Habitat effects on the population structure of *Paracentrotus lividus* and *Arbacia lixula*

M. Chiantore[a]; I. Vielmini[b]; D. Privitera[a]; L. Mangialajo[a]; R. Cattaneo-Vietti[a]

[a] DIP. TE. RIS., Università di Genova, Genova [b] Dipartimento di Biologia, Università di Pisa, Pisa, Italy

PLEASE SCROLL DOWN FOR ARTICLE

Habitat effects on the population structure of *Paracentrotus lividus* and *Arbacia lixula*

M. Chiantore[a]*, I. Vielmini[b], D. Privitera[a], L. Mangialajo[a] and R. Cattaneo-Vietti[a]

[a]*DIP. TE. RIS., Università di Genova, Genova;* [b]*Dipartimento di Biologia, Università di Pisa, Pisa, Italy*

The goal of this study was to investigate habitat effects on the population structure and condition of the sea urchins *Paracentrotus lividus* and *Arbacia lixula*. Population structure (density, biomass, size frequency distribution) of both species has been investigated in two areas along the Ligurian coast, characterised by a different level of human disturbance, representing two alternative states of the infralittoral rocky bottom habitat, the photophilic algae assemblage and the barren ground. Samplings have been carried out in two sites within each area in two times, during Spring 2006. According to this experimental design, 10 individuals per species have been collected to evaluate trophic and reproductive conditions and analyse their gut contents, and, in order to relate feeding conditions to food availability, benthic assemblages have been characterised. *P. lividus* and *A. lixula* densities are different, as much as their diets change according to the benthic assemblage the urchins live in, but their trophic and reproductive conditions are not affected by food availability. Our results suggest that top-down processes rule the population structure while bottom-up ones cause changes in the diet, but do not alter the general conditions of the urchins.

Keywords: top-down *vs* bottom-up processes; *Paracentrotus Lividus*; *Arbacia Lixula*; population structure; alternative state of the habitat; Mediterranean rocky reefs

1. Introduction

Human activities in the marine coastal system, even if acting on single components, have the potential to affect the whole natural system, causing degradation and fragmentation of habitats [1]. Complex interactions and negative feedbacks due to human impact could have a negative resonance for the whole coastal biota, leading also to strong socio-economical implications [2,3]. Assessing, interpreting and predicting these direct and indirect changes are essential to fine tune conservation activities and environmental management [4].

Subtidal rocky substrates of the Mediterranean Sea are intensively disturbed by humans for several activities, ranging from seafood collection to diving tourism [5], that can affect marine food webs by altering dynamics among trophic levels [6,7].

---

*Corresponding author. Email: chiantor@dipteris.unige.it

One of the most disruptive activities carried out in the photophilic infralittoral community of the Mediterranean Sea is the date mussel *Lithophaga lithophaga* fishery (hereafter DMF), practiced by breaking limestone rocks in which the date mussels grow. In fact, the extended clearing action of DMF causes shift from multilayered macrobenthic assemblages to coralline barren [8–11], affecting the three-dimensional structure of assemblages that switches from high-cover, multilayered systems to sparse and mono-layered ones [10]. Herein, some studies [11] reported that sea urchins show significantly greater biomass than in control areas, preventing the recovery of benthic assemblages in rocky substrates affected by DMF [9, 12]. Further, the sea urchin juveniles can shelter in holes created by the DMF, finding refuge from predators, and this shelter availability is a key factor in determining predation rates [13]. This practice has been forbidden in Italy since 1998 [14]), but it is still illegally practiced in some areas.

Such shift to a coralline barren, in the Mediterranean Sea, may be caused and/or enhanced by alternation of the linear benthic top-down trophic cascade of the infralittoral level, composed by fish (mainly Sparids and Labrids), herbivores (in particular the sea urchins *Paracentrotus lividus* and *Arbacia lixula*) and algae [15–17]. As a consequence of the intensive fishing pressure exerted on the top level of this trophic cascade, sea urchins can lack of natural direct control, thus tending, in such condition, to increase in population densities [15]. At the density of about 7–9 ind/m^2 *P. lividus* can change the structure of the benthic assemblages affecting not only composition and biodiversity, but strongly reducing total algal cover, creating bare areas of coralline encrusting algae [17–19].

As soon as this barren condition is achieved, *P. lividus* and *A. lixula* are able, even if not present at high densities, to maintain it by grazing unselectively on newly recruits [9, 20–22].

As these urchins can live both at high and low densities, respectively over barren ground and in well vegetated algal assemblages, in this study we aimed to assess weather top-down or bottom-up processes play a major role in affecting the population structure and the biological conditions of sea urchins, namely the diet and the feeding and reproductive conditions. The study was performed in two areas, representing the two levels of factor Habitat, one that was affected by the DMF and where fishery is allowed and practiced, representing the Barren Ground condition (hereafter BG) and a second one, the no take-no entry zone of a Marine Protected Area, representing the Photophilic Algal assemblage one (hereafter PA). In particular we expected that diets, feeding and reproductive conditions of the two urchins are different across the two habitats, in response to different food availability. In case that bottom up processes are relevant, we expect that the diets would be different, more resembling in BG, where their feeding and reproductive conditions would be worse.

