Substratum cavities affect growth-plasticity, allometry, movement and feeding rates in the sea urchin *Strongylocentrotus purpuratus*

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SUMMARY

We assessed the influence of rock cavities, or pits, on the growth dynamics and behavior of the purple sea urchin, *Strongylocentrotus purpuratus*. In a paired-designed, laboratory experiment, sea urchins were assigned to sandstone blocks that were either 'Flat' or had a 'Pit' drilled into the center. At the start, both groups were approximately the same shape and size. In just 2 months, the shapes of the tests were significantly different between the two treatments, with the Pit urchins having an increased height:diameter profile. This result demonstrates the plastic nature of the sea urchin test and that, despite its apparent rigidity, it is capable of deforming during growth. In addition, the presence of pits modified behavior and food consumption as well as allometric growth of the test and Aristotle's lantern. Sea urchins on Pit sandstone blocks tended to stay in the cavities and not move about the flat areas, whereas individuals on Flat blocks changed position. Sea urchins in the Pit treatment consumed less food and had relatively larger demipyramids (the 'jaw' ossicle in Aristotle's lantern). These morphological and allometric changes occurred over a short time-period (8–20 weeks). We conclude that microhabitat is an important factor in controlling the behavior and growth dynamics of the bioeroding sea urchin *S. purpuratus*.

INTRODUCTION

"The sea urchin [test] consists of a membrane, stiffened into rigidity by calcareous deposits, which constitute a beautiful skeleton of separate, neatly fitting ossicles. The rigidity of the [test] is more apparent than real, for the entire structure is, in a sluggish way, plastic..."

(Thompson, 1917; p. 662)

Thompson's (Thompson, 1917) insightful discussion of the mechanical forces influencing the morphogenesis of the echinoderm test has influenced several models of test growth and morphology (Raup, 1968; Seilacher, 1979; Telford, 1985; Dafni, 1986; Baron, 1991; Ellers, 1993; Abou Chakra and Stone, 2008; Zachos, 2009). Although these approaches can account for much of the shape variation observed among taxa, the plastic nature of the shape of the test has not been demonstrated experimentally. There are also intraspecific morphological differences (including height:diameter ratios) associated with habitat (e.g. Moore, 1935; McPherson, 1965; Lewis and Storey, 1984; Baron, 1991; Grupe, 2006), and habitat variation is often associated with substrate type and complexity.

The importance of substrate complexity, surface texture and physical properties of rocks to the composition and structure of epibenthos has long been recognized (Raimondi, 1988; Bourget et al., 1994; Sousa, 2001), and several studies have focused on the role sea urchins play as bioeroders of coral substrates (Birkeland, 1989; Bak, 1994; Mokady et al., 1996; Carreiro-Silva and McClanahan, 2001; Toro-Farmer et al., 2004; Herrera-Escalante et al., 2005). Sea urchin grazing has a profound influence on coral reef ecology and affects reef accretion and growth (Birkeland, 1989). However, few studies have examined the role of sea urchins as agents of bioerosion on rocky substrates (Krumbein and Van der Pers, 1974; Trudgill et al., 1987; Spencer, 1992). Only one study

has investigated the effect of substrate mineralogy on sea urchin abundance (Guidetti et al., 1994), and two have investigated the effect of physical microhabitat on the biology of sea urchins (Trudgill et al., 1987; Grupe, 2006).

The life-history variation and population dynamics of sea urchins can be influenced by both large-scale oceanographic patterns as well as microhabitat differences. Quantifying the effects of these different factors is necessary for population ecologists to identify spatial patterns and biogeographical variation. Previous studies have highlighted the importance of small-scale variation in sea urchin growth (Russell, 1987; Russell et al., 1998; Meidel and Scheibling, 1999; Russell, 2001), and food availability has been identified as important in controlling growth and allometry (Ebert, 1980; Black et al., 1982; Levitan, 1988; Fernandez and Bouderesque, 1997). Recently, Selden and colleagues (Selden et al., 2009) have determined that predator cues induce changes in growth, morphology and reproduction.

