

Biological cycles and recruitment of *Paracentrotus lividus* (Echinodermata: Echinoidea) in two contrasting habitats

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ABSTRACT: Two populations of *Paracentrotus lividus* (Lamarck) (Echinodermata: Echinoidea) from the Northwestern Mediterranean were compared to ascertain the plasticity and adaptive value of certain biological parameters. These populations were found in habitats which differed in terms of stability of environmental parameters and food availability. A yearly reproductive cycle was seen in both communities, with a spawning season at the end of spring that lasted up to several months. Recruitment data, inferred from abundance of post-settlement stages, indicated lack of settlement during the study period in the unstable community, while a major recruitment in summer, with less intense episodes occurring until autumn, was recorded in the stable community. The intensity of recruitment varied over an order of magnitude in the 2 consecutive years monitored. The gonadal indices were higher and the feeding indices were lower in the unstable community, indicating greater allocation of resources to reproduction, at the expense of somatic growth, in response to unfavourable conditions. The graph of the feeding and gonadal indices with size was parallel in the unstable community, while there was a lag between the sizes at which feeding activity and gonadal biomass reached their highest values at the stable site, indicating that feeding activity is not so tightly determined by gonad investment needs in the stable, food-rich community.

KEY WORDS: Reproductive biology · Recruitment · Feeding index · Echinoidea · *Paracentrotus*

INTRODUCTION

The Atlanto-Mediterranean sea urchin *Paracentrotus lividus* (Lamarck) (Echinodermata: Echinoidea) is the most abundant echinoid species in sublittoral habitats down to 20 m in the Mediterranean Sea, where its grazing activity is one of the key aspects in the dynamics of the well-illuminated communities dominated by seaweeds (Kempf 1962, Nédelec & Verlaque 1984, Verlaque 1984, Turon et al. in press). Moreover, its gonads are highly appreciated as sea-food and intense harvesting has drastically depleted the populations in some areas, especially on both the Atlantic and Mediterranean coasts of France (Le Gall 1987, Régis 1987) and on the coast of Ireland (Byrne 1990). Yet many aspects of the biology and population dynamics of this species are poorly known.

In addition, *Paracentrotus lividus* has a broad ecological distribution, ranging from rocky walls to less stable substrata such as *Posidonia oceanica* beds or loose boulders, and from areas of high hydrodynamism in the first metres of exposed shores to calmer waters in bays or deeper zones. Echinoid species can adapt their biological parameters to differing conditions such as temperature, food, wave action or predation (Ebert 1968, Gonor 1973, Régis 1979, Himmelman 1986, Kenner & Lares 1991, Levitan 1991), but little is known of the effect of habitat on the life cycle of *P. lividus*. To our knowledge, only Régis (1979) and Byrne (1990) have compared reproduction and other parameters of populations of this species in various ecological situations.

This paper is part of a study in which we ascertain the range of variation of the main life-history parameters (abundance, recruitment, growth, mortality, reproduction and feeding) of this species in naturally occurring populations belonging to 2 extremes of its

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ecological range of distribution in the Northwestern Mediterranean. Our purpose was 2-fold: to describe the biology and population dynamics of the species in these contrasting situations, and to assess the plasticity and adaptive value of the biological parameters studied. This first paper reports the results concerning recruitment, nutritional and reproductive cycles. Growth and population structure are dealt with in a second paper by Turon et al. (1995, this issue).

MATERIALS AND METHODS

Sampling sites. The study was performed on specimens from 2 localities, Tossa de Mar (41° 43.2' N, 2° 56.4' E) and Cubelles (41° 12.0' N, 1° 40.8' E), both on the northeast coast of Spain (Northwestern Mediterranean) (Fig. 1).

The site at Tossa de Mar was a zone of vertical walls of diverse orientation. The assemblages studied were found at depths between 4 and 10 m and were dominated by seaweeds, mainly *Corallina elongata* Ellis and Solander (in the first metres), *Halopteris scoparia* (Linné) Sauvageau, *Cladostephus hirsutus* (Linné) Prud'homme van Reine and *Padina pavonica* (Linné) Thivy. A more detailed description of the site is given in Turon (1990). Tossa de Mar will be referred to hereafter as the stable community, since it was sheltered from the dominating winds in the zone, and therefore exposed to low hydrodynamism, it received no direct discharge from rivers, and most of the physical variables fluctuated within the range habitual in this zone of the Mediterranean (see Ballesteros 1984 for a complete description of physical parameters).

The community studied at Cubelles consisted of a bed of small- to medium-sized boulders (approx-

mately 20 to 50 cm in the larger dimension) in a shallow (0.2 to 0.5 m in depth) zone on an open beach, near the mouth of the Foix River (which carried these boulders from the calcareous hills of the area). The upper surfaces of these boulders were occupied by a poorly developed turf of caespitous algae, mainly *Corallina elongata*. The undersurfaces were occupied by sponges, serpulids and ascidians. This site will be referred to as the unstable community, since the hydrodynamism in the zone is high (indeed, enough to move the boulders several times a year), and the shallowness and proximity of the river lead to high variability in parameters such as temperature, salinity, turbidity and inorganic contents.

The water temperature fluctuated at Tossa de Mar at a depth of 10 m between 22°C in summer (September) and 10.7°C in winter (March) during the study period. At Cubelles the temperatures were 1 or 2°C above (summer) and below (winter) those at Tossa, with more marked short-period oscillations due to the shallowness of the water.

Sampling methods. The sampling for biological cycles was performed every 2 wk at both localities. All samplings were performed during daylight, at the same hour (approximately at 13:00 h). Twenty specimens of *Paracentrotus lividus* were collected by SCUBA diving (Tossa) or by wading (Cubelles), and fixed in formalin. Ten of them were selected at random among individuals less than 30 mm in diameter (without spines) and 10 among individuals larger than 30 mm. As a result, a large range of sizes was present in each sample. For most of the variables analyzed, the results will be presented as monthly means to reduce stochastic error. Samples were taken from June 1992 to July 1993 at Tossa and from July 1992 to August 1993 at Cubelles. A total of 509 individuals from Tossa and 537 from Cubelles were included in the analyses.

Laboratory methods. The specimens were wet-weighed and dissected. The gonads and the contents of the digestive tract were wet-weighed and set aside for calculation of gonadal and feeding indices. The remaining body was dried (48 h at 120°C) and weighed.

One of the 5 gonads (the first in a clockwise direction from the madreporite) was used for histological observations. The other 4 were dry-weighed (DW = dry wt) and used to calculate a gonadosomatic index (GSI) of the form:

$$\text{GSI} = \frac{\text{DW of 4 gonads}}{\text{DW of body}} \times 100 \quad (1)$$

From microscopic observations (squash) of a portion of the fifth gonad, a maturity index (ratio between mature specimens to total number of specimens) was calculated. A specimen was scored as mature whenever sperm or ova were present in the gonads.

