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The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins

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Abstract We studied the effect of the abundance of predatory fishes and structural complexity of algal assemblages on the survival of juveniles of the sea urchin *Paracentrotus lividus* on Mediterranean infralittoral rocky bottoms. Post-settlement juveniles (2–10 mm) were placed on four distinct natural substrates with increasing structural complexity (coralline barren, algal turf, erect fleshy algal assemblages and small crevices) inside and outside the Medes Islands Marine Reserve. Predation on these sea urchins increased at greater abundance of predatory fishes, and decreased with greater structural complexity. The refuge provided by structural complexity, however, decreased with increasing size of sea urchin recruits. Predation on the smallest post-settlers was carried out almost exclusively by small fishes (< 20 cm), mainly the labrid *Coris julis*, while the dominant predator of larger juveniles was the sparid *Diplodus sargus*. Our results demonstrate the cascading effects caused by the prohibition of fishing in marine reserves, and highlight the potential role of small predatory fishes in the control of sea urchin populations.

Introduction

Sea urchin abundance is highly variable in time and space (Pearse and Hines 1987; Turon et al. 1995; Sala et al. 1998a). Small variations in sea urchin abundance can have considerable effects on benthic communities,

because sea urchin grazing beyond a particular density threshold can transform complex communities, dramatically decreasing biodiversity in many systems, such as algal communities (e.g. Lawrence 1975; Andrew and Choat 1982; Himmelman et al. 1983), seagrass beds (e.g. Camp et al. 1973; Maciá and Lirman 1999; Alcoverro and Mariani 2002) and coral reefs (e.g. Hughes et al. 1987; Carpenter 1990; McClanahan and Shafir 1990). Despite its ecological importance, the relative contributions of the processes that regulate sea urchin abundance, such as predation and recruitment, are as yet unclear.

Predation is a key process in determining sea urchin population structure and dynamics (e.g. Tegner and Dayton 1981; McClanahan and Shafir 1990; Shears and Babcock 2002). It has been suggested that predation on juveniles is the major bottleneck in sea urchin populations (Tegner and Dayton 1981; McClanahan and Muthiga 1989; Sala 1997; Lopez et al. 1998), and that it might dampen large fluctuations in density which result from variability in recruitment (Sala and Zabala 1996; Lopez et al. 1998). Therefore, sea urchin populations should be smaller in the presence of abundant predators (McClanahan and Sala 1997). In marine reserves, where predatory fishes are more abundant and larger than in unprotected areas (e.g. Halpern and Warner 2002), sea urchin densities are generally lower than outside the reserves (McClanahan and Muthiga 1989; Sala and Zabala 1996; Shears and Babcock 2002, 2003). However, predation is not the sole factor regulating sea urchin densities. Diseases (e.g. Lessios 1988) or recruitment variability (e.g. Turon et al. 1995) can also modify sea urchin populations. There is evidence of large spatial and temporal fluctuations of local sea urchin densities in marine reserves (e.g. Sala et al. 1998a) because of factors such as refuges from predation, which may reduce predation rates (Sala et al. 1998b).

The availability of shelter is a key factor in determining predation rates (Roberts and Ormond 1987; Hixon and Beets 1993; Beck 1995) and hence the distribution and abundance of sea urchins (Tegner and

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Dayton 1981; Carpenter 1984; McClanahan and Kurtis 1991; Andrew 1993). When shelter is available, sea urchins hide and graze around it, thus contributing to the formation of local barren areas (Andrew 1993; Sala 1996). The importance of shelters decreases with increasing sea urchin size because small sea urchins are more susceptible to predation by fishes than large adults (Sala and Zabala 1996; Shears and Babcock 2002). Furthermore, the availability of shelters may be limited for adult sea urchins.

