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Sutural loosening and skeletal flexibility during growth: determination of drop-like shapes in sea urchins

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The shape of sea urchins may be determined mechanically by patterns of force analogous to those that determine the shape of a water droplet. This mechanical analogy implies skeletal flexibility at the time of growth. Although comprised of many rigid calcite plates, sutural collagenous ligaments could confer such flexibility if the sutures between plates loosened and acted as joints at the time of growth. We present experimental evidence of such flexibility associated with weight gain and growth. Over 13-, 4-, and 2-week periods, fed urchins (*Strongylocentrotus droebachiensis*) gained weight and developed looser sutures than unfed urchins that maintained or lost weight. Further, skeletons of fed urchins force-relaxed more than did those of unfed urchins and urchins with loose sutures force-relaxed more than those with tight sutures. Urchins (*Strongylocentrotus franciscanus*) fed for two and a half weeks, gained weight, also had looser skeletons and deposited calcite at sutural margins, whereas unfed ones did not. In field populations of *S. droebachiensis* the percentage having loose sutures varied with urchin diameter and reflected their size-specific growth rate. The association between feeding, weight gain, calcite deposition, force relaxation and sutural looseness supports the hypothesis that urchins deform flexibly while growing, thus determining their drop-like shapes.

Keywords: sea urchin; biomechanics; collagen; ligaments; growth; morphospace

1. INTRODUCTION

Thompson (1917) proposed that the shape of an urchin is determined by patterns of mechanical forces acting on its skeleton. His idea is based on an analogy with a liquid drop sitting on a solid surface. In a drop, forces due to pressure and surface tension determine the local radii of curvature of the surface. The analogous forces in urchins are due to coelomic pressure, podia and self-weight. Also essential to the analogy is that the skeletal surface of an urchin is flexible and thus able to conform freely to the pattern of forces imposed.

Thompson's original hypothesis has been examined in several papers. Some evidence supporting the theory has

(Constable 1993). Such shrinkage under reduced food availability has also been observed in *Strongylocentrotus purpuratus* (Ebert 1967) and in *Diadema antillarum* (Levitan 1991). Similarly, 23% of bleached skeletons of urchins (*S. purpuratus*) fed seaweed *ad libitum* for one year had visible sutural gaps, whereas none of an unfed group showed gaps (Ellers *et al.* 1998). However, that study was not designed to test for an association between growth and sutural gapping. No data were kept on weight or diameter changes and no tests were done to measure the mechanical impact of the gaps. Furthermore, the 1 year period of that experiment suggests that the unfed urchins may have been in an unusual physiological condition.

In this paper we specifically test for an association between feeding, weight change, calcite deposition and sutural looseness. We present short-term experiments with relevant weight and sutural looseness measurements taken at the beginning and end of the experiments. We test whether sutural loosening is reflected in the overall mechanical properties of the skeleton by performing force relaxation tests and testing for an association with sutural looseness. We test whether looseness is associated with calcite deposition and hence growth. Finally, we test whether there is an association between size-specific growth rates and sutural looseness in field populations.

2. MATERIAL AND METHODS

(a) *Growth and sutural changes in* **Strongylocentrotus droebachiensis**

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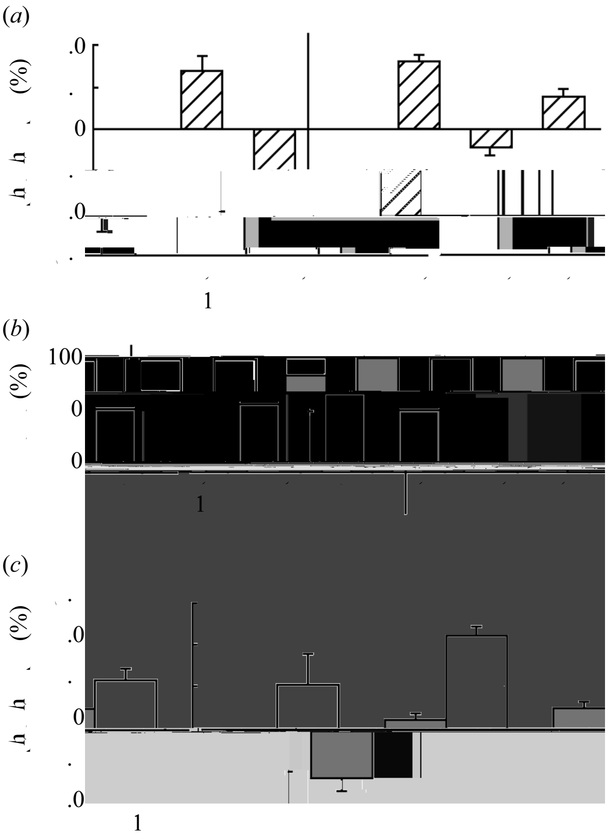


