

PUTATIVE EFFECTS OF RECREATIONAL FISHING OF *PARACENTROTUS LIVIDUS* ON POPULATIONS OF SEA URCHINS IN MEDITERRANEAN SHALLOW WATER

A. TESSIER^{1,2}, T. POISOT^{1,2,3}, P. ROMANS^{1,2}, Y. DESDEVISES^{1,2*}

¹UPMC Univ Paris 06, FRE 3355, Biologie Intégrative des Organismes Marins, Observatoire Océanologique, 66650 Banyuls/Mer, France

²CNRS, UMR 7232, Biologie Intégrative des Organismes Marins, Observatoire Océanologique, 66650 Banyuls/Mer, France

³Université Montpellier II, Institut des Sciences de l'Évolution, UMR 5554, Place Eugène Bataillon, 34095 Montpellier Cedex 05, France (present address)

* Corresponding author: yves.desdevises@obs-banyuls.fr

SEA URCHIN
PARACENTROTUS LIVIDUS
ARBACIA LIXULA
ABUNDANCE
RECREATIONAL FISHING
RESERVE EFFECT
POPULATION DENSITY
INDIVIDUAL SIZE

ABSTRACT. – The goal of this study was to assess the impact of recreational harvesting on the populations of two sea urchin species, *Paracentrotus lividus* and *Arbacia lixula*, via their population densities and mean individual size at three sites in shallow water in the Gulf of Lion (NW Mediterranean Sea) characterised by different anthropogenic pressures. We observed a positive relationship between mean size and population density for *P. lividus* at one of the three sites. The increase in anthropogenic pressure was linked to a decrease of both population density and individual size. Differences in mean size and densities were detected for *P. lividus* between a site with high anthropogenic pressure and sites with moderate to low anthropogenic pressure. These results suggest the existence of an impact of recreational sea urchin harvesting on populations of *P. lividus* and *A. lixula*, and stress the necessity of a regulation of such practices, as their effects are likely to affect local ecosystems.

INTRODUCTION

Several studies have reported that sampling activities (fishing, harvesting) have direct consequences on the benthic macrofauna, potentially decreasing density, individual size, and leading to sex ratio imbalance (Uphoff 1998, Brazeiro & Defeo 1999, Guidetti *et al.* 2004, Diele *et al.* 2005). Some indirect effects on the benthic community assemblages of rocky coasts have also been reported (Sala *et al.* 1998, Guidetti *et al.* 2003, Guidetti 2004).

Sea urchins are perhaps the most studied group of benthic macrofauna in the Mediterranean Sea (Le Direach *et al.* 1987, Lecchini *et al.* 2002, Guidetti *et al.* 2004, Pais *et al.* 2007). Their nutritional value and the delicacy of their gonads, along with the growing demand of the Japanese market (Cook & Kelly 2007), put some urchin species under intense harvesting pressure, potentially resulting in a decrease of population size in some inshore areas. In the Mediterranean Sea, *Paracentrotus lividus* (Lmk.) is sometimes intensively harvested, mostly along French, Spanish and Italian coasts (Le Direach *et al.* 1987, Palacín *et al.* 1988, Lawrence 2001, Pais *et al.* 2007). Furthermore, because they are frequently found in shallow waters, edible sea urchins are also subject to recreational fishing (Gianguzza *et al.* 2006, Pais *et al.* 2007). Recently, Duran *et al.* (2004) have suggested from population genetics that *P. lividus* population stocks are healthy on the Mediterranean and Atlantic coasts, but the increasing exploitation of edible sea urchins suggests stock monitoring along these coasts should be intensified to avoid any negative conse-

quences for stocks, such as decreases in density, biomass and individual size (Lecchini *et al.* 2002, Guidetti *et al.* 2004, Pais *et al.* 2007).

Fishing of sea urchins has indirect effects on the benthic community assemblages of rocky coasts, as they constitute keystone species of the Mediterranean infralittoral communities through their important role in the food web structuration (Kempff 1962, Lawrence 1975, Verlaque 1987). Many sea urchin species are herbivorous and graze on brown algae, calcareous algae, and seagrass species in the Mediterranean Sea (Verlaque 1987). Each urchin species has its specific diet. This herbivorous diet leads sea urchins to account for an important part of the dynamics of seaweeds (Frantzis *et al.* 1988, Palacín *et al.* 1988, Lecchini *et al.* 2002). In areas where *P. lividus* are abundant, their grazing on brown algae may trigger a shift in algal community composition, allowing the establishment of encrusting algae (Kempff 1962, Vukovic 1982, Verlaque & Nédélec 1983, Verlaque 1987, Spirlet *et al.* 1998). Some studies have shown that the presence of *P. lividus* exerts a role on the distribution of benthic assemblages (Sala & Zabala 1996, Guidetti 2004, Guidetti *et al.* 2004).

