Effect of habitat cues on the swimming behavior of pre-competent *Lacuna vincta* larvae from Friday Harbor, WA, USA

Vilhelm Fagerström*[1], Lauren Dykman*[2], Eileen Bates*[3]

FHL 548: Larval Biology of Marine Invertebrates
Summer 2019

[1]University of Gothenburg, SWE
[2]Woods Hole Oceanographic Institution, USA
[3]University of Washington, USA
*Indicates shared first authorship

Contact Information:

Vilhelm Fagerström
University of Gothenburg, Department of Marine Sciences
Carl Skottbergsgata 22 B, 413 19 Gothenburg, Sweden
vilhelm.fagerstrom@gu.se

Lauren Dykman
Woods Hole Oceanographic Institution
266 Woods Hole Rd., Woods Hole, MA 02543, USA
ldykman@mit.edu

Eileen Bates
University of Washington School of Aquatic and Fishery Sciences
1122 NE Boat St. Seattle, WA, 98105, USA
ehbates@uw.edu

Keywords: settlement cues, larvae, gastropod, Lacuna, swimming, water column, video analysis

ABSTRACT

Swimming behavior in planktonic larvae has been suggested to affect their dispersal and recruitment. Behavioral regulation of vertical distribution can affect the extent to which larvae may accumulate in or escape from vertically sheared flows or fronts. Competent larvae of many invertebrate species are known to respond to various settlement cues in the environment by regulating their behavior in order to facilitate settling in suitable habitats. The behavioral responses of pre-competent larvae to cues from the adult habitat could have implications for retention, however such responses have not been investigated. In this project we have studied the swimming behavior in pre-competent larvae from the gastropod *Lacuna vincta* in the laboratory with the objective of determining whether behavioral changes in response to potential settlement cues are present in larvae at that earlier developmental stage. Potential settlement cues included in this study are eelgrass (*Zostera marina*), the kelp *Agarum fimbriatum*, and adult *L. vincta*, in addition to a control of filtered seawater. Pre-competent *L.vincta* larvae were recorded swimming in water columns containing water in which these various cues had been soaked, and their behaviors were compared across treatments. Videos were analyzed for mean upward swimming speed, mean swimming speed along the path of travel, mean oscillatory speed, and mean axial speed for each treatment. For all metrics, there were no significant differences between all four treatments and the control. The sample size of larvae was consistently low in the kelp cue as larvae remained on the bottom of the column, possibly due to high viscosity of that cue water. Our results indicated no response to adult habitat cues when larvae are pre-competent.

INTRODUCTION

Planktonic larval stages are present in the life histories of most benthic marine invertebrates and serve many potential functions, including reducing mortality from benthic predators, dispersal away from adult competition, and contributing to population connectivity (Strathmann 1985, Pechenik 1999, Pineda et al. 2007). While passive physical transport of larvae in the water column was once considered a primary dispersal mechanism, it is increasingly recognized that planktonic larvae can regulate swimming behavior, for example controlling position in the water column to control the extent of advection or retention (Lloyd et al. 2012, Fuchs et al. 2018). When competent to settle, larvae of many taxa are known to respond to complex environmental cues that help them select viable habitat (Price 2010, Lillis et al. 2014).

Larvae across taxa have also been known to increase settlement in response to the presence of adults of their own species, another method of locating desirable habitat (Ettinger-Epstein et al. 2008, Wheeler 2016).

Although settlement in response to habitat cues has been observed in competent larvae, the possibility that pre-competent larvae may have the capacity to recognize their eventual settlement habitat, and to display behaviors that might assist in their retention in that habitat, has not been thoroughly explored. Behavioral regulation of vertical distribution throughout the planktonic phase regulates the extent to which larvae accumulate in, or escape from, vertically sheared flows or fronts (Woodson et al. 2012), or experience advection by currents (Pineda et al. 2007). The extent to which larvae can recognize adult habitat, even when not competent to settle, and alter behavior to favor retention therefore has critical implications for dispersal fate. However, precompetent responses to adult habitats in marine invertebrate larvae remain poorly understood. This study aims to examine if the presence of cues from preferred adult benthic habitat, or of cues from adults themselves, affects the swimming behavior of precompetant larvae of the species *Lacuna vincta* in the San Juan Islands, Washington.

Lacuna vincta is a common marine benthic snail that lives on subtidal algae in the Pacific Northwest, Atlantic, and Europe. Known habitat for adult *L. vincta* includes various brown algae, red algae, and eelgrass (Strathmann 1987, Fretter and Manly 1977). In England, *L. vincta* egg masses are found on the fronds of *Laminaria spp.*, *Fucus spp.*, and rhodophyceans (Fretter and Manly 1977). *L. vincta* is an annual species that reproduces year-round in the San Juan Archipelago. It produces donut-shaped egg capsules containing 1000-1500 eggs from which planktotrophic veligers hatch after 7-9 days (Strathmann 1987). Veligers become competent to settle at around 60 days (Martel & Chia 1991), and M.F. Strathmann (1987) noted that settlement may be induced by the presence of algae. The long planktonic duration of this species implies the potential for considerable physical transport, and swimming behavior during pre-competent stages could have a significant influence on dispersal outcome over this time period.

As grazers, gastropods such as *L. vincta* can have large impacts on plant and algal species on which they feed, and indirectly have impacts on whole ecosystem function and nutrient cycling. For example, on the east coast of Canada, increases in *L. vincta* populations have been associated with declines in kelp biomass, as the snails graze on kelp blades (Krumhansl & Scheibling 2011). Chenelot and Konar (2007) found that *L. vincta* in Kachemak Bay, Alaska, could have large impacts on bull kelp populations because of their high densities and grazing potential. In the San Juan Islands, *L. vincta* are also abundant on eelgrass, where they deposit egg cases. They do not feed on eelgrass under normal conditions, but rather rasp diatoms off leaf blade surfaces, thus interacting with eelgrass more indirectly through removal of epibionts (S. Seroy, pers comm).

