“Hooking” and “Sheeting:” strategies utilized by *Haminoea vesicula* to maintain stability on different substrates

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Abstract

Many marine gastropods face the challenge of adhering to substrates under adverse flow conditions. Some species live on both solid and sedimentary substrates, although how these substrate generalists resist detachment from materials with fundamentally different mechanical properties is not well studied. We used field observations and flow tank experiments to compare the capabilities and tactics of *Haminoea vesicula,* an opisthobranch gastropod, when exposed to destabilizing flow on its native sand and eelgrass. Velocities of outgoing and incoming spring tides in the tidal creeks and over and within eelgrass beds where *H. vesicula* live at False Bay, San Juan Island, WA ranged from 1 to 30 cm/s. In a flow tank, snails' resistance to current depended on substrate and orientation. On eelgrass, snails moving into flow maintained their position at velocities exceeding 40 cm/s, but were more vulnerable when facing away or sideways to flow (falling off at mean velocities of 25 and 32 cm/s respectively). In the latter orientation, snails would often rotate into flow by hooking onto the leading edge of eelgrass with the anterior edge of the cephalic shield. In this position, snails resisted flows exceeding 40 cm/s. Snails crawling on sediment and exposed to turbulent flow drew sediment-encrusted mucus sheets dorsally, completely ensheathing their bodies. "Sheeting" significantly increased snails' effective weight and ability to resist flow. On sand, snails ensheathed in sediment were least stable in the sideways orientation compared to those facing into or away from flow (mean velocities of 13 vs. 20 and 23 cm/s). Experiments on sandpaper indicated that snails were destabilized on sediment due to failure of adhesion of the sedimentary layers beneath them rather than their attachment to the sand.

Introduction

Many benthic marine gastropods face the challenge of maintaining their position on substrates while still being mobile. Success in staying attached to substrates is important and these animals otherwise run the risk of being swept away by currents. A wide range of marine substrate types exists: from sedimentary substrates such as sandy beaches or mud flats, to solid substrates including stone and seagrasses. However, particulate and solid substrates are fundamentally different in their mechanical properties. Solid substrates do not typically come apart due to external forces, while sediments can behave like either a solid or a fluid, depending on the forces that the particles in the substrate experience (Dorgan *et. al.,* 2006). This fundamental difference in how solid and particulate substrates behave under stress dictates the methods employed by gastropods in maintaining their position on either type of substrate. On solid substrates, gastropods such as limpets or abalone directly adhere to the surface of the substrate, and strength of adhesion depends on the foot-substrate connection (Branch & March, 1978; Grenon & Walker, 1981). Other gastropods, such as *Polinices* produce mucus trails on substrates and use the beating of cilia in order to adhere and move forwards (Copeland, 1922). In periods of high flow conditions, this strategy would be ill-advised to be used by animals in soft sediments, as while the animals may adhere to the sediment particles on the surface, sedimentary particles move independently from particle layers below. With sufficient shear forces, the animal could be displaced (Dorgan *et. al.,* 2006).

Because sediment particles can readily move relative to each other (in a fluid-like fashion), benthic gastropods may have difficulty remaining attached to these substrates.

However, animals across a variety of taxa exploit the fluidity of soft sediment when burrowing into the substrate in order to remain permanently or semi-permanently anchored. Through burrowing, animals expose less of their body to flow and bring their uncovered parts lower into the boundary layer, decreasing the amount of drag the animals experience. Marine gastropods were ancestrally adapted for living on hard substrates, but burrowing evolved in at least twenty families, with many groups independently evolving similar wedge-shaped foot morphology (Trueman & Brown, 1993). Compared to other burrowing mollusks that burrow vertically into sediment (e.g. bivalves and scaphopods), gastropods penetrate the sediment at shallow angles of attack using their wedge-shaped foot (Trueman & Brown, 1968).

While virtually all gastropods use their foot for locomotion, among different gastropod groups, changes in foot morphology underlie a diversity of specializations of gastropods for interacting with particular types of substrates. Brown & Trueman (1996) showed that certain marine gastropod species were specialized for their respective substrate to the point of being unable to crawl on any other type of substrate. For instance, Limpets of genus *Patella*, live on hard substrates in the rocky intertidal, and are unable to crawl when placed into sediment (Brown & Trueman, 1996). Other species of gastropod are substrate generalists, capable of crawling over both solid and sedimentary substrates. These included *Amblychilepas scutellum*, a dog whelk, and *Burnupena catarrhaca,* a gastropod that lives in rocky shores (Brown & Trueman, 1996). Gastropods capable of crawling on both solids and sediments changed their gait depending on the substrate (Brown & Trueman, 1996). To crawl on solid substrates, gastropods use pedal waves on the bottom of their foot, while gastropods that crawled on sediment used either a stepping motion over the surface or pedal waves (Brown & Trueman, 1996). Substrate generalists thus require the musculature and neural sophistication to switch between these behaviors (Brown & Trueman, 1996). Among the species of gastropod capable of living on both solid and sedimentary substrates, only a few gastropods species were capable of burrowing as well (Brown & Trueman, 1996).

