

Magnitude of herbivory in
Posidonia oceanica (L.) Delile
and factors responsible
for spatial variation



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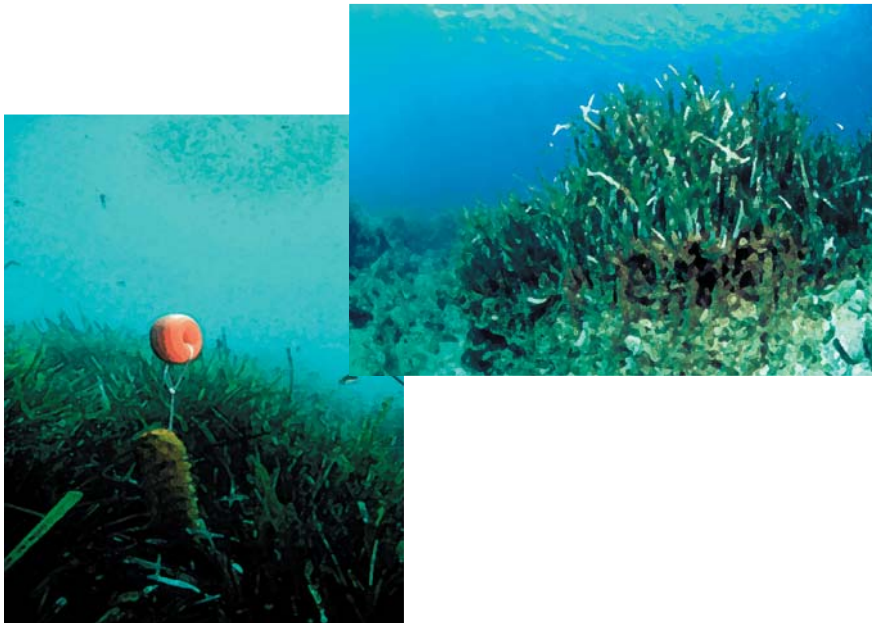
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Ecological patterns associated to the demographic structure of *Paracentrotus lividus* populations in *Posidonia oceanica* beds

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RESUM:

L'estructura poblacional de la garota *Paracentrotus lividus* (Lmk.) va ser investigada en 10 praderies superficials de *Posidonia oceanica* (L.) Delile al llarg de la costa catalana durant dos anys consecutius. L'abundància dels diferents estadis bentònics (i.e. reclutes, juvenils i adults) va ser relacionada amb diferents variables de les praderies, amb l'objecte d'establir quines són les millor candidates per explicar l'estructura demogràfica de les poblacions.

La variació natural de les poblacions va mostrar diferències importants a gran escala (ca. 2.1 a 20 ind. m⁻²) mentre que la variació interanual va ser de poca importància i amb una clara dominància dels individus de major mida. La influència dels primers estadis bentònics va ser investigada a nivell d'individus de recent metamorfosis (RMI; ≤ 15 dies des de l'assentament) i en individus juvenils (i.e. diàmetre del test de 0.5-3 cm). Els RMI es van trobar a totes les localitats durant els dos anys i van mostrar abundàncies semblants, mentre que els juvenils van estar limitats només a certes localitats, suggerint d'altres factors, a part del reclutament, com a responsables de la variació espacial observada a les poblacions de garotes.

Entre les variables de les praderies investigades, aquelles relacionades amb la qualitat de l'aliment (i.e. contingut de nitrogen en epífits, biomassa d'epífits i % de matèria orgànica en el sediment) no van mostrar cap relació amb els patrons de distribució de les poblacions, mentre que la densitat de feixos va estar associada positivament amb tots els estadis bentònics. No obstant, va ser la disponibilitat de substrat rocós més adjacent a la praderia la que va mostrar la major influència en les poblacions d'eriçons estudiades. Les densitats d'individus, incloent-hi els juvenils, van ser majors a localitats on l'eix de contacte entre ambdós hàbitats és elevat i van disminuir a distàncies creixents del substrat rocós. Aquests resultants evidencien que les poblacions de *Posidonia lividus* pertanyen al *continuum* de la biocenosis, integrat tant per la praderia com pel substrat rocós.



INTRODUCTION

Sea urchins are known to play an important role in the control of submersed aquatic vegetation (Harrold & Pearse 1987, Valentine & Heck 1991, Heck & Valentine 1995, Shears & Babcock 2003), and variations in their abundance and population structure can significantly alter the functioning of benthic communities. In turn, sea urchin populations are controlled by a range of environmental factors and ecological processes, including resource availability, predation, migration and reproductive issues.

Larval supply, settlement, and recruitment have been often identified as bottlenecks for the abundance of adult echinoids (Cameron & Rumrill 1982, Rumrill et al. 1985, Lozano et al. 1995, López et al. 1998). Hydrodynamic forces acting at multiple scales have a significant influence in larval dispersal (Botsford 2001), and differences in planktonic larval supply can produce large spatial and temporal variations in recruitment (Underwood & Fairweather 1989), resulting thus in clumped distributions of populations, especially over large geographical areas (Moberg & Burton 2000). In particular, sea urchin larvae are relatively long-lived, and can remain in the water column between 50 and 150 days (Strathmann 1978), which allows them to disperse extensively. This long-distance dispersal ability is offset by an increasing susceptibility to predation the longer larvae remain in the planktonic phase (Rumrill 1990). Once larvae settle, other factors, including predation, can exert further control on the density of urchin recruits by reducing the densities from hundreds, to only a few sea urchins per square meter (López et al. 1998, Turón et al. 1995).

Resource availability is also known to modify sea urchin population structure and dynamics, either directly or indirectly. In many sea urchin species the problem of food availability is partially circumvented by the adoption of generalist feeding strategies (review by Lawrence 1975). For instance, the diet of individuals dwelling within seagrass meadows may include leaves, epiphytes and detached seagrass debris (Shepherd 1987, Nedelec & Verlaque 1984), and feeding on macroalgae and sediment organic matter is not uncommon (Ott & Maurer 1977, Klumpp et al. 1993, Fernandez 1997). In addition to food quantity,



qualitative aspects are also of major importance. In effect, the quality of the available food resources in terms of nitrogen content (Valentine & Heck 2001), type (Harrold & Reed 1985, Shepherd 1987, Frantzis & Grémare 1992) and defences (chemical or other, Anderson & Velimirov 1982, Pelletreau & Muller-Parker 2002) may determine sea urchin rates of consumption. Moreover, food quality may alter the fitness of populations through differential gonad development and test diameter, conditioning in turn successful recruitment and adult survivorship (Beddingfield & McClintock 1998).

Another group of factors controlling sea urchin populations relates to predation. Numerous species of fishes, gastropods and crustaceans have been shown to control the size distribution and abundance of sea urchins through direct consumption (Tegner & Dayton 1981, McClanahan 1999, Guidetti 2004). Concretely, in the North-Western Mediterranean Sea, the fish *Coris julis* (Family: Labridae) and *Diplodus* spp. (Family: Sparidae), the main predators of the common sea urchin *Paracentrotus lividus*, may influence the demographic structure of populations (Sala & Zabala 1996, Sala 1997, Sala et al. 1998). The abundance of predators may indirectly induce crevice-dwelling behaviour as a sheltering mechanism (Sala 1997, McClanahan 1995, 1999), thus modifying foraging patterns and highlighting the fact that habitat complexity may play an important role in the outcome of predator-echinoid interactions in rocky habitats (McClanahan & Shafir 1990, McClanahan 1999, Hereu et al. 2005). Equally, seagrass leaf canopy may provide shelter against predation (e.g. Peterson 1982, Irlandi 1994, Bologna & Heck 1999) and the presence of juveniles within the rhizome mat (Azzolina & Willsie 1987) may be an analogous to crevice hiding behaviour in rocky substrates.

A final latter aspect to take into consideration is the inherent vagility of species and how the edges between fringing habitats (contact edge) with different resource distribution may affect their capacity to disperse (Fagan et al. 1999, D'Eon et al. 2002, Ries & Sisk 2004). In shallow seagrass beds sea urchin abundance has been proposed to relay on the supply of individuals from adjacent rocky habitats (Fernandez et al. 2001, Tomas et al. 2004) which suggest that contact edges may play an important role in controlling the



demographic structure of populations. In fact, while well-nourished individuals often display relatively limited foraging movements of ca. 0.5 to 5 m (Harrold & Reed 1985, Dance 1987), substantial foraging trips reported when food resources become limiting (e.g. Rose et al. 1999, Peterson et al. 2002) seem to support the likelihood of individual's exchanges across habitats.

The importance of these four groups of influencing variables has been largely established in numerous studies, including those cited above. However, their relative importance is probably subject to great spatial and temporal variability, and interactions among them are most likely to occur. To our knowledge, studies evaluating the relative contribution of each one of these factors to the demographic structure and size of sea urchin populations are rare.

