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RESEARCH ARTICLE

Mechanical properties of sediment determine burrowing success and influence distribution of two lugworm species

R. L. Crane[1,*] and R. A. Merz[2]

ABSTRACT

We apply new perspectives on how organisms burrow by examining the association of *in situ* variation in sediment mechanical properties with burrowing ability and species distribution of two sympatric lugworms, *Abarenicola pacifica* and *Abarenicola claparedi*. We quantified the sediment's resistance to penetration and its grain size distribution at sites inhabited by each species. *Abarenicola pacifica* individuals were found in significantly harder to penetrate, more heterogeneous sediments. We compared worm burrowing ability using reciprocal transplant experiments. Worms from firmer sediments, *A. pacifica*, were able to make successful steep burrows in sediments characteristic of either species. In contrast, *A. claparedi* individuals often failed to complete successful burrows in the firmer *A. pacifica* sediment. To examine how morphological differences could explain these patterns, we compared body wall musculature and measured how well individuals support their own bodies when draped over a cantilever. Lugworms from the firmer sediment had thicker body wall musculature and held their bodies more rigidly than did worms from softer sediments. Additionally, we observed subtle differences in the papillae on the proboscises' surfaces, which could affect worm–sediment interactions, but we found no differences in the chaetae of the two species. *Abarenicola claparedi* produced more mucus, which could be important in shoring up burrow walls in their shifting, sandy habitat. This study presents the first example of using field-based experiments to determine how sediment mechanical properties and worm burrowing ability could act to determine organismal distribution. Our findings have broader ecological implications because of the role of lugworms as ecosystem engineers.

KEY WORDS: Functional morphology, Polychaetes, *Abarenicola*, Biomechanics, Ecosystem engineer, Sediment mechanics

INTRODUCTION

Burrowing organisms play an important role in turning over sediment and determining infaunal marine communities (Krager and Woodin, 1993; Volkenborn et al., 2009; Berke et al., 2010). Their behavior affects the chemistry and bacterial composition of the sediment and surrounding water (Aller, 1982; Guitiérrez and Jones, 2006; Meysman et al., 2006; Volkenborn et al., 2010), and can alter the sediment grain sizes in the benthic habitat (Sanders, 1958; Rhoads and Young, 1970; Volkenborn and Reise, 2007). However, despite the ecological importance of burrowing organisms, we have little field-based information on their burrowing abilities in relation to the mechanical properties of the sediment.

Burrowing organisms have long been thought to extend their burrows by fluidizing sediment (i.e. suspending grains in the surrounding fluid) or scraping away burrow walls (Clark, 1964; e.g. worms: Trueman, 1966a; bivalves: Trueman, 1966b). However, a conceptual shift in our ideas about the mechanical properties of sediments has broadened our understanding of burrowing mechanisms (Dorgan et al., 2005, 2006; Dorgan, 2015). Animals living in loose granular materials (e.g. coarse sands with low organic content where adhesion between grains is minimal, and gravitational forces form stress chains between stacks of grains) often dislodge grains or fluidize the sediment locally (Dorgan et al., 2006; Dorgan, 2015). In contrast, animals entering or moving through muds and fine sands with high organic content (which behave like a composite elastic material) often crack the sediment (Johnson et al., 2002; Dorgan et al., 2005, 2006; Dorgan, 2015). Burrowing by crack propagation involves an organism expanding its body near the tip of the burrow with a wedge-like structure (shell, foot, proboscis or other morphological feature) and then exerting a force normal to the burrow walls, causing the burrow tip to crack forward. A variety of marine worms and other infaunal organisms burrow using crack propagation (Dorgan, 2015). These welcome insights have been based primarily on laboratory observations using artificial substrates, and they represent just two common alternatives of burrowing mechanisms. Depending on animal morphology and sediment characteristics, animals rely on a range of mechanisms including those described in addition to excavating the sediment by picking up and moving grains and loosening sediment to facilitate relocating it or moving through it (Dorgan, 2015).

In this study, we examine how material properties of sediment in the field relate to the distribution, success in burrowing and phenotype of two species of polychaetes, the lugworms *Abarenicola pacifica* Healy and Wells 1959 (Fig. 1A) and *Abarenicola claparedi* Healey and Wells 1959 (subspecies *vagabunda*) (Fig. 1B) (Hobson and Banse, 1981). Despite extensive morphological and behavioral similarities shared by these species, they occur in distinct but neighboring regions of the same intertidal bays. The zonation pattern of these lugworms is unusual because the *A. pacifica* region is sometimes, but not always, relatively higher in the intertidal region compared with that of *A. claparedi* (Healy and Wells, 1959; Hobson, 1967). Thus, the classic explanations of relative physiological tolerances to tidal exposure may not be the only or even primary variable in determining their intertidal distribution.

Typical of many lugworms (Wells, 1945; Jumars et al., 2015), both of these deposit-feeding species live in mucus-lined, semi-permanent J-shaped burrows (Fig. 1C). They actively pump water through their vertical burrows, which pulls surficial sediments down through a temporary head shaft. They ingest these sediments, and

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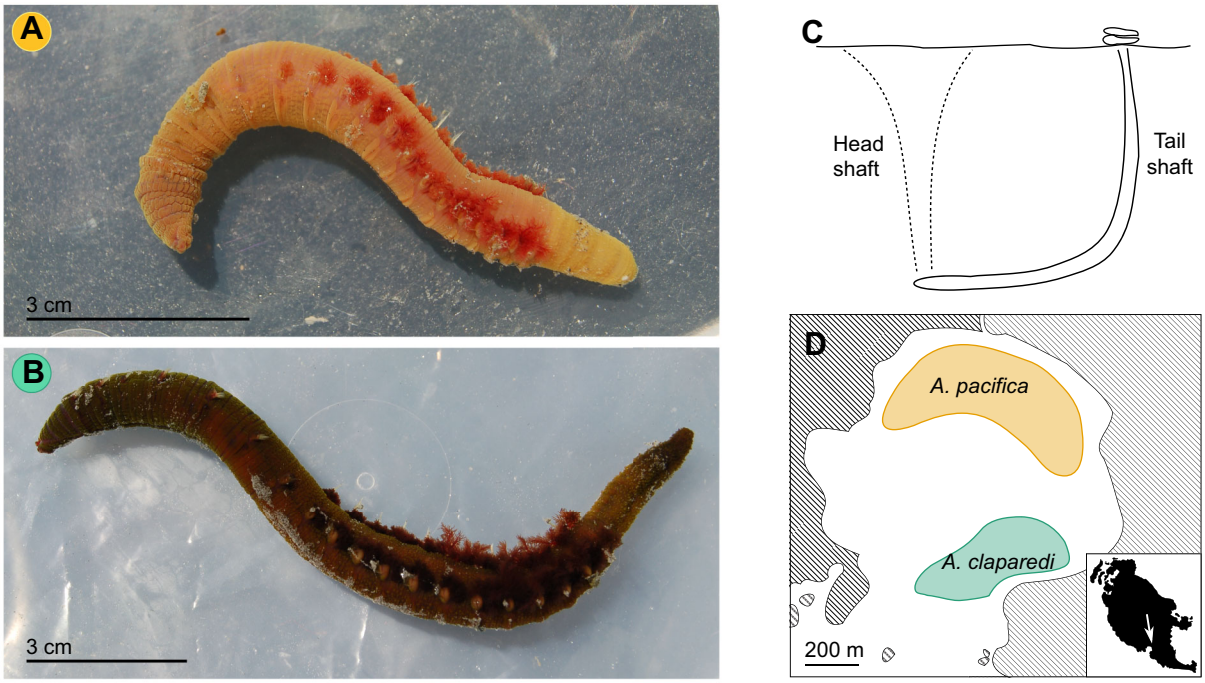

Fig. 1. Individuals of *Abarenicola pacifica* and *Abarenicola claparedi* live in J-shaped burrows in distinct areas of False Bay, WA, USA. Characteristic examples of (A) *A. pacifica* and (B) *A. claparedi* (heads pointed to the left). (C) Both deposit-feeding species live in J-shaped semi-permanent burrows. Each burrow has a temporary head shaft of shifting sediment from which the worm feeds and a steep, essentially vertical, tail shaft whose shape is maintained by mucus-reinforced walls (modified from Healy and Wells, 1959). (D) Map of False Bay showing approximate distributions of each species in 1965 (Hobson, 1967), which closely resemble distributions during this study, with inset showing the location of False Bay on San Juan Island indicated by arrow.

then defecate on the surface in characteristic coiled castings (Fig. 1C) (Wells, 1945; Healy and Wells, 1959; Woodin and Wethey, 2009).

