

## Algal cover and sea urchin spatial distribution at Madeira Island (NE Atlantic)\*

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**SUMMARY:** This study describes sea urchin spatial distribution in relation to environmental factors, and the relationship between *Diadema antillarum* density and algal abundance. Twenty-three transects around Madeira Island were surveyed by scuba divers, and sea urchin density and algal cover were determined *in situ*. Sampling sites along these transects were characterised in terms of distance from the tide line, water depth, substratum type, bottom declivity and water turbulence. *Diadema antillarum* was the dominant sea urchin species. *Paracentrotus lividus* and *Arbacia lixula* occurred at shallower depths (2-6 m), contrasting with the distribution of *Sphaerechinus granularis*, which occurs among *D. antillarum* (4-20 m). Surveys found two alternative types of communities on rocky shores: 1) a community with high algal cover and low numbers of sea urchins, along the north and south-west coasts and; 2) a community with little algal cover and high densities of sea urchins, along the south-east coast. Macroalgal cover and *D. antillarum* densities were inversely correlated (adjusted  $R^2=75.6\%$ ;  $n = 429$ ;  $p<0.05$ ). The results showed that water turbulence was the most important factor limiting the distribution of *D. antillarum* on rocky substrates. We propose a multiple non-linear regression model (using backward stepwise analysis) to explain *D. antillarum* abundance on the rocky shores:  $D. antillarum/m^2 (\sqrt{\sqrt{}}) = 0.121 - 0.209 \text{ distance from shore (in m)} (\sqrt{\sqrt{}}) + 2.052 \text{ water depth (in m)} (\sqrt{\sqrt{}}) - 1.778 \text{ water turbulence level} (\sqrt{\sqrt{}}) - 0.007 \text{ water turbulence level}^4 (\sqrt{\sqrt{}})$ ; where  $\sqrt{\sqrt{}}$  indicates data are square-root transformed (adjusted  $R^2= 60.99\%$ ;  $n = 454$ ;  $p<0.05$ ).

**Key words:** sea urchins, Madeira Island, algae, *Diadema antillarum*, distribution.

### INTRODUCTION

Several studies of sea urchin distribution and the effects of this on algal populations have been reported world-wide (e.g. Valdez and Villalobos, 1978; Bauer, 1980; Weil *et al.*, 1984; Benedetti-Cecchi and Cinelli, 1995; Turon *et al.*, 1995; Falcon *et al.*, 1996). Sea urchins are known to control the abundance and distribution of algae and can therefore have a profound influence on the structure of benthic

communities (Andrew, 1989; Vadas, 1990; Vadas and Elner, 1992; Valentine *et al.*, 1997). At Madeira Island (Portugal, north-east Atlantic), sea urchin ecology has not previously been studied in detail, although it is referred to by Augier (1985), Wirtz (1995, 1998) and Bianchi *et al.* (1998).

Sea urchin species known to occur on the rocky shores of Madeira are *Paracentrotus lividus* (Lamarck), *Arbacia lixula* (Lamarck), *Sphaerechinus granularis* (Lamarck), *Diadema antillarum* (Philippi), and the less common *Arbaciella elegans* (Mortensen) and *Centrostephanus longispis-*

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nus (Philippi) (Wirtz, 1995). *Paracentrotus lividus* and *A. lixula* have been studied in the Mediterranean Sea, where they play a decisive role in the development of benthic macrophyte communities (Kempf, 1962; Bergin, 1987; Benedetti-Cecchi and Cinelli, 1995; Turon *et al.*, 1995; Fernandez and Boudouresque, 1997). The distribution of *S. granularis* has previously been studied only at Faial (Azores), by Maciel and Gonçalves (1998).

At Madeira, empirical observations suggest that *D. antillarum* abundance is increasing (Abreu *et al.*, 1995; personal observations), which seems to be reflected by reduced seaweed abundance. This sea urchin species, and its ability to affect ecosystems, has not yet been studied around Madeira, though it has been widely studied in the western Atlantic, where it has a great impact on benthic community structure (e.g. Sammarco *et al.*, 1974; Sammarco, 1980, 1982a, b; Carpenter, 1981, 1984; Liddel and Ohlhorst, 1986, 1992; Lessios, 1988a, b, 1995). Several studies have found that the spatial distribution of *D. antillarum* correlates with a number of other factors, such as the substratum type (Valdez and Villalobos, 1978), structural morphology of the reef, food availability, predation pressure (Weil *et al.*, 1984), aggressive territorial behaviour of fishes (Sammarco and Williams, 1982), and water turbulence (Casañas *et*

*al.*, 1998). However, an integrated analysis of the major factors has not previously been undertaken. The aims of this study are to describe algal cover and sea urchin distribution around Madeira, and to investigate the importance of several environmental factors in determining *D. antillarum* abundance.

## STUDY SITE

Madeira Island is located in the northeast Atlantic Ocean, at approximately 32°38'N, 16°54'W (Fig. 1; Biscoito and Abreu, 1998). The island, of volcanic origin, is the largest of the archipelago bearing the same name, which includes Porto Santo and the smaller Desertas and Selvagens islands. Madeira extends for 58 km along a WNW to ESE axis, and its 153 km of coastline is predominantly rocky. Sea surface temperatures usually range between 17 and 22.5°C. Typically, the presence of a subtropical anticyclone over the Azores causes a northeasterly wind and ocean current, with an average velocity of 0.5 knots, to persist for most of the year at the islands (Abreu and Biscoito, 1998). The Madeira archipelago is an important biogeographical region because it contains a large number of endemic species (Baez, 1993; Beyhl *et al.*, 1995; Stock, 1995).

