

Habitat heterogeneity, sea urchin grazing and the distribution of algae in littoral rock pools on the west coast of Italy (western Mediterranean)

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ABSTRACT: The effects of habitat heterogeneity and grazing by sea urchins on the distribution of algae in littoral rock pools were investigated on the west coast of Italy (western Mediterranean) from February 1991 to April 1994. Sea urchins (*Paracentrotus lividus* and to a lesser extent *Arbacia lixula*) were removed by hand from 6 pools, chosen at random out of 12, throughout the study. The other 6 pools remained subject to natural densities of herbivores and served as controls. Two permanent plots were marked with epoxy putty in each pool. One plot was located just in front of the crevices sheltering the sea urchins while the other was marked 50 to 60 cm away. The following algal groups were monitored in these plots until March 1994: (1) articulated corallines, (2) coarsely branched algae, (3) *Cystoseira* spp., (4) filamentous algae, and (5) foliose algae. Extensive sampling of macroalgae was carried out in April 1994. Four replicated 100 cm² plots were randomly located at each distance from shelter in each pool and sampled by a nondestructive method. The results from the permanent plots indicated that the impact of sea urchins was greater close to the crevices for all the algal groups but the coarsely branched algae. In contrast, the large variability between pools often masked the importance of interactive effects between physical and biological factors at the end of the experiment. Nevertheless, reliance on shelter apparently constrained the effect of sea urchins on the filamentous algae and on *Cystoseira* spp., and thus on a conspicuous portion of the algal assemblage of the pools. The results of this study provide an example of how spatial heterogeneity and habitat complexity may affect the outcome of interactions between herbivores and algae.

KEY WORDS: Habitat heterogeneity · Sea urchin grazing · Macroalgae · Littoral rock pools · Field experiments

INTRODUCTION

Recent models of community organization have emphasized the importance of multiple causation, particularly the interplay among physical and biological processes, in explaining patterns of species distribution and diversity (Menge & Sutherland 1987, Hixon & Menge 1991). Steep gradients in the physical environment may produce variability in the abundance and distribution of populations simply as a consequence of different physiological tolerances of the species. This kind of segregation often occurs at relatively large spatial scales (Gaines & Lubchenco 1982, Barry & Dayton

1991, Dunson & Travis 1991). At smaller scales (within habitats), physical factors in the form of spatial heterogeneity may play an important role in regulating the intensity of biological interactions (Hawkins 1981, Hawkins & Hartnoll 1983, Lubchenco 1983, Sousa 1984, 1985, Connell & Keough 1985).

In marine benthic systems the intensity of predation and herbivory is often related to the presence of refuges for consumers. On emergent substrata, crevices in the rock may shelter carnivorous species that produce areas of intense predation just in front of their refuges (Menge 1978, Lively 1986, Sutherland & Ortega 1986, Fairweather 1988, Lively et al. 1993). Similarly, the availability of shelter may also affect the distribution and abundance of some species of sea urchins in subtidal habitats (Andrew 1993). The reliance on shelter by

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these species has been interpreted mainly as a defensive behavior against predation (Lawrence 1975, Vance & Schmitt 1979, Carpenter 1984, Scheibling & Hamm 1991). In these circumstances the effect of grazers is highly variable in space, being restricted to narrow areas around their refuges (Andrew 1993, Andrew & Underwood 1993). This contrasts with the dramatic impact produced by active fronts of sea urchins in other kelp beds (Chapman 1981, Dean et al. 1984, Dayton 1985, Harrold & Reed 1985, Johnson & Mann 1988). Therefore physical heterogeneity, predation and herbivory may give rise to complex interactions which explain some of the variability in community structure observed in both intertidal and subtidal habitats.

While many studies have described the effects of natural or experimental changes in the density of sea urchins in subtidal habitats (Duggins 1980, Sammarco 1980, Himmelman et al. 1983, Scheibling 1986, Fletcher 1987, Witman 1987, Andrew 1993, Andrew & Underwood 1993), little is known about their role in structuring algal assemblages in littoral rock pools (e.g. Paine & Vadas 1969). Recent investigations on the west coast of Italy (Benedetti-Cecchi & Cinelli 1992a, b unpubl.) indicated that the sea urchin *Paracentrotus lividus* may depend upon shelter in low-shore rock pools. Sea urchins aggregated in crevices in the rock and apparently grazed only in narrow areas just in front of their refuges. These areas were dominated by encrusting corallines and differed from the surrounding vegetation which was dominated by erect algae. These studies focused mainly on the effects of herbivores (including limpets) on patterns of recovery of patches of cleared space produced in dense stands of macroalgae. All these patches were relatively far from the crevices sheltering the sea urchins. Results indicated that the effects of herbivores were more evident during the early stages of colonisation but decreased with time. These effects were attributed mainly to limpets while the impact of *P. lividus* was considered minor.

