

Predation upon *Diadema* aff. *antillarum* in barren grounds in the Canary Islands

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SUMMARY: Experimental studies were carried out to determine the effects of predation on populations of the sea urchin *Diadema* aff. *antillarum* in barren grounds at the Canary Islands. The studied urchin populations were dominated by small to medium sized individuals (24-38 mm) and were variable in space. Tethering experiments showed that predation rates on *D.* aff. *antillarum* were very low and no differences were found between sites. Predation was found to be most intense on juveniles (<20 mm) and on 20-30 mm sized adults, the size range at which most individuals cease to exhibit cryptic behaviour. Urchins with test diameter >40 mm were not preyed upon whatsoever. We have experimentally demonstrated that there is an absolute predator 'escape size' of around 40 mm for *D.* aff. *antillarum* individuals in barren grounds. Predation rates obtained for juveniles show that a sufficient number may escape predation and sustain the adult population, maintaining the urchin barren habitat. Recruitment and topographic complexity, rather than predation, seem to determine the structure of urchin populations in barren grounds. We conclude that predation in fished barren grounds of the Canarian Archipelago is not of sufficient magnitude to substantially alter dense urchin populations and cause community-level effects.

Keywords: predation rate, barren grounds, population structure, cryptic behaviour, tethering experiments, 'escape size', *Diadema* aff. *antillarum*, Canary Islands.

RESUMEN: DEPREDACIÓN SOBRE EL ERIZO *DIADEMA* AFF. *ANTILLARUM* EN BLANQUIZALES DE LAS ISLAS CANARIAS. – Se realizaron unos estudios experimentales para valorar el efecto de la depredación sobre las poblaciones del erizo *Diadema* aff. *antillarum*, en zonas de blanquiales de las islas Canarias. Las poblaciones de erizos aparecieron dominadas por erizos de tallas pequeñas a medianas (24-38 mm) y resultaron variables en el espacio. Los experimentos de atado mostraron que *D.* aff. *antillarum* soporta una presión de depredación muy baja y no se encontraron diferencias entre las estaciones de estudio. La tasa de depredación fue más intensa sobre juveniles (<20 mm) y adultos de entre 20-30 mm, rango de talla en el que la mayoría de los individuos dejan de tener comportamiento críptico. Los erizos de más de 40 mm de diámetro no fueron depredados en ningún caso. Demostramos experimentalmente la existencia de una talla de escape de *D.* aff. *antillarum* frente a la depredación en zonas de blanquial en torno a los 40 mm. La tasa de depredación obtenida para juveniles indica que un número suficiente debe escapar de la depredación, manteniendo las poblaciones adultas y los blanquiales. Las tasas de reclutamiento y la complejidad topográfica, más que el nivel de depredación, parecen determinar la estructura de las poblaciones de erizos en los blanquiales. Concluimos que la depredación en los fondos rocosos sobreexplotados de las islas Canarias no tiene la magnitud suficiente para alterar substancialmente las densas poblaciones de erizos y causar efectos sobre la comunidad.

Palabras clave: depredación, blanquiales, estructura poblacional, comportamiento críptico, experimentos de atado, 'talla de escape', *Diadema* aff. *antillarum*, islas Canarias.

INTRODUCTION

Echinoids are frequently found in dense populations (Moore, 1966; Lawrence, 1975), in which they

drastically reduce the algal cover on rocky bottoms and transform wide extensions of the rocky littoral zone into areas known as "barren grounds" or "urchin-dominated zones" which are dominated by

encrusting coralline algae (Lawrence, 1975; Mann, 1982; Himmelman and Lavergne, 1985; Vadas and Elner, 1992). Therefore, they have been suggested to be involved in mediating transitions between alternate stable states (Knowlton, 1992; Knowlton, 2004), which occur when more than one type of community can stably persist in a single environmental regime (see review in Beisner *et al.*, 2003). These transitions between alternative stable states are usually sudden and difficult to reverse (Knowlton, 1992).

“Urchin barrens” have been described in coastal temperate ecosystems (Mann, 1977; Scheibling and Stephenson, 1984; Estes and Palmisiano, 1974; Vadas and Elner, 1992; Andrew, 1993); subtropical (Aguilera *et al.*, 1994; Alves *et al.*, 2003; Tuya *et al.*, 2004a,b); and tropical ecosystems (Ogden *et al.*, 1973; Sammarco, 1982; Hay, 1984; John *et al.*, 1992; McClanahan, 2000). Barren areas generated by *Diadema* aff. *antillarum* are common throughout the Canarian Archipelago (Aguilera *et al.*, 1994; Brito *et al.*, 2004; Tuya *et al.*, 2004b; Hernández *et al.*, 2006a).

Predation is one of the strongest biological processes affecting community structure and ecosystem organisation (Hariston *et al.*, 1960; Duffy and Hay, 2001; McClanahan, 1998; Guidetti *et al.*, 2005), and it may exert an important influence on the distribution and abundance of prey organisms (Paine, 1966; Levitan and Genovese, 1989; McClanahan and Muthiga, 1989; McClanahan, 1998). However, particularly in the marine environment, the influence of predators can be difficult to quantify (Aronson and Heck Jr, 1995; Aronson *et al.*, 2001). Predators can have indirect impacts on community organisation, especially when their prey interacts strongly with other species in the community (Power, 1992; Duffy and Hay, 2001). Therefore, their effects may extend beyond the prey consumed and reach an entire ecosystem throughout the so-called ‘trophic cascades’ (Paine, 1980; Menge, 1995; Witman and Dayton, 2001; Duffy and Hay, 2001; Shears and Babcock, 2002). Removal of top predator populations or severe reductions in their abundance is known to trigger trophic cascades (Steneck, 1998; Pace *et al.*, 1999; Pinnegar *et al.*, 2000; Dulvy *et al.*, 2004; Pinnegar and Polunin, 2004).

The large expansion of sea urchin populations and the reduction of algal forests is linked to the increase in fishing pressure on nature’s ‘keystone predators’, as reported for sea urchins at various latitudes

(Carpenter, 1981; McClanahan and Muthiga, 1988; McClanahan and Muthiga, 1989; McClanahan and Shafir, 1990; Sala and Zabala, 1996; Sala, 1997; Pinnegar *et al.*, 2000; McClanahan, 2000; Tuya *et al.*, 2004b; Tuya *et al.*, 2005a,b). However, other factors such as topography and substrate complexity (McClanahan, 1994; McClanahan *et al.*, 1999; Tomas *et al.*, 2004; Hernández, 2006); recruitment (Underwood and Fairweather, 1989; Hereu *et al.*, 2004); pollution and disease; and the variability of oceanographic events may also be important (see review in Pinnegar *et al.*, 2000). The increased prevalence of urchin-dominated barrens throughout the Canary Islands could also be considered as one symptom of long-standing and intense use of the littoral and fishing resources (Aguilera *et al.*, 1994; Tuya *et al.*, 2004b). Along the eastern Atlantic coast, predator removal has been linked to the subsequent creation of barren grounds as an ‘alternate stable state’ (Tuya *et al.*, 2004b, 2005b), although there is still little empirical evidence of natural reversals from the ‘barren state’ back to the macroalgal-dominated state (Tuya *et al.*, 2005b).

