Canopy structure at the edge of seagrass affects sea urchin distribution

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ABSTRACT: The purpose of this study was to add insights to the understanding of seagrass *Posidonia oceanica*–sea urchin *Paracentrotus lividus* interactions, evaluating whether the canopy structure at the edge of meadows next to rocks affects the distribution of *P. lividus*. The experiment consisted of the manipulation of seagrass structure by modifying the shoot density (20, 50, and 100%) and leaf length (natural and reduced). Plastic seagrass was used to test for the mechanism of attraction to the seagrass edge. Thus, for each treatment combination (shoot density × canopy height), 3 types of *Posidonia* were considered: natural seagrass, artificial seagrass, and natural seagrass + frame as a procedural control. The results highlighted that *P. oceanica* canopy structure influences the distribution of *P. lividus*, as the mean abundance of the sea urchin was directly proportional to the shoot density at both canopy heights. Since the type of *Posidonia* did not influence seagrass density, grazing is not the mechanism of attraction of the sea urchins towards the seagrass edge—a more plausible reason, thus, is the search for shelter. Although these findings add to the understanding of *P. oceanica*–*P. lividus* interactions at the edge of the seagrass, space use patterns in sea urchins and the structure of the seascape over which they traverse must be quantified so that a more complete understanding of species–habitat relationships and seascape connectivity can be developed.

KEY WORDS: Canopy · Edge effects · *Paracentrotus lividus* · Plant–herbivore interaction · *Posidonia oceanica* · Seascape connectivity · Spatial distribution

INTRODUCTION

The effects of habitat edges have been a topic of research for decades because they are ubiquitous features of both natural and managed landscapes (Lidicker 1999), and a key component in understanding fragmentation (Cadenasso et al. 2003, Ries et al. 2004, Laurance 2008). Understanding the functional role of edge habitats is increasingly important regarding species interaction and community dynamics, and it has become an integral part of recent landscape studies. In terrestrial landscapes, the direction (positive, neutral, or negative) and magnitude of edge effects depend on differences in resources/quality between adjacent habitats and interactions between species along habitat edges (Ries et al.

2004). Recent work also suggests that edge effects are sensitive to several contextual factors including matrix type or quality, edge orientation, edge contrast, and the presence or proximity of other edges (Sisk et al. 1997, Collinge & Palmer 2002, Reino et al. 2009).

Habitat structure influences faunal density distribution and diversity within ecosystems (Robinson et al. 1995, Lima 1998, Moksnes 2002). Seagrass meadows perform a valuable function providing an optimal habitat for the growth, survival, and reproduction of a diverse array of vertebrate and invertebrate taxa. The high habitat complexity of the canopy increases the number of niches available and, thereby, affords better protection from physical stress (Heck et al. 2003) and influences processes such as

predation and competition that dictate patterns of faunal abundance, survival, and community structure (Heck & Crowder 1991). However, studies of edge effects in seagrass systems have thus far provided inconsistent findings (Connolly & Hindell 2006) as positive (e.g. Tanner 2005, Jelbart et al. 2006), negative (Hovel & Lipcius 2002), and even neutral (Tanner 2006) responses to habitat edges have been highlighted for seagrass-associated fauna.

In general, seagrass canopy can increase food availability and living space, enhance refuge from predators (Carpenter 1984, McClanahan & Muthiga 1989) by providing shade (Jones et al. 1994, Koch 2001, Tanaka & Nakaoka 2006) and baffling currents (Papadimitriou et al. 2005, Hauser et al. 2006, de Boer 2007, Wicks et al. 2009), thus attracting juvenile reef fishes (e.g. Guidetti 2000, Verweij et al. 2006) and increasing density and diversity of epifauna (Hovel et al. 2002, Boström et al. 2006, Valentine & Duffy 2006). Variations in canopy height and shoot density on the wide spatial scale of seagrass meadows could substantially affect the abundance of common fish and invertebrates (Heck & Orth 1980, Bell & Westoby 1986, Edgar & Robertson 1992, Connolly 1994, Horinouchi & Sano 1999, Hori et al. 2009).

