SCIENTIA MARINA

Experimental evidence that intra-specific competition in seagrass meadows reduces reproductive potential in the sea urchin *Paracentrotus lividus* (Lamarck)*

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SUMMARY: To better understand the biological controls that regulate sea urchin dynamics, we studied the effects of potential inter- and intra-specific competition for food on several biological variables of the main sea urchin in the Mediterranean (*Paracentrotus lividus*). We carried out a caging experiment in which we manipulated sea urchin density (natural vs. high density) and herbivorous fish (*Sarpa salpa*) accessibility (free access vs. exclusion) in a *Posidonia oceanica* meadow. No evidence of competition between fish and urchins was detected. Neither density-dependent mortality nor changes in the somatic variables were found; however, we detected that intra-specific competition affected the reproductive potential of *P. lividus*. The gonad index of urchins at high population densities was ca. 30% lower than that of urchins at natural densities. As a spawning event had just occurred when urchins were collected, these differences probably reflect differences in reserve content, which may compromise the following reproductive period and decrease survival in the long term, as the gonads are also used as storage organs. For the time period studied, mortality rates appeared to be independent of local densities. The results indicate that a long-term negative feedback mechanism appears to take place in *P. lividus* in response to increased population density.

Keywords: competition, density-dependence, phenotypic plasticity, mortality, echinoid, *Posidonia oceanica*. Aristotle's lantern, Mediterranean.

RESUMEN: EVIDENCIA EXPERIMENTAL DE QUE LA COMPETENCIA INTRAESPECÍFICA EN PRADERAS DE FANERÓGAMAS MARINAS REDUCE EL POTENCIAL REPRODUCTIVO DEL ERIZO DE MAR *PARACENTROTUS LIVIDUS* (LAMARCK). – Para entender mejor los controles biológicos que pueden regular las dinámicas de poblaciones en erizos de mar, estudiamos los efectos de una potencial competencia inter- e intraespecífica por el alimento en algunas variables biológicas del principal erizo de mar en el Mediterráneo (*Paracentrotus lividus*) mediante un experimento con jaulas en el que manipulamos las densidades de erizos (densidad natural vs. densidad alta) y el acceso de los peces herbívoros (*Sarpa salpa*, libre acceso vs. exclusión) en una pradera de *Posidonia oceanica*. No se detectaron evidencias de competencia entre peces y erizos, ni tampoco se observó mortalidad denso-dependiente ni cambios en las variables somáticas de *P. lividus*. Por el contrario, el índice gonádico de los erizos a densidades altas fue aproximadamente un 30 % menor que el de los erizos a densidad naturales, lo cual es un efecto de la competencia sobre el potencial reproductor. Puesto que había tenido lugar un episodio de liberación de gametos antes de la recolección de los erizos, estas diferencias probablemente reflejan diferencias en el contenido en reservas de las gónadas; así, esta reducción de tamaño puede no sólo comprometer el próximo periodo reproductivo, sino también disminuir la supervivencia a largo plazo, ya que las gónadas se usan como órgano de acumulación de reservas. Los resultados indican que en *P. lividus* parece tener lugar un mecanismo de retroalimentación negativo a largo término en respuesta a un incremento en la densidad de población.

Palabras clave: competición, denso-dependencia, plasticidad fenotípica, mortalidad, equinoideos, *Posidonia oceanica*, linterna de Aristóteles, Mediterráneo.

INTRODUCTION

Sea urchins have often been considered key species in shallow water benthic communities, as they can be strong interactors (Paine, 1992; Sala and Graham, 2002), which play a major structuring role and control macrophyte abundance (Lawrence, 1975; Lawrence and Sammarco, 1982). Understanding their population dynamics is thus a basic aim in biological coastal research.

