YALE PEABODY MUSEUM

JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research,* one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at https://elischolar.library.yale.edu/.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research.*

Spatial distribution of *Alitta virens* and *Clymenella torquata* with respect to rigid boundaries in mud and sand

by Kevin T. Du Clos[1,2], Sara M. Lindsay[3] and Peter A. Jumars[1]

ABSTRACT

Recent advances in understanding of sediment material properties and of burrowing mechanics suggest likely differences in the behavior of organisms burrowing in mud and sand. The path of least resistance in the mud may lead an infaunal organism to burrow along a rigid wall. By contrast, in sand, force chains may prevent a burrowing organism from reaching a rigid wall. Burrowing in mud occurs primarily by the propagation of cracks. Cracks, and hence burrows, tend to propagate along rigid walls. In sand, force chains comprise collections of particles that experience much more stress than their neighbors. Stress chains tend to terminate at walls where their high density may inhibit burrowing. To test for differing effects of mud and sand on the spatial distribution of infauna, proximity to a rigid wall of two polychaetes, *Alitta virens* and *Clymenella torquata*, was measured in sand and mud. For both species the cumulative density distribution of burrow distances from the wall showed significantly more burrows near the wall than expected in both mud and sand. However, in direct sampling experiments, the more mobile *A. virens* showed a greater tendency to burrow at the wall in mud than in sand and strong exclusion from the immediate vicinity of the wall in sand, whereas *C. torquata* did not show a significant difference in distance from the wall in sand versus mud. The wall effect may be weaker for *C. torquata* because its limited mobility makes it less likely to encounter a wall over the course of an experiment. Our results point to the need for quantitative assessment of biases of analytical devices that rely on rigid walls, such as optodes and sediment profile imaging cameras, and suggest a possible similar bias in animal distributions around natural analogs such as rock-sediment boundaries.

1. Introduction

The term bioturbation refers to the effects of organisms on sediments and on the pore water contained within these sediments. Kristensen et al. (2012) define bioturbation as "all transport processes carried out by animals that directly or indirectly affect sediment matrices." Behaviors that lead to these transport processes include deposit feeding, crawling, burrowing and ventilation. Consequences of bioturbation are myriad. They include: ecological effects, reviewed by Meysman et al. (2006); chemical effects, including increasing the pool

1. Darling Marine Center, University of Maine, Walpole, Maine 04573-3307 USA.
2. Corresponding author *e-mail: kevin.duclos@maine.edu*
3. School of Marine Sciences, University of Maine, Orono, Maine 04469-5751 USA.

of reactive organic matter (Kristensen 2000); and, geological effects, both at the scale of individual organisms (millimeters to centimeters) and on much larger (meters to kilometers) scales (Murray et al. 2002). Actions of burrowing organisms are also major determinants of the fates of pollutants in coastal environments (Gilbert et al. 1994; Sherwood et al. 2002).

This study focuses on one aspect of bioturbation, the formation and maintenance of burrows and tubes by polychaete worms in marine sediments, and in particular on the spatial distribution of these burrows with respect to rigid boundaries. As a first approximation regarding chemical effects, the walls of a burrow are often treated as extensions of the sediment-water interface because they increase the surface area available for the diffusion of oxygen, facilitating aerobic respiration (Aller 1982; Volkenborn et al. 2007). In the absence of a burrow, diffusion is essentially one-dimensional, occurring perpendicular to the sediment surface. A burrow facilitates diffusion in the other two dimensions (Aller 1980). Areas adjacent to burrows also provide microniches that support bacterial (Bertics et al. 2010) and meiofaunal (Dittmann 1996) populations distinct from those at either the oxic sediment-water interface or within the deeper anoxic sediment. Understanding the mechanisms that control the distribution of infauna is thus crucial to explaining a wide variety of processes in the sediment column and the surrounding water.

The subjects of this study, *Alitta virens* and *Clymenella torquata*, represent two widely distributed polychaete families, Nereididae and Maldanidae, respectively. Both species are commonly studied in the laboratory and the field. *A. virens* is omnivorous (Fauchald and Jumars 1979) and is commonly found in intertidal mud flats and sand beaches in the Gulf of Maine (Larsen and Doggett 1990; Larsen 1991), the North Sea (Costello et al. 2001) and elsewhere. *A. virens* builds U-shaped burrows, often 30 cm or deeper, that it expands over the course of a few days and maintains as part of a "semi-sessile lifestyle" (Fauchald and Jumars 1979; Miron et al. 1991; Kristensen and Kostka 2005), generally remaining in its burrow at high tide and emerging at low tide to scavenge for food (Esselink and Zwarts 1989; Du Clos, unpublished). *C. torquata* is a tube-dwelling, head-down deposit feeder (Fauchald and Jumars 1979) commonly found in dense aggregations in mud and sandy mud. *C. torquata* is sessile, generally maintaining its tube in one place. If displaced from its tube, however, it rapidly reburies and forms a new one. *C. torquata* also often forms branches at the head end of its tubes and may be able to travel longer distances through prolonged or repeated tube extension (Fauchald and Jumars 1979).

In the laboratory, many infaunal species behave differently in enclosures filled with mud than in those filled with sand. When *A. virens* is kept in a mud-filled aquarium, it often burrows at the edge, with its U-shaped burrow visible through the aquarium wall. If *A. virens* is kept in the same aquarium filled with sand, however, the worm is seldom seen at the wall. One of us (PAJ) has made many casual observations of polychaetes in mud and sand aquaria, rarely seeing animals against a wall in sand aquaria. Notably, a 20 cm long *Glycera* sp. was kept in a desktop sand aquarium for over a year and never seen until the aquarium was emptied. The only readily apparent exceptions have been several species of flabelligerids and *Eupolymnia heterobranchiata* (a terebellid polychaete), that often do build burrows at the

wall in sand. How flabelligerids construct the burrow near the wall has not been seen because they do so nocturnally. *E. heterobranchiata* breaks force chains by liquefaction (Nowell et al. 1989), and that process is enhanced near an impermeable wall. Conversely, in mud, large and small tubicolous and burrowing species often are observed against the wall, including tiny *Manayunkia aestuarina*, spionids of varying sizes, terebellids, scalibregmatids, nereidids, goniadids and phyllodocids. Prior to the present study however, the effect of sediment type on infaunal behavior in the presence of a rigid wall, hereafter referred to as the wall effect, had been tested neither systematically nor quantitatively.

