

Adhesive-based selection by a tentacle-feeding polychaete for particle size, shape and bacterial coating in silt and sand

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ABSTRACT

We tested particle selection by a surface deposit-feeding, tentaculate spionid polychaete, *Pseudopolydora kempj japonica* Imajima and Hartman. In experiments with peroxide-cleaned, size-graded but otherwise natural silts and sands, individual worms showed peak preference for particles 80–99 μm in diameter, compared with previous (Self and Jumars, 1988) documentation of peak preference for particles of 7 μm in experiments conducted with plastic and glass beads. These results imply that microtektites will not in general be good tracers of mixing of mineral grains of comparable size. Animals exhibited statistically significant but not marked differences in size selectivity for subrounded versus subangular grain shapes; the size preference peak was broader in subangular grains, for which orientation of the grain can alter probabilities of both contact and retention. When one size class of grains was coated with the bacterium *Halomonas halodurans* (ATCC 29686), animals in general showed enhanced selection (relative to controls with no food value on any size class) of that size and smaller grains, even though these smaller grains lacked food value. Greatest selection, however, generally occurred for the coated size class. Results from inclusion of glass beads in some of the experiments and from separate experiments with tentacle analogs imply that this selective capability may be largely passive and mechanical. Natural grains, due to surface texture, have more surface area for adhesive contact than do smooth glass beads so that larger grains than beads are retained. Bacteria-coated grains, in turn, appear to be picked up preferentially due to adhesion with the bacterial coating; petroleum jelly-coated microscope slides also succeed in selective retention of the size class that is bacterially coated. Substantial selection by adhesive-utilizing deposit feeders apparently can be achieved without investment in complex, time- and energy-consuming sensory systems and behaviors. Experiments with natural grains showed notably more scatter than prior experiments with glass beads, but this difference is consistent with the mechanism. For nonspherical particles, both contact and retention depend on orientation as well as size.

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1. Introduction

Several studies have used glass and plastic beads in place of sediments to evaluate the selective abilities of deposit feeders (e.g., Self and Jumars, 1988). Simplicity and high precision have been the two primary reasons for resorting to smooth spheres. The size of a sphere is clearly defined by a single length dimension, whereas the size of natural sedimentary grains requires something more for accurate description. Beads are available in closely graded sizes and very uniform specific gravities, making choice experiments easy to set up and evaluate in the context of preference for one size or specific gravity of sphere over another. Although experiments with spheres have been useful in identifying mechanisms and in providing a means for careful control of biochemical treatments with restricted ranges of mechanical properties (e.g., Taghon and Jumars, 1984), they are undeniably difficult to place in the context of selection by deposit feeders for various types and sizes of natural sediment grains.

Concern regarding potential artifacts continues to be voiced in proposal and manuscript reviews involving experiments with clean, smooth-surfaced glass beads. That concern is well founded. One of us (P.A.J.), for example, has watched individuals of *Tanais* sp. from the Skagit intertidal sand flat of northern Puget Sound, Washington, spend literally hours in vain attempts to pick up spherical glass beads in their chelae for tube construction when no natural particles are available. With deposit feeders using adhesive mechanisms for particle entrainment (Jumars *et al.*, 1982) or with animals that have a scoop or sieve for particle retention (Miller, 1984), artifacts are not as blatant, yet they are present. The goal of the present paper is to assess size and shape selectivity on variously manipulated natural sediments for one deposit feeder, *Pseudopolydora kempji japonica* Imajima and Hartman, whose selective capabilities have been explored via plastic and glass beads (Self and Jumars, 1988). The manipulations involved grading by size to allow comparison of beads and sediments of similar size classes, classification of particles by shape to evaluate the role of shape in selection and culture of bacteria on individual grain-size classes to see whether selection was exhibited for food-coated grains.

We predicted *a priori* that natural grains of a given size class and specific gravity would be more easily retained by an adhesive mechanism than would glass spheres. This prediction arises from our earlier model (Jumars *et al.*, 1982) suggesting that adhesive failure results when there is too much submerged grain weight per unit of surface area contacted by adhesive. Because of their surface texture, natural grains present more surface area for contact at the molecular scale of the adhesive, and chemically roughened spheres are retained preferentially (Self and Jumars, 1978). This prediction translates into a bias toward smaller beads showing the same preference level as larger natural grains, an effect that was prominent in the data.

