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SEA) IN RELATION TO HABITAT AND MARINE
RESERVE**

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VARIATION IN ABUNDANCE AND POPULATION DYNAMICS OF THE SEA-URCHIN *PARACENTROTUS LIVIDUS* ON THE CATALAN COAST (NORTH-WESTERN MEDITERRANEAN SEA) IN RELATION TO HABITAT AND MARINE RESERVE

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SEA-URCHIN
DENSITY
SIZE DISTRIBUTION
MEDITERRANEAN SEA
MARINE RESERVE

ABSTRACT. – We surveyed the population structure of the sea-urchin *Paracentrotus lividus*, considering the impact of depth, habitat and protection on its abundance and size distribution. No difference was found between habitats (walls vs. boulders) whereas a depth gradient was highlighted for the abundance and the size distribution of the sea-urchin. Most of the population (about 80%) is located in shallow areas (less than 10 m depth) whatever the location. Shallow water populations were made of small and medium size individuals (< 50 mm in diameter) while deep water populations were made of large individuals (> 50 mm in diameter). These large individuals accounted for 57% of the population in deep areas while they only represented 11% in shallow habitats. Since the recruitment in the deep waters cannot explain the abundance of large individuals, we suggest that larger individuals originate from shallow water populations, migrating to deep habitats while growing. In addition to differences linked to depth, we also observed significant differences between localities, higher abundances of sea-urchin being observed in the marine protected area than outside (193.6 vs. 82.5 ind. per 10 m²). However, rather than a protection effect, such result seems to be the consequence of a lower recruitment outside the protected area as the lower abundance of juveniles was observed out of the protected area. This last observation demonstrates the existence of a micro-geographic variability in the population structure of *Paracentrotus lividus* and much attention should be paid on this aspect prior to test the protection effect.

OURSINS
DENSITÉ
DISTRIBUTION DE TAILLES
MER MEDITERRANÉE
RÉSERVE MARINE

RÉSUMÉ. – Nous avons décrit une population d'Oursins, *Paracentrotus lividus*, en analysant simultanément l'impact de la profondeur, de la qualité de l'habitat et de la protection sur l'abondance et la distribution des tailles. Les deux habitats sélectionnés pour présenter les plus fortes abondances d'Oursins (parois verticales-roches-blocs), n'ont pas induit de différence significative dans les populations. A l'opposé, nos résultats montrent l'existence d'un gradient d'abondance et de taille avec la profondeur. La majeure partie de la population (80%) se situe dans les zones peu profondes (< 10 m) alors que les individus les plus gros (diamètre > 50 mm) se regroupent dans les zones profondes, en dessous de 10 m. Ils représentent près de 57% de la population dans les strates profondes. Dans la mesure où le recrutement se concentre principalement dans les zones peu profondes, nous proposons que la population profonde soit formée d'individus ayant migré vers ces zones profondes au cours de la croissance. Au delà de ces caractéristiques naturelles des populations, nous avons également constaté une différence significative d'abondance en fonction de la protection avec une moyenne de 82 ind. pour 10 m² en zone non protégée contre près de 193 ind. pour 10 m² en zone protégée. Néanmoins, il convient de tempérer ce résultat par le fait que les jeunes individus (< 20 mm de diamètre) sont également plus abondants dans le site protégé, ce qui suggère que la différence d'abondance résulte en grande partie d'un recrutement plus important dans le site protégé. Il faudra donc tenir compte de cet aspect pour évaluer l'effet réserve sur les Oursins.

INTRODUCTION

In infralittoral communities of the Western Mediterranean, the sea-urchin *Paracentrotus lividus* is the key species for the control of the dynamics of seaweeds and seagrasses because of its high abundance compared to other species (Palacin *et al.* 1998). It occurs mostly in shallow waters (maximum depth 20m), where it can reach densities of up to 10 individuals per square meter (Harmelin *et al.* 1980, 1981, Verlaque 1987, Palacin *et al.* 1998). In high densities areas, it can eliminate brown algae and seagrasses and thereby induce the formation of a bare patch dominated by encrusting algae (Kempf 1962, Verlaque & Nédelec 1983, Verlaque 1987).

The gastronomic value of its gonads has led to intensive harvesting with consequent reduction of populations in some areas along the Mediterranean coasts of France and Spain (Le Direach *et al.* 1987). Because of their fishery value, the factors determining the structure of *Paracentrotus lividus* populations have been investigated, and identifying mainly the recruitment process (Azzolina 1987, Lozano *et al.* 1995) and the mortality induced by predation (Verlaque 1984, Savy 1987) as factors determining the adult subsequent population. This predation appeared mostly due to fish such as the labrid *Coris julis* that is a major predator of juveniles (Sala 1997) and sparids like *Diplodus sargus* and *D. vulgaris* being the main predators of adults (Garcia-Rubies & Zabala 1990, Garcia-Rubies 1996, Sala 1997). In addition, the intense harvesting focused on sea-urchins has direct effect on their abundances (Le Direach *et al.* 1987). Nevertheless, fisheries target *Diplodus* species in the Mediterranean sea that will reduce the natural predation on sea-urchins and may balance the potential decrease of sea-urchin populations due to human collections (Jennings & Kaiser 1998). This interaction between fisheries and sea urchin highlights indirect relationships referred to trophic cascades (Estes & Palmisano 1974).

