

# Temporal variability in abundance of the sea urchins *Paracentrotus lividus* and *Arbacia lixula* in the northwestern Mediterranean: comparison between a marine reserve and an unprotected area

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**ABSTRACT:** Sea urchin populations were monitored in the Medes Islands Marine Reserve (NW Mediterranean) and an adjacent unprotected area in order to (1) describe temporal variability in abundance and population size-structure of sea urchins within each area (from 1991 to 1997), and (2) to compare these areas to investigate the role of fish predation level in determining sea urchin population structure over time (from 1995 to 1997). Abundance of the sea urchin *Paracentrotus lividus* (Lamarck) was monitored at 7 sites (4 inside and 3 outside the reserve), and 2 distinct habitats (fields of big boulders and vertical walls). *P. lividus* exhibited significant variability in density over time on boulders, both inside and outside the reserve, whereas its density did not vary significantly on vertical walls. *P. lividus* populations differed significantly in size-structure across sites, varying from unimodal to bimodal among sites and years. Density and mean size of *P. lividus* were not significantly different between the protected and the unprotected area in either of the 2 habitats. Abundance of the sea urchin *Arbacia lixula* (L.) was monitored from 1995 to 1997 on vertical walls and boulders (4 sites inside and 3 sites outside the reserve). Density of *A. lixula* differed significantly over time on boulders, but it did not on walls. On vertical walls, density and mean size of *A. lixula* were not significantly different between areas in both habitats. This study shows that in the Medes Islands region, sea urchins exhibit striking short-term fluctuations in abundance, which can lead to misinterpretation of larger-scale temporal patterns. The comparison between the protected and the unprotected area does not support the hypothesis of fish predation as the most important factor affecting *P. lividus* populations in the Medes Islands, as patterns of lower sea urchin density relative to the unprotected area nearby were not maintained over time. These facts indicate that factors other than fish predation are very important in determining sea urchin population structure in the northwestern Mediterranean.

**KEY WORDS:** Sea urchins · Temporal variability · Marine reserves · Fish predation · Mediterranean · *Paracentrotus* · *Arbacia*

## INTRODUCTION

Ecological research suggests that fishing has important effects on the trophic structure of whole ecosystems (e.g. Dayton et al. 1995, Botsford et al. 1997). Research in marine reserves has shown that the return

to hypothetical former predation levels through prohibition of fishing may have important indirect effects on ecosystem structure through trophic cascades. For example, the recovery of predatory fish within reserves may cause a reduction in sea urchin populations (e.g. McClanahan & Muthiga 1989, McClanahan & Shafir 1990). In turn, sea urchins have important roles in determining the structure of alga-dominated benthic communities (see reviews by Lawrence 1975 and Schiel & Foster 1986). In the Mediterranean, the sea urchin *Paracentrotus lividus* (Lamarck) is a key

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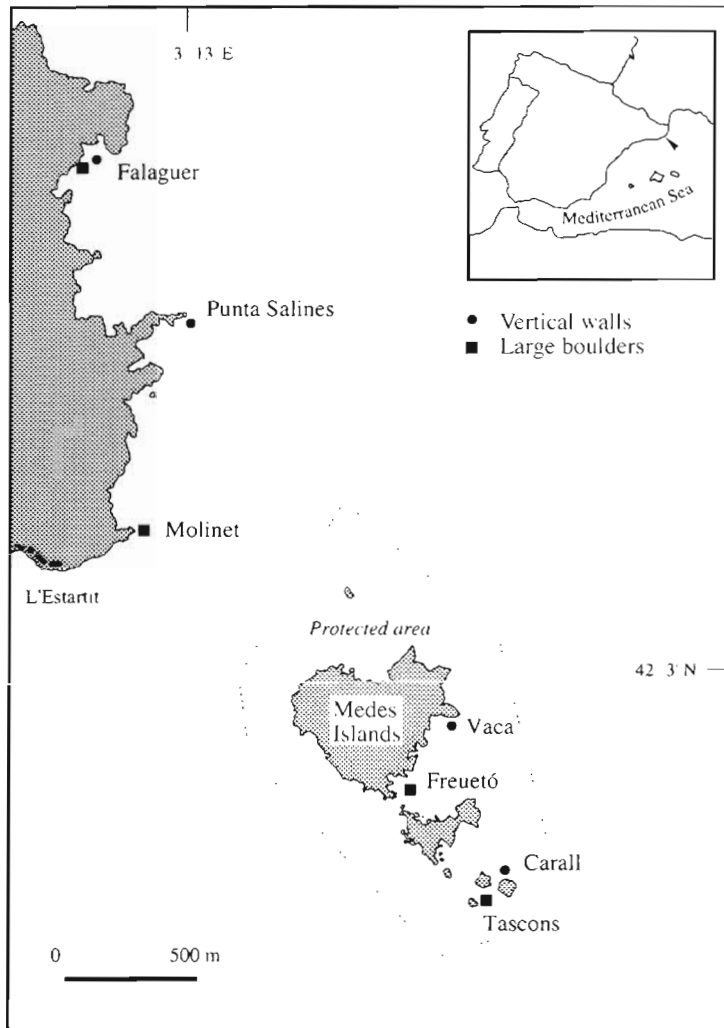


Fig. 1. Location of study sites, inside (Tascons, Freuetó, Vaca and Carall) and outside (Falaguer, Molinet, and Punta Salines) of the Medes Islands Marine Reserve, NE Spain, northwestern Mediterranean Sea. Dashed line represents the limits of the Marine Reserve, where all fishing is prohibited

species that at high densities influences the dynamics of the phytobenthos, by eliminating erect algae and seagrasses, and inducing the formation of coralline barrens (Verlaque & Nédélec 1983, Verlaque 1987), but that also exerts a significant effect on algal assemblage structure at low densities (Palacín et al. in press). The sea urchin *Arbacia lixula* (L.) generally avoids large erect algal assemblages, focusing its grazing activity mainly on encrusting algae (Kempf 1962). It has been suggested that *A. lixula* probably benefits from prior removal of erect algae by *P. lividus* (Frantzis et al. 1988). Therefore, knowledge of the effects of fishing on sea urchin populations is of fundamental importance in ecosystem management (McClanahan 1994, McClanahan & Sala 1997).