Population control exerted by predators may be different at the various stages of the prey life cycle, and certain sea urchin sizes may be particularly vulnerable to predation. Therefore, predation upon recently settled juveniles may be an important factor that limits recruitment and population structure (Tegner and Dayton, 1977; Scheibling and Hamm, 1991; Sala and Zabala, 1996). Several organisms have been identified as predators of *D. antillarum* in the western Atlantic (Schroeder, 1962; Randall, 1967; Behrens and Wells, 1984; Carpenter, 1984; Levitan and Genovese, 1989), and suggested as predators of this species in the eastern Atlantic (Brito and Falcón, 1990; Brito *et al.*, 2004; Tuya *et al.*, 2004b).

Predation also mediates sea urchin behaviour, including choice of habitat (Tegner and Dayton, 1977; Ogden *et al.*, 1973); diel movement patterns (Carpenter, 1984; Levitan and Genovese, 1989); and aggregating behaviour (Bernstein *et al.*, 1983; McClanahan, 1998; Behrens and Wells, 1984; Scheibling and Hamm, 1991; Sala and Zabala, 1996; McClanahan, 1999; Vadas and Elner, 2003). In this sense, substrate complexity and the availability of refuges mediate predation intensity on sea urchins (Ebling *et al.*, 1966; Carpenter, 1984; Levitan and Genovese, 1989; McClanahan and Kurtis, 1991).

Few experimental or observational studies have been carried out to assess the effect of predation on *D. antillarum* populations, especially in the eastern Atlantic Ocean (Behrents and Wells, 1984; Carpenter, 1984; Levitan and Genovese, 1989). The evaluation of these predatory populations in the Canary Islands comes from a study that assesses the relationships between *Diadema* aff. *antillarum* and potential predator populations (Tuya *et al.*, 2004b).

We hypothesised that (1) predation on *D. aff. antillarum* should be low or inexistent in areas with a high urchin population and (2) that predation should decrease with the increasing size of individual sea urchins. Also, (3) refuge availability, and therefore substratum rugosity, should determine the level of predation on sea urchins and the density of cryptic versus exposed individuals. The main goal of this study was therefore to evaluate whether urchin barrens of the Canarian Archipelago support any kind of predation pressure on sea urchins and, if evidence of predation is found, to assess its role as a controlling force of *D. aff. antillarum* population structure, determining which sea urchin size class is most susceptible.

MATERIAL AND METHODS

Study area

The study was carried out in shallow rocky reefs (4-10 m depth) by means of SCUBA diving from April-July 2005. Four sites were selected in the southeast of Tenerife Island (Canary Islands) in areas where urchin barren habitats were present: Boca Cangrejo, Punta Prieta, Abades and La Jaquita (Fig. 1).

Diadema aff. *antillarum* population structure

Urchin density and size structure were assessed at each site by randomly placing ten 1m² quadrats. Urchins were counted within each quadrat and the test diameter without spines of each individual was measured using vernier callipers (± 1 mm). For data analysis purposes, test diameters were categorised into size classes of 4 mm. In addition, it was noted whether individuals were located in a crevice (cryptic position), or were openly grazing the substratum (exposed position without physical protection). This information was used as a measure of the urchin's level of exposure to predators. As an environmental variable, topographic complexity of rocky reefs was

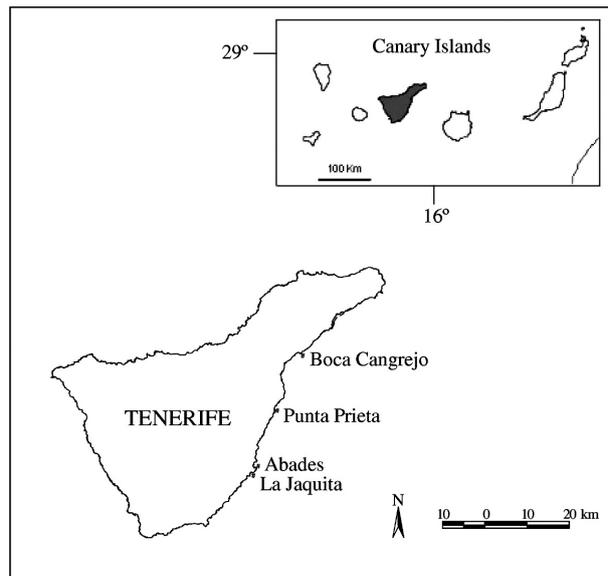


FIG. 1. – Location of study sites at Tenerife Island (Canary Islands).

estimated using the rope-and-chain method (Luckhurst and Luckhurst, 1978; Kingsford and Battershill, 1998; McClanahan and Shafir, 1990). A flexible tape was pressed along the bottom contour measuring the contour distance of eight 10 m long linear transects laid at each site. The rugosity measure was calculated as the straight-line distance per contour distance; a perfectly flat reef would consequently have a rugosity measure of 1.00.

Data from the four sites were used for comparisons of *Diadema* aff. *antillarum* density, size structure and level of exposure. Differences in density and mean test diameter between sampling sites were analysed by 1-way ANOVAs and Student-Newman-Keuls (SNK) *a posteriori* tests. Differences in size of exposed/cryptic urchins between sites were also examined using 1-way ANOVA and SNK tests. Before ANOVA analyses, the assumptions of normality and homoscedasticity were tested by Kolmogorov-Smirnov and Levene tests. When assumptions were not met and no transformation rendered variances homogeneous (Underwood, 1997), the ANOVA was carried out as it is robust to heterogeneity of variances, particularly for large balanced experiments (Underwood, 1997). The significance level was thus lowered from 0.05 to 0.01 (Underwood, 1981).

The effect of the urchin position (cryptic or exposed) on individual size was tested by means of the Mann-Whitney U non-parametric test and differences in *D. aff. antillarum* size distribution were analysed by frequency analysis (χ^2). All analyses were performed using the SPSS 12.0 statistics package.

Predation experiment

The level of predation was tested at the study sites by means of a tethering experiment. This technique, which is suitable for sedentary benthic organisms (Aronson *et al.*, 2001), has been used to test predation intensity on sea urchins in tropical ecosystems (McClanahan and Muthiga, 1989; McClanahan and Shafir, 1990; McClanahan, 1998; McClanahan, 1999; McClanahan *et al.*, 1999), in temperate systems of the Mediterranean Sea (Sala and Zabala, 1996, Guidetti, 2006) and of the Pacific Ocean (Shears and Babcock, 2002). With this technique, *D. aff. antillarum* individuals of four different size classes that included juveniles (Class 1: test diameter <20 mm) and adults (Class 2: 20-30 mm, Class 3: 30-40 mm, Class 4: 40-50 mm), were tethered to lines fixed at the substratum (McClanahan and Muthiga, 1989).

