

Walking Versus Breathing: Mechanical Differentiation of Sea Urchin Podia Corresponds to Functional Specialization

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Abstract. The podia of sea urchins function in locomotion, adhesion, feeding, and respiration; but different podia on a single urchin are often specialized to one or more of these tasks. We examined the morphology and material properties of podia of the green sea urchin, *Strongylocentrotus droebachiensis*, to determine whether, despite apparent similarities, they achieve functional specialization along the oral-aboral axis through the differentiation of distinct mechanical properties. We found that oral podia, which are used primarily for locomotion and adhesion, are stronger and thicker than aboral podia, which are used primarily for capturing drift material and as a respiratory surface. The functional role of ambital podia is more ambiguous; however, they are longer and are extended at a lower strain rate than other podial types. They are also stronger and stiffer than aboral podia. In addition, all podia become stronger and stiffer when extended at faster strain rates, in some cases by nearly an order of magnitude for an order of magnitude change in strain rate. This strain-rate dependence implies that resistance to rapid loading such as that imposed by waves is high compared to resistance to slower, self-imposed loads. Thus, the serially arranged podia of *S. droebachiensis* are functionally specialized along an oral-aboral axis by differences in their morphology and mechanical properties.

Introduction

The surface of the green sea urchin, *Strongylocentrotus droebachiensis*, like that of all urchins, is covered with five

double rows of podia, and these structures are essentially hollow tubes with terminal suckers. The wall of each podium consists of three main layers: an outer epithelium, a middle connective tissue layer, and an inner muscular layer (Florey and Cahill, 1977). Internally, the podium is connected to an ampulla, a sac-like structure that antagonizes podial movement. Contraction of the ampulla forces coelomic fluid into the podium, and thus extends it. Conversely, contraction of the longitudinal muscles shortens the podium and forces coelomic fluid back into the ampulla. All of the podia on *S. droebachiensis* share these characteristics, and all of them are similarly shaped. They exemplify the typical echinoid locomotory podia.

However, podia perform a variety of functions besides locomotion, including adhesion, feeding, shading, sensing, and respiration, and many podia are specialized for one of these functions. Podia in a particular position along the oral-aboral axis tend to perform a particular function and often exhibit morphological features that enhance performance of that function. For example, *Arbacia punctulata* has morphologically differentiated podia, reflecting the separation of respiratory, sensory, and locomotory functions. The aboral podia lack suckers and their larger surface area and thinner walls enhance respiration, the ambital podia are long with minimal suckers to allow sensation in the region around the urchin, and the oral podia are suckered to facilitate locomotion (Fenner, 1973).

Although the podia of *S. droebachiensis* lack these gross morphological differences, there may still be a division of labor between the primarily locomotory oral podia and the primarily respiratory aboral podia. We hypothesize that the podia of this species achieve functional specialization through the differentiation of distinct mechanical properties. The goal of this study was to test our hypothesis that the differences in function of oral, aboral, and ambital podia are

Received 21 October 1998; accepted 18 November 1999.

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correlated with differences in their mechanical characteristics and morphology.

Materials and Methods

Sea urchins, *Strongylocentrotus droebachiensis*, were collected subtidally near Monhegan Island, Maine. The animals, ranging in diameter from 45.4 mm to 59.7 mm, were maintained in a recirculating seawater aquarium kept at 10°C and fed *Laminaria* sp. every 2 weeks.

Natural extension

Urchins in a glass aquarium were videotaped, and the natural extension rate and initial length of podia were measured from the digitized video images. The length of a podium was measured from the base to the sucker as it was extending, and just as the podium straightened. Extension rate was quantified as the increase in length (in millimeters) per second, and strain rate was quantified as true strain (the natural logarithm of the ratio of final length to initial length) divided by the time to extend.

