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the Netherlands Institute for Sea Research

Journal of Sea Research 39 (1998) 281–290

JOURNAL OF SEA RESEARCH

# Low densities of sea urchins influence the structure of algal assemblages in the western Mediterranean

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Received 19 June 1997; accepted 25 September 1997

## Abstract

Numerous studies of interactions between urchins and algae in temperate areas have shown an important structuring effect of sea urchin populations. These studies focused almost wholly on the effect of high urchin densities on laminarian forests. In contrast, algal communities below 5–6 m depth in the northwestern Mediterranean are characterised by low sea urchin densities ($<5$ ind $m^{-2}$) and the absence of laminarian forests. No previous research has addressed sea urchin/algal interactions in this type of community. To determine the effect of the most abundant echinoid species, *Paracentrotus lividus,* on well-established algal communities in this area, we performed a removal–reintroduction experiment in rocky patches located between 13 and 16 m depth in the northwestern Mediterranean, where sea urchin densities ranged between 0.9 and 3.4 ind $m^{-2}$. After 6 months, the cover of non-crustose algae was significantly higher in the plots from which sea urchins had been removed than in control plots (84 vs 67% cover). These removal plots reverted to their original state upon reintroduction of sea urchins. The non-crustose algae consisted of turfing and frondose forms, with the former representing some 70% of the non-crustose algal cover. Change in the cover of turfing algae was responsible for the significant increase in algal development in the sea urchin removal plots. The response of frondose algae to the treatment varied between algal species. It is concluded that grazing by *P. lividus* exerts a significant effect on habitat structure, even in communities with low sea urchin densities, such as those found in vast areas of the Mediterranean sublittoral.

*Keywords:* grazing; plant–herbivore relationship; Echinoidea; *Paracentrotus lividus*; western Mediterranean

## 1. Introduction

Sea urchin herbivory has often been demonstrated to be a controlling factor in benthic algal communities, and its effect has been intensely studied in temperate and tropical communities (see reviews by Lawrence, 1975; Lawrence and Sammarco, 1982). The effect of sea urchins is best known in kelp forest communities (reviewed in Harrold and Pearse, 1985), where their activity produces barren grounds which may alternate, both spatially and temporally, with well-established kelp forests (Leighton, 1971; Mann, 1977; Tegner and Dayton, 1981; Harrold and Reed, 1985; Hart and Scheibling, 1988; Hagen, 1995; Tegner et al., 1995). Much less is known, however, about the effects of sea urchin grazing in other types of community (Valentine and Heck, 1991). In particular, very little experimental work has been done on communities where kelps are not dominant, such as Mediterranean littoral communities, where *Paracentrotus lividus* (Lamarck) is the most abundant echinoid species.

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*PII* S1385-1101(97)00061-0

*P. lividus* has been reported to produce overgrazed patches in Mediterranean and Atlantic habitats (Kitching and Ebling, 1961; Kempf, 1962; Kitching and Thain, 1983; Verlaque, 1987; Rico, 1989). They are characterised by the elimination of non-crustose algae and the formation of barren areas of rock partially or wholly covered with crustose coralline algae. These overgrazed patches have been described in shallow waters (usually $<3$ m deep) with sea urchin densities generally $>15$ ind $m^{-2}$ (Kempf, 1962; Kitching and Thain, 1983). In communities deeper than 5–6 m, however, *P. lividus* populations generally occur at low densities ($<5$ ind $m^{-2}$, see Kempf, 1962; Ballesteros, 1987; San Martin, 1995; Turon et al., 1995a,b), and a moderate to dense turf of soft algae coexists with the sea urchins. The situation in the Mediterranean contrasts, therefore, with the one found in kelp forests worldwide. In the latter, extensive areas could be converted to persistent barrens, even at depths $>10$ m (Fletcher, 1987; Witman, 1987; Leinaas and Christie, 1996). In the Mediterranean, barren areas are usually restricted to shallow waters, while coexistence of sea urchins at low densities and non-crustose algae occurs in many sublittoral communities.