Here we focus on the interactions between *Paracentrotus lividus* and macroalgae in a set of pools similar to those employed in previous investigations. Sea urchins were manipulated for 3 yr to determine whether the reliance on shelter by these herbivores affected the spatial distribution of algae within pools. Our prediction was that the removal of grazers would lead to the development of a dense stand of erect macroalgae close to crevices, while minor changes would occur far from them. The hypothesis underlying this prediction was contrasted with the alternative explanation of a negative effect of the crevices independent of the presence of sea urchins. Both hypotheses were tested against the background of natural variability in species distribution and abundance existing between pools

(see Astles 1993, Metaxas & Scheibling 1993, Metaxas et al. 1994). This procedure allowed a rigorous assessment of the ecological relevance of these hypotheses across the study site.

MATERIALS AND METHODS

This study took place on the exposed rocky shore south of Livorno, Italy (43° 30' N, 10° 20' E) from February 1991 to April 1994. Pools ranged in size from 3 to 10 m² and were located from 0.1 to 0.3 m above mean low level water (tidal range of 0.3 m). A total of 12 pools distributed along 2 km of coast was used for experiments. Detailed descriptions of this system have been reported elsewhere (Benedetti-Cecchi & Cinelli 1992a, b). Briefly, the pools supported dense stands of canopy-forming species consisting of *Cystoseira brachycarpa* var. *balearica* and *C. compressa*, interspersed among patches of encrusting and turf-forming algae. Filamentous algae also occurred as epiphytes on the other plants or as early successional species in recently disturbed gaps. The most common herbivores were the sea urchins *Paracentrotus lividus* (specimens of *Arbacia lixula* also occurred in some pools) and limpets (*Patella aspera* and *Patella caerulea*). Sea urchins were abundant in crevices while limpets occurred in patches dominated by encrusting corallines or open space.

Densities of *Paracentrotus lividus* and *Arbacia lixula* were reduced by hand removals from 6 pools chosen at random from February 1991 to April 1994. Visits every 4 wk were sufficient to maintain treatment conditions (see 'Results'). The density of sea urchins was estimated at 2 to 4 mo intervals until March 1994 in two 1 m² plots chosen at random in each pool. Abundances of *P. lividus* and *A. lixula* were combined in the results because few specimens of the second species were found during the study.

Two permanent plots were marked in each pool with small pieces of epoxy putty (Subcoat S, Veneziani) in February 1991. One plot was located at random in barren areas just in front of the refuges sheltering sea urchins. The other was located 50 to 60 cm from the crevices, usually in patches of erect macroalgae. Quadrats near the urchin refuges were 20 × 20 cm, while the more distant plots were 10 × 10 cm. This difference arose because the small plots were originally marked to follow natural fluctuations in algal abundance that were compared with changes occurring during succession in experimental clearings of the same size. The results of the colonisation experiment are reported elsewhere (Benedetti-Cecchi & Cinelli unpubl.). The quadrats were sampled at 2 to 4 mo intervals until March 1994. Plexiglas sheets the same size as the

quadrat to be sampled were used to estimate the percentage cover of the algae. A grid of 100 uniformly spaced dots was marked on the sheets and percentage values were obtained by intersection. In general, algae were combined into morphological groups (see also Benedetti-Cecchi & Cinelli 1992a, b) for representation of results and for statistical purposes. The following groups were considered: (1) articulated corallines (including *Corallina elongata* and *Halyptilon virgatum*); (2) coarsely branched algae (mainly *Halopteris scoparia* and *Laurencia obtusa*); (3) *Cystoseira* spp.; (4) filamentous algae (mainly *Cladophora rupestris*, *Polysiphonia* spp., *Sphacelaria cirrosa* and *Sphacelaria fusca*); and (5) foliose algae (consisting of *Dictyota dichotoma*, *Dictyopteris polypodioides* and *Padina pavonica*).

The data were analysed independently for each distance because of different quadrat sizes. In each case, the effect of sea urchins was tested using a multivariate analysis of variance (MANOVA) with sampling dates as the dependent vector. The Pillai trace statistic was used as it is robust to moderate violations of multinormality and multihomoscedasticity (Johnson & Field 1993). Not all dates could be incorporated into the response vector because this left no degrees of freedom for the error terms. Because minimising the number of response variables increased the power of the tests, dimensionality was reduced unless the assumption of homogeneity of within group covariance matrices was not violated. This resulted in the removal of 6 randomly chosen sampling dates from the analysis on the articulated corallines and of 4 dates from the other groups. The assumption of homogeneity of covariance matrices was tested using Bartlett's modification of the likelihood ratio test provided by the SAS statistical package (SAS 1989).