In both species, the worms typically change their positions and make new burrows over time. In *A. pacifica*, the burrows of smaller juveniles are characteristically found reaching to the upper edge of the intertidal region whereas larger individuals and adults are found to ∼0.8 m above MLLW (mean lower low water), indicating a migration that happens over the lifespan of the animals [Krager and Woodin, 1993; R.L.C. and R.A.M., personal observation; similar to the pattern seen in *Arenicola marina* (Flach and Beukema, 1994)]. Over shorter time scales, there is good evidence that individual *A. pacifica* move their burrows frequently. By making daily maps of the location of burrows as indicated by the diameter of fecal coils, Krager and Woodin (1993) followed the position of 923 worms in False Bay, WA, USA, and demonstrated that the tail shafts of *A. pacifica* individuals only remain in place for an average of 3 days (range of 1–12 days). The relocation of individual *A. claparedi* is even more obvious. This species occasionally completely exits its burrow and wanders conspicuously on the surface of the sediment during low tide. It was originally named *Abarenicola vagabunda* because of this characteristic behavior (Healy and Wells, 1959). This activity is often associated with spawning, but is also seen in pre-reproductive juveniles (Guberlet, 1934; Healy and Wells, 1959; Healy, 1963; R.L.C. and R.A.M., personal observation).

Burrowing in both species involves similar behaviors – rapid extension of the pharynx then expansion of the proboscis (Wells, 1948, 1954). These worms have chaetae-bearing parapodial ridges that can be quickly raised or relaxed. In the erect position, these form flanges that could contact the burrow wall and either anchor or propel the worms (Wells, 1944). These two species live in sediments that could potentially allow burrowing by a variety of mechanisms, including crack propagation, excavation or local fluidization (Volkenborn et al., 2010).

Variations between these two species in the proboscis, body wall and chaetae may correlate with different means of burrow extension or contribute to differences in burrowing ability, and thus determine their distribution in relation to different kinds of sediment. In muddy, cohesive sediments the extension of the pharynx could act as a wedge and the following expansion of the proboscis could crack the sediment and extend the burrow. Alternatively, in coarser sediments, these same structures could act like a rasp and disrupt the linkages among the individual sediment grains, thus dislodging them. Differences between the two species in the gross shape of the proboscis or its surface structures, papillae, may indicate these different kinds of interactions with the sediment. Worms with more robust body wall musculature should be able to generate larger hydrostatic pressures (Che and Dorgan, 2010) and therefore more effectively evert the proboscis, making them stronger burrowers. Dramatic differences in chaetal texture or position could suggest a difference in anchoring ability or in the way the body is held during burrowing and proboscis extension. Finally, differences in mucus production might relate to maintaining burrows in sediments with different properties.

MATERIALS AND METHODS

Specimen collection

We collected worms by hand from False Bay, San Juan Island, WA, USA (48°29′11″ N, 123°04′05″ W) (Fig. 1D), by carefully digging near castings visible on the sediment surface. For all experiments, observations and measurements, we used only intact animals that exhibited normal behavior (e.g. that burrowed when sediment was available). In the laboratory, the worms were housed in flow-through seawater tables within containers filled with False Bay

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sediment. We identified species using color and proportions of body regions (Fig. 1A,B), and we confirmed these identifications in a subset of worms using the number of esophageal caeca (internal glandular structures) and the presence or absence of fleshy coverings over the nephridipores (Hobson and Banse, 1981).

Sediment properties

Material properties of sediment

To quantify the mechanical properties of *in situ* sediment, we performed penetration tests in the summer of 2012 at 11 sites within False Bay that were inhabited by lugworms (*A. pacifica* N=6, *A. claparedi* N=5). Lugworm presence was judged by an occurrence of more than one fecal mound per square meter. For each measurement, we dropped a blunt-ended threaded aluminum rod (91, 68 or 22 cm long; 0.25 cm diameter) vertically into an undisturbed patch of saturated sediment. Prior to release, the rod was held upright such that the bottom of the rod was approximately 68 cm (±2.5 cm) above the sediment surface. After dropping the rod, we measured the depth it penetrated into the sediment. Attaching weights to the center of the rod modified the mass of the rod and therefore the momentum at impact. At each site, we collected data from 30–42 drops, varying the mass of the rod between 12 g and 658 g.

To compare sediment resistance to penetration, for each site we generated penetration depth versus rod mass curves – a measure of how much the sediment deformed in response to a given addition of mass. The relationship was constructed by linear regression for all instances where the mass of the dropped rod was less than 200 g, because shear strength, the parameter measured by our penetrometer, increases with compaction below the surficial bioturbated layer in marine sediments (10–15 cm in similar previously measured intertidal marine sediments; Johnson et al., 2012). Drops at less than 200 g corresponded with maximum depths of 5–11 cm in *A. pacifica* sediments and 13–20 cm in *A. claparedi* sediments.

Sediment grain size distribution

We took single cores of sediment (~3 cm diameter) at 10 sites where we measured sediment resistance to penetration (five *A. pacifica* and five *A. claparedi* sediments). We were interested in collecting samples that represented the sediment in which lugworm burrows existed at that site and so took samples to a depth of 30 cm or as deep as we could insert the core (mean depth: *A. pacifica* sediments, 23 cm; *A. claparedi* sediments, 29 cm). At one *A. claparedi* site, there was a distinct coarse layer of sediment at depths below 20 cm. Burrows did not extend into this region, so at this site we cored only to a depth of ~20 cm. We washed each core through a series of Wentworth sieves (2, 1, 0.5, 0.25, 0.125 and 0.063 mm mesh) (Fisher Scientific Company, Hampton, NH, USA). Sediments that passed through the finest sieve were allowed to settle for at least two days, after which we removed the supernatant. We placed the sediment fractions in a drying oven (70–90°C) until weights taken at 1 h intervals showed no change.

Worm burrowing ability

We compared the ability of *A. pacifica* (N=38) and *A. claparedi* (N=19) to burrow in reciprocal transplant experiments in the summers of 2012 and 2015. We watched worms burrow in unmodified saturated sediment within the beds of each lugworm species in the field. The order of trials was balanced across worms, and worms of the two species did not differ in volume (Student's t-test t=0.89, d.f.=55, P=0.38). If worms could not burrow in both sediments on the day of their collection owing to an incoming tide or temperatures of the sediment surface exceeding 18°C (a threshold suggested to be stressful by preliminary burrowing trials), they were stored overnight in the laboratory in False Bay sediment in a sea table with flow-through seawater, and were then tested the next day. We included only data from worms that completed burrows in both sediment types.

Immediately prior to a burrowing trial, we gently removed any sediment and mucus from a worm and placed it ventral-side down in an undisturbed natural depression where the sediment was saturated and the worm was resting in seawater. We recorded the times when the proboscis was fully buried and when the most posterior gills (marked by a sharp reduction in body diameter and often a color change) entered the burrow. If the worm did not complete burrowing to this depth within 20 min, we considered the burrowing attempt unsuccessful. After the last time point, we excavated the worm from the sediment and categorized the angle of its burrow as steeper or shallower than 45 deg, because lugworms typically live in vertically oriented J-shaped burrows (Fig. 1C). After burrowing trials in each sediment type, we measured the worm's volume by seawater displacement and returned it to its own habitat.

