Density, spatial distribution and size structure of sea urchins in Florida Keys coral reef and hard-bottom habitats

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ABSTRACT: The 1983-84 Caribbean-wide mortality of the long-spined sea urchin *Diadema antillarum* Philippi was followed by a 2nd mortality event during 1991 in the Florida Keys. Pre-mortality sea urchin densities were up to 5 ind. m^{-2} and the large scale decline of *D. antillarum* is considered to be 1 factor affecting community dynamics of Florida Keys reefs. During 1999-2000, we surveyed 125 sites using a stratified random sampling design in shallow-water coral reef and hard-bottom habitats. Strip transects were sampled to assess density, habitat utilization and size structure patterns among habitat types, regional sectors and between fished and protected areas. Nearly 17 yr after the mass mortality, *D. antillarum* has not recovered to pre-1983 levels, with current densities no greater than 0.05 ind. m^{-2}, and small test sizes (1 to 2 cm) dominate. Other sea urchins such as *Eucidaris tribuloides* (Lamarck) and *Echinometra viridis* Agassiz show density and habitat distribution patterns similar to historical observations.

KEY WORDS: Coral reefs · Florida Keys · Herbivory · Marine reserves · Population density · Recruitment · Sea urchins · Size structure

INTRODUCTION

Understanding the factors responsible for ecosystem change in coral reef habitats remains a challenge (Shulman & Robertson 1996, Hughes & Connell 1999). This is especially true in the Florida Keys (Dustan & Halas 1987, Porter & Meier 1992, Hughes et al. 1999), where the reefs are subtropical and subjected to substantial continental influence and densely populated shorelines (Marszalek et al. 1977, Jaap 1984). Evidence of coral reef decline is associated with: (1) diseases (Dustan 1977, Antonius & Ballesteros 1998, Richardson et al. 1998, Santavy et al. 2001); (2) physical impacts from storm events, as well as human-related impacts such as vessel groundings and anchoring (Dustan &

Halas 1987); (3) thermal stress, especially large-scale coral mortality after winter cold fronts (Roberts et al. 1982); and (4) coral bleaching during hyperthermic events (Jaap et al. 1988). Decreased herbivory, principally due to the 1983-84 mortality of the long-spined sea urchin *Diadema antillarum* (Lessios et al. 1984) is widely thought to be a major factor explaining increased macroalgal growth on reefs throughout the Caribbean (Hughes et al. 1985, Carpenter 1990a) and the Florida Keys (Lapointe 1989, Hallock et al. 1993); however, questions about the relative importance of top-down versus bottom-up control remain (Lapointe 1997, Hughes et al. 1999).

Prior to the mass mortality of *Diadema antillarum*, sea urchins attained high (>20 ind. m^{-2}) densities in many locations throughout the Caribbean (Sammarco et al. 1974, Hay 1984, Hunte et al. 1986). In the Florida Keys, however, the few historical data available indicate that

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sea urchin densities were lower (up to 4 to 5 ind. m^{-2}) (Kier & Grant 1965, Bauer 1976, 1980). However, still a general trend of increased algal cover was noted qualitatively after the 1983 urchin mortality at several upper Florida Keys bank reefs (Jaap et al. 1988) and in photomonitoring stations at 6 locations from Biscayne National Park to Looe Key (Porter & Meier 1992). Increased macroalgal cover after the urchin epidemic was also widely reported throughout the Caribbean (Hay 1981, 1984, Levitan 1992, Hughes 1994).

Seven years after the mass mortality affected the Florida Keys *Diadema antillarum* population, a 2nd disease event, after modest recovery to 0.30 to 0.58 ind. m^{-2}, once again attacked the Florida Keys population, resulting in declines to <0.01 ind. m^{-2} (Forcucci 1994). Since the 2nd mortality event, we are not aware of any large scale assessments of sea urchin densities and size structure. There is general interest in this previously ubiquitous element of the Florida Keys reef ecosystem, because there is expectation that recovery of *D. antillarum* will help to reverse the trend in macroalgal expansion at the expense of reef-building corals observed on particular reefs (Porter & Meier 1992, Edmunds & Carpenter 2001). Additionally, possible responses of other sea urchins to low *D. antillarum* densities in the Florida Keys are not documented. This study describes a large-scale assessment of sea urchin densities, habitat distribution and size structure con-

ducted during 1999-2000 throughout the Florida Keys. The surveys were 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).