Because the analyses described above were done independently for each distance from the crevices, it was not possible to test for interactions between distance and herbivores. To provide a more rigorous assessment of these interactions, the experimental pools were sampled extensively in April 1994. Four plots of 100 cm² were randomly sampled at each distance in each pool using the same technique described above. These data were analysed using 3-factor mixed model ANOVAs with herbivores (natural density vs reduced density) and distance from crevices (close vs far) as fixed, orthogonal factors, and pools nested in herbivores, but orthogonal to the distances, as the random variable. For all the analyses, percentage cover values were arcsine-transformed to remove heteroscedasticity after Cochran's test (Winer 1971). In addition, after each ANOVA the error terms were plotted against the dependent variable to check for strong deviations from normality (Sokal & Rohlf 1981).

RESULTS

Patterns in the density of sea urchins

There were no significant differences among treatments (herbivores removed and controls) in the density of sea urchins prior to manipulation, nor there were differences between pools (2-factor nested analysis of variance: $F_{(1,10)} = 2.56$, $p > 0.05$ for treatment and $F_{(10,12)} = 2.22$, $p > 0.05$ for pools). Natural densities ranged from 9.4 ± 3.4 to 24.3 ± 8.00 ind. m⁻² (means \pm SE, $n = 12$) (test diameters ranged from 1 to 8 cm) with a marked increase during the first year of monitoring and a slight decline thereafter (Fig. 1). Monthly visits were sufficient to effectively reduce the abundance of sea urchins in treatment pools. Densities fluctuated from 3.7 ± 1.3 to 0.8 ± 0.3 ind. m⁻² in pools where sea urchins were removed periodically (Fig. 1). The mean number of sea urchins found in these areas, expressed as a percentage of the number found in unmanipulated plots at each sampling date, was $11.8 \pm 4.3\%$ (mean \pm SE, $n = 13$).

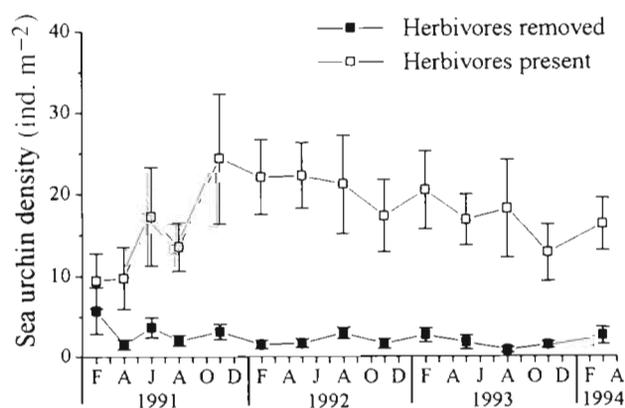


Fig. 1 Mean density (\pm SE) of sea urchins from 1 m² plots in littoral rock pools over time. Data pooled across pools, $n = 12$

Permanent plots

There were marked temporal fluctuations in the percentage cover of the articulated coralline algae (Fig. 2). Peaks of abundance occurred in November of all years, apparently as a seasonal trend. Sea urchins reduced the cover of these algae either far from (Fig. 2A) or close to (Fig. 2B) the crevices, their effect being highly significant in the latter case (Table 1) where peaks of abundance disappeared.

Removal of *Paracentrotus lividus* and *Arbacia lixula* did not exert any apparent effect on the cover of the coarsely branched algae far from the crevices (Fig. 3A).

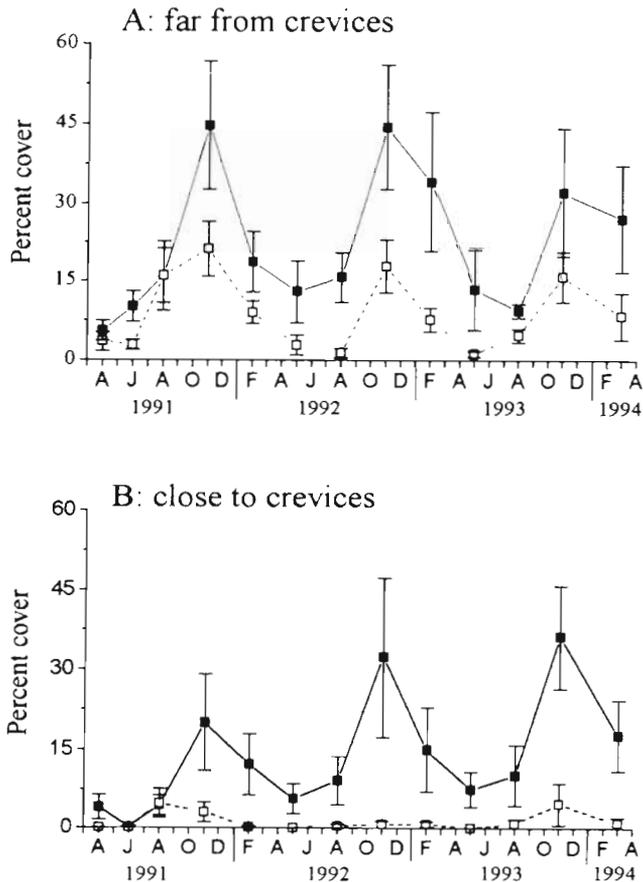


Fig. 2. Mean percentage cover (\pm SE, $n = 6$) of articulated coralline algae in littoral rock pools over time. (A) Patterns in 100 cm² plots marked at a distance of 50 to 60 cm from the crevices. (B) Patterns in 400 cm² plots marked just in front of the crevices. (■) Pools maintained at reduced densities of sea urchins. (□) Pools exposed at natural densities of sea urchins

Patterns of abundance did not exhibit any clear temporal trend, while the large standard error bars indicated a great variability between pools. Although no significant effect of sea urchins was found (Table 1), inspection of graphs suggested a greater impact of these grazers close to their refuges (Fig. 3B). However, percentage cover values were generally lower than those observed far from shelter, either in treatment or control pools.