Some experimental studies on the effect of different densities of sea urchins on algal populations have been performed (Ebert, 1977; Valentine and Heck, 1991; Andrew and Underwood, 1993). However, to our knowledge, no study has addressed the impact of sea urchin grazing at very low densities (of the order of 1–5 ind $m^{-2}$), such as those occurring in the Mediterranean sublittoral. Assessment of the influence of herbivores on algal assemblages is fundamental to the understanding of community structure and dynamics (Fletcher, 1987). Therefore, to ascertain whether sea urchin grazing can exert any controlling effect on this type of sublittoral system, we performed a removal–reintroduction experiment and studied the corresponding changes in the cover of algae, classed into either functional categories or particular species.

## 2. Materials and methods

### 2.1. Study site

The study was performed from October 1992 to October 1993, at Tossa de Mar (41°43.2′N, 2°56.4′E) on the northeast coast of Spain (northwestern Mediterranean). The biology, structure and dynamics of the local population of *Paracentrotus lividus*, as well as the algal dynamics, have been studied at this location (Ballesteros, 1984, 1991; Lozano et al., 1995; Turon et al., 1995b).

The study site had vertical walls and large rocks lying on a sandy bottom to a depth of 16 m. These large isolated boulders provide excellent natural units for experimentation, as *P. lividus* do not cross the surrounding sand to recolonise boulders where they have been removed (personal observations). An exclusion treatment could therefore be maintained over a long time without need of cages or fences. Moreover, due to their depth, these rocks were subject to low levels of water movement and never became smothered by sediment; hence the communities that developed on them were quite stable. During the study, the water temperature at a depth of 10 m fluctuated between 11.2°C (March) and 25°C (August).

We classed the algae in the following three functional categories (see Section 4): (1) encrusting coralline algae; (2) turfing algae, including all algae that carpeted the surface, but developed to less than about 2 cm in height (this category includes filamentous forms, small foliose algae and articulated corallines); and (3) frondose algae. We defined frondose algae as those whose thalli reached more than 2 cm in height, irrespective of their branching pattern.

The rocks where the 20 experimental plots were established supported a community made up of an encrusting stratum dominated by bare rock interspersed with patches of the crustose coralline *Mesophyllum lichenoides* (Ellis) Lémoine and a few encrusting invertebrates (mainly sponges and bryozoans), the sponge *Crambe crambe* (Schmidt) being the most conspicuous. The group of turfing algae occupied much of the surface available, and included *Falkenbergia rufolanosa*-stadium (Harvey) Schnitz, filaments of *Flabellia petiolata* (Turra) Nizamuddin, the articulate coralline *Jania corniculata* (L.) Lamouroux, and unidentified Ceramiaceae. The group of frondose algae was dominated by *Halopteris filicina* (Grateloup) Kützing, while *Dictyota dichotoma* (Hudson) Lamouroux and its variety *intricata* (C. Agardh) Greville, *Padina pavonica* (L.) Thivy and *Asparagopsis armata* Harvey were present in spring–summer. *Peyssonnelia squamaria* (Gmelin) Decaisne, *Codium vermilara* (Olivi) Delle Chiaje, *Sphaerococcus coronopifolius* Stackhouse, *Flabellia petiolata* (Turra) Nizamuddin, *Codium bursa* J. Agardh, *Halimeda tuna* (Ellis and Solander) Lamouroux and *Acetabularia acetabulum* (L.) Silva were also present, but in lower numbers ($<$2% cover).

### *2.2. Experimental design*

For the exclusion experiment, 20 large rocks, each at least 4 $m^2$ in surface area and surrounded by sand, were haphazardly chosen. They all lie between 13 and 16 m depth, within an area of approximately 150 × 50 m under the same physical conditions. The densities of *Paracentrotus lividus* on these boulders ranged between 0.9 and 3.4 ind $m^{-2}$, and no other echinoid species was present on them. Over all boulders within the study area, the algal community appeared quite similar. These rocks were used to place the study plots, one plot per rock. Each plot consisted of a permanent rectangular surface measuring 30 × 40 cm marked by nails. Ten rocks were used for the removal of sea urchins, and ten more were used as controls. All *P. lividus* on the exclusion rocks were removed in October 1992. Treatments were randomly assigned to the rocks, so they were adequately interspersed. Formerly undetected sea urchins were removed at subsequent visits during the first 2 months of study. Sea urchins were removed from whole rocks, not just from the plot on each rock. The sizes of removed sea urchins matched the size distribution of this species in this site (Turon et al., 1995b), with dominance of specimens $>$3 cm in diameter.

