Hydrobiologia **519:** 211–214, 2004.

Short research note

Can one species determine the structure of the benthic community on a temperate rocky reef? The case of the long-spined sea-urchin *Diadema antillarum* (Echinodermata: Echinoidea) in the eastern Atlantic

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Received 20 September 2003; in revised form 18 November 2003; accepted 1 December 2003

Key words: Diadema antillarum, sea urchins, barrens, key-herbivores, overgrazing, Canary Islands

Abstract

We sampled 36 coastal rocky reefs throughout the overall Canarian Archipelago and consider (1) the daily macroalgal consumption of the long-spined sea urchin *Diadema antillarum* and (2) the daily net production of macroalgae along temperate rocky-substrates, to provide evidence that *Diadema antillarum* plays an important role in the structure of the shallow benthic environment of the eastern Atlantic. *D. antillarum* was found to be the main key-herbivore species, as it controls by its own the algal assemblages, with negligible contribution of other grazing species.

Sea-urchins play an important role in the structure of coastal communities, transforming large shallow rocky reefs covered by fleshy erect algae into overgrazed substrates dominated by encrusting coralline algae, so called 'urchin barrens' (Lawrence, 1975; Mann, 1982; Dean et al., 1984; Andrew & Underwood, 1989, 1993; Elner & Vadas, 1990; Dayton et al., 1992; Andrew, 1993; Benedetti-Cecchi & Cinelli, 1995; Sala, 1996; McClanahan & Sala, 1997; Benedetti-Cecchi et al., 1998; Sala et al., 1998; Pinnegar et al., 2000; Shears & Babcock, 2003). Consequently, in order to understand ecological processes in coastal marine environments, a quantitative understanding of the impact of these herbivores on algal communities is necessary. Despite this fact, very few empirical attempts have been carried out worldwide to determine the threshold abundance of herbivorous species necessary to maintain an existing urchin barren completely absent of fleshy erect macroalgae (Ruitton et al., 2000; but see Shears & Babcock, 2003).

The long-spined sea-urchin *Diadema antillarum* (Philippi) has long been suggested as a key-stone species throughout coastal areas of the western Atlantic, as it plays an important role in the dynamics and structure of Caribbean coral reefs (Carpenter, 1981; Sammarco, 1982; Hay, 1984; Lessios et al., 2001). This echinoid species has been only found at the Canary Islands (Casañas et al., 1998) and the Archipelago of Madeira (Alves et al., 2001, 2003) throughout the central-east Atlantic Ocean. Rocky reefs modified to barrens are commonly observed at both archipelagos (Alves et al., 2001). Therefore, our study is an approach to address the following question: Does *D. antillarum* control the macroalgal assemblages on temperate rocky reefs along the eastern Atlantic on its own, or do other herbivores contribute significantly to grazing on rocky reefs?

To estimate the influence of *Diadema antillarum* on the structure of macroalgal assemblages on eastern Atlantic temperate rocky reefs, and therefore the mean threshold of abundance of *Diadema* sea-urchins needed to maintain an existing barren, we quantified the relationship between the fleshy erect macroalgal cover and the overall density of *D. antillarum* indi-

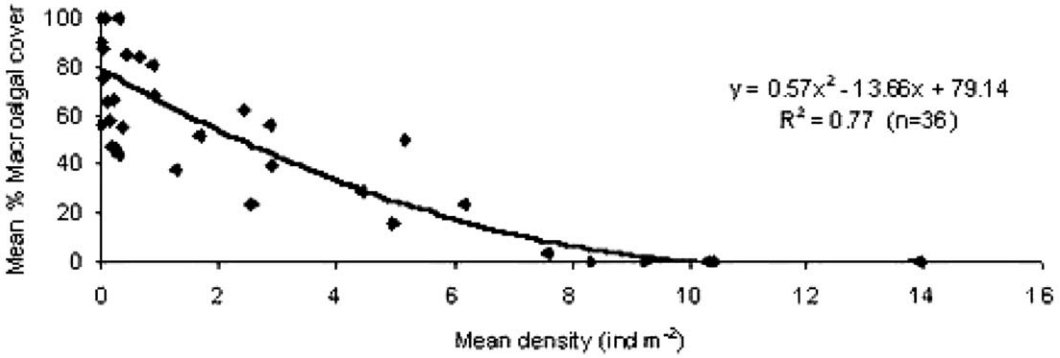

Figure 1. Non-linear regression between the mean density of total *Diadema antillarum* individuals and the mean percent of algal cover registered per location for the overall surveyed locations along the Canarian Archipelago.

Table 1. Net Primary Production and grazing rates employed in the estimation of the role of the sea-urchin *Diadema antillarum* in the structure of the rocky sublittoral environments of the Canarian Archipelago.

