Marine Biology (2006) 149: 1071–1078
DOI 10.1007/s00227-006-0279-3

RESEARCH ARTICLE

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The density and size distribution of *Diadema antillarum* in Dominica (Lesser Antilles): 2001–2004

Received: 25 January 2005 / Accepted: 15 December 2005 / Published online: 9 March 2006

Abstract *Diadema antillarum* populations at many Caribbean locations have failed to recover from a wide-spread mortality event during the early 1980s. Quantitative assessments of *Diadema* in Dominica have only recently begun and can now be put into a regional context. *Diadema* and benthic algae were monitored in 4-month intervals at six 100 m^2 sites, spread over a distance of 38 km, along the west coast of Dominica. *Diadema* density surveys began in July 2001, while algal cover was monitored as of November 2001. Mean densities of individual sites ranged from 0.81 m^{-2} (SD = 1.02) to 2.98 m^{-2} (SD = 1.33), and overall means increased from 1.50 m^{-2} (SD = 0.12) in 2001, to 2.00 m^{-2} (SD = 0.05) in 2004. The weak negative relationship observed between the *Diadema* density and macroalgal cover ($R^2 = 0.25$, $P = 0.0030$), indicates that *Diadema* play a limited role in controlling macroalgal species. In contrast, the abundance of turf algae was positively related to low *Diadema* densities, yet this relationship becomes negative beyond a critical point between 2.0 and 3.0 *Diadema* per m^2 ($R^2 = 0.25$, $P = 0.0075$). As of November 2001 size measurements of 100 randomly sampled urchins at each site were included in the surveys, resulting in overall mean test size diameters ranging between 5.54 cm (SD = 1.55) and 6.00 cm (SD = 0.96). The mean test size diameter per site ranged from 4.54 cm (SD = 1.91) at Tarou Point in November 2003 to 6.77 cm (SD = 0.83) at Salisbury November 2001. Across all sites except Tarou Point, the most commonly occurring *Diadema* sizes throughout this study were within 1 cm, in the range between 4.5 and 7.5 cm. It is unclear how this Dominica scenario fits into the context of the pathogen-induced mass mortality events of the 1980s because neither qualitative nor quantitative records exist for that time in Dominica. The recent increase in *Diadema* density may be a symptom of recovery from Hurricane Lenny. Given the indiscriminant local pressure (affecting herbivorous fishes as well as fish predators of *Diadema*) *Diadema's* role as grazer of algal turfs is highlighted. On a regional scale, its stable population of reproductive size classes may serve as source of larvae for nearby downstream islands.

Communicated by P.W. Sammarco, Chauvin

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Introduction

The wide-spread mortality of *Diadema antillarum* in the Caribbean during the 1980s (Lessios et al. 1984) has raised much concern due to the extent and longevity of its ecological and economical consequences. First, where *Diadema* was an important grazer following the overfishing of herbivorous reef fishes (Hughes 1994), its massive reduction in numbers is believed to have lead to drastic phase shifts (Hughes et al. 1987; Levitan 1988; Carpenter 1990) and the impoverishment in the community structure of coral reefs. Secondly, the recovery from this event has been extremely slow and in many regions *Diadema* populations remain far below their pre-die-off densities (Hughes et al. 1987; Karlson and Levitan 1990; Forcucci 1994; Moses and Bonem 2001). The effects of such an extensive decline in the population of this sea urchin have thus been long-lasting (Liddell and Ohlhorst 1986; Lessios 1988a, 1995, 2005), and in some cases seem irreversible (Karlson and Levitan 1990). Given the cascading ecological ramifications of such a population decrease in *Diadema*, monitoring the remaining populations where pre-die-off data is available is essential in assessing the recovery of *Diadema* as observed in Jamaica by Edmunds and Carpenter (2001), in St Croix by Miller et al. (2003) and in Curacao by Debrot and Nagelkerken (personal communication). It is equally important to survey regions previously not examined, so that the status of *Diadema* can be evaluated based on data from a wide geographical range, as regional differences and similarities in mortality and recovery may provide clues about larval sources and sinks.

This study presents preliminary findings from an ongoing *Diadema* monitoring program established in July 2001. It is based on six permanent monitoring sites along the west coast of Dominica which were surveyed 11 times up to November 2004 with the aim to assess (1) the population density of *Diadema*, (2) its size class distribution, and (3) the algal cover in *Diadema* habitats. While the spread of *Diadema* die-offs in Central America, the Greater Antilles, and Bermuda (Lessios et al. 1984; Hughes et al. 1985; Bak 1985; Lessios 1988b) has been well documented and linked to surface currents (Lessios et al. 1984; Phinney et al. 2001), fewer reports of mortality events exist for the Windward Islands (upstream) such as St Lucia (Lessios et al. 1984) and Barbados (Hunte et al. 1986). The historical context for this report is one in which Dominican fishermen and sport divers recall times when *Diadema* were "much more common than today," but in which no record of mass mortality events exist.

