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THE INFLUENCE OF SEDIMENT CHARACTERISTICS ON THE
BURROWING BEHAVIOR OF JUVENILE RAZOR CLAMS,

ENSIS DIRECTUS

by

Robert J. Hallinan

A Thesis Submitted in Partial Fulfillment
of the Requirements for a Degree with Honors
(Biology)

The Honors College

University of Maine

December 2015

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ABSTRACT

Ensis directus, the Atlantic razor clam, is an infaunal bivalve species whose geographic range extends along the Atlantic coast of North America from Canada to South Carolina. In this study, I examined the burrowing behavior of 24 large juvenile razor clams (shell length: 60-78 mm) in fine mud and coarse sand sediments. I identified four separate phases of burrowing behavior: recovery, exploration, initiation, and tunneling. Using video analysis, I estimated the proportion of clams completing each of these phases and the time it took them to complete each phase in both sediment types. All 24 clams were exposed to both sediment types; I found that the order in which sediments were presented (i.e., whether clams were presented with mud or coarse sand prior to being presented with the second sediment type) did not impact burrowing behavior. In contrast, more razor clams burrowed in the fine mud sediment and completed each phase of burrowing more quickly than they did in the coarse sand. Measurements of the sediment shear and compressive strengths determined that the coarse sand was more resistant to sediment deformation. Lastly, I utilized pressure sensors to correlate the phases of burrowing activities with changes in the pressure within sediment porewater. I found that larger changes in porewater pressure occurred while clams were burrowing in the mud compared to the coarse sand. This research determined that the burrowing behavior of this species is sediment-dependent and should be taken into account when siting facilities for razor-clam aquaculture.

This thesis is dedicated to Robert and Debra Hallinan whose support and dedication toward their careers inspired me to pursue my goals with that same passion.

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INTRODUCTION

Ensis directus, the Atlantic razor clam, is an infaunal bivalve that inhabits the intertidal and subtidal zones along the Atlantic coast. They are typically found in habitats with sandy and muddy substrate (Kenchington *et al.*, 1998). Resembling a straightedge razor, *E. directus* is an elongated suspension-feeding bivalve mollusk with a convex shell the width of which does not significantly diminish along the length of the shell, and a color that varies from yellow to dark brown (Camponelli, 2001; see Fig. 1).



Figure 1: *Ensis Directus*. The razor clam's name is indicative of its external physical characteristics. Adult razor clams are typically 4-6 in prior to harvest. Source of photograph: <http://maineoceanlover.blogspot.com/2014/08/razor-clam-escape-artist.html>.

The shell consists of two valves, hinged together by an elastic ligament, that are formed by the secretion of calcium carbonate and a protein matrix by two mantle regions that enclose the clam's body (Leavitt, 2010). Encompassing the shell is a layer of periostracum, an elastic cuticle that protects the shell from erosion within the sediment. At the anterior end of the shell, the clam can extend a muscular foot used for locomotion and burrowing (Leavitt, 2010). At the posterior end are two siphons; ciliary action on the

gills creates inward water flow through the inhalant siphon. This inhalant current passes across the gills where suspended food particles are retained and transported to the mouth (Dame, 1996). The gills are also where gas exchange (O_2 and CO_2) occurs. After passing across the gills, the water exits through the exhalant siphon. On average, *E. directus* grows up to 150-200 mm long, although the length of razor clams is temporarily increased by half their body length when the foot is fully extended (Leavitt, 2010).

Razor clams are considered to have high potential as an aquaculture species due to their increasing popularity throughout the world (da Costa *et al.*, 2011). Harvesting natural beds has caused declines in the abundance of several razor clam species in Europe, resulting in unsustainable wild harvests that cannot meet commercial demand (da Costa *et al.*, 2011). Through aquaculture, a sustainable source of razor clams can be realized, helping to achieve the Northeastern Regional Aquaculture Center's goal of increasing the "production of alternative species for the diversification of the northeastern shellfish culture industry."

In order to establish the culture of *E. directus*, growers must first determine environmental conditions that are optimal for growth. In this thesis, I investigated the influence of sediment characteristics on the burrowing behavior of *E. directus*. These sediment characteristics may differentially affect the retention and survival of razor clams in grow-out sites. If the results indicate a greater rate and frequency of burrowing in one sediment type compared to others, then farmers can select appropriate culture sites that are suitable to promote growth and development.

While razor clams are able to live outside of sediment, they typically burrow through substrate for anchorage and protection from predators. During burrowing, the clam first inserts its muscular foot (which runs lengthwise inside the shell) into the substrate below and then extends its foot to uplift the valves (Fig. 2). Meanwhile, the clam adducts its valves creating changes in hydrostatic pressure and causing swelling in the foot to serve as a pedal anchor (Trueman, 1966). Contraction of the pedal retractor muscles pulls the razor clam into the sediment and helps to compact the sides of the burrow (Trueman, 1966). Lastly, the valves relax removing blood from the foot to begin the process anew to continue burrowing.

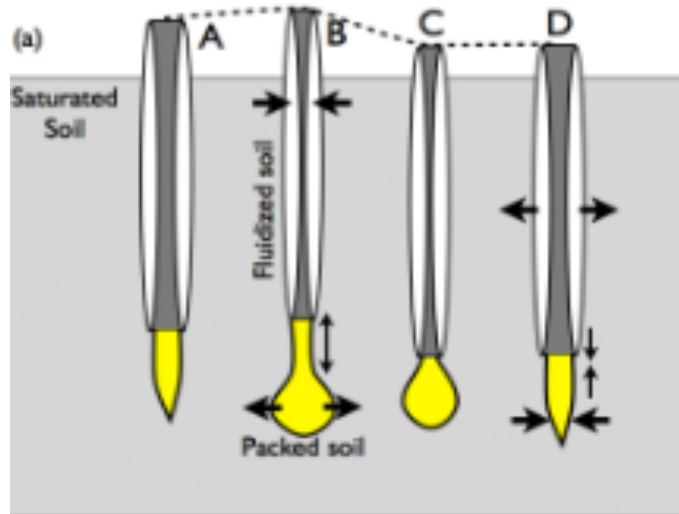


Figure 2: Schematics of *Ensis directus* Burrowing According to Jung *et al.* (2011). This image is taken directly from Jung *et al.*'s (2011) "Dynamics Of Digging In Wet Soil." (A) The muscular foot is inserted into the sediment. (B) Swelling of the foot creates an anchor, and the valves close. (C) The clam pulls itself into the sediment. (D) The valves expand, and the foot relaxes to begin the process again. See text for further details on how clam behavior creates a localized zone of fluidization that facilitates burrowing through sediment.

Jung *et al.* (2011) has described burrowing by razor clams as a two-anchor locomotion scheme, where one portion of the animal's body expands to serve as an

anchor to hold the animal in place while another portion contracts to reduce drag, thereby reducing friction that opposes its movement (Fig. 2). However, *E. directus* is capable of producing 10N of pulling force, which is insufficient to burrow in static sediment (Dorsch & Winter, 2014). While sediment behaves as a solid when undisturbed, increases in porewater pressure can suspend the sediment particles, causing them to flow, (i.e. fluidize; Dorgan, 2015). This advection of porewater occurs down a pressure gradient created by valve movement by the clams; porewater flows from areas of high to low pressure in permeable sediments (Waldbusser, 2008). As the porewater reaches the walls of the burrow, it unpacks and fluidizes the burrow causing sediment failure as a zone of localized fluidization and essentially “mushy” unpacked sediments underneath the foot (Jung *et al.*, 2011). As the incoming water mixes with the surrounding static, solid-like substrate within the burrow, the sediment failure allows the clam to travel through the newly dynamic, fluid-like state of the granular sediment before the burrow collapses (Winter *et al.*, 2012) and reducing the resistance force of drag and allowing the clam to burrow through the sediment with only 10N of force (Jung *et al.*, 2011). Because drag resistance is reduced when moving through a fluidized medium compared to static, the razor clam saves energy as it burrows. Clams are able to burrow several centimeters in static sediment, but the fluidization allows them to burrow over 70 cm (Winter, 2012).

Research on other infaunal bivalves has shown that sediment characteristics can affect morphology, energetics, and ecology. According to Thomson and Gannon (2013), there are advantages and disadvantages associated with softshell clam (*Mya arenaria*) burrowing in sediments of varying grain size. In coarser sediments, the clams must

expend more energy in order to burrow, thus their burrowing depths are shallower. However, clams that burrow in coarser sediments develop thicker shells, which reduces predation rates. In finer sediments, clams do not need to expend as much energy to burrow, so they can burrow deeper into the sediment to avoid predation. It is important to note that the depth to which clams burrowed in all sediment types increased in the presence of a predator (Thomson & Gannon, 2013), further indicating that clams can effectively sense and respond to environmental cues at various stages. To date, the impacts of sediment type on razor clam morphology, physiology, and behavior has received little attention.

In this thesis, I analyzed the changes in burrowing behavior in response to two sediment types with contrasting physical properties: fine mud and coarse sand. Whereas mud is both cohesive and elastic, sand is non-cohesive and porous, and thus more permeable than mud. These properties influence the sediment's ability to compact, thus influencing the amount of advection of porewater for localized fluidization, which ultimately affects burrowing behavior (Francoeur & Dorgan, 2014). Because the coarse sand used in this experiment was composed of particles that were heterogeneous in size, I hypothesized that razor clams would complete the burrowing process, and would do so more quickly, in the coarse sand because of the greater potential for fluidization that results from greater sediment permeability.

