

Seagrass meadow structure alters interactions between the sea urchin *Paracentrotus lividus* and its predators

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ABSTRACT: Predation on sea urchins, which are important structuring agents in seagrass communities, can be modulated by habitat structural complexity. Here we examine the importance of meadow structure (leaf length and presence of unburied root-rhizome layer) in determining predation pressure on the main invertebrate herbivore of the temperate seagrass *Posidonia oceanica* (L.) Delile, the sea urchin *Paracentrotus lividus* (Lamarck). The attributes of seagrass habitat complexity are subject to considerable spatial and temporal variability, thus affecting refuge availability. In the field, exposure of the root-rhizome layer depends on local sedimentary conditions, while changes in the leaf canopy are generally dictated by hydrodynamic regimes, light, nutrient availability as well as grazing activity. We reproduced 5 habitat conditions in the laboratory and 2 in the field by modifying leaf length and burial level of the root-rhizome layer, and we measured fish predatory efficiency under controlled conditions. In the laboratory we focused on juvenile sea urchins (0.2 to 1.2 cm test diameter, TD) while in the field we studied young adults (3 to 5 cm TD). Mortality of juveniles and young adults was significantly lower under long leaves, while the presence of an unburied root-rhizome layer appeared to provide a key refuge for juveniles, independent of leaf length. The presence of refuges thus appears to be a key factor in the interaction between sea urchins and predatory fish in seagrass meadows, and highlights the importance of local structural complexity (e.g. sedimentary regimes, fish herbivory pressure) on the regulation of predator–prey interactions.

KEY WORDS: *Posidonia oceanica* · *Paracentrotus lividus* · Herbivores · Trophic cascades · Top-down control · Refuge · Canopy

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INTRODUCTION

Predation is an important structuring agent in marine communities, and its intensity is strongly dependent on the presence of refuges, and hence spatial complexity. In seagrass meadows there are multiple elements of plant morphology or architecture that contribute to habitat structural characteristics, from the simplest (e.g. leaf surface area) to the most complex (e.g. number and size of blades, branching pattern, presence of a bare root-rhizome layer). All of these elements can provide refuge for a variety of organisms (e.g. Orth et al. 1984, Heck & Wilson 1986). In fact, sea-

grass habitat serves as refuge from predation for various prey fish and invertebrate species (Savino & Stein 1982, Orth et al. 1984, Heck et al. 1989, Orth 1992, Harris et al. 2004). Additionally, vegetation is constantly affected by multiple biotic and abiotic processes (i.e. seasonal leaf loss, leaf loss by storms or currents, grazing), which can potentially modify habitat structure and, consequently, influence predatory interactions (Savino & Stein 1982).

Sea urchins are known to play an important role in the control of submersed aquatic vegetation (Lawrence 1975, Harrold & Pearse 1987, Dayton et al. 1992, Shears & Babcock 2002), and variation in their abun-

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dance and population structure can significantly alter the structure and function of benthic communities. In seagrass meadows, sea urchin densities can vary greatly, resulting in important consequences for herbivory rates (Prado 2007); sea urchin population outbursts can result in major overgrazing events and have been implicated in decline or local extinction of seagrasses (e.g. Camp et al. 1973, Heck & Valentine 1995, Rose et al. 1999). The mechanisms governing such population outbursts in seagrass meadows are not clearly understood, although they appear to be the result of a combination of successful recruitment, refuge availability and release from predation pressure (Parker & Shulman 1986, Rose et al. 1999, Prado 2007).