Material and methods

At each of six locations, spread over a distance of 38 km along the west coast of Dominica (Fig. 1, Table 1), the end points of two 25 m transects were marked by concrete nails. Underwater site maps were drawn to assist in relocating the nails. Transect lines were temporarily installed for each survey. The sites were in depths ranging from 1 to 5 m and were monitored at 4-month intervals starting in July 2001. The density of *Diadema antillarum* was measured by counting all specimens whose test was entirely or partially within 1 m on either side of each transect. Surveys were carried out during the day. At Tarou Point and Scott's Head in November 2001, Taby Bay and Tarou Point (transect 2) in July 2002, and Tarou Point in July 2003, surveys could not be carried out because of poor visibility and/or turbulent seas. Sites were selected strategically to facilitate access while covering a wide geographic area. Density data were analyzed by using analysis of variance (ANOVA) with a randomized complete block design. Two factors which are repeated measures were included: seasons (March, July and November) and years (2001–2004). Each transect from each site represents one block (12 blocks in total).

In November 2001, November 2002, March 2003, July 2003, November 2003, March 2004, July 2004 and November 2004 test diameter measurements of 100 specimens within randomly selected aggregations were carried out at each site with the exception of Tarou

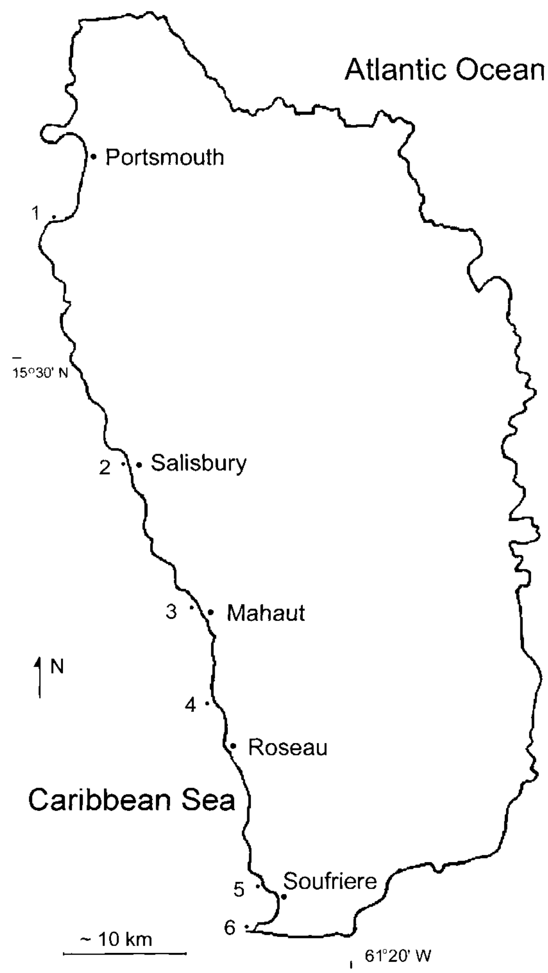

Fig. 1 Location of monitoring sites (1) Taby, (2) Salisbury, (3) Tarou, (4) Fond Colé, (5) Champagne, and (6) Scott's Head along the west coast of Dominica

Point (November 2001). A total of 4,100 measurements were obtained. Measurements were carried out in situ using Vernier calipers 50–150 m away from the permanent transects. This was done to minimize disturbance of the *Diadema* along transects. A Kolmogorov–Smirnov (K–S) two-sample test was used to examine the size distributions at the different times of measurement within each site. For each site there were 16 pairwise tests with the exception of Tauro Point (14 pairwise tests). Bonferroni correction was used to limit the experimentwise error rate.