Because of their potential to alter algal populations, understanding which species may be preferred by grazers like *L. vincta*, and understanding their capacity to be retained in and eventually settle in these habitats could have important implications for the health of different intertidal habitats and overall ecosystem function. In this study, we used video analysis and tracking of recently hatched (<1 wk) *L. vincta* veligers to determine whether they display behaviors in the plankton that may favor retention near favorable settlement habitat, even before competence.

We propose three hypotheses for response to habitat cues. First, that larvae will alter behavior in the presence of habitat cues in ways that will favor retention near future settlement sites. These include distribution lower in the water column, greater average downward swimming velocity, decreased swimming velocity along the direction of travel, and swimming in helices with a greater ratio of oscillatory movement to axial movement. Second, that larvae will display avoidance behaviors that favor advection away from adult habitat, including distribution higher in the water column, decreased average downward swimming velocity, increased swimming speed in the direction of travel, and swimming in helices with more axial versus oscillatory movement. The final hypothesis is that *L. vincta* larvae will not alter their swimming behaviors when subjected to cues.

METHODS

Larval culture

Lacuna vincta egg cases were collected from algae on the floating dock at Friday Harbor Laboratories (FHL) on July 24, 2019. Egg cases, affixed to the small piece of algae on which they were found, were kept in 800 mL glass jars containing seawater filtered through a fine-meshed filter bag. The jars were continuously stirred by paddles moving slowly at 10rpm (Strathmann 2014). Hatching from the egg cases began on July 29, 2019. Larvae were fed daily with *Isochrysis galbana* at a concentration of ~150,000 cells/mL. Water was changed every other day by reverse filtering through 15 µm mesh.

Habitat cue treatments

Three water treatments and a control were prepared to expose larvae to possible habitat cues they might experience in the Salish Sea. The treatments were: adult *Lacuna vincta*, eelgrass, kelp, and a control. The cues (50 mL of eelgrass, 50 mL of kelp and 1.1 g of adult *Lacuna vincta*) were soaked in 700 mL of filtered sea water for 24 hours at ~13°C. The cue-soaked water was then vacuum filtered through a ~1 micron filter. Both "heavy" and "light" cue water were prepared to create a stratified water column. "Heavy" water was 100% filtered seawater, while "light" water was a 1:7 ratio of fresh water to filtered seawater.

Experimental set-up

Four replicate water columns surrounded by a water jacket were used for experiments. The columns each had dimensions of 35x4x4 cm and were filled to approximately 20 cm depth with 320 ml of filtered sea water during each trial. To maintain a constant temperature and minimize convection currents, water at 13°C was pumped through the jacket surrounding the columns, beginning when the columns were filled and throughout the duration of the experiment. For each trial (6 total), treatments were randomly assigned to water columns. A column was created with a tripour each of "heavy" and "light" seawater for each cue treatment, both filled to the same level. The two tripours were connected with tubing, and the "light" cup was connected with tubing to a pipe that allowed water into the bottom of the water columns. The "heavy" and "light" cups were raised simultaneously for each treatment to gravity-fill the columns, allowing the "heavy" water to flow into the "light" water as water from the "light" cup flowed into the column. Throughout the addition of water, the "light" water reservoir was stirred vigorously to assure consistent mixing. This created 4 stratified columns, each with a salinity gradient spanning the approximate salinity interval 26.25 - 30 psu from top to bottom. The columns were allowed to equilibrate to the temperature of the water jacket, and then larvae were introduced to the bottom of each column with a syringe in ~5 mL of filtered seawater. Larval concentrations were 25-30/mL for an introduction of 125-150 per column. Columns were illuminated by four infrared light sources, two on each side of the columns.

Video collection

Video was collected using two cameras (with megapixel 8 mm IR ½" lenses) at frame rate of approximately 29 fps. At intervals of approximately 0, 20, 40 and 60 minutes after introduction of the last larvae, 6960 frames (approximately 4 minutes) were collected. The water pump through the jacket was turned off each time video was recorded to reduce bubbles in the video images. Videos were recorded using Fosica software (Wallingford Imaging Systems, Version 0.1001.1027).

Video calibration and analyses

Video files were processed using the Fosica software to isolate moving particles, which were then exported as position files providing a pixel location for each moving object in each frame of the video. Measurements of the water column were taken to calibrate pixels to true dimensions of the video using the Matlab software package Tracker3D (Grünbaum 2004). Larval positions in each frame were used to create trajectories representing each larva's movement through time for frames 2000-4000 of each video. Swimming velocity vectors were extracted to calculate the speed and direction of larval movement as well as the time spent swimming in different directions. The vertical distribution of larvae in the water columns was also analyzed using the same software package.

Statistical analyses

A MatLab program provided by Danny Grünbaum was used to calculate mean upward and downward swimming speed, mean speed along the path of travel, mean axial speed, and mean oscillatory speed. Swimming speeds were weighted by points. Each point represented the position of one larva during a single frame of video, so this was a method of weighting larval tracks by time. Each point contains information on the position and velocity of a single larvae during a single frame of video, and thus these points are used to calculate various distribution and speed metrics for the study. The mean upward swimming speed is calculated from positive vertical velocity components, averaged over all points in tracked swimming paths that had positive vertical velocities. Similarly, the mean downward swimming speed is calculated from negative vertical velocity components, averaged over all points in tracked swimming paths that had negative vertical velocities. Mean speed along the path of travel is the speed in the instantaneous direction of swimming, averaged over all points in all tracked swimming paths in each treatment. The mean oscillatory speed is a metric of movement perpendicular to the direction of net movement, while the mean axial speed is the average speed in the direction of net larval movement. The ratio of axial to osciallary speed was the metric used to quantify helical swimming patterns. Larval vertical distribution in the water column was calculated by summing the tracked points for each vertical position for all analyzed frames.

