Techniques Development for the Re-establishment of the Long-spined Sea Urchin, *Diadema antillarum*, on Two Small Patch Reefs in the upper Florida Keys

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Abstract

A project was begun in the fall of 2001 offshore of the Upper Keys to explore the feasibility and ecological results of translocating juvenile long-spined sea urchins, *Diadema antillarum*, from areas with relatively high settlement and extensive winter mortality (reef crest rubble zones), to nearby deeper water (about 25 feet, 7.5 m) patch reefs at densities approaching those on Florida reefs before the *Diadema* die-off of the early 1980s. Four patch reefs, two experimental and two controls, varying in size from about 44 to 96 m^2 were selected for the study. From September 2001 to December 2001, 434 juvenile long-spined urchins were placed on Experimental Reef (ER) #1 (96 m^2), a total potential density of 4.5/m^2, and 262 were placed on ER #2 (88 m^2), a potential density of 3.0/m^2. An additional 16 urchins were placed on ER #2 on 10/23/02 bringing the total urchins placed on ER #2 to 278, a potential density of 3.2/m^2. The translocated populations were evaluated for number and placement of surviving urchins 10 times on ER #1 and 11 times on ER #2 over various intervals from 9/8/01 to 2/5/03.

Survival of *Diadema* was roughly similar on both experimental reefs from the first count on 9/8/01 through the final count on 2/5/03. Survival rates over the first three days of 80% and 93% dropped to about 40-45% on both reefs from 11/09/01 to 05/29/02, and then, on ER #1, survival remained at about 30% from 8/8/02 to 2/5/03. On ER #2, survival remained at 40% on 8/8/02, dropped to 30% on 10/8/02, and then dropped again to 17% on 11/30/02. Survival was 20% on 2/5/03 because of placement of 16 urchins on this reef late in the study (10/23/02). The average density of urchins over the entire 17 months of the study was 1.6m/^{2} on ER #1 and 1.0/m^2 on ER #2. The highest density on ER #1 (2.1/m^2) occurred on 2/26/02; ER #2 a maximum of 1.4/m^2 occurred on 10/24/01 and on 2/26/02. The final density (2/5/03) on ER #1 and #2 was 1.2/m^2 and 0.6/m^2, respectively. Decline in survival and density on both reefs was generally gradual and stable at a similar rate of decline during the last 12 months of the study. ER #1 lost 87 urchins, a survival of 57% over the last 345 days of the study. The total loss in urchin density on ER #1 over this period, 2/26/02 to 2/5/03, was 0.9/m^2, which was a decline in density of 0.0026/m^2 per day. ER #2 lost 67 urchins during this 345-day period, a survival of 45% and a loss in density of 0.8/m^2; which was a decline in density of 0.0023/m^2 per day (the data for ER #2 includes 16 urchins released on 10/23/02).

The gradual urchin mortality over the term of the project indicated that predation was the main cause of population decline and not mortality due to storms. Population counts before and after two instances of tropical storm conditions in the fall of 2001 indicated that these storms did not cause mortality in the translocated urchin populations on the experimental deep reefs. Also, no evidence of disease-caused *Diadema* mortality was observed.

Although evidence of some movement between reef quadrants and some concentration of urchins on the more rugged and complex areas of ER #1 was evident, in general, urchins remained broadly distributed over all reef areas on each experimental reef.

The NOAA National Undersea Research Center at Key Largo (NURC) conducted rapid ecological assessments of the four project reefs on 8/31-9/1/01, before translocation of urchins and again on 9/18/02, about one year after translocation of urchins (see next chapter). The benthic ecology of the experimental reefs changed considerably during the period of exposure to "normal" pre-die-off densities of *Diadema*. These changes on the experimental *Diadema*-addition reefs over the short term of one year included a marked reduction in brown foliose algal cover, and a return toward coral-dominated benthic cover as expected from a return of *Diadema* to the reefs. They reflected changes that have occurred on limited areas of Caribbean reefs such as Jamaica where populations of *Diadema* have returned naturally. This study presents evidence that translocation of *Diadema* from environments with high risk of mortality to deeper reef areas along the Florida Keys resulted in survival and population densities that can affect change in the ecology of coral reefs, by transforming reef areas from algal dominance toward coral dominance.

Introduction

Coral reefs that compose the reef tract of the Florida Keys have been in decline for several decades. The reasons for this decline are many and varied; some are well documented and some are speculative. However, one factor strongly contributing to the decline of Caribbean, Bahamian, and Florida coral reefs has been attributed to the almost total loss, 97 to 99%, of the long-spined sea urchin, *Diadema antillarum*, in an unprecedented disease pandemic on a single marine organism that occurred in 1983-84. *Diadema* was a keystone herbivore in this region, and the loss of this animal shifted the balance on reefs from coral dominance to extensive macroalgal growth. Despite the passage of 20 years and the sporadic and variable presence of small pockets of *Diadema* in the Florida reef environment, this keystone herbivore has not repopulated reefs and macroalgae continue to dominate most coral reefs in this ecosystem.

In the fall of 2000, we began work on a project to establish a pre-die-off population level of *Diadema* on two small patch reefs in the Upper Keys. The purpose of this project was to explore the survival of translocated urchins in this environment and the effects that this urchin population may have on the benthic ecology of these reefs. The Florida Keys National Marine Sanctuary (FKNMS) and the NOAA National Undersea Research Center at Key Largo (NURC) aided in the design of the project. The rationale for the project was to collect juvenile *Diadema antillarum* from shallow rubble areas on the reef crest where they settle in the late summer and fall, but apparently do not survive the fall and winter storms that churn this area, and translocate them to deeper patch reefs. Two experimental and two control reefs were selected for this work.

The overarching goal of this project was to monitor and track the success of one technique to enhance and restore coral reef areas. Specifically, the transplantation of large numbers of small *Diadema antillarum* from shallow rubble zones to deeper patch reefs will be evaluated. An additional goal was to monitor the resulting effects of increased densities of *Diadema antillarum* to determine if a reduction of algal overgrowth will enhance coral growth and settlement.

There were four specific biological objectives in this project:

- Determine if *Diadema* survive transplantation and the size that exhibits the best survival rate after transplantation
- Estimate the survival and growth rates of transplanted *Diadema*

- Determine the distribution patterns that *Diadema* develop on test reefs
- Compare and contrast general reef condition and community level changes, including coral recruitment and growth, on the manipulated and reference reefs over time.

Methods

Patch reefs about four miles eastward and offshore of Tavernier, FL, were explored and examined during the spring and summer of 2001 and four small patch reefs were selected for this project. Two of these reefs were designated as the experimental reefs (ER #1 and #2) and two as the reference (control) reefs (CR #3 and #4). The two experimental reefs were superficially different; ER #1 (about 96 m^2) was relatively rugged and contained some large coral formations mostly at the southern end while ER #2 (about 88 m^2) exhibited lower relief without the large *Montastraea cavernosa* boulder corals that occupied ER #1. The two control reefs were located in the same vicinity as the experimental reefs. CR #3 (about 72 m^2) was generally similar to ER #2, while CR #4 (about 44 m^2) was generally similar to ER #1. The maximum relief reported by the NURC surveys (Table 1) was about 80 cm for ER #1, compared to 62 cm for CR #4, and about 43 cm for ER #2 compared to about 43 cm for CR #3.

Table 1. Physical characteristics of experimental (top) and control (bottom) patch reefs, expressed in terms of the mean (1 SE) minimum and maximum depth of surveyed transects, mean (1 SE) maximum vertical relief, and estimated mean (1 SE) percentage of site with given topographic relief. Data are based upon surveys of four 10 m x 0.4 m transects per site each year.

Experimental patch reefs

Physical variable	Experimental reef #1		Experimental reef #2		Combined experimental	
	2001	2002	2001	2002	2001	2002
Minimum depth (m)	7.5 (0.0)	7.7 (0.1)	7.4 (0.1)	7.6 (0.1)	7.5 (0.1)	7.7 (0.1)
Maximum depth (m)	7.6 (0.1)	8.0 (0.1)	7.5 (0.0)	8.0 (0.1)	7.6 (0.1)	8.0 (0.0)
Maximum relief (cm)	82 (16)	79 (13)	41 (7)	45 (4)	62 (21)	62 (17)
Relief area (%)						
< 0.2 m	72.5 (4.3)	61.3 (8.3)	63.8 (7.2)	70.0 (7.4)	68.2 (4.4)	65.7 (4.4)
0.2-0.5 m	25.0 (4.6)	23.8 (5.5)	35.0 (7.1)	28.8 (7.5)	30.0 (5.0)	26.3 (2.5)
0.5-1.0 m	1.3 (1.3)	15.0 (6.1)	1.3 (1.3)	1.3 (1.3)	1.3 (0.0)	8.2 (6.9)
1.0-1.5 m	1.3 (1.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.7 (0.7)	0.0 (0.0)
> 1.5 m	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)

Control patch reefs

Physical variable	Control reef #3		Control reef #4		Combined control	
	2001	2002	2001	2002	2001	2002
Minimum depth (m)	7.4 (0.1)	7.5 (0.0)	8.0 (0.1)	7.7 (0.1)	7.7 (0.2)	7.6 (0.1)
Maximum depth (m)	7.5 (0.0)	7.5 (0.0)	8.1 (0.0)	7.8 (0.0)	7.8 (0.2)	7.7 (0.1)
Maximum relief (cm)	42 (6)	44 (7)	63 (17)	61 (19)	53 (11)	53 (9)
Relief area (%)						
< 0.2 m	77.5 (3.2)	78.8 (4.7)	76.3 (7.2)	83.8 (5.5)	76.9 (0.6)	81.3 (2.5)
0.2-0.5 m	21.3 (2.4)	18.8 (2.4)	17.5 (6.0)	10.0 (2.0)	19.4 (1.9)	14.4 (4.4)
0.5-1.0 m	1.3 (1.3)	2.5 (2.5)	5.0 (2.0)	6.3 (3.8)	3.2 (1.9)	4.4 (1.9)
1.0-1.5 m	0.0 (0.0)	0.0 (0.0)	1.3 (1.3)	0.0 (0.0)	0.7 (0.7)	0.0 (0.0)
> 1.5 m	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)

Each of the four project reefs was carefully mapped and photographed before translocation of *Diadema* was begun. A sub-surface buoy was placed on each reef to mark the location without an attention-generating surface marker. A north–south and an east–west transect line was established at about the center of each reef, dividing each reef into four quadrants. Each of these quadrants, NW, NE, SW, and SE, was then marked off into 4-m^2 divisions to facilitate accurate recording of placement and subsequent location of *Diadema* during counts. Each experimental reef fit into a rectangle composed of 30 4-m^2 sectors, as six columns of sectors along the north–south axis and five rows of sectors along the east–west axis. On ER #1 the north–south axis was situated along the line dividing three columns of 4-m^2 sectors to the west and two columns of sectors to the east. On ER #2 the north–south axis divided the reef into two columns of sectors to the west and three columns to the east. The east–west axis on both ER #1 and #2 divided the reef in the center, three rows of sectors to the north and three rows to the south. A square pvc-pipe frame 2 m on each side was used to measure and temporarily demark each 4-m^2 sector and served as a frame for photographs. A map of the location and approximate size of the coral formations that composed each reef was recorded in situ with pencil on a plastic slate on which the 4-m^2 sectors and 120-m^2 total area were inscribed with a permanent marker. Later, representations of coral formations were traced with a permanent marker and a permanent map of each reef was drawn on a plastic slate.

These reefs were not exactly rectangular in shape; there were areas of dense hard and soft coral structure exhibiting rugged relief, areas of low relief with scattered coral formations, and some areas with only seagrass and sand bottom within the delimited grid pattern of the reef. For the purpose of determining the density of *Diadema* on each reef and on each quadrant of each reef, 4-m^2 sectors that contained little or no reef structure on the periphery of the reefs were eliminated from calculations of reef area.

Six of these 4-m^2 sectors were omitted from ER #1, resulting in a total reef area of 96 m^2: one sector from the NW quadrant (resulting reef area of 32 m^2); one from the NE quadrant (resulting in 20 m^2); three from the SW quadrant (resulting in 24 m^2; and one from the SE quadrant (resulting in 20 m^2). For ER #2, which was smaller in extent and structure than ER #1, a total of eight 4-m^2 sectors were omitted, resulting in a total reef area of 88 m^2: one sector from the NW quadrant (resulting in 20 m^2); three from the NE quadrant (resulting in 24 m^2); one from the SW quadrant (resulting in 24 m^2); and three from the SE quadrant (resulting in 20 m^2). Figure 1 illustrates the working map of each experimental reef, including demarcation of the 4-m^2 sectors omitted from reef area determinations.

Juvenile *Diadema* were collected from shallow rubble zones at the reef crest at Conch and Pickles Reefs during 10 trips to one or both sites from September to December 2001 (Table 2). Urchins were collected by carefully removing them from under or between rubble with a short aluminum rod and flipping them into a large, small-mesh hand net. When the net was full, the urchins were taken to a boat, placed in holding tanks, and sorted by size: small (test size about 1

to 2.5 cm), medium (2.6 to 4.0 cm), and large (4.5 to 6 cm). Usually, two collectors worked the rubble bottoms and one additional person in the boat helped to transfer the urchins to the holding tanks. Effort (Table 2) consists only of the total collector hours expended during each collection trip (one-three collectors). A total of 30 collection hours were expended to collect 741 urchins. There was an average yield of 25 urchins per collector-hour.