In the Mediterranean, *Posidonia oceanica* (L.) Delile is the dominant seagrass species, forming extensive meadows and structuring habitats of high complexity because of its high shoot density, length of the leaves (Heck & Orth 1980), and interlacing rhizomes that, especially when they are exposed, can provide potential refuges for species (Farina et al. 2009, Prado et al. 2009). One of the most common invertebrates occurring in *P. oceanica* meadows is the sea urchin *Paracentrotus lividus* Lamarck. *P. lividus* commonly occurs in 2 contrasting habitats: in shallow subtidal rocky habitats and in *P. oceanica* meadows. In the rocky habitats, at high densities it overgrazes complex algal assemblages turning them into barren areas dominated by a few species of encrusting algae (e.g. Benedetti-Cecchi et al. 1998, Hereu 2006). In this habitat, it shelters in crevices in the rocks or between boulders, exhibiting cryptic behaviour (Verlaque 1984, Sala & Zabala 1996). In *P. oceanica* beds, it occurs among shoots where it can find shelter from predation due to the high structural complexity (Farina et al. 2009) and the availability of food. Tomas et al. (2005, 2006) have established that the presence of epiphytes on seagrass makes the leaves more palatable to the sea urchin, as it feeds preferentially on epiphytes rather than on plant material (Nédelec & Verlaque 1984, Sheperd 1987, Alcoverro et al. 1997, Tomas et al.

2005, 2006), although recent data indicate a more intense grazing pattern on the lower portions of the leaf, near the base (Pinna et al. 2009).

Recent studies have estimated spatial distribution of *Paracentrotus lividus* in the 2 habitats (Tomas et al. 2004, Ceccherelli et al. 2009a). Specifically, higher numbers of *P. lividus* individuals have been reported at the edge of *Posidonia oceanica* meadows adjacent to rocky habitats versus the meadow interior (Ceccherelli et al. 2009a, present study) and higher frequency of large size-classes of individuals in the meadow compared to that in rocky habitats (Ceccherelli et al. 2009a). The lower abundance of settlers found in *P. oceanica* meadows (Tomas et al. 2004, Prado et al. 2012) supports the hypothesis that a considerable abundance of individuals migrate from the rocky habitats to the meadow (Fernandez et al. 2001, Ceccherelli et al. 2009b). This suggests that *P. oceanica* meadow edges could play an important role in controlling the demographic structure of populations. Indeed, migrations of the sea urchin from the rocks to seagrass patches have been estimated both in the field (Ceccherelli et al. 2009b) and in the laboratory (Pinna et al. 2012), suggesting that when *P. lividus* individuals are outside a refuge, they searched for a well-structured habitat where they could find both shelter and food.

Our goal in this study was to understand if meadow edge is chosen for sea urchin refuge or as a resource itself (or both), and if seagrass canopy structure affects urchin distribution, with important functional implications for the entire ecosystem. With this aim, we used both natural and artificial (plastic) seagrass units located at the edge of the meadow, the latter reproducing the natural structure of *Posidonia oceanica* so that shelter but no food was provided. The difference in abundance of *Paracentrotus lividus* individuals between natural and artificial units would indicate the role played by food provided by the leaves of *P. oceanica* in influencing *P. lividus* spatial distribution in this edge habitat. A higher number of individuals in the artificial units would suggest that the search for shelter triggered their movement towards the seagrass units despite the inedibility. Further, manipulation of the seagrass structure achieved by modifying the shoot density and leaf length was used to provide various understory microhabitats with intermediate (between dense seagrass canopy and open substrate) levels of shelter and food availability, reproducing the conditions offered to *P. lividus* by meadows in different states of conservation. A higher number of individuals in the more structured canopy would suggest that the benefits of

P. oceanica edge habitat are enhanced by dense and long shoots. The sea urchin abundance at the meadow edge was evaluated regardless of their origin habitat (i.e. from the rocky habitat and the meadow inside).