Assessments of algal cover were included in the surveys between November 2001 and July 2004. This was done by placing 1 m quadrat in 1 m intervals on alternating sides of each transect. The quadrat was subdivided into one hundred 10×10 cm squares to assist in determining total algal cover to the closest 5%. Algae were differentiated as macroalgae (erect fleshy and calcareous species, as well as prostrate growth forms of *Dictyota*) and turf (filamentous species). Encrusting Corallinaceae (e.g., *Porolithon*) were not included in the assessment. Dominant algal taxa within each transect

Table 1 Site characteristics, *Diadema* density and test diameter at each study site

Site and transect	Depth (m)	Habitat	Algae
Taby Bay			
Transect 1	1.5	3	FTF, DIC, GLX
Transect 2	1.5	3	FTF, DIC, GLX
Salisbury			
Transect 1	1.5	1	FTF DIC, UMA
Transect 2	1.5	2	FTF DIC
Tarou Point			
Transect 1	4.5	3	FTF DIC
Transect 2	4	2	FTF DIC
Fond Colé			
Transect 1	1	1	FTF DIC
Transect 2	1	1	FTF DIC
Champagne			
Transect 1	2	2	FTF, DIC
Transect 2	2	2	FTF, DIC
Scotts Head			
Transect 1	1	1	FTF, DIC
Transect 2	1	1	FTF, DIC

Habitat types: *1* flat or poorly structured substrate, *2* moderately structured substrate with profile amplitude of 1–1.5 m, and *3* highly structured substrate with profile amplitude of up to 2 m. Algal components: *FTF* filamentous turf algae, *DIC Dictyota* spp., *GLX Galaxaura* sp., and *UMA* unidentified macroalgae

were noted. A linear regression was used to measure the relationship between *Diadema* density and macro and turf algae cover. *Diadema* density and macroalgal cover values were log transformed.

Results

Diadema antillarum density and size classes

The mean density of *Diadema antillarum* per year ranged from 1.50 (SD = 0.12) in 2001 to 2.00 m^{-2} (SD = 0.05) in 2004 (Fig. 2). The mean density per site ranged from 0.81 m^{-2} (SD = 1.02) at Salisbury in November 2001 to 2.98 m^{-2} (SD = 1.33) at Tarou in March 2004 (Table 2). Density distribution was patchy and differed significantly between the sites (ANOVA, $P < 0.0001$). A significant difference was also found between each year (ANOVA, $P < 0.0001$) with an overall mean density increase of 33.33% and increase per site ranging from 10.19% at Fond Colé to 69.23% at Scott's Head (Table 2, Fig. 2). Yearly density peaks observed at all sites during March surveys were not significant (ANOVA, $P = 0.21$).

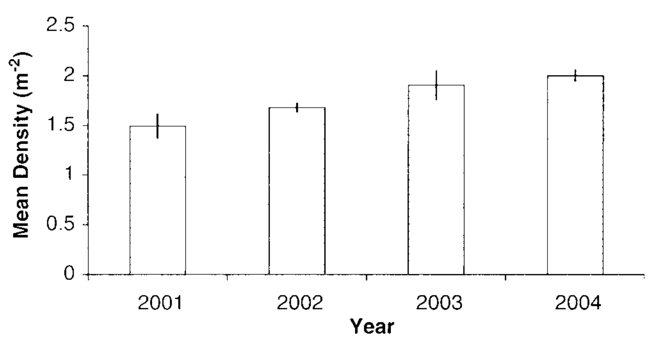

Fig. 2 Mean density of *Diadema antillarum* in Dominica between 2001 and 2004

Diadema test size diameters ranged from 0.40 cm at Tarou in July 2003 to 10.11 cm at Salisbury in July 2003. The mean test size diameter per site ranged from 4.54 cm (SD = 1.91) at Tarou Point in November 2003 to 6.77 cm (SD = 0.83) at Salisbury November 2001 (Table 3). Overall mean test size diameters were 6.00 cm (SD = 0.96) in November 2001, 5.90 cm (SD = 1.24) in November 2002, 5.80 cm (SD = 1.34) in March 2003, 6.00 cm (SD = 1.23) in July 2003, 5.54 cm (SD = 1.55) in November 2003, 5.84 cm (SD = 1.19) in March 2004 and 5.78 cm (SD = 1.08) in July 2004. Across all sites except Tarou Point, the most commonly occurring *Diadema* sizes throughout this study remained within 1 cm, in the range between 4.5 and 7.5 cm (Fig. 3a–f). Juveniles (test diameter 0.6–3.0 cm) were more abundant during the November surveys. During the test-size measurements, it was observed that *Diadema* were commonly distributed in clusters of similar size classes. Over the years, the distribution of size classes for each sampling point at each site was most stable at Taby, Champagne and Scott's Head (Fig. 4a, e, f). The least stable distribution of size classes was recorded at Tarou and Fond Colé (Fig. 4c, d), both of which experienced high disturbance levels of sediment runoff from coastal construction. Spawning was observed among 30 measured specimens at Fond Colé on March 16, 11 specimens at Salisbury on March 18 and 1 specimen at Scott's Head on March 19, 2003. In July 2001 at Scott's Head, 19 *Diadema* with test diameters of less than 1 cm were observed.