Once discussed in the context of marine protected area, therefore it becomes difficult to predict the evolution of sea-urchin populations because they will be protected from collecting but they may be exposed to more intense natural predation by fish. Many studies on the Mediterranean rocky littoral have demonstrated that large piscivorous and invertebrate-feeding fish are more abundant within marine protected areas compared to no protected sites (e.g. Bell 1983, Harmelin *et al.* 1995, Vacchi *et al.* 1998). In contrast, many studies comparing abundance and density of sea-urchin populations show variable results. Sala & Zabala (1996) monitored the abundance of *Paracentrotus lividus* within and outside the Medes islands marine reserve (NE Spain) for three years and reported a pattern of lower abundance in the reserve relative to

nearby unprotected areas. This pattern was attributed to increased predatory fish abundance in the reserve (Garcia-Rubies & Zabala 1990). Latter, a similar survey did not found any significant difference in density and mean size and conclude that these last results did not support the cascade hypothesis (Sala *et al.* 1998).

The aims of the present study were to describe the density and size structure of *Paracentrotus lividus* populations according to habitats and depths in some rocky habitats in the north-western Mediterranean Sea and ultimately to make comparisons among protected and unprotected areas using the Cerbère-Banyuls Marine Reserve as protected areas.

MATERIAL AND METHODS

Paracentrotus lividus were collected in April 1999 in the Cerbère-Banyuls Marine Reserve and a nearby unprotected area (South of France, north-western Mediterranean Sea) (Fig. 1). The study was conducted in 3 localities experiencing similar exposure to wind and waves but different constraints in terms of protection: the Totally Protected Area (TPA), the Partially Protected Area (PPA) and the Unprotected Area (UPA) (Fig. 1). In the TPA, all human activities are forbidden. In the PPA, recreational fishing is authorised for both fish and invertebrates as well as professional fisher using only fixed nets. In the UPA, no constraints are in place except those concerning spear-fishing and fishing regulations everywhere. The Cerbère-Banyuls Marine Reserve has been established in 1974 and spread over 7 km of coastline. We chose a marine protected area because we want to avoid the effect of collection on description of the natural population features. Each of the three localities (TPA, PPA and UPA) was separated from the other by 3 to 4 km. In each locality, 2 habitats were identified: "boulder" habitats (we turned them up to inspect under surfaces) that were colonised by a rich algal assemblage, and vertical and sub-vertical "walls" that supported algae as well as other invertebrates. In each habitat, collections were made at two different depths: a shallow zone between 0 to 10 meters depth, and a deeper zone between 10 to 20 meters depth.

Abundance and population size structure of sea-urchins were studied by scuba-diving along transects of 10 m long and 1 m wide. Each site was made of three transects. Altogether the sampling accounted for 36 transects that were all sampled within a month period (April 1999). The time of sampling took place before the recruitment season (Lopez *et al.* 1998) and therefore we mostly counted adults and juveniles of the previous year. For each transect, *Paracentrotus lividus* individuals were counted and their diameter (test without spines) was measured to the nearest mm with a calliper. Data were further grouped in 10 mm size classes.

To test for difference in abundance and mean size between localities, habitats and depth, a three-way ANOVA was performed after verifying the homogeneity of variance and the normality of data (Scherrer 1984).

