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NOTE

Influence of fishing and functional group of algae on sea urchin control of algal communities in the eastern Atlantic

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ABSTRACT: We address the effect of several factors influencing the depth of interfaces between the shallow photophilic brown algal assemblages and *Diadema antillarum* urchin-dominated barrens on rocky reefs of the warm-temperate central-eastern Atlantic. By means of a multifactorial observational approach, we hypothesized that it would be locally influenced by (1) the functional structure of the dominant brown algal assemblages (corticated foliose algae versus large frondose coarsely-branched fucoid species), in addition to (2) the fishing status (fished versus unfished sites) and (3) the large-scale topography of the substrate. Our results show that brown algal assemblages reach deeper waters at unfished sites, which is independent of the dominant brown algal functional group. However, monospecific algal facies dominated by large frondose coarsely branched fucoid species (mainly the genera *Cystoseira*) reach deeper waters in comparison with corticated foliose algae, at fished sites.

KEY WORDS: Sea urchins · *Diadema antillarum* · Phytobenthos · Functional groups · Ecosystem-level effects · Canary Islands

INTRODUCTION

Large, shallow, rocky areas covered by erect photophilic algae are transformed by sea urchins into overgrazed substrates dominated by encrusting coralline algae. These so-called 'urchin-grazed barrens' (e.g. Mann 1982, McClanahan & Sala 1997, Sala et al. 1998, Shears & Babcock 2003, Tuya et al. 2004a) have been widely described in coastal temperate areas (Vukovic 1982, Verlaque 1987, Andrew & Underwood 1989, Francour 1994, Sala & Zabala 1996, Sala et al. 1998, Babcock et al. 1999, Pinnegar et al. 2000, Alves et al. 2001, Shears & Babcock 2003, Tuya et al. 2004a). These authors have highlighted that the transformation of a zone from an algal-dominated system to an urchin-grazed barren is a dynamic and complex interaction of different physical and ecological mechanisms, operating at different scales of spatial and temporal variability. Processes affecting the sea urchin population structure, and thus involved in the interactions of urchin barrens with algal assemblages, are widely acknowledged in temperate coastal areas (see Shears & Babcock 2003). Fishing pressure on natural sea urchin predators, the topography and complexity of the substrate and the availability of refuges, recruitment, pollution and diseases, harvesting, and the variability of oceanographic events are the most important processes (for reviews, see Sala et al. 1998 and Pinnegar et al. 2000).

Patches of functionally (sensu Steneck & Dethier 1994) different brown algal species form a photophilic macroscopic algal bed, as a continuous and heterogeneous mosaic of different algal species, throughout the shallowest rocky seascape of the Canarian Archi-

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pelago (Haroun et al. 2003). The long-spined sea urchin *Diadema antillarum* (Philippi) has been recently identified as the main key-herbivorous species ('habitat determiner') throughout the sublittoral rocky bottoms of the warm-temperate central-eastern Atlantic, as it controls the macrobenthic algal assemblages with negligible contribution from other grazing species (Alves et al. 2003, Tuya et al. 2004b). Intensive grazing by *D. antillarum* restricts the lower edge of the photophilic algal facies to the first few meters of the subtidal (Alves et al. 2001, 2003, Tuya et al. 2004b). Hence, clear interfaces or borders (sensu Gagnon et al. 2004) between brown algal stands and urchin barrens extend parallel to the coastline. Several ecological and physical processes play a significant role in the structure and abundance of *D. antillarum* populations and, consequently, in the interaction between both habitats across the eastern Atlantic; these are water turbulence (Alves et al. 2001), fishing and the abundance of top-predators (following the classical trophic cascades paradigm, Tuya et al. 2004a), and the small-scale substrate complexity (Tuya et al. 2004a). However, the dominance of photophilic algal stands by functionally different brown algal groups, as determinants of the interplay between photophilic algal assemblages and urchin barrens, still remains to be considered.

In this paper, we address the effect of several factors influencing interfaces between the photophilic algal assemblages and urchin barrens on rocky reefs of the warm-temperate eastern Atlantic by means of a multifactorial, observational (mensurative) approach. Specifically, we hypothesized that the depth-limit between both habitats would be locally influenced by the functional structure of the dominant brown algal assemblages in addition to factors that seem, as reported in the literature, to affect the population structure of the sea urchin *Diadema antillarum*, such as the fishing pressure (unfished versus fished sites) and the physical topography of rocky reefs.

