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Role of two co-occurring Mediterranean sea urchins in the formation of barren from-*Cystoseira* canopy

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Abstract

In the Mediterranean Sea the co-occurring sea urchins *Paracentrotus lividus* and *Arbacia lixula* are usually considered to share the same ecological role in the formation of barren from *Cystoseira* canopy. However, their foraging ability may vary due to feeding behavior and species-specific morphological traits. The relative effects of *P. lividus* and *A. lixula* on *Cystoseira* canopy was tested experimentally both in the laboratory, at a density of about 20 ind./m^2, and in the field by gut content analysis. Results, both in the field and in the laboratory experiments, show that *A. lixula* is unable to affect *Cystoseira* spp. Furthermore, these results confirmed the great ability of *P. lividus* to consume *Cystoseira* canopy, thus supporting the evidence of the major role of this species in the creation of barren state.

1. Introduction

Canopy-forming brown algae are habitat formers able to locally modify physical and biological factors and understory assemblages (Ballesteros et al. 1998;; Bulleri et al. 2002) leading to biological amelioration (*sensu* Moore et al. 2007). There is concern globally about their widespread loss across many parts of the world's rocky shores (e.g. Airoldi and Beck 2007). This is a result of their sensitivity to several direct and indirect human stressors (Perkol-Finkel and Airoldi 2010).

On Mediterranean rocky reefs, such habitat formers are well represented by the genus *Cystoseira* C. Agardh (Fucales, Phaeophyceae). These algae are distributed from the intertidal to the upper circalittoral and perform numerous ecosystem services as they provide high primary production and source of food, nutrient cycling, substrata for settlement, protection from predators and shelter from disturbance (Graham 2004; Ballesteros et al. 2009).

Over the last few decades most of the *Cystoseira* species have experienced severe decline in many Mediterranean regions (Thibaut et al. 2005; **Mangialajo et al. 2008**). Urbanisation is thought to have the most disrupting effects on *Cystoseira* canopy, particularly because it affects water clarity through eutrophication and alters sedimentation and water motion (Mangialajo et al. 2008). Furthermore, anthropogenic stressors such as global warming

and overfishing have also invoked this process. **O**verfishing of large sea urchin predator fish, especially *Diplodus* spp., can cause severe sea urchin outbreaks (*Paracentrotus lividus* and *Arbacia lixula*) and promote a shift in rocky benthic community structure (Hereu et al. 2008; Sala et al. 2012**, Cardona et al. 2013**). The variation in sea urchin grazing intensity may drive switches between one complex state, dominated by a stratified assemblage of several erect algae including the *Cystoseira* genus, to a simpler one, dominated by few encrusting algae, the so-called 'barren ground' (Shears and Babcock 2002; Estes et al. 2011).

In the Mediterranean Sea *P. lividus* and *A. lixula* are commonly found in both barren grounds and erected macroalgae assemblages (Guidetti and Dulčić 2007; Agnetta et al. 2013) and traditionally they have been considered a guild of herbivores (Bulleri et al. 1999, Bulleri et al. 2002). However recent investigations have distinguished the diets and trophic positions of the two species showing that *A. lixula* is an omnivore tending to carnivory, while *P. lividus* is basically a herbivore that can turn into an omnivore both on barren and vegetated rocky areas (Agnetta et al. 2013). Recent evidence suggests that the roles of the two species in maintaining the extension of barrens overlaps (Bulleri et al. 1999; Bonaviri et al. 2011; Bulleri 2013).

Despite the fact that sea urchin grazing is generally accepted to be very important to habitat modifications on Mediterranean rocky shores, comparisons of the **relative role** of *A. lixula* and *P. lividus* to **form barrens from** *Cystoseira* **canopy** is largely overlooked and has not yet been studied in any great detail.

In order to fill this important ecological gap we performed a laboratory experiment to observe the feeding behaviour of *A. lixula* and *P. lividus* and catch interspecific differences in their approach to *Cystoseira* spp. and to assess their relative ability to consume **and dislodge** *Cystoseira* spp. **(i.e. barren formation)**. We also studied the gut content of these species in natural conditions with the aim of comparing the amount of *Cystoseira* consumed by the two predators in the field. We predicted **that** 1) different ways of approaching the algae would be demonstrated by the two species in the laboratory experiment 2) only *P. lividus* would be able to consume *Cystoseira* and 3) that *Cystoseira* spp. play a greater role in *P. lividus* **diet rather** than in *A. lixula*.