MATERIALS AND METHODS

This study was conducted in the Gulf of Alghero (northest Sardinia, Italy), near Capo Caccia-Isola Piana Marine Protected Area (MPA), in a small bay near the shore (Fig. 1). Sampling for the experiment took place 6 times between November 2009 and March 2010, when tourism was extremely low, at the edge of a 500 m wide continuous *Posidonia oceanica* meadow at a depth of 5 to 7 m. Here, rhizomes were not buried and a thin covering of bryozoans were the only epiphytes on the leaves. The rocky habitat next to the meadow edge consisted of gently sloping platforms covered mostly by algal turfs, *Codium bursa* (Agardh 1822), *Halimeda tuna* (Ellis & Sol.) JV Lamour, *Dasycladus vermicularis* (Mayhoub 1976), and *Udotea petiolata* (Turra) Borgesen. No boulders were present and crevices on the rocks were the only irregularities on the rock surface. The mean abundance (± SE) of sea urchins at the study site in the seagrass edge was higher than inside the seagrass and in the adjacent rocky habitat: 7.81 (±2.09), 4.10 (±1.06), and 4.30 (±0.84) ind. m^{-2} (n = 40), respectively ($F_{2,117}$ = 4.06, p = 0.0197).

The artificial seagrass structures reproduced the light levels and velocity of near-bottom water currents of *Posidonia oceanica* canopy, but did not provide a food resource. Artificial structures were constructed to reflect the broad characteristics of the seagrass edge habitat (i.e. the natural shoot density, leaf height, and number of leaves per shoot), which were estimated in the field at the beginning of the experiment. Mean (± SE) shoot density of *P. oceanica* in 40 × 40 cm areas was 75.67 (±4.67, n = 10), mean leaf height was 45.33 (±7.03, n = 10), while the mean number of leaves per shoot was 5.81 (±0.63, n = 10). Each artificial structure was constructed from a 40 × 80 cm frame of plastic coated iron with a 5 × 10 cm mesh to which mimics of *P. oceanica* leaves were tied. Artificial leaves were made of green plastic strips and arranged to form a shoot with the density and length of leaves resembling natural *P. oceanica* at that site: each shoot was made of 3 folded 100 cm-strips (that corresponded to 6 leaves, each 50 cm in height) and a total of 150 shoots were tied to each frame.

In the experiment, 3 types of *Posidonia oceanica* canopy were considered (Fig. 2): natural seagrass (NS), artificial seagrass (AS), and natural seagrass + frame (NS+F, the procedural control). The NS+F treatment was included to allow us to distinguish between the effect of the frame (if any) and the effect of the lower food availability in the AS treatments compared to the NS treatments. Thus, at each NS+F unit, the same plastic coated iron frame was secured in 40 × 80 cm units where natural leaves were present. Differences between NS and NS+F units would highlight the influence of the frame, such as possibly impeding *Paracentrotus lividus* locomotion. Conversely, each AS unit was placed in areas of 40 × 80 cm, where the natural seagrass vegetation was removed, and in which the frame with leaf mimics was secured at the corners with two 35-cm iron dowels driven below the substratum using a hammer. The 40 × 80 cm experimental units (replicates), were all located at the edge of the seagrass meadow: the artificial units were placed in areas cleared from *P. oceanica*, while the natural units were obtained by *in situ* manipulation of the shoots along the edge.

The entire experiment was completed over 6 randomly chosen times within the study period. To enable estimation
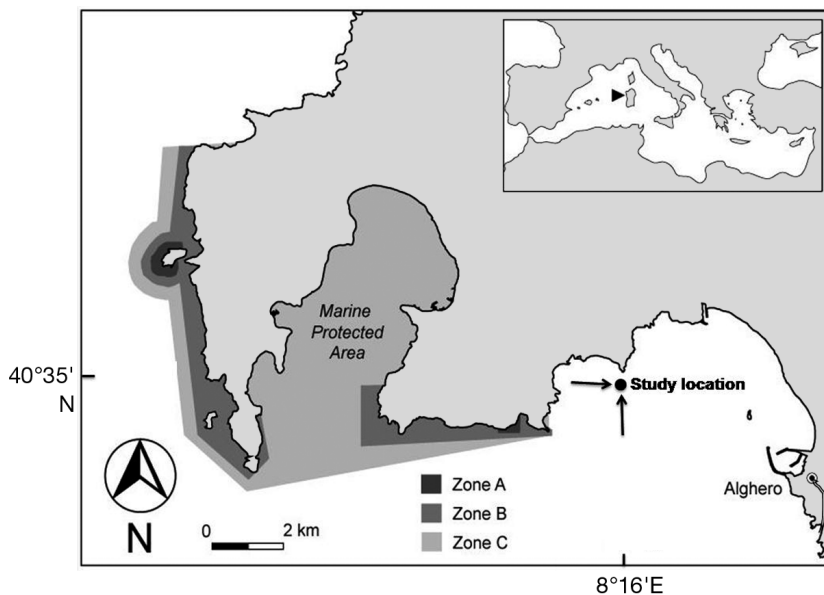