RESULTS

Qualitative Swimming Behavior Observations

When observed in their 800 mL culture jar, *L. vincta* larvae tended to swim upward and aggregate at the surface. Helical upward and downward swimming patterns were observed, similar to other veliger larvae. Larvae were phototactic, and tended to aggregate on the side of the culture jar closest to intense light. Some larvae remained at the bottom where they swam in circles. Larvae also seemed to swim upward rapidly in response to turbulence: directly after injection many ended up concentrated at the surface. On contact with the surface, they reacted by retracting the velum slightly, sinking ~0.5 cm, then continuing to swim upward again, repeating the cycle. When larvae were injected into the bottom of the column, they swam upward initially, but after an acclimatization time, they explored the length of the water column.

Number of tracked points and paths

Overall, an average of 28,614, 35,734, 8,083, and 37,928 points were recorded for Control, Eelgrass, *Agarum*, and Adult *Lacuna*, respectively (Figure 1A). Each point represents the location of a single larva during one frame of video. From these points, an average of 121, 138, 38, and 171 paths were generated for each replicate, respectively (Figure 1B). Overall, *Agarum* had the lowest number of points and paths because many of the larvae remained at the bottom of the column and did not swim. The greatest number of points and tracks were recorded in the Adult Lacuna treatment.

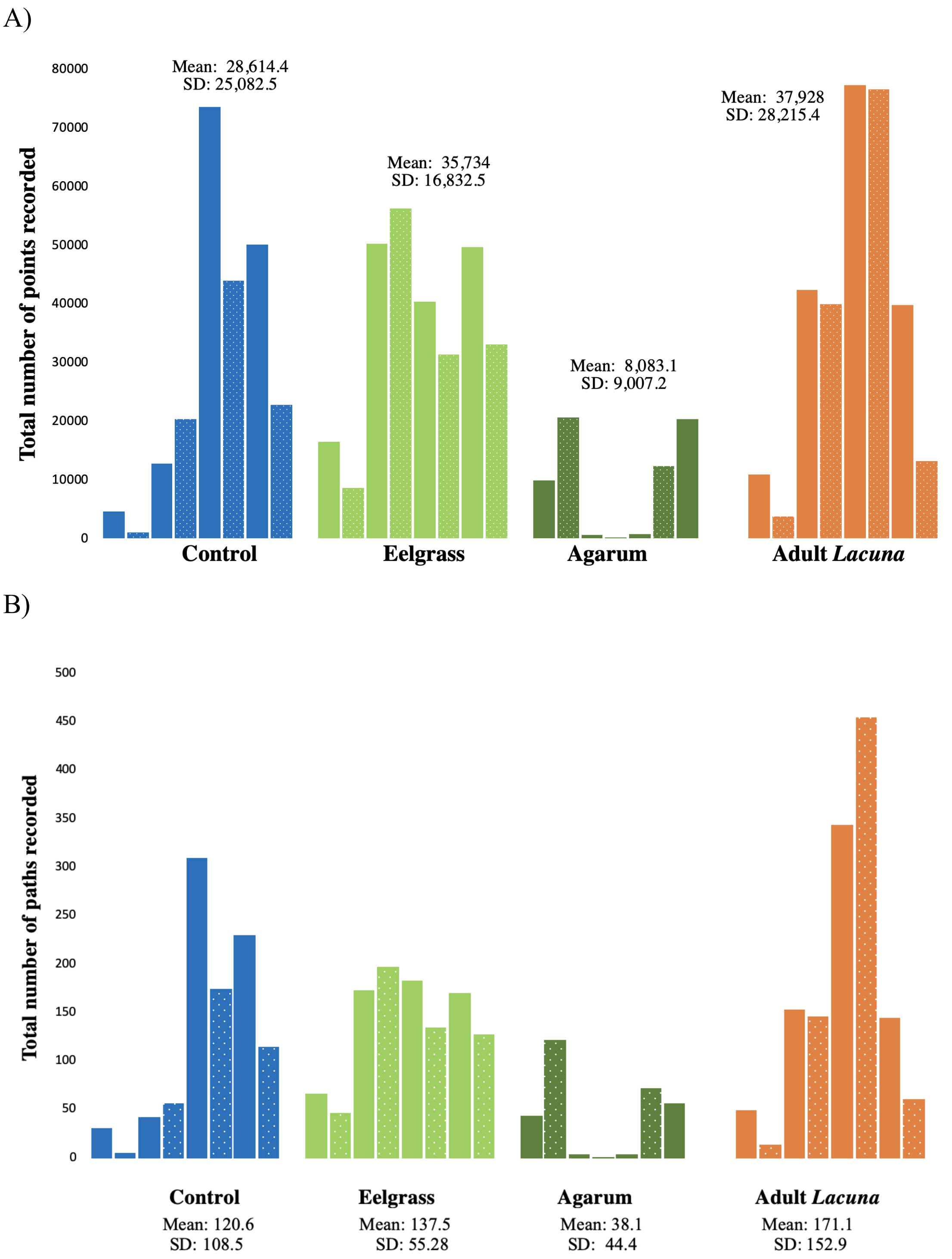

Figure 1. The average number of points (A) and paths (B) tracked in MatLab for larvae swimming in each video recorded. Solid bars are from time point 2 (20 minutes after larval introduction), and dotted bars are from time point 3 (40 minutes after larval introduction).

