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Interpopulation variability of the reproductive cycle of *Paracentrotus lividus* (Echinodermata: Echinoidea) in the south-western Mediterranean

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The spawning of *Paracentrotus lividus* has been determined on the basis of the annual gonad index cycle at three sites in the Algiers area presenting low, intermediate and strong hydrodynamism. Three biotopes (*Posidonia oceanica* beds, rocky substrate with photophilous algae and overgrazed rocky substrate) and two depths (1–3 m and 6–10 m) were considered at these sites, the sex-ratio was always strongly in favour of females (2:1 to 3:1). In all sites but one, there were marked differences in the gonad index and the spawning period between sites; the gonad index reached its maximum value at the site with the weakest hydrodynamism, and the minimum value at the site with the strongest hydrodynamism. Spawning took place in April–May and August–September at the site with the weakest hydrodynamism, in April–June and October–December at the site with intermediate hydrodynamism and only in winter at the site with maximum hydrodynamism. The coexistence, on regional scale, of these reproductive cycles might enable *Paracentrotus lividus* to compensate the mortality during planktonic larval phase by the fact that spawning of this sea urchin occurred in all seasons.

INTRODUCTION

The edible sea urchin *Paracentrotus lividus* (Lamarck) (Echinodermata: Echinoidea) is widely distributed along the Atlantic and the Mediterranean coasts (Tortonese & Vadon, 1987). The ever increasing interest in this species is due, first, to its primordial role in maintaining the equilibrium of sublittoral communities in which they are considered to be the key species (Sala et al., 1998; Pinegard et al., in press), and, second, for its economic value (Palacin et al., 1998).

Few data exist concerning the biology of this species in the southern Mediterranean (Dieuzeide, 1933; Bergin, 1987; Semroud & Kada, 1987; Semroud, 1993) and most of these studies are not related to sea urchin reproduction.

The aim of the present study was to investigate the reproductive strategy of *P. lividus* through an examination of seasonal and interstational variations of its gonad index. This index is often used to study the reproductive cycle, fluctuations in gonad size and the spawning periods (Lawrence et al., 1965; Fenaux, 1968; Semroud & Kada, 1987; Guettaf & San Martin, 1995; Lozano et al., 1995). It has been demonstrated that the gonad index usually exhibits extensive variability on both the spatial and temporal scales (Moore, 1966; Lozano et al., 1995).

In *P. lividus*, the gonad index appears to vary with the season, biotope and trophic conditions (Régis, 1979; Semroud & Kada, 1987; Semroud, 1993; Guettaf & San Martin, 1995), as well as with temperature (Byrne, 1990), hydrodynamic conditions (Fenaux, 1968), photoperiod and phytoplankton blooms (Fenaux, 1968; Régis, 1979). Some authors have observed two spawning periods for *P. lividus* (Fenaux, 1968; Crapp & Willis, 1975; Pedrotti, 1993; Semroud, 1993), whereas other authors mention only one such spawning event (Zavodnik, 1987; Byrne, 1990; Lozano et al., 1995).

In order to explain the variations of the gonad index, three parameters were investigated in this study: (1) the biotope; (2) depth and (3) hydrodynamism.

MATERIALS AND METHODS

Sea urchin sampling

Approximately 30 individuals of *Paracentrotus lividus*, with an ambitus diameter of 4.5–5.8 cm (without the spines), were sampled monthly (January–December 1994) by SCUBA diving from three sites in the Algiers region (Algeria): at Algiers Beach (Bay of Algiers), El Marsa and Aïn Tagouraït (Bou Ismail) (Figure 1). These sites differ in their hydrodynamic conditions and algal assemblages (Table 1). The dominant algal species on the rocks covered with photophilic algae (Algiers Beach and Aïn Tagouraït) include: (1) the Fucophyceae (*Cystoseira compressa* (Esper) Gerloff & Nizamuddin, *Cystoseira crinita* (Desfontaines) Duby, *Dictyota dichotoma* (Hudson) Lamouroux, *Dilophus spiralis* (Montagne) Hamel, *Padina pavonica* (L.) Thivy, *Stypocaulon scoparium* (L.) Kützing); (2) Florideophyceae (*Asparagopsis armata* Harvey, *Ceramium diaphanum* (Lightfoot) Roth, *Corallina elongata* (Ellis & Solander), *Lithophyllum incrustans* (Philippi), *Peyssonnelia squamaria* (Gmelin) Decaisne); and (3) Ulvophyceae (*Bryopsis muscosa* (Lamouroux), *Bryopsis* sp., *Codium fragile*

