

DOES DEPTH AND SEDIMENTATION INTERACT WITH SEA URCHINS TO AFFECT ALGAL ASSEMBLAGE PATTERNS ON EASTERN ATLANTIC REEFS?

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ABSTRACT A range of factors may affect the composition and abundance of macroalgae on subtidal rocky reefs. We experimentally determined the interactive effect of the occurrence of the long-spine sea urchin, *Diadema antillarum*, depth and sedimentation levels on macroalgal assemblage structure on eastern Atlantic rocky reefs. Specifically, we manipulated sea urchin densities (removal of all individuals vs. untouched controls at natural densities) on rocky reefs devoid of erect vegetation, and predicted (1) that removal of sea urchins would differently affect macroalgal assemblage structure between deep (16–18 m) and shallow (8–9 m) reef strata, and that (2) the effect of sea urchin removal on macroalgae would be altered under different scenarios of sedimentation (ambient vs. enhanced). Experimental circular plots (2 m in diameter) were set up at 3 locations at Gran Canaria (Canarian Archipelago), and were maintained and monitored every 4 wk for 1 y. At the end of the experimental period, the structure of the algal assemblages differed between urchin treatments and depth strata, with a larger cover of turf and bushlike algae where urchins were removed and at the shallow reef stratum. More important, differences in algal assemblage structure between urchin treatments were irrespective of sedimentation levels, but shifted from the shallow to the deep stratum. This interactive effect was, in turn, observed for bushlike algae, as a result of a larger magnitude of response (i.e., larger cover) in the shallow stratum relative to the deep stratum, but was not detected for either turf or crustose coralline algae. These results highlight the importance of some physical conditions (here, differences in depth) to interact with biotic processes (here, urchin abundance) to create patterns in the organization of subtidal and benthic assemblages.

KEY WORDS: macroalgae, benthic assemblages, assemblage structure, sea urchins, sedimentation, depth strata

INTRODUCTION

Subtidal temperate habitats are heterogeneous. A range of factors may facilitate or disturb the presence and abundance of subtidal macroalgae living on hard bottoms, and thereby affect their composition and assemblage structure (Lüning 1990). For example, light, sedimentation, grazing, and water flow have been repeatedly highlighted as important determinants of macroalgal assemblage structure (Schiel & Foster 1986, Witman & Dayton 2001). In turn, an appreciation of the interactive effects of physical and biological processes may assist in the development of predictive models about the assembly and maintenance of heterogeneity of subtidal communities (Connell 2005).

Depth directly affects different abiotic properties, such as light availability, nutrient concentrations, sedimentation, and temperature (Garrabou et al. 2002). For example, an increase in depth is associated with a decrease in light availability and typically in algal growth, which affect the community dominant (Witman & Dayton 2001). A considerable small-scale horizontal spatial variability (from centimeters to meters) in the structure and abundance of algal assemblages clearly indicate that other mechanisms are also relevant to influence patterns in algal abundance and assemblage structure on subtidal reefs (Fowler-Walker & Connell 2002, Schils & Coppejans 2003, Terlizzi et al. 2007). For example, sediment deposition may disturb, and so alter, algal diversity and abundance at small scales (Schiel & Foster 1986, Airoldi & Virgilio 1998), often indirectly facilitating opportunistic filamentous turfs to replace adversely affected canopy-forming, erect, macroalgae (Airoldi

& Cinelli 1997, Irving & Connell 2002), although sediment disturbance may promote diversity through preventing monopolization of space by competitively superior species (Littler et al. 1983b, Airoldi, 2003).

The presence of high sea urchin population densities has been widely advocated as a key mechanism determining the organization and functioning of temperate reefs: Overgrazing by sea urchins may cause the elimination of erect macroalgae, ultimately turning algal beds into “urchin-grazed barrens” dominated by algal crusts and sessile invertebrates (e.g., Dayton et al. 1992, Andrew 1993, Andrew & Underwood 1993, Shears & Babcock 2003, Graham 2004, Tuya et al. 2004b). The intensity of sea urchin grazing, and subsequently its effects on the organization of benthic assemblages, is, however, considerably heterogeneous through space and time (Benedetti-Cecchi et al. 1998). A range of biotic and abiotic mechanisms can alter sea urchin densities, and so grazing rates. For the former, shifts in the behavior (Sala et al. 1998) and recruitment (Ebert 1983, Balch & Scheibling 2000) patterns are two of the main studied mechanisms, whereas for the latter, differences in turbulence, wave action, substrate rugosity, and heterogeneity are factors routinely advocated to influence the effect of sea urchin grazing over algal assemblages (Lawrence 2001). For example, water turbulence typically decreases with increasing depth (Denny 1988, Roberts et al. 2006), and may therefore increase the susceptibility of erect algae to sea urchin grazing (Alves et al. 2001, Tuya et al. 2007, Shears et al., 2008). Similarly, the negative effect of sea urchin grazing over erect macroalgae can be exacerbated under scenarios of increased sediment loads that facilitate opportunistic filamentous algae through an inhibition of the recruitment of erect macroalgae (Valentine & Johnson 2005), although the effect of urchins on macroalgae can be

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reduced when high levels of sedimentation have adverse effects on larval and postsettlement survival of sea urchins (Shears et al. 2008).