In a previous study, Sala & Zabala (1996) monitored the abundance of *Paracentrotus lividus* within and outside the Medes Islands Marine Reserve (NE Spain) for 3 yr (1992 to 1994), reporting a pattern of lower abundance of sea urchins in the reserve relative to nearby unprotected areas. This pattern was attributed to differences in predatory fish abundance between the reserve and the unprotected area (García-Rubies & Zabala 1990, García-Rubies 1997). Higher abundances of predatory fish in the reserve have been maintained over time (García-Rubies 1997); have decreased sea urchin abundances been maintained as well? Sea urchin populations may exhibit significant variations in density over time due to several factors, including recruitment and disease (Lawrence & Sammarco 1982, Lessios 1988, Lawrence 1996). Thus, long-term monitoring of sea urchin populations is important for distinguishing changes in abundance due to natural fluctuations, long-term oceanographic processes, and anthropogenic impacts. The aims of this study were: (1) to describe temporal variability (from 1991 to 1997) in abundance and population size-structure of the sea urchins *P. lividus* and *Arbacia lixula* in some rocky habitats in the northwestern Mediterranean, and (2) to make comparisons among protected and unprotected areas from 1995 to 1997 to investigate the role of fish predation level in determining sea urchin population structure over time (sea urchin harvesting in this region is low, and thus we hypothesize that differences between areas may be caused by differences in predatory fish abundance).

## MATERIAL AND METHODS

The study was carried out in the Medes Islands Marine Reserve and a nearby unprotected area (NE Spain, northwestern Mediterranean Sea) (Fig. 1). The Marine Reserve (created in 1983), where fishing is prohibited (93.2 ha), is located 1 km offshore from the town of L'Estartit (42° 16' N, 03° 13' E) and encompasses a group of small islands (total surface area less than 20 ha). The study was conducted within 2 habitats: (1) fields of large limestone boulders (Tascons and Freuetó, within the reserve, hereafter 'R'; Falaguer and Molinet, outside the reserve, hereafter 'NR') and (2) vertical walls (Carall and Vaca, R; Punta Salines and

Falaguer, NR) (Fig. 1). Boulder habitats were colonized by a rich algal assemblage dominated by erect algae, articulated calcareous algae and small filamentous algae (Sala & Boudouresque 1997). Vertical walls supported algal assemblages as well as numerous suspension feeders (Ros et al. 1985).

Abundance and population size-structure of sea urchins were studied by SCUBA diving along randomly located transects ( $50 \times 1$  m each) on bottoms between 5 and 10 m depth, at each study site. Transects were divided into five  $10 \text{ m}^2$  subtransects. Within the first  $20 \text{ m}^2$  of each transect, *Paracentrotus lividus*  $>1$  cm in diameter were counted and their diameter (test without spines) measured with calipers. In the remaining  $30 \text{ m}^2$ , *P. lividus* were counted but not measured. Since *Arbacia lixula* density was lower, all individuals  $>1$  cm in diameter were counted and measured within the transects. Diameters were grouped in size classes of 1 cm, and in subtransects of  $10 \text{ m}^2$ . Sampling (3 to 5 transects per site and date) was carried out once per summer. *P. lividus* was monitored from 1991 to 1997 in Tascons (R), Freuetó (R), Carall (R), and Punta Salines (NR), from 1992 to 1997 in Falaguer (NR), and from 1995 to 1997 in Vaca (R) and Molinet (NR). *A. lixula* was monitored from 1995 to 1997 in all of the above sites. Since only one sampling could be done yearly due to logistical constraints, we decided to sample always during the same season (summer), in part because *P. lividus* shows recruitment peaks at this time (Lozano et al. 1995, Sala & Zabala 1996), and thus we expected to visually find 1 yr old individuals in our transects 1 yr after they settled. To test for temporal variability in density and mean size within sites, 1-way ANOVAs were performed on log-transformed data.

In 1995 we decided to study the effect of the protected area (i.e. the effect of high density of predatory fish) on sea urchin populations, and thus added new sampling sites to the monitoring program, in order to account for spatial heterogeneity within areas. A hierarchical sampling design (at least 2 sites within each of the areas) was needed to properly test differences in density and mean size of *Paracentrotus lividus* and *Arbacia lixula* between protected and unprotected areas. To test for differences in density and mean size between areas (protected vs unprotected), ANOVAs were performed on log-transformed data between 1995 and 1997, where data were available for 2 sites inside the reserve and 2 sites outside the reserve. Within this analysis, site (random factor) was nested within the level of protection (fixed factor; protected or unprotected) in order to account for the differences between areas.

## RESULTS

### Temporal variability in *Paracentrotus lividus* populations

Densities of *Paracentrotus lividus* for all sampling dates and sites are shown in Fig. 2. In Tascons (R), density steadily increased from 1991 to 1995, then decreased until 1997 (1-way ANOVA,  $df = 6$ ,  $F = 5.78$ ,  $p < 0.001$ ). In Freuetó (R), density also varied significantly over time ( $df = 6$ ,  $F = 6.32$ ,  $p < 0.001$ ), dropping by a factor of 2 from 1991 to 1992, then remained stable until 1994, when it increased by a factor of 2. Between 1995 and 1997 densities at Freuetó showed smaller fluctuations. In Falaguer (NR), density exhibited a significant increase from 1992 to 1993, but after