In addition, I measured the changes in porewater pressure that occur during burrowing in each sediment type. I expected changes in porewater pressure to be smaller in the mud sediment compared to that of the coarse sand sediment. In sediments with

fewer interstitial spaces where sediment particles bind together more compactly, such as mud compared to sand, there may be less of an energetic cost for burrowing. This may explain Addino *et al.*'s (2014) findings in which there was higher density of stout razor clams (*Tagelus plebius*) in areas of greater clay and silt content. Less energetic expenditures allow razor clams to exert less force while burrowing and therefore less pressure is applied to the advecting porewater. In addition, larger pores allow greater ease through which porewater flows through the sediment (i.e., greater permeability). This allows for greater advection, and thus greater changes in pressure, through the more permeable coarse sand.

Documenting the variation in razor clam behavior associated with burrowing in different sediment types may help farmers interested in culturing razor clams identify appropriate sites that will retain razor clams. Raising razor clams in areas where the clams prefer to burrow will result in a larger yield as fewer are likely to emigrate from the culture site, predation rates will be lower, and growth and development will be enhanced. Although burrowing by clams can make it more difficult to harvest them, farmers must ensure that razor clams planted in a given location will still be there at harvest. Understanding key interactions between the clams and their habitat is important for farmers to maximize the efficiency of their harvest (da Costa *et al.*, 2011) and ensuring that *E. directus* is a viable species for aquaculture.

METHODS AND MATERIALS

The razor clams used in my thesis were from a single cohort of clams produced at the Darling Marine Center in June 2012 (see Flanagan 2013 for details). In brief, ripe adult razor clams were placed in a 0.8 m x 1.2 m spawning table that contained a 12 mm layer of UV sterilized, filtered seawater (UVFSW) at 15°C. Over the course of three hours, the temperature was gradually increased to 22°C to produce a temperature shock, a method typically used to induce bivalves to spawn. Female razor clams released a string of white eggs, and male razor clams released a cloudy, white suspension of sperm. In order to control fertilization, individual razor clams were removed from the spawning table as soon as they began releasing gametes and were placed in separate 1 L beakers containing UVFSW 15°C.

A standard hatchery protocol for fertilization of marine bivalves was employed (Helm & Bourne, 2004). The eggs from each female were first captured on a 20 µm mesh sieve and rinsed with UVFSW to remove metabolic wastes that may have accumulated in the spawning beakers. The eggs from each female were then rinsed back into beakers containing fresh UVFSW. Sperm from spawning males was collected as it exited the clam and placed in a microcentrifuge tube on ice to retain sperm activity while the eggs were prepared. To reduce the chances of a polyspermy, which results in irregularities in growth and development, eggs were fertilized with sperm at a 100:1 sperm to egg ratio. As soon as fertilization was evident for a majority of the eggs from each female (extrusion of polar body), the fertilized eggs were captured on a 20 µm mesh sieve while allowing excess sperm to pass through. For the next 48 hours, the embryos were held in

20 L buckets containing UVFSW at 15°C by which time they progressed through the trochophore stage and entered the D-stage of larval development (i.e., the development of the hinged valves). After 36 hours, the water temperature was raised from 16°C to 19°C.

D-stage razor clam larvae were transferred into four tanks containing 350 L UVFSW at ambient temperature at a density of 10 larvae•ml⁻¹. Every other day, the water in each tank was drained and replaced with new UVFSW. An 80 µm mesh sieve was used to capture larvae during the draining of the tank and facilitate their transfer to the fresh UVFSW. The density of the razor clam populations was reduced to 2 larvae•ml⁻¹ as the clams continued to grow; excess clams were transferred into three additional 350 L tanks. This process allowed for the culture of 700,000 razor clams from D-stage to metamorphosis.

Once the juveniles appeared to reach competency and settled, the razor clams were set in sand containers immersed in tanks receiving ambient Damariscotta River water. The clams were then held in these flowing-seawater tanks at the Darling Marine Center until they were used in my experiment. All clams used in my project were transported on ice to the University of Maine, Orono in spring 2015. At the University of Maine, they were placed in the seawater recirculating system in the basement of Murray Hall and allowed to acclimate to the conditions (32 ppt salinity, ~15°C) in the recirculating system and recover from the transport. During the acclimation process, the razor clams were held in a submerged plastic container with a mixture of fine and coarse sediments and were fed Shellfish Diet (Reed Mariculture), *ad-libitum*.

Twenty-four razor clams (shell length: 60-78 mm) were presented with two different types of sediment to determine how sediment characteristics influence their burrowing behavior. The test subjects were placed into 1 L beakers containing one of two sediment types, fine mud from Lowe's Cove in Maine's Damariscotta River adjacent to the Darling Marine Center and coarse sand-shell hash from the mouth of Maine's Pemaquid River at the Colonial Pemaquid State Historic Site (hereafter referred to as "mud" and "coarse sand", respectively).

To begin the process, I removed four razor clams from the acclimation sediment held in the recirculating seawater system (32 psu at 14.8°C) and placed them in a submerged wood frame box with a 220 µm Nitex mesh screen bottom in the same tank. The razor clams remained here for 12 hours; this holding period was intended to reduce differences in stress among individuals that may have occurred during their removal from the acclimation sediments (or later from experimental beakers).



Figure 3: Preparation of Razor Clams for Burrowing Trials. Razor clams were removed from the acclimation sediment and held on a mesh screen prior to their placement in the experimental sediments.

The burrowing experiments were conducted in a second adjoining tank in the same recirculating system. I prepared eight 1 L plastic beakers by removing the bottom of each beaker and replacing it with a 220 μm Nitex mesh lining. The beakers were then filled with approximately 600 mL of experimental sediment. The Nitex bottom was designed to allow sufficient water flow through the sediments within the beakers to prevent the sediments from becoming anoxic (i.e., to prevent depletion of O_2 and build-up of sulfides due to microbial activity). I placed mud in four beakers and coarse sand in the other four. The beakers were held suspended just above the bottom of the tank to further promote water flow through the sediments to prevent anoxic conditions. The 12-hour recovery period also allowed the sediment sufficient time to settle in order to improve water clarity for observations of burrowing behavior.

I observed burrowing behavior in a set of six trials. For three trials I transferred four clams into four of the immersed 1 L plastic beakers (one clam per beaker) containing mud. A video camera was activated once the razor clams were introduced to the experimental sediment to record their activity. Burrowing activity was observed for a total of 20 minutes, after which the clams were removed from the experimental beakers and returned to the submerged mesh box for another 12 hours before they were presented with the coarse sand. I then introduced the same clams to the beakers of the coarse sand and their activity recorded via video camera. A second set of trials was conducted in which clams were first presented with coarse sand prior to being presented with mud. After observing the clams' behavior in both sediments, they were removed from the sediment and I measured their shell length, shell height, shell width, and wet weight.



Figure 4: Measuring Razor Clam Size. Three external shell dimensions were estimated for each clam. Shell length of a razor clam is the dimension along the longest axis of the shell (above). In addition, shell width was measured perpendicular to the length measurements at half the length of the razor clam. The height measurements were taken across the top of the valves where the siphons are exposed.

Twice more, I repeated this process of presenting razor clams first with the mud and then the coarse sand. For three additional trials, I again presented razor clams first with the coarse sand and then mud. For each trial, four new razor clams were used. The introduction of the razor clams first to one sediment type and then the other allowed me to examine whether the order of presentation affected burrowing behavior in each sediment type.

To process video files, I identified four phases of burrowing behavior, each being a distinct event shared by all razor clams in the process of burrowing. The first phase was a recovery period defined as the time between introduction of a clam to the experimental

sediment and the time the clam began to probe the sediment surface with its foot. The second phase was an exploration period between the initial probing of the sediment surface and the initiation of burrowing, indicated by the insertion of the foot into the sediment. The initiation period (3rd phase) was the time between the insertion of the foot and when the razor clam hoists itself upright into the sediment. The fourth and final stage of burrowing activity observed was tunneling, consisting of the time between being upright and complete burial. I used iMovie to analyze the video recordings and determine whether individual razor clams completed each of the phases of burrowing within the 20 minute recording period, and if they did, how much time had elapsed for the completion of each phase. Identifying these phases allowed me to compare how different stages of burrowing behavior are influenced by sediment type.

Lastly, I conducted additional trials in which I placed stainless steel pressure sensors (Sensym ICT Series 19/SPT, 5 psi gauge) near the edge of the beakers to record porewater pressure differences associated with each phase of clam burrowing (as per Wethey & Woodin, 2005) for an additional twelve clams. Positive changes in pressure occur when porewater is pumped into the sediment, and negative changes in pressure occur when porewater is discharged from the burrow onto the surface sediments (Wethey & Woodin, 2005). Any changes in pressure observed indicated changes in the porewater pressure, which is largely influenced by the permeability of the sediment and correlates with its porosity (Volkenborn *et al.*, 2010). Prior to experimentation, the pressure sensor's chamber was filled with seawater and covered with Nitex mesh to prevent the entry of any sediment. The sensor was then calibrated in a 5 gallon bucket by submerging

the diaphragm of the sensor from 0-40 cm with depth increments of 5 cm and 1 min at each depth (as per Wetthey & Woodin, 2005). I conducted a total of six trials in which I measured the behavior and pressure changes for pairs of clams. In three trials, pairs of clams were provided with mud and in the other trials they were presented with coarse sand. The purpose of using these pressure sensors was to create a better understanding of the events occurring during burrowing and the interaction between clams, the sediment and sediment pore-water.



Figure 5: Pressure Recordings of Razor Clam Burrowing. I used a video camera to track the timing of the various phases of burrowing behavior and to correlate behavior with variation in porewater pressure, (i.e., the changes in pressure within the sediment caused by clam burrowing activity).

In addition to recording razor clam activity, I also recorded characteristics of the experimental sediments. Prior to introducing clams into the experimental beakers containing the mud, I used a Torvane gauge to measure the lateral stress (the shear strength) of the sediment. Once firmly lodged into the sediment, I twisted the Torvane until the sediment gave way to the force applied and recorded the value. Then, in those same beakers, I used a S-170 Pocket Penetrometer to measure the longitudinal stress (the compressive strength) of the sediment. I placed the tip of the penetrometer on the sediment surface (in an area that had not been disturbed by the Torvane), applied a downward force until the tip was fully lodged into the sediment, and recorded the value. I then repeated this process with four beakers containing the coarse sand.