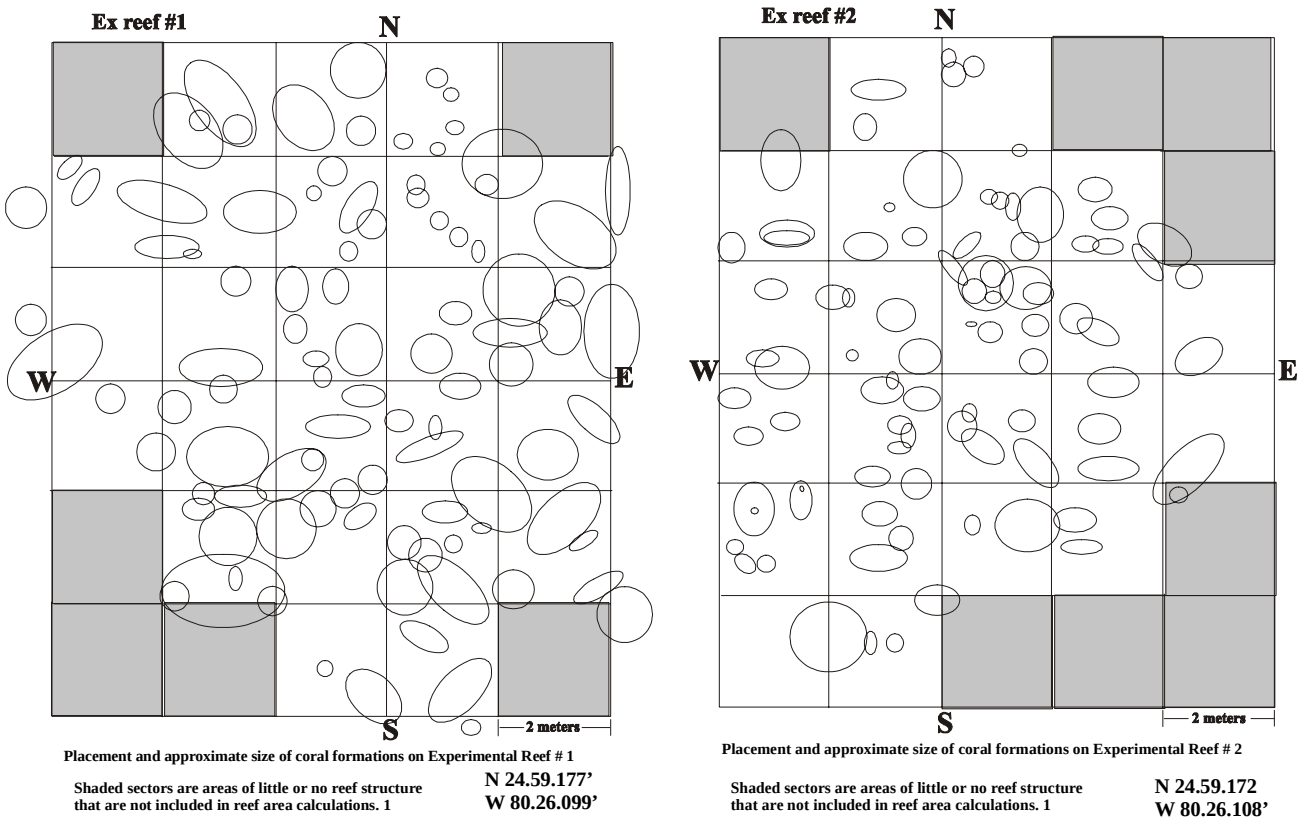


Figure 1. Working map of experimental reefs #1 and #2.

Table 2. Collection data for juvenile *Diadema antillarum* at Pickles and Conch reefs.

Date 2001	Conch Reef	Pickles Reef	small (1–2.5 cm)	medium (2.6–4.0 cm)	large (4.5–6+ cm)	effort in collector hours
09/04		162	43	102	17	6.0 hrs
09/05		123	23	93	7	6.0 hrs
09/17	11			11		0.5 hrs
09/19	75		58	13	4	2.0 hrs
09/21	105		32	33	40	6.0 hrs
09/26	78		53	14	11	1.5 hrs
10/05	41		15	5	21	1.5 hrs
10/24		55	22	14	19	2.0 hrs
12/14	17		1	6	10	0.5 hrs
12/20	74		2	15	57	4.0 hrs
Totals	401	340	249	306	186	30.0 hrs

Immediately after collection, the urchins were transported by boat to the experimental reefs. Divers carried the urchins down to the reefs, where they were placed next to coral formations. Upon being released from nets, urchins immediately moved toward and into nearby coral structures. No urchin seemed to be exposed without shelter for more than a few minutes. No predation on newly released urchins was observed. The specific location of release of each urchin was recorded a map of the reef (see Fig. 1).

Counts of urchins on the experimental reefs were made at various intervals as weather and opportunity allowed beginning a few days after the first translocation on 9/8/01 until 2/5/03 (Table 3). When a count (population evaluation) was made on the same day as a collection of juvenile urchins, the count of the surviving *Diadema* population on the reefs was made before release of the collected juvenile urchins. An exception to this occurred on 10/24/01 at ER #2. In this instance, to prevent inflation of the survival estimate, the number of urchins released was subtracted from the number counted on that date. Also, 16 urchins released on ER #2 on 10/23/02 were subtracted from the count on 11/30/02 to provide more accurate survival data.

A total of 11 counts (10 on ER #1 and 11 on ER #2) were made over the course of the project. Each quadrant of the experimental reefs was carefully surveyed and the presence and location of every urchin observed was recorded.

Table 3. Translocation and survival data of *Diadema antillarum* on the two experimental reefs, 9/4/01 to 2/5/03.

Date	Experimental Reef #1 (96 m^2)				Experimental Reef #2 (88 m^2)			
	total released before count (#R)	total count (#C)	% survival (#C/#R)	# released this date (after count)	total released before count	total count	% survival (#C/#R)	# released this date (after count)
09/04,5/01				201				85
09/08	201	160	80		85	79	93	
09/17				11				
09/19	212	172	81		85	79	93	27
09/21								105
09/26				79				
10/05				42				
10/24				34	217	134	62	21*
11/09	367	161	44		238	118	50	
12/14				17				
12/20	384	175	46	50	238	106	45	24
02/26/02	434	202	47		262	122	47	
05/29	434	181	42		262	109	42	
08/08	434	135	31		262	103	39	
10/08	434	122	28		262	77	29	
10/23								16
11/30	434	119	27		278/262	63/47	23/18	
02/05/03	434	115	26		278	55	20	
Totals				434				278/262**

*The 21 urchins released on this date were included in the count on this date. For this table these 21 urchins were subtracted from the number released and from the number counted.
**The 16 urchins released on 10/23/02 were not included in data analysis of 11/30/02.

Long view of Experimental Reef #1.

An extensive series of photographs was made of each experimental reef before placement of the urchins and then at various times after their placement. The reefs were not disturbed by collection of organisms or relocation of any urchins after initial placement. Two exceptions to this were the removal of two large spotted burrfish, *Chilomycterus atinga*, the first on 9/3/01, the day before initial placement of urchins on the reef, and the second during a night dive on 9/28/02. The first burrfish was removed from the NE quadrant of ER #1 where there was evidence (crushed coral and broken shells) that the burrfish frequently occupied a specific sheltered area under a coral formation. The second was also removed from ER #1 as it moved about this area during the night. It also apparently frequented the same sheltered coral cave area on the NE quadrant as the first burrfish, as crushed shells and urchin spines were present. Remains of freshly crushed urchins on ER #2 indicated that the burrfish also frequented this nearby reef. The second burrfish was taken immediately after feeding on urchins since bits of *Diadema* test and spines were present in the area where it was taken and also found later on the bottom of the holding tank where it was placed after capture.

Documentation of the benthic communities of the experimental and reference reefs was conducted by NURC on 8/31-9/1/01 before placement of urchins on the experimental reefs and again on 9/18/02, about one year after placement of *Diadema* on the experimental reefs. The following chapter details changes that occurred on experimental and reference reefs during the first year of this project.

Results

The results of this project fall into two basic categories: the progressive survival and status of *Diadema* populations on the experimental reefs, and the analysis and documentation of the condition and changes in benthic communities on the experimental and reference reefs (see next chapter).

Diadema *Populations on the Experimental Reefs*

Collection of juvenile *Diadema* from the shallow rubble zones during good weather and sea conditions was not physically or technically difficult. Juveniles were variously abundant in these areas during late summer, fall, and early winter depending on settlement success and occurrence and intensity of storms during this period. Table 2 (above) presents the collection data and effort in collector hours for the juvenile *Diadema* collected during the first four months of the project. Small *Diadema* (test size under about 2.5 cm in diameter) are very secretive and can be difficult to find. Although an average of 25 urchins per collector-hour were taken, an experienced collector, depending on conditions, would be considerably more productive than a novice collector. Also, the numbers of juvenile urchins in these shallow rubble zones varied considerably depending on strength of recruitment, occurrence of storms, depth, and season. When juvenile urchins were abundant, large numbers could be quickly collected and when they were scarce, collection was more time consuming.

We intended to attain a density of about 4 *Diadema* per square meter on each experimental reef to approximate reported, near-maximum, pre-die-off densities on Florida Keys reefs of 4-5/m^2. With limited collection effort, juvenile *Diadema* were available in the rubble zones of Conch and Pickles Reefs during the early fall of 2001 in just enough abundance to provide the desired pre-die-off *Diadema* density (about 3-4.5/m^2) on each reef. Despite high mortality in the first few months, a sustained average density of 1-2 urchins/m^2 (1.7/m^2 on ER #1 and 1.1/m^2 on ER #2) was maintained over the course of the project.

Table 3 (above) presents data on the total numbers of *Diadema* released on ER #1 and #2, the numbers counted at each population evaluation on each reef, and the percent apparent survival rate of the urchins on each reef at the time of each count. The survival rate is termed "apparent survival" because it is quite possible, especially when early juveniles were abundant, that some urchins were deeply hidden in the reef structure and were not observed. The survival rate may have been slightly higher, but not lower than that recorded. Figures 2 and 3 show cumulative numbers of urchins released on ER #1 and ER #2, respectively, and counts at each survey; Figure 4 combines these data for both experimental reefs. Figure 5 presents percent apparent survival based on density (#/m^2 counted/#/m^2 released x 100) for both experimental reefs, and Figure 6 shows the changes in density of *Diadema* on each experimental reef over the course of the study.

Survival, Distribution, and Movement of Diadema *on the Experimental Reefs*

Survival rates were high during the first weeks after initial translocation of urchins to the experimental reefs. The initial translocation of juvenile *Diadema* occurred on 09/04/01 and 9/5/01. A total of 201 (plus 11 on 9/17/01) were placed on ER #1 and 85 were placed on ER #2. Percent apparent survival on ER #1 by density (#/m^2 counted/#/m^2 released x 100) over the first 14 days (9/05 to 9/19/01) was 82% on ER #1 and 90% on ER #2 (Table 3).

Storm Mortality

The upper Florida Keys were brushed by two fall storms early in the project, strong Tropical Storm Gabrielle on 9/14/01, and Hurricane Michelle on 11/5/01. The Upper Keys area experienced sustained winds of about 25-30 knots and gusts of about 40 knots during both storms. There was evidence of the effects of storm surges (sedimentation, movement of some

corals and rocks, and accumulations of loose seagrass and seaweed) on the experimental reefs after both storms.

Figure 3. Reef # 2: Total Diadema released (cumulative) and counted at each population evaluation.

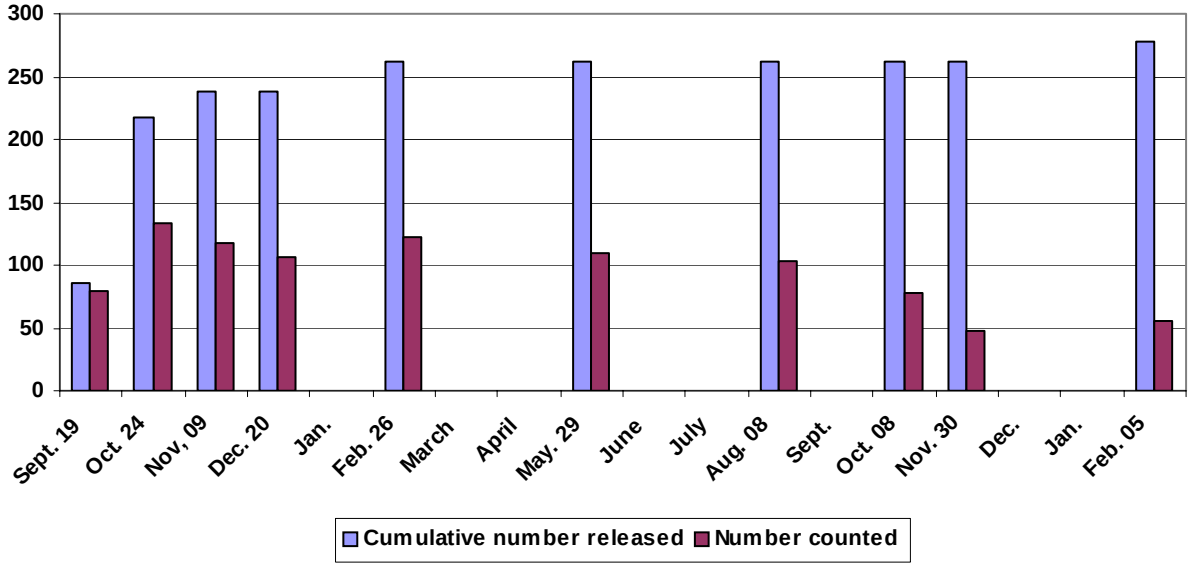


Figure 4. Reefs # 1 & #2: Combined release (cumulative) and count data at each population evaluation.