2. Materials and methods

2.1. *Sampling*

To test for the habitat effects on the *P. lividus* and *A. lixula* populations, two areas have been chosen along the Ligurian coast (Figure 1; North-western Mediterranean Sea, Italy), each representing a different alternative state of the habitat, the barren ground and the well vegetated conditions. The two study areas are the no take-no entry zone of the Portofino Marine Protected Area, Cala Oro (44°18'47.9" N – 09°10'00.5" E), representing the PA level of factor Habitat, in which human impact is only represented by no destructive research field activities (D.M. 26.04.1999) and Capo Noli (44°11'49.2" N – 08°25'31.0" E), severely damaged by a past illegal destructive date mussel *Lithophaga lithophaga* fishery (for fishery technique see [9]), where recreational fishing activities are allowed and practiced (angling and spear-fishing), representing the BG level.
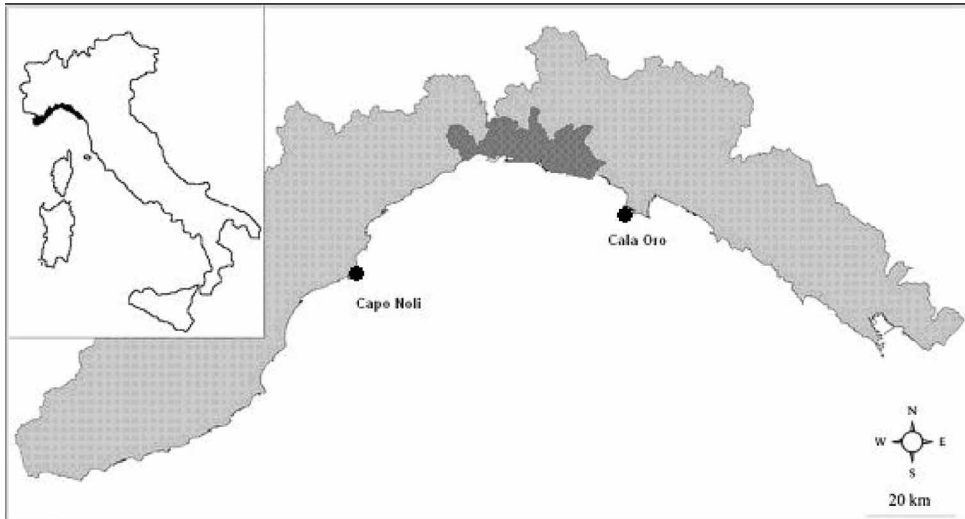
Figure 1. Sampling locations: Cala Oro: 44°18'47.94" N – 09°10'00.45" E; Capo Noli: 44°11'49.18" N – 08°25'31.04" E.

Both areas, around 100 km apart, have natural carbonatic rocky bottoms [8] and are similarly exposed to wave action.

The two sea urchin populations have been investigated by SCUBA diving, in two sites, hundreds meters apart, in each area, between 3 and 6 m depth. Sampling was performed twice in late spring (2006), when the highest algal biomass and cover are generally recorded in the Mediterranean algal assemblages [23], maximising the differences between the two levels of factor Habitat.

Densities of the two urchin species were estimated by counting specimens in three random transects (each composed by 10 quadrats, 1 m² each) per site per time, taking care of small cryptic individuals inside crevices or under boulders. Sampling of *P. lividus* and *A. lixula* was made by separate series of quadrats to insure independence of data. Size distributions were estimated by measuring test diameter, without spines, of all individuals in five quadrat replicates, per transect, site and time, using a vernier calliper, and data were grouped into 0.5 cm size classes. Ten adult specimens (>30 mm test diameter) for each species were collected in each sampling occasion in order to investigate feeding and reproductive conditions. Wet mass of total individual, gonads and gut have been weighed to calculate the repletion index (RI: gut wet weight × 100/total wet weight) and the gonado-somatic index (GSI: gonad wet weight × 100/total wet weight), according to [24] and [25]. The dissection was done as soon as possible, in order to reduce gut evacuation. Gut contents were frozen (−20°C), in order to analyse their composition in three specimens per site for each urchin species. Size-weight correlations between diameter of individuals and their volume were calculated for each site at each sampling time in order to evaluate the total population biomass on the base of the size/frequency distribution.

Benthic assemblages in the three locations have been characterised by taking five digital photos of 400 cm² area each, within each site, per time. Each digital image was analysed by superimposing a grid of 25 equal-sized small squares (each of them representing 4% of the total surface of each image). The percent cover of algae was quantified by, in each small quadrat, assigning a value comprised between 0 (no presence) and 4 (total cover) to each item present. Values of each quadrat per grid were added to obtain the final percentage.

Gut contents were characterised through binocular observation of two equal random samples of the contents from each specimen, placed on a 2.5 × 2.5 cm grid. The relative percent abundance of each gut component was thus determined as relative percent abundance. Such method was used

as a modification of the Jones' one [26], used in the past by [27] and [28], taking into account not only the percent occurrence of the different food items, but also their relative cover.

Taxa from the benthic assemblages and from the gut content analyses were identified, whenever possible, to species level; they have then been grouped in OTUs (Operative Taxonomic Units) for the data analyses: *Posidonia oceanica*, Fucales (*Cystoseira* spp.), Dictyotales (*Padina pavonica*, *Dictyota* spp., *Dictyopteris polypodioides*), other Brown Erect algae (BE, mainly *Halopteris filicina*, *Stypocaulon scoparium, Sphacelaria* spp. and *Cladostephus spongiosus*), Green Erect algae (GE, mainly *Acetabularia acetabulum* and *Codium* spp.), Red Erect algae (REr, mainly *Laurencia* complex), Articulated Corallinales (AC, including *Corallina elongata*, *Amphiroa* spp., *Jania rubens, Haliptilon virgatum*), Red Encrusting Algae (REn, Corallinales and *Peyssonnelia* spp.), Turf (including filamentous algae, mostly Ceramiales and Cladophorales), mucilage, animal taxa (such as the sponges *Spirastrella cunctatrix*, *Crambe crambe*, *Cliona* spp., hydroids, the anthozoan *Balanophyllia* spp., and the boring bivalve *Gastrochaena dubia*), Cyanobacteria. This latter OTU, as well as *Posidonia oceanica*, was found in the gut contents only, while some of the animals, such as *Gastrochaena dubia*, were found only in the benthic assemblages and not in the guts. The percent cover of each OTU was referred to the whole sampling surface, taking into account, for the benthic assemblages, also the percent cover of bare rock, organic detritus and holes, natural and caused by DMF, in order to compare the different levels of food availability to grazing organisms.