	Mean algal consumption	Mean net primary production	
	68–98 mg ww ind^{-1} h^{-1} (0.50–0.72 g dw ind^{-1} d^{-1})	2480–2500 g m^{-2} yr^{-1} [a] (≈6.8 g dw m^{-2} d^{-1})	
Source	Tuya et al. (2001) (Gran Canaria Island)	Valiela (1995) (Atlantic temperate coastal environments)	Ruitton et al. (2000) (Mediterranean Sea)
	Multi-diet *in situ* assays	Repeated harvest of standing crop	

[a]No data available for the Canarian Archipelago.

viduals throughout sublittoral hard-substratum environments along the Canary Islands. We chose 36 locations around the 8 islands of the Canarian Archipelago (27–29° N, 14–19° W; sea-water temperature ranges between 18–23 °C throughout the year), the spatial scale of the study being 100's of kilometres. In each location, 16 quadrants of 2 × 2 m^2 were randomly sampled in shallow rocky habitat (8–18 m deep, March 2003) (Ruitton et al., 2000) during daylight hours. The percentage of fleshy erect macroalgal cover (mainly large brown macroalgal species belonging to the genera *Cystoseira*, *Sargassum*, *Lobophora* and *Dictyota*) was visually quantified within each quadrant by assigning to this taxon a score ranging from 0 to 4 and adding up to 24 estimates (Benedetti-Cecchi et al., 1996). Final values were expressed as percentages.

A markedly non-linear decrease of the mean percent of macroalgal cover with increasing mean density of total *Diadema antillarum* abundance was observed (Fig. 1), and it was concluded that a total lack of fleshy erect macroalgal cover resulted from a mean density ≥10 ind m^{-2}.

To asses if the daily grazing of *Diadema antillarum* can consume the total net benthic macroalgal production, we took into consideration (1) the mean daily macroalgal consumption of *Diadema antillarum*, and (2) the average daily net primary production of macroalgae along shallow temperate rocky-substrates (Table 1). It was found that benthic daily net primary production was one order of magnitude greater than grazing rates by *D. antillarum* (6.8 g dw m^{-2} d^{-1} *Vs* 0.5–0.72 g dw ind^{-1} d^{-1}).

In conclusion, the macroalgal consumption by a mean density of about 10 *Diadema antillarum* m^{-2} equals approximately the net benthic primary production, and this density would therefore be able to maintain a rocky reef completely barren of fleshy erect algal cover. Since this estimated threshold is in agreement with our empirical recorded data (Fig. 1), *D. antillarum* can therefore be considered as the main key-herbivorous species throughout shallow rocky reefs of the Canary Islands. This result is similar to that reported by Alves et al. (2003) for the Madeiran Archipelago. In contrast to findings in the Caribbean (e.g. Hay, 1984; Carpenter, 1990), our results suggest that

the contribution of other herbivorous fauna (mainly benthic epifauna and herbivorous fish populations) to grazing on fleshy macroalgal beds is negligible along shallow sublittoral rocky reefs of the eastern Atlantic Canary Islands. Additionally, our results clearly contrast with those recently reported from other temperate waters environments (e.g. Mediterranean Sea) where the role of fishes and a wide variety of marine macroinvertebrates have been recently highlighted as contributors to determining the structure of erect fleshy macroalgal assemblages (Sala, 1996; Ruitton et al., 2000).

In conclusion, *Diadema antillarum* maintains low macroalgal coverage and has therefore a strong impact on the structure of the shallow phytobenthic populations of the Canarian Archipelago. This fact indicates a strong interaction between *D. antillarum* and macroalgae, embedded in a majority of negligible effects of others herbivorous species (Paine, 1992).

Several reasons may explain the presence of extensive urchin barrens along the subtidal rocky-substrates of the Canarian Archipelago. Firstly, overexploitation of inshore demersal fish resources (Bortone et al., 1991; Falcón et al., 1996), which in turn has been considered as one of the main explanations to the high abundance recorded for sea-urchins at different latitudes (Vukovic, 1982; Verlaque, 1987; Francour, 1994; Sala & Zabala, 1996; McClanahan & Sala, 1997; Sala et al., 1998; Babcock et al., 1999; Pinnegar et al., 2000; Jackson, 2001; Shears & Babcock, 2003). Secondly, the large macroalgal grazing daily rates of the voracious sea-urchin genera *Diadema* (0.5–0.7 g dw ind^{-1} d^{-1}) in comparison with other temperate-waters echinoid species, such as *Paracentrotus lividus* (0.1–0.3 g dw ind^{-1} d^{-1}; Ruitton et al., 2000) or *Strongylocentrotus droebachiensis* (0.02–0.48 g dw ind^{-1} d^{-1}; Larson et al., 1980). Finally, an additional explanation may be the low primary production in shallow waters around the Canarian Archipelago coastlines. The oceanographic conditions off the Canary Islands (the surrounding waters are oceanic and oligotrophic, Basterretxea & Arístegui, 2000) could therefore reflect the lack of productivity necessary to develop a complex ecological set of herbivorous.

Acknowledgements

Research was economically supported by the Spanish "Ministerio de Medio Ambiente" in the framework of the 'Canarias, por una costa viva' project (www.canariasporunacostaviva.org) in collaboration with WWF-ADENA. We gratefully thank O. Bergasa, T. Sánchez, A. Iglesias, A. López, N. Rodriguez, A. Del Rosario, G. Herrera, R. Herrera and F. Espino for help with the underwater data collection.

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