MATERIALS AND METHODS

Study area. 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 semicontinuous series of offshore bank barrier reefs (Jaap 1984). Between the islands of the Florida Keys and the reef tract is Hawk Channel, a V-shaped basin (5 to 12 m depth) dominated by sand, seagrass beds 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, Chiappone & Sullivan 1997). For example, offshore bank reefs are best developed and patch reefs most numerous in the upper and lower Keys regions (Marszalek et al. 1977, FDEP 1998).
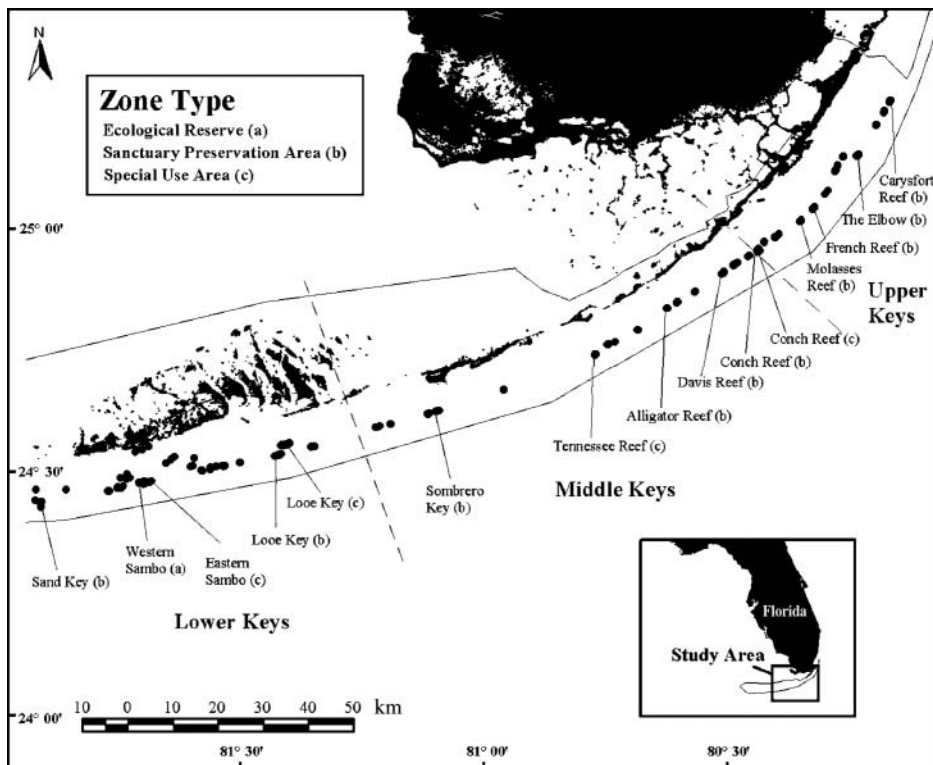

Fig. 1. Sea urchin sampling locations in the Florida Keys during 1999-2000. Illustrated are the boundaries of the Florida Keys National Marine Sanctuary, regional sectors and the location of no-fishing zones established in 1997

Twenty-three no-fishing zones were established in the Florida Keys National Marine Sanctuary in 1997 (NOAA 1996) encompassing many of the best-developed offshore bank barrier reefs, in addition to some offshore and near-shore patch reefs (Fig. 1). The zones consist of 1 Ecological Reserve (Western Sambo, 31 km^2), 18 Sanctuary Preservation Areas (SPAs, average of 0.82 km^2 in area, range of 0.16 to 3.27 km^2), and 4 special-use zones (Research Only, average of 1.15 km^2 in area, range of 0.68 to 1.77 km^2).

Sea urchin surveys and data analyses. We employed a 2-stage, stratified random sampling approach to derive mean density estimates for sea urchins at multiple spatial scales throughout the Florida Keys, following similar procedures outlined in Cochran (1977) and modified for our coral reef surveys (Miller et al. 2002). Surveys were conducted during September to December 1999 and July to September 2000. In 1999, we sampled 16 of the 23 no-fishing zones in the Florida Keys within 4 habitat strata: aggregate offshore patch reef (sampled only in the lower Keys region), inner reef line (found only in the upper Keys), shallow fore reef (4 to 7 m depth) and deeper fore reef (8 to 12 m) (Table 1). Calculations of stratum areas and random allocations of sampling stations within habitat strata were performed using a Geographical Information System (GIS) with geo-referenced benthic habitat maps (FDEP 1998). Two study sites were allocated to each no-fishing zone by randomly selecting two 200×200 m 'blocks' within each habitat stratum. Reference sites open to fishing were randomly assigned by habitat type (according to FDEP 1998 data) and regional sector (Table 1). In 2000, 45 hard-bottom and coral reef sites were surveyed in the lower Keys region from the shoreline to the deeper fore reef (12 m), using similar site selection procedures as in 1999. Five no-fishing zones (1 ecological reserve, 2 SPAs and 2 Research Only areas) were included with corresponding reference sites. Seven habitat types were sampled: nearshore hard bottom,

Table 1. Sea urchin sampling effort in the Florida Keys during 1999-2000. No-fishing zones are RO = research only area, SPA = sanctuary preservation area and ER = ecological reserve