Rocky intertidal communities exist in a mosaic of substrate types that differ in a variety of ways – for example, hard granite *versus* softer sandstones. Surprisingly, the effect of rocky substrate variability on intertidal organisms remains poorly understood despite the direct implications for coastal management and conservation. A good example is the purple sea urchin, *Strongylocentrotus purpuratus*, which is commonly found in a variety of intertidal rocky types of the Pacific coast of North America from Isla Cedros, Mexico (Caso, 1961) to Torch Bay, Alaska (Duggins, 1981). In places where the substratum is soft enough to be eroded, urchins are found living inside cavities or 'pits' (Ricketts et al., 1985). The contours of these pits fit the individuals inhabiting them, and this suggests that bioerosion from foraging activity and spine abrasion produces these cavities (Fewkes, 1890). However, there are other sites where the rock is less friable and the urchins do not form pits and are instead found distributed over the rock surface.

Sea urchin species show differences in the allometric relationship between the height and diameter of the test (Thompson, 1917; Ebert, 1988). Purple sea urchins show a high degree of intraspecific variability in this relationship. The shape of purple sea urchins found in pits is different from that of sea urchins residing outside of these cavities (Baron, 1991; Grupe, 2006). Non-pit-dwelling sea urchins have a 'lower' profile (smaller height:diameter test ratio) than sea urchins found inside pits. However, it is not known whether this association is the result of 'plastic' growth because shape-related differential mortality and/or microhabitat selection could account for this pattern (Baron, 1991). Moreover, understanding the mechanisms underlying phenotypic variations can shed light on evolutionary phenomena (Stearns, 1989; Taylor and Wilson, 2003). Nevertheless, there are no experiments exploring whether the dynamics and mechanics of growth could produce this morphological difference associated with microhabitat.

The purpose of this study is to assess whether the presence of cavities (pits) in rocks has the potential to influence the behavior and allometric growth of purple sea urchins. We used a paired-design experiment to examine: (i) whether sea urchins would occupy a pit if present; (ii) movement patterns in the presence/absence of pits; and (iii) the short-term effects of pits on growth plasticity and allometry. The results of our work experimentally demonstrate the plasticity of the sea urchin test during morphogenesis and validates D'Arcy Thompson's description (Thompson, 1917).

MATERIALS AND METHODS

Samples of small (8.63–22.75 mm in test diameter), intertidal purple sea urchins, *Strongylocentrotus purpuratus* Stimpson 1857, were collected from both pit and non-pit habitats at Bean Hollow, California, USA (37°13′N 122°24′W) on 27 July 2007 and shipped to our lab (Villanova University, Villanova, PA, USA). These sea urchins were acclimated to a recirculating seawater system (12.97±1.00°C and 31.58±0.58‰ – measured daily) for 7 weeks (these and all subsequent ± estimates of variation are standard deviations).

On 18 September 2007, urchins (N=48) were paired by first ranking individuals by diameter and assigning them to pairs in rank order (1 and 2; 3 and 4, etc.). Within pairs, individuals were assigned to one of two groups in such a way that the overall mean and variance of the height:diameter ratios of the two groups across pairs were as close as possible. Finally, the groups were assigned randomly to one of two treatments – 'Pit' or 'Flat'. All urchins were then injected with the fluorochrome calcein (4.54 mg calcein per liter of seawater) through the peristomal membrane. Calcein is incorporated into the growing edges of all ossicles and registers the size at the time of injection. Fluorescent-marking (with tetracycline and, more recently, with calcein) is the standard method of assessing sea urchin growth (e.g. Ebert, 1980; Russell and Urbaniak, 2004). The skeletal elements were cleared of all soft tissue with 5% sodium hypochlorite at the end of the experiment. Aristotle's lanterns were examined with a dissecting microscope fitted with an ocular micrometer and illuminated with UV light that reveals the fluorescent mark and the original jaw size at the time of tagging. At the start and every 2–5 weeks until the experiment ended on 14 February 2008 (21 weeks), we recorded wet mass (resolution to 0.01 g) and test height and diameter (resolution to 0.01 mm). Before weighing, individual urchins were placed on an absorbent paper towel for 2–5 min. The diameter was measured with digital knife-edge vernier calipers at the ambitus, perpendicular to the oral–aboral axis, from the center of an interambulacral column to the center of the opposite ambulacral column, making sure that the edges of the calipers were carefully

placed between spines and tubercles. The height of the test was measured along the oral–aboral axis, again making sure that the edges of the calipers were carefully placed between spines and tubercles.