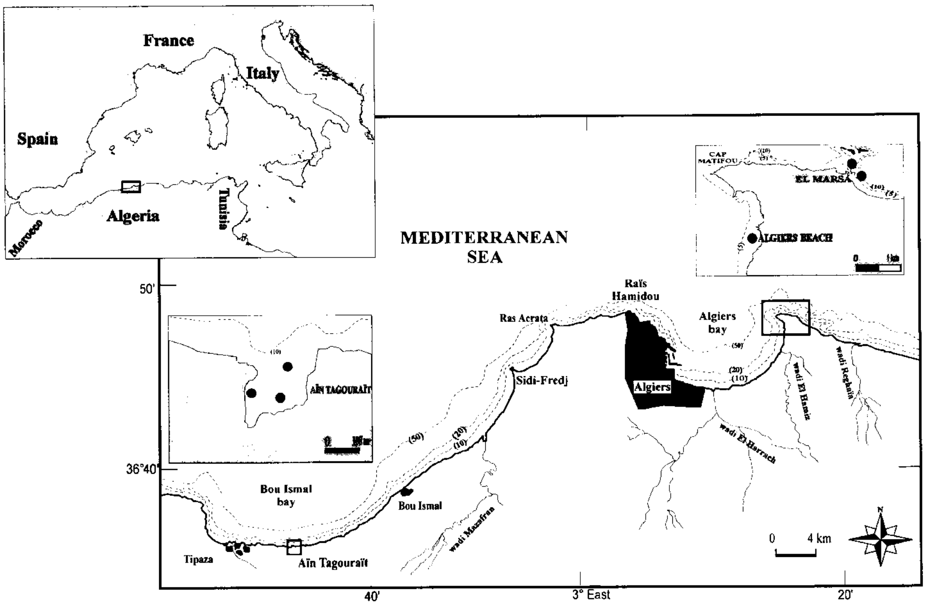

Figure 1. Localization of the sampling sites of the sea urchin *Paracentrotus lividus* around Algiers (south-western Mediterranean) on rocky substrate with photophilic algae, overgrazed rocky substrate or *Posidonia oceanica* beds.

Table 1. *Biotic and abiotic characteristics of the different sampling sites.*

Stations	Biotopes	Depth (m)	Hydrodynamism conditions	Winds (frequencies in %)		
				Directions	Autumn–winter	Spring–summer
Algiers Beach	Rock and photophilic algae	1–3	Low	East sector	12.6	49.0
El Marsa	Overgrazed rock	1–3; 6–10	Intermediate	West sector	42.4	16.4
	Posidonia oceanica	1–3; 6–10		Calm	6.3	8.8
Aïn Tagouraït	Rock and photophilic algae	1–3	Strong	East sector	24.4	27.0
	Overgrazed rock			West sector	36.0	27.7
	Posidonia oceanica			Calm	6.4	16.8

(Suringar) Hariot, *Flabellia petiolata* (Turra) Nizamuddin, *Ulva rigida* (C. Agardh) Le Jolis). The overgrazed rocks (El Marsa and Aïn Tagouraït) show encrusting Corallinaceae on which grows the alga *Ulva rigida* between May and August. Meanwhile, the Algiers Beach site is fed by two rivers (the El Hamiz and the El Harrach) which carry the domestic and industrial waste waters for the entire city of Algiers (Figure 1). Water salinity and temperature were similar in the three sites (36.2–37.0 psu and 12–27°C respectively).

The gonad index

Sampled sea urchins were immediately dissected. Gonads were placed in an oven at 70°C for 48 h, and subsequently weighed. Various gonad indexes were proposed in the literature (Moore, 1934; Lawrence et al., 1965; Fuji, 1967; Fenaux, 1968; Gonor, 1972; Régis, 1979; Semroud & Kada, 1987; Grosjean et al., 1998). Among them, the only one related to a similar region (Semroud & Kada, 1987) is used in this work in order to compare the results. This gonad index (GI) is expressed as the ratio of the gonad dry weight in mg (GDW) over the horizontal test diameter cubed (d) without the spines in cm^3:

$$IG = \frac{GDW}{d^3} \qquad (1)$$

For statistical analysis, a non-parametric Mann–Whitney test was used to compare two independent samples, whereas a Kruskal–Wallis test was used to compare several samples. The Student–Newman and Keuls (SNK) non-parametric multiple comparisons test was also used (Zar, 1999). Parametric methods were not employed as the variance homogeneity (Bartlett & Levene tests: $P < 0.01$) and normal distribution of the data (Kolmogorov–Smirnov test: $P < 0.01$), were not met. A global analysis of the variation in gonad index was made using a principal component analysis (PCA) followed by a hierarchical classification in ascending order (Escofier & Pagès, 1990). All statistical analyses were performed using Statistica software.

