

**Sediment properties and burrowing of *Abarenicola pacifica* and *A. claparedi*
vagabunda in False Bay**

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Recent research on burrowing mechanics suggests that animals may be moving through crack propagation and that the material properties of a sediment may be important for the ability of animals to move it. Two species of *Abarenicola* who inhabit distinct areas of False Bay were examined. It was hypothesized that a sediment's stiffness would be related to its grain-size composition and to animal distributions, and that worms would burrow more successfully in their own sediment. In sites with either *A. pacifica* or *A. claparedi*, grain size distribution was analyzed and a modified penetration test was used to quantify the stiffness of sediments. Additionally, each species was timed burrowing in the field in either its own sediment or the sediment of the other species. *A. pacifica* lived in stiffer, poorly-sorted sediment with a high proportion of silts and clays, while *A. claparedi* were found in less stiff, well-sorted sediments consisting mostly of fine sands. Despite living in distinct sediment types, worms did not burrow more quickly in their own sediment. However, burrowing angle and speed changes throughout burrowing suggest *A. claparedi* struggled to burrow successfully in the stiffer sediment of *A. pacifica*. Our results suggest that the material properties of sediment do vary with the grain size composition and that these material properties may play an important role in determining animal success in an area. However, the affect of the material properties of sediment on burrowing of *Abarenicola* in the field is not as simple as originally hypothesized.

Introduction

The lives of organisms buried in sediment has long interested scientists, but understanding how exactly these organisms function is challenging specifically because they are hidden from view. Traditional attempts to explain animal distributions examined grain size ranges of sediment (Sanders, 1958). Incorporating knowledge of different grain sizes, organisms living in sediment were described as living in two amensal trophic groups, which were used to account for animal distributions (Rhoads & Young, 1970).

Early models of how organisms moved through the sediment often include a step where animals liquefy or scrape the sediment in front of them in order to move forward. This process has been described in a variety of organisms from lugworms to bivalves (Trueman, 1966). However, recent work by Dorgan *et al.* has forced biologists to reconsider the mechanisms by which organisms burrow. They argue that considering sediment as its component parts through grain-size analysis does not capture the true

nature of sediments as organisms experience them. Clean, coarse beach sand will behave like a granular solid, but the particles of many marine sediments are better represented as a single composite material of larger grains embedded in a variety of fine sediments and organic particles (Dorgan *et al.*, 2006). Using clear gelatin as a proxy for sediments, Dorgan *et al.* (2005) have shown the annelid *Nereis virens* is able to burrow by using its eversible pharynx as a wedge to propagate a crack. By shooting out its pharynx, the worm exerts a normal force against the walls of the burrow, causing the tip of the burrow to crack forward. Many other burrowing organisms may use similar methods of crack propagation (Dorgan *et al.*, 2006).

The success and exact mechanics of burrowing through crack propagation will depend on the material properties of a sediment, of how it responds to stresses exerted by organisms as they burrow. If organisms are burrowing through crack propagation, then differences in sediment material properties may provide a new lens with which to examine animal distribution and behavior. In order to understand how the crack propagation model might apply to other organisms, *Abarenicola pacifica* and *A. claparedi vagabunda* were examined in False Bay, a shallow bay on San Juan Island that drains at low tide, exposing a broad mudflat (Fig. 1).

A. pacifica and *A. claparedi* are two species of lugworm who live head-down in semi-permanent mucus-lined burrows where they deposit feed and leave characteristic stacked castings on the sediment surface (Fig. 2). Both worms burrow through the sediment and may change the location of their burrows (Healy & Wells, 1959). These worms are also ideal for studying the material properties of sediment because, although they share many morphological and behavioral traits, they live in distinct areas of the bay

(Healy & Wells, 1954; Hobson, 1967). Although their exact distributions can change, in the summer of 2012, as in 1954 and 1967, *A. pacifica* were found exclusively in the shallow waters near the entrance to the bay and *A. claparedi* were found farther out near the mouth of the bay.

If *Abarenicola* are in fact burrowing through crack propagation, then we predict that each species will live in sediments with a distinct range of stiffnesses. Furthermore, if the success of crack propagation is related to previous ideas about animal-sediment interactions, then sediment stiffness and *Abarenicola* distribution should be associated with specific ranges of grain size. Finally, we predict that each species of *Abarenicola* should burrow best in its own sediment.

Materials and Methods

All field data and specimens were collected in False Bay in June and July, 2012. Based on the distribution of *Abarenicola*, the stiffness of sediment was quantified at various sites around the bay and sediment samples were collected for grain-size analysis. Burrowing behavior was also examined in the field.