Mechanical extension

Podia from three locations on the animal were tested separately: aboral podia are those on the upper surface of the urchin; ambital podia are those occupying a narrow circumferential band at the widest diameter of the urchin; and oral podia are those on the lower surface of the urchin. Urchins were placed in an isotonic solution, 7.5% $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$, at 10°C, for 15 min prior to mechanical tests of their podia and were kept in this solution during the tests (Dales, 1970). The MgCl_2 solution prevented muscle contraction, so passive material properties could be tested.

All mechanical tests were performed with an Instron material testing device (Model 4301) that loaded materials at specified rates and simultaneously measured force and extension. Force and extension signals were digitized (12-bit) at 1000 Hz and recorded in a computer. The error in the force measurements was $< \pm 0.001$ N. The error in the extension measurements was $< \pm 0.01$ mm. Tests were conducted as follows. An urchin was strapped in place, and a small, spring-loaded clip was attached to the distal end of a podium. The podium was then pulled perpendicular to the surface of the urchin (in the direction of normal extension) at a constant extension rate until it broke.

Fifteen podia—5 aboral, 5 ambital, and 5 oral—were tested on each urchin at a given extension rate. Each of five urchins were tested at three extension rates: 0.167 mm/s (minimum natural extension rate), 0.708 mm/s (halfway between the mean and the minimum natural extension rates), and 1.25 mm/s (mean natural extension rate). Another set of podia from one urchin was also tested at 3.45 mm/s (maximum natural extension rate).

In comparing lengths of different podial types and calculating strain and strain rate, initial length of the podium (measured between the body wall and the end of the clip) was defined as the point at which force started to increase (above 0.001 N) during the breaking tests, thus indicating that the podium has just started to stretch (Fig. 1a). Nominal stress on a podium was calculated by dividing the force applied by the mean tissue cross-sectional area of podia of that type from that urchin. Nominal strength is the nominal stress at which a material breaks. True strain was calculated by taking the natural logarithm of the length divided by the initial length. Stiffness is the slope of a stress-strain curve and was taken from the upper, linear portion of the J-shaped stress-strain curves (Fig. 1b). Strain rate was calculated by dividing the final strain by the time required to get from initial length to breaking.

Tissue cross-sectional area

Relaxed podia from urchins soaked in 7.5% $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$ were cut off at the base. Although this technique depressurized the podia, it allowed us to compare the three types in as similar a state as possible. The exterior and luminal diameters of the podia were measured halfway between the base and the sucker with an ocular micrometer (± 0.01 mm) on a light microscope. These diameters were used to calculate the total and luminal cross-sectional areas, and the tissue cross-sectional area was found by subtracting the luminal cross-sectional area from the total cross-sectional area. Five podia of each type were measured on each urchin.

Results

Structure and natural extension

All oral, ambital, and aboral podia had the same gross morphology (suckered tube) and similar diameters (Table 1). The ambital podia, however, were 67% longer than the aboral and oral podia, and the oral podia had thicker walls and a much greater cross-sectional area of tissue than either the aboral or ambital podia (Table 1). Urchins extended their oral, ambital, and aboral podia at the same rate. Nonetheless, because the ambital podia had the greatest initial length, they also had the lowest strain rate (Table 1).

Mechanical extension tests

All the material properties of all podia were positively dependent on strain-rate (Fig. 2, linear regression analysis, all $P < 0.05$, all d.f. = 86). For the three podial types, the slopes of breaking force, nominal strength, and breaking strain with respect to strain rate were not significantly different (ANCOVA, Table 2). For breaking force and nominal strength, the r^2 of the regressions ranged between 0.44 and 0.58; and for breaking strain, the r^2 of the regres-