I compared the frequency of clams completing each phase of burrowing in the two sediment types using R x C contingency tests. I also compared the differences in the mean time required for clams to complete each phase of burrowing using t-tests. T-tests were also used to determine the statistical significance of differences in shear and compressive strength for the two sediment types. For all of these statistical comparisons I employed Excel-based programs available from McDonald (2014).

RESULTS

The order in which razor clams were introduced to each sediment did not significantly affect burrowing behavior (i.e., previous burrowing experience did not affect the proportion of clams that completed each phase of burrowing). In the mud, all clams completed the recovery, exploration, and initiation phases of burrowing regardless of whether they were presented with the mud or coarse sand first (Fig. 6). The proportion of clams completing the tunneling phase of burrowing in mud differed among clams introduced first to the mud versus the coarse sand, but this difference was not statistically significant (r x c contingency test, $X^2=0.381$, d.f.=1, $p=0.537$). Equal proportions of clams completed the exploration, initiation, and tunneling phases in the coarse sand, independent of the order of sediment presentation (Fig. 7). The proportion of clams completing the recovery phase in coarse sand differed depending on the order of sediment presentation, however, the difference was not statistically significant (r x c contingency test, $X^2=1.04$, d.f.=1, $p=0.307$).

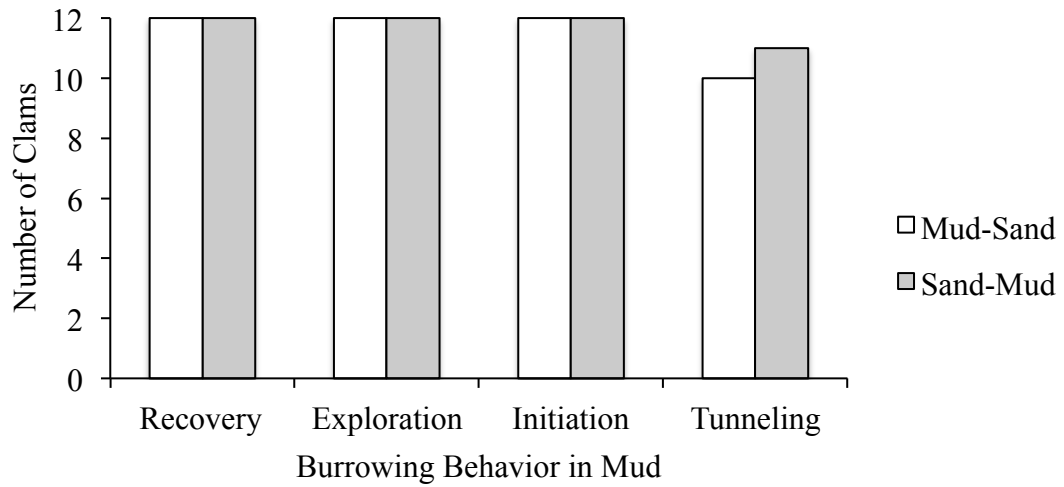


Figure 6: Order of Sediment Presentation and Burrowing Behavior Completion in Mud. The height of the bars indicates the number of razor clams that completed the given phase of burrowing behavior in the mud. The white bars indicate the number of clams completing each phase that were introduced to the mud first (mud-sand) while the grey bars indicate the razor clams introduced to the mud after being presented with the coarse sand (sand-mud).

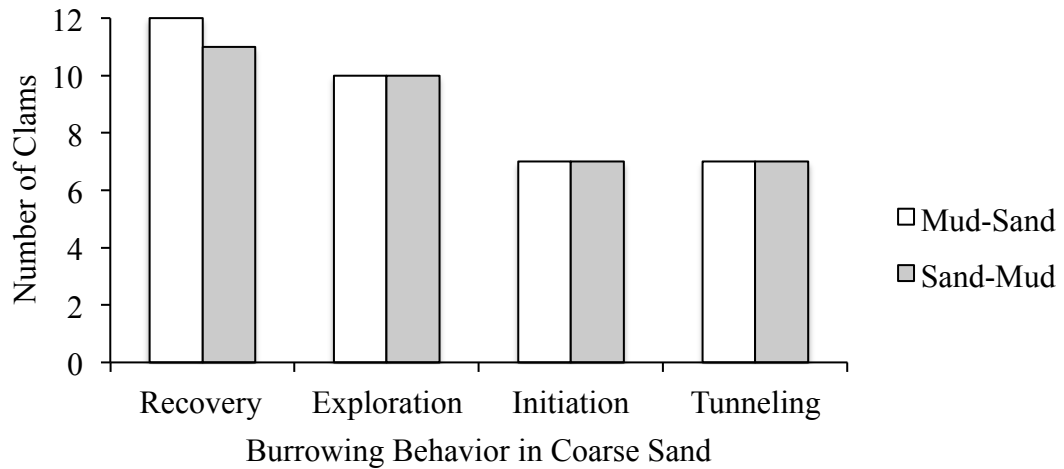


Figure 7: Order of Sediment Presentation and Burrowing Behavior Completion in Coarse Sand. The height of the bars indicates the number of razor clams that completed the given phase of burrowing behavior in the coarse sand. The white bars indicate the number of clams completing each phase that were introduced to the mud first (Mud-Sand) while the grey bars indicate the razor clams introduced to the mud after being presented with the coarse sand (Sand-Mud).

The time it took for clams to complete each of the four phases of burrowing in each sediment types was, likewise, not dependent on the order in which the sediments were presented. In the mud, the length of time it took for clams to complete the exploration, initiation, and tunneling phases of burrowing were drastically lower than the time at which they completed the recovery phase (Fig. 8). Although the time at which each phase was completed in mud varied by up to 22% among clams introduced first to the mud versus the coarse sand, there was no significant difference in the time of burrowing phase completion when comparing order of sediment presentation (t-tests; d.f.=1, $p=0.099-0.349$). In the coarse sand, the length of time it took clams to complete the exploration, initiation, and tunneling phases of burrowing was again drastically lower than the time it took them to complete the recovery phase (Fig. 9). There was more variation in the average time required for clams to complete each phase in coarse sand among clams introduced first to coarse sand versus mud. However, there was also substantially more individual variation in the time it took in coarse sand so these differences were not significant (t-tests, d.f.=1, $p=0.159-0.500$).

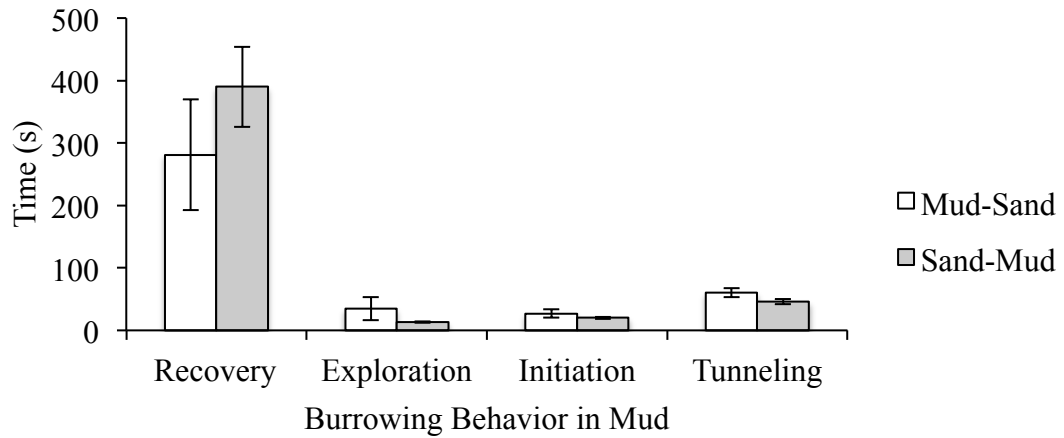


Figure 8: Order of Sediment Presentation and the Time (Mean \pm SE) of Burrowing Behavior Completion in Mud. The height of the bars indicates the average time of burrowing phase completion in the mud. Error bars represent standard error of the mean. The white bars indicate the times at which clams completed each phase when introduced to the mud first (Mud-Sand); the grey bars indicate the times at which clams completed each phase when introduced to the mud after being presented with the coarse sand (Sand-Mud).

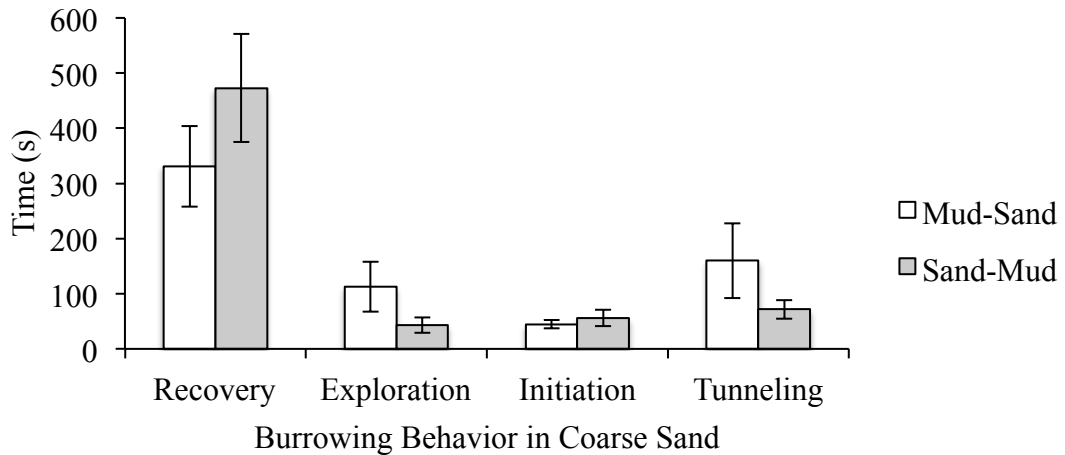


Figure 9: Order of Sediment Presentation and the Time (Mean \pm SE) of Burrowing Behavior Completion in Coarse Sand. The height of the bars indicates the average time of burrowing phase completion in the coarse sand. Error bars represent standard error of the mean. The white bars indicate the times at which clams completed each phase when introduced to the mud first (Mud-Sand); the grey bars indicate the times at which clams completed each phase when introduced to the mud after being presented with the coarse sand (Sand-Mud).