To contribute to fill this gap, we examined the roles of recruitment, food availability, refuges against predation and migration from adjacent habitats, in structuring the Mediterranean sea urchin *Paracentrotus lividus* (Lmk.) populations at different life stages in seagrass (*Posidonia oceanica* (L.) Delile) beds. We used a correlative approach undertaken in 10 shallow seagrass beds (along ca. 300 km of the Catalan coast, NW Mediterranean) over two consecutive years.

MATERIALS AND METHODS

Study sites and sampling design

Ten sites were chosen along the Catalan coast (Fig. 1) for the presence of shallow (5 to 8 m depth) *Posidonia oceanica* beds. These are largely representative of the shallow seagrass meadows of the study region, which are scarce there. Selected meadows encompassed a wide range of structural properties (see below), and two of them were located inside zones protected for more than 20 years (Marine Protected Areas, MPAs): the Medes Islands Reserve and the Banyuls Marine Reserve.

We measured sea urchin abundance and size-distribution at each site, and evaluated



the contribution of the four groups of causal factors (i.e. recruitment, food, predation and migration from adjacent habitats) to among-site variability. At each site, the recruitment input was evaluated by measuring the abundance of post-metamorphic stages. The influence of resource availability was established by measuring seagrass biomass, seagrass nitrogen content, epiphytic load and organic matter in the sediment. The influence of predation was estimated indirectly by assessing structural characteristics of the meadows providing refuge against predators. Finally, the potential of sea urchin migration from adjacent habitats was assessed by measuring the length of the contact edge between the seagrass meadows and the rocky substrate and the densities of sea urchins along transects from the fringing hard substrate.

The population size and structure, as well as the abundance of post-metamorphic stages, were evaluated in summer 2003 (all sites except Montroig, see below), and repeated in summer 2004 (all sites). Variables related to the resource availability, predation and migration potential were only investigated in 2003.

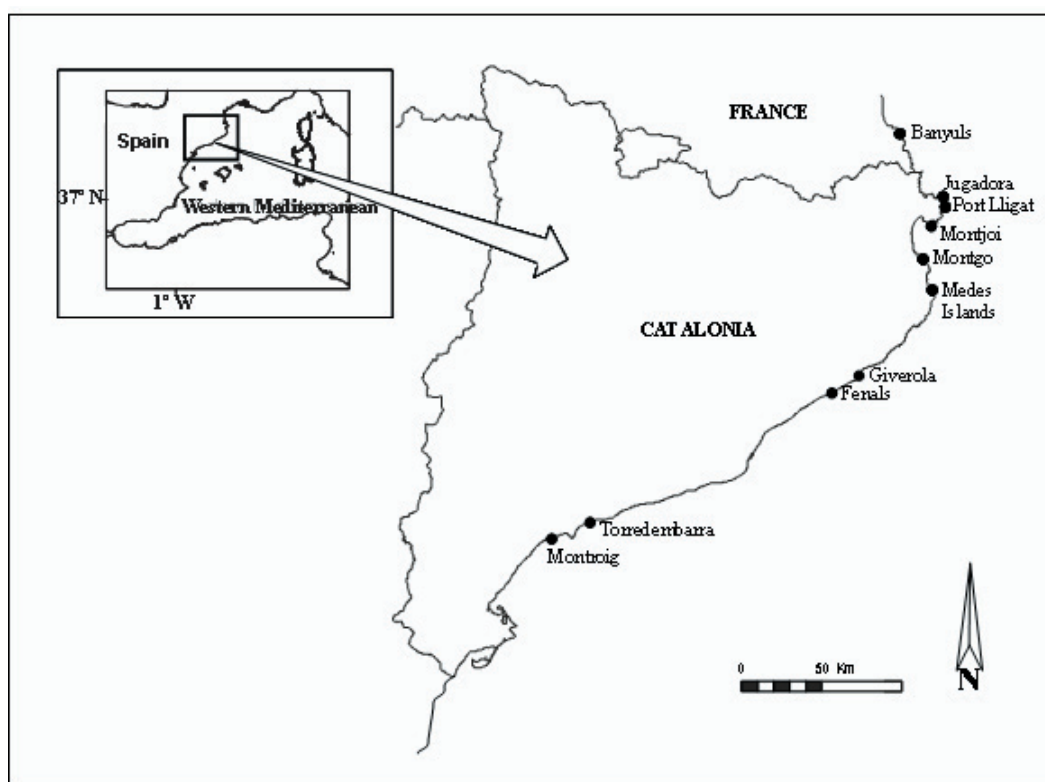


Fig. 1. Map of the western Mediterranean showing the position of the study sites.



At each study site, the sampling area (ca. 1000 m²) was established between 5 and 8 m and adapted to the meadow morphology excluding the edges of the meadow (5 m from rocks or bare sand) except when the effect of the contact edge was tested (see below).

Sea urchin population structure

At each study site, *Paracentrotus lividus* abundance and size distribution was obtained by placing haphazardly fifteen 50 x 50 cm quadrates within the study area. Sea urchin test diameter was measured in situ using a calliper. Sizes from 0.5 to 3 cm were considered as juveniles, whereas sizes greater than 3 cm were regarded as adults (size differences based on changes in the feeding ecology from Verlaque 1984). In addition, we separated adults into medium (3 to 5 cm) and large (5 to 8 cm) size classes.

Abundance of post-metamorphic stages

Differences in the abundance of post-metamorphic stages among study sites were evaluated by placing haphazardly nine replicate collectors for sea urchin recruits. The collectors consisted of scrub brushes with vegetal bristles. They were fastened to a rope and attached to a small buoy at the canopy height at one end and hammered into the sediment with a star picket at the other (Tomas et al. 2004). The collectors, always within the leaf canopy, were left in the field for two 15 days periods in June-July in each of the two consecutive sampling years, in an attempt to capture the recruitment peak which has been reported to occur between spring and early summer in this species (López et al. 1998, Hereu et al. 2004). Consequently, recovered individuals were ≤ 15 days old (hereafter RMI: recently metamorphosed individuals). By replacing the collectors we also aimed to prevent the accumulation of detritus and benthic algae and to minimise possible predation effects. We removed collectors by cutting the rope to which they were attached and placing them carefully into individual plastic bags. Special care was taken to minimise re-suspension and loss of attached organisms. The effectiveness of such devices as collectors for RMI of *P. lividus* has been tested elsewhere (Hereu et al. 2004, Tomas et al. 2004).

Bags containing the collectors were placed into an icebox and transported to the laboratory. Once in the laboratory, they were thoroughly rinsed with water, and the content filtered through a 250 μm mesh, preserved in glass containers for sorting, counting and size measurement of RMI under the dissecting microscope (Hereu et al. 2004).

Availability and quality of food

Food availability and food quality was evaluated for two of the three major components of the sea urchin diet (Verlaque 1984, Boudouresque & Verlaque 2001): seagrass and epiphytes. The third component (sediment organic matter) was only quantitatively assessed.

Seagrass and epiphyte biomass were estimated as the product of leaf (or epiphyte) biomass, shoot density and % cover of seagrass in each meadow studied. Seagrass shoot density was measured in twelve 40 x 40 cm quadrates placed at random within the sampling area (Alcoverro et al. 1995). Seagrass percent cover was assessed by visual estimation of the surface covered by *Posidonia oceanica* within twenty-seven 50 x 50 cm quadrates, also distributed at random within the sampling area. Shoot and epiphyte biomass were measured on nine haphazardly collected shoots at each study site. Additionally, nine sediment samples were collected just below the sediment surface at each study site in order to determine the organic matter content. All samples were placed in plastic bags and transported to the laboratory. Once there, epiphytes were scraped off from the *P. oceanica* leaves with a razor blade. Leaves and epiphytes were then dried, weighed separately (60 °C, 48 h), ground to a powder and analyzed for C and N contents with a Carlo-Erba CHN Analyser (see Alcoverro et al. 1995 for detailed methodology). The sediment samples were dry weighed (80 °C, 24 h) and the total organic matter in the sediment calculated as the difference between the dry weight and the residue left after combustion at 450 °C for 2 h (after Parker 1983).



Refuges against predation

The existence or accessibility of refuges in the mat was evaluated at each site. The mat is a three-dimensional net formed by overlapped vertical and horizontal rhizome axis of *Posidonia oceanica* (see Fig. 2a). Depending on the local hydrodynamic conditions, the spaces between rhizomes can be filled with sediment to a greater or lesser extent. In the case they are empty, crevices and holes among the intermingled rhizomes can be used as refuges by sea urchins. To estimate the availability of such refuges we introduced a meter stick (60 cm long by 2.5 cm diameter) within the rhizomes (Boudouresque & Meinesz 1982). We considered the refuges as present when the meter stick penetrated at least 40 cm in a least 7 (out of 10) assays. Otherwise, mostly when compact sand filled within-rhizome cervices, the refuges were considered absent. As the leaf canopy can also act as a protection by “hiding” the sea urchins from their potential predators, shoot density and seagrass cover were also considered as meadow features possibly allowing sea urchins to escape from predation, and analysed in consequence.

