Swimming performance as a constraint on larval morphology in plutei

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ABSTRACT: Understanding evolutionary mechanisms constraining larval morphology is challenging, both because morphology has many potential functional consequences and because the impacts of morphological variation on most functions are difficult to quantify. We assessed the potential importance of swimming as a factor driving larval morphology by hypothesizing that larvae of the sand dollar *Dendraster excentricus* are at or near a local maximum in swimming performance as a function of their morphological characteristics. To test this hypothesis, we used a hydrodynamic model parameterized to represent the 4-armed larval stage to predict the consequences of morphological changes on larval movement in still water and shear flows. We created 3 morphological families, consisting of series in which either larval body skeleton volume, relative arm length, or arm elevation angle were incrementally altered from observed morphologies, and used upward swimming velocity as a metric of performance. For each morphological family, a wide subset of alternate morphologies performed better than the observed morphology in still water. However, in shear flows, the observed morphology consistently fell within the narrow morphological range that minimized rapid downward velocities. These results suggest that larval swimming performance, especially performance in moving water, is a driving factor in the evolution of *D. excentricus* larval morphology. Further, our results suggest that small morphological changes resulting from environmental shifts, such as those predicted to result from ocean acidification, may have potentially large deleterious ecological consequences.

KEY WORDS: Functional morphology · Biomechanics · Shape evolution · Planktonic larvae · Hydrodymanic model · Larval swimming · Shear flow

INTRODUCTION

Larval morphology affects fitness through feeding performance, energetic costs, conspicuousness, vulnerability to predation, and other mechanisms. This suggests that larval morphology reflects compromises between multiple possible evolutionary pressures. It is seldom clear which mechanism, if any, is the dominant evolutionary driver of any given trait or set of traits.

Most planktonic larvae are weak swimmers that are unable to swim against horizontal currents. However, most larvae have some degree of control over their vertical positions in the water column, enabling them to regulate exposure to UV radiation, food availability, and other environmental factors that vary with depth (Pennington & Emlet 1986, Metaxas & Young 1998a,b,

Clay et al. 2004). Larvae also use depth control to modulate dispersal by ambient currents (Forward & Tankersley 2001, Welch & Forward 2001, Forward et al. 2003, Shanks et al. 2003). Hence, larval control over vertical position is likely advantageous for growth and survival. Because larvae with stronger vertical swimming can potentially control their vertical positions under wider ranges of environmental conditions, it is reasonable to hypothesize that swimming performance, and more specifically vertical swimming ability, may be an important factor driving the evolution of larval morphology.

Larvae are typically denser than water, and most rely on active swimming to remain in the water column. Vertical swimming abilities are functionally linked to larval morphology through the buoyancy and gravity

forces inherent in the size and shape of each larva, and through propulsion and drag resulting from bio-mechanical interactions with surrounding water. One of the few groups in which the functional relationship between morphology and swimming performance has been investigated both experimentally and theoretically is the 'armed' larvae. This group includes larvae that have long, thin, ciliated, arm-like structures, which are typically used for both swimming and feeding. Armed larvae include representatives from diverse taxonomic groups, including the pluteus larvae of ophiuroids and echinoids, larval phoronids, larvae of some mollusks such as the hairy triton, and some annelid larvae including those with the rostraria larval form (Young et al. 2002, Grünbaum & Strathmann 2003). Morphological variability within the armed larvae includes variability in arm number, arm size, and position. For example, the morphology of plutei of the sand dollar *Dendraster excentricus* changes as these larvae progress through 4-, 6-, and 8-armed stages, and also varies with environmental conditions such as food abundance (Boidron-Metairon 1988, Hart & Strathmann 1994).

Most research on larval swimming biomechanics has focused on swimming in still water (Chia et al. 1984, Emlet 1990, 1991, 1994, Pennington & Strathmann 1990, McHenry 2005, Higgins et al. 2008). In coastal species such as *Dendraster excentricus*, the relationships between larval morphology and movement are complicated by the fact that their larvae are immersed in turbulence and shear over much of their planktonic period. Moving water may significantly alter the functional consequences of morphological traits in ways that are so far poorly understood.

Oceanic energy dissipation rates typically range from 10^{-6} to 10^{0} cm^2 s^{-3} (Kiøerboe & Saiz 1995). The Kolmogorov scale, which indicates the approximate characteristics of turbulent eddies, suggests that for these energy dissipation rates the smallest turbulent eddies are on the order of 1 to 0.03 cm in length, 0.01 to 0.3 cm s^{-1} in velocity, and 100 to 0.10 s in duration (Tennekes & Lumley 1972, Kundu & Cohen 2002, Yamazaki et al. 2002). Because most larvae are smaller than the typical size of the smallest turbulent eddies (Emlet 1991) it is likely that, except under very energetic conditions, these larvae experience turbulence primarily as shear. Therefore, the mechanics of larval swimming in shear flows are an informative and tractable first approximation to larval movement in complex coastal flow environments.

Shear alters the mechanics of swimming in many planktonic organisms. Many species of motile algae (Pedley & Kessler 1992a,b, Bearon & Grünbaum 2006) and larvae (Grünbaum & Strathmann 2003, Strathmann & Grünbaum 2006, McDonald 2007, Clay 2008,

Clay & Grünbaum 2010) have been shown to tilt in shear and consequently to move horizontally toward downwelling water. These interactions of swimming and shear can lead to downward advection and therefore net downward movement, despite upward swimming. Further, high shears can cause planktonic organisms to lose stability and tumble, resulting in loss of the orientation necessary for directional swimming. Loss of orientation leads to downward transport of larvae that would swim up in still water. In both of these cases, larval morphology-flow interactions compromise behavioral control over vertical position in the water column.

Clay & Grünbaum (2010) found theoretical evidence that some larval morphologies orient in flow such that a component of their swimming velocity is directed horizontally toward upwelling water. Vertical transport resulting from such interactions could lead to upward velocities that exceed those of larvae swimming in still water. For larvae with these specialized morphologies, morphology-flow interactions could potentially increase behavioral control over vertical position in the water column.