The study plots were photographed monthly until April 1993. At that time, *P. lividus* were reintroduced on half of the ten exclusion rocks, in the same numbers (and approximate sizes) as before the experiment. The other half of the removal plots was left untouched as a control. The rationale behind reintroduction was to investigate whether, and at what rate, the algal populations reverted to their original state. The zones were monitored again from June to October 1993.

The photographic slides were projected onto a Diastar-200 (Osram) device, which reflects the image up through a glass sheet. The enlarged images were traced onto acetate sheets. The outlines of the algae of each category, bare rock, and other invertebrates (mainly sponges) were drawn, the images were digitized, and the percentage cover was calculated for each category. Furthermore, it was possible to identify and quantify the cover of some algae (particularly frondose forms) at the species level.

### *2.3. Statistical analyses*

The percentage cover of the diverse categories or species was compared between treatments and controls for the period of exclusion (before reintroduction) by a randomization version of a repeated-measures analysis of variance based on Manly (1991), which consisted of a two-stage permutation of the data: first, individuals were randomly reassigned to the two habitats, and then readings for each individual were randomly rearranged among observation times. With this two-level randomisation, the overall total sum of squares, as well as the total between- and within-subjects sums of squares, remain unchanged (Manly, 1991). The sum of squares associated with each factor and their interaction is, therefore, a suitable statistic on which to test the significance of each effect. We randomised the whole series of data 4999 times (plus the observed one) to approximate the null hypothesis distribution of the sum of squares for each factor and their interaction, and then examined how extreme were the observed values in this distribution. We judged an effect to be significant when the observed sum of squares was exceeded by less than 5% of the corresponding values in the randomization series. The randomisation program was written in Turbopascal.

We selected this non-parametric randomisation method because the usual, parametric repeated-measures analyses, either in their univariate (ANOVAR) or multivariate (MANOVAR) forms, require stringent assumptions about the variance–covariance matrix that were not met by our data even after several transformation attempts. The MANOVAR procedure also had very low power in our case. For issues relating to the assumptions and power of ANOVAR–MANOVAR see Potvin et al. (1990) and Von Ende (1993).

## 3. Results

In the control plots, non-crustose algae and bare rock were the dominant forms (62 ± 1.3% and 26 ± 1.3% cover, respectively, mean ± standard error all times pooled). The rest of the area (12 ± 0.5% of total cover) was occupied mainly by the encrusting coralline *M. lichenoides*, with some encrusting invertebrates, mostly *C. crambe* (Schmidt), a species not consumed by *P. lividus* (Uriz et al., 1996). Among non-crustose algae, the turfing category accounted for 44 ± 1.2% of the total algal cover, while the frondose category represented only 18 ± 0.8%. Aside from these functional categories, the following algae were monitored at the species level: *F. rufolanosa* for the turfing group, and *H. filicina, P. pavonica, D. dichotoma, D. dichotoma* var. *intricata* and *A. armata* for the frondose group. At the beginning of the experiment there were no significant differences in cover between the treatment and control plots for most categories or species considered (*t*-tests). However, in spite of our random assignment of treatments, the control plots had by chance a significantly greater percentage cover of *H. filicina* (mean of 14%) than the treatment plots (mean of 7%). In turn, as *H. filicina* made up most of the frondose category, the same pattern of significantly higher initial cover in the control plots was found when considering the whole frondose algae group. Treatment effects would be masked by this fact in these two cases, although we were still able to test interaction (treatment × time) effects in them.

There were no differences in density of sea urchins between control and treatment plots (*t*-test). Once the sea urchins were removed, the non-crustose algae in the treatment plots increased their cover with respect to the control plots (Fig. 1a). In the April sampling, at the time when sea urchins were reintroduced in half the plots, the cover values were: removal plots, 84 ± 3% (mean ± standard error); control plots, 67 ± 5%. The removal plots, therefore, showed about 25% more non-crustose algal cover than the unmanipulated ones. The algal cover in the plots in which sea urchins were not reintroduced remained higher than in the control plots until the end of the study (1 year after removal). On the other hand, in the plots where sea urchins were reintroduced (in the same numbers per rock as before the removal), the values of coverage reverted to those of the control plots, and by the end of the study (October) they were very similar (slightly more than 60% cover). There were no marked fluctuations in non-crustose algal cover during the study period in the controls, the highest values being found in spring (March and April) as usual in algal populations of this zone (Ballesteros, 1991).