RESULTS

Sex-ratio and variability in the gonad index

At all three sampling sites, there were significantly more females than males (Figure 2), regardless of the biotope or depth considered. The proportion of female sea urchins was significantly higher from May to October (χ^2 test, $P<0.01$) for all biotopes (Figure 2). The Mann–Whitney *U*-test shows that the gonad index was never significantly different between males and females ($P>0.05$) except for Algiers Beach and El Marsa in March ($P<0.05$) and Aïn Tagouraït in February ($P<0.05$). Consequently, the males and females of *Paracentrotus lividus* were pooled for the rest of the study.

Fluctuation in the gonad index over time

In Algiers Beach (rock covered with photophilic algae), the annual cycle for the gonad index (Figure 3) exhibits significant seasonal variations (Kruskal–Wallis test, $P<0.01$). Significant decreases in this index were observed in April–May and August–September (SNK test, $P<0.05$). These decreases in gonad index value in spring (59% of the previous peak, February–March) and in summer (77% of the previous peak, June–July), correspond to the spawning events classically found in *P. lividus* in Mediterranean.

In El Marsa (Figure 3), the annual gonad index cycle differed significantly from one month to the other (Kruskal–Wallis test, $P<0.01$). Significant decreases in the gonad index were observed in April–June and October–December (SNK test, $P<0.05$) and this regardless of the depth (1–3 m and 6–10 m) or biotope considered (overgrazed rock and *Posidonia oceanica* sea grass bed). Here again, two peaks in the gonad index were observed, one in spring (February–March) and the other in summer (July–September), and these were similarly followed by two spawning periods. It should be noted, however, that the second peak (July–September) is delayed in comparison with the second peak occurring in Algiers Beach (June–July; Figure 3). Compared to the seasonal recorded peaks of gonad indices in El Marsa (Figure 3), the decrease in gonad index were 60 and 68% lower (in spring and summer respectively). Meanwhile, the mean gonad indices observed here were lower than those recorded in Algiers Beach (Table 2).

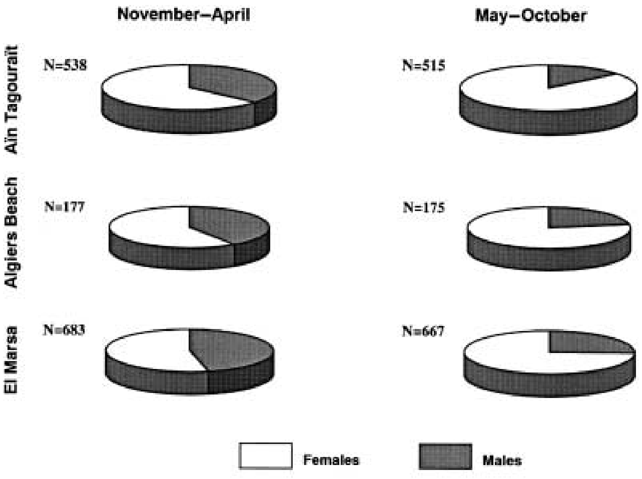

Figure 2. Frequency of male and female *Paracentrotus lividus* for the three studied sites, regardless of the biotope or depth considered.

In Aïn Tagouraït (Figure 3), during the sampling period, the gonad index shows a significant temporal variation (Kruskal–Wallis test, $P<0.01$), with a marked decrease in February–March (SNK test, $P<0.05$), regardless of biotope. The cycle of the gonad index at this site (Figure 3) shows a unique peak in January followed by a decrease of the values (72% in average) during the months of February and March which corresponded to a single spawning period. In other respects, the mean gonad index values were lower than those recorded at the two other sampling sites (Kruskal–Wallis test, $P<0.05$; Table 2).

Analysis of gonad index variability

The influence of depth on gonad index values was studied at the El Marsa site on two biotopes (overgrazed rock and *P. oceanica* sea grass beds). On overgrazed rock, for the both studied depths, the mean gonad index of *Paracentrotus lividus* were comparable except from August to November (Figure 3). Indeed, during this time, the gonad indices for sea urchins living at depths of 1–3 m was higher than those observed for urchins at 6–10 m (SNK test, $P<0.01$).

