Grazing by the sea urchins *Arbacia lixula* L. and *Paracentrotus lividus* Lam. in the Northwest Mediterranean

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Abstract

The sea urchins *Arbacia lixula* and *Paracentrotus lividus* are common on shallow subtidal reefs in the Mediterranean. Previous studies on the ecology of these species reported that *P. lividus* is generally more abundant on horizontal or gently sloping substrata, where it forages mainly on erect algae. In contrast, *A. lixula* is more common on vertical substrata and it is considered a main grazer of encrusting coralline algae. Observations on some rocky shores in the Ligurian sea indicated that *P. lividus* occurs mainly in crevices at the bottom of the vertical walls, and that neither species is present on horizontal or sub-horizontal substrata. In this study we investigated the distribution and abundance of the two species of sea urchins on vertical substrata at different spatial scales and through time. A field experiment was used to test whether *A. lixula* constrained the distribution of *P. lividus* on vertical substrata, and to test for the predicted differences in the effects of the 2 species on assemblages of algae and invertebrates. Four treatments were used: (1) control (sea urchins left untouched); (2) *A. lixula* removed, *P. lividus* present; (3) *A. lixula* present, *P. lividus* removed, and (4) both species removed. The effects of sea urchins on colonising algae and invertebrates were examined after 6, 12 and 18 months. *A. lixula* was consistently more abundant than *P. lividus* on patches of vertical substrata, but the removal of *A. lixula* did not affect the abundance of *P. lividus*. There was no effect of *A. lixula* on encrusting corallines, but the cover erect algae increased and the number of limpets decreased significantly where *A. lixula* was removed. *P. lividus* had only a minor impact on the assemblage, probably due to its low abundance. *A. lixula* had effects close to those predicted for *P. lividus*, suggesting that the ecological role of these herbivores may be more similar than previously thought. The implications of these results for the management of the edible sea urchin, *P. lividus*, are discussed. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Sea urchins have important effects on the structure and dynamics of assemblages of species in coastal habitats, including seagrass meadows (Valentine and Heck, 1991), kelp beds and other assemblages of macroalgae (Lawrence, 1975; Sousa et al., 1981; Hawkins and Hartnoll, 1983; Himmelman et al., 1983; Scheibling, 1986; Witman, 1987; Johnson and Mann, 1988; Andrew, 1993; Andrew and Underwood, 1993; Leinaas and Christie, 1996), and littoral rock pools (Paine and Vadas, 1969; Benedetti-Cecchi and Cinelli, 1995). When at high density, sea urchins can nearly eliminate erect macrophytes from large areas, producing the so-called 'barren habitat' dominated by encrusting corallines. The barren state may persist unless the abundance of sea urchins declines (Pearse and Hines, 1979; Scheibling and Stephenson, 1984).

Although qualitatively similar effects of sea urchins have been described in different regions, the direct and indirect consequences of the foraging activity of these grazers may vary greatly in space and time due to variation in their abundance, feeding preferences and behaviour (Lawrence, 1975; Duggins, 1981; Dean et al., 1984; Harrold and Reed, 1985; Andrew and Underwood, 1989). A complex set of physical and biological factors influence the foraging activity of sea urchins, including availability of food, presence of predators, water motion and availability of refuges (Vance and Schmitt, 1979; Cowen et al., 1982; Carpenter, 1984; Vadas et al., 1986; Johnson and Mann, 1988; Scheibling and Hamm, 1991; Andrew, 1993; Benedetti-Cecchi and Cinelli, 1995; Sala and Zabala, 1996). This heterogeneity may result in variable effects of sea urchins at large as well as small spatial scales (Elner and Vadas, 1990; Andrew, 1993, Hagen, 1995). Variability at small spatial scales may also be enhanced by the co-occurrence of different species of sea urchins with different ecological effects. For example, Dean et al. (1984) showed that *Strongylocentrotus franciscanus* (Agassiz) and *Lytechinus anamesus* persisted in the same barren areas by foraging on different life stages of kelps. Spatial and/or temporal variability in the relative abundance of these species is likely to introduce variability in the structure of populations of kelps.

In the Mediterranean, the sea urchins *Arbacia lixula* L. and *P. lividus* co-occur on hard substrata in shallow subtidal habitats. Although these species often coexist, *P. lividus* is generally more abundant on horizontal or gently sloping surfaces, while *A. lixula* is more common on vertical substrata (Kempf, 1962; Regis, 1978). On exposed shores, *A. lixula* sometimes occurs in the shallower part of vertical walls, while *P. lividus* is found at greater depths (Chelazzi et al., 1997). This pattern is often explained in terms of a greater resistance of *A. lixula* to wave action. The alternative explanation can be proposed that *A. lixula* restricts *P. lividus* to deeper areas of the reef, but little experimental work has been done to distinguish between the two models. *P. lividus* is reported to feed mainly on fleshy algae and suspended organic particles, while encrusting corallines seem to be the preferred food of *A. lixula* (Kempf, 1962; Regis, 1978; Verlaque and Nedelec, 1983; Frantzis et al., 1988). This evidence, however, comes mainly from correlative studies on the distribution of sea urchins and algal vegetation and from analyses of gut contents. To date, there is no clear experimental evidence to assess whether *A. lixula* and *P. lividus* have different effects on algal assemblages in the Mediterranean (but see Kempf, 1962).