Each sea urchin was associated with a Flat, square (55 mm × 55 mm) piece of sandstone of thickness 26 mm. The Pit treatment sandstone blocks had symmetrical concave cavities ~28.11±1.48 mm in diameter and 14.36±1.57 mm deep drilled into the center-surface. The Flat treatment blocks were not drilled. Individual sandstone blocks were fitted with an open-top plastic mesh-fence (diagonal openings of 10 mm) and randomly assigned to a spot in a grid system (176×65 cm) suspended in a sea table (183×92 cm). This 'suspension system' consisted of a PVC support frame (inside the sea table) that suspended the blocks from above by thin plastic tubes. The mesh-fences, tubes and blocks were secured together with elastic bands. The substrates were positioned in the sea table such that the tops were ~25 mm below the surface of the water. The tops of the mesh-fences were always above the water line and prevented sea urchins from escaping the enclosure. To promote vigorous water movement across the surface of the blocks, 10 rotating submersible pumps were installed around the suspension system, and three tracks of airstones were placed along the bottom under the replicates.

All replicates were provided with abundant food and allowed to recover from the fluorochrome injection for one week. Each day following recovery, the enclosures were monitored and the sea urchin position and relative kelp (*Macrocystis pyrifera*) consumption recorded. The positions of Flat sea urchins were recorded relative to a quadrant on the block, and Pit sea urchins were recorded either as occupying the pit or else their quadrant position occupied outside the pit was determined. Movement was scored in both groups as 0 (same position as previous day) or 1 (different position). Kelp blades were cut into strips (~16–25 cm²), frozen in seawater, defrosted before feeding and provided to each enclosure. Kelp strips were not weighed but were provided in approximately equal amounts (~4–5 strips) to each enclosure. Each day, food consumption was recorded as 'no kelp present' (all strips consumed in 24 h) or 'kelp present' (not all kelp consumed) and scored in both groups as 1 (no kelp present – more strips added) or 0 (kelp present – fewer strips added).

During the experiment, there were two maintenance/power failures to the seawater system, resulting in prolonged emersion exposures (15–24 h) of the sea urchins. These exposures caused mortalities and the loss of a single sea urchin in a pair meant the loss of the experimental unit (one replicate). These failures occurred during weeks 10 and 14 and resulted in the mortality of 2 (Flat – lost 2 pairs) and 12 (10 Flat and 2 Pit – lost 10 pairs) sea urchins, respectively. The two mortalities in the Pit replicates on week 14 were paired with urchins in the Flat mortality group that week. No power failures or further mortalities occurred from weeks 14 to 21 for the remaining 12 pairs.

To assess overall shape changes over time, we used Model II linear regressions of height *versus* diameter for the Flat and Pit treatments at the start, week 8 and at the end of the experiment (week 21). At each of these time intervals, the slopes and intercepts of these lines were compared by means of t-tests. We analyzed differences between Pit and Flat treatments on week 13 (before the second failure) to maximize the number of replicates for comparisons of movement, growth and kelp consumption (22 pairs rather than 12 pairs at week 21). The paired-design dictated that values for these variables were calculated as a difference ([Pit] – [Flat]). Normality was assessed with a Shapiro Wilk W test and, if normally distributed, then t-tests were used to assess differences from 0, with α=0.05. If a variable was not normally distributed, then a Signed Rank test was used. Values for height:diameter ratio were calculated also as [Pit] – [Flat], tested for

normality and analyzed with *t*-tests at each of the six time measurements with a Bonferroni correction (α=0.008). In addition, the height:diameter ratio was analyzed as a repeated measures ANOVA. Model II allometric regressions were calculated for test diameter *versus* jaw length at the start (using fluorescently labeled individuals) and final day of the experiment for both the pit and non-pit groups (Ebert and Russell, 1994). ANCOVA was used to compare the slopes of these regressions at both time periods. Finally, we used a χ^2 contingency to determine whether Pit or Flat was associated with mortality or survival during the two unplanned emersion events.

RESULTS

There were no significant differences in diameter, height, height:diameter ratio or mass between the Flat and Pit treatments at the start of the experiment (Table 1). Fig. 1 plots height *versus* diameter for the start, 8 week and end-points of the experiment. These plots show that, as individuals grew, the Flat treatment urchins did not change their height:diameter ratio, whereas the Pit treatment urchins got 'taller'.