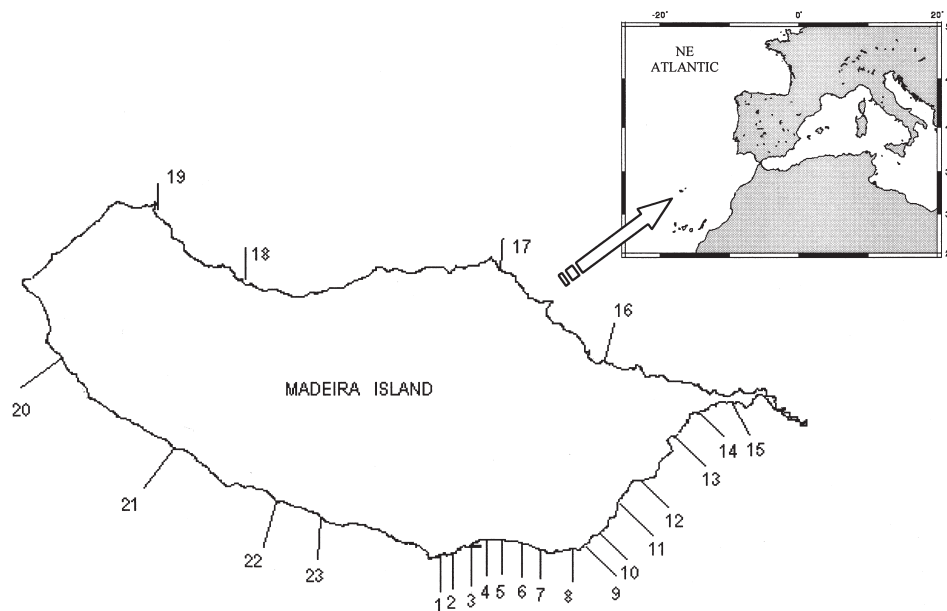


FIG. 1. – Location of transects along the Madeira coast: 1 – Clube Naval (west); 2 – Lido (west); 3 – Molhe; 4 – Barreirinha (east); 5 – Lazareto; 6 – Pináculo; 7 – Garajau; 8 – Galo; 9 – Roca-mar; 10 – Reis Magos (east); 11 – Porto Novo; 12 – Santa Cruz (east quay); 13 – Machico (quay); 14 – Caniçal (Junta quay); 15 – Quinta do Lorde; 16 – Porto da Cruz (quay); 17 – São Jorge; 18 – Seixal (quay); 19 – Porto Moniz (quay); 20 – Paúl do Mar (west); 21 – Madalena (quay); 22 – Ribeira Brava (east harbour); 23 – Campanário (islet).

## METHODOLOGY

Off Madeira Island, 23 transects were surveyed by scuba divers from July to August 1998: transects 1 to 15 were off the southeast coast (1SE–15SE); transects 16 to 19 were off the north coast (16N–19N), and transects 20 to 23 were off the southwest coast (20SW–23SW) (Fig. 1). Along each transect, the number of sea urchins per square metre, the percentage of algal cover, water depth, substratum type and bottom declivity were assessed and recorded on waterproof sheets every 10 m, starting from about 2 m distance from shore and continuing until sandy sediments (where sea urchins are scarce) occurred. When weather conditions were adverse, data collection began from 10 m distance from shore. Every 10 m along each transect, three random replicates of the number of sea urchins and of the percentage of algal cover were assessed within a 1 × 1 m quadrat and a 0.5 × 0.5 m quadrat divided into 100 5 × 5 cm squares respectively. At each sampling point, all sea urchins were identified and counted.

Six different categories of substratum were recorded: rock; big boulders; big and medium boulders; medium and small boulders; small boulders; and sand. We considered big boulders to be larger than 1 m, medium boulders between 0.2 and 1 m, and small boulders smaller than 0.2 m. Bottom declivity was measured to four levels: 1) 0–5°; 2) 6–30°; 3) 31–60°; 4) 61–90°. The degree of water turbulence at each transect was categorised from annual wave-height frequency (%) data recorded by the Portuguese Hydrographic Institute between 1961 and 1970 off the major coastal areas of Madeira (Instituto Hidrográfico, 1979). Based on these data, four categories were recognised: 1) total calm or very low disturbance, 99–100% frequency of waves less than 1.5 m in height; 2) moderate disturbance, 98% of waves less than 1.5 m and 2% from 2–3.5 m in height; 3) considerable disturbance, 77% less than 1.5 m and 23% from 2–3.5 m in height; 4) strong or very strong disturbance, 54% less than 1.5 m and 46% from 2–3.5 m.

In an attempt to determine the factors limiting the spatial distribution of *D. antillarum* on rocky shores (e.g. distance from shore, water depth, substratum type, bottom declivity and water turbulence), a multiple non-linear regression (with corresponding ANOVA) was performed. Variables used for the equation were selected based on a backward stepwise analysis using the Statistica V.5 program. Data were square-root transformed since this improved the residuals.

To test for differences in sea urchin distributions, a two-way ANOVA test was performed. Water depth and sea urchin species were the independent variables, and sea urchin density was the dependent variable.

A linear regression between the percentage of algal cover and *D. antillarum* density was performed using the Minitab 12.2 statistics program. Variables were square-root transformed as this minimised the residuals.