Several studies investigated the impact of commercial harvesting on sea urchin populations in the Mediterranean Sea (Le Direach *et al.* 1987, Gras 1987, Pfister & Bradbury 1996, Guidetti *et al.* 2004, Pais *et al.* 2007), but few considered the practice of recreational harvesting (Gianguzza *et al.* 2006, Pais *et al.* 2007). The objective of the present study was to assess the impact of recreational

harvesting on *P. lividus* and *A. lixula* by comparing population density and individual size in protected (Cerbère-Banyuls Marine Reserve) and unprotected areas along a portion of the French Gulf of Lion coast.

MATERIALS AND METHODS

Study area: Samples were collected in May 2008 along the French Catalan coast (North-Western Mediterranean Sea) both inside and outside the Cerbère-Banyuls Marine Reserve (Fig. 1) over a three weeks period. The study was conducted at three sites (Le Racou, Paulilles (Le Fourat) and Tancade) with a decreasing impact of recreational harvesting of sea urchins from Le Racou to Tancade (Table I). Le Racou is subjected to commercial and recreational fishing, Paulilles is subjected to recreational fishing only, while all fishing is prohibited in Tancade (personal communication of the managers of the Cerbère-Banyuls Marine

Reserve), which is located within a protected area.

Sampling: Mean size and abundance for both species were recorded *in situ*. The current practice of estimating size of sea urchins is to measure the diameter of the test in its widest part (ambitus) without spines (Barnes & Crook 2001, Lecchini *et al.* 2002, Barillé-Boyer *et al.* 2004, Pais *et al.* 2007). However, this technique damages the urchins, because the use of vernier callipers breaks their spines. We chose to use a non-destructive technique because part of our work was conducted in a protected area. A sample of urchins was measured with spines, using a calibration to the millimeter level. Harvesting *Paracentrotus lividus* individuals, on which the two measurement techniques were performed in the laboratory, allowed to validate this method. These urchins, used for validation, were collected at a location different from the three study sites. Pearson's correlation coefficient shows a strong linear relationship between the size with and without spines ($N = 122$, $R = 0.950$; $p = 0.001$, Fig. 2).

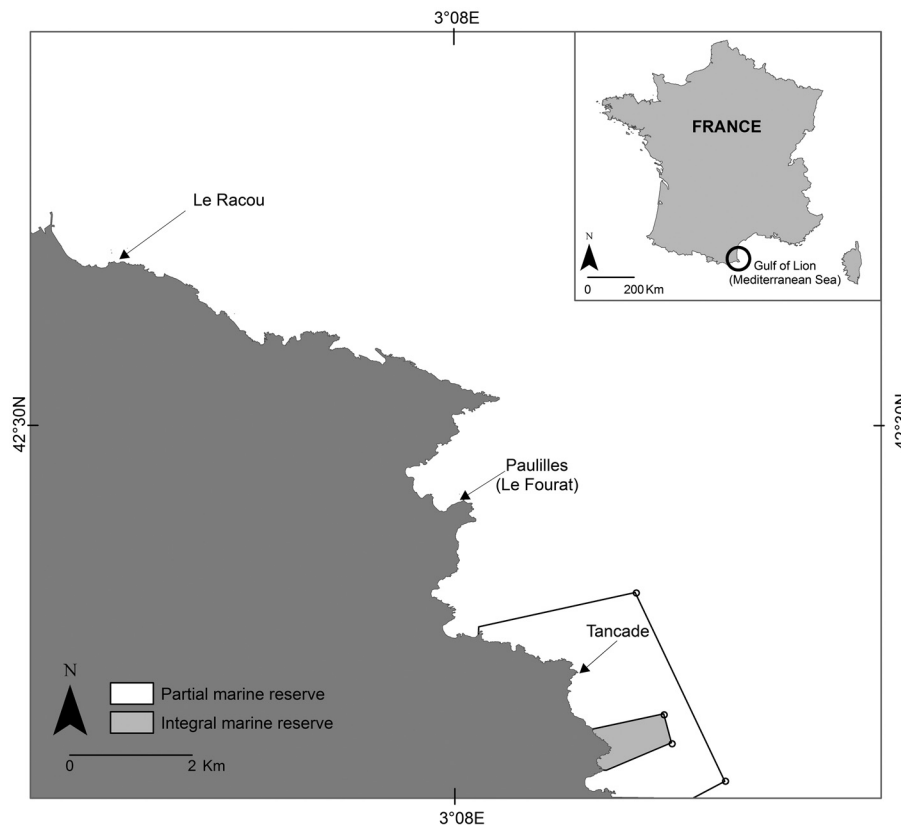


Fig. 1. – Location of the three study sites (Le Racou, Paulilles and Tancade) along the French Catalan coast; Le Racou: high anthropogenic pressure, Paulilles: moderate anthropogenic pressure and Tancade: low anthropogenic pressure