Conversely, the temporal variation of the gonad index in *Posidonia oceanica* sea grass beds was identical at the two depths examined (Figure 3; Kruskal–Wallis test, $P>0.05$). The maximum, minimum and mean gonad index values over the one year sampling period (Table 2) were statistically different at depth on the overgrazed rock (Mann–Whitney *U*-test, $P<0.01$), but not on the *P. oceanica* beds ($P>0.05$).

A global analysis of gonad index variability shows that the two first axes of the factorial analysis represent, respectively, 40.7 and 31.2%, or 72% of the total inertia. The third and fourth axes account for only 13.0 and 7.9% of the total inertia, respectively. It would thus appear that, as a general rule, the sites are grouped (or separated) as a function of the mean prevailing hydrodynamic conditions and not as a function of either biotope or depth (Figure 4).

On axis 1, the sheltered station (Lra) is compared to the more moderately exposed stations of the site (MPo3, MPo6, Mra3, Mra6). This same axis also compares the station made up of rock covered in photophilic algae (Lra, Hra) to the stations exhibiting overgrazed rock (Hov, Mov3, Mov6). On axis 2, the two sites (low and medium hydrodynamism) are opposed to the exposed site (high hydrodynamism).

Following the PCA, a hierarchical ascending classification was carried out for these same stations using the Euclidean distance. As is seen for the PCA, the final dendrogram reveals that the stations are distributed into three groups that correspond to the three sites examined (Figure 5): group A, identifiable by the assembling of the stations (Hra, Hpo, Hov) located at the most exposed site (Aïn Tagouraït), whatever the biotope (rock with photophilic algae, overgrazed rock, *Posidonia oceanica* bed); group B, characterized by four stations (Mov3, Mov6,