Individuals provided with pits tended to stay in these cavities, with 88.1% of the daily recordings for position over 13 weeks occurring in pits. By contrast, there was no pattern to quadrant position of the sea urchins on Flat sandstone blocks, with a nearly even division among the four areas (26.6%, 23.6%, 23.3% and 26.5%). In addition, the sea urchins on Flat blocks moved positions significantly more than their counterparts in the cavities (Fig. 2a). As measured by the amount of kelp added each day to the enclosures, Flat sea urchins consumed significantly more food than Pit sea urchins (Fig. 2a). We tested whether this observed difference in food consumption resulted in an overall difference in mass gain with a one-tail *t*-test (Flat predicted to be higher). At week 13, the difference in mass was normally distributed (W=0.96, P=0.43), and there was no difference between treatments (*t*=–0.74, P=0.23). Although this statistical result held true for the end of the experiment (the difference was again normally distributed, W=0.98, P=0.97), there was a trend for the Flat to weigh more than Pit (*t*=–2.13, P=0.06).

Growth patterns showed a change in test shape between the two treatments. Overall growth in diameter of the Flat treatment (3.66 mm ± 0.76) was greater than that of the pit treatment (3.03 mm ± 1.61); however, growth in height of the Pit treatment (2.50 mm ± 0.75) was greater than that of the Flat treatment (1.84 mm ± 0.76). Pit sea urchins grew significantly

Table 1. Comparison of measures between the two treatment groups used to quantify size and shape at the start of the experiment

Variable	Treatment Flat	Pit	P value
Height (mm)	7.46±1.67	7.42±1.75	0.71
Diameter (mm)	16.70±3.59	16.65±3.77	0.95
Height:diameter	0.45±0.02	0.44±0.01	0.75
Mass (g)	2.69±1.41	2.70±1.54	0.80

Values are means±1 s.d. (*N*=24). The experimental design dictated that analyses be run on the within-pair difference of these values and tested against a hypothesized value of zero. The Shapiro Wilk W indicated that the difference-variable was normally distributed for height (W=0.9673, P=0.81), height:diameter (W=0.9385, P=0.16) and mass (W=0.9735, P=0.75) but not for diameter (W=0.7181, P<0.0001). A Wilcoxon Sign–Rank test was performed on diameter, and paired tests performed on the other three difference-variables (P values reported). There were no significant differences in any of these measures between treatments.

more in height than Flat individuals (Fig. 2b). This change in test allometry is best visualized by plotting the difference between pairs in height:diameter ratio over time (Fig. 3). The results of a repeated measures ANOVA showed a significant interaction of treatment (Pit *vs* Flat) and time (using Geisser–Greenhouse adjusted *df*, $F_{3.4,143.1}$=17.32, P<0.0001). A significant difference between groups was detected as early as 6.5 weeks on 2 November (*t*=3.41, P=0.0012). At the start of the experiment, the mean height:diameter values for Pit and Flat sea urchins were 0.44±0.01 and 0.45±0.02 (Table 1); after 13 weeks (21 December), the means were 0.50±0.04 and 0.46±0.03, respectively.

Jaw length (*J*) and test diameter (*D*), transformed using natural logarithms, were used in an ANCOVA with ln(*D*) as the dependent variable, Pit *versus* Flat as a grouping variable, ln(*J*) as a covariate, and an interaction term of Pit/Flat × ln(*J*). The interaction term indicated that the slopes were homogeneous on the first day (ANCOVA: $F_{1,38}$=0.038, P=0.854) but not at the end of the experiment (ANCOVA: $F_{1,23}$=13.599, P=0.002; Fig. 4).

Through the entire 21 weeks of the experiment (Fig. 5), the growth of diameter was negatively associated with initial size in the Pit treatment but not in the Flat treatment, whereas the growth of height was negatively associated with initial size in the Flat treatment but not Pit treatment.
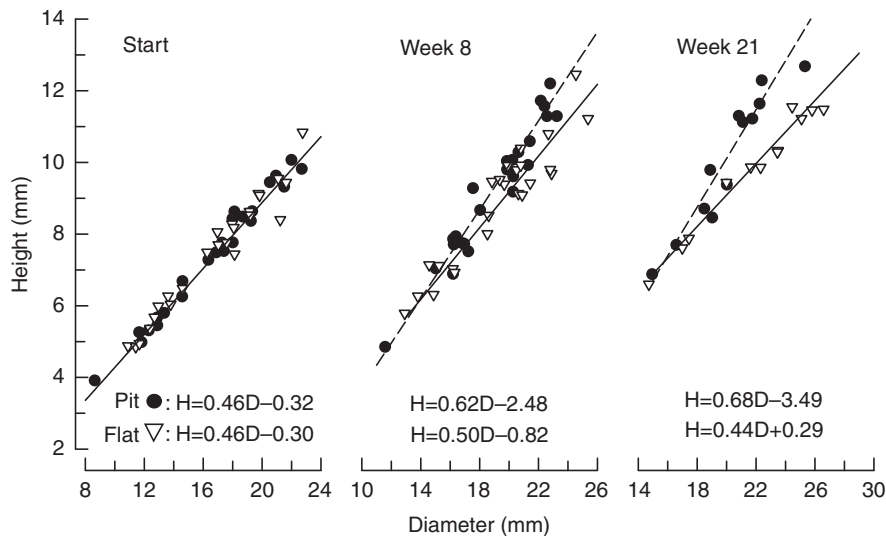

