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**30 Abstract**

31 In 1983-1984, an unknown waterborne pathogen caused the mass mortality of long-spined sea  
32 urchin (*Diadema antillarum*) across the Caribbean and western tropical Atlantic. After  
33 approximately 15 years, urchin populations began to recover at some locations, yet few have  
34 reached pre-mortality densities. To date, no study has documented a recovery in the western  
35 tropical Atlantic outside of the Caribbean. Over a 25-year period (1991-2015) we documented an  
36 8-17% population growth rate of *D. antillarum* in the central Bahamas. However, our mean  
37 observed densities, 0.06-0.38 urchins m<sup>-2</sup>, remained below pre-pandemic levels. Combined with  
38 observations from other locations in the Caribbean, it appears that *D. antillarum* populations are  
39 increasing, yet have not fully recovered from their 1980s mass mortality throughout much of  
40 their geographic range.

**42 Introduction**

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

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4 53           During the four decades since the die-off, recovery of *D. antillarum* has been slow and  
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6 54   variable. Among other factors such as low post-settlement survival (Williams et al. 2011), the  
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9 55   presumed reason for the slow recovery has been an absence of source populations resulting in  
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11 56   minimal larval production (Lessios 1988, 1995, Miller et al. 2009). In the mid to late 1990s,  
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14 57   approximately 15 years after the die-off, recovery began in several isolated locations. For  
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16 58   example, in Jamaica *D. antillarum* increased to pre-mortality densities around 2000 (Edmunds  
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18 59   and Carpenter 2001), but with local variability (Cho and Woodley 2000). The increasing  
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21 60   densities of *D. antillarum* in Jamaica corresponded with both a large reduction in macroalgae  
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23 61   abundance (Edmunds and Carpenter 2001) and increased survival and faster growth of  
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25 62   scleractinian corals (Idjadi et al. 2010). Beyond Jamaica, the recovery of urchin populations has  
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27 63   been slower, e.g. Barbados, St. Croix, (Miller et al. 2003), and Puerto Rico (Tuohy et al. 2020),  
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29 64   with many populations still below pre-mortality densities. Other locations, such as the Florida  
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31 65   Keys (Chiappone et al. 2002; Miller et al. 2009) and Panama (Lessios 2005), have not  
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33 66   experienced any observed recovery, potentially due to low or inconsistent recruitment.  
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38 67           The majority of studies on *D. antillarum* populations have occurred within the Caribbean  
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40 68   Sea proper (Carpenter and Edmunds 2006), and to date, there has been no documentation of  
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42 69   urchin recovery outside of this region (i.e., in the greater tropical western Atlantic). The  
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44 70   Bahamian Archipelago, located adjacent to and northeast of the Caribbean region, had notable  
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46 71   population sizes of *D. antillarum* consistent with those observed across the broader region prior  
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48 72   to the mass mortality event (Ray 1958; Newell et al. 1959; Bauer 1980; Hay 1984), but densities  
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50 73   have remained low through the 2000s (Harborne et al. 2009). The goal of this study was to  
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52 74   examine changes in the density of *D. antillarum* in the central Bahamas over a 25-year period  
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54 75   from 1991 to 2015.  
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4 **76 Methods**