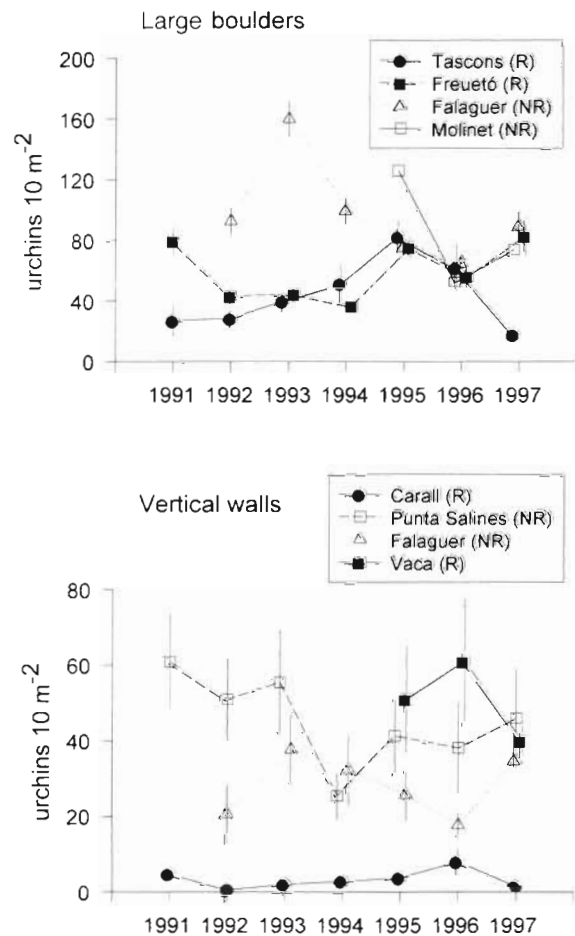


Fig. 2. *Paracentrotus lividus*. Number of sea urchins ( $>1$  cm diameter) per  $10 \text{ m}^2$  (mean  $\pm$  SE) at each site and in the 2 types of habitats studied (large boulders and vertical walls, between 5 and 10 m depth) during the monitoring period (1991 to 1997). Solid symbols represent sites within the Medes Islands Marine Reserve (R); open symbols represent sites in the nearby unprotected, fished area (NR)

1993 *P. lividus* numbers exhibited a continuous decrease until 1996, and then increased slightly in 1997 (df = 5,  $F = 13.30$ ,  $p < 0.001$ ). In Molinet (NR), density dropped from 1995 to 1996, then increased slightly (df = 2,  $F = 8.07$ ,  $p = 0.001$ ).

On vertical walls, *Paracentrotus lividus* populations showed statistically significant variations in density only within Carall (R), where density exhibited a 16-fold increase from 1992 to 1996 (Fig. 2; 1-way ANOVA, df = 6,  $F = 2.20$ ,  $p < 0.05$ ). The higher variance observed on vertical walls relative to big boulders indicates that spatial heterogeneity at the 10 m<sup>2</sup> scale is higher on vertical walls, i.e. *P. lividus* are more evenly distributed on big boulders than on vertical walls.

At Tascons (R), mean size of *Paracentrotus lividus* varied significantly over time (1-way ANOVA, df = 6,  $F = 18.41$ ,  $p < 0.001$ ). Recruitment of *P. lividus* that occurred between 1992 and 1994 greatly influenced the size distribution at Tascons (Fig. 3). The size-frequency graphs illustrate an exponential decrease from 1992 to 1993. After 1993, however, the distribution was bimodal, with a second mode of urchins between 4 and 6 cm in diameter. This second mode of large urchins after 1994 was more conspicuous due to a lower recruitment rate during these years. At Freuetó (R) mean size also varied significantly over time (df = 6,  $F = 34.29$ ,  $p < 0.001$ ). High recruitment rates in 1992 and 1993 produced a size-distribution with a very conspicuous mode of small urchins (Fig. 3). However, as recruitment declined after 1993, the size distribution was markedly bimodal, with a first mode composed of small urchins (1 to 2 cm) and a second mode of individuals of 5 to 6 cm diameter. At Molinet (NR), where mean size varied significantly from 1995 to 1997 (df = 2,  $F = 15.43$ ,  $p < 0.001$ ), small urchins were the most abundant, probably responding to good recruitment during these years. Falaguer (NR) showed a pulse of recruits in 1992 and 1993, but after 1993 recruitment was lower and the sea urchin population showed abundance peaks at larger sizes as the study progressed (df = 5,  $F = 52.65$ ,  $p < 0.001$ ).

Mean size of *Paracentrotus lividus* did not vary significantly over time at Carall (R) (1-way ANOVA, df = 6,  $F = 1.90$ ,  $p = 0.129$ ). At this site, no small urchins (less than 2 cm in diameter) were found until 1994 (Fig 4). From 1991 to 1993, the size distribution was skewed towards large size-classes, with a peak at 5 to 6 cm diameter. Low recruitment occurred every year, however, after 1993. The peak of urchins of 5 to 6 cm diameter was maintained during the 7 years of the study, except in 1994 when the population peaked at 2 to 3 cm, and in 1997 when the distribution was bimodal, with a second peak of urchins at 2 to 3 cm. At Vaca (R), where mean size varied significantly over time (df = 2,  $F = 15.99$ ,  $p < 0.001$ ), small urchins (<2 cm) were the most abundant between 1994 and 1997, especially in