However, Brown & Trueman's inquiries were focused specifically on typical shelled gastropod species and did not include the shell-reduced opisthobranch species. Opisthobranch species capable of burrowing also share the wedge-shaped foot morphology found in burrowing shelled snails, although little has been reported about opisthobranch burrowing capabilities (Brown & Trueman, 1993). An opisthobranch substrate generalist, *Haminoea vesicula* lives on solid substrates, in particular eelgrass, and is also commonly found crawling on and burrowing in sandy sediments (Fig. 1A). Adult *H. vesicula* are often found on the blades of eelgrass where they consume diatoms on the surface of the plant (Gibson and Chia 1989) (Fig. 1B). *H. vesicula* is an annual species, with veliger larvae hatching in the summer and surviving in the pelagic zone for approximately thirty days until settling in the sediment as juveniles to overwinter into the next summer season (Gibson and Chia 1991). These snails are cephalaspideans with a cephalic headshield, and a thin "bubble" shell. During periods of changing tides, adults living in eelgrass must face periods of increased flow velocities as well as the eelgrass flipping between the seaward and landward orientations. On the other hand, snails living in the sediment that have been knocked off from the eelgrass or those which are moving over the substrate must also maintain their position under adverse flow conditions. Observations of *H. vesicula* in False Bay showed that when snails were on the sediment in flow, they would sometimes cover themselves in a thin blanket or sheet of mucus and sediment while continuing to crawl. We triggered this behavior in 12/20 snails in the field using a hand-held paddle to introduce a current close to the snail. “Sheeting” can be the beginning steps of continuous gradient of burrowing behavior, but it also exists as a behavior distinct from burrowing. Snails, when “sheeting” may maintain their height on the sediment under the veil of sediment, transition back on top of the surface into crawling, or may dig deeper into the sediment by burrowing.

Description of crawl/sheet:

Cilia covering *H. vesicula* epidermis seamlessly propel the snail forward, allowing the snail to glide over the surface of substrates through a tunnel of mucus produced by sub-epithelial mucus glands on the snail’s cephalic shield and foot (Rudman, 1971). During “sheeting,” sediment becomes trapped or incorporated into the dorsal portion of this mucus tunnel, and as the snail moves forward, this covering of sediment appears to slide over the animal from anterior to posterior. This process is initiated when the snail lowers its head and angles the tip of its headshield such that the anterior edge reaches just below the surface of the sediment. The snail then flares the ciliated left and right ridges of the headshield, parting the sheet, exposing the mantle cavity openings to the surrounding water. In this manner, the snail bulldozes through surface of the sediment, lifting particles trapped within the tunnel of mucus over the cephalic shield and onto the back of the snail. Simultaneously, sediment-laden mucus slides from below the head to envelop the sides of the snail. This “sheet” eventually reaches past the tail of the snail and is left behind as the snail crawls forward, visible as an elongate sediment-coated membrane. The snail is capable of continually undergoing “sheeting” and may produce a trail many body lengths long, so long as the head is angled downwards towards the sediment. “Sheeting” ceases when the snail slightly raises its head and the snail crawls onto the surface of the sediment or when it burrows deeper into the sediment.

Description of burrowing:

Snails undergo “sheeting” as the initial step for burrowing into the sediment. Once successfully sheeted, the snail closes the anterior ridge of its headshield and drives its head deeper into the sediment. Continually lifting and lowering the anterior dorsal surface of the cephalic shield, the snail displaces sediment over the top of its head. The snail periodically flares the sides of its headshield, shifting sand to the left and right of the head, further loosening the sediment. At this point only the head has penetrated into the sediment: the shell, foot, and tail reside covered in the “sheet,” are resting on the plane of the sediment. As burrowing continues the snail crawls forward into the sediment, bringing the rest of the body deeper into the sediment.

Previous studies have primarily focused on the development and ecology of *H. vesicula* larvae, but adult *H. vesicula* remain poorly studied (Gibson, G.D., & Chia, F.S, 1989, 1991). Little is known about how opisthobranch substrate generalists maintain their position under adverse flow conditions. Here, we examine *H. vesicula* ability to maintain its position on both sedimentary and solid substrates in three orientations facing flow: side, anterior, and posterior in order to compare the relative stability of these snails on different substrates. The main contributor to destabilization, drag forces, can be described through the equation:

$F_D = \frac{1}{2} \rho v^2 C_D A$

or Drag = ½ Coef. Drag x projected surface area x velocity^2,

where ρ represents the density of the fluid (seawater); v represents velocity of flow; ρ signifies the drag coefficient, influenced by the shape of the object in flow; A is the area exposed to flow, proportional to the force of drag experienced, (Murray, J.A., *et. al.,* 2011). Given that the snails have a larger surface to induce drag in the side orientation, we expect this orientation to be the most susceptible to dislodgement (Fig. 2C). The anterior/posterior orientations present nearly the same surface area to flow, so we expect these to perform similarly (Fig. 2A,B). We hypothesize that the "sheeting" behavior is one mechanism that increases the snails' resistance to being dislodged by flow in sediment by increasing their effective mass. The sheeting behavior is not available to snails crawling on eelgrass, yet snails are subject to the same destabilizing forces caused by flow. Therefore we hypothesize that orientation to flow will be important for adhering to eelgrass, and snails would need a mode of adhesion in order to remain in place on eelgrass "fluttering" in flow.

Materials and Methods

Collection and Maintenance of snails

H. vesicula were collected by hand from the sediment and surface of eelgrass in False Bay, San Juan Islands, Washington, and brought to Friday Harbor Laboratories (San Juan Islands, Washington) over the duration of the experiments in June and July 2014. Animals were maintained in indoor sea tables with continuously flowing seawater at 10-14 °C and salinity of 34ppt. . Animals were not actively fed during this period of time, although they appeared to graze on diatoms on surfaces of the holding tanks and continuously produced fecal pellets. All experiments were conducted within two weeks of animal collection.