MATERIALS AND METHODS

Area of study and experimental design. The study was carried out on basaltic rocky bottoms between 3 and 30 m depth of the Canarian Archipelago (28° N, 15° W, central-eastern Atlantic Ocean), in October 2003. The distribution of benthic communities along the bathymetric axis shows a clear vertical zonation pattern, with the arrangement of the communities in belts with distinct species composition and abundance, as observed in many shallow temperate subtidal habitats (Garrabou et al. 2002 and references therein). Within the shallowest photophilic zone, extensive stands of perennial brown algal assemblages make up the dominant community (Haroun et al. 2003). Two main groups of photophilic, non-turfing, fleshy brown algae can be distinguished (Haroun et al. 2003), according to the classical algal functional form groups reported in the literature (Littler & Littler 1984, Steneck & Dethier 1994, Ruitton et al. 2000, Garrabou et al. 2002, McClanahan et al. 2003), occurring as distinct patches. Corticated foliose brown algae (henceforth referred to as Functional Group 1 [FG1]) consist of sheet-shaped, jointed calcareous and thick leathery-shaped species (e.g. *Cutleria multifida*, *Dyctiota* spp., *Lobophora variegata*, *Padina pavonica*, *Stypopodium* spp., *Taonia* spp., *Zonaria* spp. etc.), from 1 to 15 cm in height, which constitute either algal cushions or thin sheets with mixtures of algal species. On the other hand, corticated large brown macrophytes (henceforth referred to as Functional Group 2 [FG2]) are erect, frondose, coarsely branched fucoid species (mainly of the genera *Cystoseira* and *Sargassum*), which generally form monospecific algal stands.

We define the variable $Z_{<5\%}$ as the depth-limit (the 'edge') from which the percent (%) cover of the overall photophillic brown phytobenthos drops uniformly below 5% cover with increasing depth. This depth, therefore, represents the shallowest upper edge of grazed urchin barrens. This measure was, in all cases, determined on a homogeneous horizontal surface to avoid the local effect of small-scale substrate topography (crevices, holes etc.).

Two categories of large-scale habitat complexity were defined following the criteria of Garcia-Charton et al. (2000): (1) low (rocky platforms with low relief) and (2) high (rocky bottoms with sharp slopes). Finally, fished and unfished sites were selected outside and inside Marine Protected Areas (MPAs) from the Canarian Archipelago (http://www.mapya.es/rmarinas/index_rm.htm), where only capture of fin fish is controlled. On the other hand, sea urchins are not subjected to a fishery across the overall Canarian Archipelago.

Our experimental design tested the effect of the 2 functional groups of brown algae (FG1 versus FG2) on the dependent variable $Z_{<5\%}$ at both fished and unfished sites, with high and low bottom complexity. We selected a total of 24 sites across the Canarian Archipelago as spatial replicates of the 8 defined experimental treatments (2 functional groups of brown algae × 2 categories of fishing pressure × 2 categories of bottom complexity), with 3 sites per treatment (each MPA provided 4 sites, while unprotected adjacent areas to each MPA another 4 sites).

Sampling and data analysis. At each site, a diver swam perpendicular to the coastline until a clear transition between the shallow photophilic brown algal

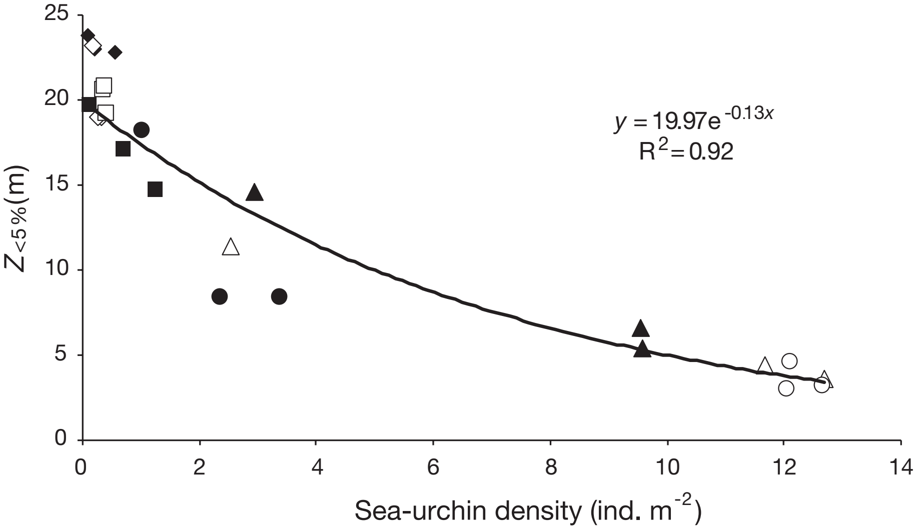

Fig. 1. *Diadema antillarum*. Non-linear regression between the mean density of total individuals per site and the depth-limit from which the percent cover of the overall brown phytobenthos drops uniformly below 5% of cover ($Z_{<5\%}$). Empty icons: Functional Group 1; full icons: Functional Group 2; □■: sites with low bottom complexity inside MPAs; ◇◆: sites with high bottom complexity inside MPAs; ○●: sites with low bottom complexity outside MPAs; △▲: sites with high bottom complexity outside MPAs

