

Spatio-temporal variability in a key herbivore, the long-spined black sea urchin (*Diadema antillarum*, Echinodermata: Echinoidea) in the Canary Islands

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Spatio-temporal variability in the population structure of long-spined black sea urchin, *Diadema antillarum*, was investigated at two islands (Gran Canaria and Tenerife) in the Canarian Archipelago over a year. The mean abundance of *D. antillarum* across all counts was 2.70 ± 0.07 ind m^{-2} (mean \pm SE, $N=1440$), while the mean biomass was 105.76 ± 3.75 g m^{-2} (mean \pm SE, $N=1440$). Abundances and biomasses of *D. antillarum* differed consistently between vegetated and unvegetated bottoms; however, locations within each habitat at each island fluctuated following different trends. For the overall study, mean densities and biomasses in the barren locations varied between 3.36 – 6.97 ind m^{-2} and 93.76 – 405.13 g m^{-2} , respectively; while mean densities and biomasses in the algal stand locations varied between 0 – 0.33 ind m^{-2} and 0 – 7.34 g m^{-2} , respectively. Striking differences existed in the size-structure among locations; however, larger size-classes (test diameter > 3.5 cm) were present at all locations, and usually dominated in terms of abundance. The majority of individuals in the algal stands were large-sized, probably as a result of the high abundance of the most palatable food. In contrast, small-sized individuals (test diameter < 1.5 cm) only occurred in the barren habitat, suggesting that recruitment of *D. antillarum* could be favoured by the presence of high densities of congeners, as a way to decrease the risk of predation.

INTRODUCTION

A common feature of the population biology of sea urchins is fluctuations in local abundance and, consequently, variability in the effects of grazing on the structure of vegetated communities (Ehner & Vadas, 1990). Such fluctuations occur both through changes in the behaviour of adults, which move into new areas of reef (Vadas et al., 1986; Lozano et al., 1995; Sala et al., 1998; Chiappone et al., 2002; Dumont et al., 2004; Gagnon et al., 2004), and also by variations in recruitment to existing populations (Lessios, 1988; Andrew & Underwood, 1989; Sala et al., 1998; Balch & Scheibling, 2000; Lawrence, 2001; Hereu et al., 2004).

The long-spined black sea urchin, *Diadema antillarum* (Philippi), is a gregarious echinoid that occurs in almost all marine habitats in the shallow subtidal across the warm-temperate waters of the eastern Atlantic, from Madeira to the Gulf of Guinea. In this region, this species plays a key role in organizing and structuring subtidal rocky reefs (Alves et al., 2001; Tuya et al., 2004), since it is directly involved in the transformation of large areas previously covered by erect algae to 'barrens' or unvegetated substrates.

In general, water turbulence considerably inhibits the presence of *D. antillarum* within the first metres of the subtidal (Alves et al., 2001; Tuya et al., 2005). As a result, the distribution of benthic communities along a depth gradient axis shows a clear vertical zonation pattern. Within the shallowest photophilic zone, extensive stands

of algal assemblages make up the dominant community (hereafter called 'algal stands') (Tuya et al., 2005), with low densities of major grazers such as sea urchins. Intensive grazing by hyperabundances of *D. antillarum* produces abrupt boundaries between these 'shallow water' algal stands and areas devoid of vegetation, resulting in the existence of barrens extending in depth until the soft bottom habitat (Tuya et al., 2005).

Previous studies describing the significant role *Diadema antillarum* plays in organizing rocky reefs in the eastern Atlantic have used correlative approaches that only incorporated spatial variability. Little attention has been given to temporal variations in the structure of *D. antillarum* populations. The goal of the present paper was to investigate spatio-temporal variability in population structure (abundances, biomasses and sizes) of the long-spined black sea urchin, *D. antillarum*, at two islands of the Canarian Archipelago (Gran Canaria and Tenerife) over a year. We hypothesized that: (1) differences in abundances, biomasses and size-structure between vegetated and unvegetated shallow rocky bottoms were consistent throughout the year; and (2) variability through time was consistent at two locations within each type of habitat at each island.