Calibration of Flow Tank

In all critical velocity trials, snails were tested in a flow tank of 124cm length x 16cm width x 19cm height constructed in the style of Vogel & LaBarbera (1978). A sediment-filled plastic tray of 36cm length x 13cm x width 4.5cm height with a 10.5cm long ramp attached for decreasing turbulence was placed into the working section of the flow tank (Fig 3A,B). The sediment was collected adjacent to eelgrass beds in False Bay (San Juan Islands, Washington) and was of density 1.36 (g/mL). The leading edge of the ramp was always within 3-8cm downstream from the hex-cell flow straighteners. The testing area of the tank was at least 15cm downstream from the trailing edge of the ramp and within the edges of the sediment-filled tray. To determine the velocity of flow speeds used in critical velocity experiments, fluorescein dye was used to visualize flow, and high speed videos of five different speed settings on the flow tank were taken and analyzed. Linear regression was performed on these velocities to determine the relationship between speed settings on the flow tank and the velocity of flow in the testing space. To extend the velocity range of the tank, a 10cm wide plate was placed vertical to flow in order to accelerate flow velocities in the working space (Fig. 3B). The plate was always 2cm above the surface of the substrate. The testing space for trials with accelerated velocities was at least 1/2cm, but no more than 4cm downstream of the plate. Velocities of flow for speed settings on the modified flow tank were found using the same methods as the unmodified flow tank.

Critical Velocity Experiments

To compare the relationship of *H. vesicula's* orientation to flow and the snail's ability to cling to sediment, we first established the critical velocity (the highest velocity at which they could maintain their position) of snails in three orientations: side, anterior (n=18), and posterior (n=20) to flow (Fig. 2). To keep height within the flow tank constant, in all trials conducted, the foot of snails was approximately 7cm from the surface of the water, or even with the top edges of the sediment-filled tray. For the side orientation, we compared both sheeted (n=50) and unsheeted (n=12) snails. Unsheeted snails were those that did not immediately sheet upon contact with the sediment and crawled instead. For each side orientation sediment trial, we placed snails within the testing range inside of the tray filled with sediment.. Snails were 7cm from the surface of the water and never less than 3cm away from the sides of the tank. Once the animals were positioned, the flow tank speed was increased at intervals of (0.028 m/s) every ten seconds (to allow the tank to equilibrate to each speed). We recorded the speed at which snails were dislodged from the sediment.

For sediment anterior (n=18) and posterior (n=20) trials, the maximum velocities of the unaltered flow tank were insufficient to successfully displace snails. The plate was inserted to modify the flow tank and increase velocity of flow within the testing area. Snails, when placed in sediment usually responded by immediately sheeting, so trials in these orientations were conducted with sheeted snails. Animals were initially placed at the center of the testing area. Velocity was increased at intervals of (0.068m/s) every ten seconds (to allow the tank to equilibrate to each speed). We recorded the speed at which snails were dislodged.

For critical velocity trials on eelgrass, eelgrass blades were strung length-wise to flow for anterior (n=25) and posterior (n=19) orientation trials and width-wise to flow for side orientation trials (n=31). These eelgrass blades were collected from False Bay and maintained in the same indoor sea tables as the snails. Ends of eelgrass blades were clamped with binder clips attached to a plastic plate and were pulled taut (Fig. 3C). This apparatus was placed into the sediment tray such that the top surface of the eelgrass was 7cm from the surface of the water. Snails were carefully placed on the eelgrass such that they were crawling lengthwise on the eelgrass. For sandpaper trials, a sheet of waterproof 180 grade sandpaper was attached to a plastic sheet and placed into the sediment-filled tray in the flow tank so that the surface of the sandpaper was 7cm from the surface of the water. Anterior (n=16), posterior (n=23), and side (n=32) orientation trials were conducted using this as the substrate. For both eelgrass and sandpaper trials, once snails were placed on their respective substrates, flow speed was increased by intervals of (0.068m/s) every ten seconds to allow flow to equilibrate. We recorded the orientation of snails before and after they rotated due to flow, and recorded the critical velocity at which snails detached.

Mass and Density Gained from Sheeting

To determine how much *H. vesicula* mass increased due to their sheeting behavior, we measured the amount of mass the animals gained from the sediment during this behavior. For each trial, we first weighed and placed the animal into a container filled with 1.36 (g/mL) density sand collected from False Bay and 1cm seawater. In approximately two-thirds of the trials, the animals would begin sheeting immediately (data not shown), however, in the cases that the animals remained crawling on the surface, we were able to consistently coax them into sheeting by gently pulsing water onto the animals' cephalic shields with a pipet without dislodging the animals from the sediment. Once the animals were fully obscured by the sediment during sheeting, we used forceps to pick up the animals in a dorsal-ventral orientation, careful not to dislodge the sediment collected in mucus on their surface, and placed the animals onto a scale to record their effective mass after sheeting (n=32).These weights did not include what could be relatively extensive mucus/sediment membrane trails left on the sediment surface and so they are a conservative measurement of the weight gained by sheeting. Every other trial, we mixed the sediment to eliminate these trails and flattened the surface of the sediment to ensure an even surface between trials. We compared the mass *H. vesicula* gained from sheeting to the mass the animals gained from sediment adhering to the bottom of their feet from crawling on the surface. We repeated the process described above, using the individuals that remained crawling on the surface for at least 15 seconds, without out sheeting behavior (n=32). We chose 15 seconds as the cut-off point, as this was comparable to the time necessary to coax the animals into sheeting, as conducted in the previous trials, and to allow the animals to stabilize in the sediment. Thus the effective mass of these "control" animals included the mass of their bodies and the mass of the sediment that adhered to their feet as would occur when they are gliding along the sediment bottom.