Given that the order of sediment presentation did not influence the number of razor clams completing each phase of burrowing or the time required to completed each behavior, I proceeded to compare the burrowing behavior of clams in each sediment type without regard to the order in which sediments were presented. There was a minor and statistically not significant difference in the number of clams completing the recovery phase in mud versus coarse sand (Fig. 10; R x C contingency test, $X^2=1.02$, d.f.=1, $p=0.312$). In contrast, up to 42% fewer clams completed the exploration, initiation and tunneling phases in coarse sand compared to those completing each phase in mud. In all three comparisons the differences were statistically significant (R x C contingency tests, $X^2=3.63-12.60$, d.f.-1, $p=0.057-<0.001$). On average, the razor clams completed all phases of burrowing behavior 1.2 to 3.2-fold faster in the mud compared to the coarse sand (Fig. 11). While there was not a significant difference among the razor clams in the time it took to complete the recovery phase of burrowing behavior in the two sediment types (t-test, d.f.=1, $p=0.443$), there was a significant difference in the time required to complete the exploration, initiation, and tunneling phases of burrowing in the different sediments (t-tests, d.f.=1, $p=0.001-0.040$).

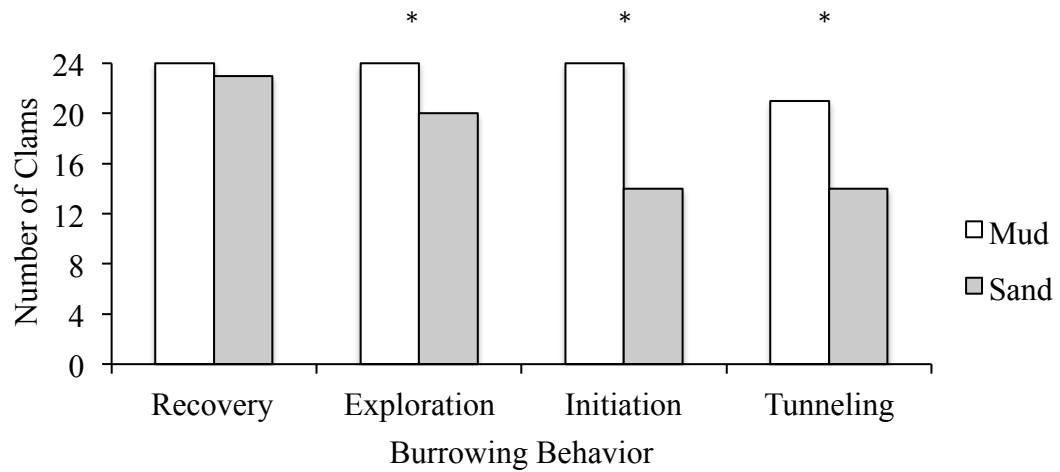


Figure 10: Completion of Burrowing Behavior in Mud and Coarse Sand. The height of each bar indicates the total number of clams (out of 24) that completed the given phase of burrowing behavior in both the mud (white bars) and coarse sand (grey bars). An asterisk indicates any difference in the number of razor clams that completed a given phase of burrowing behavior in the two sediment types that was statistically significant.

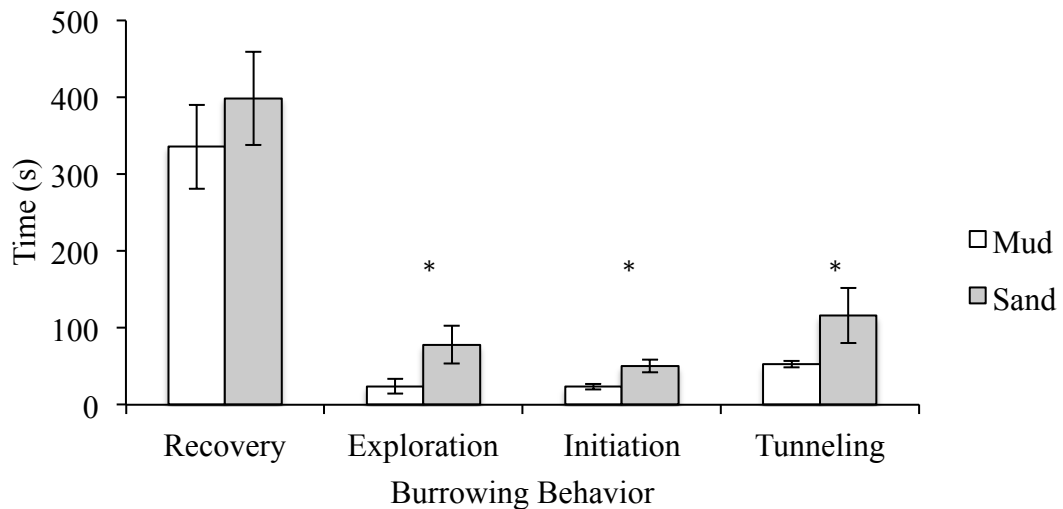


Figure 11: Average Time of Burrowing Behavior Completion in Mud and Coarse Sand. The height of the bars indicates the mean time at which the razor clams completed the given phase of burrowing behavior in mud (white bars) and coarse sand (grey bars). Error bars represent the standard error of the mean. An asterisk indicates any difference in the time required for razor clams to complete a given phase of burrowing behavior in the two sediment types that was statistically significant.

Torvane and penetrometer-based measurements indicated that the coarse sand was able to withstand more pressure, both laterally and longitudinally, prior to sediment failure compared to the mud (Fig.12). The coarse sand had greater shear strength (as demonstrated with the Torvane) and compressive strength (as demonstrated with the S-170 Pocket Penetrometer) compared to the mud used in this experiment. When comparing sediment integrity, the differences in the shear strength and the compressive strength between the two sediment types were statistically significant (t-tests, d.f.=1, $p=0.0011$ and $p=0.0001$, respectively).

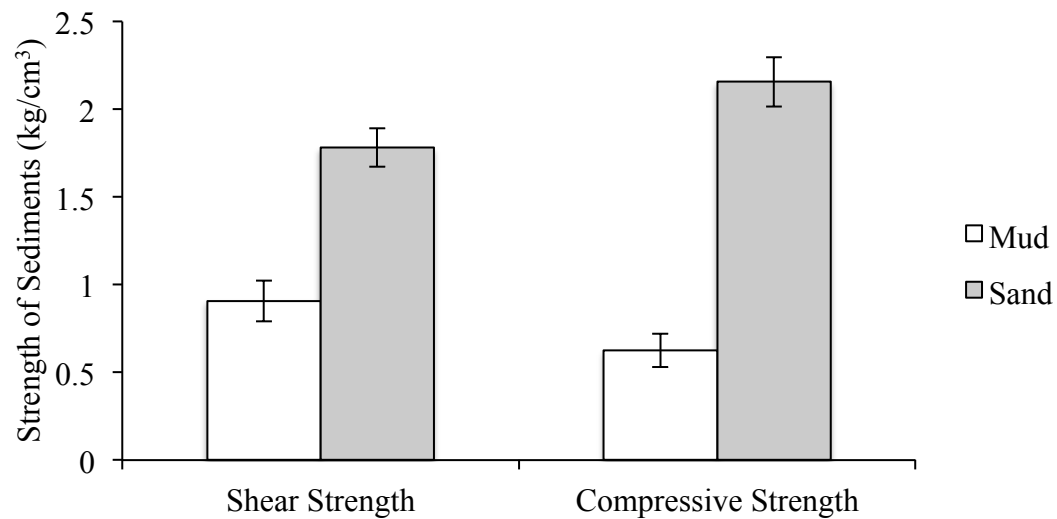


Figure 12: Shear and Compressive Strength of Mud and Coarse Sand. The height of the bars indicates the average force needed to cause sediment failure both horizontally (shear strength) and vertically (compressive strength) in the mud (white bars) and the coarse sand (grey bars). Error bars represent the standard error of the mean.

I also examined the relationship between the morphometric measurements (length and width) of the razor clams and the times at which they completed each phase of burrowing in both sediment types (for those that completed the specified behavior). There was no discernable trend between the time required to complete each phase and clam length (Fig. 13-16) or clam width (Fig. 17-20). Estimates of the correlation between the time required to complete each phase and length or width were small ($r^2=0 - 0.371551$) and not significantly different from zero. This indicates that neither the length nor width of the razor clams influenced the rate at which they completed each phase of burrowing, regardless of sediment type.

