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Grazing by *Diadema antillarum* (Philippi) upon algal communities on rocky substrates*

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SUMMARY: Grazing by *Diadema antillarum* sea urchins is well documented for coral reefs, although information is scarce for the eastern part of the Atlantic Ocean, where rocky substrate dominates the sea bottom. This study analysed grazing activity by *D. antillarum* upon the algal communities living on rock substrates, and its possible impact on the subtidal communities. Controlled feeding experiments using exclusion cages were performed between May and September 1998 at Madeira Island (NE Atlantic). Three experimental treatments were used: (1) closed cages to exclude sea urchins, (2) open cage controls, and (3) uncaged controls (nine replicates in each treatment). After four months, in September 1998, the percentage algal cover was quantified. One-way analysis of variance followed by Post Hoc Tukey (HSD) tests showed significant differences between algal abundance in the presence (uncaged and open cage controls) or absence (closed cages) of sea urchins. In the areas where *D. antillarum* was excluded (closed cages), algal abundance increased by about 10% in the four-month period. *Diadema antillarum* thus effectively reduces algal abundance, and this may have important consequences in determining the algal community structure of rocky substrate.

Key words: *Diadema antillarum*, grazing, macroalgae, Madeira Island, rocky substrate, sea urchins.

RESUMEN: DEPREDACIÓN DE COMUNIDADES DE ALGAS POR EL ERIZO *DIADEMA ANTILLARUM* (PHILIPPI) EN SUSTRATOS ROCOSOS. – La depredación por el erizo *Diadema antillarum* ha sido ampliamente descrita en arrecifes de coral, aunque escasa en la zona Este del Océano Atlántico, donde predominan los sustratos rocosos. En el presente trabajo se analiza la actividad depredadora de *Diadema antillarum* sobre las comunidades intermareales. Se han realizado experimentos de alimentación controlada empleando jaulas con exclusas, en los meses de mayo a septiembre de 1.995 en la Isla de Madeira (NE Atlántico). Se emplearon tres diseños experimentales distintos: 1) jaulas cerradas para excluir a los erizos, 2) jaulas abiertas para controles y 3) controles sin jaula (nueve replicados en cada diseño). Tras cuatro meses, en septiembre de 1.998, fue cuantificado el porcentaje de la cobertura algal. El análisis de la variancia de una entrada seguido del Test de Post Hoc Tukey (HSD) mostraron diferencias significativas entre la abundancia algal en presencia (controles de jaulas abiertas y sin jaula) y en ausencia (jaulas cerradas) de la especie. En la zona de estudios sin erizo, la abundancia algal aumentó aproximadamente un 10% en el periodo estudiado. El erizo *Diadema antillarum* produce, por lo tanto, una disminución de la abundancia algal, factor clave en la determinación de la estructura de las comunidades algales sobre sustrato rocoso.

Palabras clave: *Diadema antillarum*, depredación, macroalgas, Isla de Madeira, sustratos rocosos, erizos.

INTRODUCTION

The black sea urchin *Diadema antillarum* (Philippi, 1845) has been characterised as a keystone species in shallow subtidal ecosystems because of its effectiveness in reducing algal biomass and diversity (Bak *et al.*, 1984; Carpenter, 1990; Larsen *et al.*, 1996). However, grazing by *D. antillarum* is well-documented only for the Western Atlantic, where sea bottoms are dominated by coral reef communi-

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ties (Sammarco *et al*., 1974; Sammarco, 1980, 1982a, b; Carpenter, 1981). Although this species has been less studied in the east Atlantic, where sea bottoms are dominated by rocky substrate communities, studies in the Canary Islands (Larsen *et al*., 1996; Casañas *et al.*, 1998; Garrido-Sanahuja and Haroun, 1998) and off the Madeira Islands (Augier, 1985; Bianchi *et al.*, 1998; Alves *et al.*, 2001) have suggested a similar voracity of *D. antillarum* feeding on macroalgae. These studies also reported that *D. antillarum* may be responsible for nearly denuded substrata, which may have important consequences on the structure of benthic communities by leaving less food available for other herbivores and reducing the dissolved organic matter available for detritivores (McGlathery, 1995; Valentine *et al.*, 1997). This study aimed to analyse the grazing activity by *D. antillarum* upon the algal communities on rocky substrates, and to evaluate its possible impact on the subtidal communities off Madeira.

MATERIAL AND METHODS

Study site

Madeira Island is located in the north-east Atlantic Ocean, at approximately 32°38'N and 16º54'W (Biscoito and Abreu, 1998). It has a reduced continental shelf, and forms part of the important Macaronesian biogeographic region (Beyhl *et al.*, 1995; Stock, 1995). This 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 Island itself extends W-NW to E-SE along 58 km, and its 153 km of coastline are predominantly rocky with boulders. The surface seawater temperatures usually range between 17.0 and 22.5°C (Abreu and Biscoito, 1998).