band and the urchin barren was observed, avoiding bare haloes around the shallowest shelters of sea urchins. To ensure that the percent cover of fleshy brown algae was under 5%, we deployed a 25 × 25 cm quadrat and the percent cover was visually estimated *in situ* following standardized procedures (Foster et al. 1991, Dethier et al. 1993, McClanahan et al. 2003). This protocol was replicated 5 times per site (n = 5). Tidal corrections were further applied to compare the overall dataset. In addition, the abundance of all adult *Diadema antillarum* individuals (test diameter without spines >2 cm) were visually recorded by SCUBA divers along urchin barrens using 16 haphazardly located 2 × 2 m (4 m^2) quadrats per sampling site (Ruitton et al. 2000, Tuya et al. 2004a).

The relationship between the lower edge of the photophilic algal assemblages (quantified by means of the $Z_{<5\%}$) and *Diadema antillarum* sea urchin abundance was estimated using non-linear regression analysis.

A mixed 4-factor ANOVA model (Underwood 1997) was applied to test for differences attributable to the 3 defined experimental factors: (1) fishing status (fixed factor with 2 levels: unfished versus fished), (2) the complexity of the habitat (orthogonal and fixed factor with 'low versus high' as levels) and (3) the dominant functional group of algae (orthogonal and fixed factor incorporating the levels corresponding to the 2 categories of algae: FG1 and FG2). The random factor 'Sites' represents the spatial replication of the experimental treatments, and is therefore nested within the second-order interaction term among the 3 experimental factors. When a term of the ANOVA that included a fixed factor was significant, the SNK *a posteriori* test was applied. Before analysis, Cochran's test was used to check for homogeneity of variances. Although no transformation rendered variances homogeneous, the ANOVA was carried out as it is robust to heterogeneity of variances, particularly for large balanced experiments (Underwood 1997).

RESULTS

Grazing by the sea urchin *Diadema antillarum* determines the lower edge of photophilic brown algal assemblages, as a strong non-linear decrease with depth (as absolute values of the variable $Z_{<5\%}$) is observed with increasing sea urchin abundance (Fig. 1).

Clear overall differences in the mean depth of interfaces between photophilic algal assemblages and urchin barrens were observed between fished and unfished (MPAs) sites (Figs. 1 & 2), which was corroborated by the ANOVA model (Table 1). The mean value (±SD) of the variable $Z_{<5\%}$ across unfished sites

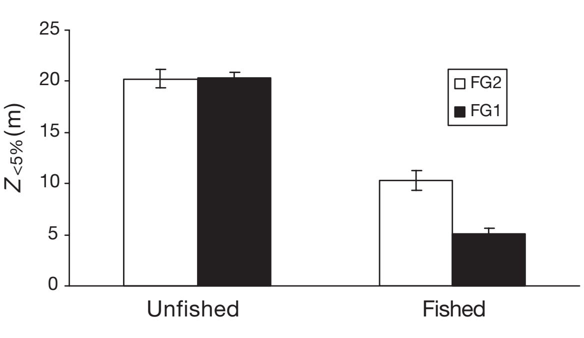

Fig. 2. Effect of fishing status (fished versus unfished MPAs and the functional group of dominant algae (FG1 versus FG2) on interfaces between photophillic brown algal stands and urchin barrens. Error bars represent ±SE

Table 1. 4-factor ANOVA on the effects of fishing status, bottom complexity and functional grouping of dominant brown algal assemblages on the mean depth of interfaces between brown algal stands and urchin-dominated barrens across the Canarian Archipelago. *p < 0.01

Source of variation	df	MS	*F*
Functional group (=FG)	1	3.85	5.98
Status (=S)	1	39.93	61.94*
Habitat complexity (=C)	1	0.44	0.69
FG × S	1	5.97	9.32*
FG × C	1	0.29	0.45
S × C	1	0.01	0.02
FG × S × C	1	2.07	3.21
Site (FG × S × C)	16	0.64	11.55*
Residual	96		

(20.26 ± 3.66) is, thus, about 2 to 3 times that at fished sites (7.65 ± 5.10) (Fig. 2). At the unfished sites, no significant differences were detected as a function of the dominance of either functional group of brown algae (FG1 versus FG2). However, significant differences were detected, at fished sites by the SNK test between both of the functional groups (Figs. 1 & 2). In fact, this difference detected solely at the fished sites implied a significant first-order interaction between the factors 'Functional group × Status, as detected by the ANOVA ($F = 9.32$, $p < 0.01$; Table 1). Brown algal stands consisting of species of the FG2 (mainly monospecific beds of the genera *Cystoseira*) reached deeper waters at the fished sites (10.3 ± 5.37 m, mean ± SD) in comparison with the brown algae belonging to the FG1 (5.03 ± 3.14 m) (Fig. 1).