Distribution in the water column

For all treatments, distribution of time spent swimming in different levels of the water column did not change notably between the 20-minute and 40-minute timepoints, suggesting larvae had reached a steady state in behavior by 20 minutes (Figure 2). The control and eelgrass treatment both had two peaks in distribution at the top and the bottom of the water column (Figure 2A). In the Agarum treatment, larval distribution was heavily bottom-skewed, with a peak at the surface in the 20-minute timepoint. This peak may have been caused by bubbles from the water bath, which were seen in one video. In adult *Lacuna* cues, larvae were more evenly distributed in the water column, without spending much time at the bottom.

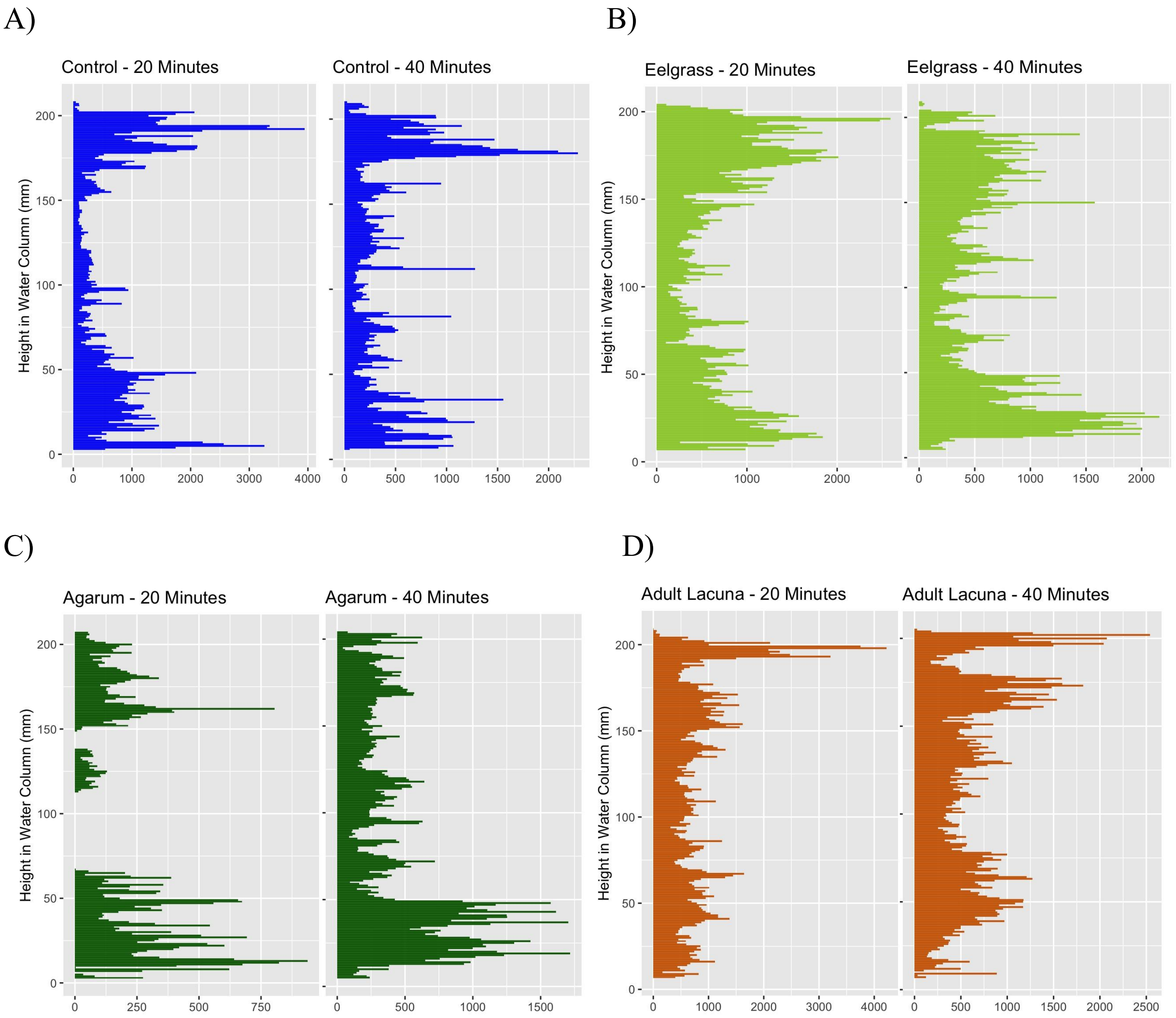

Figure 2: Histograms of time spent swimming at different heights in the water column. For each cue, data taken at 20 minutes and 40 minutes are displayed separately.

Mean upward and downward velocity

Overall, mean upward and downward swimming speeds were similar between treatments. Mean upward velocities were 0.41, 0.54, 0.53, and 0.56 mm/s for Control, Eelgrass, *Agarum,* and Adult *Lacuna*, respectively (Figure 3). Mean downward velocities were 0.58, 0.67, 0.66, and 0.78 mm/s for Control, Eelgrass, *Agarum*, and Adult *Lacuna*, respectively (Figure 3). Some trials are missing for the *Agarum* treatment because too few tracks were recorded.