P. lividus is absent from horizontal or gently sloping substrata on the exposed rocky shores south of Livorno (northwest Mediterranean), contrary to what reported for other regions (see above). Observations in this area indicate that *P. lividus* occurs mainly in crevices at the bottom of vertical walls, while *A. lixula* is more abundant on vertical substrata (Benedetti-Cecchi et al., 1998). In the present study we tested whether *A. lixula* was consistently more abundant than *P. lividus* on vertical substrata at 2 spatial scales (among sites hundreds of metres apart, and among patches of substratum tens of metres apart) over a period of eight months. The hypothesis that *A. lixula* reduces the cover of the encrusting coralline algae and *P. lividus* affects erect algae was tested in a factorial experiment involving the orthogonal removal of the two species from patches of vertical substrata. This experiment was also used as a preliminary test of the hypothesis that *A. lixula* influenced the density of *P. lividus* in this habitat.

2. Materials and Methods

2.1. Study sites

This study was done on shallow subtidal reefs on the exposed rocky shores south of Livorno, Italy (43° 30′ N, 10° 20′ E), from June 1996 to January 1998. The substratum between 1 and 5 m in depth consisted of gently sloping rock platforms covered by dense stands of turf-forming algae, interrupted by vertical walls dominated by encrusting algae. The substratum was again sub-horizontal below these walls and extended seaward up to 10–12 m in depth. The extension of the vertical substrata between 1 and 5 m was estimated subjectively as 20 to 30% of that of nearly horizontal surfaces. The sea urchins *Arbacia lixula* L. occurred almost exclusively on the vertical substrata, while *Paracentrotus lividus* Lam. was more common in crevices that originated at the bottom of the rock walls (Benedetti-Cecchi et al., 1998). Urchins were absent from the rock platform and there was no evident sign of grazing in these areas. Grazing by sea urchins was important for the maintenance of patches of encrusting algae on the vertical walls, although the relative effect of the two species was unknown (Benedetti-Cecchi et al. 1998). Patches ranged from 10–50 m^2 in size and were represented mainly by *Lithothamnion* spp., *Peyssonnelia polymorpha* (Zanardini) Schmitz and *Peyssonnelia rosa marina* Boudouresque et Denizot. The most common invertebrates on vertical substrata were the limpets *Patella caerulea* L. and *Patella aspera* Roeding, the barnacle *Balanus perforatus* Bruguiére and encrusting bryozoans, in addition to the sea urchins. The algal turfs that monopolized the gently sloping substrata were a potentially important source of colonists for replenishment of vertical patches (Benedetti-Cecchi et al., 1998). The algal turfs comprised the geniculate corallines *Corallina elongata* Ellis et solander and *Haliptilon virgatum* (Zanardini) Garbary and Johansen, the fleshy algae *Dictyota dichotoma* (Hudson) Lamouroux, *Padina pavonica* (L.) Lamouroux and *Taonia atomaria* (Woodw.) J. Agarth, and filamentous algae of the genera *Ceramium*, *Polysiphonia* and *Sphacelaria*. Further details on these sites are in Benedetti-Cecchi et al. (1998).

2.2. Distribution of sea urchins

Spatial and temporal variability in patterns of abundance of the two species of sea urchins were examined by sampling patches of vertical substrata of 20–30 m^2 (1–5 m deep) at two sites (stretches of coastline about 300 m long and 600–700 m apart) at three times: June 1996, June 1997 and September 1997. At the beginning of the study, 18 patches were randomly selected from a larger number in each site (with adjacent patches being no closer then 15 m) and assigned randomly in groups of six to the three times of sampling. At each time in each site, three patches were used to estimate the abundance of *A. lixula* and three patches were used to sample *P. lividus*. The number of individuals was counted in four replicate quadrats of 0.25 m^2 within each patch; thus, the two species of sea urchins were sampled in different patches, and a different set of patches was used each time. This design ensured that the data were spatially and temporally independent. Animals with a test diameter less than 20 mm were not counted, as they were rare during the study.

Densities were analysed using analysis of variance with the following factors: Species (*A. lixula* vs. *P. lividus*, fixed and orthogonal), Site (2 sites, random and orthogonal), Time (three times, random and orthogonal), and Patch (three patches, random and nested within the Species × Site × Time interaction). Site and Patch estimated spatial variability at scales of hundreds and tens of metres, respectively. Time was random since the three dates of sampling were randomly selected within the study period to represent temporal variability at a scale comparable to that used in the manipulative experiment (see below). In this and subsequent analyses, Cochran's C test was used to test homogeneity of variances. Densities of sea urchins were transformed to natural logarithms to stabilise variances.