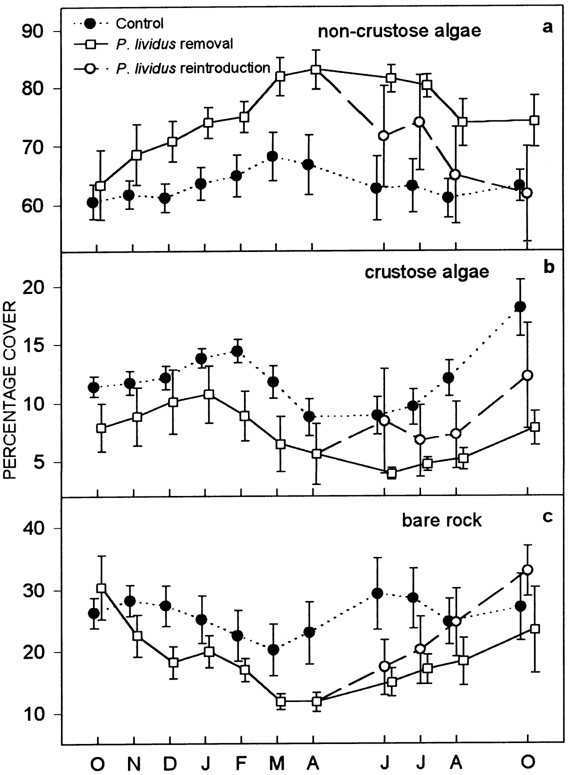

Fig. 1. Time course of the percentage cover of (a) non-crustose algae, (b) crustose algae, and (c) bare rock in the experimental and control plots. Sea urchins were reintroduced in half the treatment plots in April. Bars are standard errors ($n = 10$ for control plots and for removal plots until April; $n = 5$ for removal and reintroduction plots thereafter).

In the crustose algal category (represented by *M. lichenoides*), the differences between treatment and control were not as marked as in the case of non-crustose algae (Fig. 1b). There was a higher coverage in the control plots, but this was partly because there was already a higher development of crustose algae in the control plots at the beginning of the study. Only at the end of the survey was there a significant (*t*-test) difference between the control plots and the five plots in which the sea urchin exclusion continued for the whole year (means of 19 and 8% cover, respectively), while the reintroduction plots showed intermediate values. Bare rock, on the other hand, decreased in the treatment plots (Fig. 1c), its coverage having been halved compared to the controls in April (12 and 23%, respectively). However, by the end of the study the differences had almost disappeared.

The results of the randomisation analysis for the period (October–April) previous to sea urchin reintroduction in some plots are shown in Table 1. Treatment and time effects, as well as the interaction, were tested. The time factor was significant in all cases ($p < 0.01$) and was not included in the Table. The treatment effect was significant in the case of the non-crustose category. No significant effect of the treatment or the interaction was found for the crustose algae or the bare rock categories, although the interaction term was almost significant for the latter, suggesting a different time course in treatment and control plots. The large variation among replicates hindered the detection of significant patterns in the analyses.

Division of the non-crustose category into its two components, turfing algae and frondose algae (Fig. 2), showed that turfing species were the dominant form, and that they followed much the same pattern over time as the whole non-crustose category: an increase in cover in the removal plots, while those in which sea urchins were reintroduced in April reverted to the control-plot coverage. A significant treatment effect was found in the analyses (Table 1). As for the frondose algae (Fig. 2b), we started by chance with a situation in which there was a higher cover of frondose algae in the control than in the experimental plots. Both the control and the experimental plots experienced a decrease in cover during the first 3 months, with a subsequent increase. This increase was higher in the removal plots, and accordingly a significant interaction term appeared in the analyses (Table 1). Frondose algae were at their maximum between June and August, and there were no clear differences in cover during these months in the control, removal or reintroduction plots.