Dorgan et al. (2006) described differences in the material properties of mud and sand that may help to explain the wall effect. Fractures in mud tend to travel along smooth, rigid interfaces, so it may be easier for *A. virens* to burrow at a wall where a "preformed crack" occurs as mud separates from the wall in advance of a burrowing organism (Dorgan 2007). Sand is a granular medium, i.e., its bulk properties are determined by interactions between individual particles. An example of the importance of grains in the bulk material properties of sand is the formation of force chains, networks of particles that resist a much greater proportion of the force applied to the sediment column than do the particles that surround them. The high density of force chains at walls (where many force chains terminate) may prevent infaunal organisms from reaching a wall in sand.

Here we tested the hypotheses that *A. virens* and *C. torquata* burrow at or near rigid boundaries (walls) more often than would be expected by chance in mud, but not in sand. We predicted that the wall effect may be less important for *C. torquata* than *A. virens* because of *C. torquata's* sessile lifestyle. *C. torquata* often burrows wherever it first lands and rarely relocates its tube unless displaced from the sediment, so we expected that differences in the material properties of the sediment in which it burrows would be less important in determining its distribution.

2. Methods

A. virens were obtained either by collection from the Lowes Cove intertidal mudflat at the Darling Marine Center in Walpole, Maine, USA, or from the stock maintained at the Center for Cooperative Research and Aquaculture in Franklin, Maine, USA. The blotted wet weight of *A. virens* at the beginning of the experiments was 3.9 ± 0.3 g (mean $\pm$ s.e.m.; $n = 28$). All worms used had intact pygidia bearing anal cirri. The pygidium was identified at the end of each experiment to ensure recovery of the entire worm. Weights of worms for sand and mud experiments did not differ significantly based on a *t* test ($p = 0.12$). *C. torquata* was collected from an intertidal mudflat near Lubec, Maine, USA. As for *A. virens*, all *C. torquata* had intact pygidia before and after experiments. The blotted wet weight for *C. torquata* at the beginning of the experiments was 145 ± 14 mg (mean $\pm$ s.e.m.; $n = 27$). Weights of worms for sand and mud experiments did not differ significantly based on a *t* test ($p = 0.17$). To isolate effects of sediment properties and avoid potential complications from inter-individual interactions, all experiments used one worm per enclosure.

Mud was collected during low tide from the intertidal mudflat in Lowes Cove at the Darling Marine Center in Walpole, Maine, USA. Before use, mud was homogenized with a paint mixer mounted to an electric drill and sieved through a 2 mm mesh to remove larger solids. Sand used for experiments with *A. virens* was Quikrete "Play Sand." Before use, it was rinsed with a high volume of fresh water to remove fine particles. *C. torquata* would not burrow in pure sand, likely because the low organic content of the sand is unsuitable for deposit feeding. To create a sediment in which *C. torquata* would burrow, sand was supplemented by adding approximately 10% Lowes Cove mud by volume. The addition of mud did not appear to significantly alter the physical properties of the sand.

Stocks of both worms were maintained in a recirculating seawater system at 16–19°C at a salinity of 32–37 S_P. The same conditions were used for burrow-opening and worm-location experiments.

a. Burrow-opening experiments

Distance from the wall of each burrow opening was measured in experiments with *A. virens* and *C. torquata*. For *A. virens*, 12 pipes with 20.3 cm inner diameter (i.d.) were filled with sand and 12 with mud approximately 15 cm deep. For *C. torquata,* 14 pipes with 10.2 cm i.d. were filled approximately 10 cm deep for each sediment type. Pipes were chosen to match common experimental enclosure sizes rather than to mimic natural population densities. Smaller pipes were chosen for *C. torquata* than for *A. virens* because the former is both smaller and less mobile. All pipes were incubated in recirculating seawater for at least 12 h to allow sediment to settle and water at the top of the pipe to clear.

After addition of one *A. virens* or *C. torquata,* each pipe was incubated in recirculating seawater. A previous study of *A. viren's* burrowing behavior notes an "exploration and construction" phase of about three days in the process of burrow formation, after which the burrow morphology stabilizes (Miron et al. 1991). Thus, experiments with *A. virens* were incubated for seven days to avoid sampling during the period of most rapid change. Experiments with *C. torquata* were incubated for seven days for consistency. The incubation period proved sufficient for *C. torquata* to build a tube.

At the end of the incubation period, the surface of the sediment in each pipe was photographed. Photographs were used to measure the distance from the closest wall to each burrow opening (to the nearest millimeter) using Adobe Photoshop CS5 Extended. Distances were measured along a pipe radius to the nearest edge of the burrow. To ensure that no burrows were missed, general locations of burrows were verified by comparison of the photographs to drawings of the sediment surface.

Burrow-opening data were analyzed non parametrically because the data were not expected to fit a normal distribution. Equation 1 was used to calculate the expected cumulative distribution functions (cdf) for burrowing-opening distance for each pipe size, where x is the distance from the wall and R is the radius of the pipe minus one burrow radius.

$$cdf(x) = \frac{R^2 - (R - x)^2}{R^2} \tag{1}$$

The cdfs were calculated by dividing the area of sediment contained within a ring extending a distance x in from the edge of the pipe wall by the total area of sediment in the pipe. Distance was measured from the wall to the nearest edge of the burrow, so the burrow radius was subtracted from the pipe radius to account for the fact that no burrow can be farther from the wall than the pipe radius minus the burrow radius. For each species and sediment type, the cumulative frequency distribution of burrow-opening distances was compared with the appropriate expected cdf using a one-tailed, one-sample Kolmogorov-Smirnov test. This test is conservative where ties are present as for the data analyzed here. A significance level of 0.05 was used for this and all subsequent statistical tests. A one-tailed Mann-Whitney (MW) test was performed to compare median distance from the pipe wall for mud and sand. A one-tailed MW test was also performed to compare the median number of burrow openings per pipe for sand and mud.