Sea urchins did not exert any effect on *Cystoseira* spp. far from their refuges (Fig. 4A), while the removal of grazers induced a significant increase in algal abundance close to shelter not observed in control pools (Fig. 4B, Table 1). Temporal changes in the percentage cover of *Cystoseira* spp. were evident far from the refuges sheltering the sea urchins, with peaks of abundance occurring in spring (Fig. 4A).

Temporal variability was also a feature of the last 2 groups of plants considered in this section: the

filamentous and foliose algae. Peaks of abundance occurred during summer for the former group (Fig. 5) while temporal changes were less predictable in the latter case (Fig. 6). No significant effects of sea urchins were found far from shelter either for the filamentous or foliose algae (Figs. 5A & 6A, Table 1). In contrast, significant results emerged for both groups in front of the crevices. Finally, the large standard error bars observed for the foliose algae indicated a great variability between pools.

Extensive sampling

The extensive sampling of macroalgae carried out in April 1994 allowed formal tests on the herbivore \times distance interactions and an estimation of the natural variability between pools. Herbivores significantly reduced the abundance of the articulated coralline and coarsely branched algae (Fig. 7A, B) (Table 2) and interacted significantly with the distance from shelter in determining the distribution of the filamen-

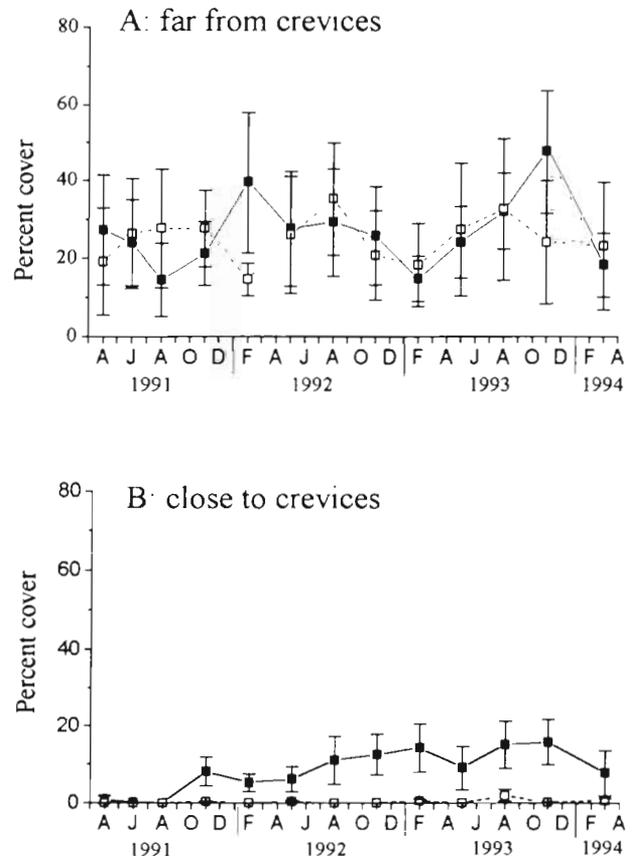


Fig. 3. Mean percentage cover (\pm SE, $n = 6$) of coarsely branched algae in littoral rock pools over time. Symbols as in Fig. 2

Table 1. Results of multivariate analysis of variance (MANOVA) on the effect of sea urchins on algal cover close to and far from crevices. Significant p-values ($p < 0.05$) are given in **boldface**

Algal groups	Close to crevices					Far from crevices				
	Pillai trace	F	Hip. df	Error df	p	Pillai trace	F	Hip. df	Error df	p
Articulated corallines	0.9985	383.2	7	4	0.0001	0.9838	13.5	9	2	0.0709
Coarsely branched algae	0.7500	1.1	8	3	0.5128	0.5012	0.2	9	2	0.9553
<i>Cystoseira</i> spp.	0.9926	29.7	9	2	0.0330	0.6307	0.4	9	2	0.8743
Filamentous algae	0.9928	30.8	9	2	0.0318	0.7103	0.5	9	2	0.7855
Foliose algae	0.9948	42.6	9	2	0.0231	0.7103	0.5	9	2	0.7855

tous plants (Fig. 7D) (Table 2). Grazing by sea urchins did not affect the percentage cover of *Cystoseira* spp. nor that of foliose algae (Fig. 7C, E) (Table 2). With the exception of the filamentous species, no other group of algae was interactively influenced by herbivores and distance from shelter (Table 2). Spatial variability was very large both between and within pools: several interactions between distance and pools were significant in the analyses (Table 2). For

example, the abundance of both the coarsely branched algae and *Cystoseira* spp. was greater far from the refuges of sea urchins in some pools, while the reverse occurred in other cases (Fig. 7B, C). Differences due to crevice effects were more consistent across pools for the filamentous and foliose algae. Interactive effects were not observed for these groups, but the differences between pools were still highly significant (Table 2).

