Contents lists available at ScienceDirect



Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Spine reorientation influences drift particle capture efficiency in sea urchins



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Matthew N. George *, Emily Carrington

Department of Biology and Friday Harbor Laboratories, University of Washington, 620 University Road, Friday Harbor, WA 98250, USA

ARTICLE INFO

ABSTRACT

Article history: Received 4 November 2013 Received in revised form 30 July 2014 Accepted 1 August 2014 Available online xxxx

Keywords: Strongylocentrotus Streamlining behavior Drag Kelp Urchin grazing Ecomechanics Many marine organisms use behavior to navigate hydrodynamic landscapes. The subtidal sea urchin *Strongylocentrotus franciscanus* reorients its spines as water velocity increases to reduce drag and remain attached to the substratum. Streamlining may be advantageous in this regard, but it is unclear how this change in drag profile will affect particle capture, a feeding strategy employed by these organisms. Streamlining in urchins results in a "spines down" posture while particle capture benefits from spines remaining erect, a difference that could potentially lead to decreased feeding rates in high water velocities. To investigate this we ran flow tank experiments with three species of urchin (*Strongylocentrotus droebachiensis, Strongylocentrotus franciscanus*, and *Strongylocentrotus purpuratus*) which differ in size and spine length. All urchins studied displayed some degree of streamlining, although the threshold water velocities. However, taking into account urchin size and the changes in particle flux at each water velocity. *S. purpuratus* was significantly more efficient at capturing particles with "spines up" — an advantage which disppeared once spines were lowered. These results show that size and spine orientation affect how particles interact with urchins in flow and imply that spine morphology plays a role in whether or not an individual adopts a streamlined posture.

Published by Elsevier B.V.

1. Introduction

Life in the subtidal zone is driven by water motion. Underwater currents interact with benthic topography to produce hydrodynamic forces that fluctuate in both time and space (Denny, 1987a). Hydrodynamic forces can remove individuals from the substratum (Denny, 1987b; Bell and Gosline, 1997; Blanchette, 1997), cause physical damage to those which remain attached (Shanks and Wright, 1986), and influence community structure (Leichter and Witman, 1997; Siddon and Witman, 2003). This challenge that marine organisms face influences their size (Gaylord et al., 1994; Blanchette, 1997; Denny, 1999), shape (Friedland and Denny, 1995; Koehl, 1996), and the performance of biomaterials (Denny and Gaylord, 2002; Boller and Carrington, 2007; Demes et al., 2011).

For suspension feeders, underwater currents present a trade-off. The movement of water makes suspension feeding possible by delivering suspended particles to the feeding structures of sessile organisms (Rubenstein and Koehl, 1977). However, as water velocity increases, drag and lift forces increase as water interacts with the shape and size of feeding structures (Denny et al., 1985). Mitigation of these forces requires that organisms living in high current areas employ

* Corresponding author. Tel.: +1 360 378 2165.

E-mail address: mngeorge@u.washington.edu (M.N. George).

morphological (Friedland and Denny, 1995; Carrington, 2002) and behavioral (Koehl, 1976; Maude and Williams, 1983) strategies to survive (Denny, 1994).

For sea urchins, water movement plays a fundamental role in their behavioral ecology. Inhabiting both the intertidal and subtidal, sea urchins are voracious, mobile herbivores, often credited with the destruction of the entire algal communities (Mann, 1977; Hagen, 1983). However, urchins move little when algal drift is abundant, take refuge in crevices, and lift their spines into currents to feed (Lawrence, 1975; Duggins, 1981; Harrold and Reed, 1985; Lowe et al., 2014). This behavioral switch in feeding mode increases the amount of drift algae present in the local environment (Vanderklift and Kendrick, 2005) and pulls nutrients out of the water column, feeding the individual, other urchin species, and the benthic invertebrate communities below them (Duggins, 1981; Nishizaki and Ackerman, 2004; Britton-Simmons et al., 2009; Kelly et al., 2012). As such, it has been hypothesized that this flux of carbon from photic zones may allow invertebrate communities to live in high current subtidal habitats where light levels are low (Bustamante et al., 1995; Vanderklift and Wernberg, 2008).

Recently it has been shown that *Strongylocentrotus franciscanus* (Agassiz, 1863) moves its spines into streamlined positions as water velocity increases to reduce drag forces and stay attached to the substratum (Stewart and Britton-Simmons, 2011). A form of streamlining, spine movement dynamically alters the urchin's drag coefficient and

cross-sectional area. This work compliments a previous study which compared the probability of dislodgment of three species of urchins with different spine morphologies (Denny and Gaylord, 1996). While these studies highlight that shape change can reduce dislodgement risk, it remains unclear how feeding performance is affected by spine posture. One possibility is, with spines up, particles are forced to flow through the gaps between spine rows, increasing the probability of encountering tube feet. Another possibility is, with spines down, urchins actually increase particle capture rate by reducing boundary layer thickness (Frechette et al., 1989).

In this study we investigate the effect of spine reorientation on particle capture using three species of sea urchin with different body sizes and spine morphologies. *S. franciscanus*, a relatively large, subtidal urchin, has long spines and readily adopts a streamlined posture in laboratory manipulation of water velocity (Stewart and Britton-Simmons, 2011). Other commonly occurring species that inhabit the subtidal and intertidal zones of the Pacific Northwest, *Strongylocentrotus purpuratus* (Stimpson, 1857) and *Strongylocentrotus droebachiensis* (Müller, 1776), are smaller by comparison, have different spine lengths, and have no previously recorded streamlining behavior. Using these three species in flow tank experiments, we ask whether spine morphology plays a role in streamlining behavior and what effect, if any, changes in spine posture have on particle capture.

