

## Selection by a deposit-feeding polychaete, *Polygordius jouinae*, for sands with relatively high organic content

Patricia A. Ramey<sup>1</sup> and Erica Bodnar

Rutgers, The State University of New Jersey, Institute of Marine and Coastal Sciences (IMCS), 71 Dudley Road, New Brunswick, New Jersey 08901

### Abstract

Field observations and flume experiments investigated whether subsurface migration and selection by adult *Polygordius jouinae* for sediment enriched with organic flocs could help explain small-scale patchiness of this deposit-feeding polychaete in rippled, sandy sediments on the inner continental shelf off New Jersey. Paired ripple crest–trough samples taken from stations located kilometers apart in several months in 1994, 1995, and in May 2006 found higher but more variable densities of *P. jouinae* in troughs compared with crests. Sedimentary particulate organic matter was also patchily distributed at similar spatial scales. In a racetrack flume under realistic flow (shear velocity = 0.32 cm s<sup>-1</sup>) and flatbed conditions, arrays of alternating, fresh ambient sediment (including natural levels of particulate organic material) and freshly sieved sediment (reduced in particulate organic content) showed significant subsurface movement of *P. jouinae* to sediment patches containing higher amounts of particulate organic matter in 48 h. Subsequent experiments showed that locating organic patches was not the consequence of a directed search. However, worms that located richer patches remained there and fed. Rate of movement in sediments indicated that *P. jouinae* could potentially travel the wavelength of a typical ripple (14–30 cm) at the Long-term Ecosystem Observatory in 15-m water depth in 35–75 min. Thus in a dynamic environment where food concentrations are low and patchy, the affinity of *P. jouinae* for particulate organic matter and its undirected, high rate of subsurface movement is a plausible mechanism to account for the similar spatial distributions of *P. jouinae* and its food resources in continental shelf sediments.

Sedimentary landscapes in high-energy, physically active continental shelf environments encompass a rich array of habitats or patch structures that appear significant to benthic organisms (e.g., Zajac et al. 2003; Barros et al. 2004). Small-scale patch dynamics and dispersal of infaunal organisms in these environments are poorly understood, even though such knowledge is critical to predicting ecological responses to long-term habitat changes on continental shelves. It is well established that infauna are

patchily distributed on many spatial scales, and population and community patterns are created and maintained by complex interactions among a host of biological and environmental factors (reviewed by Ólafsson et al. 1994; Snelgrove and Butman 1994). Moreover, ecological patterns and processes operating at one spatial scale may differ from those at another scale (e.g., Dayton and Oliver 1980) or in another environment. At larger spatial scales, primary factors responsible for patterns of distribution of infauna may include sediment grain size, larval dispersal, and habitat selection (reviews by Butman 1987; Snelgrove and Butman 1994). At relatively smaller scales, dispersal and habitat selection by mobile, postlarval juvenile and adult stages seeking food may play a central role. Availability of food can stimulate the migration of organisms to areas where food resources are more abundant (Hughes 1993; Nilsson et al. 2000), and information on the patchiness of species and resources is used in many ecological models and in generating ecological theory.

Sedimentary particulate organic matter (derived from organic-rich flocs containing phytodetritus, decomposing macroalgae, fecal pellets, microorganisms, and to a lesser extent seagrass and land-derived detritus) is an important component of the diet of many infaunal organisms. Particulate organic matter concentrations decrease with increasing grain size of the sediment. Thus its relative abundance in the coarse, sandy sediments that cover ~70% of continental shelves may be especially important in influencing patterns of distribution of infauna. Although poor in organic matter, highly permeable sands allow for concentration mechanisms such as pore-water advection, a process not possible in finer sediments. This advection can enhance the levels of fresh particulate organic matter in the

<sup>1</sup> Corresponding author (ramey@imcs.rutgers.edu).

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top several centimeters of the sediment (Eckman 1990; Pilditch et al. 1998). The main driving forces of advection are pressure gradients along the sediment surface. These develop whenever unidirectional or oscillating bottom flows are deflected by topography (Huettel and Gust 1992; Precht and Huettel 2003) and because current speed, direction, and topography on continental shelves change on timescales from seconds to seasons, particulate organic matter is often distributed in a highly patchy manner at relatively small scales. Moreover, the interaction of flow with microtopography may also enhance deposition nearby (Eckman 1990; Pilditch et al. 1998) by creating regions of reduced shear stress (Pilditch and Miller 2006). Thus, heterogeneity generated by ubiquitous and persistent microtopographic habitats such as ripples may be an important source of microhabitat specialization and resource partitioning (Hogue and Miller 1981). Biogeochemical reactions within the sediment can also further influence patchiness in organic matter as well as the availability of oxygen, nutrients, and heavy metals (Ziebis et al. 1996; Janssen et al. 2005).

Most infauna in sandy sediments are small, interstitial, relatively mobile species that are often patchily distributed horizontally at small scales (e.g., Eckman 1979), even when sediment grain size is homogeneous (e.g., Sandulli and Pinckney 1999). Studies have related spatial distribution of some infauna to food resources (Gray 1967; Decho and Fleeger 1988; Santos et al. 1995) and the supply of organic matter on continental shelves has been positively correlated with pulses of infaunal activity (Gerino et al. 1998; Stead and Thompson 2003). Patterns of distribution of infauna have also been associated with microtopography (e.g., Hogue and Miller 1981; Barros et al. 2004). However, relatively little is known about the causes of these patterns and how these habitat features affect small-scale (<1 m) patchiness of species (Hogue and Miller 1981; Barros et al. 2004; Gallucci et al. 2005). Several studies in physically active, sandy sediments suggest that active selection by postlarval stages is responsible for distribution patterns associated with microtopographic features (e.g., Sameoto 1969; Grant 1981). If active selection occurs, then patterns may be a result of faunal responses to a variety of different food patches produced by small-scale variations in water flow (Snelgrove and Butman 1994; Barros et al. 2004).