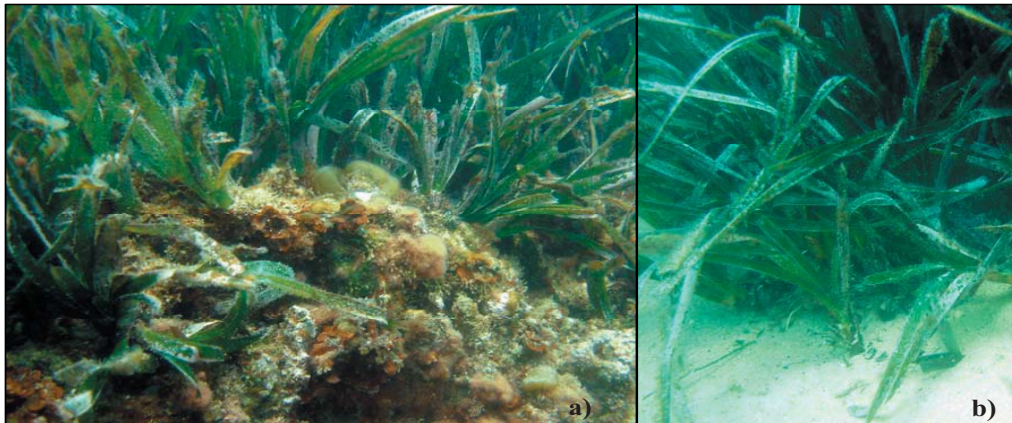


Fig. 2. a) *Posidonia oceanica* bare mat structure showing the existence of refuges; and b) mat replenished with sediments; only the top rhizome layer is accessible

Connectivity between habitats

At each meadow, the influence of the adjacent rocky substrate was established by measuring during two consecutive years (2003 and 2004) the abundance and size distribution of *Paracentrotus lividus* in seagrass meadows at increasing distance (1, 3 and 10 m) from the rocks. At each sampling distance, 15 replicate quadrates (50 x 50 cm) were placed and all sea urchins present inside counted and measured. In the more heterogeneous meadows (Torredembarra, Giverola, Fenals, Banyuls, see above), samples were obtained only at 1 and 3 meters distance, as no single point was distant >10 m from any rock.

The contact edge (CE) between seagrass and rocky substrate was also estimated at each site as the longitude, in meters, of the line along which both habitats were in direct contact within the study area (ca. 1000 m²). Data were obtained from available local cartography, and complemented with direct underwater measures whenever necessary.

Data analyses

Among-site variation. Differences in the abundance of RMI, juvenile and adult *Paracentrotus lividus* between years (2003 and 2004, fixed factor) and sites (random factor) were analysed with a 2-way orthogonal ANOVA. Differences in the distribution of sea urchins sizes (i.e. juveniles: 0.5 to 3 cm, adults from 3 to 5 cm and adults from 5 to 8 cm) among sites and years was investigated using the two-way ANOSIM permutation test (Clarke 1993). Differences between sites in seagrass biomass, shoot density, seagrass cover, percent organic matter, epiphytic biomass, seagrass leaf nitrogen content and epiphyte nitrogen content (for which we only obtained data in 2003) were investigated with a one-way ANOVA. Differences in the abundance of juvenile and adult *P. lividus* between sites (random factor) and distance from the rock (fixed factor 1, 3, and 10 meters, when present) were analysed with a 2-way orthogonal ANOVA. In that analysis, the two years (2003 and 2004) were pooled together after verifying the lack of significance of the year factor (one-way ANOVA, year fixed factor, $p > 0.05$). By doing so, potential difficulties interpreting complex third-order interactions were avoided. Differences in the size distribution of sea urchins at

increasing distances from the rocks were tested with ANOSIM analyses. However, since this procedure does not allow the analysis of more than two factors, we performed a one-way ANOSIM to test differences between years followed by a two-way ANOSIM to evaluate the influence of distance and site.

Association between variables. Correlation analyses were used to assess the relation between several variables. In particular, the following relationships were investigated: (1) the correlation between RMI and juvenile densities (only in sites where juveniles were present). This relationship was tested using RMI data from 2003 and juvenile abundance of 2004 (the juveniles expected to result from RMI of the previous year); (2) the correlation between juvenile (only when present) and adult densities; (3) the correlation between adult and juvenile densities with the food-related variables (seagrass and epiphyte biomass, nitrogen content in seagrass and epiphytes and percent of organic matter in the sediment); (4) the correlation between structural variables of the meadow (seagrass shoot density and cover) and RMI, juvenile (only in sites where present) and adult densities; (5) the correlation between sea urchins densities and the length of the contact edge (CE) between habitats, using only densities of individuals at 3 m from the rocky substrate (the furthest distance available in all study sites) to avoid as much as possible the interaction between edge width and the influence of the contact edge itself. To determine the effect of the mat rhizome structure (presence/absence) on the abundance of juvenile sea urchins a two-way orthogonal ANOVA with Year and mat Structure (yes-no) as fixed factors was used.

For all the ANOVAs, data were first tested for normality (Chi-square) and homogeneity of variances (Cochran's test) and transformed when necessary to satisfy the ANOVA assumptions, as indicated in the results section. When data transformation did not alleviate the departures from the hypothesis, the level of significance was lowered to $p=0.01$ to minimize the probability of a type II error. The existence of significant differences among site groups was investigated by Student-Newman-Keuls (SNK) post hoc comparisons.



RESULTS

Adults and juveniles

Adult densities of *Paracentrotus lividus* (i.e. sizes from 3 to 8 cm) differed considerably among sites but not between years. Densities ranged from 14 ± 2.8 [S.E] ind. m^{-2} in Giverola to 1.7 ± 0.8 in Banyuls (i.e. Fig. 3; Table 1a). Juveniles (i.e. sizes from 0.5 to 3 cm) appeared only at four sites (Torredembarra, Fenals, Giverola and Banyuls), and densities never exceeded 5 ind. m^{-2} (Fig 4a; Table 2a). Patterns were consistent between the two studied years (Fig 4a; Table 2a) except in Banyuls where juveniles were present only in 2004. No interannual differences in size class distribution of *P. lividus* were observed whereas differences among sites, although significant, were overridden by the overall dominance of large sea urchins over juvenile ones (see Fig. 4 for results). In the sites where juveniles were present (i.e. only the 4 sites mentioned above included), there was a tendency although not significant between both variables ($r= 0.817$; $p> 0.05$).

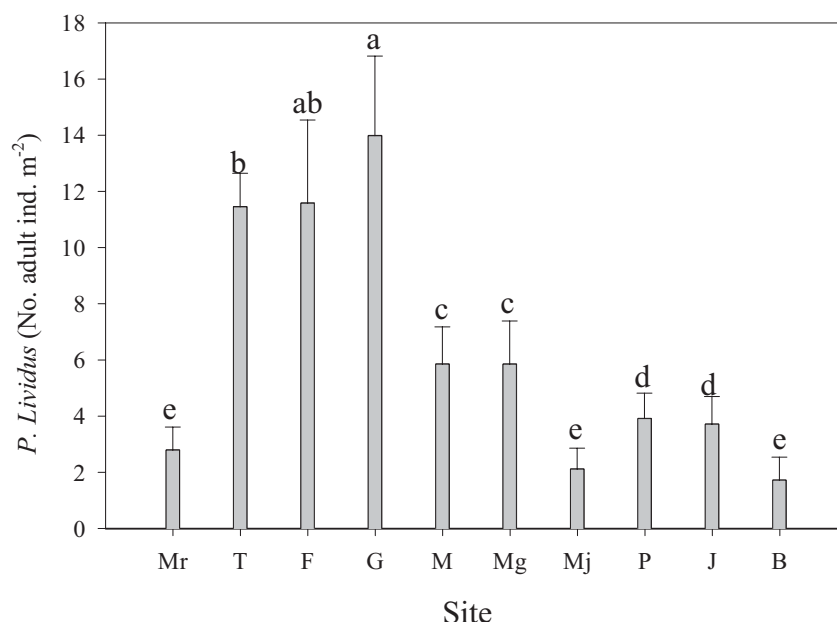


Fig. 3. Abundance of adult *Paracentrotus lividus* (i.e. sizes 3 to 8 cm) at each study site (data from 2003 and 2004 pooled). In SNK significant differences among site groups are indicated with letters (see Table. 2a). Mr = Montroig; T = Torredembarra; F = Fenals; G = Giverola; M = Medes; Mg = Montgó; Mj = Montjoi; P = Port Lligat; J = Jugadora and B = Banyuls. Error bars are S.E.