Table I. – Characteristics of the sampling sites.

Station	Protection status	Anthropogenic pressure	Topology	Principal algal coverage
Le Racou	Outside reserve	High	Bottom rough: low-depth areas (0.5 to 1 m) with sand and rock and deepest areas (1-2 m) with medium-sized pebbles	Grass algae and encrusting algae
Paulilles	Outside reserve	Moderate	Depth increasing gradually (0-2 m) with medium-sized rocks	Grass algae (0-1 m depth) and encrusting algae (1-2 m depth)
Tancade	Within reserve (harvest of sea-urchin prohibited)	Limited	Depth increasing gradually (0-2 m), large-sized rocks	Raised algae

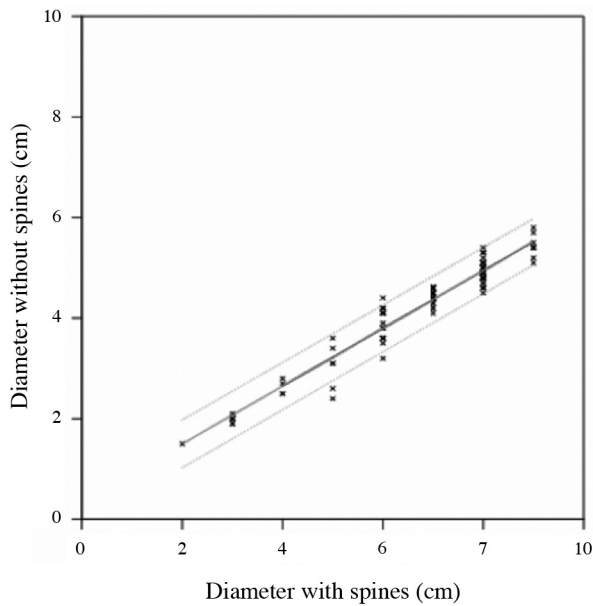


Fig. 2. – Scatterplot depicting the link between the diameter in cm of 122 *Paracentrotus lividus* individuals measured with and without spines ($R = 0.950$, $p < 0.001$)

The three sites were sampled in the 0-2 m depth range by snorkelling (because recreational fishing is usually done on foot or by snorkelling). We chose to use a random sampling design to estimate individual density and body size in the study area. In randomly chosen zones (“sample units”) of 1 meter radius circles delineated using a rope and a lead, the number and body size of all individuals of both urchin species were determined. At each site, 10 surveys of one hour each were conducted. This was repeated on four days at each site (for a total 40 replicates) and one person conducted all the samplings. Each area was randomly selected using a specially designed table listing random directions (indicated by randomly generated angles uniformly distributed in the range of 1-360 °) and distances (indicated by randomly generated fin kicks, uniformly distributed between 1 and 15).

Data analysis: The effects of species, sampling site, and interaction between these factors on density (expressed in individuals per square meter) were tested using a two-way ANOVA (random effects) with significance assessed via 999 permutations (Anderson & Legendre 1999). Because this test requires a balanced design (an equal number of observations in each condition), six datasets (corresponding to the six conditions implied by the combination of three sites and two species) containing 28 measures (size of the smallest sample) were reconstructed by random sampling within the original datasets. To ensure that sampling does not induce a bias in further analyses, means and variances of reconstructed and original datasets were compared.

Following the observation that data were not normally distributed (Shapiro-Wilk’s test), Bartlett’s test using 999 permutations was used to assess homogeneity of variances (Anderson & Legendre 1999). When two-way ANOVA resulted in a significant association between site or species and density, *a posteriori* tests were used to identify the modalities of the factor associated with the variation in the response variable. Whenever variances

were found to be equal among samples, t-tests with 999 permutations were used. Otherwise, non-parametric tests (Kruskal-Wallis and Mann-Whitney tests) were used.

