

## RESEARCH ARTICLE

# Streamlining behaviour of the red urchin *Strongylocentrotus franciscanus* in response to flow

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### SUMMARY

This work was motivated by subtidal observations of red urchins (*Strongylocentrotus franciscanus*) moving their spines into streamlined positions as water current increased in the field. Trials in a flume across flow speeds from 0 to 65 cm s<sup>-1</sup> enabled us to observe the change in overall shape of the urchins and quantify the decrease in spine angle that occurred as flow speeds increased. The effect of this behaviour on drag and lift was measured with physical models made from urchin tests with spines in the 'up' position (typical in stagnant and slow velocities) and in the 'down' position (typical of posture in high velocities). Streamlining spines decreased the drag, but increased the lift experienced by urchin models at flow speeds between 10 and 40 cm s<sup>-1</sup>, current velocities that are commonly encountered by these animals in the field in Washington, USA. Total force (combination of drag and lift) was similar for 'up' and 'down' models at all flow speeds, lift comprising the majority of the force for 'down' models, and drag slightly higher for 'up' models. Live urchins in the field routinely adopt a streamlined 'down' posture in flow, suggesting that they may be better able to cope with lift than drag. This behaviour, although affecting hydrodynamic forces and enabling *S. franciscanus* to remain attached to the substratum in high currents, may lead to reduced capture of drift kelp, which is entrapped on upright spines and then eaten, delivery of which is positively related to flow speed. Urchins living in deep subtidal habitats rely on drift kelp capture but must stay attached to the substratum to be successful in a habitat. Therefore, this streamlining behaviour may be an important factor enabling *S. franciscanus* to persist in deep, high-current areas.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/214/16/2655/DC1>

Key words: sea urchin, streamlining, behaviour, drag, lift, hydrodynamic force, current, kelp.

### INTRODUCTION

The physical environment that organisms experience in natural habitats is temporally variable on multiple time scales. Animals and plants have evolved a variety of mechanisms to cope with this temporal variability. In marine ecosystems, hydrodynamic forces generated by currents and waves can vary in strength over a range of time intervals (seconds to minutes to hours) and marine organisms must be capable of dealing with these fluctuations. Common strategies include streamlined shapes, flexible morphologies that are easily deformed, high strength to withstand forces, and behavioural adaptations (e.g. Koehl, 1984; Denny, 1987; Vogel, 1994; Siddon and Witman, 2003). Each approach has its costs and benefits, and understanding these tradeoffs can provide insight into the physical processes that are most relevant to the success of a particular species, and help us understand the mechanisms underlying species distributions (Wainwright et al., 1976; Denny et al., 1985).

The red sea urchin *Strongylocentrotus franciscanus* (Agassiz 1863) lives intertidally and subtidally on rocky shores of North America from Alaska, USA, to Baja, Mexico, across a depth range from one to several hundred metres (Morris et al., 1980). This urchin is an omnivore that primarily feeds on seaweeds, especially in shallow environments where attached algae are present. However, urchins living deeper than the photic zone (where attached algae are absent) rely primarily on delivery of detached drift macroalgae (Britton-Simmons et al., 2009). Algal drift caught on upright urchin spines is tasted with the urchin's tube feet and, if desirable, moved

to the underside side of the animal and devoured using jaws located on the oral side of the animal. Water motion is therefore an important component of algal drift delivery, but the hydrodynamic forces exerted by moving water present the challenge of remaining attached to the substratum. Urchins remain attached to the substratum *via* adhesion of many small tube feet. A typical urchin pincushion shape is not a particularly streamlined shape, and hydrodynamic forces can overcome their tenacity and detach them from the substratum (Denny and Gaylord, 1996); natural flow conditions do dictate urchin spatial distribution (Siddon and Witman, 2003). For an urchin, detachment can result in physical damage of spines, exposure of its vulnerable underside surface to potential mobile predators (e.g. fish) and capture by sessile predators (e.g. anemones) that they may encounter if detached by the current. Juvenile *S. franciscanus* have been reported to aggregate under adult conspecifics, a behaviour that confers protection from predators and may also function to shelter them against hydrodynamic forces (Nishizaki and Ackerman, 2007).

