



## Macroalgal assemblage type affects predation pressure on sea urchins by altering adhesion strength

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### ABSTRACT

In the Mediterranean, sea breams are the most effective *Paracentrotus lividus* and *Arbacia lixula* predators. Generally, seabreams dislodge adult urchins from the rocky substrate, turn them upside down and crush their tests. Sea urchins may respond to fish attacks clinging tenaciously to the substratum. This study is the first attempt to investigate sea urchin adhesion strength in two alternative algal assemblages of the rocky infralittoral and evaluated its possible implication for fish predation. We hypothesized that (1) sea urchin adhesion strength is higher in rocky shores dominated by encrusting macroalgae (ECA) than in erected macroalgae (EMA); (2) predation rates upon sea urchins are lower in ECA than in EMA; and (3) predation rate on *A. lixula* is lower than that on *P. lividus*. We observed that attachment tenacity of both sea urchins was higher in ECA than EMA and that *A. lixula* exhibited a stronger attachment tenacity than *P. lividus* in ECA. Results supported the importance of adhesion strength, as efficient defence against sea bream attacks, only for *P. lividus*. *A. lixula* adhesion strength does not seem to be an important factor in avoiding fish predation, possibly because of the low palatability of the species. These patterns may deserve particular interest in understanding the processes responsible for the maintenance of sea urchin barrens that are dominated by ECA assemblage.

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### 1. Introduction

Predation moulds community structure in ecological and evolutionary times (Vermeij, 1977; Paine, 1980). Predation risk, both perceived and actual, may induce changes in prey morphology (e.g. Hoverman et al., 2005; Andersson et al., 2006; Selden et al., 2009) behaviour (Lima and Dill, 1990; Legault and Himmelman, 1993; Lima, 2009) and the timing of hatching or metamorphosis (e.g. Peckarsky et al., 2002). Thus, it is not surprising that animals invest considerable materials and energy into attributes that counteract and reduce the effects of predation.

Sea urchins are no exception to this rule as they exploit physical, chemical, and behavioural mechanisms to reduce their vulnerability to predators (Lawrence, 1987). They contrast predation by morpho-functional features such as thickened test, accumulation of deterrent compounds in their tissues, presence of spines and globiferous pedicellariae that can inject toxic substances into the skin of their predators (Campbell, 1983). Furthermore, behavioural mechanisms, such as cryptic, escape and aggregative responses are

also common predator-avoidance strategies in sea urchins (Carpenter, 1984; Rodriguez and Ojeda, 1998). This variety of defence strategies adopted reflects the broad range of sea urchins predators (Mann, 1982; Tegner and Levin, 1983; Sala, 1997; Hori and Noda, 2007; Gianguzza et al., 2009).

In the Mediterranean, the co-occurring sea urchin species *Paracentrotus lividus* and *Arbacia lixula* are the most important grazers and there is increasing evidence that natural and human predation has the potential to directly control their populations with indirect effects, through trophic cascades, on the whole structure of benthic communities (Sala et al., 1998).

The variation in sea urchin grazing intensity may drive switches between one complex state, dominated by a stratified assemblage of several erect macroalgae, to a simpler one dominated by few encrusting algae: the so-called 'barren ground' (Sala et al., 1998; Boudouresque and Verlaque, 2001; Bulleri et al., 2002).

Despite a long list of potential predators, only the seabreams *Diplodus sargus* and *D. vulgaris* have been reported to effectively control sea urchin populations as they actively prey upon adult and juvenile urchins (Sala and Zabala, 1996; Guidetti, 2004, 2006; but see also Bonaviri et al., 2009). Different feeding habits have been reported for seabreams, depending on the sizes of both the

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predator and the prey (Sala, 1997; Guidetti, 2004). Very small urchins (<1 cm in test diameter) are generally swallowed whole using suction, whereas larger sea urchins (>3 cm in test diameter) are attacked at the base to dislodge them from the rocky substrate, turned upside down, and finally bitten on the oral side until the tests are broken (Sala, 1997). Large sea urchins may respond to fish attacks with cryptic behaviours such as clinging tenaciously with their tube feet to the substratum and sometimes into holes drilled into the substratum where they shelter during the daytime, whilst displaying a nocturnal feeding activity (Shepherd and Boudouresque, 1979; Dance, 1987; Hereu et al., 2005; Sala and Zabala, 1996). The sea urchin adhesion strength is determined by the number of tube feet involved, the tube foot tenacity and the type of substratum (Santos et al., 2005; Santos and Flammang, 2007).

While much of the literature on *P. lividus* and *A. lixula* stresses the importance of the size and shape of the sea urchin test in attachment strength and thus the probability of dislodgment in relation to hydrodynamic conditions (Smith, 1978; Santos and Flammang, 2007), little is known about the influence of the type of substrate on sea urchin adhesion strength (Santos et al., 2005) and its implications for predator success (Guidetti and Mori, 2005).

Santos et al. (2005) evaluated, under laboratory conditions, the influence of substratum roughness on the adhesion strength of tube feet in the sea urchin *P. lividus* and the sea star *Asterias rubens*, and showed a stronger adhesion on a rough substratum in comparison to a smooth counterpart, which is mostly due to an increase in the contact surface between the tube foot disc and the substrate. Guidetti and Mori (2005) through laboratory observations, provided evidence that morpho-functional features such as attachment tenacity, spine length, and test robustness and thickness were positively related to sea urchin size for both *P. lividus* and *A. lixula*, but differ between the two species. *A. lixula* appears to be structurally more resistant than *P. lividus* to sea bream crushing attacks.

