



Functional traits of two co-occurring sea urchins across a barren/forest patch system

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ABSTRACT

Temperate rocky reefs may occur in two alternative states (coralline barrens and erect algal forests), whose formation and maintenance are often determined by sea urchin grazing. The two sea urchin species *Paracentrotus lividus* and *Arbacia lixula* are considered to play a similar ecological role despite their differing morphological traits and diets. The patchy mosaic areas of Ustica Island, Italy, offer an ideal environment in which to study differences in the performance of *P. lividus* and *A. lixula* in barren versus forest states. Results show that the two sea urchin species differ in diet, trophic position, grazing adaptation, movement ability and fitness in both barren and forest patches. We confirmed herbivory in *P. lividus* and omnivory with a strong tendency to carnivory in *A. lixula*. When the sea urchin escape response to a predator was triggered, *P. lividus* responded faster in barren and forest patches. Forest patch restricted movement, especially in *A. lixula* (velocity in barren \approx 10-fold greater than in forest). A large Aristotle's lantern, indicative of durophagy, confirmed adaptation of *A. lixula* to barren state.

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1. Introduction

Temperate rocky marine ecosystems may occur alternatively as algal forest or barren, the latter being dominated by sea urchins and encrusting organisms (Beisner et al., 2003; Graham, 2004; Knowlton, 2004; Palumbi et al., 2008; Scheffer et al., 2001; Suding et al., 2004). These alternative states are dynamic, and environmental perturbations (e.g. variations in the abundance of sea urchin predators, outbreaks of disease among sea urchins, destructive harvesting of benthic organisms, deterioration of water quality, storms etc.) can trigger one state to switch to the other (Bonaviri et al., 2009; Coleman et al., 2008; Fanelli et al., 1994; Gianguzza et al., 2011; Sala et al., 1998; Steneck et al., 2002). The transition between forest and barren is usually not homogeneous, and is often characterized by a patchy intermingled mosaic of the two states (Bulleri and Benedetti-Cecchi, 2006; Hereu et al., 2008; Sala et al., 1998; Watson and Estes, 2011). During the transition, sea urchin abundance and species composition vary greatly in patches, and their grazing activity likely affects their stability, ultimately determining the shift of the whole system toward one of the two stable states (barren vs forest) (Konar and Estes, 2003; Watson and Estes, 2011).

In Mediterranean rocky infralittoral systems, *Paracentrotus lividus* and *Arbacia lixula* are the most abundant sea urchin species (Guidetti, 2006; Sala et al., 1998). These species are often considered to occupy the same trophic guild (Benedetti-Cecchi et al., 1998; Sala et al., 2012),

but their distribution differs between algal states. In forests *P. lividus* is by far more frequent and abundant than *A. lixula*, which is absent or very rare (Gianguzza et al., 2010; Guidetti and Dulčić, 2007). At low densities, *P. lividus* becomes cryptic, hiding in crevices, feeding near its refuge and creating little barren patches, or “gardens” (Verlaque, 1987; Benedetti-Cecchi and Cinelli, 1995; Hereu, 2006). At high densities, *P. lividus* switches from cryptic to active grazing, creating large patches devoid of erect algae (Kempf, 1962; Sala and Zabala, 1996; Verlaque, 1987). In contrast, *A. lixula* reaches high densities only in barrens (Guidetti and Dulčić, 2007; Micheli et al., 2005; Privitera et al., 2011) where it plays a leading role in maintaining the substrata free of new benthic settlers (Bonaviri et al., 2011; Bulleri et al., 1999). It remains unclear whether the scarcity of *A. lixula* in the forest state results from its preference for encrusting algae, which are abundant in the barren state, or from its inability to move and penetrate thick algal canopies.

The two urchin species differ morphologically. *P. lividus* has shorter and denser spines than *A. lixula* and more extendible tube feet (Gianguzza et al., 2010; Guidetti and Mori, 2005; Santos and Flammang, 2005, 2007). These features potentially make *P. lividus* better adapted to penetrate, climb, and knock down the erect algae thalli in forest patches as a result of their superior mobility.

The Aristotle's lantern is larger in *A. lixula* than in *P. lividus* (Fernandez and Boudouresque, 1997) suggesting an adaptation in *A. lixula* to feed on crustose algae (i.e.: durophagy, *sensu* Hagen, 2008). Accordingly, gut content analysis indicates a strong feeding preference for encrusting corallines by *A. lixula*, in contrast with fleshy algae by *P. lividus* (Privitera et al., 2008 and reference therein). Moreover, some demonstrated larger lantern size (which indicates an increasing ability to scrape) and lower

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gonad somatic index values (a stress response, impairing fitness) in sea urchins inhabiting food-limited habitats, such as the barren, relative to those inhabiting habitats with abundant food, such as forest algae (Agatsuma et al., 2005; Bayed et al., 2005; Brady and Scheibling, 2006; Brewin et al., 2000; Byrne, 1990; Fernandez and Boudouresque, 1997; Konar and Estes, 2003; Levitan, 1992; Sánchez-España et al., 2004).

No experimental studies have specifically tested whether diet preference and movement capability can explain the different distribution and fitness of urchin species in barren and forest states.

