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The Sea Urchin *Diadema antillarum* (Echinodermata, Equinoidea), algal cover and juvenile coral densities in La Parguera, Puerto Rico

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ABSTRACT

Grazing by the black sea urchin *Diadema antillarum* reduces algal cover and enhances coral recruitment. The overall goal of this project was to examine if there is a relationship between densities of *D. antillarum* with algal cover and abundance of juvenile corals. Population densities of the black sea urchin, juvenile coral abundances and algal cover were assessed along four 20m^2 transects at two depth intervals (0-3 and 3-8m) within each of two inner shelf coral reefs off La Parguera Natural Reserve (San Cristóbal and Enrique) in southwest, Puerto Rico using a 1m^2 quadrat (divided into 100 areas of 100cm^2, each area encompassing 1% of the quadrat). Juvenile coral densities were counted and identified to genus or species. Algal cover and composition was measured using each 1% square of the 1m^2 quadrat. Urchin population densities were significantly higher at 0-3m at the two sites studied. Population densities were higher at Enrique at 0-3m than at San Cristobal but at 3-8m *Diadema* was not seen at Enrique. A total of 30 juvenile corals belonging to eight different genera were found. Juvenile coral densities were higher at 3-8m at the two reef sites studied. Algal cover and composition was mainly composed by crustose coralline algae at 0-3m at both reef sites. Macroalgal cover was low at both reefs. The results of this study suggest that densities of coral recruits at inner shelf reefs in La Parguera, Puerto Rico are driven mainly by differences in habitats (depth).

KEY WORDS

Coral recruitment, abundance, *Diadema antillarum*, densities, composition, correlation.

RESUMEN

El pastoreo del erizo negro, *Diadema antillarum* reduce la cobertura de algas y provee sustrato disponible para el reclutamiento coralino. La meta principal de nuestro trabajo era examinar si existe una relación entre las densidades de *D. antillarum*, la cobertura de algas y el reclutamiento de corales. La densidad poblacional del *D. antillarum*, la abundancia de corales juveniles y la cobertura de algas fueron evaluados a lo largo de cuatro transectos de 20m^2, en dos intérvalos de profundidad (0-3m y 3-8m) en dos arrecifes de la zona interior de la Reserva Natural de La Parguera en el suroeste de Puerto Rico utilizando un cuadrante de 1m^2 (dividida en 100 áreas de 100cm^2, cada área abarcando 1% del cuadrante). La densidad de corales juveniles fue contada e identificada a género o especie. La cobertura y composición de algas fue medida utilizando cada cuadro pequeño representando 1% del cuadrante de 1m^2. La densidad poblacional de *D. antillarum* fue significativamente diferente en 0-3m de profundidad en ambos lugares. Dichas densidades fueron más altas en Enrique en 0-3m de profundidad. Sin embargo en 3-8m no fueron encontrados los erizos en dicho arrecife. Un total de 30 corales juveniles pertenecientes a ocho géneros diferentes fueron encontrados. La densidad de los corales juveniles fue mayor en 3-8m en ambos lugares. La cobertura y composición de algas fue dominada por algas crustosas coralinas de 0-3m en ambos arrecifes. La cobertura de macroalgas fue baja en ambos arrecifes. Nuestros resultados sugieren que las densidades de corales juveniles en arrecifes de la zona interior de La Parguera son guiados mayormente por diferencias en hábitats (profundidad).

PALABRAS CLAVE

Reclutamiento coralino, abundancia, *Diadema antillarum*, densidades, composición, correlación.