Material Properties

The stiffness of sediment was quantified at 10 sites inhabited by lugworms (5 by *A. pacifica*, 5 by *A. claparedi*) and two additional sites in very soft sediment inhabited by neither species by dropping a threaded rod (91 cm long, 0.25 cm diameter) vertically so that the bottom of the rod was 68 cm above the saturated sediment and then measuring how deep the rod was embedded in the sediment. The mass of the dropped rod (and therefore the force exerted on the sediment) was modified by adding fishing weights in different combinations as well as using rods that were three-quarter and one-quarter the

length of the original rod. At least three trials of a series of twelve different masses were performed with every weight at every site. In each trial the pattern of the addition of weights ascended and descended so that any bias in sediment properties associated with tidal height was avoided.

Sediment Collection and Grain Size Analysis

Two or three sediment cores were collected from every dropping site by inserting a 3 cm diameter copper pipe to a depth of 30 cm or until it became stuck. If, when removing the sediment from the corer, a clear transition in sediment types was apparent, only the top portion of sediment from these samples was analyzed.

Twelve cores corresponding to the 12 different dropping sites (5 with *A. pacifica*, 5 with *A. claparedi*, and 2 with neither) were sieved by hand through 2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, and 0.063 mm mesh. Sediment collected in each sieve was transferred to weigh boats and dried in a drying oven, ranging from 70-90°C. Fine sediments that ran through all the sieves were allowed to settle for at least two days, after which the supernatant was removed and the sediment dried. After drying, the sediment fractions separated by the sieves were weighed.

Burrowing Tests

Behavioral tests of burrowing by *A. pacifica* and *A. claparedi* were carried out in undisturbed sediment in the field at sites where dropping tests had previously been performed and where one worm species was present. Worms were collected by carefully digging near castings visible on the surface. Each worm was gently cleared of sediment by hand in seawater immediately after collection and stored individually in a plastic bag filled with seawater until testing. Individuals were tested in sediment characteristic of

their own species and in sediment of the other species, and the order of trials was controlled for between worms. Some worms completed their second trial the day after collection. They were returned to the lab in plastic bags, which were stored in a sea table with circulating seawater overnight, and they were returned to the field in the morning.

For every trial, an individual was placed ventral-side down in a puddle. Time points were recorded when it was placed, when the proboscis was fully buried, when the gills first entered the burrow, and when the most posterior gill entered the burrow. Water temperature was monitored regularly and all tests occurred between 15 and 21°C. After the most posterior gill entered the burrow, the worm was dug up from the sediment and the angle of its burrow was noted. After its last trial, the worm's volumetric size was measured, and the worm was returned to its own sediment.

Data Analysis

Material Properties

To characterize the stiffness (slope of the stress/strain line), the samples from each field site were analyzed. Because the relationships were typically in the form of j-shaped curves we made linear regressions of only the low stress (mass < 250 g) portion of the data because the curves were linear in this region and these forces are more representative of what a worm might encounter. Because these slopes were not normally distributed, a Wilcoxon rank sum test was used to compare the stiffnesses of the sediments of each species of worm.

Grain Size

The proportion of each sediment size fraction was compared between the sediments of the two species of *Abarenicola*. A Wilcoxon rank sum test was used for the

non-normally distributed fractions captured in the 2 mm, 1 mm, and 0.5 mm sieves as well as the sediment less than 0.063 mm. A two-tailed t-test was used for the 0.25, 0.125, and 0.063 mm sieves.

To examine the relationship between grain size and stiffness, we tested the correlation between the sediment stiffnesses and the percent mass of each of the 7 sediment fractions.

Burrowing Tests

The number of worms that failed to complete the burrowing trial was compared across sediments using a chi-squared test, and then these trials were excluded from further data analysis. Total burrowing times were compared using a Wilcoxon rank sum test, because the data were not normally distributed. Comparisons were made within each species of worm between the two sediment types as well as at specific site between each species. Burrowing time to various checkpoints were also examined. Time from placement to burial of the proboscis in the sediment was compared between species using a Wilcoxon rank sum test. Burrowing times from the proboscis to the first gills and from the first gills to the last gills were normally distributed and compared between species using a t-test. The angle of burrowing was compared across testing sites for each species of worm using a chi-squared test.

Results

Observations in the field and laboratory suggested some differences between *A. pacifica* and *A. claparedi*. *A. pacifica* seemed to have a firmer body when handled. Additionally, although both species readily produced mucus, the mucus of *A. claparedi* was both more profuse and stronger. The mucus coating individuals of *A. pacifica* was

easily broken and wiped off the worms in seawater. In contrast, individuals of *A. claparedi* were often wrapped in thick ropes of mucus that had to be slipped off the worm or cut with scissors.

Material Properties

Abarenicola pacifica and *A. claparedi* lived in sediments that describe distinct stress-strain curves (Fig. 3, 4). Examining only trials with a low stress (mass < 250 g), *A. pacifica* lived in sediment that has a significantly steeper slope (Fig. 4b)($z = 0.012$, $p < 0.05$) and was therefore stiffer.