The sea urchin *Paracentrotus lividus* (Lamarck) is the most common grazer in the Mediterranean infralittoral (e.g. Kempf 1962; Verlaque 1987). At high densities, this species overgrazes complex algal assemblages composed of several hundred species, and turns them into barren areas dominated by a few species of encrusting algae (Kempf 1962; Neill and Larkum 1965; Verlaque 1987; Sala 1996). Barren areas, together with large sea urchin populations, occur mainly in areas with few urchin predators (reviewed by Sala et al. 1998b; Pinnegar et al. 2000). However, there is also evidence of barren areas in marine reserves with large fish densities (Sala et al. 1998a). The objective of this study was to determine the effects of predator abundance and structural complexity of the habitat (algal assemblages) on the survival of juvenile *P. lividus*. We hypothesize that the survival of juveniles decreases with increasing predator abundance, and that increasing structural complexity (availability of shelter) decreases the predation rate. To test this hypothesis, we carried out experiments in the NW Mediterranean, in a marine reserve and in an unprotected area with significant differences in the abundance of predatory fishes.

Materials and methods

Study site

The study was carried out in the NW Mediterranean Sea, both in the Medes Islands Marine Reserve (where fishing is prohibited) and the nearby Montgrí unprotected area (where fishing takes place) (see Hereu et al. 2004 for a detailed map). The reserve (which was created in 1983), is located 1 km offshore from the town of l'Estartit (42°16'N, 03°13'E) and encompasses a group of small islands. The study was conducted on rocky bottoms 5–10 m deep, harbouring a mosaic of patches (10^3 – 10^5 cm²) dominated by distinct types of algal assemblages, including:

1. Coralline barrens dominated by encrusting corallines (*Lithophyllum incrustans*, *Mesophyllum alternans*, *Spongites notarisii*);
2. Turf algal assemblages dominated by small filamentous algae (e.g. Rhodomelaceae, Ceramiaceae, Ulvaceae); and
3. Erect algal assemblages dominated by a canopy of perennial (e.g. *Cystoseira compressa*, *Codium*

vermilara) and seasonal (e.g. *Dictyota dichotoma*, *D. fasciola*, *Asparagopsis armata*) macroalgae and understory species (e.g. *Corallina elongata*, *Rhodomenia ardissoni*, *Halopteris filicina*) (Sala and Boudouresque 1997).

Predatory fish abundance

To quantify the abundance of urchin-feeding fishes in the reserve and the unprotected area, we counted and visually estimated the size of all fishes along randomly located 50×5 m transects using SCUBA diving (Harmelin-Vivien et al. 1985). We conducted five transects in each of two randomly selected sites in both the reserve and the unprotected area ($n=10$ transects per level of protection). The different substrate types form small patches (<10 m²), and fishes move between patches, hence we assumed that there were no differences in fish density between substratum types within sampling sites. Fish biomass was calculated using length-biomass relationships from E. Sala (unpublished data) and Bayle et al. (2001).

Predation experiments

Juvenile *P. lividus* 2–10 mm in diameter (test without spines) were collected from crevices and beneath boulders in the study areas using SCUBA diving.

All experiments were conducted in summer because fish activity is higher (Garcia-Rubies 1996) and *P. lividus* recruitment is strongest (Lopez et al. 1998). Nocturnally active urchin-feeding fishes are uncommon (Savy 1987; Sala 1997); therefore experiments and field observations were conducted during daylight.

Juvenile *P. lividus* were placed on the bottom using tweezers and covered with 40×40×30 cm plastic cages with 1-cm mesh size. After 5 min, a diver located on the bottom 10 m away lifted the cage using a string, thus exposing the urchins to predators. We believe we avoided artefacts caused by the attraction of fishes to divers, and obtained independent estimates of predation. Fishes did not appear to be attracted to the cage, and therefore we believe that predation was not biased by the experimental procedure. A digital video camera (Sony VCR 900) in an underwater housing (Gates Diego Housing) was placed close to the cage, and experiments were filmed by remote control for 20 min (divers left the site after pulling away the cage and exposing urchins to predators). In the laboratory, we watched the videotape and noted the times at which each sea urchin was consumed by fishes, identified the predator species for each individual sea urchin, and estimated their size using a plastic ruler placed at the study site as a reference. Preliminary trials showed that in most treatments sea urchin survival showed asymptotes before 20 min after the beginning of the experiments, suggesting that the

experiments were run long enough to allow us to detect differences between treatments.