The difference in mean size among sites for *Arbacia lixula* (at Paulilles and Tancade) was assessed using a Student’s t-test with 999 permutations, as variances were homogeneous (Fligner’s test) but data were not normally distributed. The differences in mean size among sites for *Paracentrotus lividus* (sites Le Racou, Paulilles, and Tancade) were measured by a one-way ANOVA, as data were normally distributed and variances were homogeneous (according to Fligner’s test). To characterize pairwise differences between sites, Tukeys’ Honestly Significant Difference *a posteriori* tests were used.

For each species at each site, correlations between population density and individual size were assessed using Pearson’s correlation tests (using 999 permutations, as density data were not normally distributed).

Analyses were conducted using the R 2.9.0 software (R development core team 2008). All tests were declared significant for $p < 0.05$.

RESULTS

Density and size

When testing for the effects of sampling site and urchin species on population density, we found that mean population density is different both between species ($p = 0.001$) and sampling site ($p = 0.005$; Table II), but no interaction was found between these two factors ($p = 0.132$). The mean population density for *Paracentrotus lividus* (2.55 ind.m⁻²) was greater than for *Arbacia lixula* (0.14 ind.m⁻², $p < 0.0001$).

Population density varied amongst sampling sites both when considering *A. lixula* and *P. lividus* simultaneously ($p = 0.005$) and separately (*A. lixula* $p = 0.003$; *P. lividus* $p = 0.01$). Densities were similar between Paulilles and Tancade (both species, $p = 0.211$; *A. lixula*, $p = 0.601$; *P. lividus*, $p = 0.096$). Densities observed in Le Racou were significantly smaller than in the two other sites, for both species (0.80 vs. 1.35 for Paulilles, $p = 0.03$, and 1.82 for Tancade, $p = 0.01$), as well as when considering only *A. lixula* (no individuals observed, vs. 0.27 for Paulilles, $p = 0.001$, and 0.22 for Tancade, $p = 0.012$) (Fig. 3) or only *P. lividus* (1.62, vs. 2.44 for Paulilles, $p = 0.038$, and 3.43 for Tancade, $p = 0.001$) only (Table II; Fig. 4).

We found no significant difference in mean individual size for *A. lixula* between Tancade (mean size = 6.91 cm) and Paulilles (mean size = 7.30 cm; $p = 0.743$; Table II). Individual sizes were different between sites for *P. lividus* (all sites, $p < 0.0001$) (Table II). Sizes were also significantly different between each pair of sites (Tancade - Paulilles, $p < 0.0001$; Le Racou - Paulilles, $p < 0.0001$; Tancade - Le Racou, $p < 0.0001$, Fig. 5). Individuals were larger in Tancade ($n = 26$, mean size = 6.60 cm) than in

Table II. – Mean and standard deviation for density and size for *Paracentrotus lividus* and *Arbacia lixula* at the three sampling sites, and percentage of *P. lividus* at each site. N is the number of individuals and X the number of replicates. “Significance” refers to the statistical test (ANOVA) of the comparison of means.

Variable	Le Racou (N, X)	Paulilles (N, X)	Tancade (N, X)	Significance
Total density of both species (ind.m ⁻²)	0.81 ± 1.52 (194,38)	1.36 ± 1.74 (341,40)	1.82 ± 2.42 (321,28)	P = 0.005
Density of <i>P. lividus</i> (ind.m ⁻²)	1.62 ± 1.83 (194,38)	2.44 ± 1.85 (307,40)	3.43 ± 2.51 (302,28)	P = 0.01
Density of <i>A. lixula</i> (ind.m ⁻²)	- (0,40)	0.27 ± 0.50 (34,40)	0.22 ± 0.50 (19,28)	P = 0.003
Size of <i>P. lividus</i> (cm)	4.29 ± 1.33 (194,28)	5.48 ± 1.34 (307,38)	6.60 ± 1 (302,26)	P < 0.0001
Size of <i>A. lixula</i> (cm)	- (0,0)	7.30 ± 1.26 (34,13)	6.91 ± 1.64 (19,4)	P = 0.743
Percentage of <i>P. lividus</i>	100 (194,38)	91.33 ± 16.30 (307,40)	95.59 ± 9.88 (302,28)	P = 0.607