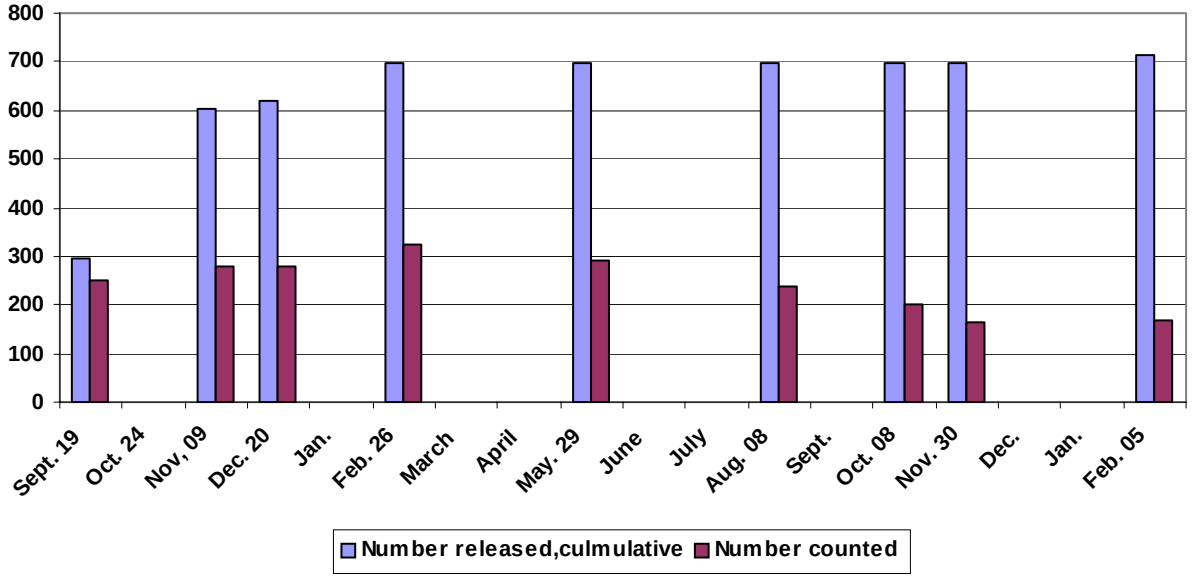


Figure 5. Percent apparent survival of Diadema by density (#/sq. m counted / #/sq. m released) at each count on reefs # 1 and # 2.

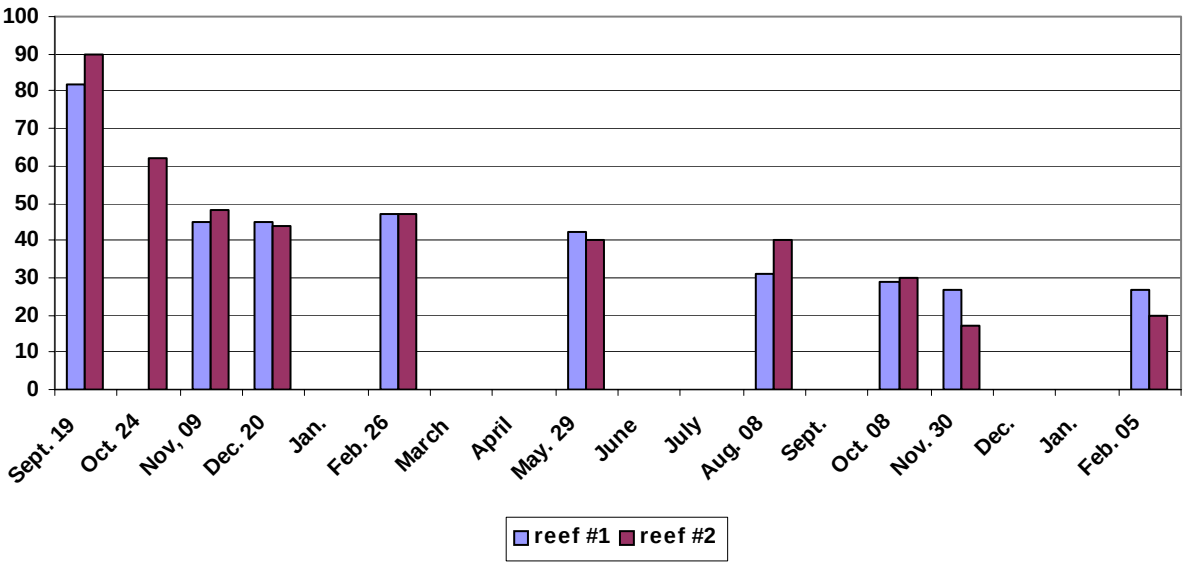
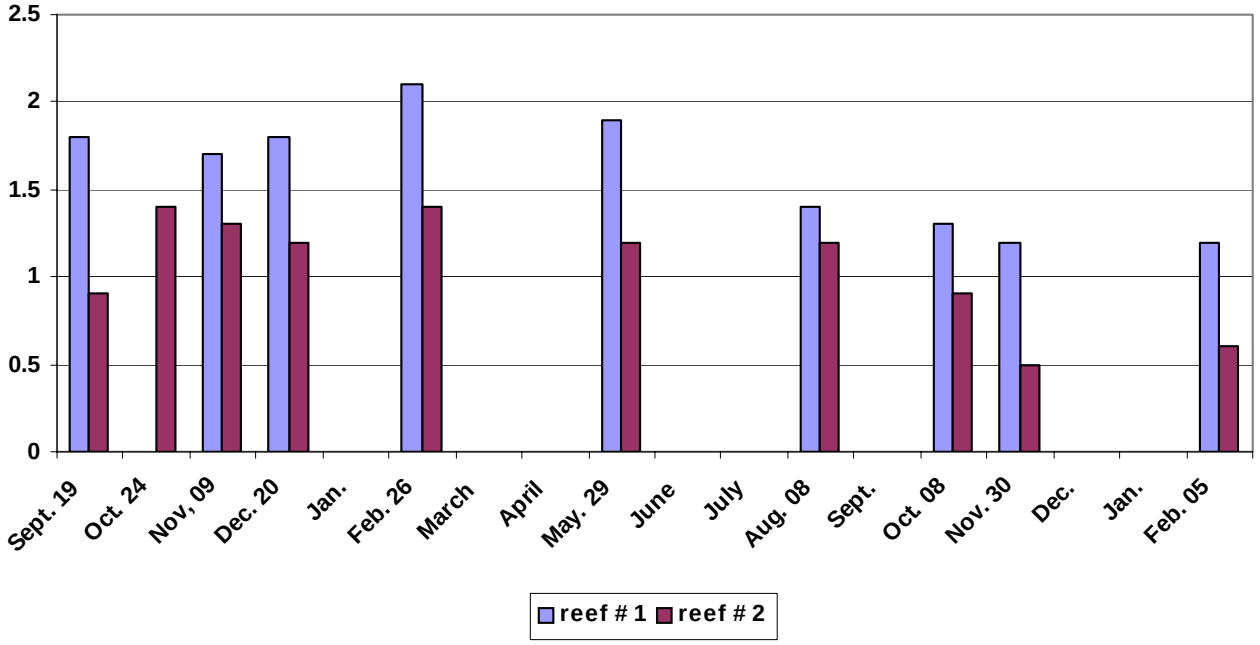


Figure 6. Density (#/sq. m) of Diadema on each experimental reef at each count.



Tropical Storm Gabrielle passed westward over the center of the Florida peninsular, well north of the Keys, which experienced the very fringes of the southern side of the storm, with winds mostly southerly. Loss of *Diadema* on the experimental reefs due to T.S. Gabrielle was minimal

or none as the percent apparent survival on ER #1 and #2 on 9/8/01 were, respectively, 81% (1.7/m^2) and 90% (0.9/m^2) and the first counts after the storm 5 days later on 9/19, were 82% (1.8/m^2) and 90% (0.9/m^2) showing no loss in density (Tables 4 and 5). There was a release of 11 urchins on the NW quadrant of ER #1 on 9/17 after the storm (Table 6), and this is reflected in the increase in density on the NW quadrant in the 9/19 count from 1.8/m^2 (82% survival) to 2.2/m^2 (88% survival) an actual increase of 15 urchins on this quadrant. There was no loss in apparent survival or density of urchins on either reef before and after the storm; apparently there was no mortality due to passage of this storm. This indicates that urchins on the deeper patch reefs can survive a significant storm event with no apparent mortality.

Table 4. ER #1: percent change in density (% Sur, apparent survival) of *Diadema* (#/m^2 counted / #/m^2 released x100) on each quadrant and on the total reef area, including density released (R#/m^2) and counted (C#/m^2) on the total reef area.

Quadrant	NW	NE	SW	SE	total reef area		
	32 sq. m	20 sq. m	24 sq. m	20 sq. m	96 sq. m		
Date	% Sur	% Sur	% Sur	% Sur	R#/m^2	C#/m^2	% Sur
09/08/01	82	78	93	68	2.1	1.7	81
09/19	88	65	67	92	2.1	1.8	82
11/09	39	49	43	47	3.8	1.7	45
12/20	33	44	65	53	4.0	1.8	45
02/26/02	41	38	73	45	4.5	2.1	47
05/29	34	36	67	41	4.5	1.9	42
08/08	25	22	57	34	4.5	1.4	31
10/08	18	24	50	32	4.5	1.3	29
11/30	16	25	40	34	4.5	1.2	27
02/05/03	14	20	47	36	4.5	1.2	27

Table 5. ER #2: percent change in density (% Sur, apparent survival) of *Diadema* (#/m^2 counted / #/m^2 released x 100) on each quadrant and on the total reef area, including density released (R#/m^2) and counted (C#/m^2) on the total reef area.

Quadrant	NW	NE	SW	SE	total reef area		
	20 sq. m	24 sq. m	24 sq. m	20 sq. m	88 sq. m		
Date	% Sur	% Sur	% Sur	% Sur	R#/m^2	C#/m^2	% Sur
09/08/01	88	80	80	140	1.0	0.9	90
09/19	125	80	70	120	1.0	0.9	90
10/24	55	79	65	42	2.3	1.4	61
11/09	55	55	29	55	2.7	1.3	48
12/20	28	48	33	69	2.7	1.2	44
02/26/02	45	52	38	53	3.0	1.4	47
05/29	52	42	31	41	3.0	1.2	40
08/08	34	42	46	38	3.0	1.2	40
10/08	21	32	35	29	3.0	0.9	30
11/30	24	19	19	12	3.0	0.5	17
02/05/03	10	19	23	29	3.2	0.6	20

Table 6. ER #1: number of *Diadema* released, cumulative (#Rel), density released (#/m^2), actual number counted, (Cnt), and number present per square meter (#/m^2) on each quadrant at each population evaluation.

Quadrant	NW				NE				SW				SE			
	32 sq. m				20 sq. m				24 sq. m				20 sq. m			
Date	#Rel	#/m^2	#Cnt	#/m^2	#Rel	#/m^2	#Cnt	#/m^2	#Rel	#/m^2	#Cnt	#/m^2	#Rel	#/m^2	#Cnt	#/m^2
09/08/01	70	2.2	56	1.8	45	2.3	36	1.8	37	1.5	34	1.4	49	2.5	34	1.7
09/19	81	2.5	71	2.2	45	2.3	30	1.5	37	1.5	25	1.0	49	2.5	46	2.3
11/09	120	3.8	47	1.5	94	4.7	46	2.3	56	2.3	23	1.0	97	4.9	45	2.3
12/20	127	3.9	43	1.3	99	5.0	44	2.2	56	2.3	35	1.5	102	5.1	53	2.7
02/26/02	142	4.4	58	1.8	109	5.5	42	2.1	71	3.0	53	2.2	112	5.6	49	2.5
05/29	142	4.4	47	1.5	109	5.5	40	2.2	71	3.0	47	2.0	112	5.6	47	2.3
08/08	142	4.4	34	1.1	109	5.5	23	1.2	71	3.0	40	1.7	112	5.6	38	1.9
10/08	142	4.4	27	0.8	109	5.5	25	1.3	71	3.0	35	1.5	112	5.6	35	1.8
11/30	142	4.4	23	0.7	109	5.5	28	1.4	71	3.0	31	1.3	112	5.6	37	1.9
02/05/03	142	4.4	19	0.6	109	5.5	21	1.1	71	3.0	35	1.4	112	5.6	40	2.0
mean				1.3				1.7				1.5				2.1

Hurricane Michelle passed westward through the Florida Straits on 11/5/01 about 100 miles SE of the upper Florida Keys. The Florida Keys were on the northern side of the storm and experienced strong northeasterly winds gusting to 50 knots (Molasses Reef) and storm surges of 1-3 feet (storm data from the NOAA Tropical Weather web site). The impact of H. Michelle to the Upper Keys appeared to be greater than the impact of T.S. Gabrielle.

