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Population status of the urchin *Diadema antillarum* in the Florida Keys 25 years after the Caribbean mass mortality

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Abstract. The 1983-84 Caribbean-wide mortality of the urchin *Diadema antillarum* Philippi was followed by a second mortality event in the Florida Keys in 1991. The demise of this once ubiquitous herbivore is one factor contributing to wider Caribbean reef change during the past 25 years. Over an 8-year period from 1999-2007, we examined densities and test sizes of *D. antillarum* at 786 sites from the northern extent of the Florida Reef Tract to the Dry Tortugas, including two National Parks and the Florida Keys National Marine Sanctuary. Visual surveys along belt transects were used to enumerate individuals and test sizes in a two-stage stratified random sampling design that incorporated cross-shelf benthic habitats, geographic regions, and no-fishing management zones. While pre-1983 densities were as high as 5 individuals/m^2, surveys since 1999 from < 1 m to 27 m depth show that current densities are still well below 1 individual/m^2. During seven different annual sampling periods, the maximum site-level density was only 0.33 individuals/m^2, with the highest densities of larger (> 5 cm test diameter) individuals reported from only a few locations. The relative contributions of larval survivorship, predation, suitable recruitment sites, and reduced fertilization success to *Diadema* recovery are still largely unknown.

Key words: Benthic, *Diadema*, marine protected area, stratified sampling, urchin.

Introduction

The 1983-84 Caribbean-wide mass mortality of the long-spined sea urchin *Diadema antillarum* represents one of the most spatially expansive and prolonged disturbances to reef ecosystems in the region (Carpenter 1988; Lessios 1988, 2005). Prior to the mass mortality event, *D. antillarum* attained high (>20 per m^2) densities in many Caribbean reef areas (Lessios 1988), but urchin abundances declined by several orders of magnitude and have remained in this state over two decades later (Lessios 2005; Weil et al. 2005; Debrot and Nagelkerken 2006). Together with physical impacts from storms, coral disease outbreaks, and severe bleaching episodes (Gardner et al. 2003), the reduction in urchin densities has had severe consequences in terms of coral-algal dominance patterns (Carpenter 1988; Lessios 1988).

In the Florida Keys, the few historical data available prior to 1983-84 indicate that *Diadema antillarum* densities were lower (up to 4-5 per m^2) (Kier and Grant 1965; Bauer 1976, 1980). However, still a general trend of increased algal cover was apparent after the urchin mortality at several Florida Keys reefs (Jaap et al. 1988; Porter and Meier 1992). Seven years after the 1983-84 event, a second disease event in the Florida Keys, after initially modest recovery to 0.30-0.58 individuals/m^2, once again depressed *D. antillarum* densities to < 0.01 individuals/m^2 (Forcucci 1994). Large-scale surveys of urchin densities across the south Florida during 1999-2001 confirmed this pattern of poor recovery (Chiappone et al. 2001, 2002).

Since the mass mortality, limited to moderate recovery in *Diadema antillarum* populations has been reported in some Caribbean reef areas (Lessios 2005; Carpenter and Edmunds 2006; Debrot and Nagelkerken 2006), but this has not occurred in the Florida Keys (Chiappone et al. 2002; Lazar et al. 2005). It is anticipated that *D. antillarum* recovery will help to promote coral recruitment and a return to pre-mortality baseline reef conditions (Carpenter and Edmunds 2006; Macia et al. 2007; Myhre and Acevedo-Gutierrez 2007). There is particular interest in the spatial and temporal patterns of recovery in the Florida Keys, as there are expectations that urchin recovery will perhaps help to reverse the trend in seaweed expansion and concurrent declines in reef-building corals. In addition, the slow and incomplete recovery of this urchin raises the question of factors limiting population recovery (Miller et al. in press).