One of the most studied grazers in coral reef ecosystems is the black sea urchin *Diadema antillarum* (Philippi, 1845). *Diadema antillarum* was distributed from the Gulf of Mexico, throughout the Caribbean, Surinam and Brazil in South America, northward to Bermuda and eastward to the Azores, Madeira and Cape Verde Islands and the Gulf of Guinea in western Africa (Carpenter, 1997; Atrill & Kelmo, 2007). *Diadema antillarum* is omnivorous, preferring to feed on algal turfs but ingesting other sessile invertebrates (Randall, Schroeder & Starck, 1964; Carpenter, 1981; Weil, Losada & Bone, 1984). This urchin usually populates holes and crevices, emerging before sunset to forage during nighttime. Higher population densities used to be found in shallow depths (0-3m) (Randall et al., 1964; Vicente & Goenaga, 1984; Carpenter, 1984, 1997; Weil et al., 1984, Weil, Torres & Ashton, 2005; Lugo-Ascorbe, 2004). Several small juveniles and species of fishes get shelter on the long spines of *Diadema* (Vicente & Goenaga, 1984) as well as some invertebrates such as copepods, mysids, amphipods, shrimps, crabs (Randall et al., 1964) and larval stages of the Caribbean spiny lobster *Panulirus argus* (Vicente & Goenaga, 1984). In 1983, a mass mortality caused by an unknown pathogen wiped out approximately 99% of *D. antillarum* in the wider Caribbean (Lessios, 1988). However, recent studies have suggested that two decades after the massive mortality, *Diadema* populations are slowly recovering (Carpenter & Edmunds, 2006; Edmunds & Carpenter, 2001; Weil et al., 2005; Martin-Blanco et al., 2010).

Grazing by *D. antillarum* and coral recruitment

Many studies have focused on the effects of grazing by *D. antillarum* on coral reef communities (Ogden et al., 1973; Sammarco, 1980, 1982; Carpenter, 1981, 1984, 1986, 1997; Hay, 1984; Foster, 1987; Hughes, Keller, Jackson & Boyle, 1987; Hughes, 1989; Williams & Carpenter, 1997; Edmunds & Carpenter, 2001; Williams & Polunin, 2001; Carpenter & Edmunds, 2006; Furman & Heck, 2009). The direct effects of grazing by *D. antillarum* are: (1) reduction of algal biomass, (2) enhancement of primary productivity rates on algal turf communities, (3) shifts of algal community composition and diversity, and (4) mortality of recruits and small juveniles of sessile marine invertebrates (Ogden et al., 1973; Sammarco, 1980; Carpenter, 1981, 1984, 1986, 1997; Foster, 1987; Hughes et al., 1987; Hughes, 1989 Williams & Carpenter, 1997; Williams & Polunin, 2001; Edmunds & Carpenter, 2001; Carpenter & Edmunds, 2006). After the mass mortality of *Diadema* in 1983, algal community structure on many affected reefs changed from algal turfs encompassed from many filamentous species and crustose coralline algae to a community dominated by macroalgal species (Lessios, 1988). Higher densities of *Diadema* are associated with a reduction in macroalgal cover and increased abundance of juvenile corals (Edmunds & Carpenter, 2001; Myhre & Acevedo-Gutiérrez, 2007). Sammarco (1980) suggested that high densities of *Diadema* could cause intense grazing, damaging juvenile corals and reducing coral recruitment, while in the absence of these sea urchins; corals could not compete with algae for substrate. As a result, intermediate densities of *Diadema* were suggested as best in regulating the abundances of corals and algae. Decreased survivorship of juvenile corals in the absence of grazing is due to overgrowth, shading and abrasion by macroalgae, smothering by sediment that accumulates on elevated algal biomass or a combination of these effects (Edmunds & Carpenter, 2001).