Previous quantitative macrofaunal sampling in sandy, rippled beds at the Long-term Ecosystem Observatory (LEO-15) on the continental shelf off New Jersey revealed species-specific differences in patterns of abundance in crests and troughs (e.g., Newby 2006; Ramey 2008). Specifically, the deposit-feeding polychaete, *Polygordius jouinae*, is commonly found in higher and more variable densities in ripple troughs compared with crests (Ramey 2008). Patches of fine, organic flocs have also been observed by divers in ripple troughs of sandy sediments at LEO-15 (Petrecca pers. comm.). Patchiness of resources coupled with the behavior of species can determine the arrangement of individuals within communities (Thrush et al. 1989), and it was the observations described above that laid the foundation for the present study. This study first set out to reconfirm distribution patterns observed for *P.*

*jouinae* in rippled beds at LEO-15 (Ramey 2008: Grassle et al. unpubl. data) and to determine ambient concentrations of food resources at the same spatial scale. Then, using a laboratory flume and a flat, sandy bed, we also tested whether these patterns could be causally related to active selection by *P. jouinae* for elevated levels of sedimentary particulate organic matter derived from the organic-rich flocs typically associated with troughs. We predicted that (1) *P. jouinae* will detect and choose a more favorable habitat (i.e., areas with relatively higher amounts of sedimentary particulate organic matter), (2) the movement of *P. jouinae* will be directed (i.e., in response to some stimulus associated with the sedimentary particulate organic matter) rather than in an undirected search pattern until sedimentary particulate organic matter is located (i.e., no stimulus detected), and (3) sediment choice will depend on the location of sedimentary organic matter in relation to a worm's starting position (downstream or upstream of the food source).

## Methods

*Study site and species*—LEO-15 (39°27.69'N, 74°15.81'W) is located on the inner continental shelf off New Jersey. Sediments in this area include well-sorted medium to coarse sands with a median grain size of 400–500  $\mu\text{m}$  (Reimers et al. 2004). Sediments are subjected to both unidirectional currents and wave-driven, oscillatory flows. During a particularly active period from August to September 1995, mean alongshore currents (measured 44 cm above the bottom) were 5 to 20  $\text{cm s}^{-1}$  and cross-shore currents associated with the tides were generally  $\leq 8 \text{ cm s}^{-1}$  (Traykovski et al. 1999). Rippled beds are the predominant bed form, with ripple heights ranging from 3 to 15 cm and wavelengths of 10 to 100 cm (Traykovski et al. 1999; Styles and Glenn 2002). Ripples are symmetrical in shape, which is the characteristic morphology created by wave-driven oscillatory flow. During the present study in 2006, ripples were 6 to 12 cm in height and had a wavelength of 14 to 30 cm.

The study species was the small (sexually mature adult body length 13.0–43.1 mm; width 0.23–0.38 mm), interstitial, deposit-feeding polychaete *P. jouinae*, which is a dominant member of infaunal communities in sandy sediments at LEO-15 and in bays and harbors from Massachusetts to southern New Jersey (Ramey et al. 2006). This species has a certain affinity to coarse, sandy sediments, and density has been shown to be significantly and positively correlated with the proportion of medium to very coarse sand and negatively correlated with fine sand at relatively large scales (Ramey et al. 2006). However, considerable variation and patchiness occurs at small spatial scales (Ramey 2008).

*Sample collection*—The observation that *P. jouinae* is commonly found in higher but more variable densities in ripple troughs compared with crests came from samples collected at LEO-15 on several dates in 1994 and 1995 (Ramey 2008; Grassle et al. unpubl.). Paired sediment cores (7 cm diameter, 10 cm deep, 38.5  $\text{cm}^2$ ) from ripple crests

and troughs (90 cores total) were randomly collected by scuba divers from Stas. 9 and 30 (see map, Ramey 2008) and processed live over a 300- $\mu\text{m}$  sieve. In May 2006, to determine if these patterns for *P. jouinae* were still present and to determine sediment parameters, which were not included in the 1994 and 1995 studies, the same methods were used to haphazardly collect paired crest–trough samples at Sta. 9 ( $n = 12$ ) and Node B ( $n = 6$ ) (Ramey 2008). To aid in setting up the experiments described below, a small amount of sediment was removed from the top layer ( $\sim 1$  cm deep) of each core before fixation and frozen for later determination of ambient concentrations of total chlorophyll *a* (Chl *a*) and pheophytin as an indirect measure of food availability. Samples were then washed over stacked 300- $\mu\text{m}$  and 32- $\mu\text{m}$  sieves and fixed, and *P. jouinae* was enumerated from the sediment retained on the 300- $\mu\text{m}$  sieve. Grain-size analysis (by dry weight percentages) was conducted for Node B samples (recombined 300- $\mu\text{m}$  and 32- $\mu\text{m}$  portions) using stacked sieves ( $\geq 2$  mm, 1 mm, 500  $\mu\text{m}$ , 250  $\mu\text{m}$ , 125  $\mu\text{m}$ , 32  $\mu\text{m}$ ,  $\leq 32$   $\mu\text{m}$ ).

Sediment to be used in the experiments and live *P. jouinae* were collected from troughs at Node B. Sediment was either frozen directly or briefly washed over a 100- $\mu\text{m}$  mesh to remove some of the particulate organic matter and then frozen, thus creating sediments with ambient and lowered low amounts of particulate organic matter. Total particulate organic carbon, Chl *a*, and pheophytin were determined for these sediments each time an experiment was run. Sediment for carbon and nitrogen analysis was first dried, ground, and acidified in silver cups to remove carbonates and then measured using a Fisons NA1500N elemental analyzer with acetanilide as a calibration standard. Sample Chl *a* and pheophytin were extracted from sediment (3–11 g) in 90% acetone and concentration determined by fluorometric analysis using the low sensitivity setting on a Hitachi F2000 spectrofluorometer.