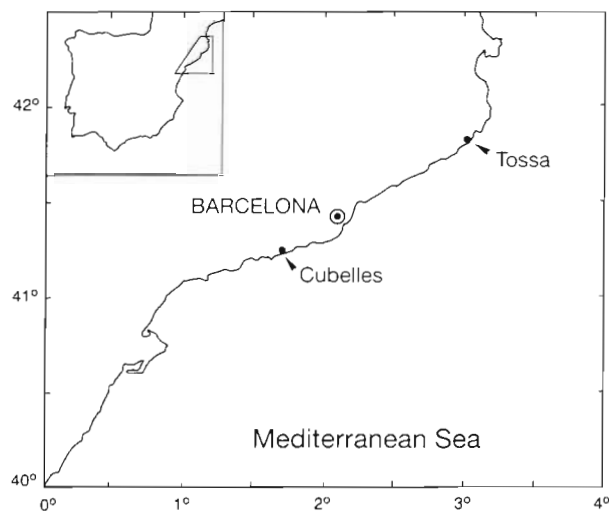


Fig. 1. Catalan coast (NE of Spain) showing sampling localities

For monthly histological studies, the fifth gonads of 5 females with a diameter (without spines) larger than 40 mm at Tossa and 30 mm at Cubelles were used. These gonads were dehydrated, embedded in paraffin, sectioned and stained with haematoxylin-eosin. The evolution of the germ cells (oogonia, oocytes and ova) was analyzed from these sections. Estimates of the diameter of the germ cells were made by measuring 100 cells per individual. The cells measured were the first to appear in the visual field under light microscopy sectioned at the nucleus (oogonia) or nucleolus (oocytes) level. Since the nuclei were usually not visible in the mature ova, they were measured along their maximum dimension irrespective of the level of sectioning (but ova sectioned clearly tangentially were not measured). Another variable estimated from the histological sections was the thickness of the layer of nutritive phagocytes that forms the wall of the gonadal follicles (Pearse & Cameron 1991). Five measurements of each of the first 5 follicles encountered in the visual field were averaged to obtain the estimate.

Feeding activity has been inferred in echinoids from indices relating washed guts, gut contents or both together, with total weight or volume (Pearse 1969a, b, Régis 1979, Semroud & Kada 1987, Guillou & Michel 1994). The rationale behind the study of washed gut weights (Régis 1979) is that the digestive tissue may act as a storage organ and thus indicate periods of reserve accumulation. For the estimation of a feeding index, however, we preferred a more direct measure of the consumption rate, and thus the gut contents of 10 specimens per sample (the remaining 10 were left for later dietary studies) were dry-weighted and used to calculate a repletion index (RI) as proposed by Kempf (1962), which has the form:

$$RI = \frac{DW \text{ of gut contents}}{DW \text{ of body}} \times 100 \quad (2)$$

Statistical analyses were performed mainly by 2-way ANOVA for unbalanced designs and Tukey tests (Zar 1984). Prior to performing parametric tests, the assumptions of normality and homoscedasticity were tested by Kolmogorov-Smirnov and Bartlett tests, respectively. No transformation of the data was necessary. The SYSTAT package (v. 5.0) was used for the analyses.

Recruitment. This study was performed at Tossa in a vertical wall. Three samples were taken at 3, 6 and 9 m depth by delimiting a 20 × 20 cm square using an aluminium frame. All the organisms present within the frame were then scraped off and placed in a plastic bag (the basal layer of crustose algae had to be removed with the aid of a hammer and chisel). At Cubelles, 2 samples were collected in the same manner, one from the upper surface of the boulders and the other from the undersurface. Samples from the sediment between

boulders were also occasionally taken by collecting the superficial layer (2 cm thick) of sediment in 20 × 20 cm squares. Sampling was performed during the period indicated for the study of biological cycles. Additional samples were obtained in October and December 1993 at Tossa. All samples were fixed in formalin and carefully examined under the stereomicroscope. The number and diameter of every juvenile (<2 mm in diameter) found was recorded.

RESULTS

The relationship between GSI and size (all months pooled) is presented in Fig. 2 (note that specimens from Cubelles were smaller than those from Tossa). There was a sharp rise in GSI at the unstable site for urchins about 30 mm in diameter, and then the GSI course reached a plateau. In the stable community the rise in the GSI occurred less abruptly and at larger sizes (from 40 mm on). The stabilization at the right hand of the curve was not as apparent as for the unstable site and the values reached were lower. The percentage of mature urchins (all months pooled) rose at Cubelles between the size class 10–20 mm and 20–30 mm, while at Tossa the same was found at sizes 2 cm larger (between 30–40 and 40–50 mm) (Fig. 2).

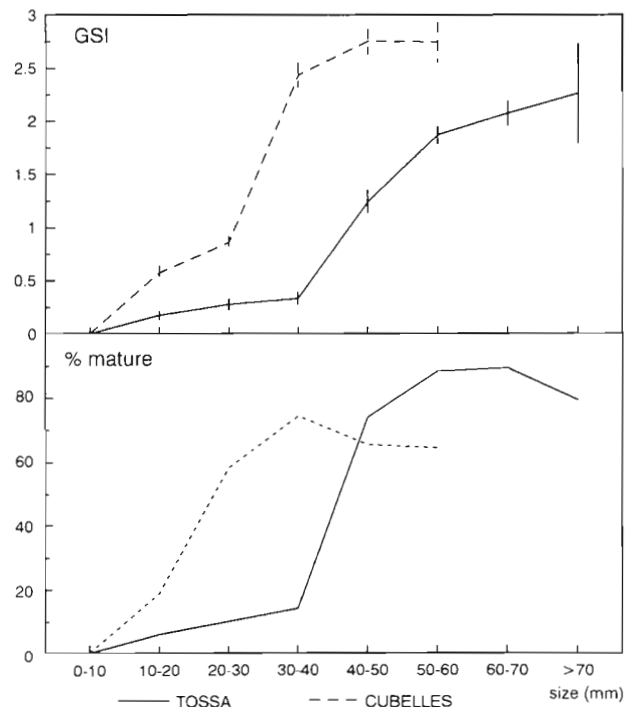


Fig. 2. *Paracentrotus lividus*. Gonadosomatic index (GSI) as a function of size (bars are standard errors) and percentage of mature individuals for each size class at the 2 sampling locations

Since the inclusion of immature specimens could alter the GSI trend, we included only individuals >30 mm from Cubelles and >40 mm from Tossa, separately for each sex, in the graph of the monthly GSI trend (Fig. 3). Separate 2-way analyses of variance on the GSI with month (excluding the first month at Tossa and the last one at Cubelles) and sex as factors at both sites revealed a strong effect of the month (Tossa: $F = 4.533$, $df = 12, 221$, $p < 0.001$; Cubelles: $F = 6.925$, $df = 13, 259$, $p < 0.001$). The overall GSI values did not differ with sex at Tossa ($F = 1.439$, $df = 1, 221$, $p = 0.232$), but the temporal trend was different with respect to sex, as revealed by a significant sex \times month interaction ($F = 2.499$, $df = 13, 221$, $p < 0.005$). On the other hand, significant differences in GSI values were found between sexes at Cubelles ($F = 7.651$, $df = 1, 259$, $p < 0.01$), with the values for males higher in most months, but the temporal trend was quite parallel, and the interaction term was not significant ($F = 0.951$, $df = 13, 259$, $p = 0.501$). As can be seen in Fig. 3, the values were higher and the variations were more marked at the unstable than at the stable site. The graph of Cubelles showed 2 peaks, one in August and the other in February–March, whereas at Tossa the trend was less clear, although a general decrease in the index for both sexes was visible from September–October to May.