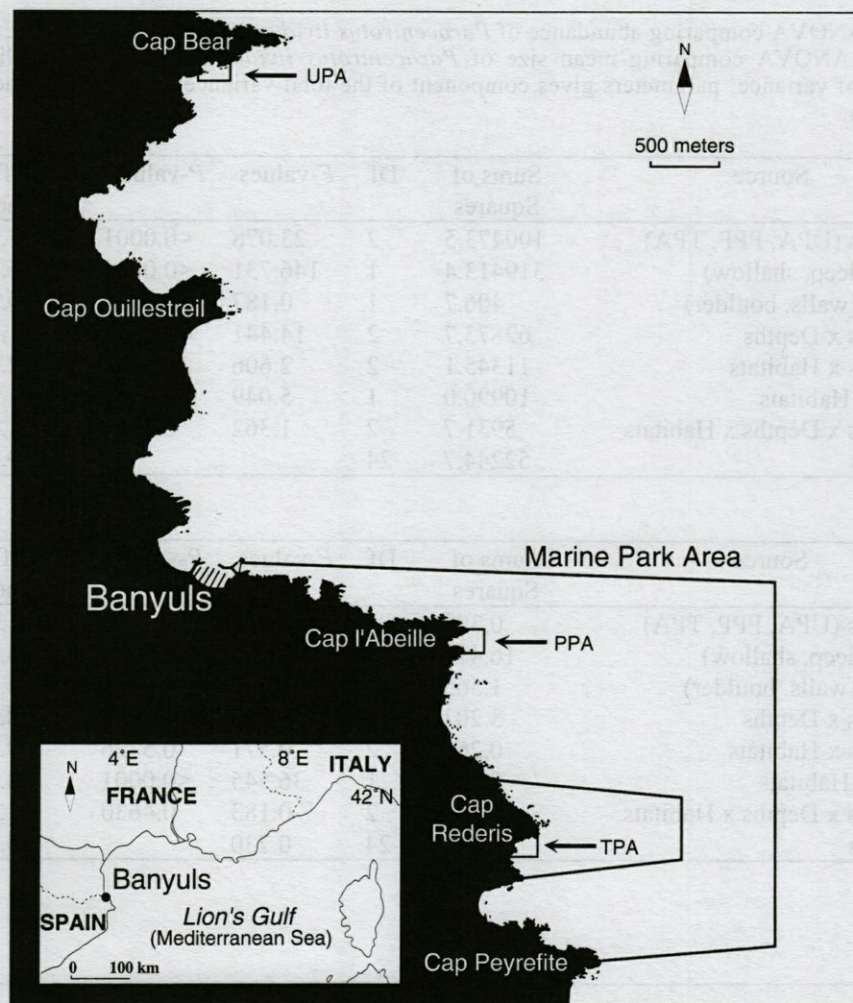


Fig. 1. – Location of the three areas where sea-urchins were counted according to depths and habitats with replicates of 10 m². UPA = Unprotected area; PPA = Partially protected area and TPA = totally protected area.

RESULTS

Over all transects, we counted and measured a total of 5637 individuals. Abundance of *Paracentrotus lividus* varied from 29 to 517 individuals per transect. In the following sections, we will use abundance values since they can be easily translated into density as each transect represented 10 square meters. Comparisons of abundance of *P. lividus* with a three-way ANOVA (Table I) demonstrated significant difference in the combined factor 'locality × depth' ($p < 0.0001$) as well as single factors 'locality' ($p < 0.0001$) and 'depth' ($p < 0.0001$). Overall, the deeper areas showed continuously lower abundance than shallow ones in all localities (mean abundance = 62.4 vs. 250.8 individuals per transect). In addition, localities exhibited significant difference with much lower abundance of urchins in the UPA (mean abundance = 82.5 individuals per transect) compared to PPA and TPA (mean

abundance = 185.3 and 202.0 individuals per transect respectively) (Fig. 2A). Among the three sources showing significant divergence of the abundance, the 'depth' accounted for 67% of the variance while 'locality' and the combined factor 'locality × depth' explained 21 and 13% of the total variance respectively. Abundance did not vary significantly according to the type of habitat, boulders and walls (Fig. 2).

Similar analysis were performed using the mean size of individuals per transect. The size of *Paracentrotus lividus* specimens recorded in this survey varied from 5 to 75 mm. The mean size of individuals collected per transect varied from 20.6 to 60.0 mm. Comparison of mean size of the populations of each transect show significant differences among habitats and depth (Table I). The three-way ANOVA demonstrated significant differences in 4 sources: the single factors 'habitat' ($p = 0.015$) and 'depth' ($p < 0.0001$) and the com-

Table I. – Three-way ANOVA comparing abundance of *Paracentrotus lividus* according to localities, depths and habitats (top). Three-way ANOVA comparing mean size of *Paracentrotus lividus* according to localities, depths and habitats (bottom). ‘% of variance’ parameters gives component of the total variance explained by each factor and the combination of factors.

Source	Sums of Squares	Df	F-values	P-values	% of variance
Localities (UPA, PPP, TPA)	100473.5	2	23.078	<0.0001	17.82
Depths (deep, shallow)	319413.4	1	146.731	<0.0001	56.67
Habitats (walls, boulder)	406.7	1	0.187	0.6694	0.07
Localities x Depths	62873.7	2	14.441	<0.0001	11.15
Localities x Habitats	11345.1	2	2.606	0.0946	2.01
Depths x Habitats	10990.0	1	5.049	0.0341	1.95
Localities x Depths x Habitats	5931.7	2	1.362	0.2751	1.05
Residuals	52244.7	24			9.27

Source	Sums of Squares	Df	F-values	P-values	% of variance
Localities (UPA, PPP, TPA)	0.391	2	0.848	0.4409	1.08
Depths (deep, shallow)	16.411	1	71.197	<0.0001	45.39
Habitats (walls, boulder)	1.565	1	6.790	0.0155	4.33
Localities x Depths	3.203	2	6.948	0.0042	8.86
Localities x Habitats	0.263	2	0.571	0.5726	0.73
Depths x Habitats	8.424	1	36.545	<0.0001	23.30
Localities x Depths x Habitats	0.367	2	0.183	0.4630	1.02
Residuals	5.532	24	0.230		15.29