*Flume and experimental setup*—All experiments were conducted in the racetrack flume at the Institute of Marine and Coastal Sciences, Rutgers University, New Jersey (<http://marine.rutgers.edu/flume/racetrk.html>) designed after the flume described by Nowell et al. (1989). Experiments were conducted in the straight working section (6.2 m long, 0.7 m wide). For each experiment, two plates (30 cm  $\times$  30 cm) were placed in the flume 1.5 m apart (plate 1 upstream of plate 2), and separated by a cross-channel bedload trap in the flume bottom (Ramey 2008). The bedload trap opening was flush with the flume bed 21.5 cm downstream of plate 1. It was designed to catch any worms moving as bedload, thus preventing worms from plate 1 being transported into plate 2. For each experiment the flume was filled with natural seawater to a depth of 14 cm, maintained at 20°C and a salinity of  $31 \pm 2$ . Flow was driven by paddles located in the return channel of the flume and free-stream velocity was set at 5 cm s<sup>-1</sup>, which is comparable with the mean flow at LEO-15 (Traykovski et al. 1999; Styles and Glenn 2002). Because of the large number of worms needed for the experiments, it was necessary to reuse worms. Individuals, however, were never used in consecutive experiments and were carefully

monitored throughout the study to make sure they remained active, undamaged, and had few intestinal parasites. *P. jouinae* used in the experiments were adults 21 to 30 mm in length. Worms were maintained at  $\sim 20^\circ\text{C}$  in small bowls with seawater and sediment that was regularly renewed. Before all experiments, worms were starved for  $\sim 24$  h.

*Experiment 1: Distribution patterns*—This experiment was designed to examine distribution patterns and determine if *P. jouinae* shows a preference for sediment type, given a choice between sediments with ambient and lowered amounts of particulate organic matter under flow (constant grain size), or moves predominantly in the upstream or downstream direction regardless of sediment type. It is also possible that movement is a result of some combination of these factors (i.e., sediment type and flow direction). Each plate, described above, was made up of two arrays (each 10 cm  $\times$  10 cm; 1 cm deep) arranged side by side (6 cm apart) (Ramey 2008). Arrays were further subdivided into four equally sized cells with a temporary plastic divider. Three of the arrays were designated as treatment arrays (three replicates) and one as a control. Cells in the treatment arrays were filled with sediment with either ambient or reduced particulate organic content in an alternating pattern. For the control, all cells contained reduced levels of organic matter. With the plastic divider present, 5 worms were placed in the center of each cell (5 worms cell<sup>-1</sup> = 20 worms array<sup>-1</sup>  $\times$  4 arrays = 80 worms trial<sup>-1</sup>) and given 30 min to burrow into the sediment. The plastic divider was then removed, flow started, and after 48 h the number of worms in each cell was counted. This experiment was performed four times (referred to as trials 1–4;  $n = 320$  worms), and each time the location of the control array was changed so that it had occupied all four possible positions after completion of the four trials. To determine if shear velocity ( $u_*$ ) was similar among arrays within and among experimental trials, flow velocities were measured in the center of  $\geq 2$  cells array<sup>-1</sup> during most experiments. Measurements were taken at 7–12-cm heights above the sediment bed with a two-axis (measuring horizontal and vertical components of velocity) laser Doppler velocimeter. Graphical presentations of the vertical flow profiles indicated that two points (8 and 12 cm above the bed) were above the log layer, and they were not used in the calculation of shear velocity (cm s<sup>-1</sup>) (Nowell et al. 1981).

*Experiment 2: Direction of movement*—This experiment was designed to determine if the patterns observed for *P. jouinae* in the first experiment were a result of *P. jouinae* moving in a directed search (i.e., in response to some stimulus associated with the sedimentary particulate organic matter) or not (i.e., did not detect a stimulus and moved in some nondirected search pattern), and if success locating an organic patch depends on the location of the patch in relation to the worm's starting position (downstream or upstream of the food resource). Here, the two plates were each divided into 12 elongate cells (24 cm  $\times$  1 cm; 1 cm deep) spaced 1.5 cm apart (Ramey 2008). Each

cell was filled with lowered organic matter sediment with the exception of a small patch (2 cm × 1 cm) containing ambient levels of organic matter. This patch was randomly placed (by flipping a coin) so that for 50% of the cells it was located 3 cm upstream of the worm (worm placed at the center of each elongate cell, at the 12-cm mark), and in the remaining 50% of the cells it was 3 cm downstream of the worm. To accomplish this, the patch was placed at a 3-cm distance from the center of each elongate cell (i.e., at distances of 7–9 or 15–17 cm along the 24-cm-long cell). Three centimeters was chosen because it is comparable with the total length of the worms. A straw ~2 cm long was inserted into the sediment in the center of each cell (at 12 cm), and a single worm was placed in each straw. Straws were flush with the bottom of the plate to prevent premature movement of the worms. Once worms had burrowed into the sediment, straws were removed, and the flow was started. Thus, worms were given a 50:50 chance of locating a patch or not, or to find a patch by moving with the flow (downstream) or against it (upstream). After 30 min the flow was stopped and a plastic divider was inserted where the worm had initially been placed. Sediment was then removed in 1-cm increments (from the side without an organic patch first) to determine if the worm had moved in the direction of the ambient patch and the distance it had moved from its starting position (1 worm cell<sup>-1</sup> × 12 cells × 2 plates = 24 worms trial<sup>-1</sup>). These worms are very active and move promptly once in contact with sediment (pers. observ.). Here we wanted to look at short-term movement patterns and therefore a time interval of 30 min was chosen to allow the worms ample time to potentially detect a chemical cue and move either left or right away from their starting positions. A longer time interval might have given the worms too much time, which could have resulted in them randomly locating the organic patch (undirected search). This experiment was performed three times (herein referred to as trials 1–3;  $n = 72$  worms). Flow velocity was not changed from experiment 1, so new profiles were not measured.

