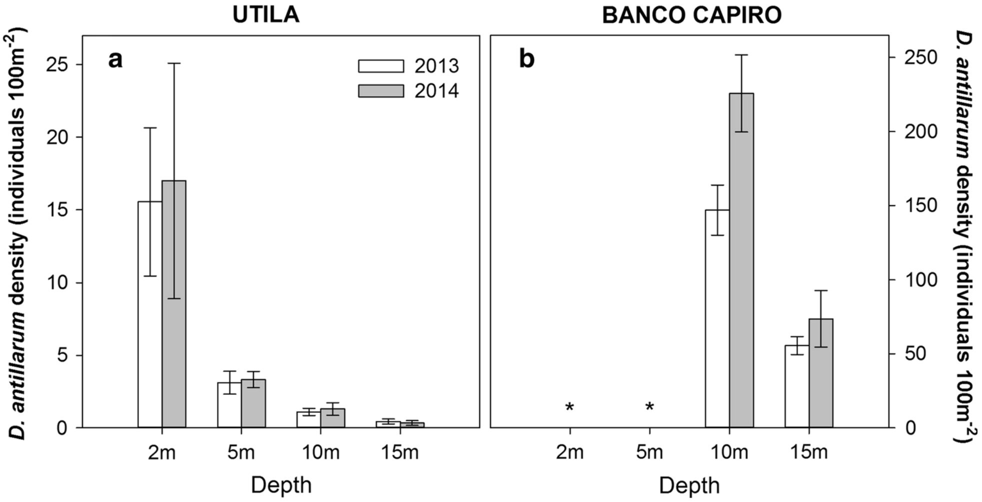

Fig. 2 Population densities of *Diadema antillarum* at varying depths on the reef systems of **a** Utila and **b** Banco Capiro, including temporal variations between 2013 and 2014. Data shown are mean values ± SE ($n = 9$) and were collected during June–August each year using 50-m × 2-m belt transects. *Asterisk* Data for 2 and 5 m on Banco Capiro were unavailable due to the deep offshore topography of the site

of juvenile *D. antillarum* 100 m^{-2} was nearly 150 % greater on Banco Capiro (5.10 ± 1.15 100 m^{-2}) than Utila (2.03 ± 0.36 100 m^{-2}; $H_1 = 4.26$, $p < 0.05$; Fig. 3).

Investigating ecological function

There was a significant positive relationship between the density of juvenile coral recruits and *D. antillarum* population density, after controlling for the effects of site and depth ($F_1 = 27.49$, $p < 0.001$). Coral recruit density on Utila was 28.89 ± 2.96 and 23.22 ± 3.14 100 m^{-2} at 10 and 15 m, respectively, an order of magnitude lower than the 343.89 ± 23.53 and 185.89 ± 13.84 100 m^{-2} observed at the same depths on Banco Capiro (10 m: $H_1 = 12.80$, $p < 0.001$; 15 m: $H_1 = 12.80$, $p < 0.001$; Table 1). Alongside the significant increase in *D. antillarum* population density at 10 m on Banco Capiro between 2013 and 2014, there was also an increase in juvenile coral recruitment at both 10 m and 15 m (10 m: $H_1 = 12.80$, $p < 0.001$; 15 m: $H_1 = 12.79$, $p < 0.001$). On Utila, the abundance of juvenile coral recruits did not change significantly between 2013 and 2014.

Scleractinian coral cover on Utila was 12.17 ± 2.04 and 12.00 ± 1.73 % at 10 and 15 m, respectively, whilst cover on Banco Capiro was up to six times greater with values of 62.17 ± 6.61 and 48.72 ± 2.93 % at the same depths (10 m: $H_1 = 12.82$, $p < 0.001$; 15 m: $H_1 = 12.82$, $p < 0.001$; Table 1). There was a significant positive relationship between *D. antillarum* population density and percentage cover of scleractinian coral after controlling for depth ($F_1 = 4.16$, $p < 0.05$) although this relationship varies slightly between sites ($F_1 = 4.07$, $p < 0.05$).