The long-spine 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 structuring subtidal rocky reefs (Alves et al. 2001, Tuya et al. 2004b, because it is directly involved in the transformation of large reef areas previously covered by erect algae to barrens, following the classic trophic cascades paradigm (Sala et al. 1998). Indeed, the contribution of other grazers (e.g., herbivorous fishes) to the generation of reef barrens is negligible when compared with the grazing caused by *D. antillarum* (Tuya et al. 2004a).

Potential interactions between different factors are often ignored in tests of hypotheses about the structure of benthic assemblages, although they might clarify a substantial amount of the spatial variability among whole assemblages. In this study, we experimentally determined the interactive effect between the occurrence (absence vs. presence) of the long-spine black sea urchin, *D. antillarum*, and differences in depth and sedimentation (ambient vs. enhanced) to create patterns in the assemblage structure of macroalgae on eastern Atlantic rocky reefs. Specifically, we manipulated sea urchin densities and predicted (1) that removal of sea urchins would differently affect macroalgae assemblage structure between deep and shallow reef strata, and that (2) the effect of sea urchin removal on macroalgae assemblage structure would be altered under different scenarios of sedimentation (enhanced vs. natural); in particular, we predicted that erect, bushlike algae would be more affected by urchin grazing than filamentous turfs, where sediment loads are heavier.

MATERIALS AND METHODS

Study Area

The study was carried out at 3 locations, 1–2 km apart, on the northeast coast of Gran Canaria (The Canarian Archipelago, 28°N, eastern Atlantic Ocean), from March 2007–March 2008. Each location encompasses rocky (basaltic) reefs denuded of vegetation (“urchin-grazed barrens”) from approximately 4–20 m depth, and are exposed to the prevailing swells and seas from the northwest and northeast, respectively. Oceanographic variables (i.e., current patterns, sea surface temperature, exposure to waves) are typically similar from one location to the other (González Barbuzano 2003). Sea surface temperature fluctuates from 18–19°C in winter to 23–24°C in summer. In this area, the distribution of benthic communities along the bathymetric axis shows a consistent vertical zonation pattern. Within the shallowest zone (0–3 m), extensive stands of algal assemblages—principally, bushlike algae (Tuya & Haroun 2006)—dominate the community, and long-spine sea urchins only occur in low densities (0–1 individuals/m²). Intensive grazing by *D. antillarum* produces clear interfaces between these shallow-water algal stands and deeper areas devoid of vegetation (from below 3 m of depth, long-spine sea urchin mean densities typically range from 4–6 individuals/m² [Tuya et al. 2004b]).

Interactive Effects Between Sea Urchin Presence and Depth: Experimental Design

At each location, circular plots (diameter, 2 m) were created by either removing all urchins (–U) or preserving urchin densities at natural levels (i.e., untouched controls, +U). All plots were set up on horizontal reef surfaces with similar densities of urchins (ranging from 4–6 individuals/m²), and devoid of erect vegetation. The center of each experimental plot was marked with a metal stake drilled into the reef and labeled for subsequent identification. Two plots of each treatment (–U and +U) were established at 2 depth strata—deep (16–18 m) versus shallow (8–9 m)—within each location (i.e., 8 experimental plots per location). All plots were created at the beginning of March 2007, and were visited approximately every 4 wk to maintain treatments and to quantify changes in assemblage structure, until the end of the experiment (March 2008). Because adult *D. antillarum* individuals show a clear “homing behavior” (Tuya et al. 2004c), colonization of urchin removal plots (–U) was mostly restricted to juveniles (personal observation) throughout the study, which hide in cryptic reef microhabitats such as cracks and crevices (Hernández 2006). Immigration of adult *D. antillarum* into urchin removal plots (–U), at any time during the 4-wk period, was, in all cases, less than or equal to 2 individuals per plot, and individuals were removed.

Interactive Effects Between Sea Urchin Presence and Sedimentation: Experimental Design

The second experiment was conducted at the same locations using the same methods described for the previous experiment, but was only conducted at a single depth stratum (12–14 m). At each location, 2 plots of each urchin treatment (–U and +U) were subjected, every 4 wk, to an “enhanced” sedimentation treatment by adding sandy (0.28 mm mean grain diameter) sediments (40.44 g wet weight per experimental plot) as a fine “rain” (Airoldi & Virgilio 1998, Connell 2005) uniformly distributed within each plot. The other 4 plots were maintained at “natural” (i.e., unmanipulated) levels of sedimentation. To determine a proxy to the level of sedimentation in the study area, 4 funnel-like sediment traps (63.58 cm² of upper circular area) were established, 30 cm above the bottom at 1 location, and the mean accumulation rate (measured in grams wet weight per square meter per day) of sediments was quantified every day for 4 successive days. Those plots assigned to the “enhanced” sedimentation treatment were subjected to a 3-fold increase in sedimentation rates (0.67 g wet weight/m²/day) relative to natural sedimentation levels (0.22 g wet weight/m²/day¹). Such an increase was selected to represent a realistic scenario in the shifts of sediment loads within the study area (González Barbuzano 2003), which lacks major runoff sources (e.g., rivers, creeks) throughout the year.