Sampling mission (date)	No. sites	Area sampled (m^2)	Total effort (%)
Platform margin (Aug–Dec 1999)			
Aggregate offshore patch reef (Lower Keys)			
No-take zones (Looe Key RO)	2	160	2.5
Reference sites	2	160	2.5
Inner reef line (Upper Keys)			
No-take zones (Grecian Rocks SPA)	2	160	2.5
Reference areas	2	160	2.5
Shallow fore reef (4 to 7 m)			
No-take zones			
Lower Keys (Looe Key SPA)	2	160	2.5
Middle Keys (Sombrero Reef SPA)	2	160	2.5
Upper Keys (Elbow Reef SPA)	2	160	2.5
Reference sites			
Lower Keys	2	160	2.5
Middle Keys	1	80	1.3
Upper Keys	2	160	2.5
Deeper fore reef (8 to 12 m)			
No-take zones			
Lower Keys (3 no-take zones)	6	480	7.5
Middle Keys (6 no-take zones)	12	960	15.0
Upper Keys (3 no-take zones)	6	480	7.5
Reference sites			
Lower Keys	9	720	11.3
Middle Keys	19	1520	23.8
Upper Keys	9	720	11.3
Total	80	6400	100.0
Lower Keys cross shelf (Jul–Sep 2000)			
Nearshore hard bottom			
Western Sambo ER	2	160	5.0
Reference sites	2	160	5.0
Mid-channel patch reef			
Western Sambo ER	2	64	2.0
Reference areas	2	64	2.0
Offshore patch reef			
Western Sambo ER	2	64	2.0
Reference areas	2	64	2.0
Aggregate offshore patch reef			
Looe Key RO	2	160	5.0
Reference areas	2	160	5.0
Back reef rubble			
Western Sambo RO	1	80	2.5
Sand Key SPA	1	80	2.5
Reference areas	7	560	17.4
Shallow fore reef (4 to 7 m)			
Looe Key SPA	2	160	5.0
Reference areas	3	240	7.5
Deeper fore reef (8 to 12 m)			
Sand Key SPA	2	160	5.0
Western Sambo ER	2	160	5.0
Eastern Sambo RO	2	160	5.0
Reference areas	9	720	22.4
Total	45	3216	100.0

mid-channel patch reef, offshore patch reef, back reef rubble, shallow fore reef and deeper fore reef (Table 1).

Within each survey block, 4 random sampling points were generated in the GIS and were located in the field using a differential global positional receiver. Paired 25 m transects were deployed at each of the 4 sampling points per block (for a total of 8 transects per block), typically perpendicular to shore and parallel to each other. In shallow and deeper spur and groove habitats, paired transects were usually placed on separate spurs, but in all habitats were separated by at least 4 m. Because of the relatively small size of mid-channel and offshore patch reefs, 10 m transects were used instead, yielding a smaller total sampling area of 32 m^2 per block compared to 80 m^2 per block for other habitat strata. Using a scale bar, a 0.4 m swath along each transect was carefully surveyed for the number and test diameter of sea urchins. Surveys were conducted using SCUBA and all identifications were made *in situ* by the same observer for the duration of the study.

Mean sea urchin densities were computed for each pair of transects to derive block level density estimates.

Statistical comparisons of mean densities were accomplished by computing confidence intervals (CI) based on the equation:

$$CI = \text{mean} \pm t_{[\alpha,\, df]} \times SE$$

where SE was estimated by the 2-stage, stratified random sampling design (Cochran 1977) and CI were adjusted for multiple comparisons using the Bonferroni procedure (Miller 1981). The experiment-wise error rate was held at $\alpha = 0.05$ 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.

RESULTS

Platform margin patterns

Diadema antillarum represented 16 of the 56 individuals recorded (29%) during 1999 (Table 2). The species was absent from 86% of the sites sampled and few locations yielded densities >0.02 ind. m^{-2} (Fig. 2). The greatest density (0.05 ind. m^{-2}) was recorded from a middle Keys reference site on the deeper fore reef at Tennessee Reef. Mean densities of *D. antillarum* were not significantly different among habitat types (comparison-wise $\alpha = 0.038$), regional sectors ($\alpha = 0.017$) or between no-fishing zones and reference areas by habitat type and regional sector ($\alpha = 0.003$) (Table 2). The 16 *D. antillarum* encountered ranged in size from 1.2 to 5.0 cm in diameter and averaged 2.1 ± 0.24 cm (mean ± 1 SE) in test diameter (TD). The modal size classes of 1.1 to 1.5 cm and 1.6 to 2.0 cm accounted for 44 and 31% of all individuals, respectively (Fig. 3).