2.3. Experimental removals of P. lividus and A. lixula

To test the hypothesis that *A. lixula* negatively affects the density of *P. lividus* on vertical substrata, and to test for the separate and joint effects of these herbivores on macroalgae and other invertebrates, patches of vertical substrata were maintained clear of one or both species from July 1996 to January 1998. At the beginning of the study, 12 patches supporting both *A. lixula* and *P. lividus* were selected at random from a larger number available along 600 m of coastline, in an area that contained one of the sites also used for sampling densities of sea urchins (see above). These patches were assigned randomly in groups of three to each of the following treatments: (1) *A. lixula* and *P. lividus* untouched (+ A + P); (2) *A. lixula* removed, *P. lividus* untouched (−A + P); (3) *A. lixula* untouched, *P. lividus* removed (+ A − P), and (4) both *A. lixula* and *P. lividus* removed (−A − P). Patches ranged in size from 15–25 m^2 and were located in water 1–4 m deep. Visits every two weeks were sufficient to maintain the experimental treatments. During these visits sea urchins were removed by hand from the appropriate patches and released far from the experimental areas. *P. lividus* was removed from the vertical walls as well as from crevices.

Sea urchins were counted in the experimental patches with four replicate quadrats of 0.25 m^2 every two months from December 1997 to December 1998. The percentage

cover of algae, the barnacle *Balanus perforatus* and bryozoans, and the density of limpets, were monitored three times during the study using 20×20 cm quadrats. Nine quadrats were marked in each patch using small pieces of epoxy putty (Subcoat S, Veneziani) at the beginning of the experiment. These quadrats were placed haphazardly in the experimental patches but with the proviso that two quadrats were no closer than 40 cm. Three replicate quadrats were sampled randomly (without replacement) in each patch, after 6, 12 and 18 months from start. Percentage cover values were determined using visual estimates (Dethier et al., 1993; Benedetti-Cecchi et al., 1996) with the aid of a 20×20 cm acrylic sheet divided into 25 4×4 cm sub-quadrats, and a score from 0 to 4% was given to each small quadrat. Algae were grouped in categories for graphical presentation and statistical analyses. The following taxa were considered: (1) filamentous algae; (2) articulated corallines; (3) fleshy algae; (4) *Peyssonnelia* spp.; (5) encrusting brown algae, and (6) encrusting corallines. Percentage cover of encrusting algae was estimated after erect species were gently removed with a plastic brush.

Treatment effects were tested using analysis of variance. The effect of *A. lixula* on the density of *P. lividus* was analysed using a three-factor mixed model with *A. lixula* (presence vs absence) as a fixed effect, Patch as a random variable nested in *A. lixula*, and Time random and orthogonal to *A. lixula* and Patch. Six dates among those at which the density of *P. lividus* was estimated were selected randomly and included in the analysis. The responses of algae, barnacles and limpets to the experimental treatments were analysed using a four-factor analysis with *A. lixula*, *P. lividus* and Time (elapsed time) as fixed, orthogonal factors, and Patch as a random factor nested in the interaction *Arbacia × Paracentrotus* and orthogonal to Time. In some cases percentage cover values were square-root transformed while densities were log transformed to stabilise variances (after Cochran's C test). When appropriate, SNK tests were used to separate means at $\alpha = 0.05$.

3. Results

A. lixula was more abundant than *P. lividus* on vertical substrata (Fig. 1A, B). This difference was significant ($F_{1,5} = 26.7$, $P < 0.01$, after post-hoc pooling of the terms Species × Site + Species × Time + Species × Site × Time which were not significant at $P > 0.25$) and consistent in space and time (no other factor was significant in the analysis). The larger abundance of *A. lixula* was also evident in the experimental patches, although patterns were more variable in this case (note the large standard error bars in Fig. 1C). Manual removals reduced the abundance of sea urchins in the appropriate patches to near zero (Fig. 1C, D). The removal of *A. lixula* had no effects on *P. lividus*, either as a main factor or in interaction (Fig. 1D; Table 1). In contrast to the previous analysis on patterns of distribution of sea urchins, there were large and temporally inconsistent differences from patch to patch in the abundance of *P. lividus* (note the significant Time × Patch interaction in Table 1).

