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Paracentrotus lividus (Echinodermata: Echinoidea) attachment force and burrowing behavior in rocky shores of SW Portugal*

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Abstract

The rock burrowing sea urchin *Paracentrotus lividus* is a common wave-swept organism that inhabits intertidal rock pools and shallow subtidal temperate shores. Here we present field data on *P. lividus* attachment force, burrow shape and test diameter measured in different rocky habitats (intertidal pools, low shore intertidal channels and shallow subtidal shores) and in two study sites with different wave-exposure conditions. These data were then analyzed to look for a possible relationship between the size of sea urchins and their attachment force and burrow shape as well as the influence of wave-exposure and habitat in the measured variables. *P. lividus* test diameter varied among habitats: urchins were smaller in mid-shore intertidal pools and bigger in shallow subtidal shores. We observed in all studied habitats that attachment force was not correlated with test size, while burrow shape index (BSI) was negatively correlated with test size. Results suggest that the attachment force of large and small urchins was similar, but smaller animals occurred in relatively deeper burrows (higher BSI values). Attachment force was positively correlated with BSI, which indicates that burrows may enhance attachment force of *P. lividus* living in rocky shores by allowing the use of spines as anchorage points and reducing the urchin area exposed to drag forces. Our results partially support the hypothesis that attachment force and BSI might be influenced by local variation in wave-exposure. Higher values for both attachment strength and BSI were measured in intertidal rock pools, the most wave-exposed habitat considered in this study, suggesting that urchins living in such habitat are more able to resist dislodgment by wave-induced forces since they occupy relatively deeper burrows and thusattach more firmly to the substrate. However, neither attachment force nor BSI were higher in the more exposed shore.

Key words: sea urchin, *Paracentrotus lividus*, wave exposure, burrowing behavior, attachment force, SW Portugal

Introduction

Stress caused by hydrodynamic forces is an important process that affects ecological structure and community dynamics in wave-swept rocky shores (Denny 1988). Wave induced hydrodynamic forces can break or dislodge organisms, opening patches of substratum for settlement and invasion (Paine & Levin 1981) and may, directly or indirectly, limit the local abundance and distribution of species (Siddon & Witman 2003), the morphology and body size of organisms (Denny 1999), the foraging behaviour (Kawamata 1998), growth (Etter 1989), reproduction (McCarthy *et al.* 2003), recruitment and survival of organisms (Jonsson *et al.* 2006). It might also modify intra- and inter-specific interactions (Robles *et al.* 2001; Wernberg & Connell 2008).

Sea urchins are common mobile organisms in coastal habitats that thrive in a wide range of envi-

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ronmental conditions, from calm bays to exposed capes. Sea urchins rely on their tube feet for locomotion and attachment to the substratum (Lawrence 1987). The strength with which sea urchins attach to a substrate is determined by the tube foot tenacity and the number of tube feet involved (Santos & Flammang 2007). Attachment strength, together with test size and shape influences the maximum hydrodynamic force that different sea urchin species are able to withstand and might account for their distribution patterns (Siddon & Witman 2003; Santos & Flammang 2007; Tuya *et al.* 2007; Santos & Flammang 2008) and their resistance to predatory attacks (Guidetti & Mori 2005; Gianguzza *et al.* 2010).

Several echinoid species (*e.g.*, *Stomopneustes variolaris*, *Paracentrotus lividus*, *Echinometra* spp., *Echinostrephus* spp., *Heliocidaris* spp., *Heterocentrotus trigonarius* and *Strongylocentrotus* spp.) exhibit a specialized behaviour that provides extra protection from hydrodynamic stress: rock burrowing by the mechanical action of both spines and teeth (Otter 1932). It has been shown that *Paracentrotus lividus* uses the teeth of its Aristotle's lantern to bore and not its spines (Märkel & Meier 1967 in Asgaard & Bromley 2008). By sheltering into burrows, sea urchins largely reduce their cross-sectional area exposed to the water flow, which decreases the drag forces acting on them (Gaylord *et al.* 1994) and diminishes the risk of dislodgement. At the same time, burrows may enhance attachment force since both tube feet and spines may be used to anchor individual urchins to the substratum (Otter 1932; Trudgill *et al.* 1987).