Effects of grazing by *D. antillarum* on algal community structure have been studied in different sites in the wider Caribbean, Belize, Cuba, Panama, Grand Cayman and Jamaica, among others (Ogden et al., 1973; Sammarco, 1980, 1982; Foster, 1987; Edmunds & Carpenter, 2001; Williams & Polunin, 2001; Carpenter & Edmunds, 2006). However, studies concerning *D. antillarum* in Puerto Rico have concentrated on determining their abundances, distribution, size structure, evaluation of potential interaction between the populations characteristics, spatial heterogeneity of various sites and habitats and evaluation of reproductive traits (Vicente & Goenaga, 1984; Lugo-Ascorbe, 2004; Weil et al., 2005; Williams, García-Sais & Capella, 2009; Williams & García-Sais, 2010; Williams, Yoshioka & García-Sais, 2010; Williams, García-Sais &Yoshioka, 2011). However, none have assessed the potential relationship between the urchin densities and coral recruitment. Coral reefs in La Parguera encompass a substantial building block in the natural resources of Southwestern Puerto Rico. These reefs are extremely important for the local economy (i.e., tourism, commercial and recreational fishing activities) and because of the high biodiversity they sustain (Ballantine et al. 2008)

Studying the *D. antillarum* densities and exploring a potential co-variation with algal cover and juvenile coral abundances can help in the ongoing worldwide effort to increase our understanding about the process of herbivory in coral reef systems. The aim of this study is to determine if there is any relationship between *D. antillarum* population densities, algal cover and composition and juvenile coral abundances at two depth intervals (0-3; 3-8m) at two fringing, inner shelf coral reefs in La Parguera, Puerto Rico. This will show at which depth (0-3m or 3-8m) *Diadema* can help in the regulation of these processes within each reef.

METHODOLOGY

Study site

The south coast of Puerto Rico is characterized by lower wave energy and a wider insular shelf than the north coast (García, Morelock, Castro, Goenaga & Hernández-Delgado, 2003). It also features embayments and submarine canyons (Acevedo & Morelock, 1988). Fieldwork of this study was conducted in two coral reefs off La Parguera Natural Reserve, in the southwest coast of Puerto Rico. La Parguera is a dry and warm area with a yearly mean surface water temperature of 28,4°C (average maximum and minimum, 31,8°C and 22,5°C respectively) and the average surface salinity is 35,2ppt (García, Schmitt, Heberer & Winter, 1998). The insular shelf of La Parguera extends 8-10km offshore. Abundant coral reefs and adjacent marine ecosystems such as seagrass beds dominated by *Thalassia testudinum* and mangrove forests dominated by *Rhizophora mangle* and fringe coral reefs encompass La Parguera. Reefs in La Parguera are aligned east to west and the insular shelf is divided into inner shelf, mid shelf and shelf edge reefs (García et al., 1998). Two inner shelf reefs were selected as the study areas: San Cristóbal Reef and Enrique Reef (Fig. 1). These sites were selected due to the abundance of *Diadema* in both sites (Lugo-Ascorbe, 2004; Weil et al., 2005). Furthermore, these two reefs have similar reef structure in both depth ranges analyzed.

Enrique Reef (17°56,658N; 67°02,213W) is a partially exposed fringing reef located 1,5 km off shore. The outer reef reaches a long shallow platform with mangrove keys and sea grass beds in an east-west direction. The reef platform is short (30-50m) with a 15m drop and a community structure of corals and octocorals. San Cristóbal Reef (17°56,450N; 67°04,659W) is a partially exposed fringing reef, with an extended platform and a drop of 20m. It is located approximately 1km off shore. Some species present are: *Diploria clivosa, D. strigosa, D. labyrinthyformis, Acropora prolifera, Montastraea annularis, Porites astreoides* and *Favia fragum*.

Experimental design

All the surveys were completed between August and December, 2009. *Diadema antillarum* individuals were counted within a $1m^2$ quadrat along four transects parallel to shore ($20m^2$) on each depth intervals (0-3 and 3-8m).