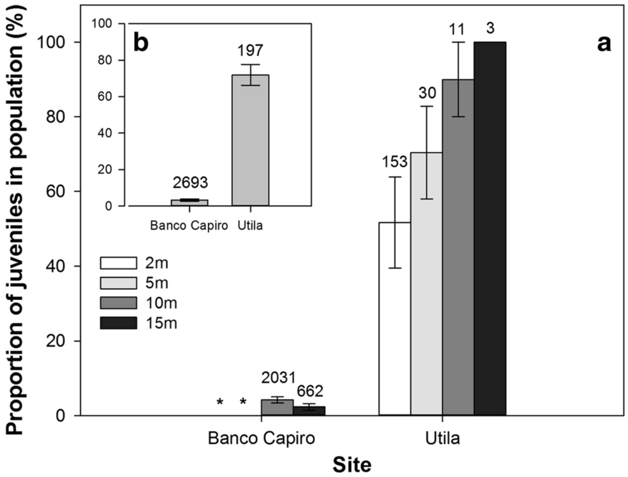

Fig. 3 Proportion of juveniles within the overall *Diadema antillarum* population on the contrasting reef systems of Utila and Banco Capiro, shown **(a)** at individual study depths and **(b)** as a proportion of the total site population across depths. Data shown are mean ± SE, and the total population size used to calculate proportions (*n*) are shown above each *bar*

Mature macroalgal cover was up to 6.6 times greater at Utila (41.06 ± 3.55 and 46.72 ± 4.62 % at 10 and 15 m, respectively) than Banco Capiro (7.06 ± 1.46 and 23.06 ± 2.89 %; 10 m: $H_1 = 12.80$, $p < 0.001$; 15 m: $H_1 = 12.18$, $p < 0.001$; Table 1). In line with expectation, mature macroalgal cover decreased with an increase in *D. antillarum* population density on both Utila and Banco Capiro when controlled for site and depth ($F_1 = 17.69$, $p < 0.001$).

Barriers preventing population recovery

No significant difference was found between the abundance of fish predators of *D. antillarum* on Utila (21.44 ± 5.52 and 6.11 ± 2.16 250 m^{-2} at 10 and 15 m, respectively) and Banco Capiro (18.89 ± 6.74 and 9.11 ± 3.03 250 m^{-2}; Table 1). There was also no significant relationship between predator abundance and *D. antillarum* population densities. Likewise, the abundance of herbivorous fish did not differ significantly between Utila and Banco Capiro at either depth. The mean abundance of herbivorous fish on Banco Capiro was 78.11 ± 6.96 and 53.11 ± 5.51 250 m^{-2} at 10 and 15 m, respectively, and 61.00 ± 6.05 and 51 ± 12.22 250 m^{-2} on Utila (Table 1). There was no relationship between herbivorous fish abundance and *D. antillarum* population size.

There was also no significant difference in the population density of *E. viridis* between Utila (69.56 ± 32.60 and 15.22 ± 9.13 100 m^{-2} at 10 and 15 m, respectively) and Banco Capiro (67.89 ± 21.74 and 4.22 ± 2.46 100 m^{-2}; Table 1). Population densities of *E. viridis* and *D. antillarum* showed no significant relationship. However, when Utila was analysed independently, incorporating data from 2 and 5 m, a significant positive relationship was observed between populations of these two echinoid species ($F_1 = 16.47$, $p < 0.001$). *T. ventricosus* were found to be present on the reefs of Utila, albeit at low population densities (0.11–2.11 individuals 100 m^{-2}), whereas the species appeared to be entirely absent from Banco Capiro (Table 1).

HAS values on Banco Capiro were 19.00 ± 0.62 at 10 m and 18.33 ± 0.66 at 15 m, which were approximately 25 % greater than the 13.39 ± 0.84 and 13.36 ± 0.70 recorded at Utila (10 m: $H_1 = 12.49$, $p < 0.001$; 15 m: $H_1 = 11.61$, $p < 0.001$; Table 1). In the full Poisson ANCOVA model, no relationship between HAS and *D. antillarum* population densities was detected. However, when Utila was analysed in isolation across all four depths, there was a positive relationship between *D. antillarum* population size and HAS ($F_1 = 22.34$, $p < 0.05$).