Statistics and Analysis

To account for trials in which snails remained attached to substrates past the highest velocities tested, the critical velocities in these trials were reported as the highest velocities experimentally available: 0.188m/s in the unaltered flow tank, and 0.432m/s for the accelerated flow tank trials. Only trials in which snails successfully crawled or sheeted on the substrates were used.

Shapiro-wilks tests were performed to determine if critical velocities were normally distributed. Performance amongst the various orientations on different substrates were compared with Kruskal-Wallis tests because the data were usually not normally distributed. Analysis of effective snail mass increase from sheeting was also conducted using the same method. Data analysis was conducted using R ver. i386 3.1.0.

Results

Snail Stability on Sediment

Snails that performed sheeting (n=48) gained on average 0.19 grams, while animals that did not sheet but were otherwise crawling on the sediment gained 0.06 grams (n=47) (H=51.2, df=1, p<0.001) (Fig. 6). The critical dislodgement velocity of sheeted (n=50) snails was significantly greater than that of unsheeted (n=12) snails in the side orientation (H=17.5, df = 1, p < 0.001,) (Table 1). Snails in the posterior (n=20) orientation performed better than those in the side (n=50) (H=40.2, df = 1, p<0.001), while anterior (n=18) was even more resistant to destabilization than posterior (n=20) (H=3.92, df=1, p=0.048) (Table 1) (Fig. 5).

On sandpaper, side (n=32), anterior (n=16), and posterior (n=23), all required higher critical velocities for stabilization than sediment in the side (n=50) (H=54.4, df=1, p<0.001), anterior (n=18) (H=28.4, df=1, p<0.001), and posterior (n=20) (H=16.9, df=1, p<0.001). None of the snails on sandpaper in the anterior orientation detached from the substrate therefore withstanding speeds of at least .0.432 m/s.

Critical Velocities to Dislodgement on Eelgrass

Comparing the posterior (n=19) and anterior (n=25) orientations (H=25.1,df=1,p<0.001), posterior was significantly more susceptible to destabilization (Table 1) (Fig. 5). There was no significant difference between all trials in the side orientation (n=31) and the anterior orientation (n=25) (H=0.2029, df=1, p=0.652) (Table 1) (Fig. 5). Although, within the side trials, as flow velocity increased, snails were rotated radially about their head as the axis of rotation, until reaching anterior orientation to flow. At this point, the part of the foot directly below the shell and tail detached and were suspended waving in the flow. Only the anterior surface of snails' heads remains attached to the eelgrass. In 16 our 31 side trials, snails travelled forward into the flow to hook the anterior edge of their headshield under the leading edge of the eelgrass (Fig. 3). Animals that performed "hooking" (n=16), were more capable of remaining attached than those that did not perform this behavior (n=15) (H=8.56, df=1, p=0.003) (Table 1).

Critical Velocities to Dislodgement Eelgrass Versus Sediment

Comparing *H. vesicula* tenacity on soft sediment and eelgrass, snails adhering to eelgrass in the side without hooking (n=15) were more resistant to dislodgement than snails adhering to sediments in the side orientation (n = 50) (H=55.4, df=1, p<0.001) and anterior (n =18) (H=31.1, df=1, p<0.001) orientations. However, there was no significant difference between snails on eelgrass (n=19) and sediment (n=20) critical velocities in the posterior orientation (H=1.5, df=1, p=0.220)(Table 1).

Discussion

Haminoea vesicula is a marine gastropod that adheres on both solid and sedimentary substrates and must retain stability on these substrates. Drag forces are the main source of destabilization and are proportional to the area perpendicularly exposed to flow (Vogel, S. LaBarbera, 1978). Although we expected the side orientation to be the most susceptible to dislodgement among the orientations we tested(because it has the greatest area exposed to flow) the adhesion of the head onto the solid substrates (eelgrass and sandpaper), allowed the snails to rotate their shell downstream in a position more nearly parallel to flow with the head facing the oncoming flow. We observed this in every eelgrass and sandpaper side orientation trial. Furthermore, the posterior orientation was the least resistant to dislodgement in the solid substrates (eelgrass and sandpaper). In these trials, drag incurred by the shell and tail lifted these upwards and snails were peeled off the sediment. This was unlike the anterior or side orientations in which snails could keep their heads attached to the substrate. These observations suggest that the ventral surface of the head was the main part of the foot by which these snails were adhering to eelgrass. These snails use cilia on their feett and epidermis to glide over mucus produced by glands around the body (Rudman, W.B. 1971). Although it is possible that cilia may be more densely packed on the underside of the head to allow for greater adhesive forces in the mucus, it remains unclear what features of the head allow the head to attach so tenaciously.