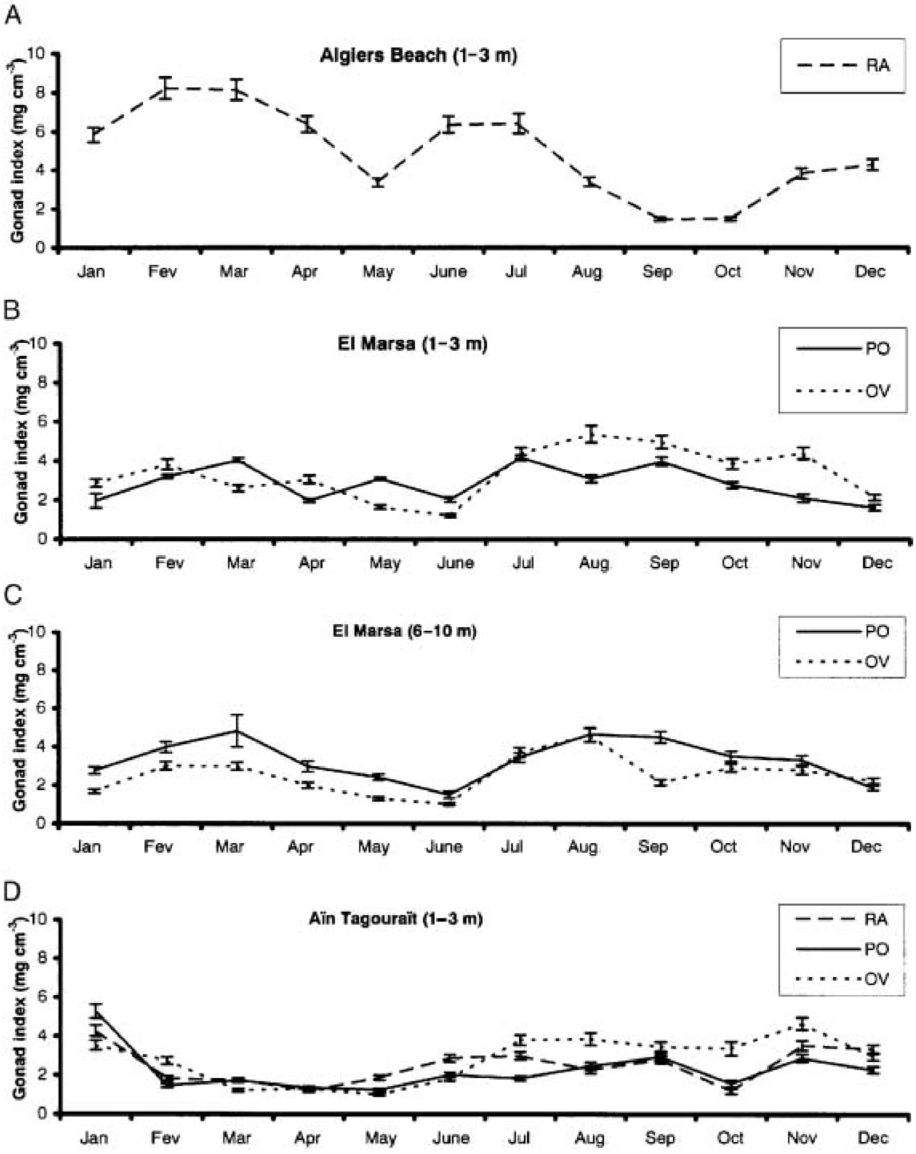

Figure 3. Changes in mean gonad index according to time and biotope: (A) at Algiers Beach 1–3 m depth; (B) El Marsa 1–3 m and (C) 6–10 m depth; and (D) Aïn Tagouraït 1–3 m depth. Bars indicate confidence interval; RA, rocky substrate with photophilous algae; OV, overgrazed rocky substrate; PO, *Posidonia oceanica* beds.

Table 2. *Maximal, minimal and annual mean values of the mean gonad index (GI), for the different biotopes, depths and sites of the three sampled sites.*

Stations	Biotopes	Max GI (mg cm^{-3})	Min GI (mg cm^{-3})	Mean GI (mg cm^{-3})
Algiers Beach	Rock and photophilic algae (1–3 m)	8.23 ±1.55 (February)	1.49 ±0.26 (September)	4.93 ±0.93
El Marsa	Overgrazed rock (1–3 m)	5.36 ±1.06 (August)	1.22 ±0.24 (June)	3.35 ±0.64
	Over grazed rock (6–10 m)	4.60 ±0.88 (August)	1.03 ±0.20 (June)	2.51 ±0.48
	Posidonia oceanica meadow (1–3 m)	4.17 ±0.79 (July)	1.62 ±0.31 (December)	2.86 ±0.55
	Posidonia oceanica meadow (6–10 m)	4.81 ±1.53 (March)	1.52 ±0.39 (June)	3.29 ±0.71
Aïn Tagouraït	Rock and photophilic algae (1–3 m)	4.27 ±0.79 (January)	1.17 ±0.28 (October)	2.53 ±0.48
	Overgrazed rock (1–3 m)	4.65 ±0.87 (November)	1.00 ±0.19 (May)	2.77 ±0.55
	Posidonia oceanica meadow (1–3 m)	5.27 ±1.00 (January)	1.24 ±0.23 (May)	2.26 ±0.44

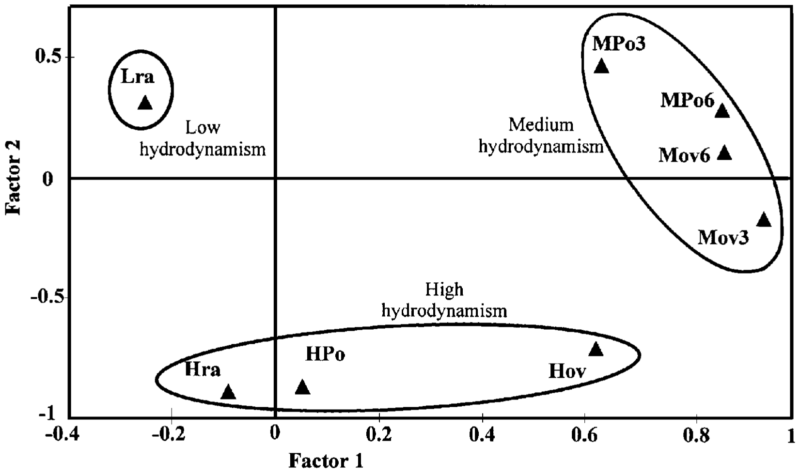

Figure 4. Two-dimensional scatterplot of factors loadings, factor 1 vs factor 2, in principal component analysis. Eigenvalue of factor 1=3.26, of factor 2=2.50. Lra, low hydrodynamic conditions and rock and algae (Algiers Beach); MPo3, MPo6, medium hydrodynamic conditions and *Posidonia oceanica* beds at 3 and 6 m depth (El Marsa); Mov3, Mov6, medium hydrodynamic conditions and overgrazed rock at 3 and 6 m depth (El Marsa); Hra, HPo, Hov, high hydrodynamic conditions and rock and algae, *P. oceanica* beds or overgrazed rock respectively (Aïn Tagouraït).