Table 1
Significance levels obtained by randomisation for the repeated-measures analyses of the growth rates (in proportion of SS from the randomised series that exceeded the observed SS)

| Source of variation | Proportion exceeding observed SS |
|---|---|
| Non-crustose algae | |
| Treatment | 0.046[b] |
| Treatment × time | 0.169 |
| Crustose algae | |
| Treatment | 0.147 |
| Treatment × time | 0.486 |
| Bare rock | |
| Treatment | 0.143 |
| Treatment × time | 0.067 |
| Turfing algae | |
| Treatment | 0.013[b] |
| Treatment × time | 0.815 |
| Frondose algae | |
| Treatment | 0.105 |
| Treatment × time | 0.000[b] |
| *Halopteris filicina* | |
| Treatment | 0.406 |
| Treatment × time | 0.001[b] |
| *Padina pavonica* | |
| Treatment | 0.695 |
| Treatment × time | 0.978 |
| *Dictyota dichotoma* | |
| Treatment | 0.179 |
| Treatment × time | 0.684 |
| *Dictyota dichotoma* var. *intricata* | |
| Treatment | 0.087 |
| Treatment × time | 0.731 |
| *Falkenbergia rufolanosa* | |
| Treatment | 0.482 |
| Treatment × time | 0.003[b] |
| *Asparagopsis armata* | |
| Treatment | 0.147 |
| Treatment × time | 0.000[b] |

[a] The time factor is omitted, as it was always significant at $p < 0.01$.
[b] Significant (at the 0.05 level) effect.

The time courses of the percentage cover of the separate species monitored are presented in Figs. 3–5. *H. filicina* (Fig. 3a) was the dominant form among the frondose algae, and showed the same pattern as the latter (Fig. 2b), with a significant interaction between time and treatment (Table 1). *P. pavonica, D. dichotoma* and *D. dichotoma* var. *intricata* (Fig. 3b and Fig. 4) appeared seasonally in spring or summer. Note the temporal succession of the two forms of *D. dichotoma* (Fig. 4). The mean percentages cover during the period analysed until reintroduction were in all cases zero or close

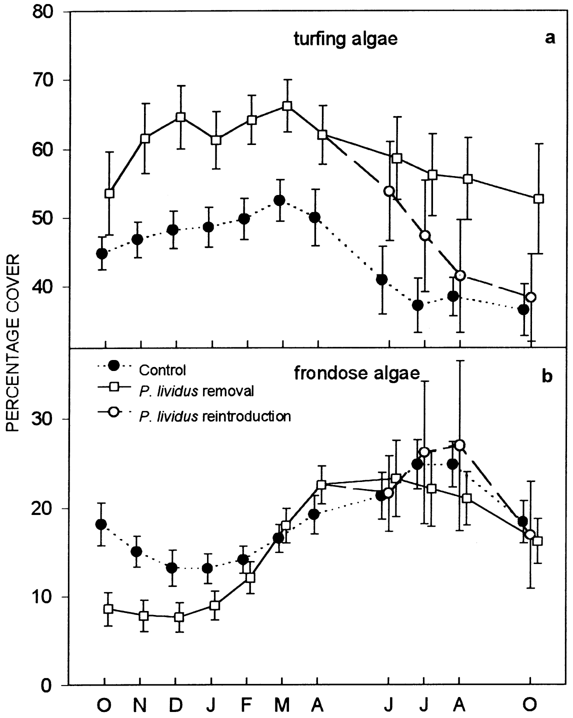

Fig. 2. Time course of the percentage cover of (a) turfing and (b) frondose algae during the experiment. Bars are standard errors ($n = 10$ for control plots and for removal plots until April; $n = 5$ for removal and reintroduction plots thereafter).