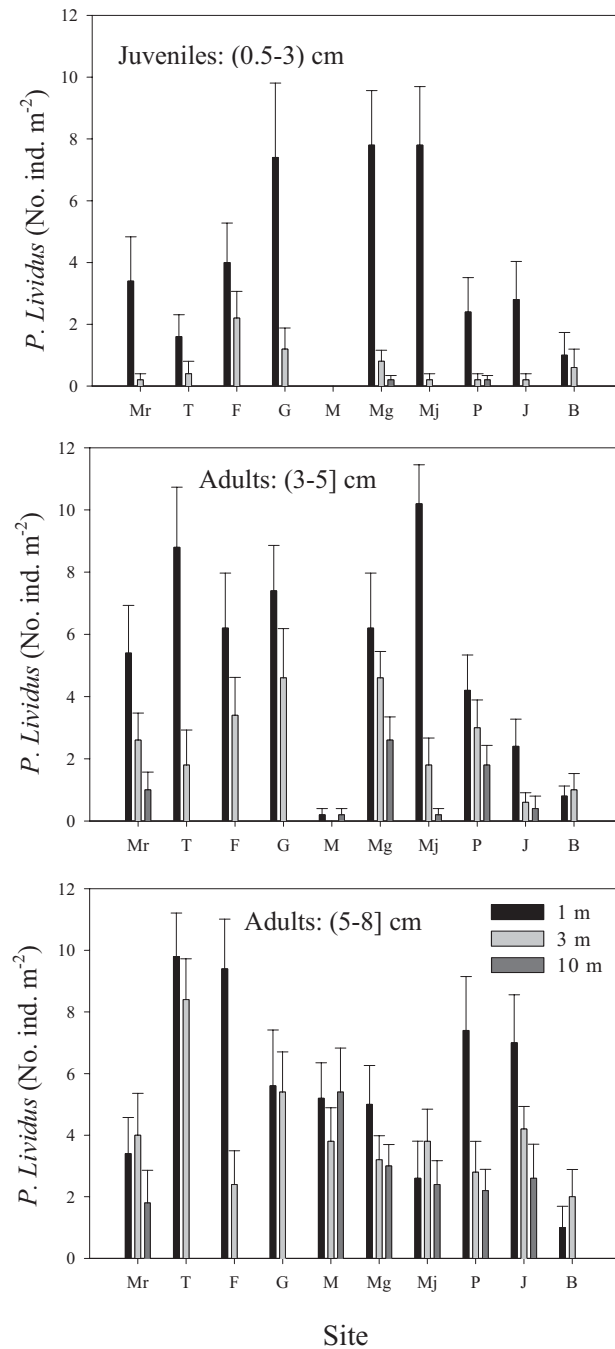


Fig. 4. Abundance of each size-age class of *Paracentrotus lividus* a) juveniles: 0.5 to 3 cm; b) adults from 3 to 5 cm; and c) adults from 5 to 8 cm at each study site (data from 2003 and 2004 pooled). In SNK for juvenile abundance, significant differences among site groups are indicated with letters (see Table. 2b). In two-way ANOSIM only spatial differences in size class distribution were significant: $R_{\text{Year}} = 0.089$; $p > 0.05$; $R_{\text{Site}} = 0.369$; $p < 0.001$. Error bars are S.E.



Table 1. Two-way orthogonal ANOVAs on the abundance of the different life-stages of *P. lividus* at each site and year: a) adults (i.e. sizes 3 to 8 cm); b) juveniles (i.e. sizes 0.5 to 3 cm); and; c) numbers of RMI in collectors. Significant differences are indicated (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

a) Adult <i>Paracentrotus lividus</i>				
Source of variation	ANOVA			
	df	MS	F	<i>p</i>
Year = Y	1	0.986	0.976	0.3489
Site = S	9	31.566	22.682	0.0000***
Y x S	9	1.009	0.725	0.6856
Transformation: \sqrt{x}				
Cochran's C: 0.079 (n.s)				
b) Juvenile <i>Paracentrotus lividus</i>				
Source of variation	ANOVA			
	df	MS	F	<i>p</i>
Year = Y	1	0.0646	0.2735	0.2100
Site = S	9	0.6269	2.6522	0.0164*
Y x S	9	0.0355	0.1500	0.9976
Transformation: $\sqrt{\sqrt{x}}$				
Cochran's C: 0.339 (n.s)				
c) RMI				
Source of variation	ANOVA			
	df	MS	F	<i>p</i>
Year = Y	1	0.62	0.016	0.9555
Site = S	9	571.42	14.73	0.0000***
Y x S	9	186.75	4.815	0.0000***
Transformation: -				
Cochran's C: 0.366 (n.s)				

Post-metamorphic stages

The number of RMI (recently metamorphosed individuals ≤ 15 days from settlement) collected largely differed among study sites, with densities ranging from 25 ± 2.5 [S.E] ind. to only 1.7 ± 0.4 ind. in Montroig. There were interannual differences, since abundance of RMI decreased at some sites (e.g. Montroig, Torredembarra and Montgó) but increased in others (e.g. Port Lligat, Jugadora and Banyuls; i.e. significant Site x Year interaction, Table 1c; Fig. 5). A significant relationship was found between RMI and both adult ($r = 0.736$; $p < 0.05$ $n = 10$) and juvenile populations ($r = 0.952$; $p < 0.05$, $n = 4$) where they were present.



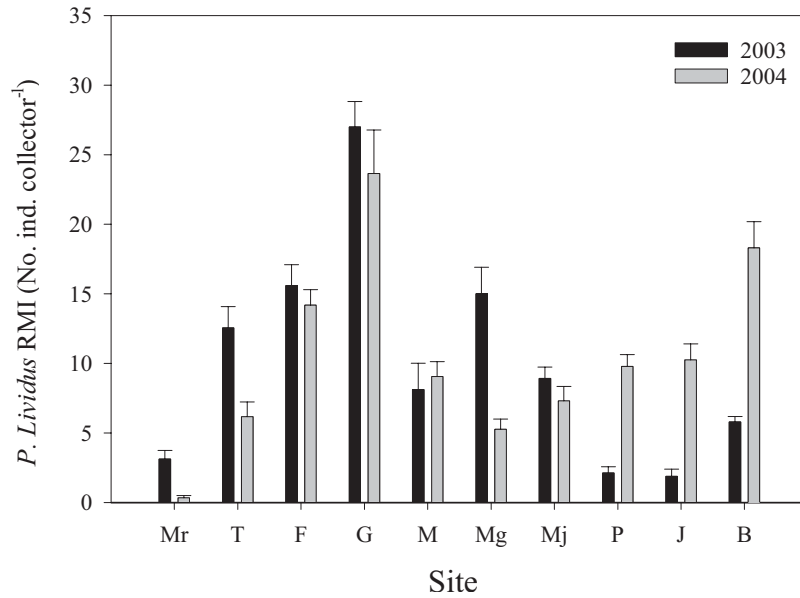


Fig. 5. Abundance of RMI (Recently Metamorphosed Individuals) ≤ 1 mm collected at each study site in 2003 and 2004. Error bars are S.E.

Availability and quality of food

There were significant differences among study sites for all variables related to the quantity and quality of food resources, including seagrass and epiphytic biomass, C: N ratio in both seagrass and epiphytes and percent of organic matter in the sediment. The SNK tests on these variables indicated the existence of multiple significantly different groupings but they were not consistent across the different variables studied (see Table 2). No correlation was found between any of these variables and the abundance of adult or juvenile sea urchins.

Table 2. Mean values of explicative variables measured at each study site, including recruitment, food variables (shoot biomass, C: N in *Posidonia oceanica* and epiphytes, epiphytic biomass and organic matter), predation (reserve vs. non reserve status) and habitat features (shoot density, cover, presence of bare mat and existence of rocky substrate). In one-way ANOVA and SNK, significantly different Site groups (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$) are indicated.