The rock burrowing sea urchin *Paracentrotus lividus* has a wide geographical distribution, occurring mostly on intertidal rock pools and shallow subtidal shores despite exhibiting highly variable spatial and temporal distribution patterns (Boudouresque & Verlaque 2007). In SW Portugal, *P. lividus* abundance and size structure patterns vary at different spatial scales. Smaller sea urchins occur at very high densities in burrows in mid-shore intertidal pools (~300 ind./m^2), while larger individuals occur in moderate densities (~30 ind./m^2; D. Jacinto, unpublished data) in shallow subtidal shores (5–8 meters depth). The proportion of sea urchins in burrows is smaller in shallow subtidal shores when compared to mid-shore intertidal pools (D. Jacinto, unpublished data).

P. lividus is an important ecological and economical resource. As an herbivore, its impact on the surrounding communities might be a density dependent process, which may profoundly affect benthic communities inducing the formation of bare patches dominated by encrusting algae (Benedetti-Cecchi *et al.* 1998). Biological and physical factors such as predation pressure (Hereu 2005) and hydrodynamic stress (Kawamata 1998) influence sea urchin foraging behavior, reducing its grazing activity and dictating the outcome of interactions with local algae populations. Like other rock burrowing species, *P. lividus* can switch from mobile (grazing) to sedentary (drift-feeding) feeding when in burrows (Boudouresque & Verlaque 2007; Asgaard & Bromley 2008). Being an agent of bioerosion, *P. lividus* can significantly effect on the topography, complexity of the substratum and associated biodiversity. *Paracentrotus* bioerosion is an important process responsible for pool deepening in the mid-intertidal zone and weakening the intertidal rock mass (Trudgill *et al.* 1987).

Rock burrowing behaviour in *P. lividus* populations is frequently observed in the highly energetic Atlantic shores (Otter 1932; Trudgill *et al.* 1987; Gago *et al.* 2003) but scarce in the Mediterranean (D. Jacinto pers. obs.), probably due to differences in the oceanographic conditions and wave regimes. Such observations suggest that rock burrowing behavior in *P. lividus* might be an adaptive response to hydrodynamic forces, enhancing their attachment force and ability to resist dislodgement in wave-swept habitats as proposed by Otter (1932).

In the present study, we collected data on *P. lividus* test diameter, attachment force, surface rugo-

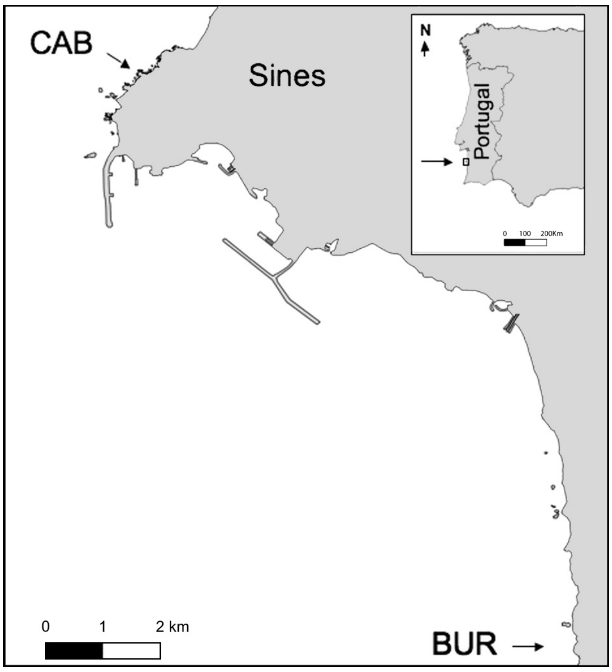

FIGURE 1. Location of study area in relation to mainland Portugal (inset). Two shores (~ 10 km apart) were sampled: CAB = Cabo de Sines and BUR = Praia do Burrinho.

sity and burrow shape in different rocky habitats (mid-shore intertidal pools, low-shore intertidal channels and shallow subtidal shores), in order to test the following hypotheses:

1) Urchin size affects attachment force. Within each studied habitat we expect a positive and significant relationship between attachment force and urchin size.

2) Burrows enhance attachment force. Within each studied habitat we expect a positive and significant relationship between attachment force and burrow shape index (BSI; a measure of the rugosity or surface profile of the substrate from where the sea urchin was dislodged). We also test for a possible relationship between BSI and urchin size.

3) Wave-exposure variation between shores and habitats influences *P. lividus* attachment force and BSI. We expect a larger attachment force and a larger BSI in more wave-exposed shores and habitats.