The strength of adhesion under the head also allows *H. vesicula* to retain stability in the side orientation by hooking onto the edge of eelgrass. This behavior was extremely successful in allowing snails to adhere to the eelgrass, as in over eighty percent of the trials in which snails hooked; snails were able to retain stability even past the fastest velocity flow available for testing (0.432 m/s) (Table 1). In trials in which snails did not hook, only a third of the snails were able to stay on eelgrass at this velocity. On eelgrass, it is unknown whether the adhesion between the foot and mucus or between mucus and eelgrass interfaces failed first. Regardless, by hooking over the leading edge of eelgrass the horizontal drag forces would press the underside of the head onto the edge, physically decreasing shear stresses on the interface. Snails may also be diverting flow with their headshield to incur less drag on the rest of its body.

A comparison between sandpaper and sediment trials shows that snails were more capable of adhering to sandpaper. This result suggests that snails' ability to maintain stability in soft sediments depends on the adhesion between the top layer of sediment that the foot was directly adhering to and the particles directly below; failure happened in the sediment-sediment adhesion rather than in the mucus-sediment connection. In sediment trials, snails were displaced when destabilizing forces overcame the force of gravity, the stabilizing force keeping snail and mucus on the surface (Dorgan, *et. al.* 2006). Snails retained a layer of sediment trapped in the mucus on the bottom of their foot even when dislodged; further suggesting that failure on sediment occurs due to separation between particles.

However, to counteract the destabilizing forces of drag, snails on sediment undergo "sheeting" in order to increase their effective mass, thus increasing the force of gravity acting on them. Although snails decreased their height in flow through sheeting, the decrease was less than or equal to 1mm and so probably did not have a large effect on the drag force. Furthermore, the sheet increased the effective surface area of the snails exposed to flow, making up this difference. Sheeting also created small ridges around the foot, but at destabilizing velocities, the sediment around the foot was blown away, exposing more of the animal to flow. This strategy of using sediment to increase effective mass and anchor the animal to the surface is shared by sand dollar juveniles, which actively select the densest particles in the sediment to store in their stomachs to presumably weigh them down and prevent destabilization (Chia, F.S. 1979). It is unlikely that *H. vesicula* actively select which particles to incorporate in their sheets. This study only measured the tenacity of "sheeted" snails in one type of sediment of density 1.36 (g/mL) and further study would be necessary to determine if higher density sediments would offer "sheeted" snails even greater stability on the substrate.

If stability on substrates in adverse flow conditions was a strong selective pressure influencing gastropod evolution, the evolution of a prehensile-like head capable of a variety of functions may have been a reason why the cephalaspideans have diverged to live on a variety of substrates, while still retaining very similar elongate body shape morphology along with their head shield (Wagele, H., & Klussman-Kolb, A., 2005). Cephalaspideans, like *H. vesicula* crawl through the movement of cilia on their epidermal surfaces and rely on the cephalic shield to plow into the sediment. This general anterior plow shape is shared by many burrowing snails, but *H. vesicula* burrowing strategy differs significantly from other gastropod burrowing behaviors (Trueman and Brown, 1992). *H. vesicula* may lack the muscles in order to burrow at a high angle of penetrance into the sediment, as seen in gastropods such as *Bullia*. However, *H. vesicula's* sheeting behavior has a low angle of penetration into the sand would allow for little shear forces and stress chains between particles in the sediment (Dorgan, K.M., 2006). This absence of forces would require less vigorous muscular behavior for burrowing (Trueman & Brown, 1991).

While previous studies have focused on the adhesion of gastropods on solid substrates, this study examined the stability of a substrate generalist gastropod, *Haminoea vesicula,* on its differing substrates (Branch & March, 1978; Grenon & Walker, 1981). We propose that two behaviors, "sheeting" and "hooking," allow this species to help maintain stability on sediment and eelgrass, respectively. However, the present study only explored a single species of cephalaspidean, and it is unclear if these behaviors are unique to this species.

