

RESEARCH ARTICLE

Impacts of hurricanes and disease on *Diadema antillarum* in shallow water reef and mangrove locations in St John, USVI

Renee D. Godard^{1*}, C. Morgan Wilson¹, Caleb G. Amstutz², Natalie Badawy¹, Brittany Richardson¹

1 Departments of Biology and Environmental Studies, Hollins University, Roanoke, Va, United States of America, **2** Community School, Roanoke, Va, United States of America

✉ These authors contributed equally to this work.

* rgodard@hollins.edu



OPEN ACCESS

Citation: Godard RD, Wilson CM, Amstutz CG, Badawy N, Richardson B (2024) Impacts of hurricanes and disease on *Diadema antillarum* in shallow water reef and mangrove locations in St John, USVI. PLoS ONE 19(2): e0297026. <https://doi.org/10.1371/journal.pone.0297026>

Editor: Jiang-Shiou Hwang, National Taiwan Ocean University, TAIWAN

Received: July 18, 2023

Accepted: December 26, 2023

Published: February 15, 2024

Peer Review History: PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: <https://doi.org/10.1371/journal.pone.0297026>

Copyright: © 2024 Godard et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: This original data is available ([10.5281/zenodo.8395238](https://zenodo.org/doi/10.5281/zenodo.8395238)).

Funding: Funding for this research was provided by the Paula Pimlott Brownlee and Janet Spear

Abstract

The 1983–1984 mortality event of the long-spined sea urchin *Diadema antillarum* reduced their population by up to 99% and was accompanied by a phase shift from coral dominated to algal dominated reefs in the Caribbean. Modest rebounds of *D. antillarum* populations in the Caribbean have been noted, and here we document the impacts of two major hurricanes (2017, Irma and Maria) and the 2022 disease outbreak on populations of *D. antillarum* found by targeted surveys in the urchin zone at nine fringing reef and three mangrove sites on St. John, USVI. *D. antillarum* populations at the reef sites had declined by 66% five months after the hurricanes but showed significant recovery just one year later. The impact of recent disease on these populations was much more profound, with all reef populations exhibiting a significant decline (96.4% overall). Fifteen months after the disease was first noted, *D. antillarum* at reef sites exhibited a modest yet significant recovery (15% pre-disease density). *D. antillarum* populations in mangrove sites were impacted by the hurricanes but exhibited much higher density than reef sites after the disease outbreak, suggesting that at *D. antillarum* in some locations may be less vulnerable to disease.

Introduction

Prior to the early 1980s, long-spined urchins, *Diadema antillarum*, were abundant macroalgae grazers in the Caribbean [1–3] with common densities ranging from of 3 up to 71 urchins m⁻² [4]. So numerous were these organisms in some areas, localized removal was once considered for the establishment of underwater marine trails [5]. This species consumes benthic algae that can compete with coral for space and plays a critical role in preventing algal overgrowth on reefs [6–9], a role that became obvious when the species collapsed in the early 1980s [3, 4, 10]. In early 1983, populations of *D. antillarum* adjacent to the Panama Canal first exhibited signs of disease, and within 13 months populations across the breadth of the Caribbean had experienced mass mortality (96–99%) by an unknown pathogen that likely spread along ocean currents and in the ballast water of boats [3, 11, 12]. This decimation of *D. antillarum* was

Professorships at Hollins University as well as support from Tom and Anna Lawson. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

associated with a phase shift in the Caribbean from coral-dominated reefs to those occupied primarily by macroalgae [3, 7, 13–16].

After the mass mortality event in the mid-1980s, rapid recovery of *D. antillarum* was anticipated as the phase shift to macroalgae released the species from food limitations and its reproductive potential (a female can produce millions of eggs per spawn) was impressive [13, 17]. However, *D. antillarum* populations have, overall, shown only modest recovery, with most populations remaining at least an order of magnitude lower than pre-1983 [2, 3, 9, 18–23]. Several non-mutually exclusive hypotheses have been proposed to explain the limited recovery of *D. antillarum* and include: suppressed recruitment resulting from low population density and their asynchronous spawning behavior [3, 24], increased competition from vertebrate reef herbivores [25], reduced populations of mutually beneficial heterospecific echinoids [3], increased vulnerability to disease due to decreased immune function [26], increased predation pressure [27], and the loss of structural complexity which reduces the availability of daytime refugia [28]. Though the Caribbean-wide recovery has been limited, several studies have reported a more modest recovery of *D. antillarum* populations associated with a localized return towards a more coral dominated community [9, 15, 29–32].

The reported impacts of hurricanes on *D. Antillarum* populations in the Caribbean have been variable. Hurricane Allen (cat 5, 1980) significantly reduced *D. antillarum* density on shallow reefs (5–8 m) in Jamaica but did not impact populations in deeper (10–20 m) water [33]. Similarly, Hurricane Irma (cat 4, 2017) caused a significant decline in already depleted *D. antillarum* populations in the Florida Keys [34]. However, the increased mortality associated with Hurricanes Hugo (cat 4, 1989) and Earl (cat 4, 2010), did not result in significant declines in density of *D. antillarum* in Lameshur Bay, St. John, U. S. Virgin Islands (USVI) [2]. And after Hurricane Dean (cat 5, 2007), density in a robust Southern Mexico *D. antillarum* population remained stable [29].

In late January 2022, another die-off of *D. antillarum* was noted, this time originating near a harbor in St. Thomas, USVI. Within four months, signs of disease similar to those of 1983 (a lack of tube feet control, slow spine reaction and loss, followed by epidermal necrosis) had occurred in populations throughout the Caribbean (1,300 km N to S and 2,500 km E to W) [35]. Current molecular techniques, combined with a veterinary pathology approach, led to the identification of a scuticociliate that resembled *Philaster apodigitiformis* as the causative agent of the 2022 disease outbreak [36]. While the full extent of the 2022 die-off is not yet known, a closely monitored *D. antillarum* population at Saba (Caribbean, Netherlands) exhibited a 99% mortality rate [35]. Similarly, Levitan and colleagues [32] reported that *D. antillarum* populations followed since 1983 in Greater and Little Lameshur Bays, St John, USVI, had exhibited a 98% decline.