Sea urchins significantly affected the percentage cover of erect coralline algae in the permanent quadrats, although the abundance of these plants remained low throughout the experiment in all treatments (Fig. 2A). The impact of *A. lixula* was larger than that of *P.*
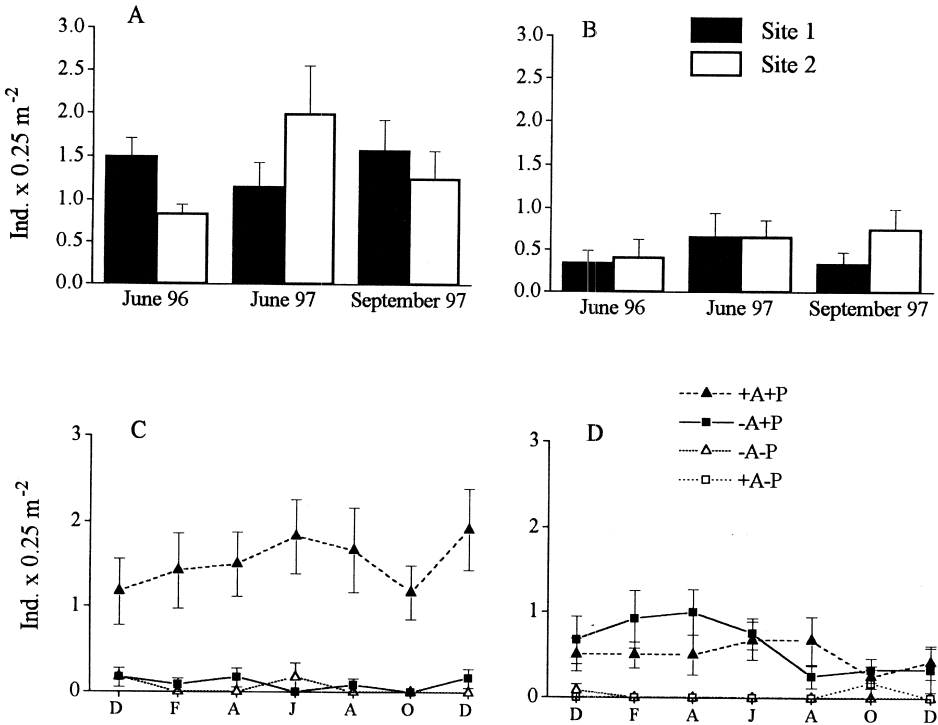
Fig. 1. Spatial and temporal patterns of abundance of *A. lixula* and *P. lividus*. Values are mean densities (and SE) of sea urchins in (A,B) two unmanipulated sites sampled at three different times (with $n = 4$ replicated quadrats pooled across three replicate patches for each species at each time), and (C,D) the experimental and control patches (with $n = 4$ replicate quadrats pooled across three replicate patches in each treatment).

Table 1
Analysis of variance on the effects of removing *A. lixula* from patches of vertical substrata on the density of *P. lividus*. Variances were homogeneous ($C = 0.07$, $P > 0.05$)

Source of variation	df	MS	F
A. lixula = Ar	1	0.694	0.22ns
Time = Ti	5	0.767	1.17ns
Ar × Ti	5	0.628	0.96ns
Patch (Ar)	4	6.430	9.81**
Ti × Patch (Ar)	20	0.655	1.75*
Residual	108		

* $P < 0.05$; ** $P < 0.01$; ns = not significant.

A Articulated corallines

B Filamentous algae

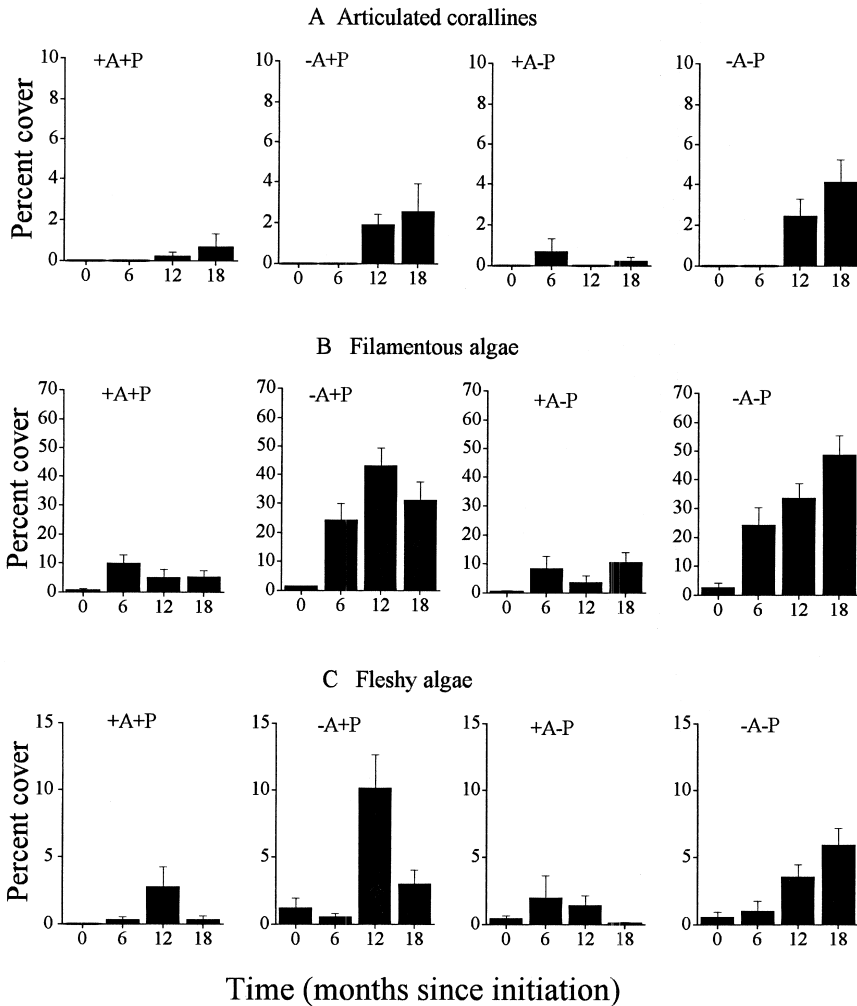

C Fleshy algae

Time (months since initiation)