Sediment Analysis

Comparing the cores taken from sediment with *A. pacifica* with those taken from *A. claparedi*, *A. pacifica* live in a more poorly sorted sediment (Fig. 5). The sediments with *A. pacifica* contained a significantly higher proportion of sediment captured in the 2 mm ($z = 2.67$, $p < 0.01$), 1 mm ($z = 2.52$, $p < 0.05$), 0.05 mm ($z = 2.09$, $p < 0.05$), and 0.063 mm sieves ($t(8) = 3.01$, $p < 0.05$) as well as sediment less than 0.063 mm ($z = 2.51$, $p < 0.05$). Sediment of *A. claparedi* was composed of significantly higher proportion of sediment captured in the 0.125 mm sieve ($t(8) = -4.37$, $p < 0.005$). There was no significant difference between the two sediment types in the amount of sediment captured in the 0.25 mm sieve.

There is no correlation between percent mass captured in a sieve and the stiffness of the four coarsest sediments (2 mm, 1 mm, 0.5 mm, 0.25 mm sieves) (Fig. 6). A negative correlation was found between percent mass captured in a 0.125 mm sieve and stiffness of the sediment ($r^2(10) = 0.51$, $p < 0.01$). A positive correlation was found

between percent mass in the two finest fractions and the stiffness of the sediment (0.063 mm sieve, $r^2(10) = 0.391$, $p < 0.05$; less than 0.063 mm, $r^2(10) = 0.511$, $p < 0.01$).

Burrowing Tests

Neither species of worm burrowed faster in its own sediment (*A. pacifica*, $p = 0.095$; *A. claparedi*, $p = 0.123$). Also, no significant difference was found between species in total burrowing time ($p = 0.128$). However, a difference did emerge between species in how they burrowed in the stiffer sediment of *A. pacifica*. No difference existed between species in the time between when the worm was placed and when the worm successfully started to burrow ($p = 0.0607$). However, once the proboscis was in the sediment, *A. pacifica* then burrowed to the gills faster than *A. claparedi* ($z = 2.50$, $p < 0.05$). This pattern flipped after reaching the first gills with *A. claparedi* reaching the last gill more quickly ($t(40) = -2.91$, $p < 0.01$). In the sediment of *A. claparedi*, no difference existed in burrowing time to get into the sediment or to reach the gills. However, *A. pacifica* burrowed faster across the gills ($t(31) = -2.32$, $p < 0.05$).

There was no significant difference in the number of incomplete trials in the two sediment types for either species of worm. In the sediment of *A. pacifica*, *A. claparedi* burrowed more shallowly than in its home sediment ($X^2(2,28) = 10.67$, $p < 0.005$). *A. pacifica* showed no difference in burrow angle in the two sediments.

Discussion

The two species of *Abarenicola* lived in distinct sediment types in False Bay. *A. pacifica* lived in a stiffer sediment that was poorly sorted and characterized by a particularly high proportion of the finest grained sediments including silts and clays (Fig. 4, 5). In contrast, *A. claparedi vagabunda* lived in a well-sorted sediment composed

almost exclusively of fine sands (Fig. 4, 5). This differentiation of sediment types between worm locations supports the hypothesis that the material properties of sediment and the grain size composition of the sediment will be important in determining worm distribution. These findings accord with the experience of previous workers (Sanders, 1958, Hobson, 1967, Rhoads & Young, 1970) that said that animal populations varied predictably with variations in sediment composition while additionally incorporating tests of the material properties of sediment.

Furthermore, significant correlations emerged between certain sediment fractions and the stiffness of the sediment. Sediments containing a high proportion of fine sands (0.125 mm sieve) tended to be less stiff while poorly sorted sediments composed with a large fraction of silts and clays (0.063 mm sieve and < 0.063 mm) tended to be stiffer (Fig. 6). The presence of a high proportion of extremely fine particles in a poorly sorted sediment could increase the stiffness by filling in the spaces between larger particles. Thinking about sediment as a single composite material (Dorgan *et al.*, 2006), the fine particles, by filling in these spaces, could increase adhesion between particles and decrease the ability of other particles to move. This relationship between the grain size distribution of the sediment and the material properties of the sediment provide evidence for a relationship between the ideas of burrowing through crack-propagation and traditional studies of animal-sediment interactions (Sanders, 1958, Rhoads & Young, 1970). Furthermore, comparing these properties of sediments provides a framework by which the models can be considered together.

Given the strong association of each species with a characteristic sediment, it is surprising that worms do not seem to burrow faster in their own sediment (Fig. 7).