Preliminary survey

Preliminary prospective Scuba dives were made along the whole coast of Madeira Island to determine a rocky substrate area that would best fit the experiment requirements in terms of *D. antillarum* abundance and feasibility for divers to perform and monitor the experiment. The selected area was on the south coast, at Lido bay (see Alves *et al.*, 2001), despite the considerable homogeneity of the benthic communities observed along almost the wholesubtidal rocky shore of the south and south-east coast of Madeira, featuring high densities of this species and nearly bare substrata. The natural density of *D. antillarum* and the percentage algal cover in the experiment area were determined by 27 random quadrats, using a square metre for *D. antillarum* abundance, and a 0.5 m x 0.5 m quadrat divided into a hundred 5 x 5 cm squares for algal cover.

Two Kolmogorov-Smirnov tests were performed to assess the normal distribution of *D. antillarum* abundance and algal cover. Both tests revealed that the data conformed to the normal distribution ($p > 0.05$), thus showing that all treatments were in the same initial conditions.

Cage design

The cages measured 0.5 0.5 m wide and 0.2 m high with a 0.2 m overhanging edge made of 2 cm mesh wire. They were built of 8 mm steel and attached to the bottom with iron nails and wire. The top was open to ensure that free-swimming herbivores could enter the cage. The cage design tried to minimise any disturbance of natural conditions on the algal colonisation and growth, such as current and light intensity. Two different cage designs were used: laterally closed cages (Fig. 1A) and open cages (controls), with the sides partly closed (Fig. 1B). The closed cages were previously tested in the experiment area for their ability to exclude sea urchins. The open cages were also tested for their ability to allow sea urchins in. This experiment was performed for two weeks, and both cage designs performed as expected.

In situ cage experiment

To estimate *D. antillarum* grazing upon the algal cover, an exclusion experiment was performed between May and September 1998. Three experimental treatments were used: (1) closed cages which excluded sea urchins; (2) open cage controls, to control any eventual side effects of the cage structures themselves; and (3) uncaged controls (small iron cross markers).

Nine replicates of each treatment were set randomly on the bottom at depths of 11–13 m in the pre-determined area (approximately 200 m^2). During the four months of the experiment, the cages were monitored weekly by Scuba divers to observe the integrity of the experiment. In September 1998, at the end of the experiment, the percentage algal

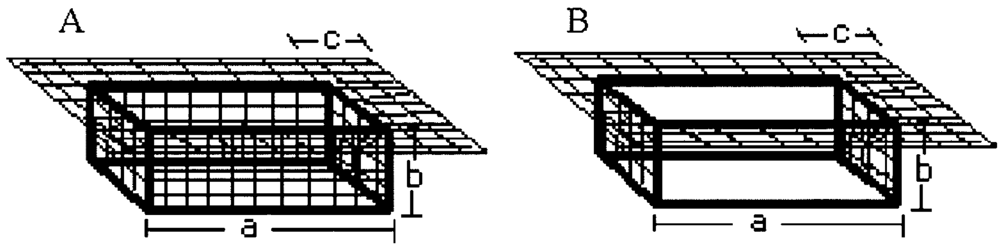

FIG. 1. – A: Closed cage for sea urchin exclusion. B: Open cage control, which allows the entrance of sea urchins. In both A and B, (a) = 0.5 m; (b) and (c) = 0.2 m; 2 cm mesh size.

cover was quantified in all replicates of all treatments, using a 0.5 m x 0.5 m quadrat divided into 100 squares (5 cm x 5 cm): the number of squares with algae was counted and the percentage cover of the total area was calculated.

Data analysis

The mean and the standard error of the percentage algal cover of each treatment were calculated. A one-way ANOVA was used to test the null hypothesis that there were no significant differences in the percentage algal cover between the three treatments. Because more than two comparisons were made, this analysis was followed by a post-hoc comparison using the Tukey honest significant differences (HSD) test. Concerning the ANOVA test assumptions, the data conformed to the normal distribution (Kolmogorov-Smirnov test, $p > 0.05$) and to homogeneity of variance (Levene's test, $p > 0.05$). The significance level assumed for all tests was 95% ($p < 0.05$). All statistical tests were performed with the Statistica V.5 software package.

RESULTS

The preliminary survey showed that the natural density of *D. antillarum* at Lido bay was 5.11 ± 1.56 individuals/m^2 (mean ± standard deviation). It was also observed that *D. antillarum* was the most abundant sea urchin and predominated as the main herbivore in the experimental area.