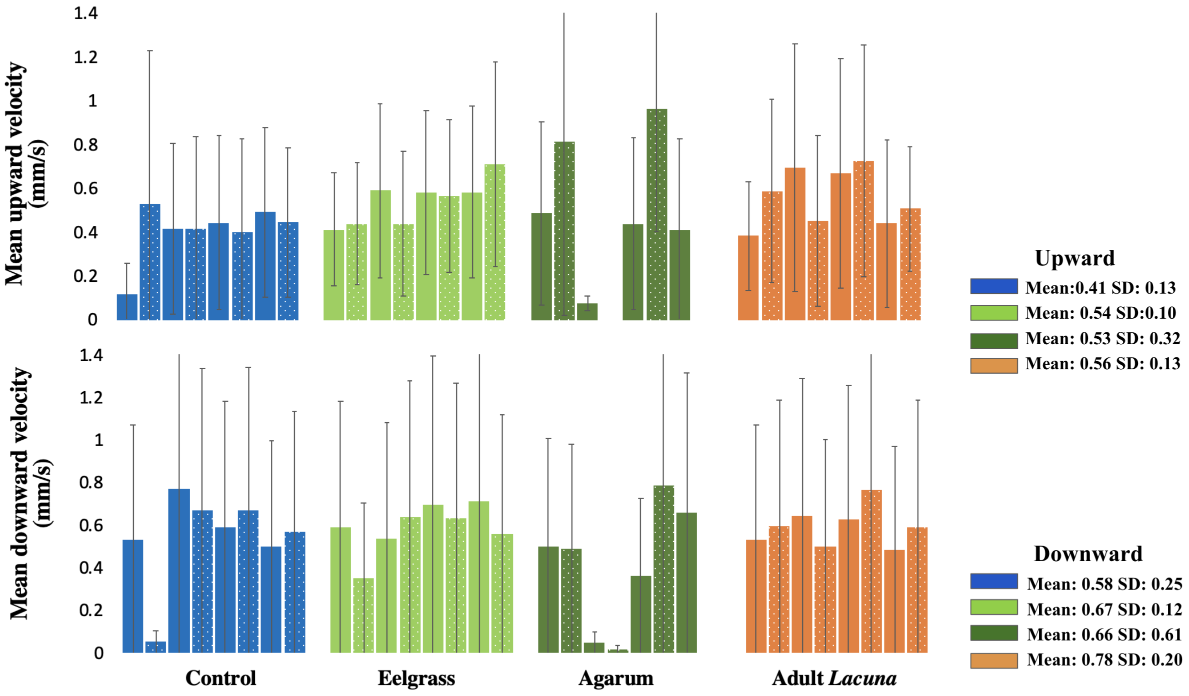

Figure 3. The mean upward and downward swimming speeds for tracked larvae in each treatment, averaged by points. Solid bars are from time point 2 (20 minutes after larval introduction), and dotted bars are from time point 3 (40 minutes after larval introduction).

Mean speed in direction of travel

The mean speed along the path of travel of tracked larval movement was 0.72 mm/s for the control, 0.74 mm/s for eelgrass, 0.84 mm/s for kelp, and 0.85 mm/s for adult snail treatment. The highest value was recorded in a kelp trial, however this result is likely recorded for bubbles which were seen at the beginning of the video. Excluding this trial, the overall highest swimming speeds were recorded in the Adult *Lacuna* treatment, although this trend is not significant.

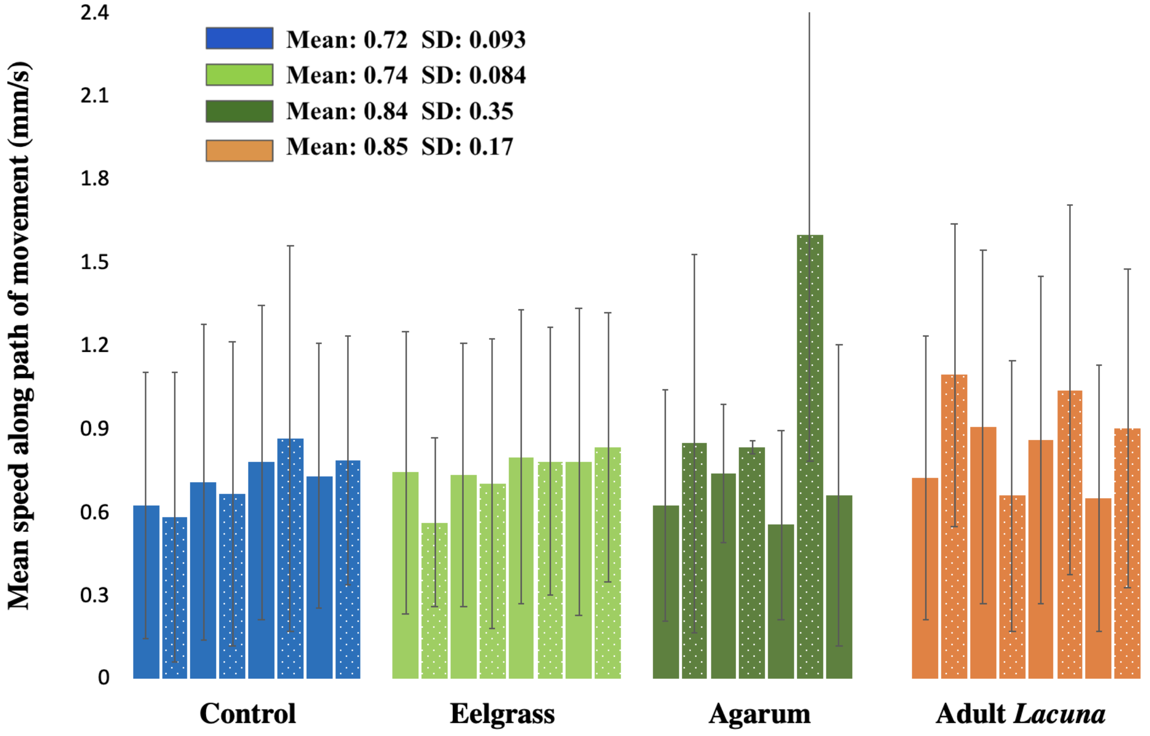

Figure 4. The mean speed along the path of movement for each treatment, averaged by points. Solid bars are from time point 2 (20 minutes after larval introduction), and dotted bars are from time point 3 (40 minutes after larval introduction).