Eucidaris tribuloides was the most abundant species during 1999, represented by 38 individuals or 68% of all sea urchins. Densities did not exceed 0.038 ind. m^{-2} and this species was absent from 54 of the 80 sites (68%) (Fig. 2). The 39 individuals surveyed had an average test diameter of 1.7 ± 0.11 cm (mean ± 1 SE) and ranged in size from 0.5 to 3.0 cm (Fig. 3). Mean densities of *E. tribuloides* were significantly different among habitat types (comparison-wise $\alpha = 0.038$), among regional sectors on the shallow fore reef ($\alpha = 0.017$) and between no-fishing zones and reference sites for both the shallow and deeper fore reef (Table 2).

Of the 3 species encountered during 1999, *Echinometra viridis* was the least abundant, accounting for <4% of all sea urchins (Fig. 2). This species was absent from all but 2 sites, both of which were
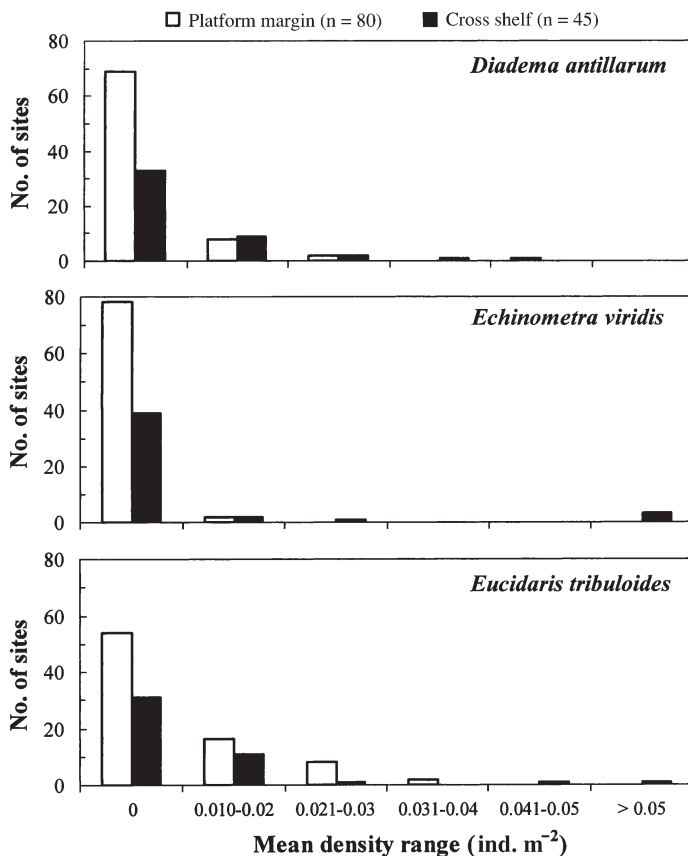

Fig. 2. Frequency distribution of mean sea urchin density ranges (ind. m^{-2}) for 80 platform margin sites during 1999 and 45 cross shelf sites during 2000 in the Florida Keys

on the shallow fore reef: a high-relief spur and groove habitat at Elbow Reef (0.013 ind. m^{-2}) and a low-relief hard-bottom habitat north of Carysfort Reef SPA (0.013 ind. m^{-2}) (Table 2). No significant differences in mean density were detected at any of the spatial scales investigated, and the 2 individuals were 0.5 and 1.0 cm in test diameter.

Cross-shelf patterns

Low densities and generally small test sizes characterized sea urchin assemblages on the Florida Keys platform margin during 1999. Overall, 73 sea urchins representing 5 species were found. Only 14 individuals of *Diadema antillarum* were found at the 45 sites dur-

Table 2. Mean sea urchin densities (ind. m^{-2}) on the Florida Keys platform margin during 1999 by habitat, regional and management strata

Spatial scale (no. sites)	*Diadema antillarum* Mean	SE	*Eucidaris tribuloides* Mean	SE	*Echinometra viridis* Mean	SE
Among habitat types						
Aggregate patch reef (4)	0.006	0.006	0.016	0.009	0	0
Inner reef line (4)	0	0	0	0	0	0
Shallow fore reef (11)	0.001	0.001	0.011	0.004	0.002	0.002
Deeper fore reef (61)	0.003	0.001	0.005	0.001	0	0
Habitat by regional sector						
Shallow fore reef						
Lower Keys (4)	0.003	0.007	0.006	0.008	0	0
Middle Keys (3)	0	0	0	0	0	0
Upper Keys (4)	0	0	0.025	0.011	0.006	0.008
Deeper fore reef						
Lower Keys (15)	0.001	0.002	0.002	0.002	0	0
Middle Keys (31)	0.004	0.004	0.005	0.003	0	0
Upper Keys (15)	0.002	0.002	0.008	0.005	0	0
Management type						
Aggregate patch reef						
Lower Keys						
No-fishing zones (2)	0.013	0.012	0	0	0	0
Reference areas (2)	0	0	0	0	0	0
Inner reef line						
Upper Keys						
No-fishing zones (2)	0	0	0	0	0	0
Reference areas (2)	0	0	0	0	0	0
Shallow fore reef						
Lower Keys						
No-fishing zones (2)	0	0	0.006	0.006	0	0
Reference areas (2)	0.006	0.006	0.006	0.006	0	0
Middle Keys						
No-fishing zones (2)	0	0	0	0	0	0
Reference areas (1)	0	0	0	0	0	0
Upper Keys						
No-fishing zones (2)	0	0	0.019	0.009	0.006	0.006
Reference areas (2)	0	0	0.031	0.006	0.006	0.006
Deeper fore reef						
Lower Keys						
No-fishing zones (6)	0	0	0	0	0	0
Reference areas (9)	0.001	0.001	0.003	0.002	0	0
Middle Keys						
No-fishing zones (12)	0.001	0.001	0.006	0.002	0	0
Reference areas (19)	0.006	0.006	0.003	0.002	0	0
Upper Keys						
No-fishing zones (6)	0	0	0	0	0	0
Reference areas (9)	0.003	0.002	0.013	0.003	0	0