**Data analysis**—Patterns of abundance for *P. jouinae* in rippled beds were compared by plotting mean ( $\pm$  SD) density for paired crest–trough samples at LEO-15. Density differences between crests and troughs at Stas. 9 and 30 were made with a Mann–Whitney *U*-test (SPSS 10.0). Experiment 1 was designed to test the prediction that the distribution of *P. jouinae* is dependent on the amount of particulate organic matter in the sediment or flow direction (upstream vs. downstream) or both. Thus, if sediment type was important then significantly more worms were expected in the ambient sediment cells, whereas if flow direction was most important, significantly more worms would be present in the two upstream cells or the two downstream cells in each array. Other patterns could result if both sediment type and flow direction were important. This interaction was tested using a Chi-squared goodness-of-fit ( $\chi^2$ ) test, described below. Experiment 2 was designed to test the prediction that movement of *P. jouinae* is associated with a chemical stimulus from sedimentary organic matter, and success in locating an organic patch

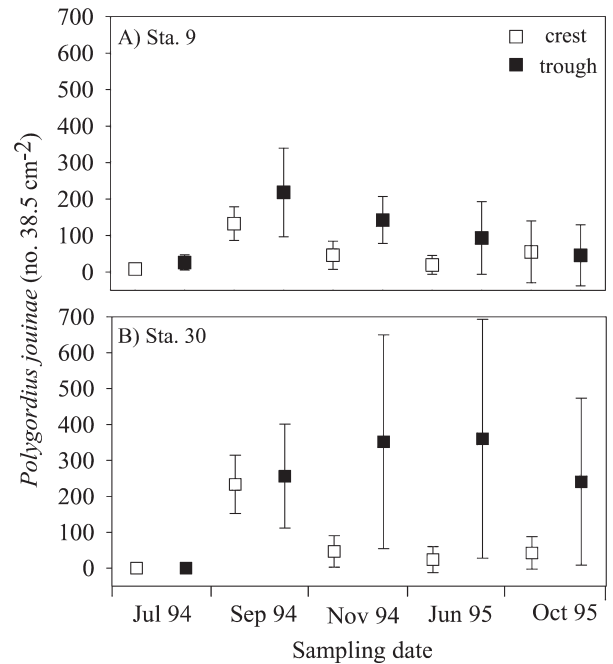


Fig. 1. Mean ( $\pm$ SD) density of *Polygordius jouinae* (number 38.5 cm<sup>-2</sup>;  $n = 9$ ) in paired crest and trough samples collected from (A) Sta. 9 and (B) Sta. 30 at LEO-15 research site located on the inner continental shelf off New Jersey, during July, September, and November 1994, and June and October 1995 (Ramey 2008; Grassle et al. unpubl.).

will be greater if the patch is located upstream of the worm's starting position. Therefore, significantly more *P. jouinae* were expected to move toward patches located upstream of their starting positions (movement against the flow). Distribution patterns (experiment 1) and direction of movement (experiment 2) were analyzed using a  $\chi^2$  test, which was calculated for each experimental trial (experiment 1: number of worms pooled for replicate treatment arrays  $n = 60$ , control  $n = 20$ ; experiment 2:  $n = 24$ ) ( $\alpha = 0.01$  and  $0.05$ ). Results and environmental parameters (i.e., sediment type, flow direction [upstream vs. downstream] and interaction between sediment type and flow) were consistent among experimental trials; thus a  $\chi^2$  test was also performed on pooled-trial data (experiment 1: number of worms pooled for treatment arrays for trials 1–4,  $n = 240$ , control  $n = 80$ ; experiment 2: trials 1–3,  $n = 72$ ). Experimental results are presented graphically for sediment type because it was the only variable that significantly affected the distribution of *P. jouinae*.

## Results

**Density of *P. jouinae* and ambient sediment parameters**—The density of *P. jouinae* at Stas. 9 and 30 was significantly greater ( $n = 90$ ,  $U$ -test = 697.5,  $p = 0.011$ ;  $n = 89$ ,  $U$ -test = 639.5;  $p = 0.004$  respectively) in ripple troughs (Sta. 9:  $\bar{x} = 105.3 \pm 107.1$ ; Sta. 30:  $\bar{x} = 239.3 \pm 265.9$ ) compared with crests (Sta. 9:  $\bar{x} = 52.6 \pm 65.4$ ; Sta. 30:  $\bar{x} = 69.2 \pm 98.0$ ) over several months during 1994 and 1995 (Fig. 1). Density was also generally more variable in replicate trough

Table 1. Means ( $\pm$  SD) for sediment parameters including v-coarse to med = very coarse to medium sand (%), fines (%), Chl *a* and pheophytin = total Chl *a* and pheophytin ( $\text{mg g}^{-1}$ ), particulate organic carbon (%), nitrogen (%), and C:N ratio for ambient and reduced organic (–organic) experimental sediment treatments and for ambient LEO-15 sediments from crests and troughs. n/a = not available.

Sediment parameters	Experiments		LEO-15 ambient	
	Ambient	–Organic	Crest	Trough
V-coarse to med (%) (250 $\mu\text{m}$ –1 mm)	89.5 (0.5)	92.0 (2.2)	Node B 93.9 (2.0)	Node B 91.2 (1.2)
fines (%) (63–125 $\mu\text{m}$ )	10.2 ( $\pm$ 0.16)	8.3 (2.2)	Node B 5.3 (2.1)	Node B 7.6 (0.6)
Chl <i>a</i> and Pheophytin ( $\text{mg g}^{-1}$ )	$0.49 \times 10^{-3}$ ( $0.12 \times 10^{-3}$ )	$0.15 \times 10^{-3}$ ( $0.04 \times 10^{-3}$ )	Sta. 9 ( $0.04 \times 10^{-3}$ ) Node B $0.49 \times 10^{-3}$ ( $0.10 \times 10^{-3}$ )	Sta. 9 ( $0.10 \times 10^{-3}$ ) Node B $2.4 \times 10^{-3}$ ( $0.56 \times 10^{-3}$ )
Organic carbon (%)	0.035 (0.002)	0.021 (0.004)	n/a	n/a
Nitrogen (%)	0.004 (0.001)	0.002 (0.001)	n/a	n/a
C:N	8.1 (1.22)	8.9 (0.41)	n/a	n/a