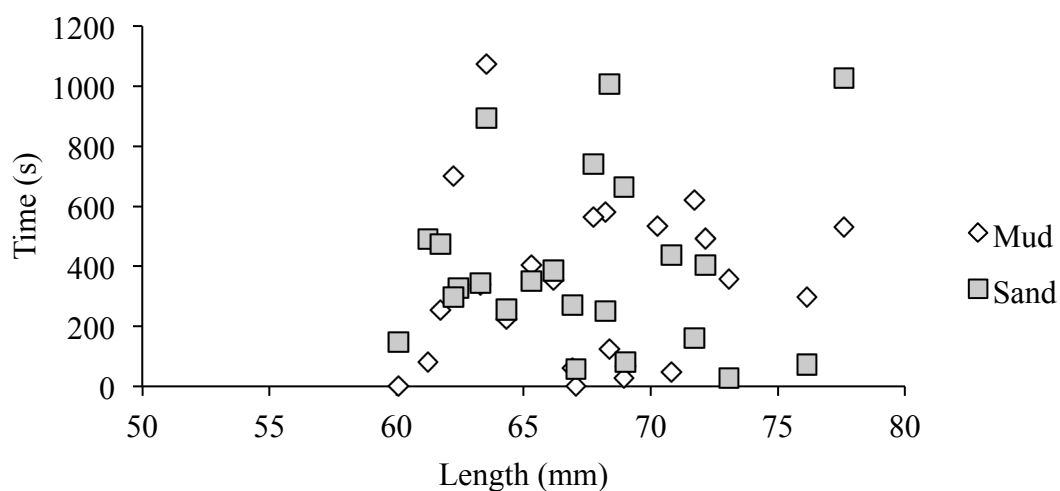


Figure 13: Relationship Between Razor Clam Length and Recovery Rate. A comparison of the length of each razor clam to the rate at which they completed the recovery phase of burrowing behavior in both the mud (white diamonds) and the coarse sand (grey squares).

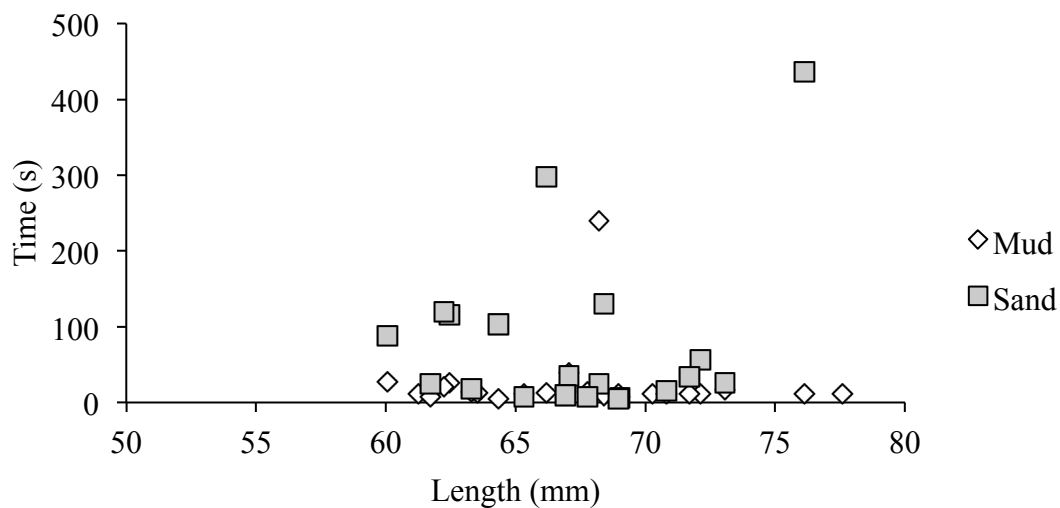


Figure 14: Relationship Between Razor Clam Length and Exploration Rate. A comparison of the length of each razor clam to the rate at which they completed the exploration phase of burrowing behavior in both the mud (white diamonds) and the coarse sand (grey squares).

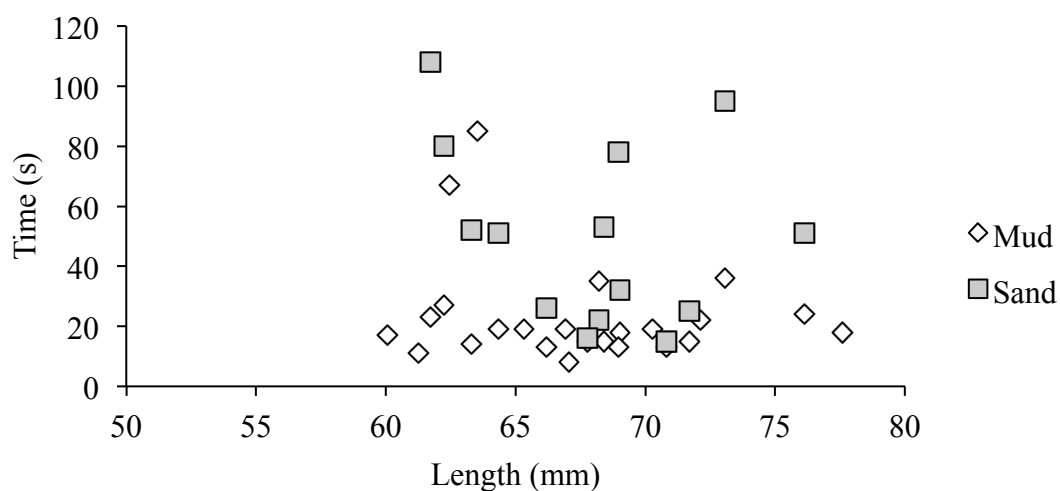


Figure 15: Relationship Between Razor Clam Length and Initiation Rate. A comparison of the length of each razor clam to the rate at which they completed the initiation phase of burrowing behavior in both the mud (white diamonds) and the coarse sand (grey squares).

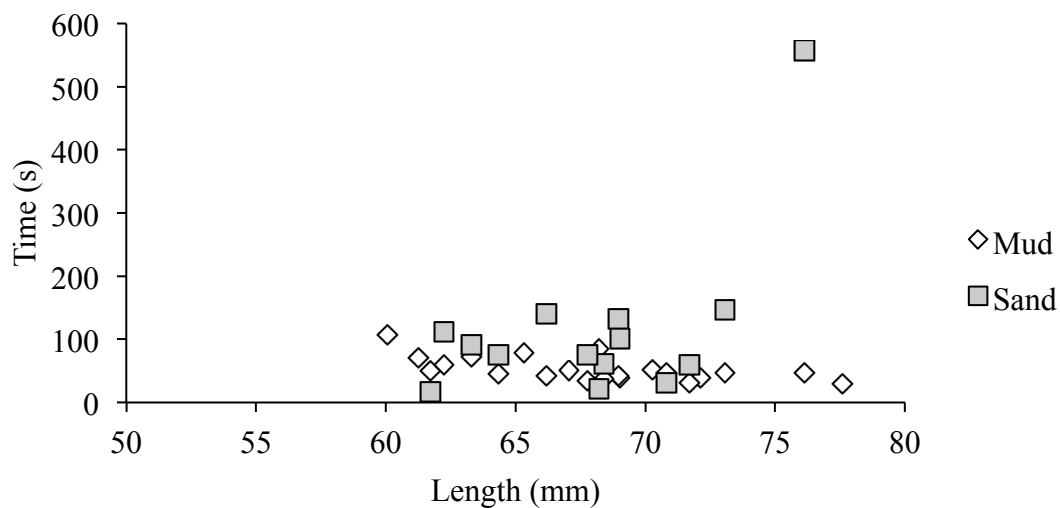


Figure 16: Relationship Between Razor Clam Length and Tunneling Rate. A comparison of the length of each razor clam to the rate at which they completed the tunneling phase of burrowing behavior in both the mud (white diamonds) and the coarse sand (grey squares).

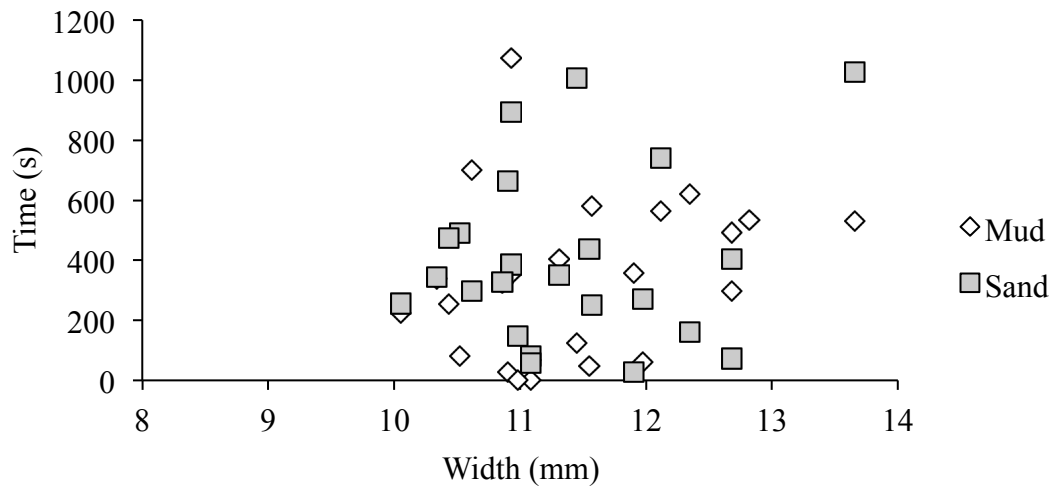


Figure 17: Relationship Between Razor Clam Width and Recovery Rate. A comparison of the width of each razor clam to the rate at which they completed the recovery phase of burrowing behavior in both the mud (white diamonds) and the coarse sand (grey squares).