Consistent differences did, however, emerge in burrowing times between species in the stiffer sediment with *A. pacifica* beginning burrowing more quickly and *A. claparedi* initiating burrowing more slowly but progressing more quickly upon reaching the gills. Interestingly, in the less stiff sediment usually inhabited by *A. claparedi*, this trend reversed, and *A. pacifica* burrowed more quickly across the gills. This pattern suggests that the two species may approach burrowing slightly differently through variations in morphology or behavior.

Evidence of further differences in burrowing emerged when examining other measures of burrowing success. In particular *A. claparedi*, who typically burrow in less stiff sediment, seem to be less successful in burrowing in the stiffer sediment of *A. pacifica*. Their burrows tended to be shallower in the stiff sediment than in their home sediment. Typical lugworm burrows are U- or J-shaped with a vertically shaft near the surface and a more level region deeper in the sediment (Healy & Wells, 1959).

Morphological observations of the two species can be used to make initial predictions about possible causes of these differences in burrowing success. *A. pacifica* seem to have a firmer body when handled, and their body wall is more resistant when cut with scissors (Healy & Wells, 1959). This firmness could help a worm to generate the higher forces necessary to propagate a crack and burrow successfully through stiffer sediment. For example, more muscle development or a firmer body wall to better manipulate coelomic fluid could help a worm to generate higher forces against burrow walls.

Finally, the material properties of sediment may be affecting other aspects of worms' lives. The stiffness as well as the viscosity of a sediment might affect long-term

burrow maintenance. Although both worms produce mucus and use it to line their burrows, *A. claparedi* seemed to produce markedly more and stronger mucus. Higher mucus production might help these worms maintain burrow shape in less stiff sediment. In the future, it would be informative to examine other aspects of worms' lives that might be affected by the material properties of sediment as well as to quantify other properties of sediment especially along other timescales. We examined only stiffness of sediment in response to a short-term stress, but sediment may respond to stresses differently over periods of time, affecting different aspects of burrowing organisms' lives differently.

Considering how the material properties of sediments might affect the lives of burrowing organisms provides a new lens with which to examine animal distribution and habitat choices. Traditional research on animal distribution in sediment has often used grain size to describe a trophic group amensalism (Sanders, 1958), placing animals with certain feeding habits in distinct areas. However, the material properties of the sediment, as described in by Dorgan *et al.* (2006), may be just as important in determining animal success in an area. Furthermore, although examinations in the field may introduce complexity, it would be important in future research to explore not only the effect of sediment material properties on burrowing success along a variety of measures but also to consider how the material properties of sediment influence other areas of a burrowing organism's life.

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A



B



Figure 1. False Bay is a shallow bay on San Juan Island that drains at low tide exposing a broad mudflat, (a) Google Earth, (b) Merz.

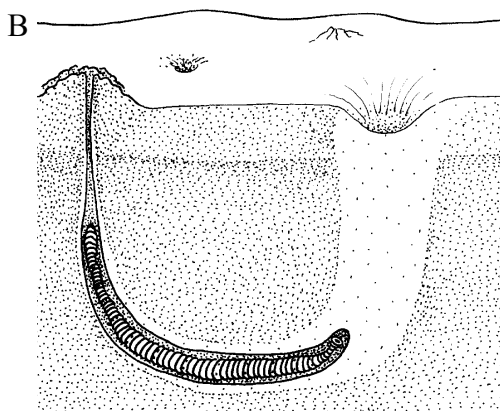


Figure 2. (a) *A. barenicola pacifica* (left) and *A. claparedi vagabunda* (right) oriented head-down. (b) The characteristic U-shaped burrow of the lugworm as it deposit feeds and (c) the castings that these worms leave on the surface. (b) http://biodidac.bio.uottawa.ca/thumbnails/fildet.htm?File_name=poly026b&File_type=gif, (c) Merz.