samples than in replicate crest samples (Fig. 1). Despite the low density of *P. jovinae* in May 2006, these patterns persisted. Mean density of *P. jovinae* in ripple troughs at Sta. 9 was  $3.5 (\pm 2.42)$  individuals ( $\text{ind.}$ )  $38.5 \text{ cm}^{-2}$  compared with  $0.33 (\pm 0.82)$   $\text{ind.}$   $38.5 \text{ cm}^{-2}$  in crests, whereas at Node B, mean density in troughs was  $7.33 (\pm 5.03)$   $\text{ind.}$   $38.5 \text{ cm}^{-2}$  and  $0.33 (\pm 0.58)$   $\text{ind.}$   $38.5 \text{ cm}^{-2}$  in crests. In the same May 2006 samples, concentrations of Chl *a* and pheophytin within the top centimeter of sediment were generally higher and more variable in troughs (Sta. 9:  $0.18 \times 10^{-3}$ – $0.48 \times 10^{-3} \text{ mg g}^{-1}$ ; Node B:  $1.9 \times 10^{-3}$ – $3.0 \times 10^{-3} \text{ mg g}^{-1}$ ) than in crests (Sta. 9:  $0.20 \times 10^{-3}$ – $0.30 \times 10^{-3} \text{ mg g}^{-1}$ ; Node B:  $0.40 \times 10^{-3}$ – $0.60 \times 10^{-3} \text{ mg g}^{-1}$ ). Chl *a* and pheophytin concentrations were  $\sim 1.33$  times greater in ripple troughs than crests at Sta. 9 and  $\sim 4.88$  times greater in troughs than crests at Node B (Table 1). Sediment grain size was similar among crests and troughs at Node B (Table 1). The coarse to medium sand fraction and fine sand fraction made up  $\sim 93.9\%$  and  $\sim 5.3\%$  respectively in crests, and  $\sim 91.2\%$  and  $\sim 7.6\%$  in troughs (Table 1).

*Sediment and flow parameters for experiments*—Sediment used in the experiments was similar in grain size to that in

rippled beds at LEO-15 and did not differ among experimental treatments (i.e., ambient vs. reduced organic matter) (Table 1). The range of total Chl *a* and pheophytin concentrations used for the ambient ( $0.32 \times 10^{-3}$ – $0.60 \times 10^{-3} \text{ mg g}^{-1}$ ) and the reduced organic treatments ( $0.12 \times 10^{-3}$ – $0.21 \times 10^{-3} \text{ mg g}^{-1}$ ) were similar to the range observed among crests and troughs, and within troughs at Sta. 9 (Table 1). Chl *a* and pheophytin concentrations were  $\sim 3.27$  times greater in the ambient treatment than the reduced organic treatment, and similar to the elevated values at Node B. Total sediment particulate organic carbon values were low and were  $\sim 1.7$  times higher in the ambient treatment ( $\bar{x} = 0.035\%$ ) compared with the reduced organic treatment ( $\bar{x} = 0.021\%$ ) (Table 1). C:N ratios were similarly low, which suggests that particulate organic matter present was relatively fresh. Shear velocity ( $u_* = 0.32 \pm 0.11 \text{ cm s}^{-1}$ ) in experiment 1 was similar among arrays within experiments and among experimental trials (Table 2).

*Experiment 1: Distribution patterns*—In each of the four trials  $>90\%$  of the *P. jovinae* were found in the ambient sediment cells after 48 h (Fig. 2). A  $\chi^2$  test on pooled data for each trial indicated that the distribution of *P. jovinae*

Table 2. Shear velocity ( $u_*$ ) ( $\pm$ SD) for  $\geq 2$  cells array $^{-1}$  (with a few exceptions,  $n = 1$ ) on the upstream and downstream plate positions in the racetrack flume, for a single array across all four experimental trials and for all four arrays in a single trial measured with a laser Doppler velocimeter during experiment 1.

Location	Experiment 1: Shear velocity $\text{cm s}^{-1}$ ( $u_*$ )				
	Trial 1	Trial 2	Trial 3	Trial 4	Trials 1–4
Upstream array 1	0.27 (0.05) $n = 2$	0.25 (0.03) $n = 2$	0.32 (0.10) $n = 3$	0.42 (0.20) $n = 3$	0.33 (0.13) $n = 10$
Upstream array 2	0.24 (0.02) $n = 3$	0.24 (0.03) $n = 2$	$0.44 \pm 0.10$ $n = 3$	0.40 (0.15) $n = 3$	0.34 (0.13) $n = 11$
Downstream array 3	0.37 (0.14) $n = 4$	0.27 (0.01) $n = 3$	$0.38 \pm 0.13$ $n = 3$	0.25 $n = 1$	0.33 (0.11) $n = 11$
Downstream array 4	0.30 $n = 1$	0.26 (0.06) $n = 4$	$0.29 \pm 0.02$ $n = 2$	0.28 $n = 1$	0.27 (0.04) $n = 8$
Total	0.30 (0.09) $n = 10$	0.26 (0.03) $n = 11$	$0.37 \pm 0.10$ $n = 11$	0.38 (0.13) $n = 8$	0.32 (0.11) $n = 40$