Site	Recruitment (RMI) ^{***}	C: N in seagrass ^{***}	C: N in epiphytes ^{***}	Epiphytic biomass ^{***} (g DW shoot ⁻¹)	Organic matter ^{***} (%)	Shoot density ^{***} (No. m ⁻²)	Cover (%) ^{***}	Shoot Biomass ^{***} (g DW shoot ⁻¹)	Presence of mat	CE length	Reserve status
Mf	1.7 ± 0.4 ^f	19 ± 0.3 ^g	11.3 ± 0.7 ⁱ	0.25 ± 6 E ^{-3 a}	0.73 ± 0.05 ^g	479 ± 62 ^d	85 ± 3 ^a	1.02 ± 0.01 ^a	No	12.7	NR
T	9.3 ± 1.3 ^d	20.2 ± 0.4 ^f	16.1 ± 0.6 ^f	0.12 ± 6 E ^{-3 b}	1.04 ± 0.04 ^e	658 ± 49 ^b	62 ± 7 ^{bc}	0.67 ± 0.02 ^c	Yes	40.7	NR
F	14.9 ± 1.3 ^b	29.7 ± 0.3 ^a	16.9 ± 0.6 ^{de}	0.03 ± 3 E ^{-3 c}	0.45 ± 0.06 ^h	559 ± 44 ^f	30 ± 7 ^d	0.65 ± 0.04 ^f	Yes	4	NR
G	25.3 ± 2.5 ^a	24.8 ± 0.9 ^e	15.9 ± 0.5 ^e	0.10 ± 6 E ^{-3 b}	1.13 ± 0.05 ^e	1001 ± 50 ^a	46 ± 8 ^c	0.64 ± 0.19 ^{cd}	Yes	50.6	NR
M	8.6 ± 1.5 ^d	27.5 ± 0.4 ^b	17.2 ± 0.5 ^d	0.06 ± 7 E ^{-3 bc}	1.80 ± 0.12 ^b	467 ± 46 ^f	66 ± 6 ^b	0.63 ± 0.02 ^c	No	10.3	R
Mg	10.1 ± 1.3 ^d	23.3 ± 0.5 ^d	9.3 ± 0.3 ^g	0.09 ± 3 E ^{-3 b}	0.95 ± 0.04 ^f	412 ± 46 ^f	62 ± 6 ^{bc}	0.85 ± 0.04 ^b	No	18.3	NR
Mj	8.1 ± 0.9 ^d	19.8 ± 0.4 ^f	18.4 ± 0.4 ^e	0.09 ± 3 E ^{-3 b}	1.48 ± 0.06 ^c	478 ± 22 ^d	55 ± 3 ^c	0.94 ± 0.12 ^b	No	13.8	NR
P	5.9 ± 0.6 ^e	27.9 ± 0.3 ^b	31.9 ± 0.8 ^a	0.22 ± 7 E ^{-3 a}	2.42 ± 0.08 ^a	361 ± 32 ^c	65 ± 4 ^b	1.06 ± 0.17 ^{ab}	No	14.6	NR
J	6 ± 0.8 ^e	24.1 ± 0.2 ^{bc}	19.8 ± 0.4 ^b	0.21 ± 7 E ^{-3 a}	2.44 ± 0.09 ^a	282 ± 28 ^f	70 ± 6 ^b	0.95 ± 0.15 ^{ab}	No	20.4	NR
B	12 ± 1.1 ^c	21.8 ± 0.3 ^c	16.1 ± 0.3 ^c	0.08 ± 4 E ^{-3 b}	1.26 ± 0.07 ^d	418 ± 47 ^{de}	37 ± 4 ^{cd}	0.54 ± 0.03 ^d	Yes	10	R



Table 3. a) Correlation analyses between numbers of RMI in collectors and structural variables of the meadow; b) correlation analyses between densities of juvenile *Paracentrotus lividus* (i.e. sizes 0.5 to 3 cm) and controlling variables related to food resources and meadow features (for further details see text). Significant differences are indicated (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

a) Variables influencing RMI					b) Variables influencing juveniles				
	df	MS	<i>F</i>	<i>r</i>		df	MS	<i>F</i>	<i>r</i>
Shoot density					Food resources				
Correlation	1	241.27	15.60	0.809***	Correlation	1	5.480	1.769	0.685
Residual	8	15.91			Residual	2	3.097		
Total	9				Total	3			
Seagrass cover					Seagrass biomass				
Correlation	1	184.03	7.97	0.706*	Correlation	1	0.168	0.029	0.014
Residual	8	23.06			Residual	2	5.753		
Total	9				Total	3			
					Epiphytic biomass				
					Correlation	1	0.348	0.061	0.172
					Residual	2	5.663		
					Total	3			
					% N in <i>P. oceanica</i>				
					Correlation	1	3.489	0.453	0.546
					Residual	2	4.092		
					Total	3			
					% N in epiphytes				
					Correlation	1	0.166	0.028	0.119
					Residual	2	5.754		
					Total	3			
					% Organic matter				
					Meadow features				
					Shoot density	df	MS	<i>F</i>	<i>r</i>
					Correlation	1	10.754	23.346	0.921*
					Residual	2	0.460		
					Total	3			
					Seagrass cover				
					Correlation	1	0.189	0.033	0.127
					Residual	2	5.742		
					Total	3			

Structural characteristics of the meadow

Seagrass shoot density varied significantly among study sites with values ranging from ca. ~ 282 shoots m⁻² in Jugadora to 1000 shoots m⁻² in Giverola. Similarly, seagrass cover, was largely variable among study sites, values ranging from ca. 30% in Fenals to 85% in Montroig (see Table 2). Shoot density was positively correlated with all benthic life stages of *Paracentrotus lividus* (i.e. RMI, juveniles and adults; see Table 3a-b; Table 4) whereas cover was positively correlated only with the abundance of RMI in collectors (Table 3a). Refuges in the mat structure were only present in Torredembarra, Giverola, Fenals and Banyuls, the only sites where juveniles were observed ($F_{\text{Structure}} = 21.07$; $p < 0.001$) in both 2003 and 2004 study years ($F_{\text{year}} = 0.01$; $p > 0.05$).

Table 4. Correlation analyses between densities of adult *Paracentrotus lividus* (i.e. sizes 3 to 8 cm) and controlling variables (see Table 3b). Significant differences are indicated (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Variables influencing adult <i>Paracentrotus lividus</i>				
Food resources	df	MS	F	r
<i>Seagrass biomass</i>				
Correlation	1	0.254	0.011	0.037
Residual	8	22.106		
Total	9			
<i>Epiphytic biomass</i>				
Correlation	1	30.495	1.664	0.414
Residual	8	18.325		
Total	9			
% N in <i>P. oceanica</i>				
Correlation	1	19.103	0.967	0.328
Residual	8	19.749		
Total	9			
% N in epiphytes				
Correlation	1	0.259	0.011	0.038
Residual	8	22.105		
Total	9			
% Organic matter				
Correlation	1	31.975	1.762	0.424
Residual	8	18.140		
Total	9			
Meadow features				
<i>Shoot density</i>				
Correlation	1	115.68	15.667	0.808**
Residual	8	7.677		
Total	9			
<i>Seagrass cover</i>				
Correlation	1	27.629	1.478	0.394
Residual	8	18.684		
Total	9			



Connectivity between habitats

Sea urchin abundance in the two study years decreased progressively with increasing distance from the rocks (see Fig. 6 for one-way ANOVA results showing the absence of interannual differences). Significant differences were detected among study sites but overall densities (i.e. all sites included) declined from 15.2 ind. m⁻² at 1 m, 7.1 ind. m⁻² at 3 m and 2.7 ind. m⁻² at 10 m from the rocks with the Medes Islands and Banyuls MAPs being exceptions to this pattern (no differences between distances; see Fig. 6 for results of the two-way ANOVA between sites and distances).

The size distribution of sea urchins did not change in the two study years, but significant differences among sites and among distances were found (see ANOSIM results in Fig. 7). In study sites without refuges in the mat (i.e. Montroig, Medes Islands, Montgó, Montjoi, Port Lligat and Jugadora), juveniles were also found close to the rocks (mostly at 1 m), excepting in the Medes Islands MPA where no juveniles were observed. Adult sizes from 3 to 5 cm were, however, the most abundant at 1 and 3 m from the rocks whereas individuals from 5 to 8 cm became more important at the largest distance from the hard substrate (see Fig. 7).

The length of the contact edge (CE) evidenced important differences among study sites (Table 2), and was significantly correlated with the densities of sea urchins at 3 m from the hard substrate (Fig. 8).