MATERIALS AND METHODS

Study area and sampling design

The study was carried out on rocky bottoms between 2 and 10 m depth at the islands of Gran Canaria and

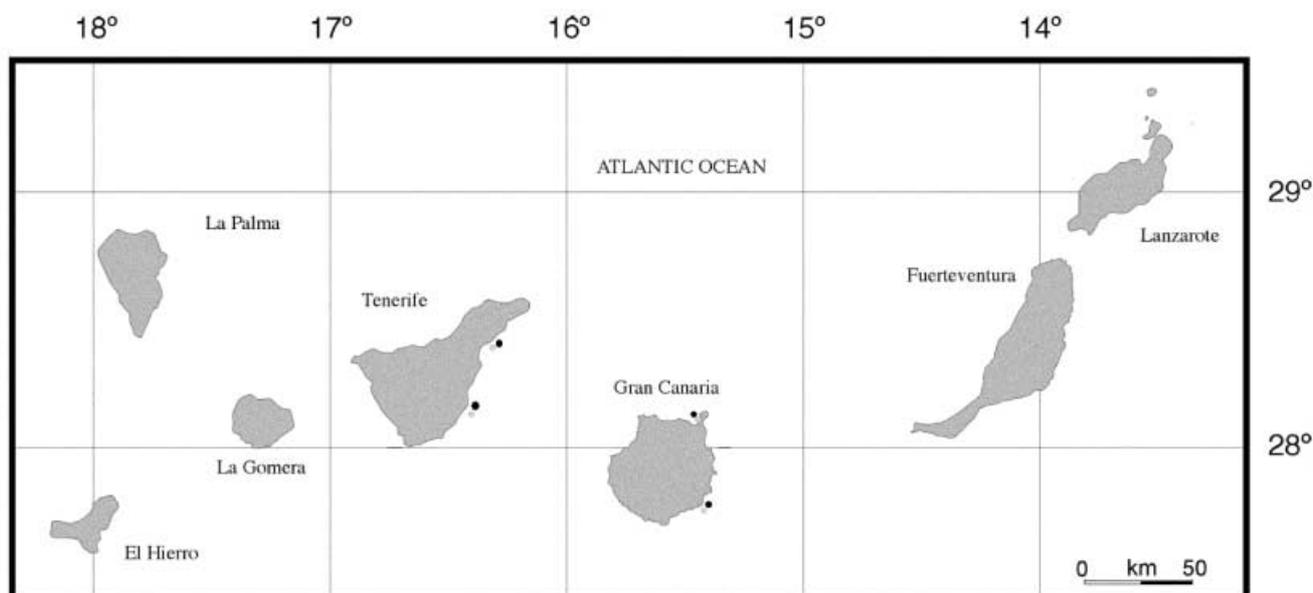


Figure 1. Map of the study area showing sampling locations at each island. Black circles, barrens; grey circles, algal stands.

Table 1. Analysis of the effects of Times (random), Habitats (barrens vs algal stands, fixed), and Locations (random and nested within habitats), on the mean abundances and biomasses of long-spined black sea urchins, *Diadema antillarum*, at each surveyed island.

	Mean abundances				Mean biomasses			
	Gran Canaria		Tenerife		Gran Canaria		Tenerife	
	MS	F	MS	F	MS	F	MS	F
Times=T	1.15	0.33*	0.79	2.39*	4.43	1.44*	27.32	1.86*
Habitats=H	530.18	No test	230.15	No test	3505.95	No test	8517.91	No test
T×H	0.25	0.44	0.79	2.39	2.22	0.72	27.32	1.86
Loc (H)	0.37	0.66	22.29	66.97*	1114.80	37.23*	244.97	16.63*
Loc (H)×T	0.56	2.00*	0.33	1.59*	3.08	1.16*	14.72	2.13*
Residual	0.28		0.20		1.92		6.90	

*, $P < 0.01$; MS, mean squares; F, F-ratios.

Tenerife (Canarian Archipelago, 28°N), from May 2004 to May 2005. Sea-water temperature ranged between 22 and 23°C in summer, and between 18 and 19°C in winter. At each island, we selected two locations, 10s of km apart (Figure 1), within both algal stands and barren habitats. All locations were outside areas closed to fishing, and were selected on the basis of accessibility. Due to logistical constraints, the sampling periodicity differed between islands. We sampled locations in Gran Canaria twice per month (a total of 24 sampling times); whereas sampling in Tenerife occurred approximately monthly (a total of 13 sampling times). Dates of sampling varied among months to optimize sampling conditions (e.g. lack of swell). For each island, our sampling design tested the effect of: (i) the date; (ii) the type of habitat (vegetated vs unvegetated rocky bottoms) on the population structure of the sea urchin *Diadema antillarum*; with (iii) two replicated locations within each habitat and island.