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Figures

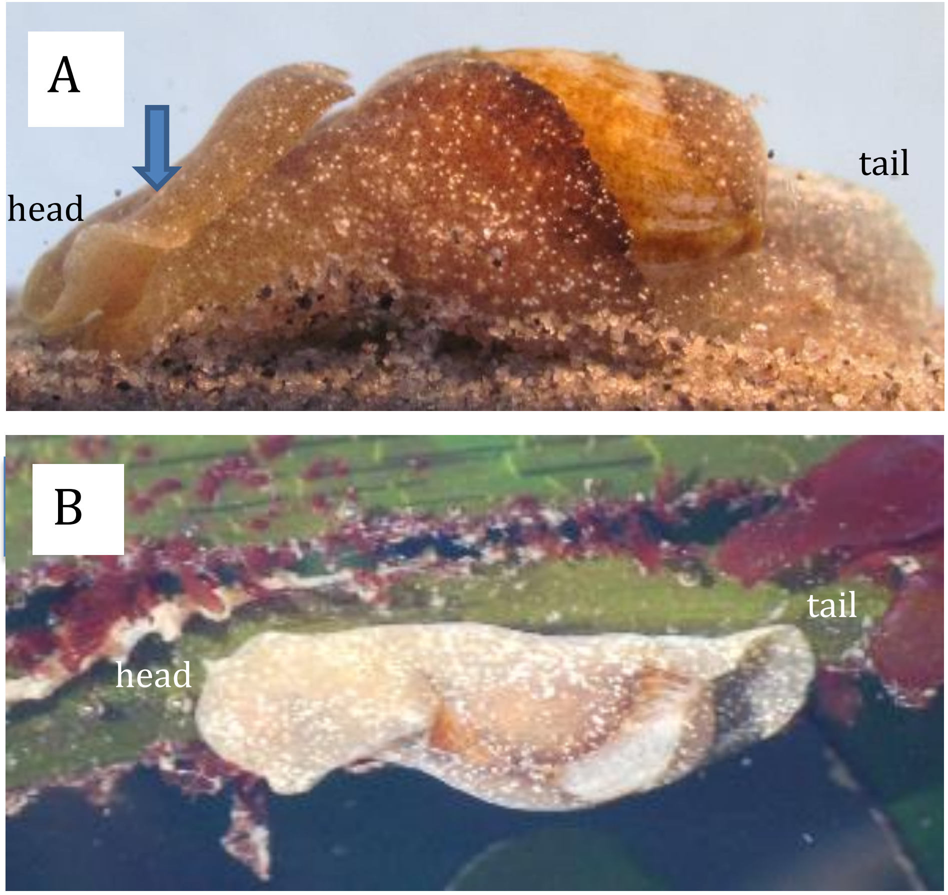

Fig 1. *H. vesicula* crawling on (A) sediment and (B) eelgrass. In both figures, anterior/head located left, posterior/tail to the right. Blue arrow indicates cephalic shield.

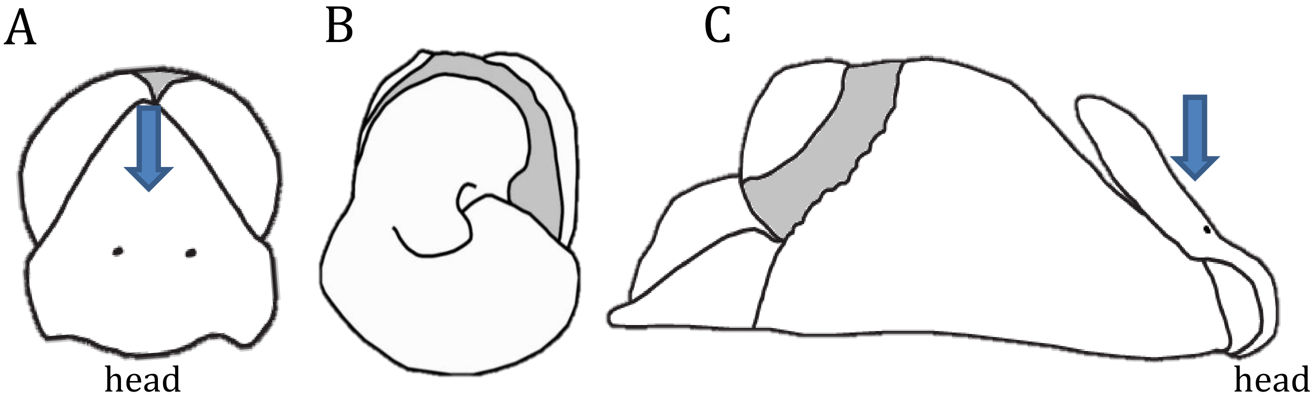

Fig 2. Diagram of *H. vesicula* (A) anterior, (B) posterior (C) side orientations. Shell colored in grey. Side orientation exposes greatest surface area to flow. Blue arrows indicate cephalic shield

