

New resource axes for deposit feeders?

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ABSTRACT

Recent work on selectivity in deposit feeders has focused on the importance of particle size. In field experiments with exotic sediments of known characteristics (glass beads), we demonstrate that selective ingestion in a multitentaculate, surface deposit feeding ampharetid polychaete depends upon particle specific gravities and surface textures. The degree of selectivity for specific gravity is shown to be dependent upon worm size. Further, particles are sorted on the basis of specific gravity in the gut of the ampharetid, particles of higher specific gravity apparently having shorter gut residence times. The latter observation impugns the use of bulk gut contents analysis as evidence of deposit feeder selectivity. Selection on the basis of surface texture is also demonstrated for two spionid species sympatric with the ampharetid.

*"I eat my peas with honey;
I've done it all my life.
They do taste rather funny,
But it keeps them on my knife!"
— Anonymous*

1. Introduction

Empirical investigations have shown that many deposit feeders utilize microbial epigrowth on sediment particles (e.g., Fenchel, 1970; Fenchel and Kofoed, 1976). Both empirical (Whitlatch, 1974; Fenchel *et al.*, 1975) and theoretical (Taghon *et al.*, 1978) studies, in turn, have suggested that particle size selection will therefore be found in deposit feeders. Given a relatively uniform cover of bacteria over the surfaces of particles of different sizes (Hargrave, 1972; Dale, 1974), more bacteria per unit volume of sediment can be ingested if smaller particles are selected.

The selective capabilities of deposit feeders, however, have been delineated in only a preliminary way. Johnson (1974, 1977) carefully documented the complexity of natural sediment particles—complexity which has forced investigators to use chemical and mechanical disaggregation to provide reproducible comparisons of deposit feeder gut contents with ambient sediments. While providing reproducibility,

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Table 1. Physical characteristics of the two glass bead types employed throughout the experiments, according to the specifications of Cataphote Division, Ferro Corporation. Size range is for 85% of beads, by number.

	Type 1	Type 2
Diameter (μm)	44-62	44-62
Specific gravity	2.99 (ρ_1)	3.99 (ρ_2)
Refractive index	1.65	1.91

these disaggregation procedures destroy the original sediment fabric and particle-size spectrum experienced by the organism. To avoid the resultant problems in evaluating deposit feeder selectivity, we chose instead to use exotic sediment particles of closely specified characteristics. This approach has proven useful in a wide variety of applications, from the study of suspension feeders (e.g.: Wilson, 1973; Timko, 1976; Frost, 1977) to granivores (e.g.: Emlen and Emlen, 1975; Mares and Williams, 1977). Use of exotic particles is not a panacea, however; it is incumbent upon the investigator to select particles that are not entirely artificial in the responses they elicit.

To test the predictions of Taghon *et al.* (1978) concerning particle size selection by deposit feeders, we had hoped to develop paired tracers, two particle types of identical size but differing in some easily recognizable way. To one particle type or the other we would attach either attractive or repellent substances. By varying the sizes of these paired particle types we had planned to determine the range of particle sizes over which selection could be demonstrated. The initial experiments involved glass beads of two different refractive indices, readily distinguishable by immersion in a liquid having the same refractive index as one of the bead types. We began these experiments with a deposit feeding ampharetid polychaete (of a new genus to be described by Banse, in press). It is a multitentaculate, surface deposit feeder (illustrated in feeding posture by Fauchald and Jumars, in press, fig. 1). The first adsorbed substance we field tested was the residue from potassium permanganate soaking, which our chemist colleagues assured us would effectively stain glass.

The unexpected results from our controls in this experiment led us, in succession, to testing several hypotheses in place of our original ideas concerning particle size. Explicitly, the null hypotheses tested herein are:

- (1) The ampharetid does not select among particles of differing specific gravities.
- (2) The ampharetid does not select among particles of differing surface textures.
- (3) Worm size is independent of the specific gravity of particles ingested.
- (4) The surface texture of particles ingested is independent of worm size.
- (5) Sorting of glass beads by specific gravity along the length of the gut of the ampharetid does not occur.

Table 2. Bead modifications and their apparent effects on bead surfaces; all treatments followed by drying on a hotplate and storing.