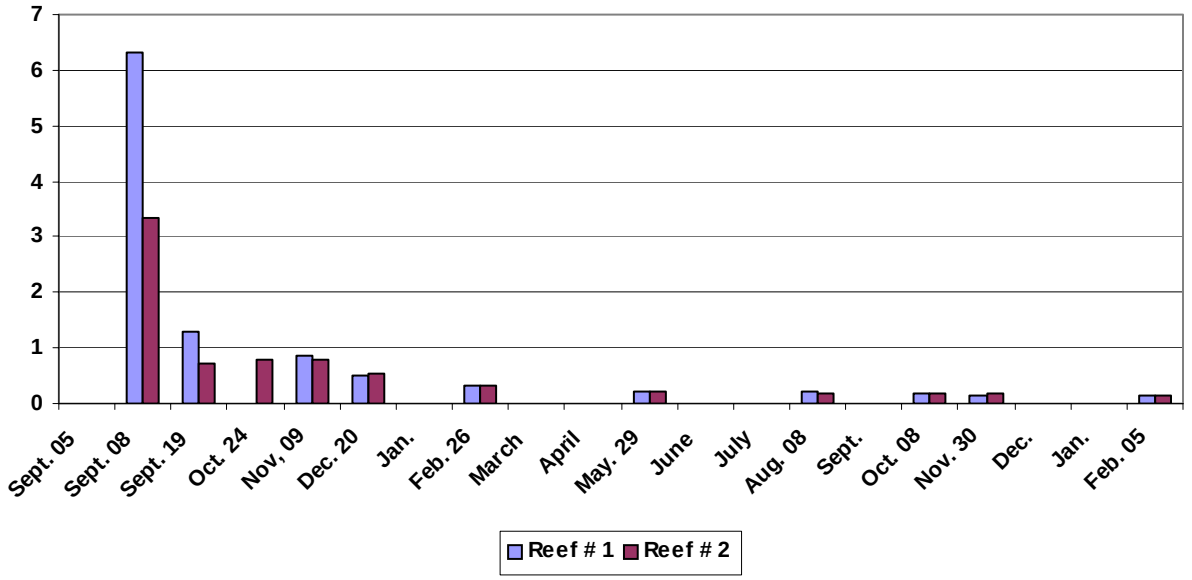
Diadema survival on ER #1 dropped from 82% on 9/19 to 45% on 11/9/01, 51 days later (4 days after H. Michelle; Table 4). During this 51 days, however, 155 additional urchins were translocated to ER #1 (between 09/26 and 10/24; Table 3), so although the percent survival (calculated as the #/m^2 counted/#/m^2 released x 100) dropped by 37% over this period, the overall density of urchins on the reef dropped by only 0.1/m^2 (1.8/m^2 to 1.7/m^2; Table 4). Even though percent survival dropped by about 37% over these 51 days, the density of urchins on ER #1 was about the same at the time of both counts, before and after the storm. The rate of decline in apparent survival on ER #1 over this 51-day period (9/19 to 11/9/01) was 0.85% per day (Table 7, Fig. 7).

The situation during this period on ER #2 was more complex, and more revealing. A count of urchins made on ER #2 on 10/24/01 (ER #1 was not counted), 12 days before H. Michelle, showed 61% survival of *Diadema* (Table 5). This was a drop of 29% apparent survival over a period of 35 days (9/19 to 10/24), but a gain in density of 0.5/m^2 from the previous count of 0.9/m^2 on 9/19 to 1.4/m^2 on 10/24. The gain in density was a result of the placement of 132 translocated *Diadema* on ER #2 on 9/19 and 9/21/01. The rate of decline of urchins on ER #2 during the 35 days before the storm was 0.8% per day (Table, 7, Fig. 7). The count on 11/9/01 (1.3/m^2), 4 days after the hurricane, showed 48% survival on ER #2 (Table 5), a drop of 13% from the 61% survival of the previous count (0.1/m^2) on 10/24/01, 16 days prior. However, the rate of decline, 0.8% per day, was the same for the 35-day period before (9/19 to 10/24/01) and the 16-day period that included the storm (10/24 to 11/9/01). This indicates that on ER #2, H. Michelle did not cause mortality great enough to increase the daily rate of mortality in the 16

Table 7. ER #1 and #2: percent rate of loss per day (mortality rate) of *Diadema* urchins on each reef at each count.

Date	Total # of days before each count	ER #1 % loss (density) from inception at each count	ER #1 % rate of loss per day (%loss/# days)	ER #2 % loss (density) from inception at each count	ER #2 % rate of loss per day (% loss/# days)
09/05/01	0	0	0	0	0
09/08	3	19	6.33	10	3.33
09/19	14	18	1.29	10	0.71
10/24	49	--	--	39	0.80
11/09	65	55	0.85	52	0.80
12/20	106	55	0.52	56	0.53
02/26/02	174	53	0.31	53	0.31
05/29	267	58	0.22	60	0.23
08/08	338	69	0.20	60	0.18
10/08	399	71	0.18	70	0.18
11/30	452	73	0.16	83	0.18
02/05/03	519	73	0.14	80	0.15

Figure 7. Percent rate of loss per day of total *Diadema* urchins released (daily mortality rate) on each reef at each count.



days that included the storm above the rate during the 35 days before the storm. The last translocation of urchins occurred 12 days before H. Michelle on 10/24, with 21 placed on ER #2, and 34 placed on ER #1.

The placement of urchins on both reefs before H. Michelle (9/19 through 10/24/01) was almost equal, 155 on ER #1 and 153 on ER #2, and the time of release was also similar. The daily rate of mortality on ER #1 (0.85% per day) over the 51-day period between 9/19 and 11/9, which included H. Michelle, was very close to the daily rate of mortality (0.8% per day) that was experienced on ER #2 during the period before (9/19 to 10/24) and the period including the

storm (10/24 to 11/9/01). Also, the overall survival rate on 11/9/01 was almost the same on both reefs, 45% on ER #1 and 48 % on ER #2 (Tables 4 and 5).

In summary, the absence of mortality on both reefs from 9/8 to 9/19/01, which included T.S. Gabrielle; the same daily percent rate of loss on ER #2 (0.8%) during the 35-day period before (9/19 to 10/24) and the 16-day period (10/24 to 11/9) that included H. Michelle on ER #2 (0.8%); the close similarity of the daily percent rate of loss on ER #1 and #2 during the 51 days between 9/19 and 11/9/01, which included H. Michelle; and the parallel survival rates (45% and 48%) on both reefs on 11/9 indicate that mortality patterns on both reefs were very similar during the 51 days from 9/19 to 11/30 and that there was no precipitous mortality of urchins on either reef immediately after either storm. The data suggest a gradual loss of urchins over time rather than a rapid loss immediately after H. Michelle on ER #2 and the pattern of loss on both reefs is so similar that if this storm did not cause considerable mortality on ER #2, then it probably didn't cause such mortality on ER #1. This analysis shows that no urchin mortality was caused by T.S. Gabrielle, and indicates, but does not conclusively prove, that precipitous mortality of *Diadema* did not occur as a result of the proximity of H. Michelle.

Storm Mortality Analysis: Time line for counts and storms, 09/08/02 through 11/09/02. G – T.S. Gabrielle, M – H. Michelle, C - count date

```
                 09/14 G                                  11/05 M
  09/08 C          !          09/19 C                    10/24 C      !      11/09 C
____!___________!__________!_________________________ !________!________!______

Survival percentage (#/m2 counted/#/m2 released x 100) and density (#/m2)
      !              !             !                            !          !          !
      !              !             !                            !          !          !
(1) 80% 1.7/m2       !         81% 1.8/m2                                !    45% 1.7/m2
(2) 93% 0.9/m2       !         93% 0.9/m2                 61% 1.7/m2     !    48% 1.3/m2
      !              !             !                            !          !          !
Daily percent rate of loss (#/m2 counted/#/m2 released x 100)/days elapsed
      !              !             !                            !          !          !
(1)  ! ----------no loss ----------!--------0.7% per day-------------------------------!
                (11 days)          !          (51 days)         !          !          !
(2)  ! ----------no loss-----------!--------0.8% per day--------!--0.8% per day----!
      !         (11 days)          !            (35 days)       !     (16 days)     !
      !              !             !                            !          !          !
Urchins added to reefs
      !              !             !                            !          !          !
(1)  201                  11                 79    42          34    (total 367)     !
(2)   85                          27  105                      21    (total 238)     !
```

The data above (approximate placement of dates) lays out the time line for counts, percent loss between counts, rate of daily loss from 09/19 to 10/24 to 11/09 (no loss from 09/08 to 09/19), and urchins added to the reefs during the period 09/08 to 11/09/01.

Although these strong storms apparently did not greatly affect *Diadema* populations on these relatively deep (about 25 feet, 7.5 m) patch reefs, the shallow rubble zones on the reef crest absorb much more storm energy and the wave surge rolls and grinds rubble and destroys small urchins that have settled on the scoured rock surfaces. The same wave energy that seems to prepare the rock surface for settlement of post-larval *Diadema* also destroys juveniles that grow and develop in this environment over the late summer and fall months. On 1/3/03, after winter storms, the rubble zone at the north end of Conch reef had few (about 10) healthy *Diadema* in the deeper areas, about 8-10 feet (3 m) deep, along with 3 dead urchins and about 7 with their spines missing. There were no urchins present in the shallow areas, 3-4 feet (1.2 m) deep. A strong sea surge was breaking over the south end of Conch reef at this time.

The initial loss over the first three days, about 19% on ER #1 and 10% on ER #2, occurred before the storms and was most likely a loss of small juveniles, presumably to predation. Small juveniles, however, can hide far under and deeply into coral and rock structures and it is possible that we could not observe all that were present and that the losses after the first three days were not as great as the count indicated. The much greater loss (81% survival) on the more rugged ER #1 compared to the smaller loss (93% survival) on the low relief of ER #2 indicates that either predation was much greater on ER #1 over these three days or that the small urchins were better hidden.

Losses of about 55% (45% survival) on ER #1 and 52% (48% survival) on ER #2 occurred during the first 65 days, and although both storms were included in this period, there was no loss of urchins from T.S. Gabrielle and apparently little, if any, direct loss from H. Michelle.

Survival rates seemed to remain constant at about 45% on both reefs during the fall and winter months. Mortality on ER #1 was apparently a bit greater since 67 additional urchins were translocated to it on 12/20/01 with only 24 urchins translocated to ER #2 on that same day. ER #1 had 43 more urchins added to its population in December 2001 than ER #2. The placement of additional urchins on these reefs during the first four months of the study accounted for the preservation of the density of urchins on the reefs despite the numerical loss of urchins between counts.

Except for the placement of 16 large urchins, test size 3.5-6 cm, on ER #2 on 10/23/02, the 12/20/02 translocations were the last placement of urchins on the experimental reefs for the duration of the study. The survival data from the last 345 days of the study, 2/26/02 to 2/5/03, were most important since few additions of urchins to the reefs affected survival rates during this period. The 16 large urchins released on ER #2 on 10/23/02 were subtracted from the count on 11/30/02 to avoid inflation of the survival calculation during this period. We felt that it was quite likely that all of these 16 large urchins could have easily survived the 38 days between release and the count on 11/30, and to include them would skew the data to indicate a higher survival rate on ER #2 at that count than had actually occurred.

Thus the total number released on ER #2 was recorded as 262 rather than 278 for the 11/30/02 count and the number surviving at this count was recorded as 47 rather than the 63 actually counted. Therefore the density on the 11/30/02 count for ER #2 was $0.5/m^2$, and the percent apparent survival at this count was 17%. The 16 urchins released on 10/23/02, however, were

included in the final count on 2/5/03 and this accounted for the apparent increase in survival from 17% to 20%, density from 0.5/m^2 to 0.6/m^2, percent mortality (as loss of density) from 83% to 80%, and the decrease in the percent loss of urchins per day from 0.18% to 0.15% between the 11/30/02 count and the final count on 02/05/03.

Elimination of these 16 urchins also changes the data for the 11/30/02 count of urchins released on the NE and SE quadrants of ER #2 (Table 8), eliminating 8 from this count on each of these quadrants. The release and count including these 16 urchins released on 10/23/02 is recorded in Table 3, but the corrected values reflecting the elimination of these 16 urchins from the data on this count are recorded in Tables 5, 7, and 8 and on the resulting graphs (Fig. 2-6) as well.

Table 8. ER #2: number of *Diadema* released, cumulative (#Rel), density released (#/m^2), actual number counted, (Cnt), and number present per square meter (#/m^2) on each quadrant at each population evaluation.

Quadrant	NW				NE				SW				SE			
	20 sq. m				24 sq. m				24 sq. m				20 sq. m			
Date	#Rel	#/m^2	#Cnt	#/m^2	#Rel	#/m^2	#Cnt	#/m^2	#Rel	#/m^2	#Cnt	#/m^2	#Rel	#/m^2	Cnt	#/m^2
09/08/01	15	0.8	14	0.7	25	1.0	18	0.8	25	1.0	20	0.8	20	1.0	27	1.4
09/19	15	0.8	20	1.0	25	1.0	19	0.8	25	1.0	17	0.7	20	1.0	23	1.2
10/24	53	2.7	30	1.5	58	2.4	46	1.9	55	2.3	36	1.5	51	2.6	22	1.1
11/09	57	2.9	32	1.6	65	2.7	37	1.5	58	2.4	17	0.7	58	2.9	32	1.6
12/20	57	2.9	15	0.8	65	2.7	32	1.3	58	2.4	20	0.8	58	2.9	39	2.0
02/26/02	57	2.9	25	1.3	75	3.1	38	1.6	62	2.6	24	1.0	68	3.4	35	1.8
05/29	57	2.9	30	1.5	75	3.1	31	1.3	62	2.6	20	0.8	68	3.4	28	1.4
08/08	57	2.9	19	1.0	75	3.1	31	1.3	62	2.6	28	1.2	68	3.4	25	1.3
10/08	57	2.9	12	0.6	75	3.1	24	1.0	62	2.6	21	0.9	68	3.4	20	1.0
11/30	57	2.9	14	0.7	75	3.1	14	0.6	62	2.6	11	0.5	68	3.4	8	0.5
02/05/03	57	2.9	5	0.3	83	3.5	15	0.6	62	2.6	15	0.6	76	3.8	20	1.0
mean				1.0				1.2				0.9				1.3

Survival rates on both reefs held constant at 45 and 47% over the winter months of December and January, and dropped to 42 and 40% by 05/29/02, about 9 months after the initial translocation. *Diadema* populations on the experimental reefs were not evaluated again until 8/8/02, about 2 months later. Apparent survival dropped to 31% on ER #1 and 40% on ER #2 during this period. Two months later, on 10/8/02, apparent survival had dropped again to 29% on ER # 1 and 30% on ER #2, and about two months later, 11/30/02, apparent survival, about a year after the initial translocation, was 27% on ER #1 and only 17% on ER #2 (excluding the 16 additional urchins that were added to ER #2 on 10/23/02). The last count on 2/5/03 showed a loss of only 4 urchins on ER #1 (119 to 115), which registered as no loss in survival, 27%, based on density of urchins. Survival, based on density, increased on ER #2 from 17% to 20%, despite a numerical loss of 8 urchins, 63 down to 55, due to the placement of the 16 urchins on 10/23/02.