2.2.   *Data analysis*

Analysis of Variance (ANOVA) was used to test for differences in sea urchins density, biomass, size structure, RI and GSI. The full model for testing Habitat effects on sea urchin populations is composed by four factors: Species (fixed, two levels: *Paracentrotus* and *Arbacia*), Habitat (fixed, crossed, two levels: Photophilic Algae-PA, Cala Oro; Barren Ground-BG, Capo Noli), Site (random, nested in Habitat, two levels) and Time (random, crossed, two levels). As the full model could not provide tests for the main factors (Species and Habitat) the two sampling times were analysed separately.

Authors are well aware that factor Habitat was not properly replicated, yet, there are not comparable areas for both date mussel fishery and for protected areas close enough (in the order of hundreds of km), in order to avoid the interplay of counfounding factors, acting beyond the regional scale. The closest Marine Protected Area, the Cinque Terre one, could not be used in an asymmetric design, as it was shown to display quite different features relative to the Portofino one [29].

Prior to analysis, the homogeneity of variances was tested by Cochran's test. When the assumption of homogeneity of variances was violated data were transformed and the assumption was checked again [30]. As transformation did never remove heterogeneity, also in these cases untransformed data were analysed, setting $\alpha = 0.01$ to compensate for the increased likelihood of Type I error. When appropriate, SNK tests were performed for *a posteriori* multiple comparisons of the means. ANOVAs were performed using the GMAV5 software package (University of Sydney, Australia).

Distance-based permutational multivariate analysis of variance (PERMANOVA, [31]) based on Bray–Curtis dissimilarities [32] on square root transformed data was used to test significance of factor effects on benthic assemblages and in the gut contents of the two species. Multivariate patterns of distribution of benthic assemblages and gut contents were plotted using a principal coordinates analysis (PCO, [33]), based on Bray–Curtis dissimilarities on square root transformed data, separately for each sampling date. PCO and PERMANOVAs were performed using Primer 6 and PERMANOVA $+ \beta 3$.

3. Results

Average density ranges from 1.6 ind/m^2 ($\pm$ 1.2 SE) to 10.2 ind/m^2 ($\pm$ 0.5 SE) and from 0.2 ind/m^2 ($\pm$ 0.9 SE) and 6.1 ind/m^2 ($\pm$ 1.1 SE), for *P. lividus* and *A. lixula* respectively (Figure 2). Densities are generally higher in the BG area, although significant effects are detected only in the second sampling time, where lowest density values are recorded in the PA area than in the BG one, and, in addition, Species effects are detected, being *Paracentrotus lividus* densities higher than *A. lixula* ones (Table 1).

The size frequency distribution of *P. lividus* (Figure 3a) shows that, in the PA area, its population is represented for about 60% by individuals belonging to the smallest classes (i.e. 10–30 mm). In contrast, the BG population is skewed towards a larger size. Differently, *A. lixula* populations (Figure 3b) show a similar uni-modal size frequency distribution across the two Habitat types,

Figure 2.   *Paracentrotus lividus* (grey) and *Arbacia lixula* (white) densities in the two habitats (Photophilic Algae and Barren Ground), separately in the two sampling times (T1 and T2).

Table 1.   ANOVA results on density of the two urchin species, separately for the two sampling times. Cochran's test significant: set $\alpha = 0.01$. Data not transformed.

Density		T1			T2			
Source	DF	MS	F	P	MS	F	P	F *versus*
Species	1	7.9350	6.92	0.1193	99.2267	194.24	**0.0051**[a]	Sp×si(ha)
Habitat	1	165.3750	12.46	0.0717	210.0417	561.36	**0.0018**[b]	Si(ha)
Site (Ha)	2	13.2675	3.59	0.0516	0.3742	0.25	0.7829	Residual
Sp × Ha	1	2.6667	2.32	0.2669	43.2017	84.57	0.0116	Sp×si(ha)
Sp × Si (Ha)	2	1.1475	0.31	0.7376	0.5108	0.34	0.7173	Residual
Residual	16	3.6992			1.5058			
Total	23							