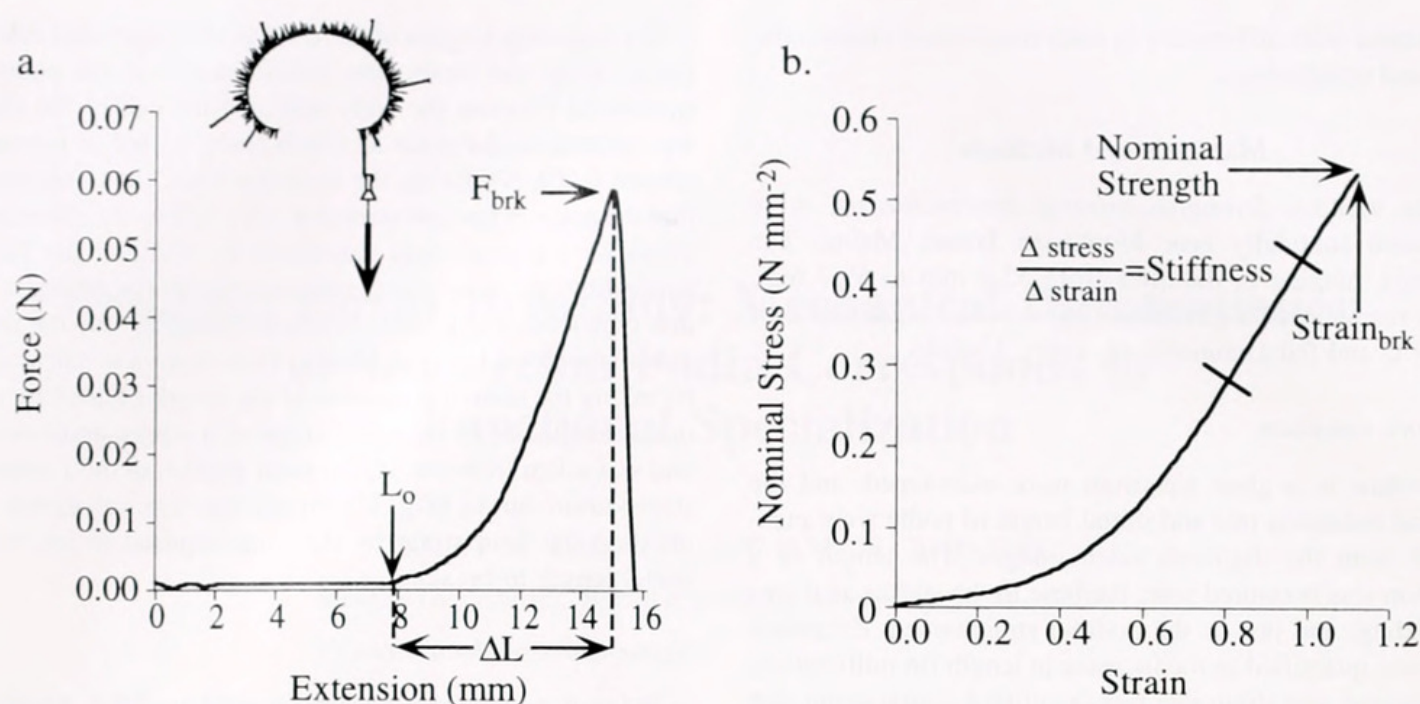


Figure 1. Force-extension (a) and stress-strain (b) curves of an oral podium. L_0 , the initial length, is the length at which the podium starts resisting extension; F_{brk} is the force at which the podium breaks, and ΔL is the change in length from L_0 to the breaking force. Nominal stress is force divided by cross-sectional area, and strain is the natural logarithm of the length divided by the initial length. Stiffness is the slope of the linear portion of this curve. Nominal strength is the stress at which the podium broke, and $Strain_{brk}$ is the strain at which the podium broke. Inset shows an urchin in the testing setup with one of its oral podia being extended.

sions ranged between 0.09 and 0.13. Thus, although nearly half of the variation in breaking force and nominal strength is explained by variation in strain rate, little of the variation in breaking strain (9%–13%) is explained by variation in strain rate. *A posteriori* comparisons of elevations using Tukey's Q (Table 2) revealed that oral podia exhibited higher breaking forces, nominal strengths, and breaking strains than aboral podia; *i.e.*, the oral podia were stronger and stretchier. The ambital podia also exhibited lower breaking forces and breaking strains than did the oral podia, but they were equally strong.