2. Materials and methods

Three species of sea urchin (*S. droebachiensis*, *S. purpuratus*, and *S. franciscanus*) were collected from subtidal field sites near Friday Harbor Laboratories on San Juan Island, WA, USA (48°32′39.92″N, 123°00′39.60″W) and held in aquaria with flowing seawater. Urchins were kept at 10 °C for two weeks and were fed drift kelp particles ad libitum. Pictures of each individual and a length standard were taken with an Olympus FE-47 digital camera in the coronal (side) and transverse (top) planes. Using Image J software (NIH, Bethesda, MD, USA), average spine length (n = 50 per individual), test diameter (transverse plane), and test height (coronal plane) were measured to the nearest millimeter. Test surface area (A, m²) was computed using the generalized equation for an oblate spheroid using test diameter and test height. Adult urchins of approximately the same diameter were selected within species (see Table 1).

2.1. Spine angle

Each urchin was placed in a 350 l, high-speed flume (Boller and Carrington, 2006) under a weighted plastic basket to restrict movement. A Sanyo VPC-E2 waterproof camcorder was placed downstream of each urchin and focused upon their resting position. After a 15 minute acclimation period the basket was removed and water velocity was increased from 0 to 79 cm s⁻¹ in nine increments (0, 8, 20, 32, 40, 46, 57, 73, and 79 cm s⁻¹), stopping at each water velocity for 2 min. Water velocity was measured in real time using an electromagnetic flow meter (Marsh-McBirney Inc., Gaithersburg, MD, USA; accuracy = ± 3 cm s⁻¹). If an urchin was dislodged or moved from the initial position the trial was restarted. Dislodgement was common with *S. droebachiensis* above 46 cm s⁻¹. Video for each individual was split into a series of images representing the urchin's orientation at each water velocity. The contrast of each image was manipulated in order

to differentiate the background from the organism, creating a silhouette. Spine angle was measured using spines from first quadrant (top right) of each urchin. Positive angles indicate that spines were above horizontal while negative values indicate a position below, as defined by Stewart and Britton-Simmons (2011).

2.2. Particle capture

For all particle capture feeding experiments a larger, 4000 liter paddle-driven flume was used (Nowell et al., 1989). The subtidal kelp *Costaria costata*, known to be consumed by all three species of urchin studied (Vadas, 1977; Britton-Simmons et al., 2009), were collected from the dock at Friday Harbor Laboratories. Blades were cut into $1 \times 1 \times 0.1$ cm ("small") and $3 \times 3 \times 0.1$ cm ("large") pieces to represent typical algal drift fragments that urchins catch in the field (Britton-Simmons, unpublished data). A total of 400 g (wet weight) of kelp particles of a single size were added to the flume and circulated for 1 h until evenly distributed along the raceway.

Urchins were acclimated and filmed in the same way as previously described. Particle capture was tested at seven flow velocities from 0 to 44 cm s⁻¹ (0, 6, 15, 24, 34, 40, and 44 cm s⁻¹), with each water velocity constituting a single trial conducted in order from slow to fast. For each trial an urchin spent 2 min at one water velocity after which the flume was turned off and the urchin was removed. The total amount of drift particles the urchin captured was blotted, weighed, counted, and returned to the flume to ensure that the same number of particles was available for the next trial. At faster flow velocities urchins were protected with a screen until the desired water velocity was reached, after which the screen was removed and the trial began.

The amount of algal drift captured by each urchin in a trial was reported as both the number of particles captured (#) and dry algal mass captured (W_{dry} , grams). Dry algal mass was calculated using a conversion factor described by the linear regression of dry to wet algal mass (W_{wet} , grams) ($r^2 = 0.98$, p < 0.001):

$$W_{dry} = 0.1006 W_{wet} + 0.002.$$
 (1)

The number of particles captured by each urchin (n, #), over the length each trial (t, seconds), was then used with urchin test surface area (A, defined earlier) to calculate the number of particles captured per unit area of capture surface per unit time $(\# m^{-2} s^{-1})$:

capture rate =
$$\frac{n}{At}$$
. (2)

Similarly, the particle flux past each urchin within a trial $(\# m^{-2} s^{-1})$ was calculated using the concentration of particles within the volume of the experimental chamber (C, $\# m^{-3}$), assuming a uniform distribution, and multiplying by water velocity (v, m s⁻¹):

particle flux =
$$Cv$$
. (3)

Particle capture rate and particle flux were then used to calculate particle capture efficiency (%):

capture efficiency =
$$\frac{\text{capture rate}}{\text{particle flux}}$$
. (4)

Table 1

Morphometric measurements (mean \pm SD) of the three species of sea urchin studied. Species with a common letter were not significantly different when compared using a post hoc Tukey HSD test ($\alpha = 0.05$).

	n	Test diameter (cm)	Tukey HSD	Spine length (cm)	Tukey HSD	Spine-body ratio	Tukey HSD
S. droebachiensis	15	6.37 ± 1.37	А	0.86 ± 0.22	А	0.14 ± 0.05	А
S. purpuratus	8	6.43 ± 1.28	A	1.53 ± 0.17	В	0.24 ± 0.04	В
S. franciscanus	13	8.65 ± 2.94	В	4.36 ± 1.27	С	0.60 ± 0.35	С

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