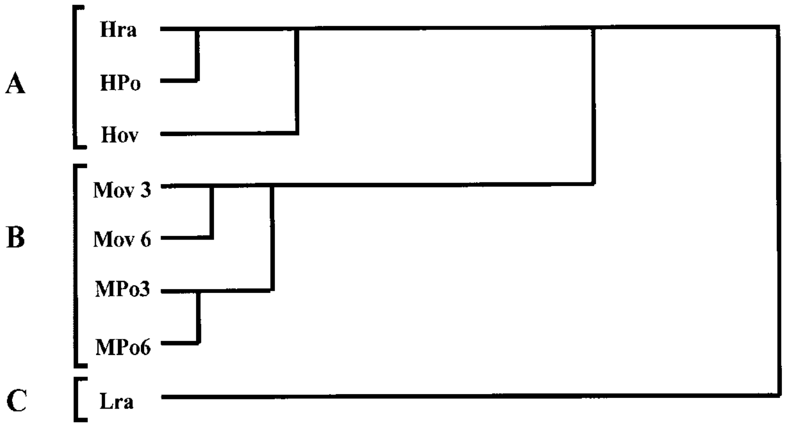

Figure 5. Hierarchical tree diagram of a joining (tree clustering) analysis performed on mean monthly values of gonad index calculated for the eight different stations. Lra, low hydrodynamic conditions and rock and algae (Algiers Beach); MPo3, MPo6, medium hydrodynamic conditions and *Posidonia oceanica* beds at 3 and 6 m depth (El Marsa); Mov3, Mov6, medium hydrodynamic conditions and overgrazed rock at 3 and 6 m depth (El Marsa); Hra, HPo, Hov, high hydrodynamic conditions and rock and algae, *P. oceanica* beds or overgrazed rock respectively (Aïn Tagouraït).

MPo3, MPo6) belonging to the moderately exposed site (El Marsa) and was not dependent on either biotope (overgrazed rock and *P. oceanica* bed) or depth (1–3 and 6–10 m); group C, single station (Lra) of rock covered in photophilic algae that was located at Algiers Beach, and corresponding to the sheltered site.

DISCUSSION

Sex-ratio

A 1:1 sex ratio is usually observed for *Paracentrotus lividus*, as was true for the majority of echinoderms (Lawrence, 1987). In the present study, the number of females was greater than that of males, regardless of biotope, site or depth; the sex-ratio (female:male) was found to be between 2:1 and 3:1. Such a female dominance has already been observed for *P. lividus* in Algeria (Semroud, 1993). Neefs (1938) in Roscoff (Brittany, France), noted that the females outnumber the males from September to November, regardless of depth. Such a disequilibrium in favour of females has also been observed in other sea urchins, including *Sphaerechinus granularis* (Semroud & Senoussi, 1989), *Tripneustes ventricosus* Lamarck (McPherson, 1965), *Eucidaris tribuloides* Lamarck (McPherson, 1968) and *Heliocidaris erythrogramma* Valenciennes (Dix, 1977a). McPherson (1965) suggested that differences in growth and mortality could explain the dominance of one sex over the other. In other respect, this dominance could be related to a delay of gonads maturation after spawning between males and females. For instance, the population would be made up of mature male sea urchins that are more numerous than there female counterparts (Brookbank, 1968).

Table 3. *Literature review of the spawning period(s) of the sea urchin* Paracentrotus lividus.

Locations	Spawning per year	Spawning period	References
Atlantic	1	Summer	Mortensen (1927)
Western Atlantic (France)	1	March–April to July–August	Neefs (1938)
Western Atlantic (south-west Ireland)	2	January–March and August–September	Crapp & Willis (1975)
Western Atlantic (Brittany, France)	1	March–December	Allain (1975)
Western Atlantic (south Brittany, France)	1	May–July/August	Spirlet et al. (1998)
Western Atlantic (south-west Ireland)	1	May–September	Byrne (1990)
Mediterranean	1	March–April	Selenka (1878) (in Boolootian, 1966)
Mediterranean	several	All year-round	Mortensen (1927)
North-west Mediterranean (Villefranche-sur-mer, France)	2	Beginning of June and end of summer–beginning of November	Fenaux (1968)
North-west Mediterranean (Marseille, France)	2	June and September–November	Régis (1979)
North-west Mediterranean (west Corsica, France)	2	May–June and September–November	Verlaque (1984)
Mediterranean (Adriatic Sea)	1	March–autumn	Zavodnik (1987)
South-west Mediterranean (Alger, Algeria)	2	March and August–September	Semroud & Kada (1987)
South-west Mediterranean (Alger, Algeria)	2	March–April and October–November	Sadoud (1988)
North-west Mediterranean (Liguro-Provençal basin, France)	2	April–May and September–October	Pedrotti (1993)
South-west Mediterranean (Algiers, Algeria)	2	March and July–August	Semroud (1993)
South-west Mediterranean (Alger, Algeria)	2	April and October–December	Chitini & Sellal (1994)
North-west Mediterranean (Barcelona, Spain)	1	April–July	Lozano et al. (1995)
North-west Mediterranean (west Corsica, France)	2	March–June and August–October	Fernandez (1996)
South-west Mediterranean (Alger Beach, Algeria)	2	April–May and August–September	Present study
South-west Mediterranean (El Marsa, Algeria)	2	April–June and October–December	Present study
South-west Mediterranean (Aïn Tagouraït, Algeria)	1	February–March	Present study