Data collection and data analysis

All *Diadema antillarum* individuals were counted and their sizes were measured by SCUBA divers in ten replicate 1×1 m (1m²) quadrats at each date and location within each type of habitat. Quadrats were haphazardly laid out 10s of metres apart. The sizes (test diameter without spines) were measured using calipers. A slight overestimation of the test diameter was unavoidable, due to the underwater working conditions and the long spines, which made the use of calipers even more difficult than with other sea urchins (e.g. *Paracentrotus lividus*, Turón et al., 1995). The size of the sampling unit and the replication used were selected based on previous studies (Tuya et al., 2004), and preliminary surveys at the specific locations. Biomasses were further calculated using our own test diameter–weight relationship. Individuals were grouped into four size-classes for further analysis (class 1:

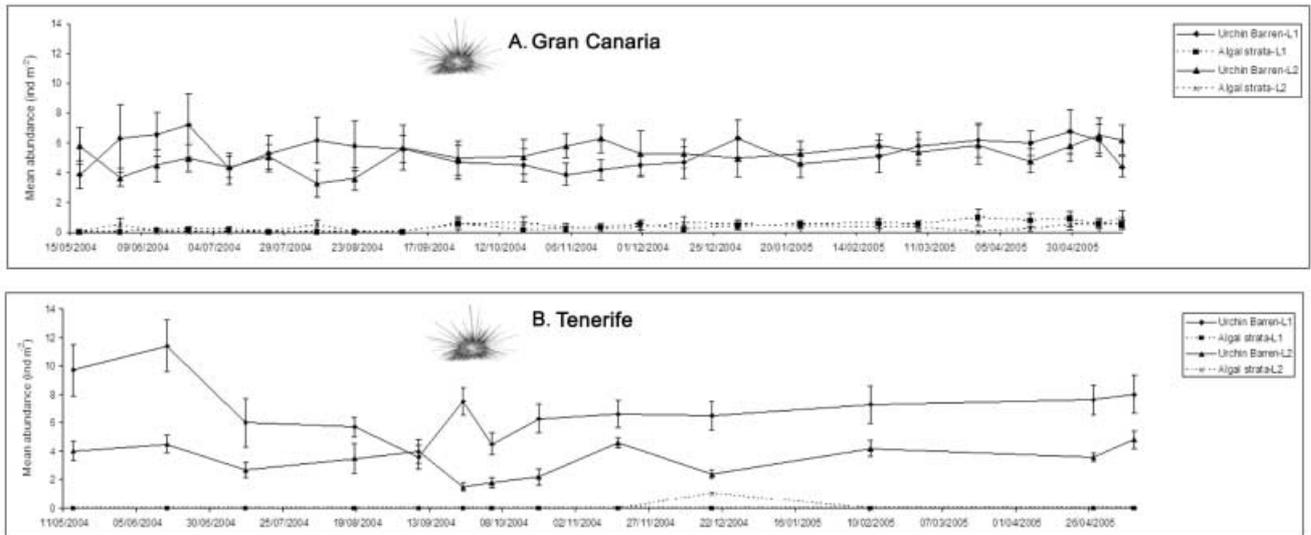


Figure 2. Mean abundances of *Diadema antillarum* at each location within each habitat and island throughout the study. Error bars are SE of mean values ($N=10$).