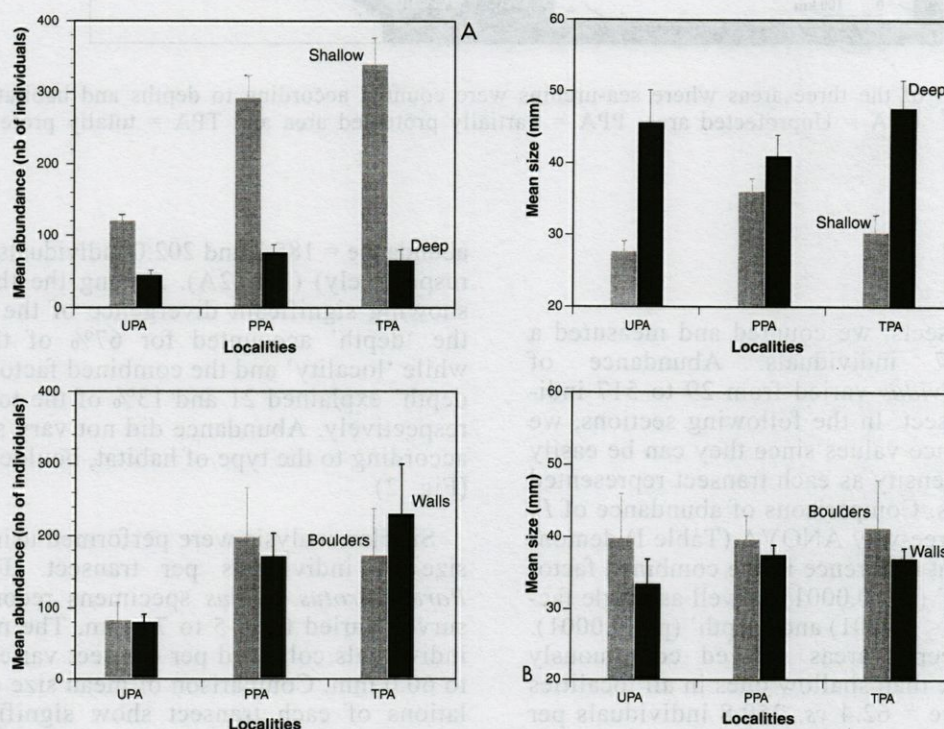


Fig. 2. – A, Mean abundance per transect of 10 m² according to depth (top) and habitats (bottom), considering each locality. B, Mean size (mm) of individuals counted in each transect according to depth (top) and habitats (bottom), considering each locality. Error bars give standard error.

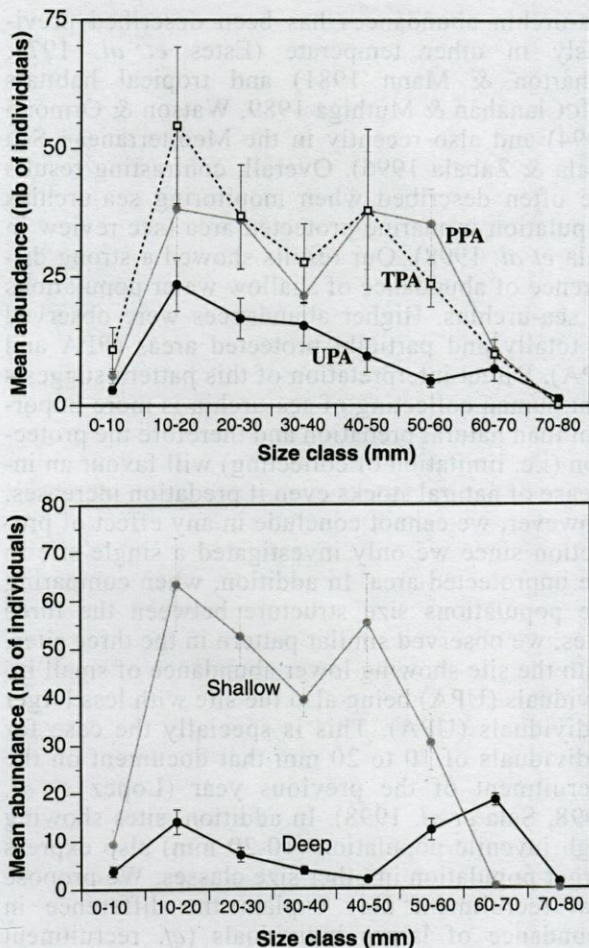


Fig. 3. – Top, Mean abundance for each size class and considering separately each locality whatever depth and habitat. Bottom, Mean abundance for each size class, considering separately each depth whatever locality and habitat. Error bars give standard error.

bined sources 'locality \times depth' ($p = 0.004$) and 'habitat \times depth' ($p < 0.0001$). Overall, these significant differences come from individuals that are much smaller in shallow areas (31.3 vs. 44.8 mm in deeper areas) and walls (36.0 vs. 40.2 mm in boulders), both whatever the locality (Fig. 2B). The depth explained most of the variance (45%) while the habitat only accounted for 4%. Mean sizes were similar between localities (Fig. 2B).