At Ustica Island, a transitional phase with a patchy mosaic pattern of barren and forest occurred in 2009, providing an excellent opportunity to study the functional traits of *A. lixula* and *P. lividus* in different states, minimizing the bias associated with natural spatial and temporal variability. With the aim of better understanding the potential role of these two species in shaping communities, we analyzed, for each state and species: (a) gut contents and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures, to assess diet and trophic positions; (b) lantern size, to estimate functional adaptation to durophagy; (c) movement ability and (d) gonadic mass to assess fitness. We predicted: (a) different diets for *P. lividus* and *A. lixula* in both forest and barren patches, with a preference for erect algae in the former species and for crustose algae in the latter; (b) larger lantern and (c) reduced movement ability in *A. lixula* and (d) small gonadic mass of *P. lividus* and *A. lixula* in barren and forest, respectively, resulting from the absence of their preferred food in these states.

2. Materials and methods

2.1. Study area

The Ustica Island MPA is located in southwest Italy. It was established in 1986 on a small volcanic island 80 km off the northern coast of Sicily, covering 16,000 ha, of which 65 are devoted to the no-take area along the northwestern part of the island (Zone "A," Fig. 1). The bottom of the no-take zone is an extensive rocky platform of gentle slope characterized by high structural complexity, which varies widely at spatial scales from centimeters to decimeters. Unlike other Mediterranean MPAs, the Ustica infralittoral zone developed in barren after protection enforcement (Gianguzza et al., 2006; Riggio and Milazzo, 2004) and until 2007 sea urchins, *P. lividus* and *A. lixula*, and encrusting corallines such as *Lithophyllum* spp., *Pseudolithophyllum expansum*, *Lithothamnium* spp., *Mesophyllum coralloides* dominated the bottom. In recent years, starfish predation reduced sea urchin abundance (Bonaviri et al., 2009; Di Trapani, 2011; Gianguzza et al., 2009a,b), likely promoting the flourishing of erect macroalgae (Agnetta et al., 2010; Gianguzza et al., 2010), forming a landscape of patches of tens of meters in diameter interspersed with barren, dominated by encrusting algae, or forest, dominated by erect algae.

The study was carried out during the second half of July 2009 on rocky reefs 3 to 6 m deep on the western side of Ustica Island

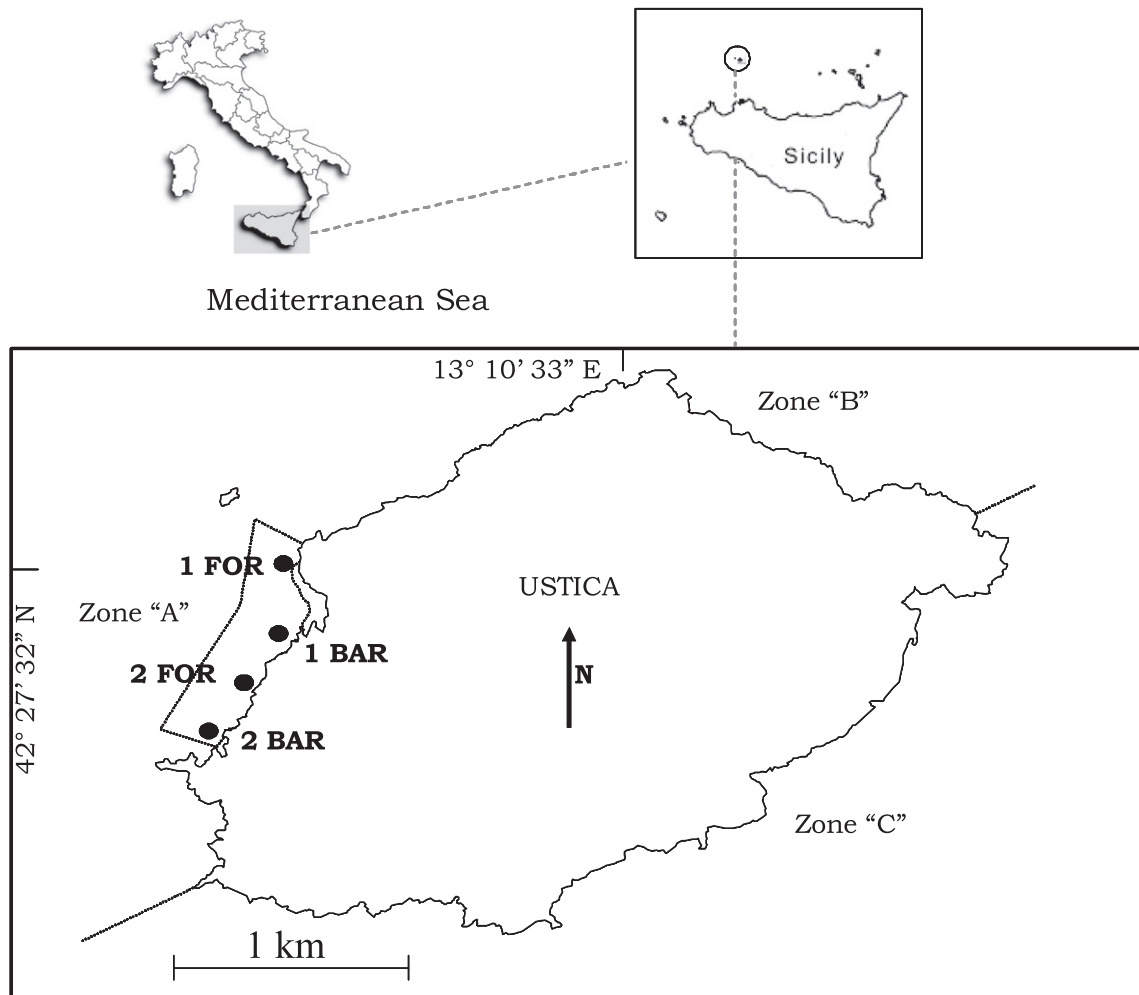


Fig. 1. Map of Ustica Island and sampling patches (1, 2) of each state (forest, FOR; barren, BAR).