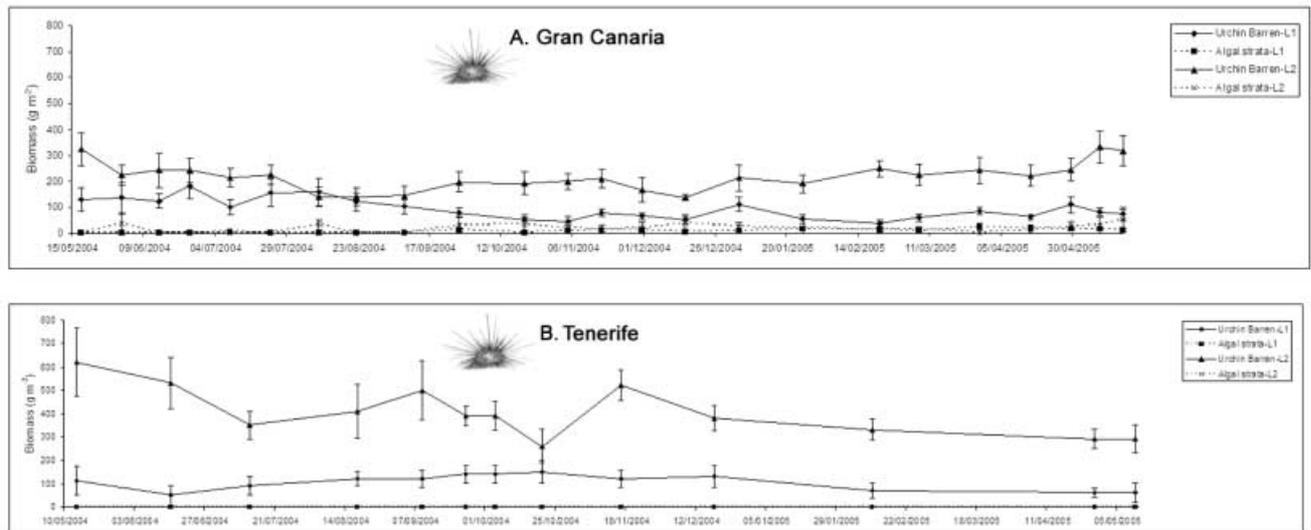


Figure 3. Mean biomasses of *Diadema antillarum* at each location within each habitat and island throughout the study. Error bars are SE of mean values ($N=10$).

< 1.5 cm test diameter without spines, class 2: 1.5–3.5 cm, class 3: 3.5–5.5 cm, and class 4: > 5.5 cm) (Tuya et al., 2004). We considered that small-sized urchins (size-class 1) were recently recruited individuals (hereafter termed ‘juveniles’), with a maximum age of 15 weeks in the benthos since settlement based on Bak’s (1985) estimation of the growth rates of *D. antillarum* recruits.

Total abundances and biomasses for each island were analysed by analysis of variance (ANOVA), testing for temporal consistency in differences between the two types of habitat, and between the locations sampled within each habitat, separately for each island. The model therefore incorporated the following factors: (1) ‘Times’ (=‘dates’ random factor with 24 levels for Gran Canaria, and 12 levels for

Tenerife); (2) ‘Habitats’ (fixed factor with 2 levels, and orthogonal to the previous factor); and (3) ‘Locations’ (random factor nested within ‘Habitats’, with 2 levels). Before analysis, Cochran’s test was used to check for homogeneity of variances. Transformations ($\sqrt{\quad}$, log, arcsine) did not render variances homogeneous for abundances and biomasses recorded at Tenerife (Cochran’s test, $P < 0.01$), so the significance level was set at $\alpha = 0.01$ instead of 0.05, as ANOVA is robust to heterogeneity of variances, particularly for large balanced experiments (Underwood, 1997).

Finally, size–frequency diagrams were plotted for each time and location within each type of habitat and island to assess the spatial and temporal differences in the population structure.