## RESULTS

### Species distribution and abundance

Four sea urchin species were found during the course of the surveys: *Diadema antillarum*, *Arbacia lixula*, *Sphaerechinus granularis* and *Paracentrotus lividus*. *Diadema antillarum* was found in high densities off the southeast coast on transects 1SE to 15SE, and also on transects 23SW (on the border of the southeast coast) and 19N (Tables 1 and 2). Mean density in these areas was  $6 \pm 4.8$  (standard deviation) individuals/m<sup>2</sup>. We only found individuals with a test diameter greater than 10 mm. Between transects 23SW to 1SE (Praia Formosa) and 14SE to 15SE (Prainha), the substratum was sandy and sea urchins were almost completely absent. On the north and southwest coasts of the island, with the exception of transect 19N, very low densities of sea urchins, particularly *D. antillarum*, were observed. In these areas, *A. lixula* was the predominant sea urchin, although it occurred in very low densities (between 0 and 1 individuals/m<sup>2</sup>). However, on the south coast, mean densities of  $17 \pm 1.5$ ,  $14 \pm 16.5$ ,  $8 \pm 1.2$  and  $6 \pm 4.5$  individuals/m<sup>2</sup> were observed. *Sphaerechinus granularis* was generally observed at densities lower than  $2 \pm 0.6$  individuals/m<sup>2</sup>. *Paracentrotus lividus* was only recorded on transect 1SE, at 1.8 m depth, with a mean density of  $11 \pm 1.5$  individuals/m<sup>2</sup> and on transect 5SE, at 3 m depth, at a mean density of  $2 \pm 4.0$  individuals/m<sup>2</sup> (Tables 1 and 2).

### Distance from tide line and water depth

Sea urchin species distribution varied with distance from tide line and water depth. *Diadema antillarum* was the dominant species at almost all distances from the shore and at all depths, except in areas shallower than 2–3 m. However, on transect 1SE, a maximum of 68 individuals/m<sup>2</sup> of *D. antillarum* was recorded at 4 m depth, and in the Porto Santo Island

TABLE 1. – Sea urchin density and percent algal cover (mean of three samples  $\pm$  standard deviation), water depth, bottom declivity (Bott. decliv.) and substrate type against distance (Dist.) from the tide line for transects 1 to 13. (Measurements were taken every 10 m until sandy sediments were reached, with the exception of those marked with an asterisk (\*). Bottom declivity was measured on a four-level scale as described in the methodology.)