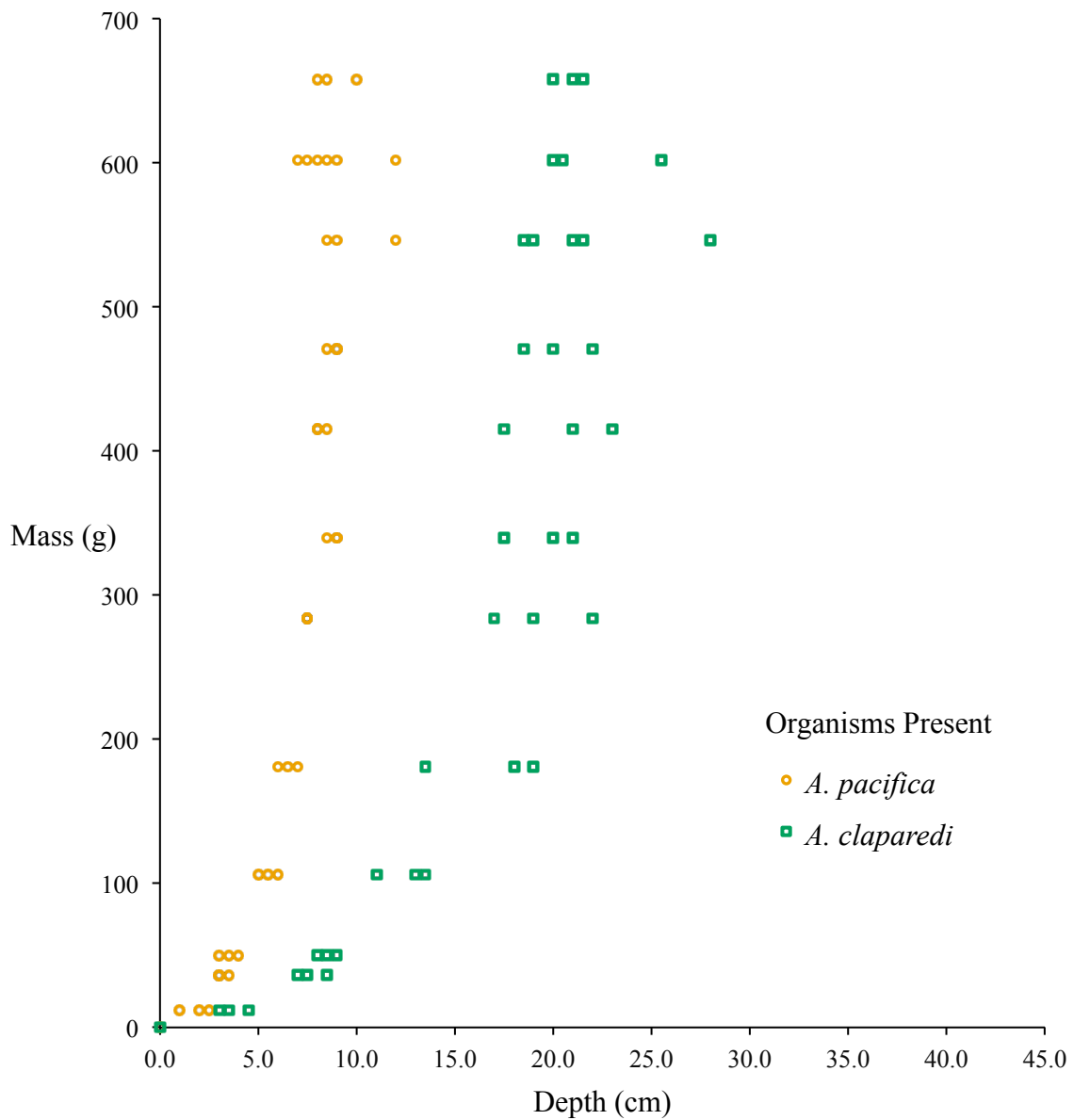


Figure 3. The stiffness of the sediment was quantified by dropping a threaded rod with various added weights into the sediment and measuring how deep the rod was embedded in the sediment. At every site, at least dropping trials were carried out at every mass. This graph shows data from just two sites, and the trials from each site describe a j-shaped stress-strain curve.