In contrast to the analysis of other material properties, the ANCOVA for nominal stiffness revealed significant differences between slopes (Table 2). In an ANCOVA, when the slopes of the lines are unequal, comparisons of elevations cannot be generalized across all variations in the independent variable (in this case strain rate). Specifically, *a posteriori* comparisons of slopes using Tukey's Q revealed that oral podia exhibited less positive strain-rate dependence than did ambital podia. For those comparisons showing no significant difference between slopes, we found that ambital podia were significantly stiffer than aboral podia at all strain

Table 1

Podial morphology and extension rates

	Aboral	Ambital	Oral	ANOVA
Initial length (mm)	7.59 (0.3) a	11.64 (0.5) b	6.26 (0.3) a	d.f. = 2, 96 $P = 0.0001$
Exterior diameter (mm)	0.67 (0.01)	0.72 (0.01)	0.70 (0.02)	$P = 0.07$
Wall thickness (mm)	0.06 (0.01) a	0.07 (0.01) a	0.11 (0.01) b	$P = 0.0001$
Cross-sect. tissue area (mm ²)	0.12 (0.007) a	0.13 (0.008) a	0.18 (0.009) b	$P = 0.0001$
Extension rate (mm s ⁻¹)	1.23 (0.16) a	1.30 (0.17) a	1.23 (0.13) a	d.f. = 2, 89 $P = 0.9$
Strain rate (s ⁻¹)	0.34 (0.05) a	0.14 (0.03) b	0.45 (0.07) a	$P = 0.0006$

Means (SE) and results of ANOVAs comparing them. Means with different letters are significantly different ($P < 0.05$) by the Fisher PLSD *a posteriori* test.