Before the 1983 disease episode, this well-studied Lameshur Bay population of *D. antillarum* had averaged 14.39 m^{-2} but collapsed to 0.08 m^{-2} by 1984 [13]. While the population here did recover, the *Diadema* density never rose above 1.15 m^{-2} [2]. Given the modest recovery in this bay in St. John, we became interested in comparing population patterns with other sites on the island. As such, in 2017 we surveyed *D. antillarum* populations at shallow-water reef sites on both the north and south sides of the island, as well as along the fringes of mangroves (*Rhizophora mangle*). This initial survey occurred nine months before the island was severely impacted by two category 5 hurricanes. On September 6, the western eyewall of Hurricane Irma tracked over St. John with estimated sustained wind speeds of 185 mph (161 kt), gusts over 220 mph (191 kt), and an atmospheric pressure of 916 mb [37–39]. Two weeks later, Hurricane Maria passed 60 miles south of St. John with an estimated wind speed of 155 mph (135kt) and an atmospheric pressure of 920 mb [38, 40]. We continued to follow patterns in *D. antillarum* density at these reef and mangrove sites through 2023 (Fig 1). Given that two major

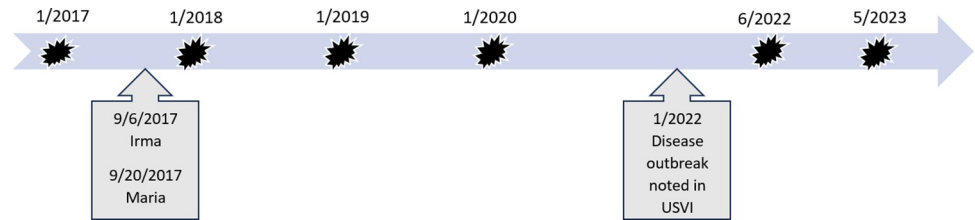


Fig 1. Timeline. Dates (month/yr) of *Diadema antillarum* surveys noted above the blue timeline, with dates of the two major hurricanes (month/day/yr) and the disease outbreak (month/yr) noted below the timeline.

<https://doi.org/10.1371/journal.pone.0297026.g001>

perturbations occurred during that time interval, we were able to: 1.) compare the impacts of hurricanes and disease on *D. antillarum* populations; 2.) explore recovery patterns following these perturbations; and 3.) examine *D. antillarum* populations in multiple reef and mangrove locations.

Methods

From 2017 to 2023 (except for 2021 due to COVID restrictions, Fig 1), we surveyed the abundance of *D. antillarum* at nine fringing reef sites (1–9) and three mangrove sites (M1–M3) in St. John, USVI (see Fig 2). The nine reef sites occurred within the boundaries of the Virgin Islands National Park and were originally chosen because of 1) their accessibility from land, 2) their coverage of both the north (sites 1–4) and south (sites 5–9) sides of the island, 3) inclusion of two areas surveyed on St. John since 1983 (site 5 is within the site “SQST” and 6 mirrors “DOBI” reported by Levitan [13]), and 4) their distance from one another (no two sites closer than 0.35 km). The three mangrove sites (Fig 2: M1–M3), separated by a minimum of 0.4 km, were in Hurricane Hole in the Virgin Islands Coral Reef National Monument and, prior to the

St. John, USVI

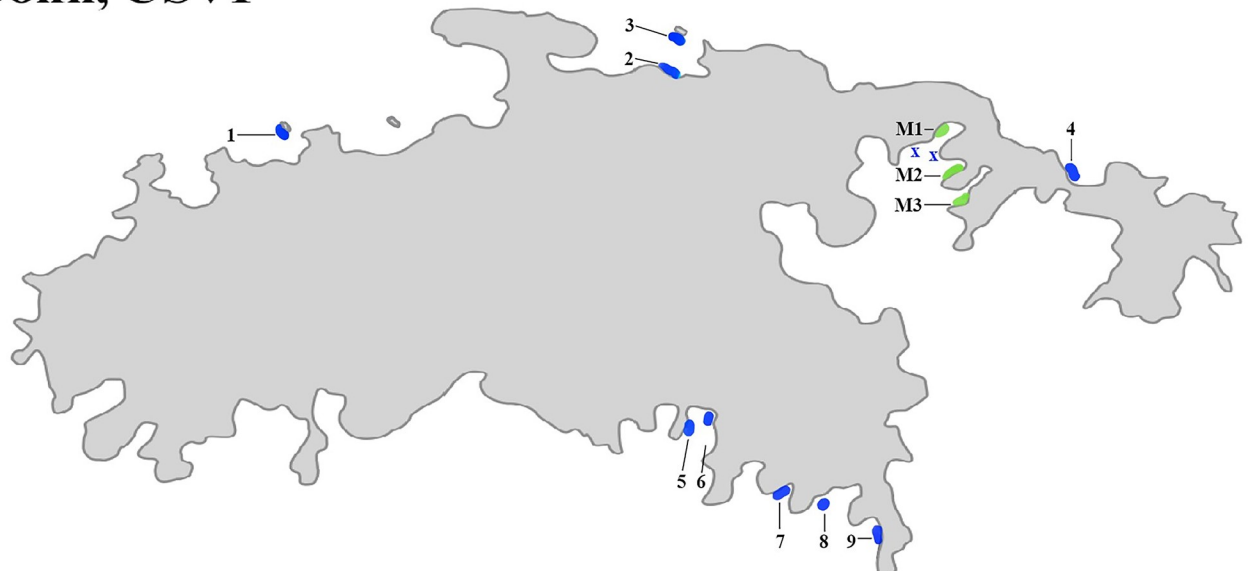


Fig 2. Map STJ. Survey sites in St John, USVI. Blue marks the numbered reef sites (1–9) and green marks the mangrove sites (M1–M3). The blue x’s mark the two reef locations in Hurricane Hole that were anecdotally surveyed in 2022 and 2023 where urchin density remained high (2022 and 2023). *Diadema* Survey Map produced by Kristen Bell (Zenodo. <https://doi.org/10.5281/zenodo.8372679>).