(Fig. 1). We selected four random patches (two characterized by barren and two by forest), each 200 m apart, from a set of patches with similar orientation (270° – 275°), water motion (Sunseri, 1995), and topography.

2.2. Preliminary survey

A preliminary survey was conducted in order to characterize benthic assemblage and urchin biomass in forest and barren patches. Benthic assemblages were assessed by superimposing a grid of 25 equal-sized small squares (each of them representing 4% of the total surface of each image) using digital image of each 400 cm² area. The percent cover of each taxa was quantified in all the small quadrats by assigning a score between 0 (no presence) and 4 (total cover) to each taxa observed. Values of each small quadrat were added to obtain the final percentage of the entire quadrat (Chiantore et al., 2008). We placed 10 replicate quadrants randomly in each patch. In order to assess the organisms present beneath the algal forest canopy (hypo-strata), we photographed the replicates ($n=10$ in each patch) after cutting all the erect algae present. Sea urchin biomass was calculated from the diameter and density of sea urchins in the field (see Cardona et al., 2007) based on the equation: $W=0.002 \times (D^{2.59})$ ($r^2=0.98$) (W : weight in grams, D : test diameter in millimeters) previously extrapolated from a sub-sample of individuals ($n=50$ in each patch) of both *P. lividus* and *A. lixula*. Densities of both *P. lividus* and *A. lixula* were independently estimated in the field by visual counts within quadrats randomly located in each patch (1 m^2 ; $n=10$).

Benthic assemblages (PERMANOVA; $P(\text{MC})=0.002$; $F_{1,36}=116.24$) and biomass of sea urchins (ANOVA species \times state $P=0.025$; $F_{1,72}=37.86$) differed significantly between barren and forest patches. Principal coordinates analysis (PCO, Appendix Fig. A1) showed that coralline algae and massive colonial and solitary invertebrates were associated with the barren patches, whereas erect algae like leathery macrophytes and corticated foliose were associated with forest (PCO1 89.7%). Cover of crustose algae and leathery macrophytes significantly contributed to dissimilarity between barren and forest states (SIMPER, Appendix Table A1). Massive colonial (McA) and sessile invertebrates (SA) were significantly more abundant in the barren, even when we only detected a state effect for McA ($F_{(1,39)}=121$; $p<0.009$). Biomass of *P. lividus* was significantly higher in barren (mean \pm SD: 113.77 ± 17.03) than in forest patches (35.32 ± 8.96). Similarly, the biomass of *A. lixula* was significantly greater in barren (123.67 ± 15.60) than in forest (8.75 ± 3.44) areas.

2.3. Sampling design

In order to test for differences between the two sea urchin species in barren and forest patches in gut content, isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), lantern index (LI) and movement ability, we utilized a sampling design with three factors. We treated “Species” (Sp), as a fixed variable with two levels (*A. lixula* and *P. lividus*); “State” (St) as fixed and with two levels (barren and forest), and “Patch” (Pa) as random and nested in “State” with two levels (P_1 and P_2).

Given that the two species differ in gonadic size and maturity cycles (author’s data unpublished), we tested for differences in gonadosomatic index (GSI) between barren and forest patches for the two sea urchins using a sampling design with only two factors: “State” (St) was treated as fixed with two levels (barren and forest) and “Patch” (Pa) as random and nested in “State” with two levels (P_1 and P_2).

2.4. Sampling procedures

In order to analyse urchin diet, we collected six adult specimens of both species (>35 -mm test diameter) in each patch and dissected them as soon as possible in order to avoid gut evacuation. After dissection gut contents were immediately frozen. We later took at random two equal volumes of gut contents from each sample and placed them on a 2.5×2.5 -cm grid in a Petri dish in order to evaluate the percent cover of each item through a binocular microscope. We then estimated the relative percent abundance of each gut item based on percent cover. This method allowed us to take into account the percent occurrence of the different food items and also their relative volume (Privitera et al., 2008). For the gut contents, we grouped animal and algal taxa a priori using the morpho-functional criteria outlined by Steneck and Dethier (1994) for algae and Jackson (1979) for animals (Table 1). We used morpho-functional criteria because we reasoned that size, shape and anatomy of prey (i.e. algae and sessile animals) control the ability of sea urchins to handle and ingest them (Steneck and Dethier, 1994). Moreover, the use of these groups could facilitate future comparisons at larger spatial and temporal scales. We were generally able to identify food items to genus level (Table 1), but when identification was not possible we used anatomical components (e.g. tissue, morphology) to place them in one of the morpho-functional groups. Completely digested material was not considered. All samples were standardized relative to total gut contents.

Table 1
Description of shared functional groups used in benthic and gut content analysis and trophic guilds for stable isotopes analysis.