Fig. 1. Model II linear regressions of height (H) *versus* diameter (D) at the outset (start), midway (week 8) and conclusion (week 21) of the experiment. The dashed line represents the Pit treatment, and the solid line represents the Flat treatment. Although the absolute values change, the ranges of the *x*-axes are the same, and so the slopes are visually comparable across plots. Sample sizes are 24 for each regression in the first two plots and 12 for the last. The R^2 values range from 0.89 for Flat at Week 8 to 0.98 for Pit at the start of the experiment. At the start, there are no differences between Flat and Pit in the slope (*t*=0.00043, P=0.9996) or intercept (*t*=–0.084, P=0.93). There also are no differences between the start and week 8 of the Flat treatment in slope (*t*=1.36, P=0.19) or intercept (*t*=–0.84, P=0.41) nor are there differences between the start and week 21 of the Flat treatment in slope (*t*=–0.39, P=0.71) and intercept (*t*=0.45, P=0.66). There are differences between Flat and Pit in both the slope and intercept at week 8 (*t*=3.52, P=0.0018; *t*=–2.72, P=0.0123) and week 21 (*t*=3.72, P=0.0029; *t*=–2.89, P=0.0135).

Within Fig. 1:
Start Pit ●: H=0.46D–0.32 Flat ▽: H=0.46D–0.30
Week 8 H=0.62D–2.48 H=0.50D–0.82
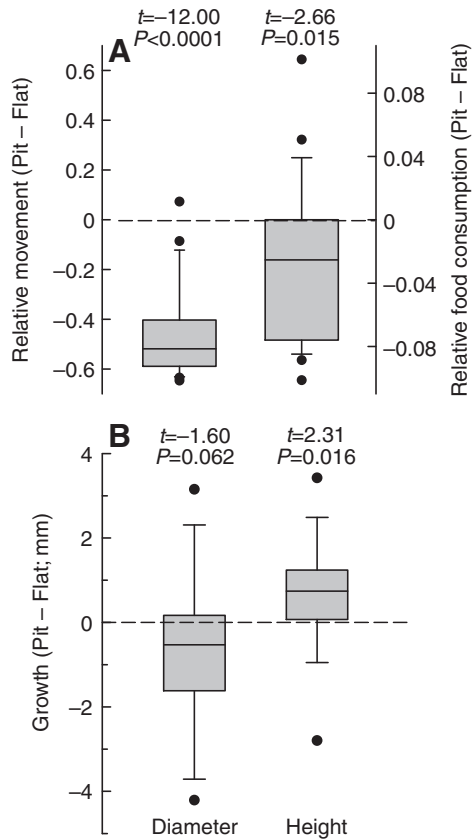Week 21 H=0.68D–3.49 H=0.44D+0.29