As it is difficult to handle *Diadema aff. antillarum* due to its morphological characteristics, a modified tagging technique was employed, which was formerly used by Olsson and Newton (1977) for the sea urchin *Strongylocentrotus franciscanus*. The method previously tested and successfully applied *in situ* to *Diadema aff. antillarum* (Clemente *et al.*, 2007), consisted in using external tags which were anchored through holes drilled in the urchin tests. This simple technique was not suitable for juvenile *D. aff. antillarum* (size class 1), because the majority of tests were broken upon piercing (Clemente *et al.*, 2007). Therefore, juvenile tests were perforated through the oral-aboral sections with a hypodermic needle (0.53x88 mm) and threaded with nylon monofilaments (0.25 mm) (McClanahan and Muthiga, 1989), which required removing these individuals temporarily from their habitat.

Ten tagged individuals of each size class were attached at 1 m intervals along 11 m transect lines laid over shallow rocky reefs at depths between 4 and 8 m. A total of four transects and 40 urchins were placed at the same time per site. Each individual was threaded with 40 cm of nylon monofilament, which allowed urchins to move in an area of approximately 0.785 m² and usually find holes or crevices to occupy in the substrate. The experiments were visited every 24 hours over 5 days to determine the number of individuals that died during each daily interval and to classify the condition of the carcass.

Examining the condition of the carcass provides crude information about the type of predator that fed on the sea urchin (McClanahan and Muthiga, 1989; Shears and Babcock, 2002). Carcasses were classified

and were typically found to be: (1) gone - if urchin body could not be found but the nylon tether was still present, which may be due to fish predators such as sparids and labrids that often consume urchins whole (McClanahan, 1995), but the source of predation was unknown; (2) broken - if urchin body was present but broken, which is often attributable to fish predators such as balistids that methodically break open the carcass and leave part of the test (McClanahan, 1995); or (3) with intact test but patches of freshly stripped spines - attributable to predation by starfish *Coscinasterias* or *Marthasterias* (Shears and Babcock, 2002). Daily monitoring of the individuals enabled urchins that appeared to be dying as a result of the piercing procedure to be identified. Individuals damaged by the procedure were characterised by intact, bleached tests with spines missing around the hole through which they were pierced (Clemente *et al.*, 2007). Adult sea urchins that lost their tag in the period 1-4 hours before the beginning of the predation experiment were also detected. In order to minimise these effects, these individuals were replaced with new ones and removed from the data analysis.

Survival rate was calculated for each individual urchin; defined as the number of days each *D. aff. antillarum* individual survived in the experiment. Predation rate was calculated as the total length of the experiment (5 days) minus the survival rate in days. Finally, a relative predation intensity index was calculated for each site and size class dividing predation rate by the length of the experiment (IP = (5 - S)/5). The index produces a value between 0 and 1, where 0 corresponds to no sea urchin eaten over the whole experiment, and 1 to all individuals eaten during the first experimental day.

Differences in survival rate of *D. aff. antillarum* individuals between size classes and sites were analysed using a 2-way ANOVA and Student-Newman-Keuls (SNK) *a posteriori* test. The factor 'size' (4 levels) was treated as a fixed effect and the factor 'site' (4 levels) as a random effect. The statistical package GMAV5 for windows was used under the specifications of Underwood *et al.*, 2002.

RESULTS

Diadema aff. antillarum population structure

Densities of *Diadema aff. antillarum* in barren ground habitats varied highly between studied sites

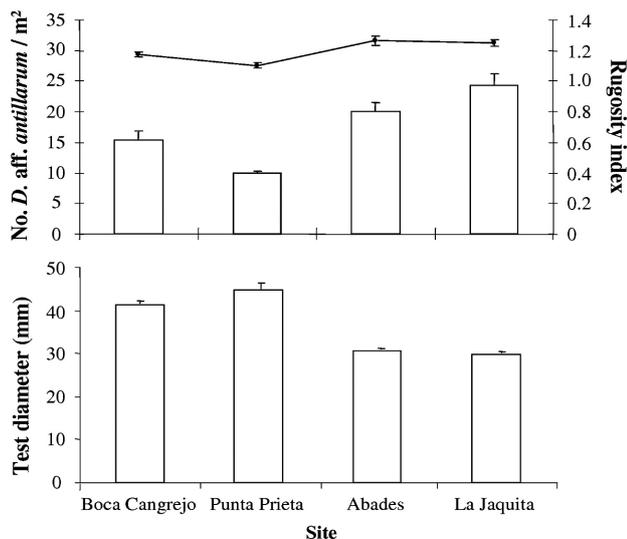


FIG. 2. – Mean *Diadema* aff. *antillarum* density (\pm SE) and test diameter (\pm SE) at studied sites (bars) and mean substrate rugosity index measurements (\pm SE) (line plot).

($F= 18.871$; $p<0.001$) (Fig. 2). The SNK test shows that the lowest urchin densities were recorded at Boca Cangrejo and Punta Prieta sites ($p=0.290$), which were significantly different ($p<0.01$) from the higher values obtained at La Jaquita and Abades sites ($p=0.100$) (Fig. 2). The substrate rugosity index was also significantly different between sites ($F= 11.766$; $p<0.001$); values obtained in Abades and La Jaquita ($p=0.601$) were significantly different ($p<0.01$) from those registered at Boca Cangrejo and Punta Prieta ($p<0.05$) (Fig. 2). In fact, a positive correlation between *Diadema* aff. *antillarum* density and the substrate rugosity index was obtained ($r= 0.928$, $p<0.05$). The overall density of exposed urchins was significantly higher than the density of cryptic urchins ($U= 284.500$; $p<0.001$) (Fig. 3).

There was significant variation in urchin size between sites ($F= 171.720$, $p<0.001$) (Fig. 2). The SNK test shows that the smallest urchin sizes were recorded at La Jaquita (29.70 ± 0.35 mm) and Abades (30.46 ± 0.45 mm) sites ($p=0.329$), which were significantly different from those at Boca Cangrejo (41.30 ± 0.58 mm) ($p<0.01$) and from the largest sized urchins recorded at Punta Prieta (44.78 ± 1.21 mm) ($p<0.01$) (Fig. 2). Likewise, pooled data showed significant variation in size of exposed and cryptic urchins ($U=24771.50$; $p<0.001$); test diameters of individuals that remained cryptic were lower (28.74 ± 0.52 mm) than those of urchins categorised as exposed (37.84 ± 0.41 mm) (Fig. 3). The relationship between *Diadema* aff. *antillarum* size and density was found to be significant and negative ($r= -0.949$, $p<0.05$).