b. Worm-location experiments

Direct sampling experiments were performed to determine the location of the worm itself with respect to the wall. Fourteen experimental pipes were sampled for each combination of organism and sediment type. Although *C. torquata* locations were sampled from the same experimental pipes used for the burrow-location experiments described above, we refer to worm-location "experiments" for convenience. In the case of *C. torquata*, at the termination of each of the burrow-opening experiments, after removing the water at the top of the pipe with a siphon, sediment in the pipe was divided into inner and outer volumes by pressing a 6.6 cm diam. cylinder (0.2 mm wall thickness) into the center of the sediment to the bottom of the pipe. The location (edge or center) of the worm was then recorded. When a worm was cut during sampling and found in multiple sections, its position was scored according to the location of the larger of the two worm sections by weight. Assuming that the wall has no effect on the distribution of worms in the sediment (the null hypothesis), the likelihood of finding a worm in one of the two sections should be proportional to the area of that section. Thus, a binomial test was performed using the ratio of the area of the outer section to that of both sections combined (0.58) as the expected probability of finding a worm in the outer section based on chance alone.

We noted during many of the burrow-opening experiments in mud (described above) that upon reaching the bottom of its container *A. virens* often continued to burrow along the bottom of the container, as would be expected if cracks follow a rigid wall. Therefore, the bottom of the pipe was treated as an extension of the wall in determining the location of *A. virens* within the sediment. Pipes (i.d. 20.3 cm), split at 5 cm from the bottom, were used to test whether a worm was at the wall, the center or the bottom of the pipe (Fig. 1). Split pipe sections were sealed with duct tape and band clamps. Pipes were then filled to 15 cm with mud or sand and incubated in flowing seawater with one *A. virens* each. After seven days, pipes were sampled. First, band clamps and duct tape were removed and a metal divider was slid between the split sections of the pipe. Then, with the metal divider still in place, a 12 cm diam. cylinder (1.8 mm wall thickness) was pressed down into the center of the pipe.
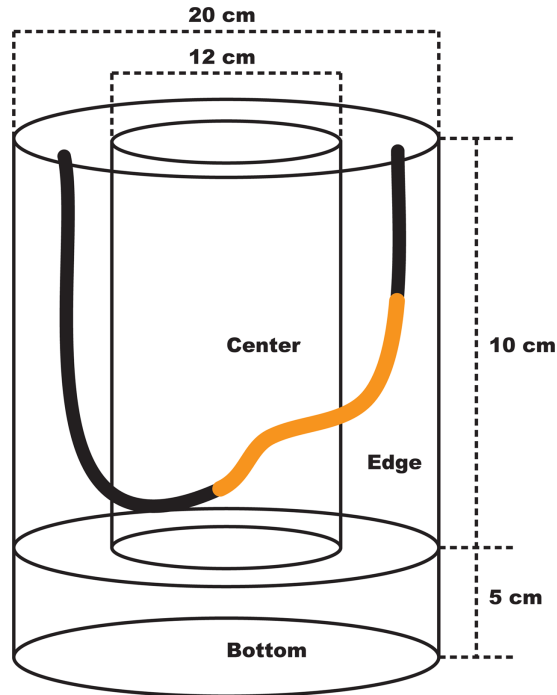
Figure 1. The sampling scheme used for the worm-location experiment with *A. virens* illustrates the
dimensions of each sediment section sampled from a 20.3 cm inner diameter pipe. The bottom
section is 5 cm tall. The remaining 10 cm tall top section is subdivided into an inner 12 cm diameter
center section and an outer edge section.

Finally, the pipe was removed, and the position of the worm (bottom, wall or center) was
noted. As for *C. torquata*, the position of a worm found in multiple sections was assigned
to that pipe section containing the larger section of the worm. Again, a binomial test was
performed using the expected probability of finding a worm in the wall or bottom section
vs. the entire pipe. In this case, the expected probability was found by dividing the volume
of the combined wall and bottom sections by the volume of all sections combined (0.67).