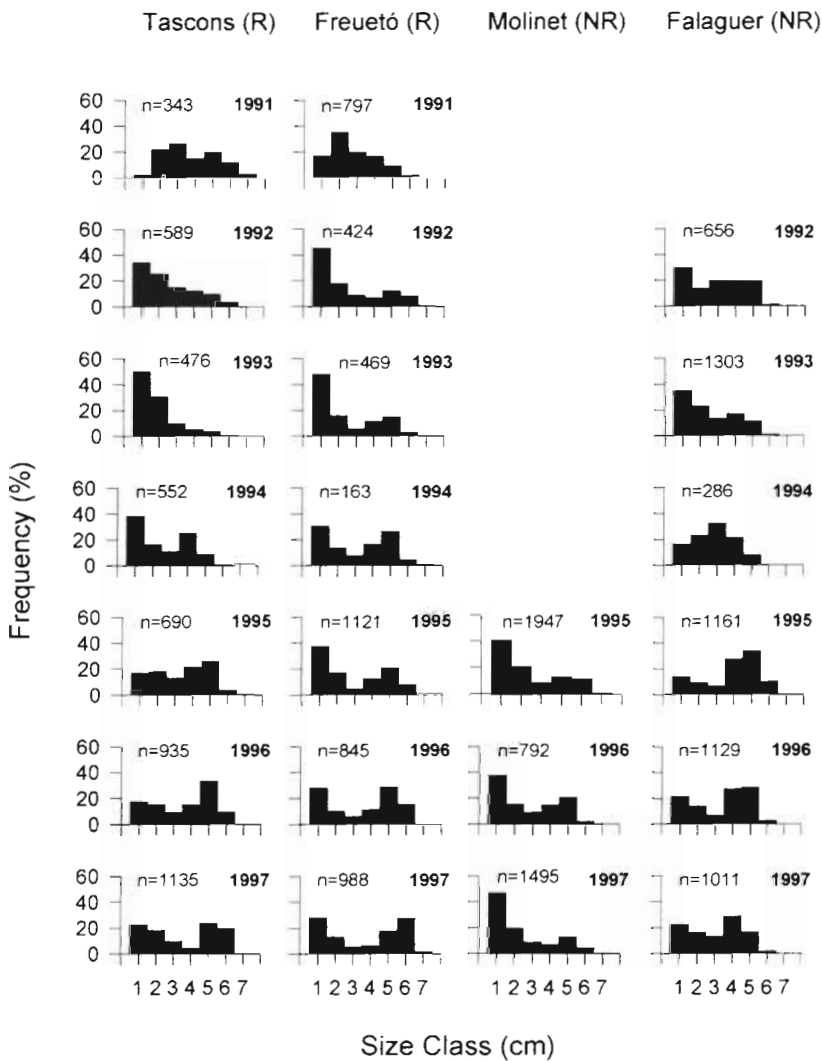


Fig. 3. *Paracentrotus lividus*. Sea urchin (>1 cm) test size frequency from 1991 to 1996 on large boulders (between 5 and 10 m depth) within (Tascons and Freuetó) and outside (Falaguer and Molinet) the Medes Islands Marine Reserve. Size classes: 1 = 1–1.9 cm, 2 = 2–2.9 cm, 3 = 3–3.9 cm, 4 = 4–4.9 cm, 5 = 5–5.9 cm, 6 = 6–6.9 cm, 7 = 7–7.9 cm

1995, where half of the total number of urchins were small (Fig. 4). The distribution was bimodal from 1995 to 1997, with a second mode at 5 to 6 cm. At Punta Salines (NR), the size distributions indicated variations in population size over time (Fig. 4;  $df = 6$ ,  $F = 30.99$ ,  $p < 0.001$ ). In 1991 the size distribution was bimodal, with a first mode comprised of small urchins and a second mode of large urchins 6 to 7 cm in diameter. In 1993 the pattern was blurred, and low recruitment occurred every year from 1993 to 1997, with the major pattern in size distribution being an accumulation of individuals in larger size-classes. At Falaguer (NR), the size distributions were skewed, with few small individuals and a mode of urchins between 4 and 6 cm in diameter (Fig. 4). Although mean size differed significantly over time ( $df = 5$ ,  $F = 8.74$ ,  $p < 0.001$ ), this pattern was maintained from 1992 to 1997.

#### Comparison of *Paracentrotus lividus* populations among areas

Comparison of *Paracentrotus lividus* densities on large boulders from 1995 to 1997 showed significant differences in density among sites within areas (Table 1a). Mean density did not differ between the protected and the unprotected area. There was a significant variation in density over time, but temporal trends were not significantly different among areas. Comparison of densities on vertical walls (1995 to 1997) showed a different pattern (Fig. 2, Table 1b). Although there were no significant differences in density over time, density varied significantly among sites within areas, where differences among sites were higher inside than outside the reserve. However, density did not differ significantly between the protected area and the unprotected area from 1995 to 1997.

Comparison of mean size of *Paracentrotus lividus* on large boulders showed significant differences over time, and among sites within areas (Fig. 3, Table 2a). However, there were no significant differences between the protected and the unprotected area. On vertical walls, the comparison of mean size of *P. lividus* showed significant differences over time, and among sites within areas (Fig. 4, Table 2b), but, as on large boulders, mean size

did not differ significantly between the protected and the unprotected area.

#### Temporal variability in *Arbacia lixula* populations

Densities of *Arbacia lixula* for all sampling sites and dates are shown in Fig. 5. Densities on large boulders showed significant differences over time (from 1995 to 1997; Table 3a). Density did not change at Tascons (R) from 1995 to 1997 (Fig. 5; 1-way ANOVA,  $df = 2$ ,  $F = 0.98$ ,  $p = 0.38$ ) or at Molinet (NR) ( $df = 2$ ,  $F = 2.05$ ,  $p = 0.13$ ). At Freuetó (R), density significantly varied from 1996 to 1997, where mean density increased by 3 times ( $df = 2$ ,  $F = 6.79$ ,  $p < 0.001$ ). At Falaguer (NR), density increased steadily from 1995 to 1997 ( $df = 2$ ,  $F = 4.34$ ,  $p = 0.019$ ). On vertical walls, density did not vary