<https://doi.org/10.1371/journal.pone.0297026.g002>

2017 hurricanes, were considered among the most diverse mangrove sites in the Caribbean [39, 41].

Our surveys were conducted by snorkel, and like Carpenter and Edmunds [15], we targeted the “urchin zone” at each site. Specifically, before collecting data, we surveyed each site for 30 minutes, noting locations of *D. antillarum* aggregations. After the 30 min survey was completed, we counted all *D. antillarum* in three different 10 x 2 m transects. Each transect was separated by at least 15 m and selected for high aggregation. Because it is more difficult to safely place a weighted transect by snorkel in a way that avoids damaging benthic organisms, transects were established by a 10 m nylon rope stretched between two snorkelers above the substrate. All *D. antillarum* (juvenile and adult) within 1 m of either side of transect were then counted, including those hidden under rocks and crevices within the transect (see Fig 3A). The depth at each end of the transect was measured (to nearest 0.25 m) and the transect location was marked with a handheld global positioning system (GPS) unit (Garmin GPS 72H) in a waterproof bag. Mangrove sites were linear by nature, and the prop root fringe extended 1.5–2.5 m from the shoreline before the hurricanes. After the hurricanes, the mangrove fringe remained linear but at sites M2 and M3 the substrate was eroded and the prop root fringe was compressed. The transects included most of the urchin habitat within the prop roots given the distance of the fringe from the shoreline. Unlike the hard pavement that characterized the reef sites, the benthos of the mangrove fringe was primarily sand with scattered scleractinian coral heads.

After the 2022 disease outbreak, *D. antillarum* populations were extremely depleted at our sites (Fig 3B), prompting the establishment of transects whenever an urchin was encountered during the 30 min survey period. If more than three transects at a site were surveyed, the three transects with the highest counts were used for analysis. Water conditions (wave action and turbidity) and time limitations prevented population assessment at the following sites (year): 1 (2020); M1 (2019, 2020); M2 (2023); M3 (2023).

For each year at each reef site, we calculated the density (*D. antillarum* m⁻²) by averaging the urchin counts from the three transects. As we were interested in comparing the impacts of the hurricanes and the disease outbreak on *D. antillarum*, we conducted two separate analyses



Fig 3. Photos. A) *D. antillarum* reef site 6 (2016, pre-hurricane) B) *D. antillarum* reef site 7, spines and test (2022) C) *D. antillarum* mangrove site M1 (2022) D) *D. antillarum* shallow reef adjacent to M1 (2022).

<https://doi.org/10.1371/journal.pone.0297026.g003>

of the data from the reef sites. To assess the impact of the hurricanes on and subsequent recovery of *D. antillarum* populations, we compared the density in 2017 to that found in 2018 and 2019 using a repeated measure ANOVA with a Greenhouse-Geisser correction, as the data were normally distributed (Shapiro-Wilks $p > 0.05$). Because we were unable to sample in 2021, we compared the data collected in 2020 to that collected in 2022 and 2023, a timeline that mimics that of the hurricanes (Fig 1). As these data were normally distributed, we used a repeated measures ANOVA with a Greenhouse-Geisser correction. All analyses were performed using IBM SPSS statistics Version 27 [42]. *D. antillarum* densities at the three mangrove sites in each sampling year were also calculated. The mangrove sample size prevented statistical comparisons, but patterns at reef sites were compared to those at mangrove sites graphically.

Results

All our reef and mangrove transects were in shallow water (0.25–3.0 m), with most *D. antillarum* occurring at depths of 0.25–1.5 m and typically wedged into, or under, crevices generated by rubble, rocky pavement, and living scleractinian coral (Fig 3A, 3C and 3D).

Occasionally, *D. antillarum* were found sheltering in the open in aggregations > 5 individuals, a pattern that was more likely to occur at mangrove sites and at reef sites before the hurricanes Irma and Maria. While we did not collect and measure *D. antillarum*, we did note variation in the size of adults across sites and years and consistently noted that the population at all sites was composed primarily of adults ($> 95\%$).

Prior to the hurricanes, *D. antillarum* density varied between reef sites (Fig 4). Some locations (sites 2, 4, 9) had fewer than 0.2 m^{-2} while others ranged from 1.6 m^{-2} (site 3) to 8.5 m^{-2} (site 7, Fig 3A and 3C). After the hurricanes (2018), the average *D. antillarum* density dropped 66%, from the pre-hurricane (2017) average of 2.97 (S.E. ± 0.98) m^{-2} to 1.05 (± 0.98) m^{-2} . Seven sites experienced moderate to dramatic declines in *D. antillarum* abundance, while two (sites 3 and 4) showed modest increases in abundance (Fig 5). By 2019, the density had increased at all sites, with two (sites 5 and 7) exhibiting relatively robust populations ($> 3.5 \text{ m}^{-2}$). A repeated measures ANOVA revealed a marginally significant impact of time from hurricane on *Diadema* density ($F(1.184,7) = 4.479$, $p = 0.057$). Pairwise comparisons indicated a significant increase in *D. antillarum* density only between 2018 and 2019 ($p = 0.042$).