Our study is one of the first attempts to measure attachment force of the sea urchin *P. lividus* in the field (but see Guidetti & Mori 2005; Santos & Flammang 2007; Gianguzza *et al.* 2010) and to assess the importance of urchin burrows as an adaptive strategy to resist dislodgment in wave-swept habitats.

Methods

The field study was carried out between August to October 2009 on intertidal and shallow subtidal rocky shores of SW Portugal (Fig. 1). Two shores were considered, *Cabo de Sines* (CAB) and *Praia do Burrinho* (BUR), about ten kilometres apart (Fig. 1). CAB is a headland, mainly consisting of igneous rock formations (gabbro) with a complex topography, while BUR is a metamorphic rocky shore (mainly schist) situated southwest from CAB in the lee of the headland. Location of the shores relatively to the prevalent income wave and wind direction (from NW) and previous observations and measurements on the variability of subtidal hydrodynamic forces in SW Portugal (D. Jacinto, unpublished data) suggest that hydrodynamic stress is higher in CAB. Three habitats were considered in each shore: mid-shore intertidal pools (IP), low-shore intertidal channels (< 1 m deep; IC), and shallow subtidal shores (6 m depth; SS). Empirical data show that wave induced flow decreases

FIGURE 2. Metal grab used to clamp *P. lividus* and measure attachment force when connected by a hook to a spring dynamometer. The gear consists of a steel compass modified as a grabbing claw that allows a proper grip to sea urchins even when inside tight burrows.

with depth (Siddon & Witman 2003). Here, we assume that the studied habitats are subjected to variable wave-induced hydrodynamic stress (higher in mid-shore intertidal pools and lower in shallow subtidal shores).

In each shore and habitat, individual sea urchins (n = 50) were sampled. For each individual, we measured the following variables: 1) attachment force; 2) test diameter; and 3) Burrow Shape Index (BSI), a measure of the rugosity or surface profile of the substrate from where the sea urchin was dislodged (regardless of urchins being sampled inside or outside of burrows).

Attachment force was measured by clamping a metal grab (a steel compass modified as a grabbing claw that allows a proper grip to sea urchins even when inside tight burrows; Fig. 2) to the sea urchin's test, connected by a hook to a spring dynamometer, and pulled normally to the substratum at an approximate constant speed. The maximum force (Newton) required to dislodge each sea urchin was recorded.

Test diameter of the dislodged urchin was measured with a caliper to the nearest millimeter.

A plastic profile copy gauge, or profilometer, was used to measure BSI, the topographical rugosity of the substrate from where the sea urchin was dislodged. By pressing the profile gauge against the surface where the urchin was laying on, we were able to transfer the profile of the surface or burrow where the urchins were found to an underwater slate, and later analyze it with image analysis software (ImageJ; Abràmoff *et al.* 2004).Two perpendicular profile measurements were made for each surface or burrow. We considered the variable burrow shape index (BSI) as the average ratio between the length of the surface or burrow profile (BP) and the length of the burrow opening (BO), *i.e.*, contoured-to-linear distance of the topography of the surface or burrow where the urchins were found (BSI = BP/BO). BSI is higher than one when urchins occur in burrows (concave surfaces) and approaches the unity when urchins are found on very shallow burrows or outside burrows (flat surfaces).

The hypotheses of a relation between attachment force and BSI with urchin size, and of attachment force with BSI were tested by non-parametric Spearman's rank correlation (r_s) for each habitat. The hypothesis that wave-exposure variation between shores and habitats influences *P. lividus* attachment force and BSI was tested by ANOVA in an experimental design with 2 factors: 1) habitat (H), a fixed factor with 3 levels (IP, IC and SS); 2) Shore (S), a fixed factor with 2 levels (CAB = *Cabo de Sines* and BUR = *Praia do Burrinho*) (n = 50). Homogeneity of variance was assessed using Cochran's C-test and Student-Newman-Keuls (SNK) tests were used when appropriate (Underwood 1997). The package GAD (Sandrini-Neto & Camargo 2011) for R software (R Development Core Team 2011) was used to perform the analysis (according to Underwood 1997).