Diadema and algal cover

There was a significant polynomial relationship between *Diadema* and turf algal cover ($R^2 = 0.25$, $P = 0.0075$; Fig. 5). A liner relationship was detected between *Diadema* density and macroalgal cover ($R^2 = 0.25$, $P = 0.0030$; Fig. 6).

Discussion

From July 2001 to November 2004, the overall mean density of *Diadema antillarum* increased by 33.33% and has been consistently higher than the population densities from Caribbean locations with documented post-mortality surveys (see Karlson and Levitan 1990 for St John; Forcucci 1994 for the Florida Keys; Moses and Bonem 2001 for Jamaica; Chiappone et al. 2001 for the Dry Tortugas). *Diadema* in Dominica are also consistently larger than those from populations affected by mass die-offs (cf. Lessios et al. 1984; Carpenter 1990), approximately equal in size to those measured prior to

Table 2 *Diadema antillarum* density (m^{-2}) and standard deviations (SD) at all study sites

Site and transect	Jul 2001	Nov 2001	Mar 2002	Jul 2002	Nov 2002	Mar 2003	Jul 2003	Nov 2003	Mar 2004	Jul 2004	Nov 2004
Taby Bay											
Transect 1	1.38	1.72	1.82	N/A	1.38	1.90	1.88	1.48	1.70	1.70	1.64
Transect 2	1.22	1.80	1.94	N/A	2.10	3.14	3.50	2.80	2.60	2.36	2.60
Mean	1.30	1.76	1.88	N/A	1.74	2.52	2.69	2.14	2.15	2.03	2.12
SD	1.26	1.39	1.18	N/A	1.18	1.43	1.63	1.37	1.21	1.13	1.15
Salisbury											
Transect 1	0.56	0.84	0.88	0.72	1.18	0.76	0.84	1.00	1.20	1.68	1.50
Transect 2	1.62	0.78	0.86	1.12	0.94	1.20	1.28	1.36	1.08	1.52	1.28
Mean	1.09	0.81	0.87	0.92	1.06	0.98	1.06	1.18	1.14	1.60	1.39
SD	1.48	1.02	0.77	0.94	1.04	0.77	0.82	1.01	0.95	1.09	0.96
Tarou Point											
Transect 1	1.92	N/A	2.56	2.50	2.66	2.80	N/A	2.56	3.02	2.86	2.20
Transect 2	2.38	N/A	2.54	N/A	2.56	2.64	N/A	2.20	2.94	2.32	2.24
Mean	2.15	N/A	2.55	2.50	2.61	2.72	N/A	2.38	2.98	2.59	2.22
SD	0.88	N/A	1.27	1.11	1.01	1.12	N/A	1.12	1.33	0.94	0.95
Fond Colé											
Transect 1	1.72	1.26	1.20	1.76	1.12	1.34	1.28	1.42	1.20	1.30	0.86
Transect 2	2.80	2.46	2.48	3.28	3.76	3.38	2.64	4.08	3.40	3.38	3.48
Mean	2.26	1.86	1.84	2.52	2.44	2.36	1.96	2.75	2.30	2.34	2.17
SD	0.82	0.86	0.85	1.11	1.59	1.28	1.01	1.92	1.45	1.40	1.69
Champagne											
Transect 1	1.36	1.12	1.36	1.14	1.14	1.40	1.44	1.26	1.32	1.18	1.56
Transect 2	1.40	1.28	1.58	1.30	1.26	1.42	1.52	1.72	1.60	1.58	1.52
Mean	1.38	1.20	1.47	1.22	1.20	1.41	1.48	1.49	1.46	1.38	1.54
SD	0.69	0.76	0.73	0.77	0.73	0.70	0.93	0.87	0.80	0.91	0.58
Scotts Head											
Transect 1	1.10	N/A	1.06	0.64	1.00	1.54	1.10	1.78	1.44	2.16	2.30
Transect 2	1.50	N/A	1.64	1.52	1.70	1.82	1.88	2.06	2.78	2.38	2.14
Mean	1.30	N/A	1.35	1.08	1.35	2.00	1.49	1.92	2.11	2.27	2.22
SD	0.60	N/A	0.58	0.80	0.70	0.78	0.82	0.95	0.98	0.79	0.94