Fig. 1. Study location at Punta Negra near Capo Caccia-Isola Piana Marine Protected Area in Alghero (NW Sardinia, Italy)
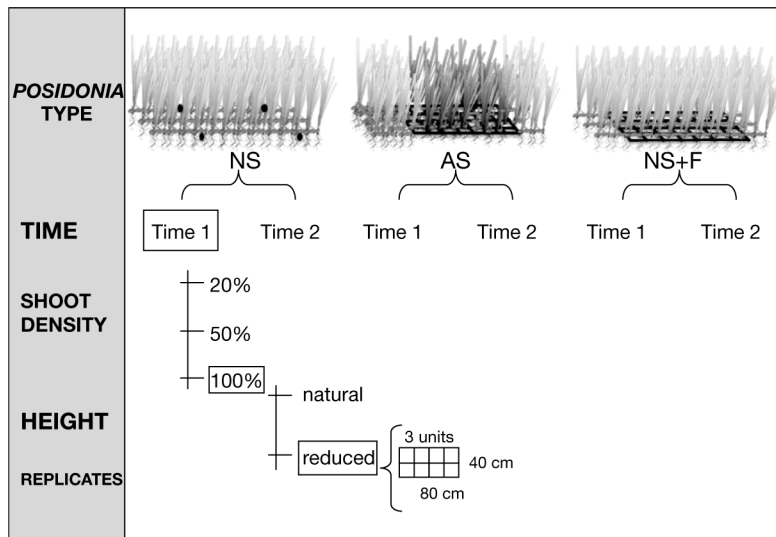
Fig. 2. Experimental design indicating all 4 factors considered and the levels of each factor: *Posidonia* type (natural seagrass: NS; artificial seagrass: AS; natural seagrass + frame: NS+F), time (2 levels within each *Posidonia* type), shoot density (20, 50, and 100%), and canopy height (natural and reduced). Each combination of treatments had 3 replicates

of temporal variability, each '*Posidonia oceanica*' type (NS, AS, and NS+F) was deployed twice (Fig. 2). At each time, 6 combinations of shoot density × height were newly established. For manipulation of NS and NS+F *P. oceanica* types, (1) shoot density (100, 50, and 20%) was altered by clipping shoots using scissors, and (2) canopy height (natural and reduced to half) by cutting leaves. For AS units, the canopy height was reduced by tying 50-cm plastic strips to the frame, while bundles of 75 and 30 strips were used to reproduce the 50 and 20% shoot densities, respectively. Each treatment combination was measured in triplicate, so that 18 experimental units were obtained at each experimental period (Fig. 2).

During the establishment of the experimental units, care was taken to ensure that no *Paracentrotus lividus* individuals were present within the study areas. *P. lividus* were counted after 1 wk at the same time of day (from 10:00 to 11:00 h). This time span (i.e. 1 wk) was judged to be more than sufficient to reflect the actual pattern of sea urchin movements measured in rocky habitats (up to 220 cm d^{-1} in unprotected areas; Hereu 2005), while there are only preliminary estimates on *P. lividus* movements in seagrass habitats as a result of predator avoidance (Scianna et al. 2007). A 4-way ANOVA was performed on *P. lividus* abundance: '*Posidonia*' type (NS, AS, and NS+F), shoot 'density' (20, 50, and 100%), and canopy 'height' (natural and reduced)

which were treated as fixed and orthogonal, while the factor 'time' was treated as random (2 levels) and nested in the '*Posidonia*' type. Cochran's test was performed to check for homogeneity of variances, while the Student-Newman-Keuls (SNK) test was utilized to make *a posteriori* comparisons of mean values (Underwood 1997).