The large-scale substrate complexity in the studied sites appears not to play a significant role in the depth of borders between algal stands and urchin barrens. Thus, neither any detectable interaction with other experimental factors nor the main effect of this factor has been involved in any significant term in the ANOVA (Table 1). Finally, it is important to recognize that differences between sites for each treatment explain a significant amount of the variability within our experimental design ($F = 11.55$, $p < 0.01$; Table 1). This inter-site variability within each established treatment is greater across fished sites (right side of Fig. 1) than across unfished sites (left side of Fig. 1).

DISCUSSION

Depth-related trends in community structure respond to strong changes in community determining factors (Garrabou et al. 2002). Human-induced disturbances through fishing appear to be a significant factor regulating the structure of shallow phytobenthic communities at opposite levels of fishing pressure (Shears & Babcock 2003 and references therein). Our study has shown that fished sites present shallow interfaces between photophilic brown algal stands and urchin-dominated barrens, whereas this border is deeper in sites protected from fishing (sites inside MPAs). This result is not surprising as sites protected from fishing activities show diverse and highly structured assemblages of large-sized predatory benthophagous organisms (e.g. fish or crustaceans). These populations have the potential of controlling the key-grazing species *Diadema antillarum* throughout infralittoral rocky reefs of the warm-temperate central-eastern Atlantic (Tuya et al. 2004a). This trend has been similarly reported with other key-herbivorous sea urchins at other coastal systems in a large body of scientific literature covering the cold-temperate mid-latitudes in both of the hemispheres (e.g. Andrew & Choat 1982, Bernstein et al. 1983, Sala & Zabala 1996, Estes et al. 1998, Sala et al. 1998, Babcock et al. 1999, Steneck et al. 2002, Shears & Babcock 2003) by following the classical trophic cascades paradigm (as reviewed by Sala et al. 1998, Pinnegar et al. 2000).

Despite the fact that habitat complexity favours the impact of grazers (e.g. sea urchins) governing the structure of erect brown macroalgae (as reviewed by Sala et al. 1998 and Steneck et al. 2002), large-scale (≥100 m) habitat complexity does not seem to have an important effect on the depth of the interfaces between brown algal facies and urchin barrens. This lack of significance is attributable to the selection of a descriptor operating at large spatial-scales (≥ 100 m) instead of medium (1 to 10 m) or small (< 1 m) spatial-scales, which would more readily reflect the availability of refuges (crevices, boulders etc.). Marine organisms respond to variations of different descriptors according to their body size and life characteristics (Garcia-Charton et al. 2000).

Unfished sites have shown brown algal stands with a depth-related extension which is independent of the dominant brown algal functional group. In contrast, the functional group to which the dominant brown algal species belong (FG1 versus FG2) may play a significant role in determining the depth of interfaces between shallow photophilic brown algal assemblages and urchin-grazed barrens, at fished sites. Algal stands, dominated by large frondose coarsely branched fucoid species (FG2, mainly 4 and 2 species of the genera *Cystoseira* and *Sargassum*, respectively), significantly reached deeper waters in comparison with corticated foliose brown algae (FG1). We propose 2 complementary mechanisms to explain this observation. Firstly, it can be related to the wave-induced sweeping motion of large erect canopy-forming fucoid algae (FG2); algal stands of this functional group restrict both sea urchin movement and suitable space to graze, as has been suggested for large brown macrophytes in temperate waters (Steneck & Dethier 1994, Konar 2000, Gagnon et al. 2004). Secondly, the sea urchin *Diadema antillarum* has shown lower feeding preference for species belonging to FG2 (e.g. *Cystoseira*) than those from FG1 (Tuya et al. 2001). This avoidance is attributable to the rather coarse and tough body of the genera *Cystoseira* (physical factor), as well as to the presence of polyphenols (chemical factor; Winter & Estes 1992, Knoess & Glombitza 1993) as defenses against herbivores (Shunula & Ndibalema 1986). Despite the potentially confounding effects of chemical and morphological traits (Hay 1997), this hierarchy is in agreement with the susceptibility to being eaten as a function of algal morphology (algal functional groups) reported by Steneck & Dethier (1994), mainly for large invertebrates such as sea urchins in temperate seas.

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