To test how predation may be modified by the structural complexity of the habitat, four types of substrate (see above for details) were selected on each area, by increasing degree of protection from predation: (1) coralline barrens without shelter (no crevices); (2) algal turfs; (3) erect macroalgal assemblages; and (4) crevices (0.5–3 cm width). In the treatment with crevices, sea urchins were placed inside the crevices; in all other treatments sea urchins were placed on the substrate. In both areas (inside and outside the marine reserve), we conducted five experiments randomly placed in each habitat type. In each experimental replicate, 10 juvenile sea urchins (2–4 mm diameter) were placed in each treatment (habitat type). To test for differences in survival of juvenile *P. lividus* between treatments and degree of predator abundance, two-way ANOVAs were performed, with predator abundance (reserve, unprotected area) and habitat type as independent variables, and survival at the end of the experiment as the dependent variable. Cochran's test was conducted prior to ANOVA to test the assumption of homogeneity of variance. Data were log-transformed to satisfy this assumption.

To determine the relationship between the sizes of sea urchins consumed by fish of particular size classes, we conducted experiments as described above, using two size classes of sea urchins (2–6 and 6–10 mm), in the marine reserve ($n = 3$ replicates per size class and habitat type). To test for differences in sea urchin survival among sizes and substrata, two-way ANOVAs were performed. Cochran's test was conducted prior to ANOVA to test the assumption of homogeneity of variance. When necessary, data were log-transformed to satisfy this assumption.

To determine the relationship between predatory fish size and sea urchin size, we conducted a non-linear regression between fish length and sea urchin diameter, using data from experiments where sea urchin size was

measured and estimation of fish size was possible. We also conducted additional experiments using sea urchins from 10 to 13 mm in diameter.

Results

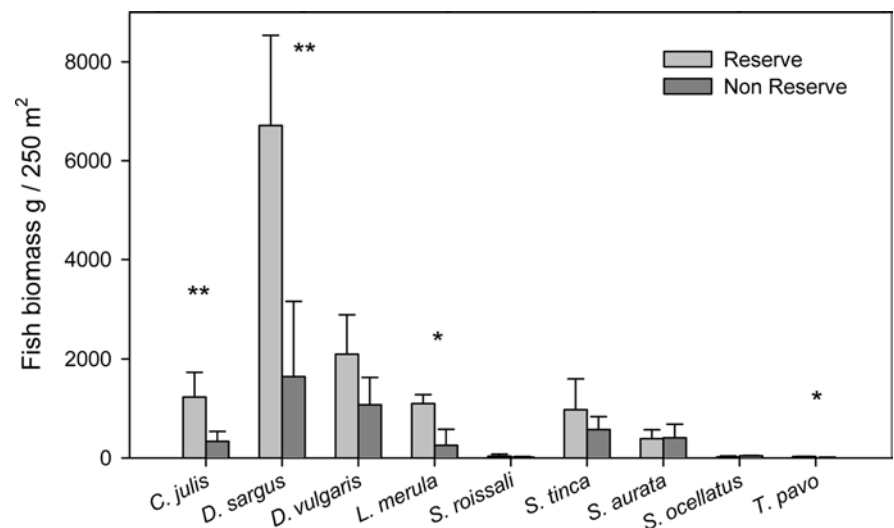
Abundance of predatory fish

The major *P. lividus* predator, *Diplodus sargus*, showed similar densities in the reserve and the unprotected area (ANOVA: $F_{1,18} = 1.36$, $P = 0.26$). However, mean size was significantly larger in the reserve, and hence biomass was higher in the reserve ($F_{1,18} = 13.02$, $P = 0.002$; Fig. 1). The biomasses of *Coris julis* ($F_{1,18} = 10.8$, $P = 0.005$), *Labrus merula* ($F_{1,18} = 7.57$, $P = 0.013$) and *Thalassoma pavo* ($F_{1,18} = 7.56$, $P = 0.013$), the other main *P. lividus* predators (Sala 1997), were also significantly greater in the marine reserve than in the nearby unprotected area (Fig. 1). The biomass of other known predators was not statistically different between the reserve and unprotected area. Nevertheless, the total biomass of predator fishes was higher in the reserve, mainly due to the contribution of *D. sargus* (Fig. 1).

