RESEARCH ARTICLE

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Morpho-functional defences of Mediterranean sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, against fish predators

Abstract Morpho-functional features potentially involved in defence mechanisms against fish predators (i.e. attachment tenacity, spine length, and test robustness and thickness) have been assessed in two Mediterranean sea urchins, *Paracentrotus lividus* and *Arbacia lixula*. All four morpho-functional features were significantly and positively related to individual size for both species of sea urchins. Test robustness (i.e. static load needed to break sea urchin tests) was significantly greater for *A. lixula* (from 3,450 to 15,000 g depending on size) than for *P. lividus* (1,180–11,180 g). Attachment tenacity (i.e. force needed to dislodge sea urchins from the rocky substrate) was greater in *A. lixula* (280–3,300 g) than in *P. lividus* (110–1,450 g), and the difference tended to decrease in relation to smaller sea urchin size. Spine length was greater in *A. lixula* (1.5–2.9 cm) than in *P. lividus* (0.5–2.3 cm), but the difference decreased for larger sea urchin size. Test thickness was slightly greater (but not significantly) in *A. lixula* (0.35–1.10 mm) than in *P. lividus* (0.12–0.90 mm). These results provide evidence that morpho-functional features of sea urchins could be involved in affecting predation rates by fishes upon *P. lividus* and *A. lixula*, with potential implications for the population structure and distribution patterns of the two sea urchins in shallow rocky reefs.

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Introduction

Sea urchins are important grazers in most marine benthic sublittoral communities (Lawrence 1975; Tegner and Dayton 1981; Sala et al. 1998a and references therein). In many temperate areas they can cause the transition between macroalgal forests and coralline barrens, with important repercussions for the structure and functioning of rocky-reef ecosystems (Tegner and Dayton 1981; Scheibling 1986; Verlaque 1987; McClanahan and Shafir 1990; Leinaas and Christie 1996; Sala et al. 1998a; Shears and Babcock 2002; Guidetti and Boero 2004). Besides other factors (e.g. diseases, physical factors, recruitment; Hart and Scheibling 1988; Hagen 1992; Sala et al. 1998a; Hereu et al. 2004), predation (including human exploitation; see Guidetti et al. 2004 and references therein) has been shown to affect density, behaviour, and population structure of sea urchins (Tegner and Dayton 1981; McClanahan and Shafir 1990; Estes and Duggins 1995; Scheibling 1996; Sala et al. 1998a; Shears and Babcock 2002). Predators, from this point of view, have the potential to influence the structure of benthic communities indirectly by directly affecting the activity of grazers through cascading effects (Pinnegar et al. 2000; Witman and Dayton 2001; Sala 2004).

Benthic communities in the shallow Mediterranean rocky sublittoral range from coralline barrens (dominated by sea urchins and encrusting algae) to complex macroalgal beds (which harbour hundreds of species of algae and animals). It has been suggested that sea urchins may drive the transition between these two community states (Sala et al. 1998a; Sala 2004; but see Bulleri et al. 2002). The sea urchins *Paracentrotus lividus* and *Arbacia lixula* may coexist in Mediterranean subtidal rocky reefs, in spite of some differences in their microhabitat preferences (Bulleri et al. 1999 and references therein) and geographical distribution (Francour et al. 1994; Boudouresque and Verlaque 2001). Most of the available studies took into account *P. lividus* to

explain the distribution of barrens and the structure of macroalgal communities in shallow Mediterranean rocky reefs (Verlaque 1987; Palacin et al. 1998; Sala et al. 1998a; Hereu 2004). Nevertheless, *A. lixula* may also exert an important role (Guidetti et al. 2003). Different patterns of grazing have been observed between the two sea urchins (Frantzis et al. 1988), but this issue is still a matter of debate (see Bulleri et al. 1999). A potentially different efficiency with which natural predators can control each of the two sea urchin species could have implications for their overall grazing effects on macroalgal assemblages.