At the end of the experiment, the mean algal cover (± standard error) was 4.4 ± 1.2% in the uncaged controls, 5.8 ± 1.5% in the open cage controls, but as high as 14.6 ± 2.7% in the closed cages (where sea urchins were excluded) (Fig. 2). One-way ANOVA showed that algal cover differed significantly between treatments (Table 1). However, the Tukey (HSD) test revealed that significant differences only occurred between closed cages with

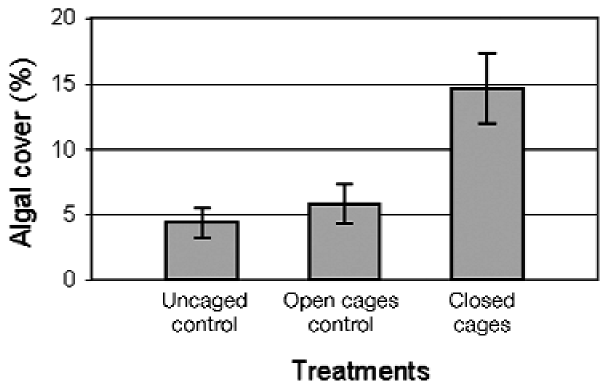

FIG. 2 – Algal cover (means ± standard errors, n = 9) in uncaged controls, open cage controls, and closed cages that excluded sea urchins, in September 1998, four months after the experiment was started.

either of the controls. The mean percentage algal cover was not significantly different between uncaged controls and open cage controls (Table 1). The percentage algal cover observed in the closed cages, compared with the uncaged and open cage controls, allows us to conclude that, in the area where *D. antillarum* was excluded (closed cages), the algal abundance increased by about 10% in the four-month period.

During the experimental period, it was registered that adult *D. antillarum* individuals (measuring approximately 10 cm in test diameter) were com-

TABLE 1. – Summary of all effects for a one-way ANOVA test and the probabilities for the Post Hoc Tukey (HSD) test, of the percentage algal cover between three treatments (uncaged control, open cages control, and closed cages); *df*, degrees of freedom; MS, Mean Square; *, significantly different ($p < 0.05$).

One-way ANOVA - Summary of all effects

df effect	Ms effect	*df* error	MS error	F	p-level
2	277.8	24	32.45	8.56	0.0016*

Tukey HSD test - Probabilities for post hoc tests

	Uncaged control (1)	open cages control (2)	Closed cages (3)
(1)		0.8410	0.0023*
(2)			0.0089*
(3)			

monly observed invading the control replicates (both uncaged and open cage controls).

DISCUSSION

Studies in the Caribbean have also used cages to exclude *Diadema antillarum* (Sammarco, 1980, 1982a; Carpenter, 1981), as well as to eliminate an entire *D. antillarum* population efficiently (Sammarco *et al.*, 1974; Sammarco, 1982b). Also, our attempts to maintain *D. antillarum* exclusion from the closed cages, and at natural densities inside controls (both uncaged and open cage controls), were successful, demonstrating that the cage design was efficient because it excluded predators and did not significantly influence algal growth. Because of the low annual seasonal variations in weather conditions and seawater temperature off Madeira (Instituto Hidrográfico, 1979; Abreu and Biscoito, 1998; Carita, 1998), we consider that the present results will only be slightly and non-significantly affected by seasonal variations.

The present study documented an increase in algal cover in the areas where *D. antillarum* were excluded (closed cages). Similar results were described in Caribbean waters by Sammarco (1980, 1982a, b) and Carpenter (1981).

Liddell and Ohlhorst (1986) studied algal recovery in Discovery Bay (Jamaica) immediately after a mass urchin cull on coral reefs, and described an increase in algal cover of about 40% over a four-month period. In our study we observed a 10% increase in algal abundance. Differences in water temperature between sites may justify the different levels of algal increase.

The results obtained from the present study, together with the negative relation observed by Alves *et al.* (2001) between percentage algal cover and densities of *D. antillarum* in Madeira, suggest that *D. antillarum* grazing pressures control algal abundance on rocky substrates (such as Madeira, Canary and Cape Verde – East Atlantic archipelagos) and not just in coral reef communities (West Atlantic). The impact of *D. antillarum* on the structure of rocky shore benthic communities may have important consequences for the ecosystem. Thus, benthic communities will probably undergo significant changes if *D. antillarum* abundance significantly increases or decreases.

If a similar event to the one that happened in the Western Atlantic, where entire populations of *D. antillarum* suffered the most extensive and severe mass mortality ever recorded for a marine animal (Levitan, 1988; Lessios, 1995), occurred in the Madeira Archipelago, an increase in the total algal abundance could probably be expected. If this happened, the present study would be significant, as it would be possible to compare *D. antillarum* densities, algal abundances and increase rates. For the above reasons, we consider that the management of sea urchin abundance (such as *Diadema antillarum*) on rocky substrates (such as Madeira Island) is important in order to prevent unfavourable ecosystem changes.

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