By December 2001, 434 juvenile urchins had been released on ER #1 (reef area of about 96 m^2), which without any subsequent losses would have been a density of 4.5/m^2. The highest *Diadema* density recorded on ER #1 was 2.1/m^2 and occurred on 2/26/02. After about 17 months, the urchin density on ER #1 was 1.2/m^2 (the lowest recorded density) with an apparent survival rate of 27%. The density of urchins on ER #1 at the first count on 9/8/01, was 1.7/m^2 and 1.2/m^2 at

the last count on 2/5/03. The average density of *Diadema* on ER #1 over the duration of the project was 1.6/m^2.

A total of 278 urchins (including the 16 released on 10/23/02) were released on ER #2, (reef area of about 88 m^2), which without any subsequent losses would have been a density of 2.98/m^2. The highest *Diadema* density recorded on ER #2 was 1.4/m^2 and occurred on 10/24/01 and again on 2/26/02 (45 urchins were released on ER #2 between these counts). After 17 months the urchin density on ER #2 was 0.6/m^2 with an apparent survival rate of 20%. The average density of *Diadema* on ER #2 over the duration of the project was 1.0/m^2.

The total area of reef structure of both experimental reefs was 184 m^2. By number, 61% (434) of the 712 urchins were placed on ER #1 and 39 % (278) were placed on ER #2. Numerically, by 2/5/03 ER #1 lost 74% of the urchins placed on it, and ER # 2 lost 80%. The potential density of the release of 712 urchins combined for both reefs was 3.9/m^2 and at the end of the study, the surviving density for both reefs combined was 0.9/m^2. Despite considerable differences in numbers of urchins placed on each reef, a total potential density of 4.5/m^2 on ER #1 and 3.2/m^2 on ER #2, the average density of *Diadema* on both experimental reefs over the 17-month term of the project was 1.6/m^2 on ER #1 and 1.0/m^2 on ER #2, a difference of 0.6/m^2. The total loss of density on ER #1 (4.5/m^2 down to 1.2/m^2) over the course of the study was 3.3/m^2 compared to the loss of 2.6/m^2 (3.2/m^2 down to 0.6/m^2) on ER #2, a greater loss of potential density of 0.7/m^2 on ER #1 than on ER #2.

A difference of 0.6/m^2 separated the total density of urchins on ER #1 (1.2/m^2), from ER #2 (0.6/m^2) 17 months after initial placement of urchins on these reefs. The overall urchin density was greater on ER #1 than on ER #2 at each count (Fig. 6), but the percent apparent survival of urchins on each reef was very similar until the 8/8/02 count (Fig. 5). After excluding the 16 urchins added to ER #2 on 10/23/02 for the 11/30/02 count, ER #2 had a 58% decline in urchin density from 1.2/m^2 down to 0.5/m^2, between 8/8/02 and 11/30/02. ER #1, however, with a density loss of 1.4/m^2 down to 1.2/m^2, a decline of only 14%, did not experience a similar loss over the same period. Predation seems the most likely cause for the precipitous decline on ER #2; perhaps the relative scarcity of complex reef structure on ER #2 made the urchins more available to predators on this reef.

Overall, however, the rate of loss of urchins on both reefs was similar. The daily rate of loss of percent density of urchins on both reefs was calculated by dividing the percent loss (mortality) of urchins (100 – (#/m^2 counted / #m^2 released x 100) on each experimental reef at the time of each count by the number days elapsed since the first translocation of urchins. This provided the daily rate of loss from the beginning of the project of the percent mortality at the time of each count (Table 7 and Fig. 7).

The initial rapid loss of urchins is evidenced in the high daily rate of loss over the first 3 days after the first translocation. Although survival rates were relatively high over these 3 days, 81% on reef # 1 and 90% on reef # 2, the short time period of 3 days produced a high daily rate of loss, 6.3% per day on reef # 1 and 3.3% per day on reef # 2. It may be that the small juveniles that were translocated succumbed rapidly to predation or that many of these smallest urchins were not detected in the complex reef structures on the first count. Interestingly, despite the

structural and areal differences in the two reefs; the differences in the numbers of urchins released and counted on these reefs; and the varying number days between counts, after the initial period of 65 days; the daily rate of percent mortality on each reef is very close from Nov., 2001 to Feb. 2003 (Table 7). And this daily rate of loss was relatively stable on both reefs at about 0.2% from 5/29/02 through 11/30/02. The average percent rate of loss per day from the total number of urchins that were placed on both reefs from 2/26/02 through 11/30/02, 278 days, was 0.21% on ER #1 and 0.22% on ER #2, and the average loss of density from 2/26/02 to 11/30/02 was $0.9/m^2$ on both reefs, a daily rate of density loss of $0.003/m^2$ per day on both reefs. In the 67-day period between the last two counts, 11/30/02 and 2/5/03, ER #2 continued to lose urchin density (8 urchins, $0.09/m^2$) more rapidly than ER #1 (4 urchins, $0.04/m^2$).

Mortality due to predation is assumed to the major cause of loss of urchins on the experimental reefs. However, it is possible that some urchins moved off the reefs onto other nearby reefs. A few large urchins were observed on CR #3 during a night dive on 8/28/02, but such movement would have had to occur over 40 to 50 feet (12 to 15 meters) of seagrass bed that separated ER #1 from CR #3, so we consider movement of urchins off the experimental reefs as possible, but unlikely.

Our primary interest in this project was to investigate survival of the translocated *Diadema* on the experimental reefs and the effect that these urchins may have on the benthic ecology of these reefs. Growth rates, movement of urchins on the reefs, preference for particular microhabitats, and distribution of urchins on the reefs were also of considerable interest, but the frequent monitoring and detailed experimental design required to fully explore these considerations were beyond the scope of this project. Analysis of the survival and/or movement of translocated *Diadema* within each of the 4-m^2 sectors was not possible. However, analysis of the numbers of urchins released and the numbers counted in each quadrant of the experimental reefs at each population evaluation did yield interesting results.

Changes in urchin populations in each quadrant of each reef would be due, in varying measure, to differential survival and/or movement of urchins between quadrants. The boundary line between quadrants often ran through coral reef structures so, in some areas, urchins moving from one side of a coral head or complex coral structure to the other would move from one quadrant to another with relatively little actual linear movement. However, despite the inherent vagaries of urchin populations in the quadrants, some understanding of the distribution of urchins on the reefs can be gleaned from this data.

Movement of an urchin from one quadrant to another registered as a loss to one quadrant and a gain to another. A gain in population would result from either movement into that quadrant or settlement of new recruits in that area. After the first two months, the presence of new recruits on any area of the experimental reefs would have been quite obvious, and newly settled *Diadema* would not have been noticeable on the reef during the first month. In a study of settlement of *Diadema* off Curacao, Bak (1985) reported growth of newly settled *Diadema* at about 3-6 mm in a two-week period, and Forcucci (1994) estimated an early growth rate of about 7 mm per month for urchins on Florida Keys reefs. We would not have noticed newly settled *Diadema* until they had attained a test size of at least 5 mm, probably a month or so after settlement and such small

urchins would have been quickly identified as recent recruits. We are reasonably certain that few *Diadema* settled and survived on these reefs until early fall of 2002.

Increases in populations on any quadrant are assumed due to movement to more "desirable" environments with better shelter and/or stronger algal growth. Decreases in populations may be due to urchin movement out of a particular quadrant or loss from predation (or other cause of mortality) within that quadrant. A study using spine tags to track individual urchins by Carpenter (1984) demonstrated that *Diadema* returned with remarkable fidelity to the same daytime shelter and that the urchins avoided grazing on the same areas that were foraged the previous night.

Tables 6 and 8 list the cumulative numbers of *Diadema* released in each quadrant of ER #1 (Table 6) and ER #2 (Table 8) and the numbers of urchins observed in each of the quadrants on each reef at each count (population evaluation). Also listed in these tables are the density (#/m^2) of urchins released (cumulative) in each quadrant and the density (#/m^2) of urchins on the reef area of each quadrant at each count.

This data from each quadrant of each experimental reef is expressed as line graphs of the changes in density on each quadrant at each count. Figures 7 (above) and 8 show changes in density of urchin populations on each quadrant of ER #1 and ER #2. These line graphs compare the density of urchins cumulatively released on each quadrant with the density of urchins present on each quadrant at each population evaluation. Figures 9 and 10 show the changes in the percent density of urchin populations, (#/m^2 counted/#/m^2 released x 100) on each quadrant of ER #1 and ER #2, and on the total reef area. These line graphs compare increases and/or decreases in density of urchin populations relative to the density of the total number of urchins released on each experimental reef and on each quadrant of each reef at the time of each population evaluation. They illustrate relative survival and/or accumulation of urchins in these areas.

Figure 8. Reef # 1: Density of Diadema urchins (#/sq. m) cumulative total released (R) and number counted (C) on each quadrant at each count.

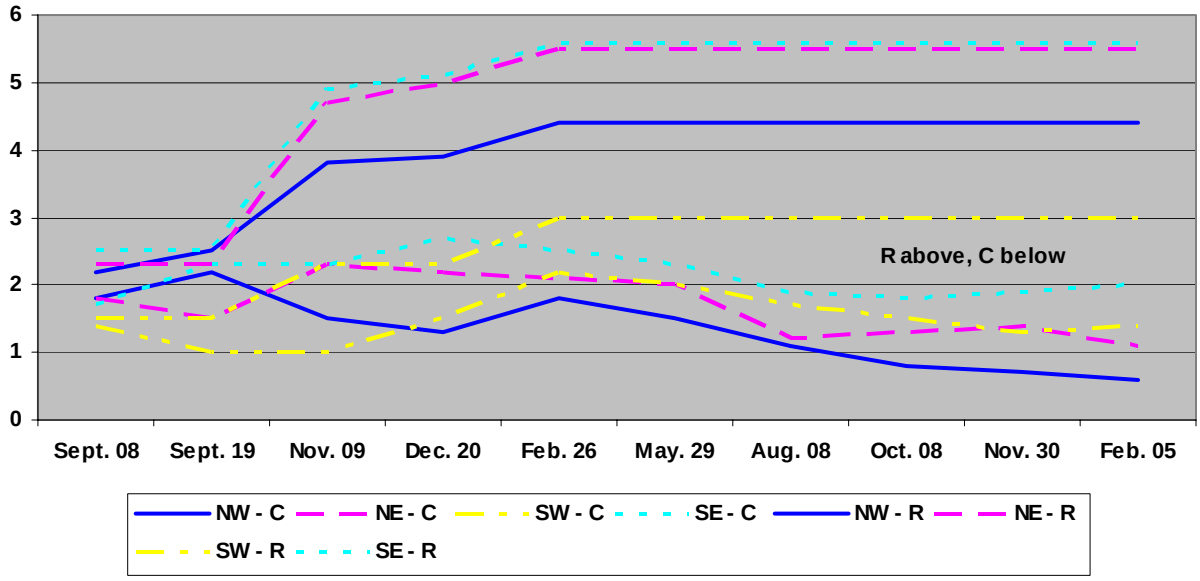


Figure 9. Reef # 2: Density of Diadema urchins (#/sq. m) released (R) and number counted (C) on each quadrant at each count.