Sampling

For both experiments, and at each sampling time (i.e., every 4 wk from March 2007 to March 2008), a scuba diver quantified *in situ* the percent cover of algae in four 50 × 50-cm quadrats (0.25 m²) within each plot, following point-quadrat procedures previously implemented for the study area (a grid of 121 points per quadrat was used in all cases [Tuya and Haroun 2006]). Quadrats, tens of centimeters apart, were haphazardly laid out

within each plot. This is a rapid, nondestructive technique to assess assemblage structure and dominance of sessile biota (Fowler-Walker & Connell 2002, McClanahan et al. 2003). Final values for each taxon were expressed as percentages. Taxa presented in less than a 4% cover were omitted. Responses of algae can be identified, without loss of significant information, through taxonomic groups instead of species (Terlizzi et al. 2003). Macroalgae were thus categorized into 3 morphological groups, by taking into account the algal form groups reported in the literature (Steneck & Dethier 1994, Fowler-Walker & Connell 2002, McClanahan et al. 2003; Vaselli et al. 2008), and previously implemented in the study area (Tuya and Haroun 2006). Turf algae (hereafter referred to as TA) consist of small cushion-shaped and filamentous species, usually less than 5 cm in height (e.g., *Colpomenia sinuosa*, *Dasycladus vermicularis*, *Jania* spp., *Ceramium* spp.). Bushlike algae (hereafter referred to as BA) are erect, coarsely branched algae (e.g., *Asparagopsis* spp., *Corallina elongata*, *Dyctiota* spp., *Padina pavonica*, *Stypocaulon scoparium*, *Stypopodium zonale*, *Zonaria tournefortii*), from 1–15 cm in height, which constitute either large algal cushions or thin sheets. Finally, coralline algae (hereafter referred to as CA) consisted of algal crusts (e.g., the genera *Lithothamnion*, *Lithophyllum*, *Neogoniolithon*, *Titanoderma*), and were counted when not overgrown by other algae.

Statistical Analyses

For each experiment, differences between categories (and combinations) of predictive factors were evaluated using multi- and univariate analysis of variance (ANOVA). Permutational analysis of variance (PERMANOVA [Anderson 2001]) was used to partition both multivariate and univariate variability, because this approach allows multivariate testing for interactions, and uses permutations to calculate *P* values. The latter was preferable because the data were from unknown distributions and were overdispersed. The test statistic (pseudo *F*) is a multivariate analogue of the univariate Fisher's *F* ratio, and in the univariate context the two are identical when using Euclidean distance as the dissimilarity measure (Anderson 2001). Because data collected from the same experimental units through time are often autocorrelated, and so assumptions of

analyses may not be met, we analyzed data at the end of the experimental period according to a mixed effects, 4-factor ANOVA model, incorporating (1) location (random factor with 3 levels), (2) urchins (fixed factor with 2 levels; –U vs. +U and orthogonal to the previous factor), (3) depth (deep vs. shallow strata) or sedimentation (ambient vs. enhanced) (fixed factor with 2 levels, and orthogonal to the previous factors), and (4) plots (random factor with 2 levels, nested within the 2nd order interaction between location, urchin, and depth or sedimentation). Raw data were square root transformed to down-weight the most abundant taxa, and multivariate (the entire macroalgal assemblage) and univariate (percent coverage of TA, BA, and CA) analyses were based on Bray-Curtis dissimilarities and Euclidean distances, respectively. *P* values were calculated from 4,999 unrestricted permutations of the raw data. When appropriate, pairwise *a posteriori* comparisons were executed using 4,999 permutations to test for differences among levels of fixed factors. To visualize multivariate patterns, non-metric multidimensional scaling ordination was carried out on the square root transformed data. Differences in variability (dispersion) in assemblage structure between treatments were tested through pairwise comparisons with the PERMDISP routine (Anderson 2004) via 4,999 permutations of the raw data. All analyses were performed using the PRIMER 6.0 (PRIMER-E Ltd, UK) statistical package.

RESULTS

Effects of Urchin Removal on Algal Assemblages Between Shallow and Deep Strata

Differences in algal assemblage structure between urchin removal and untouched (control) plots at the end of the experiment shifted from the shallow to the deep stratum (Table 1, PERMANOVA, Ur × De, *P* < 0.05); this interactive effect was consistent among locations (Table 1, PERMANOVA, Lo × Ur × De, *P* > 0.1), although the effects of urchins and depth shifted among locations (Table 1, PERMANOVA, Lo × Ur and Lo × De, *P* < 0.01). In general, the structure of the algal assemblages at the shallow stratum was more variable (i.e., dispersed) relative to those algal assemblages at the deep strata

TABLE 1.