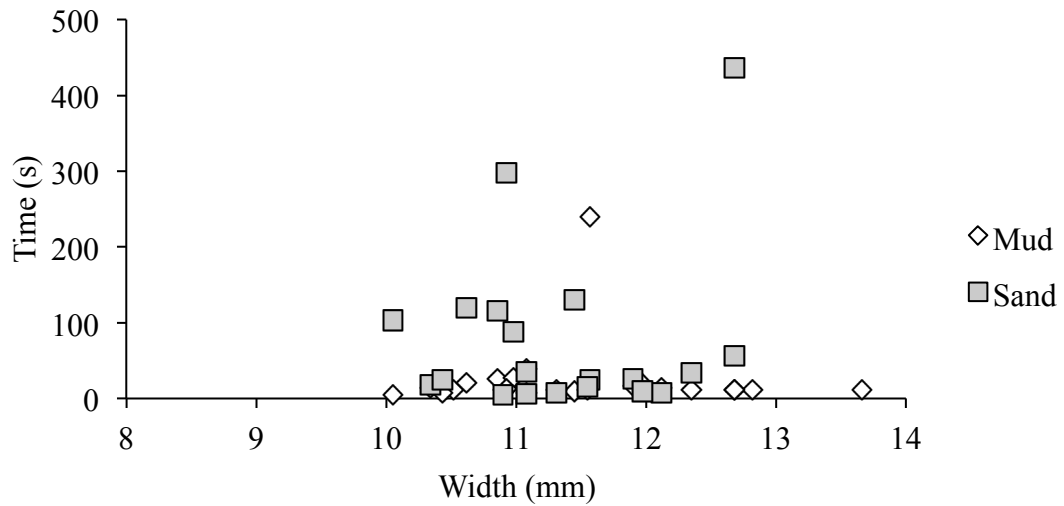


Figure 18: Relationship Between Razor Clam Width and Exploration Rate. A comparison of the width of each razor clam to the rate at which they completed the exploration phase of burrowing behavior in both the mud (white diamonds) and the coarse sand (grey squares).

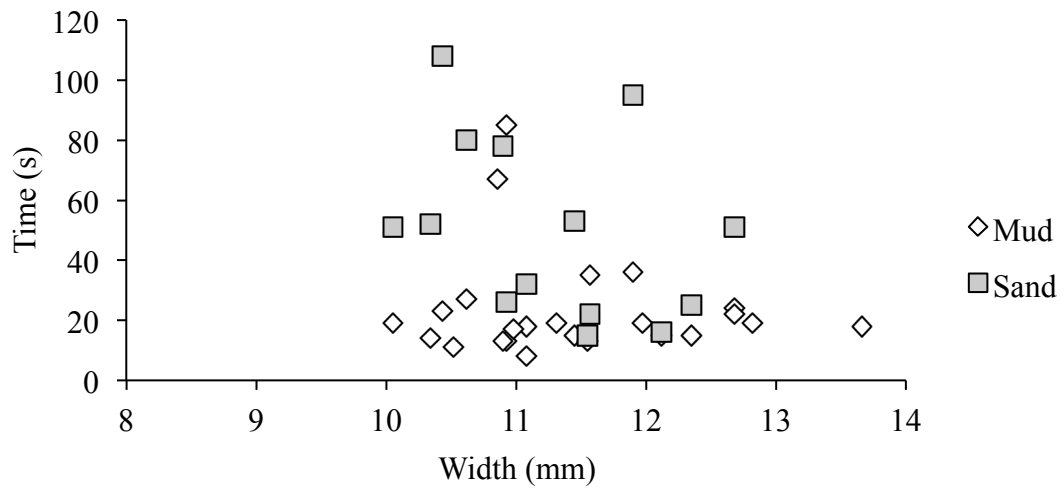


Figure 19: Relationship Between Razor Clam Width and Initiation Rate. A comparison of the width of each razor clam to the rate at which they completed the initiation phase of burrowing behavior in both the mud (white diamonds) and the coarse sand (grey squares).

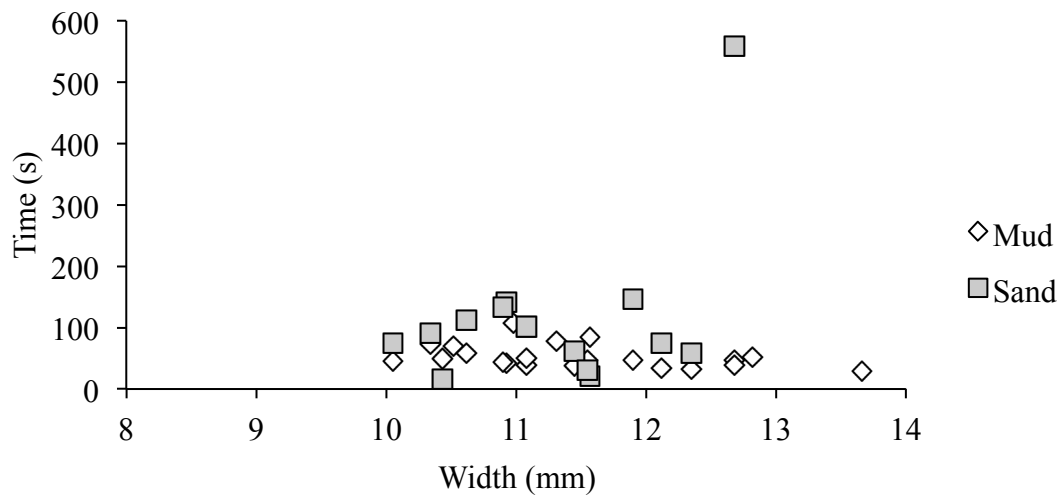


Figure 20: Relationship Between Razor Clam Width and Tunneling Rate. A comparison of the width of each razor clam to the rate at which they completed the tunneling phase of burrowing behavior in both the mud (white diamonds) and the coarse sand (grey squares).

Lastly, I analyzed the changes in porewater pressure that result from razor clam burrowing. There were only small changes in the pressure signal detected during the recovery, exploration, and initiation phases of burrowing, indicating that surface activity does not create large changes in porewater pressure. The tunneling phase, along with activity once the clams are within the burrow, created a large pressure gradient that was detected by the sensors (Figs. 21 & 22). Of the six razor clams introduced to the mud with pressure sensors, three produced measurable changes in porewater pressure while burrowing (Fig. 21), whereas only two of the six razor clams introduced to the coarse sand with pressure sensors produced measurable changes in porewater pressure (Fig. 22).

Of the three razor clams that produced measurable pressure changes during burrowing in the mud, two produced large changes in porewater pressure (total change ~ 0.6 to 1.0×10^3 Pa; Fig. 21A and B). The third produced much smaller porewater pressure changes ($\sim 0.3 \times 10^3$ Pa; Fig. 21C). . For both of the clams burrowing in coarse sand, the pressure signals were relatively weak (total change $\sim 0.12 - 0.14 \times 10^3$ Pa; Fig. 22). The decrease in pressure observed for the third clam in mud and the two clams in coarse sand could have been due to the dissipation of pressure propagation if the clam burrowed far from where the pressure sensor was located. The more consistent data, in both sediment types, occurred when burrowing took place closer to the sensor. Even so, my results suggest razor clams produce larger changes in the porewater pressure when burrowing in the mud compared to the coarse sand in both the tunneling phase of burrowing and the activity that follows this phase.

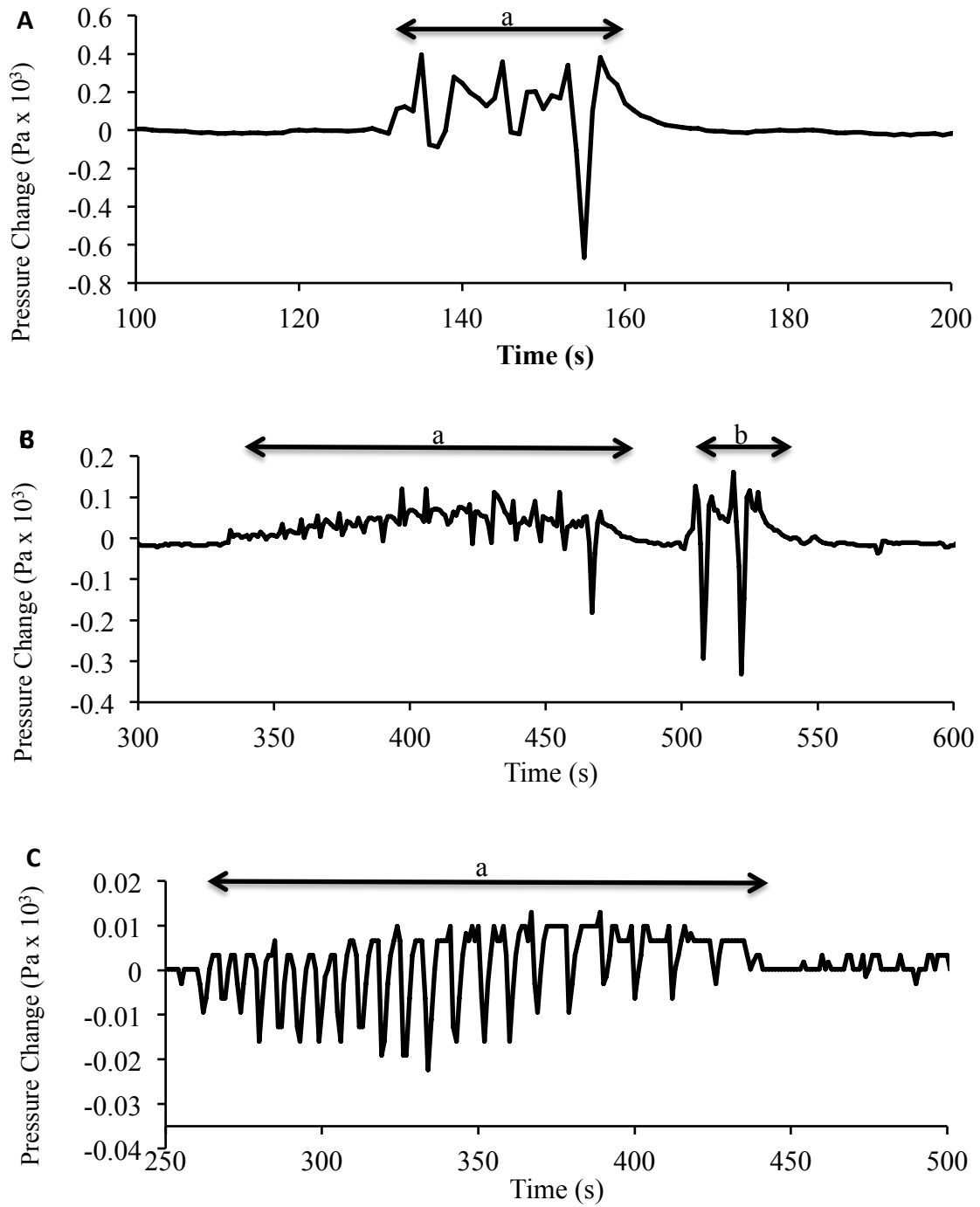


Figure 21: Changes in Mud Porewater Pressure During Razor Clam Burrowing. Three razor clams (A-C) successfully burrow in the mud, displaying changes in pressure associated with both the tunneling phase of burrowing (a) and activity once the tunneling phase is completed (b).