Populations in 2020 continued to increase at five sites (2, 3, 6, 7, 9; Fig 5), but five months after the disease event (2022), *D. antillarum* populations declined dramatically (96.4% reduction), from a site average of 2.51 (S.E. ± 0.61) m^{-2} to 0.09 (S.E. ± 0.03) m^{-2} (Fig 4). Though numerous *D. antillarum* tests and spines were found at each site (Fig 3B), no living urchins were found at site 2, density was less than 0.1 m^{-2} at five locations (sites 1, 3, 5, 7, 9) and no locations had densities $> 0.3 \text{ m}^{-2}$ (Fig 5). Eleven months later (2023), *D. antillarum* density had increased to 15% of the pre-disease average ($0.39 \pm 0.05 \text{ m}^{-2}$), with $> 0.2 \text{ m}^{-2}$ found at all locations and $> 0.4 \text{ m}^{-2}$ found at four sites (1, 2, 5, 8). A repeated measures ANOVA revealed a strongly significant impact of disease on urchin density ($F(1.015,7) = 13.439$, $p = 0.006$). Pairwise comparisons indicated significant differences in urchin density between all three sampling periods (2020:2022 $p = 0.015$; 2020:2023 $p = 0.026$; 2022:2023 $p = 0.005$).

D. antillarum populations in the mangroves appeared to exhibit a different pattern than those of the reef sites over the same sampling time period (Fig 6). Prior to the disease outbreak, mangrove sites had lower *D. antillarum* densities than reef sites; however, after the disease event (2022), one mangrove site (M1) had *D. antillarum* populations that were 7.5 times higher ($2.1 \pm 0.85 \text{ m}^{-2}$) than any reef site, and this high density persisted 16 months later (2023).

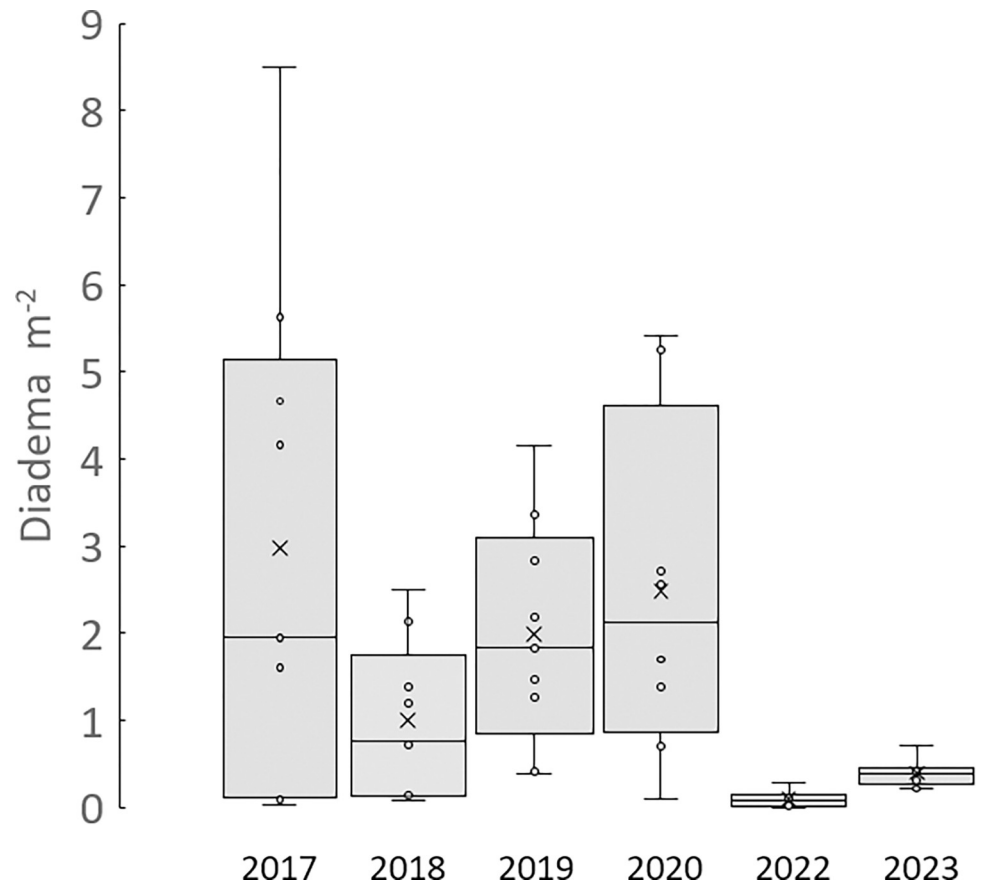


Fig 4. Box-whisker overall reef sites. Box-and-whisker plots of *D. antillarum* m⁻² at the nine reef sites in St. John sampled 2017–2023. The median value is indicated by the horizontal bar and the X marks the mean value.

<https://doi.org/10.1371/journal.pone.0297026.g004>

Discussion

Given that *D. antillarum* aggregate [43] and prefer to seek shelter in crevices [28] that can vary over small distances [44], we chose to survey *D. antillarum* in the aggregation areas which we determined by a standardized preliminary survey. As such, our density values represent a maximum abundance and don't lend themselves to comparison to values from studies using randomly placed transects. However, this method allows for reliable comparisons within sites and between years.

Prior to the back-to-back hurricanes of 2017, *D. antillarum* density at two thirds of our reef sites were similar to density patterns reported from the “urchin zones” sampled in Jamaica, St. Croix, Barbados, Belize, Bonaire, and Grenada [15]. Our overall site average of 2.97 (S.E. ± 0.98) m⁻² indicated that, at least in pockets, *D. antillarum* were at densities that might support more successful reproduction in this prolific, yet asynchronous broadcast spawner. Five months after Hurricanes Irma and Maria, *D. antillarum* populations at the reef sites declined by 66%, like the losses reported after Hurricanes Hugo (1989) and Earl (2010) for *D. antillarum* at different depths (2–9 m) in Lameshur Bay [2]. And 17 months later, *D. antillarum* populations were increasing in density at all our sample sites in contrast to *D. antillarum* populations in the Florida Keys that exhibited a significant decline after Irma passed through at lower wind speeds (cat 4 in the Keys). Unlike populations in St. John, *D. antillarum* in the Florida Keys have remained at very low density and have shown very few signs of growth [45],