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6 77 We recorded *D. antillarum* abundances on three types of shallow (<5 m depth) patch  
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8 78 reefs during the early summer from 1991 to 2015 as part of annual surveys of the regional reef  
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10 79 community. These surveys recorded all vertebrates, several invertebrate species (e.g., urchins,  
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12 80 lobster), as well as unquantified descriptions of other notable features. Reefs were located within  
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14 81 7 km of Lee Stocking Island, Bahamas (Fig. 1) and ranged in size from 1.0-13.1 m<sup>2</sup>. The first  
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16 82 type of reef, hereafter natural patch reefs (n = 9), were coral bommies (6.0 – 13.1 m<sup>2</sup>, 9.4 ± 1.3  
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18 83 [mean ± standard error]) found on sand and limestone benches at depths between 2 to 4 m. Each  
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20 84 was approximately 50 m from the nearest adjacent reef, and remained unmanipulated for the  
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22 85 entire 25-year period. The other types of reefs formed an experimental array (established in the  
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24 86 early 1990s) of 1 m<sup>2</sup> concrete-block artificial reefs (n=16) and 3.5 m<sup>2</sup> translocated coral patch  
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26 87 reefs (n=32) arranged in a sand-seagrass flat with each reef at least 200 m from the nearest reef.  
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28 88 The artificial reefs rapidly became colonized by corals, sponges, and other benthos as well as  
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30 89 fishes (Carr and Hixon 1997). The translocated patch reefs consisted of ≥ 0.5 m diameter coral  
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32 90 heads of *Orbicella annularis* and *Porites astreoides* (see Carr and Hixon 1995 & Hixon and Carr  
33  
34 91 1997 for a full description). While the experimental array has been used for experimental  
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36 92 manipulations of reef fishes (e.g., Hixon and Carr 1997), *D. antillarum* and their predators (e.g.,  
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38 93 queen triggerfish, *Balistes vetula*) have never been manipulated. Across the 25-year study, we  
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40 94 conducted visual surveys on the natural patch reefs over 22 years and on the artificial and  
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42 95 translocated reefs over 15 years. Surveys were conducted during the day when two divers using  
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44 96 SCUBA counted all *D. antillarum* on the reefs, thoroughly inspecting all holes and crevices with  
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46 97 the aid of a dive light to ensure all urchins were counted.  
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4 98 We used generalized linear mixed models (GLMM) to describe the change in urchin  
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6 99 density as a function of the fixed effect of time (years) and the random effect of reef  
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9 100 identification. We conducted a separate analysis for natural patch, artificial, and translocated  
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11 101 reefs because we were interested in the change in *D. antillarum* density over time, controlling for  
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14 102 reef types. See Appendix I for a full description of our statistical methods and *R* packages used.  
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16 103 All analyses were conducted within the *R* statistical environment (R Core Team 2021, version  
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19 104 4.1.2).  
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## 22 23 106 **Results and Discussion**

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26 107 Over the 25-year study period, we observed the lowest densities, mostly  $< 1$  urchin  $m^{-2}$ ,  
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28 108 during the first 10 years of monitoring (i.e., the 1990s) and then higher *D. antillarum* densities in  
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31 109 the 2000s (Fig. 2). Several recruitment pulses occurred in the 1990s (Fig 2ab), but these episodic  
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34 110 events did not result in sustained population growth, similar to pulses observed in St. Coix  
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36 111 (Miller et al. 2003), Panama, and the Florida Keys (reviewed by Lessios 2016). Sustained  
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38 112 population growth developed towards the end of our study, despite persistent low densities on  
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41 113 the natural patch and translocated reefs in 2015 (Fig 2ab) that did not affect the overall pattern.  
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43 114 The high variation among reefs is not surprising given the small size of individual reefs, and is  
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46 115 likely representative reefs in this region which is dominated by small patch reefs. We found a  
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48 116 significant population growth rate of *D. antillarum* on the natural patch and translocated reefs  
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51 117 (Fig. 2, Supplemental Table 1,2). On natural patch reefs, *D. antillarum* density increased on  
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53 118 average by 8% per year (95% Confidence Interval [CI]: 4%–14%), while on translocated reefs  
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56 119 they increased by 17% per year (95% CI: 9%–26%). While some of the highest densities were  
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58 120 observed on the artificial reefs, we did not detect a significant increase of *D. antillarum* on them  
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4 121 (Fig 2b). Yet, we did document large local population pulses in 1996 and 2015 (Fig 2b). This  
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6 122 pattern may be due to the cinder block construction that created numerous holes in a small area  
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9 123 (Fig. 1). At the end of our study, the observed mean densities were 0.24 urchins m<sup>-2</sup> (95% CI:  
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11 124 0.03–1.76) on natural patch reefs, 0.38 urchins m<sup>-2</sup> (95% CI: 0.11–1.32) on artificial reefs, and  
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13 125 0.06 urchins m<sup>-2</sup> (95% CI: 0.02–0.22) on translocated reefs. In comparison, pre-mortality  
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15 126 densities of *D. antillarum* in the Bahamas ranged from <1 urchin m<sup>-2</sup> (Hay 1984) to 2.9 urchins  
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17 127 m<sup>-2</sup> (Bauer 1980), both higher than our mean densities. Though not directly quantified in their  
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19 128 reports, both Ray (1958) and Newell et al. (1959) included photographs that showed clearly high  
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21 129 densities of *D. antillarum*, and Newell et al. (1959) qualitatively described the urchins as being  
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23 130 “abundant.” Nonetheless, we observed higher urchin densities on all reef types during our study  
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25 131 than the first post-mortality census of 0.006 urchins m<sup>-2</sup> from 1997-1998 (Kramer 2003) and 0.04  
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27 132 urchins m<sup>-2</sup> in 2007 (Harborne et al. 2009). Although not from our specific study location, the  
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29 133 previously reported densities from throughout the Bahamas suggest general patterns and trends  
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31 134 for the region and represent the best available comparison. More surveys on larger reef systems  
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33 135 across the entire Bahamas, as well as the greater Caribbean, would provide a clearer trend of *D.*  
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35 136 *antillarum* populations in the region. Nevertheless, our study is the first to document a long-term  
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37 137 trend in urchin density in the Bahamas, which indicated the start of a recovery.