The seagrass meadows of the Mediterranean Sea are characterised by the high physical complexity of the dominant species, *Posidonia oceanica* (L.) Delile, which typically has dense leaf canopy (Heck & Orth 1980) and robust rhizomes coated with the remains of old leaf sheaths. The net of interlacing rhizomes, roots and sediment form a dense root-rhizome layer (Romero et al. 1994) that can be either buried or partially exposed. When exposed, its crevices can provide potential refuges for prey species. Hence, in *P. oceanica* meadows, in addition to leaf canopy, gaps and burrows within the root-rhizome layer structure can be a potentially important factor in the survival of prey. However, the availability of these possible shelters often varies according to the biological features of the meadow and local environmental variables. Seagrass burial levels, for instance, can vary depending on the hydrodynamic regimes or sedimentation rates (Gacia et al. 1999), and the root-rhizome layer structure may be completely buried or exposed at different levels. In addition, shoot density and leaf length can be controlled by abiotic (e.g. hydrodynamic regimes, light conditions or water turbidity; Den Hartog 1970) or biotic conditions (e.g. herbivore activity; Heck & Valentine 2006). In particular, herbivory pressure in the Mediterranean exhibits strong seasonal patterns, and can substantially modify seagrass leaf length (Tomas et al. 2005), thus altering refuge suitability of the seagrass canopy and opening the possibility of complex interactions between herbivores.

Posidonia oceanica meadows are commonly inhabited by the sea urchin *Paracentrotus lividus* (Lamarck), the most important invertebrate herbivore in the Mediterranean (Boudouresque & Verlaque 2001). This sea urchin has been reported to consume up to an average of 17% of the annual leaf production, thus playing a central role in the trophic dynamics of the system; however, consumption withstands considerable spatial variation (from ca. 6 to 36% of the annual leaf production; Prado et al. 2007). Juvenile sea urchins seem to be

present only in those meadows where the root-rhizome layer is unburied (Tomas et al. 2004, Prado 2007), which highlights the potential effect of this structure as a refuge for juveniles. In contrast, young adults are too large to hide within the root-rhizome layer (e.g. Tomas et al. 2005), yet not large enough to deter predators (Sala & Zabala 1996). In the present study we investigated the relative refuge potential of different seagrass structural features for the sea urchin *P. lividus* against fish predation. We examined the role of the existence of the root-rhizome layer in order to confirm previous correlation results (Prado 2007), and the role of leaf length to explore possible indirect interactions among herbivores. We used a combination of field- and laboratory-based manipulative experiments, manipulating under controlled conditions these 2 features of seagrass habitat.

MATERIALS AND METHODS

The role of structural elements of *Posidonia oceanica* meadows (i.e. leaf canopy and root-rhizome layer) as refuges against predation for sea urchins was evaluated in different experiments, according to the size of the organisms involved. For small sea urchins (juveniles, 0.2 to 1.2 cm test diameter, TD) we tested the effects of leaf canopy and the presence of the root-rhizome layer on survival. For young adults (3 to 5 cm TD), we only investigated the effects of leaf canopy, as the crevices in the root-rhizome layer are too small to allow young adult sea urchins to enter (Tomas et al. 2004). Predation experiments were conducted both in the field and the laboratory. For young adults, experiments were performed in a Marine Protected Area (Medes Islands Marine Reserve, 42° 16' N, 03° 13' E) where large predators (consumers of adult sea urchins) are abundant (Hereu et al. 2005). Juvenile sea urchins were too small to be successfully manipulated under field conditions, and predation experiments on these individuals were conducted in an aquarium, with a high density of potential predators.

Predation on juveniles. Two experiments were conducted with juvenile sea urchins within the aquaria facilities of the Aquàrium de Barcelona. Sea urchins, seagrass and sand were collected in February 2005 between 5 and 7 m depth off Blanes (NE Spain) using SCUBA and immediately transported to the Aquàrium for further sorting. Experimental units consisted of open transparent plastic boxes (25 cm wide × 30 cm long × 16 cm high) with thin net walls (2 × 2 mm mesh size) in which different seagrass structures were constructed (see below and Fig. 1). A preliminary experiment revealed that juveniles were not able to escape from such experimental units.

