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Arenicolid behaviors: similarity of *Arenicola marina* and *Abarenicola pacifica*

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Abstract

The hydraulic activities of two arenicolid polychaetes, *Abarenicola pacifica* and *Arenicola marina,* result in strikingly similar pressure waveforms. The principal hydraulic activities are defecation, burrowing and feeding/burrow maintenance. Both the duration and magnitudes of the pressures are very similar. The behavioral periodicities of the two species are also quite similar, although burrowing is more common in *A. pacifica* than in *A. marina.* Additionally burrowing activities in *A. marina* appear to be more influenced by tidal stage than those in *A. pacifica*. The link between burrowing and pore-water pressure reductions makes this difference potentially important in terms of drawing oxygenated water into surface sediments.

Key words: bioirrigation, bioturbation, infauna, lugworm, pore-water

Introduction

Arenicolid polychaetes are obvious residents of sedimentary habitats worldwide (Wells 1964). Two species in particular are of interest, in the north Pacific *Abarenicola pacifica* Wells, 1959 and in the north Atlantic *Arenicola marina* (Linnaeus, 1758). They are very abundant; densities of > 50 m^{-2} are common for even *A. marina,* the larger of the two species. An important aspect of both species is that they feed from subsurface pockets often 10 to 25 cm below the surface and defecate onto the surface, thus bringing sediment from depth onto the sediment surface. However, as numerous investigators have described (Ashworth 1912; Hylleberg 1975; Wells 1945), they are actually primarily feeding on surface material moved to the depth of the feeding pocket by the activities of the individual; thus they greatly increase the rate at which labile organic material is buried (Riisgård & Banta 1998; Banta et al. 1999; Hylleberg 1975). Their effects on sediments are thus several fold. First, they create areas of elevated sediment turnover surrounding the exit of the tail shaft of the burrow, where defecation occurs approximately every 15 to 45 min when the animal is feeding (Wells 1953; Woodin 1985). Second, they both move subsurface sediment back onto the surface, exposing it to oxic mineralization and move potentially labile materials on the sediment surface rapidly to depth, potentially reducing its exposure to oxic processes, depending on the “sloppiness” with which the individual feeds on the subducted materials. Third, their activities, both feeding and irrigation, are known to affect the biogeochemical gradients in the vicinity of the burrow and those of *A. marina* in particular have been the subject of considerable modeling effort with regard to biogeochemical effects and rates of pore-water flux (Timmerman et al. 2002; Meysman et al. 2006; Huettel et al. 1996). Finally, their activities create surface topographic features that in permeable sediments alter flows through surface sediments (Huettel et al. 1996).

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A variety of field experiments have been done with these obvious ecosystem engineers, ranging from altering their rates of activity (e.g., Woodin 1985) to altering densities (Reise 1983; Volkenborn & Reise 2007), asking the degree to which these species drive the rest of the assemblage in terms of composition, densities and interactions. One typically obtains the expected result from these manipulations, i.e., altering the density or activity of the source of bioturbation generates a discernible effect. A lingering question, however, is the degree of similarity of these species and thus the manner of their impact on systems. From the earliest workers such as Ashworth (1912), investigators have commented upon the similarity of life style, burrow structure, feeding and defecation of the two species, their broad boreal and north temperate geographic distributions. However, these species have distinct body morphologies, belong to different genera, have differences in the mechanism of proboscis eversion, length of neuropodia, numbers of gut caecae, and ability to retract the prostomium (Wells 1959). Given these morphological differences, our primary purpose in this research was to ask whether the activities of the two species are really as similar as previous authors have stated. This question has three parts: (1) what are the activities, (2) are the activities similar in their frequency of occurrence and (3) are the activities comprised of similar components. By the "components" of the activity we mean the positive and negative pressure waveforms associated with hydraulic activities, actions of the worms seen in side view in thin aquaria of acrylic plastic in the laboratory, and surface traces such as fecal mounds or areas of subsidence known as feeding pits. Given the results reported for changes in assemblages when densities or activities of these arenicolid polychaetes are altered (e.g., Volkenborn & Reise 2007; Wilson 1981), we expected to find great similarity, and we did.