Several processes such as predation (e.g. Tegner and Dayton, 1981; McClanahan, 1994, 1998; Scheibling, 1996), recruitment (e.g. Raymond and Scheibling, 1987; Watanabe and Harrold, 1991; Kenner, 1992), migration (e.g. Odgen et al., 1973; Vadas et al., 1986; Hagen, 1995), and disease (e.g. Lessios et al., 1984; Hagen, 1995; Scheibling et al., 1999) greatly influence sea urchin population size and structure. These processes can favour both population outbreaks as population limitations are released (e.g. Harmelin et al., 1981; Watanabe and Harrold, 1991; Levitan, 1992; Sala and Zabala, 1996), and limit population numbers through increased mortality due to disease (e.g Lessios et al., 1984; Scheibling and Raymond, 1990; Scheibling and Hennigar, 1997), enhanced predation pressure (e.g. Pearse and Hines, 1987), or competition for resources (e.g. Keller, 1983; McClanahan and Kurtis, 1991). Sublethal effects which diminish the general fitness and reproductive output of individuals can also occur (e.g. Ebert, 1977; Himmelman, 1986; Andrew, 1986; Levitan, 1989; McClanahan and Kurtis, 1991; Lawrence and Vasquez, 1996).

Echinoids have a marked phenotypic plasticity, as a response to the different environmental conditions (Ebert, 1996). Changes in somatic (e.g. decrease in body size or increase in the size of the food-gathering apparatus) and reproductive variables often take place when food is scarce (e.g. Ebert, 1968, 1980; Levitan, 1988; Edwards and Ebert, 1991; George, 1996; Fernandez and Boudouresque, 1997). Increased population densities can have contrasting effects on the reproductive output of free-spawning invertebrates such as sea urchins (reviewed by Levitan, 1995). High densities can negatively affect gamete production due to food limitation (e.g. Levitan, 1989; Wahle and Peckham, 1999; Brewin et al., 2000). On the other hand, fertilization rates generally increase with adult density (e.g. Pennington, 1985; Levitan et al., 1992; Levitan and Young, 1995; Wahle and Peckham, 1999).

Given the high plasticity of echinoids, the relative importance of the different mechanisms that regulate the populations still need further understanding.

The echinoid *Paracentrotus lividus* (Lamarck) is a key species that influences macrophyte structure and dynamics (Kitching and Ebling, 1961; Verlaque, 1987; Palacín et al., 1998a), and it is one of the most abundant invertebrate grazers in the Mediterranean. This specie is found in a variety of shallow habitats and is a typical inhabitant of the endemic seagrass *Posidonia oceanica* (L.) Delile meadows. Under natural conditions, densities of *P. lividus* are generally low in such beds (0 to 6 ind m^{-2}, e.g Azzolina et al., 1985; Ballesteros, 1987; Maggiore et al., 1987; Palacín et al., 1998b). However, various sea urchin outbreak events which have resulted in overgrazing of the seagrass have been observed (Verlaque and Nédelec, 1983; Shepherd, 1987; Ruiz et al., 2001), indicating the existence of an important interaction network.

When inhabiting *Posidonia oceanica* meadows, *Paracentrotus lividus* preferentially feeds on the distal parts of the seagrass leaves and their epiphytes (Ott and Maurer, 1976; Traer, 1980; Nédelec and Verlaque, 1984), and it apparently obtains most of its nitrogen from the epiphytes (Tomas et al., in press). The other main macroherbivore present in these meadows is the sparid fish *Sarpa salpa* (Linnaeus, 1758), the adults of which also feed on *P. oceanica* leaves and their epiphytes (Verlaque, 1981, 1985; Velimirov, 1984; Havelange et al., 1997). Although interspecific competition is generally less important than intraspecific competition in marine herbivores (Gurevitch et al, 1992), there is nevertheless a potentially significant competitive interaction between the sea urchin *P. lividus* and the sparid fish *S. salpa* for food (i.e. seagrass and epiphytes).

This paper is part of a study that uses caging experiments to evaluate the importance and effects of the two main macroherbivores (*Paracentrotus lividus* and *Sarpa salpa*) on *Posidonia oceanica* and its epiphytes (see Tomas et al., 2005a). We present here an experimental study of the effects of potential inter- and intra-specific competition for food on the sea urchin *P. lividus*. We aim to provide new data for a better understanding of the biological mechanisms that can regulate population dynamics of this important species. In this study we have assessed the effect of increasing sea urchin density as well as competition with the herbivorous fish *S. salpa,* on regulating the trade-off between investment in reproduction versus investment in somatic variables in *P. lividus*.