It has been suggested that the transition from macroalgal beds to barrens in the Mediterranean is enhanced by the removal of predatory fishes that feed upon sea urchins (Sala et al. 1998a). The sparid fishes *Diplodus sargus* and *D. vulgaris* are the most effective predators capable of controlling sea urchin populations as they actively prey upon adult and juvenile urchins. Wrasses (chiefly *Coris julis* and *Thalassoma pavo*), instead, prey only upon juveniles (Sala 1997; Sala et al. 1998a; Guidetti 2004a) and they may thus affect post-settlement mortality (Hereu et al. 2005). Depending on the size of the fish predator relative to the size of the sea urchin prey, different feeding habits of *Diplodus* fishes have been reported (Sala 1997; Guidetti 2004b): very small urchins (< 1 cm) are generally swallowed whole using suction, whereas larger sea urchins are attacked at the base to dislodge them from the rocky substrate, turned upside down, and finally bit in the oral side until tests are broken. The success of attacks is negatively related to sea urchin size (Sala and Zabala 1996; Guidetti 2004a). When fish predators are offered already opened sea urchins, approximately the same fish species feed with similar patterns upon *P. lividus* and *A. lixula* (Guidetti 2004a). Tethering experiments, however, showed that predation rates are far greater over *P. lividus* than *A. lixula* (Guidetti 2004b).

The above issues suggest that the two species of sea urchins have a similar palatability, but also that some defence strategy against fish predators could determine different predation rates between *P. lividus* and *A. lixula*, which are likely to be also related to sea urchin individual size.

In this study, therefore, we assessed the relationships between morpho-functional features potentially involved in defence mechanisms against fish predators (i.e. attachment tenacity, spine length, test thickness and robustness) and sea urchin individual size and tested for possible differences between *P. lividus* and *A. lixula*.

Materials and methods

Data collection in the laboratory

Specimens of *Paracentrotus lividus* (n = 68; test diameter without spines ranging from 0.9 to 6.1 cm) and *Arbacia lixula* (n = 68; test diameter: 1.0–6.4 cm) were collected by scuba diving in shallow rocky reefs in southern Apulia (SE Italy, Mediterranean Sea). Sea urchins were carefully detached from the rocky substrate to avoid ripping off podia (which may bias measures of attachment tenacity in the laboratory), or damaging spines. They were then quickly transported to the laboratory and allowed to acclimate for some days in aquaria (located in a thermostatic room), to limit the shock due to sampling.

Sea urchins were first measured (test diameter without spines, centimetres) using a vernier calliper. Attachment tenacity was then measured by means of spring dynamometers. For this purpose, sea urchins were put in large aquaria (about 200 l) in which limestone plates had been placed on the bottom, mimicking the natural rocky substrate. Experimental trials showed that it takes about 1 h for sea urchins to find an appropriate place and attach firmly to the substrate (i.e. for the attachment tenacity in the aquaria to be comparable to the values measured in the field; unreported data). Two hours later, two thin plastic bands were carefully inserted orthogonally under each sea urchin. The bands were connected to the spring dynamometer, which was then gently pulled normal to the substratum until the sea urchin was detached, and the force (in grams) necessary to dislodge the sea urchin was recorded. Spine length (centimetres) was measured for each sea urchin by subtracting the test diameter from the total maximum diameter (test with spines) and dividing by two.

According to Strathmann (1981), sea urchin skeletons have to resist static loads whenever they are attacked by crushing predators (as is the case when *Diplodus* fishes attack adult sea urchins). Test robustness was measured by a custom-made device as the static force necessary to crush sea urchin tests. Sea urchins were positioned upside down (see the Introduction for a description of fish predator attacks upon sea urchins) in a special box clamp and increasing pressure was applied by the progressive filling of a piston, until the crushing of the test. The weight (grams) of the water contained in the piston was used as a surrogate of the static force needed to crush sea urchin tests.

Finally, thickness (millimetres) of each sea urchin test was measured with a vernier calliper: five measures were performed on each sea urchin test, and the mean value was then used as the datum (Strathmann 1981).