Effects of predation and habitat structural complexity on sea urchin survival

The predatory fishes observed eating juvenile sea urchins during the experiments were the labrids *C. julis*, *L. merula*, *Symphodus roissali* and *T. pavo*, and the sparids *D. sargus* and *D. vulgaris*. Predation rates on juvenile *P. lividus* were significantly greater in the marine reserve than in the unprotected area for all substrate types except crevices (Fig. 2; Table 1). In the reserve, the survival of sea urchins was higher with increasing structural complexity of the algal assemblage, being minimal on coralline barrens where shelter was absent,

Fig. 1 Biomass of predatory fishes (mean $\pm$ SD) inside and outside the Medes Islands Marine Reserve. Asterisks indicate statistical significance in an ANOVA analysis (* $P < 0.05$; ** $P < 0.01$)



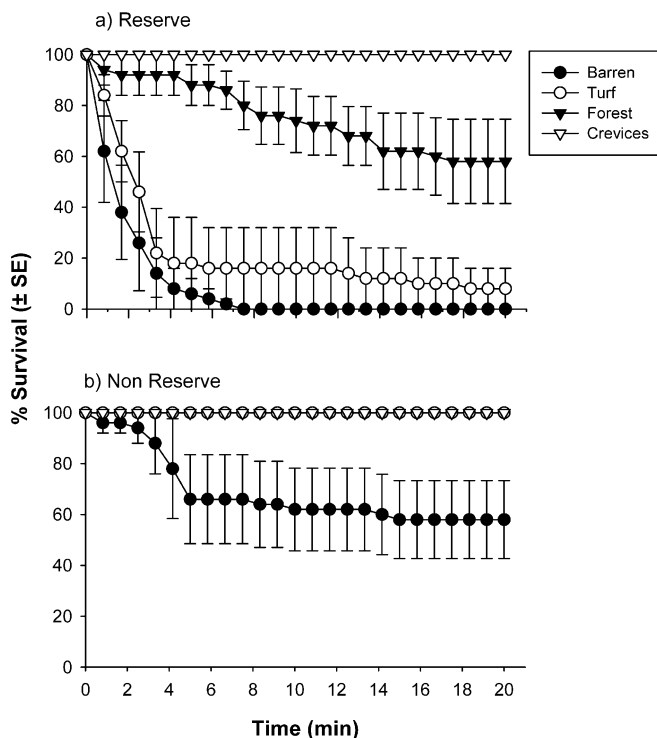


Fig. 2 Mean survival ($\pm$ SE, $n = 5$) of juvenile *Paracentrotus lividus* in distinct habitat types in **a** the Medes Islands Marine Reserve and **b** the unprotected area nearby

and maximal inside crevices which provided the highest degree of physical protection. In the unprotected area, where predatory fishes were less abundant, all juvenile *P. lividus* on vegetated substrates survived the experiment, whereas in the reserve they experienced predation in all vegetated treatments (Fig. 2; Table 2). In the reserve, the percentage survival for turf assemblages and

barrens was very low, in contrast with erect algae habitats and crevices (Table 2).

Predation was highest during the first 5 min of the experiments (Figs. 2, 3).

In the reserve, predation on sea urchins 6–10 mm in diameter was greater than on smaller ones (2–6 mm) except on crevices (Fig. 3; Table 3). Sea urchin survival was similarly low in barrens and algal turfs regardless of size, whereas survival of smaller sea urchins was greater in erect algal assemblages. Crevices provided effective refuge for both size classes.