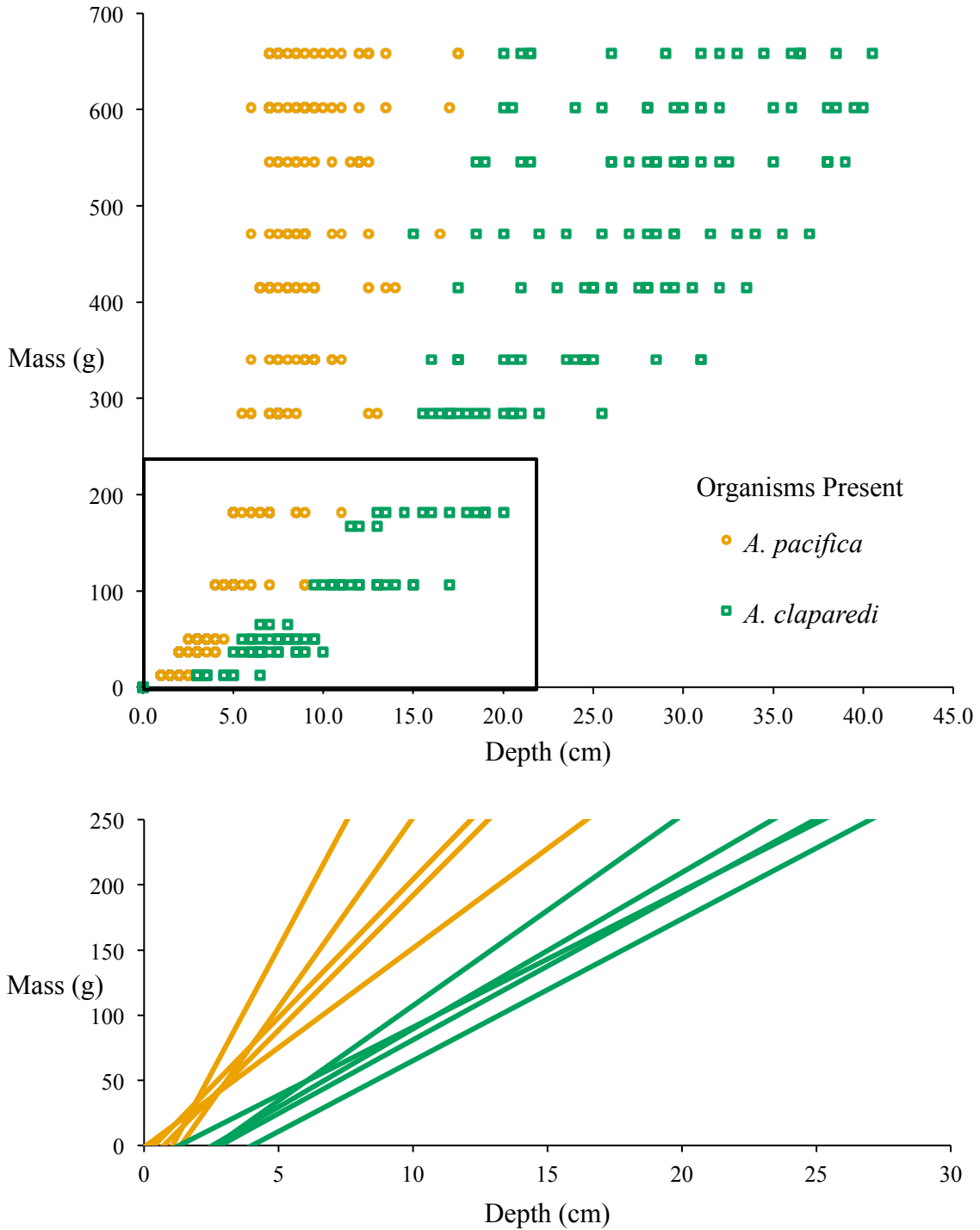


Figure 4. (a) Depth to which a dropped threaded rod fell into the sediment with different additional weights. Trials were conducted at five sites with *A. pacifica* (orange) and five sites with *A. claparedi* (green). (b) Linear regression was used to fit lines to curves from each site at low stresses (mass < 250 g). The slopes of the curves were significantly different between sediments with each species ($p < 0.05$).