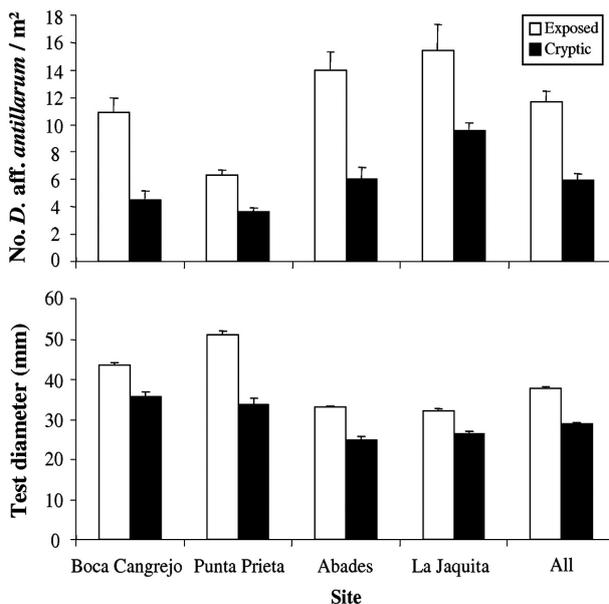


FIG. 3. – Mean density and test diameter of exposed and cryptic *Diadema* aff. *antillarum* individuals at studied sites.

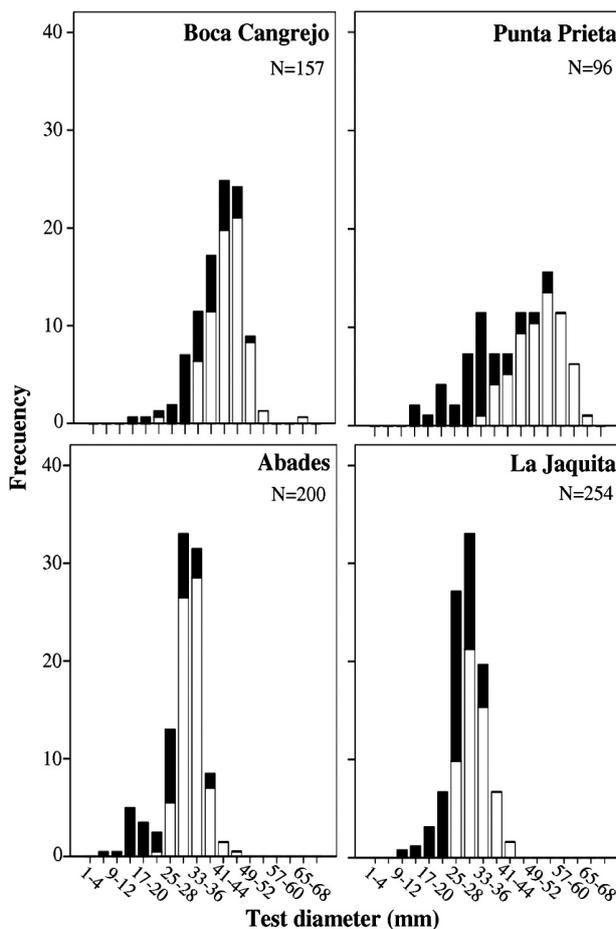


FIG. 4. – *Diadema* aff. *antillarum* size frequency distribution at each site. Shaded bars indicate the proportion of cryptic urchins and white bars the proportion of exposed individuals.

Populations of *Diadema* aff. *antillarum* at the studied sites were unimodal; very few urchins had test diameters below 25 mm and those that did generally remained in cryptic positions (Fig. 4). The size-frequency distribution showed significant variations among the 4 sampling sites ($\chi^2=587.220$, $p<0.001$) (Fig. 4). The general pattern in terms of sea urchin exposure to predators was that the smallest individuals were cryptic, while exposed urchins usually belonged to larger size classes (Fig. 5).

Predation experiment

From carcass observations, it was easy to distinguish between death caused by tethering and death caused by predation; therefore, individuals dying from the tagging procedure were able to be removed from the data analysis. Only 1.87% of the experimental individuals in all sites died from the handling and tethering procedure.

We registered predation events on *Diadema* aff. *antillarum* at all studied sites but only in sea urchin size classes 1-3, as none of the urchins bigger than 40 mm test diameter were consumed (Fig. 6).

Predation intensity was highest for size class 1 (0.19 ± 0.04) and no predation occurred for size class 4. In the latter all individuals remained alive until the end of the experimental period (Fig. 6). Comparison of relative predation intensity indices by 2-way ANOVA shows that 'size' was a significant factor ($F=$

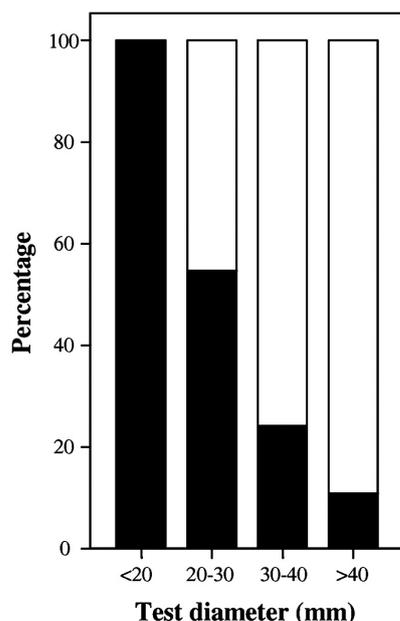


FIG. 5. – Percentage of the presence of cryptic urchins (shaded bars) and exposed individuals (white bars) within urchin size classes.

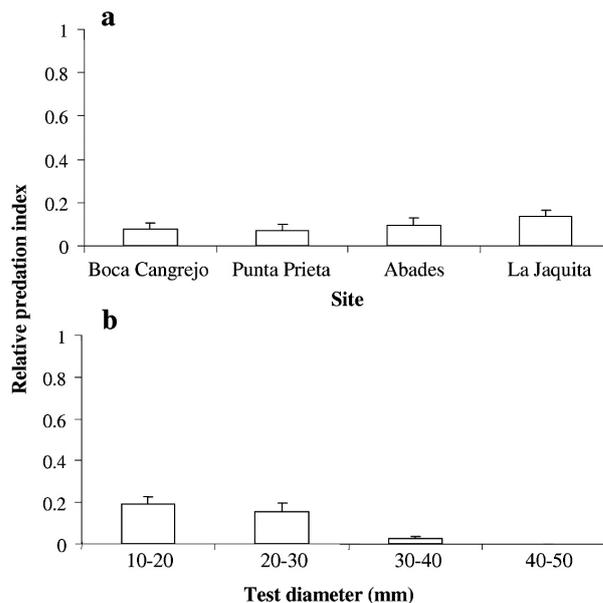


FIG. 6. – Mean survival rates \pm SE of *Diadema* aff. *antillarum* obtained within (a) sites and (b) sea urchin size classes with predation experiments.

22.17, $df= 3$, $p<0.001$). The SNK test differentiates ($p<0.01$) between urchins belonging to size classes 1 (<20 mm) and 2 (20-30 mm) ($p=0.515$), which had the highest predation rates, and the less predated size classes 3 and 4 ($p=0.396$) (Fig. 6).