Temporally, mature macroalgal cover increased between 2013 and 2014 at both Utila (10 m: $H_1 = 11.56$, $p < 0.001$; 15 m: $H_1 = 10.41$, $p < 0.01$) and Banco Capiro

Table 1 Echinoid population and broad ecosystem parameters at multiple depths on two highly contrasting Honduran coral reef systems: Utila (representing a typical contemporary Caribbean reef) and Banco Capiro (a unique example of isolated *Diadema antillarum* recovery)

Ecological variable	Utila				Banco Capiro		*p* values for differences in means between sites	
	2 m	5 m	10 m	15 m	10 m	15 m	10 m	15 m
D. antillarum population density (100 m^{-2})	17.00 ± 8.09^{a}	3.33 ± 0.55^{ab}	1.22 ± 0.43^{bc}	0.33 ± 0.17^{c}	255.67 ± 26.06^{d}	73.56 ± 19.11^{e}	<0.001	<0.001
D. antillarum biomass (100 m^{-2})	1429.7 ± 680.78^{a}	280.33 ± 46.49^{ab}	102.79 ± 36.49^{bc}	28.03 ± 14.01^{c}	17724.0 ± 2046.90^{d}	5777.10 ± 1500.10^{e}	<0.001	<0.001
Hard coral cover (%)	19.83 ± 1.51^{a}	22.55 ± 2.96^{a}	12.17 ± 2.04^{ab}	12.00 ± 1.73^{b}	62.17 ± 6.61^{c}	48.72 ± 2.93^{d}	<0.001	<0.001
Macroalgal cover (%)	33.78 ± 2.51^{a}	36.00 ± 5.56^{a}	41.06 ± 3.55^{a}	46.72 ± 4.62^{a}	7.06 ± 1.46^{b}	23.06 ± 2.89^{c}	<0.001	<0.0001
Predatory fish abundance (250 m^{-2})	35.78 ± 9.11^{a}	9.11 ± 4.12^{ab}	18.89 ± 6.74^{ab}	9.11 ± 3.03^{ab}	21.44 ± 5.52^{a}	6.11 ± 2.16^{b}	0.310	0.449
Herbivorous fish abundance (250 m^{-2})	102.89 ± 11.34^{a}	93.89 ± 11.34^{a}	61.00 ± 6.05^{ab}	51.56 ± 12.22^{ab}	78.11 ± 6.96^{a}	53.11 ± 5.51^{b}	0.078	0.507
Juvenile coral recruit density (100 m^{-2})	14.78 ± 0.74^{a}	14.89 ± 0.74^{a}	28.89 ± 2.96^{a}	23.33 ± 3.14^{a}	343.89 ± 23.53^{b}	185.89 ± 13.84^{c}	<0.001	<0.001
Habitat Assessment Score (HAS)	14.78 ± 0.74^{a}	14.89 ± 0.74^{a}	13.39 ± 0.84^{a}	13.36 ± 0.70^{a}	19.00 ± 0.62^{b}	18.33 ± 0.66^{b}	<0.001	<0.001
E. viridis abundance (100 m^{-2})	308.89 ± 117.95^{a}	101.22 ± 39.50^{a}	69.56 ± 32.60^{ab}	15.22 ± 9.13^{b}	67.89 ± 21.74^{ab}	4.22 ± 2.46^{c}	0.216	0.528
T. ventricosus abundance (100 m^{-2})	2.11 ± 0.68^{a}	1.11 ± 0.32^{ab}	0.00 ± 0.00^{ab}	0.11 ± 0.11^{b}	0.00 ± 0.00^{ab}	0.00 ± 0.00^{ab}	0.145	0.317
Proportion of juveniles in *D. antillarum* population (%)[a]	71.87 ± 5.77^{a}				3.25 ± 0.90^{b}		<0.001	