2. Materials and methods

a. Collection site

Adult *Pseudopolydora kempji japonica* (250–270 μm prostomium width), and sediments (500- μm mesh sieved) immediately surrounding the worms were collected at low

tide from the upper intertidal sand flats of False Bay, San Juan Island, Washington (48° 29' N, 123° 04' W). Collected materials were brought to the University of Washington's Friday Harbor Laboratories, San Juan Islands. All of the feeding experiments were conducted in an indoor water table with continuous flow of fresh seawater.

b. Sediment preparation and sample analysis

Sediments collected from False Bay were washed thoroughly in fresh water and were soaked overnight in 30% hydrogen peroxide solution to remove the organic matter associated with the sand grains (i.e., mucus, microbes, diatoms and other organic debris). The cleaned sediments were sieved (NitexTM mesh) in fresh water into 8 size classes of 18–42, 42–63, 63–80, 80–105, 105–125, 125–163, 163–202, 202–300 μm , and then oven dried at 75°F. Aliquots of the individual size classes were taken and placed in separate, well aerated, 1-liter beakers that contained filtered (0.2- μm NucleporeTM) seawater enriched with 0.1% bactopeptone and 1.0% yeast extract inoculated with the bacterium *Halomonas halodurans* (ATCC 29686; Hebert and Vreeland, 1987). The beakers were placed on top of a shaker operating at 20–25 rpm. Microbial growth was monitored using acridine orange direct counts (Hobbie *et al.*, 1977). Cultures were incubated for 8 d at room temperature to ensure that all of the particles were densely colonized by *H. halodurans*. These bacteria-coated particles are referred to here as “particles with food value” and are represented in all the figures as filled symbols. Open symbols, by contrast, represent particles with no appreciable food value.

Particle size and shape were analyzed microscopically. To determine particle size, the projected width of the grain was measured. This choice corresponds approximately with the second major axis of the particle in three dimensions. It is the dimension that corresponds most clearly to both the ability of the particle to pass through a sieve of a given mesh size and, for similar reasons, the ability of an organism to swallow the particle (confirmed by pretest, results not shown). Particle shapes were classified according to standard geologic criteria (Powers, 1953; Shepard, 1963). Although we originally classified particles into four shape categories (i.e., angular, subangular, subrounded and rounded), the results that we present cover only subangular and subrounded types. The majority of the particles were subangular (42–62%) or subrounded (38–58%). Whenever encountered, angular (0–4%) and rounded (1–5%) particles were pooled, respectively, with the subangular and subrounded particle types because they did not occur with sufficient frequency for meaningful analysis. Subrounded and subangular particles were never sorted and run separately; results are analyzed and displayed separately both for clarity and because of statistical evidence that the two were selected slightly differently by the worms.

c. Experiments with a broad spectrum of natural particles

Proportions of particles within the various size classes in the experimental particle mixtures were made approximately equal by number. Whereas natural grain-size mixtures

are approximately lognormal in size-frequency distribution, a uniform distribution affords greater statistical sensitivity in evaluating selection. Eight size classes were used in the preparation of experimental particle mixtures, but the data that we present exclude the largest size class (250–300 μm) because its proportions in the particle mixtures turned out to be 2–3 times greater than the rest of the other size classes—and yet it was ingested too rarely for reliable quantification. In the control, none of the particle size classes contained any food value. This control is an approximate natural-sediment analog of the bead experiments previously carried out with *Pseudopolydora kempii japonica* (Jumars *et al.*, 1982; Self and Jumars, 1988). In the treatments, one size class had food value (coated with *H. halodurans*), while the remaining size classes did not. Food value was placed in a different particle size class in each treatment. All of the feeding experiments under this set-up were conducted in the summer of 1986.