3. Results

a. Burrow-opening experiments

Burrow openings for *A. virens* were distributed significantly closer to the wall than
predicted from the expected cdf for both mud (Fig. 2a) and sand (Fig. 2b) ($p = 1.4 \times 10^{-14}, 5.9 \times 10^{-5}$, respectively). In the mud experiments, a total of 29 burrow openings
were counted with a median distance from the wall of 0.0 cm. In the sand experiments, 22
burrow openings were counted with a median distance from the wall of 0.6 cm (Fig. 3a).
The difference between these distances is significant based on a MW test ($p = 0.0043$).
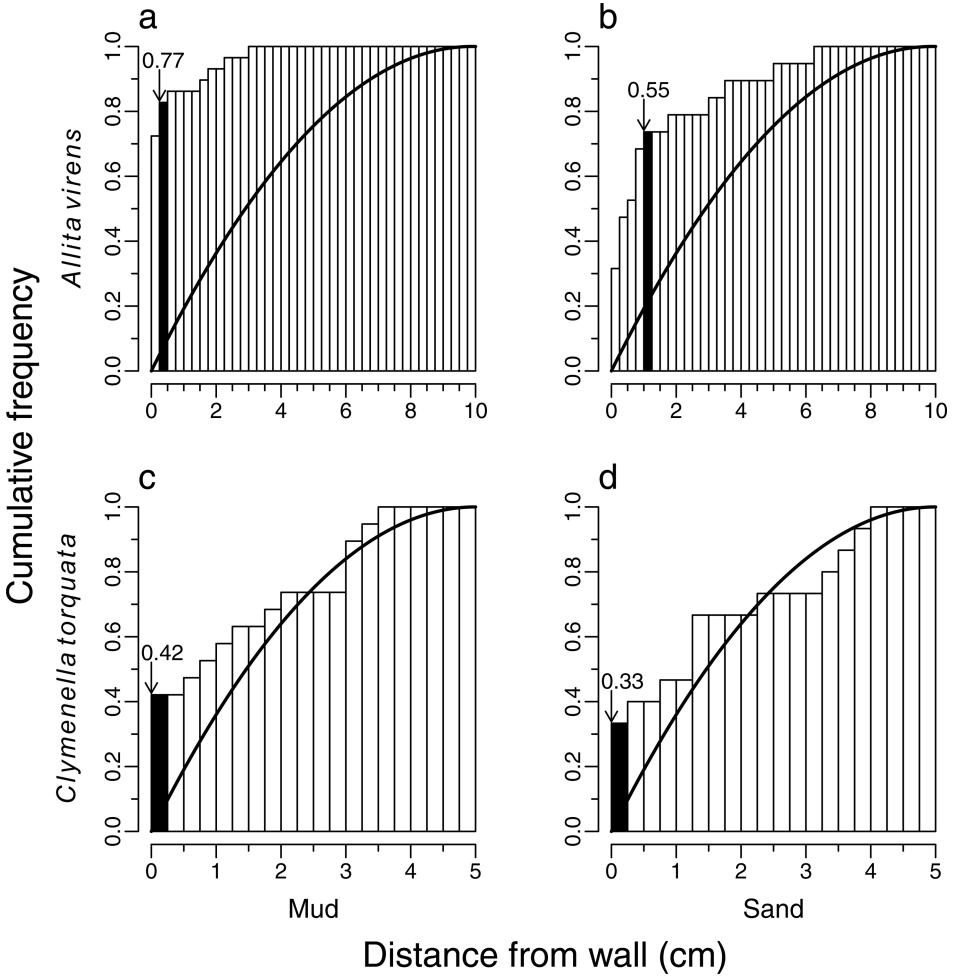
Figure 2. Cumulative frequency plots for distance from the wall of burrow openings in experiments with *Alitta virens* in mud (a) and sand (b) and *Clymenella torquata* in mud (c) and sand (d). The expected cumulative density function (cdf) is indicated by a curve on each plot. The distance at which the maximum difference between the expected cdf and the actual frequencies occurs is indicated by a black bar and arrow with the distance above. Each of the four frequencies is greater than its corresponding expected cdf based on results of Kolmogorv-Smirnov tests ($p = 1.4^{-14}$; $p = 5.9 \times 10^{-5}$; $p = 5.9 \times 10^{-5}$; $p = 0.020$).

The median total number of burrow openings per pipe was higher for mud (2.0) than sand (1.5) (Fig. 4a). This difference is significant based on a MW test ($p = 0.026$).

Burrow openings for *C. torquata* were also significantly closer to the wall than predicted from the expected cdf for both mud (Fig. 2c) and sand (Fig. 2d) ($p = 5.9 \times 10^{-5}$, 0.020, respectively). Median distance from the wall for the 18 burrow openings in the experiments
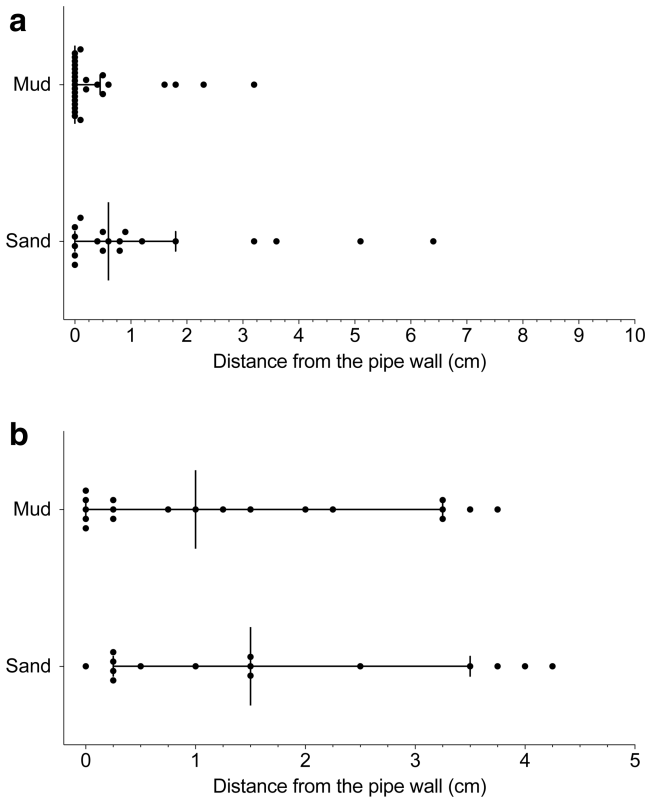
Figure 3. Distance from the wall for each burrow opening for *Alitta virens* and *Clymenella torquata* in mud and sand. Median distance and interquartile range are indicated for each sediment type. For *A. virens* (a), the median distances are 0.0 and 0.6 cm for mud and sand respectively. The lower end of the interquartile range for mud is obscured by the median. The distance for mud is significantly less than that for sand based on a Mann-Whitney test ($p = 0.0041$). For *C. torquata* (b), the median distances are 1.0 and 1.5 cm for mud and sand respectively. The lower end of the interquartile range for mud is obscured by the median. The distances for mud and sand are not significantly different based on the results of a Mann-Whitney test ($p = 0.19$).

with mud ($n = 14$) was 1.0 cm. Median distance for the experiments for the 16 burrow openings in the experiments with sand ($n = 14$) was 1.5 cm (Fig. 3b). These distances are not significantly different based on a MW test ($p = 0.19$), although the trend is in the same direction as for *A. virens*. The median number of burrow openings per pipe was 1.0 for both mud and sand (Fig. 4b).