In this study, we used the 4-armed stage larvae of the sand dollar *Dendraster excentricus* to evaluate whether swimming performance is an important functional constraint driving the evolution of larval morphology. We addressed this question by posing the hypothesis that larvae are at or near a local maximum in swimming performance in still water and/or shear, as a function of their morphological characteristics. An implication of this hypothesis is that morphological shifts from observed values decrease swimming performance. We tested this hypothesis by quantifying the functional consequences for swimming performance of altered morphologies in 4-armed *D. excentricus* larvae. More specifically, we systematically incremented each of 3 larval morphological characteristics — body skeleton volume, relative arm length, and arm elevation angle — and used the resulting performance-morphology relationships to compare observed to hypothetical larval forms.

METHODS

Model description. Our hydrodynamic model was a modified version of that used by Grünbaum & Strathmann (2003), and the same as that used by Clay & Grünbaum (2010). A complete quantitative description of the model can be found in Grünbaum & Strathmann (2003). Key modifications from Grünbaum & Strathmann (2003) were that our version of the model was dimensional (rather than non-dimensional), and was parameterized to specifically represent 4-armed *D. ex-*

centricus larvae. We approximated the larval form as a set of slender cylinders, allowing the flow and force distribution around each cylinder segment to be calculated using low Reynolds number slender body theory. For cylinders representing ciliated arm sections, we based calculations on an extension of slender body theory by Grünbaum (1995) in which ciliary propulsion is approximated by a tangential velocity at the cylinder surface. These 'ciliated' cylinders created a 'traction velocity' that provided the propulsive force of the larva.

We specified larval arm positions by the arm elevation angle, which we defined as the angle of the arm above the horizontal (x-y) plane, and arm sweep angle,

which we defined as the orientation of the arm within that plane (Fig. 1). We assumed bilateral symmetry between the 2 arms within each pair of arms. We defined the relative arm length as the ratio of the ciliated arm length allocated to the postoral arms over one half of the total ciliated arm length. Thus, a value of 0 indicates that the total ciliated arm length is allocated to the anterolateral arms, a value of 1 indicates equal allocations to the postoral and anteolateral arms, and a value of 2 indicates that the total length is allocated to the postoral arms.

We approximated the hydrodynamic effects of the larval body with non-ciliated cylinders in the shape of
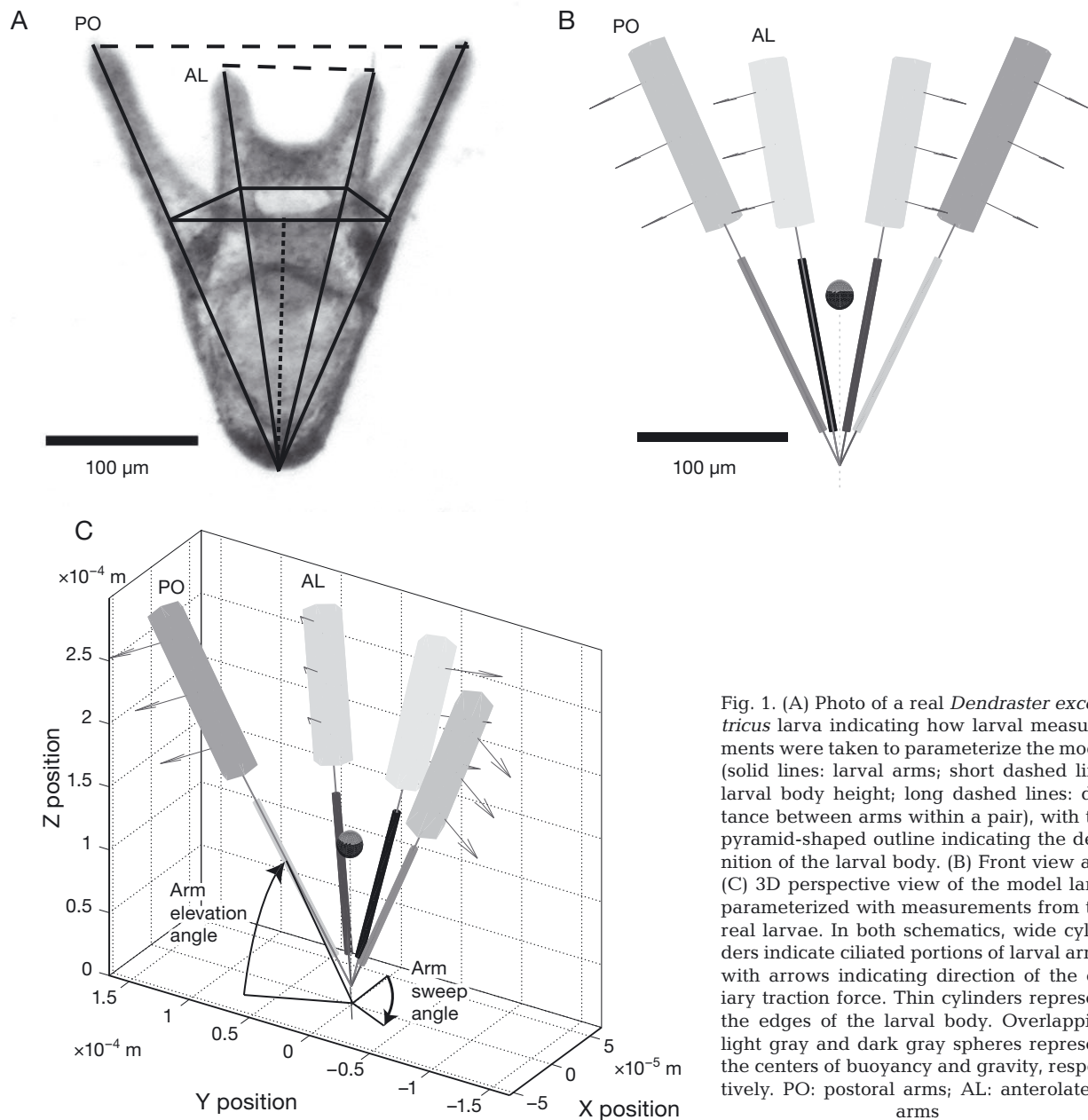