Mean oscillatory and axial speed

Oscillatory motion was quantified as a unitless ratio of oscillatory velocity (perpendicular to the path of net travel) and axial velocity (along the path of net travel). A lower value indicates greater oscillation component of motion relative to directed travel. Conversely, a higher value indicates less oscillation relative to directed travel. The mean values for these ratios for each treatment were highly consistent, with 0.36 for the control, 0.38 for the eelgrass, 0.39 for the kelp, and 0.38 for the adult snail treatment. These data had great variation within each trial, and there was no significant difference between trials or treatments.

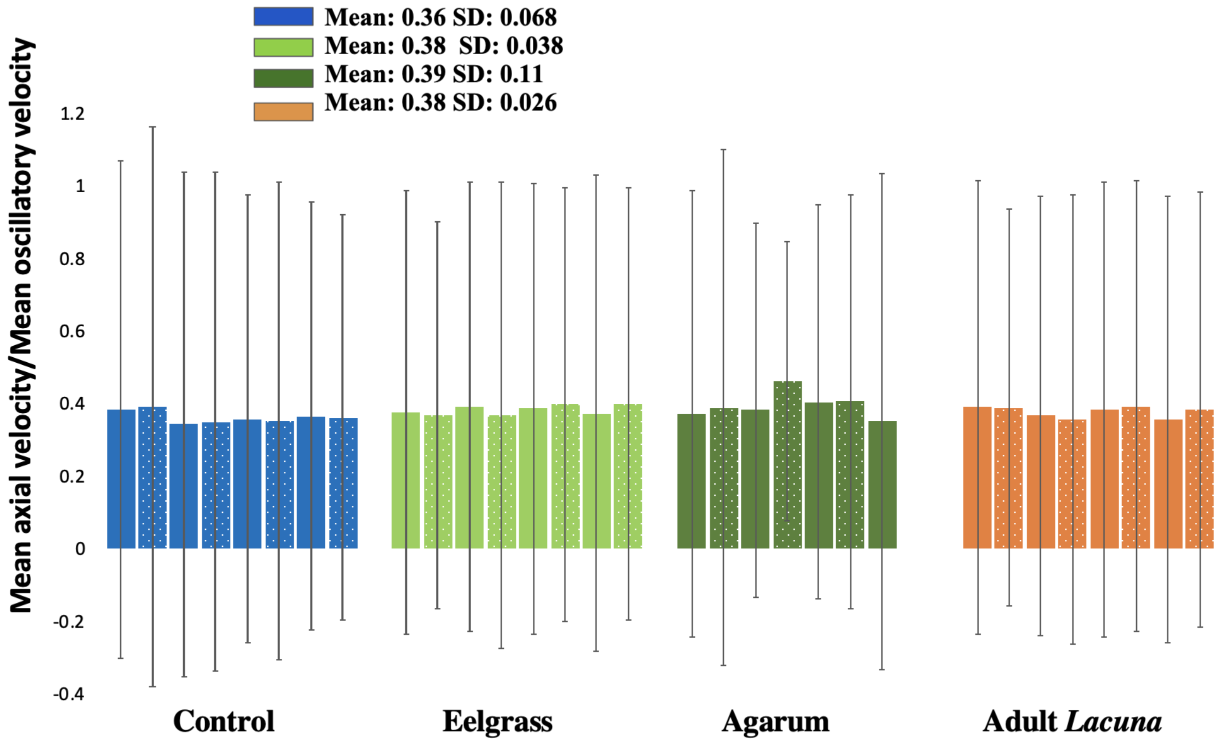

Figure 5. The mean axial speed over the mean oscillatory speed for larvae swimming in each treatment, averaged by points. Solid bars are from time point 2 (20 minutes after larval introduction), and dotted bars are from time point 3 (40 minutes after larval introduction).

DISCUSSION

Larvae of many taxa are known to respond to food, biofilm, or adult conspecific chemical cues when competent to settle to assure settlement in favorable habitat. Most larvae swim too slowly to overcome horizontal current velocities, but they are capable of altering their horizontal movement by vertical swimming to position themselves in distinct current regimes at different levels in the water column. Based on spatially explicit physical models, behaviors to regulate vertical position in the water column are important determinants of dispersal fate. Despite the importance of larval behavior throughout the planktonic duration in determining advection and concentration in sheared flows and fronts, it remains unknown whether larvae respond to cues from adult habitat during their pre-competent stage. Behaviors such as downward swimming, distribution lower in the water column, and more frequent changes of direction may function to maximize retention near favorable future settlement sites. Such behavior could be advantageous if transport far from viable habitat is likely in the physical oceanographic setting, or if habitat is rare, patchy, or limited in spatial extent. Such habitat recognition in early larval life could be significant, as it would increase expectations of larval retention, and provide important evidence that invertebrates respond to signatures of future habitat throughout life. Conversely, behaviors such as upward swimming, distribution higher in the water column, and less frequent changes of direction to favor advection away from benthic habitat. This would be advantageous for avoiding high rates of predation near the benthos or for dispersing to new habitat away from dense adult populations.