About 1.5 in (3.8 cm) of experimental particle mixture was poured in all of the feeding trays ($3.5 \times 4.0 \times 3.0$ in = $8.9 \times 10.2 \times 7.6$ cm), and freshly collected worms were laid on top of the mixtures. Worms were spaced to avoid any possible overlap of feeding areas. Although new tubes were built quickly (5–15 min), a number of the worms remained inside for 1 h or more without obvious feeding bouts. After 2–3 h the top 1 cm of the surface sediment near each worm was sampled with the aid of a soda straw (6 mm diam.) and the worms were sieved out of the sediment and preserved in a 5% seawater formalin solution for future gut analysis. The first (i.e., hindmost) 50–75 particles encountered in the gut of each worm and per ambient sediment sample in each experiment were classified microscopically according to size class and particle shape, and their proportions were determined. As in our prior work (Jumars *et al.*, 1982; Self and Jumars, 1988), variability in proportions found in the worms exceeded variability in ambient sediment proportions. Because spatial variation in proportions within the ambient sediments did not show systematic spatial pattern, we pooled the particles counted in ambient sediment samples. For each of the controls (no food value), 12 worms were counted. For the experiment in which food value was on the smallest size class, 11 worms were counted; for all other food-containing experiments, 9 were assayed.

d. Experiments with restricted size classes and glass beads

To answer more specific questions about the adhesive mechanism of selection, a limited number of particle size classes was used [i.e., natural particles 4–34, 63–80 and 125–163 μm long and glass beads (purchased from Cataphote Division, Ferro Corporation, Jackson, Mississippi) 4–37 and 74–105 μm in diameter]. We restricted the number of size classes to three because we could generate explicit, *a priori* hypotheses of the rank order of selection expected if worms changed adhesive strength of mucus to select the food-containing particle. In the first such experiment, only natural grains were used. The idea was to obtain clearer separation of size classes than is achieved with greater diversity of particle sizes. In the second, glass beads were included as an internal control. The idea was to reveal any change in adhesive strength of the glue as a change in retention efficiency for

larger or smaller beads. Natural grains and beads were made equal by weight and so approximately equal by volume. Bacteria were attached only to natural particles and only to the largest or smallest size class. None of the glass beads in the mixture held food value. The specific gravity of the glass beads used was 2.42, near that of quartz (2.65). Microscopic examination of the sand grains of False Bay sediment revealed on the basis of color, transparency and refractive index that 87–96% of the particles were composed of quartz material.

Unlike the previous experimental procedure (summer 1986), the worms were initially set on trays containing fresh False Bay sediments (sieved through a 500- μm mesh screen). After allowing the animals to acclimate for 2 d, surficial sediment was covered with 500- μm glass beads (1.5–2.0 cm thick) to impede feeding access to the underlying sediments. We knew from prior tests that these beads were too large for the worms to ingest. An hour later, the experimental particle mixture was laid on top of the glass beads (1.5–2.0 cm thick) as a seawater-based slurry (Self and Jumars, 1978). The top 1 cm of the surface sediment near each worm was sampled, and again little systematic spatial variation was found, so ambient size-class proportions were pooled. At the end of the feeding run (1.0–1.5 h), the worms were sieved out of the sediment and preserved in a 5% seawater formalin solution. The size and shape of the first (i.e., hindmost) 150–170 particles found in the gut of each worm and per ambient sediment sample from each experiment were determined microscopically. The increased sample size of grains was used to improve precision. We also increased the number of worms in each treatment to 20. All of the feeding experiments under this set-up were conducted in summer 1987.

e. Selectivity measures

For the food-free mixtures of cleaned sediment grains, we first quantified particle selectivity in *P. kempji japonica* as the base-ten log odds ratio (LOR):

$$LOR = \log_{10} \frac{Q_{ig} S_a}{S_g Q_{ia}}, \quad (1)$$

where Q_{ig} = proportion of the i^{th} particle size and shape class found in the gut of the animal;

S_g = proportion of the rest of the size and shape classes found in the gut of the animal;

Q_{ia} = proportion of the i^{th} particle size and shape class found in the ambient particle mixture; and,

S_a = proportion of the rest of the size and shape classes found in the ambient particle mixture.

Log odds ratios (equivalent to method 4 of Cock, 1978) were used for their well established statistical behaviors (Fleiss, 1973) and straightforward interpretation: Positive values indicate preference for the particle, negative values indicate selection against the particle,

and nonselective behavior equates with a value near zero. A log odds ratio of 1.0 indicates that a particle is taken 10 times more frequently than one would expect without selection, whereas a value of 2 indicates that it is taken 100 times more frequently. Since only 10^2 particles were counted per sample, the log odds ratio in our present application cannot exceed a range of about -2 to 2 . They were also used to allow ready comparison with our previous results for deposit feeders selecting clean glass and plastic beads (Jumars *et al.*, 1982; Self and Jumars, 1988).