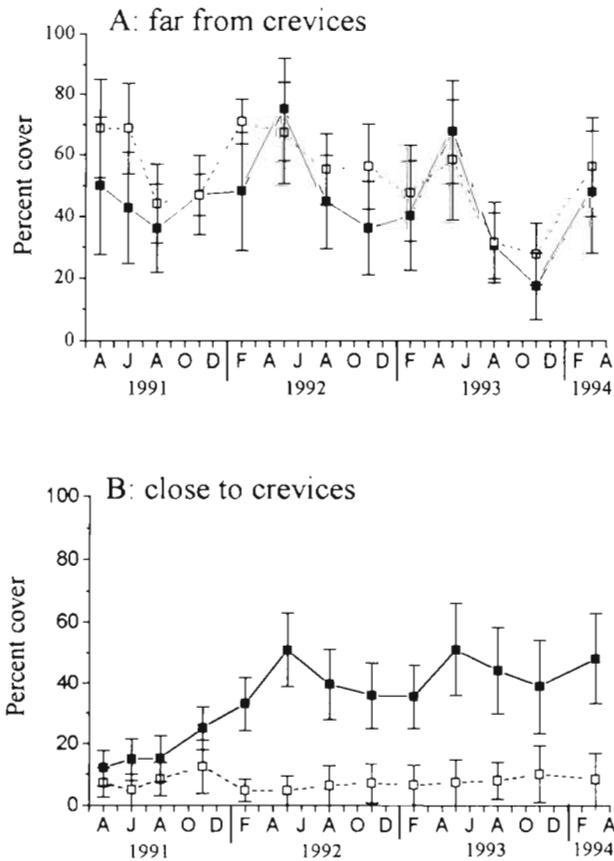


Fig. 4. Mean percentage cover (\pm SE, $n = 6$) of *Cystoseira* spp. in littoral rock pools over time. Symbols as in Fig. 2

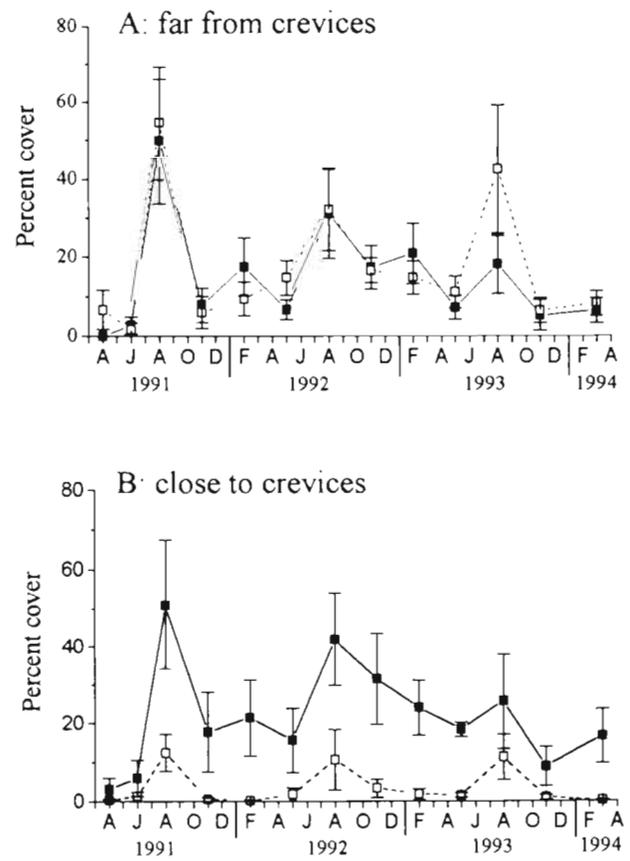


Fig. 5. Mean percentage cover (\pm SE, $n = 6$) of filamentous algae in littoral rock pools over time. Symbols as in Fig. 2