Nevertheless, this was not the case for *P. lividus* as the maturation of gonad seems to be identical for the two sexes according to the gonad index (Guettaf & San Martin, 1995; present study).

Effects of environmental parameters

At a given site, no biotope effect was observed on the gonad index of *P. lividus*. This result was rather surprising as the food resources would appear to vary substantially from one site to the next. Therefore, the reason behind this result could be the exportation of leaves from *Posidonia oceanica* beds in the vicinity of the stations of this study. Indeed, Pergent et al. (1994) estimated that 29% of the primary production of a *P. oceanica* bed was exported in this manner. This exportation might induce an abundant available resources. Thus, *P. oceanica* leaves can contribute up to 40% of the digestive gland contents in *Paracentrotus lividus* individuals living at a distance of several hundred metres from a sea grass bed (Verlaque & Nédélec, 1983).

The gonad index does not also vary significantly with depth. These results were in agreement with those obtained by Dix (1977b) for *Heliocidaris erythrogramma*. On overgrazed rock (El Marsa), a significant difference was observed for the different depths examined from August to September. During this period, water temperatures were high and the assemblages of the alga *Ulva rigida* became considerably abundant at shallow depths. *Ulva rigida* is readily eaten by *P. lividus*. The seasonal development of this alga in mild shallow waters could, therefore, explain the differences observed among the gonad index values. Such an increase in this index, correlated with depth and algal abundance, has been observed in *Strongylocentrotus droebachiensis* (Keats et al., 1984).

Conversely, the gonad indices were significantly different among the sites. The lowest values were calculated for the site exhibiting the harshest hydrodynamic conditions (Aïn Tagouraït). This was in agreement with the results obtained by Lozano et al. (1995) which indicated that the repletion index in *P. lividus* decreased with increasing hydrodynamic pressures. When adverse hydrodynamic conditions prevail, *P. lividus* cease to feed. Identical results have been observed in other species, such as *S. droebachiensis* (Keats et al., 1984) and *Echinus esculentus* (Nichols, 1981).

In this study, the highest gonad indices were observed in the most sheltered site (Algiers Beach). Previously, the gonad index was linked to nutrition of *P. lividus* (Semroud & Kada, 1987). Lawrence et al. (1992) for *P. lividus* and Meidel & Scheibling (1999) for *S. droebachiensis* demonstrated that the gonad and somatic production was high when food resources were not limiting. The sea urchins of Algiers Beach, in addition to being able to feed in a conventional pattern, use the available macroalgae, including the genera *Cystoseira, Dictyota, Dilophus, Padina* and *Stypocaulon*. These algae are considered to be a preferred food source for *P. lividus* by Frantzis & Grémare (1992). In addition, this site is rich in particulate organic matter that is brought by the El Harrach and El Hamiz rivers (Figure 1) (Samson & Dahmani, 1995). In El Marsa, which presents intermediate hydrodynamic conditions when compared to the other two sites, the gonad indices were similarly intermediate.

Spawning periods

Each site exhibits its own model of spawning cycle. In Algiers Beach site, the gonad index presents two peaks, followed by two substantial decreases that correspond to two spawning periods in spring and in summer. A second type of spawning cycle was observed in El Marsa site (intermediate hydrodynamism) where two peaks in the gonad index were similarly found, followed by two spawning periods, however a delay of one to two months was observed between the gonad index peak of fall and the spawning. The third and last type of spawning cycle was observed in Aïn Tagouraït (high hydrodynamism) where a single spawning period was observed in winter according to the gonad index values.