Data shown are mean values ± SE ($n = 9$) and were collected during June–August 2014. Data for 2 m and 5 m on Banco Capiro were unavailable due to the deep offshore topography of the site. Superscript letters denote results of Steel–Dwass test (a nonparametric pairwise comparison) used because of non-normality of the distribution of all ecological variables. If the letters are the same, there is no difference in the mean value of the variable between the corresponding depths/sites

[a] Data pooled across depths at each site due to the small sample size available on Utila

(10 m: $H_1 = 8.04$, $p < 0.01$; 15 m: $H_1 = 10.99$, $p < 0.001$; Table 1).

Discussion

Banco Capiro represents a unique contemporary reef system

Despite their close proximity, Utila and Banco Capiro have very different *D. antillarum* population densities, clearly demonstrating continued suppression of populations on Utila and augmentation of populations on Banco Capiro. Banco Capiro represents the highest reported post-mortality population density beyond the shallowest reef environments anywhere in the Caribbean. Crucially, our data also show that *D. antillarum* is fulfilling its expected role as a keystone species on both of these reef systems through a clear positive relationship between population density and both live scleractinian coral cover and juvenile coral recruit density, coupled with a negative relationship with macroalgal cover.

There are no pre-mortality data available for Honduran reefs, and it is therefore possible that the *D. antillarum* populations of Banco Capiro were never impacted by the Caribbean-wide mass mortality. However, given the ubiquity of the disease throughout the region, coupled with the fact that Banco Capiro is located just 60 km away from Utila, where the low urchin densities allow us to assume that populations were impacted, it is highly likely that Banco Capiro was also left affected by the mass die-off.

Banco Capiro boasts a scleractinian coral cover of 48–62 %, impressive in a region where averages are estimated to be as low as <10 % (Gardner et al. 2003). The current dominance of corals of the genera *Agaricia* and *Undaria*, coupled with the increase in juvenile coral recruitment, suggests that Banco Capiro is a reef system that is either (1) newly emerging, or (2) in the process of regeneration. *Agaricia* spp. and *Undaria* spp. are opportunistic plate corals with high reproductive outputs that recruit easily, meaning that they are often pioneers in the establishment of new reefs (Darling et al. 2012).

Although urchin populations on Banco Capiro increased over the last 2 yr, macroalgal abundance has also increased. This finding is not unprecedented as it mirrors the findings of a recent study in Puerto Rico, where the extent of macroalgal coverage was found to be uncorrelated with *D. antillarum* population size (Ruiz-Ramos et al. 2011). This result highlights the multifaceted nature of threats to coral reef ecosystems and shows that restoration of *D. antillarum* populations alone is unlikely to cause wholesale phase-shift reversal. However, augmentation of *Diadema* populations and reintroduction of their associated ecosystem services may help to buy time to elucidate and mitigate other threats to coral reefs.

It is likely that recent increases in scleractinian coral cover, juvenile coral recruitment, and *D. antillarum* population size have all occurred concurrently and that a positive feedback loop has been established. The significant increases in *D. antillarum* population size and juvenile coral recruit abundance that occurred on Banco Capiro between 2013 and 2014 support this assertion. However, initiation of this positive feedback loop likely relies on Banco Capiro's release from a historical barrier to *D. antillarum* recovery, initiating a population threshold to be exceeded that reinstates their ecosystem services. This barrier is likely to be related either to reproduction/recruitment dynamics, or to a change in the level of one or more ecological variables that have historically been suppressing population recovery.

Barriers preventing widespread population recovery

The spawning behaviour of, and volume of gametes produced by, *D. antillarum* before and after the mass mortality event were similar (Lessios 1988), and experimental manipulations of *Strongylocentrotus droebachiensis* have demonstrated that when spawning adult sea urchins are separated by more than 2 m there is little chance of fertilisation success (Pennington 1985). Lessios (1988) therefore postulated that the observed lack of post-mortality juvenile recruitment might occur, not because of changes in reproductive dynamics, but because of gamete dilution caused by post-mortality increases in nearest-neighbour distance.