Worm characteristics

Proboscis and chaetae

We compared features of the proboscis and the chaetae of *A. pacifica* and *A. claparedi* worms using scanning electron microscopy (SEM). We collected worms in the autumn of 2014 and spring of 2015, weighed them and then preserved them for comparison. The animals were relaxed in a solution of isotonic $MgCl_2$ and seawater. When the worms were limp and unresponsive, we extracted most of the $MgCl_2$ solution, leaving a minimal covering around the worm, and then added formalin (5%) slowly to their dishes at a rate of approximately 10 drops h^{-1} for several hours. The specimens were kept in formalin under refrigeration for at least 24 h and then were transferred to an ethanol series and dehydrated (30%, 50%, 70%, 85%, 95% and three washes of 100% ethanol). Specimens for SEM were submerged in 100% hexamethyldisilazane for at least 24 h, after which they were allowed to air dry (Nation, 1983; Barré et al., 2006) and then mounted on stubs using double-sided tape, silver paint, or adhesive carbon or copper tabs, sputter coated with gold–palladium, and viewed with a Philips XL 20 SEM at the University of Pennsylvania. From SEM images, we examined the chaetae and the surface of the proboscis of individuals of both species.

Body proportions

We collected worms in November 2014 to compare body proportions between the two species. We measured their volume by seawater displacement in a graduated cylinder, gently patted the worms dry and weighed them, and then after relaxing them in isotonic $MgCl_2$ measured their length (*A. pacifica* N=13, *A. claparedi* N=15). In field experiments, we measured worm volume but converted those values to masses using the robust correlation between mass and volume, which held for both species (linear regression model: mass=1.05×volume–0.0036, where the mass is in g and the volume is in ml; $F_{1,22}$=2033, P<0.001, R^2=0.99).

Body wall muscle thickness

We measured the width of the circular and longitudinal muscle layers of the ventral body wall from hand-cut cross-sections of the first gill-bearing segments of worms preserved as described above (*A. pacifica* N=10, *A. claparedi* N=8). Preliminary observations of sagittal sections indicated that the circular muscle layer diminishes in thickness at the boundaries of major (segmental) and minor

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annuli but has relatively constant thickness between boundaries. Therefore, the measurements were made away from annular boundaries. Worms were preserved and images were collected by the same procedure as describe above for SEM images. Larger specimens were measured using an ocular micrometer on a Wild dissection microscope whereas smaller specimens were measured from SEM images using NIH ImageJ (Schneider et al., 2012).

Worm rigidity

We measured the bending rigidity of the bodies of live worms (*A. pacifica* N=20, *A. claparedi* N=21) collected in November 2014 and June 2015. The worms did not differ in mass between species (Wilcoxon rank sum test, W=240, P=0.44). We gently removed any surface mucus or sediment from a worm's body. Then, supporting its head and tail, we draped and then released it over a plastic pipette (7.5 mm diameter) that was held as a horizontal cantilever beam. Each worm was positioned ventral-side down at its midpoint so that it would balance for at least 30 s while being videotaped using a camera that was aligned with the axis of the pipette. From single video frames, we measured the angles each worm assumed immediately after being draped on the pipette (approximately a second after it was placed on the beam and usually the moment when its head and tail were farthest apart) and when the head and tail came in closest proximity within the following 30 s (i.e. the most acute angle that was achieved). Using ImageJ (Schneider et al., 2012), we measured the angle formed by the points defined by the tip of the head, the midpoint of the body where it rested on top of the pipette and the tip of the tail. The worm's volume was then measured by seawater displacement and it was weighed.

Mucus production

We compared mucus production over an hour-long period by measuring change in mass of *A. pacifica* (N=31) and *A. claparedi* (N=23) worms collected in September 2014 and May and June 2015. In the laboratory on the same day as collection, we gently separated each worm from any mucus or sediment, and holding the worm mid-body, blotted its head and tail. The worm was then weighed in a clean Petri dish, after which seawater was added to cover it. The worm and water were maintained at 12°C. After 1 h, the worm (including the newly secreted layer of mucus adhering to its body) was removed from the Petri dish. Its head and tail were blotted as described above and it was reweighed.

Statistical analyses

For all appropriate comparisons, a Student's t-test was used when data were normally distributed and a Wilcoxon rank sum test when they were not. The slopes of the penetration depth versus rod mass curves of sediments characteristic of each species were compared using a Welch two-sample t-test, to account for unequal variances. To examine sediment grain size distributions, the percentage of the total mass of the core that was captured at each grain size was compared between sediments characteristic of each species using Wilcoxon rank sum tests.

For worms used in burrowing experiments, a Wilcoxon rank sum test was used to assess the effect of burrowing order. Burrowing times were compared between sediments using a paired t-test for *A. pacifica* worms and a paired Wilcoxon signed-rank test for *A. claparedi* worms. Burrowing times were compared between species using a Wilcoxon rank sum test. Finally, separately for each species, we used McNemar's paired χ^2 test to compare the frequency of steep burrows between sediment types.

We examined the body proportions of the two species by fitting linear models for each species to plots of the natural log of body mass versus the natural log of length. We compared the slopes of the two models. If the slopes were not significantly different, we generated models that assumed identical slopes and tested whether the intercepts differed significantly (parallel regression lines model). To compare longitudinal and circular muscle layer thicknesses

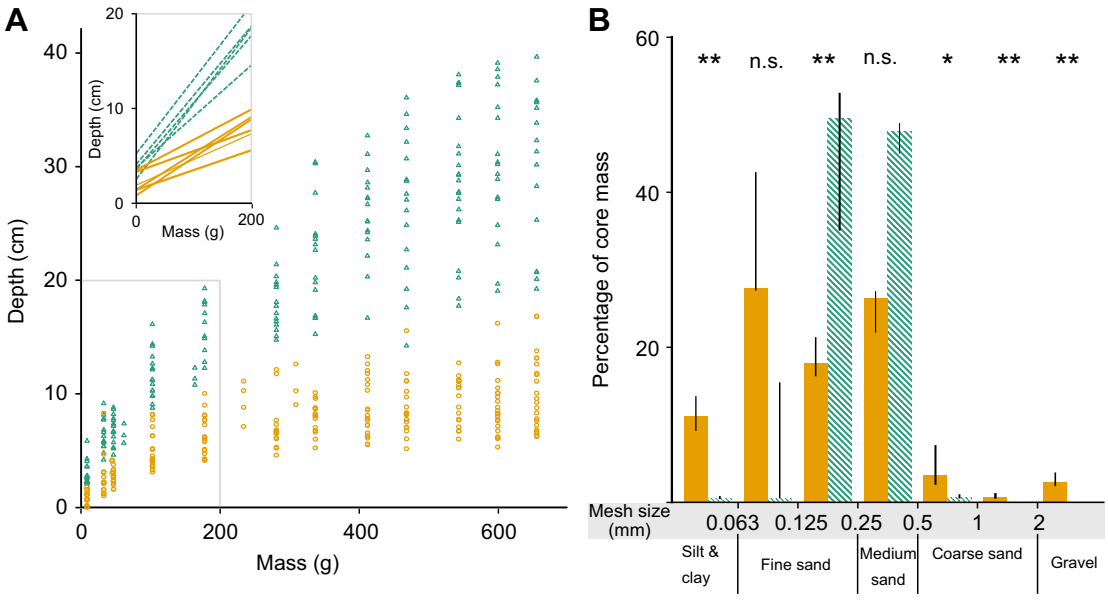

Fig. 2. Sediments characteristic of the habitats of *A. pacifica* and *A. claparedi* differ in resistance to penetration and grain size distribution. (A) The depth a threaded rod of varied masses penetrated the sediment when dropped from a consistent height onto sediment at six *A. pacifica* sites (orange circles; drops per site=32, 36, 38, 39, 39, 39) and five *A. claparedi* sites (green triangles; drops per site=36, 38, 39, 40, 42). The gray-outlined box indicates boundary for data included in linear regression. Inset: slopes of penetration depth versus rod mass were calculated using linear regression of drops performed at less than 200 g at *A. pacifica* (orange solid) and *A. claparedi* sites (green dashed). (B) Sediment size class distributions collected from habitats characteristic of *A. pacifica* (orange solid; N=5) and *A. claparedi* (green barred; N=5). Data are represented as median [±interquartile range (IQR)] percentages and were compared with a Wilcoxon rank sum test (*P<0.05, **P<0.01, n.s., not significant).