The fate of the juvenile urchins (10-20 mm) which were preyed upon was unknown as the tests were completely removed from the tethers (Table 1). This could have resulted from predation by sparid fishes, such as *Diplodus cervinus* and *D. sargus*, which are relatively abundant in barren grounds and which completely engulf the urchin, or from predation by invertebrate predators such as *Coscinasterias tenuispina*, the clearly dominant asteroid at the studied sites, which breaks up or removes small urchins. Of the adult individuals found dead, 66.67% of the 20-30 mm size class and 25% of the 30-40 mm size class were gone, which may be due to fish predation; 33.33% and 75% respectively were present with test intact and patches of stripped spines, a state attributable to *C. tenuispina* predation (Table 1).

TABLE 1. – Source of predation on tethered urchins, based on the study of the condition of the carcass in predation experiments.

	Size class (mm)			
	10-20	20-30	30-40	40-50
Number preyed	19	15	4	0
Proportion				
Unknown	100.00	66.67	25.00	0.00
<i>Coscinasterias tenuispina</i>	0.00	33.33	75.00	0.00

The relative predation intensity index ranged within sites between 0.07 ± 0.03 in Punta Prieta and 0.13 ± 0.03 in La Jaquita (Fig. 6). However, the analysis shows no significant effect of the factor 'site' on urchin survival ($F = 1.01$, $df = 3$, $p = 0.389$) (Fig. 6), and the overall mean predation intensity obtained at barren grounds was 0.09 ± 0.02 .

DISCUSSION

The studied sea urchin populations were variable in space in terms of density and size structure. However, the spatial variation seen in urchin density and size in barren ground habitats did not seem to be influenced by predation, as predation pressure was found to be low throughout with no differences found between sites. McClanahan (1998) found similar results in tropical populations of *Echinometra mathaei* in which the echinoid was the most abundant and dominant species. At the lowest levels of predation *E. mathaei* individuals often show signs of food limitation and consequently it is thought that their populations are regulated by food resource availability and intra- and inter-specific competition for these resources (McClanahan and Kurtis, 1991; McClanahan, 1998). Not only this species but many echinoids are able to continue to survive with low levels of food (Lawrence, 1975; Ebert, 1980; Black, 1984; Levitan, 1991). Field experiments with *Diadema antillarum* have shown that this species has the ability to reduce and adjust skeletal body size and metabolic costs as population density fluctuates (Levitan, 1988; Hernández *et al.*, 2006b). The density and size results obtained here for *D. aff. antillarum* at different sites in the Canary Islands are further evidence of urchin's capability to continue to survive when density increases by shrinking in size, as seen in La Jaquita and Abades. There is also evidence of urchins increasing in size under decreased density, noticed at Punta Prieta and Boca Cangrejo. Moreover, density seems to be higher in sites where reefs have higher topographic complexity, probably as a result of there being more space available to support more dense populations, according to Hernández (2006), who found that the number of recruits positively correlates with rocky reef complexity, possibly enhancing higher number of small individuals.

The size structure of *Diadema aff. antillarum* populations was clearly unimodal in habitats with high densities which conform barren grounds, typi-

cal of fished sites with low levels of size-specific predation (Andrew and Choat, 1982; Shears and Babcock, 2002). Populations were dominated by small to medium sized individuals (24-38 mm), in concordance with the size class spectrum of Tuya *et al.*, (2004b) (15-55 mm). Moreover, that *Diadema aff. antillarum* was frequently observed exposed on the substrate may be explained by several factors common to barren grounds, as mentioned by Carpenter (1984) and Alves *et al.*, (2001), such as the high urchin densities and the low predation levels reported here along with low abundance of predators (Tuya *et al.*, 2004b).

Juveniles (individuals up to 20 mm test diameter) were always observed in crevices at barren grounds, as has been previously found for *Diadema antillarum* in the Caribbean (Bak, 1985; Hunte and Younglao, 1988) and for *D. aff. antillarum* in the Canary Islands (Hernández, 2006). Our tethering experiment results suggest that this is a predator-avoidance response by the most susceptible size class; a strategy which is also common in other echinoids in the presence of predators (Ogden *et al.*, 1973; Tegner and Dayton, 1977; Carpenter, 1984; Hunte and Younglao, 1988; Levitan and Genovese, 1989; McClanahan and Kurtis, 1991; Sala and Zabala, 1996; Tomas *et al.*, 2004). As demonstrated for other species and systems, the presence of shelter can reduce the amount of mortality caused by predation (McClanahan and Shafir, 1990; Hixon and Beets, 1993; Andrew, 1993). In this sense, habitat complexity, in terms of substrate rugosity and availability of spatial refuges, is an important factor determining juvenile escape from predation (Hereu *et al.*, 2005).

Urchins of 20-30 mm diameter were often observed in open areas of the rocky sublittoral. This exposed behaviour pattern in small sized sea urchins indirectly suggests that *D. aff. antillarum* may regularly escape from predation after having achieved approximately 20 mm in test diameter. Based on the extent of exposure displayed by urchins sized between 20-30 mm, it is thought that overall predation upon them is very low. In addition, 'hyperabundance' of *Diadema aff. antillarum*, as we found in Abades and La Jaquita, seems to induce a physical stress caused by the saturation of refuges, so that these small sizes are found out of refuges.

Urchins over 40 mm test diameter were not preyed upon at all and predation was very low on individuals sized between 30-40 mm test diameter. Consequently, we have experimentally demonstrated the existence of

a predator 'escape size' (sensu Sala, 1997) of around 40 mm test diameter for *D. aff. antillarum* individuals in barren ground habitats beyond which small fishes cannot effectively predate on sea urchins. These results therefore support the hypothesis that there is a lack of top predators specialised in feeding on such large sized urchins in barren grounds (Tuya *et al.*, 2004b). This is in concordance with the low abundance and small sizes of potential predatory fishes currently found in overexploited barren grounds of the Canary Archipelago (Falcón *et al.*, 1996; Tuya *et al.*, 2004b). Alternatively, the abundance of these predators is so low that the characteristics of this experimental design did not allow us to detect their effect on the urchin populations investigated.

In most cases, the specific predators responsible for attacks on tethered *D. aff. antillarum* individuals could not be identified by examining the carcass condition. However, a substantial percentage of predation events on adult urchins, especially of those between 30 and 40 mm, were probably carried out by the starfish *Coscinasterias tenuispina*. Taking into consideration that *C. tenuispina* is by far the most abundant invertebrate predator in the Canary Islands (Clemente *et al.*, unpublished manuscript), most predation by fish species is probably limited to sea urchins <30 mm.

In general, predation pressure is very low on *Diadema aff. antillarum* populations in barren grounds (0.09 ± 0.02) compared with results obtained from tethering experiments using other sea urchin species. Sala and Zabala (1996) found a higher predation rate of 0.36 on *Paracentrotus lividus* in a marine protected area of the Mediterranean Sea, but a similar value to ours of 0.07 at fished sites. McClanahan (1998) reported an average predation index for *Echinometra mathaei* in coral reefs off southern Kenya of 0.5. In a study on *Echinometra viridis* in the Caribbean (Belize) the same author found a mean predation index that ranged between 0.19 and 0.51 depending on the location along the patch reefs (McClanahan, 1999).