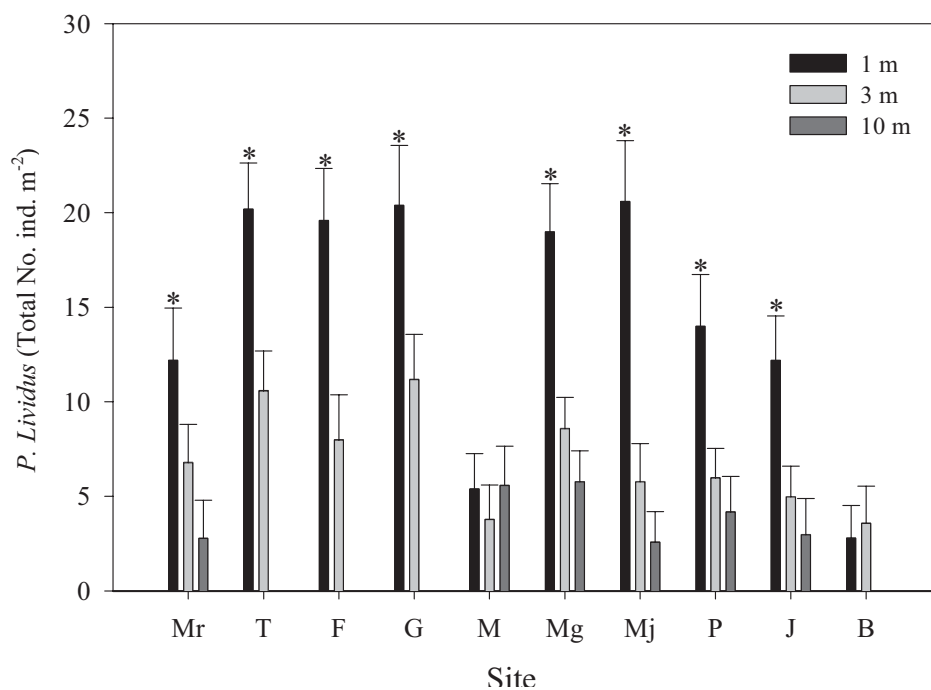


Fig. 6. Abundance of *Paracentrotus lividus* measured in 50 x 50 cm quadrates at 1, 3 and 10 m from the rocky substrate at each study site (data from 2003 and 2004 pooled; $F= 2.9051$; $p= 0.0891$, $n = 30$). Two-way ANOVA, displayed significant differences among sites ($F= 20.802$; $p< 0.0001$), distances ($F= 28.157$; $p< 0.005$) and their interaction ($F= 5.667$; $p< 0.0001$). In SNK, significant differences among distances at each site are shown. Error bars are S.E.

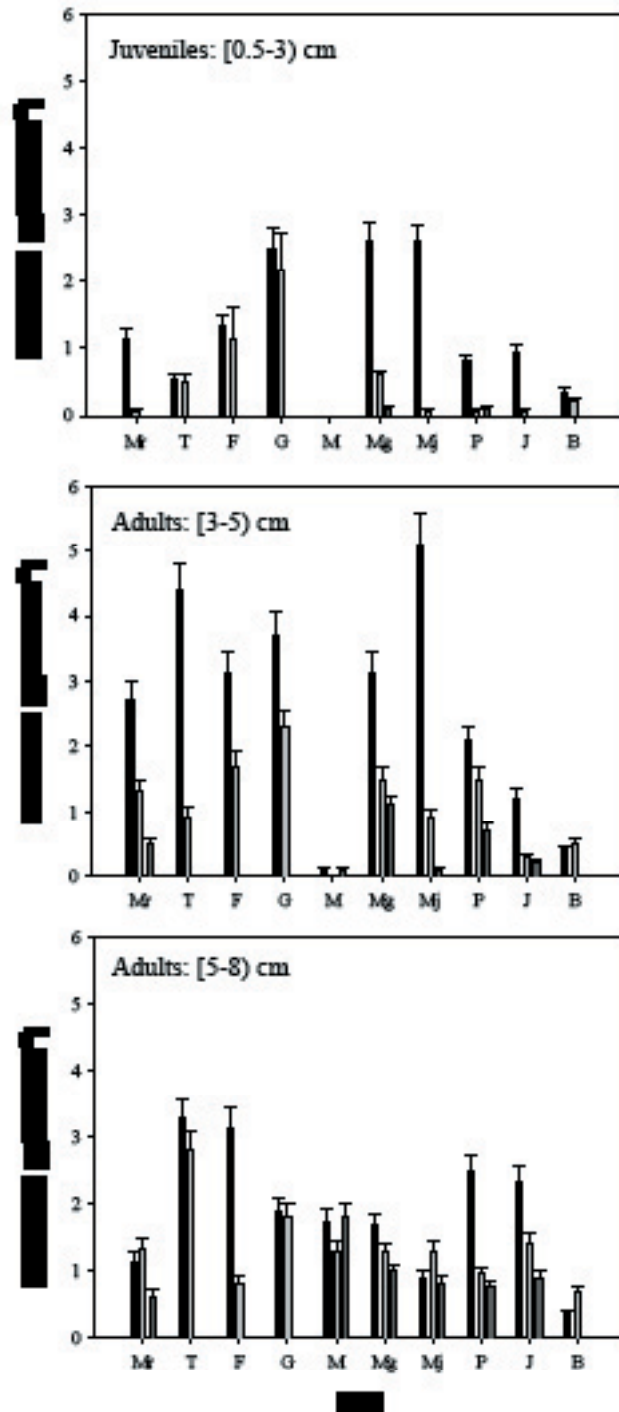


Fig. 7. Abundance of each size-age class of *Paracentrotus lividus* at 1, 3 and 10 m from the rocky substrate at each study site (data from 2003 and 2004 pooled; ANOSIM $R_{\text{Year}} = 0.031$; $p > 0.05$). In two-way ANOSIM analysis, there were significant differences in the size class distribution of *P. lividus* among Sites ($R_{\text{Site}} = 0.426$; $p < 0.001$) and Distances ($R_{\text{Distance}} = 0.488$; $p < 0.001$). Error bars are S.E.



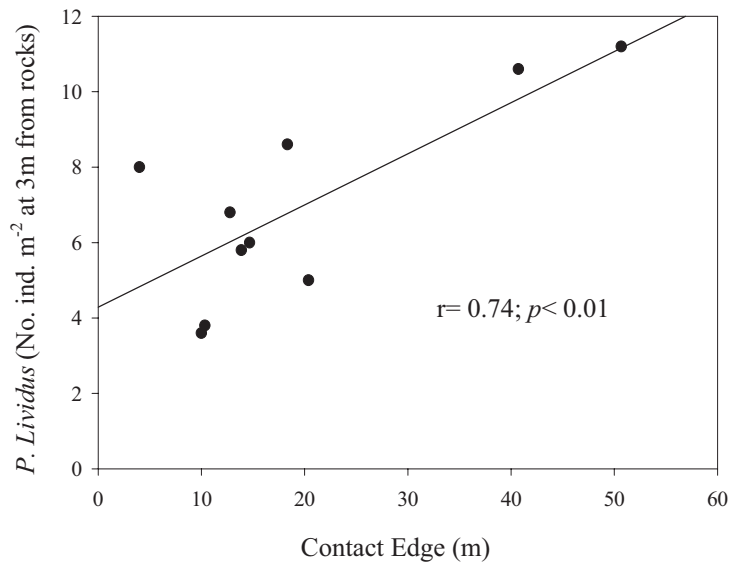


Fig. 8. Correlation between the Contact Edge (meters) between seagrass and hard substrate and the within-meadow densities of *Paracentrotus lividus* at 3 m from rocks at each study site.



DISCUSSION

The structure and abundance of populations of *Paracentrotus lividus* within shallow seagrass meadows appears to be highly variable at the spatial scales of meters and kilometres examined, and seems basically controlled by the supply of individuals, either through in situ recruitment (in meadows with a bare mat offering refuges to juveniles) or through migration from adjacent rocky habitats. Mortality is important at the early sea urchin stages whereas predation on adult individuals shows little contribution to explain sea urchin abundance. The quality and the quantity of food evidenced no role in determining the abundance of this species.

Migration of *Paracentrotus lividus* from adjacent rocky habitats where recruitment is more successful seems to be the main source of individuals in the studied seagrass beds. We base this assertion on the finding that recruitment of juveniles within meadows occurs only very rarely. In effect, not only juveniles (0-1 cm, ca. 1 year) were absent from most seagrass beds far from the rocks but also densities of early adults (<5 cm, ca. 4 years old, Crapp & Willis 1975) decreased considerably with increasing distance. Furthermore, the high association observed between sea urchins abundance and the contact edge between seagrass and rocky habitats confirms the importance of sea urchin flux between both habitats to explain the population structure. Densities of adults (2-20 ind. m⁻²: this study) and recently metamorphosed individuals (0-76 ind. m⁻²: Azzolina & Willsie 1988, this study) in seagrass meadows are consistently lower than in nearby rocky habitats (adults: 10-80 ind. m⁻² Boudouresque & Verlaque 2001; RMI: 400-700 ind. m⁻²: López et al. 1998), suggesting the existence of a spill over or mass effect (i.e. density-mediated migration; Shimida & Wilson 1985) as already proposed to account for patterns of *P. lividus* populations in other meadows (e.g. Fernandez et al. 2001, Tomas 2004).