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Table 1. Grain size distribution for sediments characteristic of *Abarenicola pacifica* and *Abarenicola claparedi*

Grain size (mm)	*A. pacifica* median %	*A. claparedi* median %	Wilcoxon test statistic	*P*
>2	**2.5**	0	25	**<0.01**
1–2	**0.8**	0	25	**<0.01**
0.5–1	**3.4**	0.6	23	**<0.05**
0.25–0.5	26.4	47.8	5	0.15
0.125–0.25	17.9	**49.5**	0	**<0.01**
0.063–0.125	27.5	0.5	22	0.06
<0.063	**11.1**	0.4	25	**<0.01**

The median percentage of sediments captured in each fraction out of the total core mass is compared across the two sediment types using a Wilcoxon rank sum test. Significant *P*-values are shown in bold. Significantly different comparisons (the median percentage of the sediment in which that fraction is more common) are shown in bold.

between species, we used this same process to examine plots of the natural log of muscle layer thickness versus the natural log of body mass. For worms used in bending experiments, we compared worm masses between the two species with a Wilcoxon rank sum test. We compared initial and minimum bending angles between species by fitting linear regression models of the effect of weight on bending angle and testing slope and intercept as described above. The times when worms reached minimum angle after being released were compared between species with a Student's *t*-test. The effects of worm mass and species on mucus production were examined by fitting linear regression models for each species then comparing slopes. Additionally, the quantity of mucus produced as a proportion of body mass was compared between species with a Wilcoxon rank sum test.

All statistical tests were performed in R (version 3.3.2, http://www.R-project.org/), and plots were generated with the R package ggplot2 (Wickham, 2009).

RESULTS

Sediment properties

Material properties of sediment

Sediments characteristic of *A. pacifica* and *A. claparedi* differed in mechanical properties, with sediments characteristic of *A. pacifica* deforming less (Fig. 2). Sediments characteristic of *A. pacifica* were only penetrated to maximum depths of 5–10 cm, yet sediments characteristic of *A. claparedi* showed high variation in the degree to which the weighted rod penetrated the sediment, and had maximum depths of 20–40 cm (Fig. 2A). The slopes of the mass–penetration relationships of the sediments associated with each species differed significantly (t=7.2, d.f.=7.5, P<0.001; Fig. 2A). Sediments characteristic of *A. pacifica* were firmer (slope mean±s.d.=0.0298±0.0081) than sediments characteristic of *A. claparedi* (slope mean±s.d.=0.0708±0.0105; Fig. 2B).

Sediment grain size distribution

Sediments characteristic of the habitats of *A. pacifica* and *A. claparedi* had different grain size distributions (Fig. 2B). Sediments from within the *A. pacifica* bed were more heterogeneous, containing significantly more of both of the coarsest grains, including gravel and coarse sand, as well as the finest silts and clays as compared with sediments from within the *A. claparedi* bed (Fig. 2B, Table 1). Sediments characteristic of the habitat of *A. claparedi* were well sorted and were composed primarily of fine and medium sands (0.125–0.5 mm diameter) (Fig. 2B, Table 1).

Worm burrowing ability

Both species completed burrows more quickly in *A. claparedi* sediment than in *A. pacifica* sediment (Fig. 3A). The median burrowing times for *A. pacifica* worms were 85 s faster in *A. claparedi* sediment (paired *t*-test, t=−2.70, d.f.=37, P<0.05), and the median burrowing times for *A. claparedi* worms were 40 s faster in *A. claparedi* sediment (paired Wilcoxon signed-rank test, V=164, N=19, P<0.01). However, the burrowing times did not differ between species in either sediment (in *A. pacifica* sediments: W=334, P=0.65; in *A. claparedi* sediments: W=399, P=0.53; Fig. 3A). There was no effect of sediment order on burrowing time (Wilcoxon rank sum test for *A. pacifica* worms in *A. pacifica* sediment, W=231, P=0.15 and in *A. claparedi* sediment, W=176, P=0.90; for *A. claparedi* worms in *A. pacifica* sediment W=57, P=0.36 and in *A. claparedi* sediment W=32, P=0.32).

Although the two species showed no difference in total burrowing time, *A. pacifica* completed steep burrows more

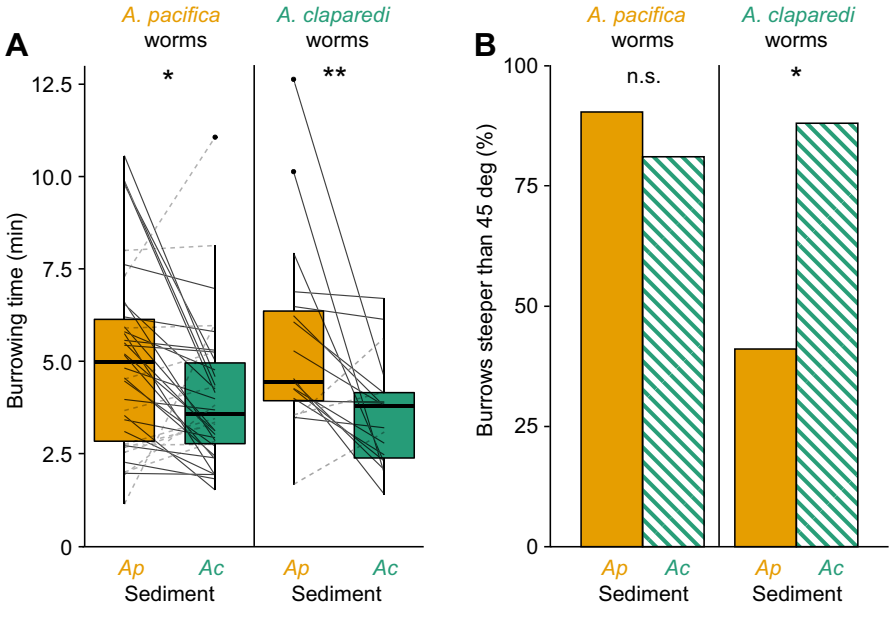

Fig. 3. Burrowing behavior of *A. pacifica* (orange solid) and *A. claparedi* (green barred) during reciprocal transplant experiments in the field. (A) Individuals of both species burrow from the surface to their last gill segment in less time when burrowing in the softer sediment associated with *A. claparedi* than in the firmer sediment characteristic of *A. pacifica* (*A. pacifica* worms: N=38, paired *t*-test, t=−2.70, P<0.05; *A. claparedi* worms: N=19, paired Wilcoxon signed-rank test, V=164, P<0.01). Lines connect burrowing times for the same individual in each sediment type (animals indicated by solid lines burrowed more slowly in sediment characteristic of *A. pacifica*; those indicated by dashed lines burrowed more slowly in sediment characteristic of *A. claparedi*). Boxplots show median±IQR. (B) *Abarenicola pacifica* are equally likely to generate successful steep burrows in either sediment (N=32, McNemar's χ^2=0.57, P=0.45); in contrast, *A. claparedi* generate more successful steep burrows in *A. claparedi* sediment than in *A. pacifica* sediment (N=17, McNemar's χ^2=6.13, P<0.05) (*P<0.05, **P<0.01, n.s., not significant).

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frequently than *A. claparedi*. *Abarenicola pacifica* individuals were just as likely to successfully create the typical steep burrows in the harder to penetrate sediment characteristic of *A. pacifica* (29/32 burrows) as in the softer sediment characteristic of *A. claparedi* (26/32 burrows) (McNemar's χ^2=0.57, d.f.=1, P=0.45; Fig. 3B). In contrast, *A. claparedi* worms created steep burrows much less frequently in the firmer *A. pacifica* sediment (7/17 burrows) than in their own looser sediments (15/17 burrows) (McNemar's χ^2=6.13, d.f.=1, P<0.05; Fig. 3B).

Worm characteristics

Proboscis and chaetae

The morphology of the inflated proboscis of these two species differed markedly only in the shape and distribution of the papillae (Fig. 4). Both species displayed the largest papillae in the region of the proboscis that is contiguous with the outer body wall, which is the region that is first extended into the sediment, pressed into the sides and tip of the extending burrow and then pushed posteriorly as the rest of the proboscis is expanded. In *A. pacifica* these large papillae had a simple cone shape (Fig. 4A,B), whereas those of *A. claparedi* were typically broader and presented a more paddle-like surface (Fig. 4D,E). In both species, the pattern of papillation of the proboscis defined an 'equator' which functions as a fold-line during extension and retraction of the proboscis (Fig. 4A,C,F). The pattern of the small papillae depended on species. In *A. pacifica*, the posterior hemisphere that connects to the outer body wall had a mixture of interspersed larger and smaller papillae (Fig. 4A). In contrast, the region of the proboscis nearer the mouth was covered by a nearly uniform field of relatively smaller papillae (Fig. 4A,C). In *A. claparedi* both the proximal and distal regions of the proboscis were covered with an interspersed mixture of large and small papillae (Fig. 4F,G).