We tested the hypotheses that pre-competent larvae would respond to habitat cues by spending more time lower in the water column (favoring retention) or by spending more time higher in the water column (favoring advection). Our results indicate no significant change in distribution in the water column between control columns and cue columns, indicating that pre-competent *L. vincta* larvae do not respond to these particular habitat cues early in their planktonic period. Larvae spent more time swimming higher in the water column in the presence of adult *Lacuna* cues, which might indicate a propensity to try to leave adult habitat in early life stages. Because these studies were conducted in a confined water column, a greater proportion of upward to downward swimming would lead to the observed distribution higher in the water column. However, these differences were slight, and more work is needed to explore this relationship.

We also expected that larvae would respond to habitat cues by either increasing downward swimming speed (favoring retention) or decreasing downward swimming speed (favoring advection). Similarly, we expected larvae to decrease upward swimming speed (favoring retention) or increase upward swimming (favoring advection) when exposed to habitat cue. We found no difference in upward or downward swimming speed between the control and three cues, supporting the hypothesis that *L. vincta* larvae do not respond to these cues by altering vertical swimming speed. Overall across treatments, downward swimming speeds tended to be greater than upward swimming speeds (Figure 3). Although their buoyancy has not been quantified, observationally the larvae appear to be negatively buoyant, which could be responsible for this greater downward swimming speed.

We expected that larvae would respond to adult habitat cues by decreasing (favoring retention) or increasing (favoring advection) mean swimming speed along the path of travel. We saw no significant difference in this metric between the control and three cues, after removing one spurious trial caused by bubbles in the *Agarum* treatment. The mean swimming speed was slightly higher in the presence of adult *Lacuna*, but once again this trend was not significant and requires further study.

Helical swimming has been described in many marine invertebrate larvae, but its implications are not yet well understood (Wang et al. 1987). This behavior may help larvae detect the presence of light and gravity, sense gradients of habitat cues, search for habitat, or control their swimming velocity and direction by changing the height and diameter of the helix. Additionally, more frequent direction changes lead to a greater likelihood of retention (D. Grünbaum, lecture notes). We therefore expected that a greater proportion of oscillatory movement relative to axial movement would favor retention, and the opposite relationship to favor advection in the presence of cues. Our results showed minimal difference between treatments, supporting the hypothesis that *L. vincta* larvae do not change helical geometry in response to the queried cues.

Our results showed no evidence that swimming behavior of pre-competent *L. vincta* larval swimming is affected by chemical cues in the water column. Further studies on the ability of *L. vincta* larvae to alter swimming behavior in response to cues should still be completed, both to test additional cues and to see at what point if any during development *L. vincta* do begin to change their swimming behavior in response to cues. An important caveat of this study is that larval swimming was studied in still water in a confined water column. Swimming behavior in nature, however, will have more complicated implications in the physical oceanographic settings. Retention can be enhanced when larvae are concentrated in sheared fronts, eddies, and internal tidal bores. Moreover, turbulent mixing complicates directional swimming behavior as it changes larval orientation. If habitat cues are well-mixed in the water column, as was the case with our experimental columns, increased downward swimming can lead to greater prevalence of *L. vincta* larvae closer to substrate, where advective currents may be weaker. Future studies should look at the response of these larvae to turbulence and discontinuities in the water column such as haloclines, pycnoclines, and thermoclines, or response to cues in flume experiments with moving water.

One complication with our design was the tendency of larvae to remain on the bottom of the *Agarum* column following injection. To test the cause of this pattern, *Agarum* conditioned water was added to a small dish, and ten larvae were introduced. All quickly retracted their velum and remained at the bottom. Some continued ciliary movement, while in others cilia stopped. When the *Agarum* treatment was diluted to half concentration and veligers were added, they swam normally, indicating a difference in reaction with concentration. Future studies should decrease the concentration of this cue. While the concentration used in this study is likely unrealistic in most field settings, ripped algae can accumulate in mass along coastlines during certain tidal conditions in *L. vincta* habitat. We hypothesize that increases of water viscosity from kelp slime may be a mechanism for larval entanglement and mortality, which may be relevant in intertidal and nearshore subtidal habitat where *L. vincta* hatch. The much smaller number of tracks found by the video analysis confirmed our observations that larvae were not actively swimming in the *Agarum* treatment. The larger velocities and standard deviations associated with the various speed metrics for the *Agarum* treatment may have been due to occasional bubbles in the video that may have been moving faster. Anomalies like these might have been hidden in the other treatments, where the vast majority of tracks were actually from larvae, but were more apparent in the *Agarum* videos where they may have made up the majority of the tracks.

Lacuna are abundant grazers and population booms might affect the species on which they settle. In subtidal kelp beds of Nova Scotia, Canada, large populations of *L. vincta* damage kelp blades, decrease kelp biomass, and increase blade loss during periods of heavy wave action. This has also been shown for kelp in Vancouver, B.C., Canada where newly settled *L. vincta* occured on kelp (Martel & Chia 1991). In Alaska, *L. vincta* densities can reach 1,540 snails/m^2 on juvenile blades of *Nereocystis* (Chenelot and Konar, 2007). The ability to recruit in large numbers may be enhanced if larvae have mechanisms to remain near their natal site throughout development, thus increasing the likelihood of population booms, and affect which algaes or plant populations are grazed. In addition to the role they provide as marine habitat, marine macroalgaes are recognized for their potential as carbon sinks through their eventual transport to the deep ocean (Krause-Jensen & Duarte 2016). *Lacuna* impacts on kelp biomass on large scales may have more global implications.