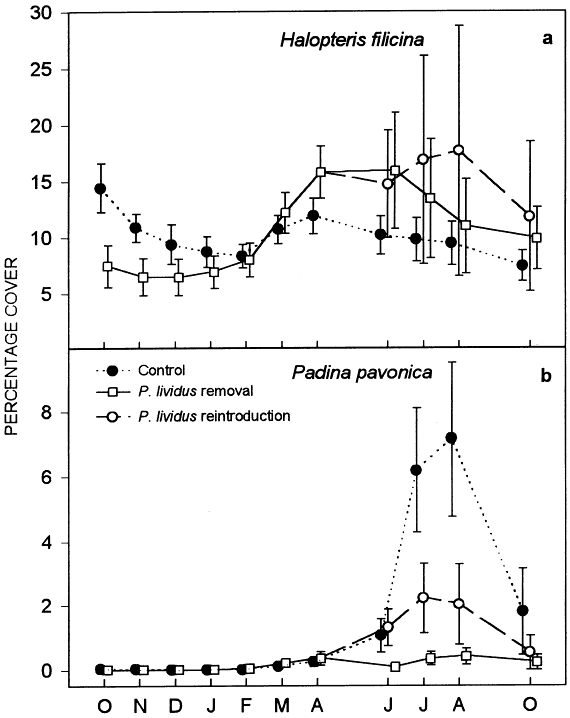

Fig. 3. Time course of the percentage cover of (a) *Halopteris filicina* and (b) *Padina pavonica* during the experiment. Bars are standard errors ($n = 10$ for control plots and for removal plots until April; $n = 5$ for removal and reintroduction plots thereafter).

to zero and, accordingly, no significant effect was found in the randomisation analyses (Table 1). The increase in cover of these species occurred during the reintroduction part of the study. In *P. pavonica* and *D. dichotoma*, there was a tendency towards higher cover in the controls during this period (June–October). The variances, however, were large, and only in *P. pavonica* in August was the difference between control plots (7% cover) and the plots in which exclusion of sea urchins was continued (0.4% cover) significant (*t*-test).

*F. rufolanosa*, the tetrasporophyte form of *A. armata*, peaked in late winter–spring (Fig. 5a), while the gametophyte form peaked in late spring (Fig. 5b). *F. rufolanosa* was the only turfing algae quantified at the species level. In both cases, the increase in the treatment plots was higher than in the control plots, as revealed by a significant interaction between treatment and time (Table 1).

In general, the plots in which the sea urchins were reintroduced in April showed, at the end of the study, percentages cover for the different species or categories which were either intermediate between the controls and the plots in which the exclusion was continued, or closer to the controls. This can be especially seen in categories with total cover above 10%. When considering algae with low cover, however, random variation was high in the reintroduction part of the study and no clear patterns could be discerned.

## 4. Discussion

Sea urchins were a significant structuring force in the system studied. In our removal zones, the densities of sea urchins were <5 ind m$^{-2}$. These values are representative of large areas along this coast at depths >6 m (Turon et al., 1995a). We have demonstrated that the exclusion of sea urchins produced about 25% increase in non-crustose algal

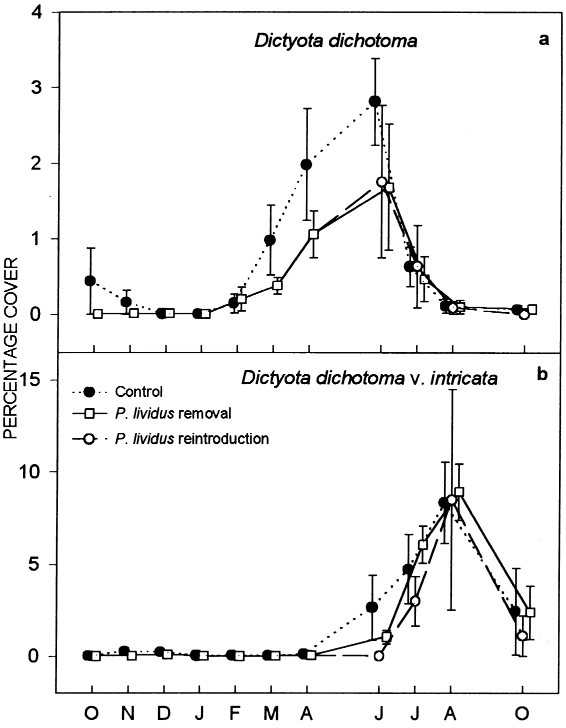

Fig. 4. Time course of the percentage cover of (a) *Dictyota dichotoma* and (b) *D. dichotoma* var. *intricata* during the experiment. Bars are standard errors ($n = 10$ for control plots and for removal plots until April; $n = 5$ for removal and reintroduction plots thereafter).