b. Worm-location experiments

For experiments with *A. virens* in the mud, the worm was found in the wall or bottom sections in all 14 enclosures (Fig. 5). These results are significantly different from the
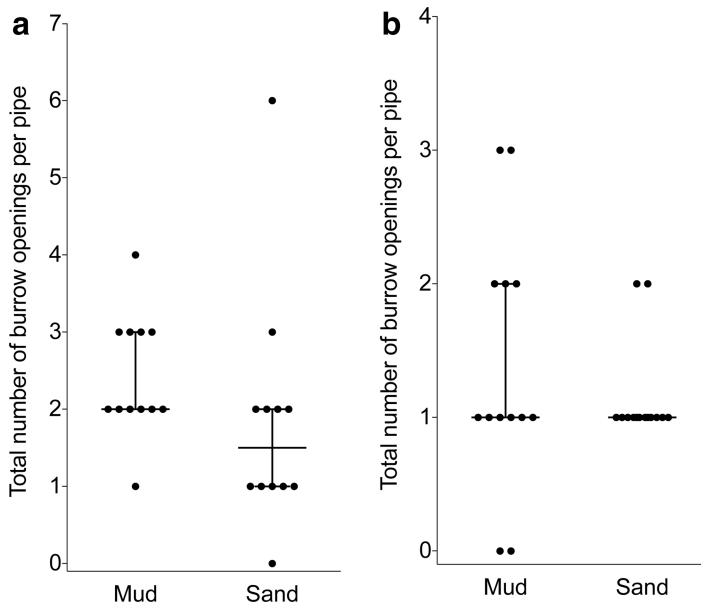
Figure 4. Total number of burrow openings per pipe for *Alitta virens* and *Clymenella torquata* in mud and sand. Median and interquartile range are indicated for each sediment type. For *A. virens* (a), the median numbers are 2.0 and 1.5, for mud and sand respectively. The lower end of the interquartile range for mud is obscured by the median. The number of burrow openings per pipe is significantly greater for mud than for sand based on a Mann-Whitney test ($p = 0.028$). For *C. torquata* (b), the median number is 1.0 for both mud and sand. The lower end of the interquartile range for mud and both ends of the interquartile range for sand are obscured by their respective medians.

expected probability of 0.67 ($p = 0.0074$). For sand, the worm was found in the center section in 3 out of 14 enclosures. This result is not significantly different from the expected probability ($p = 0.57$).

In the experiments with *C. torquata* the worm was found in the edge section in 6 out of 14 enclosures in mud and 7 out of 14 enclosures in sand (Fig. 7). These results are not significantly different from the expected probability of 0.58 ($p = 0.29$ and $p = 0.59$, respectively).

4. Discussion

In both the burrow-opening and worm-location experiments, *A. virens* showed a stronger tendency to burrow near rigid walls in mud that was seen in the experiments in sand. The difference between *A. virens's* behavior in mud and sand might be attributed, at least in part, to the distinct mechanical properties of the two sediment types. Although mud and sand are superficially similar, they differ mechanically. In mud, a worm generally burrows by forming a crack that propagates in advance of the worm's head (Dorgan et al. 2005
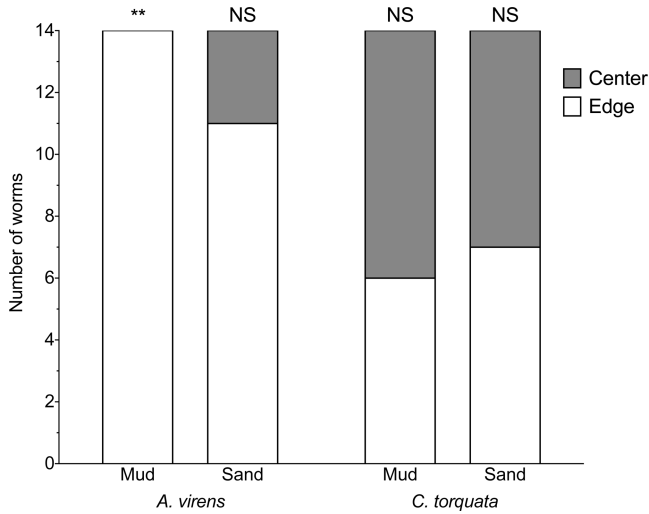
Figure 5. Number of experiments in which a worm was found in the edge (white) or center (gray) section for each species and sediment type. For each group, the total number of experiments was 14, the number found in the edge section was 14 for *Alitta virens* in mud, 11 for *A. virens* in sand, 6 for *Clymenella torquata* in mud, and 7 for *C. torquata* in sand. Of the four groups, the ratio of worms found in edge vs. center sections was significantly different from the expected probability only for *A. virens* in mud, based on a binomial test ($p = 0.0074$).

and 2007). When not near a wall in mud, an organism must break the cohesive-adhesive bonds between grains to form a burrow (Fig. 6a). Cohesive-adhesive forces are stronger in mud than in sand because mud's smaller particle size leads to a larger contact area between grains per unit of volume. To burrow at a wall, an organism needs only to overcome the relatively weaker adhesive forces between grains and the wall (Fig. 6b). Because burrowing at a wall requires less force than burrowing away from a wall, once a burrowing organism encounters a wall it is likely that it will burrow "downhill" by staying at the wall rather than exerting the greater force required to move away. According to the crack-propagation model for mud, as the crack formed by a burrowing worm approaches a wall, mud separates from the wall, and forms a void even before the initial crack reaches the wall. The initial crack eventually merges with the void, causing the crack to follow the wall (Dorgan 2007; Dorgan et al. 2007).

Unlike mud, sand is a granular material in which interactions between individual particles compound to determine bulk material properties. In granular materials, the matrix of the grains resists applied forces. Within this matrix, a subset of grains that make up "force chains" resists a disproportionate fraction of the total load. Force chains are commonly described as any assemblage of three or more particles, each of which exceeds a certain pressure threshold, that approximates a line (e.g., forms an angle larger than 150°; Pöschel and Schwager 2005). In experiments and model runs in closed containers, force chains often
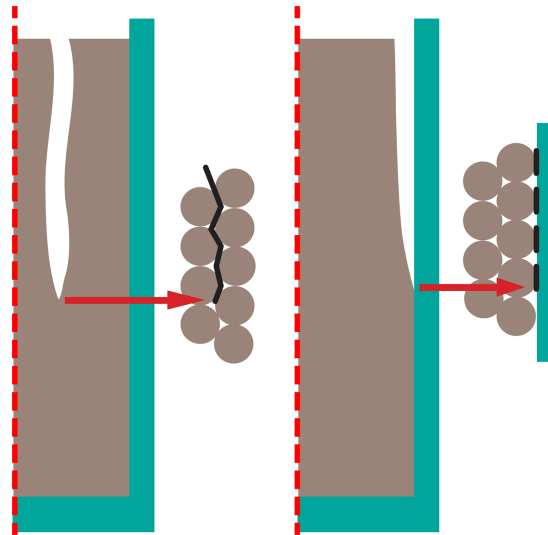
Figure 6. Schematic half-pipe sections (with detail inset) showing locations of cracks in mud away from and at a wall. To burrow at a distance from a pipe wall (a), an organism must break the cohesive-adhesive bonds between mud grains. To burrow at the pipe wall (b), an organism must break fewer and possibly weaker adhesive bonds between the mud grains and the wall.