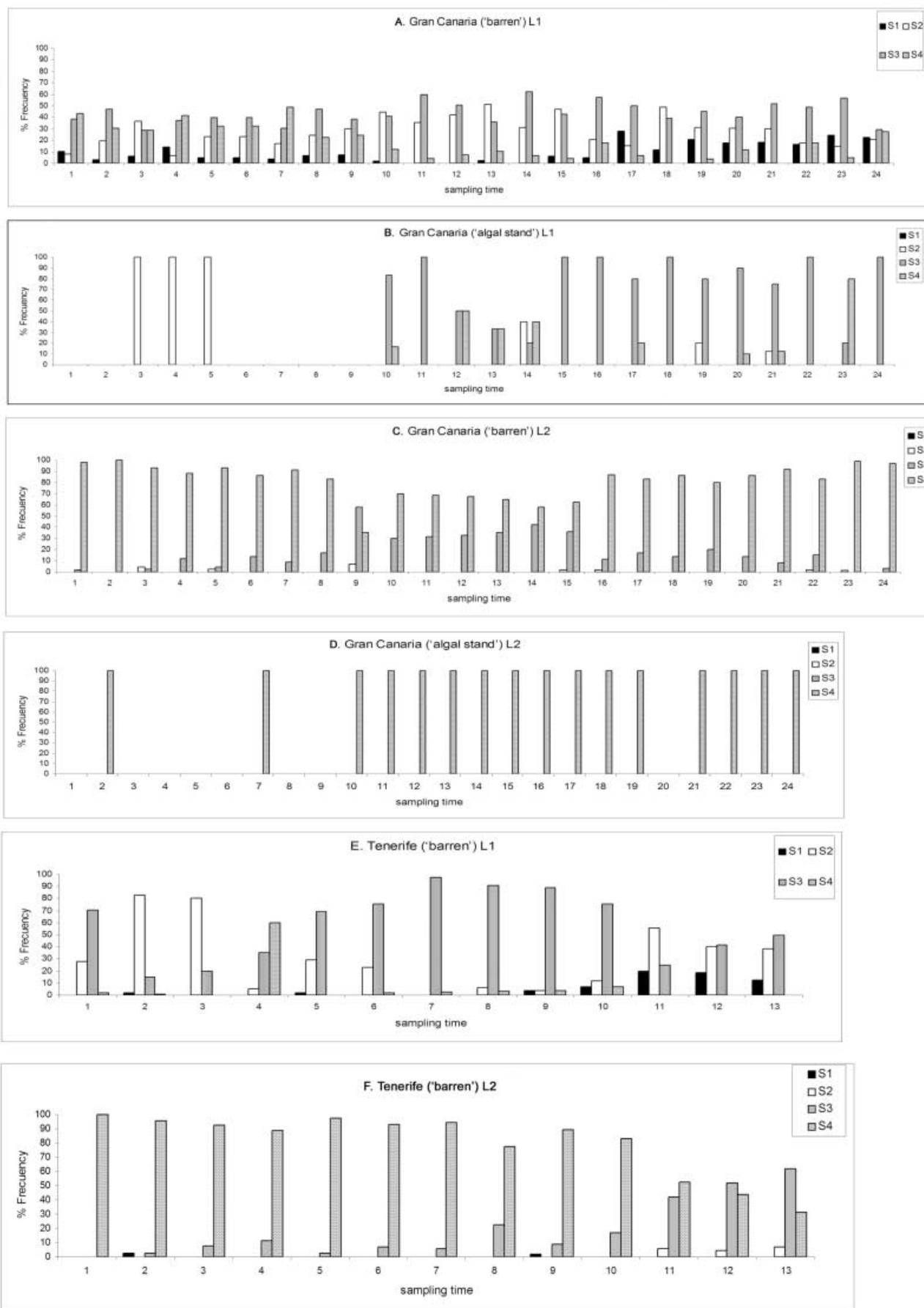


Figure 4. Size–frequency distributions of *Diadema antillarum* at each location within each habitat and island throughout the study. Class 1, < 1.5 cm test diameter without spines; class 2, 1.5–3.5 cm; class 3, 3.5–5.5 cm; and class 4, > 5.5 cm.

RESULTS

The mean density of *Diadema antillarum* for the study (all counts pooled) was 2.70 ± 0.07 ind m^{-2} (mean \pm SE, $N=1440$), which ranged between 0 and 6.97 ind m^{-2} per location. Similarly, the mean biomass of *D. antillarum* for the entire study was 105.76 ± 3.75 g m^{-2} (mean \pm SE, $N=1440$), which varied between 0 and 405.13 g m^{-2} per location.

Mean densities and biomasses of *D. antillarum* per date and location are shown in Figures 2 and 3, respectively. As indicated by ANOVA (Table 1), differences in the mean abundances and biomasses of *D. antillarum* between the two habitats (barrens vs algal stands) were consistent through time at both islands ('Time \times Habitats', $P > 0.01$, Table 1). Quantitatively, mean abundances and biomasses were ~ 17 and 13 times greater in the barrens compared to the algal stands, respectively, at Gran Canaria (Figures 2 & 3); whereas we did not find sea urchins at both locations within the algal stand habitat at Tenerife (Figures 2 & 3). Mean densities and biomasses per date in the barren locations varied during the 12-month survey between 3.36 – 6.97 ind m^{-2} and 93.76 – 405.13 g m^{-2} , respectively; while mean densities and biomasses per date in the algal stand locations varied between 0 – 0.33 ind m^{-2} and 0 – 7.34 g m^{-2} , respectively.

Although densities and biomasses of *D. antillarum* appeared consistent at each location throughout the survey (the factor 'Times' was non-significant as a 'main effect'), the two locations within each habitat and island fluctuated following different trends (Figures 2 & 3), as revealed by ANOVA ('Loc (H) \times Times', $P < 0.01$, Table 1). As a result, the differences between the two locations within each habitat and island were not consistent each time they were surveyed. Nonetheless, seasonality was not apparent in the fluctuations of the mean abundances and biomasses of this invertebrate at both islands (Figures 2 & 3).