Statistical treatment of data

For both *P. lividus* and *A. lixula*, we first tested the relationship between the four variables investigated and the sea urchin size by regression analysis, using the least-square regression method. As data were balanced, homogeneity of variances in each data set was tested by Cochran's test (Underwood 1997). Even in the single case (i.e. attachment tenacity; see Results) where variances were slightly, but significantly, heterogeneous, we

did not transform the data, as transformations are scale dependent (Box and Cox 1964), and the regressions would not be estimated with the same precision if the scale is changed (Underwood 1997). A homogeneity of slopes test was used to compare regressions obtained for *P. lividus* and *A. lixula*, taking into account that the heterogeneity of regressions prevents an analysis of covariance (ANCOVA) being done (Underwood 1997). As the regressions describing the relationships of the four variables investigated with sea urchin size were heterogeneous between *P. lividus* and *A. lixula* (see Results), the Wilcox procedure, according to the Johnson–Neyman technique (Johnson and Neyman 1936), was used to determine the regions of significance between lines. In particular, this procedure was used for determining the limits of the covariate for which there is 95% confidence that the difference between two lines at any point below or above the two limits, respectively, is significant (Huitema 1980; Wilcox 1987). This technique is considered straightforward when there are two samples (the two sea urchin species in our study) being compared, and one covariate (i.e. test size; Underwood 1997).

Results

The attachment tenacity varied from 110 to 1,450 g for *Paracentrotus lividus*, and from 280 to 3,300 g for *Arbacia lixula*. Regression analyses revealed that the

relationship between the attachment tenacity and sea urchin size was significant for both *P. lividus* and *A. lixula* (Fig. 1a; *P. lividus*: $y = 237.03x - 140.36$, $r^2 = 0.69$, $F_{1,66} = 146.94$, $P < 0.001$; *A. lixula*: $y = 432.76x + 16.00$, $r^2 = 0.79$, $F_{1,66} = 15.61$, $P < 0.001$). Variability in the measures of tenacity was slightly heterogeneous between *A. lixula* and *P. lividus* (Cochran's test, C: 0.73, $P > 0.05$). There were significant differences in slopes (homogeneity of slopes test: $F_{1,133} = 30.04$, $P < 0.001$), and the Wilcox test showed that lines were not statistically different ($P < 0.05$) in the covariate (i.e. $x = $ test size) range of between −3.71 and 0.52. This means that the attachment tenacity of *P. lividus* is significantly lower than that of *A. lixula* in the observed range of test sizes, and that the larger sea urchins are, the more differences are evident (Fig. 1a).

Spine length, ranging from 0.5 to 2.3 cm for *P. lividus* and from 1.5 to 2.9 cm for *A. lixula*, was related to sea urchin size for both *P. lividus* and *A. lixula* (Fig. 1b). Regression analyses revealed that the relationship was significant for both species (*P. lividus*: $y = 0.30x + 0.50$, $r^2 = 0.88$, $F_{1,66} = 469.78$, $P < 0.001$; *A. lixula*: $y = 0.18x + 1.54$, $r^2 = 0.48$, $F_{1,66} = 60.63$, $P < 0.001$). Cochran's test did not detect any significant variability in spine length for *A. lixula* and *P. lividus* (Cochran's test, C: 0.58, n.s.). The homogeneity of slopes test revealed significant differences in slopes between *P. lividus* and *A. lixula* ($F_{1,133} = 20.15$, $P < 0.001$). The Wilcox test showed that lines are not statistically different ($P < 0.05$) within the covariate interval between 6.81 and 14.30, suggesting that spine length of *P. lividus* is significantly smaller than that of *A. lixula* in the whole range of the observed values of sea urchin individual size, but also that such a difference tends to decrease with increasing sea urchin size (Fig. 1b).