Fig. 1. (A) Photo of a real *Dendraster excentricus* larva indicating how larval measurements were taken to parameterize the model (solid lines: larval arms; short dashed line: larval body height; long dashed lines: distance between arms within a pair), with the pyramid-shaped outline indicating the definition of the larval body. (B) Front view and (C) 3D perspective view of the model larva parameterized with measurements from the real larvae. In both schematics, wide cylinders indicate ciliated portions of larval arms, with arrows indicating direction of the ciliary traction force. Thin cylinders represent the edges of the larval body. Overlapping light gray and dark gray spheres represent the centers of buoyancy and gravity, respectively. PO: postoral arms; AL: anterolateral arms

an inverted pyramid, constrained at the top by the area encompassed by the larval arms (Fig. 1). Because the model assumed a low Reynolds number, there was minimal leakage between cylinders (Cheer & Koehl 1987), making this a reasonable first approximation to a solid larval body. For hypothetical larval forms, the height of the body was constrained such that model larval body volume matched observed larval body volume. The magnitude and centers of buoyant and gravitational forces (Fig. 1) were calculated from the distribution of tissue and calcium carbonate in the arms and the larval body.

This hydrodynamic model provided reasonable approximations of larval swimming in flowing water using a minimal amount of computational power. The design of our study required 174 080 simulated swimming trajectories; our simplified model made this experimental design computationally feasible.

Model parameterization. We used measurements of cultured 3 d old, 4-armed *Dendraster excentricus* larvae to establish a baseline morphology (Clay 2008, Clay & Grünbaum 2010). Briefly, larvae were cultured at a density of approximately 2 larvae per ml in a 5 µm bag with filtered water under continuous, gentle stirring. Water changes and feedings (*Rhodomonas lens*, at a concentration of approximately 5000 cells ml^{-1}) took place 12 to 24 h post-fertilization and 2 to 3 times per week thereafter. We preserved the larvae in a 70% ethanol and seawater solution buffered (supersaturated) with sodium bicarbonate and imaged 31 individuals under 10x magnification. We used the image processing and analysis software ImageJ version 1.36b (National Institutes of Health) to measure the digital images in pixel dimensions. We used a digital image of a stage micrometer to convert pixel dimensions to physical dimensions. We measured arm length, width between arms within a pair, arm diameter, and body height (distance from the base of the larva to the low point of the ventral transverse band between the postoral arms) from the image of each larva (Fig. 1). We used the fine-focus microscope knob, calibrated with a capillary tube of known diameter, to measure the distance from the plane of the tips of the arm pairs projecting upwards toward the microscope and the plane of the arms lying flat on the slide. We used these distances and projected lengths to calculate the lengths of larval body parts that were above the plane of the slide. Each larva had small asymmetries in arm length within both arm pairs. Because the model assumed bilateral symmetry, we used the average arm length for each pair as a representative value. In all instances skeletal rods were intact, but a few larvae had slight tissue shrinkage due to preservation. In these cases, we used the tip of the skeletal rods to indicate arm length.

Direct observations enabled us to determine the total arm length (length from base of larval body to arm tips); total postoral and anterolateral arm length (for each arm pair, distance from base of larval body to arm tips); height that the body extended up each pair of arms; total length of ciliated arm (total arm length minus the body height on each arm); relative arm length (ratio of the ciliated band length allocated to the postoral arms to one half the total length of ciliated arm length); arm elevation angle for each pair of arms (angle of each arm above horizontal); sweep angle (the position of each arm on the x-y plane); body volume (volume of the assumed pyramid-shaped body); and arm diameter.

A few parameters could not be determined from direct observations. We followed Pennington & Strathmann (1990) by assuming skeletal density was the same as mineral calcite (2.71 g ml^{-1}). We based the volume of skeleton in the arm spicules on reports of *Dendraster excentricus* having simple spicules with a diameter of 3 µm in their anterolateral arms, and having fenestrated spicules containing twice as much skeletal material per unit length in their postoral arms (Emlet 1982). For the baseline larva, we assumed that 6% of the larval body is made up of skeletal material, based on estimates that the skeleton of 4-armed *D. excentricus* plutei may contribute as much as 77% of their excess density (Pennington & Emlet 1986, Pennington & Strathmann 1990). For hypothetical larval forms we assumed the body skeleton remains attached to the base of the larval body, maximizing its contribution to larval stability. Because traction velocity in the hydrodynamic model does not correspond exactly to ciliary tip speed or any other directly observable morphological trait, we determined the traction velocity indirectly by requiring that the swimming velocity of the baseline model larvae in still water matched observed values (Clay 2008, Clay & Grünbaum 2010).

Assessment of performance metrics. We constructed 3 families of model larval morphologies by incrementally altering one of 3 focal morphological parameters: body skeleton volume, relative arm length, and arm elevation angle. We varied the body skeleton volume as a percentage of the total body volume by 1% increments from 1% to 10% (compared to the observed value of 6%). We varied relative arm length in increments of 0.1 from 0.1 to 1.9 to include morphologies in which either the postoral arms or the anterolateral arms were much longer than observed (the observed value of relative arm length was 1.08). Finally, we varied arm elevation angle as a percentage of the angle observed in real 4-armed *Dendraster excentricus* larvae (65° for postoral arms, 78° for anterolateral arms). We modeled arm elevation angle in increments of 10% from 10% to 110% of the observed values, so that arms ranged from nearly horizontal to nearly vertical.

We modeled movement of each family of morphologies in still water, and at 16 levels of vertical shear (horizontal gradients in vertical velocities) and of horizontal shear (vertical gradients in horizontal velocities) from 0 to 10 s^{-1}, representing the range of typical oceanic shear levels (Kiørboe & Saiz 1995, Yamazaki et al. 2002). We generated 128 random initial orientations, and calculated the swimming trajectory from each initial orientation for each morphology at each shear. We simulated each trajectory for 120 s, of which the first 100 s were included to enable initial transients in orientation to subside. We used the final 20 s of each simulated trajectory to collect swimming performance data.