Groups	Gut content/benthic assemblage	Stable isotopes
Crustose algae (CA)	<i>Lithophyllum</i> , <i>Lithothamnium</i>	<i>Lithophyllum</i> , <i>Lithothamnium</i>
Filamentous algae (Fil)	<i>Ceramium</i> spp., <i>Bryopsis</i> spp., <i>Spachelaria</i> spp., <i>Cladophora</i> spp.	<i>Ceramium</i> spp., <i>Bryopsis</i> spp., <i>Spachelaria</i> spp., <i>Cladophora</i> spp.
Foliose algae (Fol)	<i>Anadyomene stellata</i> , <i>Flabellia petiolata</i>	<i>Anadyomene stellata</i>
Corticated foliose algae (CoFo)	<i>Padina pavonica</i> , <i>Dictyopteria membranacea</i> , <i>Dictyota</i> spp.	<i>Dictyota</i> spp. (CoFoF) and <i>Padina pavonica</i> (CoFoC)
Corticated macrophyte (CoMa)	<i>Laurencia</i> spp., <i>Stypocaulon scoparium</i>	<i>Laurencia</i> spp.
Leathery macrophyte (LM)	<i>Cystoseira</i> spp.	<i>Cystoseira</i> spp.
Articulated calcareous Algae (ACA)	<i>Corallina</i> sp., <i>Jania</i> sp., <i>Amphiroa rigida</i> , <i>Halimeda tuna</i>	<i>Liagora viscida</i> , <i>Amphiroa rigida</i>
Solitary animals (SA)	Anthozoans such as <i>Anemonia viridis</i> , vermetids, polychaetes, foraminiferans (gut)	
Sheet-like colonial animals (ScA)	Such as encrusting bryozoans, didemnids	
Massive colonial animals (McA)	Sponges, anthozoans such as <i>Cladocora caespitosa</i> , bryozoans such as <i>Myriapora truncata</i>	
Tree-like colonial animals (TA)	Colonial stoloniferous, colonial hydroids	
Particulate feeders (PF)		<i>Anemonia viridis</i> , <i>Aiptasia</i> spp.
Meso herbivores (MH)		<i>Cerithium</i> spp., columbellidae
Detritivores (DS)		Sipunculids
Crustaceans omnivores (CrOm)		<i>Calcinus tubularis</i> and other small crustaceans
Suspension feeders (SF)		Vermetids, serpulids, stoloniferous
Filter feeders (FF)		<i>Protula</i> sp., <i>Spirastella cunclatrix</i>
Rock (RK)	Denuded substrate (benthic assemblage)	
Other animals (OA)	Animal fragments in the gut contents	

The diet of the two sea urchins was also investigated through stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). While not providing the dietary resolution of gut content observation, stable isotope analysis produces an averaged measure, by time and space, of what has been assimilated. Five individuals of each adult *P. lividus* and *A. lixula* and their potential prey (five pieces of each algae and five individuals for each animal species) were hand-collected from all patches and separately sealed in plastic bags. Faunal specimens were sampled by slicing a small portion of the foot of *Anemonia viridis* and *Aiptasia* sp. and of sea urchins' lantern muscles (Tomas et al., 2006). For any other animal the whole body (excluding shell) was used. For the algae various pieces of thalli were used. Samples of sedimentary organic matter (SOM) were collected in 50 ml plastic pumps from each patch ($n = 5$). Sediment samples were filtered through 0.45- μm GF/F filters to extract the particulate portion. Half of the samples, with the exception of sea urchin muscles, were washed with 2 N HCl to remove inorganic carbonates and analysed for $\delta^{13}\text{C}$. Given that the acid wash could alter $\delta^{15}\text{N}$ values (Tomas et al., 2006), untreated parts were used to analyse $\delta^{15}\text{N}$. All samples were rinsed with distilled water and dried at 60 °C (48 h approximately). Measurements of stable isotope abundances were performed using a continuous-flow isotope-ratio mass spectrometer (Thermo Delta Plus XP) coupled to an elemental analyser CHN (Thermo EA 11112). Experimental precision, based on the standard deviation of replicates of the internal standard, was 0.2‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Isotope ratios were expressed relative to PeeDee Belemnite (PDB) standard for carbon and to N_2 in air for nitrogen. Ratios were calculated as: $\delta X = [(R_{\text{sample}}/R_{\text{standard}} - 1)] \times 1000$ where X is ^{13}C or ^{15}N , and R is the corresponding ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. With the aim of visualizing trophic relationships between sea urchins and their prey, tropho-dynamic diagrams were constructed by grouping the organisms into trophic guilds as derived from morpho-functional features and isotopic signatures (Table 1).

The lantern index (LI) (lantern height/test diameter) was calculated for six individuals (>35-mm test diameter) of each species per patch. Lantern length and test diameter were measured with a calliper at 0.05-mm precision according to Levitan (1991, 1992). Wet gonado-somatic index (GSI) (gonad wet weight/total body wet weight) was calculated for the same individuals.

In order to measure the movement ability of the two species, we used the escape response of sea urchins induced by *M. glacialis*. Although this method measures the maximal locomotory performance of sea urchins under extreme circumstances, it facilitates a comparison of the movement ability of species in different substrata directly in the field, without manipulation of individuals. Moreover, no others alternative stimuli have been described in literature. The variable measured was the route covered by the sea urchins after contact with *M. glacialis*, which affects *P. lividus* and *A. lixula* urchins in that they immediately extend and open their globiferous pedicellariae (activation), lower their spines and flee from the point of contact. The route covered by six individuals of each species in five minutes was measured with a thin chain, in both barren and forest patches for a total of 48 replicates. Replicates were scattered, tens of meters apart, in the southern part of Ustica, where *M. glacialis* is abundant and benthic assemblage is similar to the "A" zone (Agnetta et al., 2010; Gianguzza et al., 2009a,b).