Site	Dist. from shore (m)	Sea urchins/m <sup>2</sup> (mean $\pm$ standard deviation)				Algal cover (%)	Depth (m)	Bott. decliv.	Substratum type
		<i>D. antillarum</i>	<i>A. lixula</i>	<i>S. granularis</i>	<i>P. lividus</i>				
1	2	0.0 $\pm$ 0.0	17.3 $\pm$ 1.5	0.0 $\pm$ 0.0	10.7 $\pm$ 1.5	68.3 $\pm$ 17.6	1.8	1	rock
	10	50.7 $\pm$ 18.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	14.3 $\pm$ 2.1	3.8	3	rock
	20	21.0 $\pm$ 5.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	10.3 $\pm$ 13.1	6	1	rock
	30	15.7 $\pm$ 2.1	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	20.3 $\pm$ 17.6	6.5	3	rock
	40	11.3 $\pm$ 3.1	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	10	2	big boulders
2	2	0.0 $\pm$ 0.0	1.0 $\pm$ 1.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	86.0 $\pm$ 14.4	1.5	2	big and med. bld.
	10	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	1.3 $\pm$ 0.6	0.0 $\pm$ 0.0	96.3 $\pm$ 2.5	4	2	big and med. bld.
	20	4.0 $\pm$ 1.0	0.7 $\pm$ 1.2	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	87.3 $\pm$ 10.7	5.5	2	big and med. bld.
	30	2.3 $\pm$ 2.1	0.0 $\pm$ 0.0	2.0 $\pm$ 0.0	0.0 $\pm$ 0.0	5.7 $\pm$ 2.1	6.5	2	big and med. bld.
	40	5.0 $\pm$ 1.0	0.0 $\pm$ 0.0	0.7 $\pm$ 0.6	0.0 $\pm$ 0.0	8.3 $\pm$ 4.7	9	3	big and med. bld.
	50	5.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	7.0 $\pm$ 2.0	10	2	big and med. bld.
	60	7.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	8.3 $\pm$ 2.9	12	2	big and med. bld.
	70	5.7 $\pm$ 2.1	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	5.3 $\pm$ 3.2	12.9	2	big and med. bld.
3	2	5.3 $\pm$ 2.3	5.7 $\pm$ 4.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	3.3 $\pm$ 2.5	5	3	big boulders
	10	14.0 $\pm$ 2.0	0.7 $\pm$ 1.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	3.7 $\pm$ 1.5	9	3	big boulders
	20	8.0 $\pm$ 4.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	2.3 $\pm$ 0.6	19	3	big boulders
4	2	0.0 $\pm$ 0.0	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	98.0 $\pm$ 1.0	3.5	2	big and med. bld.
	10	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.7 $\pm$ 1.2	0.0 $\pm$ 0.0	75.0 $\pm$ 9.6	5.7	2	med.andsmall bld.
	20	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	6.7 $\pm$ 1.2	0.0 $\pm$ 0.0	4.3 $\pm$ 1.5	6	2	small boulders
	30	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	3.3 $\pm$ 3.1	0.0 $\pm$ 0.0	7.3 $\pm$ 1.5	7.5	2	small boulders
	40	1.0 $\pm$ 1.0	0.3 $\pm$ 0.6	1.0 $\pm$ 1.0	0.0 $\pm$ 0.0	86.3 $\pm$ 8.1	9	2	big and med. bld.
	50	1.0 $\pm$ 1.0	0.0 $\pm$ 0.0	0.7 $\pm$ 1.2	0.0 $\pm$ 0.0	90.7 $\pm$ 1.2	10	2	big and med. bld.
5	2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	84.7 $\pm$ 9.0	1.5	2	big boulders
	10	0.0 $\pm$ 0.0	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	2.3 $\pm$ 4.0	91.3 $\pm$ 3.1	3	2	big boulders
	20	2.7 $\pm$ 0.6	0.0 $\pm$ 0.0	0.7 $\pm$ 1.2	0.0 $\pm$ 0.0	14.0 $\pm$ 15.6	4	2	big boulders
	30	4.0 $\pm$ 1.0	0.0 $\pm$ 0.0	2.3 $\pm$ 0.6	0.0 $\pm$ 0.0	12.3 $\pm$ 5.1	5	2	big boulders
	40	4.3 $\pm$ 1.5	0.3 $\pm$ 0.6	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	17.0 $\pm$ 7.8	8	2	big boulders
	50	2.3 $\pm$ 2.5	0.0 $\pm$ 0.0	0.7 $\pm$ 1.2	0.0 $\pm$ 0.0	10.7 $\pm$ 2.3	12	3	big boulders
6	2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	78.0 $\pm$ 3.0	2	2	big boulders
	10	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	63.0 $\pm$ 14.4	3.9	2	big boulders
	20	3.0 $\pm$ 1.0	1.0 $\pm$ 1.7	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	3.0 $\pm$ 3.5	4.9	2	big and med. bld.
	30	5.7 $\pm$ 2.1	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	6.3 $\pm$ 5.9	5.5	2	big and med. bld.
	40	3.7 $\pm$ 1.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	4.3 $\pm$ 2.1	6.5	2	big and med. bld.
	50	4.7 $\pm$ 1.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	1.7 $\pm$ 1.2	9	3	big and med. bld.
	60	2.7 $\pm$ 1.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	3.3 $\pm$ 1.5	11.1	2	big and med. bld.
	70	5.0 $\pm$ 1.7	0.0 $\pm$ 0.0	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	3.7 $\pm$ 0.6	14.3	3	big and med. bld.
	80	2.7 $\pm$ 1.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	2.7 $\pm$ 0.6	19.3	3	big and med. bld.
7	10	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	66.0 $\pm$ 3.6	2	2	small boulders
	20	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	65.7 $\pm$ 4.7	5.6	3	small boulders
	30	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	88.0 $\pm$ 3.6	7.1	2	big boulders
	40	5.7 $\pm$ 1.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	2.0 $\pm$ 1.7	8.9	2	big boulders
	50	9.3 $\pm$ 2.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	4.0 $\pm$ 5.2	9	2	big boulders
	60	6.7 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	5.7 $\pm$ 2.5	10.5	3	big boulders
	70*	8.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	7.7 $\pm$ 4.2	11.8	3	big boulders
8	2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	81.0 $\pm$ 3.5	5	2	med.andsmall bld.
	10	8.0 $\pm$ 3.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	33.7 $\pm$ 3.2	5.6	2	med.andsmall bld.
	20	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	60.3 $\pm$ 12.9	6.3	2	med.andsmall bld.
	30	11.7 $\pm$ 2.1	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	9.9	3	big and med. bld.
	40	12.3 $\pm$ 2.1	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	13	3	big and med. bld.
	50	6.0 $\pm$ 1.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	16	3	big and med. bld.
	60	7.7 $\pm$ 2.1	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	18.5	3	big boulders
	70	8.0 $\pm$ 5.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	20.5	3	big boulders
9	2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	4.7	2	big and med. bld.
	10	6.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	6.8	2	big and med. bld.
	20	9.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	9.9	2	big and med. bld.
	30	15.3 $\pm$ 4.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	11.8	4	big boulders
	40	7.3 $\pm$ 4.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	15.6	2	big boulders
	50	6.3 $\pm$ 3.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	16.6	3	rock
	60	4.3 $\pm$ 3.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	20.1	4	rock
10	2	10.0 $\pm$ 4.4	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	15.7 $\pm$ 2.1	5.2	2	med.andsmall bld.
	10	7.0 $\pm$ 1.7	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	1.3 $\pm$ 0.6	6.6	2	small boulders
	20	8.0 $\pm$ 2.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	5.7 $\pm$ 3.1	7.7	2	small boulders
	30	6.0 $\pm$ 3.6	0.0 $\pm$ 0.0	1.3 $\pm$ 1.5	0.0 $\pm$ 0.0	1.7 $\pm$ 1.2	9.2	2	small boulders
	40	6.3 $\pm$ 2.9	0.3 $\pm$ 0.6	2.3 $\pm$ 0.6	0.0 $\pm$ 0.0	1.0 $\pm$ 0.0	10.8	2	small boulders
	50	8.3 $\pm$ 1.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	12	2	small boulders
	60	6.7 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	14.5	2	small boulders
11	2	11.7 $\pm$ 3.1	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	7	3	big boulders
	10	22.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	14.1	3	rock

TABLE 1 (Cont.) – Sea urchin density and percent algal cover (mean of three samples  $\pm$  standard deviation), water depth, bottom declivity (Bott. decliv.) and substrate type against distance (Dist.) from the tide line for transects 1 to 13. (Measurements were taken every 10 m until sandy sediments were reached, with the exception of those marked with an asterisk (\*). Bottom declivity was measured on a four-level scale as described in the methodology.)