Materials and methods

Submersible pressure sensors (Wethey & Woodin 2005) recorded pressure waves in pore-waters both in the field adjacent to arenicolids and in the laboratory with single worms confined within aquaria. In the field, pressure sensors were implanted within 5–10 cm of active individuals identified from feeding funnels and fecal mounds. A syringe core was used to remove a cylinder of sediment the width of the sensor, and the sensor was placed into the hole and the sediment packed gently around it. The opening leading into the sensor was covered with 64-µm mesh to prevent sediment clogging, and the passage was filled with seawater. Deployment depth in beds of *Abarenicola pacifica* was 10–12 cm versus 15–20 cm in beds of *Arenicola marina*. In the laboratory fresh sediments from field arenicolid beds were placed into aquaria made from 40-cm wide by 30-cm tall sheets of 1.25-cm-thick acrylic plastic with a 1- to 1.5-cm thick gasket of Tygon® tubing. Typical sediment dimensions were 30 cm wide by 20 cm tall by 1.2 cm thick with an overlying 3–4 cm of flowing seawater. Sediments were allowed to rest at least 24 h prior to animal addition. To allow identification of signals, only one individual was placed in each aquarium. Pressure sensors were screwed into a threaded hole on the back of the aquarium at a depth of 10 cm. Time-lapse images (one image per 30 s) were taken of the front of the aquarium to record shifts in sediment and any visible animal motions. Typically grains could be seen moving during periods of intense activity. Clocks of the cameras and pressure-sensor dataloggers were synchronized by computer at each data download. See Wethey & Woodin (2005) for complete pressure sensor specifications.

Time-lapse images were viewed both as single images and as movies using Premiere Pro 1.0 and 2.0 (© Adobe Systems). Images in which distinct behaviors could be observed were identified as to time and type of behavior. Using ten such periods each from three different individuals per species, pressure-sensor records were scanned to determine whether the pressure waveforms associated with each behavior were distinguishable and predictable. After confirming the relations between behaviors captured on camera and specific pressure waveforms with an additional ten behavioral episodes, the known waveforms for each behavior were used to analyze the pressure record. Analysis of the video record alone is not sufficient for behavioral analysis even in the laboratory because individuals are not visible most of the time if their normal sediments are present. All hydraulic activities produce pore-water pressure changes, however, and thus are detectable from the pressure record if one can determine that unique behaviors are associated with particular waveforms (Wethey & Woodin 2005). Additionally, the pressure sensors are field deployable, allowing analysis of activities of unrestrained individuals in the field.

Pressure records for 24 h from laboratory recordings of three individuals per species were used to document patterns of behavior. Individuals were allowed 2 d to acclimate to the aquarium for burrow establishment prior to analysis of behavior.

Field records of behavior are from unknown numbers of unrestrained individuals within arenicolid beds in the field at intertidal sites at Königshafen, Sylt, Germany (55°02′13″N, 8°24′34″E) for *Arenicola marina*, and False Bay, San Juan Island, Washington State, USA (49°29′19″N, 123°03′57″W) for *Abarenicola pacifica*. As in the laboratory, hydraulic activities of animals in the field result in pore-water pressure changes recorded on pressure sensors deployed in the sediment. As depicted in Fig. 1, the resulting waveforms correspond to those seen in the laboratory, where the behavior can be verified from analysis of independent video recordings.

Results

Five common behaviors were seen in the time-lapse imagery and had distinctive waveforms in pressure sensor recordings. They were defecation, burrowing, feeding and burrow maintenance, sediment cracking and resting. Defecation and burrowing produce pressures of the greatest magnitude. As is evident from Fig. 1, defecation comprises a series of pulses prior to a large negative pressure spike often >6 cm of water but of very short duration, typically <10 s, followed by a series of pulses 1–2 cm of water above baseline (ambient static) pressure. The total period is 2–4 min (Table 1B). In actively feeding animals defecation is frequent, occurring every 15–45 min depending on individual size (Wells 1945; Woodin 1985), but it still accounts for only 15–16% of the behavioral episodes and only 4–7% of an individual’s time expenditure (Table 1). In both species, defecation is more common during ebb than during flood (Table 2B–C). Kymograph traces from the work of Wells (1953) clearly show the large reduction in pressure associated with defecation, and Wells (1953) occasionally observed large flows of water into the burrow from the feeding funnel during defecation, as one would expect given the large negative pressure pulse generated by defecation (Fig. 1). Wells (1953) also observed the series of positive pressure pulses immediately following defecation, seen as tail-to-head pumping on his kymograph traces.