terminate at the walls of containers, e.g., Geng et al. (2001), in a process known as jamming (Albert et al. 2000; Corwin et al. 2005). A burrowing organism therefore must break or reorient many force chains to burrow near the wall of a container. The number of chains that the worm must break increases as the worm descends into deeper sediment because the concentration of force chains increases with depth, as the deeper particles support the weight of overlying particles (Geng et al. 2001). *A. virens* often starts its burrow at a much shallower angle (with respect to the sediment surface) in sand than in mud (Jumars, unpublished). This behavior may be a method by which a worm can avoid the need to break more abundant force chains present below the surface. Similarly, once the worm has burrowed, it might have difficulty approaching walls due to the jamming that results from the presence of the rigid structure. Considering the results of the burrow-opening experiments, this distance is likely to be less than one centimeter.

These results clarify the burrowing behaviors of *A. virens* observed at the sediment-water interface. In both sand and mud, *A. virens* tends to begin to burrow near the wall of an enclosure, which helps to explain why the burrow openings for both sediment types clustered closer to the pipe wall than expected by chance alone. The worm may be able to gain leverage from the wall, making it easier to break the surface. Alternatively or in addition, the worm may be responding to containment. When placed in an enclosure, such as the pipes used for this study, *A. virens* often crawls around the perimeter several times before beginning its burrow. *A. virens's* initial burrowing behavior is qualitatively different

in mud versus sand. Effects of containment should be similar for both sediment types; it is not evident how they could explain the observed differences. The sampled position of the worm is likely to be affected by an escape response resulting from handling of the pipe. However, the worm is likely to retreat into a preformed burrow rather than forming a new one, so the results should still reflect the locations of the burrows. The presence of oxidized rinds surrounding dissected burrows provides strong evidence for the existence of such preformed burrows.

Divergence in behavior between sediment types observed at the sediment surface appears to extend to the sediment column below, as demonstrated by the results of the worm-location experiments. When beginning to burrow in mud, the worm burrows nearly perpendicularly to the sediment surface. In sand, the worm burrows at a shallower angle and moves its head back and forth, loosening the top grains, rather than progressing through crack-propagation (Dorgan et al. 2007). After beginning to burrow at the wall of its enclosure in mud, *A. virens* continues to burrow along the wall, forming a U-shaped burrow that traces the wall's form (Fig. 7a). In a representative burrow dissection (Fig. 7b), the burrow begins near the edge of the sediment column but redirects toward the center of the pipe at a depth of approximately 2 cm. This commonly observed pattern may result from *A. virens's* response to the vertical gradient in force chain abundance in the sediment column resulting from the weight of overlying sediments. Although *A. virens* can readily burrow near a wall at the surface, force chains likely prevent it from doing so at depth. Results from the burrow-opening experiments suggest that the worm may often continue its burrow at about 1 cm from the wall where the force chains are less dense. *A. virens* could potentially break force chains at the wall of the pipe by fluidizing the sand, but we are not aware of evidence that they are able to do so.

C. torquata, unlike *A. virens*, showed no significant difference in the distance from the wall at which it burrows in mud vs. sand. The difference between the results for the two species may result from the different lifestyles of the two organisms. Not as adept as *A. virens* at crawling on the sediment surface, *C. torquata* was observed in this study to build its burrow near where it initially landed; whereas *A. virens* generally crawled along the surface before beginning to burrow, often encountering a wall in the process. In addition, once *C. torquata* has burrowed and formed its tube, it may not move enough to encounter the wall of the aquarium over the remaining course of the experiment. Though it sometimes forms subsurface branches off the primary tube shaft, the tube generally maintains its overall position. The disproportionate burrowing of *C. torquata* near the wall found in the burrow-location experiments may reflect some bias in where the worms were dropped at the start of the experiment or an effect of the fluid circulation in the pipe. The presence of the tube itself may also play an undetermined role in the behavior of *C. torquata* at the wall of the enclosure. Some polychaetes (e.g., many terebellids) often attach their tubes to surfaces, such as boulders, but *C. torquata* did not do so in this study. *C. torquata's* deliberate, head-down, tube-building habit likely explains why the median number of burrow openings it produced was one per pipe in both mud and sand. It is not clear whether the larger number
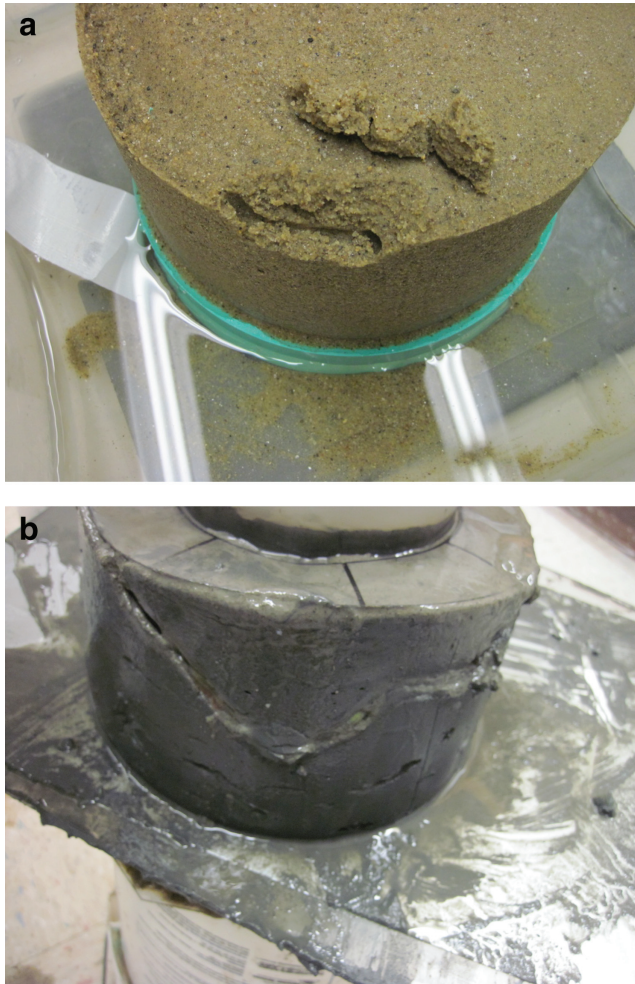
Figure 7. *Alitta virens's* burrows in sand and mud columns formed in 20.3-cm i.d. pipes, which
   have been removed. In sand (a), the worm has started its burrow near the edge of the column and
   redirected it toward the center of the pipe after reaching about 2 cm deep. Part of the top of the
   burrow has been dissected away. The direction of burrowing is from left to right. In mud (b), the
   U-shaped burrow is visible around the perimeter of the column.