Fig. 1 Relationship between morpho-functional features (**a** attachment tenacity; **b** spine length; **c** test robustness; **d** test thickness) of the sea urchins *Paracentrotus lividus* and *Arbacia lixula*, and individual size (test diameter without spines)
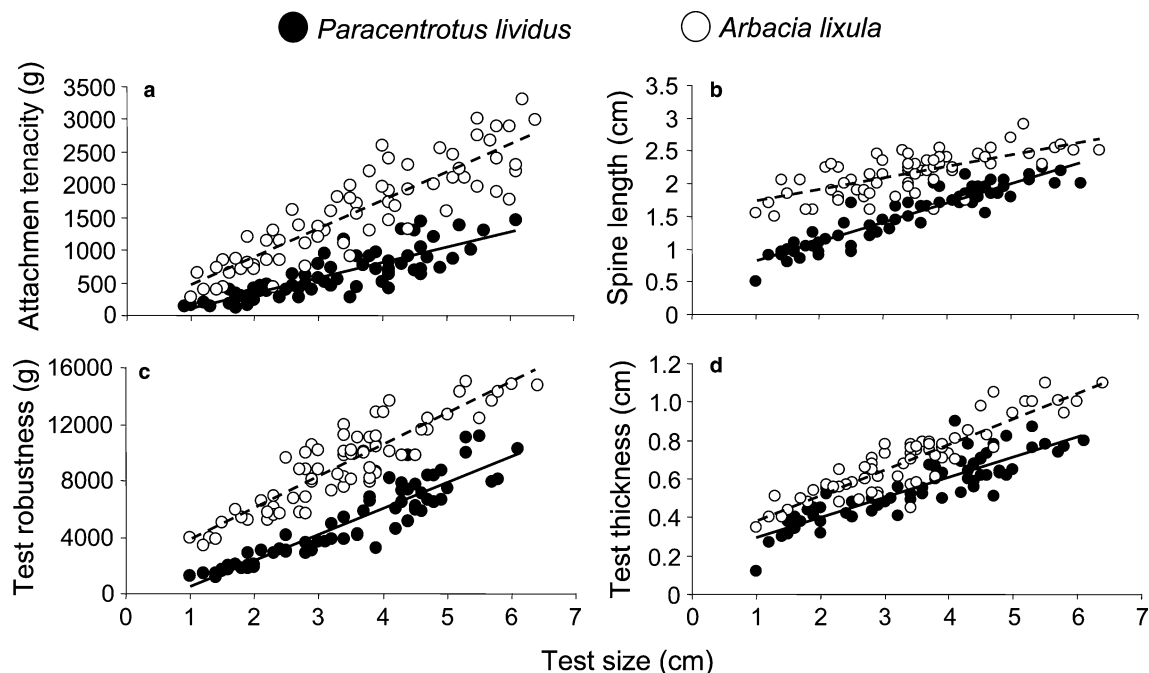
Test robustness ranged from 1,180 to 11,180 g for *P. lividus*, and from 3,450 to 15,000 g for *A. lixula*. The relationship between test robustness and the individual sea urchin size for both *P. lividus* and *A. lixula* is shown in Fig. 1c. Regression analyses revealed that the relationship was significant for both species (*P. lividus*: $y = 1870.0x - 1366.2$, $r^2 = 0.85$, $F_{1,66} = 365.56$, $P < 0.001$; *A. lixula*: $y = 2251.9x + 1538.3$, $r^2 = 0.81$, $F_{1,66} = 281.40$, $P < 0.001$). Variability in test robustness was homogeneous between *A. lixula* and *P. lividus* (Cochran's test, *C*: 0.53, n.s.). The homogeneity of slopes test showed significant differences in slopes between the two sea urchins ($F_{1,133} = 5.41$, $P < 0.05$), although such a difference in slope was less pronounced than for the other variables investigated (see Fig. 1a–d). The Wilcox test showed that the two lines are not statistically different ($P < 0.05$) within the range of the covariate of between – 1493.7 and –2.05. This suggests that *P. lividus* tests are significantly less robust that those of *A. lixula* whatever the sea urchin test size (Fig. 1c).