We assessed swimming performance using 3 metrics: (1) the range of horizontal and vertical shears over which upswimming occurred, (2) larval net vertical velocity in still water, horizontal shear, and vertical shear, and (3) larval horizontal velocity in vertical shear. We used net vertical velocity and the range of shears in which upswimming occurred as our primary performance metrics. In vertical shear, larval net vertical velocity results from a combination of larval vertical swimming and, if there is horizontal movement, by vertical advection. Therefore, in vertical shear, larval horizontal velocity quantifies the contribution of this indirect movement mechanism. For larval vertical and horizontal velocities, we report the median, 10th and 90th percentile velocities to reflect morphology-flow combinations in which initial orientations had persistent consequences for swimming movements.

RESULTS

Swimming performance in still water

In still water, all modeled body skeleton volume morphologies swam upward, with lower body skeleton volumes resulting in faster upswimming (Fig. 2). In contrast, only a narrow range of relative arm lengths, those similar to observed morphologies (between 1.0 and 1.3), moved upward in still water (Fig. 3). Outside this range, larvae had negative upswimming velocities. Morphologies with arm elevation angles down to 40% of observed had positive vertical velocities, with angles near 65% maximizing upswimming in still water (Fig. 4).

Swimming performance in shear: body skeleton volume

In both vertical and horizontal shear, increases or decreases in body skeleton volume improved one swimming performance metric, but compromised another
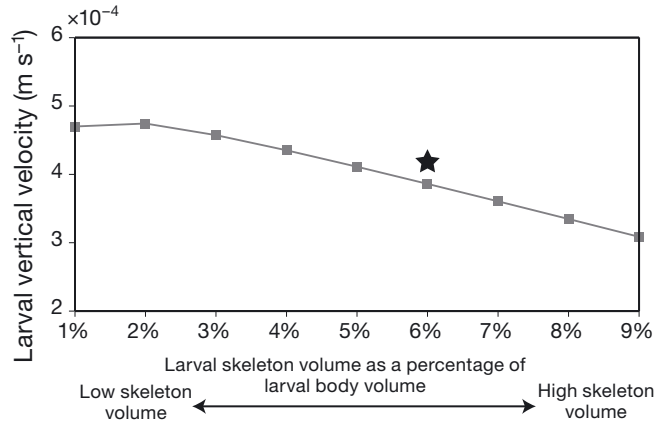

Fig. 2. Model results for the vertical velocity in still water of larval morphologies with skeleton volumes ranging from 1 to 9% of the total body volume swimming. Vertical velocities are reported as the median (gray line) for 128 runs for each morphology, each started at a random initial orientation. In this and succeeding figures, the area between the 10th and 90th percentiles is shaded gray. Variability in velocity, when present, results from larvae tumbling and/or having multiple stable orientations. The morphology marked with a star corresponds to measurements of real larvae
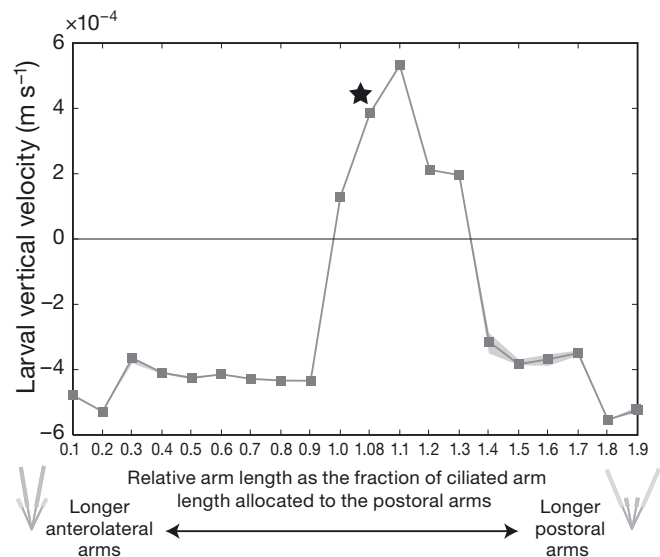

Fig. 3. Model results for the vertical velocity in still water of larval morphologies with relative arm lengths ranging from 0.1 to 1.9. Details are as described for Fig. 2

(Fig. 5). In vertical shear, increased body skeleton volume increased the range of shears in which larvae moved vertically upward, due to increased horizontal movement toward upwelling water. However, when failure to swim upward did occur, larvae moved downward at increasing velocities with increases in body skeleton volume. In horizontal shears, larvae with higher body skeleton volumes moved upward at a greater range of shears, while larvae with lower body skeleton volumes had higher maximum upward velocities.
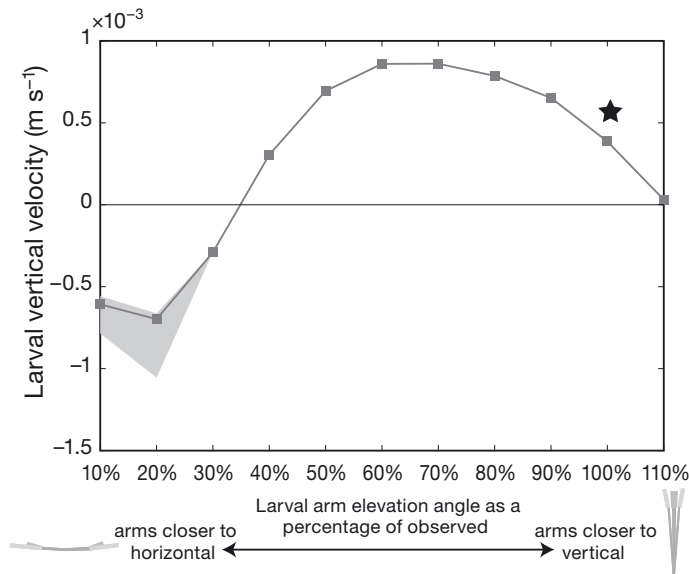
Fig. 4. Model results for the vertical velocity in still water of larval morphologies with arm elevation angles ranging from 10% to 110% of that observed in real larvae. Details are as described for Fig. 2

Swimming performance in shear: relative arm length

Larval morphologies with relative arm lengths near 1.0 swam up faster in low horizontal and vertical shears, while most morphologies with large or small relative arm lengths had greater net vertical velocities in high shears (Fig. 6). The exception to this pattern was that larvae with extremely long postoral arms had downward velocities in high horizontal shear. In both vertical and horizontal shear, the same morphologies (those with much longer postoral arms) had both the highest and lowest velocities, reflecting a strong and persistent dependence upon initial orientation.