For the experiments that incorporated food, we sought a means to focus more closely on particle retention rather than particle contact by appendages, as we expected most of the food effect to be in the latter. Jumars *et al.* (1982) proposed a two-step, heuristic, stochastic model describing the mechanics of particle selection in adhesive-using deposit feeders. The first step of their model involves the probability of contact $P(C_i)$ of the i^{th} particle size class by the animal's tentacles in the ambient particle mixture. They suggested based on stereological principles (Underwood, 1968; Weibel, 1963) and a simplified geometric model that this probability could be calculated as

$$P(C_i) = \frac{n_i}{\sum_1^N n_i}, \quad (2)$$

where $n_i = F(d_i) \times d_i$,

$F(d_i)$ = proportion of the i^{th} particle size class,

d_i = geometric mean size of the i^{th} particle size class and

N = the number of size classes.

In words, the formula implies that the probability of contacting a particle is related linearly to both its relative abundance and its diameter. This formula assumes constant particle shape. Because our shape differences were not extreme, we did not attempt to incorporate shape into this calculation.

The contact bias toward larger particles can be extreme and can mask subsequent steps in selection, so we attempted to remove it. If the contact model (Jumars *et al.*, 1982) is accurate and there is no active rejection or passive loss after physical contact, then one should observe a frequency (proportion) of ingestion equal to $P(C_i)$. In our calculations, $P(I_{ij})$ is the j^{th} worm's observed (proportional) gut content of the i^{th} particle size class. We define the residual retention, R_{ij} , as

$$R_{ij} = P(I_{ij}) - P(C_i). \quad (3)$$

That is, residual retention is the difference between the observed proportion and the expected proportion based on this contact model.

For several reasons we would not expect this "correction" to be accurate. It does not take into account contact biases for grains whose diameters approach the palp width (Hentschel,

1996). It also does not take into account any subsequent steps. Therefore we took the additional step of calculating the difference in residual retention between experiments and controls:

$$ED_{ij} = \text{Experimental } R_{ij} - \text{Median Control } R_i. \quad (4)$$

This “experimental difference” as a function of grain size i and experimental worm j subtracted the median residual retention for that size class over all the control worms, as there is no means to pair experimental with control worms. More subtly, ambient size class and bead proportions varied slightly between experiment and control, and these variations were suppressed through the effects of Eq. 3 separately on each of the residual retention terms in Eq. 4.

Because of the differences that we document in this paper between retention of beads and retention of sediment grains of the same nominal size, within our own results we compared only sediments with natural sediments and beads with beads, both across sizes. That is, Eq. 2–4 never combined beads and natural grains. As would be expected from the forms of Eq. 3 and 4, they tend to make the data more amenable to parametric analysis by improving fit to a normal distribution.

f. Analog model

In the process of exploring the mechanics of particle selection, Jumars *et al.* (1982) developed simplified analogs of the feeding tentacles of surface deposit feeders. Their analogs were made of standard glass microscope slides coated with two types of adhesives; two-sided adhesive tapes, and VaselineTM petroleum jelly. Using the latter analog and their method, we carried out replicates of two of the feeding experiments employed with *P. kempji japonica* in the bead and natural sediment mixtures (i.e., the control without food value and the treatment with food value on the 125–163- μm particles). The weights (metal bolts) placed on top of the glass slides while the jelly-coated side of slide was applied to the surface sediment were 95.8 (heavy pressure) or 37.5 g (light pressure). The bolts were not submersed but the petroleum jelly was fully immersed. Particles that adhered to the jelly were sampled from 10 different sites along the slides. Size classes of the particles were analyzed and their proportions, determined.