In order to explain differences in sea urchin abundance, irradiance under the AS and NS+F *Posidonia* types at the different canopy manipulations were measured. Light measurements were taken at 12:00 h on a sunny day in February using an underwater quantum photometer: 2 replicate readings were recorded for each of the 6 combinations of 'density × height', at both *Posidonia* types. Light irradiance was analysed with a 3-way ANOVA with '*Posidonia*' type (AS and NS+F), shoot 'density' (20, 50, and 100%), and canopy 'height' (natural and reduced) as fixed and orthogonal factors. Cochran and SNK tests were run as above.

RESULTS

Overall, the abundance of *Paracentrotus lividus* in the *Posidonia oceanica* experimental units was quite consistent with natural abundance at the edge of the seagrass meadow. In particular, presence of *P. lividus* ranging from 1 up to 7 ind. occurred in most of the units, while their absence was recorded only very rarely (Fig. 3). The type of *Posidonia* (NS, AS, and NS+F) did not have any significant effect on the abundance of sea urchins; neither the main nor any interactive effect was detected from the analysis (Table 1). Nevertheless, there was a significant effect of the density of *P. oceanica* on the abundance of *P. lividus*; indeed, density had a significant effect and SNK test highlighted that there was an increase in mean abundance of *P. lividus* with the increase in *P. oceanica* shoot density, regardless of the canopy height (Table 1). Finally, consistency in *P. lividus* abundance within each type of *Posidonia* was found between experimental periods (Table 1). Post hoc pooling of various non-significant interactions did not alter the patterns of significance, although tests were more powerful.
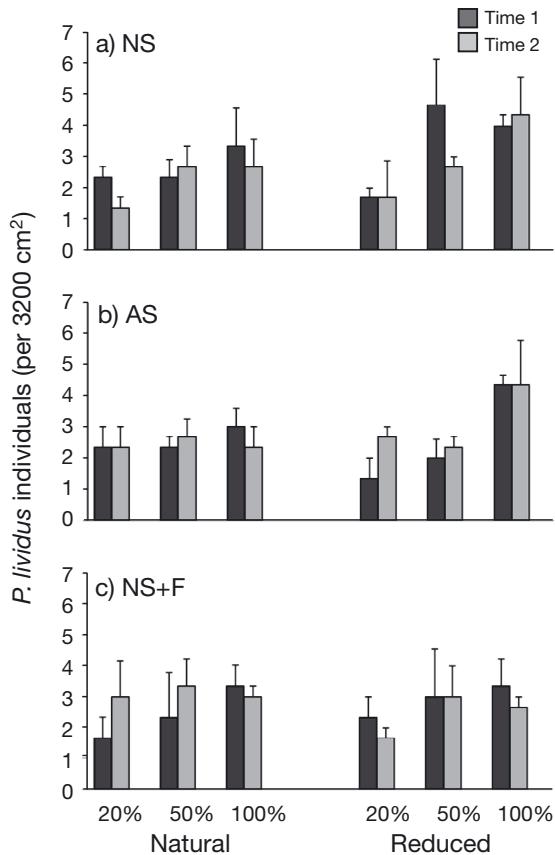
Fig. 3. Mean (+SE) *Paracentrotus lividus* abundance for all combinations of *Posidonia* type, canopy height, and shoot density. *Posidonia* types: (a) natural seagrass (NS), (b) artificial seagrass (AS), and (c) natural seagrass + frame (NS+F). Canopy height: natural and reduced. Shoot density: 20, 50, and 100%

The analysis did not detect any significant influence of *Posidonia* type on the irradiance (Table 2). However, differences in irradiance depended highly on *Posidonia oceanica* structure (Fig. 4); a significant 'density × height' interaction indicated that light intensity was directly related to the shoot density as significant increases in irradiance were found between 100 and 50%, and between 50 and 20% at both canopy heights (Table 2; SNK test). Also, higher irradiance was found at reduced rather than natural height where shoot density was left unaltered (100%), while at 50 and 20% there were no differences in irradiance between heights (Table 2; SNK test).