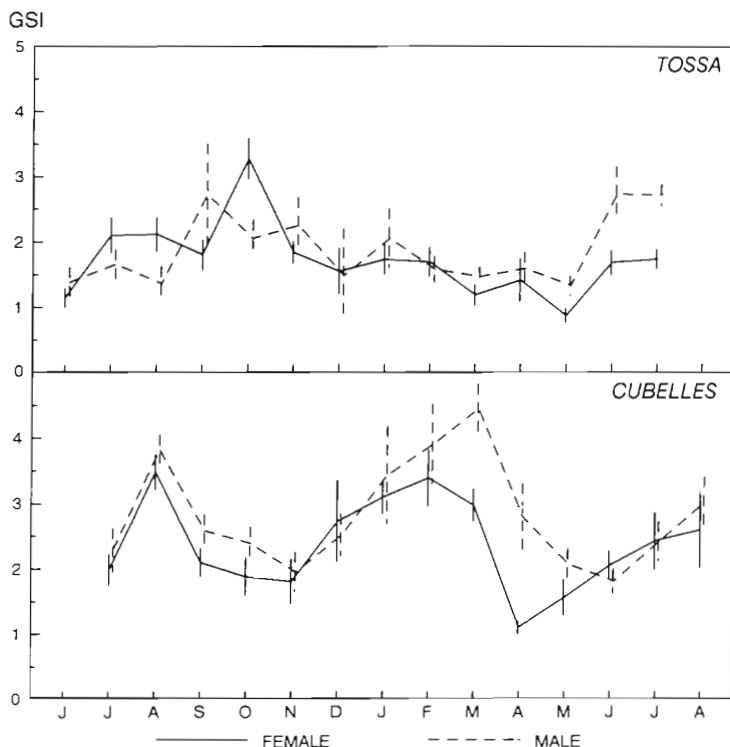


Fig. 3. *Paracentrotus lividus*. Temporal trend of the gonadosomatic index (GSI), for each sex, during the study period at both localities. Only specimens >40 mm at Tossa and >30 mm at Cubelles are included in this graph. Bars are standard errors

Comparison of the GSI values (both sexes combined) across localities by 2-way ANOVA showed a highly significant effect of the main factors (locality: $F = 55.569$, $df = 1, 480$, $p < 0.001$; month: $F = 4.238$, $df = 12, 480$, $p < 0.001$), as well as of the interaction between month and locality ($F = 7.196$, $df = 12, 480$, $p < 0.001$), indicating different temporal trends in the 2 communities. This finding was confirmed by a non-significant Spearman rank correlation coefficient between the GSI values in both communities ($r_s = -0.027$, $n = 13$, $p > 0.5$). In the presence of a significant interaction term, comparisons of means should be done for the levels of one factor within each level of the other factor (Underwood 1981). Tukey tests among localities within each month revealed that the differences were not significant only in July, October and November 1992 and in April, June and July 1993. Roughly speaking, the GSI values at Cubelles were always higher than at Tossa except in the months in which a decrease in the former locality coincided with an increase in the latter.

The time course (monthly means) of the maturity index during the study period followed a different pattern from that of the GSI (Fig. 4). In both habitats the higher percentages were found in spring, the lower ones at the end of summer, and the pattern was similar in both sexes.

The temporal trend of the thickness of the layer of nutritive phagocytes in females was quite the reverse from the pattern of the maturity index (Fig. 5), with minimum values (reaching less than 20 μm) in spring, and highest values (more than 120 μm) in summer and the beginning of autumn.

As for the histological observations, a similar pattern of development in the female gonads was observed for both localities. The cycle began in spring, in which some ova of the previous cycle were still present, the nutritive layer was poorly developed, and a number of oogonia (<5 μm in diameter) appeared in the basal part of the follicular walls. During summer-beginning of autumn the nutritive tissue increased steadily in thickness, while the oogonia grew into oocytes (>10 μm). From autumn to winter, the oocytes increased in diameter and finally became mature ova (>70 μm). They were distinguished from large oocytes because the former had a much smaller (often not visible) nucleus and accumulated in the lumen of the follicles. During this period, which lasted all winter, the nutritive tissue layer regressed to a minimum. During the spring and beginning of summer the lumens were found with progressively fewer ova, indicating release, and

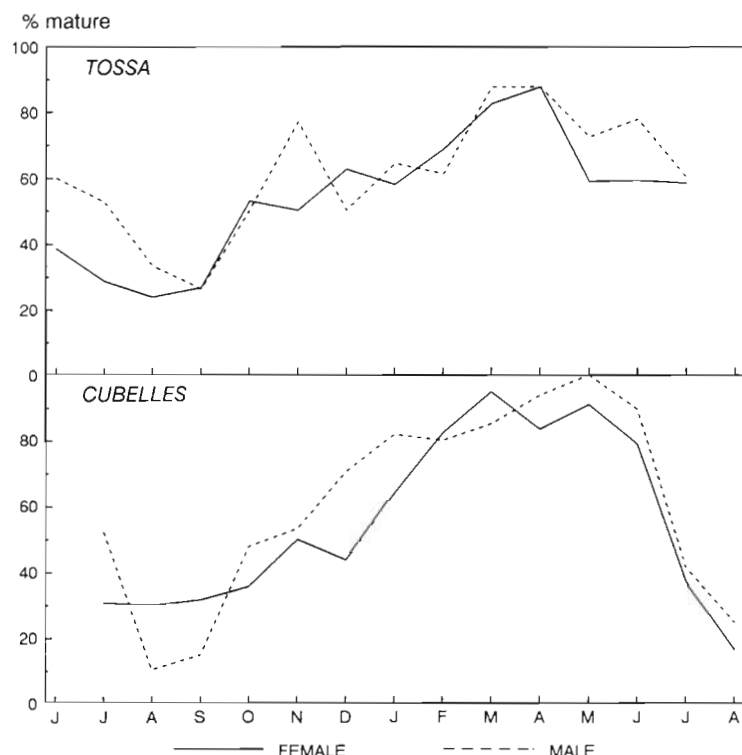


Fig. 4. *Paracentrotus lividus*. Percentage of mature individuals, for each sex, during the study period at both localities

the cycle started again. Figs. 6 to 11 show selected features of this process. Although not so systematically, we also performed sporadic histological observations on male gonads, which matched the pattern of development of females.