g. Statistical analysis

A diversity of parametric and nonparametric approaches (Sokal and Rohlf, 1981) was used to assess selectivity for size, shape and food value. We used analysis of variance (ANOVA) as an initial exploratory tool for testing dependence of selectivity on particle characteristics. Based on Self and Jumars (1988) and Jumars *et al.* (1982), our *a priori* prediction was that a quadratic regression would adequately describe the dependence of the animal’s preference (log odds ratio) on particle size. All tests were run and initial graphs drawn using SYSTATTM for the Macintosh, Version 5.2 (Wilkinson *et al.*, 1992). We exported figures to Adobe IllustratorTM 10 for addition of further detail and for stylistic

uniformity. Rather than present extensive text discussion of which specific differences are statistically significant, we made extensive use of notched box-and-whisker plots (McGill *et al.*, 1978) of the experimental difference, ED_{ij} (between experiment and control without bacterial coatings). The narrowed waist of the notch in such plots reveals the nonparametric 95% confidence limits for the median. When these limits do not overlap zero, the individual effect is significant, and when they do not overlap each other, selection for two grain sizes, shapes or food covers is significantly different. Nonoverlap of confidence limits is a conservative estimator of significant difference at the nominal confidence level, but the reader is warned that if many contrasts are made a correction should be implemented for multiple testing.

Case-specific nonparametric statistics were used for further hypothesis testing (Conover, 1980; Hollander and Wolfe, 1973). In particular, the selectivity pattern of the animals, expressed as the experimental difference (ED_{ij}) in the first part of the summer of 1987 experimental set-up were analyzed using a nonparametric test of predicted order (Sarris and Wilkening, 1977). We suspected that the bacteria-coated particles (**bolded**) would correspond with the highest preferences. The following explicit, *a priori* null (0) and alternative (*a*) hypotheses were tested. The alternatives are based on the hypothesis (Jumars *et al.*, 1982) that mucous adhesive or cohesive strength is adjusted by the animal to permit retention of the food-containing size fraction and that therefore any smaller particles will be retained as well:

1. with food value present in the 4–34- μm fraction,

$$H_0: \mathbf{ED}_{4-34} \leq ED_{63-80} \leq ED_{125-163},$$

$$H_a: \mathbf{ED}_{4-34} > ED_{63-80} > ED_{125-163};$$

2. with food value present in the 63–80- μm fraction,

$$H_0: \mathbf{ED}_{63-80} \leq ED_{4-34} \leq ED_{125-163},$$

$$H_a: \mathbf{ED}_{63-80} > ED_{4-34} > ED_{125-163};$$

3. with food value present in the 125–163- μm fraction,

$$H_0: \mathbf{ED}_{125-163} \leq ED_{63-80} \leq ED_{4-34}$$

$$H_a: \mathbf{ED}_{125-163} > ED_{63-80} > ED_{4-34}.$$

Since there were 3 particle size classes, there were 3! or 6 possible combinations of rank orderings. The probability that any one of the 6 combinations would occur was therefore 1/6 ($P = 0.167$), assuming that all combinations were equally likely. In each of the experiments with food value in one size class, 20 worms were analyzed. If the level of significance is set at $\alpha \leq 0.05$, by the conservative Bonferoni criterion, rejection of the null hypothesis (H_0) should be set at an α level of $0.05/20$ or ≤ 0.0025 . This test is even more conservative because the ordered ranking combination of the selectivity pattern in the alternative hypothesis in each of the experiments is strict.

Table 1. ANOVA of log odds ratios (LOR_{ij}) for the 1986 experiment with the outlier of Figure 1 removed, assuming that each size and shape class is independent within each of the 12 worms. The number of observations was reduced to 155 because those values for which the denominator of $LOR_{ij} = 0$ were not used. Numbers in parentheses use the conservative correction of decrementing the error degrees of freedom by three times the number of worms used in the experiment to account for the fact that once the proportions of six particle size classes of each shape in each worm are known, so is the seventh, and similarly once the proportion of subangular particles is determined, so is the proportion of subrounded ones.

Source	Sum of squares	Degrees of freedom	Mean square	<i>F</i> ratio	<i>P</i>
Size	4.259	6	0.710	11.22 (8.41)	<0.0001 (<0.0001)
Shape	0.007	1	0.007	0.116 (0.087)	0.73 (0.77)
Size × Shape	0.962	6	0.160	2.535 (1.902)	0.023 (0.087)
Error	8.856	141 (105)	0.0633 (0.0843)		