Fig. 2. Percentage cover of erect algae in the four experimental treatments, with *A. lixula* (+ A) and *P. lividus* (+ P). Data are mean values (+ SE, $n = 9$) from three independent plots pooled across three replicate patches at each time.

lividus and these effects were more evident after 12 and 18 months from the beginning of the experiment, resulting in a significant *Arbacia × Paracentrotus × Time* interaction (Table 2 and SNK tests). The removal of *P. lividus* had minor effects on these algae (compare $+ A - P$ to $+ A + P$ in Fig. 2C).

The abundance of the filamentous algae was low in control patches and in patches where only *P. lividus* was removed. In contrast, the removal of *A. lixula* led to a drastic increase in the percentage cover of these algae through time (Fig. 2B). This resulted in a significant *Arbacia × Time* interaction with significantly more filamentous algae in $- A + P$ and $- A - P$ patches than in the other treatments (Table 2 and SNK tests).

Table 2
Analysis of variance on the effects of *A. lixula* and *P. lividus* on erect and encrusting algae

Source of variation	df	Articulated corallines		Filamentous algae		Fleshy algae		Encrusting brown algae		Encrusting corallines		*Peyssonnelia* sp.	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
A. lixula = Ar	1	5.148	34.78***	19710.01	39.22**	30.577	19.40**	6.750	0.09ns	1316.009	2.43ns	0.022	0.01ns
P. lividus = Pa	1	0.256	1.73ns	73.34	0.15ns	0.150	0.09ns	90.750	1.25ns	690.083	1.28ns	1.932	0.90ns
Ar × Pa	1	0.256	1.73ns	18.75	0.04ns	0.021	0.01ns	98.231	1.35ns	700.232	1.29ns	9.198[a]	4.35*
Patch (Ar × Pa)	8	0.148	0.49ns	502.50	2.49*	1.576	1.81ns	72.824	1.26ns	540.833	2.21*	2.154	1.02ns
Time = Ti	2	2.051	23.29***	501.40	2.61ns	12.804	30.970***	269.620	4.96*	1048.620	2.50ns	0.881	0.44ns
Ti × Ar	2	1.919	21.79***	990.29	5.15*	7.873	19.04***	54.528	1.00ns	377.120	0.90ns	0.481	0.24ns
Ti × Pa	2	0.069	0.79ns	659.45	3.43ns	3.883	9.39**	87.028	1.60ns	825.028	1.96ns	1.519	0.75ns
Ti × Ar × Pa	2	0.327	3.71*	225.08	1.17ns	1.947	4.71*	29.898	0.55ns	182.565	0.43ns	1.791	0.89ns
Ti × Patch (Ar × Pa)	16	0.088	0.29ns	192.10	0.95ns	0.413	0.47ns	54.366	0.94ns	420.153	1.71ns	2.013	0.95ns
Residual	72	0.301		0.871		2.109		57.602		244.889		201.96	
Cochran's test:		$C = 0.20$; $P > 0.05$		$C = 0.18$; $P > 0.05$		$C = 0.16$; $P > 0.05$		$C = 0.15$; $P > 0.05$		$C = 0.12$; $P > 0.05$		$C = 0.19$; $P > 0.05$	
Transformation:		Square root		None		Square root		None		None		Square root	

[a] Tested against the pooled term: Patch (Ar × Pa) + Residual (MS = 2.113; df = 80).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = not significant. Pooling procedure have been used according to Underwood (1997).

There were also significant differences among patches in the distribution of these algae (Table 2).

There were more fleshy algae in patches where *A. lixula* was removed ($-A + P$ and $-A - P$) than in the other treatments (Fig. 2C). These effects were more evident after 12 months from the start of the experiment and resulted in a significant *Arbacia* $\times$ *Paracentrotus* $\times$ Time interaction (Table 1 and SNK tests).