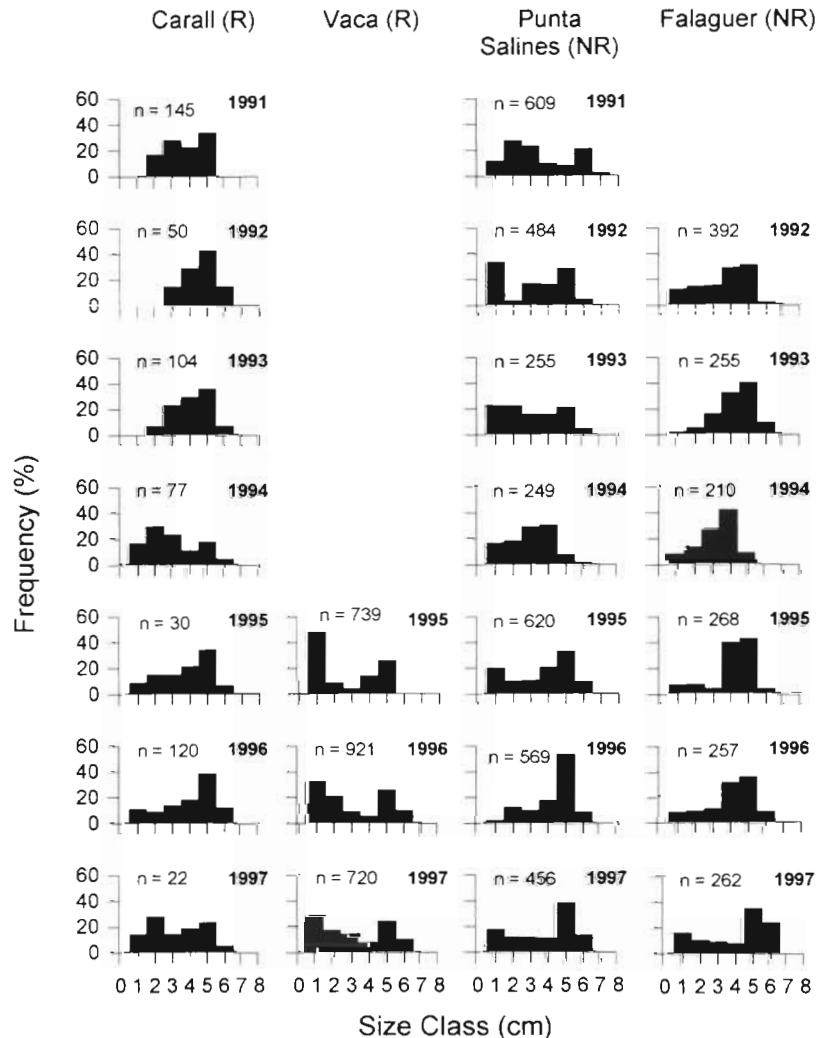


Fig. 4. *Paracentrotus lividus*. Sea urchin (>1 cm) test size frequency from 1991 to 1996, on vertical walls (between 5 and 10 m depth) within (Carall and Vaca) and outside (Falaguer and Punta Salines) the Medes Islands Marine Reserve. Size classes as in Fig. 3

Table 1 Density of *Paracentrotus lividus*. Results of nested ANOVA comparing densities between protected and unprotected areas and over time (1995 to 1997) on (a) large boulders and (b) vertical walls

Factor	df	MS	F	p
<b>(a) Large boulders</b>				
Time	2	0.68	11.31	<0.001
Area	1	0.82	1.84	0.308
Site(Area)	2	0.44	7.38	0.001
Area × Time	2	0.16	2.59	0.078
Error	170	0.06		
<b>(b) Vertical walls</b>				
Time	2	0.01	0.08	0.92
Area	1	0.83	0.25	0.667
Site(Area)	2	3.32	33.54	<0.001
Area × Time	2	0.15	1.49	0.23
Error	173	0.10		

Table 2. Size of *Paracentrotus lividus*. Results of nested ANOVA comparing mean size between protected and unprotected areas and over time (1995 to 1997) on (a) large boulders and (b) vertical walls

Factor	df	MS	F	p
<b>(a) Large boulders</b>				
Time	2	0.73	18.97	<0.001
Area	1	4.81	0.38	0.601
Site(Area)	2	12.67	328.62	<0.001
Area × Time	2	2.89	75.08	<0.001
Error	3241	0.04		
<b>(b) Vertical walls</b>				
Time	2	1.21	34.33	<0.001
Area	1	2.61	2.94	0.229
Site(Area)	2	0.89	25.21	<0.001
Area × Time	2	0.39	11.06	<0.001
Error	4976	0.04		

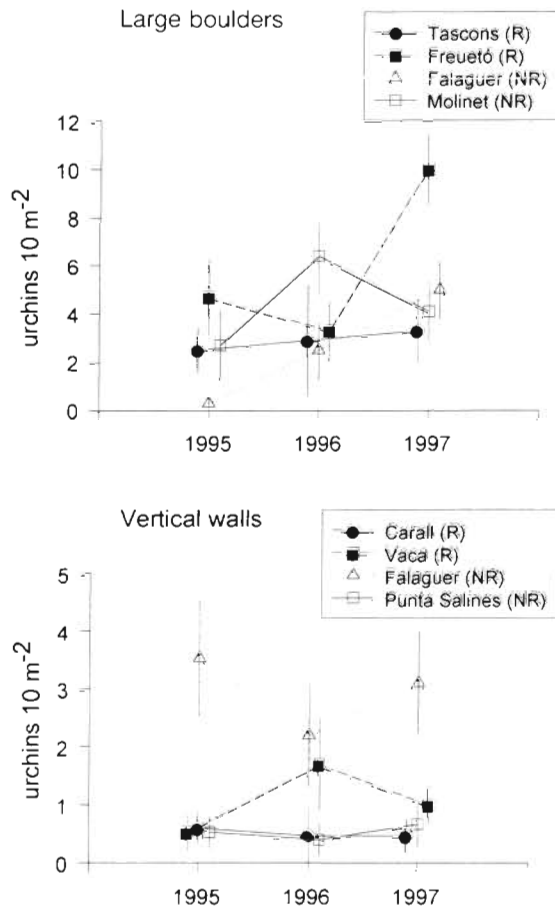


Fig. 5. *Arbacia lixula*. Number of sea urchins (>1 cm diameter) per 10 m<sup>2</sup> (mean ± SE) at each site and in the 2 types of habitats studied (large boulders and vertical walls, between 5 and 10 m depth) during the monitoring period. Solid symbols represent sites within the Medes Islands Marine Reserve (R); open symbols represent sites in the nearby unprotected, fished area (NR)

Table 3. Density of *Arbacia lixula*. Results of nested ANOVA comparing densities between protected and unprotected areas and over time (1995 to 1997) on (a) large boulders and (b) vertical walls

Factor	df	MS	F	p
<b>(a) Large boulders</b>				
Time	2	1.43	8.97	<0.001
Area	1	0.33	0.22	0.685
Site(Area)	2	1.49	9.32	<0.001
Area × Time	2	0.96	6.02	0.003
Error	172	0.16		
<b>(b) Vertical walls</b>				
Time	2	0.02	0.25	0.777
Area	1	0.49	0.45	0.571
Site(Area)	2	1.10	12.08	<0.001
Area × Time	2	0.07	0.77	0.466
Error	172	0.09		

significantly over time at any of the sites (1-way ANOVA,  $p > 0.05$ ).