A steady unidirectional current exerts the hydrodynamic forces drag and lift on an urchin. Drag is caused by the difference in pressure between the upstream and downstream sides of the animal and works in a direction parallel to the direction of flow. Lift is created by a drop in pressure as flow velocity increases as water passes up and over an urchin, creating a force perpendicular to the direction of flow. Drag and lift are proportional to the square of water velocity and to the area of the organism projecting in the direction of the force. The

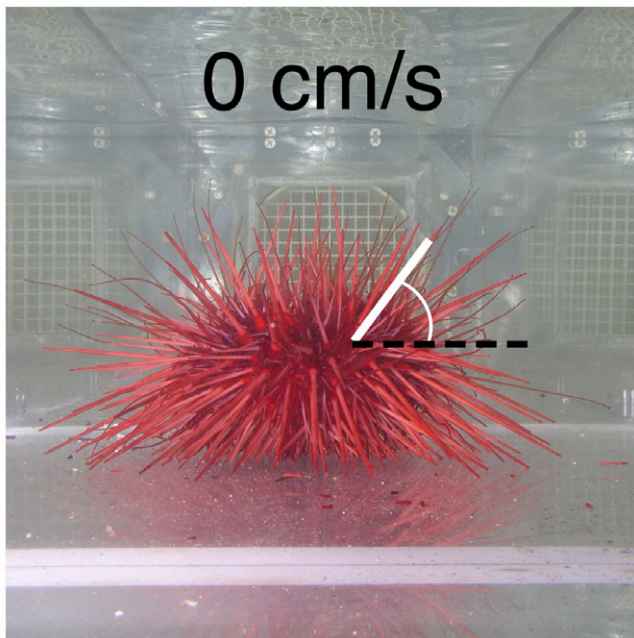
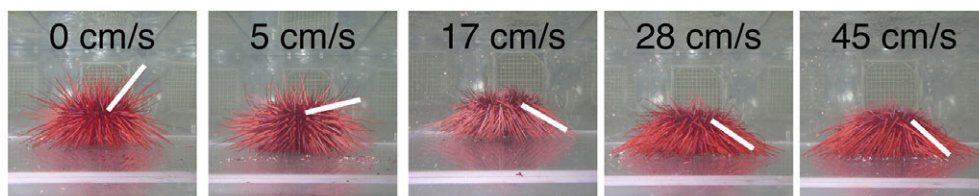


Fig. 1. Spine angle was measured from the horizontal (0 deg; dashed line) for spines in the top right quadrant of live *Strongylocentrotus franciscanus* responding to flow in the flume (white line).



total force experienced by an urchin in steady flow is a combination of lift and drag and works in a direction between parallel and perpendicular, depending on the strength of each.

This work was motivated by subtidal observations of *S. franciscanus* moving into streamlined postures as flow speed increased in the field in the San Juan Islands, WA, USA (see supplementary material Movie 1 for video of urchin streamlining behaviour in the field). This area is characterized by strong tidal currents that move water in and out of the Juan de Fuca Strait and create unpredictable flow dynamics around the many islands in the area. Flow is generally unidirectional (changing direction with the tide  $4\times$  per 24h), and can increase velocity significantly over a few minutes or even tens of seconds, from stagnant flow to speeds in excess of  $1\text{ m s}^{-1}$  (Eckman et al., 2003; Britton-Simmons et al., 2008). This streamlined posture is a previously unreported behaviour by any species of sea urchin. This work addressed two questions: (1) do red urchins predictably change their spine orientation in response to increased water flow; and (2) does this behaviour affect the hydrodynamic forces (drag and lift) experienced by an urchin?

## MATERIALS AND METHODS

### Field observations

Observations of streamlining behaviour in *S. franciscanus* in response to flow in the field were made at subtidal sites between 20 and 30m depth near Friday Harbor Laboratories on San Juan Island, WA, USA ( $48^{\circ}32'39.92''\text{N}$ ,  $123^{\circ}00'39.60''\text{W}$ ).

