NOTE

Protracted recovery of long-spined urchin (*Diadema antillarum*) in the Bahamas

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Abstract In 1983–1984, an unknown waterborne pathogen caused the mass mortality of long-spined sea urchin (*Diadema antillarum*) across the Caribbean and western tropical Atlantic. After approximately 15 years, urchin populations began to recover at some locations, yet few have reached pre-mortality densities. To date, no study has documented a recovery in the western tropical Atlantic outside of the Caribbean. Over a 25-year period (1991–2015), we documented an 8–17% population growth rate of *D. antillarum* in the central Bahamas. However, our mean observed densities, 0.06–0.38 urchins m^{-2}, remained below pre-pandemic levels. Combined with observations from other locations in the Caribbean, it appears that *D. antillarum* populations are increasing, yet have not fully recovered from their 1980s mass mortality throughout much of their geographic range.

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Introduction

In 1983–1984, the long-spined urchin (*Diadema antillarum*) experienced a massive mortality event likely caused by an unknown waterborne pathogen (Lessios 1988). This die-off began near Panama (Lessios 1983) and then spread throughout the Caribbean and western tropical Atlantic, resulting in a 98% average reduction in *D. antillarum* populations across the region (Lessios 1988). *D. antillarum* is an ecologically important herbivore (Ogden 1973). Combined with overfishing of parrotfishes and other herbivorous fishes, the drastic decline in *D. antillarum* corresponded with a rapid proliferation of macroalgae and a decline in corals on many reefs (Liddell and Ohlhorst 1986; Knowlton, 2001; Carpenter and Edmunds 2006). The loss of *D. antillarum* populations is considered one of the major factors that have led to the overall degradation of coral reefs in the region over the last few decades (Knowlton, 2001).

During the four decades since the die-off, recovery of *D. antillarum* has been slow and variable. Among other factors such as low post-settlement survival (Williams et al. 2011), the presumed reason for the slow recovery has been an absence of source populations resulting in minimal larval production (Lessios 1988; 1995, Miller et al. 2009). In the mid to late 1990s, approximately 15 years after the die-off, recovery began in several isolated locations. For example, in

Jamaica *D. antillarum* increased to pre-mortality densities around 2000 (Edmunds and Carpenter 2001), but with local variability (Cho and Woodley 2000). The increasing densities of *D. antillarum* in Jamaica corresponded with both a large reduction in macroalgae abundance (Edmunds and Carpenter 2001) and increased survival and faster growth of scleractinian corals (Idjadi et al. 2010). Beyond Jamaica, the recovery of urchin populations has been slower, e.g., Barbados, St. Croix, (Miller et al. 2003), and Puerto Rico (Tuohy et al. 2020), with many populations still below pre-mortality densities. Other locations, such as the Florida Keys (Chiappone et al. 2002; Miller et al. 2009) and Panama (Lessios 2005), have not experienced any observed recovery, potentially due to low or inconsistent recruitment.

The majority of studies on *D. antillarum* populations have occurred within the Caribbean Sea proper (Carpenter and Edmunds 2006), and to date, there has been no documentation of urchin recovery outside of this region (i.e., in the greater tropical western Atlantic). The Bahamian Archipelago, located adjacent to and northeast of the Caribbean region, had notable population sizes of *D. antillarum* consistent with those observed across the broader region prior to the mass mortality event (Ray 1958; Newell et al. 1959; Bauer 1980; Hay 1984), but densities have remained low through the 2000s (Harborne et al. 2009). The goal of this study was to examine changes in the density of *D. antillarum* in the central Bahamas over a 25-year period from 1991 to 2015.

Methods

We recorded *D. antillarum* abundances on three types of shallow (< 5 m depth) patch reefs during the early summer from 1991 to 2015 as part of annual surveys of the regional reef community. These surveys recorded all vertebrates, several invertebrate species (e.g., urchins, lobster), as well as unquantified descriptions of other notable features. Reefs were located within 7 km of Lee Stocking Island, Bahamas (Fig. 1), and ranged in size from 1.0–13.1 m². The first type of reef, hereafter natural patch reefs ($n = 9$), was coral bommies (6.0 – 13.1 m², 9.4 ± 1.3 [mean ± standard error]) found on sand and limestone benches at depths between 2 and 4 m. Each was approximately 50 m from the nearest adjacent reef and remained unmanipulated for the entire 25-year period. The other types of reefs formed an experimental array (established in the early 1990s) of 1 m² concrete-block artificial reefs ($n = 16$) and 3.5 m² translocated coral patch reefs ($n = 32$) arranged in a sand-seagrass flat with each reef at least 200 m from the nearest reef. The artificial reefs rapidly became colonized by corals, sponges, and other benthos as well as fishes (Carr and Hixon 1997). The translocated patch reefs consisted of ≥ 0.5 m diameter