The diameters of the germ cells, expressed as frequency histograms, provided a good indication of the gonadal changes (Fig. 12). At the beginning of the study at Tossa (July 1992) the smaller size classes were the most abundant. The increase in size was rapid, and during most of the winter and spring, ova of the larger size classes were found. In July a new generation of small cells appeared. At Cubelles the pattern was similar, but the ova started to decline beginning in May 1993, while at the same time the small oogonia and oocytes of the following cycle appeared. The main spawning at Cubelles took place from May to July 1993, and a retardation was observed with respect to the previous year, the pattern of August 1993 being very similar to that of July 1992. This phenomenon was also apparent at Tossa: at the end of the study (July 1993) the gonads still contained a fair number of ova, while in July 1992 most of the germ cells belonged

to the smaller size classes and the gonads appeared to be discharged. The time courses of both the maturity index and the thickness of the nutritive layer in Tossa (Figs. 4 & 5) also show this retardation of development in 1993.

The values of the repletion index varied markedly with size, but followed a different pattern at each locality (Fig. 13, the GSI trend is also presented for comparison). There was a constant increase in RI values from the initial size classes at Tossa, and the curve leveled off from sizes ≥ 30 mm. A lag was visible between the sizes at which the feeding activity increased and the sizes at which the gonadal development was appreciable. At Cubelles, on the other hand, there was a sharp increase in the RI values between the size classes of 20–30 mm and 30–40 mm. The trend of RI and GSI indices was parallel in this community (apart from the fact that the numerical values were nearly coincident), indicating a coincidence between the life stages at which there was an increase in feeding activity and in gonadal development.

To eliminate differences due to smaller specimens, we again considered only specimens > 40 mm at Tossa and > 30 mm at Cubelles in the graph of the RI with time (Fig. 14). The GSI graph is also added for comparison. At both localities, the factor month proved significant in a 2-way ANOVA with sex and month as factors (Tossa: $F = 4.06$, $df = 12, 128$, $p < 0.001$; Cubelles: $F = 2.673$, $df = 13, 112$, $p < 0.005$). However, no overall differences were detected for sexes (Tossa: $F = 2.75$, $df = 1, 128$, $p = 0.09$; Cubelles: $F = 1.367$,

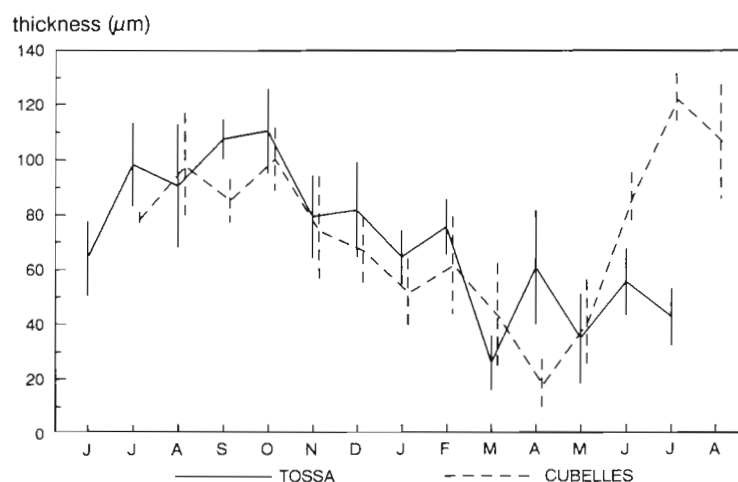
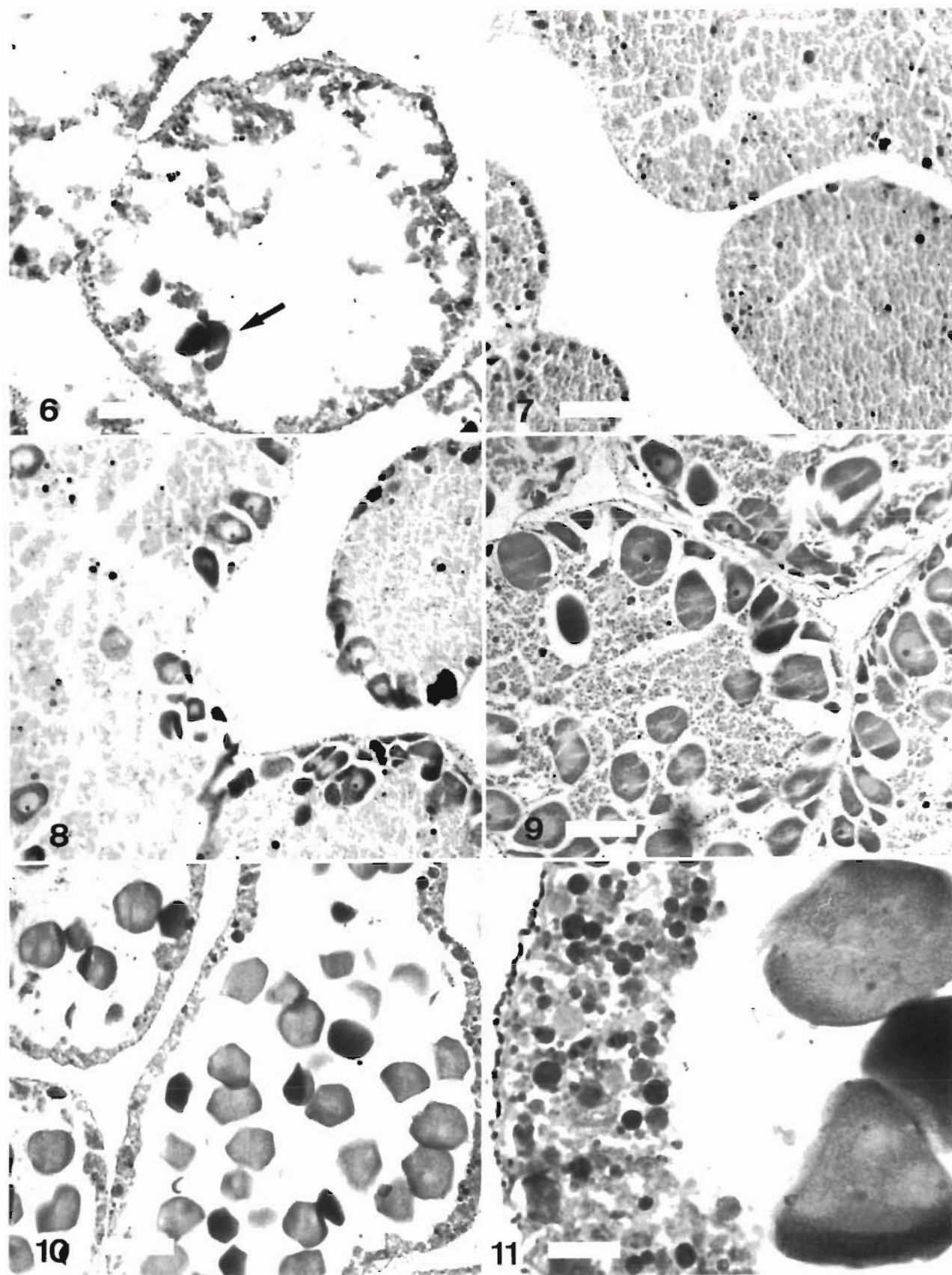