### Posture and spine angle of urchins in flow tank

Urchins were collected from subtidal field sites and held overnight in aquaria with running seawater. Eight urchins of similar size (9.1–10.6cm test diameter) were selected for flume trials. Each

urchin was placed in the centre of the flume under a weighted wire retainer to let it acclimate and keep it from moving too far from the centre of the flume. After 30 min, the retainer was removed and flow in the flume was adjusted from 0 to  $63\text{ cm s}^{-1}$  in 12 increments (0, 1, 5, 11, 14, 17, 19, 23, 28, 40, 45,  $63\text{ cm s}^{-1}$ ). After 2 min at each flow speed, a head-on photo of the urchin was taken from upstream in the flume using an underwater camera (Xacti, Sanyo, San Diego, CA, USA). Simultaneous video of the side view of the urchin was also taken at each flow speed from outside the flume through the clear Plexiglas<sup>®</sup> wall, using a video camera (Handicam, Sony, New York, NY, USA). Head-on pictures of each urchin were taken from upstream in the flume. This allowed us to get enough distance from the urchin to photograph the entire individual, without having to deal with any air/water/Plexiglas<sup>®</sup> distortion as would have been the case if we attempted to use photos from the side, which would have had to be taken from outside the flume. The response of spines was similar all the way around the urchin.

The angle of spines from the top quadrant of each urchin (Fig. 1) was analyzed from the upstream photos to quantify the position of spines at each flow speed using Image J software (NIH, Bethesda, MD, USA). Only pictures in which the urchin was in the centre of the flume were used, as proximity to either sidewall affected the behaviour and posture of the urchin. Spine angle was only calculated for spines that were projecting sideways, and were therefore moving relatively perpendicular to the plane of the photograph, and minimized the effect of azimuth.

### Drag and lift of urchin models

Urchin models were made from the tests and spines of real urchins from our field sites. Four models of posture ('up' and 'down') were constructed from similar sized (9.1–10.6cm test diameter)



Fig. 2. Example urchin models in the spine 'up' posture (left) and the spine 'down' posture (right).

urchins collected from our field sites. Each model was made by first removing the Aristotle's lantern, internal organs and soft tissue from the inside of the urchin. The spines remained attached during this process and were positioned into 'up' or 'down' postures that represent the two extremes of the range of spine orientations observed in the flume trials using live animals (Fig. 2). Models were then dried and coated with one layer of BullsEye Shellac (Zinsser, Northridge, CA, USA) followed by two coats of 1015 Captain's varnish (Kop-Coat Inc., Pittsburg, PA, USA). Urchin models were allowed to dry completely between applications. To attach the models to the force transducer, the head of a bolt was embedded in the centre of a short length of PVC using Z-Spar splash zone epoxy (Z-Spar Coatings, St Louis, MO, USA) so that the threaded end of the bolt extended beyond the end of the PVC pipe. Once the epoxy had cured the PVC end of this device was inserted into the peristomial opening of the urchin test and secured to the top inside surface of the test using Z-Spar. The PVC/bolt devices were custom made for each model so that the head of the bolt was in the vertical centre of the urchin. Models were attached to a force transducer by the bolt on a false bottom that was suspended just below the water's surface in a flow tank (i.e. urchins models were upside down in the tank). Models were positioned as close as possible (<5 mm) to the false bottom without touching it. Lateral displacement (drag) and vertical displacement (lift) were recorded simultaneously from deflection of the sting of a two-axis force transducer on LabVIEW 2009 National Instruments Version 9 (32 bit), using a National Instruments USB-6009 data acquisition device (Austin, TX, USA).

The force transducer was calibrated from voltage by hanging weights from the sting of the transducer from the same position as the centre of the models in lateral and vertical direction, and converted using the equation:

$$F = ma, \tag{1}$$

where  $F$  is force,  $m$  is mass and  $a$  is acceleration due to gravity ( $9.8\text{ms}^{-1}$ ).

To normalize for size, drag ( $D$ ) and lift ( $L$ ) were converted to coefficients using:

$$C_d = \frac{2D}{\rho v^2 A} \tag{2}$$

and

$$C_l = \frac{2L}{\rho v^2 A}, \tag{3}$$

where  $C_d$  is the drag coefficient and  $C_l$  is the lift coefficient,  $\rho$  is the density of the water ( $\text{kgm}^{-3}$ ),  $v$  is the water velocity ( $\text{ms}^{-1}$ ),  $A$  is the two-dimensional area of the urchin in a plane perpendicular to the flow and  $A_p$  is the plan form, or the area of the urchin as viewed from directly above.

Total force was calculated as:

$$F_{\text{dt}} = \sqrt{(0.5\rho v^2 C_d A)^2 + (0.5\rho v^2 C_l A)^2}. \tag{4}$$

## RESULTS

### Spine angle

Urchins consistently assumed a streamlined position and reduced the angle of their spines at higher flow speeds in the flume (ANOVA,  $F=46.36$ ,  $\text{d.f.}=11$ ,  $P<0.01$ ; Fig. 3).