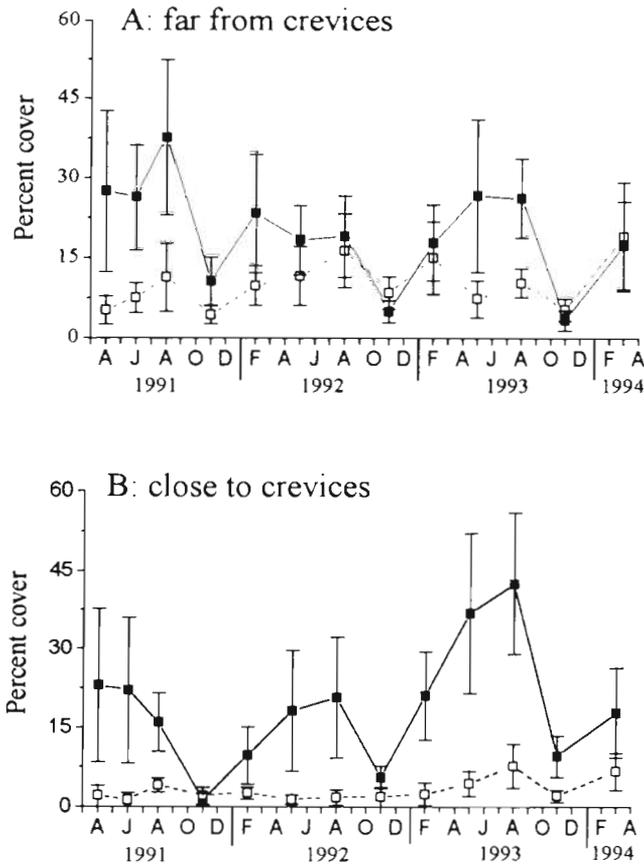


Fig. 6. Mean percentage cover (\pm SE, $n = 6$) of foliose algae in littoral rock pools over time. Symbols as in Fig. 2

DISCUSSION

A major goal of this investigation was to test whether the reliance on shelter by sea urchins constrained their impact on the algal assemblage. Qualitative comparisons of the overall effect of treatments at different distances from shelter indicated that the impact of herbivores was greater close to their refuges for all groups of plants but the coarsely branched algae. More detailed analyses were done by examining interactions between the factors herbivores and distance from shelter by the end of the study. A significant interactive effect was found only for the filamentous algae, but the large variability between pools might have masked the importance of these interactions. This seems particularly true for *Cystoseira* spp. The percentage cover of these algae was drastically reduced by sea urchins in front of their refuges, while the removal of herbivores could result in a greater abundance of *Cystoseira* spp. close to the crevices. Despite this, the interaction between herbivores and distance was not significant ($p = 0.071$).

The brown algae of the genus *Cystoseira* are among the most intensively grazed plants in subtidal habitats of the Mediterranean. Although formal experimental investigations are not common in this basin, correlative and observational data suggest that *Paracentrotus lividus* may transform dense beds of *Cystoseira* into barren areas dominated by encrusting corallines (Verlaque & Nedelec 1983, Verlaque 1984). Verlaque (1984) reported that densities of sea urchins ranging from 7 to 20 ind. m^{-2} (~5 cm test diameter)

Table 2. Effects of treatments on the cover of articulated corallines, coarsely branched algae, *Cystoseira* spp., and filamentous and foliose algae in April 1994 (data were angular transformed to meet the assumption of homoscedasticity after Cochran's test). Herbivores (H) and distance (D) were fixed factors; pools were nested within herbivores and were random. For filamentous algae, the interaction among distance and pools [D \times Pools (H)] was not significant at $p = 0.25$ and the mean square and degrees of freedom for this term were pooled with those of the residual (Winer 1971, Underwood 1981). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns: $p > 0.05$

Source of variation	df	Articulated corallines		Coarsely branched algae		<i>Cystoseira</i> spp.		Filamentous algae		Foliose algae	
		MS	F	MS	F	MS	F	MS	F	MS	F
Herbivores	1	0.7483	5.92*	2.6069	8.43*	0.8183	0.52ns	0.6058	5.04*	1.5339	3.57ns
Pools (H)	10	0.1264	3.95***	0.3091	5.07***	1.5735	18.70***	0.1202	3.49***	0.4299	6.78***
Distance	1	1.1068	11.09**	0.5285	3.35ns	3.7295	8.76*	0.1018 ^a	2.89ns	0.0391	0.33ns
H \times D	1	0.0103	0.10ns	0.0363	0.19ns	1.7386	4.09ns	0.1873 ^a	5.31*	0.1567	1.33ns
D \times Pools (H)	10	0.0998	3.12**	0.1576	2.58**	0.4251	5.05***	0.0413	1.20ns	0.1176	1.85ns
Residual	72	0.0320		0.0610		0.0842		0.0344		0.0634	
Pooled ^b	82							0.0353			
Cochran's test		C = 0.21 $p > 0.05$		C = 0.14 $p > 0.05$		C = 0.14 $p > 0.05$		C = 0.14 $p > 0.05$		C = 0.14 $p > 0.05$	