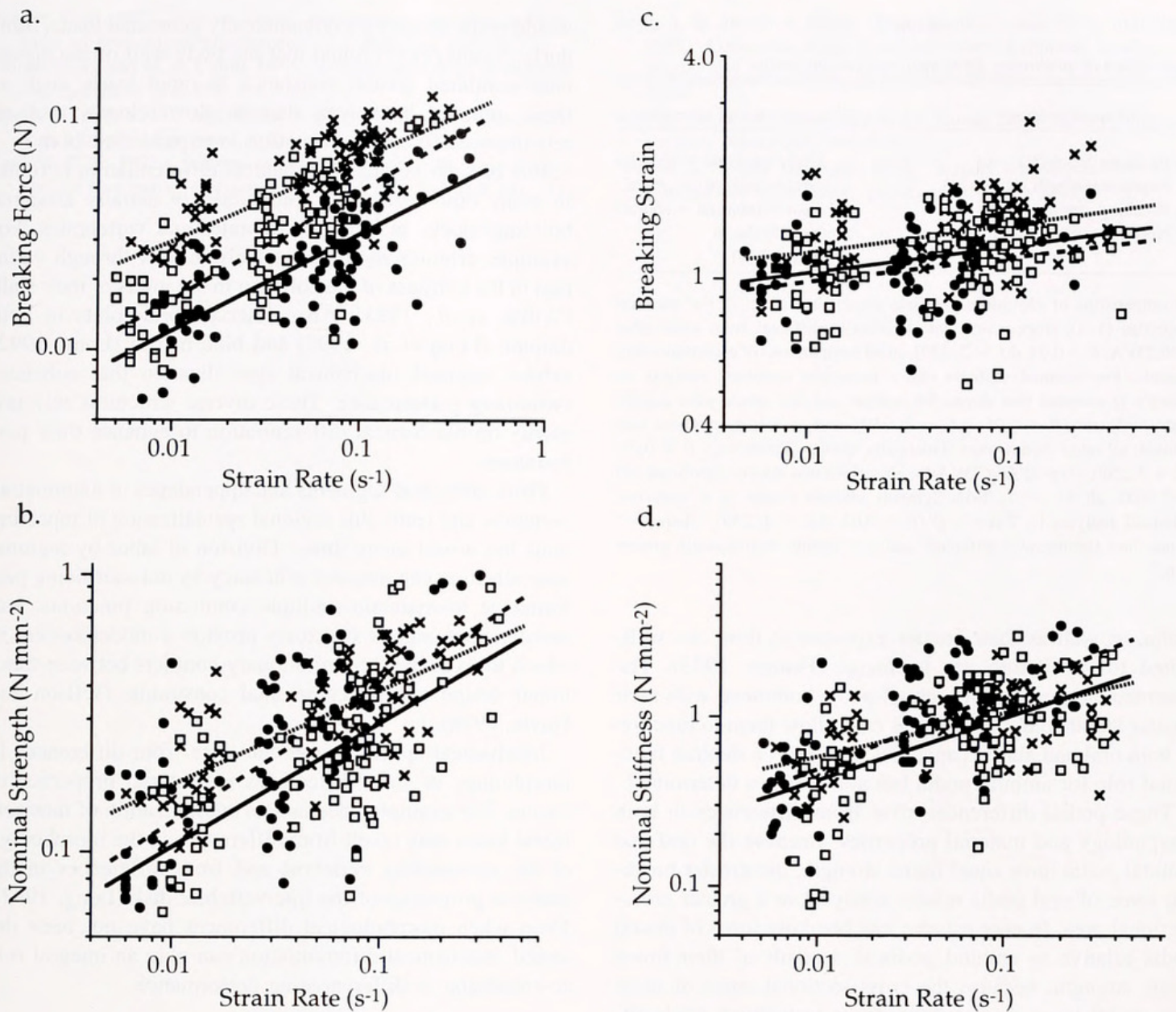


Figure 2. Breaking force (a), nominal strength (b), breaking strain (c), and nominal stiffness (d) are plotted on a log-log scale against strain rate for oral (crosses, dotted line), ambital (filled circles, dashed line), and aboral (open squares, solid line) podia. Lines are least-squares linear regressions. Line slopes and elevations were compared by ANCOVA (Table 2).

rates, and aboral podia were significantly stiffer than oral podia at all strain rates; r^2 values for these regressions ranged from 0.30 to 0.43.

Discussion

Some of the morphological differences found among the podia of other urchins (e.g., presence *versus* absence of suckers) are absent in *Strongylocentrotus droebachiensis*, possibly because the aboral podia, in addition to acting as a respiratory surface, perform other functions that require suckers. For example, drift algae captured by aboral podia may be the primary food source for some urchins (De Ridder and Lawrence, 1982). Furthermore, urchins like *S.*

droebachiensis, that live in high-flow environments, may require suckered aboral podia to secure themselves in cracks and to right themselves (Fenner, 1973). Thus, aboral podia, though performing a different set of tasks from oral podia, would still require the same gross morphology.

Although all podia in *S. droebachiensis* do possess suckers, they still exhibit mechanical and morphological differentiation consistent with their location and functional specialization for locomotion or respiration. The greater strength and thicker walls of the oral podia presumably enhance one of their primary functions, which is to resist hydrodynamically generated forces on the urchin (Denny and Gaylord, 1996). Similarly, the thin walls of the aboral

Table 2

Comparison of strain-rate dependent material properties

Material property	Comparison of elevations
(1) Breaking force (N)	Oral > ambital > aboral
(2) Nominal strength (N mm ⁻²)	(Oral = ambital) > aboral
(3) Breaking strain	Oral > (ambital = aboral)
(4) Nominal stiffness (N mm ⁻²)	Ambital > aboral Aboral > oral