Taking into consideration the high urchin densities in fished barren grounds, it is likely that *Diadema aff. antillarum* population structure cannot be modified by the low level of predation reported in this study. This has facilitated the demographic explosion of *D. aff. antillarum* on the unprotected coasts of the Canary Islands, as shown for other barren grounds (Andrew and Choat, 1982; Andrew and MacDiarmid, 1991). In this sense, Tuya *et al.*, 2004b found that low abundance and biomass of potential

top predatory fish were common in well developed urchin-grazed barrens, which appears to be related to high densities of sea urchins and in turn, to low cover of fleshy macroalgae. The consequence is the establishment of 'undesired' alternate stable states (Knowlton, 2004) in which systems shift from complex, highly diverse and productive states to simplified, low diversity, low productive states. This is another case in which anthropogenic disturbance by removal of top predators has caused dramatic shifts in the organisation and structure of the coastal community. The result has been damage to the resilience of the marine system (Myers and Worm, 2003; Hughes *et al.*, 2005) with the subsequent establishment of 'undesired' organisational states (Knowlton, 2004; Hughes *et al.*, 2005). Furthermore, knowledge of these phase shifts has important implications for future management strategies focused on mediating transitions between alternate states, as 'undesired' states may be highly resistant to restoration.

We conclude that predation in barren grounds in fished areas of the Canary Archipelago is not of sufficient magnitude to substantially alter such dense urchin populations and cause community-level effects. Moreover, and considering the high settlement rates obtained by Hernández *et al.* (2006a), the predation rate registered for juvenile urchins shows that sufficient numbers of juveniles may be escaping predation and sustaining the adult population to maintain the urchin barren habitat. Therefore, we suggest that the recruitment rate and topographic complexity, rather than predation, determine the structure of urchin populations in barren grounds as proposed by Hereu *et al.*, 2004 and Hernández 2006. Further observational and experimental approaches should be used to specifically identify *D. aff. antillarum* predators both in overexploited barren grounds and at sites with high density and well structured fish populations. It is therefore suggested that research should focus on urchin populations in Marine Protected Areas of the Canary Islands, where controlled fishing effort would result in higher abundances of top predators.