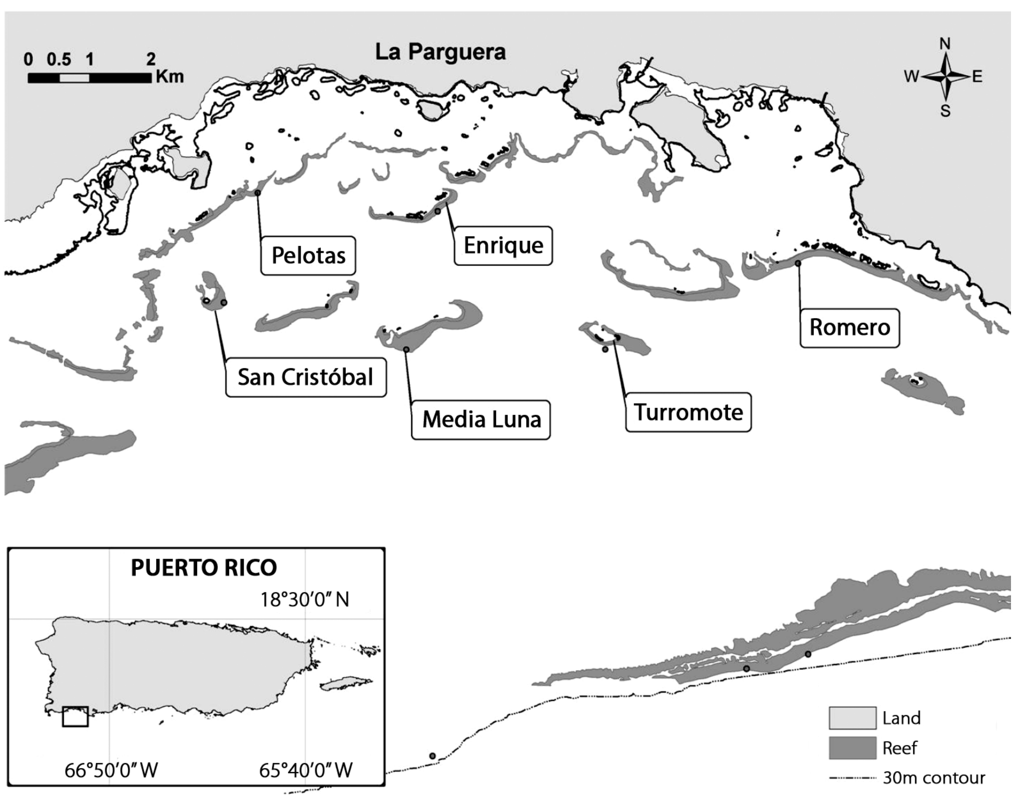

FIG. 1. Study sites at La Parguera, Puerto Rico.

The quadrat was deployed randomly ten times along each of the four transects (n=40) in each of the 2 depth intervals (n=80) and used to estimate urchin densities. Urchins were counted in all places found (holes, rock crevices and pavement) during daylight.

Juvenile coral densities were measured using the same 1m^2 quadrat but divided it into 100 areas of 100cm^2, each area encompassing 1% of the sampling area. Depending on the species and its average size/area, a condition of minimum size was applied. For instance, colonies less than 5cm in diameter for large-sized species (*Montastraea* spp., *Colpophyllia natans*, *Diploria* spp., etc.) and less than 2cm for medium-small-sized colonies (*Siderastrea* spp., *Porites* spp., etc.) were considered juvenile corals not confusing this criterion with ramets resulting due to partial mortality of colonies. Percent algal cover (i.e., macroalgae, filamentous turf algae and crustose coralline algae or CCA) was determined by using the same 1m^2 quadrat used to collect juvenile coral densities.

Data did not fulfill the assumptions of parametric tests. A Permutational Analysis of Variance (PERMANOVA) was used to test differences on *Diadema* densities, juvenile coral densities and coral cover and composition between depth intervals and reef sites. PERMANOVA is a novel statistical approach for testing the concurrent response of one or more variables to one or more factors in an ANOVA experimental design of any distance measurement by using permutation methods (Anderson, 2001). Spearman's correlation analyses were used to look for relationships between algal cover and juvenile coral and *D. antillarum* densities.