MATERIALS AND METHODS

Study site

The study was carried out in a *Posidonia oceanica* meadow located in the Medes Islands Marine Reserve (NE coast of Spain, north-western Mediterranean, 42º2'N, 3º13'E) at a depth of 5-6 m, near the upslope limit of the meadow. Shoot density in this meadow at this depth is between 450 and 600 shoots m^{-2} (Alcoverro *et al.*, 2000). Within the depth range mentioned, the meadow hosts a population of the sea urchin *Paracentrotus lividus* with an average density of about 5 individuals m^{-2}, which consist mainly of adult individuals (i.e. 5 to 7 cm in diameter without spines) (Romero *et al.*, 1999; Tomas *et al.*, 2004). Dense schools of the sparid fish *Sarpa salpa* are commonly found in this meadow. The schools reach densities of between 30 and 60 individuals 100 m^{-2} (Tomas *et al.*, 2005b).

Experimental design

To assess the effect of increased sea urchin population density and the presence of concurrent fish on some key variables of the sea urchin *Paracentrotus lividus*, we set up a caging experiment, in which manipulated both sea urchin density and fish accessibility to the seagrass. Four experimental conditions were set: two sea urchin density treatments (natural, i.e. ca. 5 ind m^{-2} and high, ca. 15 ind m^{-2}) combined with two different conditions in terms of fish presence: free access and exclusion. The high density level was chosen according to recent *P. lividus* population outbreaks reported by Ruiz *et al.* (2001). Three replicate cages were used for each experimental condition. The 12 cages were placed at a minimum distance of 3 m from each other. The cages were 1.5 m x 1.5 m (2.25 m^2), 0.5 m high and delimited at the corners by iron bars. Fences were constructed with 2 cm plastic mesh attached to the seafloor with iron pegs. Plots that excluded *Sarpa salpa* were roofed with 5 cm plastic mesh attached to the cage by elastic rope. Treatments were assigned randomly to each cage. Sea urchins found in the cages at the beginning of the experiment were counted and other individuals were added if needed from an area of the same meadow located 300 m away.

As this experiment was part of another study (see Tomas *et al.,* 2005a), the cages that stopped fish from entering were deployed later than the cages with no roofs. As a result, one set of urchins (i.e. those in cages without roofs, in the potential intra- and inter-specific competition experiment) were manipulated for a longer period of time (ca. 475 days, i.e. from May 2000 to October 2001) than the other set (i.e. those in roofed cages, in the potential intra-specific competition only experiment, for 380 days, i.e. from November 2000 to October 2001). However, this should not influence our results, since changes to the variables assessed usually occur in much shorter times (e.g. after 1.5-3 months; Keller, 1983; 2 months; Andrew, 1986, and 6 months; Levitan, 1989). Therefore, we assume that the experimental period of more than one year is long enough for any effect to be established, and as the experiments ended at the same time (October 2001), we compared the sea urchin variables at this point in time. In fact, no large differences were observed between urchins at both experimental times under the same population density conditions (see Results), which supports our assumption that both experiments are (statistically) comparable despite being carried out for different time periods.

Cages can petentially introduce artefacts into the experimental results. Although most previously published works did not report caging effects on sea urchins (Levitan, 1988, 1989; Andrew, 1986; but see Keller, 1983), we evaluated this possible cage effect on the biological variables of *Paracentrotus lividus* by comparing the urchins from the natural density plots at the end of the experiment with urchins collected randomly within the study site. We also made efforts to avoid interferences by periodically cleaning the roofs and walls (every 15 days) to remove fouling organisms which could reduce the light entering the cages and/or become a possible food source for urchins, and repairing any damage as soon as it was detected. Light intensity inside the cages was measured using a spherical quantometer, and it was, on average, about 10-15% less than outside. At this depth (5 m), this reduction is not important enough to affect plant vitality (Ruiz and Romero, 2001). In fact, no pernicious effects were detected in the seagrass variables measured (Tomas *et al.,* 2005a). Cages were also checked periodically to maintain the desired sea urchin densities. Drifting leaves that accumulated inside the cages were periodically removed to keep their abundance within natural levels (Mateo and Romero, 1997).