Test thickness (ranging from 0.12 to 0.90 mm for *P. lividus*, and from 0.35 to 1.10 mm for *A. lixula*) was related to sea urchin size for both *P. lividus* and *A. lixula* (Fig. 1d). Regression analyses revealed that the relationship was significant for both species (*P. lividus*: $y = 20.10x + 0.19$, $r^2 = 0.78$, $F_{1,66} = 236.54$, $P < 0.001$; *A. lixula*: $y = 0.13x + 0.24$, $r^2 = 0.82$, $F_{1,66} = 300.61$, $P < 0.001$). Cochran's test did not show any significant heterogeneity in test thickness between *A. lixula* and *P. lividus* (Cochran's test, *C*: 0.56, n.s.). The homogeneity of slopes test revealed that there were significant differences in slopes ($F_{1,133} = 7.83$, $P < 0.01$). The Wilcox test, in this case, was unable to find a range of the covariate where the lines were not statistically different. This means that although *A. lixula* appeared to have slightly thicker tests, such a difference was not statistically significant for any sea urchin size (Fig. 1d).

Discussion

The present study provides evidence that morpho-functional features of adult sea urchins that could be involved in defence against predatory fishes (i.e., attachment tenacity, spine length, and test robustness and thickness) are positively related to sea urchin size for both *Paracentrotus lividus* and *Arbacia lixula*. In addition, this study shows that attachment tenacity, spine length, and test robustness differ significantly between the two species of sea urchins. *A. lixula*, from this point of view, appeared to be structurally more resistant to crushing predator attacks.

Experimental studies have shown that the smaller the sea urchin, the higher the rate at which they are preyed upon, for both *P. lividus* and *A. lixula* (Sala and Zabala 1996; Guidetti 2004b). From this perspective, the positive relationship we found between morpho-structural defence features and sea urchin size could explain the differences in predation rates related to size (Sala 1997;

Guidetti 2004a). However, it has to be considered that the above-mentioned experimental studies (Sala and Zabala 1996; Guidetti 2004b) were done using tethering, which artificially exposes sea urchins to predators. In natural conditions, small sea urchins are able to escape efficiently from predators by sheltering in refuges (e.g. crevices). When growing, their ability to occupy shelters decreases, leaving sea urchins (e.g. medium-sized individuals) more exposed to predation until they reach very large sizes, which provides them another form of predatory escape (Connell 1972; Tegner and Dayton 1981; Sala and Zabala 1996; Sala 1997). All the above issues suggest that juvenile and, to a lesser extent, medium-sized sea urchins in natural conditions could compensate for their less-efficient morpho-functional defences against predators by sheltering. This also suggests how important the availability of shelters (i.e. the structural complexity of rocky reefs) is in affecting sea urchin population density, chiefly in areas characterised by high density of predatory fishes (e.g. marine reserves; Sala et al. 1998a and references therein; P. Guidetti and E. Sala unpublished data). These results could also explain the general relationship between the cryptic behaviour of sea urchins as a function of size and the density of fish predators observed in the Mediterranean and elsewhere (Tegner and Dayton 1977; McClanahan and Kurtis 1991; Sala and Zabala 1996; Shears and Babcock 2002; Guidetti 2004b, 2004c).

Differences in attachment tenacity, spine length, and test robustness between *P. lividus* and *A. lixula* suggest the latter species to be more structurally defended than the former against the attacks of *Diplodus* fishes (see the Introduction for the specific technique fish predators use to dislodge sea urchins and break their tests). Although there are no previous quantitative data available, the results for attachment tenacity are consistent with the observation by Bulleri et al. (1999 and personal communication), who noted that, while performing experimental removals, the force necessary to dislodge *A. lixula* was much greater than that required to remove *P. lividus*. Attachment tenacity, from a general perspective, could also be an adaptation allowing *A. lixula* to colonise shallower habitats than *P. lividus*, where sea swell is particularly intense (Kempf 1962), but it has to be also noted that in some areas (e.g. Tremiti Archipelago, central Adriatic) *A. lixula* may live at depths greater than 15–20 m (personal observation). *A. lixula*, therefore, appears to be more firmly attached to the rocky substrate and to have longer spines and a more robust test than *P. lividus*. All these features make *P. lividus* potentially much more prone to predation by crushing predators such as *Diplodus* fishes (Sala 1997). These outcomes are consistent with the results of tethering experiments within protected areas (i.e. areas of high density of large *Diplodus* fishes) that revealed far greater predation rates by fish predators upon *P. lividus* than upon *A. lixula* (Guidetti 2004b). The fact that morpho-functional features typical of *A. lixula* and *P. lividus* may affect the rates at which the two sea urchins are subject to