3. Results and discussion

a. Experiments with a broad size spectrum of uncoated, natural particles

The difficulty that we had with the largest size class (250–300 μm) left us with much smaller sample sizes (total number of grains counted) in this preliminary experiment than we had wished, and four of the ambient samples were lost. A total of 68 subrounded and 111 subangular particles were counted from the 6 ambient samples. Respective totals were 173 and 316 from the total of 12 worms. Nevertheless, with these cleaned natural particles belonging to the remaining seven size classes and two shape classes, ANOVA reveals a significant effect of particle size on LOR_{ij} (Table 1). One outlier (Fig. 1) was deleted to conform to the assumptions of ANOVA. Leaving in this outlier inflates the sum of squares for the shape effect, but it does not reach significance even then ($P = 0.58$). It has no appreciable influence on the probabilities associated with the size or shape-size interaction effects. Although the effect of shape is not significant on its own, the interaction verges on significance. Inspection of the curves (Fig. 1A, B) suggests greater selection for subrounded grains over most of the upper size range, reversing for the smallest size categories. The interaction, then, likely masks any shape effect with this sample size and design.

This ANOVA confirms our qualitative expectation with respect to particle size. Our earlier work (Jumars *et al.*, 1982; Self and Jumars, 1988) revealed preference for particles of intermediate size. Indeed, quadratic regression showed significant dependence of log odds ratio on particle size in both the subangular and subrounded grains ($P < 0.001$), with roughly equal precision (multiple $R^2 = 0.25$, $n = 73$ for the subrounded; multiple $R^2 = 0.22$, $n = 81$ for the subangular with the outlier again omitted from the calculation).

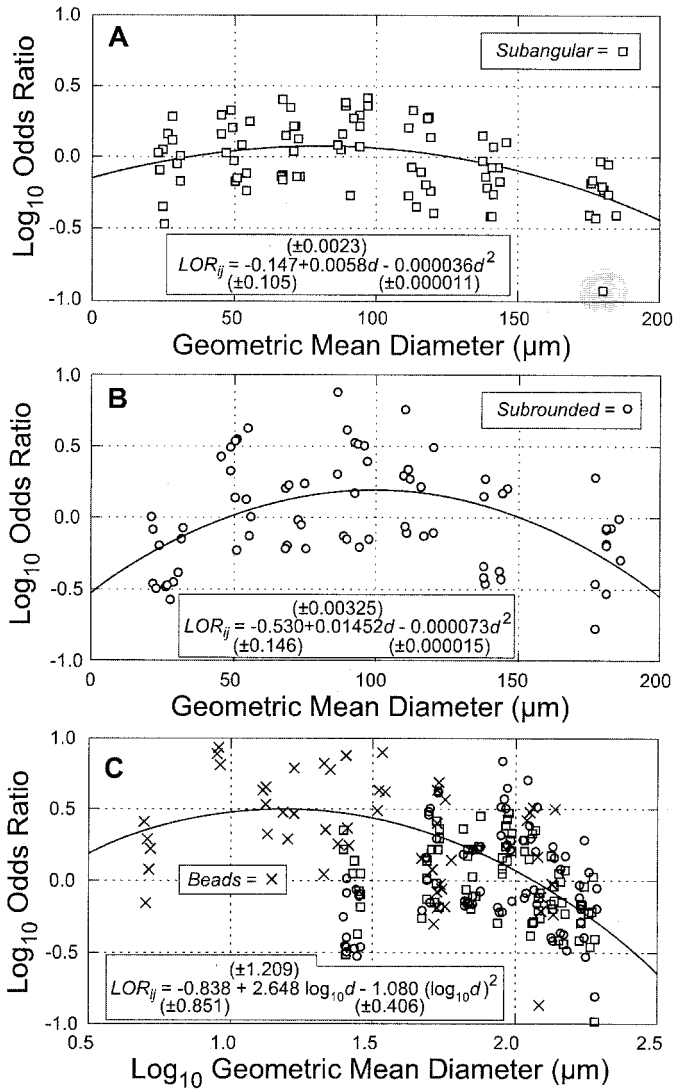


Figure 1. Log odds ratios (LOR_{ij}) versus particle size for (A) subangular and (B) subrounded sediment particles in the present experiment, with nonlinear least-squares fits to a second-order polynomial. The bottom panel (C) combines the data from A and B on a log scale for diameter with data for glass beads from Self and Jumars (1988). Those data are not corrected here for variations in specific gravity among beads or between beads and the sediments, and the curve plotted is for the beads only. Numbers in parentheses are 95% confidence limits of the vertically adjacent coefficients, and the point surrounded by a gray halo is the outlier mentioned in the text (and excluded from the regression). Note the shifting of the size of peak selection in sediments to substantially higher particle size than the peak for beads. All points are “jittered,” i.e., plotted with some variation around their geometric mean diameters (d) in order to reduce vertical overlap in plotting.