The density and size frequency distribution of the sea urchin population in this meadow was monitored for four years (2000 to 2003). The mean size (test

diameter) was highly constant over time with a remarkable uniformity, being 63.3 mm ± 4.1 (SD) in May 2000 (beginning of "fish and urchin" experiment), and 63.3 mm ± 7.4 (SD) in November 2000 (beginning of "urchins only" experiment) (Tomas *et al.*, 2004). Therefore, although we did not measure the individuals placed in each plot at the beginning of the experiment, we can assume that all cages had similarly sized animals prior to the experiment. At the end of the experiment, all individuals were measured and no differences in test diameter (TD) were found between the treatments (mean TD for all individuals 66.6 ± 4.7 (SD) mm; F = 1.04, a = 0.05 d.f.11, 186, p = 0.42; one-way ANOVA, random factor cages).

Variables measured and sampling procedures

When the experiment (October 2001) was completed, sea urchins from all the experimental plots were harvested. In the laboratory, sea urchins were measured using a vernier caliper (to the nearest 0.1 millimetre) and dissected into various components: gonads, Aristotle's lantern and test. One of the 5 gonads removed was kept in formaldehyde (4%) and used for histological observations. The other 4 gonads, the muscle, the Aristotle's lantern and the test were dry-weighed (100°C until constant weight), and used to calculate the relationship between body parts. The indices calculated were:

a) Aristotle's lantern Index (LI)
LI = (DW of lantern / DW of body) * 100

b) Gonadic Index (GI)
GI = (DW of 5 gonads / DW of body) * 100

LI was considered to reflect investment in feeding (e.g. Ebert, 1980; Levitan, 1991), whereas GI was considered to reflect reproductive performance (e.g. Vadas, 1977). The dry weight of the 5 gonads was estimated by multiplying the DW of the four dried gonads by 5/4. Microscopic observations of the gonads were performed to assess the sex of animals by squashing a portion of the gonad as described by Lozano *et al.* (1995). In addition, the preserved gonads of three to four randomly selected females from the cages from the plots that allowed free access to *Sarpa salpa* were embedded in paraffin wax for histological examination. The other dried gonads of these females were used for C and N analysis (Carlo Erba autoanalyzer) to assess potential differences in qualitative composition of the gonads. Prior to dehydrating and embedding, the volume of the gonad was estimated from the weight of water displaced when the gonad was placed under the water surface of a bowl held over a set of scales (Andrew, 1986; Levitan, 1989). Transverse sections 7 mm thick were then cut at three levels of the gonad (approximately at one third, the centre and two thirds of the gonad major axis) and stained with haematoxylin / eosin (H/E)

Our experiment did not allow us to measure the urchins' growth, which can be affected by population density and limited food availability (Levitan, 1989). The sea urchins used in our experiment were large and uniformly-sized. We did not expect significant changes in growth because *Paracentrotus lividus* grows very little after reaching 5-6 cm in diameter (Crapp and Willis, 1975; Kitching and Thain, 1983; Turon *et al.*, 1995). However, to avoid possible alometric effects (e.g. Gonor, 1972), the analysis was restricted to data from individuals of a single, modal class (6 cm i.e. diameter >59.5 mm and < 69.6 mm), which represented the main size structure that occurred in the meadow.

Statistical analysis

To test for a potential caging effect on the biological variables measured, we performed a one-way ANOVA (factor caging) comparing LI, test DW, and GI of individuals (replicates) from plots with a natural density and with free access to *Sarpa salpa* with the same variables of urchins collected randomly within the study site.