### Force

Streamlined urchin models ('down' position) experienced a significant reduction in drag (up to one-third) (ANOVA, spine position  $\times$  flow,  $F=48.01$ ,  $\text{d.f.}=11$ ,  $P<0.01$ ; Fig. 4A), but an increase in lift (up to 2 $\times$ ) relative to models with spines in the 'up' (non-streamlined) position over much of the range of flows they were exposed to in the flume (ANOVA, flow,  $F=5.56$ ,  $\text{d.f.}=11$ ,  $P<0.01$ ;

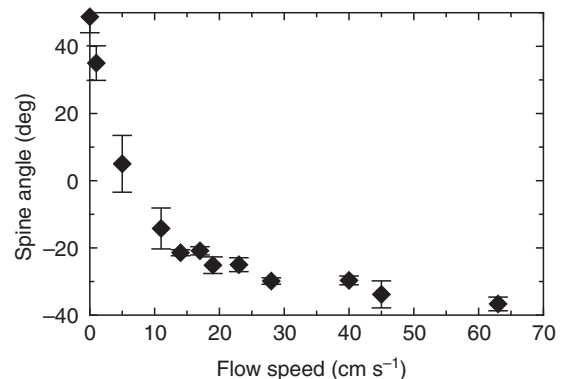


Fig. 3. Spine angle of live *S. franciscanus* across flow speeds in the flume (mean  $\pm$  s.e.m.,  $N=5$ ).

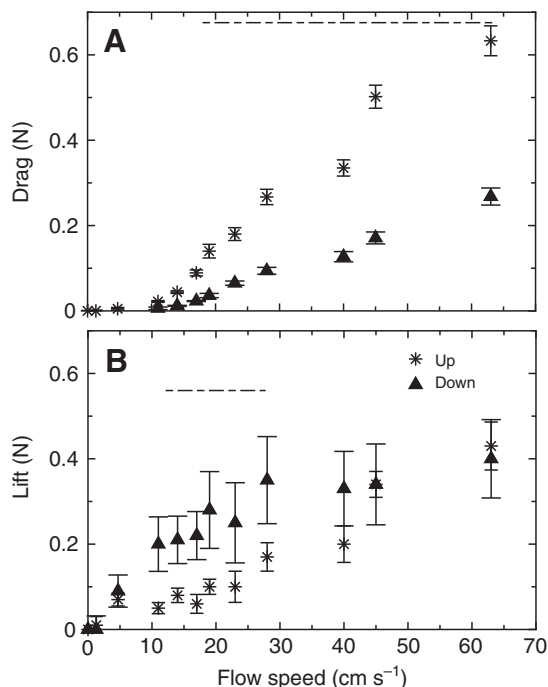


Fig. 4. (A) Drag and (B) lift on urchin models in the spine 'up' ( $\Omega$ ) and spine 'down' ( $\sigma$ ) postures across flow speeds in the flume (mean  $\pm$  s.e.m.,  $N=4$ ). Dashed line indicates values that are significantly different between spine 'up' and spine 'down' models at the same flow speed, as determined by *post hoc* least squares means pairwise comparisons.

Fig. 4B). The largest differences in lift occurred at flow speeds between 10 and 28  $\text{cm s}^{-1}$ . At higher flow speeds, lift was the same for 'up' and 'down' models, whereas differences in drag began at 10  $\text{cm s}^{-1}$  and increased with increasing flow speed, and were maximal at the highest flow speed, 63  $\text{cm s}^{-1}$  (Fig. 4A,B).

However, total force was similar between 'up' and 'down' models at all but the highest two flow speeds, when total force was higher on 'up' models (ANOVA, flow,  $F=16.11$ , d.f.=11,  $P<0.01$ ; Fig. 5).

$C_d$  was lower for 'down' models than for 'up' urchin models at almost all flow speeds (ANOVA, spine position  $\times$  flow,  $F=3.85$ , d.f.=11,  $P<0.01$ ; Fig. 6A).  $C_L$  was similar between 'up' and 'down' models at most flow speeds, but was higher for 'up' models at flow speeds from 4 to 11  $\text{cm s}^{-1}$  (ANOVA, flow,  $F=3.06$ , d.f.=11,  $P<0.01$ ; Fig. 6B).