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39 138         The slow pace of recovery of *D. antillarum* populations in the Bahamas could be due to a  
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41 139 number of abiotic or biotic factors. Successful recruitment, driven by upstream larval sources,  
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43 140 larval survival, successful settlement, and juvenile survival are all critically important. Given the  
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45 141 moderate isolation between the Bahamas and the Caribbean (e.g. Cowen et al. 2006, Galindo et  
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47 142 al. 2006; but see Schill et al. 2015), there may be few upstream larval sources. Thus, it is  
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49 143 unlikely that the growing populations in Jamaica or St. Croix would serve as a larval source  
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144 based on prevailing ocean currents (Lessios et al. 1984; Lessios 1988). Self-recruitment from  
145 local populations in the Exuma Sound may be the best source to sustain the population in the  
146 future (Colin 1995), due to its importance for other species in this region: the bicolored  
147 damselfish *Stegastes partitus* (Pusack et al. 2014; Johnson et al. 2018) and the spiny lobster  
148 *Panulirus argus* (Lipcius et al. 2001; Stockhausen and Lipcius 2001). Therefore, it is likely that  
149 low adult *D. antillarum* densities in the Exuma Sound have limited capacity for rapid recovery,  
150 and improved population growth will require populations to reach larger sizes.

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

163         In spring 2022, widespread mortality of *D. antillarum* were first reported in St. Thomas  
164 and subsequent reports occurred throughout the Antilles (AGRRA 2022). There have not been  
165 any reports of this ongoing die-off in the Bahamas, but if it happens, then recovery in the region  
166 will likely slow or even reverse. Documenting new occurrences of death or recovery of *D.*

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167 *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  
declines of *D. antillarum* would likely result in increased macroalgal cover and further stress to  
already degraded Caribbean coral reefs.