While *L. vincta* in the San Juan Islands are found on a number of algal species, they also occur on eelgrass where they rasp diatoms from the surface of the blades. As such, if there is a possible chemical cue inducing *L. vincta* settlement on eelgrass habitat, it could be associated with the surface diatoms. In this experiment, the algae and seagrass surfaces were coarsely cleaned by gently scrubbing to remove large particles, epibionts, and *Lacuna* egg cases. Small encrusting algae and biofilms were not removed. Therefore, our results do not isolate the exact plant in question per-se, but rather chemical signatures from the eelgrass or kelp community. Filtering through a 1 micron mesh assured animals, bacteria, and large particles from the cue samples did not end up in the cue water. However chemical signatures of these epibionts may have remained. The goal of the experiment was focused on chemical cues associated with *L. vincta* habitats in a broader sense, as opposed to attempting to isolate what specific cues were responsible for possible behavioral changes within a given habitat. Further studies should investigate in more detail if there are particular diatoms, biofilms, or other microorganisms that may affect settlement more than the habitat species itself. In addition, future research should expand to study whether *L. vincta* larvae of different ages respond differently to chemical cues.

In conclusion, although behaviors throughout the larval lifespan can have implications for dispersal fate, most studies investigate larvae at a time near settlement. This study provides the first measurements of larval swimming behavior of a relatively understudied gastropod species at early stages in the planktonic duration, and demonstrates that these larvae show no significant alteration in swimming behavior in response to the cues tested as signatures of adult habitat.

REFERENCES

Cahill, A.E. and Keoury, S.A. (2016). Larval settlement and metamorphosis in a marine gastropod in response to multiple conspecific cues. *Peer J* DOI:10.7717/peerj.2295.

Chenelot, H. and Konar, B. (2007). *Lacuna vincta* (Mollusca, Neotaenioglossa) herbivory on juvenile and adult Nereocystis luetkeana (Heterokontophyta, Laminariales). *Hydrobiologia 583*(1):107-118.

Ettinger-Epstein, P., Whalan, S., Battershill, C. N., and de Nys, R. (2008). A hierarchy of settlement cues influences larval behaviour in a coral reef sponge. *Marine Ecology Progress Series*, *365*, 103-113.

Fretter, V. and Manly, R. (1977). Algal associations of *Tricolia pullus, Lacuna vincta* and *Cerithiopsis tubercularis* (Gastropoda) with special reference to the settlement of their larvae. *Journal of the marine biological association of the United Kingdom*, *57*(4), 999-1017.

Fuchs, H.L., Gerbi, G.P., Hunter, E.J., and Christman, A.J. (2018). Waves cue distinct behaviors and differentiate transport of congeneric snail larvae from sheltered versus wavy habitats. PNAS. 115(32): E7532-E7540.

Grünbaum, D. (2004). Tracker 3D* Movement Analysis Software.

Krause-Jensen, D., and Duarte, C. M. (2016). Substantial role of macroalgae in marine carbon sequestration. *Nature Geoscience*, *9*(10), 737.

Krumhansl, K. A. and Scheibling, R. E. (2011). Spatial and temporal variation in grazing damage by the gastropod *Lacuna vincta* in Nova Scotian kelp beds. *Aquatic Biology 13*(2):163-173.

Lillis A, Eggleston DB, Bohnenstiehl DR (2014) Oyster Larvae Settle in Response to Habitat-Associated Underwater Sounds. *PLOS ONE* 9(1):10.1371.

Lloyd, M.J., Metaxas, A. and deYoung, B. (2012). Physical and biological factors affect the vertical distribution of larvae of benthic gastropods in a shallow embayment. Marine Ecology Progress Series 464:135-151.

Martel, A. and Chia, F.S., (1991). Oviposition, larval abundance, in situ larval growth and recruitment of the herbivorous gastropod, *Lacuna vincta* in kelp canopies of Barkley Sound, Vancouver Island (British Columbia). *Marine Biology* **110**:237-247.

Pechenik, J.A. (1999). On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Mar. Ecol. Prog. Ser.* 177:269-297.

Pineda, J., Hare, J.A., and Sponaugle, S. (2007). Larval Transport and Dispersal in the Coastal Ocean and Consequences for Population Connectivity. *Oceanus* 20(3): 22-39.

Price, N. (2010). Habitat selection, facilitation, and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. *Oecologia* 163(3): 747–758.

Strathmann, M.F. (1987) *Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast: Data and Methods for the Study of Eggs, Embryos, and Larvae.* University of Washington Press.

Strathmann, R.R. (1985). Feeding and Nonfeeding Larval Development and Life-history Evolution in Marine Invertebrates. *Ann. Rev. Ecol. Syst.* 16:339-61.

Strathmann, R. R. (2014). Culturing larvae of marine invertebrates. In *Developmental Biology of the Sea Urchin and Other Marine Invertebrates* (pp. 1-25). Humana Press, Totowa, NJ.

Wang, W.X. and Xu, Z.Z. (1987) Larval swimming and postlarval drifting behavior in the infaunal bivalve *Sinonovacula constricta*. *Mar Ecol Prog Ser* 148:71-81.

Wheeler, J.D. (2016) Behavioral Responses of Invertebrate Larvae to Water Column Cues. PhD Thesis. MIT/WHOI Joint Program in Oceanography, Applied Ocean Science, and Engineering.

Woodson, C.B., McManus, M.A., Tyburczy, J.A, Barth, J.A., Washburn, L., Caselle, J.E., Carr, M.E., Malone, D.P., Raimondi, P.T., Menge, B.A., and Palumbi, S.R. (2012). Coastal fronts set recruitment and connectivity pattern across multiple taxa. *Limnology and Oceanography* 57(2):582–596.