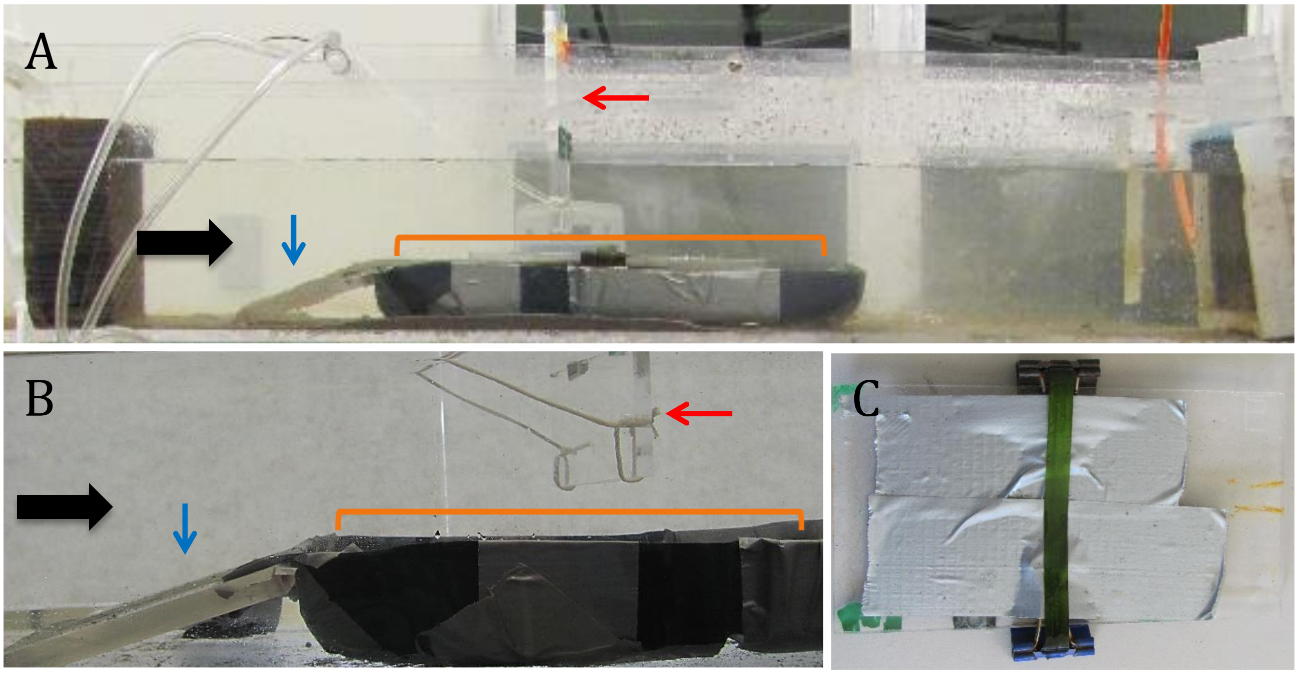

Fig 3. Flow tank and equipment for critical velocity experiments. Modified flow tank (A) flow (black arrow) travelled left to right and included (B) vertically suspended plate (red arrow), ramp (blue arrow), sediment tray (orange bracket). (C) Eelgrass was suspended on two office paper clamps attached to plastic plate.

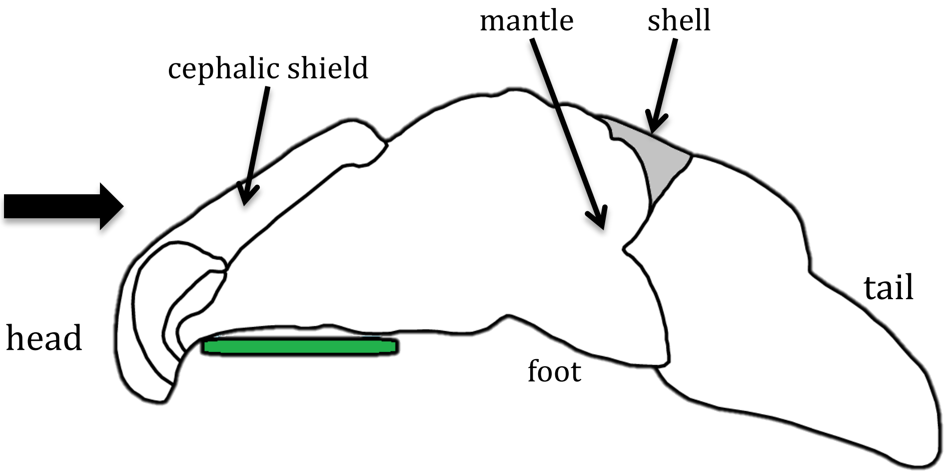

Fig 4. *H. vesicula* "hooking" behavior. The snail wraps anterior edge of cephalic shield over the leading edge of the eelgrass (shown in green). Flow travelling left to right (black arrow).

Orientation	**Condition**	**N**	**Median Critical velocity (m/s) to destabilization ± IQR**	**Percent snails did not destabilize (%)**
Side	Sediment (unsheeted)	12	0.106 ±0.028	0.0
	Sediment (sheeted)	50	0.133 ±0.027	12.0
	Eelgrass (hooked)	16	0.432 ±0.0	81.3
	Eelgrass (unhooked)	15	0.296 ±0.204	33.3
	Sandpaper	32	0.432 ±0.102	64.5
Posterior	Sediment (sheeted)	20	0.228 ±0.0	0.0
	Eelgrass	19	0.228 ±0.068	5.3
	Sandpaper	23	0.364 ±0.136	12.5
Anterior	Sediment (sheeted)	18	0.228 ±0.068	0.0
	Eelgrass	25	0.432 ±0.068	36.0
	Sandpaper	16	0.432 ±0.0	100

Table 1. Median critical velocities to destabilization of snails in side, anterior, and posterior facing flow orientations, on sediment, eelgrass, or sandpaper substrates. Percent snails did not destabilize past highest velocities in flow tank: above >80% (dark blue), 60-80% (light blue), 0.0% (pink). *Statistical differences between conditions within text.