Arenicolids typically have rows of long-handled dentate hooks in the neuropodium and variously ornamented capillary chaetae arrayed in notopodial bundles (Hutchings, 2000; Rouse and Pleijel, 2001). *Abarenicola pacifica* and *A. claparedi* were similar in these features. The long-handled hooks could be protruded from the surface of the body (Fig. 5A) and had a single large fang with finer dentition (Fig. 5B). In both species, the texture of the surface of a capillary chaeta varied along its length. In the regions nearest the body where the chaetae move in and out of the body wall within the capillary bundle, the surface was relatively smooth compared with the pilose distal tips that were more commonly in contact with the sediment (Fig. 5C,D).

Body proportions

For a given mass, individual *A. pacifica* were shorter and stouter than the more slender, elongate *A. claparedi*. The slopes of the ln (mass) versus ln(length) curves were not significantly different between species (t=0.559, d.f.=24, P=0.581; model reported in Table 2). The significant difference in intercepts suggests the median mass of *A. pacifica* worms was 2.20 times as great as

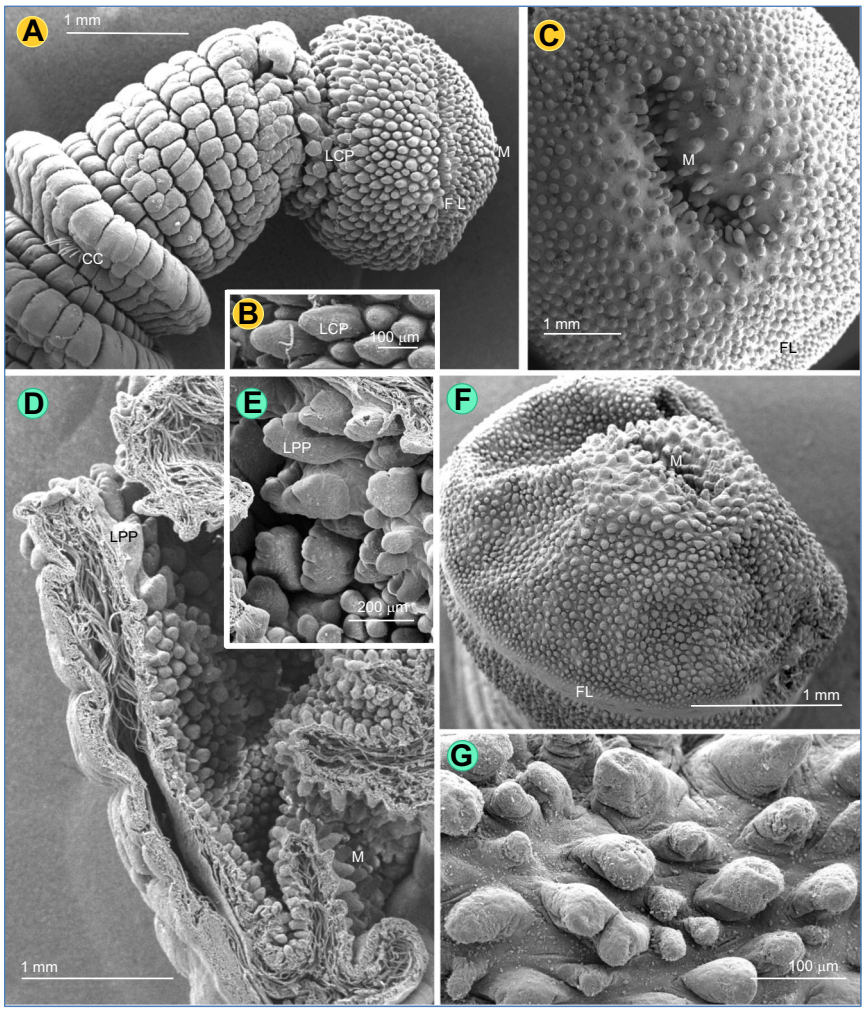

Fig. 4. Surface structures of the proboscises of preserved lugworms. (A) Anterior segments illustrating the capillary chaetae and inflated proboscis of *A. pacifica*. Papillae vary in size over the surface of the proboscis. (B) The largest papillae are adjacent to the body wall and are conical in shape (LCP) and are interspersed with smaller papillae. Beyond the fold line of the proboscis, the papillae become smaller and uniform in size near the mouth in this species. (C) Uniformly small papillae surrounding the mouth of *A. pacifica*. (D) Longitudinal section of an uninflated proboscis of *A. claparedi*, showing (E) the broad, paddle-like large papillae adjacent to the body wall (LPP). (F,G) Small and large papillae are intermingled over the whole surface of a partially inflated proboscis of an *A. claparedi* individual. Circles associated with each image label indicate species (orange for *A. pacifica*, green for *A. claparedi*). CC, capillary chaetae; FL, fold line; M, mouth; LCP, large conical papillae; LPP, large paddle-like papillae.

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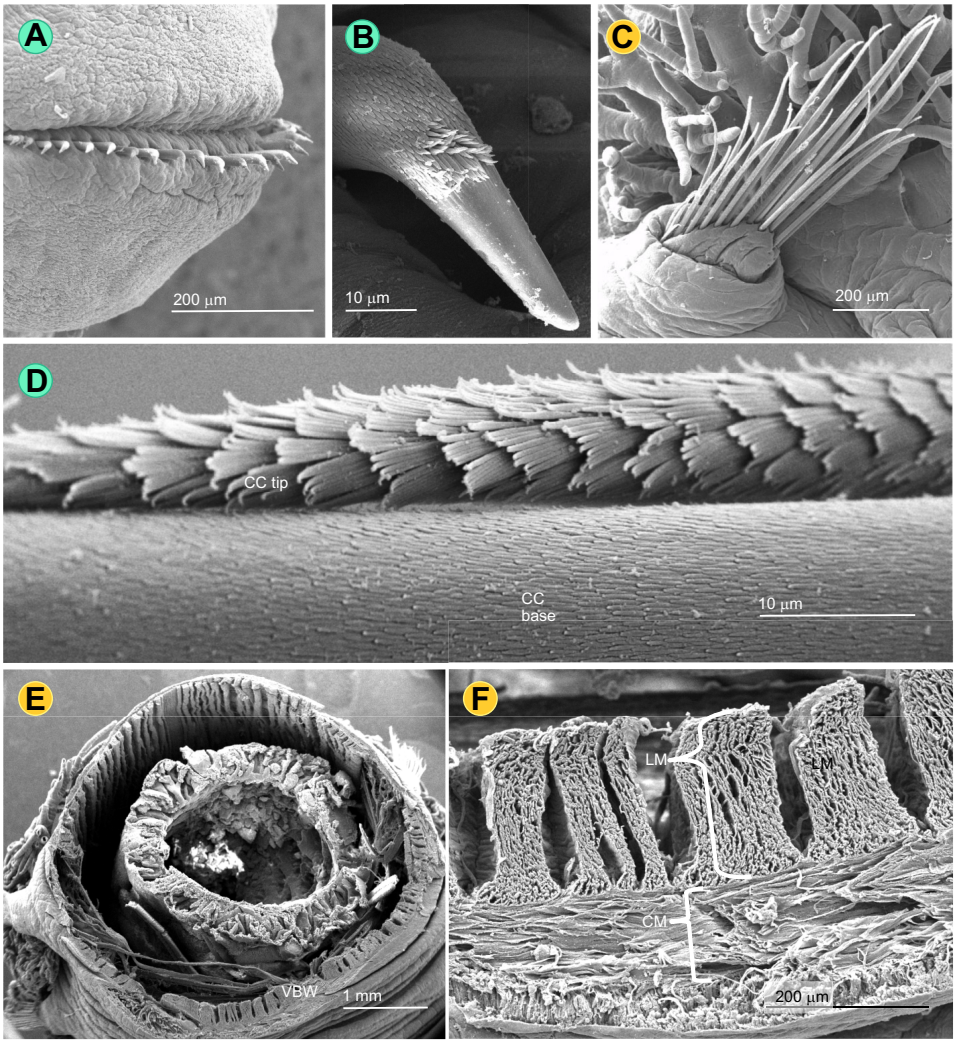