Results of multivariate and univariate ANOVA testing the effects of location (random factor), urchins (fixed factor with 2 levels and orthogonal to the previous factor), depth (fixed factor with 2 levels and orthogonal to the previous factors), and plots (random factor with 2 levels, nested within the 2nd order interaction between location, urchins, and depth) on the structure of algal assemblages and the percent coverage of each algal morphological group at the end of the experiment.

Source	df	Algal Assemblage			Turf Algae			Bush Algae			Crustose Algae		
		MS	F	<i>P</i>	MS	F	<i>P</i>	MS	F	<i>P</i>	MS	F	<i>P</i>
Lo (location)	2	17,479	39.37	0.0002	0.41	2.25	0.1475	66.21	10.11	0.0027	4.35	12.28	0.0013
Ur (urchins)	1	25,678.2	5.77	0.0462	39.47	37.99	0.0253	799.26	24.49	0.039	0.09	0.86	0.4513
De (depth)	1	59,751	4.75	0.0762	52.01	45.95	0.0211	1186.76	11.87	0.0478	18.4	4.08	0.1808
Plot (Lo × Ur × De)	12	443.94	2.58	0.0004	0.18	3.97	0.0001	65.521	5.60	0.0000	0.35	1.69	0.0866
Lo × Ur	2	4,448.1	10.02	0.0002	1.03	5.71	0.0181	32.00	4.98	0.0266	0.10	0.31	0.7413
Lo × De	2	12,581	28.33	0.0002	1.14	6.22	0.014	95.57	14.59	0.0006	4.52	12.78	0.0011
Ur × De	1	5,863.4	11.30	0.0268	2.09	7.94	0.1062	341.26	11.74	0.0757	1.01	1.85	0.3072
Lo × Ur × De	2	518.8	1.16	0.3696	0.26	1.45	0.2723	29.07	4.44	0.0361	0.54	1.55	0.2529
Residual	72	172.27			0.04			1.17			0.20		

(Table 2, PERMDISP, most pairwise comparisons, $P < 0.01$), which, indeed, tended to cluster together in the ordination space (Fig. 1).

For TA, the direction and magnitude of differences between urchin treatments (-U vs. +U) was consistent between depth strata (Table 1, Ur \times De and Lo \times Ur \times De, $P > 0.10$, Fig. 2). We detected differences in the percent coverage between urchin treatments (-U vs. +U) and depth strata (Table 1, urchin and depth, $P < 0.05$, Fig. 2). Those plots where urchins were removed (-U) contained 3.1 times more algal cover than untouched (control) plots (+U), whereas plots at the shallow reef stratum contained 1.6 times more algal cover than the deep reef stratum (Fig. 2). These differences between urchin treatments and depth strata, however, differed slightly in magnitude among locations (Table 1, Lo \times Ur, Lo \times De, $P < 0.05$, Fig. 2).

In the case of BA, differences between urchin treatments varied from the deep to the shallow reef stratum (Table 1, Ur \times De, $P = 0.07$, Fig. 2), as a result of a larger magnitude of response (i.e., larger percent of coverage) in the shallow relative to the deep stratum (Fig. 2), which even varied among locations (Table 1, Lo \times Ur \times De, $P < 0.05$, Fig. 2). We detected differences in the percent coverage between urchin treatments (-U vs. +U) and depth strata (Table 1, urchin and depth, $P < 0.05$, Fig. 2). Those plots where urchins were removed (-U) had 3.4 times more cover of algae than plots where urchins were not eliminated (+U), whereas those plots at the shallow reef stratum had 5.7 times more cover of algae than the deep reef stratum (Fig. 2). These differences between urchin treatments and depth strata differed in magnitude among locations (Table 1, Lo \times Ur, Lo \times De, $P < 0.05$, Fig. 2).

Finally, and for CA, location no. 1 contained a larger percent coverage than the other locations at the end of the experiment (Table 1, location, $P < 0.01$, Fig. 2), particularly at the shallow stratum, which resulted in an interactive effect between these 2 factors (Table 1, Lo \times De, $P < 0.01$, Fig. 2). No other significant effects were detected.

Effects of Urchin Removal on Algal Assemblages Between High and Low Levels of Sedimentation

The effect of urchin manipulations (-U vs. +U) on algal assemblage structure was irrespective of sedimentation levels at the end of the experiment (Table 3, PERMANOVA, Ur \times Se, $P > 0.05$) (Fig. 3), although it varied among locations (Table 3, PERMANOVA, Lo \times Ur, $P < 0.05$). Moreover, differences in dispersion in assemblage structure were not observed among

TABLE 2.

Results of pairwise comparisons of multivariate dispersion between sea urchin treatments (removals [-U] vs. untouched controls [+U]) from shallow to deep strata.