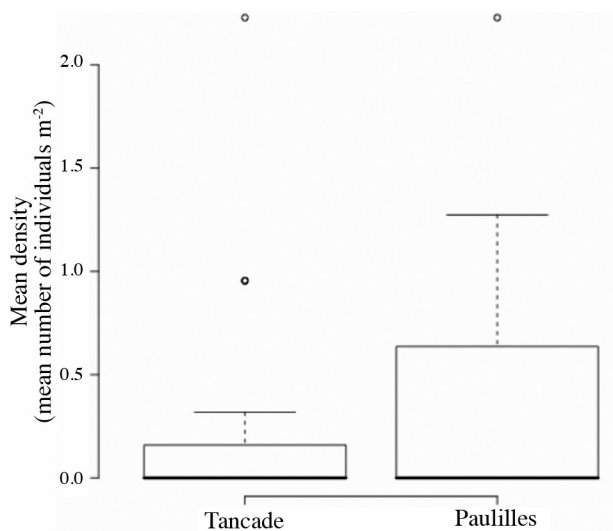


Fig. 3. – Mean density (mean number of individuals.m⁻²) of *Arbacia lixula* at the sites of Tancade and Paulilles. No significant difference was found between the sites ($p = 0.71$)

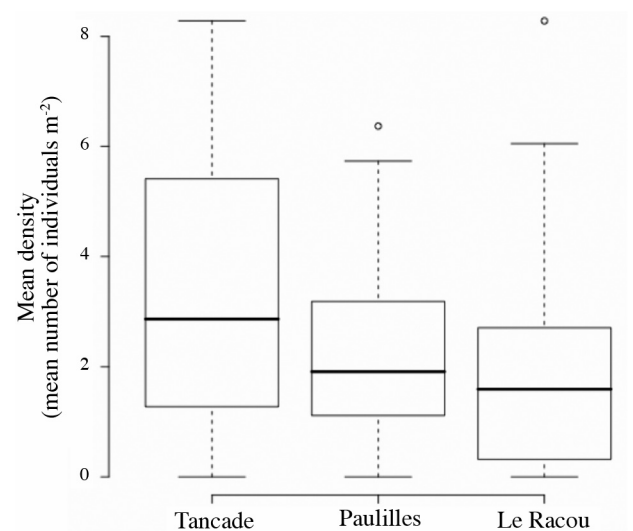


Fig. 4. – Mean density (in number of individuals.m⁻²) of *Paracentrotus lividus* at the sites of Tancade, Paulilles and Le Racou. No significant difference was found between Tancade and Paulilles ($p = 0.25$), but mean density at Le Racou was significantly lower ($p = 0.04$)

Paulilles ($n = 38$, mean size = 5.48 cm) and Le Racou ($n = 28$, mean size = 4.29 cm).

Relation between density and size

Except for a positive correlation for *Paracentrotus lividus* in Paulilles ($p = 0.004$), we found no correlation between density and mean individual size in any configuration (sites-species).

DISCUSSION

While slightly less precise, size with spines was found to be a good estimator of the test diameter, allowing *in situ* measurements of live animals. Previous studies have shown that echinoderm spines regenerate (Heatfield

1971, Dubois & Ameye 2001), for example after an environmental perturbation triggering their loss. Regeneration could induce some variability in the ratio of the diameter at the ambitus with and without spines (in that mature individuals may nonetheless display shorter spines than expected). Future research should characterize this variability within and between sampling sites and seasons to better estimate the effect of this process on the spine size pattern.

We observed a significant difference in the density of individuals of *Paracentrotus lividus* and *Arbacia lixula*, between a site with a high anthropogenic pressure and two sites with moderate and low anthropogenic pressure. This observation supports the hypothesis that anthropogenic pressure has an impact on sea urchin populations in the study area. The impact of recreational fishing, as well as commercial fishing, on the density of the sea urchins

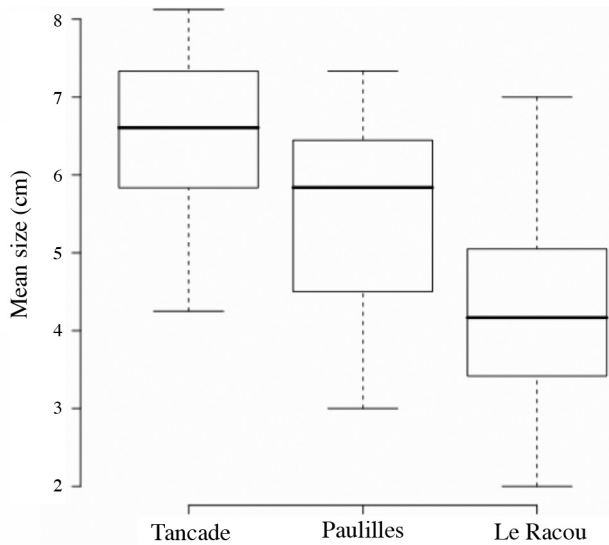


Fig. 5. – Mean sizes of *Paracentrotus lividus* individuals at the sites of Tancade, Paulilles and Le Racou. Mean sizes at all sites were significantly different and all pairwise tests indicate significant differences; individuals at Tancade were bigger ($p = 0.0001$), and individuals at Le Racou were smaller ($p = 0.0003$).