ing 2000. *D. antillarum* was absent from 73% of the sites, and only 1 individual was recorded at 9 of the 45 sites (20%) (Fig. 2). One site, a mid-channel patch reef within the Western Sambo Ecological Reserve, yielded densities >0.03 ind. m^{-2}. Of the 7 habitat strata sampled, *D. antillarum* was absent from nearshore hard bottom, offshore patch reefs and the shallow fore reef. Mean densities of *D. antillarum* did not differ significantly among habitat strata (comparison-wise $\alpha = 0.002$) or between no-fishing zones and reference sites by habitat type ($\alpha = 0.05$) (Table 3). Similar to the 1999 results, individuals recorded during 2000 were generally small (<4 cm TD) (Fig. 3). The 14 individuals surveyed had an average test diameter of 2.4 ± 0.42 cm (mean ± 1 SE) and ranged in size from 1.0 to 5.4 cm.

In contrast to the 1999 surveys, *Echinometra viridis* was the most abundant sea urchin (36 ind., 49% of total) recorded during the 2000 cross-shelf surveys in the lower Keys (Table 3). Site level densities were as high as 0.59 ind. m^{-2} and 2 sites, a back reef rubble habitat north of Pelican Shoal (0.59 ind. m^{-2}) and 1 of the 2 aggregate offshore patch reef sites surveyed within the Looe Key Research Only zone

(0.10 ind. m^{-2}), accounted for 75% of all individuals recorded. Although local densities were relatively high in a few locations (3 locations or 7% had densities >0.05 ind. m^{-2}), *E. viridis* was absent from 87% of the sites and 3 of the 7 habitat types sampled (Fig. 2). No significant differences in mean density were detected among habitat strata (comparison-wise $\alpha = 0.002$) or between no-fishing zones and reference sites by habitat type ($\alpha = 0.05$). The 36 individuals surveyed averaged 2.7 ± 0.13 cm TD (mean ± 1 SE) and ranged in size from 1.3 to 4.3 cm (Fig. 3).

Nineteen individuals of *Eucidaris tribuloides* were recorded during 2000 (Table 3). This species was absent from 69% of the sites, and only 1 individual was recorded from 11 of the 45 sites (24%) (Fig. 2). The greatest site level density (0.063 ind. m^{-2}) was in a mid-channel patch reef north of Maryland Shoal. *E. tribuloides* occurred in all habitat strata except offshore patch reefs. No significant differences in mean density were detected among habitat strata (comparison-wise $\alpha = 0.002$). Mean densities were greater on nearshore hard-bottom sites within the Western Sambo Ecological Reserve compared to fished sites ($\alpha = 0.05$), but no significant differences were detected between no-fishing zones and reference sites for the 6 other habitat strata. The 19 individuals recorded averaged 1.9 ± 0.17 cm TD (mean ± 1 SE) and ranged in size from 1.1 to 4.2 cm (Fig. 3).

Echinometra lucunter and *Lytechinus variegatus* were also found during 2000, but only 2 individuals of each were recorded from the 45 sites. *E. lucunter* was recorded from an offshore patch reef within the Western Sambo Ecological Reserve and from a reference aggregate offshore patch reef site near the Looe Key Research Only zone, while *L. variegatus* was only recorded from 1 reference nearshore hard bottom site east of the Western Sambo Ecological Reserve in an area of scattered hard bottom with patches of sand and sparse to dense seagrass (*Thalassia testudinum*).