Modification	Result
<u>Coating (bead types 1 and 2):</u>	
Soaking in saturated KMnO_4 solution, drying on hotplate (3 repetitions), followed by tapwater rinse	Brownish MnO_2 coating, frosted surface appearance under $200\times$ magnification
<u>Etching (type 1 beads only):</u>	
Boiling 3 hr in 2.3N acid-dichromate cleaning solution, followed by tapwater and acetone rinses [showed no effect on type 2 beads]	Obvious frosting and pitting under $200\times$ magnification
<u>Etching (type 2 beads only):</u>	
Soaking overnight in 2.3N acid-dichromate cleaning solution, followed by tapwater and acetone rinses [caused disintegration of type 1 beads]	Obvious frosting and pitting under $200\times$ magnification
<u>No modification (bead types 1 and 2):</u>	
Additional (to tapwater rinse) acetone rinse for etching experiment	No change

(6) Sorting of glass beads by surface texture along the length of the gut of the ampharetid does not occur.

We were also able to test some of these hypotheses in two spionid polychaete species sympatric with the ampharetid.

2. Methods

a. Bead preparing and dispensing. The beads (Table 1) were variously modified. After modification (Table 2), two bead types were mixed in approximately equal proportions by volume for each treatment and each control to make a total of roughly 60 cm^3 . In the first experiments (1/20/77, 4/21/77, 4/25/77), these beads were dispensed dry from salt shakers. Because of obvious differences in wettability between bead types, subsequent mixtures (7/15/77) were dispensed as a seawater-based slurry from a plastic squeeze bottle.

b. Field procedure. All experiments were conducted at the +5 to +6 tidal level (1.5-1.8 m) above mean low water within a mudflat between the north and south forks of the Skagit River, northern Puget Sound, Washington. At low tide, when all the experiments were performed, the mudflat is dotted with small pools, a few centimeters to a few meters in diameter and 1-5 cm deep. To collect an adequate num-

ber of individuals for the experiments, areas where high densities of ampharetid fecal mounds occurred were selected as experimental sites. Within the pools, a foot square (929 cm²) metal frame was pressed into the sediment to mark a sample site and to decrease wind-caused disturbance during particle dispensing. Two replicate quadrats were used for each treatment and each control to estimate between-site variability. Treatments and controls were randomly assigned to the preselected high ampharetid density quadrats.

The glass bead mixtures were dispersed over the sediment surface, forming as even a cover as possible within the metal frame. The frame was then removed, and surface sediment cores were taken with soda straws (6 mm diameter) at random positions within the quadrat. In the first experiment (4/21/77), surface sediment cores were taken again 1-2 hours later, just prior to the end of the experiment, for comparison with the initial straw cores. This step was deleted in subsequent experiments because no significant difference was found (Mann-Whitney *U* test, $P > 0.10$, 2-tailed) between median proportions of bead types in the before and after cores.

Experiments were terminated after approximately 2 hours, when animals were collected with a plastic tube corer (4.7 cm diam.). At least the surface 2-cm layer of these cores was retained and immediately fixed in a 20-40% formalin solution with rose Bengal, and virtually the entire 929 cm² of sediment was collected. Our experience indicates that a formalin solution of lower strength than 20% does not adequately fix specimens in their closely fitting tubes, resulting in partial decomposition of the gut wall and the possibility of redistribution of glass beads within the body cavity.

c. Laboratory procedure. Fixed sediment samples were sieved on a 351- μ m screen. Ampharetids were sorted out under a dissecting microscope and stored in 70% ethanol awaiting gut content analysis.

To obtain a rapid but relatively precise estimate of an individual's size, five morphological measurements were made on 13 specimens for multiple least squares regression against worm volume. Volume measurement was chosen instead of wet or dry weight because it is neither destructive nor sensitive to the weight of ingested sediments. Specimens were immersed in 100% glycerol in a depression slide for measurement ($\pm 10 \mu$ m) or count of (1) interocular distance (between prostomial eyespots in focus), (2) width at the sixth setiger (dorsal view), (3) length from the last thoracic setiger to the anal opening (dorsal view), (4) number of abdominal segments, and (5) number of uncinni on the sixth (first uncinnigerous) setiger. Only entire specimens were used.