A number of seagrass shoots, including their respective rhizome and roots, similar to the natural density of local shallow meadows (i.e. 400 to 500 shoot m^{-2}) and bearing, on average, 5.9 ± 0.7 leaves shoot $^{-1}$ (Alcoverro et al. 1995) were placed in each of the boxes and anchored with cable ties. If necessary, sand was added to completely cover the rhizomes in order to eliminate crevices or other potential refuges. In the first experiment, we evaluated the role of seagrass canopy in decreasing fish predatory efficiency. To simulate different canopy conditions, leaves were cut as appropriate, and 3 treatments, each with 3 replicate units (boxes), were assembled: absence of leaves (0 cm), short leaves (all leaves longer than 7 cm were cut to 7 cm length) and long leaves (all leaves longer than 20 cm were cut to 20 cm length). In all 3 treatments, the rhizome layer was completely covered with sand (Fig. 1a). In the second experiment, we combined 2 treatments of leaf canopy (long leaves vs. short leaves) with 2 treatments of root-rhizome layer (presence vs. absence) in which rhizome crevices were available or filled with sand respectively (Fig. 1b). For each combination of treatments 3 replicates (independent experimental units, i.e. boxes) were used.

All boxes were placed in the bottom of a large tank (3500 l, 2 m diameter) with continuous seawater flow and containing the main guild of fish species known to prey on juvenile sea urchins (Boudouresque & Verlaque 2001). Specifically, the tank contained a total of 31 *Coris julis* (L.), Labridae; 7 *Diplodus sargus* (L.) and 7 *D. vulgaris* (Geofr.), Sparidae, which were starved for 1 wk prior to the start of the experiment. In addition, to reduce potential behavioural artefacts, boxes with no urchins were left inside the tank to allow acclimation of fish. After 4 d, sea urchins ($n = 15$) were added to each box and the experiment started. Three empty plastic

control boxes with sea urchins ($n = 15$) adhered to the bottom (using 2-component Ivergor putty) were also placed in the tank. These boxes allowed for the monitoring of predation when urchins were readily available to predators; these controls were used to determine the end-point of the experiments. After 15 h, ca. 90% of individuals had been consumed in the controls, and experimental boxes were closed with a fine plastic mesh cover and removed from the tank; the number of remaining individuals in each treatment was then counted.

Predation on young adults. The protective effect of seagrass canopy against fish predation for young adults was evaluated in a shallow *Posidonia oceanica* meadow (ca. 5 m depth) at the Medes Islands Marine Reserve, where predators are very abundant and large enough to prey on young adults (Garcia-Rubies & Zabala 1990). In addition, the experiment was conducted in summer (August 2005), when predators are more active (Sala & Zabala 1996) and predatory potential is highest. We compared predation rates between plots (in natural stands) with short leaves (cut to 7 cm) and plots with long leaves (cut to 20 cm), and we also built control plots where urchins were totally exposed; the latter determined the end-point of the experiments (Fig. 1c).

Plots were 180 × 180 cm in size, and 3 replicated plots were used for each treatment and control. Seagrass treatments (i.e. short leaves and long leaves) were marked with metal stakes and always carried out in areas where rhizomes were covered by sand. Control plots were set on unvegetated patches within the meadow, in which we placed a plastic mesh (2 cm pore size, attached to the sand with stakes) to facilitate tethering of urchins.

Sea urchins (3 to 5 cm TD) were collected from rocky substrates near the study site using SCUBA. For each experimental plot, 12 ind. were pierced through the test with a hypodermic needle, threaded with monofilament line (50 cm length) and tied to a metal stakes (Aronson & Heck 1995). Each tethered urchin was uniquely identified with a number and placed randomly inside the plot. The experiment concluded when more than 50% of individuals in the control plots had been consumed. This occurred within a 4 d period, after which stakes were removed and the remaining sea urchins counted.

Data analyses. We used ANOVA to assess the significance of differences among treatments, using sea urchin mortality (as a percentage relative to the initial number) in each box as the dependent variable. For the aquarium experiments, the effects of leaf length on predation pressure were tested with a 1-way ANOVA with leaf length as a fixed factor (3 levels: no leaves, short leaves and long leaves). Subsequently, the con-