predation is further supported by the observed differences in cryptic behaviour between *P. lividus* and *A. lixula* related to size. *A. lixula*, in fact, tends to come out from shelters for foraging in open space at a smaller size than *P. lividus* (Guidetti 2004b). This behavioural pattern may be explained by the former species exhibiting much more efficient defences against predators, in spite of a similar palatability between the two sea urchins when fish are offered opened sea urchin tests (Guidetti 2004a). These results about morpho-functional features of the two sea urchins, therefore, fit with the theory that for a defence feature to be effective, it should increase prey fitness or survival (e.g. increase the predator handling time; Tollrian and Harvell 1999). This has also been observed for other marine invertebrates, such as limpets, for which a measure of resistance to predators is also dependent on how much force and effort are needed to dislodge them from the rocky shore (Coleman et al. 2004). It thus appears increasingly clear that size and morpho-functional and behavioural traits (or their combinations) typical of each sea urchin species may concur in the response of *P. lividus* and *A. lixula* against fish predators. Such mechanisms appear to be very common in cases in which predators are much more mobile than their prey (e.g. sea birds and limpets, fishes and sea urchins), where morpho-functional features exhibited by slow-moving invertebrates are aimed at dissuading predators and/or at increasing the cost to the predator via reducing success rate or increasing handling time.

These results, finally, may have implications for management of fishery and sea urchin exploitation. With regard to fishery, there are many studies showing that overexploitation of fish predators in rocky reefs may trigger trophic cascades, with repercussions reverberating through the entire food web (Sala et al. 1998a). This should lead managers to bear in mind that control of sea urchin populations, which may prevent transition from macroalgal beds to coralline barrens, may also require the recovery of populations of predatory fishes (Sala and Zabala 1996). The human exploitation of sea urchins, considering that only *P. lividus* is edible, in addition, could not exert an efficient control of sea urchin populations since *A. lixula* may increase in density in rocky reefs where *P. lividus* is heavily fished (Guidetti et al. 2004). So, *P. lividus* fishery could cause ecological changes even where *P. lividus* coexists with *A. lixula*. Notwithstanding the specific roles of the two sea urchins that have not yet been clarified (Bulleri et al. 1999, Boudouresque and Verlaque 2001), there is increasing evidence that the non-edible *A. lixula* is far less preyed upon than *P. lividus* by fish predators (Guidetti 2004a, 2004b). Therefore, where *P. lividus* is intensively fished in shallow rocky reefs in the Mediterranean sublittoral, *A. lixula* could be released from competitive control by *P. lividus*. Such dynamics, although plausible in the regions where both urchins are abundant in subtidal reefs (e.g. SE Italy), might not be general. Many reports from the north-west Mediterranean, in fact, show that even in marine reserves and areas subject to heavy sea urchin exploitation, *P. lividus* may be more abundant than *A. lixula* (e.g. Sala et al. 1998b; Palacin et al. 1998; Ruitton et al. 2000).

In conclusion, because *A. lixula* is likely to be less efficiently controlled by fish predators (probably due to its more efficient defences), there could be considerable increase in the size of populations of this species, with possible repercussions for the entire benthic community. Density and related ecosystem effects of sea urchins, however, are not only attributable to predation, but also to other processes (e.g. settlement dynamics, post-settlement mortality, microhabitat availability) that should also be taken into account before drawing any conclusions.

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