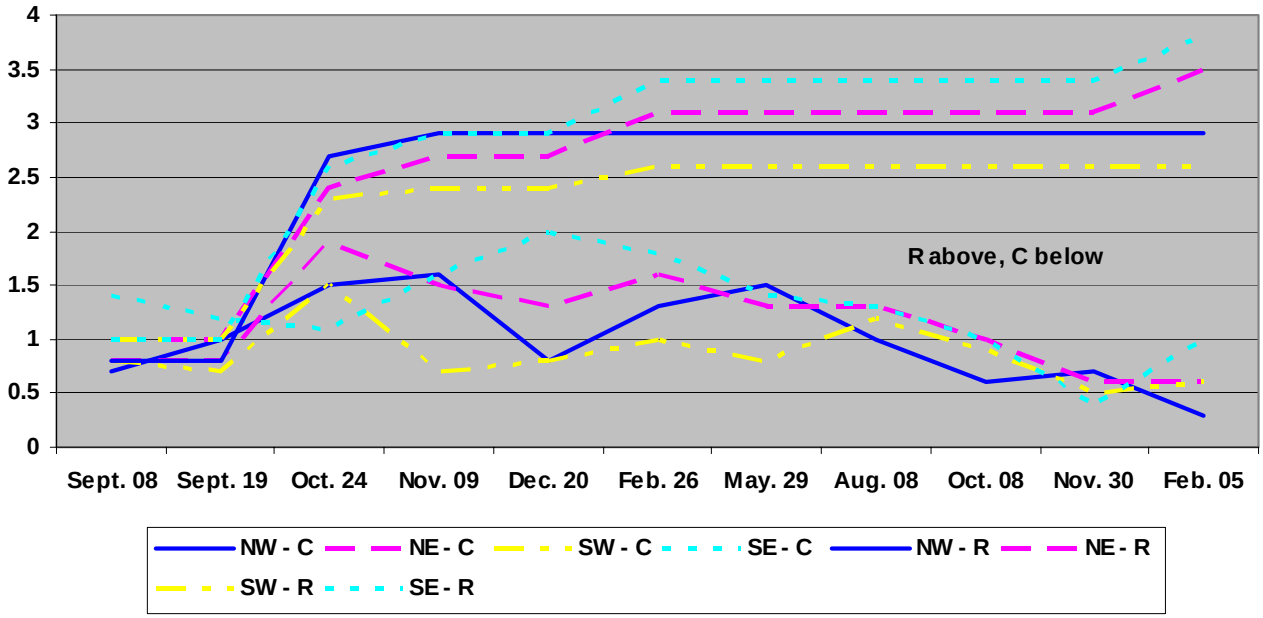
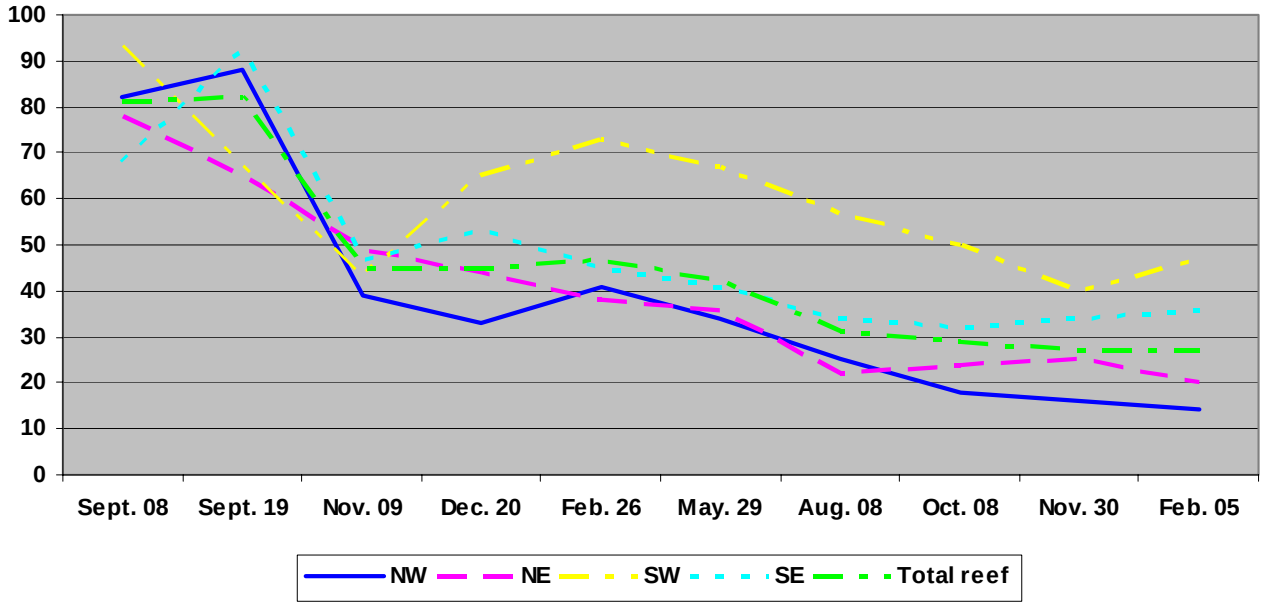


Figure 10. Reef # 1: Percent change in density of Diadema (#/sq. m counted / #/sq. m released on quadrant and on the total reef area at each count.



Without marking individual urchins, it is not possible to know definitively whether a loss of urchins in a quadrant between counts was due primarily to movement or to mortality. However, an increase in the number of urchins in a quadrant in the absence of release of additional urchins

in that quadrant must be due to movement of urchins into it. Also, an increase in urchin density in one quadrant over the same period as a decline in density in another quadrant may be due to movement rather than differential mortality. A decline in density of urchins in a quadrant that was markedly less than declines in other quadrants and less than the reef-wide decline, may be due to a movement of urchins into that quadrant, although significantly less mortality in that quadrant than in others cannot be discounted.

Experimental Reef #1

The data on placement and count of urchins in each quadrant of ER #1 over the course of the project is summarized in Tables 4 and 6 and in Figures 8 and 10. There was evidence of some movement of *Diadema* on ER #1 after initial placement. On ER #1 the density of urchins in the SE quadrant increased from 1.7/m^2 to 2.2/m^2 (0.5/m^2, an increase from 68 to 92) between 9/8 and 9/19/01 without the addition of new urchins. The density of urchins on the SW quadrant declined by 0.4/m^2 and the density on the NE quadrant declined by 0.3/m^2 without addition of new urchins, so it seems likely that urchins moved from the NE and SW quadrants into the SE (which has a border common to both NE and SW quadrants) over the 11 days between counts. The increase in urchin density of 0.4/m^2 in the NW quadrant was likely due to the placement of 11 urchins in this quadrant on 9/17/01.

The SE quadrant of ER #1 contains large and complex boulder coral formations, *Montastraea cavernosa*, and covers a relatively small area, 20 m^2. It would be expected that this complex reef structure would attract and contain a higher density of *Diadema* because of the shelter that these structures offer. The SW quadrant of ER #1 also contains large boulder coral structures and was a bit larger in total reef area, 24 m^2, and the NE quadrant, with the same area as the SE quadrant, also contained some large coral structure. The NW quadrant, with lower and less complex coral structure, also covered 24 m^2.

Placement density of urchins in the quadrants of ER #1 (5.6/m^2 SE, 5.5/m^2 NE, 4.4/m^2 NW, and 3.0/m^2 SW; Fig. 7) varied considerably (Table 4, Fig. 8). The two quadrants with the highest placement densities, NE and SE, had the highest average densities, NE 1.7/m^2 and SE 2.1/m^2, over the course of the project. The quadrant with the lowest placement density, NW, had the lowest density, 0.6/m^2, only about half the density of the other three quadrants at the last count on 2/5/03. Evidently, urchins on the NW quadrant experienced a higher mortality rate or moved into the more rugged nearby quadrants. The percent apparent survival (47% and 36%) and the final density (1.4/m^2 and 2.0/m^2) were greatest in the SW and SE quadrants at the end of 17 months. These were the quadrants on ER #1 with high and rugged coral growth.

The percent urchin density (Fig. 10) declined rapidly in the SW quadrant from initial placement of urchins on 9/4/01 (93% on 9/8/01) through 11/9/01 (43%), but then rapidly increased back up to 73% on 2/26/02. Despite receiving the lowest number of translocated urchins (71, 3.0/m^2), the percent density (47% after 17 months, Fig. 10) in the SW quadrant remained considerably higher than the other quadrants and higher than the total density on the reef. Percent urchin density in the SE quadrant was also greater than that on the total reef while quadrants NE and NW were below the density on the total reef (Fig. 10).

Although some movement into the SE and especially the SW quadrants seems to have occurred (Fig. 10), in general, a gradual and similar decline in urchin densities in the SW and NW quadrants occurred while urchin densities on the NE and SE quadrants did not decline and even slightly increased from 8/8 to 11/30/02 (Fig. 8 and 10). Between 11/30/02 and 2/5/03, however, density in the SW quadrant increased while density in the NE quadrant declined by about the same amount. A departure from this picture of gradual decline or little change in the density of urchins on each quadrant after 2/26/02 is evident in a marked decline in density in the NE quadrant that occurred between 5/29 (2.2/m^2) and 8/8/02 (1.2/m^2). This quadrant contains the sheltered site within a large coral structure that was occupied by both large Atlantic burrfish and this quadrant may have been a focus for predation during that time prior to the removal of the second one on 9/28/02.

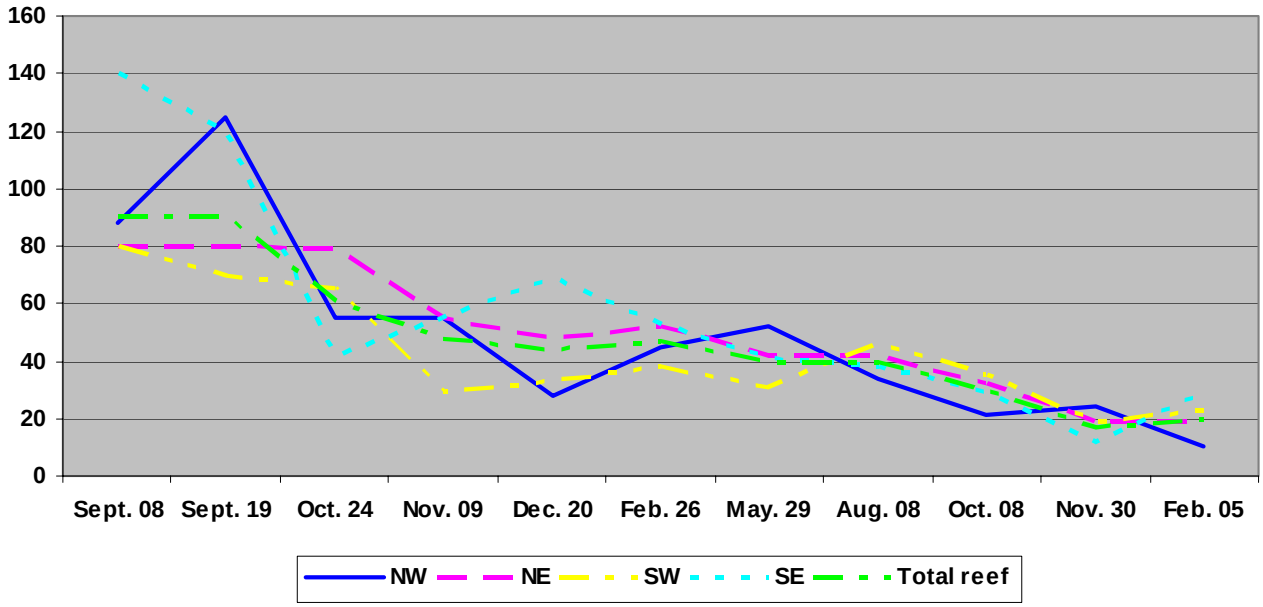
In general, the pattern of distribution and changes in density of urchins on ER #1 over the course of the study showed a tendency for accumulation of urchins in the SW and SE quadrants, especially in the SW quadrant, and a greater loss or movement out of the NW and to a lesser degree the NE quadrants (Fig. 10). Urchins are probably attracted to the high relief and rugged coral formations of the SW and SE quadrants, and/or have better survival in these areas.

Experimental Reef #2

Data on placement and counts of urchins on each quadrant of ER #2 over the course of the project is summarized in Tables 5 and 8 and in Fig. 9 and 11. ER #2 is more homogenous in reef structure than ER #1. There are no large, complex coral structures and the coral structures that are present have low relief. Considerably fewer *Diadema* were translocated to ER #2 and they were distributed more evenly over the quadrants (2.9/m^2 NW, 3.5/m^2 NE, 2.6/m^2 SW, and 3.8/m^2 SE) than on ER #1. Density of urchins was always less on ER #2 than on ER #1 (Fig. 6) with the closest density, 1.4/m^2 on ER #1 and 1.2/m^2 on ER #2 occurring on 8/8/02 (Tables 4 and 5

Within the first 15 days or so there was strong movement of the translocated urchins into the NW and, in the first 3 days, especially into the SE quadrant of ER #2. Although relatively few urchins were released on this reef (85) in the first translocation on 9/4 and 9/5/01, and no further urchins were placed on the reef until 9/19/01, density in the SE quadrant increased to 140% of the density at release on 9/8/01 (3 days after release), and then declined to 120% on 9/19/01 (14 days after release). The population in the NW quadrant was 88% of the release density on 9/8/01, but then climbed to 120% of the release density on 9/19. In contrast, the population densities of the NE and SW quadrants were relatively static at 80% and 70% of the release densities over the period from 9/8 to 9/19/01. In actual numbers, these figures represent a gain of 7 urchins to the SE quadrant and a loss of 1 urchin to the NW quadrant between 9/5 and 9/8/01 and a loss of 5 urchins to the SE quadrant and a gain of 6 urchins to the NW quadrant between 9/8 and 9/19/01. Some urchins did move, however, from the NE and SW quadrants to the NW and SW quadrants very soon after translocation.

Figure 11. Reef # 2: Percent change in density of *Diadema* (#/sq. m counted / #/sq. m released) on each quadrant and on the total reef area at each count.



In general, after 10/24/01, urchin density declined gradually at a similar rate in all quadrants during the rest of the study. A notable exception, however, was a rapid loss of density in the NW quadrant (1.6/m^2 to 0.8m^2) from 11/9 to 12/20/01. The NE and SW quadrants also lost density during this period. In contrast, the SE quadrant gained density from 10/24 to 12/20/01 (1.1/m^2 to 2.0/m^2), an indication that some movement toward the SE quadrant occurred.