Since 1999, we have conducted intermittent, large-scale surveys of urchin density and size structure in a diversity of habitats across the south Florida shelf encompassing hundreds of sites. This short communication describes the population status of *Diadema antillarum* as of 2007 along ~200 km of the

Florida Reef Tract, but also provides a temporal comparison of population densities and size structure since 1999 in both the Florida Keys and Dry Tortugas regions. These results are a follow-up to previous reports on the population status of urchins in the Florida Keys (Chiappone et al. 2001, 2002) and are part of an ongoing assessment and monitoring program to evaluate large-scale ecological patterns in community structure and the responses of small reef areas to protection from fishing pressure (Miller et al. 2002).

Material and Methods

The Florida Keys are an archipelago of limestone islands stretching more than 360 km from Key Biscayne to the Dry Tortugas. Along the seaward edge of the south Florida shelf is the reef tract, a semi-continuous series of offshore bank-barrier reefs interspersed with sand, rubble, and low-relief hard-bottom (Shinn et al. 1989). Between the islands of the Florida Keys and the reef tract is Hawk Channel, a V-shaped basin (5-12 m depth) dominated by sand, seagrasses, and patch reefs (FDEP 1998). Coral reef distribution and community structure in the Florida Keys reflect exchange processes between Florida Bay and the Atlantic Ocean affected by the size and orientation of the Pleistocene islands and the proximity of the Florida Current to the platform margin (Shinn et al. 1989).

During 1999-2007, a series of research expeditions were carried out to quantify, among other variables, urchin density and size distribution patterns across the south Florida shelf. A two-stage, stratified random sampling approach was used to derive mean density estimates for urchins at multiple spatial scales throughout the Florida Keys, following similar procedures outlined in Cochran (1977) and modified for our coral reef benthic surveys (Miller et al. 2002; Smith et al. in press). Surveys were carried out in the Florida Keys, excluding the Dry Tortugas, in 1999-2001 and 2005-07, and in the Dry Tortugas during 2000 and 2006 (Figs. 1-2). The sampling domain was partitioned by habitat type using available bathymetry and benthic mapping data (FDEP 1998). The habitat classification scheme accounted for features that correlate with benthic fauna distributions, including cross-shelf position, topographic complexity, and the proportion of sand interspersed among hard-bottom structures. Additional stratification variables included regional location and management zones, the results of which are reported elsewhere. Map resolution was such that the survey domain was divided into a grid with individual cells of size 200 m by 200 m (40,000 m^2) that defined unique habitat classes. Table 1 provides the classification system used during the 2007 surveys at 235 sites in the Florida Keys.

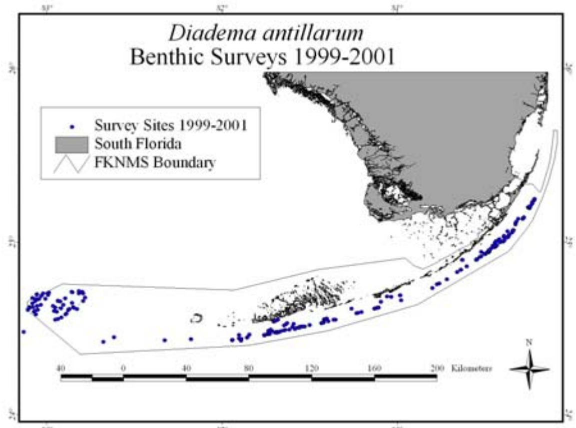


Figure 1: *Diadema* urchin survey sites in the Florida Keys National Marine Sanctuary (FKNMS) sampled during 1999-2001.