In Algiers beaches, the abundance and availability of the nutritional resources allows the gonad to be rapidly replenished following the emission of gametes. This was in agreement with Fox (1924) who shows that when conditions are favourable, *P. lividus* can produce mature oocytes only nine days after a spawning event. Thus, the lesser food availability in the site presenting intermediate hydrodynamic conditions, could explain the delay in the fall spawning event. Therefore, in the site exhibiting harsh hydrodynamic conditions, the food resources were probably not sufficient to allow a second such spawn. Or, may be the spawning is concentrated in a unique spawning event to give fertilization a better chance, because of the bad hydrodynamism conditions.

Authors who have examined the spawning cycle of *P. lividus* in the Mediterranean have observed either one or two spawning events (Table 3). The timing of these spawning events appears to vary between regions. Indeed, the results of the present study demonstrate that such variability can occur between relatively close sites within a given region. Generally, for all the sites combined, *P. lividus* seems to experience spawning events throughout all the year (Table 3), but for a given site these spawning events seem to be closely linked to the energetic resources availability (algae in particular) and, indirectly, to the prevailing hydrodynamic conditions.

It would appear that *P. lividus* adopts a very different reproductive strategy depending on hydrodynamic conditions and food availability. This could represent a strategy for staggering the risks associated with spawning. By producing larvae throughout the year, in a given region, *P. lividus* maximizes the probability of seeing larvae from at least one of its spawning events survive hazards such as currents, meteorology and predation (Pedrotti & Fenaux, 1992) and reach biotopes favourable to recruitment. This would result in a yearly recruitment that is fairly regular in its occurrence. However, for another urchin, *Arbacia lixula* in Corsica, recruitment seems to occur less than once every five years (C.F. Boudouresque, personal communication). This interannual variability is also observed for *Sphaerechinus granularis* in Brittany (Guillou & Michel, 1993), where it appears to be linked to winter storms and to the thickness of the spring algal layer that can prevent fixation of the juveniles (Lumingas & Guillou, 1994). Another explanation for the great variability in recruitment is through a dilution of the gametes as a result of hydrodynamic conditions (which will result in a decrease in fertilisation success). Moreover, in *Strongylocentrotus purpuratus*, the hydrodynamic conditions can interfere with normal larval development (Mead & Denny, 1995).

Although for a given region spawning occurs all year long, these spawning events are not of equal magnitude. In the Algiers region (present study), and as is seen in the Villefranche-sur-Mer region (France) (Fenaux, 1968), two particularly important spawning events are observed: spring–summer and in spring–autumn, respectively. These spawning events coincide with phytoplanktonic blooms (Pedrotti, 1993). Indeed, a number of authors have suggested that phytoplankton could stimulate spawning in echinoderms (Himmelman, 1981; Starr et al., 1990). The periods of maximal benthic recruitment that have been observed in the Mediterranean generally coincide with both the spawning periods and the larval peaks within the phytoplankton (Lozano et al., 1995; Turon et al., 1995). Nevertheless, larva are also present within the plankton at other times of the year, although in far lesser number (Pedrotti, 1993). Similarly, Lozano et al. (1995) observed some benthic recruitment in winter whereas San Martin (1995) observed recruitment between March and July. The recruits observed in March are probably the result of a winter spawning event. As a general rule, and at least on the scale of a given region, recruitment of *P. lividus* would appear to be a yearly phenomenon as has been suggested by Turon et al. (1995) for the Catalonia region (Spain).

CONCLUSION

The gonad index for *Paracentrotus lividus*, as well as the number and the timing of the spawning events, does not appear to be influenced by either the depth or biotope for the three sites examined in the Algiers region. The hydrodynamic conditions seem to be the determining factor, although indirect as it would allow or prevent access to the food resources. Three different reproduction cycles were observed for the three sites, with one or two spawning events being recorded. Such cycles have already been observed in other regions of the Mediterranean. It thus appears that such plurality in spawning periods can exist within a given region and it is hypothesized that the same is true throughout the Mediterranean. The coexistence of these different reproductive cycles results in the occurrence of spawning events throughout the year, albeit of varying importance. For a given region, this reproductive strategy could help explain why planktonic larvae and benthic recruitment have been observed year-round. This staggering of reproductive events throughout the year, result in a reduction of the risks associated with the planktonic larval phase. This could explain the annual benthic recruitment observed for *P. lividus*, whereas such an annual recruitment is not observed for other benthic invertebrates.

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