Fig. 2. Relative movement, food consumption and growth. The boxes span the 25th to 75th percentiles, the median is the horizontal line in the box, the error bars are the 5th and 95th percentiles, and all outliers are plotted. Values for paired *t*-tests appear above each plot. (a) Relative movement and food consumption. Between days, individuals were scored as being in the same position (0) or in a different position (1); and no kelp present (1 = added more food) or kelp present (0 = added fewer kelp strips). The difference between pairs (Pit–Flat) shows a highly significant (negative) tendency for greater movement of Flat sea urchins (data significantly different from normal distribution: W=0.7891, P=0.0002, t for Wilcoxon Sign–Rank). Significantly more kelp was added to the Flat enclosures, indicating more food consumption in this group (data normally distributed: W=0.9335, P=0.14). (b) Growth at the end of 13 weeks between pairs showed significantly greater increases in height for Pit sea urchins (data normally distributed: W=0.9438, P=0.23). The trend was for greater growth in diameter in Flat sea urchins, but this tendency was not statistically significant (data normally distributed: W=0.99720).
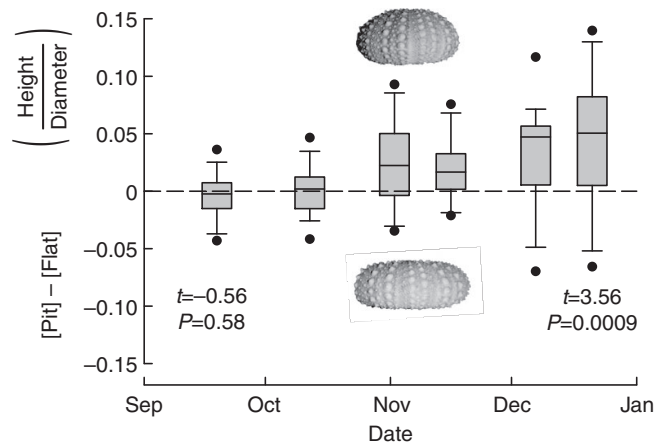

Fig. 3. Box plots of the difference between pairs in height:diameter ratio over 13 weeks – the boxes span the 25th to 75th percentiles, the median is the horizontal line in the box, the error bars are the 5th and 95th percentiles, and all outliers are plotted. The difference variable was not significantly different from a normal distribution on each of the six dates (Shapio Wilk W tests, P values range from 0.74 on 21 December to 0.10 on 7 December). Values for *t*-tests at the beginning and at the end of the experiment, testing whether the means are significantly different from zero, appear below each plot. The images of the tests represent a pair-difference of +0.07 on the *y*-axis.

DISCUSSION

Thompson (Thompson, 1917) first described the shape of the sea urchin test using the analogy of a liquid drop on a flat surface and ascribed the forces producing this shape to coelomic pressure, podia (tube feet) and 'self-weight' (Dafni, 1986; Ellers and Telford, 1992; Ellers, 1993; Johnson et al., 2001). As an urchin grows, the sutures between test ossicles loosen (Ellers et al., 1998; Johnson et al., 2001) and "the entire structure is, in a sluggish way, plastic" [Thompson (Thompson, 1917) p. 662]. The flexibility in the test resulting from this kind of growth is capable of producing rapid changes in height:diameter ratios and morphological plasticity (Figs 1, 3).

Ellers and Telford (Ellers and Telford, 1992) measured the coelomic pressure in *Strongylocentrotus purpuratus* relative to the surrounding seawater. They found that it fluctuates with the movements of Aristotle's lantern and the associated tension and curvature changes of the peristomal membrane, and is negative overall (mean = –8 Pa). They also found no difference in coelomic pressure between fed (actively growing) and starved (not growing) urchins. Their results suggest that there is no difference in coelomic pressure between the Pit and Flat treatments in our experiment. There was also no difference in self-mass between our two treatments at the outset of the experiment and at weeks 8 and 13 when significant differences in shape were apparent (Figs 1, 3). Therefore, the remaining sources of difference between the forces acting on the morphogenesis of test shape are those attributable to the tube feet.

Tube feet "like so many long cables, moor the animal to the ground [and] constitute a symmetrical system of forces, with one resultant downwards, in the direction of gravity, and another outwards in a radial direction" (Thompson, 1917). At the start of the experiment, the mean test height of urchins in pits was 7.42 mm ± 1.75, the mean depth of the pits was 14.36 mm ± 1.57, and the heights of all urchins in pits were below the level of the plane of the top of the substrate – that is, they were totally 'submerged' within the cavities. We observed that the ambital tube feet of the urchins in the pits were anchored to the sides of the pits, whereas the tube feet of the urchins on Flat substrates could only anchor to the bottom. This difference should result in a greater degree of forces associated with the tube feet in the radial direction for urchins in pits and might account for the different shapes produced on the two types of substrates (Fig. 3).