Despite the fact that the adult population is nearly 190 times greater on Banco Capiro than on Utila, the density of juvenile *D. antillarum* is only 150 % higher. This indicates that the rate of recruitment per individual is higher on Utila than on Banco Capiro. Whilst a potentially low level of juvenile *D. antillarum* recruitment on Utila is undoubtedly contributing to slow rates of population recovery, these data indicate the presence of a major ecological barrier that is suppressing recovery by operating to prevent juvenile survival into adulthood.

The time taken for juveniles to reach maturity is estimated to be roughly 12 months (Ogden and Carpenter 1987). However, despite the fact that in 2013 45 % of the Utilan *D. antillarum* population was juvenile, there was no significant increase in adult population size between 2013 and 2014. This fact, coupled with the observation that the proportion of juvenile *D. antillarum* in the Utilan population increased from 45 to 72 % between 2013 and 2014, indicates that at least low-level recruitment is occurring around Utila and that the resultant juvenile recruits are not surviving into adulthood.

On Utila, there is a positive relationship between *E. viridis* and *D. antillarum* population densities that does not exist on Banco Capiro. This fact, coupled with the observation that *T. ventricosus* is entirely absent from Banco Capiro, suggests that Tela Bay might be a successional stage ahead of Utila or on a different ecosystem trajectory. In the initial stages of population recovery, a positive relationship between *D. antillarum* and both *E. viridis* and *T. ventricosus*, as seen on Utila, is expected as their generalist feeding habits clear areas of substratum for recruitment of palatable food resources for *D. antillarum* (Haley and Solandt 2001).

Competition from herbivorous fish fails to explain patterns of *D. antillarum* densities. Currently, densities of neither *D. antillarum* nor herbivorous fishes are sufficient for shared food resources to be a limiting factor. However, as *D. antillarum* (and fisheries) continue to recover on Banco Capiro competition will likely, at least partially, begin to regulate populations. With recently introduced fishing restrictions in Tela Bay, and improvements in fisheries management on Utila, the relationships between *D. antillarum* population and levels of competitive herbivory may change over time.

Banco Capiro is significantly more structurally complex than Utila, but HAS only relates positively to *D. antillarum* density on Utila. This can be explained by the fact that Banco Capiro is highly homogeneous with lower variation in HAS than Utila, meaning that a significant relationship could be masked. Several studies highlight the importance of structural complexity for numerous echinoid species for the facilitation of juvenile survival through the provisioning of shelter from predation (e.g., Andrew 1993; Hereu et al. 2005; Scheibling and Robinson 2008). Shelter enables urchins to develop until their test diameter is large enough to avoid predation when not hidden (Scheibling and Robinson 2008). Whilst our results indicate that predator abundance is not suppressing populations on Utila, observations of hiding behaviour on our study sites suggest that urchins are reliant on shelter provided by the reef architecture as a key component of their ecology (Fig. 4).

The lack of relationship between *D. antillarum* and the abundance of predators on Banco Capiro may be elucidated by three, non-mutually exclusive, explanations: (1) the system is structurally complex enough that microhabitat availability still outweighs demand, meaning that predator avoidance is effective across the system; (2) other predators not accounted for in this study (e.g., *Panulirus argus*; spiny lobster) may effect *D. antillarum* population densities and explain the timid behaviour of the urchins, and/or (3) there is a high proportion of juvenile urchins in Utila compared to adults, suggesting that predation is acting on the population at this developmental stage, reducing numbers of mature individuals. If *D. antillarum* are most vulnerable to predation at this stage of their life history, it is possible that there is a link between habitat complexity and the provision of refugia from predation. Observations indicate that there is a positive relationship between *D. antillarum* population size and HAS on Utila. The low structural complexity of Utila's reefs may create a dearth of appropriate hiding places required by juveniles to develop test diameters that exceed the predation escape threshold.