There were striking differences in the sizes of *D. antillarum* among the six locations where it was found throughout the study (Figure 4). In all populations, the larger size-classes (sizes 3 and 4, test diameter > 3.5 cm) dominated in terms of overall abundance (Figure 4). At barren Location no. 1 at Gran Canaria, juveniles (size 1) were almost always present, suggesting that there was a smooth and regular recruitment at this location. The sizes of *D. antillarum* at this location contrasted to those at barren Location no. 2 at Gran Canaria, where there was no evidence of recruitment during the survey. The lack of juveniles in this population suggests that there had been little recruitment into the population for at least 1 y prior to the start of this study, based on Bak's (1985) growth rates. Similarly, barren Location no. 2 at Tenerife was dominated by large-sized individuals (size-class 4, test diameter > 5.5 cm), with a low presence of juveniles. In contrast, few individuals of size-class 4 were found at barren Location no. 1 at Tenerife throughout the study period. This location was dominated initially by individuals within size-class 2, and later by individuals within size-class 3. It is worth noting, moreover, that small-sized *D. antillarum* individuals (size 1, test diameter < 1.5 cm) were only recorded on the barren habitat. In all cases, however, the presence of juveniles showed an inconsistent

trend through time at each location where they appeared (Figure 4). The specimens detected in the algal stands locations belonged mainly to the large size-classes (3 and 4), with the exception of Location no. 1 at Gran Canaria where we observed a large proportion of individuals within size-class 2 at the beginning of our survey.

DISCUSSION

Our study provides evidence to suggest that differences in *Diadema antillarum* abundances and biomasses between vegetated (algal stands) and unvegetated (barrens) shallow rocky bottoms were consistent year-round. Mean abundances and biomasses of *D. antillarum* did not remain stable at each location within each type of habitat throughout the sampling programme; there were differences among months, but no trends were evident through time. In this sense, variability through time was not consistent between locations within each habitat and island, especially in the case of the barrens. Within barrens at each island, *D. antillarum* was not consistently more abundant at a specific location. As a result, there was significant variation in mean abundances and biomasses of *D. antillarum* over 12 months at the four barren locations. This result is similar to changes in mean abundances among successive months observed for other echinoid species in barren habitats (Andrew & Underwood, 1989; Benedetti-Cecchi et al., 1998). This fact may reflect the temporal effect of different processes operating at diverse temporal scales. We can only speculate on the nature of these factors driving the temporal dynamics of *D. antillarum* populations. Nonetheless, changes in abundances of sea urchins can be attributable to mortality, movements, and high levels of successful recruitment. In the present study, the latter explanation appears most probable in view of the fact that we recorded substantial numbers of juveniles (size-class 1) at almost all barren locations. In the Canary Archipelago, *D. antillarum* is almost-mature year-round (Garrido et al., 2000) and propagules are probably released throughout the entire year. Despite the occurrence of two main peaks of settlement over a 1 y period at some locations at the Canary Islands, planktonic larvae of this invertebrate can settle consistently through time in collectors above barren habitats (Hernández et al., 2004). As a result, frequent settlement events could help to explain the observation of differences among sampling times at each barren location; this pattern has been extensively recorded for other echinoid species (reviewed by Ebert, 1983; Balch & Scheibling, 2000). Observations of sea urchin populations need to span several decades, or even more, before such conclusions can be made (Elner & Vadas, 1990; Sala et al., 1998; Edmunds & Carpenter, 2001; Vanderklift & Kendrick, 2004).

In contrast to Gran Canaria, where some individuals were observed inhabiting the algal stand strata, we did not register *D. antillarum* within this habitat in the two locations at Tenerife. The different 'architecture' of the algal species that dominated this habitat may be responsible for this discrepancy. The 'shallow water' algal stands in the two locations surveyed at Tenerife were dominated by large, frondose, coarsely-branched furoid species (mainly the genera *Cystoseira* and *Sargassum*); however,

foliose algae (principally *Dyctiota* spp. and *Lobophora variegata*) dominated the algal stands in the two locations surveyed at Gran Canaria. The wave-induced sweeping motion of large, canopy-forming, furoid algae likely restrict both sea-urchin movement and suitable space to graze in the Canarian Archipelago (Tuya et al., 2005), as do large brown macrophytes in temperate waters (Konar, 2000; Gagnon et al., 2004).