Groups	t	P
+U shallow versus -U shallow	51.606	0.001
+U shallow versus +U deep	61.981	0.001
+U shallow versus -U deep	35.019	0.009
-U shallow versus +U deep	29.805	0.012
-U shallow versus -U deep	0.61471	0.724
+U deep versus -U deep	22.442	0.10

2D Stress: 0,04

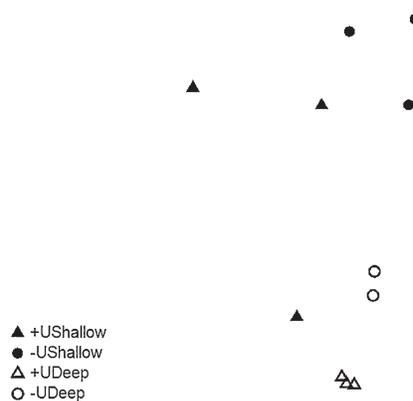


Figure 1. Two-dimensional nonmetric multidimensional scaling plot showing centroids of algal assemblages that were subjected to sea urchin removals (circles) or preserved at natural densities of sea urchins (untouched controls, triangles) at shallow (open symbols) and deep (filled symbols) strata at the end of the experimental period. Replicated plots have been averaged within each treatment for each of the 3 locations.

treatments (all pairwise comparisons, $P > 0.05$, PERMDISP, Table 4, except between -U -sediments and +U +sediments).

For both TA and BA, we observed a significantly larger cover, at the end of the experiment within those plots where urchins were removed (Table 3, urchins, $P < 0.05$, 2.1 times for TA and 2.5 times for BA, Fig. 4), irrespective of levels of sedimentation (Table 3, Ur \times Se, $P > 0.05$, Fig. 4). Differences between levels of sedimentation did not cause a significant change in the cover of both algal groups (Table 3, sedimentation, $P > 0.05$, Fig. 4). Finally, location no. 1 contained more CA than the other locations at the end of the experiment (Table 3, location, $P < 0.01$, Fig. 4), which even resulted in an interactive effect with urchin treatments (Table 3, Ur \times Lo, $P < 0.05$, Fig. 4). No other significant effects were detected.

DISCUSSION

Effects of Urchin Removal on Algal Assemblages Between Shallow and Deep Strata

The key role that sea urchins play in determining algal assemblage structure has been experimentally demonstrated throughout temperate latitudes (e.g., Dayton et al. 1992, Andrew 1993, Benedetti-Cecchi et al. 1998, Alves et al. 2001, Bulleri et al. 2002, Graham 2004). Typically, an increase in the cover of erect algae, including both turf and bushlike algae, within plots where sea urchins were eliminated (or reduced) has been observed, which is consistent with our observations from subtidal rocky reefs at Gran Canaria. Similarly, differences in the composition and structure of erect macroalgae between bathymetric strata have been observed at temperate subtidal reefs (e.g., Garrabou et al. 2002, Balata and Piazzini 2008, Vergés et al. 2009). More important, our study demonstrated that the magnitude of differences in algal assemblage structure between plots subjected to urchin manipulations (removal vs. untouched controls) shifted from shallow to deep waters. These results highlight, therefore, the capacity for physical conditions (i.e., depth) to interact with biotic processes (i.e., urchin abundance)