RESULTS

Diadema antillarum population densities

Diadema antillarum population densities were significantly higher at 0-3m than at 3-8m at the two sites studied (PERMANOVA; p=0,0002). Population densities were higher at Enrique at 0-3m (2,35 ± 0,63ind./m^2) than San Cristobal (1,75 ± 0,49 nd./m^2) but at 3-8m *Diadema* was not seen at Enrique (Fig. 2). However, significant differences between sites were not found (PERMANOVA; p= 0,2184).

Juvenile coral densities

A total of 30 juvenile corals belonging to eight different genera were found. Juvenile coral densities were significantly higher at 3-8m than at 0-3m at the two sites studied (PERMANOVA; p=0,0037). San Cristóbal showed higher juvenile coral densities at 3-8m than at 0-3m (0,35±0,04col./m^2 and 0,175±0,03col./m^2 respectively). Same pattern was observed for Enrique (0,075 ± 0,03col./m^2 at 0-3m and 0,225 ± 0,03 col./m^2 at 3-8m) (Fig. 3).

Significant differences among juvenile coral densities were not found when comparing both sites (PERMANOVA; p=0,2747). *Siderastrea* sp. and *Montastraea* sp. were the dominant scleractinian recruits between the two depths studied (Fig. 4).

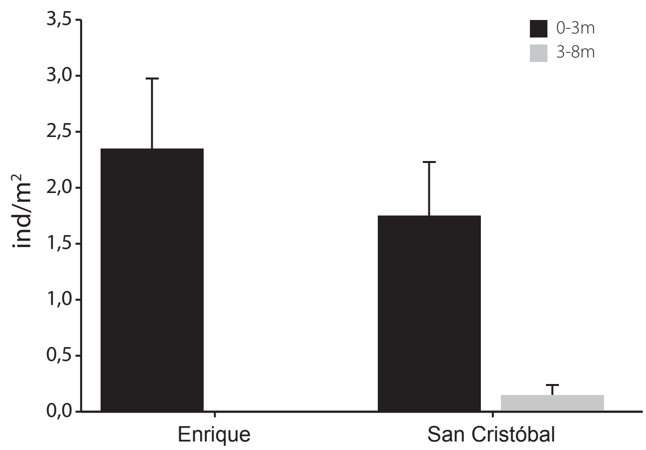

FIG. 2. Mean (+SE) of *Diadema antillarum* population densities at the two sites studied and depth intervals.

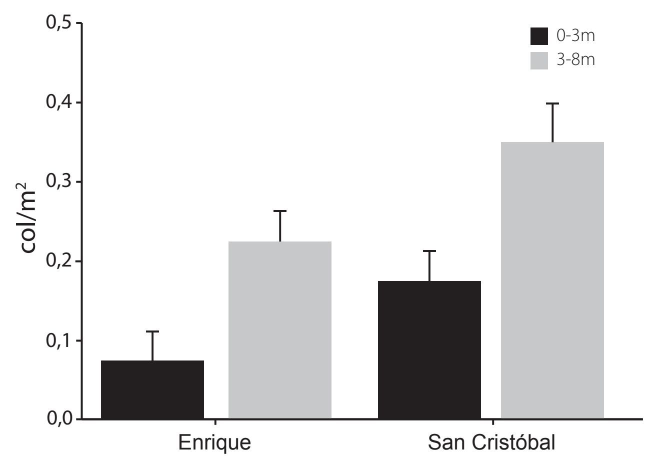

FIG. 3. Mean (+SE) juvenile coral densities at the two sites studied.

Algal cover and composition

Algal cover and composition was mainly composed by crustose coralline algae (CCA) at 0-3m and turf algae at 3-8m within both sites (Fig. 5). Macroalgal cover was mainly composed of *Dyctiota* sp., *Halimeda opuntia*, *H. incrasata* and *Galaxaura* sp. and was not significantly different when comparing sites (PERMANOVA; p=0,0610) nor depths (PERMANOVA; p=0,1070). CCA (i.e. *Porolithon* sp.) showed significant differences between depths (PERMANOVA; p=0.04).