Microscopic examination for color and refractive index revealed that 86–97% of the particles were composed of quartz, supporting the assumption of uniform specific gravity.

Peak selection (Fig. 1) was at 99 μm for subrounded particles and 80 μm for subangular ones. The peaks are so broad that they cannot be located with high precision (cf. Self and Jumars, 1988). Hence the sizes at which peak values occur are not significantly different, but the curve for the subrounded particles is significantly more peaked (cf. the second-order term in each equation in Fig. 1). We suspect that the curve flattening for subangular grains is due to their less accurate description by a single grain dimension (orientation being important to both contact and retention). By contrast, however, the peak drawn for glass and plastic beads in *P. kempji japonica* is centered at 17 μm . This size is larger than the 7 μm given by Self and Jumars (1988) because in this redrawing (for simplicity) no correction is made for variations in specific gravity among the beads that they used. Even so, the peaks for natural grains are far enough from the regression equation for the glass and plastic beads that it does not fit the present data and vice versa (by comparison of regression and residual sums of squares, *F*-test $P < 0.05$). An important caveat is that grain sizes in the sieved sediments did not reach sizes as small as those of the glass beads in the earlier experiments (Self and Jumars, 1988); for that reason we could plot their data on a linear rather than logarithmic size scale.

We have no reason, however, to suspect bimodality of selection or any other complex pattern on smaller natural particles. The results agree qualitatively with the heuristic model of Jumars *et al.* (1982). The rising limb of the curve in this interpretation is due to the increase in probability of encounter with increasing particle size, while the falling limb is due to adhesive failure or insufficient tensile strength of the adhesive to retain a contacted particle that is heavy. Failure sets in at a smaller particle diameter when the particle is a smooth sphere rather than a natural grain, suggesting strength of adhesion rather than tensile strength as the weak link. This roughness effect was demonstrated previously by Self and Jumars (1978), who etched beads to make their surfaces rougher. We hesitate to pursue further quantitative comparison between selection for beads in their study versus natural grains, however, because the experimental designs with beads differed substantially from ours. Self and Jumars (1988) used equal volumes of beads and commercially prepared (highly angular) sand, with the bead volume comprising equal numbers of beads of two sizes. For *P. kempji japonica*, one of these beads as an internal control was always of 88 μm diameter and a specific gravity of 2.42, and the other bead size and specific gravity varied among independent experiments. Moreover, we cannot assert that our results apply quantitatively to fully natural sediments because we cleaned the grains of their natural coatings.

Despite these caveats, it is evident that natural grains show greater inherent variability in selection. Although we do not dispute that some other experimental design might reduce unexplained variance, variability in grain shape and orientation must add to variability in both contact and retention. Thus at least some of the variability that we portray must be real

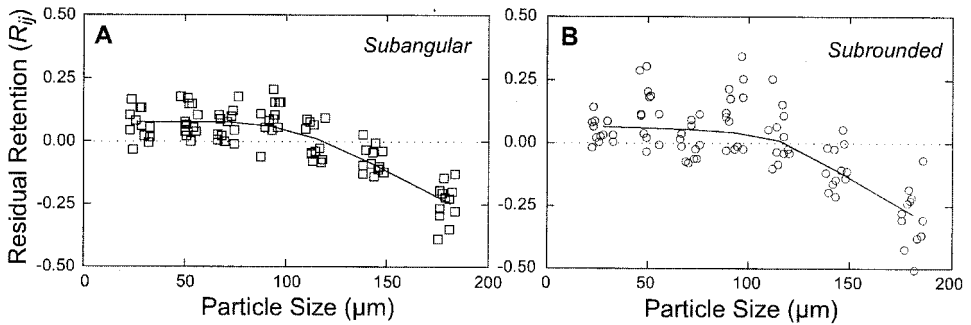


Figure 2. Residual retention (R_{ij}) versus particle size for (A) subangular and (B) subrounded particles. Solid curves are LOWESS smoothings (Cleveland, 1979). The flat-lying limb of the curve is consistent with uniform retention of beads below the size for which peak preference is shown (Fig. 1), and the falling limb indicates only partial retention of beads above that peak size. All points are “jittered,” i.e., plotted with some variation around their geometric mean diameters (d) in order to reduce vertical overlap in plotting.

and is a factor supporting the observation of (only) partial preference for particles of any given size class.