2.5. Data analysis

Gut contents were analyzed by distance-based permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). The analysis was computed on a similarity matrix among samples, obtained by applying the Bray-Curtis index on the square root-transformed percentage of each animal and algal morpho-functional group of gut contents. Where appropriate, pair-wise tests (at $\alpha = 0.05$) were used as a posteriori check of significant effects.

The untransformed isotopic signatures of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and the transformed $\text{Ln}(X + 1)$ distance covered by sea urchins were analyzed

by ANOVA (Underwood, 1997) after checking for homogeneity of variances using Cochran's C test. Student–Newman–Keuls (SNK) tests (at $\alpha = 0.05$) were used, where appropriate, for a posteriori comparisons of the means (Underwood, 1997; Winer et al., 1991). Untransformed lantern and gonadosomatic indices values, resembled by Euclidean distance, were both analyzed by ANCOVA in relation to sea urchin size (test diameter) or total weight, respectively (see Ebert et al., 2011).

In order to assess the contributions of each trophic guild (Table 1) and SOM to the assimilated diet of sea urchins, linear mixing models were used. We examined all possible combinations of each source contribution (0–100%) in small increments of 1% and tolerance of 0.1 to 0.5 as recommended by Phillips and Gregg (2003). Enrichments of 1.3 for carbon and 2.2 for nitrogen were considered to correct for isotope fractionation across trophic levels. In particular, we based our fractionation parameters on recommended estimates by McCutchan et al. (2003), for carbon (type of tissue analysed) and nitrogen (type of consumer diet, respectively). Mixing models were carried out using Iso-Source software version 1.3.1 (Phillips and Gregg, 2003). The trophic level of both sea urchins was calculated according to the equation developed by Hobson and Welch (1992): $\text{TL} = 1 + (\text{Nm} - \text{Nb})/\text{TE}$, where TL = trophic level of the species, Nm = mean $\delta^{15}\text{N}$ value of the species, Nb = average basis $\delta^{15}\text{N}$ value of producers (algae) and TE = trophic enrichment factor (see Section 2.2).

3. Results

3.1. Gut contents

Gut contents analysis revealed a diet dominated by crustose algae for *A. lixula* and by erect fleshy algae for *P. lividus* (Fig. 2). The diet composition of the two species differed significantly in both states. The gut contents of *A. lixula* were similar in barren and forest, but differed significantly for *P. lividus* (Table 2, Sp \times St interaction and pair-wise tests). *P. lividus* individuals collected in barren patches

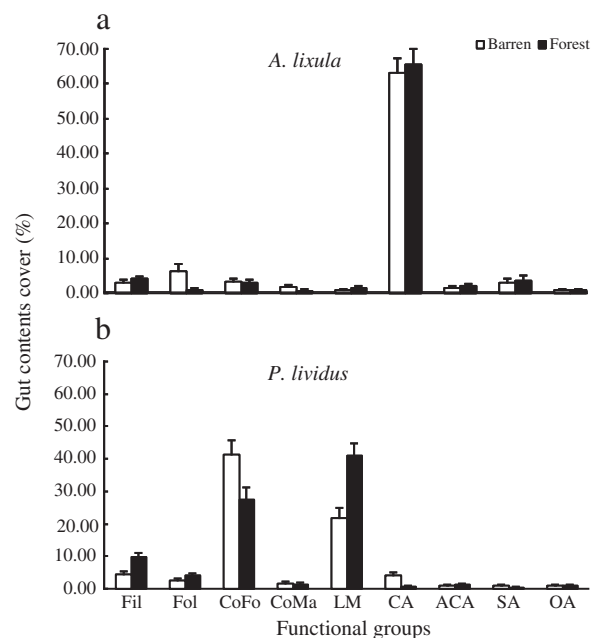


Fig. 2. Gut contents cover (\pm S.E.) of sea urchin species in the two states. Fil = filamentous algae, Fol = foliose algae, CoFo = corticated foliose algae, CoMa = corticated macrophyte algae, LM = leathery macrophyte, CA = crustose algae, ACA = articulated calcareous algae, SA = solitary animal, OA = other animal.

Table 2

Results of PERMANOVA testing for differences in sea urchin gut content cover considering the fixed factors “Species” with two levels (*P. lividus* and *A. lixula*) and “State” with two levels (barren and forest) and the random factor “Patch” (Pa) nested in “State” with two levels (P_1 and P_2).

Source	df	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Species (Sp)	1	39,085.0	1568.80	0.03	713	0.00
State (St)	1	519.7	0.73	1.00	3	0.56
Patch (Pa) (St)	2	709.7	1.74	0.12	9944	0.13
Sp×St	1	1498.5	60.15	0.04	798	0.00
Sp×Pa (St)	2	24.9	0.06	0.96	9951	0.96
Res	40	406.91				
Total	47					

contained corticated foliose algae, whereas those coming from forest patches had ingested mostly leathery macrophyte (Fig. 2).

3.2. Stable isotopes

Mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ significantly differed between the two sea urchin species, with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values higher for *A. lixula* than *P. lividus* in both barren and forest patches (Table 3, Fig. 3, Table A2).