Feeding/burrow maintenance (‘pumping’ in tables) consists of pulses above and below baseline that are of small magnitude, typically with amplitudes less than ±1 cm of water and periods of 10–20 s. The first minute of each defecation record in Fig. 1 illustrates this behavior. This behavior is the most common (Table 1), occupying >60% of the animal’s time budget and conforms primarily to periods of pumping from tail to head as described by Wells for *Arenicola marina* (1949).

Burrowing has two components, large, short pulses of several centimeters of water amplitude, with higher-frequency, small-amplitude pulses interspersed. Unlike defecation, in both species the large pulses are of two types, and a burrowing episode may have only one or both forms present. One type has both large negative and large positive components with the positive component often exceeding the negative in size; in contrast the other form has a rather small, positive component and a large, negative spike. The example shown in Fig. 1 for *Abarenicola pacifica* in the laboratory consists primarily of the first type, while that for *A. pacifica* in the field has primarily the second type. The examples for *Arenicola marina* both in the field and in the laboratory have both types represented. Burrowing is often associated with a reduction in baseline, indicating a drop in pore-water pressure resulting from the arenicolid pumping in a head to tail direction. Wells (1953) saw these reversals of pumping direction in his laboratory kymograph recordings of *A. marina*. Examples of the resulting reduction in pore-water pressure are shown in Fig. 2 for field recordings of *A. pacifica* and *A. marina*. The duration of this reduction in pore-water pressure is quite variable, 1–4 min to over 20 min. The latter are seen in *A. marina* during flood but not ebb and conform to the reversal of "water flow" in burrows captured in field recordings by Krüger (1964). The importance of such flow reversals are discussed in Wethey et al. (2008).

Burrowing bouts are more common in both species than defecation, representing 34–36% of the behaviors observed (Table 1A). Those of *Arenicola marina* are typically 25% shorter than burrowing bouts of *Abarenicola pacifica* (Table 1B), and in general *A. marina* spends only 12% of its time burrowing versus 29% for *A. pacifica* (Table 1C). An additional potentially important difference in burrowing activities between the two species is with regard to tidal stage. In the laboratory both species appear to burrow more often during flood than during ebb, though individuals clearly vary (Table 2A). The same pattern is very clear in field recordings of *A. marina,* which has 0.05 burrowing bouts h^{-1} on average during ebb versus 2.26 bouts h^{-1} during flood (Table 2B). The pattern is less clear in field recordings for *A. pacifica,* which has 1.32 burrowing bouts h^{-1} during ebb versus 1.17 burrowing bouts h^{-1} during flood (Table 2C). However, burrowing bouts in *A. pacifica* during flood are 5.59 min long, whereas those during ebb are on average 3.8 min, resulting in approximately 30% more time in burrowing during flood than ebb by *A. pacifica*. Thus the difference in burrowing between flood and ebb is less striking in the field than in the laboratory but still is observed in *A. pacifica*.

Periods of inactivity or "resting" did not appear to follow any pattern and were not seen in all animals but were on one occasion >36 h in duration with no discernable irrigative behavior. Sediment cracking also did not appear to follow a temporal pattern though it was often common during initial establishment of the burrow in both species and was typically associated with burrowing.