Finally, we detailed the size distribution looking at variations between localities, habitats and depth. Regarding localities, the lower value of abundance found in UPA compared to the other sites (PPA and TPA) was consistent in all size classes except for large individuals (Fig. 3). The three localities showed similar distribution pattern, small individuals (10 to 20 mm in diameter) being the most abundant. Among the 8 single-factor ANOVA computed for each size class between localities, only the 50-60 mm size class showed significant differ-

ence ($p = 0.006$) mostly because this size class was under-represented in the UPA samples. The size class of recruit of the previous year (10 to 20 mm) show also significant difference between localities ($p = 0.01$) with UPA population being less abundant than the two others (PPA and TPA). The size classes distribution varied significantly according to depth. As previously observed, most of the population was located in the shallow transects and only large individuals (50 to 70 mm in diameter) were more abundant in the deeper habitats (Fig. 3). After exclusion from the data, the very small individuals that were not targeted in our sampling design (lower than 10 mm diameter), shallow habitats showed a decrease of individuals as they become larger. Deeper habitats showed similar decrease in smaller through to medium size classes but larger individuals became the most abundant size class. Larger individuals (> 50 mm diameter) accounted for 57% of the population in the deeper habitats while they only represented 11% in the shallow habitats. Among the 8 single-factor ANOVA computed for each size class among the depth distribution, all size classes exceeding 20 mm diameter differed significantly between shallow and deep habitats. Finally the size class distribution did not differ according to the habitat structure (boulder vs. walls).

DISCUSSION

Overall, our results demonstrated significant differences in abundance and size distribution of *Paracentrotus lividus* according to localities and depths but not depending on substrates. Differences among localities and depth appeared highly significant, and little affected by micro-geographic variation since the variance among transects within the same site only accounted for 15 and 9% of the total variance in abundance and size respectively (see the residuals in three-way ANOVA, Table I).

The recruits of the year are smaller than 10 mm and often appear to be the most numerous in the population (Lopez *et al.* 1998, Barnes *et al.* 1999). In the present work, this size class is one of the less abundant because our sampling protocol did not include total cleaning of some surface and observation under binocular. Therefore, analysis of this class is not representative of the recruitment. The upper size class (10-20 mm) appears to be the most abundant in shallow waters (and almost in deeper waters). Individuals belonging to this size class are assumed to be recruits of the previous year like suggested by Lopez *et al.* (1998) and Sala *et al.* (1998). Our data showed that they preferentially occurred in shallow waters, whatever the habitats considered. This difference, according to depth range, can result from variation in the number of recruits settling at each depth, or from a differen-

tial predation on a similar number of recruits. The main predator of juveniles *P. lividus* in the north-western Mediterranean Sea is *Coris Julis* (Sala 1997). Previous fish survey in the same areas where we prospected for sea-urchin populations did not show significant differences in density of *C. Julis* (Dufour *et al.* 1995). Therefore, the difference according to depth in the recruits density mainly result from recruitment processes in shallow waters (Lopez *et al.* 1998). However, a differential abundance of predators other than *C. julis* (fishes or invertebrates) may also contribute to enhance this difference.

The difference in density between shallow and deep areas remains stable in all small and medium size classes including all individuals smaller than 50 mm in diameter. Larger individuals (> 50 mm in diameter) were equally distributed between shallow (31.8 ind. per 10 m²) and deeper (30.7 ind. per 10 m²) areas. Such similarity in population density of large individuals is opposed to the strong divergence found in smaller individuals and can result from migration of larger individuals to deeper habitats or from higher predation on large individuals in shallow habitats. Major predators of adults *Paracentrotus lividus* and *Diplodus sargus* and *D. vulgaris* (Sala 1997), which occur uniformly between the surface and 20 meters depth (Dufour *et al.* 1995, Jouvenel 1997) and cannot explain the shift in density of sea-urchins. In addition to natural predation, we must also consider that human collection which is significant in the Mediterranean Sea would be more intense in shallow water (Palacin *et al.* 1998). However, in our survey we found more large individuals in deep water than small ones at the same depth (average of 31.8 large individuals vs. 30.6 small ind.). Therefore, the recruitment itself, in deep habitats, cannot explain the abundance of large individuals and some migrations have also contributed to the deeper populations. The human collection will contribute to decrease the shallow populations but this decrease is also due to migration of larger individuals into deeper habitats. This migration was already described in sea-urchins and more specifically in *Paracentrotus lividus* (Dance 1987, Crook *et al.* 2000, Barnes & Crook 2001). Such change in habitats will be linked to change in feeding and other biological features that is still to be investigate.

