Diadema antillarum on St. Croix, USVI: Current Status and Interactions with Herbivorous Fishes

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The 1983-84 mass mortality of the long-spined sea urchin, Diadema antillarum, intensified the loss of herbivory that was a major factor in the degradation of coral reefs in the wider Caribbean. As determined from recent surveys, densities of D. antillarum populations at back reef locations on St. Croix, US Virgin Islands, are higher than densities immediately following the die-off – but still about an order of magnitude below pre-die-off densities and patchy in both time and space. Comparisons to similar surveys during the past twelve years and to earlier historical records indicate that recovery on St. Croix continues at the very slow rate that typified the first decade after the mass mortality. Populations of herbivorous fishes on St. Croix surged following the D. antillarum die-off but have experienced heavy fishing pressure ever since then. Reciprocal densities of D. antillarum versus roaming grazers (parrotfishes and surgeonfishes) on survey transects and stationary point counts indicate that negative interaction between these two groups is present despite the reductions to their populations during the last 35 years.

INTRODUCTION

Since the early 1980s, macroalgae have been replacing corals on Caribbean reefs – a phase shift more rapid and widespread than anything observed in the Caribbean fossil record [1]. Structural complexity has been reduced as algae-covered skeletons of branching Acropora and massive Orbicella (Montastrea) and Diploria corals are further degraded through bioerosion and wave action, leading to reduced diversity of the vertebrate and invertebrate inhabitants [2-5].

Reduced herbivory is an unequivocal promoter of algal growth. When herbivores, such as parrotfishes, surgeonfishes, and the sea urchin Diadema antillarum Philippi, 1845, are excluded, experimental plots are quickly overgrown by macroalgae [6,7]. The harvesting of many large parrotfishes and surgeonfishes contributes to the transition to macroalgal dominance by reducing the size structure of these grazers to mostly small individuals that are unable to constrain macroalgae growth [8,9]. Overharvest of herbivorous fishes may even be responsible for the high densities of D. antillarum observed shortly before the 1983-84 mass mortality event [10], and it is likely that the role of D. antillarum in limiting macroalgae became more important as herbivorous fishes declined in size and numbers. When D. antillarum populations suffered the famous mass mortality, herbivory...
was reduced to negligible levels and macroalgae surged [11]. More recently, where _D. antillarum_ has shown some recovery, macroalgae have declined and coral settlement has increased [12], but this has occurred in only a few locations [13,14].

Before the mass mortality and overharvesting, _D. antillarum_ and grazing fishes were strong competitors. When _D. antillarum_ were removed from experimental sites, parrotfishes and surgeonfishes showed significant increases, and densities of these grazing fishes declined as _D. antillarum_ recolonized the sites [15]. Adult populations of two surgeonfish species increased significantly on Panamanian reefs after the mass mortality of _D. antillarum_ [16] and herbivory by parrotfishes and surgeonfishes increased immediately following the mass mortality of _D. antillarum_ on St. Croix [17,18]. Few studies have examined the status of this competitive interaction since the mass-mortality.

We have examined densities of both _D. antillarum_ and herbivorous fishes using both transect surveys and stationary point counts on St. Croix, USVI, in order to: (1) Determine the current state of recovery of _D. antillarum_ and, (2) Explore the current relationship between populations of _D. antillarum_ and herbivorous fishes.

**MATERIALS AND METHODS**

**Transect Surveys**

As part of an ongoing survey of _D. antillarum_ recovery on St. Croix, USVI, SCUBA divers conducted surveys using haphazardly placed 25 x 2m transects at four back-reef sites from May 29 to June 13, 2013 (Figure 1). Rod Bay, Columbus Landing, and Turner Hole are part of a long-term study of _D. antillarum_ recovery [19-21]. Split Cove was added in 2013 to increase geographic coverage of that monitoring study. The number of transects placed varied due to surface conditions at the time surveys occurred and ranged from 10 at Split Cove and Turner Hole to 11 at Rod Bay and 12 at Columbus Landing. On April 1 and 2, 2016, five additional transects were carried out at Rod Bay and 11 were carried out at Columbus Landing.

To determine whether competitive interactions between _Diadema_ and herbivorous fishes could be influencing population densities, all fishes moving through an area 1m to either side of the transect line and 1m above the transect line were identified and enumerated by two divers before counting _Diadema_. Patchiness of _Diadema_ along most transects – with sections of high and low densities – makes this a weak method for the detection of any density complementarity.