The SE quadrant had by far the greatest number of urchins (27) and greatest density (1.4/m^2) at the first count on 9/8/01 and the least number of urchins (8) and lowest density (0.4/m^2) at the count on 11/30/02. However, on the final count on 2/5/03, the number of urchins on the SE quadrant rose from 8 to 20, a gain in density from 0.5/m^2 to 1.0/m^2. The addition of 16 urchins to this reef on 10/23/02 as well as movement to this quadrant probably accounted for this gain. After 2/26/02 the density of urchins on all quadrants of ER #2 varied from 1.8/m^2 in the SE quadrant to 1.0/m^2 in the SW quadrant, but on 11/30/02, 278 days later, the distribution of urchins over the reef was almost equal in all quadrants, from the highest in the NW quadrant of 0.7/m^2 to the lowest in the SE quadrant of 0.4/m^2. Between 11/30/02 and 2/5/03 there was a marked decline in density in the NW quadrant (0.7/m^2 to 0.3/m^2) and an increase in density (0.5/m^2 to 1.0/m^2) in the SW quadrant. The decline was even and gradual in the NE and SE quadrants and more variable with opposite peaks and dips in the NW and SW quadrants (Fig. 9). The average density of urchins on each quadrant over the course of the project was very similar (NW 1.0/m^2, NE 1.2/m^2, SW 0.9/m^2, and SE 1.3/m^2). Thus in general, the population of *Diadema* on ER #2 maintained a variable, but generally homogeneous distribution over the reef over the last 12 months of the project. The lack of high relief and rugged coral formations on this reef probably contributed to this pattern of distribution.

Diadema *Recruitment*

There has been speculation on the role, if any, that a population of adult *Diadema* may have in stimulating settlement and/or survival of post-larval *Diadema* in the area of the adults through preparation of the substrate (including stimulation of the growth of coralline algae) and/or release of pheromones (perhaps stimulation to begin metamorphosis). In addition, adults may directly aid in the survival of newly settled juveniles through protection under the spines of the adults. Three or four small, apparently newly settled *Diadema* urchins were observed on ER #1 during the course of the study, and on 11/30/02 we found 6 new juveniles on ER #1 and 4 on ER #2. On 2/5/03 there were 3 small juveniles on ER #1 and 1 on ER #2; no juveniles were observed on the control reefs. They were not found in the immediate presence of adults and it was not obvious that the presence of the now adult *Diadema* on these reefs influenced settlement in any way, but the presence of these juveniles is suggestive of an adult influence. These juveniles were included in the counts on those dates.

It has been noted that *Diadema* larvae prefer to settle in areas cleared of filamentous algae (Bak 1985; Lessios 1995) and this may be the main reason why settlement occurs in the reef crest rubble zones where the coral rock substrate is cleaned of algae by frequent movement and abrasion caused by high sea states. The rocky substrates of these shallow rubble areas and reef areas with dense populations of *Diadema* are both relatively clear of algal growth. Lessios (1995) reported on extensive research conducted with *Diadema* and other urchins that occupy similar reef environments, in particular *Echinometra viridis*, which competes with *D. antillarum* for food and substrate. Lessios' research showed that high densities of *E. viridis*, which graze the substrate more intensively than *Diadema*, produced areas with greater rates of *Diadema* recruitment than areas with both *E. viridis* and *D. antillarum* and *D. antillarum* alone. Areas with only *D. antillarum*, however, had greater recruitment than areas with no urchin populations. Lessios (1995) concluded that lack of recruitment months after the 1983-84 die-off was due to extreme paucity of *Diadema* larvae in the waters of the Caribbean.

Our study indicates that on Florida reefs, the presence of adult *Diadema* is, or should be, helpful to the recruitment of juvenile *Diadema*. Many juveniles settle on the shallow rubble areas of Conch and Pickles Reefs during late summer and fall of each year. There is an absence, or extreme dearth, of recruits, however, on the deeper patch reefs where our study took place only a mile or so inshore from these reefs. If some larvae nearing settlement are present in the waters of Conch and Pickles Reefs, which they must be, then there should also be some larvae present that could, and probably do, settle on nearby reefs as well. Small juveniles 1 to 2.5 cm test diameter, translocated to these reefs survived in large numbers for many days after translocation, thus there is nothing intrinsic in the environment of these patch reefs that would prevent significant survival of juvenile *Diadema*, at least not after a test size of 1.5 to 2 cm is attained. In November, 2002, about one year after translocation and maintenance of an increased population level of *Diadema*, we observed a number of juvenile *Diadema* that had settled on the experimental reefs. The number of new juveniles was not great, 10 to 12, roughly about $0.07/m^2$, but this demonstrates that *Diadema* post-larvae will settle and survive on Florida reefs where populations of adults are present. However, according to the survival data in our study, settlement and survival of about 1.2 *Diadema* urchins per year on each square meter of reef area is required to maintain a population of about 1 to 2 urchins/m^2 on the patch reefs of our study. Mortality immediately after

settlement is probably very high, so settlement of post-larval *Diadema* in numbers far greater than 1.2/m^2 is no doubt necessary to secure survival of 1.2 urchins/m^2. We feel that the scarcity of *Diadema* recruits on Florida Keys patch reefs is due to both paucity of larvae in the water mass and a lack of proper substrate and/or settlement stimulus on reefs without an adult population. In all probability, however, given the occurrence of scattered individuals and small groups of urchins in various locations on Keys reefs, the scarcity of late stage larvae in the water is a more significant factor in the failure of *Diadema* to repopulate Florida reefs than the lack of prepared substrate.

An adult female *Diadema* can produce 10 million eggs every month (Levitan 1988) and Tom Capo (personal communication) in rearing experimentation with *Diadema* reports the fecundity of some individuals at 15 to 20 million eggs per spawn. When *Diadema* were present on most reefs of the Caribbean, Florida, and the Bahamas at densities from about 1/m^2 up to perhaps 20/m^2, the larval load of *Diadema* in these waters must have been immense. (One can only wonder at the changes that must have occurred in the planktonic ecology of these waters upon the abrupt elimination of this immense component of the zooplankton population.) Despite such extraordinary fecundity, small populations of adults scattered widely over reef areas are not capable of producing large numbers of larvae. This is because *Diadema* are sessile spawners; males and females release gametes into the water without physical contact and without regard to proximity of individuals. When males and females are more than about a meter apart, fertilization is severely compromised and few viable larvae result. Also, the scarcity of large adults greatly reduces the fecundity of populations (Levitan 1991).

Small populations and widely spaced individuals are not able to produce the numbers of larvae necessary for recovery of populations to pre-die-off levels. Natural recovery of dense *Diadema* populations will depend on the chance coalescence of many factors that are favorable to successful settlement and survival of larvae. It will be necessary for these factors to merge frequently in order to maintain established populations.

Growth

Growth rates of *Diadema* under natural conditions depend on many factors including genetics, temperature, water quality, reef structure, and quantity and quality of benthic algal communities. Accurate determination of growth rates of *Diadema* under well defined natural conditions would require tagging of a significant number of individual urchins, probably at least 30, and frequently and accurately measuring the test diameter of each urchin over an extended period, at least 6 months to a year. Repeating these experiments under differing conditions of depth, benthos, and seasonality would also be necessary to characterize variability of growth rate potential for this species in various locations.

Although we were not able to conduct such detailed experimentation on growth, we did make estimates of the size range of the *Diadema* collected and translocated to the experimental reefs. Table 2 lists the size ranges of the collected urchins, 249 (34%) were in the small range (1-2.5 cm), 306 (41%) were in the medium range (2.6-4.9 cm), and 186 (25%) were in the large range (4.5-6 or more cm). This collection data illustrates that by far the large majority of the translocated urchins were young juveniles of small test diameter since 75% had a test diameter of less than 4 cm. Very few were larger than 4.5 to 5 cm. We noticed during the 12/20/01

population evaluation that very few, if any, of the urchins observed were in what we had defined as the small and medium size ranges. Although it is possible that smaller sized urchins sustained the greatest mortality due to predation, it is unlikely that all the smallest urchins would have been lost and only the larger ones survived during the first three to four months. Survival rates on 12/20/01 were 46% on ER #1 and 45% on ER #2, so many urchins in the small and medium size ranges must have survived to that point. It is likely that many small urchins in the 2 cm test size range grew to test diameters of 3.5-4 cm within the first 4 months. Also, the benthic survey by NURC (next chapter) showed that by far the greatest test size range of *Diadema* found on the experimental reefs in September 2001 were in the 4.0-4.9 cm range. So, in general, *Diadema* on Upper Keys offshore patch reefs appear to attain a test size of 4-5 cm within about one year. Forcucci (1994) reported a growth rate of over 4 mm per month for juveniles with test diameters up to 24.0 mm, and our observations roughly agree with this rate for urchins in the 2.0-4.0 cm test diameter range. In general, *Diadema* achieve a test diameter of about 3-4 cm within the first year and about 4-5 cm in the second year, and a low estimate of longevity is 4 years with a test diameter of about 10 cm (Ogden and Carpenter 1987).

Discussion

There were four specific biological restoration objectives in this project. We feel we have succeeded in attaining these objectives to a large degree during the conduct of this project. Each of these objectives is listed below with a brief comment on what this study has revealed on these topics.

1. Determine if *Diadema* survive transplantation and the size that exhibits the best survival rate after transplantation.

Diadema clearly survive transplantation. The initial survival rates of 80 to 90 percent over the first few weeks after translocation and continued survival at levels of about 1.0/m^2 over the entire year of the project demonstrate that adequate survival of translocated *Diadema* is attainable. We were not able to definitively determine the best size for translocation, but the indications are that larger urchins, test size greater than 2 cm, survive better than smaller urchins.

2. Estimate the survival and growth rates of transplanted *Diadema*.

Survival rates on each experimental reef and on each quadrant of each reef were carefully analyzed. The initial high loss rates (presumably mortality) over the first two to three months leveled off at about 50% and, over the last 12 months of the study, survival dropped to about 25%. Densities, however, were maintained at about 1-2/m^2 on both experimental reefs throughout the sturdy. The daily rate of percent reduction in density of urchins on both reefs after the first two months was the same. Over the 9-month period, 2/26/02 to 11/30/02, the density of urchins declined 0.9/m^2 on both experimental reefs, a daily rate of loss of density of about 0.0032 urchins/m^2 on both reefs. To maintain a population of *Diadema* at a density of about 1/m^2 on a reef area, a recruitment rate that would support survival of about 1.17 urchins/m^2 of reef area per year would be required.

It is tempting to speculate that translocation of *Diadema* on Florida Keys reefs, especially larger urchins, should be targeted at densities of about 2/m^2. Densities greater than 2/m^2 may

experience undue loss and densities less than $1/m^2$ may be too few to establish persistent and biologically effective populations. This speculation is based more on intuition and experience than analysis of data. Also, Lessios (1995) reported that the average density on all reefs censused in the San Blas area of Panama before the die-off was close to $1.0/m^2$. However, population densities much greater than $1/m^2$ were not uncommon in the Caribbean. Bak (1985) reported that densities of *Diadema* along the southwest coast of Curacao were $4\text{-}12/m^2$ during the period 1975 to 1983. Although populations much greater than $1.0/m^2$ have been reported, healthy populations over broad areas containing varied types of reef structure and hard bottom in the Florida Keys may have a "climax density" of about $1.0/m^2$. The various types of reef structure present in Florida Keys reefs, various exposures to predation, and perhaps most important, varied incidence of recruitment may greatly affect the density of urchins on specific reef areas in various locations. Research on the response of urchin populations translocated to various reef types and locations is needed.

Estimates of growth rates observed in this study indicate that only about 4-6 months are required for juveniles (1.5 to about 2.0 cm test diameter) to attain a small adult size of 3-4 cm test diameter.

3. Determine the distribution patterns that *Diadema* develop on test reefs.

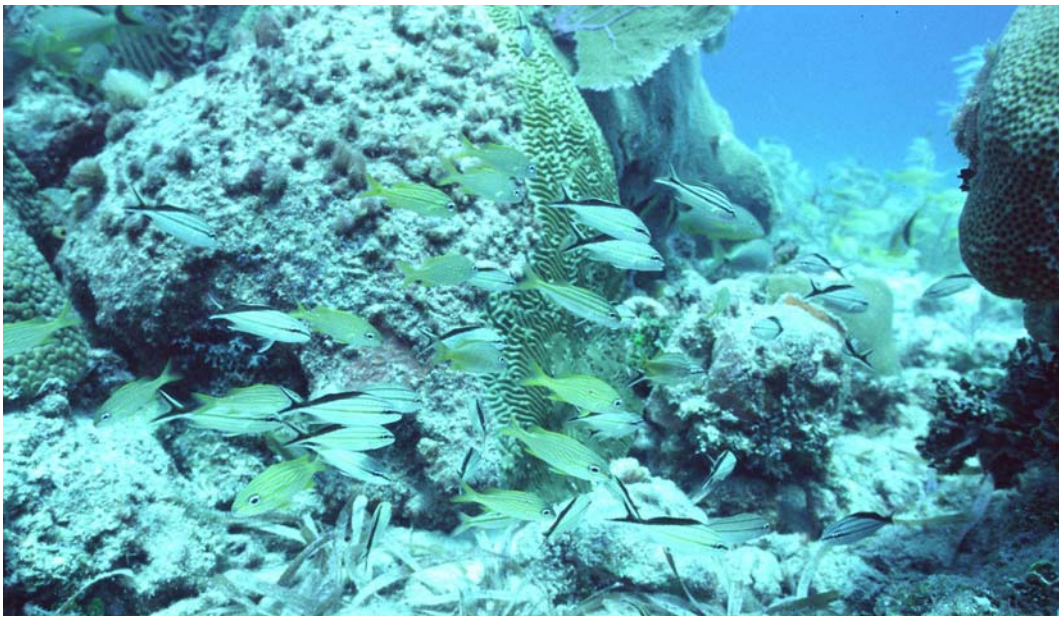
The distribution patterns of *Diadema* on these patch reefs were indicated by data on the density of urchins in the four quadrants of each experimental reef. In general, although there was movement of urchins from quadrant to quadrant, and indications of concentration in quadrants with high and complex coral formations, for the most part, urchins remained relatively evenly distributed over all the quadrants of each experimental reef.