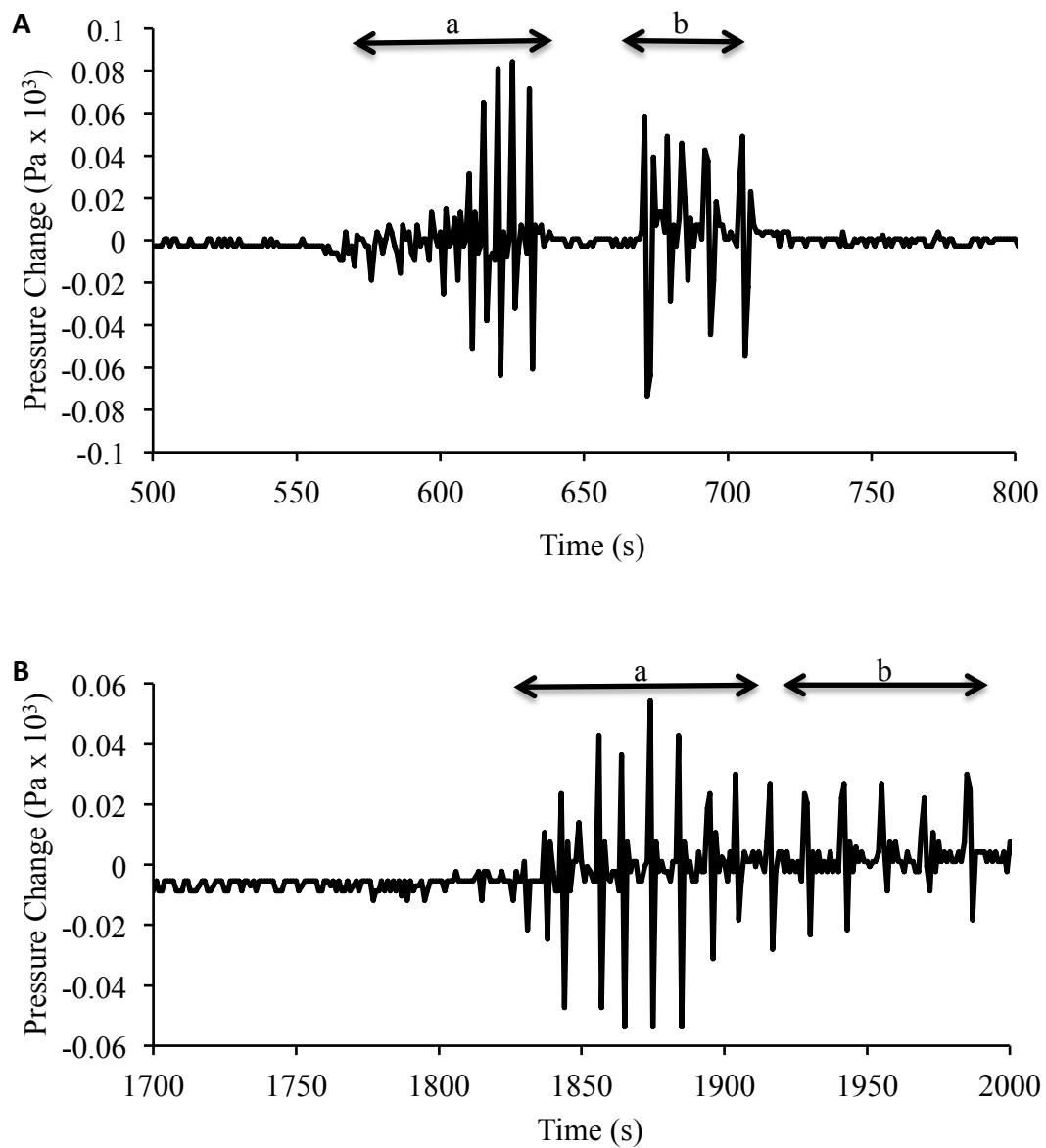


Figure 22: Changes in Coarse Sand Porewater Pressure During Razor Clam Burrowing. Two razor clams (A and B) successfully burrow in the coarse sand, displaying changes in pressure associated with both the tunneling phase of burrowing (a) and activity once the tunneling phase is completed (b).

DISCUSSION

The burrowing behavior of razor clams is highly dependent on sediment type and the age and size of the clams. In her honors thesis, Flanagan (2013) showed that small juvenile razor clams (shell length 12.0-18.5 mm) completed burrowing more often and burrowed faster in fine-grained commercial play sand and a sand-mud mix than they did in fine mud sampled from the Lowes Cove near the Darling Marine Center. In particular, she found that it took longer for small juvenile razor clams to initiate burrowing and the overall burrowing cycle took longer in mud because of the time required to initiate burrowing in mud. Based on Flanagan's results, I initially hypothesized that larger juvenile clams (shell length 60-78 mm) would also be more likely to burrow and would complete burrowing more quickly in sand sediments. However, the results of my research run counter to the findings of Flanagan (2013). Not only did the larger juvenile razor clams complete all phases of burrowing more quickly in mud (significantly so in the case of the exploration, initiation and tunneling phases) compared to the coarse sand, a higher proportion of the clams in my experiment completed burrowing in the mud. Perhaps there is an ontogenetic shift in burrowing behavior so that larger clams prefer mud sediments as opposed to sandy sediments. This developmental shift in sediment preference has been observed in several bivalve species, including *Macoma balthica* for which there was a greater abundance of juveniles in high intertidal mud habitats and a greater abundance of adults in lower intertidal sandy flats (Compton *et al*, 2009).

The variation in the "quality" of sediments used in my experiment relative to those used by Flanagan (2013) may also account for our different findings. While the

mud sediments in both experiments were sampled from Lowes Cove, Flanagan used a much finer, more polished commercial grade “play sand” while the sand used in my experiment was a very coarse sand with lots of shell hash. A substantial proportion (42%) or larger juvenile clams did not start exploring sediments and nearly as many did not initiate burrowing in the coarse sand I used in this experiment while all of the clams in Flanagan’s (2013) project completed burrowing in the play sand. It is important to note that adult razor clams have regularly been observed at the Ft. Pemaquid site where the coarse sand sediments were obtained. As Flanagan (2013) notes, if clams take longer to burrow in a particular sediment type, they are more prone to predation and damage. Thus, clams that take longer to burrow or completely reject the sediment are at higher risk of mortality whether it is in natural populations or aquaculture settings.

Razor clams have been called “the Ferrari of diggers” because of the speed with which they can burrow, not to mention that large juvenile and adult razor clams may have a burrow that can extend upward of 3 feet into the sediment (Leavitt, 2010). As discussed in the introduction, valve contraction while burrowing creates a localized zone of fluidization, particularly in the region surrounding the extended foot (Winter *et al.*, 2012). This reduces the resistance through the sediment, draws water toward the foot, creating a zone of fluidized sediment around and below the foot, thus allowing the clam to burrow through the sediment.

The porosity of the sediment can influence the extent of sediment fluidization. A complex relationship exists between the porosity of the sediments and how that porosity influences razor clam burrowing. More porous sediment, such as the coarse sand, has a

larger degree of seawater already surrounding the razor clam while burrowing compared to the less porous fine mud. While burrowing in the mud, the razor clams may experience more rapid fluidization as seawater enters the burrow because of the greater concentration gradient that exists; the low porosity of the sediment creates a void when the valves contract where seawater rapidly flows towards through the sediment. However, the method of fluidization is essential to the burrowing process because static sediment creates greater resistance to burrowing. One might expect the razor clams to burrow more quickly in the more porous sediment because the larger degree of porosity prevents the sediment from becoming too static, and greatly reduces the friction of burrowing.

My results demonstrated that the coarse sand I used had greater resistance to both vertical and longitudinal stress (i.e., it contained greater compressive and shear strength compared to the fine mud), as a result of the greater size of the sediment particles. Sediment “strength” may also play a role in how hard a clam has to work to penetrate the sediment. The significantly higher shear and compressive force required to cause failure in the coarse sand, as indicated by the Torvane and penetrometer measurements, may require a greater expenditure of energy by a clam in order to cause the sediment failure needed to burrow. These measurements were taken after the sediments were introduced to the experimental beakers and allowed to settle for 12 hours. Thus, they represent the sediment shear and compressive strength at the time the clams were introduced to each sediment type, but do not necessarily reflect differences in sediment packing and shear and compressive strength that might be experienced in natural settings. Unfortunately, I did not have access to the equipment to measure these parameters in the field.

My findings are consistent with those of Sassa *et al.* (2011) who investigated the criteria necessary for proper burrowing by various infaunal bivalve species. They found that local sediment conditions, such as the hardness of surface sediment influenced clam burrowing behavior. For example, as sediment hardness increased adjustments in burrowing behavior were made, most notably the burrowing angle and depth. Both the burrowing angle and burrowing depth decreased with increased sediment hardness as a means to compensate for the excessive energy required for burrowing (Sassa *et al.*, 2011). This may explain the longer time it took razor clams to complete burrowing and the reduced frequency of burrowing for razor clams in the coarse sand compared to the mud in my experiment; they were essentially exhibiting a response to the greater energy requirements needed to burrow in the coarse sand compared to the mud.