2. Material and Methods

2.1. Study area

The study was performed in the upper infralittoral (3- 6 m) of the Ustica Island, located off the north coast of Sicily (Western Mediterranean, 38°42'20''N -10°43'43'' E), where crustose algae are interspersed with pools of *Cystoseira* spp. patches (mainly *Cystoseira brachicarpa var. balearica* and *Cystoseira compressa*) forming a binary patchy landscape (Gianguzza et al. 2010).

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The sea urchins *P. lividus* and *A. lixula* co-occur in this system (annual mean density of adults $\times$ m^{-2} $\pm$ SE was 2.70 $\pm$ 0.63 and 3.10 $\pm$ 0.72, respectively N = 160 **individuals** $\times$ species) providing an optimal opportunity to assess their grazing on *Cystoseira* spp.

2.2. Laboratory trials

A laboratory experiment was done from May to July 2011 to evaluate the ability to consume *Cystoseira* canopy by *P. lividus* and *A. lixula* (Fig. 1). The experiment was set up randomly collecting adult sea urchins (both *P. lividus* and *A. lixula* 35–50 cm in test diameter without spines) and cobbles covered by *Cystoseira* spp. (external face from about 10×10 cm to 18×15 cm) from a small bay of Ustica Island. After field collection cobbles were placed in large sealed plastic tanks containing oxygenated seawater for transportation to the laboratory. The sea urchins were brought to the same laboratory packed in ice. Before starting the experiment *P. lividus* and *A. lixula* were starved for 2 weeks and kept in separate tanks (300 **L**) to ensure that the two species had experienced similar conditions and to prevent changes in natural feeding responses (Rochette et al. 1994). Sessile organisms on cobbles, or on *Cystoseira,* were removed. *Cystoseira* were maintained in different storage tanks (300 **L**). All organisms were maintained with circulating natural seawater, at ambient light (12 h light and 12 h darkness) and at a temperature of 20°C for the whole duration of the experiment.

The experiment was aimed at assessing both the feeding behaviour and the relative ability of sea urchins to consume *Cystoseira* and consisted of a treatment with three levels of urchin presence carried out in replicated (n= 3) aquaria: 1) only *A. lixula* present, 2) only *P. lividus* present and 3) no urchins (controls) present. Each **aquarium** was 90 $\times$ 50 $\times$ 50 cm in size (ca. 200 **L** of sea water). In each aquarium a cobble covered with *Cystoseira* spp. was positioned. Twenty individuals of one sea urchin species (a density of about 20 ind./m^2) were then supplied where needed according to the experiment protocol. Controls were considered in order to assess the performance of *Cystoseira* (i.e. weight loss) in the absence of sea urchins. The cobbles with *Cystoseira* were weighed before being introduced in the aquarium, then sea urchins were allowed to forage until either the canopy disappeared, or a maximum of thirty days, whichever occurred first. When *Cystoseira* disappeared, we **recorded** the number of days spent for total consumption. Moreover, in order to estimate consumption of *Cystoseira* (g), cobbles were re-weighed when the canopy disappeared, or at the end time of the experiment. To ensure the independence of data each pool of sea urchins was used only once (Underwood 1997). **A total of 18 hours was spent** observing the feeding behaviour of the sea urchins. Observation times were equally distributed between the morning and afternoon for each of the first 3 days of the experiment. Each observation was ten minutes in duration and dedicated to each aquarium where sea urchins were present.

2.3. *Cystoseira* spp. gut contents

The sea urchins were collected over four seasons: summer and autumn 2007, winter and spring 2008. For each season collection took place on two random dates. Each time two sites, 400 m apart with similar orientation and hydrodynamic conditions, were randomly selected on the western side of Ustica Island (as in Gianguzza et al. 2013). In order to analyse sea urchin gut contents we collected six adult individuals of both species (> 35 mm test diameter) at each site and time, **at 3-6 m of depth**. Sea urchins were dissected 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 under a 40 × microscope in order to discern the gut items ingested and to evaluate the percentage of *Cystoseira* spp. out of the whole content.

2.4 Data analysis

Differences in percent *Cystoseira* wet weight from the beginning to the end of the laboratory experiments were analysed using a 2 - way ANOVA with "Urchin" (Ur; three levels: *P. lividus*, *A. lixula* and no urchins) treated as a fixed factor, and "Aquarium" (Aq; three levels) as a random and nested factor (n = 3).