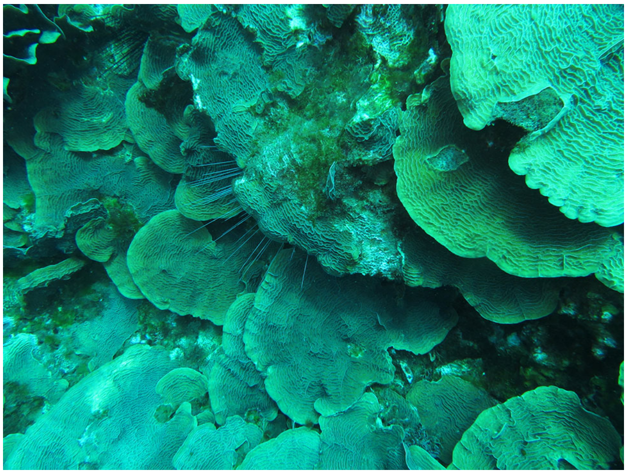

Fig. 4 Photograph of adult *Diadema antillarum* exhibiting hiding behaviour on Banco Capiro by seeking shelter within a shelf created by a plate coral. This behaviour was commonly observed during data collection at this site

Although AGRRA data used to create Fig. 1 do not include a specific measure of habitat complexity (e.g., HAS), percentage cover of scleractinian coral can be used as a proxy for 3-D structure because of the strong positive relationship that exists between these two variables (Lee 2006). All sites with *D. antillarum* population densities <1 individual m^{-2} represented in Fig. 1 (i.e., all sites excluding Banco Capiro) had low mean scleractinian coral cover of 7–25 %. This means that Banco Capiro, the only site exhibiting *D. antillarum* densities >1 individual m^{-2}, is also the only site with scleractinian coral cover >25 % (10 m average of 62 %). This strengthens our proposal that a lack of structural complexity across the MABR may be a key contributing factor to the near ubiquitous lack of *D. antillarum* population recovery and that continued "reef flattening" is likely to exacerbate this problem.

With this in mind, it is possible that adult *D. antillarum* populations could be augmented through the use of artificial reef systems designed specifically to protect juveniles from predation. Doing this would enable *D. antillarum* ecosystem functions to be reinstated, which in turn would lead to increased stony coral cover and habitat complexity that would provide shelter for future generations of *D. antillarum* recruits. Enhancing *D. antillarum* population densities in this way would also help populations to overcome problems associated with low levels of juvenile recruitment, which is almost certainly an underlying barrier to recovery. High adult *D. antillarum* densities will lead to decreased nearest-neighbour distances, which in turn will increase fertilisation success rates and reduce the extent to which recruitment failure contributes to population suppression.

Our data suggest that future research efforts should focus on the relationship between reef structural complexity and survival of *D. antillarum* to the adult stage. Reduced habitat complexity may increase the impact of predation, thus increasing mortality rates amongst juvenile *D. antillarum*, and driving the barrier to maturation. If widespread population increases can in fact be stimulated via conservation interventions, Utila and Banco Capiro could provide a model for a wider-scale improvement in coral reef health throughout the Caribbean and sustain, if not improve, the socioeconomic circumstances of the millions of people who rely on its reef systems for survival.

Acknowledgments This work was funded by Operation Wallacea and conducted in collaboration with Tela Marine Research Centre and Coral View Research Centre, Honduras. We would like to thank Operation Wallacea staff and volunteers for contributions to data collection in Honduras and Mexico, as well as Centro Ecológico Akumal (CEA) for logistical support in Mexico. We are particularly grateful to Antal Borcsok, Maria Arroyo-Gerez, Caitlin Marsteller, Rich Astley, and Sarah Laverty for facilitating this research through logistical support. Special thanks goes to the Atlantic and Gulf Rapid Reef Assessment (AGRRA) team for providing regional data on *D. antillarum* population densities and to Ian Drysdale (Healthy Reefs Initiative) and Jenny Myton (Coral Reef Alliance) for their constant support of this work and their tireless efforts to protect Banco Capiro. We also thank the two anonymous reviewers whose suggestions have enabled us to make significant improvements to the manuscript.