Volume of individual worms was estimated for the regression analysis during their immersion in 70% ethanol in a well slide. With a camera lucida, a tracing of the projected image of the animal was made. The tracing was divided into three or four parts corresponding as closely as possible to two-dimensional projections of

cylinders or hemispheres. Three to five replicate estimates of the projected surface area of each segment were made with a planimeter. The mean projected area for each of the three or four parts was then used to compute volume of that part, assuming a cylindrical or hemispherical shape. Since the projected radius of a segment varied along the length of the tracing, a mean radius was employed. Summing the partial volumes produced the final estimate.

Based on stepwise multiple regression (Dixon, 1973, pp. 305-330) of the logarithm of worm volume (mm^3) against the logarithms of the measurements and counts, we determined that interocular distance was a good ($r = 0.97$) estimator of body volume and that the estimate could not be substantially improved with the addition of the other measurements.

In the 7/15/77 experiment, sufficient specimens of the spionids *Pseudopolydora kempj japonica* and *Pygospio elegans* were obtained to allow analysis of their selectivities. Their body volumes, estimated as for the ampharetid, were regressed against (1) interocular distance (between anteriormost eyespots in focus), (2) width at the fourth (*Pseudopolydora*) or second (*Pygospio*) setiger, (3) total length, (4) number of segments with hooded hooks, and (5) prostomial length (anteriormost point to anterior of first setiger in *Pygospio* versus midpoint of second setiger in *Pseudopolydora*). Prostomial length ($r = 0.93$) proved to be a good estimator of *Pseudopolydora* volume, and counts of segments with hooded hooks ($r = 0.90$) a good estimator of *Pygospio* volume, in a log-log plot.

For the 4/21/77 experiment, all ampharetid individuals sampled were subjected to gut content analysis. The larger number of individuals collected in the 4/25/77 and 7/15/77 experiments required subsampling. Ampharetid individuals were partitioned into three groups on the basis of size, and equal numbers of individuals were chosen randomly from each group. Specimens were immersed in 100% glycerol in a depression slide and cleaned of adherent sediment particles and glass beads. Interocular distance was measured after removal of the branchiae. The worms were then placed in a drop of water for dissection. Care was taken to isolate foregut (anterior to any gut diverticulum or loop) contents from hindgut (far posterior, straight section of the gut) contents. Contents of the midgut were not analyzed. Foregut beads were removed from the anteriormost location of gut contents until at least 50 were obtained or until the midgut was reached, whichever occurred first; an analogous procedure was used for the hindgut. The number of beads removed and counted per foregut or per hindgut actually varied from 5 to 125. The total was counted before their drying on a hotplate. Immersion in 1-bromonaphthalene (refractive index 1.65) left only ρ_2 (the higher specific gravity) beads visible, and their proportion in the total was calculated. Etched beads (Table 2) were determined directly under $200\times$ magnification, but proportions of ρ_1 and ρ_2 beads were verified by immersion, in those treatments where both specific gravities were used.

Gut material in the spionids invariably was not retained in the anatomical foregut.

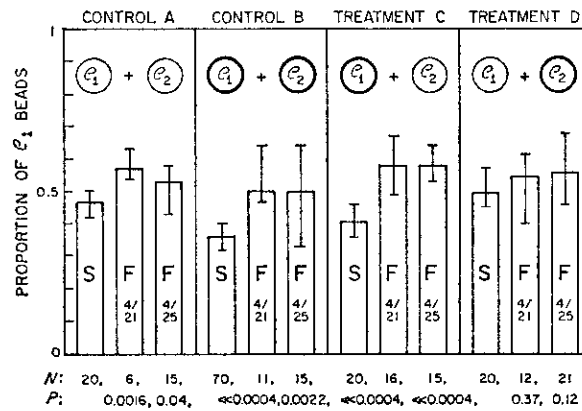


Figure 1. Median proportions of ρ_1 beads in sediment cores (S) and animal foreguts (F) in April experiments; error bars: 96% nonparametric confidence limits of medians; P: two-tailed Mann-Whitney *U* probability that sediment and foregut proportions were drawn from distributions having the same median; N: number of cores or foreguts analyzed; thick circles: permanganate-treated beads; thin circles: untreated beads.

First appearance of gut material in preserved specimens was in the midgut region (approximately fifteenth setiger). Etched bead determinations otherwise followed the same procedure as for the ampharetid.

A subsample of 50 beads was taken from each straw core sample. They were identified as to bead type in the same manner as were the beads recovered from the worm guts.