Spearman's correlation analyses

Correlation analysis between *D. antillarum* densities and juvenile coral densities were not significant at 0-3m (Spearman's R=0,05; p=0,60) nor at 3-8m (Spearman's R=-0,03;p=0,75). However, a significant negative correlation was found when comparing *D. antillarum* densities and macroalgal cover at 0-3m (Fig. 6). Moreover, a significant positive correlation was found between *D. antillarum* densities and CCA cover at 0-3m (Fig. 7). Also, a significant negative correlation was found between *D. antillarum* densities and turf algae cover at 0-3m (Fig. 8).

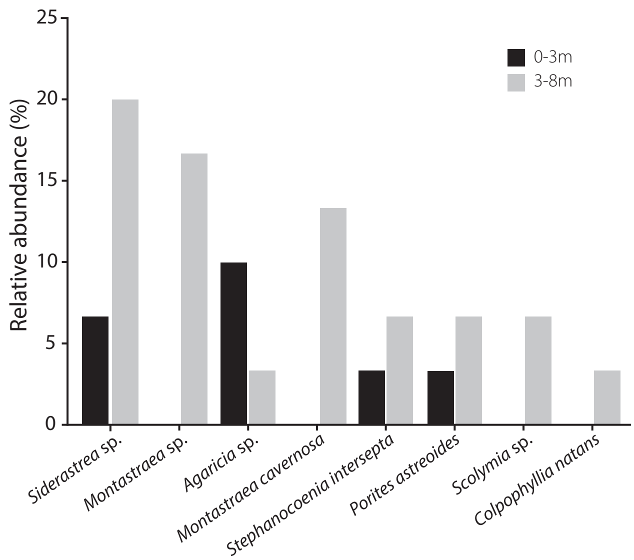

FIG. 4. Relative abundance (%) of scleractinian recruits between the two depths studied.

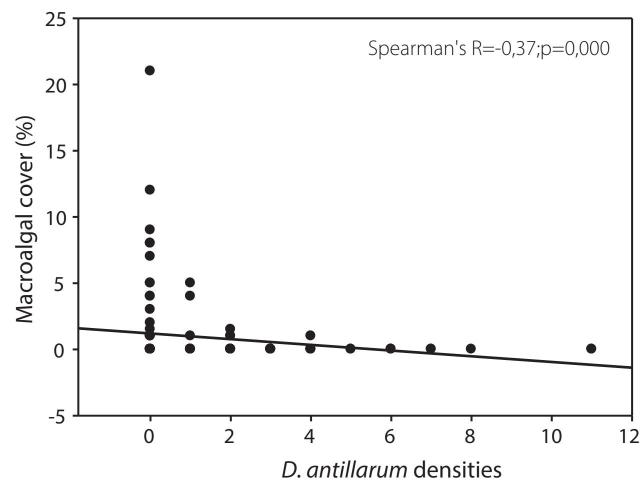

FIG. 6. Spearman's R correlation analysis between *D. antillarum* densities and macroalgal cover at 0-3m.

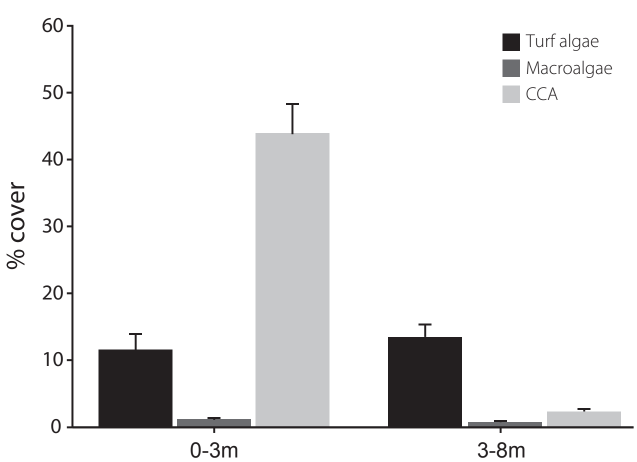

FIG. 5. Algal cover (%mean±SE) between the two depths studied.