Swimming performance in shear: arm elevation angle

In vertical shear, morphologies with low arm elevation angles moved upward only at low shear, and moved rapidly downward as shear intensified (Fig. 7). When morphologies failed to swim upward, they moved downward at increasingly greater velocities as the arms became more horizontal. In horizontal shear, morphologies with low arm elevation morphologies moved upward at most shears, but when arm elevation angles decreased to 10% of observed, these morphologies had rapid downward movement at low and moderate shears. Morphologies with intermediate arm elevation angles moved downward at nearly all shear levels, with downward speed decreasing at higher arm elevation angles. The 2 morphologies with the highest

modeled arm elevation angles (100% and 110%) moved upward over the widest range of vertical shears. Low arm-elevation angle morphologies had the greatest upward movement at higher horizontal shears, while medium arm-elevation angles had the greatest upward velocities at low shears. High arm-elevation angles had consistently low, predominantly upward velocities in horizontal shear.

DISCUSSION

Many evolutionary mechanisms constrain larval morphology, and the relative functional importance of these mechanisms is rarely understood. Because swimming performance appears to have strong direct and indirect implications for larval ecology, we hypothesized that swimming performance is a dominant factor driving the evolution of larval morphology. We used a hydrodynamic model of sand dollar larval swimming in still water and shear flows to test an implication of this hypothesis, namely that larvae are at or near a morphological optimum, and that shifts from observed morphologies will result in decreased swimming performance. The results of our swimming analysis suggest upswimming and related performance measures exert different selective pressures on morphologies in still water than in shear. Observed larval morphologies appear to represent a reasonable compromise between the differing requirements for swimming in still and moving water.

Larval swimming in small-scale flow can change ambient conditions

We chose larval upward swimming velocity as our primary performance metric because relatively small changes in vertical position in the water column can lead to dramatic changes in ambient conditions. We hypothesized that maximized upwards swimming is advantageous because it maximizes control over water column position.

Our results highlight the potentially disproportionate consequences of relatively small larval horizontal swimming velocities in flows that contain vertical shears (horizontal gradients in vertical velocities). Net vertical movement of larvae in vertical shear followed trends of horizontal movement in vertical shear for each morphological parameter examined. Net vertical velocity in vertical shear was consistently 2 to 3 orders of magnitude larger than velocity components resulting solely from larval swimming (horizontal velocity in vertical shear and vertical velocity in horizontal shear).
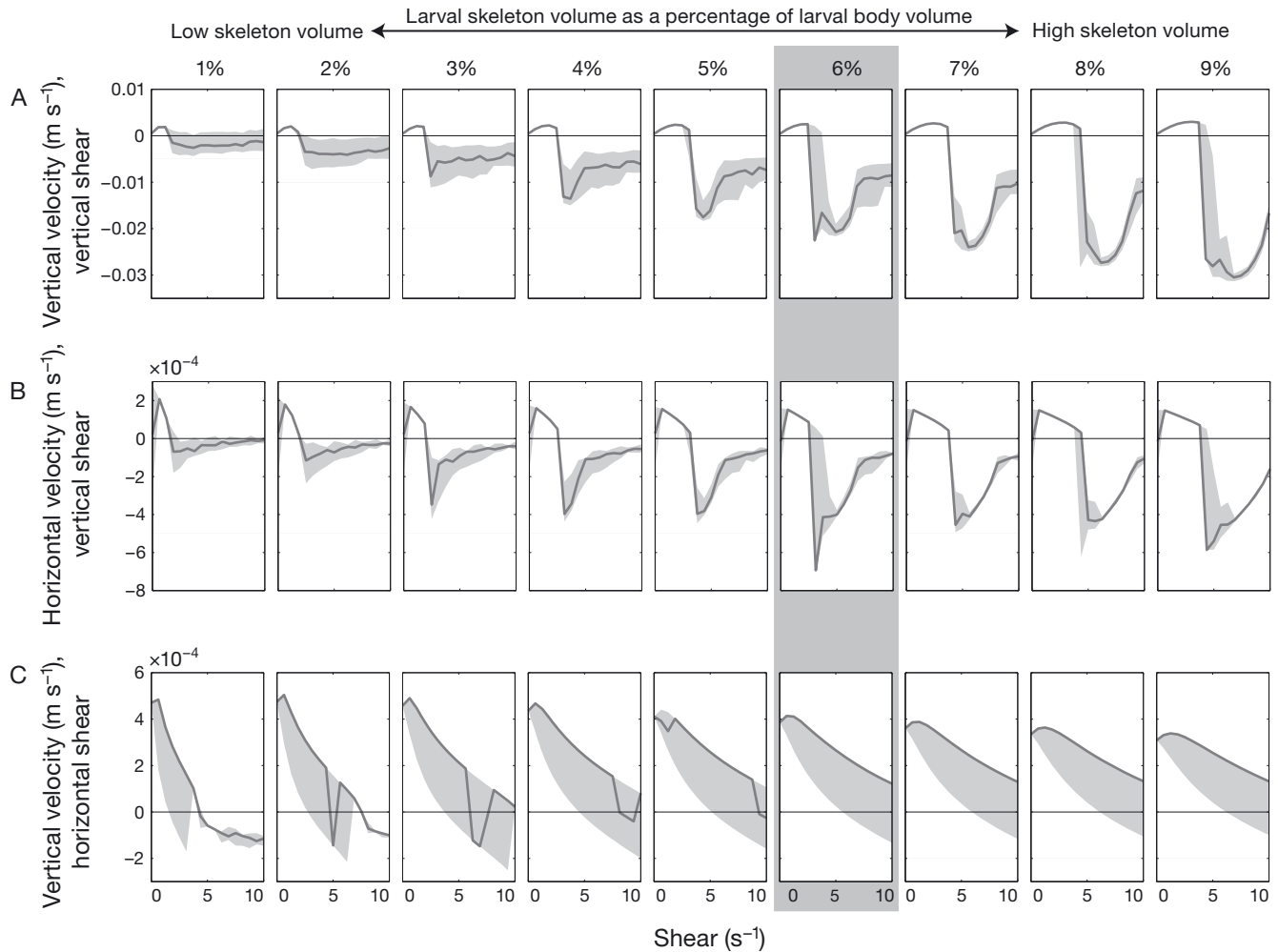
Fig. 5. Model results for swimming velocities in shear flow of larval morphologies with skeleton volumes ranging from 1% to 9% of the total body volume. (A) Larval vertical velocity in vertical shear; (B) larval horizontal velocity in vertical shear; (C) larval vertical velocity in horizontal shear. Each row shows median larval velocity (dark gray line) for 128 runs for each morphology at each of 16 shear levels ranging from 0 to 10 s^{-1}, each started at a random initial orientation. In this and succeeding figures, the area between the 10th and 90th percentiles is shaded gray. Variability in velocity, when present, results from larvae tumbling and/or having multiple stable orientations