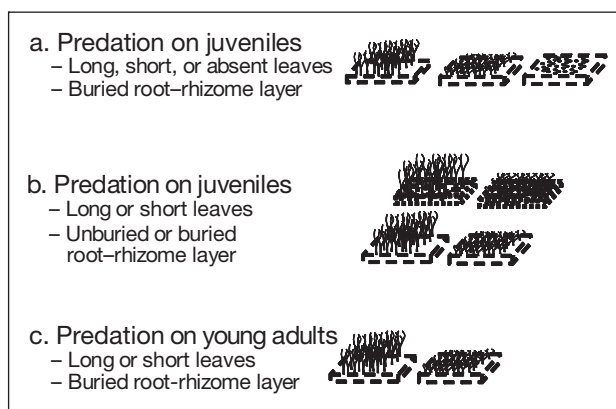


Fig. 1. Setup of predation experiments for juvenile and young adult sea urchins in different refuge conditions. Substrate type: buried (dashed) or unburied (dotted) root-rhizome layer. Leaf canopy length: long (20 cm), short (7 cm) or absent.

current influence of leaf canopy and availability of unburied root-rhizome layer structure on predation pressure was assessed using a 2-way ANOVA (with leaf length and root-rhizome layer structure as fixed factors, with 2 levels each).

For the field experiment, the effect of the seagrass canopy on predation pressure was assessed using a 1-way ANOVA with leaf length as a fixed factor (2 levels: short leaves and long leaves)

For all analyses, data were first tested for normality (Kolmogorov-Smirnov test) and homogeneity of variance (Cochran's test). When overall significant differences were detected, *a posteriori* pairwise comparisons of means were performed using a Student-Newman-Keuls (SNK) test (Zar 1989).

RESULTS

In the absence of exposed root-rhizome layer (first experiment), we detected that predation activity on juveniles was highly influenced by the presence of leaves. Mortality of juveniles was significantly lower when leaves were long ($29.1 \pm 11.0\%$ mortality, mean \pm SE) than when they were either short ($68.0 \pm 6.6\%$ mortality) or absent ($56.7 \pm 5.1\%$ mortality; SNK, $F = 6.327$, $p = 0.033$) (Fig. 2).

When the effects of leaf canopy and root-rhizome layer were tested simultaneously (second experiment), both variables showed a strong influence on the predation of juveniles. Predation was lowest (mortality reaching values as low as $11 \pm 4.4\%$) when the unburied root-rhizome layer was present, independent of leaf length (Table 1, Fig. 3). When the root-rhizome layer was buried, the treatment with long leaves showed less predation than that with short leaves (i.e.

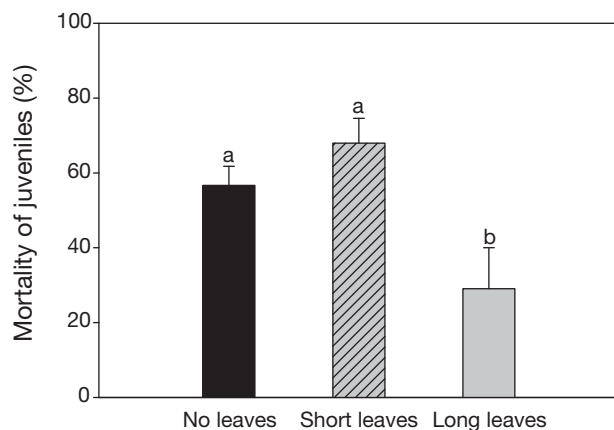


Fig. 2. *Paracentrotus lividus*. Percent mean (\pm SE) mortality of juvenile sea urchins (0.2 to 1.2 cm test diameter, TD) under different canopy conditions. Different letters indicate significant differences between treatments (SNK)

Table 1. Two-way factorial ANOVA used to assess differences in predation pressure (% mortality) on juvenile sea urchins by fish between substrate (root-rhizome layer: buried in sand vs. unburied) and canopy conditions (leaf length: short vs. long) and their interaction

Source	df	MS	F	p
Substrate (S)	1	0.2896	25.5850	0.0009
Leaf length (L)	1	0.0778	6.8950	0.0304
S \times L	1	0.0792	7.0090	0.0293
Error	8	0.1132		