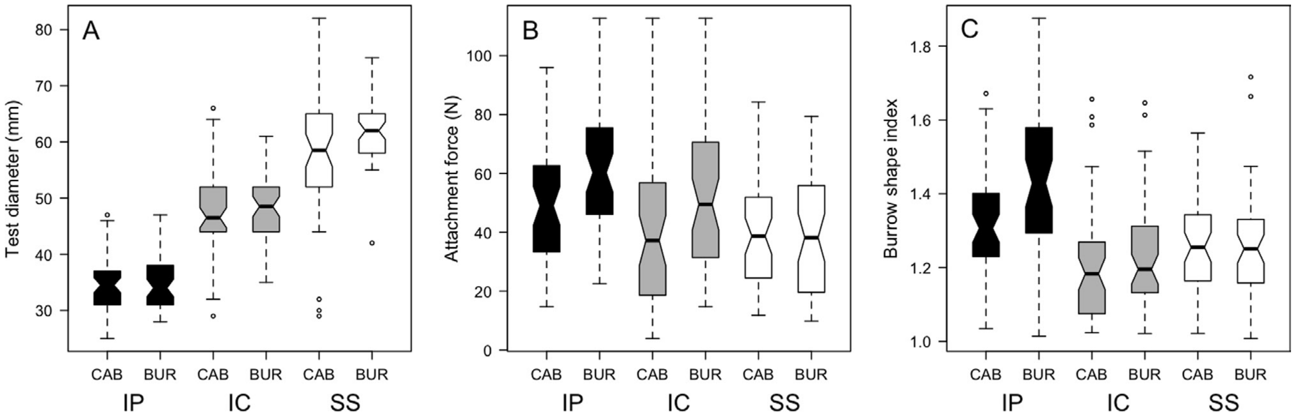

FIGURE 3. *Paracentrotus lividus*. Boxplots of (A) Test diameter (mm), (B) attachment force (N) and (C) Burrow shape Index per habitat (IP = mid-shore intertidal pools; IC = low-shore intertidal channels and SS = shallow subtidal shores) and study site (CAB and BUR) in SW Portugal (n = 50).

Results

Urchin size (test diameter) distribution varied amongst studied habitats and shores (Fig. 3A; Fig. 4 D–F; Tables 1 and 2). Overall, smaller urchins were sampled in mid-shore intertidal pools (34.6 ± 4.88 mm, mean ± SD; range: 25–47 mm), medium sized urchins in low-shore intertidal channels (48.0 ± 6.57 mm, mean ± SD; range: 29–66 mm) and larger individuals in shallow subtidal shores (59.8 ± 8.42 mm, mean ± SD; range: 29–82 mm). Differences on sea urchin mean test diameter were also detected between shores, suggesting that sea urchins sampled in CAB were smaller than the ones sampled in BUR (Tables 1 and 2; Fig. 3A).

P. lividus attachment force was highly variable within each habitat and shore (Fig. 3B; Fig. 4 A–C; Tables 1 and 2): in IP, it varied between 14.7 N and 112.7 N (mean ± SE: 49.0 ± 2.54 N and 62.2 ± 2.92 N, CAB and BUR, respectively); in IC, it varied between 3.9 N and 112.6 N (mean ± SE: 38.5 ± 3.47 N and 53.5 ± 3.62 N, CAB and BUR, respectively); and in SS, it varied between 9.8 N and 84.3 N (mean ± SE: 39.3 ± 2.49 N and 38.3 ± 2.87 N, CAB and BUR, respectively). Results show a strong interaction effect ($p < 0.01$; Tables 1 and 2) between the two main factors, habitat and shore, on the distribution patterns of mean attachment force values (SNK tests for the interaction H x S, Table 2). Both in CAB and BUR, the force required to dislodge sea urchins from the substrate was on average higher in IP than any other habitat. However, while in BUR significant differences were found between average attachment forces measured in intertidal channel and shallow subtidal rocky shores (IP > SS), no such differences were found on CAB (IP = SS). Higher mean attachment force values were measured in intertidal pools (IP) of BUR than those of CAB. The same was true for urchins sampled in intertidal channels (IC) while on shallow subtidal rocky habtitat (SS) no differences were found between study shores.