In spite of the fact that *P. lividus* and *A. lixula* can live on barren grounds and vegetated rocky shores (Chiantore et al., 2008), recent data have shown a positive correlation between barren extent and sea urchin densities and this pattern was more evident for *A. lixula* (Fanelli et al., 1994; Micheli et al., 2005; Guidetti and Dulčić, 2007). These findings might suggest a different predation vulnerability between the two sea urchin species in distinct algal assemblages. The rationale is that erect macroalgae would leave less available adhesive surface area to sea urchin tube foot discs and the rocky bottom. Consequently sea urchin adhesion strength was expected to be lower in erect macroalgae-dominated shores rather than area dominated by encrusting algae. This is because a large proportion of bare rock is available for sea urchin anchoring in the later. Nevertheless, this mechanism would be of unequal relevance for each of the sea urchin species, because the number and position of tube feet differ between them. For example, *A. lixula* presents tube feet exclusively on the oral side, where they are numerous. In contrast, *P. lividus* shows less densely packed tube feet, but they are distributed all around the test (Santos and Flammang, 2007).

We carried out two experiments in the Marine Protected Area (MPA) “Ustica Island” (Southern Tyrrhenian Sea, Italy), where both encrusting corallines algae (ECA) and erect macroalgae (EMA) assemblages were simultaneously present as a mosaic of interspersed patches. The following hypotheses were tested: (1) sea urchin adhesion strength is higher in ECA than in EMA; (2) predation rate upon *P. lividus* and *A. lixula* is lower in ECA than in EMA and (3) as a consequence of the greater attachment tenacity of *A. lixula* than *P. lividus* (Guidetti and Mori, 2005) we also predicted a lower predation rate for this species compared to *P. lividus*.

## 2. Materials and methods

### 2.1. Study area

The study was carried out at Ustica Island the protruding part of an extinct volcano located in the southern Tyrrhenian Sea (Western Mediterranean, 38°42'20"N–10°43'43" E), 60 km north of the Sicilian coast. Its base lies at about 2000 m depth and it is composed mainly of alkaline basalts and sedimentary rocks (Riggio and Milazzo, 2004).

Our investigation was done in the no-take zone of the Marine Protected Area of Ustica Island from June to August 2007. In this area, about 10 yr after the harvesting ban (1991), *P. lividus* and the co-occurring *A. lixula* achieved their maximum density ( $8 \pm 3.5$  individuals/m<sup>2</sup> and  $12 \pm 4.0$  individuals/m<sup>2</sup> mean density  $\pm$  S.E. respectively). As a consequence, a barren status spread extensively from the shallow to moderately deep rocky sublittoral (Riggio and Milazzo, 2004; Gianguzza et al., 2006). However, during the latest years densities of both sea urchins dramatically decreased (Bonaviri et al., 2009). An aftermath of such fluctuations was the resurgence of small *Cystoseira* spp. dominated patches. This configuration provided a binary landscape were either ECA or EMA dominated, forming a mosaic of interspersed patches of about 1.5 m in diameter. By 2007, when the work reported herein was done, in the no-take zone *P. lividus* density was  $3.5 \pm 0.5$  individuals/m<sup>2</sup> (mean density  $\pm$  S.E.) and that of *A. lixula*  $2.5 \pm 0.8$  individuals/m<sup>2</sup> (mean density  $\pm$  S.E.).

Two sites were randomly selected from the no-take zone, called Sbarramento (S<sub>1</sub>) and Acquario (S<sub>2</sub>, Fig. 1). The sites were chosen approximately 600 m apart with other important factors (depth, topography, orientation, water motion, sea urchin and predator density) unchanged. The EMA assemblage was dominated by *Cystoseira brachycarpa* var. *balearica* and *C. compressa*, whereas ECA was dominated by encrusting coralline algae such as *Lithothamnion* spp. and *Lithophyllum* spp.

### 2.2. Adhesion strength

The effect of the algal assemblage on the sea urchin adhesion strength was tested for both sea urchin species through an *in situ* experiment. The experimental design considered three factors: Algal assemblage (Al), fixed with two levels (EMA and ECA); sea urchin species (Sp), fixed with two levels (*A. lixula* and *P. lividus*); and Site (Si), orthogonal and random with two levels (S<sub>1</sub> and S<sub>2</sub>). There were 10 replicates per cell. Due to the interspersed of ECA and EMA patches in the two selected sites, levels of factor algal assemblages faced similar sea urchin and sea urchin predator densities.

The experiment was thus performed using 80 *P. lividus* and 80 *A. lixula* (test diameter without spines ranging from 3 to 3.5 cm) randomly collected by SCUBA diving in shallow rocky reefs, between 1 and 3 m in depth, of the no-take zone. Sea urchins were carefully detached from the rocky substrate to avoid ripping off podia (which may bias measures of attachment tenacity), or damaging spines. After collection, one thin plastic band was carefully inserted longitudinally under each sea urchin and then they were quickly placed on shallow rocky substrates (about 1 m depth) each representing the two different algal assemblages. Care was taken in order to give each sea urchin time enough to properly attach to the bottom (Guidetti and Mori, 2005) and to connect the plastic band to the spring dynamometer. This was gently pulled normal to the substratum and manually moved upwards at a constant speed (Flammang and Walker, 1997). In this study we evaluated the echinoid attachment strength as scaled attachment force (force expressed in N) according to the protocol described in

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