Predator-prey size relationship

The identity of the major predators changed with increasing sea urchin size (Fig. 4). Although *D. sargus* was the most important predator of adult *P. lividus* (Sala and Zabala 1996; Sala 1997), it did not feed effectively on small juveniles (< 4 mm). The labrid *C. julis* was the most effective predator of small juvenile *P. lividus*. The importance of *C. julis* as a predator decreased, while that of *D. sargus* increased, with increasing sea urchin size. As reported previously by Sala (1997), *P. lividus* of > 10 mm diameter are consumed mostly by *D. sargus*. Other fish species made a limited contribution to total predation (0–20%) (Fig. 4). Although *L. merula* was not observed eating sea urchins of > 11.5 mm diameter in this study, they are known to prey on large sea urchins, including this size (Sala 1997).

The relationship between the size of the predatory fish (all species) and the size of sea urchins consumed by them was statistically significant although the variance explained by the model was low (Fish = $13.361 + 1.679 \times \text{Urchin}$; $r^2 = 0.31$, $P < 0.001$; Fig. 5). There was a significant correlation between predator

Table 1 Results of ANOVA comparing the effect of substrate type in protected and unprotected areas on the survival of juvenile *Paracentrotus lividus*

Factor	df	MS	F	P level	Tukey post-hoc test
Protection (P)	1	40.83	45.10		Barren (B): R $\neq$ NR Turf (T): R $\neq$ NR Algae (A): R = NR Crevices (C): R = NR
Substrate (S)	3	18.27	20.19		Reserve (R): B = T $\neq$ A = C Non-reserve (NR): B = T = A = C
P $\times$ S	3	9.19	10.16	< 0.01	
Error	32	0.905			

Table 2 Survival of juvenile *P. lividus* in each substrate type and size class inside (MR) and outside (NR) the Medes Islands Marine Reserve. Barren Coralline barren; Turf algal turf; Erect erect palatable algae

		2–6 mm		6–10 mm	
		Mean %	SD	Mean %	SD
MR	Barren	0.00	0.00	0.00	0.00
	Turf	6.66	16.32	0.00	0.00
	Erect	58.00	33.11	11.66	16.02
	Crevices	100	0.00	100	0.00
NR	Barren	56.66	30.76		
	Turf	100	0.00		
	Erect	100	0.00		
	Crevices	100	0.00		

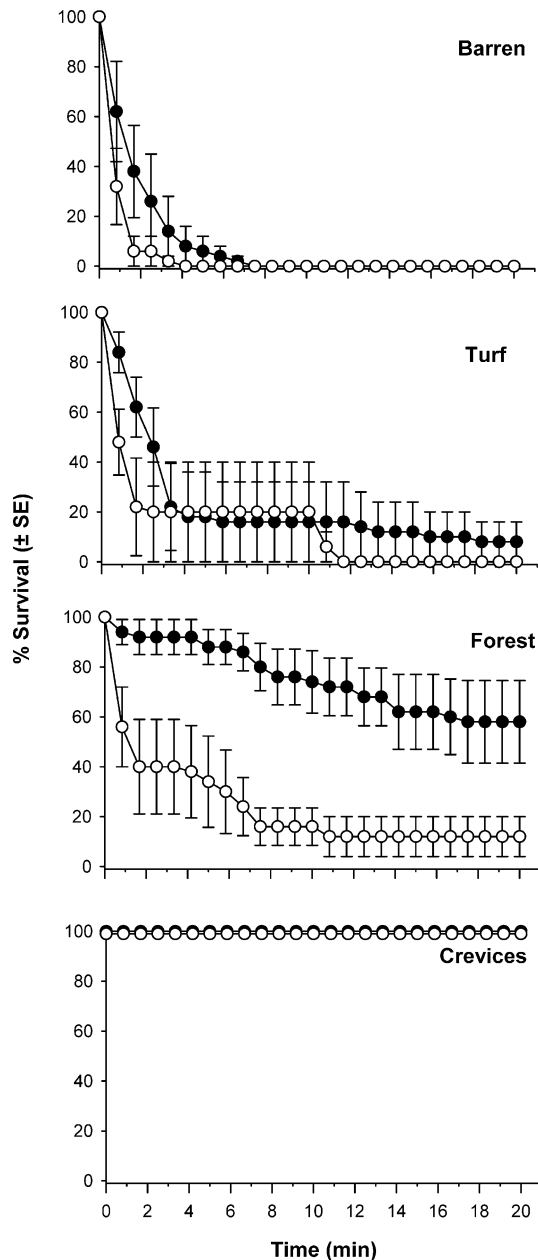


Fig. 3 Mean survival ($\pm$ SE, $n=5$) of juvenile *P. lividus* belonging to two size classes (2–6 mm and 6–10 mm) in distinct habitat types in the Medes Islands Marine Reserve