We carried out factorial ANOVAs with two fixed orthogonal factors (sea urchin density, and presence/absence of *Sarpa salpa*): the first factor indicating intra-specific and the second factor inter-specific competition, as well as a nested factor (cages) on the dependent variables LI, test DW and GI measured (for each sea urchin) at the end of the experiment.

We also tested whether the effect of population density was the same for both sexes. As the cages and the presence of *Sarpa salpa* were found to have no effect (see Results), and as the number of females available in the natural density cages was 16 in total, we randomly chose 16 males from these same cages, and 16 males and females from the high density cages. Therefore, we ended up with a balanced design analysed with a Two-Way ANOVA (fixed factors density and sex) for the variables LI, test DW and GI, where sea urchins were the replicates (i.e. n = 16).

TABLE 1. – Nested ANOVA performed to assess significant differences in *Paracentrotus lividus* biological variables due to: increased sea urchin density (D), the presence of the herbivorous fish *Sarpa salpa* (F), their interaction (D x F), and the cages (nested factor). p-value: ns = not significant; df = degrees of freedom; MS, mean square.

Variable	Effect	df	MS	F	p-value
LI	Density	1	0.198	0.232	ns
	Fish	1	0.415	0.484	ns
	D x F	8	0.856	1.627	ns
	Cage (DF)	1	0.070	0.081	ns
	Error	186	0.526		
Test DW	Density	1	12.127	0.964	ns
	Fish	1	26.083	2.073	ns
	D x F	8	12.585	0.995	ns
	Cage (DF)	1	6.923	0.550	ns
	Error	186	12.646		
GI	Density	1	12.399	7.178	0.028
	Fish	1	0.618	0.358	ns
	D x F	8	1.727	0.695	ns
	Cage (DF)	1	0.060	0.035	ns
	Error	186	2.484		

To test for possible differences in gonad volume, we carried out a nested ANOVA (one fixed factor, i.e. sea urchin density, and a nested factor, i.e. cages) on urchins from the cages which allowed free access to *Sarpa salpa*, whose gonads had not suffered breakage and thus their volume could be estimated. A nested ANOVA (one fixed factor, i.e. sea urchin density, and a nested factor, i.e. cages) was performed to test for differences in %C, %N and C/N content of gonads from three randomly selected females from the cages that *S. salpa* could access freely.

When overall significant differences were detected, *a posteriori* pair-wise comparison of means was performed using the Student-Newman-Keuls (SNK; Zar, 1989), comparison test.

Prior to the statistical analyses, normality and homogeneity of variance were checked for all data (Kolmogorov-Smirnov Test and Cochran's test respectively). All differences were considered significant at $p < 0.05$. All analyses were run with the Statistica v.4 package.

RESULTS

We did not find any caging effects when we compared the urchins from the natural density plots at the end of the experiment with the urchins collected randomly within the study site. No significant differences were found for any of the variables tested (LI, test DW, GI) ($p > 0.05$ for all variables). In addition, no mortality was found in any of the cages,

judging from the absence of dead sea urchins during the experimental period.

No effect of the presence of *Sarpa salpa* (i.e. potential inter-specific competition) or the interaction between the presence of *S. salpa* and sea urchin density was detected in either of the biological variables measured for *Paracentrotus lividus* (Table 1).