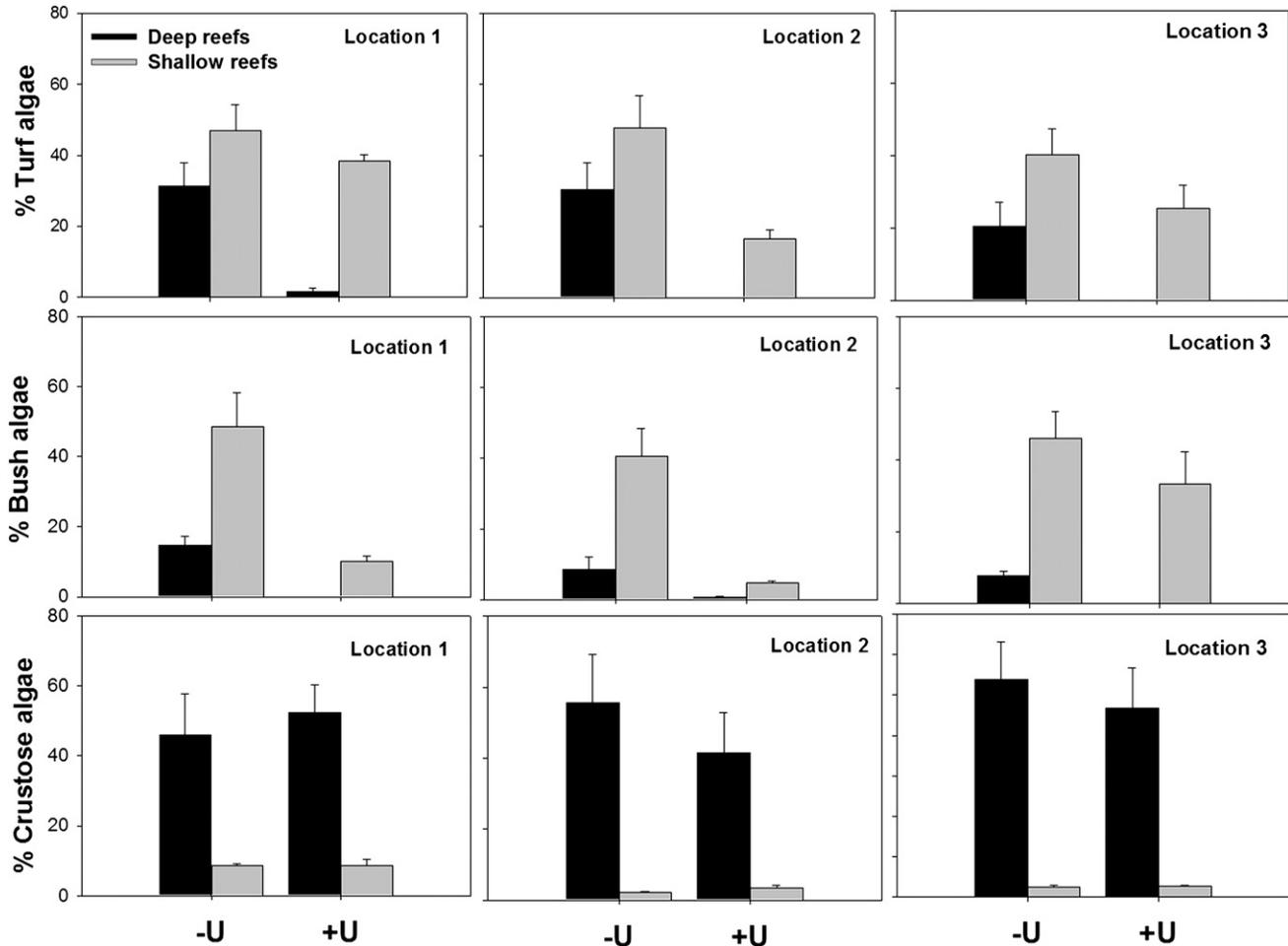


Figure 2. Mean percent coverage of each morphological group subjected to sea urchin removal (-U) or preserved at natural densities of sea urchins (+U) at shallow (gray bars) and deep (black bars) strata at the end of the experimental period. Error bars are \pm SE of means ($n = 8$).

to create patterns in the organization of subtidal, benthic assemblages. Differences in depth not only maintain differences in the composition and structure of algal assemblages, but can also give rise to divergence during succession when the densities of major grazers are altered. In this context, bushlike algae increased more in abundance (i.e., cover) in the shallow than deep waters when urchins were removed; a pattern that was not observed for turf algae. Such a result demonstrates the capacity for depth to impose a strong synergistic effect that facilitates the assembly and maintenance of bushlike algae in shallow waters.

Typically, large patches where major grazers are excluded are colonized by a range of algal species, mainly via arrival of propagules from adjacent populations (Airoidi 2000). Differences in their abilities to survive and grow subsequently affect patch colonization. Because an increase in depth is linked with a decrease in light availability, and then a decline (limitation) in algal growth, the results of our experiment suggest that growth is more light limited for bushy algae relative to turf algae. This perception is in agreement with their different morphologies and ecologies (Steneck & Dethier 1994, McClanahan et al. 2003), and could partially explain the comparatively large increase in the cover of bushlike algae where sea urchins were removed, from the deep to the shallow stratum. In general, a filamentous (or a cushion-shaped) morphology is more efficient

than a bushy one to capture photosynthetically active radiation (PAR) light (Littler et al. 1983b; for example, self-shading is more limited relative to bushlike algae (Littler & Arnold 1980). Moreover, it is also possible that proximity to the source of propagule donors could explain some of these observations. Because extensive stands of bushlike algae dominate the community within the shallowest zone (0–3 m) in the study area (Tuya & Haroun 2006), these zones could supply propagules to the immediately adjacent strata (i.e., the shallow stratum in our experiment), because the dispersion of algal propagules generally shows a sharp, exponential decrease several meters away from the algal donor (Santelices 1990, Kendrick & Walker 1991, Coleman 2003). Obviously, several other potential factors (or even combinations) that vary with depth (e.g., wave-induced turbulence) could also affect each group differentially. Further experimental approaches are necessary to unravel the various proposed mechanisms behind the observed patterns. The lack of response observed for encrusting coralline algae may be explained by the short duration of the experiment. It is likely that both turf and bushlike algae did not have sufficient time to monopolize the entire available space within plots, which prevented the competitive exclusion of encrusting coralline algae. In addition, encrusting coralline algae are able to reduce settlement of

TABLE 3.

Results of multivariate and univariate ANOVA testing the effects of location (random factor), urchins (fixed factor with 2 levels and orthogonal to the previous factor), sedimentation (fixed factor with 2 levels and orthogonal to the previous factors), and plots (random factor with 2 levels nested within the 2nd order interaction between locations, urchins, and sedimentation) on the structure of algal assemblages and the percent coverage of each algal morphological group at the end of the experiment.