[a]SNK test: *Paracentrotus>Arbacia***
[b]SNK test: BG>PA**
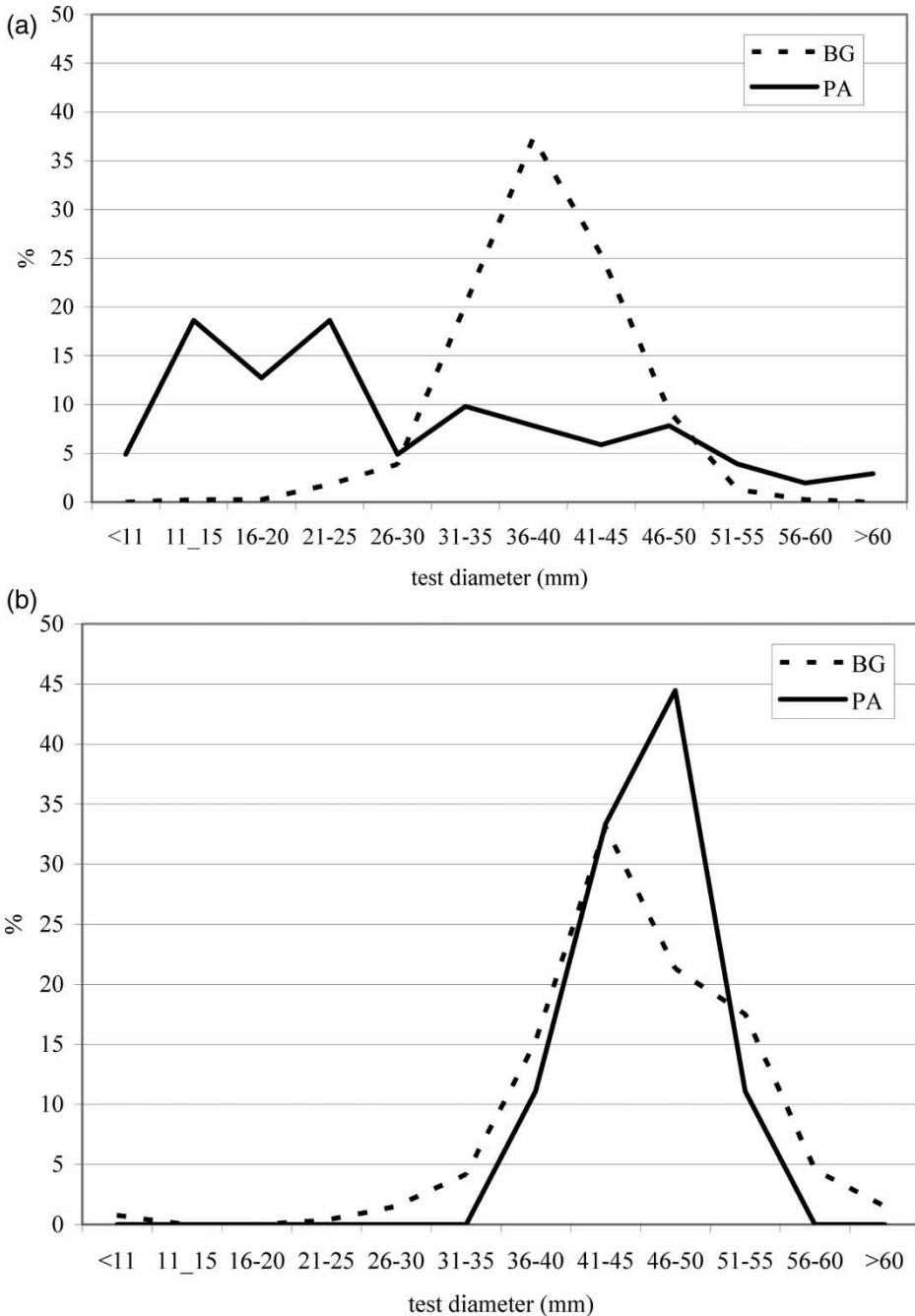
Figure 3.   Size frequency distribution of the two urchin species in the two habitats (Photophilic Algae and Barren Ground) averaged on the two sampling times: (a) *Paracentrotus lividus*; (b) *Arbacia lixula*.

always lacking the small-size individuals. Yet, ANOVA (Table 2) performed on modal size of the two urchins shows no effects of both Species and Habitat, showing that this population parameter cannot be considered a good descriptor of population structure. Biomass values (Figure 4) range from 34.4 gWW/m² (± 16.8 SE) in the PA area, to 244.1 gWW/m² (± 23.4 SE) in the BG one

Table 2. ANOVA results on modal size of the two urchin species, separately for the two sampling times. Cochran's test significant: set $\alpha = 0.01$. Data not transformed.

Modal size		T1			T2			
Source	DF	MS	F	*P*	MS	F	*P*	F *versus*
Species	1	1254.2604	74.10	0.0132	90.2968	2.50	0.2544	sp×si(ha)
Habitat	1	742.5938	32.04	0.0298	137.5095	13.11	0.0685	si(ha)
Site (Ha)	2	23.1771	0.91	0.4221	10.4873	0.12	0.8902	Residual
Sp × Ha	1	536.7604	31.71	0.0301	1.7889	0.05	0.8444	sp×si(ha)
Sp × Si (Ha)	2	16.9271	0.67	0.5278	36.0651	0.40	0.6749	Residual
Residual	16	25.4479			89.4766			
Total	23							

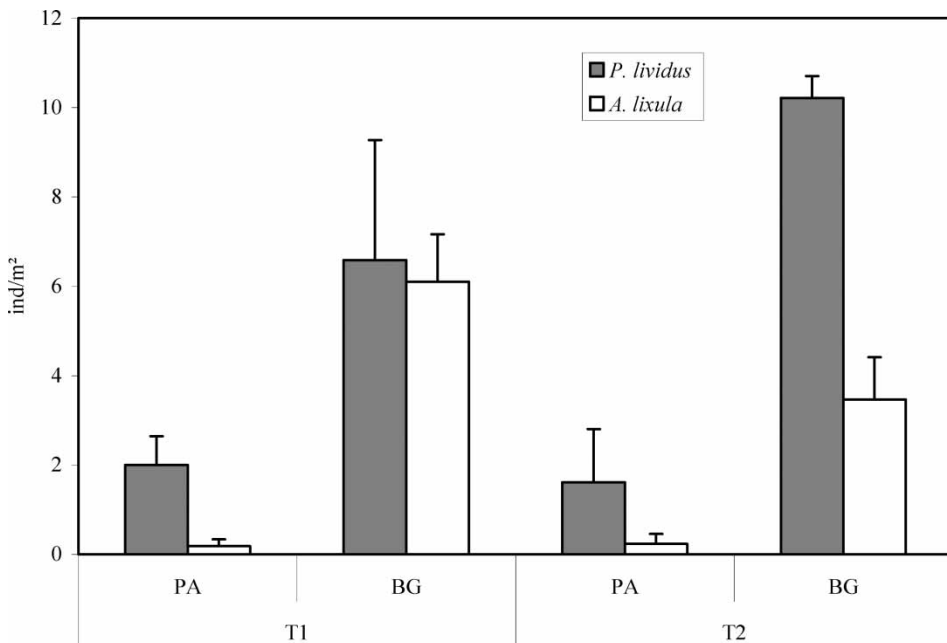Figure 4. *Paracentrotus lividus* (grey) and *Arbacia lixula* (white) biomass in the two habitats (Photophilic Algae and Barren Ground), separately in the two sampling times (T1 and T2).

for *P. lividus*, while *A. lixula* biomass ranges from $6.0 \, \text{gWW/m}^2$ (± 4.3 SE) in the PA area to $212.5 \, \text{gWW/m}^2$ (± 39.2 SE) in the BG one (Figure 4). A significant Species × Habitat effect is detected only in Time 2 (Table 3), when biomasses of both species are higher in BG than in PA; in BG *P. lividus* shows higher biomass than *A. lixula*, while in PA the two species do not show significant differences in terms of biomass.