of burrow openings in mud versus sand for *A. virens* results from a higher rate of burrow
production or a longer lifetime of visible burrow openings in mud.

   Biogeochemical mechanisms may reinforce the aforementioned physical mechanisms
in determining the spatial distributions of *A. virens* and *C. torquata* in mud and sand.
By building its burrow against a wall in mud, *A. virens* reduces the area of its burrow
wall available for exchange with surrounding sediments, which decreases the diffusion of

solutes into its burrow from those sediments and similarly the diffusion of oxygen out of its burrow to those sediments. An infaunal organism must irrigate its burrow with a flux proportional to that of the diffusive flux of solutes to maintain solute concentrations near those of the overlying water (Aller 1982), so reducing the diffusion of solutes by building near a wall could provide an energetic benefit by decreasing the necessary irrigation flux. This mechanism is likely to be more important in mud than sand because in coarser sediments, advective irrigation dominates over less efficient diffusive irrigation (Kristensen and Hansen 1999). *C. torquata's* tube is less permeable than the surrounding sediment (Zorn et al. 2006), so it would not likely derive the same benefit as *A. virens* from burrowing at a wall in mud.

Further work will be needed to determine whether wall effects extend to the field. Several studies have examined differences in invertebrate assemblages based on proximity to boulders. These studies cite differences in organic-matter concentration (Motta et al. 2003) and fluid dynamics (Cusson and Bourget 1997) as possible explanations for observed differences. Neither of these studies was performed with sufficiently fine spatial resolution to detect a wall bias due to local sediment mechanics that is likely to operate on the scale of centimeters at most. Past laboratory bioturbation studies using tracers (reviewed by Maire et al. 2010) may have missed the wall effect because of their tendency to average horizontally by slicing cores into vertical layers and homogenizing each slice before quantifying tracers. Future studies could employ core subsamples to provide further information on the small-scale spatial distribution of particle displacement. In addition, more mechanical studies will be needed to clarify the effects of sediment type on burrowing behavior and to test our proposed mechanisms for the differences between sediment types.

Detecting the wall effect in the field and relating the wall effect to bioturbation rates will require experiments designed specifically to account for small-scale spatial variation and possibly special techniques for infaunal sampling at the interface with boulders and other obstructions. It should also be noted that adhesion of mud to natural, rough stone may be far greater than to smooth, man-made surfaces, increasing the mechanical costs of burrowing near the interface. Our results suggest that sensor measurements that rely on proximity to a rigid wall may be biased, particularly when used to interpret phenomena on scales larger than that of the individual organism, such as the ecology or bioturbation activity of a system. At least one study that used sediment-profile imaging (SPI) has acknowledged the effect of the wall may have yielded elevated measures of bioturbation compared to the surrounding sediment: "The burrow formation rate, observed in this study, may be a liberal estimate since burrow formation at the sediment-camera-faceplate interface is facilitated along the interface" (Sturdivant et al. 2012). Comparing organism densities taken from SPI experiments with those from traditional sampling methods, such as core sampling, may provide a method for testing for the wall effect in the field and could help calibrate results from SPI and optode measurements, making the methods more widely applicable. Most problematic is recalibration or reinterpretation of luminophore-based estimates of bioturbation rates made through a transparent faceplate (e.g., Schiffers et al. 2011). Only

the immediately adjacent grain layers, wherein mechanical wall biases reach their maxima, are visible. Moreover, through the mechanical interactions discussed above, the magnitude and direction of bias are likely to vary with grain size. The differential responses of *A. virens* and *C. torquata* to rigid boundaries indicate that behavioral studies will be needed to determine the importance of wall effects for the behavior of other important infaunal taxa.

REFERENCES

Albert, I.; P. Tegzes; B. Kahng and R. Albert. 2000. Jamming and fluctuations in granular drag. Phys. Rev. Lett., *84*, 5122–5125.

Aller, R. C. 1980. Quantifying solute distributions in the bioturbated zone of marine sediments by defining an average microenvironment. Geochim. Cosmochim. Acta, *44*, 1955–1965.

Aller, R. C. 1982. The effects of macrobenthos on chemical properties in marine sediment and overlying water. Animal-Sediment Relations: The Biogenic Alteration of Sediments. P. L. McCall and M. J. S. Tevesz, New York: Plenum Press: 53–102.

Bertics, V.; J. Sohm; T. Treude; C. Chow; D. Capone; J. Fuhrman and W. Ziebis 2010. Burrowing deeper into benthic nitrogen cycling: the impact of bioturbation on nitrogen fixation coupled to sulfate reduction. Mar. Ecol. Prog. Ser., *409*, 1–15.