Aquarium observations through a dissecting microscope provided a qualitative impression of the particle selection process. Both natural sediments and glass beads were used.

3. Results and discussion

To clarify the reasoning behind particular experiments, we will develop the hypotheses in the order in which they were generated. The first experiments (4/21/77 and 4/25/77) were intended to reveal whether a manganese dioxide coating was selected for or against by the ampharetid. The results of these experiments are summarized in Figure 1. It quickly became apparent that specific gravity (cf. controls) has at least as large an effect as the coating (cf. controls versus treatments) in influencing selection.

To more clearly display the treatment effects and to investigate potential interaction (in the statistical sense), we examined residuals, i.e., the proportion of ρ_1 beads in the foregut minus the median proportion of ρ_1 beads in the straw cores (Fig. 2). Because we chose nonparametric methods in the analysis, the residuals were left in the easily interpreted terms of proportions, not arcsine transformed as

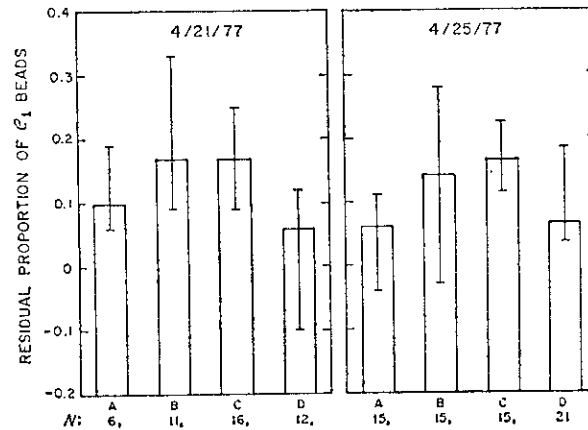


Figure 2. Residual proportions from Fig. 1. (foregut minus median from sediment cores); error bars: 96% nonparametric confidence limits of medians; N : number of foreguts analyzed.

might be desirable for parametric applications (Sokal and Rohlf, 1969). There are obvious differences among the controls and treatments (Kruskal-Wallis test: $P \ll 0.001$, 4/21/77; $P \cong 0.008$, 4/25/77). On both days the ordering of treatments versus controls is similar. It can be summarized as follows, where the ordering indicates increasing selection of the ρ_1 beads from left to right, and underlining in common indicates no significant difference (experimentwise $\alpha < 0.05$) in pairwise comparisons between median proportions:

$$\begin{array}{cc}
 4/21/77 & 4/25/77 \\
 \underline{D \ A \ B = C} & \underline{A \ D \ B \ C}
 \end{array}$$

Coated beads and ρ_1 beads are selected for, and no strong statistical interaction is apparent between specific gravity and coating in the treatments we were able to perform (Controls A and B give comparable results). It was impossible, however, to run two hypothetical controls, ρ_1 beads of which half were coated and ρ_2 beads of which half were coated, for further indications of the coating effect. The manganese dioxide was variably removed by the combination of conditions in the gut and preservation in formalin, and the beads could not be adequately distinguished on the basis of the minor pitting observed (Table 2).

The results of the 4/21/77 and 4/25/77 experiments changed the focus of our experiments from the search for an attractive or repulsive coating to the testing of the influence of factors other than size on the selection process. They allowed us to reject the null hypothesis of no selection on the basis of particle specific gravity, but the mode of the effect of acid-permanganate soaking remained unclear. Was the effect due to the slight pitting produced or to the manganese dioxide coating?