In contrast to the patterns described above, sea urchins had no effects on encrusting brown algae and encrusting corallines (Fig. 3A, B; Table 2). There were significant temporal changes in the percentage cover of the encrusting brown algae which were
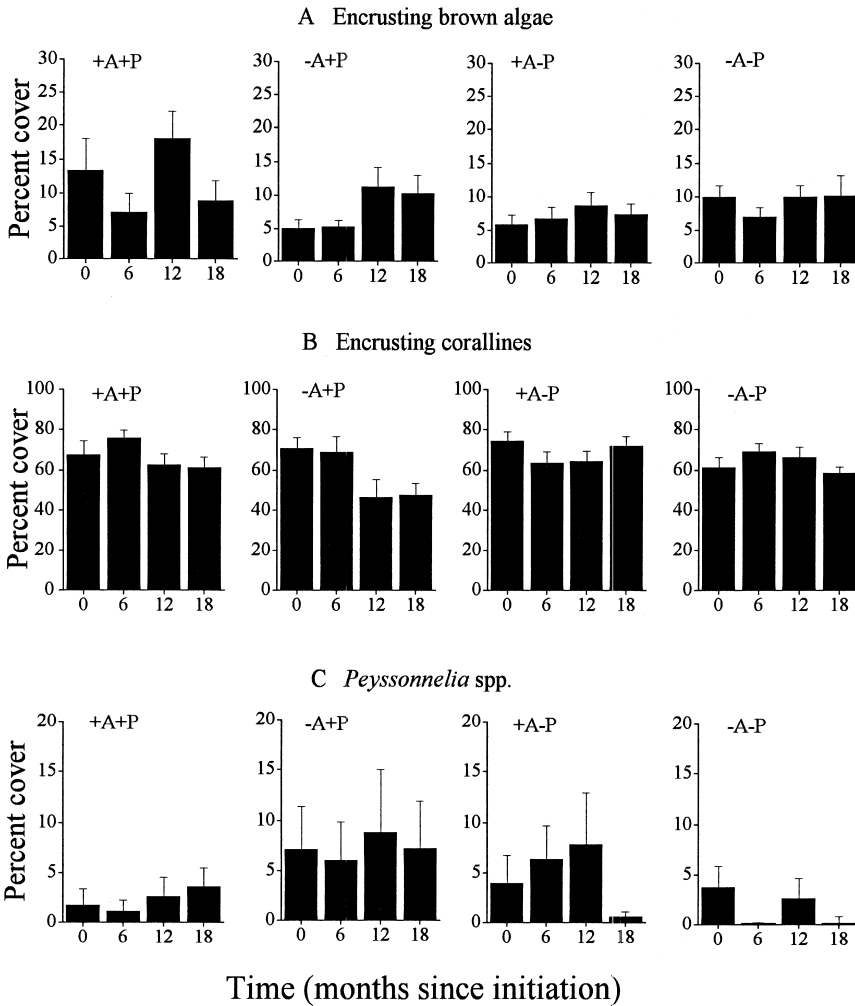

Fig. 3. Effects of *A. lixula* and *P. lividus* on the percentage cover of encrusting algae. Data are mean values ($+$ SE, $n = 9$) from three independent plots pooled across three replicate patches at each time. Codes for treatments as in Fig. 2.

more abundant after 12 months since the start of the experiment than at other times (Table 2 and SNK test). There were significant differences among patches in the distribution of the encrusting corallines (Table 2).

The 2 species of sea urchins interactively affected the percentage cover of *Peysson-nelia* spp. (Fig. 3C). Removing *A. lixula* in the presence of *P. lividus* had larger effects than removing both species simultaneously. That is, *Peyssonnelia* spp. was more abundant in $-A + P$ and $+A - P$ patches than in the other treatments, resulting in a significant *Arbacia* $\times$ *Paracentrotus* interaction (Fig. 3C; Table 2).

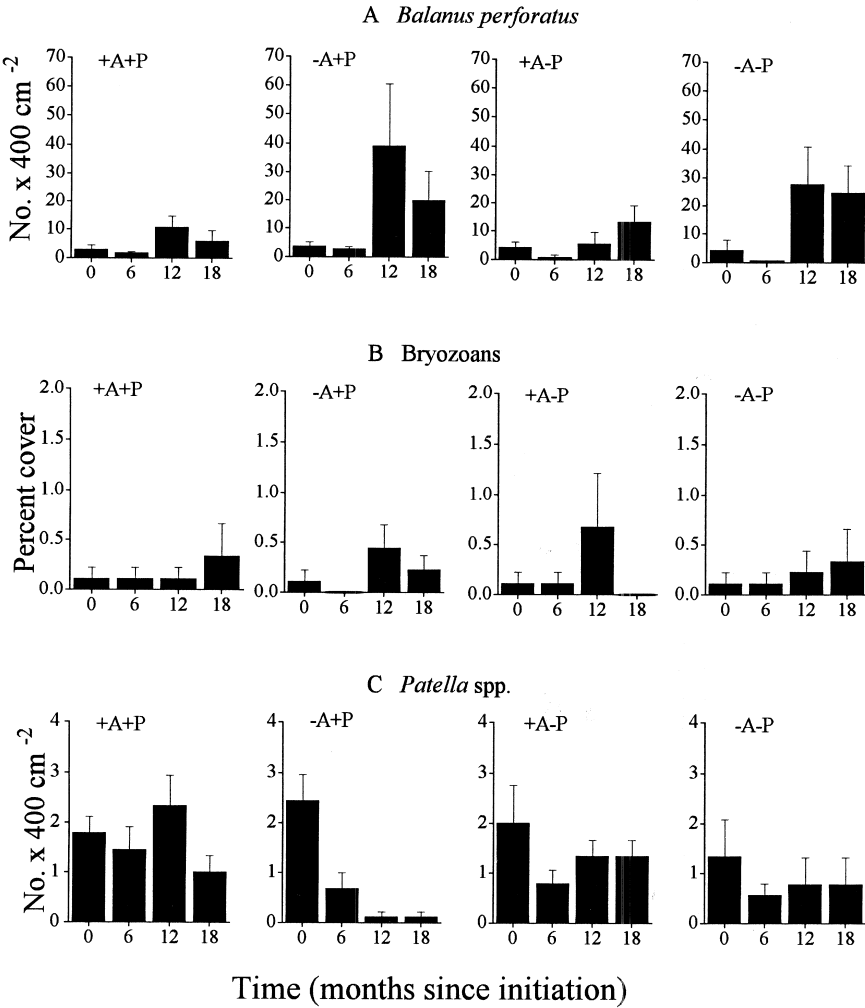There were no effects of sea urchins on *B. perforatus* and bryozoans (Fig. 4A, B;