On large boulders there were no significant differences in *Arbacia lixula* mean size over time. All sites showed a dominance of individuals >3 cm, with the sites in the unprotected area showing a strong peak at 4 to 5 cm. The size-frequency distributions at Tascons and Freuetó (R) between 1995 and 1996 reflect low recruitment of *A. lixula*. Falaguer and Molinet (NR) exhibited a very narrow unimodal distribution in 1995 and 1996 (Fig. 6). Only individuals between 3 and 5 cm diameter were found at this time, suggesting a lack of recruitment in preceding years. However, the size distribution in 1997 indicates a low recruitment. Only Freuetó (R) showed significant variations on

mean size over time (1-way ANOVA,  $df = 2$ ,  $F = 6.79$ ,  $p = 0.001$ ).

Mean size did not vary significantly over time at any site on vertical walls (1-way ANOVA,  $p > 0.05$ ). All sites showed a unimodal size-distribution, with a peak at 4 to 6 cm diameter (Fig. 7). Small individuals (<2 cm) were only detected at Punta Salines (NR) in 1996 and Vaca (R) in 1997. Aside from these 2 sites, the remaining sites and years showed a consistent pattern of dominance of large individuals and lack of recruitment.

#### Comparison of *Arbacia lixula* populations among areas

On large boulders, there were no significant differences in *Arbacia lixula* density between the reserve and the unprotected area (Fig. 5, Table 3a). However, there were significant differences among sites within areas, although significant differences were detected only among the sites inside the reserve (Tukey's test,  $p = 0.03$ ). On vertical walls, there were significant differences in density among sites within areas (Fig. 5, Table 3b); in this case, density was significantly different among sites in the unprotected area (Tukey's test,  $p = 0.006$ ). However, there were no significant differences in density between areas or over time.

The comparison of sizes of *Arbacia lixula* on large boulders showed no significant differences among sites within areas, or among areas (Fig. 6, Table 4a).

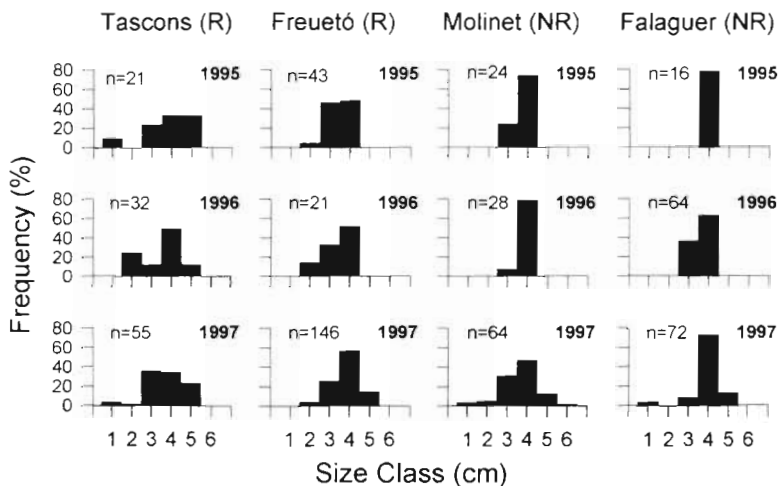


Fig. 6. *Arbacia lixula*. Sea urchin (>1 cm) test size frequency from 1995 to 1997 on large boulders (between 5 and 10 m deep), within (Tascons and Freuetó) and outside (Falaguer and Molinet) the Medes Islands Marine Reserve. Size classes as in Fig. 3

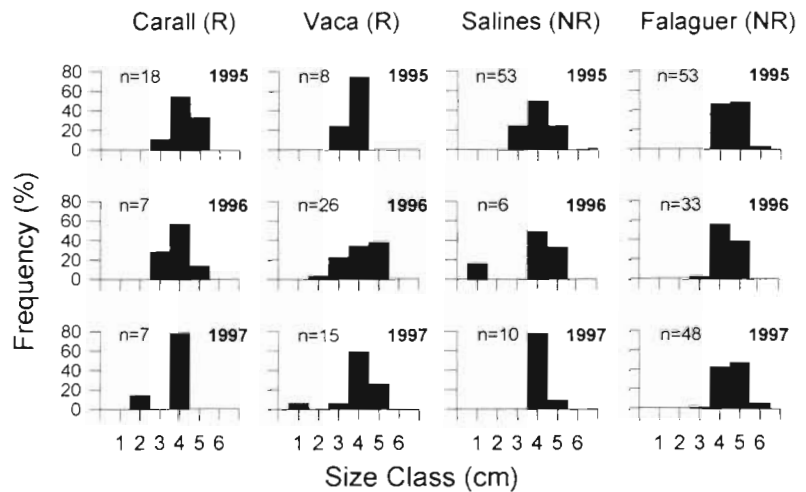


Fig. 7. *Arbacia lixula*. Sea urchin (>1 cm) test size frequency from 1995 to 1997 on vertical walls (between 5 and 10 m deep), within (Carall and Vaca) and outside (Falaguer and Salines) the Medes Islands Marine Reserve. Size classes as in Fig. 3

On vertical walls, the comparison of mean size of *A. lixula* across sites showed significant differences among sites within areas, but there were no significant differences among areas (Fig. 7, Table 4b).