Fig. 5. *Paracentrotus lividus*. Thickness of the nutritive layer of the gonadal follicles of female urchins at both localities. Bars are standard errors



Figs. 6 to 11. *Paracentrotus lividus*. Selected images of the stages of the female gonads at the locality of Tossa. Fig. 6. Spent condition in June 1992, arrow points to a residual ovum. Fig. 7. Phase of gonadal reconstitution in September 1992: the nutritive layer has attained its maximum thickness and oogonia are visible as intensely stained cells near the basal zone. Fig. 8. Oocyte maturation in October 1992, note the large nuclei. Fig. 9. Advanced state of maturation in February 1993: large oocytes and the first ova are visible. Fig. 10. Mature state in June 1993: lumen of follicles filled with ova. Fig. 11. Enlarged image of the nutritive layer in July 1993, at the beginning of its reconstitution. Phagocytes are abundant in the wall. Scale bars: Figs. 6, 8, 9 & 10 = 100 μm ; Fig. 7 = 250 μm ; Fig. 11 = 25 μm

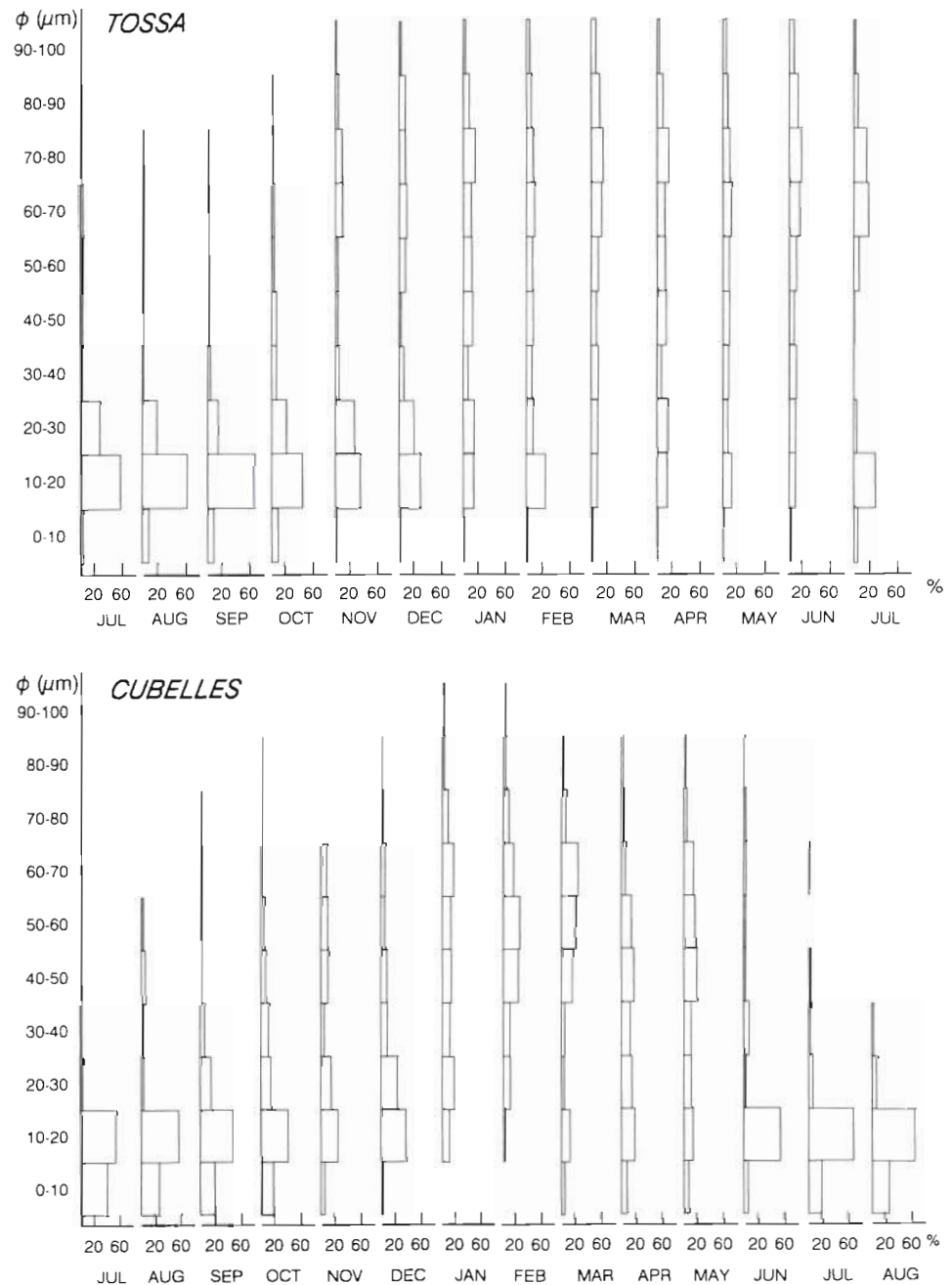


Fig. 12. *Paracentrotus lividus*. Oocyte size-frequency distributions at both localities during the study period

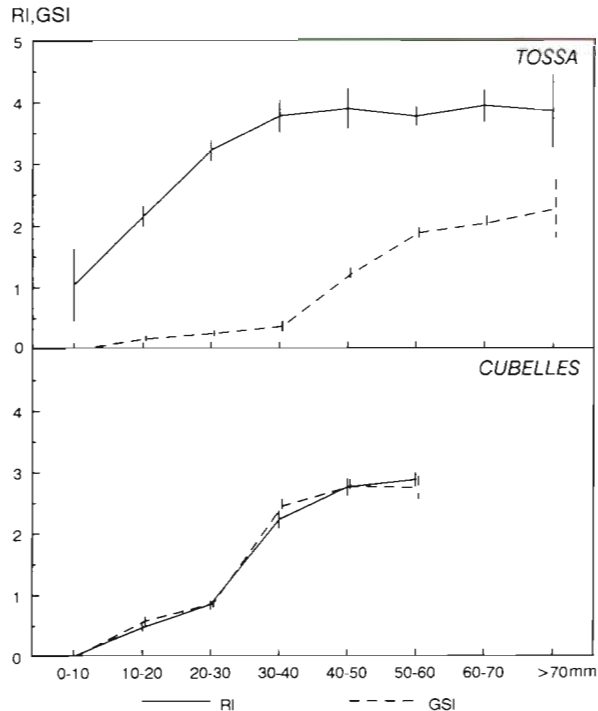


Fig. 13. *Paracentrotus lividus*. Graph of the repletion index (RI) as a function of size at the 2 localities studied. The GSI values are also represented. Bars are standard errors