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REFERENCES

- Aguilera, F., A. Brito, C. Castilla, A. Díaz, J.M. Fernández-Palacios, A. Rodríguez, F. Sabaté and J. Sánchez. – 1994. *Canarias, economía, ecología y medio ambiente*. Francisco Lemus Editor, La Laguna.
- Alves, F.M.A., L.M. Chicharro, E. Serrao and A.D. Abreu. – 2001. Algal cover and sea urchin spatial distribution at Madeira Island (NE Atlantic). *Sci. Mar.*, 65: 383-392.
- Alves, F.M.A., L.M. Chicharro, E. Serrao and A.D. Abreu. – 2003. Grazing by *Diadema antillarum* (Philippi) upon algal communities on rocky substrates. *Sci. Mar.*, 67: 307-311.
- Andrew, N.L. – 1993. Spatial heterogeneity, sea urchin grazing, and habitat structure on reefs in temperate Australia. *Ecology*, 74: 292-302.
- Andrew, N.L. and J.H. Choat. – 1982. The influence of predation and conspecific adults on the survivorship of juvenile *Evechinus chloroticus* (Echinoidea: Echinometridae). *Oecologia*, 54: 80-87.
- Andrew, N.L. and A.B. MacDiarmid. – 1991. Interrelations between sea urchins and spiny lobsters in northeastern New Zealand. *Mar. Ecol. Prog. Ser.*, 70: 211-222.
- Aronson, R.B. and K.L. Heck Jr. – 1995. Tethering experiments and hypothesis testing in ecology. *Mar. Ecol. Prog. Ser.*, 121: 307-309.
- Aronson, R.B., K.L. Heck Jr and J.F. Valentine. – 2001. Measuring predation with tethering experiments. *Mar. Ecol. Prog. Ser.*, 214: 311-312.
- Bak, R.P.M. – 1985. Recruitment patterns and mass mortalities in the sea urchin *Diadema antillarum*. *Proc. 5th Int. Coral Reef Congr.*, 5: 267-272.
- Behrens, K.C. and R.A. Wells. – 1984. The influence of fish predators on the distribution and abundance of *Diadema antillarum*. *NOAA Tech Mem OAR NURP-2*.
- Bernstein, B.B., S.C. Schroeter and K.H. Mann. – 1983. Sea urchin (*Strongylocentrotus droebachiensis*) aggregating behaviour investigated by a subtidal multifactorial experiment. *Can. J. Fish. Aquat. Sci.*, 40: 1975-1986.
- Beisner, B.D., D.T. Haydon and K. Cuddington. – 2003. Alternative stable states in ecology. *Front. Ecol. Environ.*, 1: 376-382.
- Black, R., C. Codd, D. Hebbert, S. Vink S and J. Burt. – 1984. The functional significance of the relative size of Aristotle's lantern in the sea urchin *Echinometra mathaei* (de Blainville). *J. Exp. Mar. Biol. Ecol.*, 77: 81-97.
- Brito, A. and J.M. Falcón. – 1990. Contribución al conocimiento de la distribución y ecología de *Chilomycterus atringa* (Pises, Diodontidae) en las Islas Canarias. *Vieraea*, 19: 271-275.
- Brito, A., J.C. Hernández, J.M. Falcón, N. García, G. González-Lorenzo, M.C. Gil-Rodríguez, A. Cruz-Reyes, G. Herrera, A. Sancho, S. Clemente, E. Cubero, D. Girard and J. Barquín. – 2004. El Erizo de Lima (*Diadema antillarum*) una especie clave en los fondos rocosos litorales de las Islas Canarias. *Makaronesia (Bol. Asoc. Am. Mus. Cienc. Nat. Tje.)*, 6: 68-86.
- Carpenter, R.C. – 1981. Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. *J. Mar. Res.*, 39 (4): 749-765.
- Carpenter, R.C. – 1984. Predator and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum*. *Mar. Biol.*, 82: 101-108.
- Clemente, S., J.C. Hernández and A. Brito. – 2007. An external tagging technique for the long-spined sea urchin *Diadema aff. antillarum*. *J. Mar. Biol. Ass. U. K.*, 87: 5334/1-3.
- Duffy, J.E. and M.E. Hay. – 2001. The ecology and evolution of marine Consumer-Prey interactions. In: M.D. Bertness, S.D. Gaines and M.E. Hay (eds.), *Marine community ecology*, pp. 131-157. Sunderland Mass, Sinauer.
- Dulvy, N.K., R.P. Freckleton and N.V.C. Polunin. – 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecol. Lett.*, 7: 410-416.
- Ebert, T.A. – 1980. Relative growth of sea urchin jaws: an example of plastic resource allocation. *Bull. Mar. Sci.*, 30: 467-474.
- Ebling, F.J., A.D. Hawkins, J.A. Kitching, L. Muntz and V.M. Pratt. – 1966. The ecology of Lough Ine XVI. Predation and diurnal migration in the *Paracentrotus* community. *J. Anim. Ecol.*, 35: 559-566.
- Estes, J. and J.F. Palmisiano. – 1974. Sea otters: their role in structuring near shore communities. *Science*, 185: 1058-1060.
- Falcón, J.M., S.A. Bortone, A. Brito and C.M. Bundrick. – 1996. Structure of and relationships within and between the littoral, rock-substrate fish communities off four islands in the Canarian Archipelago. *Mar. Biol.*, 125: 215-231.
- García-Rubies, A. – 1996. *Estudi ecològic de les poblacions de peixos sobre substrat rocós a la Mediterrània Occidental: Efecte de la fondària, el substrat, l'estacionalitat i la protecció*. Ph. D. thesis, Univ. Barcelona.
- Guidetti, P. – 2006. Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. *Ecol. Appl.*, 13 (3): 963-976.
- Guidetti, P., S. Bussott and F. Boero. – 2005. Evaluating the effects of protection on fish predators and sea urchins in shallow artificial rocky reefs habitats: a case study in the northern Adriatic Sea. *Mar. Environ. Res.*, 59 (4): 333-348.
- Hay, M.E. – 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology*, 65: 446-454.
- Hariston, N.G., F.E. Smith and L.B. Slobodkin. – 1960. Community structure, population control, and competition. *Am. Nat.*, 94: 421-425.
- Hernández, J.C. – 2006. Estrategia reproductiva de la población canaria del erizo *Diadema aff. antillarum* Philippi, 1845: maduración gonadal, asentamiento larvario y reclutamiento. PhD. thesis, Servicio de Publicaciones de la Universidad La Laguna.
- Hernández, J.C., A. Brito, E. Cubero, N. García, D. Girard, G. González-Lorenzo and J.M. Falcón. – 2006a. Temporal patterns of larval settlement of *Diadema antillarum* (Echinodermata: Echinoidea) in the Canary Islands using an experimental larval collector. *Bull. Mar. Sci.*, 78 (2): 271-279.
- Hernández, J.C., A. Brito, N. García, M.C. Gil-Rodríguez, G. Herrera, A. Cruz-Reyes and J.M. Falcón. – 2006b. Spatial and seasonal variation of the gonad index of *Diadema antillarum* (Echinodermata: Echinoidea) in the Canary Islands. *Sci. Mar.*, 70 (4): 689-698.
- Hereu, B., M. Zabala, C. Linares and E. Sala. – 2004. Temporal and spatial variability in settlement of the sea urchin *Paracentrotus lividus* in the NW Mediterranean. *Mar. Biol.*, 144: 1011-1018.
- Hereu, B., M. Zabala, C. Linares and E. Sala. – 2005. The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. *Mar. Biol.*, 146: 293-299.
- Himmelman, J.H. and Y. Lavergne. – 1985. Organization of rocky subtidal communities in the St. Lawrence estuary. *Nat. Can.*, 112: 143-154.
- Hixon, M.A. and J.P. Beets. – 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol. Monogr.*, 63: 77-101.
- Hughes, T.P., D.R. Bellwood, C. Folke, R.S. Steneck and J. Wilson. – 2005. New paradigms for supporting the resilience of marine ecosystems. *Trends Ecol. Evol.*, 20: 380-386.
- Hunte, W. and D. Younglao. – 1988. Recruitment and population recovery of *Diadema antillarum* (Echinodermata, Echinoidea) in Barbados. *Mar. Ecol. Prog. Ser.*, 45: 109-119.
- Knowlton, N. – 1992. Thresholds and multiple stable states in coral reef community dynamics. *Am. Zool.*, 32: 674-682.
- Knowlton, N. – 2004. Multiple 'stable' states and the conservation of marine ecosystems. *Prog. Oceanogr.*, 60: 387-396.
- John, D.M., J.H. Price and G.W. Lawson. – 1992. Tropical east Atlantic and Islands: plant-animal interactions on tropical shores free of biotic reefs. In: D.M. Jonh, S.J. Hawkins, and J.H. Price (eds.), *Plant-Animal Interactions in the Marine Benthos*, pp. 87-99. Oxford Clarendon Press, Oxford.
- Kingsford, M.J. and C.N. Battershill. – 1998. Subtidal habitats and benthic organisms of rocky reefs. In: M. Kingsford and C. Battershill (eds.), *Studying temperate marine environments. A handbook for ecologists*, pp. 83-114. Canterbury University Press, New Zealand.
- Lawrence, J.M. – 1975. On the relationships between marine plants and sea urchins. *Oceanogr. Mar. Biol. Annu. Rev.*, 13: 213-286.