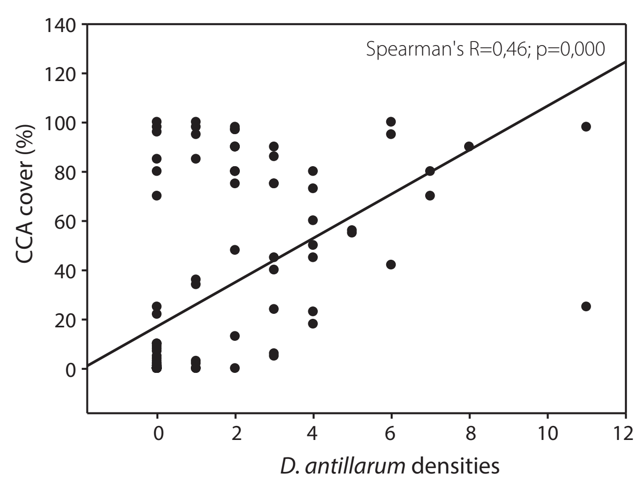

FIG. 7. Spearman's R correlation analysis between *D. antillarum* densities and CCA cover at 0-3m.

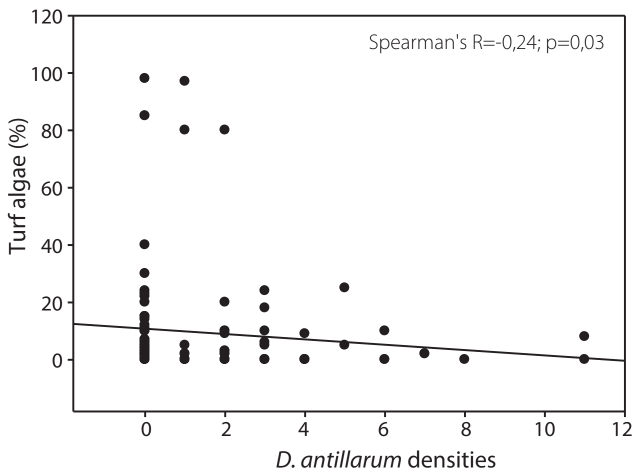

FIG. 8. Spearman's R correlation analysis between *D. antillarum* densities and turf algae cover at 0-3m.

DISCUSSION

Different studies have shown that *D. antillarum* can help in the regulation of coral reef communities (Ogden et al., 1973; Sammarco, 1980, 1982; Carpenter, 1981, 1984, 1986, 1997; Foster, 1987; Hughes et al. 1987; Hughes, 1989; Williams & Carpenter, 1997; Edmunds & Carpenter, 2001; Williams & Polunin, 2001; Carpenter & Edmunds, 2006). Moreover, it has been suggested that in some places in the Caribbean, *Diadema* densities can regulate the recruitment of corals by providing macroalgal free substrate so that coral recruits can settle faster (Edmunds & Carpenter, 2001; Carpenter & Edmunds, 2006).

The present study shows contrasting results within the two inner shelf reefs in La Parguera, Puerto Rico. This contrast is observed when comparing densities of *Diadema* and juvenile coral densities at the two depths studied. At 0-3m *Diadema* densities (2,35ind./m^2 for Enrique and 1,75ind./m^2 for San Cristóbal) were higher than 3-8m (0 for Enrique and 0,15ind./m2 for San Cristóbal) at both reefs. However, juvenile coral densities were higher at 3-8m (1,75col. /m^2 for San Cristóbal and 0,225 col./m^2 for Enrique) at both reefs.

