

Patch recolonization through migration by the echinoid Paracentrotus lividus in communities with high algal cover and low echinoid densities.

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Abstract: We examined the recolonization of patches which had been artificially cleared of the echinoid *Paracentrotus lividus*. Our aim was to mimic an extraction event such as those produced by harvesters and to examine how long it took for the sea urchin to recolonize the cleared areas. We selected a community in which there was a low echinoid density (ca. 2 ind.m⁻²) and high algal cover. These conditions are typical of many rocky Mediterranean assemblages at depths below 4-6 m. The experimental patches varied in the degree of isolation from neighbouring sea urchin. In these circumstances we found that recolonization was slow, and only in the most accessible zones did the sea urcchin abundance recover within 18 months. After 4 and a half years, the population had recovered to less than 46% of the original abundance in the most isolated area. Settlement and growth of urchins, rather than migration, may account for recolonization in isolated zones. We conclude that extraction of this species may have a long-lasting effect on the local populations of echinoids which, in turn, may influence algal communities.

Résumé : Recolonisation par migration de l'échinide Paracentrotus lividus (Lamarck) dans une communauté à forte couverture algale et faibles densités d'oursins.

Nous avons examiné la recolonisation de zones expérimentales après les avoir dégagées artificiellement de tous les spécimens *Paracentrotus lividus*. Notre but était de mimer un prélèvement normal de pêche et d'examiner à quelle vitesse les peuplements d'oursins peuvent recoloniser l'habitat. Nous avons choisi une communauté où la densité des oursins était faible (2 ind.m-2 environ) et la couverture algale bien développée. Ces conditions sont typiques du biotope sublittoral rocheux méditerranéen au-dessous de 4-6 m de profondeur. L'accessibilité de chaque zone par mouvement latéral des oursins était différente. Dans ces circonstances, la recolonisation est très lente; la zone la plus accessible est la seule à avoir récuperé la densité initiale d'oursins en 18 mois, tandis que la zone la moins accessible ne retrouve, après quatre ans et demi, qu'une densité de seulement 46 % de la densité initiale. La croissance *in situ* de nouvelles recrues, plutôt que la migration latérale, est probablement responsable des taux de recolonisation observés dans les zones isolées. En conclusion, l'extraction de cette espèce peut avoir des effets de longue durée sur les peuplements locaux, ce qui a, en retour, un effet sur les communautés algales.

Keywords: Paracentrotus lividus, Echinoidea, migration, recolonization, western Mediterranean.

Introduction

can be found from sea level down to 80 m on rocky shores and in beds of *Posidonia oceanica* (L.) Delile, although it is most abundant in the first 20 m depth. The roe of this species is highly appreciated as seafood and intense harvesting has led to a reduction in populations in some areas, especially on the Atlantic and Mediterranean coasts of France (Le Gall, 1987; Régis, 1987) and on the coast of Ireland (Byrne, 1990). Moreover, diseases have contributed to marked declines in the stock of this species, especially on the French Mediterranean coast (Boudouresque *et al.*, 1990; Maes & Jangoux, 1984). These effects seem to have been offset in recent years by the intense fishing of some species that prey on *P. lividus* (Sala & Zabala, 1996), which has led to an increase in sea urchin densities in many western Mediterranean rocky shores.

The extent of movements of echinoids is poorly know. It depends on span of their grazing excursions, on whether they return to the same site after foraging, and on the extent to which they disperse over new areas due to exhaustion of local food resources. In conditions of poor algal development (food shortage) and high density of sea urchins, P. lividus is able to travel daily distances in the range of one to several meters (Shepherd & Boudouresque, 1979). Little is known, however, about their movement patterns in zones without food limitation (i.e., high algal cover) and low sea urchin density, a condition prevailing in many rocky Mediterranean assemblages below 4-6 meters depth. In addition, P. lividus may feature the sheltering behavior described for other species (Vance & Schmidt, 1979; Scheibling & Hamm, 1991; Andrew, 1993), whereby they return to their shelters in holes or crevices after shortrange foraging, possibly as a defense against predation. This phenomenon has recently been studied in P. lividus inhabiting littoral rock pools in the Mediterranean (Benedetti-Cecchi & Cinelli, 1995).