Fig. 5. Chaetal structures and internal musculature of lugworms. (A) The hooked chaetae of both species are quite similar morphologically (*A. claparedi* illustrated in this scanning electron micrograph). Hooks occur in rows associated with the neuropodium and can be extended away from the body wall. (B) The sculptured surface of a hook. (C) The capillary chaetae of both species are very similar and occur in bundles associated with the notopodium (*A. pacifica* pictured here). (D) A smooth base and hairy tip are characteristic of capillary chaetae of both species. (E) Mid-body cross-section of an *A. pacifica* individual; note the well-developed circular and longitudinal muscles of the ventral body wall. (F) The interior longitudinal muscles and more distal circular muscles of the ventral body wall of *A. pacifica*. The arrangement of muscle layers is the same in *A. claparedi*, but the layers are significantly thinner (Fig. 6) for worms of the same mass. Circles associated with each image label indicate species (orange for *A. pacifica*, green for *A. claparedi*). CC, capillary chaetae; CM, circular muscles; LM, longitudinal muscles; VBW, ventral body wall.

A. claparedi worms of a similar length (t=−6.32, d.f.=25, P<0.001; 95% confidence interval: 1.70–2.84).

Body wall muscle thickness

The circular and longitudinal muscle layers were readily visible in light and in scanning electron microscopy (Fig. 5E,F). For worms of similar sizes, the cross-sectional width of the circular and longitudinal muscle layers of *A. pacifica* were greater than those of *A. claparedi* (Fig. 6A,B). The slopes of the ln(muscle layer width) versus ln(mass) lines were not significantly different between species for the longitudinal muscle layer (t=1.64, d.f.=14, P=0.124) or for the circular muscle layer (t=1.47, d.f.=14, P=0.164; model reported in Table 2). Significant differences in intercepts suggest the median longitudinal muscle

Table 2. Fits of linear models to compare morphological characteristics between *A. pacifica* and *A. claparedi*

	x (units)	*y* (units)	Species	Intercept	Slope	d.f.	*F*	*P*	R^2
Body proportions	ln(length) (cm)	ln(mass) (g)	*A. pacifica*	−4.40	2.33	2,25	82.7	<0.001	0.869
			A. claparedi	−5.18	2.33				
Body wall muscle thickness	ln(mass) (g)	ln(longitudinal muscle width) (μm)	*A. pacifica*	5.23	0.505	2,15	23.3	<0.001	0.756
			A. claparedi	4.84	0.505				
	ln(mass) (g)	ln(circular muscle width) (μm)	*A. pacifica*	5.00	0.336	2,15	27.6	<0.001	0.787
			A. claparedi	4.65	0.336				
Worm rigidity	Mass (g)	Initial angle (deg)	*A. pacifica*	104.0	−7.4	2,38	12.7	<0.001	0.401
			A. claparedi	51.1	−7.4				
	Mass (g)	Minimum angle (deg)	*A. pacifica*	41.7	−5.3	2,38	13.5	<0.001	0.414
			A. claparedi	16.5	−5.3				
Mucus production	Initial mass (g)	Mass change (g)	*A. pacifica*	−0.063	0.092	1,29	99.0	<0.001	0.774
			A. claparedi	0.032	0.182	1,21	76.0	<0.001	0.784

For each species and in each comparison, linear regression models were fit to the form: y=slope×x+intercept. Presented here are the intercepts and slopes of the models as well as their significance and R^2 values. If the slopes of the two models were not significantly different between species, then models were fit that assumed the same slope.

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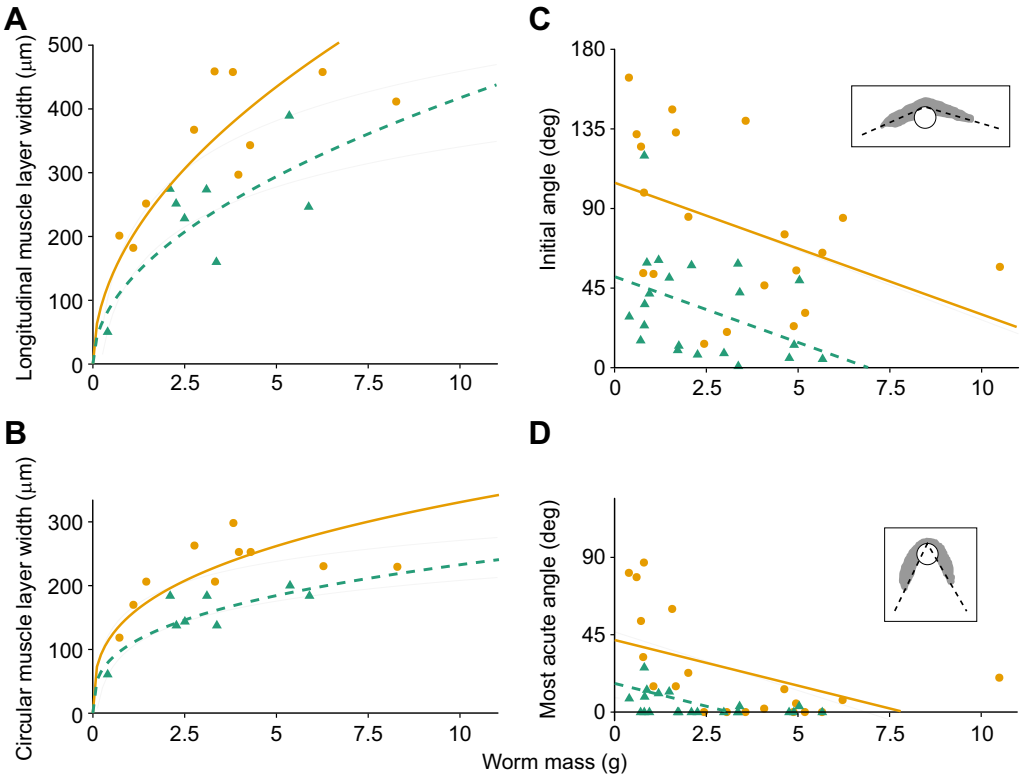

Fig. 6. Thickness of body wall musculature and worm rigidity of *A. pacifica* (orange circles) and *A. claparedi* (green triangles). *Abarenicola pacifica* possess (A) thicker longitudinal muscle layers (t=−2.98, d.f.=15, P<0.01) and (B) thicker circular muscle layers (t=−4.03, d.f.=15, P<0.01). (C) *Abarenicola pacifica* (N=20) bent less acutely over a cantilever than *A. claparedi* (N=21) immediately after being placed (t=−4.69, d.f.=38, P<0.001) and (D) at their most acute angle (t=−4.23, d.f.=38, P<0.001). Insets show example worms (gray) draped over cantilevers (circle) at each time point with dashed black lines drawn to measure the angle. All regressions are reported in Table 2.

layer thickness of *A. pacifica* worms was 1.48 times as great as *A. claparedi* worms of a similar mass (t=−2.98, d.f.=15, P<0.01; 95% confidence interval: 1.12–1.96), and the median circular muscle layer thickness of *A. pacifica* worms was 1.42 times as great (t=−4.03, d.f.=15, P<0.01; 95% confidence interval: 1.18–1.71).

Worm rigidity

When the worms were placed onto the cantilever beam, their bodies were typically taut and contracted to a minimum length, indicating that their longitudinal muscles were fully contracted. *Abarenicola pacifica* individuals were significantly stiffer than *A. claparedi* individuals (Fig. 6). Compared with the *A. claparedi* worms, the *A. pacifica* animals held their bodies in significantly less acute angles immediately upon release onto the cantilever beam with some small individuals holding their bodies nearly horizontally (Fig. 6C). The slopes of the initial angle versus mass plots were not significantly different (t=0.276, d.f.=37, P=0.784; model reported in Table 2). Differences in intercepts suggest the initial bending angle of *A. pacifica* worms was 52.8 deg less acute than initial bending angles of *A. claparedi* worms of a similar mass (t=−4.69, d.f.=38, P<0.001; 95% confidence interval: 30.0–75.7 deg).