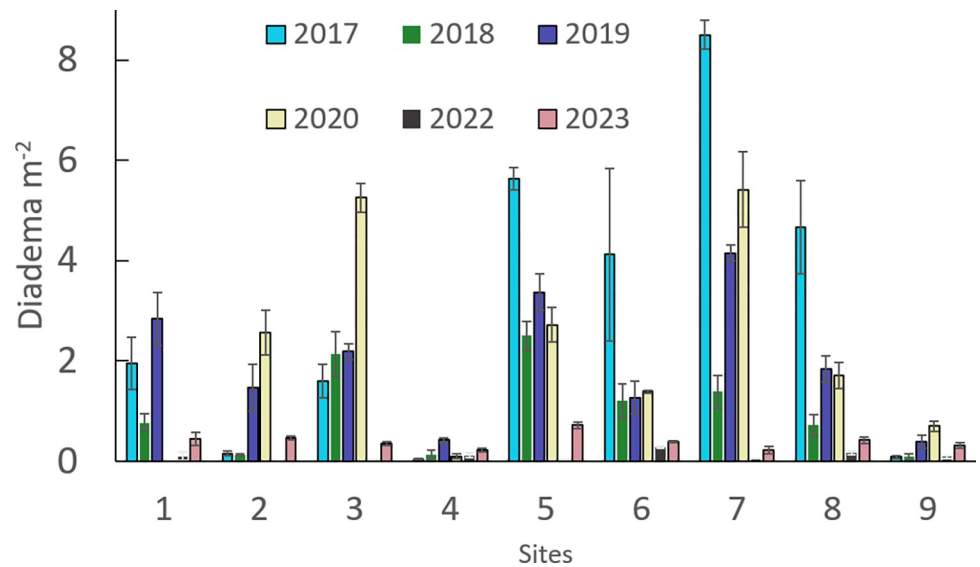


Fig 5. Average individual reef sites. Average (\pm S.E.) *D. antillarum* m⁻² (3 transects per site) for the 9 reef sites in St. John, USVI, sampled in 2017–2023. Wave action prevented sampling at Site 1 in 2020. Original data available (<https://zenodo.org/records/8395238>).

<https://doi.org/10.1371/journal.pone.0297026.g005>

potentially leaving them more vulnerable to the impacts of hurricanes. A reduction of reef complexity because of a decrease in scleractinian coral health and abundance has been associated with reduced *D. antillarum* density [9, 46]. This reduction in reef crevices could reduce refugia for *D. antillarum*, making them more vulnerable to sediment abrasion, predation, and dislodgement [34, 47]. *D. antillarum* populations on reefs in southern Mexico remained robust after Hurricane Dean (2007), which could be attributed to the relatively high coral cover, which increases habitat complexity [28, 29]. The threat of hurricanes on struggling *D.*

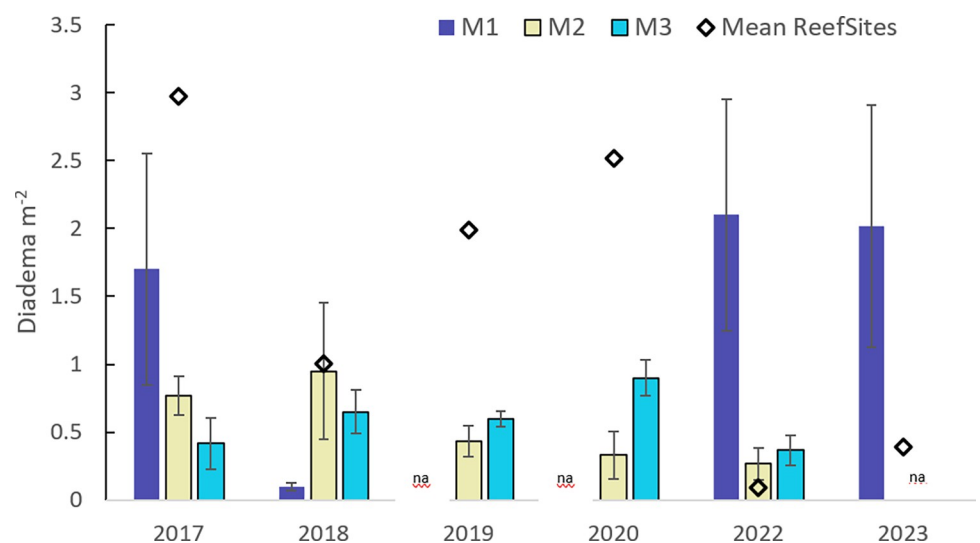


Fig 6. Mangrove sites. Average (\pm SE) *D. antillarum* m⁻² at the three mangrove sites (M1, M2, M3) 2017–2023. The diamond indicates the average *D. antillarum* m⁻² of the nine reef sites in each year. M1 was not sampled in 2019 or 2020 due to turbidity and debris, and in 2023 time constraints prevented sampling at M2 and M3. Original data available (<https://zenodo.org/records/8395238>).

<https://doi.org/10.1371/journal.pone.0297026.g006>

antillarum populations remains of significant concern, as models predict that anthropogenic changes to the atmosphere are likely to increase the strength of hurricanes [48].

The 2022 disease outbreak devastated the rebounding *D. antillarum* population by 96.4% reduction, just slightly less than that reported for Saba, Caribbean Netherlands (99%) [35] and for deeper water sites in the Lameshur Bays, St. John, USVI (98%) [32]. These differences may be attributable to the fact that we targeted our samples to the “urchin zone” rather than along randomly placed transects, and all our sites were in shallow water (< 3 m). In 2023, we found modest but significant increases in *D. antillarum* density at all nine reef sites sixteen months after the disease outbreak was first noted. Overall, the *D. antillarum* population had increased to 0.39 m^{-2} , a mere 15% of the pre-disease density outbreak. While these density values remain low compared to pre-disease values, and remain at levels that challenge population growth, the increase in density at all reef sites was encouraging. We are aware of no other published studies that have reported patterns of *D. antillarum* density in 2023.