P. lividus repletion index values range from 7.5 (± 1.8 SE) to 12.4 (± 3.5 SE), both values in PA, in Time 2 and 1 respectively. Differently, *A. lixula* repletion index values change from 5.3 (± 1.7 SE) in the BG area to 10.8 (± 3.5 SE) in the PA one (Figure 5). Yet, ANOVA performed on the repletion index does not detect any Species or Habitat effects (Table 4).

P. lividus gonado-somatic index values (Figure 6) range between 2.2 (± 1.3 SE) and 8.9 (± 1.7 SE) in PA and BG respectively, while *A. lixula* GSI values range between 5.1 (± 1.9 SE) and 7.7 (± 3.7 SE) in BG and PA respectively. Yet, ANOVA performed on gonado-somatic index does not detect any Species or Habitat effect (Table 5), and only a little small

Table 3. ANOVA results on biomass (gWW/m^2) of the two urchin species, separately for the two sampling times. T1: Cochran's test significant: set $\alpha = 0.01$. Data not transformed. T2: Cochran's test not significant on untransformed data.

Biomass		T1			T2			
Source	DF	MS	F	P	MS	F	P	F *versus*
Species	1	370.9792	0.05	0.8441	44222.2703	173.89	0.0057	sp×si (ha)
Habitat	1	73303.2310	14.07	0.0643	140624.3956	81.54	0.0120	si(ha)
Site (Ha)	2	5210.9676	2.08	0.1571	1724.5505	1.60	0.2330	Residual
Sp × Ha	1	55223.7160	7.41	0.1126	19216.8091	75.56	**0.0130**[a]	sp×si (ha)
Sp × Si (Ha)	2	7448.8309	2.98	0.0796	254.3132	0.24	0.7928	Residual
Residual	16	2502.1719			1079.4042			
Total	23							

[a] SNK: factor Habitat: BG: *Paracentrotus>Arbacia***, PA: NS; Factor Species: *Paracentrotus*: BG>PA**, *Arbacia*: BG>PA**.
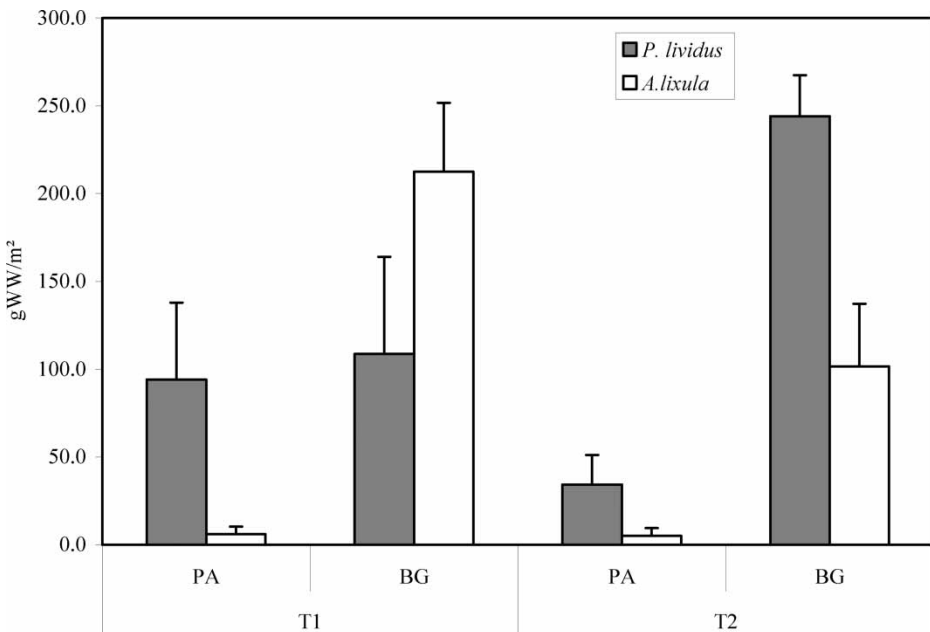

Figure 5. *Paracentrotus lividus* (grey) and *Arbacia lixula* (white) repletion index in the two habitats (Photophilic Algae and Barren Ground), separately in the two sampling times (T1 and T2).

Table 4. ANOVA results on repletion index (RI) values of the two urchin species, separately for the two sampling times. Cochran's test not significant on untransformed data.