has been shown globally (Carter & Blaricom 2002). The low density of sea urchins at Le Racou could, if recreational fishing intensifies, lead to a total stock loss at this site, provoked by either the loss of reproductive individuals or a greater impact of stochastic population size variation. However, to assess the reality of such a risk, further work is required to understand population dynamics at this site. It must be assessed whether or not the individuals found at this site are reproducing, as fishermen tend to pick the larger, sexually mature, individuals, thus potentially decreasing the fraction of breeders in the population. If no reproducers are present in Le Racou, an extinction/colonization balance might nonetheless maintain the population of *P. lividus*. Difference between population density between the sites may also be explained by their topography, which although being rocky, is mainly horizontal. This should affect more *A. lixula*, known to live mostly on vertical rock walls (Kempf 1962, Bulleri *et al.* 1999, Guidetti & Mori 2005), than *P. lividus*, which possesses fewer adhesive tube feet and a larger test diameter and colonizes rather horizontal rocky areas (Bulleri *et al.* 1999). The difference in density observed between Le Racou and the two other sites contrasts with previous studies that found the opposite pattern: a higher density in an unprotected area compared to a protected area (Sala & Zabala 1996, Guidetti *et al.* 2004). In these studies, the difference may be explained by a cascade effect: the establishment of a protected status in an area leads to an increase in the density, biomass and diversity of fish due to a decrease in fishing pressure (Polunin & Roberts 1993), leading in turn to an increase in predators of sea urchins such as *Coris julis* and *Diplodus* spp. (Sala 1997, Barrett *et al.* 2009), therefore resulting in a lower

density of sea urchins in protected areas. We report the opposite, most likely because our study was carried out at low depths where such sea-urchin predators are rare, suggesting that their effect is low or absent. Such higher urchin densities in protected *vs.* unprotected areas has been previously observed in the same location (Lecchini *et al.* 2002), as well as in other regions (Gianguzza *et al.* 2006, Pais *et al.* 2007). This suggests that the dynamics of urchin population in protected (*vs.* unprotected) area is controlled by a balance between the effects of biodiversity conservation on the food chain [the so-called “reserve effect”, see e.g. Harborne *et al.* (2008)] and the release of direct anthropogenic pressure.

Only *P. lividus* presents a difference in mean size, at each site. The individual size of *P. lividus* individuals is 1.5 times lower at Le Racou than at Tancade and 1.2 times lower at Paulilles compared to Tancade, suggesting that individual size varies along a gradient of anthropogenic pressure. Such an effect is predictable, as fishermen tend to pick the largest individuals. In shallow Mediterranean rocky reefs, intense (and unregulated) exploitation probably leads to a reduction in the mean size of *P. lividus* (Gras 1987, Guidetti *et al.* 2004, Pais *et al.* 2007). Harvesting mainly takes place during the spawning period, between May and August. Previous studies indicate that the main spawning period of *P. lividus* is in spring and summer (Lozano *et al.* 1995, Lopez *et al.* 1998, Spirlet *et al.* 1998). This harvesting of the largest individuals may lead to a lower rate of reproduction, strengthened by the fact that urchins are harvested during the spawning season. The reduced reproduction rate may cause an irreversible decline of the population, which will in turn impact the local food web. The lack of significant differences of mean size of *A. lixula* between Tancade and Paulilles is to be taken with caution, as the numbers of replicates for this condition is low ($n = 4$). We could have expected an inverse relationship between population density and mean individual size, as shown for *Diadema antillarum*, consistent with the hypothesis that urchin body size is regulated by food availability (Levitan 1988). However, we observed that mean size increases with density for *P. lividus* at Paulilles. This could be linked to the shallow depth at which our study was carried out: larger (older) individuals are indeed found deeper than the smaller (young) specimens (Lecchini *et al.* 2002). This pattern is also expected if the difference in individual size and population density observed between sites is due to harvesting, because fishermen sample the largest individuals, then impacting both density and size.