The aim of the present study is to simulate the effects of intensive harvesting of *P. lividus* in a typical northwestern Mediterranean sublittoral community, with low sea urchin densities and well-developed algal cover (i.e., no food shortage). We aimed to ascertain how fast echinoids can recolonize a cleared patch and, consequently, how long the effect of fishing populations of sea urchins is likely to last.

Materials and Methods

The study was performed at Tossa de Mar (41° 43.2' N, 2° 56.4' E) on the northeast coast of Spain (northwestern Mediterranean), in an area where rocky vertical walls extend down to sand at 16 m depth. On the vertical walls studied, a photophilic algal community dominated by *Halopteris filicina* (Grateloup) Kützing, with a variety of other algal species (*Dictyota dichotoma* var. *intricata* (C. Agardh) Greville, *Falkenbergia rufolanosa* stadium

(Harvey) Schmitz and *Padina pavonica* (L.) (Thivy)) is found above 14 m depth, while a sciaphilous community dominated by crustose coralline algae (*Mesophyllum lichenoides* Lémoine) develops between 14 and 16 m of depth. The water temperature, at 10 m depth, fluctuated between 11.2 °C (March) and 25 °C (August) during the study period.

The recolonization study was carried out in two areas with similar algal communities. One of them was a vertical wall between 4 and 16 m depth. On this wall, two zones were delimited: zone B was a 35 m² area (3.5 x 10 m) ranging from 6 to 16 m depth; zone A was a 55 m² buffer area that formed a 2 m-wide band surrounding zone B (Fig. 1). These zones were delimited by ropes. The corners of the zones were marked with nails driven into the rock, and the ropes were deployed at each sampling time and then removed. The second area was an isolated rock, between 9 and 12 m depth, lying on a sandy bottom. We will subsequently refer to this rock as zone C, and it measures ca. 125 m². The three zones were therefore designed because they provide different degrees of accessibility (A>B>C) for lateral recolonization.

All specimens of *P. lividus* within the three zones were removed in September 1992 (crevices and holes were scrutinized for the presence of hidden individuals), and the number of them larger than 2 cm in diameter was recorded. After this removal, the number of individuals larger than 2 cm in each zone was monitored after one week, then

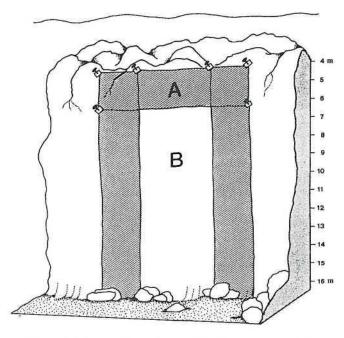


Figure 1. Scheme of two (A, B) of the three zones marked for the recolonization experiment.

Figure 1. Schéma de deux (A, B) des trois zones marquées pour l'expérience de recolonisation.

fortnightly during one month and a half, and later monthly over 18 months. Recolonization rates were estimated for every zone following the population recovery. Eventually, two further observations of the three zones were made: 18 months (September 1995) and three years (March 1997) after the end of the monitoring (i.e., three and four and a half years, respectively, after the removal of sea urchins).

The study site was selected on the basis of previous knowledge of the biology, population structure and dynamics of P. lividus (Lozano et al., 1995; Turon et al., 1995). The main recruitment of sea urchins at Tossa takes place in spring (Lozano et al., 1995), and the sea urchins take about 3 years to reach a diameter of 2 cm (Turon et al., 1995). Because we carefully cleared the experimental zones of all visible sea urchins, only hidden juveniles a few mm in diameter could have escaped detection. As we only censused recolonization by sea urchins larger than 2 cm in diameter, we can be confident that the results were not confounded with recruitment or in situ growth of juveniles, except perhaps on the last sampling dates. Our experimental site was adjacent to a zone previously monitored by us during a complete yearly cycle (Lozano et al. 1995), so that we could be confident that the zone is representative of the structure and dynamics of the sea urchin populations in this area.

Results and Discussion

The initial densities of *Paracentrotus lividus* in the three sampling zones were: zone A, 1.89 ind.m⁻²; zone B, 1.77 ind.m⁻²; zone C, 1.88 ind.m⁻². These densities corresponded well with the mean estimated for the *P. lividus* population at Tossa within the same depth range, ca. 2 ind.m⁻² between 4-16 m depth (unpublished). The time course of the recolonization of the three zones is depicted in Fig. 2 as percentages of the initial abundance. The three zones featured a slow recovery in urchins abundance. By the end of the initial monitoring, 549 days after the initial removal, only zone A featured a recolonization value near 100%, while recolonization values for the less accessible zones, B and C, were 46% and 21% respectively. The ordering of the final recolonization values matched the differential accessibility of the three sampled zones.