Source	df	Algal Assemblage			Turf Algae			Bush Algae			Crustose Algae		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P
Lo (location)	2	5,414	42.78	0.0002	1.09	4.73	0.0306	6.70	18.43	0.0002	483.29	119.90	0.0001
Ur (urchins)	1	5,649.7	7.21	0.0310	13.65	38.65	0.0249	27.33	28.82	0.0330	49.59	2.27	0.2711
Se (sedimentation)	1	1,861.4	5.32	0.0924	0.05	0.14	0.7485	0.67	4.12	0.1794	12.76	1.08	0.4075
Plot (Lo × Ur × Se)	12	126.5	0.81	0.7261	0.23	4.59	0.0000	0.36	2.51	0.0081	4.03	1.16	0.3265
Lo × Ur	2	784.1	6.19	0.0002	0.35	1.53	0.2564	0.94	2.60	0.1150	21.87	5.43	0.021
Lo × Se	2	349.7	2.76	0.0033	0.38	1.68	0.2275	0.16	0.45	0.6481	11.79	2.93	0.0923
Ur × Se	1	1,303.9	1.63	0.2876	1.29	1.47	0.3489	4.35	3.03	0.2237	0.84	0.05	0.8487
Lo × Ur × Se	2	800.93	6.32	0.0004	0.88	3.81	0.0524	1.13	3.13	0.0982	14.00	3.47	0.1055
Residual	72	156.7			0.05			0.14			3.46		

potential competitors, suggesting that they do not rely on grazing by herbivores (e.g., sea urchins) to prevent a complete swamping by erect algal species (Bulleri et al. 2002).

Finally, results from this experiment indicated that the structure of the algal assemblages at the shallow stratum was considerably more variable compared with algal assemblages at the deep stratum. These results support the notion that shallow environments are typically more variable, and more extreme, than deeper ones (Garrabou et al. 2002). Indeed, shallow habitats are notoriously affected by fluctuations in a suite of environmental factors, such as seawater temperature, turbulence and exposure to hydrodynamic forces, salinity, light, and so forth, through annual cycles (Denny 1988). As a result, substantial fluctuations in such a range of factors induce a high degree of environmental, and thus ecological, heterogeneity.

Effects of Urchin Removal on Algal Assemblages Between High and Low Levels of Sedimentation

An increase in the cover of both turf and bushlike algae was detected, again, where sea urchins were eliminated. However, patterns in the structure of these assemblages were irrespective of sedimentation levels. Filamentous algae may tolerate heavy sediment accumulations (Airoldi & Virgilio 1998, Airoldi 2003, Connell 2005). Similarly, encrusting coralline algae have been also experimentally observed to be unaffected by large sedimentation (Kendrick 1991, Vaselli et al. 2008), although negative effects of sediment are possible for some taxa (Airoldi

2003). For bushlike algae, the lack of response to a change in the level of sedimentation is somehow unexpected, particularly when coupled with a change in the densities of major grazers (Valentine & Johnson 2005). Several reasons can explain this outcome. First, it is possible that the dose added was insufficient to detect a significant change in these algal assemblages; it is also possible that the duration of the experimental period, and even the frequency of sediment additions, were not sufficient to detect a perceptible change in their macroscopic cover. The duration and intensity of sediment treatments greatly affect the outcome of these experiments (Airoldi & Cinelli 1997, Airoldi 2003, Vaselli et al. 2008). For example, the frequency of sediment additions might have been considerably long; it is possible that sediments were swept away by swells between any 2 consecutive additions. Second, it is also possible that bushlike algae in the study area may tolerate sedimentation more efficiently than previously suspected. Third, we cannot rule out the possibility that the experiment was carried out at a depth too deep for BA. At the moment, it is difficult to estimate the relative importance of these explanations. For example, despite

2D Stress: 0,1

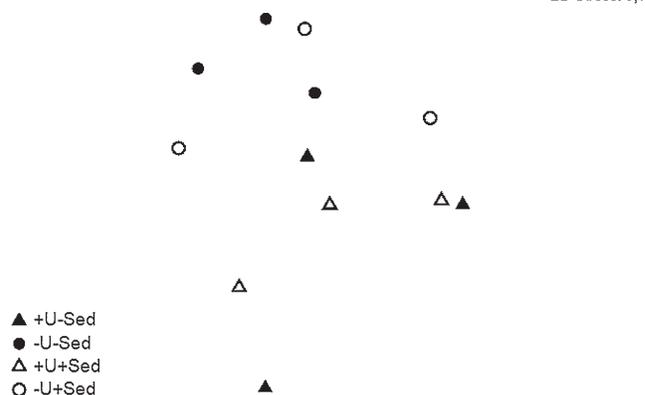


Figure 3. Two-dimensional nonmetric multidimensional scaling plot showing centroids of algal assemblages that were subjected to sea urchin removal (circles) or preserved at natural densities of sea urchins (untouched controls, triangles) at enhanced (open symbols) or ambient (filled symbols) levels of sedimentation at the end of the experimental period. Replicated plots have been averaged within each treatment for each of the 3 locations.

TABLE 4.

Results of pairwise comparisons of multivariate dispersion between sea urchin treatments (removals [-U vs. untouched controls [+U]) and levels of sedimentation.