## DISCUSSION

#### *Paracentrotus lividus* populations

Fishing pressure on sea urchin predators (mostly fin fish) has been identified as a major factor in determining the abundance of sea urchins in sublittoral communities (Tegner & Dayton 1981, Breen et al. 1982, Cowen 1983, Hay 1984). Comparisons of marine reserves (where fishing is prohibited) and unprotected areas have shown a general pattern of lower sea urchin abundance within marine reserves in tropical (McClanahan & Muthiga 1989, McClanahan & Shafir 1990, McClanahan 1995) and temperate (Boudouresque et al. 1992, San Martin 1995, Sala & Zabala 1996) seas. Most studies conducted in temperate seas, however, carried out short-term comparisons (up to 3 yr) between protected and unprotected areas. In the Medes Islands Marine Reserve, fish density was higher than in nearby unprotected areas for 8 yr (1989 to 1996; García-Rubies & Zabala 1990, García-Rubies 1997), and density of the sea urchin *Para-*

Table 4. Size of *Arbacia lixula*. Results of nested ANOVA comparing mean size between protected and unprotected areas and over time (1995 to 1997) on (a) large boulders and (b) vertical walls

Factor	df	MS	F	p
<b>(a) Large boulders</b>				
Time	2	0.010	1.58	0.207
Area	1	0.040	12.42	0.072
Site(Area)	2	0.003	0.50	0.609
Area × Time	2	0.018	2.77	0.064
Error	516	0.007		
<b>(b) Vertical walls</b>				
Time	2	0.001	0.34	0.714
Area	1	0.018	0.75	0.477
Site(Area)	2	0.024	5.60	0.004
Area × Time	2	0.005	1.26	0.287
Error	222	0.004		

*Paracentrotus lividus* was lower (3 times) between 1992 and 1994 (Sala & Zabala 1996). The present study shows that after 1994 an increase in density within the reserve coupled with a decrease in density outside the reserve led to similar sea urchin abundances on boulders between the 2 areas. The size distributions suggest that the strong increase in *P. lividus* abundance in boulder habitat at Falaguera (NR) from 1992 to 1993 was due to the 1992 extraordinary recruitment episode (when *P. lividus* <1 cm were found at an average density of 1160 ind. m<sup>-2</sup> at this site; Sala & Zabala 1996), whereas the later decrease until 1996 was coupled to lower recruitment rates. On vertical walls, the addition of a new sampling site within the reserve (Vaca) showed strong spatial heterogeneity, because *P. lividus* densities at this site were higher than at any other site, including those outside the reserve. That also resulted in lack of significant differences in density between the protected and the unprotected area on walls.

Differences in density among sites within areas for both habitats suggest that differences in microhabitat features, recruitment rate, and/or fish predation rate might exist at a scale of hundreds of meters. Sala & Zabala (1996) reported significant differences in recruitment rate between 2 sites on boulders inside the reserve (Tascons and Freuetó) located 500 m apart. Likewise, fish densities were different among sites within the reserve (García-Rubies 1997), which can result in different predation rates. Sites were selected for similar substrate, size of boulders, orientation, and water motion, but unnoticed differences in microhabitat (such as microshelters) might result in differences in survival rate of recruits.

Bimodal size distributions in sea urchin populations have been attributed to several factors, including inter-

annual variability in recruitment rate (Underwood & Fairweather 1989), predation (Tegner & Dayton 1981, Sala & Zabala 1996) and accumulation of large year-classes where longevity is high (Himmelman et al. 1983). In our study, the alternation between uni- and bimodal distribution may be due to all 3 factors. First, high recruitment rates imply a mode of small urchins. A high recruitment episode would be recognizable as a peak in the size distribution traveling through time. Second, when predation is high, early mortality could impact small sea urchins, with no expression of recruitment episodes in later years, resulting in decreasing size distributions (Sala & Zabala 1996). However, a second mode formed by large individuals may be explained by a change in vulnerability of sea urchins to predation (e.g. when they reach a size at which they leave shelters; Tegner & Dayton 1981). *Paracentrotus lividus* attains an escape in size between 4 and 5 cm (Sala 1997). Third, *P. lividus* exhibits asymptotic growth (Azzolina 1988), and thus large size-classes are actually formed by several age-classes. Therefore, when longevity is increased (by low predation rates or by attaining an escape in size) the largest sea urchins accumulate in a second mode. To ascertain the relative importance of these factors would require further study.

At most sites on vertical walls (except Vaca), both within and outside the reserve, and at most times, the size distributions showed modes for large size-classes, suggesting that recruitment was low in this habitat. Vertical walls are a habitat where physical factors may be more important in determining the structure of sea urchin populations. The availability of shelters is meager on vertical walls, and therefore both topography and exposure to predators may contribute to the lower numbers of *Paracentrotus lividus* populations within the reserve. The maintenance of densities may thus be explained by adult immigration. Immigration at Carall (R) was important during the monitoring period, since *P. lividus* density increased by a factor of 4 in only 1 yr (from 1992 to 1993), without signs of apparent recruitment. Although recruitment of *P. lividus* occurs within this depth range (5 to 10 m) (Lozano et al. 1995, Sala & Zabala 1996), immigration of adult urchins may be important in determining the population structure (Azzolina 1988), as on vertical walls within our study sites. Outside the reserve (Punta Salines), recruitment occurred regularly, as evidenced by addition of small individuals to the population. The Vaca (R) site also showed a dominance of small individuals through most of the study period, coupled to a very high density. Later examination of the site showed that Vaca has a high amount of suitable microhabitat for juveniles (small crevices and holes). This suggests that shelters, favoring the survival of high numbers of small individ-



uals at sites with high fish predation pressure, are also important in determining population structure of *P. lividus*.

Interpretation of the size distribution results may be biased by the fact that growth rate of *Paracentrotus lividus* may not be the same for all individuals of a cohort. Indeed, *P. lividus* exhibited density-dependent growth rates in the first years when held in an aquarium (Grosjean et al. 1996). If density-dependent growth rates also occur in the field, small sea urchins sheltered in small crevices may have reduced growth rates and therefore not all individuals from a single settlement episode could be detected as recruits at the same time. Therefore, our assumptions concerning recruitment could be biased with regard to the size at which we recorded recruits. However, recruitment episodes of *P. lividus* can be very intense, and we detected an increase in the smallest sizes in boulders 1 yr after a large recruitment episode [that of 1992, when Sala & Zabala (1996) monitored the appearance of smallest recruits]. Thus, we assume that even if an unknown number of sea urchins were not detected the first year after settlement, we were still able to detect and estimate the intensity of such settlement episodes from the abundance of the smallest sea urchins.