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FIGURE 1. Pore-water pressure waveforms caused by burrowing and defecation in *Abarenicola pacifica* and *Arenicola marina*. Pore-water pressures (cm H_2O) are plotted as a function of time (minutes). The left column illustrates data recorded in laboratory, thin-walled aquaria either in Friday Harbor, Washington, USA, using *A. pacifica* collected at False Bay, San Juan Island, Washington, USA or in List, Germany, using *A. marina* collected at Königshafen, Sylt, Germany. The right column illustrates data from field recordings of unrestrained *A. pacifica* in False Bay, San Juan Island, Washington, USA or unrestrained *A. marina* on the mid shore at Königshafen, Sylt, Germany. Burrowing is characterized by rhythmic positive and negative pressure spikes of 30 s to 1 min periodicity, interspersed with lower-amplitude fluctuations. Defecation is characterized by a sharp decrease in pore-water pressure, preceded and followed by small, positive pressure waves.

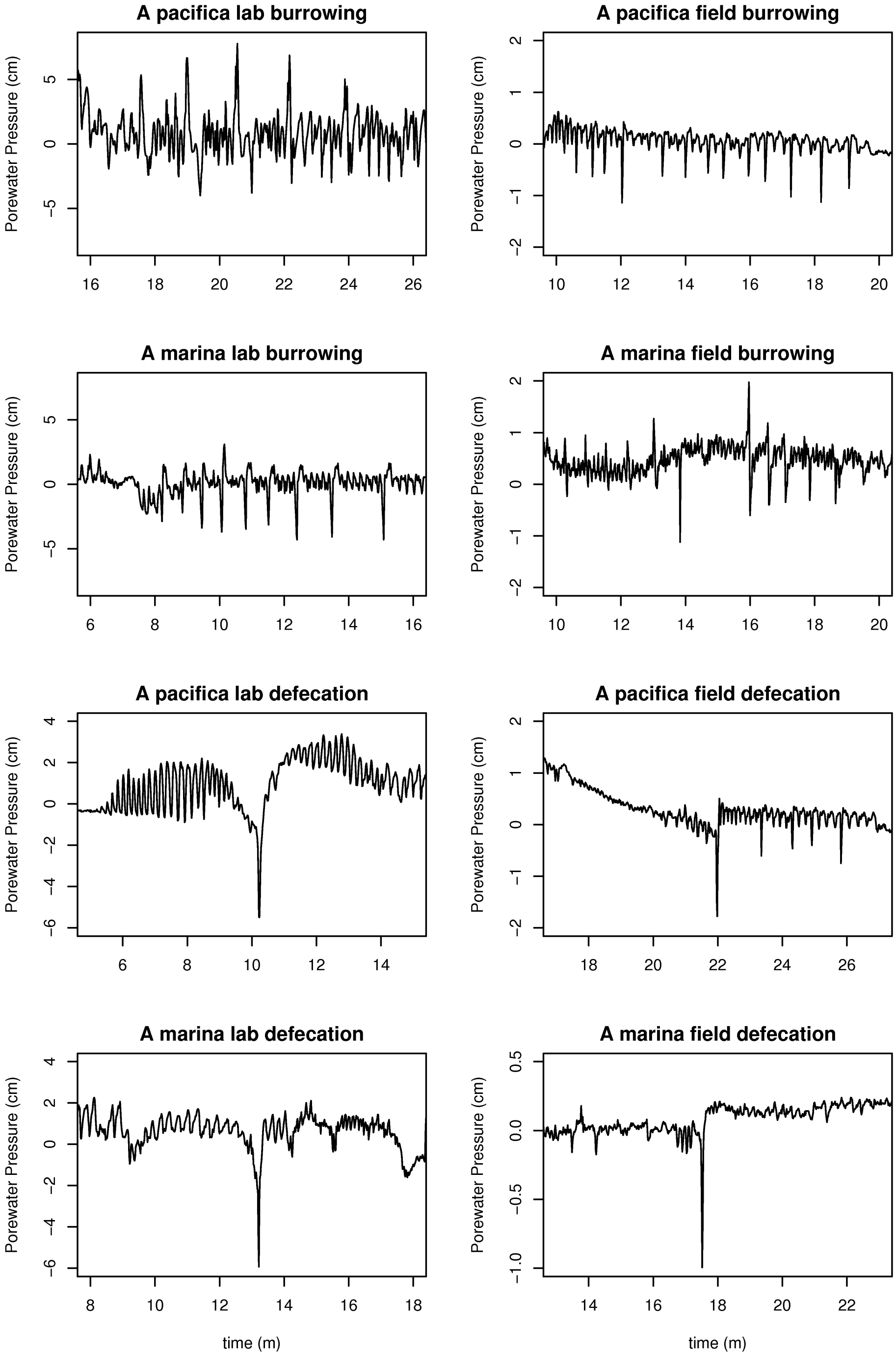
A pacifica lab burrowing
Porewater Pressure (cm)
−5
0
5
16
18
20
22
24
26
A pacifica field burrowing
Porewater Pressure (cm)
−2
−1
0
1
2
10
12
14
16
18
20
A marina lab burrowing
Porewater Pressure (cm)
−5
0
5
6
8
10
12
14
16
A marina field burrowing
Porewater Pressure (cm)
−2
−1
0
1
2
10
12
14
16
18
20
A pacifica lab defecation
Porewater Pressure (cm)
−6
−4
−2
0
2
4
6
8
10
12
14
A pacifica field defecation
Porewater Pressure (cm)
−2
−1
0
1
2
18
20
22
24
26
A marina lab defecation
Porewater Pressure (cm)
−6
−4
−2
0
2
4
8
10
12
14
16
18
time (m)
A marina field defecation
Porewater Pressure (cm)
−1.0
−0.5
0.0
0.5
14
16
18
20
22
time (m)