Groups	t	P
+U -sediments vs. -U -sediments	58.242	0.058
+U -sediments vs. +U +sediments	14.399	0.078
+U -sediments vs. -U +sediments	16.404	0.067
-U -sediments vs. +U +sediments	60.828	0.003
-U -sediments vs. -U +sediments	39.072	0.088
+U +sediments vs. -U +sediments	0.501	0.438

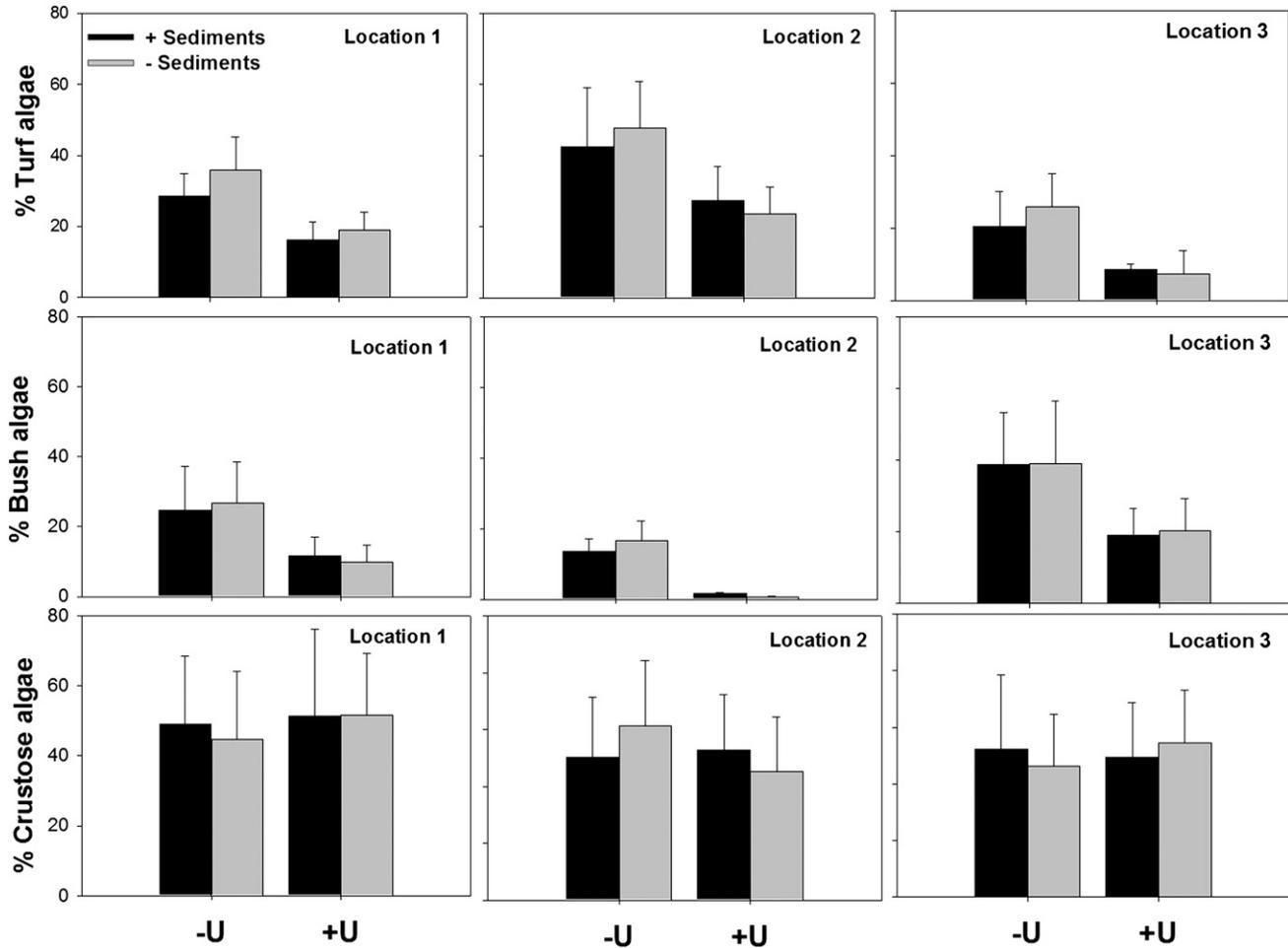


Figure 4. Mean percent coverage of each morphological group subjected to sea urchin removal (-U) or preserved at natural densities of sea urchins (+U) at enhanced (+sediments) or ambient levels (- sediments) of sedimentation at the end of the experimental period. Error bars are \pm SE of means ($n = 8$).

the fact that most studies dealing with the effects of sedimentation on macroalgae have experimentally added doses 1–2 orders of magnitude larger than ours (Airoldi & Virgilio 1998, Connell 2005), a slight reduction in the amount of sediments sinking over algal assemblages can affect the diversity and dominance of algae, particularly with regard to colonization of patches of bare rock (Airoldi & Cinelli 1997), similar to those plots where sea urchins were removed. Because species-specific responses to sediment-induced disturbances and the local characteristics of the regime of sedimentation considerably affect the response (Airoldi 2003), it is obvious that further experimental approaches are necessary to address the interac-

tive potential of sedimentation with biotic mechanisms (i.e., grazing, competition) shaping the organization of subtidal benthic assemblages in the study area.

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