The foregoing suggests that greater exertion is required for clams to burrow in the coarse sand. If so, exertion by clams did not directly correlate with the magnitude of porewater pressure changes that I observed for clams presented with the two different sediment types. Substantially higher pressure signals were detected among the three clams observed in mud compared to the signals detected for the two clams that burrowed in coarse sand. This observation contradicted my hypothesis that larger changes in porewater pressure were likely to occur in the coarse sand compared to the mud. According to Wethey and Woodin (2005), bioadvection due to the burrowing of bivalves in sediments with lower permeabilities (such as mud) was lower than that advection in sediments of greater permeabilities (such as coarse sand), although they still observed pressure signals as clams burrowed in the mud sediments. With greater alteration of

porewater flux, and thus pressure fields, caused by bioadvection in more permeable sediments (as per Wethey & Woodin, 2005), I predicted that the larger porewater pressure changes would result from greater sediment porosity. These unanticipated results may be explained by the physical properties of the different sediments used.

While the coarse sand is non-cohesive and porous, the cohesive nature of mud allows it to behave like an elastic solid (Dorgan *et al.*, 2005). Razor clams may burrow in mud using the foot as a wedge to extend the burrow via crack propagation (Dorgan *et al.*, 2005). As the spade-shaped foot initiates the crack, stress intensifies at the crack tip, propagating the crack into the mud, which behaves as a solid. Because the mud more closely resembles a solid, it serves as a more rigid boundary. Therefore, as this elastic solid deforms under stress, a more rigid boundary requires greater exertion to cause displacement (Dorgan *et al.*, 2005). A greater force applied would create a greater flux of porewater pressure.

The cohesive properties of mud make it more resistant to erosion; the small particle size and higher proportion of clay minerals allows the sediment to withstand greater current speed required for erosion (Wright *et al.*, 1999). Therefore, greater forces are required to penetrate cohesive sediment, which, in turn, creates greater changes in porewater pressure. It is important to note that I was not able to measure energetic expenses of burrowing in the two sediment types; however, incorporation of such measures into future projects is warranted.

My findings were consistent with those of Volkenborn *et al.* (2010) who observed that as sediment permeability increased, the magnitude of pressure oscillations decreased.

As the coarse sand is more porous, and thus more permeable than the mud, there were larger pressure changes while burrowing in low-permeability mud compared to the high-permeability coarse sand. The cracks created in the mud allow the enhanced transport of porewater to create greater porewater advection. This pressurization occurs through water injection into the burrow, a characteristic seen only in medium- to low-permeability sediments (Volkenborn *et al.*, 2010).

Perhaps because of the less solid-like, non-cohesive state of the coarse sand, some razor clams were simply unable to complete the initiation phase in this sediment. Although clams that completed initiation typically completed the tunneling phase as well, it took razor clams longer to complete these phases in the coarse sand compared to in the fine mud. Difficulties in anchoring the foot into the sediment to hoist the clam upright may result from a less static sediment, such as the coarse sand.

My findings are also consistent with those of Pfitzenmeyer and Drobeck (1967). In their study, the reburrowing rates of the softshell clam *Mya arenaria* were determined in sediments of varying grain sizes (0.5-4 mm). They found that clams exhibited progressively slower rates of burrowing as the particle grain size increased (Pfitzenmeyer & Drobeck, 1967). In their experiment, Pfitzenmeyer and Drobeck (1967) also compared burrowing in sediment with relatively heterogeneous grain size to burrowing by clams in four different sediments with a much more homogenous grain size. They observed that if the sediment is very homogenous in size greater compaction occurs making it more difficult for the clam foot and valves to penetrate the sediment surface. In contrast, if the sediment is very heterogeneous in size, less compaction occurs

creating large interstitial spaces that make it difficult for the clams to properly anchor the foot to pull the valves through the sediment.

In my experiment, both sediments were sampled from natural settings and I did not control for grain size homogeneity. While the compaction of the fine mud is greater than that of the coarse sand in natural settings, it is important to note that my samples of mud were only allowed to settle and compact for 12 hours prior to the burrowing trials, possibly creating a more water-saturated sediment. Thus, limited compaction of the mud may have facilitated the anchoring of the foot by clams during initial stages of burrowing, leading to a higher overall completion of burrowing in mud, whereas the compaction of the coarse sand may have created too many large pores that inhibited the sufficient anchoring of the foot to initiate burrowing.

Factors other than the physical aspects of the sediment influence whether infaunal species burrow in a given location. Compton *et al.* (2009) found that feeding strategy is associated with the sediment type in which bivalves burrow. Suspension feeders were primarily found in sandy sediment, which lacks much organic matter (Compton *et al.*, 2009). Suspension feeding bivalves typically rely on siphons that extend through the burrow to the surface to filter-feed. Their feeding efficiency may be decreased when there are higher loads of suspended sediments, which is more likely to occur in mud versus sand sediments. In contrast, deposit feeders such as *Macoma balthica* were primarily found in muddy sediment, which contains more organic matter to feed on (Compton *et al.*, 2009); these bivalves do not have long siphons but instead feed on organic detritus on the surface of the sediment or within the burrow. Some bivalves are capable of utilizing

both mechanisms for feeding (Dame, 1996). In fact, stout razor clams, *Tagelus plebeius*, have the ability to employ both feeding mechanisms to meet its nutritional requirements depending on the intensity of currents. Razor clams (*E. directus*) are considered suspension feeders. However, they have siphons that do not extend very far past their shell and so must move through to the sediment surface to feed. They are thus likely highly susceptible to sediment load. This may explain why smaller clams (as in Flanagan 2013) more readily burrow in sand; they may be less tolerant of suspended sediments during feeding than are larger clams. Future research should investigate ontogenetic changes in tolerance to suspended sediments for razor clams.

Changes in porewater pressure after the completion of the tunneling phase of burrowing behavior denote further activity within the burrow. Further tunneling may explain some of the large pressure changes for those razor clams that completely burrowed. To prevent burrow collapse burrow maintenance is required. Addino *et al.* (2014) suggested that without mucus secretions, stout razor clams must rely on the cohesion and compaction of the sediment particles to prevent sediments from constantly collapsing into the burrow. In order to maintain the established burrow, razor clams exert pressure along the walls of the burrow by both moving vertically through the column and valve gaping (Addino *et al.*, 2014). This exerted pressure may explain the changes in porewater pressure I observed for *E. directus* after clams completed the tunneling phase of burrowing. It is also important to note that changes in the local pressure field within the porewater can arise from advection caused by feeding and defecation (Wetthey &

Woodin, 2010), but these activities would likely create smaller pressure changes than I was able to observe in my experiment.

In addition, the influences of biotic and abiotic factors have been known to influence burrowing behavior. Prior to burrowing, *E. directus* may decide where and whether to burrow, and such decisions are likely to be based on environmental cues. Woodin *et al.* (1995) demonstrated in their study on recruitment cues in marine sedimentary environments that settling larvae of the polychaete worm *Arenicola cristata* and the hard clam *Mercenaria mercenaria* are able to detect negative cues associated with the disturbance of sediments by other infaunal inhabitants and adjust their behavior in response to such disturbances. These infaunal species preferred to burrow in locations where the sediment was not disturbed, as indicated by the increased time to burrow, or complete rejection of burrowing in disturbed sediments. Woodin *et al.* (1995) suggested that environmental cues stem from process-specific events, such as feeding tracks, burrowing tails, erosion and mixing of surface sediments, and fresh feces, and allowed settling clams and worms to differentiate sites where post-settlement survival was likely to be compromised. Such environmental cues may also affect whether *E. directus* burrows; in my experiment sediments were sampled from locations where adult razor clams are commonly found and I did not expect nor control for any potential differences in chemical cues in the two sediment types.

In addition, it is also important to note the influence that pollutants may have on clam burrowing. When copper was introduced to sediment, the burrowing behavior of littleneck clams (*Protothaca staminea*) was severely inhibited. Exposure to polluted

sediment drastically increased the time needed to complete burrowing (Phelps *et al.*, 1983). When previously exposed clams were reintroduced to copper-polluted sediment, their tolerance decreased and their burrowing time further increased. I did not test for the presence of pollutants in the sediments I used. However, appropriate siting of razor clam culture operations will need to take such factors into account.

With variables such as water temperature, salinity, and water flow rate controlled, the analysis of the differing burrowing behavior of *E. directus* in different sediments can be attributed to different characteristics between the two different sediment types. Although further investigations are needed to optimize the aquaculture potential of this species, the results of my work help to elucidate the burrowing behavior of this species. My findings are an important contribution to the future aquaculture of this clam species as growers have further evidence of the sediment characteristics that are optimal for burrowing.

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AUTHOR'S BIOGRAPHY

Robert Joseph Hallinan was born in Bath, Maine on April 23, 1993. He grew up in the small coastal town of Boothbay Harbor, Maine where his father taught him the challenging, but rewarding, work of lobstering which was his first introduction into marine science. After years of working alongside his father and brothers on the boat, Robert decided to find a job in aquaculture at Glidden Point Oyster Sea Farm where he has worked for four years and counting. After graduating from Boothbay Region High School in 2011 as Salutatorian of his class, Robert attended the University of Maine where he majored in biology and minored in chemistry, as well as being a member of the Honors College. During his sophomore year at the University of Maine, Robert became a brother of the agricultural fraternity Alpha Gamma Rho, where he held the position of Philanthropy Officer for three terms. After graduating from the University of Maine, Robert plans on remaining in the field of aquaculture to continue to pursue his interests in marine science.