Our results suggest that the shapes of sea urchin tests conform to the recently occupied microhabitat, which determines the relative direction of tube feet attachment. In this sense, urchin shape could be used to infer recent microhabitat conditions and probably other factors that affect tube feet attachment, such as wave action and incidence of storms. As reflex control of tube feet musculature is activated by mechanical stimulation (Florey and Cahil, 1980), changes in the magnitude and frequency of stimuli are predicted to change the attachment tenacity and, consequently, modify sea urchin tests. Moreover, the morphological plasticity of the test could also be used to describe paleoenvironments of fossilized urchins. However, further investigations are needed to identify the forces and their potential for driving test shapes.
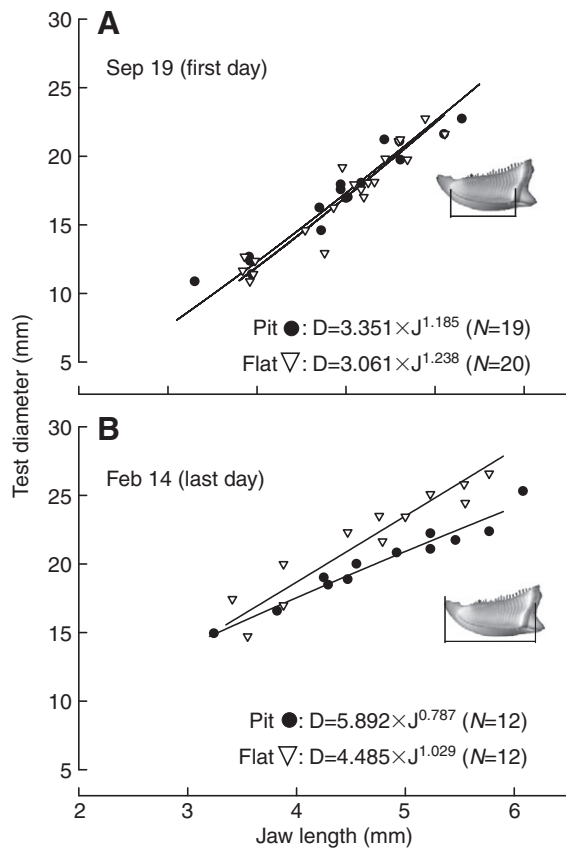
Fig. 4. Allometric relationships of test diameter (D) *versus* jaw (half-pyramid of Aristotle's lantern) length (J). Photo insets show fluorescent marks on jaw and length estimates. (a) Jaw length at the start of the experiment determined from fluorescently tagged individuals. Although all the urchins were injected with calcein at the start of the experiment, not all of them were tagged. Four were not tagged in the Flat and 5 were not tagged in the Pit treatments. (b) Jaw length at the end of the experiment from all 12 remaining pairs of Pit and Flat sea urchins. Regressions of the ln-transformed data showed that the slopes (allometric exponents) were homogenous at the start but not at the end of the experiment.

Divergent growth patterns over a short period (8–12 weeks; Fig. 2B, Figs 3, 4) produced morphological and allometric differences between sea urchins occurring in pits and those on flat surfaces. Sea urchins on substrates with pits also had adjacent flat surfaces available but showed a high degree of fidelity to these cavities (observed in pits 88% of the time). The Pit treatment had five locations, and the Flat treatment had four; and, from a bird's eye view, these were distributed over the same surface area. If movement were random and not different between the two groups, then the unequal areas between treatments would result in scoring the Pit urchins as moving more often, not less often, because the same surface area was subdivided more finely in the Pit treatments. This difference would bias the analysis against the pattern we found. The analysis clearly shows that the Pit urchins tended to stay in the cavities, whereas the Flat urchins were found to move more frequently (Fig. 2) and distributed themselves evenly among the four quadrants. The 'bias' in the design and analysis would lead to finding more, not less, movement in the Pit treatment.

Phenotypic plasticity has been observed in many urchin species – for example, *Echinometra mathaei* (Black et al., 1984), *Strongylocentrotus droebachiensis* (Russell et al., 1998; Meidel and Scheibling, 1999; Russell, 2001), *S. purpuratus* (Russell, 1987;
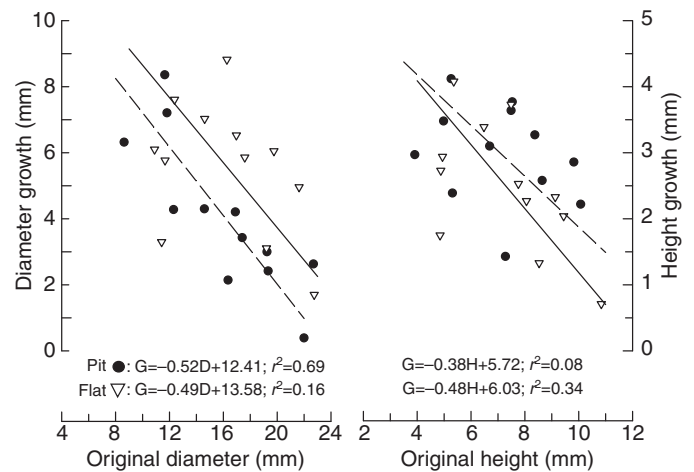