DISCUSSION

Results of the present study have highlighted that the abundance of *Paracentrotus lividus* at the edge of a *Posidonia oceanica* meadow is influenced by sea-

Table 1. Results of 4-way ANOVA on the effect of *Posidonia* type (NS, AS, and NS+F; see Fig. 2), time (2 within each *Posidonia* type), canopy height (Natural and Reduced) and shoot density (20, 50, and 100%) on the number of *Paracentrotus lividus* individuals. Student-Newman-Keuls (SNK) test results for shoot density (SE = 0.1351). Significant values in **bold**

Source of variation	df	MS	F	P
Posidonia = P	2	0.17	0.19	0.8376
Time = T(P)	3	0.93	0.52	0.6695
Height = H	1	2.67	2.11	0.2423
Density = D	2	16.73	25.45	**0.0012**
P × H	2	1.56	1.23	0.4065
P × D	4	1.62	2.46	0.1551
H × T(P)	3	1.27	1.26	0.5514
D × T(P)	6	0.66	0.65	0.8981
H × D	2	3.06	2.53	0.1599
P × H × D	4	1.45	1.20	0.4006
D × H × T(P)	6	1.21	0.68	0.6700
Residual	72	1.79		
Cochran's test	C = 0.1082 ns			

***P. lividus* abundance SNK test**
Shoot density
20% < 50% < 100%

grass shoot density. Particularly, regardless of the seagrass canopy height, higher shoot density of seagrass led to a greater abundance of sea urchins. Also, our results indicate that sea urchins do not go to the edge of *P. oceanica* to feed; indeed, *Posidonia* type was not found to influence the abundance of sea urchins as no significant difference in *P. lividus* abundance was found among NS and AS *Posidonia* types. Since the artificial material of the AS canopy did not produce any effect on sea urchins distribution, grazing is not the mechanism of attraction of sea urchins towards the seagrass meadow. Therefore, a more plausible explanation for going to the edge of the seagrass may be the search for shelter. The reliability of these data is given by the lack of differences between NS and NS+F types, indicating that the frame had no detectable effect.

Although we do not know whether the distribution of sea urchins at the edge of the seagrass meadow reflects their habitat preference, Pinna et al. (2012) show that when *Paracentrotus lividus* individuals are given a choice between *Posidonia oceanica* and boulders covered with palatable algae, they prefer the shelter of the seagrass and readily consume it. Other authors have suggested that *P. lividus* behaves fundamentally as an important feeder able to adapt widely to availability of food resources (Zupo & Fresi 1984). Field experiments demonstrate both depletion of algal species by *P. lividus* grazing (Benedetti-

Table 2. Results of 3-way ANOVA on the effect of *Posidonia* type (NS, AS, and NS+F; see Fig. 2), canopy height (Natural and Reduced) and shoot density (20, 50, and 100%) on irradiance. Student-Newman-Keuls (SNK) test result for H × D interaction (SE = 0.0087). Significant values in **bold**

Source of variation	df	MS	F	p
Posidonia = P	1	0.0006	2.32	0.1534
Density = D	2	0.0489	189.16	0.0000
Height = H	1	0.0002	0.58	0.4608
P × D	2	0.0001	0.19	0.8266
P × H	1	0.0001	0.26	0.6207
H × D	2	0.0032	12.39	**0.0012**
P × D × H	2	0.0002	0.84	0.4561
Residual	12	0.0003		
Cochran's test	*C* = 0.2581 ns			

Irradiance SNK test

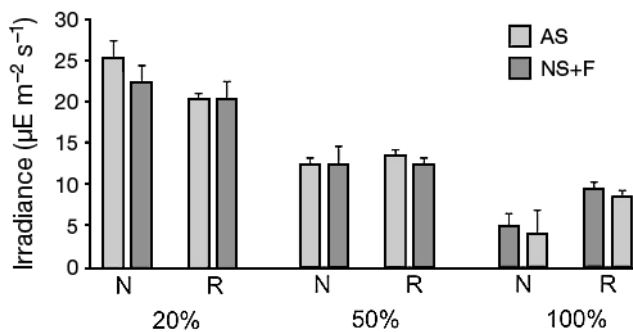| Canopy height	Shoot density	Shoot density	Canopy height
Natural	100% < 50% < 20%	100%	Natural < reduced
Reduced	100% < 50% < 20%	50%	Natural = reduced
		20%	Natural = reduced

Fig. 4. Mean (+SE) irradiance for the combinations of *Posidonia* type (AS: artificial seagrass; NS+F: natural seagrass + frame), canopy height (N: natural; R: reduced), and shoot density (20, 50, and 100%)

Cecchi et al. 1998, Bulleri et al. 1999, Hereu 2006) and the importance of *P. lividus* feeding on *P. oceanica* leaves (Alcoverro et al. 1997, Prado et al. 2007a,b). Further, Vergés et al. (2007) highlighted the chemical deterrence of *P. oceanica* on *P. lividus* and several other predators.