In addition, the further observations 1115 days after the initial removal (ca. 3 years), revealed a similar sea urchin density to that observed initially in the most accessible zone (A), while the least accessible ones reached values of 77% (zone B) and 39% (zone C). At the final observation (March 1997, after four and a half years from the beginning of the experiment), the densities of urchins larger than 2 cm were 116% (Zone A), 87% (Zone B) and 46% (Zone C) of the initial ones.

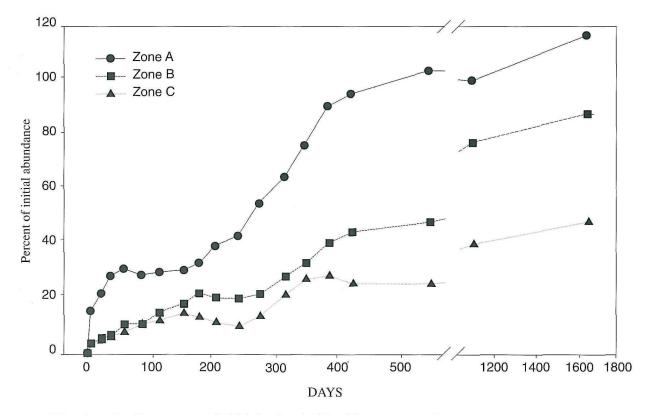


Figure 2. Recolonization (in percentage of initial abundance) of the different zones studied over time. **Figure 2.** Recolonisation (en pourcentage des abondances initiales) des différentes zones au cours du temps.

This experiment clearly showed that the recovery rates (resulting from lateral migration) of *Paracentrotus lividus* in a zone with low sea urchin densities and without food limitation, following a removal event, are very slow. In fact, zone B, which was only 2 m from undisturbed areas, featured less than 50% recovery after 18 months following removal. Even after three years, the recovery rate was only 77%, and 87% after four and a half years. These values were even lower in zone C (see Fig. 2), because migration across sand is apparently very slow. Hence our study indicates that the populations in the most isolated zones considered (zones B and C) should rely on recruitment and *in situ* growth of juveniles rather than on lateral migration from neighbouring populations for the recovery of their original sea urchin densities.

Movement in sea urchins has been shown to be a response to low food supply (Mattison *et al.*, 1977; Harrold & Reed, 1985), or high food supply (Klinger & Lawrence, 1985), or to bear no relationship at all with feeding (Shepherd & Boudouresque, 1979; Dance, 1987; Tertschnig, 1989). In any case, it is clear that sea urchins do not travel far when foraging, and that the sheltering behavior featured by *P. lividus*, possibly as a defense against predation, affects the recolonization of cleared areas. In a removal experiment of *P. lividus*, Kitching & Ebling (1961) registered that the zone cleared of sea urchins remained free of them at least during the summer after the removal event, which is consistent with the low recovery rates here reported.

The low rates of recolonization observed may have resulted from the tendency of sea urchins to return to the same shelter, and from an abundance of food, obviating the need for long foraging trips. Our finding contrasts with another experimental removal of *P. lividus* in a shallower Mediterranean community with higher sea urchin densities (leading to the existence of overgrazing facies and hence food limitation), where a much faster recolonization rate (less than two months) was found in most of the plots deprived of sea urchins (Kempf, 1962).

In conclusion, the results can be considered representative of the pattern of recolonization by migration of sea urchins in a community with low *P. lividus* densities and no food limitation. These conditions are typical of many Mediterranean assemblages below 4-6 m in depth. The results show that even moderately isolated areas may be mainly recolonized, after a removal event (i.e. by sea urchin harvesters), by *in situ* growth of recruits, and not by lateral migration as in shallower areas with higher sea urchin densities (Kempf, 1962) and food limitation (Kempf, 1962; Mattison *et al.*, 1977; Harrold & Reed, 1985). Therefore, harvesting activities below 4-6 m depth, which typically produce patches cleared of sea urchins, may cause longlasting effects on sea urchin communities, which in turn

may decrease the grazing pressure on local algal populations (Palacin *et al.*, in press).

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