Fig. 4. Effects of *A. lixula* and *P. lividus* on the abundance of invertebrates. Data are mean values (+ SE, $n = 9$) from three independent plots pooled across three replicate patches at each time. Codes for treatments as in Fig. 2.

Table 3
Analysis of variance on the effects of *A. lixula* and *P. lividus* on invertebrates

Source of variation	df	*Balanus perforatus*		Bryozoans		*Patella* spp.	
		MS	F	MS	F	MS	F
A. lixula = Ar	1	40.356	4.40ns	0.011	0.07ns	26.009	9.52*
P. lividus = Pa	1	0.474	0.05ns	0.001	0.01ns	0.454	0.17ns
Ar × Pa	1	0.057	0.01ns	0.011	0.07ns	2.676	0.98ns
Patch (Ar × Pa)	8	9.161	1.39ns	0.158	1.36ns	2.731	2.36*
Time = Ti	2	52.409	10.14**	0.158	1.36ns	2.259	1.72ns
Ti × Ar	2	14.216	2.75ns	0.030	0.27ns	1.815	1.38ns
Ti × Pa	2	7.366	1.43ns	0.035	0.31ns	0.704	0.53ns
Ti × Ar × Pa	2	2.115	0.41ns	0.168	1.49ns	2.259	1.72ns
Ti × Patch (Pa × Ar)	16	5.164	0.78ns	0.113	0.97ns	1.315	1.14ns
Residual	72	6.587		0.116		1.157	
Cochran's test:		C = 0.25; P > 0.05		C = 0.19; P > 0.05		C = 0.17; P > 0.05	
Transformation:		Square root		Ln (x + 1)		None	

* P < 0.05; ** P < 0.01; ns = not significant.

Table 3). There were temporal changes in the abundance of *B. perforatus* with significantly more animals after 12 and 18 months from the start of the experiment (Table 3 and SNK test). In contrast, the removal of *A. lixula* determined a significant decrease in the abundance of *Patella* in the experimental patches (Fig. 4C; Table 3). There were also significant differences among patches in the distribution of limpets (Table 3).

4. Discussion

The results indicated that *A. lixula* was consistently more abundant than *P. lividus* on patches of vertical substrata at the study sites. The model that *A. lixula* reduced the density of *P. lividus* in this habitat was not supported by the experimental results and must be rejected. Also the model that *A. lixula* affected the coverage of encrusting coralline algae while *P. lividus* foraged mainly on erect algae was not supported by the experimental evidence and must be rejected.

Previous studies on the distribution of these species of sea urchins in the Mediterranean have shown that *A. lixula* is generally more abundant on vertical substrata while *P. lividus* is common on horizontal or gently sloping surfaces in shallow subtidal habitats (Kempf, 1962; Regis, 1978). In contrast, *P. lividus* was nearly absent from subhorizontal substrata at our study sites while it occurred in crevices at the bottom of the vertical walls and intermixed with *A. lixula* on the vertical substrata. Although our experiment was not appropriate to test any specific mechanism of interaction between the two species of sea urchins, the lack of an increase in density of *P. lividus* after the removal of *A. lixula* suggested that factors other than interactions with this species restricted *P. lividus* to the bottom of the rocky walls. Physical processes may be invoked as an alternative explanation for these patterns. In particular, water motion may be more

detrimental to *P. lividus* than *A. lixula*. Regis (1978), argued that *A. lixula* is adapted to withstand wave shock due to the particular features of the sutures that connect the calcareous plates of the test of this species. In addition, during the experimental removal of sea urchins we observed that the force necessary to dislodge *A. lixula* from the substratum was much greater than that required to remove *P. lividus*. Possibly, this reflected the fact that *A. lixula* had, on average, a larger test diameter at our study sites (Benedetti-Cecchi et al., 1998), which translated into larger tube feet for adhesion to the substratum. Also, preliminary studies indicated that *A. lixula* tended to aggregate much more than *P. lividus* on these substrata, forming clumps of 4–5 individuals whose spines became highly intermingled (Bulleri et al., unpubl. data). It is likely that these clumps were more resistant to dislodgement by waves than single individuals. This model, however, requires formal experimental tests and is offered here only as a possible explanation for the observed patterns.