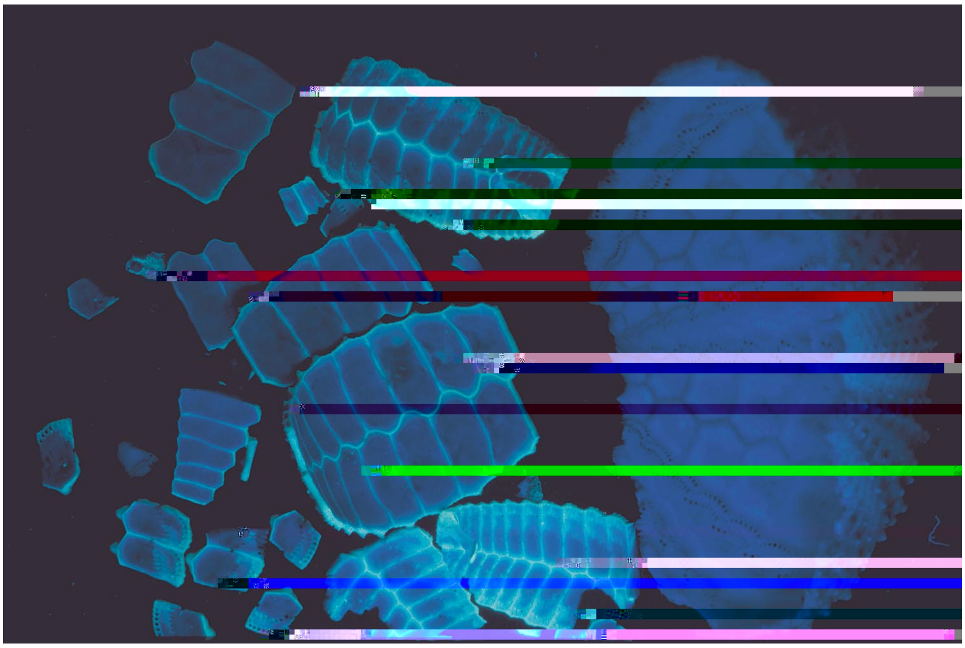
Figure 1. Growth and sutural looseness in *S. droebachiensis*. Fed urchins gained weight and unfed urchins lost weight (*a*). Feeding tended to loosen sutures (*b*) with the percentage remaining intact when bleached (grey bars) decreasing in all fed groups. Weight gains were highest in loose-sutured urchins (*c*). Error bars indicate one standard error.

experiment ($p = 0.52$, U-test; fed: $n = 25$, mean $= 68.7 \pm 2.4$ g; unfed: $n = 28$, mean $= 69.3 \pm 3.1$ g) or the four- and two-week experiment ($p = 0.57$, Kruskal–Wallis test; fed: $n = 38$, mean $= 69.1 \pm 2.9$ g; unfed: $n = 22$, mean $= 69.8 \pm 3.6$ g; unfed-then-fed: $n = 12$, mean $= 74.7 \pm 5.2$ g).

During the 13-week period, weight change differed between fed and unfed *S. droebachiensis* ($p = 0.0001$, U-test), with fed urchins gaining 2.2 ± 0.7 g ($p = 0.005$, paired t-test) and unfed urchins losing 3.7 ± 0.4 g ($p < 0.0001$, paired t-test; figure 1*a*). Fed urchins were more likely to disarticulate under their own weight after bleaching than were unfed urchins ($p = 0.02$, χ^2-test; figure 1*b*). The weight gain (figure 1*c*) of urchins that disarticulated was higher than the weight gain of those that remained intact ($p = 0.008$, U-test; 17 disarticulated with a mean weight change of 1.9 ± 1.1 g and 36 remained intact with a mean weight change of -2.2 ± 0.5 g). Both disarticulation and the feeding regime were predictive of weight change (multiple regression of weight change versus disarticulation and feeding regime: $r^2 = 0.57$; effect tests: disarticulation, $p < 0.01$; feeding regime $p < 0.0001$).

During the four-week period, weight change differed between fed and unfed urchins ($p = 0.0001$, U-test) with fed urchins gaining 2.5 ± 0.3 g ($p = 0.0001$, paired t-test) and unfed urchins losing 0.7 ± 0.1 g ($p = 0.0001$, paired t-test; figure 1*a*). Fed urchins were more likely to disarticulate under their own weight after bleaching than were either unfed urchins ($p < 0.0001$, χ^2-test, figure 1*b*) or the initial controls (19 initial urchins, $p < 0.0001$, χ^2-test). No unfed urchins and no initial controls disarticulated.

For both the four- and the two-week experiments, the change



ENDNOTES

[1] The Tanaka function given in eqn (1) in Russell *et al.* (1998) contains a misprint. For the correct function see eqn (2) of Ebert *et al.* (1999). Furthermore, the correct Tanaka function used with the parameters reported in Russell *et al.* (1998) must be multiplied by a conversion of 10 (to convert cm to mm) to obtain the units for jaw height as shown in their fig. 5. Tanaka function parameters used were: $a = 34.448$; $d = -0.1616$; $f = 38.883$; $c = 11.7$ yr.

[2] Sample calculation: growth rate of 2.9% per two weeks by weight, if sustained, corresponds to a factor of $1.029^{26} = 2.1$ times per year and, assuming isometry, that fractional weight change corresponds to a diameter change of $2.1^{(1/3)} = 1.28$, or an increase of 28%.

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Errata

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