Site	Dist. from shore (m)	Sea urchins/m <sup>2</sup> (mean $\pm$ standard deviation)				Algal cover (%)	Depth (m)	Bott. decliv.	Substratum type
		<i>D. antillarum</i>	<i>A. lixula</i>	<i>S. granularis</i>	<i>P. lividus</i>				
12	20	13.3 $\pm$ 3.1	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	16	2	small boulders
	30	10.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	17.1	2	rock
	40*	10.3 $\pm$ 2.1	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	17.7	2	rock
	2	0.3 $\pm$ 0.6	7.7 $\pm$ 1.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	1.0 $\pm$ 0.0	2.5	3	big and med. bld.
	10	7.7 $\pm$ 2.1	0.0 $\pm$ 0.0	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	1.3 $\pm$ 0.6	8	3	big and med. bld.
	20	5.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	4.7 $\pm$ 1.5	9.1	2	big boulders
	30	3.7 $\pm$ 1.5	0.0 $\pm$ 0.0	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	1.0 $\pm$ 1.0	10.2	2	big and med. bld.
13	40	2.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.7 $\pm$ 0.6	0.0 $\pm$ 0.0	5.3 $\pm$ 0.6	12.9	2	big and med. bld.
	50	2.0 $\pm$ 1.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	7.0 $\pm$ 4.4	16.2	3	big boulders
	2	8.3 $\pm$ 2.1	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	9.7 $\pm$ 7.4	4.5	2	small boulders
	10	7.3 $\pm$ 2.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	2.3 $\pm$ 2.3	6	2	med.andsmall bld.
	20	6.3 $\pm$ 1.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	1.0 $\pm$ 0.0	6.5	2	med.andsmall bld.
	30	5.0 $\pm$ 1.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	3.3 $\pm$ 0.6	8.3	3	med.andsmall bld.
	40	3.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	2.2 $\pm$ 1.6	10.8	2	small boulders
	50	3.7 $\pm$ 0.6	0.0 $\pm$ 0.0	0.7 $\pm$ 0.6	0.0 $\pm$ 0.0	16.3 $\pm$ 11.0	12.4	2	small boulders

dock, this species was observed at water depths of less than 1 m. In cliff areas (i.e. declivity close to 90°) close to the tide line, *D. antillarum* was commonly observed at depths of 1-2 m. On boulder beaches, where declivity is generally low, this species only appeared below 5-7 m water depth.

*Arbacia lixula* and *Paracentrotus lividus* preferred shallower depths, being found close to the shore. *Sphaerechinus granularis* was always found at very low densities and typically occurred 30–40 m from the shore at depths of approximately 6 m. Two-way ANOVA results show that there were significant differences ( $p < 0.05$ ) between sea urchin densities and water depth, between sea urchin species, and between both these sets of parameters (Table 3). Algal cover did not show a clear trend with distance from shore or water depth (Tables 1 and 2). On average, sandy sediments were found from about 80 m along transects from the tide line.

### Substratum type

*Diadema antillarum*, *Arbacia lixula* and *Paracentrotus lividus* were found living on almost all recorded substrata, particularly on rock floors and big boulders (Tables 1 and 2). *Sphaerechinus granularis* occurred mostly on small boulders. In general, seaweed and sea urchins were absent from sandy substrata.

### Water turbulence

Water turbulence was assessed as being level 2 for transects 1-15SE and 22-23SW; level 3 for tran-

sect 19N (which lies in a sheltered area) and 21SW; and level 4 for transects 16N, 17N, 18N and 20SW.

### Factors limiting spatial distribution of *Diadema antillarum*

All of the environmental factors analysed were integrated in a single non-linear equation. The independent variables selected were: distance from tide line, water depth, and water turbulence. The remaining variables were eliminated since they did not contribute significantly to the adjusted R<sup>2</sup>. The multiple non-linear regression equation describing the spatial distribution of *D. antillarum* on the rocky shores is:

$$D. antillarum/m^2 (\sqrt{\sqrt{\phantom{x}}}) = 0.121 - 0.209 DS(\sqrt{\sqrt{\phantom{x}}}) + 2.052 D(\sqrt{\sqrt{\phantom{x}}}) - 1.778 WT(\sqrt{\sqrt{\phantom{x}}}) - 0.007 WT^4 (\sqrt{\sqrt{\phantom{x}}})$$

where DS is distance from tide line (in m), D is water depth (in m), WT is water turbulence categorised according to the four-point scale (defined above) and  $\sqrt{\sqrt{\phantom{x}}}$  indicates data are square-root transformed. The adjusted R<sup>2</sup> was 60.99% and the number of samples (n) used for the equation was 454. The corresponding ANOVA test (95% confidence interval) was significant ( $p < 0.05$ ).

### Sea urchin vs. macroalgae abundance

In general, sea urchin densities and algal cover were negatively correlated (see Tables 1 and 2; R<sup>2</sup> is 75.6%). Due to the predominance of *D. antillarum* among sea urchins, the assessment of sea urchin

TABLE 2. – Sea urchin density and percent algal cover (mean of three samples  $\pm$  standard deviation), water depth, bottom declivity (Bott. decliv.) and substrate type against distance (Dist.) from tide line for transects 14 to 23. (Measurements were made until sandy sediments were found, except those marked with an asterisk (\*). Bottom declivity was measured on a four-level scale described in the methodology.)