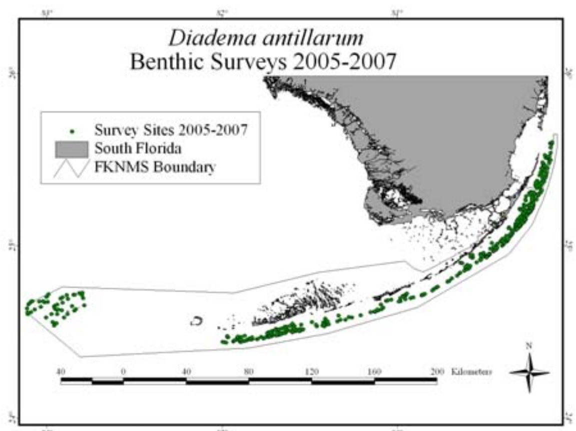


Figure 2: *Diadema* urchin survey sites in the Florida Keys National Marine Sanctuary (FKNMS) sampled during 2005-07.

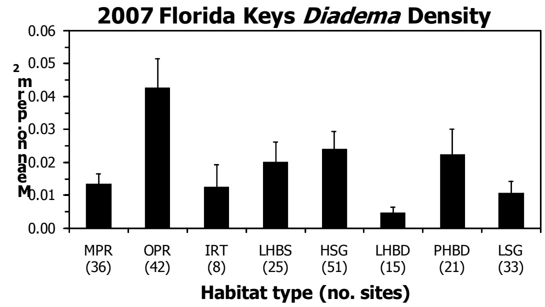
During each sampling mission, four random sampling points were generated in a GIS and were located in the field using a differential global positional receiver. During 1999-2001, paired 10 m or 25 m transects, depending on the site area, were deployed at each of the four sampling points. A 0.4 m scale bar was used to sample along both transect sides for the number and test diameter of urchins. During 2005-07, four 15-m x 1 m belt transects were sampled per site. Urchin density calculations were calculated for each site and for each stratum, consisting of combinations of habitat, regional location, and management zone. Data reported herein emphasize habitat-related patterns in density from the 2007 surveys, but also temporal comparisons between 1999-2001 and 2005-2007. Statistical comparisons of mean densities were accomplished by computing confidence intervals (CI) based on the equation: CI = mean ± $t_{[\alpha,\ df]}$ *standard error. Standard errors were estimated by the two-stage, stratified random sampling design (Cochran 1977) and confidence intervals were adjusted for multiple comparisons using the Bonferroni procedure. The experiment-wise error rate was held at α = 0.05 and the comparison-wise error rate was adjusted based on the number of multiple comparisons as follows: comparison-wise error rate = α/c, where c = k (k-1)/2 and k = number of categories (e.g. habitat classes).

Table 1: Characteristics of *Diadema* urchin survey sites in the Florida Keys sampled during 2007. Available sites reflect the number of 200 m x 200 m cells containing particular habitat types based upon FDEP (1998) mapping data

Habitat	Depth (m)	Sites (% effort)	Sites available
Mid-channel patch reef (MPR)	0.9-2.7	36 (15.3)	3,532
Offshore patch reef (OPR)	2.1-14.6	42 (17.9)	1,170
Hard-bottom/rubble/sand matrix	2.7-5.8	4 (1.7)	79
Shallow hard-bottom (LHBS)	2.7-7.0	25 (10.6)	972
Inner line spur and groove (IRT)	1.5-6.1	8 (3.4)	87
High-relief spur and groove (HSG)	0.6-9.4	51 (21.7)	238
Deeper hard-bottom (LHBD)	6.7-13.7	15 (6.4)	1,962
Patchy hard-bottom (PHBD)	4.6-11.3	21 (8.9)	956
Low-relief spur and groove (LSG)	7.6-16.2	33 (14.0)	2,825
Sampling Design Total	0.6-14.6	235 (100)	11,821