## DISCUSSION

Streamlining of spines changes the overall shape of an urchin from a typical 'pincushion' urchin shape to a shape more like a limpet; an effectively streamlined form (Warburton, 1976). We have observed in the field and documented in the laboratory that this is a predictable, common behaviour for *S. franciscanus* from deep subtidal habitats in this area. This is, to our knowledge, the first record of this streamlining behaviour of *S. franciscanus*. Our laboratory experiment with live animals showed that this behaviour is predictable; it was exhibited by every individual we tested. Streamlining by urchins was most dramatic between flow speeds of 1 and 10  $\text{cm s}^{-1}$ , and continued to increase at higher flow speeds (Fig. 3). However, we have only observed this behaviour in the field during periods of strong and rapidly fluctuating currents, conditions that are usually avoided by divers, which probably explains why it has not been previously reported.

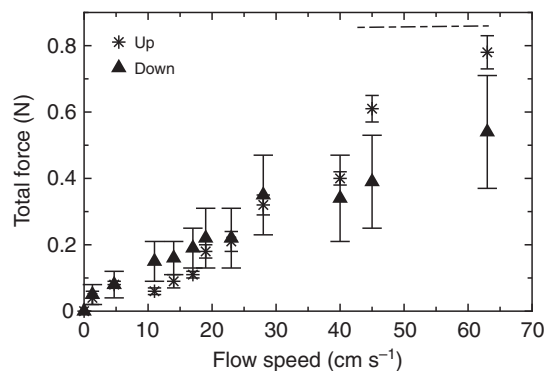


Fig. 5. Total force experienced by urchin models in the spine 'up' ( $\Omega$ ) and spine 'down' ( $\sigma$ ) postures across flow speeds in the flume (mean  $\pm$  s.e.m.,  $N=4$ ). Dashed line indicates values that are significantly different between spine 'up' and spine 'down' models at the same flow speed, as determined by *post hoc* least squares means pairwise comparisons.

Total force on the models was similar for spine 'up' (low velocity posture) and spine 'down' (high velocity posture) models, although the composition of the force was not the same. 'Up' models experienced primarily drag and 'down' models experienced primarily lift. Streamlining behaviour is a predictable behaviour in response to increasing flow speed, suggesting that red urchins may have an easier time dealing with lift forces than drag forces. Indeed, we have found during our collections of red urchins in the field that pulling an urchin in a direction perpendicular to the substrate is extremely difficult and sometimes results in catastrophic test damage wherein the oral surface actually separates from the rest of the test. In contrast, sliding the animal horizontally to break their attachment is relatively easy and never causes test damage. Although we did not measure urchin tenacity in the present study, and such studies are sparse in the literature (but see Santos and Flammang, 2005), studies of limpet tenacity (with general overall shape similar to a streamlined *S. franciscanus* but different modes of attachment – many tube feet for urchins, one big sucker-like foot in limpets) found that limpets were able to generate substantial adherence tenacity against a vertical lift force, but are relatively weak in resisting horizontal shear forces, those created by drag (Warburton, 1976; Denny, 1987) [but see Denny and Blanchette (Denny and Blanchette, 2000) for an example of a limpet with similar resistance to both lift and drag].

Several previous studies have investigated the force experienced by different species of urchins (e.g. Denny and Gaylord, 1996; Nishizaki and Ackerman, 2007). In each case, however, the overall shape of the urchin is assumed to be static, and distribution limitations were inferred from these assumed typical shapes. For example, Denny and Gaylord compared the hydrodynamic forces in three species of urchin, two of conventional urchin morphology (*Echinometra mathaei* and *Strongylocentrotus purpuratus*) and a third (*Colobocentrotus atratus*) in which the aboral surface spines are much reduced, yielding an overall shape similar to the streamlined posture of *S. franciscanus* (Denny and Gaylord, 1996). *Colobocentrotus atratus* lives in wave-swept intertidal habitats and its shape increases the lift it experiences in high-energy flow situations (Denny and Gaylord, 1996). The urchin in the present study, *S. franciscanus*, lives in subtidal habitats that experience strong, tidally generated currents that vary greatly in strength over minutes or even seconds. The streamlining behaviour described in this study decreases the drag these urchins experience in high