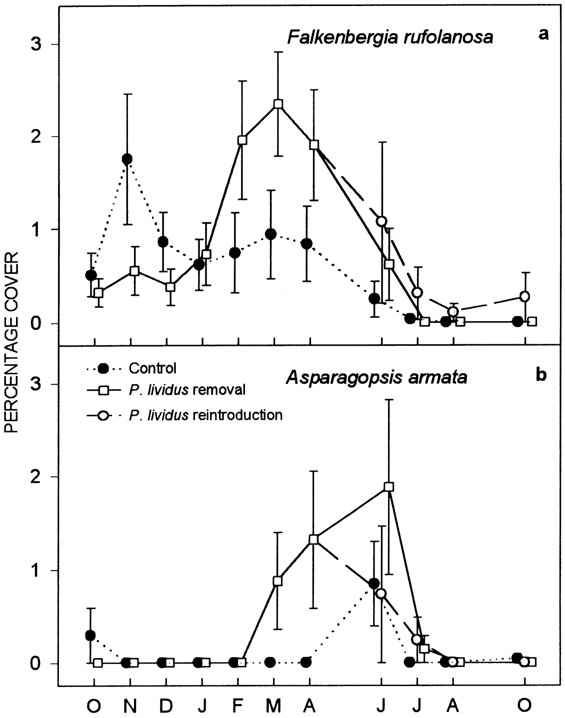

Fig. 5. Time course of the percentage cover of (a) the tetrasporophyte (*Falkenbergia rufolanosa* – stadium) and (b) the gametophyte of *Asparagopsis armata* during the experiment. Bars are standard errors ($n = 10$ for control plots and for removal plots until April; $n = 5$ for removal and reintroduction plots, thereafter).

cover. This moderate, but significant, effect clearly contrasts with the complete elimination of the soft algae found in other areas and with other species (e.g. Harrold and Reed, 1985; Fletcher, 1987; Witman, 1987; Levitan, 1988) or at higher *P. lividus* densities in Mediterranean communities ($>15$ ind $m^{-2}$, compare Kempf, 1962), which led Kitching and Thain (1983) to conclude that *P. lividus* is likely to exert a marked influence where its population density is high. This study, however, shows that the foraging activities of *P. lividus* exert a significant influence on the structure and dynamics of the algal assemblages, even in communities with naturally low densities of this species.

The degree of development of the algal assemblage studied was moderate: non-crustose algae always left bare patches in between plants, and their cover never exceeded a mean value of 70% in the control plots. Among them, frondose algae presented $<20\%$ cover most of the year in the controls. These algae were not canopy-forming, their heights never being more than 10–15 cm. It can therefore be assumed that a two-dimensional imaging method such as our slides will be accurate enough to trace relative changes in algal biomass, which were the ones of interest in this study. The third, vertical dimension was poorly developed in this community. In spite of this, we acknowledge that the figures for crustose algae and bare rock could be slightly underestimated if they are partially covered by erect algae. However, estimating actual algal biomasses would require destructive methods that would preclude the use of permanent quadrats, resulting in an added variance component. The interval chosen for successive samplings was adequate for monitoring changes in these algal populations, which are known to fluctuate on a seasonal basis (Ballesteros, 1991);

therefore no abrupt changes in algal cover that could go undetected between samplings were expected.

A treatment of algae as classes of functional groups is more meaningful than considering separate species (Littler and Littler, 1980), and several authors have considered the effects of sea urchins on different categories of algae (e.g. Ayling, 1981; Fletcher, 1987; Hughes et al., 1987; Andrew and Underwood, 1993; Benedetti-Cecchi and Cinelli, 1995). The turfing algae form a discontinuous carpet on the rocky surfaces that provides the most readily available food for the sea urchins. The frondose algae, which were more than 2 cm in height, are not large enough for the sea urchins to climb on, so they could eat only at the bases (normally richer in tough structural materials) or try to bend over the algal thalli.

There was, in general, a high variability among replicates, which hindered the detection of significant patterns. In spite of this, there was a clear effect of the exclusion of sea urchins on non-crustose algae. The turfing category (the most abundant) was responsible for the pattern found. This category, made up of a mixture of filamentous and low erect forms, can respond more quickly to changes in grazing pressure than the larger frondose algae. Several authors have reported a rapid increase in opportunistic and filamentous forms after sea urchin exclusion (Ayling, 1981; Fletcher, 1987; Andrew and Underwood, 1993). The only species monitored separately in the turfing category, *F. rufolanosa*-stadium, increased at a significantly higher rate in the growing season in the plots deprived of sea urchins than in control plots. Higher values of non-crustose algal cover in the urchin removal plots as compared to the control plots were maintained throughout the year of study. In contrast, after reintroduction of sea urchins in some plots, the values decreased again in a few months to a mean coverage similar to the controls. The results of such an experiment may, of course, vary according to the time of extraction and reintroduction. Urchins were removed in the season of slow algal growth and reintroduced in the season of high algal growth (Ballesteros, 1991). Besides, the date of reintroduction coincided with the beginning of the period of low feeding activity of *P. lividus* in this zone (Turon et al., 1995b). All this may counteract the potential effect of sea urchins, so our results are conservative.