Variability in *Cystoseira* spp. gut content between the two sea urchins was evaluated performing a 4 - way ANOVA including the factors: "Species" (Sp; two levels: *P. lividus*, *A. lixula*) treated as a fixed factor, "Season" (Se; four levels: Summer, Autumn, Winter, and Spring) as a fixed and orthogonal factor, "Time" (Ti; two levels) as a random factor nested in "Se", and "Site" (Si; two levels) as a random factor nested in Ti (n = 6). ANOVAs were calculated after checking for homogeneity of variances (Cochran's C test) **and fourth root transformation was performed for the two ANOVAs.** Student-Newman-Keuls (SNK) tests (at α=0.05) were used, where appropriate, for *a posteriori* comparisons of the means (Winer et al. 1991; Underwood 1997).

3. Results

In the laboratory experiments, *P. lividus* consumed 100% of *Cystoseira* (30–35 g) within three days. On the contrary, the algae remained untouched by *A. lixula* over a 30 day period. The consumption of *Cystoseira* spp. was vastly different between sea urchin species (ANOVA, Tab. 1 and Fig. 1). Also, the general behaviour exhibited in the aquaria by the two species was completely different. For example, *P. lividus* was able to rise up and climb on arborescent *Cystoseira* spp., flexing down the fronds whilst trying to anchor them to the substrate by its tubular feet. This afforded *P. lividus* better handling of its prey, from the fronds to the holdfast. Contrarily, *A. lixula* exhibited a scraping behaviour all around the thalli base of *Cystoseira*, possibly looking for other prey on the cobbles.

The average percent cover of *Cystoseira* spp. in the gut content of sea urchins varied significantly between the two species (ANOVA, $F_{1,160} = 151.92$, $P = 0.0002$). Overall, mean (± SE) percent cover of *Cystoseira* spp. in the gut content was 2.16 ± 0.46 for *A. lixula* and 26.47 ± 2.07 for *P. lividus* suggesting higher grazing by **the latter species**. This result was consistent through seasons and times (Fig. 2).

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4. Discussion

Factors affecting the feeding biology of echinoids have long been a subject of interest in marine ecological literature. This is due to the fact that sea urchin grazing is frequently responsible for the destruction of canopy-forming algae and the formation of barrens in shallow marine ecosystems (Lawrence 2013 and references therein). Several studies have indicated a spatio-temporal variability of feeding behaviors (Konar and Estes 2003, **Flukes et al. 2012**) and there is evidence that this may depend on local threshold density (Bulleri 2013).

As expected, field and laboratory results have consistently shown that *P. lividus* is more efficient in consuming *Cystoseira* spp. than *A. lixula*. Although gut content analysis creates uncertainty, due to possibly confounding effects (density, food selection, etc.), a significant difference in the ingested *Cystoseira* was found between the two sea urchins. In the laboratory, *A. lixula* at density of 20 ind./m^2 was unable to consume *Cystoseira* even though starved for 2 weeks and maintained for 30 days in the presence of the alga. Conversely *P. lividus* was able to consume *Cystoseira* within 3 days. Whether this is a consequence of a greater ability of *P. lividus* to feed on *Cystoseira* algae or a much greater palatability of the alga for *P. lividus* is **still to be evaluated**. As regards feeding choice, it is widely acknowledged that many sea urchins strongly display selection **for** some seaweed species over others, and this has been linked to nutritive value and physical – **chemical** properties of food (Frantzis **and Gremare** 1992). Furthermore, it is well known that food manipulation by the different feeding traits (Aristotle's lantern and tube feet) is an important step in the echinoid feeding process and algae species that are easily caught and transferred to the mouth would be favored (Lawrence 2013). Moreover, three basic feeding behaviors have been documented for sea urchins (1) **capture** of sediment or - dissolved organic material, particularly in term of amino acids, with their sulcated spines and aboral tube feet and adsorbed by dermal-skeleton, (2) removal of erect algae thalli and/or sessile invertebrates from hard substrate by means of the powerful teeth of the Aristotle's lantern and (3) capture of drift algae, "drift-trapping behaviour", by the ambulacral tube feet and spines and the subsequent transport of this material to the mouth (Conteras and Castilla 1987; Lawrence 2013). Regarding this, the two urchin species differ morphologically: *P. lividus* has shorter and denser spines, more extendible aboral tube feet and a weaker Aristotle's lantern than *A. lixula* and it is likely that such differences affect their feeding behaviors (Santos and Flammang **2005; 2007**).