Sea urchin juveniles seem to be rare within study meadows and restricted to those sites in which bare mat with crevices and holes exists (i.e. Torredembarra, Fenals, Giverola



and Banyuls). Only at those sites, juveniles of ca. 1 cm in diameter are found apart from the rock. This limited distribution of juveniles evidences the existence of large mortality early in the life-history, as RMI were found, in highly variable numbers, in all the studied sites. The agents of such mortality are unknown (see also Andrew & Choat 1985, Turón et al. 1995, López et al. 1998), but predation by invertebrates (possibly crustaceans, gastropods and poliquetes; Harrold et al. 1991) and small fish (Sala & Zabala 1996, McClanahan 1999, Guidetti 2004) appears a probable cause. Once adults, predation does not seem to play an important role. In effect, our results show that adult density in the Medes Islands MPA is dominated by larger sizes (5 to 8 cm) (Sala 1997) whereas the population structure in the Banyuls MPA is best explained by other habitat factors (see below) and a lower contact edge. The association between the existence of bare mat and the presence of juveniles indicates the importance of mortality on early stages of sea urchins, but is by no means conclusive on the agent causing it. Mat structure can play multiple roles, providing at once, stable surface for settlement, refuge from predation (i.e. the crevice behaviour described in rocky substrates: Sala & Zabala 1996, McClanahan 1995, 1999), or food, by increasing organic matter sedimentation or by enhancing the abundance of rhizome algae (see Fig. 2). Indeed, since the food preferred by early stages (ca. 1mm diameter, Verlaque 1984) seems to be encrusting and endolithic algae, which are abundant in the rhizomes, the mat can also contribute to juvenile abundance for trophic reasons.

Where recruitment was successful in supplying juveniles (i.e. Torredembarra, Fenals, Giverola and Banyuls), variability in these juveniles' abundance seemed to be explained by variability in RMI from the previous year. Although this evidence is weak due to the low number of valid observations (n= 4), it suggests that, when refuges (and perhaps adequate food for early stages) exist, settlement success may result in high late recruitment. Nonetheless, while considering the initial abundance of RMI in collectors, mortality rates can be estimated to be as large as >99%, which is in agreement with values obtained in hard substrates over comparable periods of time (López et al. 1998). The abundance of RMI is lower in seagrass meadows (2-26 ind. per collector, Tomas et al. 2004) than in nearby

rocky substrates (80-200 ind. per collector, Hereu et al. 2004; Tomas et al. 2004). Although the causes of such differences are unclear, they may involve either mechanisms of active selection by planktonic larvae (e.g. Swanson et al. 2004) or hydrodynamic conditions. Within seagrass beds, structural properties of the seagrass bed seem to favour the abundance of RMI, as shown by its significant correlation with shoot density, which may enhance RMI abundance through a hydrodynamic effect, increasing the resistance to the water flow and favouring the retention of RMI analogously to the retention of sediment particles (Gacia & Duarte 2001).

Among the structural meadow features, shoot density showed to be also associated with the abundance of adult individuals (see also Ballesteros 1987). However, this should be viewed with care, since several possible influencing variables may exist or co-exist. Shoot density can protect juveniles against predation (Farina et al. 2006), but this is less probable for individuals larger than 4 cm (Guidetti 2004) which were, nonetheless the dominant size class in all study sites. Since higher contact edge occurred in the sites with higher shoot density, the correlation between density and sea urchin abundance can be a spurious result of the statistical association between both variables. In fact, meadows with low SRC and high shoot density (ca. 900 shoots m⁻²; Alcoverro et al. 2001) are common elsewhere (e.g. the Balearic Islands) but they support very low numbers of individuals (<1 ind. m⁻², unpublished personal observations).

Food quality and resource abundance descriptors investigated were unrelated to patterns of sea urchin abundance. However, food quality is known to influence sea urchin populations, as revealed by results from manipulative experiments in the laboratory showing that feeding on different species of macrophytes causes changes in the growth of the test and in gonad weight of echinoids (Fantzis & Grémare 1992, Beddingfield & McClintock 1998). Overgrazing events resulting from organic matter and nutrient inputs have also been repeatedly reported (Kirkman & Young 1981, Rose et al. 1999, Ruiz et al. 2001, Peterson et al. 2002), suggesting that feeding on macrophytes with lower C: N ratios can induce population increases, which is consistent with observations on food preferences (Nedelec &



Verlaque 1984, Shepherd 1987). Our results do not support the hypothesis of the control by food quality or quantity, probably due to the narrow range of variability of these variables found in the natural communities sampled. Natural values of food quality estimated in this study were much lower than values found in the studies mentioned above. For instance, overgrazing reported by Peterson et al. (2002), was coupled with ca. 20 cm of sediment organic matter, and 3-10 mg g DW⁻¹ of epiphyte biomass on leaves, which is several orders of magnitude above the values reported in Table 2. Therefore, we conclude that the narrow variability of food quality in our study was substantially below the potential threshold able to cause significant modifications in sea-urchins populations patterns, and that any possible effect is overridden by other much more variable factors.

Sea urchin abundance in seagrass meadows seems to be controlled by the supply of individuals to adult populations, at least within the range of meadows investigated. This occurs through two distinctive processes, migration from the adjacent hard substrate and successful local recruitment, both related to landscape properties of the meadow. Recruitment seems to be curtailed by mortality on RMI and juvenile phases, likely due to predation and therefore, strongly dependent on the existence of refuges (i.e. rhizome mat). The presence of bare mat seems to be limited to a few sites and could possibly be regulated by changes in sediment dynamics operating at different spatial and temporal scales. Therefore, density dependent migration from rocky substrates appears as the main mechanism through which seagrass bed populations are maintained, and highlights the importance of connections between habitats in the marine environment. The functional link between shallow seagrass and rocky habitats implies the existence of a biocenosis continuum. Based on these results, further research is needed to advance our understanding on the landscape, habitat and species properties controlling the ecological phenomena in the transition zone between habitats. This vision should have special consideration when approaching major ecological questions such as the scaling of ecological processes, biological diversity and the conservation of species in the long-term.



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LITERATURE CITED

- Alcoverro T, Duarte CM, Romero J (1995) Annual growth dynamics of *Posidonia oceanica*: contribution of large-scale versus local factors to seasonality. *Mar Ecol Prog Ser* 120: 203-210
- Alcoverro T, Cebrián E, Ballesteros E (2001) The photosynthetic capacity of the seagrass *Posidonia oceanica*: influence of nitrogen and light. *J Exp Mar Biol Ecol* 261: 107-120
- Anderson RJ, Velimirov B (1982) An experimental investigation of the palatability of kelp bed algae to the sea urchin *Parechinus angulosus* Leske. *PSZN I: Mar Ecol* 3: 357-373
- Andrew NL, Choat JH (1985) Habitat related differences in the survivorship and growth of juvenile sea urchins. *Mar Ecol Prog Ser* 27: 155-161
- Azzolina JF, Willsie A (1987) Abondance des juveniles de *Paracentrotus lividus* au sein de l'herbier a *Posidonia oceanica*. In: Boudouresque CF (ed) Colloque International sur *Paracentrotus lividus* et les oursins comestibles. GIS Posidonie publ, p 159-167
- Ballesteros E (1987) Distribución of *Paracentrotus lividus* (LMK.) y *Arbacia lixula* (L.) (Echinodermata Echinoidea) en la zona infralitoral de la Costa Brava. *Cuad Marisq Publ Tec* 11: 225-232
- Beddingfield SD, McClintock JB (1998) Differential survivorship reproduction growth and nutrient allocation in the regular echinoid *Lytechinus variegatus* (Lamarck) fed natural diets. *J Exp Mar Biol Ecol* 226: 195-215
- Bologna PAX, Heck KL (1999) Differential predation and growth rates of bay scallops within a seagrass habitat. *J Exp Mar Biol Ecol* 239: 299-314
- Botsford LW (2001) Physical influences on recruitment to California Current invertebrate populations on multiple scales. *ICES J Mar Sci* 58: 1081-1091
- Boudouresque CF, Meinesz A (1982) Découverte de l'herbier de Posidonies. *Cah Parc Natl Port-Cros* 4: 1-79
- Boudouresque CF, Verlaque M (2001) Ecology of *Paracentrotus lividus*. In: Lawrence J



- M (ed) Edible sea urchins: biology and ecology. Developments in aquaculture and fisheries science-32. Elsevier, Amsterdam, p 177-216
- Cameron RA, Rumrill SS (1982) Larval abundance and recruitment of the sand dollar *Dendraster excentricus* in Monterey Bay California USA. Mar Biol 71: 197-202
- Clarke KR (1993) Non-Parametric multivariate analyses of changes in community structure. Aust J Ecol 18: 117-143
- Crapp GB, Willis ME (1975) Age determination in the sea urchin *Paracentrotus lividus* (Lamarck) with notes on the reproductive cycle. J Exp Mar Biol Ecol 20: 157-178
- Dance C (1987) Patterns of activity of the sea urchin *Paracentrotus lividus* in the Bay of Port-Cros (Var France Mediterranean). PSZNI Mar Ecol 8: 132-142
- D'Eon RG, Glenn SM, Parfitt I, Fortin M-J (2002) Landscape connectivity as a function of scale and organism vagility in a real forested landscape. Conserv Ecol 6: 10
- Fagan WF, Cantrell RS, Cosner C (1999) How habitat edges changes species interactions. Amer Nat 153: 165-182
- Fernandez C (1997) Effect of diet on the biochemical composition of *Paracentrotus lividus* (Echinodermata: Echinoidea) under natural and rearing conditions (Effect of diet on biochemical composition of urchins). Comp Biochem Physiol 118A: 1377-1384
- Fernandez C, Caltagione A, Johnson M (2001) Demographic structure suggests migration of the sea urchin *Paracentrotus lividus* in a coastal lagoon. J Mar Biol Ass UK 80: 3713-3714
- Farina S, Tomas F, Prado P, Alcoverro T, Romero J (2006) Role of predation in determining sea urchin size structure in a seagrass meadow: the importance of refuges and leaf length. In: Mediterranean seagrass workshop 2006. Abstracts volume p 39, Marsascale, Malta
- Frantzis A, Grémare A (1992) Ingestion absorption and growth rates of *Paracentrotus lividus* (Echinodermata: Echinoidea) fed different macrophytes. Mar Ecol Prog Ser 95: 169-183
- Gacia E, Duarte CM (2001) Sediment retention by a Mediterranean *Posidonia oceanica*