Morphological shifts from observed parameters compromise swimming performance

According to the model, larvae have strong swimming performance-driven reasons to avoid morphological extremes in skeleton volume. Small volumes had fast swimming velocities and slow sinking speeds in still water, but low stability in shear. Large volumes had greater stability, but when loss of stability occurred, larger volumes led to increased downward velocities. For larvae that must function effectively in both still water and shear, the observed body volume appears to be at or near an optimum in swimming performance. The volume of larval skeleton likely has functional consequences other than swimming performance, such as the metabolic cost of acquiring and maintaining calcite. The values found in real larvae are consistent with a dominant evolutionary role for swimming performance in shaping this morphological feature.

In the case of arm length distribution, the morphology of real larvae was similar to those that maximize upward movement in low shear. Larvae with more extreme asymmetry in arm length had stable orientations with rapid upward velocities in flow, but tumbled in the absence of stabilizing flow. Morphologies with more symmetrical arm lengths lacked stability and tumbled in vertical shear. The strong performance of the observed larval morphology in low shear is consistent with the hypothesis that swimming performance in still water and at low shears has the greatest selective importance. This may be because larvae spend
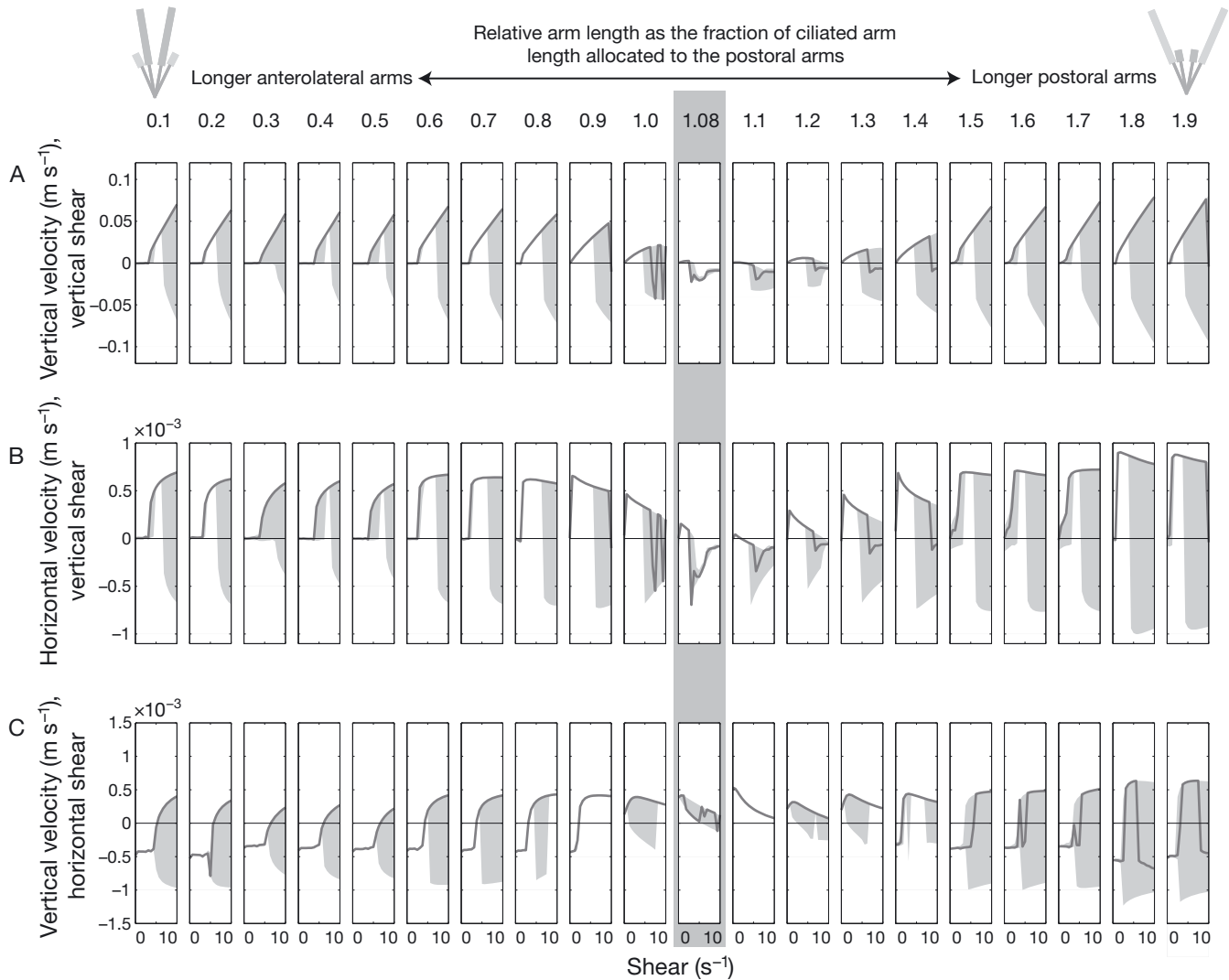
Fig. 6. Model results for swimming velocities in shear flow of larval morphologies with relative arm lengths ranging from 0.1 to 1.9. (A) Larval vertical velocity in vertical shear; (B) larval horizontal velocity in vertical shear, (C) larval vertical velocity in horizontal shear. Details are as described for Fig. 5

significantly more time in these flow conditions than in high flow conditions, or because larval swimming is relatively less important in vigorous, high-shear ambient flows.