Table 3 *Diadema antillarum* test size measurements (cm) and SD at all study sites

Site	Nov 2001	Nov 2002	Mar 2003	Jul 2003	Nov 2003	Mar 2004	Jul 2004	Nov 2004
Taby Bay	6.06	6.28	5.82	6.24	6.29	5.96	5.96	5.96
SD	0.74	0.93	1.33	1.08	0.92	1.14	0.98	1.13
Salisbury	6.77	6.18	6.40	6.85	5.89	5.93	6.04	6.45
SD	0.83	1.44	1.19	1.18	1.97	1.63	1.20	1.25
Tarou Point	N/A	6.65	6.14	5.93	4.54	5.56	5.67	5.64
SD	N/A	1.00	1.47	1.64	1.91	1.28	1.20	1.20
Fond Colé	5.93	5.28	5.76	5.71	5.85	6.03	5.92	5.10
SD	0.85	1.03	1.24	0.83	1.05	0.78	0.74	1.21
Champagne	5.76	5.06	4.94	5.14	4.89	5.61	5.09	5.13
SD	0.96	1.39	1.16	0.77	1.10	0.79	0.79	0.71
Scotts Head	5.43	5.97	5.83	6.14	5.75	5.97	6.01	5.98
SD	0.87	1.01	1.17	0.97	1.28	1.12	1.18	1.10

the mass mortality in St Croix (Ogden et al. 1973; Carpenter 1990) and larger than those recorded in Boca Raton (Bauer 1976), Cozumel (Bauer 1980), and Panama (Lessios 1995). Interestingly, adult *Diadema* (>4 cm) have been reported to be more severely affected by mortality events than juveniles (Hunte et al. 1986) and post-mortality populations are characterized by smaller urchins than those in Dominica, while the presence of adult echinoids (Highsmith 1982; Pearce and Scheibling 1990), specifically *Diadema* (Hunte and Younglao 1988; Forcucci 1994), is among the main cues for larval settlement. It thus remains unclear how this "Dominica scenario" fits into the context of the pathogen-induced mass mortality events of the 1980s because neither qualitative (taphonomy) nor quantitative (density) records exist for that time in Dominica. Evidently, the spread of *Diadema* mortality events followed the direction of Caribbean surface currents (Lessios et al. 1984; Phinney et al. 2001). Given Dominica's upstream location, vectors other than surface currents may have introduced a *Diadema*-killing pathogen. The introduction of such a pathogen via ballast waters was reported for Curacao by Bak et al. (1984) and could have occurred in Dominica which receives over 90% of its processed goods via shipments from the southern and northern Caribbean. Reductions in Dominica's *Diadema* population have likely been caused by storms. The island's narrow shelf and reef habitats are characterized