References

Alvarez-Filip L, Dulvy NK, Gill JA, Cote IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proc R Soc Lond B Biol Sci 276:3019–3025

Andrew NL (1993) Spatial heterogeneity, sea urchin grazing, and habitat structure on reefs in temperate Australia. Ecology 74:292–302

Bak RPM, van Eys G (1975) Predation of the sea urchin *Diadema antillarum* Philippi on living coral. Oecologia 20:111–115

Bak RPM, Carpay MJE, de Rutter van Steveninck ED (1984) Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curacao. Mar Ecol Prog Ser 17:105–108

Betchel JD, Gayle P, Kaufman L (2006) The return of *Diadema antillarum* to discovery bay: patterns of distribution and abundance. Proc 10th Int Coral Reef Symp 1:367–375

Bologna P, Webb-Wilson L, Connelly P, Saunders J (2012) A new baseline for *Diadema antillarum*, *Echinometra viridis*, *E. lucunter*, and *Eucidaris tribuloides* populations within the Cayos Cochinos MPA, Honduras. Gulf Caribb Res 24:1–5

Carpenter RC (1984) Predator and population density control of homing behaviour in the Caribbean Echinoid *Diadema antillarum*. Mar Biol 82:101–108

Carpenter RC (1988) Mass mortality of a Caribbean sea urchin: immediate effects on community metabolism and other herbivores. Proc Natl Acad Sci USA 85:511–514

Carpenter RC (1990) Mass mortality of *Diadema antillarum*. Mar Biol 104:67–77

Carpenter RC (2005) Sea urchin mass-mortality: effects on reef algal abundance, species composition, metabolism and other coral reef herbivores. NOAA Marine Systems Laboratory, Smithsonian Institute, Washington DC, pp 53–60

Carpenter RC, Edmunds PJ (2006) Local and regional scale recovery of *Diadema* promotes recruitment of Scleractinian corals. Ecol Lett 9:271–280

Chiappone M, Miller S, Swanson D, Ault J, Smith S (2001) Comparatively high densities of the long-spined sea urchin in the Dry Tortugas, Florida. Coral Reefs 20:137–138

Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Cote IM (2012) Evaluating life-history strategies of reef corals from species traits. Ecol Lett 15:1378–1386

Debrot A, Nagelkerken I (2006) Recovery of the long-spined sea urchin *Diadema antillarum* in Curacao (Netherlands Antilles) linked to lagoonal and wave sheltered shallow rocky habitats. Bull Mar Sci 79:415–424

Edmunds P, Carpenter R (2001) Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proc Natl Acad Sci USA 98:5067–5071

Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301:958–960

Gratwicke B, Speight MR (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. J Fish Biol 66:650–667

Haley MP, Solandt JL (2001) Population fluctuations of the sea urchins *Diadema antillarum* and *Tripneustes ventricosus* at Discovery Bay, Jamaica: a case of biological succession? Caribb J Sci 37:239–245

Hereu B, Zabala M, Linares C, Sala E (2005) The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. Mar Bio 146:293–299

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742

Hughes TP, Keller BD, Jackson JBC, Boyle MJ (1985) The mass mortality of the Echinoid *Diadema antillarum* Philippi in Jamaica. Bull Mar Sci 36:377–384

Iliffe TM, Pearse JS (1982) Annual and lunar reproductive rhythms of the sea urchin, *Diadema antillarum* (Philippi) in Bermuda. Int J Invertebr Reprod 5:139–148

Lacey EA, Fourqurean JW, Collado-Vides L (2013) Increased algal dominance despite presence of *Diadema antillarum* populations on a Caribbean coral reef. Bull Mar Sci 89:603–620

Lee SC (2006) Habitat complexity and consumer-mediated positive feedbacks on a Caribbean coral reef. Oikos 112:442–447

Lessios HA (1988) Population dynamics of *Diadema antillarum* (Echinodermata: Echinoidea) following mass mortality in Panama. Mar Biol 99:515–526