^a Tested against the pooled mean square

^b Pooled term = D \times Pools(H) + Residual

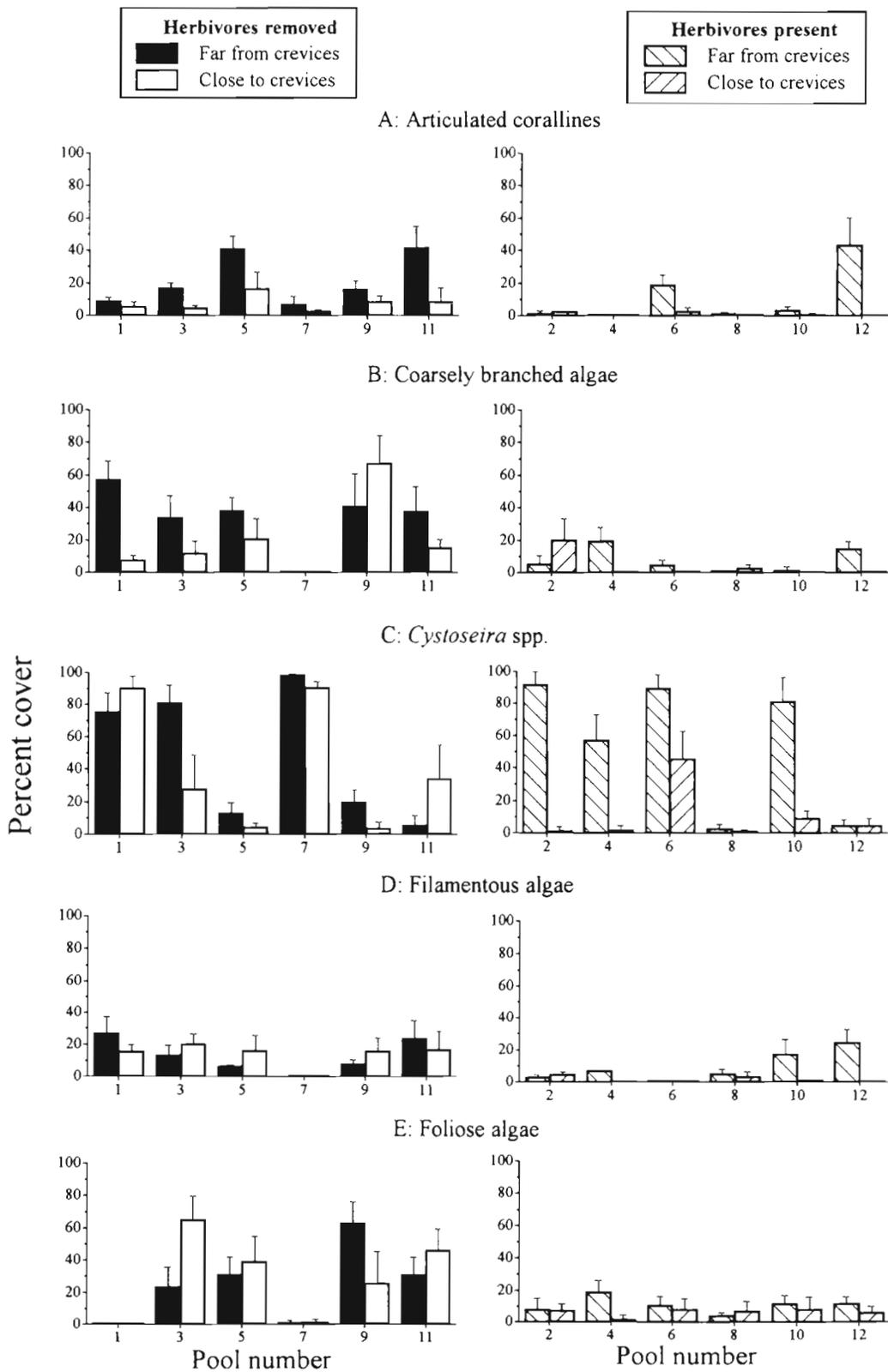


Fig. 7. Mean percentage cover (+SE, n = 4) of: (A) articulated corallines, (B) coarsely branched algae, (C) *Cystoseira* spp., (D) filamentous algae and (E) foliose algae in rock pools exposed at natural and reduced densities of sea urchins and at different distances from the crevices. Data from March 1994

may completely remove dense populations of erect macroalgae from the substratum in Corsica. Additional evidence indicating that sea urchins are involved in the maintenance of barren areas in the Mediterranean comes from recent studies carried out along the southeast coast of Italy (Fanelli et al. 1994, pers. comm.). There, denudation mainly occurred as a consequence of human activity, but sea urchins rapidly invaded the disturbed areas probably affecting the subsequent patterns of recolonisation. In contrast, complete removal of erect macroalgae by sea urchins was never observed in rock pools. Despite the high densities of these grazers (up to 24.3 ± 8 ind. m^{-2}) (mean \pm SE), stands of *Cystoseira* spp. persisted throughout the study just 50 cm from crevices sheltering the sea urchins. The removal of grazers, however, allowed the development of *Cystoseira* spp. also in areas very close to the refuges (Figs. 4B & 7C, Table 1). These results suggested that the sheltering behavior of sea urchins was a key factor allowing their coexistence with *Cystoseira* spp. in the same pools. Similar conclusions have been drawn for the filamentous algae, for which all the analyses highlighted a remarkable interactive effect between grazing and distance from crevices (Figs. 5B & 7D) (Tables 1 & 2). These results provide an example of how spatial heterogeneity and habitat complexity may affect the outcome of interactions between herbivores and algae (e.g. Sousa 1979, Moreno & Sutherland 1982, Underwood & Jernakoff 1984, Andrew 1993).