Population density (i.e. potential intra-specific competition) did not affect the somatic variables measured. Neither the Aristotle's lantern index (LI), nor the test dry weight showed significant differences for the different experimental conditions (Fig. 1, Table 1). However, there was a significant
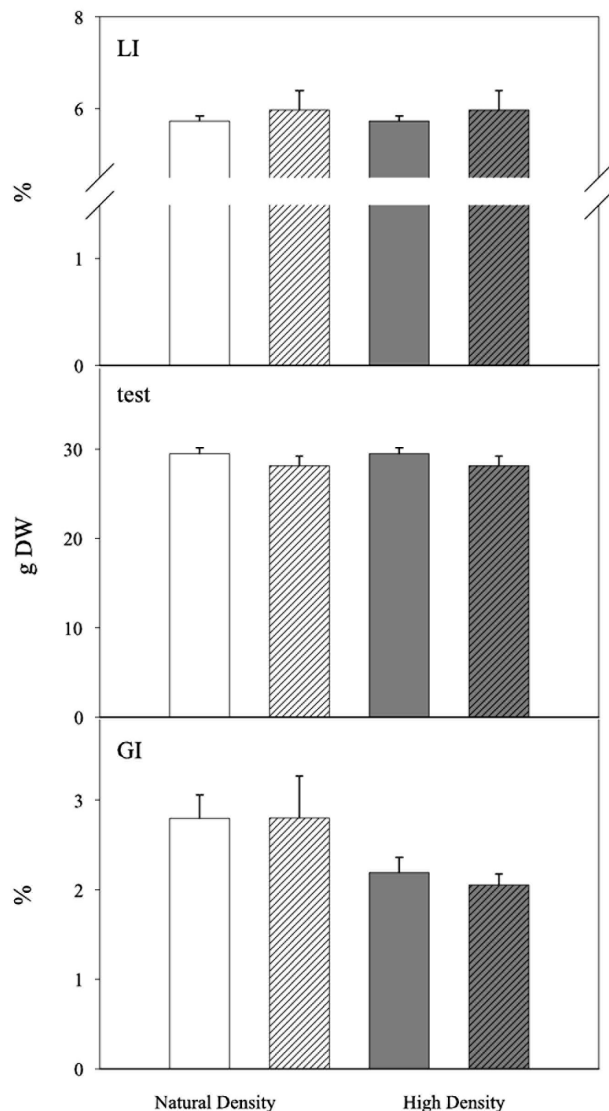

FIG. 1. – *Paracentrotus lividus*. Biological variables for sea urchins submitted to different population densities (5 ind m^{-2}, white; 15 ind m^{-2}, grey) and presence (void) / absence (striped) of herbivorous fish: Aristotle's lantern Index (LI, %; mean + SE), test DW (g; mean + SE), and Gonad Index (GI, %; mean + SE). DW = dry weight. Bars are standard errors.

TABLE 2. – Summary of the factorial two-way ANOVA to assess significant differences in *Paracentrotus lividus* biological variables comparing sea urchin densities (D), sex (S) , and their interaction (D x S). p-value: ns = not significant; df = degrees of freedom; MS, mean square.

Variable	Effect	df	MS	F	p-value
LI	Density	1	0.137	0.267	ns
	Sex	1	0.830	1.622	ns
	D x S	1	0.174	0.340	ns
	Error	60	0.512		
Test DW	Density	1	0.319	0.026	ns
	Sex	1	0.260	0.021	ns
	D x S	1	10.192	0.824	ns
	Error	60	12.375		
GI	Density	1	11.516	7.380	0.009
	Sex	1	0.288	0.184	ns
	D x S	1	0.222	0.142	ns
	Error	60	1.560		

TABLE 3. – Nested ANOVA to assess significant differences in gonad volume of *Paracentrotus lividus* from plots of different sea urchin densities (D) with free access to the fish *Sarpa salpa*, and cages (nested factor). p-value: ns = not significant; df = degrees of freedom; MS, mean square.

Variable	Effect	df	MS	F	p-value
Gonad Volume	Density	1	0.259	4.230	ns
	Cages (D)	4	0.061	0.569	ns
	Error	66	0.107		

TABLE 4. – Nested ANOVA to assess significant differences in C and N content of gonads of female *Paracentrotus lividus* from plots of different sea urchin densities (D) with free access to the fish *Sarpa salpa*, and cages (nested factor). p-value: ns = not significant; df = degrees of freedom; MS, mean square.