**Stationary Point Counts**

To look for density complementarity of _D. antillarum_ and herbivorous fishes at a scale more commensurate with _Diadema_ dispersion, counts were made of _Diadema_ and fishes in stationary 1m-radius circles. Each point count circle was centered in a larger circle (1.5m radius) that could be characterized as either _D. antillarum_-dense (>

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Figure 1. Location of St. Croix U.S. Virgin Islands in the Caribbean Sea and our study sites on the eastern half of the island. CB = Cane Bay, CL = Columbus Landing, TB = Teague Bay, SC = Split Cove, TH = Turner Hole, RB = Rod Bay.
15 urchins) or D. antillarum-sparse (< 5 urchins), so that the full range of D. antillarum was included. All herbivorous parrotfishes, surgeonfishes, and damselfishes that entered a circle were counted, and then the Diadema were counted. On April 3, 2016, snorkelers conducted eight stationary point counts at a single location – Cane Bay – to minimize environmental differences among count circles that might effect densities of fishes or Diadema (a ninth count was discarded when it was discovered that the selected point included a cleaning station where many surgeonfishes were visiting to be cleaned).

**Data Analysis**

Comparison of the density of D. antillarum among sites was performed using One-way ANOVA in the Systat 11 Statistics package, with SITES as the independent variable and Diadema per m² as the response variable and transects as the units of analysis. Density relationships between D. antillarum and roaming herbivorous fishes and between D. antillarum and territorial fishes were analyzed using linear regression in Microsoft Excel, with number of Diadema as the independent variable and number of territorial fish herbivores as the dependent variable in one analysis, and roaming fish grazers as the dependent variable in a separate analysis.

**RESULTS**

**Recovery of D. antillarum on St. Croix**

Data on D. antillarum densities in 2013 contribute to a general picture of irregular and asynchronous fluctuations observed since monitoring began in 2000 (Figures 1 and 2). As in previous years, Diadema were patchily distributed in 2013, with significant differences among sites (ANOVA: F = 14.06, df = 3, p = 0.000), and with similar values for mean density and standard deviation for transects in any given site. Highest densities were at Columbus Landing (0.94 individuals per m², SD = 0.480) and the lowest densities at Split Cove (0.02 individuals per m², SD = 0.029). At Rod Bay and Columbus Landing, D. antillarum densities increased compared to the most recent prior surveys (in 2010), while in Turner Hole densities declined compared to the most recent survey in that area (in 2008). The pattern of temporal variation continues into the 2016 sampling (Figure 2): D. antillarum densities at Columbus Landing were unchanged at 0.70 individuals per m² (SD = 0.622) while densities at Rod Bay increased to 1.15 individuals per m² (SD = 0.757). While these temporal variations are considerable, it appears that populations in the surveyed areas have recovered, overall, to about 0.1/m² since the die-off, and despite wide variation from year to year, at no time have all densities dropped all the way back to immediate post-mortality levels. It is more striking that during the last 16 years, overall densities of D. antillarum in the surveyed area, although higher
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Figure 3. (a) Total number of roaming grazers versus number of D. antillarum and (b) Total number of territorial fish herbivores versus number of D. antillarum (b) on 42 transects (2m x 25m) at four sites on St. Croix, USVI. The study sites are denoted [ Split Cove ( ○ ), Turner Hole ( □ ), Rod Bay ( ◊ )]. Least squares regression performed on untransformed data indicates a low, but significant slope in 3a: (y = - 0.4163x + 31.82, R² = 0.08, p = 0.033) and a slope that was not significant in 3b: (y = -0.0077x + 9.588, R² = 0.0006, p = 0.86).

than recorded immediately after the 1983 die-off, are still an order of magnitude below the densities observed prior to the mass mortality event, and that the amount of variation from site to site and from year to year are enormous (Figure 2) [19-21].

Grazing fishes/D. antillarum complementarity on St. Croix

Transect Surveys

Numerous herbivorous fishes were found at all sites (36.9 fish m⁻² to 63.7 fish m⁻²), although densities and species composition differed among sites and among transects within sites. A negative association between density of grazing fishes and density of D. antillarum was observed among sites. As expected the relationship between fish and D. antillarum densities were different for roaming grazers compared to the territorials. We found a significant negative relationship between roaming herbivorous fishes and D. antillarum among transects (least squares regression; y = -0.42x + 31.82, R² = 0.08, p = 0.033) (Figure 3a). Least squares regression analysis of total numbers of densities of territorial herbivorous damselfishes and D. antillarum were not significantly associated (least squares regression; y = - 0.0077x + 9.588, R² = 0.0006, p = 0.86) (Figure 3b). Together these analyses suggest that the presence of D. antillarum appears to have no effect on territorial herbivorous fishes, but could be negatively affecting roaming grazers.

Point Counts

The eight stationary point counts again revealed a significant negative association between roaming herbivorous fishes and D. antillarum (least squares regression; y = -0.61x + 27.30, R² = 0.57, p = 0.030) (Figure 4a). In addition, territorial herbivorous damselfishes were significantly associated with D. antillarum (least squares regression; y = 1.12x + 7.66, R² = 0.60, p = 0.024) (Figure 4b).