The positive but not significant relationship between *D. antillarum* densities and juvenile coral densities suggests that at both depths (0-3m and 3-8m) juvenile coral densities are driven by other ecological parameters and not by the presence or absence of *D. antillarum*. Other parameters that can affect coral recruitment can be depth, rugosity of the substrate, competition and local and regional atmospheric conditions (Irizarry-Soto, 2006). At 0-3m in both reefs, the substrate was composed primarily of skeletons of *Acropora palmata* which was covered mainly by CCA. At this habitat (depth) we also found a significant positive correlation between CCA and *D. antillarum* densities. This is consistent with past studies that have suggested that *Diadema* foraging favors the growth of CCA and increases coral settlement (Edmunds & Carpenter, 2001; Ruiz-Ramos et al., 2011). However, *Agaricia* sp. was the only coral species to show higher juvenile coral densities at 0-3m than 3-8m. This suggests that *D. antillarum* foraging may be favoring the settlement of only certain coral species at 0-3m. However, further research needs to be done to sustain this hypothesis.

At 3-8m at both sites, the substrate was mainly composed by turf algae (5,7 and 21,9% for Enrique and San Cristóbal, respectively) although a zoanthid (e.g., *Palythoa caribbaeorum*) and adult scleractinians were the main competitors.

Macroalgal cover was low at both reefs. At 0-3m the significant negative correlation between macroalgal cover and urchin densities suggests that *D. antillarum* appears to control the abundances of this type of algae at this depth range. This finding concurs with past studies in the Caribbean (Edmunds & Carpenter, 2001). However, our results on juvenile coral densities were lower at 0-3m than 3-8m. This means that competition for space by juvenile corals and macroalgae was not necessarily a factor driving the settlement of the juvenile scleractinian community at these inner shelf reefs. *Diadema antillarum* densities were not a factor either since higher juvenile coral densities were found at 3-8m where none to low *Diadema* densities were found and no significant correlation found. In our study, higher diversity of juvenile corals were found in 3-8m, which is considered an intermediate depth range in these reefs (Irizarry-Soto, 2006). This concurs with past studies in La Parguera where the highest juvenile coral diversity was found at intermediate depths (Irizarry-Soto, 2006). Furthermore, the high abundance of the dominant juvenile scleractinians found in this study (*Siderastrea* sp. and *Montastrea* sp.) is consistent with past studies at inner shelf reefs in La Parguera (Irizarry-Soto, 2006). Moreover, this study showed that juvenile *Montastraea* sp. individuals are likely to be observed between 3-8m (intermediate habitats) under conditions that needs to be elucidated and may help to understand *Montastraea* sp. dynamics, especially when these species are now considered to be listed as endangered.

None to low juvenile coral densities at 0-3m at both sites may be due to extreme wave action and to more vulnerability and exposure to hurricanes and storms which can affect the larval settlement. Also, highest densities of *Diadema* concentrating at 0-3m at both sites may be a factor affecting coral recruits due to the intense grazing that these urchins can sustain (Sammarco, 1980). However, correlation between the two factors was not significant, probably due to the low numbers when entering juvenile coral densities in the equation. The significant negative correlation between *Diadema* densities and turf algal cover suggest that *Diadema* may be maintaining at a low cover the turf algae at 0-3m by their intense grazing on this type of algae (Carpenter, 1986). Ruiz-Ramos and others (2011) mention that areas with higher abundance of corals provide higher refuge for urchins but less algae to feed on. In our study, higher abundance of corals (pers. obs.), none to low *D. antillarum* densities and higher juvenile coral densities were found at 3-8m.

Our results suggest that habitat (depth) may be driving juvenile coral densities at inner shelf coral reefs in La Parguera. At this depth coral recruitment is probably higher irrespective of the presence of *D. antillarum*. Further research needs to be done on other zones (mid shelf and shelf edge) in La Parguera to see if there is any relationship between *D. antillarum* densities and juvenile coral densities at different habitats (depths) and over time.

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