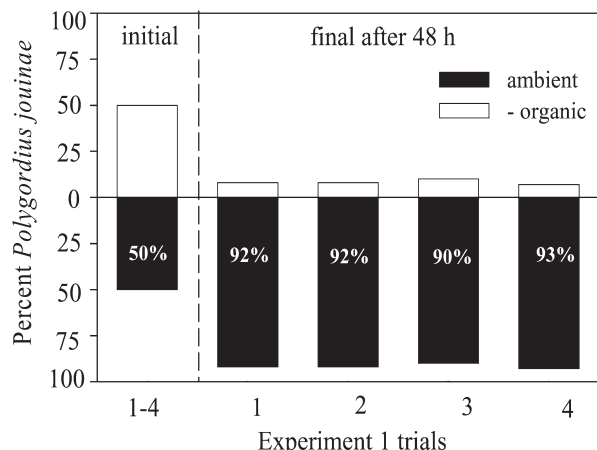


Fig. 2. Percentage of *P. jouinae* present in ambient and reduced organic content sediment treatments at the beginning of the experiment (initial conditions) and after 48 h, under flow conditions (free-stream velocity 5 cm s<sup>-1</sup>; shear velocity  $u_* = 0.32 \pm 0.11$  cm s<sup>-1</sup>) in racetrack flume for four trials in experiment 1 ( $n = 80$  trial<sup>-1</sup>;  $n = 320$ ).

was dependent on sediment type ( $\alpha = 0.01$ ) and independent of flow direction (Table 3). In a single trial (trial 2) distribution was also dependent ( $\alpha = 0.05$ ) on the interaction between sediment type and flow direction. A  $\chi^2$  test on pooled data from trials 1–4 produced the same results for sediment type and flow direction; however, there was no significant interaction between these two variables (Table 3). At the end of 48 h, fecal pellets produced by the worms were concentrated on or near the surface of cells with the ambient organic matter (Fig. 3). In the four control arrays *P. jouinae* remained relatively evenly distributed among the four cells in each trial, and worm

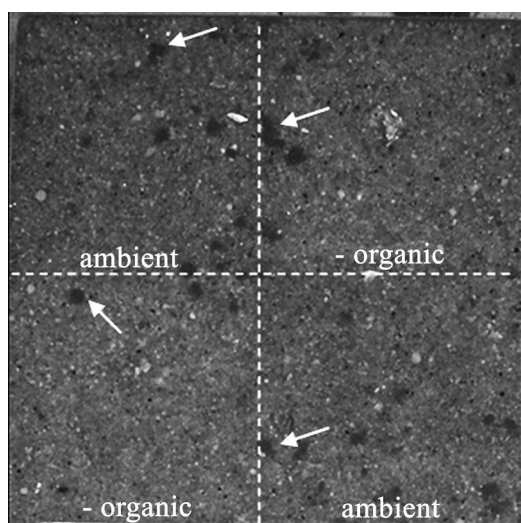


Fig. 3. Distribution and aggregation of fecal pellets (shown with arrow) on sediment surface of ambient sediment patches of a representative treatment array (each 10 cm × 10 cm; 1 cm deep) after 48 h, experiment 1. Array is subdivided into four equally sized cells (shown with dashed lines) containing ambient and reduced organic sediments.

Table 3. Chi-squared goodness-of-fit ( $\chi^2$ ) values for four environmental parameters including sediment type (ambient vs. reduced organic content;  $df = 1$ ), flow (up = upstream and down = downstream;  $df = 1$ ), interaction between sediment type and flow ( $df = 1$ ), and total ( $df = 3$ ) calculated for treatment arrays ( $n = 3$ ) and control arrays ( $n = 1$ ) in four trials ( $[\chi_{\text{trial1}}]^2$ ,  $[\chi_{\text{trial2}}]^2$ ,  $[\chi_{\text{trial3}}]^2$ ,  $[\chi_{\text{trial4}}]^2$ ) conducted in experiment 1 (i.e., number of worms were pooled for replicate treatment arrays  $n = 60$ , control  $n = 20$ ). Results were consistent among trials ( $n = 4$ ), and therefore a Chi-square test was also performed on pooled trial data ( $\chi_{\text{tot(1-4)}}^2 = \chi^2$  for trials 1–4,  $n = 240$ , control  $n = 80$ ).

Experiment 1: Distribution patterns						
Treatment						
Source	df	$(\chi_{\text{trial1}})^2$	$(\chi_{\text{trial2}})^2$	$(\chi_{\text{trial3}})^2$	$(\chi_{\text{trial4}})^2$	$(\chi_{\text{tot(1-4)}})^2$
Sediment type	1	40.02*	40.02*	36.82*	43.35*	165.00*
Flow (up or down)	1	0.15	0.42	0.42	0.017	0.038
Interaction	1	1.83	4.23**	3.43	1.70	1.76
Total	3	42.00*	44.67*	40.67*	45.07*	166.80*
Control						
Source	df	$(\chi_{\text{exp1}})^2$	$(\chi_{\text{exp2}})^2$	$(\chi_{\text{exp3}})^2$	$(\chi_{\text{exp4}})^2$	$(\chi_{\text{tot(1-3)}})^2$
Flow (up or down)	1	0.05	0.45	1.25	0.05	1.01
Total	3	0.40	2.80	4.40	1.20	4.90

\*  $\alpha = 0.01$ ; \*\* $\alpha = 0.05$ .

distribution was independent of flow (Table 3). All the worms were recovered from sediment arrays at the end of each trial and were never lost or found in the bedload trap.

*Experiment 2: Direction of movement*—In each of the three experimental trials 43% to 45% of worms were found in or on their way to the ambient patch after 30 min (Fig. 4). Similar numbers of worms were present in patches located upstream (percentage of worms = 60%, 50%, 50%, trials 1–3, respectively) and downstream (percentage of worms = 40%, 50%, 50%, trials 1–3, respectively) of the

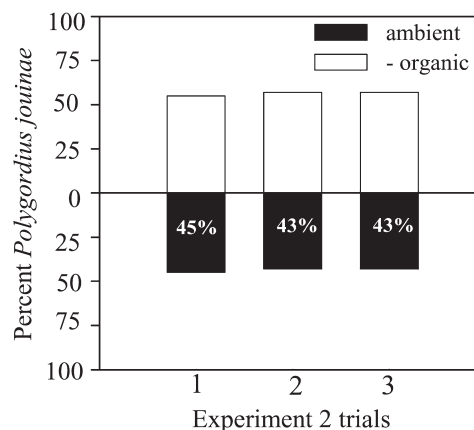


Fig. 4. Percentage of *P. jouinae* present in sediments of ambient and reduced particulate organic contents after 30 min under flow conditions (free-stream velocity 5 cm s<sup>-1</sup>) in racetrack flume for three trials in experiment 2, irrespective of positions upstream or downstream of the worm's starting position ( $n = 24$  trial<sup>-1</sup>;  $n = 72$ ).