BSI values were also highly variable within habitats and shores (Fig. 3C; Fig. 4D–F; Tables 1 and 2). Despite a large span of BSI values within each habitat and shore (between 1.02 and 1.88), mean BSI values measured in IP (mean ± SE: 1.31 ± 0.021 and 1.44 ± 0.021, CAB and BUR, respectively) were higher in comparison to IC (mean ± SE: 1.20 ± 0.018 and 1.23 ± 0.021, CAB and BUR, respectively) and SS (mean ± SE: 1.26 ± 0.022 and 1.25 ± 0.028, CAB and BUR, respectively). Again, a strong interaction effect was detected ($p < 0.01$; Table 1) between the two main factors, habitat and shore, on the distribution patterns of mean BSI values (SNK tests for the interaction H x S, Table 2). Mean BSI values were higher in intertidal rock pools (IP) of BUR than in CAB. In intertidal channels

(IC) and shallow subtidal rocky habitat (SS) no differences between shores were found in mean BSI values. Significant differences were also detected in mean BSI values between habitats within each shore. In BUR, mean BSI values were higher in IP than in IC and SS. In CAB, the mean BSI values were similar between IP and SS, and higher than the ones measured in IC.

No significant correlations were found between attachment force and test diameter for urchins sampled in each of the studied habitats (IP: $r_s=0.14$, $p=0.17$; IC: $r_s=-0.15$, $p=0.13$; SS: $r_s=-0.10$, $p=0.33$; $n=100$), refuting our hypothesis, and suggesting that factors other than size (which is related with the number and area of attachment discs) influence *P. lividus* attachment force in the field.

As hypothesized, positive significant correlations were found between *P. lividus* attachment force and Burrow Shape Index (Fig. 4A–C) for sea urchins sampled in each habitat (IP: $r_s=0.36$, $p<0.01$; IC: $r_s=0.36$, $p<0.001$; SS: $r_s=0.27$, $p<0.01$; $n=100$), suggesting that burrowing enhances attachment force in *P. lividus,* since individuals in relatively deeper burrows require higher force to be dislodged.

Negative significant correlations (Fig. 4D–F) were found between BSI and test diameter within each habitat (IP: $r_s=-0.27$, $p<0.01$; IC: $r_s=-0.30$, $p<0.01$; SS: $r_s=-0.26$, $p<0.01$; $n=100$ pairs of data for each habitat), suggesting that smaller individuals occupy relatively deeper burrows while larger individuals may be found in relatively shallower burrows or outside of burrows.

ANOVA and SNK tests results (Tables 1 and 2), partially support the hypothesis that wave-exposure variation between shores and habitats influences *P. lividus* attachment force and BSI. While higher values of BSI and attachment strength were measured in intertidal pools (IP), presumably the most exposed habitat, when comparing between shores, there is no evidence that the study variables are influenced by shore exposure as expected. In fact, when significant differences were detected between shores (Table 2), both attachment strength and BSI, values were higher in BUR (the least exposed shore).

Discussion

Rock burrowing behavior in sea urchins has been described as an adaptation for life in wave swept rocky shores (Otter 1932). In SW Portugal, coastal habitats are largely exposed to normal Atlantic swell and may be considered highly stressful environments (Instituto Hidrográfico 2006). In this region *P. lividus* is frequently found in burrows. Few studies on *P. lividus* attachment force have been conducted in the field (Santos & Flammang 2007; Gianguzza *et al.* 2010) and to our knowledge the

TABLE 1. Analysis of variance on *P. lividus* test diameter, attachment force and burrow shape index (BSI) in SW Portugal in relation to habitat (H) and shore (S). Data Transformation: Attachment force data transformed to the fourth root(x); BSI data transformed to squared root(x); Cochran's test, $p<0.05$ (test diameter), $p > 0.05$ (attachment force and burrow shape index). $n=50$. df = degrees of freedom; MS = mean square; F = test statistic. Test statistic significance levels: * ($p<0.05$); ** ($p<0.01$); ***($p<0.001$); ns ($p > 0.05$).

ANOVA		**Test Diameter**			**Attachment Force**			**BSI**		
Source of variation	**df**	**MS**	**F**		**MS**	**F**		**MS**	**F**	
H	2	15810,1	352,3	***	1,777	16,6	***	0,138	30,5	***
S	1	274,6	6,1	*	1,285	12,0	***	0,036	8,0	**
H x S	2	88,5	2,0	ns	0,599	5,6	**	0,023	5,1	**
Residual	294	44,9			0,107			0,005		