This angle diminished over the 30 s period but continued to be less acute than that of the *A. claparedi* worms (Fig. 6D). Slopes of the minimum angle versus mass plots were not significantly different (t=1.70, d.f.=37, P=0.098; model reported in Table 2). The difference in intercepts suggests the minimum bending angle of *A. pacifica* worms was 25.2 deg less acute than bending angles of *A. claparedi* worms of a similar mass (t=−4.23, d.f.=38, P<0.001; 95% confidence interval: 13.1–37.2 deg).

Within 30 s of resting on the cantilever beam, regardless of size, most of the *A. claparedi* individuals bent so acutely that their head and tail touched. There was no difference between the species in the time it took to achieve their minimal angle within 30 s (t=0.24, d.f.=39, P=0.81).

Mucus production

After an hour of resting in seawater, individuals of both species produced a coating of clear mucus that was easily visible when the worms were removed from the seawater. In both species, mucus production increased with worm size, and large *A. claparedi* produced relatively more mucus than large *A. pacifica* (Fig. 7). The slopes of the curves describing mucus production differed significantly between species (t=−3.84, d.f.=50, P<0.001; model reported in Table 2). Additionally, *A. claparedi* produced significantly more mucus as a percentage of body mass [W=578, P<0.001; median (interquartile range) for *A. pacifica*, 6.4% (3.9–9.3%); for *A. claparedi*: 14.3% (9.4–27.6%)].

DISCUSSION

The separation and distribution of *A. pacifica* and *A. claparedi* in False Bay present a puzzle: how can two worms with similar morphologies and deposit-feeding lifestyles separate False Bay into such distinct regions? One possibility is that their physiological tolerance to tidal exposure defines each species' distribution. However, in other locations (Healy and Wells, 1959; Hobson, 1967), the relative tidal height positions of the species are reversed (with *A. pacifica* residing in the lower intertidal region and *A. claparedi* in the higher intertidal position). At other sites on San Juan Island (Eagle Cove, R.A.M., personal observation), *A. claparedi* is found in the high intertidal region and *A. pacifica* is absent. The conceptualization of sediments as elastic solids (Dorgan et al., 2006) provides a new paradigm that gives insight into the distribution of these species and a framework in which to interpret some of their morphological features and burrowing behaviors.

Sediment properties

The drop-test penetration data in combination with sediment grain analyses allow us to appreciate the dramatic differences in the sediment qualities characteristic of each species' microhabitat in

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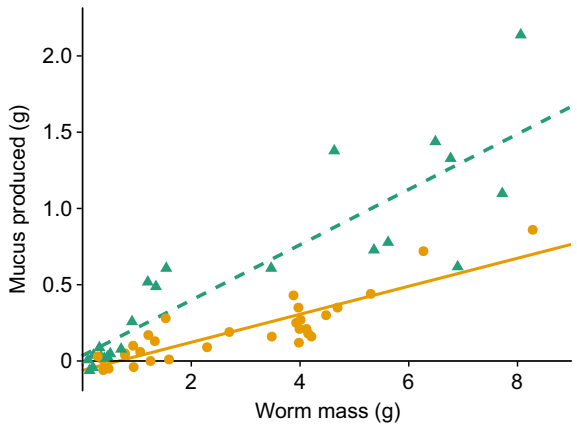

Fig. 7. Mucus produced by *A. pacifica* (orange circles) and *A. claparedi* (green triangles) measured as mass change over 1 h. *Abarenicola claparedi* showed a greater mass increase (i.e. produced more mucus) than *A. pacifica* (t=−3.84, d.f.=50, P<0.001). Regressions are reported in Table 2.

False Bay. Individuals of *A. pacifica* live in firm sediments composed of a broad grain size distribution of coarse and fine sediments, and individuals of *A. claparedi* live in easily penetrated sediment composed almost exclusively of fine and medium sands (Table 3, Fig. 2). The presence of muds (silt and clay particles) mixed with sands characteristically contributes to firmer substrata because the small particles impede the movement of larger sand grains.

Since the earliest descriptions of these species (Healy and Wells, 1959), the sediment associated with *A. pacifica* has been described as firm or stiff, and contrasted with the softer, loose, well-washed sandy sediment in which *A. claparedi* is found (Healy and Wells, 1959; Healy, 1963; Hobson, 1967). Hobson (1966) extensively sampled sediments in association with the species' distributions at a variety of soft-bottom locations around San Juan Island. She found five sites where *A. pacifica* existed. All of these were in protected settings and correspondingly had relatively high percentages of mud (defined as sediment particle sizes less than 0.06 mm) mixed in with sands. In particular, she reports the median percentages of mud at these sites as: Wescott Bay 2.5, Mitchell Bay 2.6, high intertidal of False Bay 6.7, Argyle Lagoon 15.5 and Garrison Bay 92.4. In contrast, *A. claparedi* was found in more exposed sites with coarser sediments that contained little to no mud (median percentage of mud: near the mouth of False Bay 0.2, unnamed bay near False Bay 0.7, and Eagle Cove 0.1). Nearly half a century later, lugworms are currently found only in False Bay and at Eagle Cove, but not at any of these other sites (R.A.M., personal observation; personal communication from Gustav Paulay, who has recent experience teaching the Invertebrate Biology course at the Friday Harbor Laboratories). Our values for percentages of mud associated with the species at False Bay are quite similar to those of Hobson (median 11% for *A. pacifica* sites and 0.4% for *A. claparedi* sites) (Fig. 2).

Table 3. Summary of our results demonstrating the differences between *A. pacifica* and *A. claparedi* and the sediments in which they are found

	A. pacifica	*A. claparedi*
Sediment mechanics	Harder to penetrate	Easier to penetrate
Grain distribution	Heterogeneous, gravels to clays	Homogenous sands
Burrowing ability	Stronger burrowers	Weaker burrowers
Proboscis papillae	Cone-shaped	Paddle-like
Chaetae structure	Similar	Similar
Body proportions	Short, squat	Long, slender
Body wall thickness	More muscular	Less muscular
Worm rigidity	More rigid	Less rigid
Mucus production	Less mucus	More mucus

Primarily laboratory-based studies have revealed that sediments, depending on their component parts and history, have a breadth of mechanical responses ranging from those that act like elastic solids to loose granular sands that are easily disrupted, displaced or fluidized. It has been difficult to apply those findings to natural habitats because of the challenge of characterizing sediments. Bringing sediment into the laboratory can disturb the mechanical relationship of the sediment particles to each other by breaking mucus or other organic connections between sediment grains, causing a redistribution of particles as a function of their size and altering the degree of hydration of the sediment. Making measurements of the mechanical properties of the sediment *in situ* has previously required the deployment of large equipment that is expensive and is not commercially available (Johnson et al., 2012).

To describe sediment mechanical properties *in situ*, we employed a simple penetrometer that was easy to use in the field over relatively fine spatial scales, gave repeatable results and characterized sediment in mechanical terms. Our penetrometer does not capture fine variations in material properties with depth; however, parameters relevant for burrowing that have previously been measured in field analyses have not varied significantly across the depths we consider here (Johnson et al., 2012). Additionally, although we are not directly replicating the forces a worm would generate with its proboscis, our measurements provide a consistent and quantitative way to mechanically distinguish the sediments inhabited by these two worms. Considering the penetrometer and grain size results, both *A. pacifica* and *A. claparedi* sediments lie between the distinct alternatives of elastic solids and loose grains studied previously, potentially allowing organisms to burrow using a combination of crack propagation and disruption of grain linkages (Dorgan et al., 2006) and, furthermore, they differ from each other in their position on this continuum. Based on sediment grain size, sediment characteristic of *A. pacifica* may be more tightly packed and cohesive than the looser sediment characteristic of *A. claparedi*, qualities that have been associated with a greater tendency of a sediment to crack (Volkenborn et al., 2010). However, because these sediments are more heterogeneous in grain size and include unknown organic components, it is impossible to compare them directly with theoretical results developed using proxies in the laboratory (Dorgan et al., 2005; Dorgan, 2015).