Although patterns of movement of *Paracentrotus lividus* and *Arbacia lixula* were not monitored in this study, the results discussed above indicated that the feeding activity of these consumers was limited in space. Probably, their reliance on shelter was in response to light that can be very intense in these shallow habitats. On several occasions individuals of *P. lividus* were seen covering themselves with objects such as algae, valves of mussels or plastic fragments. Circumstantial observations, however, suggested that sea urchins did not emerge at night to forage (Benedetti-Cecchi pers. obs.). Wave action could also have affected the activity patterns of these herbivores. Pools low on the shore were highly disturbed during storms at this exposed site (see below) and this could have restricted the urchins to crevices. Finally, large predators were absent from the rock pools and other potential consumers, such as crabs, often were found in the same crevices with sea urchins. Therefore, predation was probably of minor importance in determining the sheltering behavior of these herbivores.

The results were less clear for the articulated, coarsely branched and foliose algae. No significant

effects due to the removal of sea urchins were found close to the crevices for the coarsely branched algae, nor were there significant interactions between grazing and distance from shelter for all these groups by the end of the study. In addition, there was some evidence indicating that the impact of sea urchins on the articulated coralline algae was not restricted in areas close to shelter. A possible explanation for these results would be that sea urchins explored the whole habitat surrounding their refuges with very short visits (undetected by our frequent and long-term observations) that permitted removal of small plants but not canopy species. An alternative but not mutually exclusive interpretation would involve competitive interactions between *Cystoseira* spp. and the other groups of plants. As indicated by early experiments (Benedetti-Cecchi & Cinelli 1992a, b) an adult canopy of *Cystoseira* spp. may greatly reduce the cover of the other groups of algae, collectively referred to as turfs. Therefore, the occurrence of dense stands of canopy species in the experimental pools, and their rapid increase in abundance after the removal of sea urchins near to crevices, could have buffered the response of the other plants (particularly that of the coarsely branched algae) to any interactive effect of grazing and distance from shelter. These considerations did not apply to the filamentous algae probably because competitive interactions between these plants and *Cystoseira* spp. were negligible due to the epiphytic habitat of the former species (Benedetti-Cecchi & Cinelli unpubl.). Further studies involving manipulation of the physical environment (e.g. shelter; see Andrew 1993) and also focusing on the foraging behavior of sea urchins would help to elucidate interactions between urchins and macroalgae.

Distance from shelter also affected the distribution of macroalgae independently of the presence of sea urchins. Although patterns were highly variable between pools (note the significant distance \times pools interactions in Table 2) the abundances of the articulated corallines, the coarsely branched algae and *Cystoseira* spp. were all generally greater far from the crevices. There are several potential explanations for these results. First, the areas close to the refuges could have represented a microhabitat of low quality for settlement and recruitment of macroalgae, e.g. because of shading, eddies in the circulation of water, sedimentation. Some studies have highlighted the negative effects of these physical factors on algal propagules (Vadas et al. 1990, 1992 & references therein, Brawley & Johnson 1991). Second, herbivores other than sea urchins might have used the crevices as refuges, although this was not supported by direct observation (Benedetti-Cecchi pers. obs.).

Low numbers of limpets, close to the refuges but virtually absent far from them because of the dense stands of algae (Benedetti-Cecchi & Cinelli 1992b), might have contributed to spatial variability within pools. Third, the areas close to shelter could have experienced different regimes of physical disturbance than the others. In some pools refuges were represented by boulders arranged one over the other rather than by cracks in the rock. During storms, these boulders might have scoured the substratum and removed some adjacent algae. Although rare, these events occurred during the study (Benedetti-Cecchi pers. obs.).

Rock pools are often described as very variable systems (Dethier 1984, Astles 1993, Metaxas et al. 1994) and the results presented here are consistent with this view. Variability in the physical environment of the pools (e.g. the different nature of the refuges mentioned above), heterogeneity in the distribution of grazers other than sea urchins and patchiness in algal recruitment (Underwood & Denley 1984, Reed et al. 1988, Menge et al. 1993) are all potential explanations for the significant differences between pools and distance \times pools interactions reported above. These results highlight the importance of random factors and multiple causation in affecting the distribution of macroalgae in littoral rock pools. They also warn against generalizations about the role of single ecological processes, even at the small spatial scale. Given the high degree of variability, considerable effort must be planned for future studies in this system, particularly if ecological processes are to be detected with powerful experimental tests.

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