Our data also revealed significant difference in population density between the three sites surveyed. The three sites varied mostly in their protection status. Protection usually leads to increases of density, biomass, diversity and/or longevity of populations experiencing fishing pressure (Polunin & Roberts 1993, Roberts 1995). Regarding sea-urchin populations, reserve effect is more complex to estimate since it is necessary to integrate "cascade effect" (Francour 1989, Sala & Zabala 1996). The relationship between predator (fish or human) and

sea-urchin abundances has been described previously in other temperate (Estes *et al.* 1978, Wharton & Mann 1981) and tropical habitats (McClanahan & Muthiga 1989, Watson & Ormond 1994) and also recently in the Mediterranean Sea (Sala & Zabala 1996). Overall, contrasting results are often described when monitoring sea-urchins population in marine protected area (see review in Sala *et al.* 1998). Our results showed a strong difference of abundance of shallow water populations of sea-urchins. Higher abundances were observed in totally and partially protected areas (PPA and TPA). Direct interpretation of this pattern suggests that human collecting of sea-urchin is more important than natural predation and therefore the protection (i.e. limitation of collecting) will favour an increase of natural stocks even if predation increases. However, we cannot conclude in any effect of protection since we only investigated a single site in the unprotected area. In addition, when comparing the populations size structure between the three sites, we observed similar pattern in the three sites, with the site showing lower abundance of small individuals (UPA) being also the site with less larger individuals (UPA). This is specially the case for individuals of 10 to 20 mm that document on the recruitment of the previous year (Lopez *et al.* 1998, Sala *et al.* 1998). In addition, sites showing high juvenile population (10-20 mm) also express larger population in other size classes. We propose that recruitment may explain the difference in abundance of larger individuals (*cf.* recruitment limitation theory). Finally, the variation in abundance seems to result from variation in recruitment between sites rather than any effect of predation or collecting.

Our results have been analysed in term of recruitment, fish predation and human predation. These are not the only perspectives in understanding spatial variation in population structure. Behavioural aspects have been also emphasised in sea-urchins (Barnes & Crook 2001). However, this study highlights micro-geographic variations in the abundance of the population while the habitat does not seem to affect this difference. Micro-geographic variations in the distribution of marine organisms are now been observed in many surveys dealing both with population dynamics and population genetics (David *et al.* 1997, Lenfant & Planes 2002). Such aspect needs now to be considered while looking at any scale survey and when looking at the impact of some specific aspect such as the effect of protection.