Lessios HA (1995) *Diadema antillarum* 10 years after mass mortality: still rare, despite help from a competitor. Proc R Soc Lond B Biol Sci 259:331–337

Lessios HA, Robertson DR, Cubit JD (1984) Spread of *Diadema* mass mortality through the Caribbean. Science 226:335–337

Levitan DR (1988a) Algal-urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at St John, U.S. Virgin Islands. J Exp Mar Bio Ecol 119:167–178

Levitan DR (1988b) Asynchronous spawning and aggregative behaviour in the sea urchin *Diadema antillarum* Philippi. In: Burke RD (ed) Echinoderm biology. Balkema Press, Rotterdam, pp 181–186

Levitan DR (1991) Influence of body size and population density on fertilisation success and reproductive output in a free-spawning invertebrate. Biol Bull 181:261–268

Levitan DR, Edmunds P, Levitan K (2014) What makes a species common? No evidence of density-dependent recruitment or mortality of the sea urchin *Diadema antillarum* after the 1983–1984 mass mortality. Oecologia 175:117–128

Liddell WD, Ohlhorst SL (1986) Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. J Exp Mar Bio Ecol 95:271–278

Macia S, Robinson MP, Nalevanko A (2007) Experimental dispersal of recovering *Diadema antillarum* increases grazing intensity and reduces macroalgal abundance on a coral reef. Mar Ecol Prog Ser 348:173–182

McClanahan TR (1999) Predation and the control of the sea urchin *Echinometra viridis* and fleshy algae in the patch reefs of Glovers Reef, Belize. Ecosystems 2:511–523

Miller RJ, Adams AJ, Ebersole JP, Ruiz E (2007) Evidence for positive density-dependent effects in recovering *Diadema antillarum* populations. J Exp Mar Biol Ecol 349:215–222

Myhre S, Acevedo-Gutierrez A (2007) Recovery of sea urchin *Diadema antillarum* population is correlated to increased coral and reduced macroalgal cover. Mar Ecol Prog Ser 8329:205–210

Ogden JC, Lobel PS (1978) The role of herbivorous fishes and urchins in coral reef communities. Environ Biol Fish 3:49–63

Ogden JC, Carpenter RC (1987) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (south Florida)—long-spined black sea urchin. US Fish Wildl Serv Biol Rep, US Army Corps Eng TR EL 82:4–17

Pennington JT (1985) The ecology of fertilisation of Echinoid eggs: the consequences of sperm dilution, adult aggregation, and asynchronous spawning. Biol Bull 169:417–430

Randall JE, Schroeder RE, Starck WA (1964) Notes on the biology of the Echinoid *Diadema antillarum*. Caribb J Sci 4:421–433

Robertson DR (1987) Responses of two coral reef toadfishes (Batrachoididae) to the demise of their primary prey, the sea urchin *Diadema antillarum*. Copeia 3:637–642

Robertson DR (1991) Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panama indicate food limitation. Mar Biol 111:437–444

Ruiz-Ramos DV, Hernandez-Delgado EA, Schizas NV (2011) Population status of the long-spined urchin *Diadema antillarum* in Puerto Rico 20 years after a mass mortality event. Bull Mar Sci 87:113–127

Samoilys MA, Carlos G (2000) Determining methods of underwater visual census for estimating the abundance of coral reef fishes. Environ Biol Fishes 57:289–304

Scheibling RE, Robinson MC (2008) Settlement behaviour and early post-settlement predation on the sea urchin *Strongylocentrotus droebachiensis*. J Exp Mar Biol Ecol 365:59–66

Shulman MJ (1990) Aggression among sea urchins on Caribbean coral reefs. J Exp Mar Biol Ecol 140:197–207

Weil E, Torres JL, Ashton M (2005) Population characteristics of the sea urchin *Diadema antillarum* in La Parguera, Puerto Rico, 17 years after the mass mortality event. Rev Biol Trop 53:219–231

Williams AH (1981) An analysis of competitive interactions in a patch back-reef environment. Ecology 62:1107–1120