To separate the effect of pitting, the 7/15/77 experiment was run. Etched beads

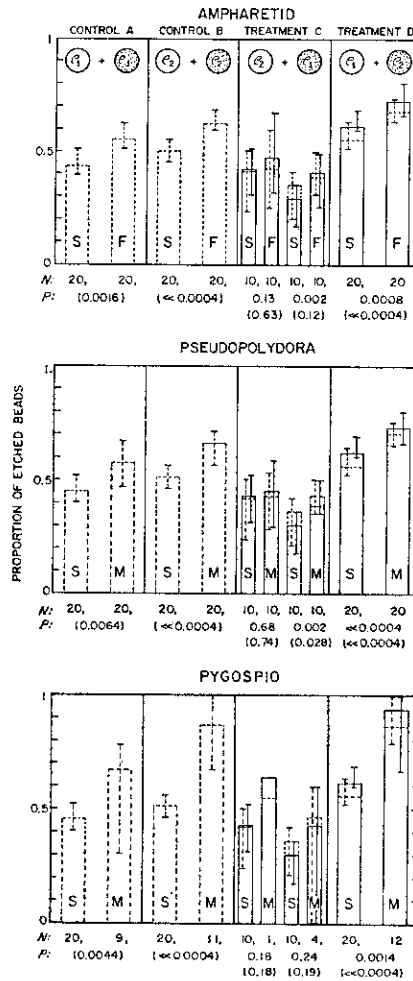


Figure 3. Median proportions of etched beads in sediment cores (S) and animal foreguts (F) or midguts (M) in July experiment; error bars: 96% nonparametric confidence limits of medians; P : two-tailed Mann-Whitney U probability that sediment and gut proportions were drawn from distributions having the same median; N : number of cores or guts analyzed; stippled circles: etched beads; plain circles: untreated beads; dashed lines and parenthetical probabilities: based on discrimination of etching *per se*; solid lines: based on more reliable immersion method. Treatment C replicates could not be combined because sediment core (S) proportions differed significantly ($P < 0.05$, Mann-Whitney U test).

were invariably selected in greater median proportion by the amphetamine than were the smooth beads (Fig. 3). Etching thus did not produce the same selection pattern as did acid-permanganate soaking. Etching apparently overrode the specific gravity effect (Treatment D), and the null hypothesis of no surface texture effect can be firmly rejected. The residuals for the amphetamine, in turn (Fig. 4), do not suggest

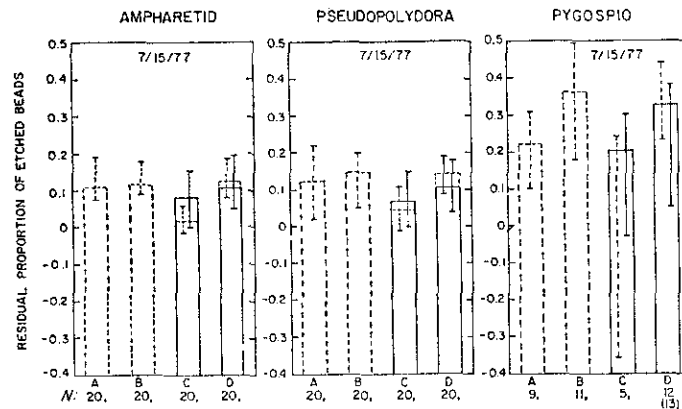


Figure 4. Residual proportions from Fig. 3. (foregut or midgut minus median from sediment cores); error bars: 96% nonparametric confidence limits of medians; dashed lines: based on discrimination of etching *per se*; solid lines: based on immersion method; *N*: number of foreguts (ampharetid) or midguts (spionids) analyzed.

any significant differences among the degrees of preference for etched beads in the various treatments (Kruskal-Wallis test: $P > 0.70$).

Pygospio and *Pseudopolydora* also selected etched glass beads over smooth-textured beads (Fig. 3). Analysis of residuals (Fig. 4) again did not indicate varying preference for etched beads among the treatments (Kruskal-Wallis test: *Pseudopolydora*, $P = 0.74$; *Pygospio*, $P = 0.11$). The degree of preference for etched beads differs, however, among the three species, with *Pygospio* showing the highest preference for etched beads in all treatments.

While processing the April samples, we attempted to find reasonable alternative hypotheses which might discredit our interpretation concerning the strong role of specific gravity in particle selection by the ampharetid. One such alternative is that the few (≤ 5) centimeters of water column might be sufficient for introduction of a partial layering of the beads due to specific gravity and skin friction differences among beads during settling. Worms in the April experiments tended to choose particles that would have had the slower settling rate in each treatment. All results of the July and April experiments, however, cannot be explained in this way (e.g., Treatment D, Fig. 3).

Another alternative we entertained in an attempt to discredit both the specific gravity and the surface texture conclusions was that glass bead size was altered by the modifications. Although preliminary measurements after the treatments showed no apparent differences between modified and unmodified beads, more careful study revealed one marked exception (Table 3). The etched ρ_1 beads had a mean diameter 13% smaller than that of the unmodified beads, resulting in a 33% decrease in average particle volume and weight. Again, however, the altered particle size cannot be used to explain all the July results.