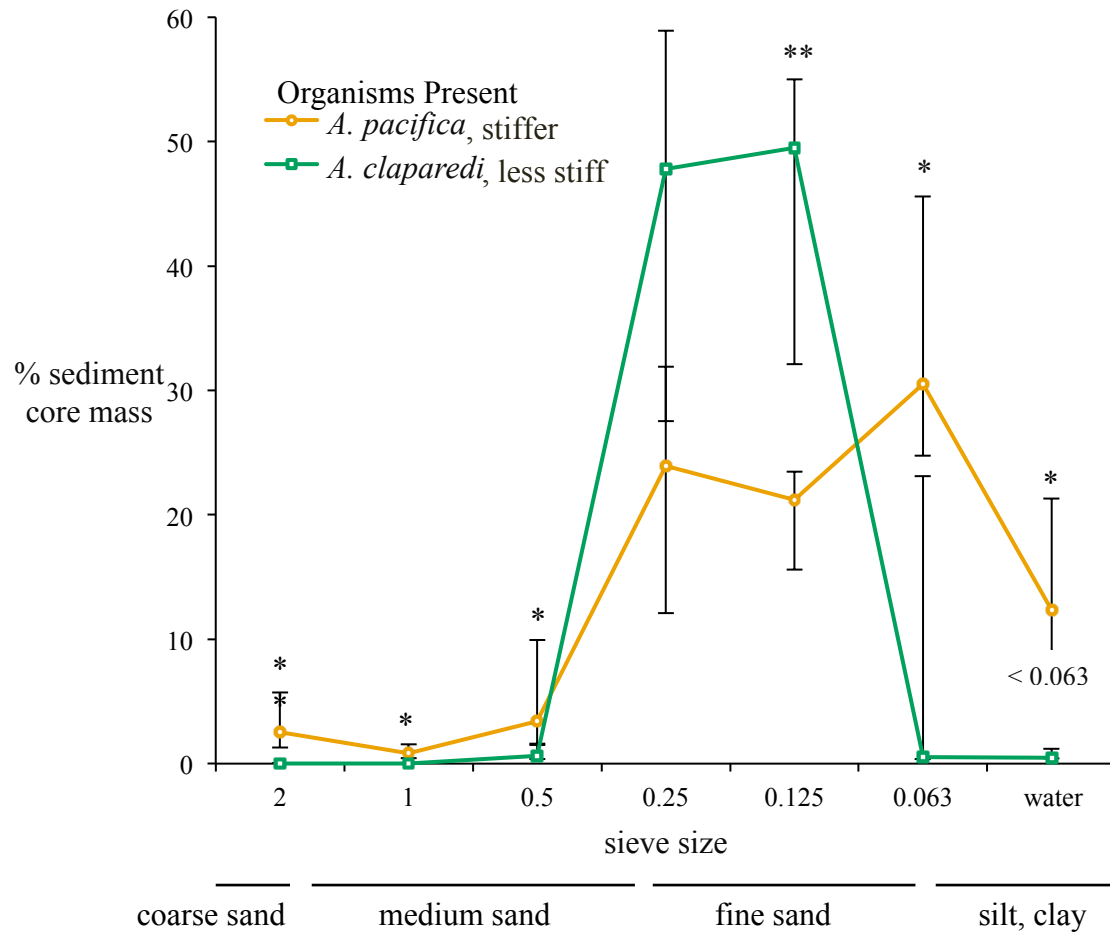


Figure 5. Percent sediment core mass captured in different sediment fractions in five sites with *A. pacifica* (orange) and five sites with *A. clarepedi* (green). * p < 0.05, ** p < 0.01