- meadow: the balance between deposition and resuspension. *Estuar Coast Shelf Sci* 52: 505-514
- Guidetti P (2004) Consumers of sea urchins *Paracentrotus lividus* and *Arbacia lixula* in shallow Mediterranean rocky reefs. *Hegol Mar Res* 58: 110-116
- Harrold C, Pearse JC (1987) The ecological role of echinoderms in kelp forests. *Echino Stud* 2: 137-233
- Harrold C, Reed DC (1985) Food availability sea urchin grazing and kelp forest community structure. *Ecology* 66: 1160-1169
- Harrold C, Lisin S, Light KH, Tudor S (1991) Isolating settlement from recruitment of sea urchins. *J Exp Mar Biol Ecol* 147: 81-94
- Heck KL, Valentine JF (1995) Sea urchin herbivory: evidence for long-lasting effects in subtropical seagrass meadows. *J Exp Mar Biol Ecol* 189: 205-217
- Hereu B, Zabala M, Linares C, Sala E (2004) Temporal and spatial variability in settlement of the sea urchin *Paracentrotus lividus* in the NW Mediterranean. *Mar Biol* 144: 1011-1018
- Hereu B, Zabala M, Linares C, Sala E (2005) The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. *Mar Biol* 146: 293-299
- Irlandi EA (1994) Large- and small-scale effects of habitat structure on rates of predation: How percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* 98: 176-183
- Kirkman H, Young PC (1981) Measurement of health and echinoderm grazing on *Posidonia oceanica* (L) Delile. *Aquat Bot* 10: 329-338
- Klumpp D, Salita-Espinosa JT, Fortes MD (1993) Feeding ecology and trophic role of sea urchins in a tropical seagrass community. *Aquat Bot* 45: 205-229
- Lawrence JM (1975) On the relationships between marine plants and sea urchins. *Oceanogr Mar Biol Ann Rev* 13: 213-286
- López S, Turón X, Montero E, Palacín C, Duarte CM, Tarjuelo I (1998) Larval abundance recruitment and early mortality in *Paracentrotus lividus* (Echinoidea) Intra-annual



- variability and plankton-benthos coupling. *Mar Ecol Prog Ser* 172: 239-251
- Lozano J, Galera J, López S, Turón X, Palacín C, Morera G (1995) Biological cycles and recruitment of *Paracentrotus lividus* (Echinodermata: echinoidea) in two contrasting habitats. *Mar Ecol Prog Ser* 122: 179-191
- McClanahan TR, Shafir SH (1990) Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* 83: 362-370
- McClanahan TR (1995) Fish predators and scavengers of the sea urchin *Echinometra mathaei* in Kenyan coral reef Marine parks. *Environ Biol Fish* 43: 187-193
- McClanahan TR (1999) Predation and the control of the sea urchin *Echinometra viridis* and fleshy algae in the patch reefs of Glovers Reef Belize. *Ecosystems* 2: 511-523
- Moberg PE, Burton RS (2000) Genetic heterogeneity among recruit and adult red sea urchins *Strongylocentrotus franciscanus*. *Mar Biol* 136: 773-784
- Nedelec H, Verlaque M (1984) Alimentation de l'oursin *Paracentrotus lividus* (Lamarck) dans un herbier a *Posidonia oceanica* (L.) Dellile en Corse (Mediterranee-France). In: Boudouresque C F De Grissac J A and Olivier J (eds) International workshop in *Posidonia oceanica* beds 1. GIS Posidonie publ, p 349-364
- Ott J, Maurer L (1977) Strategies of energy transfer from marine macrophytes to consumer levels: The *Posidonia oceanica* example. In: Keegan BF O'Ceidigh P, Boaden P (eds) *Biology of benthic organisms*. Pergamon Press, p 493-502
- Parker JG (1983) A comparison of methods used for the measurement of organic matter in marine sediment. *Chem Ecol* 1: 201-210
- Pelletreau KN, Muller-Parker G (2002) Sulfuric acid in the phaeophyte alga *Desmarestia munda* deters feeding by the sea urchin *Strongylocentrotus droebachiensis*. *Mar Biol* 141: 1-9
- Peterson TH (1982) Clam predation by whelks (*Busycon* spp): experimental test of the importance of prey size prey density and seagrass cover. *Mar Biol* 66: 159-170
- Peterson BJ, Rose CD, Rutten LM, Fourqurean JW (2002) Disturbance and recovery following catastrophic grazing: studies of a successional chronosequence in a seagrass



- bed. *Oikos* 97: 361-370
- Ries L, Sisk TD (2004) A predictive model of edge effects. *Ecology* 85: 2917–2926
- Rose CD, Sharp WC, Kenworthy WJ, Hunt JH, Lyons WG, Prager EJ, Valentine JF, Hall MO, Whitfield PE, Fourqurean JW (1999) Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in outer Florida Bay. *Mar Ecol Prog Ser* 190: 211-222
- Ruiz JM, Pérez M, Romero J (2001) Effects of fish farm loadings on seagrass (*Posidonia oceanica*) distribution growth and photosynthesis. *Mar Poll Bull* 42: 749-760
- Rumrill SS, Pennington JC, Chia FS (1985) Differential susceptibility of marine invertebrate larvae: laboratory predation of sand dollar *Dendraster excentricus* (Eschsholtz) embryos and larvae by zoeae of the red crab *Cancer productus* Randall. *J Exp Mar Biol Ecol* 90: 193-208
- Sala E, Zabala M (1996) Fish predation and the structure of the sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. *Mar Ecol Prog Ser* 140: 71-81
- Sala E (1997) Fish predators and scavengers of the sea urchin *Paracentrotus lividus* in protected areas of the north-west Mediterranean Sea. *Mar Biol* 129: 531-539
- Sala E, Boudouresque CF, Harmelin-Vivien M (1998) Fishing trophic cascades and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos* 82: 425-439
- Shimida A, Wilson MV (1985) Biological determinants for species diversity. *J Biogeogr* 12: 1-20
- Shears NT, Babcock RC (2003) Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Mar Ecol Prog Ser* 246: 1–16
- Shepherd A (1987) Grazing by the sea-urchin *Paracentrotus lividus* in *Posidonia* beds at Banyuls France. In Boudouresque CF (ed) *Colloque International sur Paracentrotus lividus et les oursins comestibles*. GIS Posidonie publ, p 83-86
- Strathmann RR (1978) The length of pelagic period in echinoderms with feeding larvae from the northeastern Pacific. *J Exp Mar Biol Ecol* 34: 23-27

- Swanson RL, Williamson JE, de Nys R, Kumar N, Bucknall MP, Steinberg PD (2004) Induction of settlement of larvae of the sea urchin *Holopneustes purpurascens* by histamine from a host alga. *Biol Bull* 2006: 161-172
- Tegner MJ, Dayton PK (1981) Population structure recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. *Mar Ecol Prog Ser* 5: 255-268
- Tomas F, Romero J, Turón X (2004) Settlement and recruitment of the sea urchin *Paracentrotus lividus* in two contrasting habitats in the Mediterranean. *Mar Ecol Prog Ser* 282: 173-184
- Turón X, Giribet G, López S, Palacín C (1995) Growth and Population Structure of *Paracentrotus lividus* (Echinodermata: echinoidea) in two contrasting habitats. *Mar Ecol Prog Ser* 122: 193-204
- Underwood AJ, Fairweather PG (1989) Supply-side ecology and benthic marine assemblages. *Tree* 4: 16-20
- Valentine JF, Heck KL (1991) The role of sea urchin grazing in regulating subtropical seagrass meadows: evidence from field manipulations in the northern Gulf of Mexico. *J Exp Mar Biol Ecol* 154: 215-230
- Verlaque M (1984) Biologie des juveniles de l'oursin herbivore *Paracentrotus lividus* (Lamarck): sélectivité du broutage et impact de l'espèce sur les communautés algales de substrat rocheux en Corse (Méditerranée France). *Bot Mar* 27: 401-424