Table 4. Chi-squared goodness-of-fit ( $\chi^2$ ) values for environmental parameters including sediment type (ambient vs. reduced organic content;  $df = 1$ ), flow (up = upstream and down = downstream;  $df = 1$ ), interaction between sediment type and flow ( $df = 1$ ), and total ( $df = 3$ ) calculated for each trial 1–3 ( $[\chi_{\text{trial1}}]^2$ ,  $[\chi_{\text{trial2}}]^2$ ,  $[\chi_{\text{trial3}}]^2$ ) conducted in experiment 2 (i.e., worms pooled for replicate treatment arrays  $n = 24$ ). Results were consistent among trials ( $n = 3$ ), and therefore a Chi-square test was also performed on pooled trial data ( $\chi_{\text{tot}(1-3)}^2 = \text{trials 1-3, } n = 72$ ).

Experiment 2: Direction of movement					
Source	df	$(\chi_{\text{trial1}})^2$	$(\chi_{\text{trial2}})^2$	$(\chi_{\text{trial3}})^2$	$(\chi_{\text{tot}(1-3)})^2$
Sediment type	1	0.17	0.17	0.42	1.18
Flow (up or down)	1	0.17	0	0.08	0.01
Interaction	1	0.49	0.31	0.50	0.37
Total	3	0.83	0.48	1.00	1.54

worm's starting position. A  $\chi^2$  test on pooled data for each trial indicated that direction of movement by *P. jouinae* was independent of sediment treatment and flow (upstream vs. downstream) (Table 4). In 30 min worms showed a wide range in movement, ranging from 1 to 11 cm ( $2.93 \pm 2.02$ ;  $n = 42$ ) from their starting positions. Worms that reached the ambient patch were never found beyond it, whereas worms that moved in the opposite direction were often found >3 cm from their starting positions. It is important to note that it is unknown what path the worms took during this experiment, and if they were found at the end of the 12-cm cell, whether they had traveled >12 cm during the experiment. Average rate of movement was  $0.1 \text{ cm min}^{-1}$  and the highest rate was  $0.4 \text{ cm min}^{-1}$ .

## Discussion

This study was motivated by unpublished observations in 1994 and 1995 that showed certain infaunal species to have distribution patterns associated with either crests or troughs in rippled beds at the LEO-15 research site off New Jersey (Ramey 2008; Grassle et al. unpubl.). Specifically, the deposit-feeding polychaete, *P. jouinae*, occurred in higher but more variable densities in ripple troughs compared with crests in inner continental shelf sandy sediments (Ramey 2008). This pattern was confirmed with samples taken for the present study in 2006. We hypothesized that this small-scale distribution pattern might be established by an interaction between the behavior of the worm and the effects of unidirectional, near-bottom, and Brinkman-layer flows on the distribution and concentration of particulate organic matter within the sediments.

Replicated flume experiments showed that, contrary to our initial expectations, worms did not detect patches of organic-rich sediment at a distance of as little as 3 cm, even when patches lay upstream of the worm. Yet, in the absence of a directed search, worms were clearly capable of moving rapidly through the interstices of these coarse sandy sediments under realistic flow conditions (free-stream velocity of  $5 \text{ cm s}^{-1}$ ; shear velocity  $[u_*] = 0.32 \text{ cm s}^{-1}$ ). In the field, the bottom microtopography can cause spatial differences in pressure-driven flows in sediments deeper

than 1 cm. Once worms found an organic-rich patch of sediment they remained in it and fed long enough to produce small mounds of fecal pellets on the sediment surface. Thus, *P. jouinae* was capable of habitat choice, even though discovery of patchy sediment resources appears to be a chance process.

Spatial and temporal variations in the distribution and concentration of particulate organic matter are likely key determinants in influencing patterns of distribution of infauna in high-energy, physically active, shallow coastal and continental-shelf benthic environments characterized by a rich array of microtopographic features. The significant role that microtopography plays in advective transport of water through the interstices of the sediment has been identified as an important process enhancing the deposition, transport, and patchiness of particulate organic matter in permeable shelf sands (Huettel et al. 1996; Pilditch et al. 1998; Reimers et al. 2004). In sandy rippled beds, near-bottom water containing particulate organic matter and oxygen is pumped into the sediments on the upstream side of ripples, where the organic matter may become trapped, whereas pore water is pumped out at the apex of crests (Huettel et al. 1996; Ziebis et al. 1996). Particulate organic matter may also accumulate in troughs by settling there as a result of reduced shear stress. In the present study, we found concentrations of Chl *a* and pheophytin up to five times higher in ripple troughs compared with crests. Similar patterns in total Chl *a* and pheophytin concentrations have been found for paired crest–trough samples collected at LEO-15 ( $39^\circ 27.0' \text{N}$ ,  $74^\circ 4.27' \text{W}$ ) in October 2005 with higher ( $\sim 6.6$  times) and more variable concentrations in troughs ( $3.6 \times 10^{-3} \pm 3.2 \times 10^{-3} \text{ mg g}^{-1}$ ) relative to crests ( $0.55 \times 10^{-3} \pm 0.10 \times 10^{-3} \text{ mg g}^{-1}$ ) (Taghon pers. comm. unpubl.). Although percentages of particulate organic carbon in sediments were not compared among ambient crests and troughs at LEO-15 in the present study, sediment treatments contained amounts similar to those determined for samples haphazardly collected at Node B, LEO-15 by Rusch et al. (2003), with values of 0.015% to 0.030% depending on sediment depth and season. Such low levels are typical of sandy sediments. In the North Sea, percentages of particulate organic carbon in sediments with coarse (i.e.,  $672 \pm 78 \mu\text{m}$ ) and medium ( $299 \pm 8 \mu\text{m}$ ) grain sizes and a variety of microtopographical features such as mounds, pits, and ripples were 0.030% and 0.023% respectively (Janssen et al. 2005).