df = 1,112, $p = 0.245$), and the interactions were also non-significant (Tossa: $F = 0.647$, df = 12,128, $p = 0.798$; Cubelles: $F = 0.68$, df = 13,112, $p = 0.755$). Data presented in Fig. 14 were therefore pooled across sexes. It can be seen that the RI values were higher at the stable site than at Cubelles. The locality factor had a significant effect in a 2-way ANOVA on the RI values with month and locality as main factors ($F = 93.866$, df = 1,266, $p < 0.001$), but the interaction term was not significant ($F = 1.615$, df = 12,266, $p = 0.087$), indicating that the temporal trend of the RI was not significantly different at the 2 localities. No relationship between RI and GSI was clear in the stable community. If any, there appeared to be an inverse evolution, as indicated by a nearly significant negative Spearman correlation coefficient ($r_s = -0.508$, $n = 13$, $p = 0.08$). The trends of both indices at the unstable site had no clear relationship ($r_s = 0.055$, $n = 13$, $p > 0.5$), although a rise in the RI values could be seen 1 mo before the rise of GSI in December, and the decrease in GSI values in spring was followed, again with a lag of 1 mo, by the RI.

As for the study of recruitment, no juveniles were found in the samples collected at Cubelles during the 14 mo of study. The sediment sam-

ples collected occasionally during this period did not contain any young specimen either. The number of juveniles collected at Tossa and their size distribution is shown in Fig. 15. The data are presented in number of individuals per 400 cm² sample. The samples from each month (3 samples were taken every 2 wk, except for periods of bad weather) were averaged to obtain a monthly estimate. The juveniles of *Paracentrotus lividus* are very similar to those of another species, *Genocidaris maculata* Agassiz, but they can be distinguished by the shape of the valves of the globiferous pedicellariae (Mortensen 1977). This character was examined in doubtful specimens and an almost total dominance of *P. lividus* was found (only half a dozen juveniles of *G. maculata* were found in the samples).

A heavy recruitment of juveniles in 1992 is evident from Fig. 15, starting in July and lasting until November. The size distributions showed the growth (and also the high mortality during this stage) of the first recruits, but specimens of the smaller size classes (<0.5 mm) were still present until November, indicating that new arrivals could have appeared during summer and autumn, although the main recruitment event was clearly between June and July. During the winter months, no appreciable recruitment was

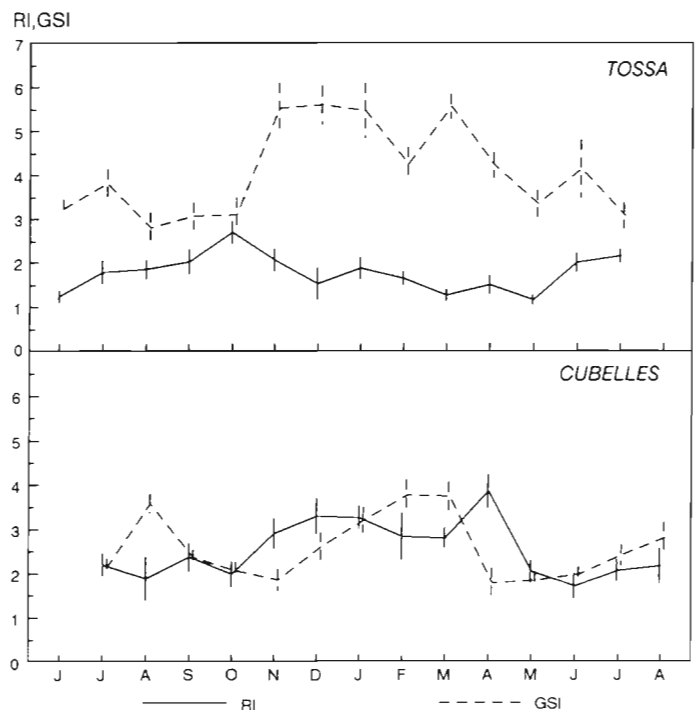


Fig. 14. *Paracentrotus lividus*. Time course of the RI index, both sexes pooled, during the study period at both localities. The GSI values are also represented. Only specimens >40 mm in Tossa and >30 mm in Cubelles are included in this graph. Bars are standard errors