Table 3. Statistics of bead sizes, calculated from ocular micrometer measurements of 50 beads of each type.

	Median Diameter (μm)	Mean Diameter (μm)	Parametric 95% Confidence Limits for the Mean (μm)	
			Lower	Upper
ρ_1 , unmodified	55.0	55.3	53.2	57.5
ρ_2 , unmodified	56.5	55.1	53.0	57.1
ρ_1 , coated	53.0	52.6	50.5	54.7
ρ_2 , coated	54.5	54.8	52.1	57.5
ρ_1 , etched	49.0	48.3	46.4	50.3
ρ_2 , etched	50.0	52.9	50.7	55.2

Corroborating the idea that the observed selection was not a methodological artifact are the results of comparisons of individual ampharetid volume with apparent selection (Table 4). Worm volume data had originally been gathered with the idea of comparing particle size selection with worm size over a broad range of particle sizes. After the April experiments, however, the results of a pretest (1/20/77 in Table 4) were re-interpreted to indicate a selectivity for specific gravity dependent upon worm size, with larger worms showing greater selectivity for ρ_1 particles. This pretest allowed one-tailed testing (in those subsequent treatments where both ρ_1 and ρ_2 beads were presented) of the null hypothesis that larger worms ingest a greater proportion of ρ_2 beads than do smaller worms (or that worm size and selectivity are unrelated). This null hypothesis was firmly rejected in some individual experiments and in aggregate by virtue of the high frequency with which the sign of the correlation coefficient (τ) was in accord with the alternate hypothesis (9/10, binomial $P = 0.011$, Table 4).

Unfortunately, the test of changing selectivity for etched beads with worm size was more equivocal. The data (Table 4) did not allow rejection of the null hypothesis of independence of etched bead ingestion and worm size, but the small number of treatments with etching as the only variable leaves this question open.

An additional worry we entertained is that we might have underestimated the selective capabilities of the organisms. If ampharetid individuals were able to change the relative concentrations of bead types within their reaches, the initial straw core proportions no longer provided a reliable indication of particle availability. Although the follow-up cores taken at the end of the 4/21/77 experiment showed no apparent depletion, they were unlikely to have fallen within the small, cardioid-shaped feeding territories of the ampharetid. Aquarium observations suggested that significant depletion of the applied amounts would not occur during the two-hour experiment, but we sought verification from the field results.

We reasoned that if an individual ampharetid showed selection for ρ_1 versus ρ_2 beads, depletion of the preferred beads might be apparent along the length of the

Table 4. Kendall's rank correlation statistic (τ) for worm size (mm^3) versus proportion of type X below; N: number of worms in treatment; α : descriptive level of significance, one (†) or two (††) tailed.

Bead Types Applied		N	τ	α	Experiment Date
X	Y				
<i>Ampharetid</i>					
ρ_1 , unmodified	ρ_2 , unmodified	6	0.00	>0.50 †	4/21/77
		15	0.07	0.39 †	4/25/77
ρ_1 , coated	ρ_2 , coated	11	0.25	0.16 †	4/21/77
		15	-0.19	>0.50 †	4/25/77
ρ_1 , coated	ρ_2 , unmodified	23	0.44	<0.002††	1/20/77
		16	0.55	0.001†	4/21/77
		15	0.06	0.40 †	4/25/77
ρ_1 , unmodified	ρ_2 , coated	12	0.11	0.34 †	4/21/77
		21	0.40	0.005†	4/25/77
		20	0.14	0.40 ††	7/15/77
ρ_1 , etched	ρ_2 , unmodified	20	-0.15	0.36 ††	7/15/77
ρ_2 , etched	ρ_1 , unmodified	20	0.08	0.32 †	7/15/77
ρ_1 , etched	ρ_2 , unmodified	20	-0.28	0.04 †	7/15/77
ρ_2 , etched	ρ_1 , unmodified	20			
<i>Pseudopolydora kempii japonica</i>					
ρ_1 , etched	ρ_2 , unmodified	20	-0.05	0.77 ††	7/15/77
ρ_2 , etched	ρ_1 , unmodified	20	-0.026	0.90 ††	7/15/77
ρ_1 , etched	ρ_2 , unmodified	20	0.27	0.06 †	7/15/77
ρ_2 , etched	ρ_1 , unmodified	20	0.13	0.23 †	7/15/77
<i>Pygospio elegans</i>					
ρ_1 , etched	ρ_2 , unmodified	10	-0.38	0.16 ††	7/15/77
ρ_2 , etched	ρ_1 , unmodified	11	-0.15	0.58 ††	7/15/77
ρ_1 , etched	ρ_2 , unmodified	5	0.30	0.32 †	7/15/77
ρ_2 , etched	ρ_1 , unmodified	12	-0.35	0.06 †	7/15/77