Mixing models (mean and 1st to 99th percentiles) indicated that CoFo (24% ± 18%; 0–75%), SOM (18% ± 14%; 0–57%) and CoMa (26% ± 10%; 0.2%–48%) were the principal sources of carbon and nitrogen assimilated by *P. lividus*, followed by LM (16% ± 9%; 0–36%), while animal guilds such as MH, DS and SF provided a minor contribution (≈ 5% each). On the contrary, results showed animals as the main food assimilated by *A. lixula*; DS (sipunculids) provided 71% ± 7% (55%–88%) of the carbon and nitrogen while the other animal guilds (SF, CrOm, MH and PF) and calcareous algae (CA and CoFoC) represented ≈ 5% each. The trophic level for *A. lixula* (TL = 3.05) was about one point greater than that for *P. lividus* (TL = 2.18).

3.3. Lantern index, movement ability and gonadosomatic index

Lantern index was higher for *A. lixula* (mean ± S.E.; 0.33 ± 0.01) than for *P. lividus* (0.27 ± 0.004), while State had no significant effect on this variable (Table 4). Although co-variable Size resulted significant, it never interacted with any of the considered factors (Table 4).

Although the two sea urchins were equally activated by the presence of the starfish in both patch types, the average distance covered by the two species was significantly different. The distance covered by *P. lividus* was higher than that of *A. lixula* in both barren and forest patches (Table 5; Fig. 4; SNK tests $p < 0.01$). Moreover, *A. lixula* and *P. lividus* were faster in barren than in forest (Table 5; Fig. 4; SNK tests $p < 0.01$ for *A. lixula*, $p < 0.05$ for *P. lividus*).

GSI of *A. lixula* (mean ± S.E.; 1.72 ± 0.16) and *P. lividus* (6.16 ± 0.55) was not affected by the factor State (Table 6).

Table 3

Results of ANOVA testing for differences in sea urchins stable isotopes $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition considering the fixed factors “Species” with two levels (*P. lividus* and *A. lixula*) and “State” with two levels (barren and forest) and the random factor “Patch” (Pa) nested in “State” with two levels (P_1 and P_2).

Source	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$			
	df	MS	F	p	df	MS	F	p
Species (Sp)	1	100.20	232.27	0.00	1	25.84	305.22	0.00
State (St)	1	3.32	2.67	0.24	1	0.00	0.00	0.98
Patch (Pa)	2	1.25	1.63	0.21	2	7.12	54.83	0.00
Sp×St	1	0.33	0.76	0.47	1	0.02	0.20	0.70
Sp×Pa (St)	2	0.43	0.56	0.57	2	0.08	0.65	0.53
Res	32	0.77			32	0.13		
Total	39				39			

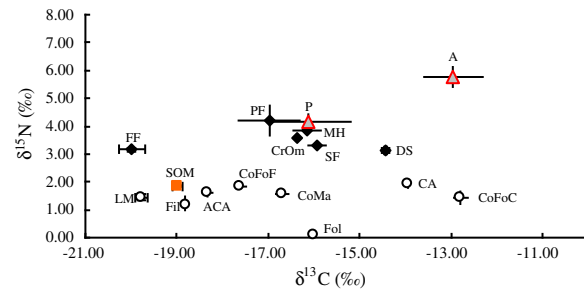


Fig. 3. Tropho-dynamic diagram of consumers and prey (pooled states and patches). A = *A. lixula*, P = *P. lividus*, PF = particulate feeders, MH = meso-herbivores, DS = detritivores, CrOm = crustaceans omnivores, SF = suspension feeders, FF = filter feeders, LM = leathery macrophyte, Fi = filamentous algae, ACA = articulated calcareous algae, CoFoF = corticated foliose flashy algae, CoMa = corticated macrophyte algae, Fol = foliose algae, CA = crustose algae, CoFoC = corticated foliose calcareous algae, SOM = sedimentary organic matter.

4. Discussion

The functional traits of *P. lividus* and *A. lixula* were estimated during a transitional phase between forest and barren state. This phase was characterized by a patchy barren/forest system in which the two species co-occurred. Our results show that, regardless of the state of the patches where urchins were present, the two species were characterized by different: (1) diet, (2) trophic position, (3) lantern traits and (4) movement ability.

Previous manipulative experiments have highlighted the leading role of *A. lixula* in maintaining the barren state, but the relative role of the two species in the dynamic between forest and barren has generally been overlooked (Bonaviri et al., 2011). Indeed, the two species are often considered to belong to the same trophic guild and, therefore, to play the same role in shaping benthic communities (Sala et al., 2012). The results of this study, however, support the hypothesis that the two species belong to different trophic guilds and fulfil differing roles in the formation of barren.

The results of the gut contents and stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analysis clearly indicate that diet of the two species differ in both barren and forest states. In agreement with previous studies, the gut contents of the two sea urchins were dominated by algae, with a prevalence of fleshy erect algae in *P. lividus* and encrusting algae in *A. lixula* (Privitera et al., 2008 and references therein). In particular, gut contents did not always correspond to the benthic cover of each state: *A. lixula* largely consumed encrusting algae also in forest, where this group was scarcely present, and *P. lividus* ingested corticated foliose algae in barren, despite this group representing less than 5% of cover in this state. These findings suggest that the two species are somehow able to select different food sources.

The results of isotopic signatures did not match the gut contents outcomes and $\delta^{15}\text{N}$ showed that the trophic position occupied by *A. lixula* was higher than that of *P. lividus*. In particular, in *A. lixula* $\delta^{15}\text{N}$ signatures were higher than those expected for a herbivore. The mixing model confirmed that *A. lixula* mainly fed on several animal guilds. Contrarily, $\delta^{15}\text{N}$ signatures of *P. lividus* were consistent with those expected for a herbivore. The mixing model indicated that this species fed principally on erect algae and that SOM played an important role in its diet. The mixing model also revealed a negligible contribution of invertebrates to the diet of *P. lividus*. From analysing results of both gut contents and isotopes, the two species should be considered omnivores with a strong tendency to carnivory for *A. lixula* and to herbivory in the case of *P. lividus*.