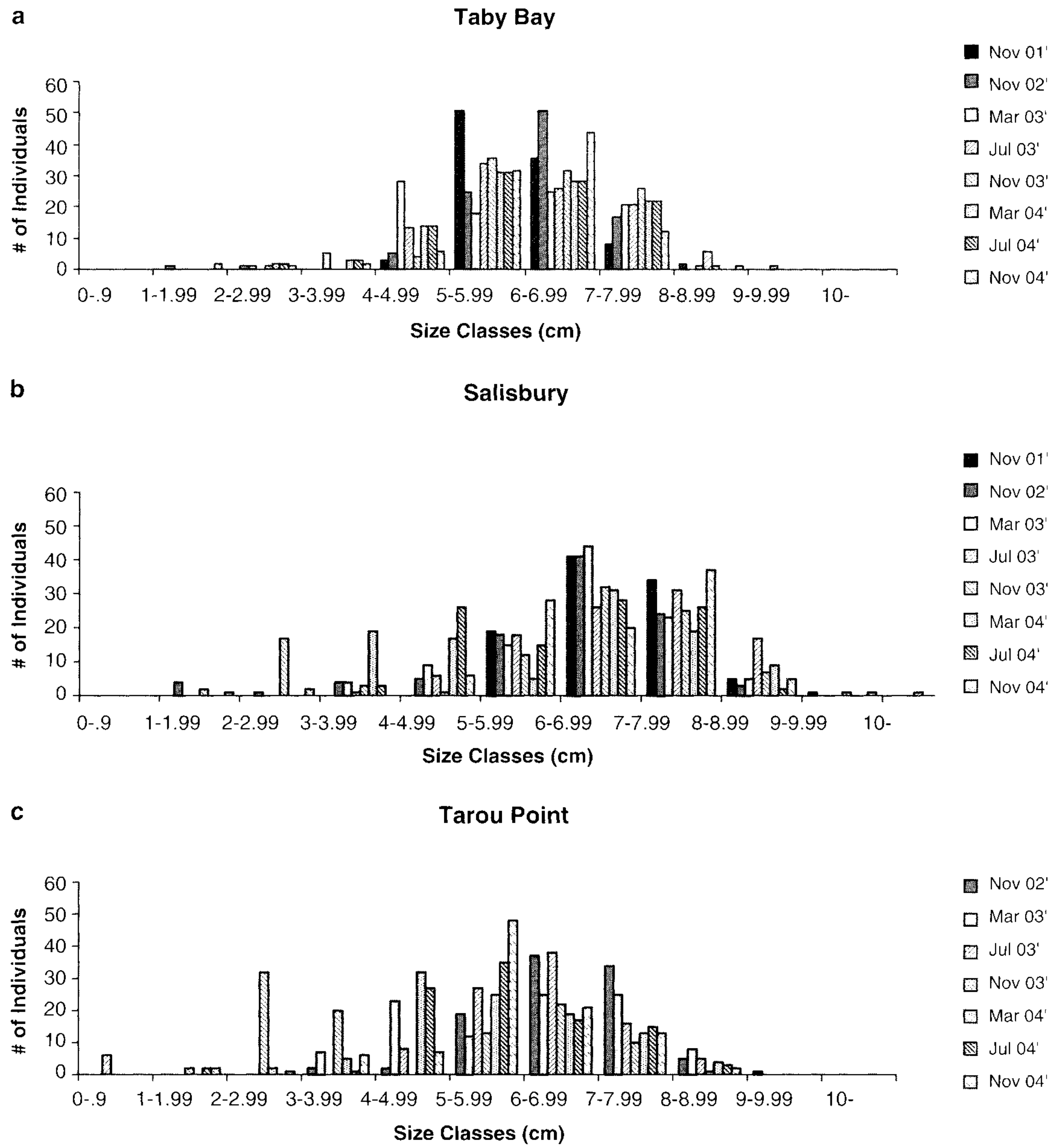

Fig. 3 a–f Size class distribution of *Diadema* at study sites between 2001 and 2004 ($n = 100$ for each data point)

by the lack of energy-dissipating structures, such as wide fringing or barrier reefs, and reef communities have little structural protection from storm-related disturbances (Steiner 2003). Hence, the recent density increase may be part of the recovery from Hurricane Lenny 1999, as no major storms have affected Dominica since then. This is supported by quantitative records from Castle Comfort (2 km south of Roseau) by J. Ware (personal communication) in 1997, 1999, and 2003, which show a sharp decline in *Diadema* after Hurricane Lenny, followed by a recovery of the population. Similar observations were made at Taby Bay, Salisbury and Fond Colé which were examined in June 1999 before Hurricane Lenny (Steiner, unpublished data).

The larval duration of the *Diadema* echinoplutei has been reported to be between 4 and 7.5 weeks (Hunte and Younglao 1988; Carpenter 1990; Eckert 1998) and post-settlement growth rates of 1 mm per week have been measured by Bak (1985). Therefore, the presence of a greater number of small (< 1 cm) *Diadema* in July 2001 (personal observation) as well as July 2002, 2003, and 2004 (this study) indicates that spawning commenced several months earlier in Dominica (as witnessed during March surveys 2003) and/or at upstream islands (e.g., Martinique). This is also supported by peaks in gonad volume of *D. antillarum* in March–April, followed by a completion of spawning by June–July as observed in Barbados by Lewis (1966). Aggregative behavior (Levitan 1988) among spawning *Diadema* may explain the seasonal density peaks observed in March surveys. Consequently, lower densities seen in November may be due to a "dismantling" of spawning aggregations. Given