coral heads of *Orbicella annularis* and *Porites astreoides* (see Carr and Hixon 1995; Hixon and Carr 1997 for a full description). While the experimental array has been used for experimental manipulations of reef fishes (e.g., Hixon and Carr 1997), *D. antillarum* and their predators (e.g., queen triggerfish, *Balistes vetula*) have never been manipulated. Across the 25-year study, we conducted visual surveys on the natural patch reefs over 22 years and on the artificial and translocated reefs over 15 years. Surveys were conducted during the day when two divers using SCUBA counted all *D. antillarum* on the reefs, thoroughly inspecting all holes and crevices with the aid of a dive light to ensure that all urchins were counted.

We used generalized linear mixed models (GLMM) to describe the change in urchin density as a function of the fixed effect of time (years) and the random effect of reef identification. We conducted a separate analysis for natural patch, artificial, and translocated reefs because we were interested in the change in *D. antillarum* density over time, controlling for reef types. See Appendix I for a full description of our statistical methods and *R* packages used. All analyses were conducted within the *R* statistical environment (R Core Team 2021, version 4.1.2).

Results and discussion

Over the 25-year study period, we observed the lowest densities, mostly < 1 urchin m⁻², during the first 10 years of monitoring (i.e., the 1990s) and then higher *D. antillarum* densities in the 2000s (Fig. 2). Several recruitment pulses occurred in the 1990s (Fig. 2ab), but these episodic events did not result in sustained population growth, similar to pulses observed in St. Croix (Miller et al. 2003), Panama, and the Florida Keys (reviewed by Lessios 2016). Sustained population growth developed toward the end of our study, despite persistent low densities on the natural patch and translocated reefs in 2015 (Fig. 2a b) that did not affect the overall pattern. The high variation among reefs is not surprising given the small size of individual reefs, and is likely representative of reefs in this region which is dominated by small patch reefs. We found a significant population growth rate of *D. antillarum* on the natural patch and translocated reefs (Fig. 2, Supplemental Tables 1, 2). On natural patch reefs, *D. antillarum* density increased on average by 8% per year (95% confidence interval [CI]: 4%–14%), while on translocated reefs they increased by 17% per year (95% CI: 9%–26%). While some of the highest densities were observed on the artificial reefs, we did not detect a significant increase in *D. antillarum* on them (Fig. 2b). Yet, we did document large local population pulses in 1996 and 2015 (Fig. 2b). This pattern may be due to the cinder block construction that created numerous holes in a small area