Site	Dist. from shore (m)	Sea urchins/m <sup>2</sup> (mean $\pm$ standard deviation)				Algal cover (%)	Depth (m)	Bott. decliv.	Substratum type
		<i>D.antillarum</i>	<i>A.lixula</i>	<i>S.granularis</i>	<i>P.lividus</i>				
14	2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	64.0 $\pm$ 20.5	2.5	2	big and med. bld.
	10	14.3 $\pm$ 2.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	3.5	2	big and med. bld.
	20	12.0 $\pm$ 3.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	5.4	2	big and med. bld.
	30	7.7 $\pm$ 1.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.3 $\pm$ 0.6	7.5	2	med.andsmall bld.
	40	8.3 $\pm$ 1.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	7.9	2	med.andsmall bld.
	50	8.0 $\pm$ 1.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	2.7 $\pm$ 2.1	8.4	2	med.andsmall bld.
	60	6.7 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	11.3	3	med.andsmall bld.
15	70	4.7 $\pm$ 1.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	2.0 $\pm$ 1.0	17.6	3	med.andsmall bld.
	2	0.7 $\pm$ 1.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	88.3 $\pm$ 7.6	5.9	2	rock
	10	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	67.0 $\pm$ 57.2	7.8	2	big and med. bld.
16	20	1.3 $\pm$ 1.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	34.0 $\pm$ 57.2	8.2	3	big boulders
	30	2.0 $\pm$ 2.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	26.3 $\pm$ 43.9	10.3	2	big boulders
	2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	73.7 $\pm$ 5.5	4.1	1	med.andsmall bld.
17	10	0.0 $\pm$ 0.0	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	43.0 $\pm$ 10.8	4.4	1	med.andsmall bld.
	20	0.0 $\pm$ 0.0	1.0 $\pm$ 1.7	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	78.7 $\pm$ 5.9	4.9	1	med.andsmall bld.
	30	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	64.7 $\pm$ 7.8	6.2	1	med.andsmall bld.
	40	0.0 $\pm$ 0.0	0.7 $\pm$ 1.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	39.3 $\pm$ 1.5	6.8	1	med.andsmall bld.
	50	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	40.7 $\pm$ 1.5	6.9	1	med.andsmall bld.
	10	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	7.7 $\pm$ 6.7	3.4	1	med.andsmall bld.
	20	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	24.3 $\pm$ 21.5	3.6	1	med.andsmall bld.
18	30	0.0 $\pm$ 0.0	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	25.7 $\pm$ 22.5	4.1	2	med.andsmall bld.
	40	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	40.3 $\pm$ 30.2	6.3	1	big and med. bld.
	50	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	49.3 $\pm$ 32.5	6.5	1	big and med. bld.
	60	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	37.0 $\pm$ 28.8	6.6	1	big and med. bld.
	70	0.0 $\pm$ 0.0	1.0 $\pm$ 1.7	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	32.7 $\pm$ 9.7	7.5	2	big and med. bld.
	80	0.0 $\pm$ 0.0	1.0 $\pm$ 1.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	40.7 $\pm$ 33.6	8.2	2	big and med. bld.
	90	0.0 $\pm$ 0.0	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	97.7 $\pm$ 1.2	9	2	big and med. bld.
	100 *	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	96.3 $\pm$ 1.5	10.1	2	big and med. bld.
	2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	68.0 $\pm$ 2.6	5.5	1	big and med. bld.
	10	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	97.0 $\pm$ 2.0	5.3	1	big and med. bld.
	20	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	97.7 $\pm$ 1.5	5.2	1	big and med. bld.
19	30	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	67.0 $\pm$ 2.6	5.4	1	big and med. bld.
	40	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	84.7 $\pm$ 6.5	5.8	1	big and med. bld.
	50	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	37.0 $\pm$ 4.0	7.2	2	med.andsmall bld.
	60	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	35.7 $\pm$ 4.7	7.3	2	med.andsmall bld.
	70	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	95.0 $\pm$ 3.0	8	2	big and med. bld.
	80	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	92.3 $\pm$ 1.5	8.5	2	big and med. bld.
	90	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	97.3 $\pm$ 2.1	10.3	2	big boulders
	100	4.7 $\pm$ 2.1	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	2.0 $\pm$ 1.0	10.2	2	big boulders
	110	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	95.7 $\pm$ 2.1	11.7	2	big boulders
	2	6.7 $\pm$ 3.2	0.0 $\pm$ 0.0	1.3 $\pm$ 0.6	0.0 $\pm$ 0.0	1.0 $\pm$ 0.0	7.2	2	med.andsmall bld.
	10	4.7 $\pm$ 0.6	0.0 $\pm$ 0.0	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	1.0 $\pm$ 0.0	8.5	2	med.andsmall bld.
20	20	3.0 $\pm$ 1.0	0.0 $\pm$ 0.0	0.3 $\pm$ 0.6	0.0 $\pm$ 0.0	1.0 $\pm$ 0.0	9.9	2	small boulders
	30	2.0 $\pm$ 1.0	0.0 $\pm$ 0.0	1.3 $\pm$ 0.6	0.0 $\pm$ 0.0	1.0 $\pm$ 0.0	11.1	2	small boulders
	40	2.3 $\pm$ 1.5	0.0 $\pm$ 0.0	0.7 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	13.5	2	small boulders
	10	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	97.7 $\pm$ 2.5	1.8	2	big and med. bld.
	20	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	93.3 $\pm$ 11.5	3.1	2	big and med. bld.
	30	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	100.0 $\pm$ 0.0	5.2	1	big and med. bld.
	40	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	100.0 $\pm$ 0.0	5.3	1	big and med. bld.
	50	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	100.0 $\pm$ 0.0	4.8	1	big and med. bld.
	60	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	100.0 $\pm$ 0.0	4.7	1	big and med. bld.
	70	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	100.0 $\pm$ 0.0	7.3	2	big and med. bld.
	80	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	100.0 $\pm$ 0.0	8.5	2	big and med. bld.
	90	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	100.0 $\pm$ 0.0	9.7	2	big and med. bld.
	100	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	100.0 $\pm$ 0.0	10	2	big and med. bld.
	110	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	100.0 $\pm$ 0.0	10.2	2	big and med. bld.
120	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	100.0 $\pm$ 0.0	10.5	2	big and med. bld.	
21	130	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	100.0 $\pm$ 0.0	11.4	2	big and med. bld.
	140	0.7 $\pm$ 1.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	67.3 $\pm$ 56.6	12.8	2	big and med. bld.
	150 *	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	100.0 $\pm$ 0.0	13.1	2	big and med. bld.
	2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	86.7 $\pm$ 3.8	2.8	2	small boulders
	10	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	83.0 $\pm$ 3.0	4.1	2	small boulders
	22	2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	75.7 $\pm$ 30.1	3.4	1
23	10	0.0 $\pm$ 0.0	13.7 $\pm$ 16.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	63.0 $\pm$ 52.8	3.7	1	big and med. bld.
	20	0.0 $\pm$ 0.0	3.3 $\pm$ 5.8	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	64.3 $\pm$ 54.8	4.3	2	big and med. bld.
	30	0.3 $\pm$ 0.6	1.3 $\pm$ 2.3	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	88.3 $\pm$ 15.9	8	3	big and med. bld.
	40	0.7 $\pm$ 1.2	0.0 $\pm$ 0.0	0.7 $\pm$ 1.2	0.0 $\pm$ 0.0	53.7 $\pm$ 45.6	8.5	2	big and med. bld.
23	2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	1	2	big and med. bld.
	10	0.0 $\pm$ 0.0	0.7 $\pm$ 1.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	20.0 $\pm$ 34.6	1.8	2	big and med. bld.
	20	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	74.7 $\pm$ 37.8	3.1	2	big and med. bld.
	30	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	86.7 $\pm$ 7.1	5.3	2	big and med. bld.
	40	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	51.3 $\pm$ 32.3	5.5	2	big and med. bld.
	50	0.7 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	2.0 $\pm$ 2.0	6.9	2	big and med. bld.
	60	1.3 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	10.8	3	big and med. bld.
70	0.7 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	12	3	big and med. bld.	