The behavior of urchins appears to be a good indicator of local predation rate: sea urchins exhibit cryptic behavior, sheltering in the presence of predators, and foraging in exposed sites when predators are absent (Tegner & Dayton 1981, Cowen 1983, McClanahan & Kurtis 1991). *Paracentrotus lividus* also adopts this predator avoidance strategy, sheltering during daylight and grazing away from shelters at night (Kempf 1962, Dance 1987). During the day in the Medes Islands Reserve most *P. lividus* are sheltered, whereas they occupy exposed sites outside the reserve (Sala & Zabala 1996). We therefore suggest that density alone may not be a good indicator of predation level in habitats with a high availability of shelters, because sea urchin densities may be similar in fished and unfished areas, but the actual urchin stock available to predatory fish (i.e. in exposed sites) can be much lower within reserves. In that case, the combined study of density, size distribution, and spatial distribution of urchins seems more appropriate.

### ***Arbacia lixula* populations**

The urchin *Arbacia lixula* dramatically increased (more than 10-fold) its abundance in western Mediterranean waters from 1983 to 1992 (Francour et al. 1994). Francour et al. (1994) hypothesized that this increase was due to an increase in seawater temperature in shallow waters over the last 20 yr. The densities found

during this study were, on average, lower (3.99 ind. per 10 m<sup>2</sup> on boulders, 1.27 ind. per 10 m<sup>2</sup> on vertical walls; range between 0.3 and 10 ind. per 10 m<sup>2</sup>) than those reported at Corsica (10 *A. lixula* per 10 m<sup>2</sup>; Francour et al. 1994). However, Kempf (1962) found densities greater than 10 ind. m<sup>-2</sup> in Marseille (France) in the early 1960s, which suggests that long-term fluctuations in *A. lixula* abundance have occurred.

Fenaux & Pedrotti (1988) found planktonic larvae of *Arbacia lixula* in areas far from the coast. Further, *A. lixula* larvae are extremely rare along the Catalan coast (X. Turon pers. comm.). These facts and the accumulation of large size-classes at our study sites suggest that recruitment of *A. lixula* may not be annual. A similar pattern was found by Kempf (1962) in Marseille, with a lack of individuals <3 cm in diameter, and a peak between 4 and 5.5 cm. One of us (E.S.) found *A. lixula* juveniles (<1 cm in diameter) in the Cabrera National Park (Balearic Islands, Spain) in May 1996, beneath rocks in the first meter of water in a sheltered bay. This suggests that recruitment areas may be restricted, and that arrival of individuals could be mainly via immigration of adults from nursery areas. Our data show, nonetheless, that low recruitment occurred in the boulder habitat studied.

*Arbacia lixula* is seldom found in fish gut contents (Savy 1987, Sala 1996), and it appears to have morphological adaptations (better attachment to substrate, denser spines) that make it less susceptible to fish predation than *Paracentrotus lividus* (E. Sala unpubl. data). Furthermore, adult *A. lixula* are almost always found at exposed sites, independent of predatory fish abundance. We suggest that *A. lixula* may not be a good indicator of the 'reserve effect', although there might be untested, indirect effects associated with reduction of *P. lividus* density due to fish predation. Therefore, we are not able to fully discuss the lack of differences in density and mean size of *A. lixula* between the protected and the unprotected area.

### **Conclusions: fish predation and temporal dynamics of sea urchin populations**

*Paracentrotus lividus* exhibited significant variability in density and mean size over short time scales at most sites. *Arbacia lixula* only showed such dramatic changes over small time scales on boulders, while populations on walls were more stable. Our results indicate that sea urchin populations in infralittoral bottoms in the northwestern Mediterranean are very dynamic, and that a long-term perspective is needed in order to draw conclusions from comparisons between areas with different levels of fishing. Our results do not support the hypothesis of predation as the most important

factor affecting *P. lividus* populations in the Medes Islands (Sala & Zabala 1996), as patterns of lower sea urchin density relative to the unprotected area nearby were not maintained over time. Furthermore, mean size of *P. lividus* did not show differences between the reserve and the unprotected area in boulders.

Sea urchin recruitment exhibits significant differences across space and time in the northwestern Mediterranean: recruitment rate may be strikingly different between very close sites (hundreds of meters; Sala & Zabala 1996) and consecutive years (Lozano et al. 1995, Turon et al. 1995). These differences may create a dynamic mosaic in space, leading to patches with differential recruitment rates, under different predation rates, etc. These differences in historical processes which persist over time complicate the interpretation of urchin abundance patterns. Our results show that variations in abundance and population size-structure at small spatial and temporal scales may lead to misinterpretation of what is happening at larger scales.

These facts warn us again about the danger of drawing general conclusions from short-term studies (sensu Dayton & Tegner 1984). Sala & Zabala (1996), who monitored *Paracentrotus lividus* on boulders from 1992 to 1994 and carried out a predation experiment, arrived at the conclusion that fish predation played an important role in determining urchin abundance. Our results suggest that recruitment rate, shelter, migration, and other factors causing mortality should be seriously considered. All these factors are also interacting in unprotected areas, hence increases in sea urchin density should not be attributed solely to overfishing (Sala et al. 1998). Fish predation is a process that may have an absolute importance by itself (i.e. biomass of urchins eaten per unit of time and area), but whose relative importance depends on the absolute importance of other processes (such as recruitment rate). The next step would require factorial experiments with predation rate, recruitment rate, and shelter as factors to be manipulated.

Coupling of different processes might reduce the differences in community structure between areas with different levels of fishing. For instance, fish predation may not be able to counteract high sea urchin recruitment, because there are other factors that help urchins to survive, such as shelters. As well, there could be spatial and temporal variations in fish predation pressure on sea urchins. It should be taken into consideration that reserves do not represent equilibrium points. Real reserves only lack human harvesting. They are, though, susceptible to oceanographic events. Although the lack of human predation within reserves may help communities to recover after disturbances, it may not prevent strong fluctuations due to strong events.

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