DISCUSSION

Few significant differences in mean sea urchin densities among habitat types, regional sectors and between no-fishing zones and reference areas were detected in the Florida Keys during 1999-2000. These results are not surprising given the low densities of sea urchins observed.
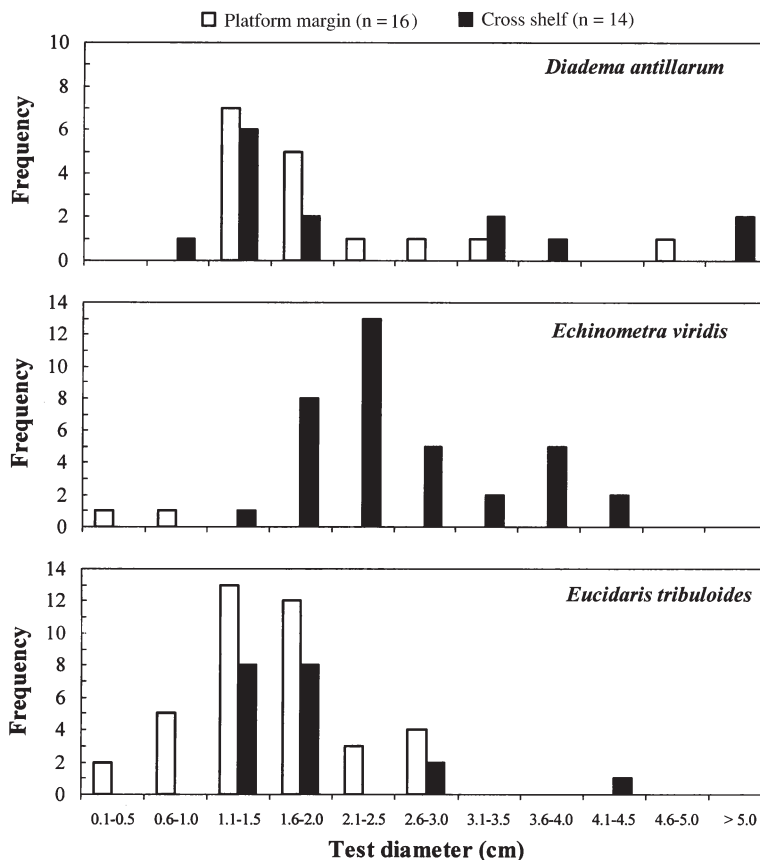

Fig. 3. Sea urchin size distribution (test diameter) in the Florida Keys from platform margin surveys during 1999 and cross shelf surveys during 2000

Table 3. Mean sea urchin densities (ind. m^{-2}) during 2000 by habitat strata and between no-fishing zones and fished areas across the continental shelf in the lower Florida Keys. No-fishing zone types are ER = Ecological Reserve and SPA = Sanctuary Preservation Area

Habitat types (no. sites)	Diadema antillarum		Eucidaris tribuloides		Echinometra viridis	
	Mean	SE	Mean	SE	Mean	SE
Nearshore hard bottom (4)	0	0	0.006	0.004	0.013	0.005
Western Sambo ER (2)	0	0	0.013	0.005	0.019	0.008
Reference sites (2)	0	0	0	0	0.006	0.006
Mid-channel patch reef (4)	0.008	0.008	0	0	0.172	0.141
Western Sambo ER (2)	0.016	0.016	0	0	0	0
Reference sites (2)	0	0	0	0	0.344	0.249
Offshore patch reef (4)	0	0	0	0	0	0
Western Sambo ER (2)	0	0	0	0	0	0
Reference sites (2)	0	0	0	0	0	0
Aggregate patch reef (4)	0.009	0.005	0.006	0.004	0.025	0.023
Looe Key RO (2)	0.006	0.006	0.013	0.006	0.050	0.046
Reference sites (2)	0.013	0.011	0	0	0	0
Back reef rubble (9)	0.006	0.002	0.015	0.008	0.007	0.007
No-fishing zones (2)	0.006	0.006	0	0	0	0
Reference sites (7)	0.005	0.003	0.020	0.010	0.009	0.009
Shallow fore reef (5)	0	0	0.003	0.002	0	0
Looe Key SPA (2)	0	0	0	0	0	0
Reference sites (2)	0	0	0.004	0.004	0	0
Deeper fore reef (15)	0.005	0.002	0.005	0.002	0	0
No-fishing zones (6)	0.004	0.003	0.002	0.002	0	0
Reference sites (9)	0.006	0.002	0.007	0.003	0	0

Conclusions from this study are also confined because of the paucity of historical density data for sea urchins. However, our results provide evidence that *Diadema antillarum* has not recovered, despite 16 yr since the 1983-84 Caribbean-wide mortality and 8 yr since the 2nd mortality event in the Florida Keys. Florida Keys sea urchin densities for the habitat types surveyed yielded low densities for all species and generally small test sizes. The size distribution of *D. antillarum* indicated recent recruitment, but poor post-settlement survivorship, as indicated by the paucity of individuals >1 yr of age. Densities of other sea urchins exhibited habitat distribution patterns consistent with historical observations (Kier & Grant 1965, McPherson 1968, 1969).