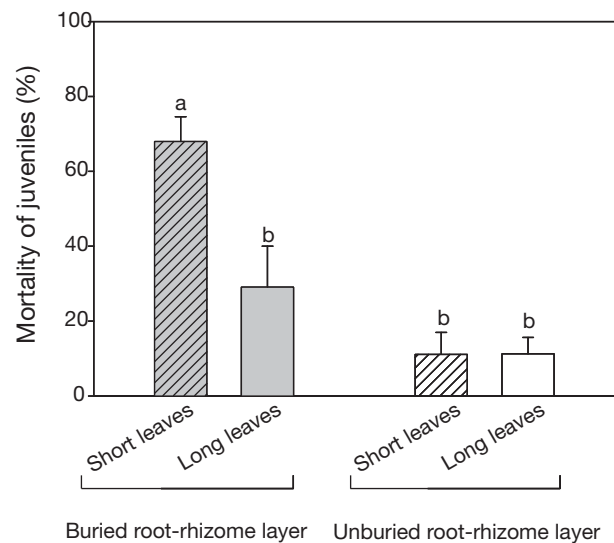


Fig. 3. *Paracentrotus lividus*. Percent mean (\pm SE) mortality of juvenile sea urchins (0.2 to 1.2 cm TD) under different refuge conditions (i.e. rhizome habitat and canopy length). Different letters indicate significant differences between treatments (SNK)

significant leaf length \times root-rhizome layer interaction) (Table 1). Similarly, in the field experiment we observed that mortality of young adults was significantly lower in plots with long leaves ($27.8 \pm 5.6\%$ mortality) than in the treatment with short leaves ($80.6 \pm 12.1\%$ mortality; ANOVA, $F = 22.26455$, $p = 0.009$) (Fig. 4).

DISCUSSION

The present study provides strong support for the importance of refuges in alleviating predation pressure on sea urchins in seagrass meadows. Rates of predation on juvenile and young adult sea urchins were strongly influenced by variations in leaf canopy and the presence of bare rhizomes. Although we only manipulated leaf length to modify canopy structure, it is plausible that other structural features, such as shoot density, also influence the capacity of leaf canopy to

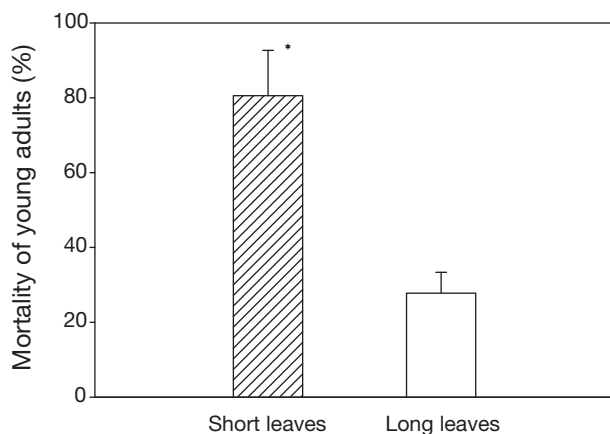


Fig. 4. *Paracentrotus lividus*. Percent mean (\pm SE) mortality of young adult sea urchins (3 to 5 cm TD) under different canopy conditions. *: significant differences

provide refuge against predation, particularly when rhizomes are buried. In fact, other authors have observed the existence of a threshold level in vegetation density which reduces predation intensity in other organisms inhabiting seagrass meadows (see Heck & Orth 2006).

In the present study, the unburied root-rhizome layer appeared to be a key refuge for juvenile sea urchins, as its presence drastically reduced mortality, independently of leaf length. However, when this structure was unavailable to juveniles (i.e. buried by sand), dense seagrass canopy still provided some degree of protection. In contrast, dense seagrass canopy was the only effective refuge for young adults. These individuals are too large to hide within the root-rhizome layer (e.g. Tomas et al. 2005), yet not large enough to deter or resist predators (Sala & Zabala 1996). Indeed, survival of young adults was significantly lower when leaf canopy was reduced or absent.