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REFERENCES

- Azzolina JF 1987. Evolution à long terme des populations de l'oursin comestible *Paracentrotus lividus* dans la Baie de Port-Cros (Var, France). In Coll Intern sur *Paracentrotus lividus* et les Oursins comestibles. Edited by CF Boudouresque, GIS Posidonie Publishers, Marseille: 257-269.
- Barnes DKA, Crook AC 2001. Quantifying behavioural determinants of the coastal European sea-urchin *Paracentrotus lividus*. *Mar Biol* 138: 1205-1212.
- Barnes DKA, Steele S, Maguire D, Turner J 1999. Population dynamics of the urchin *Paracentrotus lividus* at Lough Hyne, Ireland. Proc 5th European Echinodermata Conf, Milan, Italy. Balkema, Rotterdam: 427-431.
- Bell JD 1983. Effect of depth and marine reserve fishing restriction on the structure of the rocky reef fish assemblage in the North Western Mediterranean Sea. *J Exp Mar Bio Ecol* 107: 45-59.
- Crook AC, Long M, Barnes DKA 2000. Quantifying daily migration in the sea-urchin *Paracentrotus lividus*. *J Mar Biol Assoc UK* 80: 177-178.
- Dance C 1987. Pattern of activity of the sea-urchin *Paracentrotus lividus* in the Bay of Port-Cros (Var, France, Mediterranean). *P.S.Z.N. Mar Ecol* 8: 131-142.
- David P, Perdieu MA, Pernot AF, Jarne P 1997. Fine-grained spatial and temporal population genetic structure in the marine bivalve *Spisula ovalis*. *Evolution* 51: 1318-1322.
- Dufour V, Jouvenel JY, Galzin R 1995. Study of reef fish assemblage. Comparison of population distributions between depths in protected and unprotected areas over one decade. *Aquat Living Resour* 8: 17-25.
- Estes JA, Palmisano JF 1974. Sea otters: their role in structuring nearshore communities. *Science* 185: 1058-1060.
- Estes JA, Smith NS, Palmisano JF 1978. Sea otter predation and community organisation in the Western Aleutian Islands, Alaska. *Ecology* 59: 822-833.
- Francour P 1989. Les peuplements ichtyologiques de la réserve de Scandola: influence de la réserve intégrale. *Trav Sci Parc Naturel Régional Corse* 31: 33-93.
- Garcia-Rubies A 1996. Estudi ecológic de les poblacions de peixos litorals sobre substrat rocos a la Mediterrània Occidental: Efecte de la fondària, el substrat, l'estacionalitat i la protecció. PhD thesis, Univ Barcelona.
- Garcia-Rubies A, Zabala M 1990. Effects of total fishing prohibition on the rocky fish assemblages of Medes Island marine reserve (NW Mediterranean). *Bull Mar Sci* 54: 317-328.
- Harmelin JG, Bouchon C, Duval C, Hong JS 1980. Les échinodermes des substrats durs de l'île de Port-Cros, Parc National (Méditerranée nord-occidentale). Eléments pour un inventaire quantitatif. *Trav Sci Parc Nation Port-Cros* 6: 25-38.
- Harmelin JG, Bouchon C, Hong JS 1981. Impact de la pollution sur la distribution des échinodermes des substrats durs en Provence (Méditerranée nord-occidentale). *Téthys* 10: 13-36.
- Harmelin JG, Bachet F, Garcia F 1995. Mediterranean marine reserves: Fish indices as test of protection efficiency. *PSZN Mar Ecol* 16: 233-250.
- Jennings S, Kaiser MJ 1998. The effect of fishing on marine ecosystems. *Adv Mar Ecol* 34: 201-352.
- Jouvenel JY 1997. Ichtyofaune de la côte rocheuse des Albères (Méditerranée N.O., France). PhD Thesis, Univ Paris VI.
- Kempf M 1962. Recherche d'écologie comparée sur *Paracentrotus lividus* (Lmk.) et *Arbacia lixula* (L.) *Rec Trav Stn Mar Endoume, Fac Sci Mars* 25: 47-116.
- Le Direach L, Boudouresque CF, Antolic B, Kocatas A, Panayotidis P, Pancicci A, Semroud R, Span A, Zaqali J, Zavodnik D 1987. Rapport sur l'exploitation des Oursins en Méditerranée. In Coll intern sur *Paracentrotus lividus* et les oursins comestibles. Edited by CF Boudouresque, GIS Posidonies, Marseille: 199-220.
- Lenfant P, Planes S 2002. Temporal genetic changes between cohorts in a natural population of a marine fish, *Diplodus sargus*. *Biol J Linnean Soc* 76: 9-20.
- Lopez S, Turon X, Montero E, Palacin C, Duarte C, Tarjuelo I 1998. Larval abundance, recruitment and early mortality in *Paracentrotus lividus* (Echinoidea). Interannual variability and plankton-benthos coupling. *Mar Ecol Prog Ser* 172: 239-251.
- Lozano J, Galera J, Lopez S, Turon X, Palacin C, Morera G 1995. Biological cycles and recruitment of *Paracentrotus lividus* (Lamarck) (Echinodermata: Echinoidea) in two contrasting habitats. *Mar Ecol Prog Ser* 122: 179-191.
- MacClanahan TR, Muthiga NA 1989. Patterns of predation on a sea-urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs. *J Exp Mar Biol Ecol* 126: 77-94.
- Palacin C, Turon X, Ballesteros M, Giribet G, Lopez S 1998. Stock evaluation of three littoral echinoid species on the Catalan coast (North-Western Mediterranean). *PSZN Mar Ecol* 19: 163-177.
- Polunin NV, Roberts CM, 1993. Greater biomass and value of target coral reef fishes in two small Caribbean marine reserves. *Mar Ecol Prog Ser* 100: 167-176.
- Roberts CM, 1995. Rapid build-up of fish biomass in a Caribbean marine reserve. *Cons Biol* 9: 815-826.
- Sala E 1997. Fish predator and scavengers on the sea-urchin *Paracentrotus lividus* in protected areas of the north-western Mediterranean Sea. *Mar Biol* 129: 531-539.
- Sala E, Zabala M 1996. Fish predation and the structure of the sea-urchin *Paracentrotus lividus* populations in the NW Mediterranean. *Mar Ecol Prog Ser* 140: 71-81.
- Sala E, Ribes M, Hereu B, Zabala M, Alva V, Coma R, Garrabou J 1998. Temporal variability in abundance of the sea-urchin *Paracentrotus lividus* and *Arbacia lixula* in the northwestern Mediterranean: Comparison between a marine reserve and an unprotected area. *Mar Ecol Prog Ser* 168: 135-145.
- Savy S 1987. Les prédateurs de *Paracentrotus lividus* (Echinodermata) In Int Coll on *Paracentrotus lividus* and edible sea-urchins, Carry Le Rouet, France, 21 Feb. 1987. Edited by CF Boudouresque: 413-423.
- Scherrer B 1984. Biostatistique. *Gaëtan morin* ed., 850 p.
- Vacchi M, Bussotti S, Guidetti P, Mesa GL 1998. Study of the coastal fish assemblage in the marine reserve of the Ustica Island (southern Tyrrhenian Sea). *Italian J Zool* 65: 281-286.