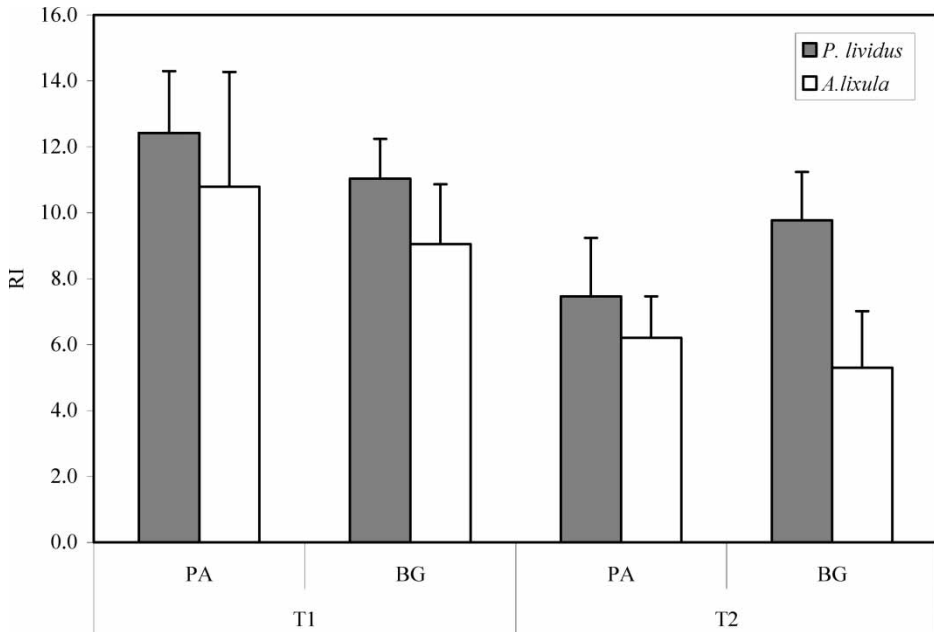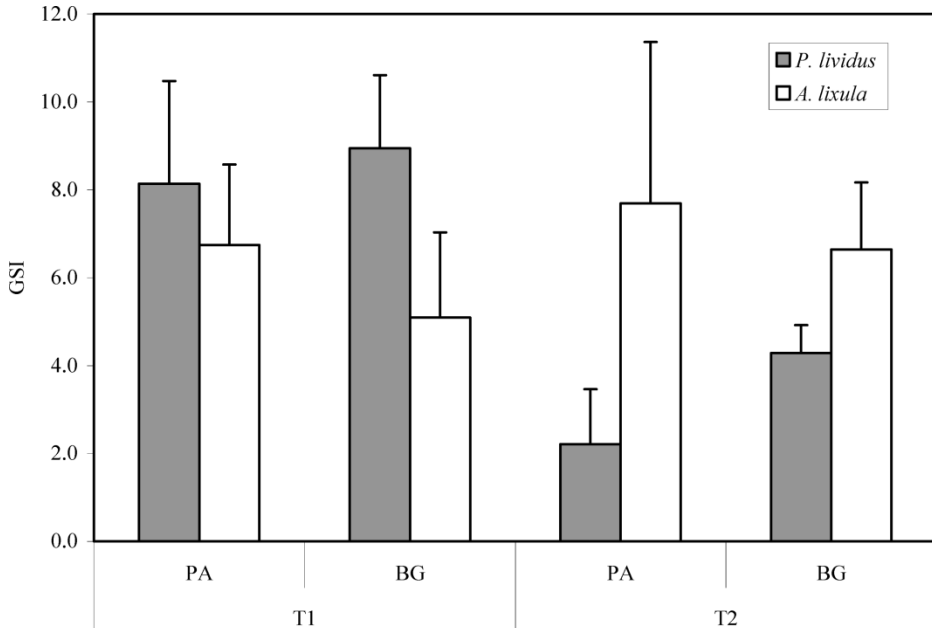| Repletion Index		T1			T2			
Source	DF	MS	F	P	MS	F	P	F *versus*
Species	1	19.2426	1.15	0.3959	49.3430	16.85	0.0545	Sp × si (ha)
Habitat	1	14.8681	3.54	0.2007	3.0726	0.47	0.5646	Si(ha)
Site (Ha)	2	4.2006	0.41	0.6679	6.5688	1.32	0.2935	Residual
Sp × Ha	1	0.1820	0.01	0.9265	15.7021	5.36	0.1466	Sp × si (ha)
Sp × Si (Ha)	2	16.7391	1.65	0.2232	2.9285	0.59	0.5656	Residual
Residual	16	10.1488			4.9586			
Total	23							

Figure 6. *Paracentrotus lividus* (grey) and *Arbacia lixula* (white) gonado-somatic index in the two habitats (Photophilic Algae and Barren Ground), separately in the two sampling times (T1 and T2).

Table 5. ANOVA results on gonado-somatic index (GSI) values of the two urchin species, separately for the two sampling times. Cochran's test not significant on untransformed data.

Gonado-somatic Index		T1			T2			
Source	DF	MS	F	*P*	MS	F	*P*	F *versus*
Species	1	0.0383	1.16	0.3946	0.1336	1.06	0.4108	Sp × si (ha)
Habitat	1	0.2220	2.31	0.2682	0.0029	0.06	0.8358	Si (ha)
Site (Ha)	2	0.0963	2.15	0.1492	0.0516	1.57	0.2385	Residual
Sp × Ha	1	0.0016	0.05	0.8467	0.0004	0.00	0.9579	Sp × si (ha)
Sp × Si(Ha)	2	0.0331	0.74	0.4937	0.1256	3.82	**0.0441**[a]	Residual
Residual	16	0.0448			0.0329			
Total	23							

[a] SNK: factor Species: PA Site1: *Arbacia>Paracentrotus**, PA Site 2: NS, BG Site1: *Arbacia>Paracentrotus**, BG Site 2: NS.

scale effect is detected during the second sampling time (significance of the interaction term SpeciesXSite(Habitat)).

The benthic assemblages in the two areas widely differ in both sampling times, being the algal cover much higher in the PA than in the BG area, with very similar values in the two sampling times (91.9% ± 1.6 SE and 91.0% ± 4.0 SE in PA and 46.8% ± 17.1 SE and 47.0% ± 6.4 SE in BG, in the two times respectively). Largest differences are found, in particular, for Dictyotales and AC, more abundant in PA (32.8% ± 1.6 SE and 22.3% ± 3.6 SE, respectively, mean on both sampling times) than in BG (0.8% ± 0.7 SE and 1.7% ± 1.1 SE, respectively, mean on both sampling times). REn and animal taxa relative cover is, instead, larger in BG (26.2% ± 7.4 SE and 38.6% ± 7.6 SE, respectively, mean on both sampling times) than in PA (8.1% ± 4.2 SE and 2.7% ± 0.8 SE, respectively, mean on both sampling times). PCO plots performed on benthic assemblages are reported in Figure 7a and 7b and PERMANOVA results are reported in

Figure 7. (a) PCO plot performed on benthic assemblages in Time 1; (b) benthic assemblages in Time 2; (c) PCO plot performed on gut contents of the two urchin species in Time 1; (d) gut contents in Time 2. In plots (a) and (b) symbols refer to the Habitat (Barren Ground-BG and Photophilic Assemblage-PA) and labels to the Sites. In plots (c) and (d) symbols refer to the urchin species and labels to the Habitat.

Table 6. PERMANOVA results on the benthic assemblages, separately for the two sampling times.