Results

Results presented herein detail *Diadema antillarum* population density and size structure based upon 2007 surveys, as well as temporal comparisons encompassing 1999 through 2007. Surveys of 235 sites from the northern Florida Reef Tract to SW of Key West during 2007 yielded relatively low densities, but slightly larger test sizes compared to previous sampling periods. A total of 299 individuals were recorded, with individuals distributed among all nine habitats sampled. The maximum site-level density was 0.267 individuals/m^2 from an upper Florida Keys offshore patch reef. Relative to previous years, an appreciable increase was apparent in the number of sites where *D. antillarum* was found and a general trend towards larger test sizes. Densities were greatest on offshore patch reef and high-relief spur and groove reefs (Fig. 3). However, habitat-level densities were so low that, despite the relatively large sample size, the only significant difference detected was between the offshore patch reef and deeper hard-bottom habitats ($P < 0.0018$, Bonferroni-adjusted α). Of the 299 *D. antillarum* recorded, test sizes ranged from 0.3-10.0 cm, with a mean ± 1 SE test size of 3.6 ± 0.1 cm. The test size distribution, in contrast to previous years, included a relatively large proportion (~33%) of individuals > 5 cm TD (Fig. 3).



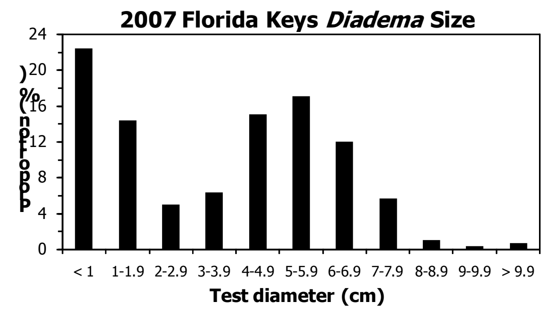


Figure 3: Mean *Diadema antillarum* densities by habitat (top) and test size distribution (bottom) from surveys of 299 individuals at 235 Florida Keys sites during 2007. Error bars are +1 SE and numbers in parentheses on the x-axis (top) are the number of sites sampled in each habitat. See Table 1 for habitat abbreviations.

Table 2 summarizes the temporal in *Diadema antillarum* density and size structure during two time periods in the Florida Keys and Dry Tortugas. In the Florida Keys, a greater proportion of sites yielded no *D. antillarum* in 1999-2001 (75%) compared to 2005-07 (62%). However, very few sites in either time period (≤ 1%) yielded densities greater than 0.2 individuals/m^2. The range in test size, the maximum test size, and the mean test size has increased since 1999-2001. The largest apparent changes are the ~42% increase in mean test size and the proportion of urchins larger than 5 cm TD in 2005-07 (32%) compared to 1999-2001 (9%).

For the Dry Tortugas region, including both shallower (< 15 m) habitats within the National Park and deeper (> 15 m) habitats on the Tortugas Bank, there are temporal similarities in density distribution, but differences in size distribution with the rest of the Florida Keys (Table 2). A greater proportion of sites yielded no individuals in 2000 (59%) compared to 2006 (44%), and very few sites in either time period (< 5%) yielded densities greater than 0.2 individuals/m^2. In terms of size structure, the most notable differences between the two time periods were the dramatic (58%) decrease in mean test size, as well as 28% change in the proportion of individuals larger than 5 cm TD, a pattern opposite to that documented in the rest of the study area.

Table 2: Temporal summary of *Diadema antillarum* density and size structure in the Florida Keys and Dry Tortugas regions during 1999-2001 and 2005-07. Site-level densities are the number (proportion) of sites with a given mean density value