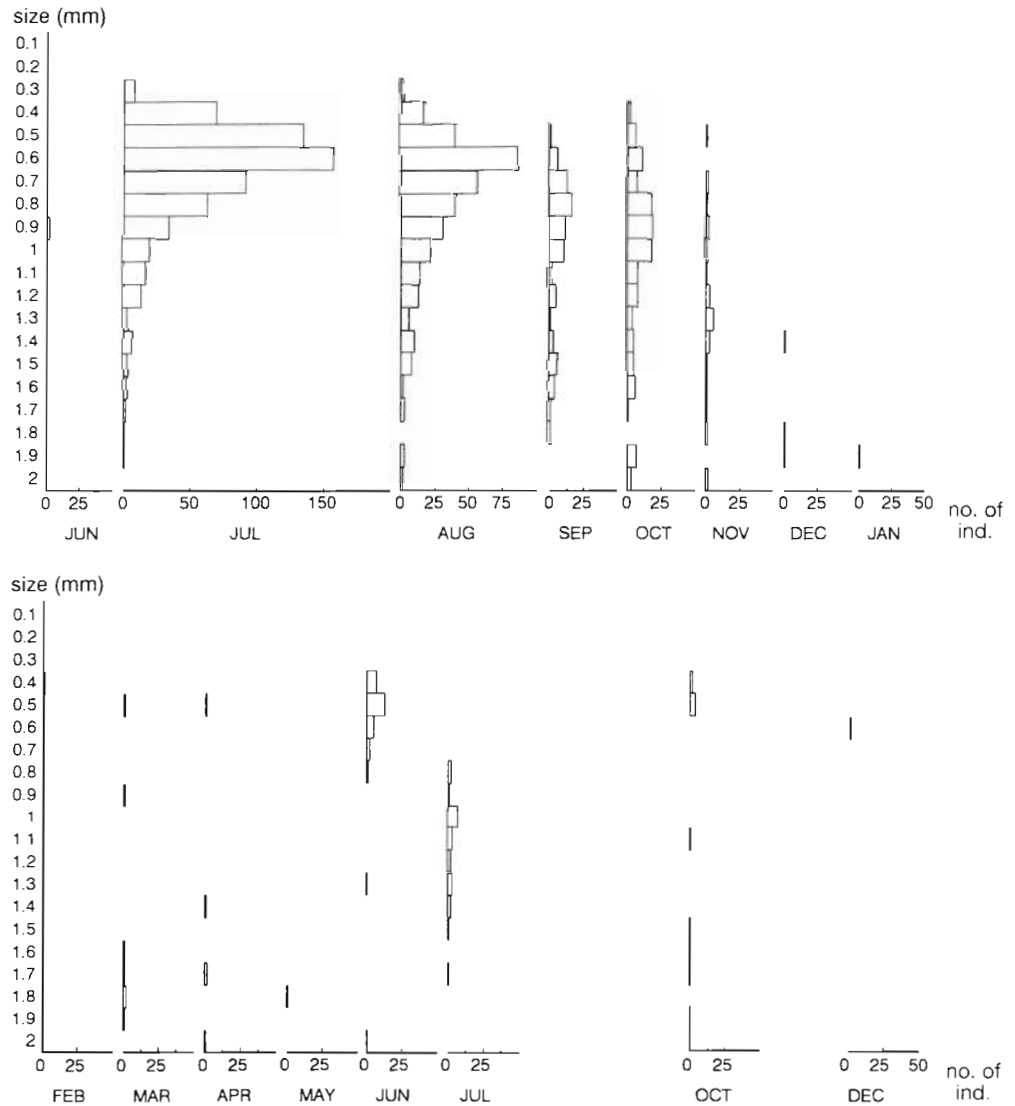


Fig. 15. *Paracentrotus lividus*. Size distributions of post-settling stages found in the samples from Tossa during the study period. All samples for each month were pooled. The values of abundance refer to number of ind. per 400 cm²

observed (only isolated individuals were found), and in June 1993 a new recruitment episode was found, although about 1 order of magnitude lower than the previous year. In July 1993 the histograms showed the growth of this cohort, but no evidence of new settlers. The original study ended at that time and, upon examination of the material during the immediate months, we decided to perform supplementary samplings (3 samples in October and 3 in December) to rule out the possibility of heavy recruitment, comparable to that of 1992, after July. The October samples showed no indication of high recruitment in the preceding months. However, some small individuals were present in this sample, again suggesting that recruitment could take place until autumn, although in fewer numbers than the spring episode. In December there were practically no juveniles in the samples.

DISCUSSION

The reproductive cycle of *Paracentrotus lividus* followed a clear annual pattern with gonad development occurring during summer and autumn, mature gonads being found all winter, and a main spawning episode seen during spring or beginning of summer. The pattern was similar at both localities, although the maturity period was shorter at the unstable site, and lags of up to 1 mo were found between communities and between years. It is possible that the unusually cold winter of 1993 accounted for the delay observed in the gonadal cycle. Phytoplankton abundance may also modulate the onset of spawning in echinoids (Starr et al. 1993).

The maturity index, the thickness of the gonad walls and the histological observation of the gonads provided the most reliable methods for assessing the

reproductive cycle of this species. The gonadal index was less reliable due to the fact that it is greatly affected by the nutritive tissue of the gonad (Pearse 1969b, Gonor 1973). Further, the use of the GSI method is flawed in many studies because some inherent assumptions were not contrasted. In particular, the relationship between size and GSI must be known, and only animals of similar sizes should be compared (Gonor 1972). This was accomplished in this study by comparing only individuals with complete gonadal development, according to the graph of GSI with size. In general, the temporal pattern of the GSI was fluctuating, and the peaks may have been produced for reasons that have little to do with the gametogenic cycle. For instance, the peak in August at Cubelles had no apparent meaning in the gametogenic course of this year, since the gonad histology, the maturity index and the thickness of the gonadal nutritive layer of the same specimens clearly show a single annual cycle (Figs. 4, 5, & 12). The peak could be a reflection of the strong storms in September of this year, which could have provoked a decrease in nutritive storage in this species. King et al. (1994) also reported drops in GSI in another species not related to spawning but to changes in nutrients stored in the gonads. Gametogenesis is probably the last process stopped in sea urchins (Bennett & Giese 1955).

While some authors have reported very neat annual cycles of GSI in *Paracentrotus lividus* (Byrne 1990) and other species of echinoids (e.g. Keats & Steele 1984, Guillou & Michel 1993), it is not uncommon to find fluctuating GSI values (Régis 1979, Semroud & Kada 1987), which should be interpreted carefully. Caution should be exercised when interpreting GSI results in this group, and the best way to define the reproductive rhythms is through the simultaneous study of several sources of evidence (viz. the thorough study by Giese 1969a, b on echinoids from the Gulf of Suez).

The present study does not support the theory that *Paracentrotus lividus* has 2 spawning periods per year. Incidentally, the graph of the monthly changes in GSI at Cubelles could have been interpreted as strongly supporting the presence of such 2 spawning periods, if this parameter alone was investigated. This example illustrates the problem with the GSI, which may have been responsible for the present confusion about the reproductive periodicities of this species. The seminal paper of Fénaux (1968) reporting 2 spawning periods has been uncritically accepted by later workers. Close examination of Fénaux graphs showed that neither her data on GSI nor her plankton observations clearly supported her conclusions, while her results on maturity indices actually revealed that there was only one maturity cycle per year. Following Fénaux's (1984) paper, all the reports of 2 yearly gonadal cycles or at

least 2 yearly spawning episodes simply accepted these results, or were based on recruitment data (Verlaque 1984, and references below) or gonadal indices (Crapp & Willis 1975, Régis 1979). When the gonads were studied histologically, a single annual gametogenic cycle (as is prevalent in temperate echinoids; Pearse & Cameron 1991), with spawning during spring-early summer, was found (Byrne 1990, and our results).

The most consistent data that we have found in the literature supporting 2 spawning seasons for *Paracentrotus lividus* in the Mediterranean are the results of larval abundances in plankton net tows in the French Mediterranean coast (Fénaux & Pedrotti 1988, Pedrotti & Fénaux 1992, Pedrotti 1993), indicating a period of larval abundance in autumn of 1984 and 1986. Either this species featured, in this zone, a different gametogenic cycle from that of the littoral studied (which is unlikely, considering the geographical proximity), or the autumn peak must be explained as an artifact in the sampling procedure. The distribution of plankton is patchy, as is the recruitment in the communities. It is not surprising, then, that high interannual variability was found in studies of larval abundances in the plankton (Pedrotti & Fénaux 1992), while studies on recruitment based on plankton abundances can lead to multi-, bi- or unimodal recruitment patterns for the same reason. Our data indicate that, while small spawnings are possible during the winter months, the gonad condition made the existence of an autumnal spawning impossible. What is possible is that gametes released from spring to the beginning of summer could lead to the presence of larvae and recruitment episodes from early summer to autumn, recruitment events in autumn being especially patchy. The study of the larval recruitment at Tossa indicated that the main settlement took place in both years at the beginning of summer, and that sporadic recruitment events can take place until late autumn. The autumn peak of larvae reported for this species in the French coast is not reflected in our study by a distinct peak of recruits. It is also worth noting that in 1993 the spring recruitment at Tossa was advanced 1 mo with respect to the previous year, while the spawning of the autochthonous population was retarded approximately 1 mo. This suggested that the recruitment in the population of Tossa came, at least in part, from allochthonous larvae.