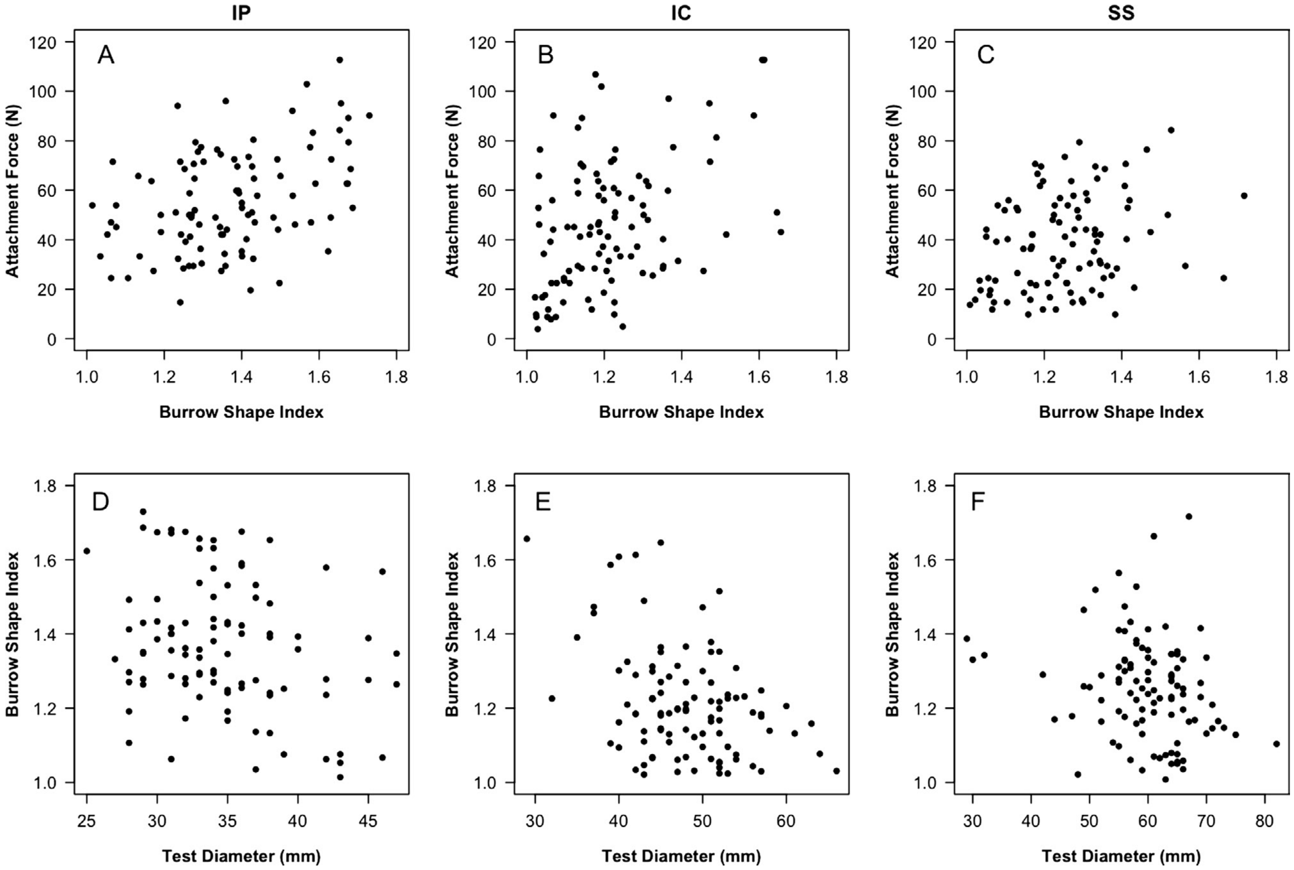

FIGURE 4. *Paracentrotus lividus*. Bivariate scatter plots of (A–C) Attachment force (N) against Burrow Shape Index (all significant positive correlations at $p < 0.05$) and (D–F) Burrow Shape Index against test diameter (mm) (all significant negative correlations at $p < 0.05$) per habitat (IP = mid-shore intertidal pools; IC = low-shore intertidal channels and SS = shallow subtidal shores) and study site (CAB and BUR) in SW Portugal ($n = 50$).

attachment force of urchins in burrows has never been measured in field studies. The method used in this study allowed us to successfully detach urchins within burrows and provide a data set of field measurements regarding the rock burrowing echinoid *P. lividus* attachment force to the substratum in different habitats.

P. lividus test diameter varied among habitats: urchins were smaller in mid-shore intertidal pools and bigger in shallow subtidal shores. Such results are concordant with what has been observed in previous studies in the same region (D. Jacinto, pers. obs.).