TABLE 1. Common behaviors of *Abarenicola pacifica* and *Arenicola marina*. A. Percentage representation of each type of behavioral bout. B. Duration in minutes of each type of behavioral bout. C. Percentage of time per type of behavior per species over 24 h.

A. Percentage by bout type		
Species	*A. pacifica*	*A. marina*
Pumping	45%	49%
Burrowing	36%	34%
Defecation	16%	15%
B. Duration of bouts (min)		
Species	*A. pacifica*	*A. marina*
Pumping	10.6	17.0
Burrowing	4.8	3.5
Defecation	2.8	2.4
C. Percentage of time per behavior		
Species	*A. pacifica*	*A. marina*
Pumping	64%	83%
Burrowing	29%	12%
Defecation	7%	4%

Discussion

As expected from their similarity in external body form and life habit, the pore-water pressure waveforms associated with the hydraulic activities of *Arenicola marina* and *Abarenicola pacifica* were strikingly similar (Fig. 1). Defecation in both species, for example, is typified by a single, short, very large, negative spike preceding and followed by a series of much smaller, positive pulses. The similarity of the waveforms both in shape and magnitude as seen in Fig. 1 implies that the effect of that activity on the pore-water of the surrounding sediments will also be very similar (see Wethey et al. 2008 for an elaboration of this point).

The activity cycles of the two species are also quite similar, particularly in frequency of occurrence of types of behavior (Table 1A). Bout duration and percentage of time per behavior show some differences (Table 1B and 1C). Perhaps the potentially most important is that of burrowing which is much more common in *Abarenicola pacifica* than *Arenicola marina* (29% versus 12%, of observation time, Table 1C). As illustrated in Fig. 2, burrowing is often associated with reductions in pore-water pressure that may draw oxygenated water into surficial sediments from above the bed (see Wethey et al. 2008). If so, then this difference in time spent burrowing is important. Additionally, burrowing also appears to lead to cracking of the sediments, perhaps resulting in creation of macropores that would enhance permeability, again an important effect, magnified by the frequency of burrowing.