- Levitán, D.R. – 1988. Density-dependent size regulation and negative growth in the sea urchin *Diadema antillarum* Philippi. *Oecologia*, 76: 627-629.
- Levitán, D.R. – 1991. Skeletal changes in the test and jaws of the sea urchin *Diadema antillarum* in response to food limitation. *Mar. Biol.*, 111: 431-435.
- Levitán, D.R. and S.J. Genovese. – 1989. Substratum-dependent predator-prey dynamics: patch reefs as refuges from gastropod predation. *J. Exp. Mar. Biol. Ecol.*, 130: 111-118.
- Luckhurst, B.E. and K. Luckhurst. – 1978. Analysis of the influence of substratum variables on coral reef communities. *Mar. Biol.*, 49: 317-323.
- Mann, K.H. – 1977. Destruction of kelp-beds by sea urchins, a cyclical phenomenon or irreversible degradation. *Helgoländ. Wiss. Meer.* 30: 455-467.
- Mann, K.H. – 1982. Kelp, sea urchins and predators: a review of strong interactions in rocky subtidal systems of eastern Canada, 1970-1980. *Neth. J. Sea Res.*, 16: 414-423.
- McClanahan, T.R. – 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral Reefs*, 13: 231-241.
- McClanahan, T.R. – 1995. Fish predators and scavengers of the sea urchin *Echinometra mathaei* in Kenyan coral-reef marine parks. *Environ. Biol. Fish.*, 43: 187-193.
- McClanahan, T.R. – 1998. Predation and the distribution and abundance of tropical sea urchin populations. *J. Exp. Mar. Biol. Ecol.*, 221: 231-255.
- McClanahan, T.R. – 1999. Predation and the control of the sea urchin *Echinometra viridis* and fleshy algae in the patch reefs of Glovers Reef, Belize. *Ecosystems*, 2: 511-523.
- McClanahan, T.R. – 2000. Coral reef use and conservation. In: T.R. McClanahan, C.R.C. Sheppard and D.O. Obura (eds.), *Coral reef of the Indian Ocean. Their ecology and conservation*, pp. 39-80. Oxford University Press, New York.
- McClanahan, T.R. and N.A. Muthiga. – 1988. Changes in Kenyan coral reef community structure and function due to exploitation. *Hydrobiologia*, 166: 269-276.
- McClanahan, T.R. and N.A. Muthiga. – 1989. Patterns of predation on a sea urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs. *J. Exp. Mar. Biol. Ecol.*, 126: 77-94.
- McClanahan, T.R. and S.H. Shafir. – 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia*, 83: 362-370.
- McClanahan, T.R. and J.D. Kurtis. – 1991. Population regulation of the rocky-boring sea urchin *Echinometra mathaei* (de Blainville). *J. Exp. Mar. Biol. Ecol.* 147: 121-146.
- McClanahan, T.R., N.A. Muthiga, A.T. Kamukuru, H. Machano and R.W. Kiambu. – 1999. The effects of marine parks and fishing on coral reefs of northern Tanzania. *Biol. Conserv.*, 89: 161-182.
- Menge, B.A. – 1995. Indirect effects in marine intertidal interaction webs: patterns and importance. *Ecol. Monogr.*, 65: 21-74.
- Moore, H.B. – 1966. Ecology of echinoids. In: R.A. Booolootian (ed.), *Physiology of Echinodermata*, pp. 73-85. Interscience Publications, New York.
- Myers, R.A. and B. Worm. – 2003. Rapid worldwide depletion of predatory fish communities. *Nature*, 423: 280-283.
- Ogden, J.C., R.A. Brown and N. Salesky. – 1973. Grazing by the echinoid *Diadema antillarum* Philippi: Formation of halos around West Indian path reefs. *Science*, 182: 715-717.
- Olsson, M. and G. Newton. – 1977. A simple, rapid method for marking individual sea urchins. *Calif. Fish. Game.*, 65: 58-63.
- Pace, M.L., J.E. Cole, S.R. Carpenter and J.F. Kitchell – 1999. Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.*, 14: 483-488.
- Paine, R.T. – 1966. Food web complexity and species diversity. *Am. Nat.*, 100: 65-75.
- Paine, R.T. – 1980. Food webs linkage interaction strength and community infrastructure. *J. Anim. Ecol.*, 49: 667-685.
- Pinnegar, J.K., N.V.C. Polunin, P. Francour, F. Badalamenti, R. Chemello, M.L. Harmelin-Vivien, B. Hereu, M. Milazzo, M. Zabala, G. D'Anna and C. Pipitone. – 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environ. Conserv.*, 27: 179-200.
- Pinnegar, J.K. and N.V.C. Polunin – 2004. Predicting indirect effects of fishing in Mediterranean rocky littoral communities using a dynamic simulation model. *Ecol. Model.*, 172: 249-267.
- Power, M.E. – 1992. Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology*, 73: 733-746.
- Randall, J.E. – 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.*, 5: 665-847.
- Sala, E. – 1997. Fish predators and scavengers of the sea urchin *Paracentrotus lividus* in protected areas of the North-West Mediterranean Sea. *Mar. Biol.*, 129: 531-539.
- Sala, E. and M. Zabala. – 1996. Fish predation and the structure of sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. *Mar. Ecol. Prog. Ser.*, 140: 71-81.
- Sammarco, P.W. – 1982. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. *J. Exp. Mar. Biol. Ecol.*, 61: 31-55.
- Scheibling, R.E. and R.L. Stephenson. – 1984. Mass mortality of *Strongylocentrotus droebachiensis* (Echinodermata: Echinoidea) off Nova Scotia, Canada. *Mar. Biol.*, 78: 153-164.
- Scheibling, R.E. and J. Hamm. – 1991. Interactions between sea urchins (*Strongylocentrotus droebachiensis*) and their predators in field and laboratory experiments. *Mar. Biol.*, 110: 105-116.
- Schroeder, R.E. – 1962. Urchin killer. *Sea Front.*, 8: 156-160.
- Shears, N.T. and R.C. Babcock. – 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia*, 132: 131-142.
- Steneck, R.S. 1998. Human influences on coastal ecosystems: does overfishing create trophic cascades? *Trends Ecol. Evol.*, 13: 429-430.
- Tegner, M.J. and P.K. Dayton. – 1977. Sea urchin recruitment patterns and implications of commercial fishing. *Science*, 196: 324-326.
- Tomas, F., J. Romero and X. Turón. – 2004. Settlement and recruitment of the sea urchin *Paracentrotus lividus* in two contrasting habitats in the Mediterranean. *Mar. Ecol. Prog. Ser.*, 282: 173-184.
- Tuya, F., A. Boyra, P. Sánchez-Jerez, C. Barbera and R.J. Haroun. – 2004a. 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. *Hydrobiologia*, 519: 211-214.
- Tuya, F., A. Boyra, P. Sánchez-Jerez, C. Barbera and R.J. Haroun. – 2004b. Relationships between rocky-reef fish assemblages, the sea urchin *Diadema antillarum* and macroalgae throughout the Canary Archipelago. *Mar. Ecol. Prog. Ser.*, 278: 157-169.
- Tuya, F., A. Boyra, P. Sánchez-Jerez and R.J. Haroun. – 2005a. Influence of fishing and functional group of algae on sea urchin control of algal communities in the eastern Atlantic. *Mar. Ecol. Prog. Ser.*, 287: 255-260.
- Tuya, F., R.J. Haroun, A. Boyra and P. Sánchez-Jerez. – 2005b. Sea urchin *Diadema antillarum*: different functions in the structure and dynamics of reefs on both sides of the Atlantic. *Mar. Ecol. Prog. Ser.*, 302: 307-310.
- Underwood, A.J. – 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Annu. Rev.*, 19: 513-605.
- Underwood, A.J. – 1997. *Experiments in ecology: Their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge.
- Underwood, A.J., M.G. Chapman and S.A. Richards. – 2002. *GMAV-5 for Windows. An analysis of variance programme*. Centre for Research on Ecological Impacts of Coastal Cities. Marine Ecology Laboratories, University of Sydney, Australia.
- Underwood, A.J. and P.G. Fairweather. – 1989. Supply-side Ecology and benthic marine assemblages. *Trend Ecol. Evol.*, 4: 16-20.
- Vadas, R.L. and R.W. Elnor. – 1992. Plant-animal interactions in the north-west Atlantic. In: D.M. Jonh, S.J. Hawkins and J.H. Price (eds.), *Plant-Animal Interactions in the Marine Benthos*, pp. 33-60. Oxford Clarendon Press, Oxford.
- Vadas, R.L. and R.W. Elnor. – 2003. Responses to predation cues and food in two species of sympatric, tropical sea urchins. *Mar. Ecol.* 24 (2): 101-121.
- Witman, J.D. and P.K. Dayton. – 2001. Rocky subtidal communities. In: M.D. Bertness, S.D. Gaines and M.E. Hay (eds.), *Marine community ecology*, pp. 131-157. Sunderland Mass, Sinauer.

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