The results clearly confirmed that *P. lividus* feeds mainly by gentler "grazing" and by "drift-trapping" *Cystoseira* algae with its aboral tube feet. *A. lixula*, owning a strong Aristotle's lantern and tube feet exclusively on the oral side, adopted a scraping behaviour (Privitera et al. 2008) all around the thalli of *Cystoseira*, possibly looking for sessile prey on the cobble. Interestingly, results indicated a deep difference in *Cystoseira*, handling and dislodging ability between the two sea urchins, probably affected not only by differences in feeding traits themselves but also by movement ability.

As observed, these features make *P. lividus* better adapted to penetrate, climb and knock down the erect thalli of *Cystoseira* as a result of its superior mobility (Agnetta et al. 2013).

The findings evidenced that **the ability to consume and dislodge *Cystoseira* spp. belongs merely to *P. lividus***. The fact that *Cystoseira* **remained intact**, notwithstanding the high *A. lixula* density in aquarium (20 urchins/m^2), is worthy of consideration and in contrast with previous manipulative studies that had indicated a redundant role of the two sea urchins in controlling this algae (Bulleri et al. 1999; Bonaviri et al. 2011). Such inconsistency might depend on the initial conditions of the studied habitat: in our case *Cystoseira*-barren mosaic in the field, and cobbles covered by *Cystoseira* spp. in the aquaria, whereas in the other two studies the habitat was a barren dominated by turf and corallines respectively (Bulleri et al. 1999; Bonaviri et al., 2011).

From an ecological point of view, **the** results suggest that the likelihood of initial **barren** patch formation could be a direct consequence of local *P. lividus* grazing: this species, by consuming and removing the entire canopy and the base of the alga, prepares naked substratum which can later be colonized by encrusting algae and its associated "cryptic fauna" (Agnetta et al. 2013). Then *A. lixula*, which settles preferentially in encrusting coralline algae, can colonize the barren (Privitera et al. 2011) and maintain it (Bonaviri et al. 2011). According to this facilitative model, in contrast to the traditional hypothesis of a competitive scenario, the decrease in *P. lividus* density, currently affected by cumulative human impact, should reduce the likelihood of widespread barren formation. Furthermore, because *Cystoseira* spp. needs naked substratum to recruit (Perkol-Finkel and Airoldi 2010) the timing of bare halos formation could be crucial in promoting the recovery of these algal forests. Thus another possible scenario is that when at low density *P. lividus* grazing on *Cystoseira* spp. (high density would make propagules more likely to be grazed) can trigger different habitat formation (algal forest *vs.* barren) depending on the seasonal time the substratum becomes naked

5. Conclusions

Foraging ability of the two sea urchins on *Cystoseira* canopy is very different and these algae can be particularly threatened by *P. lividus* grazing rather than *A. lixula*. This supports the hypothesis that *P. lividus* has a leading role in the formation of barren. Knowledge gained in this study fills important gaps in the understanding of functioning of rocky infralittoral ecosystems in particular barren formation process and furnishes new perspective to resources management also in Mediterranean Marine Protected Areas.

Acknowledgements

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Figure legends

Fig. 1 Not consumed *vs* consumed *Cystoseira* spp. (arrows) canopy by *A. lixula* (A) and *P. lividus* (B) at the end of the foraging experiment (30 and 3 days respectively).

Fig. 2 Percentage of *Cystoseira* spp. in sea urchin gut contents from the field study. Differences between the two sea urchin species were consistent with season: Summer (S), Autumn (A) 2007 and Winter (W), Spring (Sp) 2008.

Table legends

Table 1 Results of the 2 - way ANOVA on consumed *Cystoseira* spp. (percent wet weight (g)) **at the end of the experiment**. Factors include: "Urchin" (Ur; three levels: *P. lividus*, *A. lixula* and no urchins), fixed, and "Aquarium" (Aq; three levels), random and nested in Ur (n = 3). **Transformation: x^ 0.25, Cochran's Test: C = 0.3743 ns**

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Source of variation	*df*	MS	*F*	*P*
Urchin = Ur	2	23.0361	209.64	0.0000
Aquarium(Ur)	6	0.1099	0.43	0.8493
Residual	18	0.2555		
Total	26			