The frondose alga *H. filicina* showed an effect of the sea urchin removal, increasing in cover significantly more than in the controls in spring. The other frondose species monitored were seasonal forms, which, in general, appeared at the beginning of summer. Their seasonal cycle obscured any effect due to the presence or absence of sea urchins. There is even an indication that some of them (*P. pavonica* and *D. dichotoma*) grew more in control than in treatment plots. Both species are readily consumed by *P. lividus* (Verlaque and Nédelec, 1983), so that the pattern found may, in part, be due to indirect effects of the absence of sea urchins. It is possible that the increase in turfing algae in treatment plots prevented settlement of propagules of these seasonal species. Hence their appearance may be favoured in the presence of patches of bare space and crustose algae, as in our control plots. Kitching and Thain (1983) similarly reported indirect benefits of the presence of *P. lividus* on some algae. The higher cover of *A. armata* in the treatment plots may also be explained by indirect causes: this effect was unexpected, in principle, since this species had been reported as being avoided by *P. lividus* (Rico, 1989; however, in the paired choice experiments performed by this author, *A. armata* was indeed consumed by the sea urchin, although at lower rates than other algae).

Other herbivores may interact with the grazing activity of sea urchins (Ayling, 1981; Andrew and Underwood, 1993). Verlaque (1987) found that in Mediterranean shallow water communities the critical sea urchin densities at which overgrazing occurred were halved in the presence of limpets at natural densities. However, no limpets occurred at the depths studied here; large benthic herbivores (e.g. other gastropods) are rare in this area and none have been recorded in the experimental zones. On the other hand, no other sea urchin species was present on the experimental rocks. *Arbacia lixula* (L) was abundant in the area, but in shallower waters. While sparse individuals of *Sphaerechinus granularis* (Lamarck) were present in the area, none occurred on our rocks. In the (rather theoretical) case that the absence of sea urchins caused any behavioural change in other herbivores (e.g. fishes or mesograzers such as some amphipods), an effect different from the absence of sea urchin grazing per se would be introduced and the observed changes would also reflect indirect effects of sea urchin exclusion in this community.

A strong effect of *P. lividus* has been found in Atlantic waters (Ireland) by Kitching and Ebling (1961), who introduced a variety of densities of this species into 0.275 $m^2$ cages with rocks and shells free of seaweeds. Algae (mainly filamentous forms) became established within the cages without sea urchins, but a single specimen of *P. lividus* ($= 3.63$ ind $m^{-2}$) could halve algal development, while six specimens ($= 21$ ind $m^{-2}$) completely prevented algal growth. Although this study lacked replication, these findings indicate the potential effects of low densities of this sea urchin. However, they are not directly comparable to our data as they relate to the ability of *P. lividus* to interfere with algal settlement and growth, while we have investigated an already well-developed algal assemblage. Verlaque (1987) estimated that in Mediterranean communities the critical density above which there would be severe overgrazing of erect algae was in the order of 15–20 ind $m^{-2}$ for specimens 5 cm in diameter. Wherever these densities (or higher) are found in the Mediterranean, the barren ground of rock and crustose coralline algae appears (Verlaque, 1987; and personal observation). Densities $>20$ sea urchins $m^{-2}$ can also result in the regression of seagrass meadows (Azzolina et al., 1985; Shepherd, 1987). We have shown that lower densities of sea urchins, although they do not result in an elimination of the soft algal carpet, can nevertheless influence the degree of development of algal communities.

## Acknowledgements

Dr. E. Ballesteros (CEAB, Blanes, Spain) kindly helped with the identification of the algal species. We thank A. Davis (University of Wollongong, Australia) for insightful comments on the manuscript. This study was initiated and funded by the Fisheries Department of the Catalan Government. Financial support was also provided by Project PB94-0015 of the Spanish Government.

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