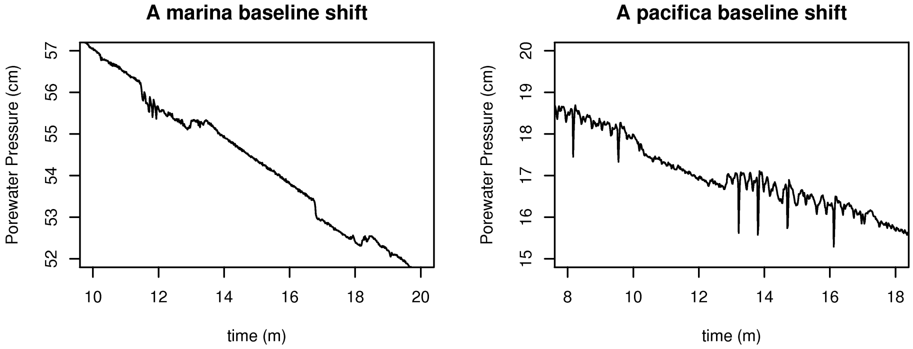

FIGURE 2. Examples of reduction in pore-water pressure baseline during pumping from head to tail in the field by unrestrained *Arenicola marina* (left) and *Abarenicola pacifica* (right). Pore-water pressures (cm H_2O) are plotted as a function of time (minutes). Pore-water pressure was reduced by 4.1 mm during minutes 11–13 and 17–18 in the left panel and was reduced by 2.8 mm during minutes 10–12.5 in the right panel. The *A. pacifica* individual was burrowing before (minutes 8–10) and after (minutes 13–17) the pore-water pressure reduction. The long-term changes in pore-water pressure were due to tidal changes in water depth.

The final difference, again associated with burrowing, is the degree of behavioral differentiation relative to tide stage. In both species defecation is more common during ebb, and burrowing during flood. For *Abarenicola pacifica*, however, the reduction in burrowing during ebb versus flood is much less pronounced than in *Arenicola marina*, perhaps partially accounting for the difference in emphasis on burrowing in the activity cycles.

In summary the two arenicolid species engage in strikingly similar hydraulic activities (Figs. 1–2). Investigators have emphasized the sediment turnover activities of these species with regard to their effects on other infauna (e.g., Woodin 1985) but it may be that the pore-water pressure changes associated with the animals' movements are more important and better explain patterns such as those of meiofauna positively associated with beds of arenicolids (Reise 1983) and apparent aggregated distributions of adult *Abarenicola pacifica* (Krager & Woodin 1993). There are differences in behavior frequencies, but the importance of those differences must await evaluation of the importance of pore-water flow reversals and the frequency of those reversals.

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TABLE 2. A. Episodes of burrowing relative to tidal state in *Abarenicola pacifica* and *Arenicola marina* in the laboratory. B. Episodes of burrowing and defecation in *A. marina* in the field relative to tidal stage. C. Episodes of burrowing and defecation in *A. pacifica* in the field relative to tidal stage. In the field, due to waves and other pore-water disturbances, not all recordings are interpretable as to organism activities, so the interpretable hours are much less than the total hours recorded. Times reported in parts B and C are the interpretable hours.

A. Percentage of burrowing minutes during ebb and flood tidal stages in three independent individuals per species in the laboratory. Total time of recording per individual was approximately 24 h.

A. pacifica		***A. marina***	
Ebb	**Flood**	**Ebb**	**Flood**
51%	49%	60%	40%
28%	72%	35%	65%
26%	74%	35%	65%

B. Burrowing bouts and defecations of *Arenicola marina* relative to tidal stage in the field over 4.8 d. Total number of bouts and bouts per hour are shown for each behavior as well as recording period. Minutes of burrowing per hour are also shown for burrowing bouts. During ebb and flood burrowing bouts are 3.68 and 3.33 min in duration, respectively.

	Hours	**Defecations**	**Burrowing Bouts**
Ebb	19	60 bouts	1 bout
		3.2 bouts/h	0.05 bouts/h
			0.2 min/h
Flood	11.5	20 bouts	26 bouts
		1.7 bouts/h	2.3 bouts/h
			7.7 min/h

C. Burrowing bouts and defecations of *Abarenicola pacifica* relative to tidal stage in the field over 5.6 d. Total number of bouts and bouts per hour are shown for each behavior as well as recording period. Minutes of burrowing per hour are also shown for burrowing bouts. During ebb and flood burrowing bouts are 3.80 and 5.59 min in mean duration respectively.

	Hours	**Defecations**	**Burrowing Bouts**
Ebb	36.5	76 bouts	48 bouts
		2.1 bouts/h	1.3 bouts/h
			5.0 min/h
Flood	6	9 bouts	7 bouts
		1.5 bouts/h	1.2 bouts/h
			6.5 min/h

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