● Natural Patch Reef

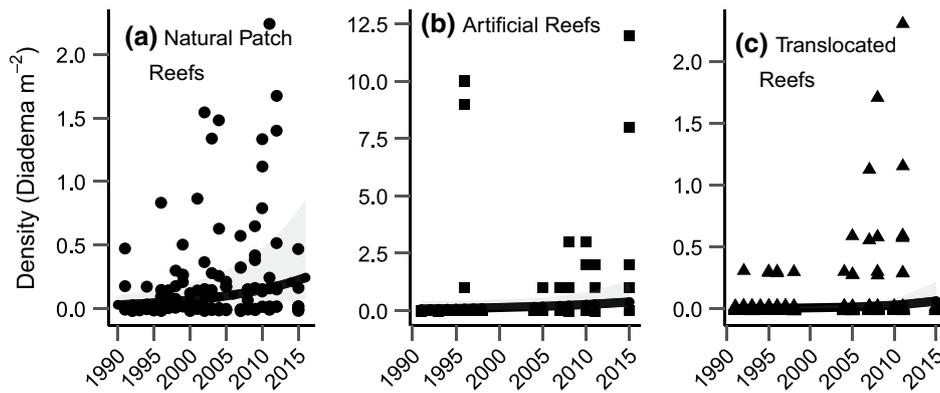

■ Artificial Reef
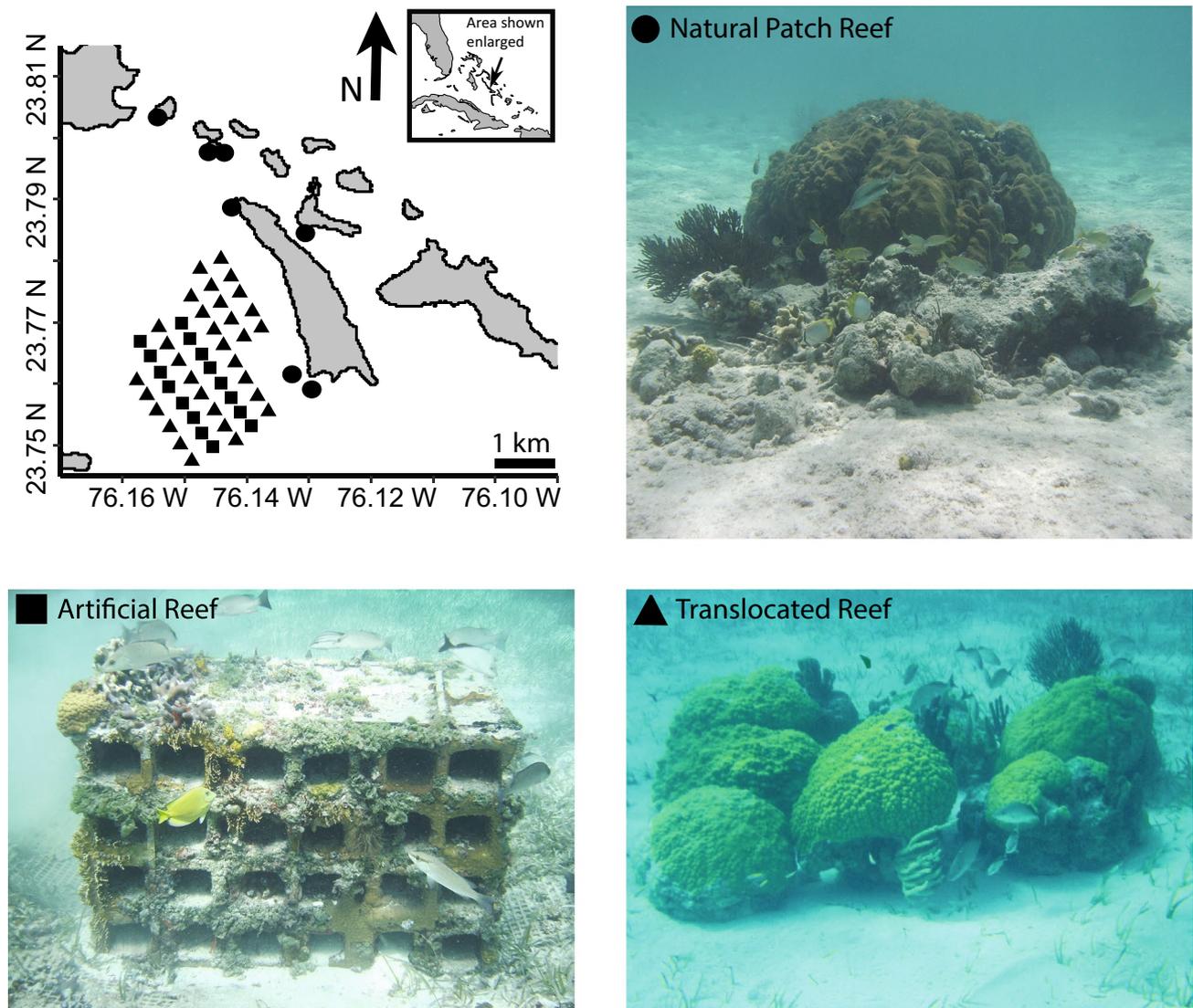
▲ Translocated Reef

Fig. 1 Map of study locations in the Bahamas and photographs of example reef types that show natural patch reefs (circles), artificial (square), and translocated (triangles) reefs. At the map scale, three of the natural patch reefs appear as overlapping circles, and extra spacing was included for visualization of the artificial and translocated reefs

(Fig. 1). At the end of our study, the observed mean densities were 0.24 urchins m^{-2} (95% CI: 0.03–1.76) on natural patch reefs, 0.38 urchins m^{-2} (95% CI: 0.11–1.32) on artificial reefs, and 0.06 urchins m^{-2} (95% CI: 0.02–0.22) on translocated reefs. In comparison, pre-mortality densities of *D. antillarum* in the Bahamas ranged from < 1 urchin m^{-2} (Hay 1984) to 2.9 urchins m^{-2} (Bauer 1980), both higher than our mean densities. Though not directly quantified in their reports, both Ray (1958) and Newell et al. (1959) included photographs that showed clearly high densities of *D. antillarum*, and Newell et al. (1959) qualitatively described the urchins as being "abundant." Nonetheless, we observed higher urchin densities on all reef types during our study than the first post-mortality census of 0.006 urchins m^{-2}