Only a few published studies of historical *Diadema antillarum* densities exist for the Florida Keys, some of which are either limited in spatial extent or are qualitative in nature. Despite these limitations, there is evidence that densities prior to 1983 were perhaps 2 orders of magnitude greater (>1 ind. m^{-2}) in some Florida Keys shallow water habitats. In the early 1960s, *D. antillarum* densities averaged 1.2 ind. m^{-2} in near-shore seagrass beds between Lower Matecumbe and Indian Key (Randall et al. 1964). Kier & Grant (1965) surveyed 55 stations from the shoreline to the deeper fore reef (33 m depth) off Key Largo during the early 1960s. These authors characterized *D. antillarum* as

'…the most ubiquitous echinoid in the area of the coral reef preserve, living at all observed depths in rocky niches along the shore and on reefs' (Kier & Grant 1965). Densities at French Reef during August 1965 (before Hurricane Betsy), September 1965 (after the hurricane) and July 1966 were 0.86, 0.00 and 0.08 ind. m^{-2}, respectively (McPherson 1968). Bauer (1980) quantified density patterns on offshore, high relief spur and groove (4 to 8 m) and deeper fore reef areas (7 to 11 m), with mean densities (ind. m^{-2}) of 1.4 to 4.5 at Molasses Reef and 1.0 at Elbow Reef (none were found during our 1999 surveys). On the deeper fore reef, densities were 0.5 at Crocker Reef, 0.2 at Molasses Reef (buttress zone), 0.1 at French Reef (*annularis-cervicornis* zone) and 0.6 at Elbow Reef (octo-coral-algal hard bottom). A small scale survey during 1993-94 was conducted at several upper Keys bank reef sites and yielded similar density and size structure results as the 1999-2000 effort (M. Chiappone unpubl. data). *D. antillarum* densities were low in 3 shallow spur and groove reefs (0.002 ± 0.001 ind. m^{-2}, mean ± 1 SE) and 2 offshore relict reef flats (0.002 ± 0.001, mean ± 1 SE), with a predominance of individuals <2 yr old.

Size distribution patterns for the 30 *Diadema antillarum* individuals recorded during this study indicate a population dominated by small (<2 cm TD) individuals. The modal size class for both years was 1.1 to 1.5 cm and the paucity of larger individuals (>5 cm TD) is

evidence of poor post-settlement survivorship, particularly when one considers that *D. antillarum* can grow to 10 cm TD (Ogden & Carpenter 1987). Using an average monthly growth rate range of 3.2 to 3.5 mm mo^{-1} for recruits within 1 yr of settlement (Lewis 1966, Bauer 1976, 1982), 94% of the individuals during 1999 and 79% during 2000 were <1 yr old. Only 1 of the 16 individuals recorded during 1999 and 3 of the 14 individuals surveyed during 2000 were probably 2 yr of age, and only 1 individual during 2000 was 3 yr of age. Assuming maturity is attained between 3.2 and 3.4 cm TD (Randall et al. 1964), 13% of the urchins surveyed during 1999 and 36% of the urchins surveyed during 2000 were likely to be mature. These results contrast with size distribution data prior to the 1991 mortality event, where the population was bimodal, with cohorts in the 3.1 to 4.0 cm and 6.1 to 7.0 cm size classes (Forcucci 1994).

The habitat distribution patterns of sea urchins besides *Diadema antillarum* were generally consistent with historical observations. In their assessment of urchin distribution patterns at 55 stations in the upper Florida Keys, Kier & Grant (1965) characterized *Eucidaris tribuloides* as generally solitary, but widely and sparsely distributed in rocky niches and seagrass beds. McPherson (1968) observed specimens on seagrass and sand, shallow offshore reefs and deeper fore reef environments to 55 m depth: densities ranged from 0.32 to 1.86 ind. m^{-2}. During 1999-2000, *E. tribuloides* was found in 6 of the 8 habitat strata sampled, but densities were lower (<0.07 ind. m^{-2}) than historical observations.