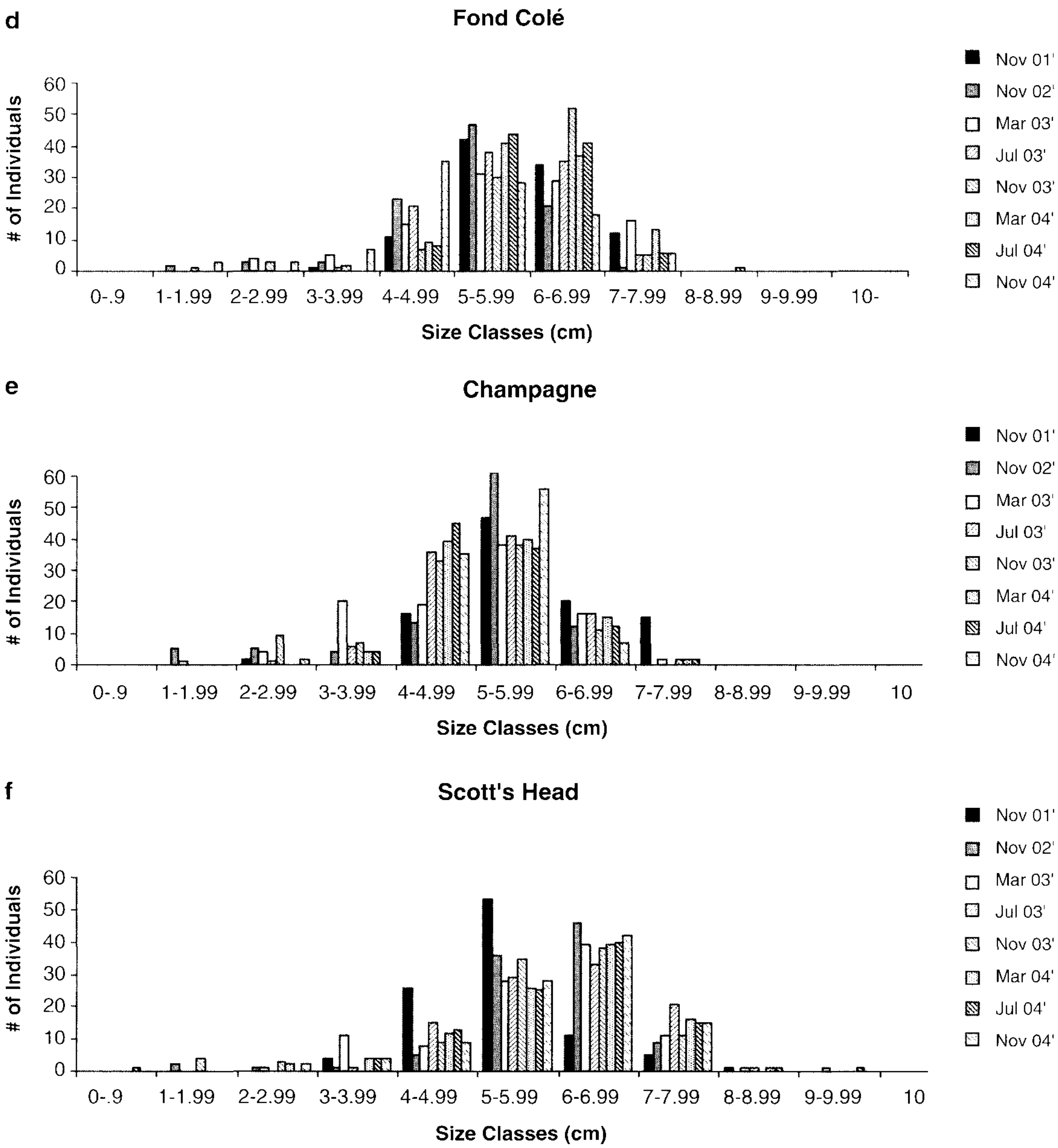

Fig. 3 (Contd.)

a larval dispersal range of hundreds of kilometers (Lessios 1988a), Dominica's current *Diadema* population may be of regional importance as source of larvae for downstream islands such as The Saints (18 km north of Dominica).

On a local scale, the relationship between *Diadema* density and algal cover was varied. The weak negative relationship observed between the *Diadema* density and macroalgal cover ($R^2 = 0.25$, $P = 0.0030$) indicates that *Diadema* play a limited role in controlling the growth of macroalgae, at least with regards to the algal species at the study sites. In contrast, the abundance of turf algae was positively related to low *Diadema* densities, yet this relationship becomes negative beyond a critical point between 2.0 and 3.0 *Diadema* per m^2. Long-lasting decreases in the *Diadema* populations of Dominica could therefore lead to algal overgrowth of many reefs, as other grazers do not seem to compensate for the seasonal density fluctuations of *Diadema*. The low density of herbivorous reef fishes (Komoroske 2002) and fish predators of *Diadema* (Petterson 2002) related to overfishing (H. Guiste, Fisheries Division, personal communication) may account for this situation.