The apparent contradiction found between gut contents and isotopic signatures may have more than one plausible explanation. First, animal tissue is digested more rapidly than algae tissue (Fernandez and Boudouresque, 2000), animals are not ingested as a whole but only

Table 4

Results of ANCOVA testing for differences in sea urchin lantern index considering the fixed factors “Species” with two levels (*P. lividus* and *A. lixula*) and “State” with two levels (barren and forest) and the random factor “Patch” (Pa) nested in “State” with two levels (P₁ and P₂), considering the sea urchins size as covariate.

Source	df	MS	Pseudo-F	P(perm)	Unique perms
Size (Si)	1	0.026	50.76	0.00	9852
Species (Sp)	1	0.018	22.22	0.04	7712
State (St)	1	0.000	0.02	1.00	24
Patch (Pa) (St)	2	0.001	0.98	0.40	9950
Si×Sp	1	0.000	0.52	0.47	9831
Si×St	1	0.001	1.33	0.27	9848
Sp×St	1	0.001	1.56	0.31	4253
Si×Pa (St)	2	0.000	0.29	0.74	9949
Sp×Pa (St)	2	0.001	1.29	0.30	9948
Si×Sp×St	1	0.000	0.52	0.48	9840
Si×Sp×Pa (St)	2	0.000	0.57	0.56	9956
Res	24	0.001			
Total	39				

parts are scraped off by the lantern (e.g. proboscid of sipunculids, fan of serpulids, etc.) and different types of algae are also characterized by different digestibility (Arafa et al., 2006; Frantzis and Gremare, 1992). Therefore, the proportion of animal and algal tissue ingested and rapidly digested by sea urchins might be underestimated by gut contents analysis. For example, leathery macrophyte, a slowly digested food, was the most abundant group in gut contents of *P. lividus* in forest, despite the fact that this group represents the least consumed food, as detected by the mixing model. Likewise, crustose algae were the most abundant item in the gut contents of *A. lixula* (60%), although they represented less than 5% of the assimilated food (Cabral de Oliveira, 1991; Ganteaume et al., 1998; Knoepffler-Peguy et al., 1987; Otero-Villanueva et al., 2004). A second explanation could be that unidentifiable calcareous material, attributed to crustose algae, could actually derive from animal shells (such as suspension feeders like serpulids and meso herbivores). In accordance with this hypothesis, Wangenstein et al. (2011) individuated a large proportion of fragments of barnacle shells among the calcareous materials in the gut contents of *A. lixula* by using a scanning electron microscope.

The fact that *A. lixula* and *P. lividus* are two omnivores with a strong tendency to carnivory (i.e. *A. lixula*) and to herbivory (i.e. *P. lividus*) is in accordance with a recent study conducted in erect algae-dominated systems in the Western Mediterranean, which also reported that *A. lixula* consumes primarily animals but *P. lividus* mainly algae (Wangenstein et al., 2011). The fact that the two species also maintain these feeding habits in barren states undermines the assumption that these co-occurring species are two herbivores that, sharing the same ecological role, avoid competition with a selective interspecific partitioning of algae. We can now reasonably state that *A. lixula* and *P. lividus* have different diets and occupy distinct trophic positions; in other words, they do not compete for resources, neither in forest nor in barren states. These results are comparable to those found by Vanderklift et al. (2006) in

Table 5

Results of ANOVA testing for differences in sea urchin length covered route considering the fixed factors “Species” with two levels (*P. lividus* and *A. lixula*) and “State” with two levels (barren and forest) and the random factor “Patch” (Pa) nested in “State” with two levels (P₁ and P₂).

Source	df	MS	F	p
Species (Sp)	1	632.75	16,166.82	0.0001
State (St)	1	155.84	15.79	0.0579
Patch (Pa) (St)	2	0.9868	2.09	0.1373
Sp×St	1	125.99	3219.08	0.0003
Sp×Pa (St)	2	0.0039	0.01	0.9918
RES	40	0.4728		
TOT	47			

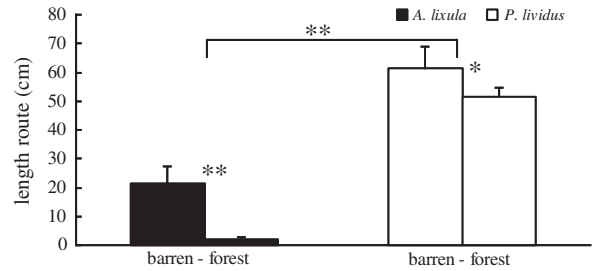


Fig. 4. Sea urchin length travelled route (cm ± S.E.) in the two studied states. SNK test: **p*<0.05; ***p*<0.01.

southwestern Australia, where the co-occurring sea urchin *Centrostephanus tenuispinus* and *Phyllacanthus irregularis*, commonly considered herbivores, exhibit an omnivorous habit tending to carnivory and are thus ecologically dissimilar to the almost exclusively herbivore *Helicoidaris erythrogramma*.