Discussion

In the areas we have surveyed on St. Croix, densities of D. antillarum are still less than ten percent of those prior to the mass mortality event, despite a nearly ten-fold increase of D. antillarum since the 1983-84 die-off. Since surveys began sixteen years ago, population densities on St. Croix have shown large variations among sites over...
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by Robertson, et al. [23], suggesting that grazing defended damselfish territories may not be worthwhile now that algae are flourishing and competitive pressure is low. Despite the changes in size, abundance, and behavior in both urchins and parrotfishes/surgeonfishes we found that densities of D. antillarum and grazing fishes are inversely related. Why should complementarity of these herbivores persist when exploitation of their common resource has become so low?

We are proposing here that spatial avoidance – practiced by parrotfishes and surgeonfishes but not damselfishes – now underlies the reciprocal densities of D. antillarum and herbivorous fishes. As in the past, the present negative interaction between roaming grazers and D. antillarum seems to have greater impact on the fishes than on the urchin. Studies conducted prior to and during the mass mortality [16-18,21] strongly support the position that abundant D. antillarum suppressed population densities of herbivorous fishes, with parrotfishes and surgeonfishes especially inhibited. Small parrotfishes and surgeonfishes may avoid areas where D. antillarum are present, not because there is no food to consume, but

Figure 4. (a) Total number of roaming fish grazers versus number of D. antillarum and (b) total number of territorial fish herbivores versus number of D. antillarum during 8 stationary point counts (1m radius, 15-minute observation) at Cane Bay on St. Croix, USVI. The point counts revealed a significant negative association between roaming herbivorous fishes and D. antillarum [least squares regression (4a); y = -0.61x + 27.30, R² = 0.57, p = 0.030]. In addition, territorial herbivorous damselfishes were significantly associated with D. antillarum [least squares regression (4b); y = 1.12x + 7.66, R² = 0.60, p = 0.024].

Diadema antillarum continues to interact significantly with roaming herbivorous parrotfishes and surgeonfishes on St. Croix despite the combination of severe reduction in abundance of D. antillarum due to mass mortality and gradual decline in size of herbivorous fishes due to fishing pressures [10]. Anecdotally, during our 2013 surveys on St. Croix we rarely observed surgeonfishes larger than 21 centimeters or parrotfishes larger than 36 centimeters, and most were juveniles smaller than 10 cm (JIO and JPE, pers. obs.), and we saw no raids inside damselfish territories by groups of juvenile parrotfishes as observed by Robertson, et al. [23], suggesting that grazing defended damselfish territories may not be worthwhile now that algae are flourishing and competitive pressure is low. Despite the changes in size, abundance, and behavior in both urchins and parrotfishes/surgeonfishes we found that densities of D. antillarum and grazing fishes are inversely related. Why should complementarity of these herbivores persist when exploitation of their common resource has become so low?

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because the foraging is suboptimal when compared with sites not containing *D. antillarum*. Damselﬁshes, on the other hand, discourage *D. antillarum* from entering their algal gardens [24–26], and the territories are so small (ca. 1.0 m$^2$) [27] that each transect has ample unguarded area available for the low numbers of *D. antillarum*. The positive association between *D. antillarum* and territorial damselﬁshes found for stationary point counts at Cane Bay may also be understood in these terms: For damselﬁshes, direct competition from *D. antillarum* is less important than the indirect beneﬁt derived from reductions in densities of competing parrotﬁshes and surgeonﬁshes. In our backreef/lagoon sites, only the most mobile component of the grazing guild, the roaming parrotﬁshes and surgeonﬁshes, seems to be responding to this negative effect of competition at the scales examined here (transsects and point counts: <= 50 m$^2$). In comparisons at much larger scales, Rogers and Lorenzen [28] have determined that competition with herbivorous ﬁshes may help to account for the much slower and more variable recovery of *Diadema* on fore-reefs as compared to back-reef/lagoonal habitats.

This study indicates that the recovery of *D. antillarum* from the massive mortality event of 1983 continues to be slow and patchy along northern and eastern coasts of St. Croix. *D. antillarum* has not recovered enough to facilitate a reversal of the coral-to-macroalgal phase shift at any of the sites we have monitored on St. Croix. Lack of full recovery seems to characterize many other locations throughout the Caribbean, with current *D. antillarum* densities of 0.1 to 5.0 urchins/m$^2$ [10,14,19,21,29–42] though the reasons behind this lack of recovery are still unknown. Even though the increased densities of *D. antillarum* since the mass mortality have been sufﬁcient to facilitate a reversal to coral dominance at our research areas on St. Croix, the reduced populations of *D. antillarum* and grazing ﬁshes appear to be interacting competitively, as described prior to the mass mortality and more recently in back-reef sites in Curaçao [43] where *Diadema* are beginning to recover.

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