Benthic assemblages		T1			T2		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Habitat	1	11599	7.9762	**0.012**	24585	26.762	**0.011**
Site (Habitat)	2	1454.2	2.9267	**0.014**	918.65	1.5086	0.195
Residual	16	496.88			608.94		
Total	19						

Table 6: the two Habitats are significantly different in each sampling time, and a significant spatial variability at the Site scale is detected in T1.

The diets of the two urchin species are consistently different in both habitats, being both Species and Habitat effects significant (Figure 7c and d; Table 7). Yet, in the second sampling time a small scale variability is detected, being the term Species × Site (Habitat) significant. The species belonging to the order Dictyotales mostly make the two diets different, representing the 41.6% ± 29.4 SE and 32.9% ± 32.9 SE of gut content in *P. lividus* on PA and BG, respectively, and the 6.4% ± 4.5 SE and the 0.5% ± 0.4 SE in *A. lixula*, respectively in the two habitats.

4. Discussion and conclusions

The two investigated habitats are confirmed to be quite different in terms of benthic assemblage structure, being algal cover much higher in the PA area than in the BG one. Yet, the population

Table 7. PERMANOVA results on the gut contents of the two urchin species, separately for the two sampling times.

Gut contents		T1			T2		
Source	df	MS	Pseudo-F	*P*(perm)	MS	Pseudo-F	*P*(perm)
Species	1	7747.4	11.346	**0.004**	6981.8	6.3163	**0.007**
Habitat	1	8133.8	10.38	**0.003**	5645	10.934	**0.004**
Site (Habitat)	2	783.61	1.337	0.209	516.3	0.9827	0.467
Species × Habitat	1	647.78	0.94867	0.506	1706.3	1.5436	0.224
Species × Site(Habitat)	2	682.83	1.165	0.333	1105.4	2.1039	**0.024**
Residual	16	586.1			525.38		
Total	23						

structure of the two urchins shows significant Habitat and Species effects only in the second sampling time. At this time, densities of sea urchins are higher in BG than in PA and a Species effect is detected, being *P. lividus* significantly more abundant than *A. lixula*. These effects are detected also in terms of biomass. In contrast, the size of the modal class does not show any Habitat or Species effect, although the size/frequency distributions of the two species are quite different in the two habitats (especially in PA), showing that this population parameter cannot be considered a good descriptor of population structure. *A. lixula* populations are mainly composed of 40–50 mm (test diameter) individuals, in both habitats, while *P. lividus* shows smaller individuals in PA than in BG, where the middle size classes, the most affected by fish predation [22], are the most abundant. In BG, *P. lividus* size frequency distribution is skewed towards large size, suggesting the lack of a direct control by top predators. In contrast, in the PA area, the no take-no entry zone of Portofino MPA, in which fishing is not allowed, *P. lividus* population is well represented by juvenile size classes, while larger ones are less conspicuous, confirming that a top-down control on sea urchins is effective [17]. The lack of Habitat effect on *A. lixula*, less predated by fish, because of morpho-functional defences [34], showing similar size frequency distribution patterns across the two areas, supports our conclusions.

The diets of the two species are different and remain different across the two habitats, with a strong selectivity of *P. lividus* for Dictyotales, particularly in BG, where this food item, although representing only the 0.8% of total cover in the benthic assemblage sums up to 32.9% of the gut content. Repletion index, instead, as well as the gonado-somatic index, is not affected at all by the habitat. These findings do not support the hypothesis of Habitat effects on feeding and reproductive conditions of the two urchins, showing that both species cope well and share food resources in the two alternative habitat conditions and suggesting that bottom-up control plays a minor role in affecting the two urchins. Bottom-up processes cause changes in the diet, but do not alter the general conditions of the urchins.

Instead, our results indicate that the differences in population structure of these two common sea urchin species between the PA and the BG conditions are a response of their different sensitivity to fish predation [34] and to the larger abundance of urchin fish predators in the undisturbed assemblage [17,35], suggesting the most relevant role played by top-down vs bottom-up processes.

References

[1] L. Watling and E.A. Norse, *Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting*, Conserv. Biol. 12 (1998), p. 6.

[2] R.S. Steneck and J.T. Carlton, *Human alteration of marine communities – students beware!* in *Marine Community Ecology*, M.D. Bertness, S.D. Gaines, and M. Hay, eds, Sinauer Associates, Sunderland, MA, 2001, pp. 445–468.

[3] J.D. Witman and P.K. Dayton, *Rocky subtidal communities*, in *Marine Community Ecology*, M.D. Bertness, S.D. Gaines, and M. Hay, eds, Sinauer Associates, Sunderland, MA, 2001, pp. 339–363.

[4] L. Benedetti-Cecchi, F. Pannacciulli, F. Bulleri, P.S. Moschella, L. Airoldi, G. Relini, and F. Cinelli, *Predicting the consequences of anthropogenic disturbance: Large-scale effects of loss of canopy algae on rocky shores*, Mar. Ecol.-Prog. Ser. 214 (2001), p. 137.

[5] J. Garrabou, E. Sala, A. Arcas, and M. Zabala, *The impact of diving on rocky sublittoral communities: A case study of a bryozoan population*, Conserv. Biol. 12 (1998), p. 302.

[6] T.R. McClanahan and E. Sala, *A Mediterranean rocky-bottom ecosystem fisheries model*, Ecol. Model. 104 (1997), p. 145.

[7] J.B.C. Jackson, et al., *Historical overfishing and the recent collapse of coastal ecosystems*, Science 293 (2001), p. 629.

[8] G.F. Russo and F. Cicogna, *Il dattero di mare,* Lithophaga lithophaga *e gli effetti distruttivi della sua pesca sull'ambiente marino costiero: problemi e prospettive*, Boll Museo Istituto Biol Uni Genova 56 (1992), p. 165.

[9] G. Fanelli, S. Piraino, G. Belmonte, S. Geraci, and F. Boero, *Human predation along the Apulian rocky coast (SE Italy): Desertification caused by* Lithophaga lithophaga *(Mollusca) fisheries*, Mar. Ecol.-Prog. Ser. 110 (1994), p. 1.