All populations of *Diadema antillarum* sampled were comprised mainly of large urchins: there was a peak in the size-distributions in size-classes 3 and 4 (>3.5 cm test diameter) in the majority of sampling times at each location. This peak appeared stable throughout the 1 y survey, suggesting that individuals within this size-range grew little over the period they were sampled. Similar peaks in size-frequency distributions are typical of other sea urchins such as *Evechinus chloroticus* in temperate eastern Australia (Andrew & Choat, 1982), *Paracentrotus lividus* in the western Mediterranean (Sala et al., 1988) and in Ireland (Barnes & Crook, 2001), *Lytechinus variegatus* and *Arbacia punctulata* in the Gulf of Mexico (Hill & Lawrence, 2003), and species belonging to the *Strongylocentrotus* genera in North America (Dumont et al., 2004). The majority of individuals in the algal stands were large-sized (size-classes 3 and 4), probably as a result of the high abundance of the most palatable food within this habitat (foliose brown algae, Tuya et al., 2001). *Diadema antillarum* adjusts its body size as a function of the availability of food as an adaptive strategy that buffers the adverse effects of increases in population density and/or decreases in food (Levitán, 1991).

Considerable variation existed in the presence of juveniles (size-class 1, test diameter <1.5 cm) among the sampled locations. Some locations appeared to be 'sources' of juveniles whereas others seemed to act as 'sinks'. In other words, some locations appeared to be more recruitment-dependent, while others were apparently more migration-dependent. However, these results should be considered with caution: echinoids can exhibit low levels, or even total absence, of recruitment over periods of years punctuated by sporadic events (Ebert, 1983; Lozano et al., 1995). As a result, locations with no evidence of recruitment are either maintained by intermittent recruitment events, which could be separated in time by years, or are dependent on migration of large-sized specimens. It is worth noting, however, that small-sized individuals were only registered at barrens. This fact suggests that recruitment of *D. antillarum* is favoured by the presence of high densities of congeners as a way of decreasing the risk of predation and increasing the survivorship of juvenile urchins. This pattern has been extensively described for other echinoids inhabiting temperate waters in studies comparing recruitment between barrens and nearby vegetated areas (Balch & Scheibling, 2000; Dumont et al., 2004). Juveniles of *D. antillarum* may be very vulnerable to predators as they are found only in holes and crevices in the substratum (personal observations), with the apparent existence of an escape size from predators in the Canarian Archipelago (Tuya et al., 2004). This cryptic behaviour has also been described in the western Atlantic (Bauer, 1976), and is typical of sea urchins in different oceans and latitudes (see Lawrence, 2001, for a review).

Spatio-temporal variability in recruitment of echinoids has been documented in a wide number of species and places; the causes of variability remain largely unexplained and have been the core focus of extensive research (Lessios, 1988; Andrew & Underwood, 1989; Lozano et al., 1995; Sala et al., 1998; Balch & Scheibling, 2000; McEdward & Miner, 2001, and references therein; Hereu et al., 2004). A complex interplay between supply of pelagic larvae, habitat selection by larvae and post-metamorphic mortality probably play key roles in explaining the great variations in recruitment of sea urchins from place to place and from time to time. This unpredictability in space and time may be particularly high for *D. antillarum*; larvae are probably subject to offshore planktonic transport for longer periods compared to other echinoids as a result of the longer development time of their pelagic larvae (~2 months, Eckert, 1998). Alternatively, the crevice-dwelling behaviour of *D. antillarum* juveniles could contribute to the patchiness observed among reefs. Both processes may add more uncertainty to the detection of specific spatio-temporal trends in their distribution patterns. Specific studies using appropriate devices to quantify settlement (Hernández et al., 2004) are desirable in this regard, coupled by scrape techniques to carefully measure recruitment through time (Lozano et al., 1995). The establishment and continuation of visual monitoring of the populations of *Diadema antillarum* is thus an important step to estimate and model the standing stock, population structure, and recruitment of this key invertebrate.

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). L.O.B. was financed by a postgraduate fellow grant provided by the Cabildo de Gran Canaria. Linguistic suggestions by T. Dempster improved previous drafts of this paper. We gratefully thank Dr M.A. Vanderklift and P. Sanchez-Jerez for their ideas and comments.

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Submitted 10 November 2005. Accepted 10 April 2006.