Fig. 5. Size-specific growth rates. Model II regressions of growth (G) as a function of original diameter (D) and height (H) from the start of the experiment to the end. Sample sizes are 12 for both Pit (dashed line) and Flat (solid line) for each plot. The slopes for Pit diameter ($t=-4.77$, $P<0.001$) and Flat height ($t=-2.25$, $P<0.05$) are significantly different from zero, whereas the slopes for Flat diameter ($t=1.36$, $P=0.20$) and Pit height ($t=-0.95$, $P=0.37$) are not.

Edwards and Ebert, 1991; Ebert, 1996; Grupe, 2006), *Diadema antillarum* (Levitan, 1991) and *Paracentrotus lividus* (Fernandez and Bouderesque, 1997). In all these cases, morphological plasticity was attributed to food availability; however, we have observed that urchins with identical food availability change their morphology and allometry owing to the presence of a cavity.

Associated with food availability is the relationship between jaw length and test diameter. Sea urchins in habitats containing limited food possess relatively larger jaws than conspecifics in habitats with abundant food (Ebert, 1980; Black et al., 1994; Pederson and Johnson, 2007). This allometric relationship is also different between species (Contreras and Castilla, 1987; Hagen, 2008). The functional significance of jaw size is related to the adaptation of Aristotle's lantern for increased feeding capacity in resource-limited habitats, such as barrens (Black et al., 1984; Pederson and Johnson, 2007), or for durophagous capability (Hagen, 2008). However, our results clearly show that microhabitat features can influence jaw–test allometry when food availability is constant (Fig. 4).

In our experiment, *Strongylocentrotus purpuratus* showed a high degree of fidelity to pits and only occurred out of them 12% of the time, whereas the Flat urchins moved more frequently. These urchins are commonly found in tidepools and on exposed rocky reefs within the wave-swept zone. Options for protection from direct wave impact include living in cracks, crevices or in cavities in the rock. This sedentary strategy seems common for other intertidal sea urchins, such as *Echinometra mathaei* (Carreiro-Silva and McClanahan, 2001) and *Paracentrotus lividus* (Trudgill et al., 1987), which prefer living in pits and feeding on drift algae. Although pits might afford protection from waves, they also provide a more hospitable microhabitat during emersion at low tide by retaining water and moderating temperatures and desiccation. An unintended demonstration of this microhabitat advantage came from the power failures to our seawater system. The seawater in the table dropped below the levels of the substrates, but the cavities in the Pit treatment retained water, whereas the Flat surfaces became dry. Of the 12 pairs affected by these unplanned emersion episodes, no individuals in the no-pit treatment survived, whereas 10 in the pit treatment survived. This difference is highly significant ($\chi^2=17.14$, $P<0.0001$).

It is much more difficult to extract an urchin living in a pit than one living on a flat surface, and the survival advantages of cavities also might involve biotic factors such as refuge against predation. Refuge availability in the context of rock hardness, friability and erosion patterns could affect population-level parameters such as habitat-specific survival rates. Although substratum mineralogy does not affect the abundance of *Paracentrotus lividus* and *Arbacia lixula* (Guidetti et al., 2004) in the Mediterranean, habitat relief has been noted as an important factor in controlling the abundance of *Centrostephanus rodgersii* in Australia (Andrew, 1993) and *Diadema* aff. *antillarum* (Hernández et al., 2008) in the Canary Islands. However, other substrate features such as surface microstructure, mineral composition and grain size and shape have not been studied and could influence microtopography, water retention and biofilm communities. These microhabitat effects could influence sea urchin reproduction, settlement, recruitment, growth and survival. Surprisingly, the role of substrates and its potential for shaping communities in temperate reef systems remains poorly understood despite its relationship with the biology and ecology of the resident organisms.

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