   A. lixula had a strong influence on the abundance of several groups of algae on vertical substrata. The most drastic effects of this species were on filamentous algae. These plants increased in cover up to 40–50% in patches where *A. lixula* was removed, while in control patches their cover was never greater than 10%. In some cases there were interactive effects between *A. lixula* and *P. lividus*. For example, the removal of *P. lividus* enhanced the abundance of the articulate corallines and fleshy algae, but only when *A. lixula* was also removed. In contrast, the removal of *A. lixula* resulted in a significant increase in the abundance of these plants independently of the manipulation of *P. lividus*. Also the abundance of *Peyssonnelia* spp. was interactively affected by the 2 species of sea urchins, but the nature of this interaction was different. Specifically, the coverage of *Peyssonnelia* increased when either *A. lixula* or *P. lividus* were removed, but these algae did not grow as well when the 2 species of grazers were removed simultaneously. At present we do not have any solid explanation for this pattern that deserves further attention.

   In addition to influencing the abundance of macroalgae, *A. lixula* also affected the density of *Patella* in the experimental patches. Clearly, the presence of *A. lixula* significantly enhanced the number of limpets, possibly through the removal of macroalgae. Several studies have shown that sea urchins may have positive indirect effects on grazing gastropods and other invertebrates by removing erect algae that otherwise would monopolize the substratum (Ayling, 1981; Himmelman et al., 1983; Fletcher, 1987; Andrew and Underwood, 1993). Interestingly, we did not find any evidence of this effect in a previous study on grazing by sea urchins on shallow subtidal reefs south of Livorno (Benedetti-Cecchi et al., 1998). In the previous experiment we did not attempt to separate the effects of the 2 species of sea urchins, and this may explain the difference between that study and the present one.

   In several cases the effects of *A. lixula* (either alone or in interaction with *P. lividus*) changed through time. It is likely that these interactions reflected differences in patterns of growth of algae between patches where sea urchins were removed and control patches. The percentage cover of algae increased through time where grazing was reduced while remaining relatively constant (at low values) in the presence of sea urchins. The alternative explanation of temporal variability in the effects of sea urchins seems less likely to account for the observed results (see Fig. 2).

From the preceeding discussion, it is clear that *A. lixula* played a major role in regulating the distribution and abundance of erect algae and limpets in this system, while the effects of *P. lividus* were of minor importance. These outcomes contradict the findings of previous ecological studies on *A. lixula*, which predicted strong effects of this species on encrusting coralline algae but little to no effects on other components of the assemblage (Kempf, 1962; Regis, 1978; Verlaque, 1987). Also the proposition that *A. lixula* requires the cleaning of erect algae by *P. lividus* to persist, as suggested by Frantzis et al. (1988), was not supported by our results. These inconsistencies might reflect the fact that previous investigations derived conclusions about the ecological role of *A. lixula* mainly from observations and from the analysis of gut contents. These approaches may lead to erroneous conclusions about the effects of a species in his habitat.

In contrast, the lack of strong effects of *P. lividus* were probably due to the low density of this species on vertical substrata. Lack of an effect might also result from sea urchins feeding on drifting algae when in crevices (Dean et al., 1984; Harrold and Reed, 1985; Johnson and Mann, 1988). Again, there are several studies to suggest that *P. lividus* is one of the most important grazers in shallow subtidal habitats in the Mediterranean (Kempf, 1962; Verlaque and Nedelec, 1983; Verlaque, 1987), but experiments are needed to test this hypothesis formally and to assess the relative importance of *A. lixula* and *P. lividus* in habitats where these species coexist. The orthogonal manipulation of *A. lixula* and *P. lividus*, as it was done in the present study, is not appropriate to assess their relative importance because the 2 species were maintained at different densities in the experimental patches and their effects were not directly comparable.

That the effects of *A. lixula* were similar to those predicted for *P. lividus* has important practical consequences. *P. lividus* is a commercial species that is harvested in several areas of the Mediterranean contributing to the maintenance of local, small fisheries (Kempf, 1962; Boudoresque, 1987). As with other species of sea urchins, intensive harvesting may lead to drastic changes in the structure and composition of assemblages. The predicted effect is an increase in cover of erect algae at the expenses of several encrusting organisms, resulting in a general loss in diversity of coastal habitats (Himmelman et al., 1983; Johnson and Mann, 1988; Andrew, 1993). Appropriate management decisions are required to mitigate the indirect effects associated with the collection of sea urchins. The results of the present study suggest that *P. lividus* should be harvested primarily in areas where *A. lixula* is also present, because the latter species is, on its own, capable to prevent undesired changes to the habitat. Before embarking in such a management, however, it is necessary to assess whether the findings of the present study are general or not. This requires additional experiments on the relative importance of *A. lixula* and *P. lividus* in different places at different times.

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