D. antillarum density at mangrove locations in Hurricane Hole appear to have followed a different pattern. Prior to the hurricanes, only one of the three mangrove sites (M1) had *D. antillarum* densities $> 1 \text{ m}^{-2}$. The western eye wall of Irma passed directly through Hurricane Hole and though the track of Maria was further south, this hurricane had a larger fetch area, which models suggest resulted in 2–3 m waves near the entrance of Hurricane Hole [38]. The combination of waves and winds from these two hurricanes uprooted mangrove trees, toppled coral, scoured the prop root communities, and transported rocks into shallow nearshore areas [39]. The wind and wave action also deposited human-made debris (e.g., boats, mooring lines, gasoline motors, etc.) in Hurricane Hole which further damaged many mangrove trees (authors’ personal observations). Deposition of debris under the prop roots in the nearshore shallows of Otter and Water Creeks (M2 and M3, respectively) was more dramatic than at M1 and likely reduced habitat for organisms including *D. antillarum* [39]. Though damage was severe, *D. antillarum* density at M2 and M3 did not show dramatic declines post-hurricane, perhaps because pre-hurricane density was relatively low ($< 1 \text{ m}^{-2}$). *D. antillarum* density at M1 exhibited a more dramatic decline (1.7 m^{-2} to 0.1 m^{-2}). However in 2022, *D. antillarum* populations at M1 were remarkably high ($> 2 \text{ m}^{-2}$) and populations at M2 and M3 were higher than at most reef sites. Unlike at reef sites, we did not observe clusters of *D. antillarum* tests and spines at the mangrove sites, but several dying *D. antillarum* (dropping spines) were noted beside an isolated coral head in the grassbed adjacent to M1, suggesting the disease was present in Hurricane Hole. Remarkably, *D. antillarum* density at M1 remained stable when resurveyed in 2023, suggesting that this population was somehow more resistant to the disease. In addition, we also noted robust populations of *D. antillarum* at two shallow water fringing reef sites located between grassbeds in Hurricane Hole (locations noted with an x in Fig 2). These two sites had notably less macroalgae than at any of our surveyed reef sites.

It is not clear why *D. antillarum* is faring so much better in Hurricane Hole than in other locations in St. John. Recent research has shown that extensive seagrass ecosystems can reduce the bacterial pathogen load in the water column and are associated with improved coral health [49]. Perhaps the extensive grassbeds in Hurricane Hole and Coral Bay (comprised primarily of *Thalassia testudinum*, *Syringodium filiforme*, and *Halophila stipulacea*) reduced the concentration of the scuticociliate that has been associated with the 2022 disease outbreak [36]. Scuticociliates are ubiquitous marine organisms and have not previously been associated with mass disease outbreaks in *D. antillarum*. Given that the disease first appeared near calm water ports and harbors, it is possible that these nutrient-rich environments may have fostered an explosive growth of a *Philaster*-like ciliate, which then dispersed rapidly throughout the Caribbean [36]. Much more research is needed to understand how ocean conditions, host factors, and

other ecosystem actions might impact this pathogen and *D. antillarum* populations, both at local and Caribbean-wide levels.

The full extent of the impacts of the 2022 scuticociliate disease on *D. antillarum* populations remains to be seen. While some populations rebounded from the 1983 disease outbreak, the rebound was modest and remained an order of magnitude lower than pre-disease density in most locations. However, there has been an increase in restoration efforts Caribbean-wide, and artificial structures have been shown to support and maintain *D. antillarum* populations [12, 16]. This suggests that, if remaining *D. antillarum* find adequate refugia and nearest-neighbor density can be increased, it is possible that *D. antillarum* may rebound from this disease-outbreak. However, given the degraded state of Caribbean reefs and the increasing frequency of hurricanes, it is also possible that the remaining corals will continue to decline as algal-free zones disappear, further reducing the habitat viability for *D. antillarum* [50]. Only time will tell what the ultimate impact of this disease will be on *D. antillarum* populations.

Acknowledgments

We thank Natasha Bestrom for help with field work and comments on a draft of the manuscript. We also thank Kristin Bell for producing the map of our study sites and Bonnie Bowers for advice on statistical analyses. We also thank Cheryl Taylor for technical support. Thanks to Thomas Kelley for help with obtaining research permits (VICR-2018-SCI-0001) to work in the Virgin Islands National Park and for the Virgin Islands Environmental Resource Station (VIERS) which provided support for research prior to the hurricanes in 2017.

Author Contributions

Conceptualization: Renee D. Godard, C. Morgan Wilson, Natalie Badawy, Brittany Richardson.

Formal analysis: Renee D. Godard, C. Morgan Wilson.

Funding acquisition: Renee D. Godard.

Investigation: Renee D. Godard, C. Morgan Wilson, Caleb G. Amstutz, Natalie Badawy, Brittany Richardson.

Methodology: Renee D. Godard, C. Morgan Wilson, Caleb G. Amstutz, Natalie Badawy, Brittany Richardson.

Supervision: Renee D. Godard, C. Morgan Wilson.

Visualization: Renee D. Godard.

Writing – original draft: Renee D. Godard.

Writing – review & editing: Renee D. Godard, C. Morgan Wilson, Caleb G. Amstutz, Brittany Richardson.