TABLE 3. – Results of two-way ANOVA test of water depth and the densities of four sea urchin species. (df = Degrees of freedom, MS = Mean Square.)

Statistic	Two-Way ANOVA		1-Depth, 2-Sea urchins		F	p-level
	Effect	df	MS	Error		
1	20	16.78	1812	10.35	1.62	0.0401
2	3	994.14	1812	10.35	96.08	0.0000
12	60	28.51	1812	10.35	2.76	3.9E-11

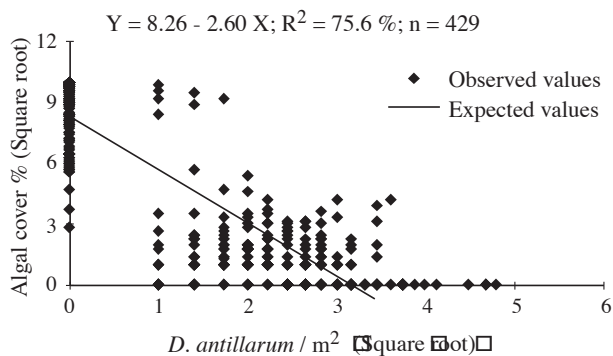


FIG. 2. – Linear regression between the density of *Diadema antillarum* and algal cover. Percent algal cover (square-root transformed) =  $8.26 - 2.60 \text{ Diadema antillarum}/\text{m}^2$  (square-root transformed);  $R^2 = 75.6\%$ ;  $n = 429$ .

density against macroalgae abundance focuses upon this species.

High algal cover was found only in those areas where *D. antillarum* was absent. However, with densities of 1 individual/ $\text{m}^2$  or higher, the percentage of algal cover decreased markedly and the linear regression between the percentage of algal cover and *D. antillarum* density shows an inverse relationship (Fig. 2). The linear regression equation is:

$$A (\sqrt{\sqrt{\quad}}) = 8.26 - 2.60 D (\sqrt{\sqrt{\quad}})$$

where A is the percentage of algal cover, D is the number of individuals of *Diadema antillarum* per square metre, and  $\sqrt{\sqrt{\quad}}$  indicates data are square-root transformed. The adjusted  $R^2$  is 75.6%, and the number of observations is 429.

## DISCUSSION

Among the less abundant sea urchin species, *Sphaerechinus granularis* reached its higher densities at 30-40 m from shore at depths of approximately 6 m. Similar results were found by Maciel and Gonçalves (1998) at the Azores Islands, and this is probably related to the lower water turbulence that

occurs at this depth. *Diadema antillarum* exhibits aggressive behaviour towards other urchin species (Shulman, 1990), which might explain the low densities of *S. granularis* in the vicinity of high densities of *D. antillarum*.

The other less abundant sea urchin species found in this study were *P. lividus* and *A. lixula*, showing a very similar distribution in terms of water depth. One possible explanation for their distribution in shallower water is the distribution of their prey species: *Cystoseira* spp., which live in very shallow waters off Madeira (Levring, 1974; Augier, 1985; Morton *et al.*, 1998), and appear to be the preferred diet of these sea urchin species (Bergin, 1987; Benedetti-Cecchi and Cinelli, 1995). However, where *D. antillarum* is absent (i.e. along the major northern coastal area) *A. lixula* were found down to 9 m, suggesting that their restricted distribution might also be mediated by competition with *D. antillarum*. Shulman (1990) recorded similar observations with the *D. antillarum* and Keller (1983) with other sea urchin species in the Caribbean reefs.