Of the parameters examined, arm elevation angle had the most complex effect on larval vertical velocity. Arm elevation angle affected the torque exerted on a larva in flow. Larvae with higher arm angles experienced greater torque in horizontal shear, and larvae with lower arm angles experienced greater torque in vertical shear. Changes to arm elevation angle also affected larval stability by causing changes in larval body shape, which altered the centers of buoyancy and gravity. Because our model held body volume to the observed value, larvae with higher arm elevation angles had longer, narrower bodies. This conferred

greater stability, by increasing separation between the centers of buoyancy and gravity. Overall, only morphologies with arm elevation angles as observed or slightly greater than observed performed well in terms of upswimming in both still and shear flow conditions. As with the other 2 morphological families, the observed morphology was consistent with those predicted by our model to maximize swimming performance across variability in flow conditions.

While these model results suggest a somewhat complicated functional relationship between larval morphology and swimming performance, observed morphologies of 4-armed *Dendraster excentricus* larvae are consistent with those predicted by our model to maximize swimming performance. This consistency supports the hypothesis that these larvae are at or near
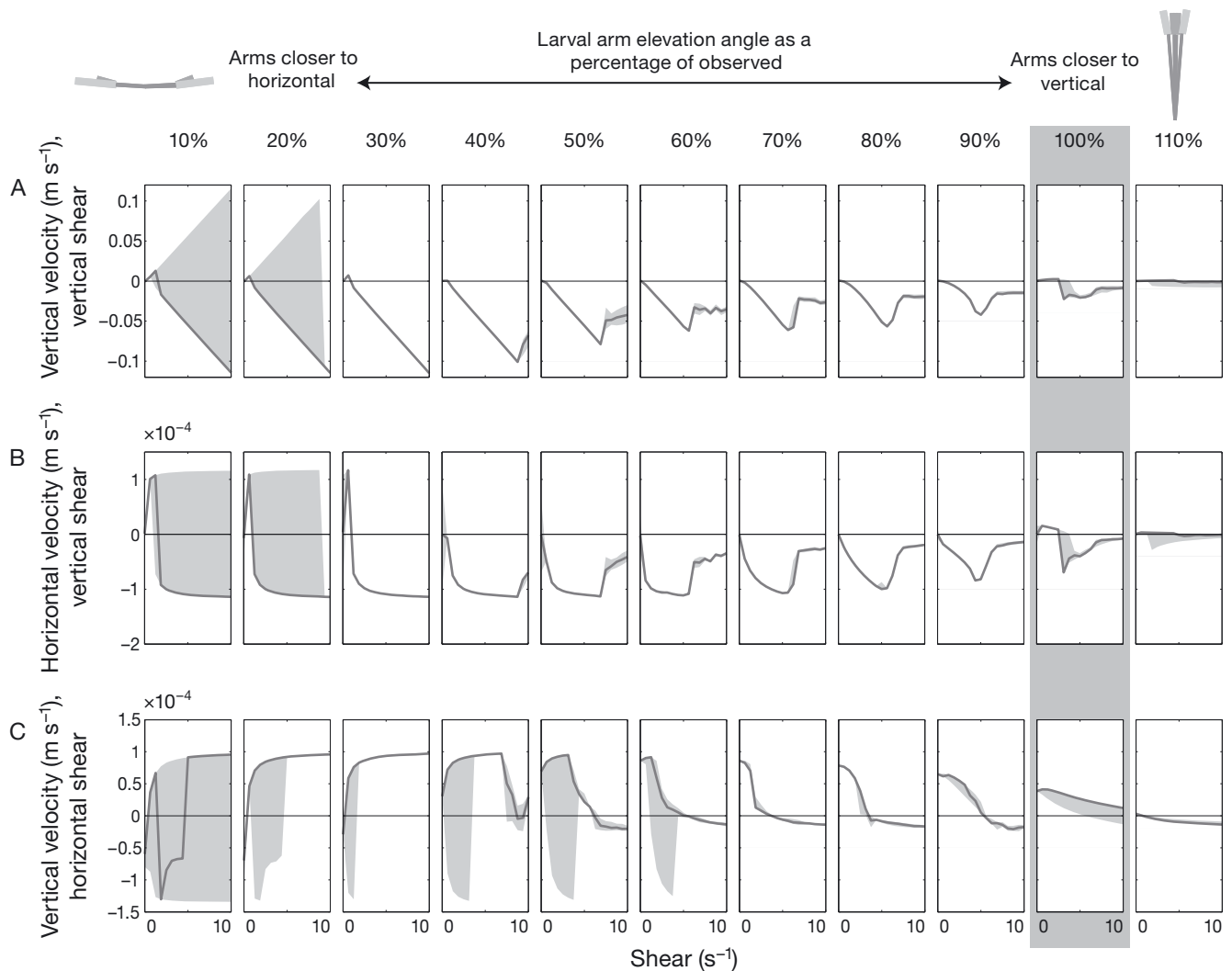
Fig. 7. Model results for swimming velocities in shear flow of larval morphologies with arm elevation angles ranging from 10% to 110% of that observed in real larvae. (A) Larval vertical velocity in vertical shear; (B) larval horizontal velocity in vertical shear; (C) larval vertical velocity in horizontal shear. Details are as described for Fig. 5

a local maximum in swimming performance as a function of morphological characteristics. Our hypothesis is only partially supported when considering swimming performance in any single flow condition. Support for the hypothesis and insights into selective pressures constraining larval morphologies are made clear only in the combined context of still and moving flow conditions. According to our model results, each morphological parameter we examined appears to be specifically adapted in real *D. excentricus* larvae to balance ability to move upward with avoidance of rapid downward movement across the expected range of flow conditions.