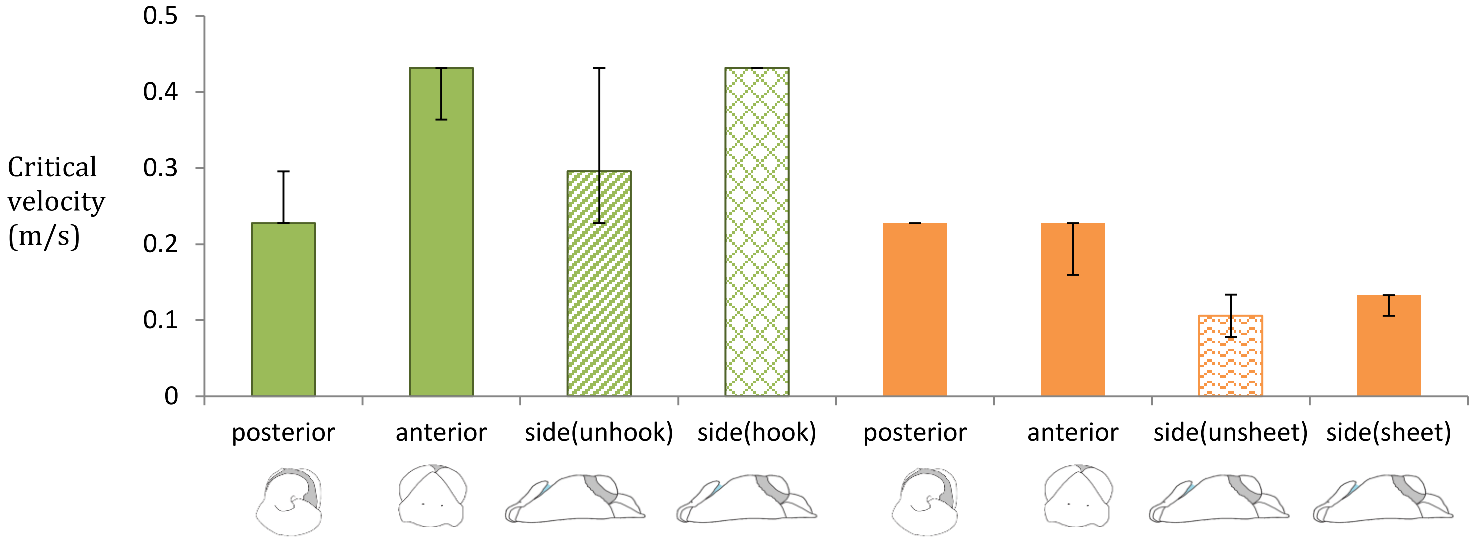

Fig 5. *H. vesicula* median critical velocities in posterior, anterior, and side orientations to flow on eelgrass (green) and sediment (orange). Error bars indicate upper and lower IQR. Icons below each condition depict the area of snails perpendicular to flow.

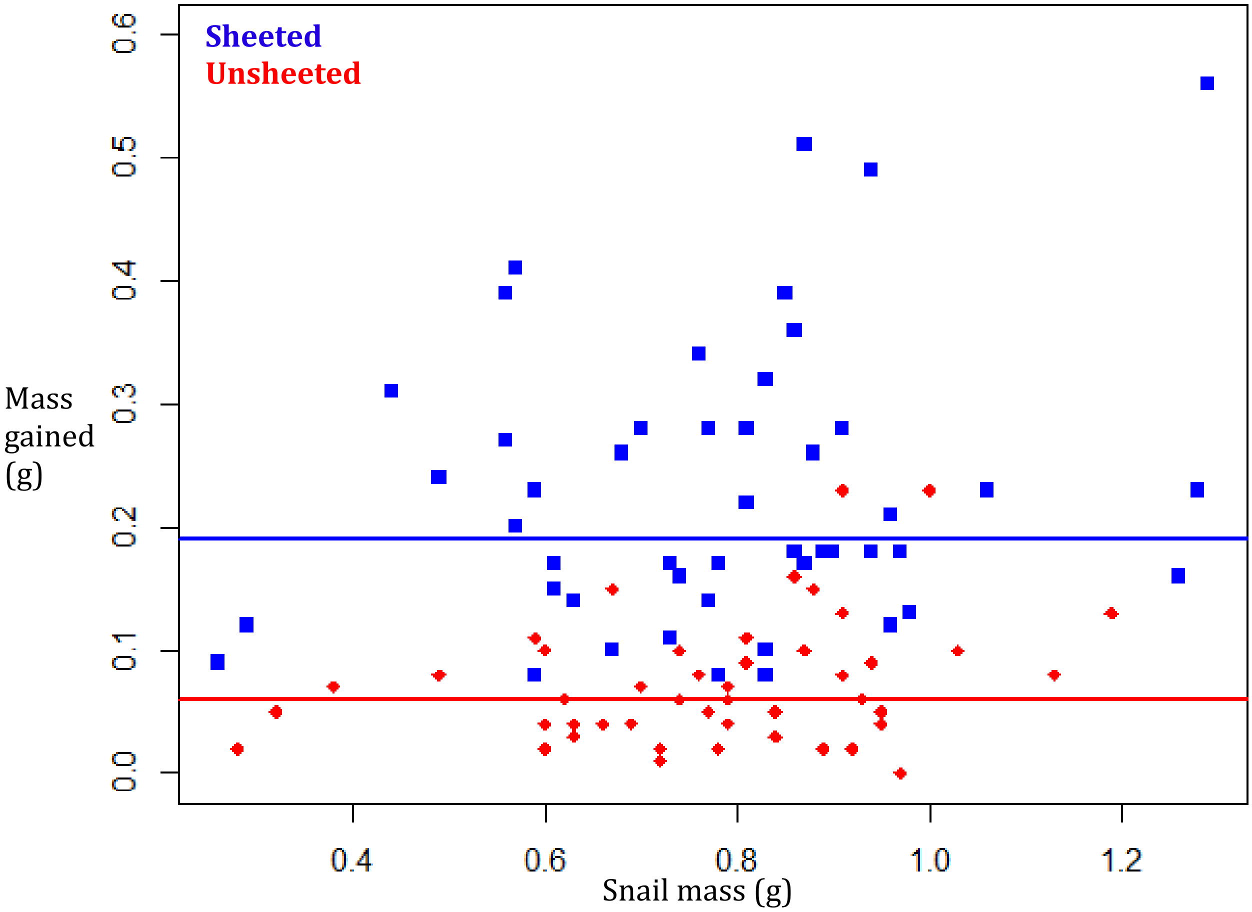

Fig 6. *H. vesicula* increases effective mass significantly during sheeting compared to crawling ($p<0.001$). Sheeted snails (blue squares), unsheeted snails (red diamonds). Lines indicate median mass gained for sheeted snails (blue) and unsheeted snails (red).