Corwin, E. I.; H. M. Jaeger and S. R. Nagel. 2005. Structural signature of jamming in granular media. Nature, *435*, 1075–8.

Costello, M.; C. S. Emblow; J. Dowse and R. J. White. 2001. European register of marine species.

Cusson, M. and E. Bourget. 1997. Influence of topographic heterogeneity and spatial scales on the structure of the neighbouring intertidal endobenthic macrofaunal community. Mar. Ecol. Prog. Ser., *150*, 181–193.

Dittmann, S. 1996. Effects of macrobenthic burrows on infaunal communities in tropical tidal flats. Mar. Ecol. Prog. Ser., *134*, 119–130.

Dorgan, K. M. 2007. Mechanics of burrowing in muddy sediments. PhD. dissertation. University of Maine.

Dorgan, K. M.; S. R. Arwade and P. A. Jumars. 2007. Burrowing in marine muds by crack propagation: kinematics and forces. J. Exp. Biol., *210*, 4198–212.

Dorgan, K. M.; P. A. Jumars; B. Johnson; B. Boudreau and E. Landis. 2005. Burrowing mechanics: Burrow extension by crack propagation. Nature, *433*, 475–475.

Dorgan, K. M.; P. A. Jumars; B. D. B. D. Johnson and B. P. Boudreau. 2006. Macrofaunal burrowing: the medium is the message. Oceanogr. Mar. Biol. Annu. Rev., *44*, 85–121.

Esselink, P. and L. Zwarts. 1989. Seasonal trend in burrow depth and tidal variation in feeding activity of Nereis diversicolor. Mar. Ecol. Prog. Ser., *56*, 243–254.

Fauchald, K. and P. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Annu. Rev., *17*, 193–284.

Geng, J.; D. Howell; E. Longhi; R. P. Behringer; G. Reydellet; L. Vanel; E. Clément and S. Luding. 2001. Footprints in sand: the response of a granular material to local perturbations. Phys. Rev. Lett., 1–5.

Gilbert, F.; L. Rivet and J. Bertrand. 1994. The in vitro influence of the burrowing polychaete Nereis diversicolor on the fate of petroleum hydrocarbons in marine sediments. Chemosphere, *29*, 1–12.

Kristensen, E. 2000. Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. Hydrobiologia, *426*, 1–24.

Kristensen, E. and K. Hansen. 1999. Transport of carbon dioxide and ammonium in bioturbated (Nereis diversicolor) coastal, marine sediments. Biogeochemistry, *45*, 147–168.

Kristensen, E. and J. E. Kostka. 2005. Macrofaunal Burrows and Irrigation in Marine Sediment: Microbiological and Biogeochemical Interactions. Interaction Between Macro- and Microorganisms in Marine Sediments. E. Kristensen, R. R. Hease and J. E. Kostka. Washington, DC, American Geophysical Union. *60*: 125–157.

Kristensen, E.; G. Penha-Lopes; M. Delefosse; T. Valdemarsen; C. Quintana and G. Banta. 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar. Ecol. Prog. Ser., *446*, 285–302.

Larsen, P. F. 1991. The macroinvertebrate fauna associated with the mud flats of the Gulf of Maine. Journal of Coastal Research, *7*, 365–375.

Larsen, P. F. and L. F. Doggett. 1990. Sand beach macrofauna of the Gulf of Maine with inference on the role of oceanic fronts in determining community composition. Journal of Coastal Research, *6*, 913–926.

Maire, O.; P. Lecroart; F. Meysman; R. Rosenberg; J. Duchêne and A. Grémare. 2010. Quantification of sediment reworking rates in bioturbation research: a review. Aquatic Biology, *2*, 219–238.

Meysman, F. J. R.; J. J. Middelburg and C. H. R. Heip. 2006. Bioturbation: a fresh look at Darwin's last idea. Trends Ecol. Evol., *21*, 688–95.

Miron, G.; G. Desrosiers; C. Retière and R. Lambert. 1991. Evolution spatio-temporelle du réseau de galeries chez le polychète Nereis virens (Sars) en relation avec la densité. Can. J. Zool., *69*, 39–42.

Motta, J. J. C.; A. J. Underwood and M. G. Chapman. 2003. Benthic assemblages in sediments associated with intertidal boulder-fields. J. Exp. Mar. Biol. Ecol., *286*, 383–401.

Murray, J. M. H.; A. Meadows and P. S. Meadows. 2002. Biogeomorphological implications of microscale interactions between sediment geotechnics and marine benthos: a review. Geomorphology, *47*, 15–30.

Nowell, A. R. M.; P. A. Jumars; R. F. L. Self and J. B. Southard. 1989. The effects of sediment transport and deposition on infauna: Results obtained in a specially designed flume. Lecture Notes on Coastal and Estuarine Studies, *31*, 247–268.

Pöschel, T. and T. Schwager. 2005. Computational granular dynamics: models and algorithms. Springer.

Schiffers, K.; L. R. Teal; J. M. J. Travis and M. Solan. 2011. An Open Source Simulation Model for Soil and Sediment Bioturbation. PLoS ONE, *6*, e28028–e28028.

Sherwood, C.; D. Drake; P. Wiberg and R. Wheatcroft. 2002. Prediction of the fate of p, p′-DDE in sediment on the Palos Verdes shelf, California, USA. Cont. Shelf Res., *22*, 1025–1058.

Sturdivant, S. K.; R. J. Díaz and G. R. Cutter. 2012. Bioturbation in a declining oxygen environment, in situ observations from Wormcam. PloS one, *7*, e34539–e34539.

Volkenborn, N.; S. I. C. Hedtkamp; J. E. E. van Beusekom; K. Reise and J. Vanbeusekom. 2007. Effects of bioturbation and bioirrigation by lugworms (Arenicola marina) on physical and chemical sediment properties and implications for intertidal habitat succession. Estuarine, Coastal and Shelf Science, *74*, 331–343.

Zorn, M. E.; S. V. Lalonde and M. K. Gingras. 2006. Microscale oxygen distribution in various invertebrate burrow walls. Geobiology, *4*, 137–145.