To demonstrate that *Paracentrotus lividus* primarily uses *Posidonia oceanica* to find shelter and that it feeds on it only opportunistically, the use of artificial seagrass structures of different dimensions would be needed. The small patch structures of artificial seagrass used in this study could have served as suitable shelters, with the nearby algae on rocky reefs and natural *P. oceanica* providing substrate for grazing. In this way, these artificial structures could have functioned for *P. lividus* merely as rocky crevices. Patches of artificial seagrass larger than the calcu-

lated home range of *P. lividus* (several square metres; Hereu 2005) are expected to host most of the sea urchins at the edge, with the nearest adjacent habitat serving for grazing. However, to estimate the influence of seagrass patch arrangement on sea urchin distribution, the *P. lividus* home range should be estimated in artificial seagrass units of different patch sizes fixed on rocky substratum with crevices available at different levels, precisely in the manner Kenyon et al. (1999) proceeded to investigate nursery effects on seagrass.

As highlighted by many studies, structural complexity may be an important determinant for fish and invertebrate communities. In particular, as suggested by Ruitton et al. (2000), for the shelter to be effective, its size must be proportional to the size of the invertebrate and, further, the abundance increases with increasing structural complexity. In Mediterranean rocky habitats, this has also been shown for juveniles of *Paracentrotus lividus* (Hereu et al. 2005). Indeed, the occurrence of high predator pressure and the consequent need for shelter initiates a cryptic behaviour of *P. lividus* (Guidetti et al. 2003) and a successful reduction in predation rate (Sala et al. 1998). At the study site, although the rocky platforms probably do provide secure shelters since irregularities in the rock are small and rare, they are covered by algal turfs that are highly palatable to *P. lividus* (Benedetti-Cecchi et al. 1998, Bulleri et al. 1999, Hereu 2006). The conformation of this rocky habitat supports the hypothesis that *P. lividus* could consider a *Posidonia oceanica* meadow primarily as a refuge and that the abundance of this sea urchin species found in this seagrass edge could mostly be due to its migration from the rocky habitat. In this regard, it is worth highlighting that this experiment was carried out in an unprotected area and that at this site the search for a shelter for *P. lividus* was not likely influenced by particularly high predation pressure. However, if the importance of *P. oceanica* as a refuge was established outside an MPA (present study), it is certainly more feasible in reserve areas.

In this study, a higher number of sea urchins went to the edge of meadows where the seagrass canopy was denser, probably attracted by the reduced irradiance. As suggested by some authors, shade is an important factor affecting *Paracentrotus lividus* dis-

tribution (Barnes & Crook 2001, Verling et al. 2002) and dense shoots of seagrasses could provide such conditions (Ceccherelli & Cinelli 1999, Verweij et al. 2006). Therefore, in this study, the lower *P. lividus* abundance at 20% density rather than at 50 and 100% could be related to the higher irradiance. This would provide evidence of the importance of the light regime on sea urchin distribution at the edge of seagrass meadows.

This study found that the seagrass edge contained greater abundances of *Paracentrotus lividus* than both the interior and the rocks, as if these individuals could benefit from the intermediate environmental conditions of the edge or from periodic visits to one or both adjacent habitats. However, in this experiment, we did not evaluate whether the sea urchins at the experimental units came from the meadow or the rocks and we cannot support either one or the other hypothesis. Although these findings add important facts to the understanding of *Posidonia oceanica–P. lividus* interactions at the edge of the seagrass, further studies are required to determine whether routine migratory movements, foraging movements between habitats, or ontogenetic shifts occur in sea urchins in order to provide insights into the role of the seagrass edge habitat on their distribution. Space use patterns in sea urchins and the structure of the seascape over which they traverse must be quantified so that a more complete understanding of species–habitat relationships and seascape connectivity can be developed.

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