4. Compare and contrast general reef condition and community level changes, including coral recruitment and growth, on the manipulated and reference reefs over time.

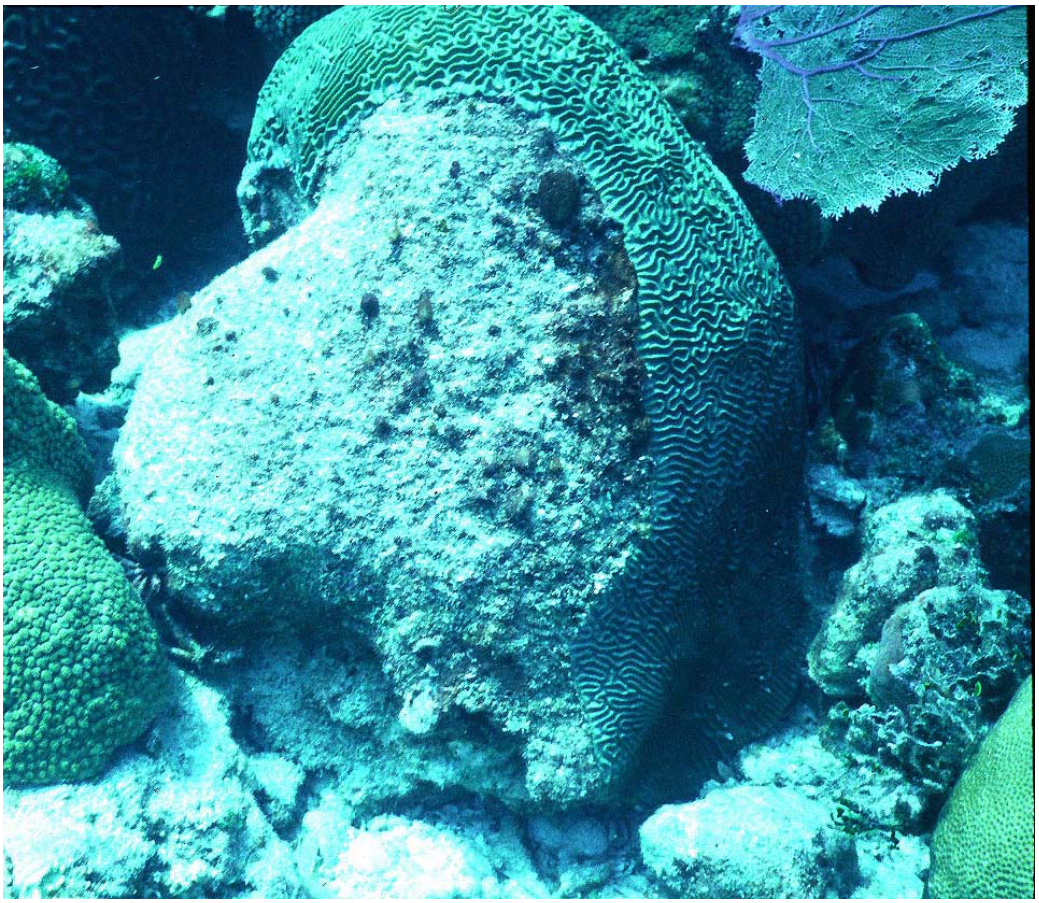
The before and after benthic assessments by NURC (next chapter) demonstrated that, among other positive changes on the experimental reefs, algal cover was markedly decreased, coralline algal cover markedly increased, stony coral cover increased, and the density of juvenile corals increased significantly over that of the control reefs.

Coral head on ER #1 in September 2001 before translocation of *Diadema*. Note the heavy algal growths.

Same coral head as above in August 2002. Note great reduction in algal growth.

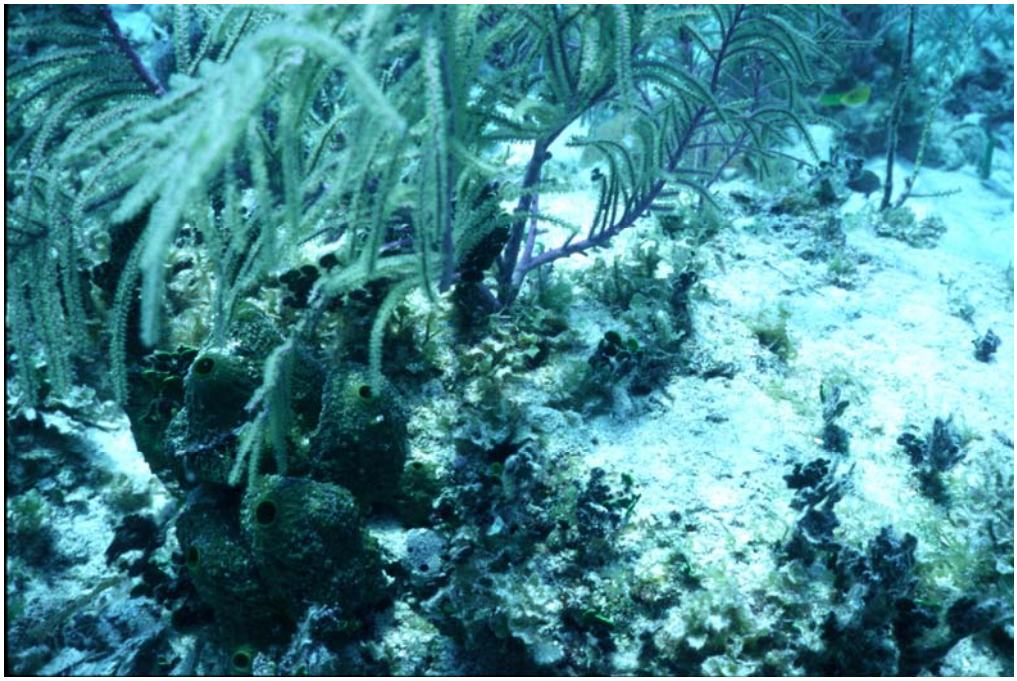


Dying coral head on ER #1 in September 2001. Note extent of erosion of living coral tissue and growth of algae on rock surfaces.



Same coral head as above on August 2002. Note removal of algae on rock surfaces and regeneration of coral tissue on upper section of formation.

Typical algal fouling on rock on ER #1 before translocation of urchins.



Typical rock reef area on ER #1 in August 2002 one year after urchin translocation.

Diadema are relatively immobile during the day and move about as they feed at night. They may return to a particular sheltered area during the day or may simply find an adequate shelter as dawn approaches. At the beginning of the project we observed a particular juvenile that had apparently settled naturally and that occupied a specific small cavity in a rock structure on the SE quadrant of ER #1over a period of several months. This indicates that at least juveniles tend to remain in the same area and occupy the same shelter during the day. Large adults probably have a greater range and may occupy various sheltered areas during the day.

In this study, once *Diadema* attained an adult size of about a 4 cm test diameter and above, mortality rates declined to slightly less than 1.0 urchin/m^2/year, a rate of about 0.0025 urchin/m^2/day.

A major concern on repopulation of *Diadema* on Florida reefs is the potential for the return of the presumed pathogen that decimated populations of these urchins in 1983-84. This is a real concern, especially since there was a secondary mortality of *Diadema* in 1990-01 (Forcucci 1994). The mortality caused by this epizootic is rapid and affects almost all *Diadema* within a very broad area. The mortality we observed on the experimental reefs during this study was gradual and persistent, but affected only a relatively small number of urchins at any one time. We also never observed the disintegration of urchins leaving a mass of disarticulated tests and spines, thus disease apparently did not cause urchin mortality during our study.

Predation was evidently the major cause of mortality of urchins on the experimental reefs. We directly observed predation on the urchins by the Atlantic burrfish, *Chilomycterus atinga*, and other predators such as triggerfish, hogfish, permit, grunts, spiny lobsters, and spider crabs may have also actively preyed on the urchins, especially on small juveniles, but active predation by other predators was not observed during our study. Such predators once accustomed to feeding on *Diadema* and upon finding a relatively dense population, may quickly remove a significant number of urchins before moving on to other areas. Without consistent recruitment adequate to maintain an effective population, these small isolated populations dwindle in number over a period of months to years. Populations of *Diadema* that occur in areas with some protection from predators, such as shallow protected areas or rugged and complex reef areas may better resist predation and persist in numbers over a longer period. Also, very low levels of recruitment would be more effective in maintaining populations in such areas.

Restoration

The importance of healthy populations of *Diadema* to the coral reefs of the Florida Keys cannot be overstated. The following summation by Ogden and Carpenter (1987) based on over 20 years of experiments and observations is a strong testimony to the need for restoration of this species:

"Through direct effects on algal communities or indirect effects on other benthic reef organisms, grazing by *Diadema* is a major factor controlling the community structure of coral reefs. ….. perhaps no other single species in the coral reef environment has such profound effects on the other organisms composing the reef community."

The major underlying purpose of this study was to explore the results and possibilities of restoration of *Diadema* to reefs of the Florida Keys. As noted in the literature for Caribbean

reefs, and as demonstrated in this study, the benthic ecology of coral reefs shifts away from dominance by macroalgae back toward dominance of coral growth relatively quickly after populations of *Diadema antillarum* at densities of about $1/m^2$ are present on the reefs. It is obvious that the reefs of the Florida Keys would benefit immensely from restoration of *Diadema* to reef areas. Restoration may occur naturally, and there are indications that some recovery is occurring in isolated areas of the Caribbean, Jamaica, Belize, and other areas, and even some small areas in the Dry Tortugas have populations of large urchins about two years old that were in densities of 0.4-0.8 urchins/m^2 (Chiappone et al. 2001). These remote populations are probably the source of the recruits that appear on the rubble zones of Keys reefs in the late summer and fall months.

Restoration of *Diadema*, however, has not occurred in the 20 years since the Caribbean-wide mass mortality of 1983-84, and very low larval densities and extensive predation on juvenile and adult urchins may prevent (Lessios 1995) or greatly delay natural restoration of pre-die-off densities of this species. Our study demonstrates that a program of continuous movement of juveniles from settlement on reef crest rubble zones to specific deeper reef areas can establish and maintain relatively dense populations of *Diadema* in small reef areas. The continuous placement of juvenile urchins on these areas after initial translocation of a population of about $2/m^2$ at a rate of about $1/m^2$ per year would substitute for natural recruitment and maintain a reproductively effective population. This would serve two purposes. First, it would restore small reef areas, perhaps in marine protected areas, to a coral-dominated ecology that will allow settlement and growth of corals under historical environmental conditions, which would be an important research tool and a reservoir of natural coral growth. And second, it would establish small populations of reproductively active *Diadema* that will increase the density of larval *Diadema* in the waters downstream of these populations. The immense fecundity of adult female *Diadema* greatly enhances the importance of even small populations of reproductively active adults. Such translocation and monitoring programs would not be expensive and could be done with volunteer personnel, and could be instrumental in aiding the recovery of this keystone herbivore to the reefs of the Florida Keys.

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References
Carpenter, R.C. 1984. Predator and population density control of homing behavior in the Caribbean echinoid, *Diadema antillarum*, Philippi. Mar. Biol. 82: 101-108.

Chiappone, M., S.L. Miller, D.W. Swanson, J.S. Ault, and S.G. Smith. 2001. Comparatively high densities of the long-spined sea urchin in the Dry Tortugas, Florida. Coral Reefs 20: 137-138.

Chiappone, M, D.W. Swanson, and S.L. Miller. 2002. Density, spatial distribution and size structure of sea urchins in Florida Keys coral reef and hard bottom habitats. Mar Ecol Prog Ser. 235: 117-126.

Bak, R.P.M. 1985. Recruitment patterns and mass mortalities in the sea urchin, *Diadema antillarum*. Proc. 5th Int. Coral Reef Cong. 5: 267-272.

Forcucci, D. 1994. Population density, recruitment and 1991 mortality event of *Diadema antillarum* in the Florida Keys. Bull. Mar. Sci. 54(3): 917-928.

Lessios, H.A. 1995. *Diadema antillarum* 10 years after mass mortality: still rare despite help from a competitor. Proc. R. Soc. Lond. B 259: 331-337.

Levitan, D.R. 1988. Asynchronous spawning and aggregative behavior in the sea urchin *Diadeama antillarum*. Pages 181-186 *in* R.D. Burke, P.V. Mladenov, P. Lambert, and R.L. Parsley, eds. Echinoderm biology, A.A. Balkema, Rotterdam.

Levitan, D.R. 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. Biol. Bull. 181: 261-268.

Ogden, J.C., and R.C. Carpenter. 1987. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Florida). Long-spined black sea urchin. U.S. Fish and Wildlife Service. Biol. Rep. 82 (11.77). U.S. Army Corps of Engineers, TR EL-82-4. 17 pp.