Worm burrowing ability

After finding consistent differences between sediments, the fundamental question is whether the worms respond to these mechanical differences; in particular, the harder to penetrate *A. pacifica* sediment would seem to present a much more challenging medium for a soft-bodied burrower. Because *A. pacifica* live in this firmer sediment, they obviously can burrow and survive in it. Our reciprocal transplant experiment revealed the interesting pattern that both species can burrow in either medium, but in the harder to penetrate sediment, only *A. pacifica* frequently generated the typical vertical burrow whereas 59% of *A. claparedi* were unable to do so. Instead, *A. claparedi* generated a more horizontal burrow that often skimmed just below the surface (Table 3, Fig. 3). Sediment resistance to penetration decreases

dramatically when tested at angles shallower than 45 deg (Brown and Trueman, 1991), so we interpret *A. claparedi*'s shallow burrows as an indication of their limited ability to penetrate the more mechanically challenging sediment.

In order to facilitate direct observation, many studies of burrowing mechanics have been conducted in sediment transported to the laboratory or in artificial substrates. Organisms have been observed burrowing in cryolite, a mineral with a refractive index similar to that of water (Francoeur and Dorgan, 2014), and in glass beads, to replicate loose granular materials, or in artificial gels, to mimic elastic muds (Dorgan et al., 2005, 2008; Francoeur and Dorgan, 2014). However, transporting sediment changes its mechanical properties, and artificial materials differ from the sediments they are replicating. Beads lack the organic matter usually encrusting sands (Johnson, 1974), and gelatins lack granularity and have to date been less stiff and tough but more elastic than their sediment counterparts (Johnson et al., 2012). These laboratory-based scenarios typically present burrowing animals with a medium that is uniform in its properties as compared with sediment in the natural world where sediment properties may change on small spatial or temporal scales.

Worm characteristics

The morphological observations of these two species offer insight into their differences in burrowing ability. *Abarenicola pacifica*, which live in the firmer sediment, tend to be shorter than *A. claparedi* of the same mass (Tables 2 and 3). This is somewhat surprising because hypotheses based on mechanical advantage for comparably sized worms would predict that worms burrowing through firmer sediment would be thinner in order to minimize strain hardening of the sediment and maximize force generation by longitudinal muscles (Kurth and Kier, 2014, 2015). Earthworms display this predicted relationship, with larger individuals being relatively thinner than smaller juveniles, and burrowing species being thinner than epifaunal species (Kurth and Kier, 2014, 2015). In contrast, small cirratulids that may have difficulty generating sufficient force concentration to fracture sediments tend to be shorter and blunter; however, these worms are significantly smaller than *A. pacifica* and *A. claparedi* and the same burrowing mechanics and limits are unlikely to apply (Che and Dorgan, 2010). The reasons that *A. pacifica* and *A. claparedi* differ from what is predicted are unknown but perhaps arise from the fundamentally different burrowing mechanism involving the rapid expansion of the proboscis or the mechanical differences in terrestrial and marine substrata. The relative sizes of *A. pacifica* and *A. claparedi* may also result directly from the thicker body wall musculature of *A. pacifica*.

Lugworms burrow by contracting their circular then longitudinal muscles, increasing coelomic hydrostatic pressure in order to evert the proboscis (Wells, 1948, 1950, 1952, 1954). *Abarenicola pacifica* possessed thicker longitudinal and circular muscle layers (Table 3, Fig. 6A,B), suggesting that they can generate higher forces within their hydrostatic skeleton. By draping worms over a cantilever beam, we found *A. pacifica* to be more rigid (Table 3, Fig. 6C,D). The worms were at their shortest at the beginning of the test, suggesting contraction of the longitudinal muscles, and thus their rigidity represented their ability to generate hydrostatic pressure. Possessing thicker body walls and being more rigid may allow *A. pacifica* to more forcefully expel their proboscises and burrow more effectively in challenging sediments.

The surface structures of the proboscis and cheatae may also offer insight into the differences in how these species interact with sediment. The papillae closest to the body wall that contact the sediment first differ markedly in shape between species (Table 3, Fig. 4A,B,D,E). These papillae are reported to initially push the sediment to the side and then backwards as the proboscis expands forwards (Wells, 1948). We suggest that the large conical papillae typical of *A. pacifica* may be better suited to anchoring in and cracking a firm and heterogeneous sediment and that the broad paddles of *A. claparedi* may be more effective at pushing aside well-sorted looser sands. Another less dramatic difference in proboscis morphology is the size variation in papillae covering the region closest to the mouth (Table 3, Fig. 4A,C,F,G). It is unclear what, if any, functions are served by the differences in papilla size. Examining how these papillae interact with the sediment may illuminate their role or the consequence of this difference between species.

The chaetae, which protrude from the sides of the worms' bodies, show no differences between species, but do suggest mechanisms of interacting with the sediment. Both species possess two kinds of chaetae that can be protruded into sediments. The long-handled dentate chaetae with a single hook and the distally pillose capillary chaetae may be acting as anchors holding segments of the worm in place as other segments move forward (Table 3, Fig. 5).

Abarenicola claparedi struggled to generate steep burrows in the firm *A. pacifica* sediment, suggesting a mechanism limiting their distribution to their own loose sediment. However, although *A. pacifica* successfully generated vertical burrows in both sediment types, they are not found in *A. claparedi* sediments and do not survive long-term transplant experiments in *A. claparedi* sediments (Hobson, 1967). While biotic, abiotic or experimental factors could have been responsible for this lack of survival, it is clear that the soft, loose, sandy habitat of *A. claparedi* makes it easy for burrow walls to cave in (Healy and Wells, 1959; Healy, 1963). Both species produce mucus with which they line their burrows (Healy, 1963). We suggest that the copious mucus (Table 3, Fig. 7) produced by *A. claparedi* may be important in shoring up burrow walls as *A. claparedi* move through a shifting, sandy habitat prone to collapse. In this way, inadequate burrow maintenance could limit *A. pacifica*'s ability to inhabit sediment characteristic of *A. claparedi*.

Conclusions and broader implications

We have shown that two closely related species of lugworms differ in burrowing ability and that those differences correspond to mechanical characteristics in the sediments where those worms are found. New perspectives on sediment mechanics have provided a novel way to envision and distinguish habitats in soft-bottom marine ecosystems. We provide an important example of how these differences can act to define the distribution of even closely related species by tracing from microhabitat characteristics determined by sediment mechanical properties to worm morphology and burrowing ability in the field.

Our findings about how the mechanical properties of the sediment can affect lugworm distribution have broad ecological repercussions. Lugworms are often considered ecosystem engineers in soft-bottom marine systems (Wilson, 1981; Berke et al., 2010). Because they are relatively large worms that burrow and move through the sediment, turning it over as they feed, and actively pumping water through the sediment, lugworms can have significant and cascading effects on their surroundings. The presence or absence of lugworms has been linked to changes in sediment stability and composition (Volkenborn et al., 2009), nutrient and oxygen availability (Volkenborn et al., 2010), macrofaunal community (Volkenborn and Reise, 2007;

Volkenborn et al., 2009; Berke et al., 2010) and bacterial presence in sediments (Gutiérrez and Jones, 2006). Although individual lugworms move frequently, patches of lugworms can show high temporal persistence (Krager and Woodin, 1993), allowing them time to significantly shape their surroundings. Our research highlights a new perspective on sediment characteristics that could be limiting lugworm distribution, which, as lugworms then shape the sediment, can in turn have far-reaching consequences for benthic community ecology. Considering how sediment mechanical characteristics can shape the marine community raises new questions about how a changing climate could affect marine systems. Climate change will alter currents and flow patterns, affecting sediment deposition and grain size distribution. Temperature changes will concurrently determine microbiota, bacteria, and the kinds and qualities of mucus that glue sediment grains together. As these changes alter sediment composition and material properties, they can ultimately shift the presence of key ecosystem engineers, like lugworms, and change entire communities.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: R.L.C., R.A.M.; Methodology: R.L.C., R.A.M.; Formal analysis: R.L.C., R.A.M.; Investigation: R.L.C., R.A.M.; Resources: R.A.M.; Data curation: R.L.C.; Writing - original draft: R.L.C., R.A.M.; Writing - review & editing: R.L.C., R.A.M.; Visualization: R.L.C., R.A.M.; Funding acquisition: R.L.C., R.A.M.

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