SNK test: *P. lividus* > *A. lixula* = Control

Figure1

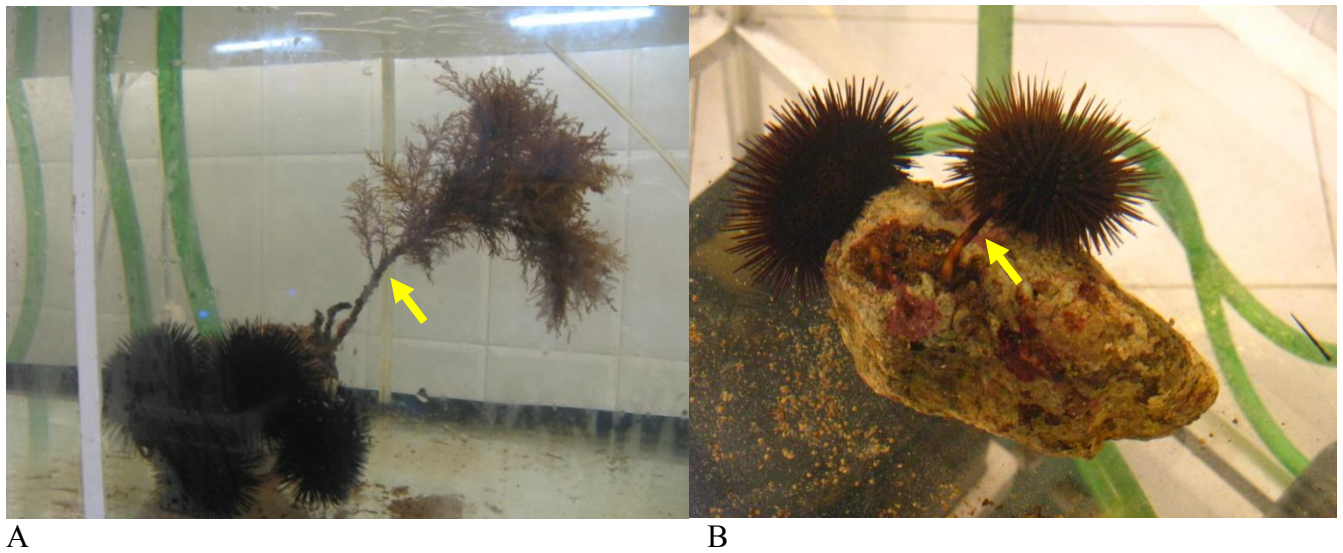A   B

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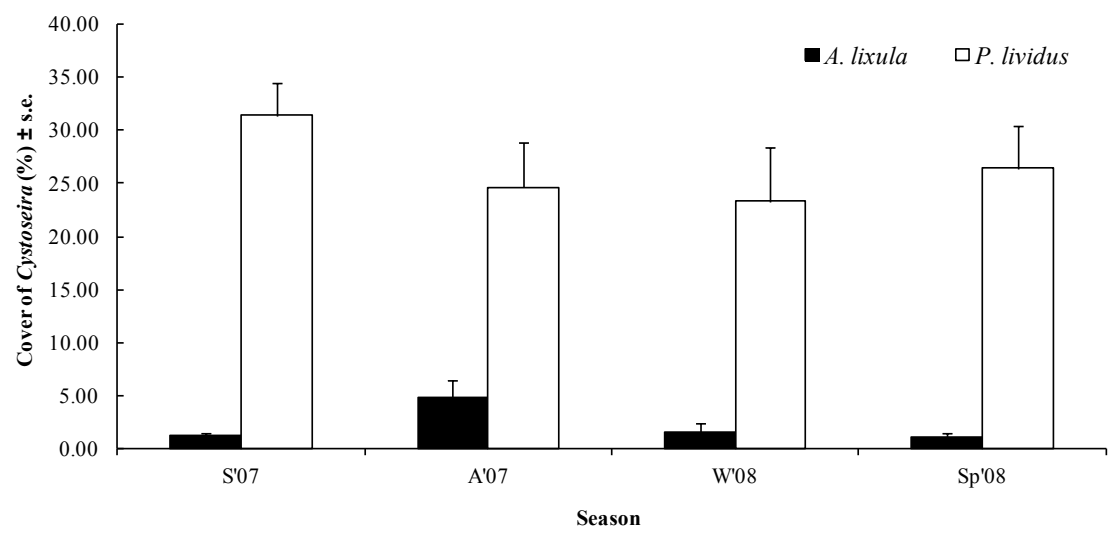
Figure2

Fig. 2 Percentage of *Cystoseira* spp. in sea urchin gut contents from the field study. Differences between the two sea urchin species were consistent with season: Summer (S), Autumn (A) 2007 and Winter (W), Spring (Sp) 2008.