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4 Figure 1. Map of study locations in the Bahamas and photos of example reef types that show  
5 natural patch reefs (circles), artificial (square), and translocated (triangles) reefs. At the map  
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7 scale, three of the natural patch reefs appear as overlapping circles, and extra spacing was  
8  
9 included for visualization of the artificial and translocated reefs.  
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16 Figure 2. *Diadema antillarum* density across the 25-year study period at each (a) natural patch  
17 reef – circles, (b) artificial reef – squares, and (c) translocated reef – triangles. Solid black curves  
18 show the prediction based on the model from Table 2 with 95% confidence intervals shown with  
19 the grey shaded regions. Points jittered to avoid overlap for visualization. Surveys were not  
20 conducted in years without data points.  
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31 Supplemental Figure 1. *Balistes vetula* per reef on the translocated reefs from 1991 to 2011.  
32 Surveys were not conducted in years without data points.  
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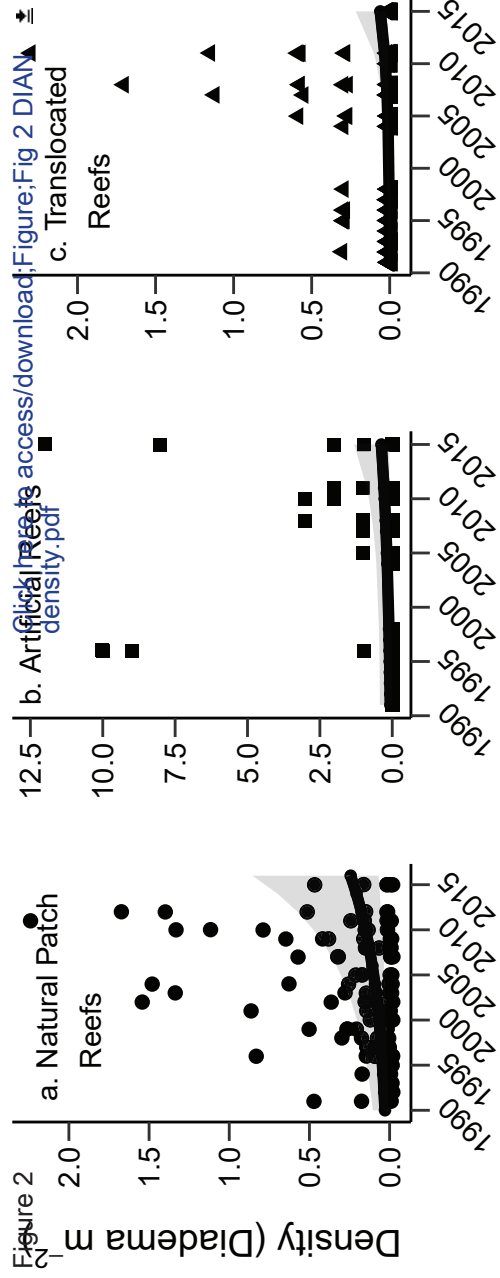
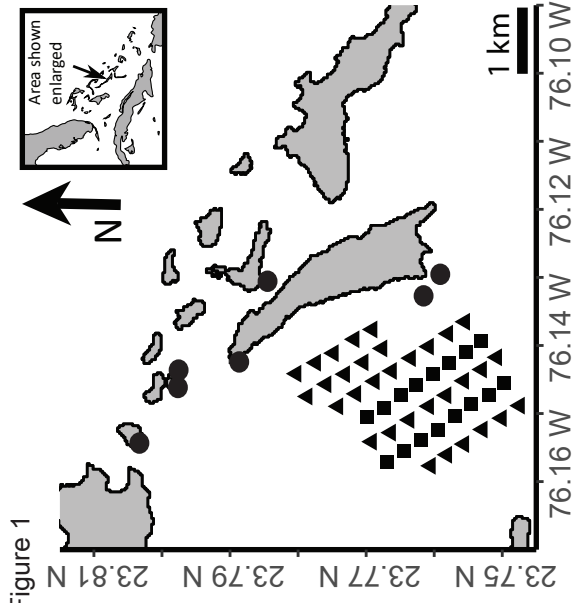


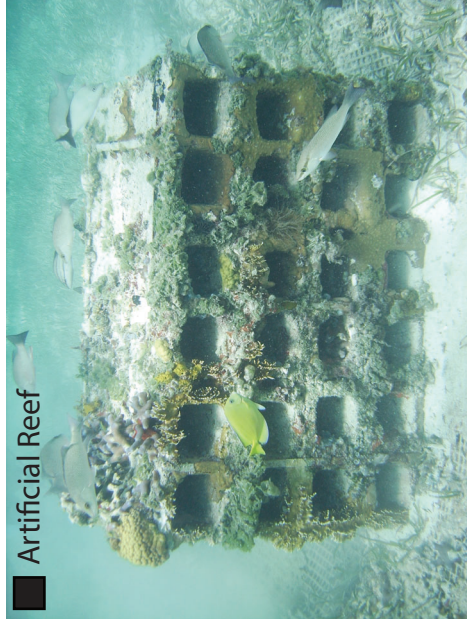
Figure 1



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ma Natural Patch Reef

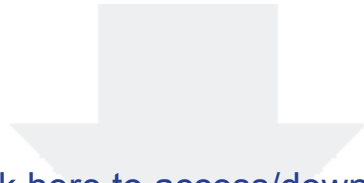


Artificial Reef

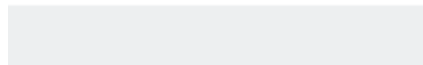


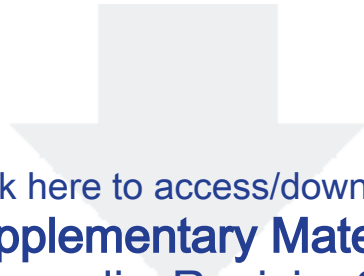
Translocated Reef





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