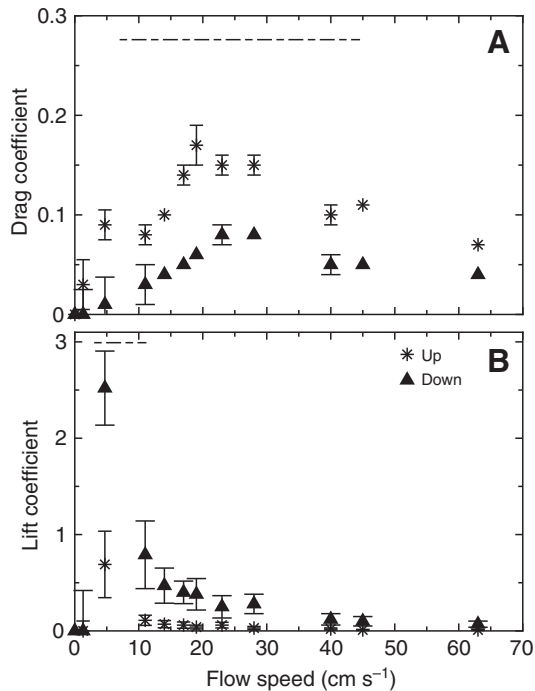


Fig. 6. (A) Drag and (B) lift coefficients for urchin models in the spine 'up' ( $\Omega$ ) and spine 'down' ( $\sigma$ ) positions across flow speeds in the flume (mean  $\pm$  s.e.m.,  $N=4$ ). Dashed line indicates values that are significantly different between spine 'up' and spine 'down' models at the same flow speed, as determined by *post hoc* least squares means pairwise comparisons.

velocities. However, these urchins cannot afford to adopt this shape permanently as they feed primarily on drift algae, which they entrap on upright spines (Duggins, 1981; Britton-Simmons et al., 2009). Upright spines also confer protection against predators. Dislodgement from the substratum is dangerous for urchins; if they are flipped over, this can lead to exposure of their unprotected oral surface to predators. Rolling around in the current can also damage spines and, with no way to control where they go, may lead to capture by predatory anemones and sea stars. However, evolving a permanent streamlined shape, such as the limpet-shaped intertidal urchin *C. atratus*, would likely reduce the ability of *S. franciscanus* to capture drift algae on upright spines. *Colobocentrotus atratus* is not similarly constrained because it lives in intertidal habitats where it grazes on attached, benthic algae.

Streamlining of spines by *S. franciscanus* represents a behavioural analog to the evolutionary solution of spine adaptation by *C. atratus* discussed in Denny and Gaylord (Denny and Gaylord, 1996). This behavioural mechanism allows *S. franciscanus* to meet the contrasting requirements of staying attached in variable, strong currents and capturing flow-delivered drift algae. Although it is likely that hydrodynamics is a major reason behind this behaviour, there may be other consequences. Although the much-touted hydrodynamic-force-reducing 'limpet shape' is relatively streamlined, limpets are often not optimally shaped from a hydrodynamic perspective (Denny, 2000). Other selective factors such as defending territories and reducing desiccation likely also drive limpet morphology (Denny and Blanchette, 2000). Subtleties of limpet shape are also affected by water motion, and can be more or less streamlined and resistant to wave impacts depending on their flow habitat (Moore, 1934; Durrant, 1975; Warburton, 1976). A key difference between limpets and urchins is

their mechanism of attachment. Limpets attach with a single muscular foot and can therefore adjust their attachment strength quickly. In contrast, sea urchin attachment is achieved by the collective action of many tiny tube feet. Tube foot tissue mechanics adjust to hydrodynamic conditions (Santos and Flammang, 2005); urchins exposed to higher flow may have higher tenacity than urchins in exposed habitats (Smith, 1988). The number and arrangement of tube feet also likely affect the ability of an urchin to stay attached in high flow. Increasing overall attachment strength is a relatively slow process for urchins because each tube foot must independently attach to the substratum, a process that is especially difficult during periods of strong current because tube feet get carried downstream by strong water flow. Thus, streamlining may be a short-term response to flow that reduces drag until the urchin can more firmly attach with its tube feet.

In summary, this streamlining behaviour is a common, predictable response to flow for *S. franciscanus* that enables this urchin to respond to the temporally variable currents it encounters in its habitat.

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