Variable	Effect	df	MS	F	p-value
% C	Density	1	3.929	0.202	ns
	Cages (D)	4	19.434	1.306	ns
	Error	12	14.880		
% N	Density	1	0.411	0.734	ns
	Cages (D)	4	0.560	0.734	ns
	Error	12	0.661		
C/N	Density	1	0.140	1.433	ns
	Cages (D)	4	0.098	0.137	ns
	Error	12	0.712		

decrease in the reproductive performance of *Paracentrotus lividus* as a response to increased sea urchin density (Table 1). The GI of sea urchins whose population density increased to 3-fold the natural density decreased by approximately 30% (Fig. 1). When examining the effects of increased population density separately for each sex, we found no significant differences between males and females (non-significant factor sex, Table 2).

No difference was observed regarding the gametogenic conditions of gonads. Histological examination of females revealed that a spawning event had occurred shortly before the individuals were collected, as all the gonads were either empty (no ova left) or in different post-spawning stages (Spirlet *et al.*, 1998). Although gonad volume tended to be higher in natural density plots than in high density plots (mean value 0.70 ± 0.06 cm^3 SE and 0.59 ± 0.09 cm^3 SE respectively), no significant differences between treatments were found (Table 3).

Neither the carbon content (49.6 ± 0.9 SE %), nor the nitrogen content of the gonads (7.4 ± 0.2 SE %), nor their ratio (C/N = 7.9 ± 0.2 SE) differed significantly between treatments (Table 4).

DISCUSSION

The results presented in this study indicate that increased population density and therefore, potential intra-specific competition in the sea urchin *Paracentrotus lividus* does not appear to affect somatic variables, but it does result in a decrease in its reproductive potential, at least within the range of the densities studied (5 to 15 ind m^{-2}) and in the meadow studied.

When food is limited, somatic responses seem to be a common fact widely reported in the literature; these include the food gathering apparatus increasing in size (e.g. Ebert, 1980; McClanahan and Kurtis, 1991; Minor and Scheibling, 1997), and a reduction in growth rate or even negative growth (shrinking; e.g. Levitan, 1988, 1989, 1991; Edwards and Ebert, 1991). None of these effects were found in our experiment, although sea urchins in cages which fish could access freely tended to have larger and less varying tests than sea urchins that had no contact with fish (Fig. 1). This could explain the greater and more heterogeneous values of LI in the latter, since a negative allometric relationship exists between test size and Aristotle's' lantern size (Régis, 1981). The lack of changes in somatic variables could also be attributed to the weak growth rates of the large *Paracentrotus lividus* (Turon *et al.*, 1995). Nonetheless, our study shows that there is a density-dependent effect on gonad weight, which suggests some kind of intra-specific competition.

The fact that the gonad index is ca. 30% lower in sea urchins maintained at high densities, coupled with the fact that gonads were in the post-spawning stage, indicates a decreased store of nutrients that may compromise the recovery and gametogenic

phases of the gonads. The scope for reproductive output, at least in the forthcoming cycle, was clearly much lower for the sea urchins in the high population density environments. George *et al.* (1990), found in laboratory experiments that a decrease in food availability led to a significant drop in the number of eggs *Paracentrotus lividus* produced, as well as to egg quality differences, which affected larval performance (George, 1996). The decrease in biomass observed in our study was not, however, reflected in terms of volume, which suggests that urchins in high population densities have gonads that are not as dense as gonads from urchins at natural densities. This could mean that there was a lower reserve content at the time when the samples were collected in high population density urchins, as spawning had already occurred.

Gonads are used as storage organs in sea urchins (Lares and Pomory, 1998; Russell, 1998; Fernandez, 1998; Montero-Torreiro and Garcia-Martinez, 2003), and hence their mass can decrease when there is a food shortage. Therefore, under limited food conditions we could expect a decrease in nutritive phagocytes due to the urchins using their reserves (e.g. Guillou *et al.*, 2000). Thus, a long-term negative feedback mechanism appears to take place in *Paracentrotus lividus* in response to increased population density. Reduced gonad biomass might not only affect reproductive potential but also compromise survival in the long term by reducing the reserve stocks. This contrasts with the faster response to increased population density described for *Diadema antillarum,* which affects body size (after 6 months approximately, Levitan, 1989).