from 1997–1998 (Kramer 2003) and 0.04 urchins m^{-2} in 2007 (Harborne et al. 2009). Although not from our specific study location, the previously reported densities from throughout the Bahamas suggest general patterns and trends for the region and represent the best available comparison. More surveys on larger reef systems across the entire Bahamas, as well as the greater Caribbean, would provide a clearer trend of *D. antillarum* populations in the region. Nevertheless, our study is the first to document a long-term trend in urchin density in the Bahamas, which indicated the start of a recovery.

The slow pace of recovery of *D. antillarum* populations in the Bahamas could be due to a number of abiotic or biotic factors. Successful recruitment, driven by upstream

Fig. 2 *Diadema antillarum* density across the 25-year study period at each **a** natural patch reef—circles, **b** artificial reef—squares, and **c** translocated reef—triangles. Solid black curves show the prediction based on the model from Table 2 with 95% confidence intervals shown with the gray shaded regions. Points jittered to avoid overlap for visualization. Surveys were not conducted in years without data points

larval sources, larval survival, successful settlement, and juvenile survival are all critically important. Given the moderate isolation between the Bahamas and the Caribbean (e.g., Cowen et al. 2006, Galindo et al. 2006; but see Schill et al. 2015), there may be few upstream larval sources. Thus, it is unlikely that the growing populations in Jamaica or St. Croix would serve as a larval source based on prevailing ocean currents (Lessios et al. 1984; Lessios 1988). Self-recruitment from local populations in the Exuma Sound may be the best source to sustain the population in the future (Colin 1995), due to its importance for other species in this region: the bicolored damselfish *Stegastes partitus* (Pusack et al. 2014; Johnson et al. 2018) and the spiny lobster *Panulirus argus* (Lipcius et al. 2001; Stockhausen and Lipcius 2001). Therefore, it is likely that low adult *D. antillarum* densities in the Exuma Sound have limited capacity for rapid recovery, and improved population growth will require populations to reach larger sizes.

Recovery of *D. antillarum* is also influenced by factors affecting juvenile survival, such as availability of suitable habitat (Miller et al. 2003; Debrot and Nagelkerken 2006), and post-settlement predation (Harborne et al. 2009; Williams et al. 2011). Most of the individuals we recorded were adults, with only 0.04% being juveniles. The rarity of juveniles on our study reefs suggests that settlement has been low and possibly limited to other shallow, wave-protected back reefs or lagoons (Debrot and Nagelkerken 2006), which are numerous in the Bahamas. We observed *D. antillarum* predators (e.g., *Balistes* spp. triggerfishes) primarily on the translocated reefs compared to our other reef types. The densities of these predators were inversely related to that of *D. antillarum* with a clear decline in total abundance of *B. vetula* during the study (Supplemental Fig. 1). Thus, triggerfishes and other predators that consume urchins may have played a role in limiting

the recovery of *D. antillarum* populations, but it is unclear to what extent.

In spring 2022, widespread mortality of *D. antillarum* was first reported in St. Thomas and subsequent reports occurred throughout the Antilles (AGRRA 2022). There have not been any reports of this ongoing die-off in the Bahamas, but if it happens, then recovery in the region will likely slow or even reverse. Documenting new occurrences of death or recovery of *D. antillarum* across the Caribbean and tropical western Atlantic is critical for management of coral reefs. As an important herbivore on overfished and degraded coral reefs, larger densities of *D. antillarum* can reduce macroalgal cover (e.g., Carpenter and Edmunds 2006; Williams 2021). We did not quantify algal cover on the natural patch reefs, but qualitative notes suggest an inverse relationship with *D. antillarum* densities. However, we also occasionally observed little to no algae on reefs lacking *D. antillarum* and reefs covered in algae that had moderate to high urchin densities. Combining long-term monitoring of *D. antillarum* with corresponding data such as predator abundance and benthic habitat composition will help identify factors that promote urchin recovery and better understand how coral reef systems ultimately respond. Collecting more data from the Bahamas and other locations peripheral to the Caribbean Sea will elucidate the long-term population dynamics of this ecologically important species. This task is especially critical considering the potential of another large-scale die-off that may be starting. Large decline in *D. antillarum* would likely result in increased macroalgal cover and further stress to already degraded Caribbean coral reefs.

Conflict of interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Declarations

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