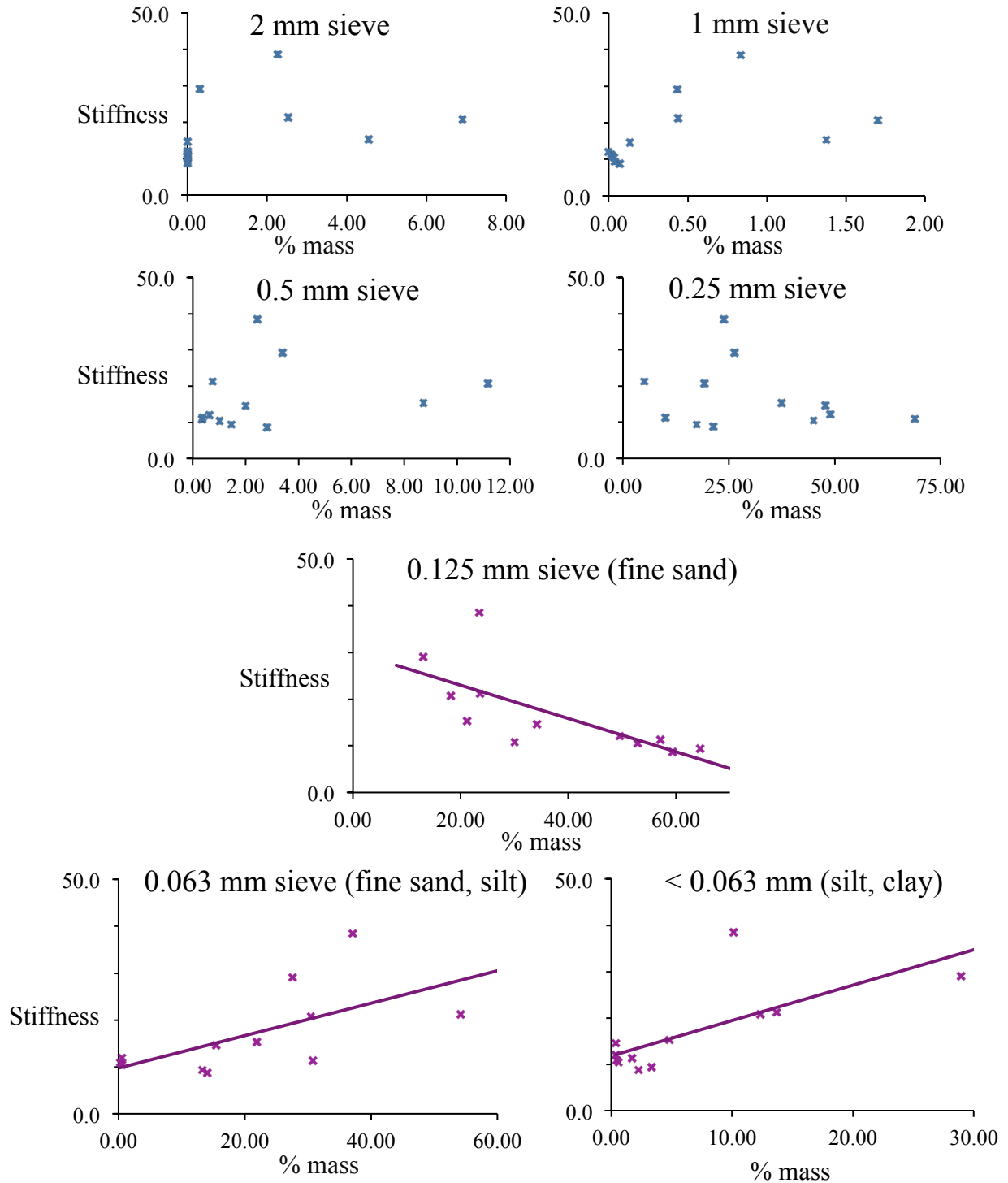


Figure 6. Correlation between amount of sediment captured in a fraction and stiffness of the sediment at 12 sites around False Bay. Correlations are insignificant for the four coarsest sediments. The fraction captured in 0.125 mm mesh showed a negative correlation ($r^2 = 0.51$, $p < 0.01$), and the two finest fractions showed a positive correlation (0.063 sieve, $r^2 = 0.39$, $p < 0.05$; < 0.063 , $r^2 = 0.51$, $p < 0.01$).

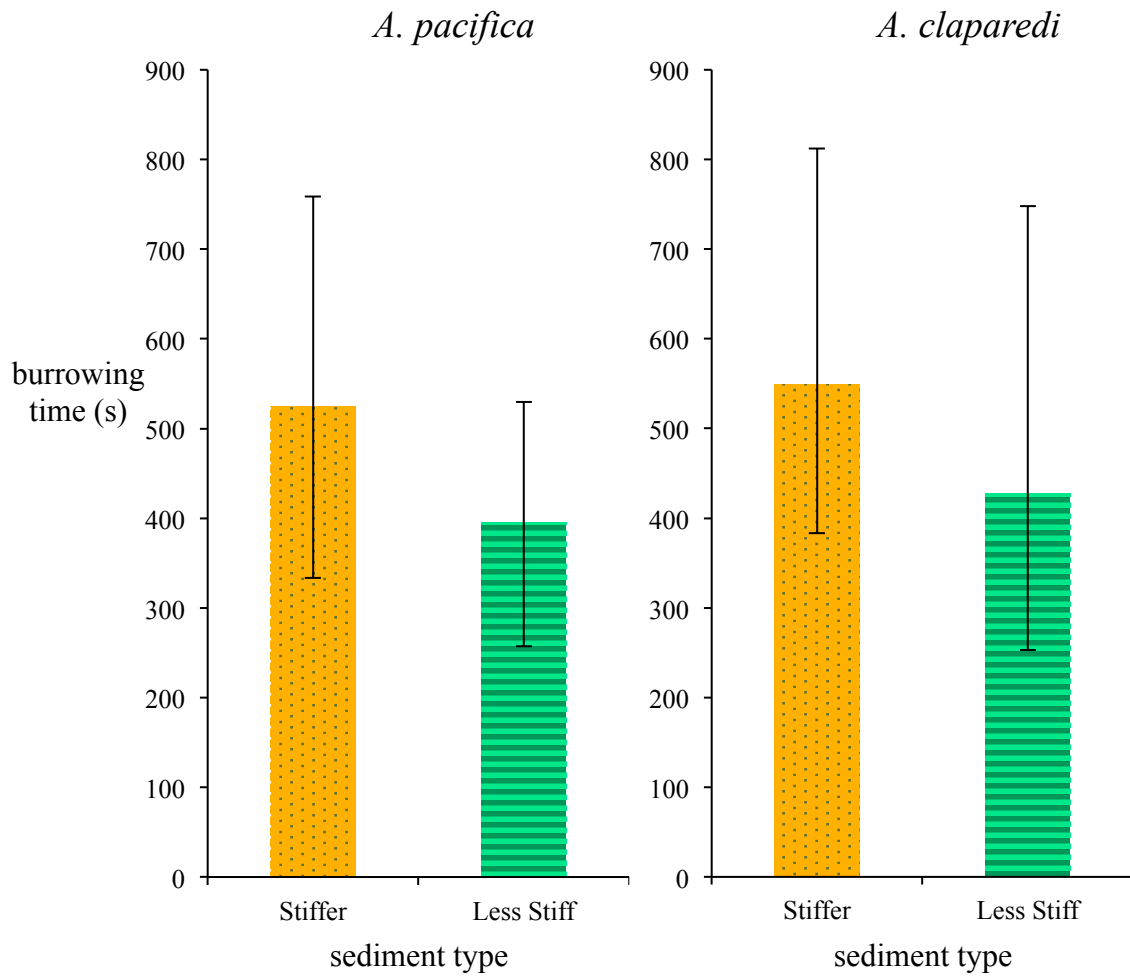


Figure 7. Total burrowing times for *A. pacifica* and *A. claparedi* in the field for the stiffer sediment with *A. pacifica* and the less stiff sediment of *A. claparedi*. Neither worm burrowed significantly faster in its own sediment.