gut. Given selection for ρ_1 beads, a higher proportion of ρ_1 beads might be expected to occur in the hindgut versus the foregut, giving, in effect, a time-lapse record of depletion and making the hindgut proportions the most reliable in estimating the strength of the selection (electivity). Precisely the opposite occurred: a relatively higher proportion of ρ_1 beads was found in the foregut for both the April experiments (Fig. 5). Rather than indicating local depletion of the favored particle type, these results suggest a sorting mechanism in the gut.

Hanson (1948), in a study of the musculature of the alimentary canal in serpulid and sabellid polychaetes, observed that cilia in the ventral groove of the gut beat toward the posterior of the animal but that muscles outside the sinus, contracting antiperistaltically, tend to hinder the transport of gut contents toward the anus. Dales (1955), in a study of terebellid polychaetes (closely related to ampharetids), also

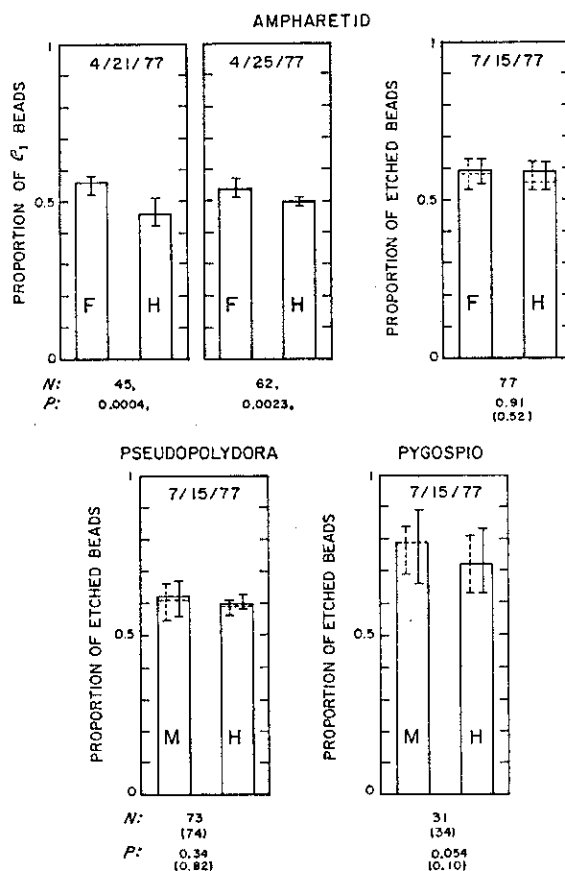


Figure 5. Median foregut (F), midgut (M), and hindgut (H) proportions from April and July experiments; error bars: 96% nonparametric confidence limits of medians; P : two-tailed Wilcoxon signed-rank probability that paired foregut and hindgut proportions (ampharetid) or paired midgut and hindgut proportions (spionids) were drawn from distributions having the same median; N : number of animals examined; dashed lines and parenthetical probability: based on discrimination of etching *per se*; solid lines: based on more reliable immersion method.

found antiperistalsis in the foreintestine (midgut) region and suggested that, "the ciliary gutter may be of use in rapidly removing indigestible material from the site of absorption." The internal morphology of the ampharetid has not been described, but it does exhibit antiperistalsis and has a ciliated ventral gutter (personal observations). Particles of higher specific gravity might thus be moved selectively toward the posterior of the ampharetid while less dense particles could be retained in the midgut by antiperistalsis. Such a mechanism is in accord with the observations; ρ_1 particles are more concentrated in the foregut of the ampharetid than in the hindgut,

but no selection ($P > 0.05$) along the gut is detected with respect to surface etching, either in the ampharetid or in the spionids (Fig. 5).