Andrew (1989), pointed out that the great plasticity of echinoids makes them less vulnerable to density-dependent mortality than other invertebrates such as gastropods. Our results support the contention that density-dependent mortality in sea urchins is not a predominant event (e.g. Ebert, 1977; Andrew, 1986; Levitan, 1989; McClanahan and Kurtis, 1991). However, had we worked with higher densities such as those reported for some sea urchin outbreaks in *Posidonia oceanica* meadows (e.g. 30 to 100 ind m^{-2}; Ott and Maurer, 1976; Boudouresque *et al.*, 1980; Traer, 1980; Verlaque and Nédelec, 1983), we might have observed more notable responses to intra-specific competition. In fact, only Keller (1983), has presented experimental evidence for density-dependent mortality in the tropical sea urchin *Tripneustes ventricosus*, which was not observed for *Lytechinus variegatus* in the same

experiment. He also suggested that male and female sea urchins differ according to the energy allocated to growth and reproduction, particularly under crowded conditions when growth is limited. Likewise, Minor and Scheibling (1997), also found differences in the GI between sexes in *Strongylocentrotus droebachiensis*. Females had greater GI than males in limited-food treatments, whereas no difference between sexes was observed in non-limited food conditions. In contrast, we did not observe different density-dependent responses for males and females of *Paracentrotus lividus*, which is consistent with Andrew's (1986), findings for *Evechinus chloroticus*.

No effects of a potential competition with *Sarpa salpa* were detected, as no differences for any variable were found when plots that could and could not be accessed by *S. salpa* were compared. This is in accordance with the results obtained in experiments conducted in the same meadow in relation to epiphyte abundance (see Tomas *et al.*, 2005a), which is the main potential food source of sea urchins. In this experiment it was observed that natural sea urchin densities (5 ind m^{-2}) were enough to control epiphyte biomass and that *S. salpa* only exerted a significant effect on epiphyte biomass in the cages in which there were no sea urchins. However, it has to be taken into account that the higher mobility of *S. salpa* compared to sea urchins allows the fish to spread out their feeding area, probably minimizing possible competitive effects.

As *Paracentrotus lividus* in the meadow studied obtains most of its nitrogen from the epiphytes (Tomas *et al.*, in press), a decrease in epiphyte biomass due to increased sea urchin density, and thus a potential decrease in N availability, could translate into a reduced N content in the gonads. However, we did not find any significant variation in the relative C/N content of the gonad in the two densities assayed. Fernandez (1997), found that when *P. lividus* was fed with artificial diets, the percentage of protein in the gonads did not differ in the different treatments, whereas changes in lipid and carbohydrate content were observed depending on the different diets. In our case, no qualitative differences in the relative C and N content were found. Nevertheless, total nitrogen in the gonads of urchins submitted to high densities was lower, given their lower biomass.

In summary, we found few changes in biological variables of *Paracentrotus lividus* under high densities in the meadow studied; this was particularly true

for the somatic variables analysed. For the time period studied, mortality rates appeared to be independent of local densities, and local food availability did not seem to regulate local population size. We could, however, substantiate a quantitative (but not qualitative) change in gonad production. A 3-fold increase in population density translated to a lower reproductive potential. Moreover, as gonads can have a storage function in addition to their reproductive role, a reduced gonad biomass may not only directly compromise the reproductive output of urchins but also jeopardize survival in the long term. We tested densities that were 3 times higher than the natural ones, and it seems clear that even higher densities are needed to trigger more drastic responses in sea urchins from the community studied (e.g. Boudouresque *et al.*, 1980). Our results therefore suggest that biological control of sea urchin populations due to intra-specific competition may not be a fast-response mechanism but a feedback response that occurs in the long term, which can contribute to limiting population size as a response to increased densities. Other processes (e.g. settlement and recruitment, Tomas *et al.*, 2004), may also be crucial for limiting sea urchin populations in *Posidonia oceanica* meadows. More studies are needed to elucidate the mid- and long-term effects of these controls on sea urchin populations and to further examine possible threshold densities where intra-specific competition controls could be fast and dramatic.

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