Verlaque M 1984. Biologie des juvéniles de l'oursin *Paracentrotus lividus* (Lamarck): sélectivité du broutage et impact de l'espèce sur les communautés algales de substrat rocheux en Corse (Méditerranée, France). *Bot Mar* 27: 401-424.

Verlaque M 1987. Relations entre *Paracentrotus lividus* (Lamarck) et le phytobenthos de Méditerranée occidentale. In Int Coll on *Paracentrotus lividus* and edible sea-urchins, Carry Le Rouet, France, 21 Feb. 1987. Edited by CF Boudouresque: 5-36.

Verlaque M, Nédelec H 1983. Note préliminaire sur les relations biotiques *Paracentrotus lividus* (Lmk.) et herbier de posidonies. *Rapp Comm Int Mer Médit* 28: 157-158.

Watson M, Ormond RFG 1994. Effect of an artisanal fishery on the fish and urchin populations of a Kenyan coral reef. *Mar Ecol Prog Ser* 109: 115-129.

Wharton WG, Mann KH 1981. Relationship between destructive grazing by the sea-urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus americanus*, on the Atlantic coast of Nova Scotia. *Can J Fish Aquat Sci* 38: 1339-1349.

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Lanfani P, Planes S 2002. Temporal genetic changes between cohorts in a natural population of a marine fish, *Gobius niger*. *Mar Ecol Prog Ser* 241: 9-20.

Lopez S, Turon X, Moreno E, Planes S, Duran C, Turon J 1998. Larval abundance, recruitment and early mortality in *Paracentrotus lividus* (Echinodermata: Echinodermata) in the NW Mediterranean Sea. *Mar Ecol Prog Ser* 172: 239-251.

Lozano J, Gillet J, Lopez S, Turon X, Planes S, Moreno E 1995. Biological cycles and recruitment of *Paracentrotus lividus* (Lamarck) (Echinodermata: Echinodermata) in two contrasting habitats. *Mar Ecol Prog Ser* 125: 179-191.

MacClanahan TR, Mumby NA 1999. Patterns of predation on a sea-urchin, *Echinomaster scaber* (Planorbata: Echinodermata), on a Kenyan coral reef. *J Exp Mar Biol Ecol* 236: 77-94.

Planes S, Turon X, Ballesteros M, Gillet J, Lopez S 1995. Stock evaluation of three littoral echinoid species on the Catalan coast (North-Western Mediterranean). *ICES J Mar Sci* 52: 163-177.

Palumbo NV, Roberts CM 1993. Greater biomass and value of target coral reef fishes in two small Caribbean marine reserves. *Mar Ecol Prog Ser* 100: 167-176.

Roberts CM 1992. Rapid build-up of fish biomass in a Caribbean marine reserve. *Cons Biol* 6: 812-820.

Sala O 1997. Fish predator and scavengers on the sea-urchin *Paracentrotus lividus* in protected areas of the north-western Mediterranean Sea. *Mar Biol* 129: 221-229.

Sala O, Zabala M 1999. Fish predation and the structure of the sea-urchin *Paracentrotus lividus* population in the NW Mediterranean Sea. *Mar Ecol Prog Ser* 180: 71-81.

Sala O, Ribes M, Hixon B, Zabala M, Aiza V, Garcia R, Garmón I 1998. Temporal variability in abundance of the sea-urchin *Paracentrotus lividus* and effects of the northwestern Mediterranean. Comparison between a marine reserve and an unprotected area. *Mar Ecol Prog Ser* 168: 137-143.

Sala O 1987. Les prédateurs de *Paracentrotus lividus* (Echinodermata) in the Coll on *Paracentrotus lividus* and edible sea-urchins. Carry Le Rouet, France, 21 Feb. 1987. Edited by CF Boudouresque: 43-45.

Schroter B 1984. Bioturbation. *Coastal marine ecology*, 830 p.

Vaschi M, Busconi S, Guidetti F, Moss G 1998. Study of the coastal fish assemblage in the marine reserves of the Ustica Island (northwestern Sicilian Sea). *Ital J Zool* 65: 281-286.

Watson M, Ormond RFG 1994. Effect of an artisanal fishery on the fish and urchin populations of a Kenyan coral reef. *Mar Ecol Prog Ser* 109: 115-129.

Wharton WG, Mann KH 1981. Relationship between destructive grazing by the sea-urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus americanus*, on the Atlantic coast of Nova Scotia. *Can J Fish Aquat Sci* 38: 1339-1349.

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