Study area/metric	1999-2001	2005-07
Florida Keys		
No. sites	211	495
No. habitats	9	10
Depth range (m)	1.2-14.0	0.6-27.0
Area sampled (m^2)	16,400	29,700
Site-level density		
Absent	158 (74.9)	307 (62.0)
0.01-0.05 per m^2	50 (23.7)	153 (30.9)
0.06-0.10 per m^2	1 (0.5)	24 (4.8)
0.11-0.15 per m^2	0	6 (1.2)
0.16-0.20 per m^2	2 (0.9)	3 (0.6)
0.21-0.25 per m^2	0	1 (0.2)
0.26-0.30 per m^2	0	1 (0.2)
0.31-0.35 per m^2	0	0
0.36-0.40 per m^2	0	0
0.41-0.45 per m^2	0	0
Size structure		
No. individuals	88	474
Range in test size (cm)	0.3-6.7	0.3-10.0
Mean test size (cm)	2.4	3.4
SE test size (cm)	0.2	0.1
% of urchins > 5 cm TD	9.1	32.4
Dry Tortugas		
No. sites	34	46
No. habitats	9	11
Depth range (m)	4.0-24.1	2.7-26.1
Area sampled (m^2)	1,360	2,760
Site-level density		
Absent	20 (58.8)	20 (43.5)
0.01-0.05 per m^2	11 (32.4)	19 (41.3)
0.06-0.10 per m^2	1 (2.9)	4 (8.7)
0.11-0.15 per m^2	0	0
0.16-0.20 per m^2	1 (2.9)	1 (2.2)
0.21-0.25 per m^2	0	0
0.26-0.30 per m^2	0	0
0.31-0.35 per m^2	1 (2.9)	0
0.36-0.40 per m^2	0	2 (4.3)
0.41-0.45 per m^2	0	0
Size structure		
No. individuals	34	98
Range in test size (cm)	0.9-9.0	0.3-7.8
Mean test size (cm)	4.3	1.8
SE test size (cm)	0.4	0.2
% of urchins > 5 cm TD	44.1	16.3

Discussion

Large-scale surveys encompassing hundreds of sites across the south Florida shelf since 1999 indicate that the *Diadema antillarum* population exists at densities well below values reported before the two mortality events in 1983-84 and 1991 (Kier and Grant 1965; Bauer 1980; Forcucci 1994). For the Florida Keys there has been an increase the proportion of sites with *D. antillarum* present, as well an increase in mean test size, with a greater proportion of larger individuals in the population. Earlier reports and recent observations indicate that other urchin species show density and habitat distribution patterns similar to pre-1983 observations, indicating that other species have not compensated for the loss of *D. antillarum* (Chiappone et al. 2002).

In the Dry Tortugas, the past six years have witnessed a decline in average size, possibly indicative of a recruitment event, perhaps in 2005, or poor survivorship to larger sizes, or both. It is noteworthy that Dry Tortugas surveys conducted in 2006 followed a very active tropical cyclone season in 2005, where several named storms passed directly over or in close proximity to the Dry Tortugas. In areas with relatively high (> 0.1 individuals/m^2) and larger (> 5 cm TD) *Diadema antillarum*, there are obvious effects of grazing on the substratum, particularly the removal of turf and macroalgae and exposure of reef rock (Chiappone et al. 2001). It remains unclear at this time whether increasing urchin densities and sizes will lead to other changes such as increased coral recruitment.

The very slow and prolonged recovery in the Florida Keys, especially compared to several recent studies in other Caribbean reef areas, raises several questions pertaining to the possible factors inhibiting recovery. Lessios (1988) and others have discussed the merits of hypotheses concerning population recovery, among them poor larval survivorship, lack of adult conspecifics and hence protection from predators, suitable recruitment sites, and inter-specific competition. The sources of urchin larvae to the south Florida shelf are not known, but may include both local and regional sources (Lee et al. 1994). Nonetheless, it is apparent that *D. antillarum* have continually recruited to benthic habitats, even after the 1991 mortality event (Chiappone et al. 2002). A recent study of *D. antillarum* larval settlement rates in the Florida Keys, however, indicate that low larval supply may be one factor limiting recovery (Miller et al. in press). The predominance of relatively small test sizes from 1999-2007 indicate post-settlement recruits have poor survivorship, perhaps due to predation pressure or physical disturbance from storms. Because *D. antillarum* was historically significant as a grazer it will be important to monitor its change in abundance and size structure over time, as well as the possible effects on benthic community structure in the Florida Keys.

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