Historical density data for both *Echinometra* species in the Florida Keys are limited to 2 studies by McPherson (1968, 1969). He reported the following densities (ind. m^{-2}) during 1965-66, with lower values recorded after Hurricane Betsy: Virginia Key (12), Pigeon Key (0.9 to 2.7), Margot Fish Shoal (6) and French Reef (0.06 to 1.40). No *E. lucunter* were found during the 1999 platform margin surveys and across the continental shelf in the lower Keys region; indeed, only 2 individuals were recorded (1.2 to 1.3 cm TD), both from offshore patch reefs. Historical densities of *E. viridis* were quite high (24 to 25 ind. m^{-2}) on some Caribbean reefs (Sammarco 1982), as well as on those Florida Keys patch reefs with abundant staghorn coral rubble (McPherson 1969). McPherson (1968, 1969) recorded densities (ind. m^{-2}) during 1965-66 at Margot Fish Shoal (21) and French Reef (0.06 to 1.40), with lower values at the 2nd site after Hurricane Betsy. Only 2 *E. viridis* (0.5 and 1.0 cm TD) were recorded from the platform margin during 1999, both from shallow spur and groove. During 2000, *E. viridis* was present in 4 of the 7 habitat strata and attained relatively high densities (up to 0.59 ind. m^{-2}) at some sites. *E. viridis*

reaches sexual maturity at >1.5 cm (McPherson 1969). Data from the 2000 surveys suggest that, in contrast to other urchins, more than 95% of the sampled individuals were sexually mature.

Historical distribution data indicate that *Lytechinus variegatus* is generally limited to soft sediment habitats, especially seagrass beds, like several other echinoid genera (e.g. *Leodia*, *Encope*, *Clypeaster*, *Meoma* and *Tripneustes*; Kier & Grant 1965). Although *L. variegatus* generally occurs in low densities on the seaward side of the Florida Keys, large aggregations within dense *Syringodium filiforme* beds have recently been documented in western Florida Bay (Macia & Lirman 1999). We found 2 individuals at 1 site close to the Boca Chica shoreline in a hard bottom area with sparse to dense seagrass patches.

What are the prospects for *Diadema antillarum* recovery in the Florida Keys and how might the sanctuary no-fishing zones affect population trajectories? Poor *D. antillarum* population recovery in the Florida Keys exhibits both similarities and differences with Caribbean reefs. It is apparent that sea urchins are recruiting to several shallow water benthic habitats, similar to observations in Curacao after the 1983-84 mass mortality (Bak et al. 1984), but contrasting with earlier observations in Jamaica (Hughes 1994) and Panama (Lessios 1988b). In particular, small size classes, but poor survivorship to reproductive size characterize the Florida Keys population size structure. Anecdotal information from marine aquarium collectors confirms that small sizes are observed seasonally in some shallow back reef rubble zones of the upper Keys, confirming that recruitment still occurs, but storms eventually redistribute the rubble and kill the urchins before they can migrate to more stable substrata (K. Nedimyer pers. comm.). The presence of recruits observed by Forcucci (1994), aquarium collectors and this study is considered significant because even after almost 20 yr of adult absence from these reefs, new individuals continue to appear. Sources of recruits are not known, but adult populations were recently discovered in the Dry Tortugas (Chiappone et al. 2001). In contrast, Hughes (1994) found poor recruitment and a dominance by large size classes in Jamaica, as did Forcucci (1994) prior to the 1991 Florida Keys mortality event.

Poor population recovery may reflect several factors. Lessios (1988b) discussed the merits of several mortality hypotheses, among them poor larval survivorship (Lessios et al. 1984), lack of adult conspecifics and hence protection from predators (Tegner & Dayton 1976, Quinn et al. 1993), suitable recruitment sites (Bak 1986, but see Cameron & Schroeter 1980) and inter-specific competition (Williams 1981, but see Hughes et al. 1987). In Panama, Lessios (1988a) con-

tended that the paucity of recruits was not due to elevated levels of competition or predation. Instead, poor population recovery was due principally to low numbers of larger individuals available for reproduction, reduced fertilization success due to low densities (Pennington 1985, Levitan 1988, 1991) and hence, inadequate numbers of larvae available for settlement to offset post-settlement mortality from storms and predation (Hunte & Younglao 1988, Lessios 1988b). While Karlson & Levitan (1990) concluded that the return of urchin densities to pre-1983 levels is not likely and would require either massive recruitment (2–3 ind. m^{-2} yr^{-1}) or very low mortality, recent reports of recovery in Jamaica (Edmunds & Carpenter 2001, Haley & Solandt 2001) suggest that large-scale surveys at other sites are warranted.

Possible responses of Florida Keys sea urchins to the Sanctuary no-fishing zones are speculative at best. The implementation of no-fishing zones does, however, provide an opportunity to evaluate the responses of fishery target species to protection and possible community level effects such as changes in competition and predation that may result (Bohnsack 1997). *Diadema antillarum* apparently competed with herbivorous fishes on many Caribbean reefs, and after 1983-84, fish grazing intensity and population densities increased 2- to 4-fold in some areas (Carpenter 1990b). On Panamanian reefs, densities of 2 surgeonfish species increased, and because juvenile recruitment during the study did not change, Robertson (1991) concluded that these fishes were limited by competition with *D. antillarum*. Because *D. antillarum* was historically significant as a grazer, it will be important to monitor its recruitment, potential for recovery and effects on community structure as marine-protected areas mature in the Florida Keys.

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