High densities of *D. antillarum* (up to a maximum record of 68 individuals/ $\text{m}^2$ ) were observed during this study, and similar densities have been recorded in Jamaica by other authors (e.g. Sammarco, 1980; Sammarco and Williams, 1982). It is generally accepted that human activities are responsible for high sea urchin densities because of the removal of predators through over-fishing (e.g. Mann, 1977; Hughes, 1994; Casañas *et al.*, 1998; Sala *et al.*, 1998; Steneck, 1998). Nevertheless, on the basis of paleontological and early historical reports, Jackson (1997) considered *D. antillarum* to have always been the most abundant sea urchin in the Caribbean. At Madeira Island, adult *D. antillarum* do not have any specific predator, which may be related to over-fishing. According to Carpenter (1984), high sea urchin densities, together with the absence of predators, may explain the frequent presence of *D. antillarum* on exposed rocks, a phenomenon observed on Madeira's rocky shores, which contrasts with the "homing" behaviour described by Carpenter (1990).

In this study, algal cover was not considered a limiting factor for *D. antillarum* distribution, but rather a result of the urchin's presence. We found evidence of two distinct and alternative rocky shore communities off Madeira Island. Where *D. antillarum* occurred in large numbers, algae were prevented from reaching any great abundance, where-

as sea urchins were not present where algae formed a dense cover. We suggest that a dense cover of algae does not prevent *D. antillarum* from occurring in high densities, but that there are other limiting factors (e.g. water turbulence) that do so. However, Wirtz (1995) considers that the types of community structure observed at Madeira Island are an example of alternative stable states, with shifts occurring only after catastrophic events. The negative relationship observed between the percentage of algal cover and the density of *D. antillarum* has been previously described in Caribbean waters by Carpenter (1981), Sammarco (1982a) and Johnson and Mann (1993).

The predominantly rough waters off the north and west coasts of Madeira Island (Instituto Hidrográfico, 1979; Abreu and Biscoito, 1998; Caldeira and Lekou, 2000) may be responsible for differences in *D. antillarum* abundance between the north and south coasts. The species was absent from many shallow areas, where wave action has its greatest impact, but in places where there is no wave action, such as in the Porto Santo dock, *D. antillarum* were found to occur at depths of less than 1 m. Weil *et al.* (1984) and Casañas *et al.* (1998) have also recorded this species in shallow waters on a Venezuelan coral reef and at the Canary Islands respectively.

For substratum type, the results showed that *D. antillarum* was found living in high densities on several kinds of rocky shores, mainly preferring rock platforms and, to a lesser extent, areas of large boulders. However, sandy sediments are avoided and limit their habitat.

Bottom declivity is linked to several of the other factors considered. It affects water depth and consequently exposure to water turbulence, which occurs mainly in shallow waters. For example, in cliff areas, where declivity is around 90°, *D. antillarum* appeared at depths of 1-2 m, whereas on boulder beaches, where declivity is low, it appeared only below 5-7 m, and this distribution pattern may be dependent upon the degree of water turbulence.

The multiple non-linear regression resulting from our study reveals that distance from the tide line, together with water depth and water turbulence, explained 60.99% of the observed sea urchin distribution. We propose four possible explanations for this low adjusted R<sup>2</sup> value. (1) Sea urchin densities were measured from July to August, while the water turbulence scale is an annual average, which may account for some of the variation in this depen-

dent variable. (2) Although previous studies have suggested some factors that might explain the distribution of *D. antillarum*, there are other factors that might have equal importance, such as the aggressive behaviour of territorial pomacentrid fishes (Sammarco and Williams, 1982), and the density of other invertebrate species (Casañas *et al.*, 1998). (3) Neither recruits nor juveniles (test diameter <10 mm) were found during the sampling months, and the inclusion of both recruits and juveniles in addition to adults should be considered in future studies since this may increase the adjusted R<sup>2</sup> value. (4) *D. antillarum* is highly adaptable to different environmental conditions and inhabits a number of different marine communities: shallow coral reefs, rocky shores, seagrass beds, sandy bottoms, mangrove roots, and even water depths down to 400 m (Weil *et al.*, 1984). *Diadema antillarum* has a variety of successful adaptive strategies (Ebert, 1985), including the ability to increase the relative size of the Aristotle's lantern compared to the size of the test when food is limited. Moreover, high population density leads to reduced body size and gamete production; body size can be adjusted quickly (by positive or negative growth) to a given resource or density-dependent factors (Levitan, 1988, 1989, 1991a, b). Populations using this life history strategy tend to closely track environmental carrying capacity (Levitan, 1989).

Another possible adaptive theory to explain the high *D. antillarum* densities on the "blanquial" (bare-ground) areas observed off the southeast coast of Madeira involves its feeding behaviour. Though it is preferentially herbivorous (Sammarco, 1982a, b; Kullen, 1996), *D. antillarum* can also be omnivorous (Carpenter, 1981), in what Lawrence (1975) considers as opportunistic feeding behaviour. Absorption of dissolved nutrients by the spines has been observed in *P. lividus* (De Burgh, 1975; Anonymous, 1996) and is yet another possible adaptive theory.

Future investigations into the spatial distribution of *D. antillarum* should consider additional variables, such as temperature, aggressive territorial pomacentrid fishes, density of all invertebrate species, surface of the substratum, the number and size of refuges, local current velocity, and dissolved nutrients in the water. Further studies on the ecology of *D. antillarum* would be of great interest and would contribute towards a better understanding and management of the rocky shore ecosystems of Madeira Island.



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