Our results suggest that larval morphologies have evolved to perform well, or at least not fail badly, in a mixture of flow regimes. In environments where the relative frequency of flow regimes differs from the coastal environments we considered, the overall evolutionary optima may also differ. For example, in the deep sea, where strong turbulence and associated shears may be relatively rare, larvae may evolve morphologies that more closely reflect performance in still or slow-moving water, sacrificing an ability to cope with more vigorous water motion.

Broader perspectives

If, as our results suggest, small changes to larval morphology have significant functional consequences, what can we conclude about constraints on larval development? In general, larval morphology likely re-

flects not only functional but also developmental constraints. Larval *Dendraster excentricus* have fenestrated spicules in their postoral arms, but simple spicules in their anterolateral arms. These 2 spicule types differ structurally: fenestrated spicules contain twice as much skeletal material per unit length (Emlet 1982). Despite the differences in spicules, these arm pairs grow at nearly the same rate, maintaining a slight asymmetry in length between arm pairs throughout development (Clay & Grünbaum 2010). Our results indicate that there likely are functional consequences to slight changes in relative arm lengths in terms of swimming performance. A functional constraint that relative arm lengths remain close to 1.0, despite differences in the amount of skeletal material required to lengthen distinct types of arms, suggests that larvae have complex regulatory machinery for spicule construction.

The developmental and functional constraints of this skeleton arrangement are currently unclear. The inclusion of both fenestrated and simple spicules appears to be an ancestral condition (Wray 1992). However, it is unclear how such complex skeleton-building machinery might impose developmental constraints on larval morphology, and over what time scales. Emlet (1983) tested the hypothesis that fenestrated spicules may provide required structural support for larval swimming, but found the presence of fenestrated spicules to be an unlikely requirement for swimming. As an alternate hypothesis, Emlet proposed that fenestrated spicules provide defensive benefits, but this hypothesis has not yet been tested. Our results suggest a third hypothesis, namely that the inclusion of both spicule types is maintained because changes to the spicule types, in the absence of other major adjustments to arm geometry and position, would have prohibitive negative consequences for swimming performance.

Our results indicate that changing single morphological parameters has strong, generally negative consequences for larval swimming performance. Nonetheless, larvae do exhibit substantial morphological variability across taxonomic groups, across stages within species, and even among closely related individuals reared under different environmental conditions (McEdward 1984, Hart & Strathmann 1994, McEdward & Herrera 1999, Young et al. 2002, Miner 2005, 2007). This variability suggests that diverse morphological parameters, such as arm number, arm size, arm orientation, and distributions of skeleton, tissue, and ciliary band are tightly regulated so that they co-vary in specific ways that preserve swimming function. If so, developmental constraints on one morphological parameter could functionally constrain multiple, biomechanically linked morphological parameters.

Global climate change is predicted to have potentially significant sub-lethal effects on larval morphology. For example, pluteus larvae have altered morphologies in response to the increases in ocean acidity predicted by the Intergovernmental Panel on Climate Change (Kurihara et al. 2004, Kurihara & Shirayama 2004, Dupont et al. 2008, O'Donnell et al. 2010). The functional consequences of these morphological shifts are as yet unknown. However, the results presented here suggest that altered swimming performance is likely to be one such consequence. Our results indicate that larval swimming performance is sensitive to changes in larval morphology, and suggest that existing larval morphologies have been selected for larval swimming performance. Global climate change — and the consequent morphological changes — are predicted to occur on time scales shorter than the time scales over which these larval morphologies have evolved. An important but currently unanswered question is whether the complex regulatory mechanisms that orchestrate larval growth and development within functional constraints such as swimming performance can evolve on correspondingly rapid time scales. If not, altered swimming performance may cause large changes to both larval and adult population dynamics. Understanding and predicting such functional changes in larval biology may have important benefits for responsible management of sensitive species in changing environmental conditions.

Areas of future research

The modeling approach used here can be readily expanded to address many related questions about the relationship between larval morphology and larval swimming performance in still water, and shear and turbulent flows. We are currently expanding the model to examine larval swimming performance in turbulence. This will allow better understanding of how model predictions and experimental observations of larval swimming in shear flows translate to more complex turbulent flows.

An interesting expansion of the work presented here would be to perform similar investigations using different baseline morphologies. This would allow for comparisons between taxa, between larvae that share a basic larval form (such as the pluteus larvae), between stages within a given species, and between morphologies that vary with environmental conditions. Expanded model results would allow for more generalized predictions about which morphological parameters co-vary to maintain swimming performance, and which morphologies reflect compromises between swimming performance and other evolutionary pressures. It may become possible to predict a space of morphologies that are functional in terms of swimming

performance for various flow conditions. These predictions could be tested against existent morphologies, including those typically found in calm versus more energetic flow conditions.

A good first step would be to conduct a similar experiment to the one presented here, but on later-staged larvae that have muscular control over arm position. The model predictions of favorable morphologies in terms of upswimming in various levels of shear could then be compared against observations of the arm angles assumed by larvae swimming in various levels of shear.

One simplification in the model used here is the assumption of bilateral symmetry within arm pairs. Pluteus larvae have been observed to have asymmetries in the arm lengths within a pair (Collin 1997, Emlet 2009). The consequences of this asymmetry on larval swimming are not yet described, but preliminary results suggest that arm-length asymmetries in larval *Dendraster excentricus* may cause larvae to swim in spirals. In low shear flows, 4-, 6-, and 8-armed *D. excentricus* larvae have been qualitatively observed to swim in spirals, possibly mitigating the effects of shear on larval movement trajectories (Clay & Grünbaum 2010). We are currently investigating how length asymmetries within arm-pairs affect model predictions for larval swimming performance in shear flow.

The results presented here raise interesting questions about which morphological parameters co-vary, and how this co-variation is regulated at the developmental level. A useful approach to addressing these questions would be to develop hypotheses that are based on gene regulatory networks, and that are informed by swimming biomechanics. One such hypothesis is that morphological features which share developmental regulatory mechanisms are bound up in specific geometrical relationships (like the relative lengths of larval arms) that must be preserved to maintain swimming performance. A complementary hypothesis is that geometrical relationships are maintained because the underlying morphological features have common regulatory systems. If so, larval morphology may be functionally more robust in the face of developmental perturbations than either biomechanics or morphometrics alone would suggest.

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