In conclusion, the present study suggests that anthropogenic pressure such as recreational harvesting affects negatively the density and mean size of the urchin populations, especially *P. lividus*, at the sampling sites with a high or moderate anthropogenic pressure. This study is preliminary and it would be necessary to characterize precisely the nature of this pressure along the French Cata-

lan coast (relevant measures include number of harvesters, time spent harvesting, and mean number, size and sex ratio of harvested individuals). Some replicates of potentially harvested vs. non harvested sites should be included, and more environmental variables at each sites should be taken into account in the analysis and interpretation of the results. The effect of predators should also be more thoroughly investigated. In this study, we cannot rule out that this variation between sites is due to other factors such as population dynamics or seasonal processes, but previous data for comparison are lacking. However, our results suggest that, given the key role of these sea urchins in the coastal ecosystems, recreational harvesting should be more closely monitored in this area.

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REFERENCES

- Anderson MJ, Legendre P 1999. An empirical comparison of permutation methods for tests of partial regression coefficients in a linear model. *J Stat Comput Simul* 62: 271-303.
- Barillé-Boyer AL, Gruet Y, Barillé L, Harin N 2004. Temporal changes in community structure of tide pools following the "Erica" oil spill. *Aquat Living Resour* 17: 323-328.
- Barnes D, Cook A 2001. Quantifying behavioural determinants of the coastal European sea-urchin *Paracentrotus lividus*. *Mar Biol* 138: 1205-1212.
- Barrett N, Buxton C, Edgar G 2009. Changes in invertebrate and macroalgal populations in Tasmanian marine reserves in the decade following protection. *J Exp Mar Biol Ecol* 370: 104-119.
- Brazeiro A, Defeo O 1999. Effects of harvesting and density dependence on the demography of sandy beach populations: the yellow clam *Mesodesma mactroides* of Uruguay. *Mar Ecol Prog Ser* 182: 127-135.
- Bulleri F, Benedetti-Cecchi L, Cinelli F 1999. Grazing by sea urchins *Arbacia lixula* L. and *Paracentrotus lividus* Lam. in the Northwest Mediterranean. *J Exp Mar Biol Ecol* 241: 81-95.
- Carter S, Blaricom G 2002. Effect of experimental harvest on red sea urchins (*Strongylocentrotus franciscanus*) in northern Washington. *Fish Bull* 100: 662-673.
- Cook E, Kelly M 2007. Enhanced production of the sea urchin *Paracentrotus lividus* in integrated open-water cultivation with Atlantic salmon *Salmo salar*. *Aquaculture* 273: 573-585.
- Diele K, Koch V, Saint-Paul U 2005. Population structure, catch composition and CPUE of the artisanally harvested mangrove crab *Ucides cordatus* (Ocypodidae) in the Caeté estuary, North Brazil: Indications for overfishing? *Aquat Living Resour* 18: 169-178.
- Dubois P, Ameys L 2001. Regeneration of spines and pedicellariae in Echinoderms: a review. *Microscopy Res Tech* 55: 427-437.
- Duran S, Palacin C, Becerro M, Turon X 2004. Genetic diversity and population structure of the commercially harvested sea urchin *Paracentrotus lividus* (Echinodermata, Echinoidea). *Mol Ecol* 13: 3317-3328.
- Frantzis A, Berthon J, Maggiore F 1988. Relation trophique entre les oursins *Arbacia lixula* et *Paracentrotus lividus* (Echinoidea Regularia) et le phytobenthos infralittoral superficiel de la baie de Port-Cros (Var, France). *Sci Rep Port-Cros Natl Park* 14: 81-140.
- Gianguzza P, Chiantore M, Bonaviri C, Cattaneo-Vietti R, Vielmini I, Riggio S 2006. The effects of recreational *Paracentrotus lividus* fishing on distribution patterns of sea urchins at Ustica Island MPA (Western Mediterranean, Italy). *Fish Res* 81: 37-44.
- Gras G 1987. Evolution des stocks de l'Oursin comestible *Paracentrotus lividus* dans le quartier maritime de Marseille (France), soumis à une pêche intensive, entre les campagnes 1984-1985 et 1986-1987. In CF Boudouresque ed., Coll intern sur *Paracentrotus lividus* et les Oursins comestibles. GIS Posidonie Publ, Marseille: 363-370.
- Guidetti P 2004. Consumers of sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, in shallow Mediterranean rocky reefs. *Helgoland Mar Res* 58: 110-116.
- Guidetti P, A. Terlizzi, Boero F 2004. Effects of the edible sea urchin, *Paracentrotus lividus*, fishery along the Apulian rocky coast (SE Italy, Mediterranean Sea). *Fish Res* 66: 287-297.
- Guidetti P, Frascchetti S, Terlizzi A, Boero F 2003. Distribution patterns of sea urchins and barrens in shallow Mediterranean rocky reefs impacted by the illegal fishery of the rock-boring mollusc *Lithophaga lithophaga*. *Mar Biol* 143: 1135-1142.
- Guidetti P, Mori M 2005. Morpho-functional defences of Mediterranean sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, against fish predators. *Mar Biol* 147: 797-802.
- Harborne A, Mumby P, Kappel C, Dahlgren C, Micheli F, Holmes K, Sanchirico J, Broad K, Elliott I, Brumbaugh D 2008. Reserve effects and natural variation in coral reef communities. *J Appl Ecol* 45: 1010-1018.
- Heatfield BM 1971. Growth of the calcareous skeleton during regeneration of spines of the sea urchin *Strongylocentrotus purpuratus* (Stimpson) a light and scanning electron microscope study. *J Morphol* 134: 57-90.
- Kempf M 1962. Recherches d'écologie comparée sur *Paracentrotus lividus* (Lmk.) et *Arbacia lixula* (L.). *Rec Trav Stn Mar Endoume Fac Sci Mars* 25: 47-116.
- Lawrence JM 1975. On the relationships between marine plants and sea urchins. *Oceanogr Mar Biol Annu Rev* 13: 213-286.
- Lawrence JM 2001. Edible sea urchins: biology and ecology. Elsevier, Amsterdam.
- Lecchini D, Lenfant P, Planes S 2002. 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. *Vie Milieu* 52(2/3): 111-118.
- Le Direach L, Boudouresque CF, Antolic B, Kocatas A, Panayotidis P, Pancicci A, Semour R, Span A, Zaquali J, Zavodnik D 1987. Rapport sur l'exploitation des Oursins en Méditerranée. In CF Boudouresque ed., Coll intern sur *Paracentrotus lividus* et les Oursins comestibles. GIS Posidonie Publ, Marseille: 199-220.