A large recruitment at the beginning of summer, with smaller episodes extending through summer and autumn, as found in our study, is consistent with the gametogenic evolution observed here, and with literature reports (Azzolina 1988 also found a single prolonged recruitment period from July to November). It is unclear, however, how the larvae can remain in the plankton for several months, especially since a

complete cycle of larval development (from 4 arms to post-larvae) has been documented in the plankton for October to November 1986 (Pedrotti 1993). Indeed, the length of the planktonic period indicated by this author (23 to 29 d) is much shorter than that reported for other echinoid larvae reared in the laboratory (Strathmann 1978: maxima from 21 to 36 wk for 4 species, with a wide range in development times). Echinoid larval growth may be influenced by many factors, food limitation (Fénaux et al. 1994) among them. It is conceivable that development of larvae can be stopped at an early stage if they are removed from favourable environments, while they can grow and metamorphose quickly if kept near habitats suitable for settlement. Fénaux et al. (1994) reported, for nearby waters (S of France), evidence for food-limitation in echinoid larvae, especially in larvae from the autumn plankton.

The lack of recruitment at the unstable site during the study should be considered with caution. It is known that echinoids can feature low levels or even absence of recruitment during several years, punctuated by episodic highs (Ebert 1983, Pearse & Hines 1987). Small-scale (of the order of thousands of metres) variation in recruitment is also documented for echinoids (Ebert 1983, Keesing et al. 1993). Either the population is maintained by episodic recruitment events, or it is dependent on migration of larger-sized forms. It seems, therefore, that the unstable community acted as a 'source' of larvae (as found by Sewell & Watson 1993, for asteroids), since it does not receive a return on its own annual production of embryos. A similar situation is described by Gonor (1973) for intertidal populations of *Strongylocentrotus purpuratus*, although Himmelman (1986) found indications of a higher recruitment in exposed than in sheltered populations of *S. droebachiensis*, which was attributed to water movement and to higher temperatures at the sheltered site.

Remarkable differences in the parameters studied have been found between the stable and the unstable communities. In short, the gonadal indices were higher and the nutritional indices lower in the unstable community. This implies a higher investment in reproduction, even in less favourable nutritional conditions. It is not surprising, then, to find that the sizes attained were smaller at the unstable habitat, which could be partly accounted for by an increased mortality of the larger specimens, but also by a decreased growth rate (Turon et al. 1995). Growth rates in sea urchins are highly sensitive to food quality and hydrodynamism (Ebert 1968, Himmelman 1986). We consider that the unstable community is more food-limited than the stable one, both by the quantity and the quality of the algae present. The vegetation at Cubelles is poorly developed and mainly composed of turfs of *Corallina elongata*, a species with high calcitic and low caloric

contents, and not preferred by *Paracentrotus lividus* (Verlaque & Nédelec 1983). Thus, not only are the RI values lower, but the absorption rate of this calcified alga per weight ingested is lower than that of fleshy macrophytes (Frantzis & Grémare 1992), abundant at the stable site. Moreover, studies using fixed transects revealed that the densities of *P. lividus* were higher (although of the same order of magnitude) at the unstable locality (Turon et al. 1995), which contributed to the food shortage.

Little is known about the size at which sea urchins become reproductive in the field, and the information available shows that considerable variation, tied to habitat characteristics such as food (Buchanan 1966, Dix 1970, Kawamura 1973) and predator pressure (Kenner & Lares 1991), can be found. *Paracentrotus lividus* appeared to have a noticeable plasticity in this character, according to the changes in gonadal and maturity indices with size, which indicates that reproductive competence is attained at sizes between 1 and 2 cm smaller at the unstable community. This may be due to an adaptation to higher mortality at this site, which favours advancement of reproductive episodes, or else be a mere result of the lower quantity and quality of the food available, resulting in individuals of the same age being smaller. Our growth data (Turon et al. 1995) indicated that the reduced growth at the former locality cannot alone account for the pattern observed and that there is also a true advancement in the age at which reproduction begins. It is especially interesting to find that the trends of the gonadal and nutritional indices with size are tied in the specimens from the unstable locality, while at the stable community a lag appeared between both curves. That the nutritive index values jumped to the plateau of the curve at sizes 2 cm smaller than the gonadal indices indicated, most probably, that when faced with favourable conditions and abundant food supply, this species can delay gonadal investment in favour of a period of somatic growth before the onset of reproductive activities. This period may contribute to the larger sizes observed in the stable community.

The trends of repletion, gut or feeding indices and gonadal indices have been found to be quite different, even opposed, in some cases (Gonor 1973, Guillou & Michel 1994), and coincident in others (Pearse 1969a, Régis 1979). Temperature and reproduction have been claimed as important parameters regulating feeding activities (Gonor 1973). In our results the trends were, if any, divergent in the stable community, while the timing of feeding and reproductive indices was more similar in the unstable one, which indicates that allocation to gonadal development explained a good deal of the variability in feeding activities, while this was not the case in the food-rich habitat.

The existing reports on variation in reproductive investment with habitat conditions indicate that opposite strategies can be displayed by echinoid species. Ebert (1968) and Gonor (1973) found that more exposed and food-limited populations of *Strongylocentrotus purpuratus* developed smaller gonads. Pearse et al. (1986) also showed that rich food yields larger gonads in the laboratory. On the other hand, Thompson (1982) showed a higher allocation to reproduction in *S. intermedius*, at the expense of somatic growth, with poor diet, which is quite coincident with the situation found here. Kenner (1992) did not find a depressed gonadal index in *S. purpuratus* inhabiting communities with scarce food. For *Paracentrotus lividus*, apparently contradictory results have been obtained by Régis (1979) (higher GSI in habitats with less food) and Byrne (1990) (larger gonads in subtidal, well-fed populations). Maturation at the same age at sites with different growth rates can produce the effect of increased GSI at equal sizes (but different ages). Thus field data should be correlated with estimates of growth rates in the habitats to be compared. Notwithstanding this cautionary remark, it seems that the echinoid species can display different responses to unfavourable conditions (especially with respect to food availability), either investing preferentially in reproduction, or allocating resources to other purposes. Sea urchins are less sensitive to food shortage than other invertebrates (Andrew 1989), and gametogenesis is probably the last process to be interrupted in starving sea urchins (Bennett & Giese 1955). Besides, there are mechanisms to ensure a short-term recovery of gametogenic activity following pulses of available food (Bishop & Watts 1992). Therefore, it seems that the shift from reproduction to somatic investment in unfavourable environments must be controlled by a factor other than food availability. We suggest that a limiting degree of hydrodynamism may be the key factor. Above this level, energy must be allocated preferentially to repair and test production (Himmelman 1986) to compensate the effects of wave exposure. Our unstable site, in spite of its higher exposure, may be under this threshold level.

Experimental work is necessary to ascertain the factors responsible for the fact that, in some populations, sea urchins respond to unfavourable conditions by decreasing gonadal volume, while in others reproductive activity is enhanced in such conditions. In our 2 site comparison, we found that the response of *Paracentrotus lividus* to more limiting environmental conditions (in terms of food and hydrodynamism, among other parameters) is a higher investment in reproduction, and a smaller size at maturity, together with a closer coupling between feeding activity and gonad production.

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