and sea urchin size within taxa (Fish = $11.517 + 0.791 \times \text{Urchin}$; $r^2=0.32$, $P<0.001$ for *C. julis* and *T. pavo*; and Fish = $21.829 + 0.666 \times \text{Urchin}$; $r^2=0.06$,

$P=0.003$ for *D. sargus*). In *C. julis*, females predominantly ate the smallest sea urchins, while males, which are larger, monopolized predation of 9- to 10-mm diameter urchins.

Discussion

The abundance of predatory fishes and the structure of algal assemblages influenced survival of juvenile *P. lividus*. Survival was higher with increasing habitat complexity and at lower fish biomass. Adult *P. lividus* also had greater mortality rates in the presence of abundant predatory fishes (Sala and Zabala 1996). Our results support the hypothesis that smaller fishes such as labrids can play a major role in the regulation of recruitment by eating the smaller size classes, although medium to large fishes are the most effective predators of adult sea urchins (Sala 1997).

As demonstrated for other species and systems, the presence of shelter can reduce predation mortality (McClanahan and Shafir 1990; Hixon and Beets 1993; Andrew 1993; Beck 1995). In the present study, increasing structural complexity of the habitat also increased survival of juvenile sea urchins, at least in the short term. Because *P. lividus* larvae do not appear to exhibit habitat preferences for settlement (Hereu et al. 2004), we would expect the density of sea urchin recruits to be larger at sites with shelter. However, the substantial mortalities of *P. lividus* settlers during the first weeks after settlement in erect algal assemblages (Sala and Zabala 1996; Hereu et al. 2004) may be due to other factors, such as predation by micropredators such as polychaetes and crustaceans, which inhabit erect algal assemblages.

Our results involve only the first 20 min after the beginning of experiments. The fact that predation by fishes had virtually ended after less than 20 min suggests that the sea urchins secured shelter and were no longer detected by fishes. However, the presence of micropredators probably causes additional mortality over time. Absolute predation rates were not obtained from our experiments because algal assemblages are not the only shelter available to juvenile sea urchins: crevices and spaces beneath small boulders also provide abundant shelter. In fact, predation in marine reserves with a high abundance of predatory fishes may not reduce absolute sea urchin densities, because most are sheltered in

Table 3 Results of ANOVA comparing the effect of substrate type on the survival of small (2–6 mm) and larger (6–10 mm) juvenile *P. lividus*

Factor	df	MS	F	P level	Tukey post-hoc test
Substrate	3	25,328.44	125.13		Small (S): B = T $\neq$ A $\neq$ C Large (L): B = T = A $\neq$ C Barren (B): S = L Turf (T): S = L Algae (A): S $\neq$ L Crevices (C): S = L
Size	1	2,091.80	10.33		
Substrate $\times$ size	3	1,484.06	7.33	<0.01	
Error	40	1,484.06			

Fig. 4 Proportion of mortality caused by major predatory fish species on juvenile *P. lividus* of different sizes