- Levitan D 1988. Density-dependent size regulation and negative growth in the sea urchin *Diadema antillarum* Philippi. *Oecologia* 76: 627-629.
- Lopez S, Turon X, Montero E, Palacín C, Durate 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, Palacín C, Moreta G 1995. Biological cycles and recruitment of *Paracentrotus lividus* (Lamarck) (Echinodermata: Echinoidea) in two contrasting habitats. *Mar Ecol Prog Ser* 122: 179-191.
- Pais A, Chessa L, Serra S, Ruiu A, Meloni G, Donno Y 2007. The impact of commercial and recreational harvesting for *Paracentrotus lividus* on shallow rocky reef sea urchin communities in North-western Sardinia, Italy. *Estuar Coast Shelf S* 73: 589-597.
- Palacín C, Turon X, Ballesteros M, Giribet G, Lopez S 1988. Stock evaluation of three littoral echinoid species on the Catalan coast (North-Western Mediterranean). *PSZN Mar Ecol* 19: 163-176.
- Pfister C, Bradbury A 1996. Harvesting red sea urchins: recent effects and future predictions. *Ecol Appl* 6: 298-310.
- Polunin N, Roberts C 1993. Greater biomass and value of target coral reef fishes in two small Caribbean marine reserves. *Mar Ecol Prog Ser* 100: 167-176.
- 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, Boudouresque CF, Harmelin-Vivien M 1998. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos* 82: 425-439.
- 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.
- Spirlet C, Groslean P, Jangoux M 1998. Reproductive cycle of the echinoid *Paracentrotus lividus*: analysis by means of the maturity index. *J Invert Reprod* 34: 69-81.
- Uphoff JHJ 1998. Stability of the blue crab stock in Maryland's portion of Chesapeake Bay. *J Shellfish Res* 17: 519-528.
- Verlaque M 1987. Relations entre *Paracentrotus lividus* (Lamarck) et le phytobenthos de Méditerranée occidentale. In CF Boudouresque ed., Coll intern sur *Paracentrotus lividus* et les Oursins comestibles. GIS Posidonie Publ, Marseille: 5-36.
- Verlaque M, Nédélec H 1983. Note préliminaire sur les relations biotiques *Paracentrotus lividus* (Lmk.) et herbier de posidonies. *Rapp Comm Int Mer Médit* 28: 157-158.
- Vukovic A 1982. Florofaunistic changes in the infralittoral zone after the sea urchin *Paracentrotus lividus* (L.) population explosion. *Acta Adriat* 23: 237-241.

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