Comparisons of elevations for data shown in Figure 2. For material properties (1–3), slopes were not statistically different from each other (ANCOVA, $P > 0.05$, d.f. = 2, 259), so all comparisons of elevations were possible. For nominal stiffness (4), a *posteriori* statistical analysis by Tukey's Q revealed that slopes for ambital and oral podia were significantly different ($P < 0.05$, d.f. = 3, 259), and so that comparison was omitted; all other slopes were statistically similar (Tukey's Q , $P > 0.05$, d.f. = 3, 259). Overall ANCOVA for elevations was always significant (all $P < 0.05$, all d.f. = 2, 261). Symbols indicate results of a *posteriori* statistical analyses by Tukey's Q ($P < 0.05$, d.f. = 3, 259), where "=" means "not significantly different" and ">" means "significantly greater than."

podia, as well as their greater exposure to flow, are well-suited to facilitating gas exchange (Fenner, 1973). The intermediate position of ambital podia combined with their greater length and thinner walls may allow them to function in both oral and aboral capacities; however, a distinct functional role for ambital podia has not yet been determined.

These podial differences arise from differences in both morphology and material properties. Because the oral and ambital podia have equal tissue strength, the greater breaking force of oral podia results solely from a greater cross-sectional area. In contrast, the low breaking force of aboral podia relative to ambital podia is a result of their lower tissue strength, because the cross-sectional areas of these two podial types do not differ from each other. Such differences in tissue strength may be due to fine-scale variation in morphology (*e.g.*, collagen fiber orientation) or tissue composition (*e.g.*, proportion of muscle relative to connective tissue).

All the material properties, especially strength and stiffness, varied positively with strain-rate over the range of natural extension rates observed. In some cases, there was nearly an order of magnitude increase in stiffness or strength for an order of magnitude increase in strain rate. The consequence of this strain-rate dependence to the performance of a given podium is that slow extensions require less energy than do rapid extensions. For a given strain rate, ambital podia require more energy to extend, but because they are extended at lower strain rates, it is unclear whether there are energetic differences in the urchin's own use of different types of podia.

If the strain-rate dependence we quantified extends to the range of strain rates applied by waves, then this mechanical difference would facilitate slower, self-imposed loads but

would resist faster, hydrodynamically generated loads. Similarly, Koehl (1977) found that the body wall of sea anemones exhibited greater resistance to rapid loads, such as those imposed by waves, than to slower loads, such as self-imposed forces that function to expand their body.

In a broader context, mechanical differentiation is found in many other structures constructed of serially arranged building blocks in both invertebrates and vertebrates. For example, crinoids reorient passively in flow through variation in the stiffness of the collagen in the joints of their stalk (Wilkie *et al.*, 1993). Also, intervertebral joints in both dolphin (Long *et al.*, 1997) and blue marlin (Long, 1992) exhibit regional mechanical specialization that enhances swimming performance. These diverse structures rely primarily on mechanical differentiation to enhance their performance.

From arthropod segments and appendages to mammalian vertebrae and teeth, this regional specialization of repeating units has arisen many times. Division of labor by regional specialization can increase efficiency by not sacrificing performance to maintain multiple conflicting functions, and serially homologous structures provide a model system in which to examine the evolutionary conflicts between functional design and developmental constraints (Wilson and Hoyle, 1978).

Mechanical specialization can arise from differences in morphology or from differences in material properties of tissues. For example, mechanical specialization of intervertebral joints may result from differences in the morphology of the surrounding vertebrae and from differences in the material properties of the intervertebral disk (Long, 1992). Even when morphological differences have not been detected, mechanical differentiation can play an integral role in enhancing or differentiating performance.

Acknowledgments

This work would not have been possible without the ideas, insight, and comments of O. Ellers and C. K. Johnson. Thanks to E. Archie, Z. Cardon, P. Dickinson, and M. Pratt for their insightful comments on the thesis version of this work and to C. Fuller for urchins. Thanks also to three anonymous reviewers for many helpful comments. This work was supported by a SURDNA Undergraduate Research Foundation Fellowship to H.A.L.

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