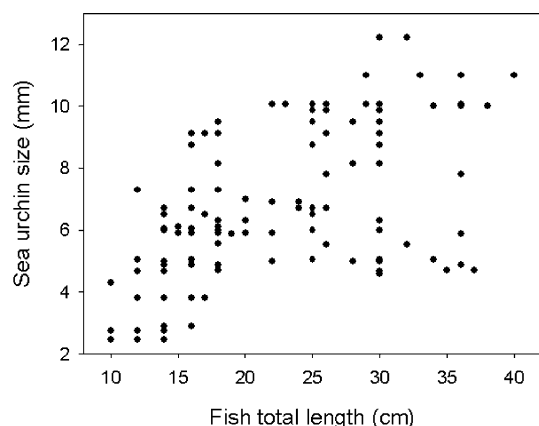
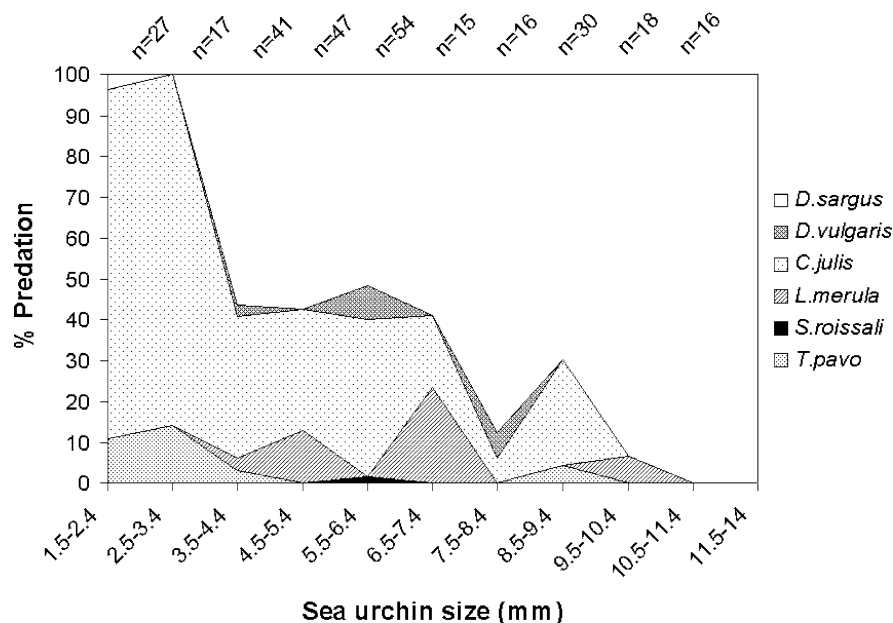


Fig. 5 Size relationship between *P. lividus* and predatory fishes during predation experiments in the Medes Islands Marine Reserve

crevices and beneath boulders (Sala and Zabala 1996; Sala et al. 1998a). However, simple predation experiments, like those carried out here, can provide a standardised protocol to assess the strength of predation in coastal ecosystems.

The partitioning of predation on *P. lividus* by fish species and sizes can have implications for the regulation of sea urchin populations as a function of fishing pressure. Small fishes eat small juveniles, and there is an escape size beyond which small fishes cannot effectively kill sea urchins (Sala 1997; this study). Therefore, sea urchins will reach a refuge from predation at smaller sizes in fished areas because predators in unprotected areas are smaller (García-Rubies 1996; Sala 1997). Our results also support the idea that the commonly neglected effects of line fishing, which mainly targets small fishes such as *C. julis* (Harmelin et al. 1995; Harmelin 1999), could influence *P. lividus* populations (Sala 1997) and, subsequently, the structure of the benthic community (Sala et al. 1998b).

Our results support the potential role of marine reserves in the regulation of sea urchin populations, and hence in preventing the development of sea urchin barrens, as predicted by models (McClanahan and Sala 1997; Sala et al. 1998b). In Mediterranean marine reserves, predatory fishes are more abundant and greater in size than in unprotected areas (e.g. García-Rubies and Zabala 1990; Francour 1991; Harmelin et al. 1995), therefore predation rates on sea urchins are greater in these reserves (Sala and Zabala 1996; this study). The significantly lower survival observed in the Medes Islands Marine Reserve relative to that in unprotected sites is a clear example of the predation effects that follow effective protection of coastal habitats (Pinnegar et al. 2000). We believe that the strength of predation on juvenile sea urchins by fishes is a good estimator of fish build-up and trophic changes in marine reserves.

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