Dales (1955, quoted above) neatly summarized the advantage of a gut sorting mechanism to the organism, but the consequent problems in studying selection by deposit feeders deserve underlining. For those organisms capable of sorting in the gut, analysis of total gut contents will not give a reliable indication of selective ingestion. Indigestible particles having long residence times in the gut will show high concentrations in the total gut contents as compared to their respective proportions immediately upon ingestion (Gaare *et al.*, 1977; Peterson and Bradley, 1978).

We are currently investigating the mechanisms which result in the selection patterns documented above. Specifically, we are testing the hypothesis that selection for specific gravity and surface texture in tentaculate deposit feeders is a mechanical process which can be understood by separating the acts of particle capture and handling. Capture (or entrainment) is basically an incipient sediment motion problem for a deposit feeder. The organism may entrain a grain mechanically (e.g., by dabbing it with a mucus-coated appendage) or hydraulically (e.g., by the siphoning mechanism of tellinid bivalves). The ampharetid and the two spionids appear to use a combination of these two modes, apparently picking up some particles with muscular movement and mucus and entraining others with the currents produced by tentacular cilia. We conjecture that less dense (closer to the specific gravity of the ambient seawater) and rougher particles are the more readily picked up by the muscle-mucus method and that less dense particles are the more easily entrained by the cilia-produced flows. Support for the latter supposition comes from recent observations on echiuran feeding. Jaccarini and Schembri (1977) suggest that nutrient-rich organic particles are more easily entrained by *Bonellia viridis* than are mineral grains. Crustacean deposit feeders (e.g., some mysids) which utilize feeding currents for particle entrainment are also likely to be more successful in capturing less dense particles.

Handling in tentacle feeders is usually done with the appendages held above the bed. Contrary to intuition, tentacle feeders with grooved appendages (e.g., spionid polychaetes) often hold their appendages with the grooved, heavily ciliated surfaces facing the sediment. This posture makes good sense as a method for allowing those particles of high specific gravity (relative to seawater) to drop back to the bed. Shear forces applied to the particles on the appendages by ambient flows would control the efficiency of this sorting, and these shear forces are sometimes augmented by muscular flailing of the feeding tentacles. *Pygospio elegans* frequently exhibits such flailing, perhaps explaining its deficit of smooth-surfaced beads relative to *Pseudopolydora kempji japonica* or to the ampharetid (Fig. 4). In tellinids (e.g., Hughes, 1975), however, these sorting flows are generated exclusively by the animal itself and are isolated by the shell from the ambient flow regime. It is tempting to speculate that this homeostatic and presumably energetically expensive, internal (to the

shell) sorting mechanism best adapts tellinids to high-food environments of variable flow velocities. Sorting on the basis of specific gravity is also likely to occur as particles are passed from appendage to appendage in deposit-feeding crustaceans. The selection that has already gone on during capture and handling may in part explain the composition of the tube of some polychaetes; we suggest that this pre-selection may explain the enigmatic observation of Featherstone and Risk (1977) that worm tubes are often depauperate in heavy minerals. Where particular shapes are required, however, heavier minerals may be preferentially incorporated (e.g., in *Owenia*, where the careful selection of flat grains is required to maintain the flexibility of the imbricated tube; Fager, 1964).

4. Conclusions

Through field experiments with glass beads, an ampharetid polychaete, and two species of spionid polychaetes, we have demonstrated the following:

- (1) The ampharetid selectively ingests particles on the basis of specific gravity.
- (2) All three species selectively ingest particles on the basis of surface texture.
- (3) The degree of selectivity for specific gravity by the ampharetid is dependent upon form size.
- (4) Sorting of particles according to specific gravity also takes place in the gut of the ampharetid (particles of higher specific gravity apparently having shorter gut residence times), invalidating analysis of bulk gut contents in evaluating selective ingestion.

Although allusions to such abilities have been made in the deposit feeding literature and comparable capacities have been demonstrated in suspension feeders (e.g., Bernard, 1974), recent efforts in evaluating deposit feeder selectivity have focused on particle size. Our results suggest that particle specific gravity, particle surface texture, and other particle characteristics are likely to be important parameters in accurately evaluating the resources utilized by deposit feeders.

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