The carnivorous habit observed here for *A. lixula* fits well with other *Arbacia* species (Penchaszadeh, 1979; Silva et al., 2004) and other *A. lixula* populations. Cabral de Oliveira (1991) found that 71% of the guts of *A. lixula* collected from Brazil consisted of the cirriped *Chtamalus* spp. and thus the species was defined “mostly carnivorous.”

Apparently, fleshy algae are not a limited resource in the barren patches for *P. lividus* as they constitute the bulk of the diet in this species (as observed in both gut contents and stable isotope analysis). Accordingly, the reproductive condition (GSI) of *P. lividus* was not affected by the state. This finding is in agreement with Chiantore et al., 2008. In that study, the GSI of *P. lividus* was similar in barren and forest states. A likely explanation is that drifting fragments of fleshy algae can be captured by *P. lividus* even when it is residing in barren patches. Actually, this “drift-trapping behaviour” was observed in other sea urchin species occurring in areas where erect algae abundance is low (Vanderklift and Wernberg, 2008). Besides drift algae, sediment or re-suspended organic material could also be caught by *P. lividus* with its sulcated spines and numerous aboral tube feet (Régis, 1978). This scenario is supported by the values of SOM assimilated by this species (18%). Moreover, the fact that leathery macrophyte were largely ingested but not assimilated by *P. lividus* in forests could indicate a “mower” activity of this species, aimed at easily reaching its preferred food (i.e. soft algae) or creating a suitable patch where it can better attach (Gianguzza et al., 2010) and feed

Table 6

Results of ANCOVA testing for differences in sea urchin GSI considering the fixed factor “State” with two levels (barren and forest) and the random factor “Patch” (Pa) nested in “State” with two levels (P₁ and P₂) considering the sea urchins total weight as covariate.

Source	df	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
<i>A. lixula</i>						
Tot wet weight (To)	1	0.62	33,699.00	0.16	9848	0.15
State (St)	1	25,629.00	13,024.00	0.00	24	0.07
Patch (Pa) (St)	2	0.15	0.35	0.71	9946	0.72
To×St	1	32.04	75.59	0.93	9833	0.93
To×Pa (St)	2	0.99	23,309.00	0.13	9947	0.14
Res	12	0.42				
Total	19					
<i>P. lividus</i>						
Tot wet weight (To)	1	15,846.00	30,241.00	0.12	9836.00	0.19
State (St)	1	962.13	13.61	1.00	24.00	0.98
Patch (Pa) (St)	2	93,623.00	66,499.00	0.01	9963.00	0.01
To×St	1	10,988.00	0.78	0.39	9823.00	0.39
To×Pa (St)	2	24,147.00	17,151.00	0.22	9950.00	0.23
Res	12	14,079.00				
Total	19					

on delivered material. There are at least two main reasons explaining why *A. lixula* prefers the barren patches: (a) this species cannot move in forest as fast as *P. lividus* (i.e. reduced movement ability) and (b) endolithic species, associated to encrusting algae, are abundant only in the barren. Notably, in volcanic basaltic substrates, such as our case study area, endolithic fauna mainly occurs at the expense of calcareous organisms. In particular, it was recently observed that the biomass of sipunculids living under coralline hypostrata appears to be very high in the Ustica barren (Badalamenti personal observations). A recent work conducted in the shallow subtidal zone of the Auletians Islands revealed that barrens support a rich cryptic invertebrate community, composed mainly of spionids and sipunculids (Chenelot et al., 2011). It was proposed that encrusting algae form several crevices, cavities, interstices colonized by bryozoans, polychaetes, echinurans, molluscs and ophiuroids. In addition, Ojeda and Deaborn (1989) and Taylor (1988) also observed that crustose coralline communities support a high diversity of species and sustain high secondary productivity. In this context, it could be suggested that the Aristotle's lantern of *A. lixula*, larger than that of *P. lividus* and able to scrape off corallines and consume benthic organisms, could be considered an evolutive adaptation to durophagy (Hagen, 2008).

Overall, our results suggest a dynamic scenario during state transition from forest to barren in mosaic patches. Initially, *P. lividus* may find sufficient food in the barren state (e.g. drift algae, SOM) (result of the present study, Chiantore et al., 2008). However, when the abundance of this species increases, it may suffer intra-specific competition (Privitera et al., 2008). This may lead to a behavioral switch from passive feeding in barren patches to active grazing in forest patches, where *P. lividus* can penetrate to obtain food (results of the present study, Kempf, 1962; Verlaque, 1987; Sala and Zabala, 1996). By consuming and removing the erect algae canopy, *P. lividus* prepares a bare space, which is then colonized by encrusting algae and its associated "cryptic fauna." At this point *A. lixula*, which settles preferentially in encrusting coralline algae, can colonize the barren (Privitera et al., 2011) and maintain it (Bulleri et al., 1999; Bonaviri et al., 2011). According to this facilitative model, and in contrast to the traditional hypothesis of a competitive scenario, the decrease of *P. lividus* recorded in recent years at Ustica MPA did not trigger any increase in *A. lixula* (Agnetta et al., 2010; Bonaviri et al., 2009; Gianguzza et al., 2006). Our results suggest that the expansion of the barren state may be driven by facilitation processes (Bruno et al., 2003; Duggins, 1981) between the two co-occurring sea urchins. Interestingly, our results indicate that the barren does not seem to be a poor and unproductive system. More research, on larger spatial and time scales, is needed to confirm the findings shown here, and overall to better understand the general functioning of the barren ecosystem. This would provide useful data for the effective management of Mediterranean rocky reef.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.seares.2012.08.009>.

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