References

1. Lessios HA. Mass Mortality of *Diadema antillarum* in the Caribbean: What Have We Learned? *Ann Rev Ecol Syst.* 1988 Nov; 19(1):371–93. Available from: <http://dx.doi.org/10.1146/annurev.es.19.110188.002103>
2. Levitan DR, Edmunds PJ, Levitan KE. 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.* 2014; 175:117–28.
3. Lessios HA. The Great *Diadema antillarum* Die-Off: 30 Years Later. *Ann Rev Mar Sci* [Internet]. 2016; 8(1):267–83. Available from: <http://dx.doi.org/10.1146/annurev-marine-122414-033857>

4. Bak R, Carpay M, De Rutter Van Steveninck ED. Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curacao. *Mar Ecol Prog Ser*. 1984; 17:105–8.
5. Randall JE, Schroeder RE, Starck WA. Notes on the biology of the echinoid *Diadema antillarum*. *Caribb J Sci*. 1964; 4(2–3):421–33.
6. Hay ME, Taylor PR. Competition between herbivorous fishes and urchins on Caribbean reefs. *Oecologia* [Internet]. 1985; 65(4):591–8. Available from: <https://doi.org/10.1007/BF00379678> PMID: 28311871
7. Aronson RB, Precht WF. Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. *Limnol. and Oceanogr*. 2000 Jan; 45(1):251–5.
8. Ostrander GK, Armstrong KM, Knobbe ET, Gerace D, Scully EP. Rapid transition in the structure of a coral reef community: the effects of coral bleaching and physical disturbance. *Proc Natl Acad Sci U S A*. 2000; 97(10):5297–5302. <https://doi.org/10.1073/pnas.090104897> PMID: 10792043
9. Edmunds PJ, Carpenter RC. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proc Natl Acad Sci U S A* [Internet]. 2001; 98(9):5067–71. Available from: <http://dx.doi.org/10.1073/pnas.071524598>
10. Carpenter RC. Mass mortality of a Caribbean sea urchin: Immediate effects on community metabolism and other herbivores. *Proc Natl Acad Sci U S A* [Internet]. 1988; 85(2):511–4. Available from: <https://doi.org/10.1073/pnas.85.2.511> PMID: 16593907
11. Lessios HA, Robertson DR, Cubit JD. Spread of *Diadema* mass mortality through the Caribbean. *Science* [Internet]. 1984; 226(4672):335–7. Available from: <http://dx.doi.org/10.1126/science.226.4672.335>
12. Hylkema A, Debrot AO, van de Pas EE, Osinga R, Murk AJ. Assisted Natural Recovery: A Novel Approach to Enhance *Diadema antillarum* Recruitment. *Front Mar Sci*. 2022 Jul 15; 9.
13. Levitan DR. Algal-urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at St. John, U.S. Virgin Islands. *Exp Mar Bio Ecol*. 1988; 119:167–78
14. Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS. Rising to the challenge of sustaining coral reef resilience. *Trends Ecol Evol*. 2010 Nov; 25(11):633–42. <https://doi.org/10.1016/j.tree.2010.07.011> PMID: 20800316
15. Carpenter RC, Edmunds PJ. Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals: Recovery of *Diadema*. *Ecol Lett* [Internet]. 2006; 9(3):271–80. Available from: <http://dx.doi.org/10.1111/j.1461-0248.2005.00866.x>
16. Hylkema A, Debrot AO, Pistor M, Postma E, Williams SM, Kitson-Walters K. High peak settlement of *Diadema antillarum* on different artificial collectors in the Eastern Caribbean. *J Exp Mar Bio Ecol* [Internet]. 2022; 549(151693):151693. Available from: <http://dx.doi.org/10.1016/j.jembe.2022.151693>
17. Lessios HA. Presence and absence of monthly reproductive rhythms among 8 Caribbean echinoids off the coast of Panama. *J Exp Mar Biol Ecol*. 1991; 153:27–47.
18. Chiappone M, Miller S, Swanson D, Ault J, Smith S. Comparatively high densities of the long-spined sea urchin in the Dry Tortugas, Florida. *Coral Reefs* [Internet]. 2001; 20(2):137–8. Available from: <http://dx.doi.org/10.1007/s003380100162>
19. Weil E, Torres JL, Ashton M. Population characteristics of the sea urchin *Diadema antillarum* in La Parguera, Puerto Rico, 17 years after the mass mortality event. *Rev Biol Trop*. 2005; 53 Suppl 3:219–31.
20. Debrot A, Nagelkerken I. 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*. 2006; 79:415–24.
21. Idjadi JA, Haring RN, Precht WF. Recovery of the sea urchin *Diadema antillarum* promotes scleractinian coral growth and survivorship on shallow Jamaican reefs. *Mar Ecol Prog Ser* [Internet]. 2010; 403:91–100. Available from: <http://dx.doi.org/10.3354/meps08463>
22. Bologna PAX, Webb-Wilson L, Connelly P, Saunders JE. A New Baseline for *Diadema antillarum*, *Echinometra viridis*, *E. lucunter*, and *Eucidaris tribuloides* Populations Within the Cayos Cochinos MPA, Honduras. *Gulf Caribb Res* [Internet]. 2012; 24. Available from: <http://dx.doi.org/10.18785/gcr.2401.01>
23. Tuohy E, Wade C, Weil E. 2020. Lack of recovery of the long-spined sea urchin *Diadema antillarum* Philippi in Puerto Rico 30 years after the Caribbean-wide mass mortality. *PeerJ* 2020; 8:e8428 <https://doi.org/10.7717/peerj.8428>
24. Levitan DR. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biol Bull* [Internet]. 1991; 181(2):261–8. Available from: <https://doi.org/10.2307/1542097> PMID: 29304646
25. Robertson DR. Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panama indicate food limitation. *Mar Biol*. 1991 Oct; 111(3):437–44.