As these seagrass features are highly variable in space and time, the susceptibility of sea urchins to predation in seagrass meadows will depend not only on the abundance and size of predators and sea urchins, but also on the temporal availability of refuge sites. Burial of the root-rhizome layer depends on the sedimentary budget, which, in turn, is driven by local conditions (Gacia et al. 1999). For instance, a recent extensive survey of shallow seagrass meadows along 500 km of coastline in the NW Mediterranean reported that only 4 seagrass meadows, out of 10 sampled, showed a conspicuous presence of an exposed root-rhizome layer (Prado 2007). Leaf canopy structure, determined by leaf length and shoot density, is still more variable, as a result of light and nutrient availability (Alcoverro et al. 1997), grazing activity (see Heck & Valentine 2006) and environmental conditions such as hydro-

dynamic regimes and water turbidity (Longstaff & Dennison 1999). *Posidonia oceanica* canopies can, for example, be strongly reduced by the grazing activity of herbivorous fish (Tomas et al. 2005, Prado et al. 2007) and, consequently, this can stimulate predation on young sea urchins. However, to adequately understand the effects of predation on sea urchins it should be recognised that predators of juveniles are different from those of young adults and adults. In effect, predation on juveniles is exerted by small fishes such as *Coris julis* and other small labrids (Hereu et al. 2005), while for young adults the most frequent predators are large sparids; while the latter are strongly affected by overfishing, the former are not (García-Rubies 1996, Sala 1997). Therefore, predation on juvenile sea urchins is likely of general occurrence and the abundance of juveniles may be dependent on the presence of the unburied root-rhizome layer. This contention is supported by Prado (2007), who reported that juveniles were only detected in meadows where a prominent root-rhizome layer was present.

In contrast, due to the loss of large predators as a result of fishing (Sala & Zabala 1996), predation pressure on young adult and adult sea urchins is probably low in most seagrass meadows. However, the abundance of large fish predators is higher inside marine reserves than elsewhere (e.g. Sala & Zabala 1996), and this can impact urchin populations. Again, this contention finds support in a large-scale survey of this region, which found lower densities of young adults as well as lower seagrass consumption rates by sea urchins inside marine reserves than elsewhere (Prado 2007).

In marine reserves, predation is enhanced both directly, by the increased abundance of predators, and indirectly, by the lower availability of dense canopies: the density of the herbivorous fish *Sarpa salpa* (L.) increases in marine protected areas (García-Rubies & Zabala 1990), to the point that it has the capacity to strongly affect *Posidonia oceanica* canopies of shallow meadows, significantly reducing leaf length (Tomas et al. 2005). As our results indicate, this reduction in shoot length could significantly increase predation pressure on young adult sea urchins. This could be critically important during the summer months, when grazing activity by fish increases dramatically (Tomas et al. 2005) and predatory fish exert the highest predation pressure on sea urchins (Sala & Zabala 1996). Although this hypothesis needs further experimental evidence, the existence of an indirect interaction between herbivorous fishes and the survival of young adult sea urchins seems consistent with the findings reported here and evidenced from the literature.

It has been well established for rocky bottom communities that the availability of refuges interacting

with the size and behaviour of both predator and prey is crucial to the regulation of sea urchin populations and, consequently, in determining the state of algal communities (Witman & Dayton 2001, Hereu 2004, Guidetti 2006, and references therein). In contrast, predator–prey interactions and their potential consequences are less studied in seagrass ecosystems and, within this context, the data presented here constitute a first step towards understanding this potentially important interaction. The present study has shown that the biotic (i.e. herbivory) and abiotic (i.e. sedimentation and hydrodynamic regime) processes that influence meadow architecture or structure have the potential to significantly affect predators' ability to control sea urchin population density. Any mechanism affecting a strongly interactive consumer (i.e. those potentially capable of causing community-wide effects) may have repercussions for the entire trophic dynamic of seagrass ecosystems. Through predation processes, herbivores are directly controlled by carnivores which, therefore, indirectly regulate plant abundance. This study highlights the existence of other factors and interactions that can indirectly alter this general top-down control. In this case, seagrass habitat structural complexity is a crucial element in regulating predation of a key herbivore in time and space by providing different refuges for different life stages.

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