[10] S. Fraschetti, C.N. Bianchi, A. Terlizzi, G. Fanelli, C. Morri, and F. Boero, *Spatial variability and human disturbance in shallow subtidal hard substrate assemblages: a regional approach*, Mar. Ecol.-Prog. Ser. 212 (2001), p. 1.

[11] P. Guidetti, S. Fraschetti, A. Terlizzi, and F. Boero, *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 (2003), p. 1135.

[12] T.R. McClanahan, A.T. Kamukuru, N.A. Muthiga, M. Gilagabher Yebio, and D. Obura, *Effect of sea urchin reductions on algae, coral, and fish populations*, Conserv. Biol. 10 (1995), p. 136.

[13] B. Hereu, M. Zabala, C. Linares, and E. Sala, *The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins*, Mar. Biol. 146 (2005), p. 293.

[14] P. Guidetti, S. Fraschetti, A. Terlizzi, and F. Boero, *Effects of desertification caused by* Lithophaga lithophaga *(Mollusca) fishery on littoral fish assemblages along rocky coasts of South-eastern Italy*, Conserv. Biol. 18 (2004), p. 1417.

[15] E. Sala, C.F. Boudouresque, and M. Harmelin-Vivien, *Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm*, Oikos 82 (1998), p. 425.

[16] B. Hereu, *Depletion of palatable algae by sea urchins and fishes in a Mediterranean subtidal community*, Mar. Ecol.-Prog. Ser. 313 (2006), p. 95.

[17] P. Guidetti and E. Sala, *Community-wide effects of marine reserves in the Mediterranean Sea*, Mar. Ecol.-Prog. Ser. 335 (2007), p. 43.

[18] M. Verlaque, *Relations entre* Paracentrotus lividus *(Lamarck) et le phytobenthos de Mediterranée occidentale*, in *Colloque international sur* Paracentrotus lividus *et les oursins commestibles*, C.F. Boudouresque, ed., GIS Podidonie Publications, Marseille (1987, pp. 5–36.

[19] J.M. Lawrence, *On the relationship between marine plants and sea urchins*, Oceanogr. Mar. Biol. 13 (1975), p. 213.

[20] D. Privitera, M. Chiantore, L. Mangialajo, N. Glavic, W. Kozul, R. Cattaneo-Vietti, and G. Albertelli, *Spatial scale of variability of sea urchins and algal communities in the Dubrovnik Area*, 15th Meeting of the Italian Society of Ecology, Torino, Italy, 2005.

[21] P. Gianguzza, M. Chiantore, C. Bonaviri, R. Cattaneo-Vietti, I. Vielmini, and S. Riggio, *The effects of recreational* Paracentrotus lividus *fishing on distribution patterns of sea urchins at Ustica Island MPA (Western Mediterranean, Italy)*, Fish. Res. 81 (2006), p. 37.

[22] P. Guidetti and J. Dulcic, *Relationships among predatory fish, sea urchins and barrens in Mediterranean rocky reefs across a latitudinal gradient*, Mar. Environ. Res. 63 (2007), p. 168.

[23] E. Ballesteros, *Structure and dynamics of North-Western Mediterranean phytobenthic communities: a conceptual, model*, in *Homage to Ramon Margalef, or, why there is such pleasure in studying nature?* J.D. Ros and N. Prat, eds, Oecol. Aquat. 10 (1991), p. 223.

[24] H. Nedelec, *Sur un nouvel indice de réplétion pour les oursins réguliers*, Rapp. Comm. Int. Mer Médit. 28 (1983), p. 149.

[25] M. Guillou and L.J.L. Lumingas, *Variation in the reproductive strategy of the sea urchin* Sphaerechinus granularis *(Echinodermata: Echinoidea) related to food availability*, J. Mar. Biol. Assoc. UK 79 (1999), p. 131.

[26] R.S. Jones, *A suggested method for quantifying gut contents in herbivorous fishes*, Micronesica 4 (1968), p. 369.

[27] M. Verlaque and H. Nedelec, *Biologie de* Paracentrotus lividus *sur substrat rocheux en Corse (Mediterranee, France): Alimentation des adultes*, Vie Milieu 33 (1983), p. 191.

[28] J. Cobb and J.M. Lawrence, *Diets and coexistence of the sea urchins* Lytechinus variegatus *and* Arbacia punctulata *(Echinodermata) along the central Florida gulf coast*, Mar. Ecol.-Prog. Ser. 295 (2005), p. 171.

[29] L. Mangialajo, N. Ruggieri, V. Asnaghi, M. Chiantore, P. Povero, and R. Cattaneo-Vietti, *Ecological status in the Ligurian Sea: The effect of coastline urbanisation and the importance of proper reference sites*, Mar. Pollut. Bull. 55 (2007), p. 30.

[30] A.J. Underwood, *Experiments in Ecology: Their logic design and interpretation using analysis of variance*, Cambridge University Press, Cambridge, 1997.

[31] M.J. Anderson, *A new method for non-parametric multivariate analysis of variance*, Aus. Ecol. 26 (2001), p. 32.

[32] J.R. Bray and J.T. Curtis, *An ordination of the upland forest communities of Southern Wisconsin*, Ecol. Monogr. 27 (1957), p. 325.

[33] M.J. Anderson, *PCO: A FORTRAN computer program for principal coordinate analysis*, Department of Statistics, University of Auckland, New Zealand, 2003. Available at: http://www.stat.auckland.ac.nz/∼mja/Programs.htm

[34] P. Guidetti and M. Mori, *Morpho-functional defences of Mediterranean sea urchins,* Paracentrotus lividus *and* Arbacia lixula*, against fish predators*, Mar. Biol. 147 (2005), p. 797.

[35] F. Micheli, L. Benedetti-Cecchi, S. Gambaccini, J. Bertocci, C. Borsini, C.G. Osio, and F. Romano, *Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages*, Ecol. Monogr. 75 (2005), p. 81.