26. Beck G, Miller R, Ebersole J. Mass mortality and slow recovery of *Diadema antillarum*: Could compromised immunity be a factor? *Mar Biol* [Internet]. 2014; 161(5):1001–13. Available from: <http://dx.doi.org/10.1007/s00227-013-2382-6>
27. Rodríguez-Barreras R. Demographic implications of predatory wrasses on low-density *Diadema antillarum* populations. *Mar Biol Res*. 2018 Feb 26; 14(4):383–91.
28. Bodmer MDV, Wheeler PM, Anand P, Cameron SE, Hintikka S, Cai W, et al. The ecological importance of habitat complexity to the Caribbean coral reef herbivore *Diadema antillarum*: three lines of evidence. *Sci Rep* [Internet]. 2021; 11(1):9382. Available from: <http://dx.doi.org/10.1038/s41598-021-87232-9>
29. Jorgensen PJ, Espinoza-Ávalos J, Bahena-Basave H. High population density survival of the sea urchin *Diadema antillarum* (Philippi 1845) to a category 5 hurricane in southern Mexican Caribbean. *Hidrobiológica*. 2008; 18(3):257–260.
30. Bodmer MDV, Rogers AD, Speight MR, Lubbock N, Exton DA. Using an isolated population boom to explore barriers to recovery in the keystone Caribbean coral reef herbivore *Diadema antillarum*. *Coral Reefs* [Internet]. 2015; 34(4):1011–21. Available from: <http://dx.doi.org/10.1007/s00338-015-1329-4>
31. Pusack TJ, Stallings CD, Albins MA, Benkwitt CE, Ingeman KE, Kindinger TL, et al. Protracted recovery of long-spined urchin (*Diadema antillarum*) in the Bahamas. *Coral Reefs* [Internet]. 2023; 42(1):93–8. Available from: <http://dx.doi.org/10.1007/s00338-022-02321-z>
32. Levitan DR, Best RM, Edmunds PJ. Sea urchin mass mortalities 40 y apart further threaten Caribbean coral reefs. *Proc Natl Acad Sci U S A* [Internet]. 2023; 120(10):e2218901120. Available from: <https://doi.org/10.1073/pnas.2218901120> PMID: 36848553
33. Woodley JD, Chornesky EA, Clifford PA, Jackson JB, Kaufman LS, Knowlton N, et al. Hurricane allen's impact on Jamaican coral reefs. *Science* [Internet]. 1981; 214(4522):749–55. Available from: <https://doi.org/10.1126/science.214.4522.749> PMID: 17744383
34. Kobelt JN, Sharp WC, Miles TN, Feehan CJ. Localized Impacts of Hurricane Irma on *Diadema antillarum* and Coral Reef Community Structure. *Estuaries Coast*. 2019 Nov 15; 43(5):1133–43.
35. Hylkema A, Kitson-Walters K, Kramer PR, Patterson JT, Roth L, Sevier MLB, et al. The 2022 *Diadema antillarum* die-off event: Comparisons with the 1983–1984 mass mortality. *Front Mar Sci*. 2023 Jan 5; 9.
36. Hewson I, Ritchie IT, Evans JS, Altera A, Behringer D, Bowman E, et al. A scuticociliate causes mass mortality of *Diadema antillarum* in the Caribbean Sea. *Sci Adv* [Internet]. 2023; 9(16):eadg3200. Available from: <http://dx.doi.org/10.1126/sciadv.adg3200>
37. Cangialosi J, Latta A, Berg R. Hurricane Irma VIIRS satellite image of hurricane Irma when it was at its peak intensity and made landfall on Barbuda at 0535 UTC. [Internet]. 2017 [cited 2023 Jul 6]. Available from: http://www.nhc.noaa.gov/data/tcr/AL112017_Irma.pdf
38. Browning TN, Sawyer DE, Brooks GR, Larson RA, Ramos-Scharron CE, Canals-Silander M. Widespread deposition in a coastal bay following three major 2017 hurricanes (Irma, Jose, and Maria). *Sci Rep* 2019; 9 (7101). Available from: <https://doi.org/10.1038/s41598-019-43062-4>
39. Rogers CS. Immediate Effects of Hurricanes on a Diverse Coral/Mangrove Ecosystem in the U.S. Virgin Islands and the Potential for Recovery. *Diversity*. 2019; 11(8):130. <https://doi.org/10.3390/d11080130>
40. Pasch R, Penny A, Berg R. Tropical cyclone report Hurricane Maria (AL152017). National Hurricane Center Miami, FL; 2018. Available at: https://www.nhc.noaa.gov/data/tcr/AL152017_Maria.pdf
41. Rogers C. A unique coral community in the mangroves of hurricane hole, St. John, US Virgin Islands. *Diversity (Basel)* [Internet]. 2017; 9(3):29. Available from: <http://dx.doi.org/10.3390/d9030029>
42. IBM. SPSS statistics for Windows. Version 27.0. Armonk, NY: IBM; 2020.
43. Weil E, Losada F, Bone D. Spatial variations in density and size of the echinoid *Diadema antillarum* Philippi on some Venezuelan coral reefs. *Bijdr Dierkd* [Internet]. 1984; 54(1):73–82. Available from: <http://dx.doi.org/10.1163/26660644-05401006>
44. Edmunds PJ, Bruno JF. The importance of sampling scale in ecology: kilometer-wide variation in coral reef communities. *Mar Ecol Prog Ser*. 1996; 143: 165–71
45. Chiappone M, Rutten L, Miller S, Swanson D. Recent trends (1999–2011) in population density and size of the echinoid *Diadema antillarum* in the Florida Keys. *Fla Sci*. 2013; 76:23–35.
46. Hughes TP. Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. *Science*. 1994 Sep 9; 265(5178):1547–51. <https://doi.org/10.1126/science.265.5178.1547> PMID: 17801530
47. Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc Biol Sci* [Internet]. 2009; 276(1669):3019–25. Available from: <https://doi.org/10.1098/rspb.2009.0339> PMID: 19515663
48. Knutson TR, McBride JL, Chan J, Emanuel K., Holland G, Landsea C, et al. Tropical cyclones and climate change. *Nat Geosci*. 2010; 3 (3):157.

49. Lamb JB, van de Water JAJM, Bourne DG, Altier C, Hein MY, Fiorenza EA, et al. Seagrass ecosystems reduce exposure to bacterial pathogens of humans, fishes, and invertebrates. *Science*. 2017 Feb 16; 355(6326):731–3. <https://doi.org/10.1126/science.aal1956> PMID: 28209895
50. Edmunds PJ. Three decades of degradation lead to diminished impacts of severe hurricanes on Caribbean reefs. *Ecology* [Internet]. 2019; 100(3):e02587. Available from: <https://doi.org/10.1002/ecy.2587> PMID: 30737954