These surrogate measures of food concentrations and measured densities of *P. jouinae* were patchily distributed in sediments at similar spatial scales at LEO-15 and, despite low overall concentrations of total Chl *a*, pheophytin, and particulate organic carbon, our experiments indicate that a difference of  $\sim 3.0$  and 1.5 times, respectively, between sediment patches (values consistent with ambient concentrations) appears to affect the behavior of *P. jouinae*. Active selection by infauna for food resources has often been implicated, rather than experimentally tested, in explaining observed patterns associated with rippled beds (e.g., Hogue and Miller 1981; Fenwick 1984).

For organisms living in such a dynamic, heterogeneous, and patchy environment with oscillatory flow, a strategy of undirected movement such as exhibited by *P. jouinae* rather

than a response to a chemical stimulus from a distance seems advantageous. This, in combination with high mobility, likely allows *P. jouinae* to respond relatively quickly to changing local conditions such as exhaustion of a food resource. Even though movement was undirected, it is likely that different patterns of behavior in sediments containing higher versus lower amounts of particulate organic matter allow this worm to aggregate, at least for a time, in more favorable, organic-rich sediments. The capability of *P. jouinae* to remain in a favorable sediment patch was further examined by placing a single worm in the center of one of the cells reduced in particulate organic content using the same array as in experiment 1 and recording the appearance of new fecal pellets at ~3-h intervals for 7 d (Ramey 2008). The first fecal pellet(s) were found after 21 and 33 h, and they along with the worm and successive pellets were present in or on the surface of one of the ambient patches for the entire week. The polychaete *Protodrilus hypoleucus* was shown to glide along with little variation in speed of movement in unfavorable sands (i.e., sterile sands), whereas, upon entering more favorable sands with associated bacteria, it moved much more slowly and intermittently stopped to sample the sediment within its reach by moving its head in various directions (Gray 1967). It is likely that *Polygordius jouinae* uses a similar pattern of behavior.

Relatively little is known about this interstitial environment or how organisms react to it (Vogel 1981). Interstitially, viscous forces predominate (low Reynolds numbers ~0.2) and meiofaunal organisms (size classes, i.e., 0.01–0.10 cm) typically experience flows of about one body length  $s^{-1}$  and shear stresses of ~0.003 to 0.05  $N m^{-2}$  (Crenshaw 1980; Vogel 1981). Crenshaw (1980) found meiofauna to have higher mobility at high flows and that movement in sandy sediments is predominantly in the upstream or downstream direction rather than across the flow. In our system, where the patch of ambient sediment filled the elongate channels in experiment 2, a worm that moved toward a patch regardless of whether it was upstream or downstream of the worm's starting position would be bound to encounter it after moving 3 cm (i.e., approximately one body length). Life in sandy sediments has been described as living in an array of parallel channels (Crenshaw 1980; Vogel 1981). Rates of movement up to 0.4  $cm min^{-1}$  for *P. jouinae* mean that a worm could potentially travel the wavelength of a typical ripple (14 to 30 cm) at LEO-15 in 35–75 min. Members of the family Polygordiidae are often considered part of the meiofaunal community because they spend their postsettlement life interstitially. However, their length (1.0 to 10.0 cm) makes them part of the macrofaunal community as it is usually defined. Perhaps the relatively large size of *P. jouinae* (sexually mature adult body length 1.3 to 4.3 cm) may allow it to move with relative ease through coarse but not finer sandy sediments.

Very few selection experiments involving subsurface movement of postlarval polychaetes have been conducted since those of Gray in the mid-1960s (e.g., Gray 1967), where *Protodrilus rubropharyngeus* and *P. hypoleucus* were shown to actively select for particular grain sizes and

organic surface films on sand grains produced by certain species of bacteria. Although microorganisms were not identified or quantified in the present study, it is unlikely that the microbial composition of the sediment was changed significantly by washing it over a 100- $\mu m$  sieve to create the reduced organic treatment, and thus sediment choice is believed to be based on the amount and quality of the particulate organic matter and associated bacteria. In an experiment more similar to the present research, Nilsson et al. (2000) tested whether the oligochaete *Paranais litoralis* could choose patches of sediment on the basis of sediment quality at small spatial scales (patch diameter 2.5 cm) over 48 h in still water. Worms selected more favorable sediment patches containing sediment from the field that was renewed every 3 d over nutrient-exhausted sediment (sediment from the field that was not renewed over 30 d). However, depletion of resources also triggered a swimming response. Worms emerged from the sediments into the water column and upon settling selected sediment that was not resource depleted.

There is some evidence that recently settled juvenile *Polygordius jouinae* (length categories 6 and 9 mm) may be transported to ripple troughs from surrounding sediments via resuspension or bedload transport in the field (Ramey 2008). In a reciprocal sediment transplant experiment at LEO-15 (Snelgrove et al. 1999), hydrodynamically unbiased trays placed in ripple troughs contained recently settled juvenile *P. jouinae* within 3 to 5 d (Ramey 2008). Tray design precluded movement through the sediment by these worms. Juvenile worms concentrated in the upper sediment layer may be more easily resuspended than adults living deeper in the sediment. The present study could not determine the relative importance of active or passive resuspension vs. subsurface migration in creating and maintaining the higher density of this deposit feeder in ripple troughs compared with crests. It does show that the affinity of adult *P. jouinae* for higher levels of particulate organic matter and its undirected, high rate of subsurface movement is a plausible mechanism for creating and maintaining observed patchiness of this species in continental shelf sediments.

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