It has been observed that under similar laboratory conditions, *P. lividus* attachment force varied with test size (Guidetti & Mori 2005), possibly due to an increase in number of tube feet with test diameter (Santos & Flammang 2007). Yet, we observed in all studied habitats that attachment force was not correlated with test size, but burrow shape index was negatively correlated with test size. The attachment force of large and small urchins is similar, but smaller animals occur in relatively deeper burrows. These results suggest that smaller individuals create or occupy relatively deeper burrows (higher BSI values) to properly attach to the substrate and resist dislodgment, while larger individuals may occur in relatively shallower burrows or even free over the substrate, as other factors like foot tenacity and the number of tube feet involved in attachment, might suffice to provide the necessary attachment force.

In all studied habitats, attachment force was positively correlated with BSI, which supports our hypothesis and indicates that burrows can enhance attachment force of *P. lividus* living in rocky shores, by allowing the use of spines as anchorage points and reducing the area exposed to drag forces.

Our results partially support our hypothesis regarding attachment force and burrow shape index being influenced by local variation in wave-exposure. Higher values for both attachment strength and burrow shape index were measured in intertidal rock pools, the most wave-exposed habitat considered in this study, suggesting that urchins living in such habitat are more able to resist dislodgment by wave-induced forces since they occupy relatively deeper burrows and thus attach more firmly to the substrate. However, neither attachment force nor burrow shape index were higher in the more exposed shore (CAB). In fact, when there were differences (both variables in mid-shore intertidal pools and attachment force in low-shore intertidal channels), the opposite was observed (higher values in the less exposed shore—BUR). Other factors might explain the observed pattern in mid-shore intertidal pools. Intertidal pools of BUR are shallower than in CAB. Despite CAB being more exposed than BUR, at a smaller scale, water flow might be higher in tidepools of BUR due to local topography and tidepool characteristics. Small-scale water flow measurements should be made in order to explain burrowing behaviour variability. Another possible confounding factor between CAB and BUR is the geological formation of tidepools in both shores. CAB is made of volcanic rocks, while tide pools of BUR have been excavated in the smoother schists. Consequently, it is much easier for an urchin to excavate deeper burrows in BUR than in CAB. Mineral composition of the substrate has been shown to influence burrowing depth in *Strongylocentrotus purpuratus* (J. Hernandéz, pers. com.), another rock burrowing sea urchin, which is able to excavate deeper burrows in softer rocky shores.

Another important factor that might potentially explain the observed patterns is predation pressure. As proposed by Menge & Sutherland (1987) predation pressure is expected to be higher in more benign physical environments. It is plausible to admit that predation pressure (potential predators include fishes, sea stars and birds) might be higher in BUR (the less exposed shore). If burrowing behavior enhances urchin attachment strength preventing the success of putative predatory attacks, then the observed patterns of BSI variability between the study sites might have been shaped by local variation in predation pressure (*e.g.*, sea urchins in relatively shallow burrows or outside burrows might be heavily predated in intertidal pools of the less environmental stressful shores, and as a result only urchins in relatively deeper burrows are found, hence the higher BSI values observed in BUR).

Our study supports the model that burrowing behavior enhances sea urchin attachment force, and might be an adaptive response to hydrodynamic stress as proposed by Otter (1932). However, alternative models including the influence of predation pressure in sea urchin burrowing behavior should be properly addressed in future studies. Additional research is needed to elucidate the processes responsible for variability in attachment force and burrowing behavior of sea urchins, considering the combined effect of exposure to hydrodynamic forces and predation pressure on burrowing behavior,

TABLE 2. SNK tests for the main terms habitat (H) and shore (S) (test diameter) and interaction term H x S (attachment force and BSI = burrow shape index). = (p>0.05); > or < (p<0.05). IP = intertidal rock pool; IC = low shore intertidal channel; SS = shallow subtidal rocky shore; CAB = Cabo de Sines; BUR = Praia do Burrinho.

Test Diameter	Attachment Force	BSI
H: IP < IC < SS	BUR: SS < IC < IP	BUR: SS = IC < IP
S: BUR > CAB	CAB: SS = IC < IP	CAB: IC < SS = IP
	SS: BUR = CAB	SS: BUR = CAB
	IC: BUR > CAB	IC: BUR = CAB
	IP: BUR > CAB	IP: BUR > CAB

while accounting for possible confounding effects like the type of rocky substrate and characteristics of the studied populations and habitats.

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