This study highlights the importance of long-term studies based on consistent methodology applied at the same locations as demonstrated by Lessios (1995, 2005). The patchy distribution of *Diadema* within and between reefs indicates that biotic and abiotic factors shaping *Diadema* habitats should be considered closely (see also Edmunds and Carpenter 2001) to improve regional comparisons and monitoring. For example, *Diadema* habitats from Dominica (narrow shelf, marginal reef

Fig. 4 K–S results for size distributions at each study site. For all sites except Tauro ($D_{0.004}$ = 0.257), $D_{0.003}$ = 0.265. Different *letters* (a, b, c) indicate significant difference. **a** Taby Bay, **b** Salisbury, **c** Tauro Point, **d** Fond Colé, **e** Champagne, **f** Scott's Head

a. Taby Bay

March 03'	a	
July 04'	a	b
March 04'	a	b
July 03'	a	b
November 04'	a	b
November 02'		b
November 03'		b
November 01'		b

b. Salisbury

March 04'	a		
July 04'	a	b	
March 03'	a	b	c
November 02'	a	b	c
November 03'	a	b	c
July 03'		b	c
November 04'		b	c
November 01'			c

c. Tauro Point

November 02'	a	
July 03'	a	b
March 03'		b
March 04'		b
July 04'		b
November 04'		b
November 03'		

d. Fond Colé

November 04'	a		
November 02'	a	b	
March 03'	a	b	c
July 03'	a	b	c
November 01'		b	c
July 04'		b	c
March 04'			c
November 03'			c

e. Champagne

November 01'	a	
November 02'	a	b
July 03'	a	b
March 04'	a	b
March 03'	a	b
November 04'		b
July 04'		b
November 03'		b

f. Scott's Head

November 01'	
November 02'	a
March 03'	a
July 03'	a
November 03'	a
March 04'	a
July 04'	a
November 04'	a

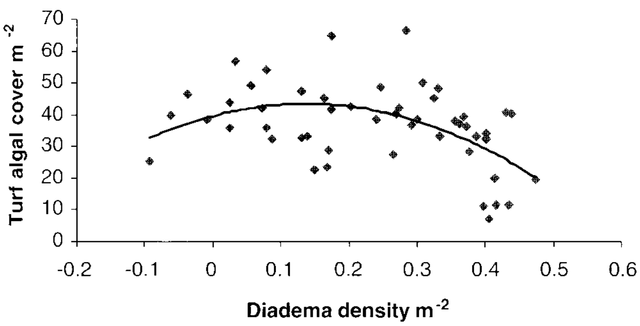

Fig. 5 Polynomial relationship between *Diadema* density and turf cover per m^2. R^2 = 0.25, P = 0.0075

systems, and little carbonate substrate) are very different from *Diadema* habitats in San Blás, Panama (wide shelf, extensive reef systems, and carbonate frameworks). Therefore, a direct comparison of such populations may not be the best approach to weigh pre- and post-mortality populations as reference points of reef health. In Dominica, "habitat preference" of *Diadema* (possibly based on turbulence regimes) is exemplified by its virtual absence on the windward side of the island, while the leeward side harbors a well-developed population. The

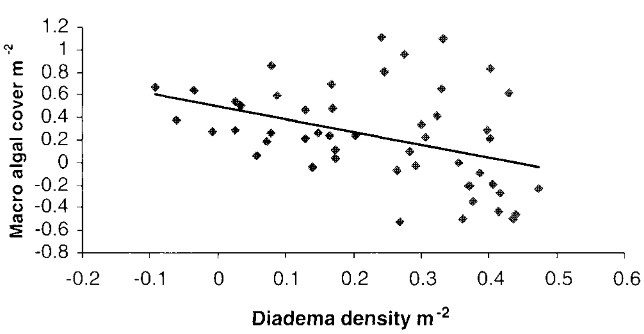

Fig. 6 Linear relationship between *Diadema* density and macroalgal cover per m^2. R^2 = 0.25, P = 0.0030

assessment of the carrying capacity of individual *Diadema* habitats would be a significant improvement in the direct comparisons of these important echinoid herbivore populations across the Caribbean. Habitat classifications in terms of rugosity, size of reef system, turbulence regimes, terrestrial, and oceanic influences (e.g., storms, hyposalinity, sediments, fertilizers, pesticides, defoliants, etc.) may be a first step.

Acknowledgments We thank F. Mastagni and T. Milloy for their help in the initial set up of the monitoring sites. J. Borger, P. Yoshioka, C. Moses and two anonymous reviewers provided helpful critiques of the manuscript. This project was funded by the Institute for Tropical Marine Ecology, Inc. (ITME RP04-01).

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