Microtektites are sometimes used as tracers of bioturbation (e.g., Ruddiman *et al.*, 1980). Our results suggest that they will not in general be handled similarly to mineral grains of similar size. If our results generalize to other adhesion-utilizing deposit feeders and to natural grains, then very small microtektites as analogs of glass beads likely will be ingested more frequently by surface deposit feeders than are mineral grains in the same size category (Fig. 1C) and so would be buried more slowly. Small differences in selectivity can produce substantial effects over multiple ingestion events (cf. Jumars *et al.*, 1981; Shull 2001).

Qualitatively, residual retention curves (Fig. 2) also conform to the shapes anticipated from the two-step (contact plus retention given contact) mechanical model of Jumars *et al.* (1982). If the model fit perfectly and the glue were strong enough to retain all particles smaller than some threshold size, however, one would expect all particles smaller than that threshold to show zero residual retention (i.e., to be picked up if contacted). The data suggest a minor bias toward slightly more frequent contact of small particles than Eq. 2 predicts. This offset could be due to details of the geometries of the grains, of grain packing, of the tentacle or of its mucous coating. We were unable to detect significant differences in selection between angular and subangular grains by ANOVA on the control worms (Table 1), but the sample size is quite small (12 worms) and the shape differences, rather subtle.

b. Experiments with a broad size spectrum and bacterial coatings

We therefore repeated ANOVA also for the treatments (Table 2), where we had a total of 65 worms, to pursue the shape issue further as well as for our primary aim of testing the

Table 2. ANOVA of residual retention (R_{ij}) results for the 1986 experiment (food value on one grain size). Each worm ($n = 65$) was assumed to act independently. Numbers in parentheses use the conservative correction of decrementing the error degrees of freedom by twice the number of worms used in the experiment to account for the fact that once the proportions of six particle size classes of each shape in each worm are known, so is the seventh, and similarly once the proportion of subangular particles is determined, so is the proportion of subrounded ones.

Source	Sum of squares	Degrees of freedom	Mean square	<i>F</i> ratio	<i>P</i>
Size	29.6	6	4.93	41.5 (30.7)	<0.0001 (<0.0001)
Food	4.41	1	4.41	37.2 (27.5)	<0.0001 (<0.0001)
Shape	3.48	1	3.48	29.4 (21.7)	<0.0001 (<0.0001)
Size × Shape	6.82	6	1.14	9.58 (7.07)	<0.0001 (<0.0001)
Food × Shape	0.678	1	0.678	5.72 (4.22)	0.017 (0.040)
Size × Food	3.69	6	0.615	5.19 (3.83)	<0.0001 (0.00095)
Size × Food × Shape	1.91	6	0.319	2.69 (1.98)	0.014 (0.066)
Error	88.243	744 (549)	0.119 (0.161)		

effect of the food addition to one size category. We had proposed (Jumars *et al.*, 1982) that adhesive-using deposit feeders might achieve selection for a particular size fraction that contains food by altering the strength of their adhesives; a stronger adhesive will shift the peak of selection toward a larger grain size. A stronger adhesive sufficient to retain the food-containing particle will also increase or leave unchanged selection for particles smaller than those at the peak. Conversely, weakening the adhesive will shift selection toward smaller grains sizes.

Size, bacterial coating, shape, and the size-food and size-shape interactions all reach unquestionable statistical significance, even if we conservatively remove 195 degrees of freedom. Doing so would account for the fact that after all but one of the size categories are measured in each worm its proportion already is known by difference, and likewise once the fraction in one shape category is known, so is the fraction in the other. Significance levels of the food-shape and the three-way interaction become borderline, however. The effect of coatings on selection drops with increasing grain size, explaining at least part of the size-food interaction (Fig. 3). There also is a significant trend in subangular grains of Figure 3 toward enhanced selection of uncoated grains sizes smaller than the coated one (15/21 cases, binomial $P = 0.039$ one tailed), as per the idea that adhesives may be strengthened when larger grains are food coated. This trend, however, is not apparent for

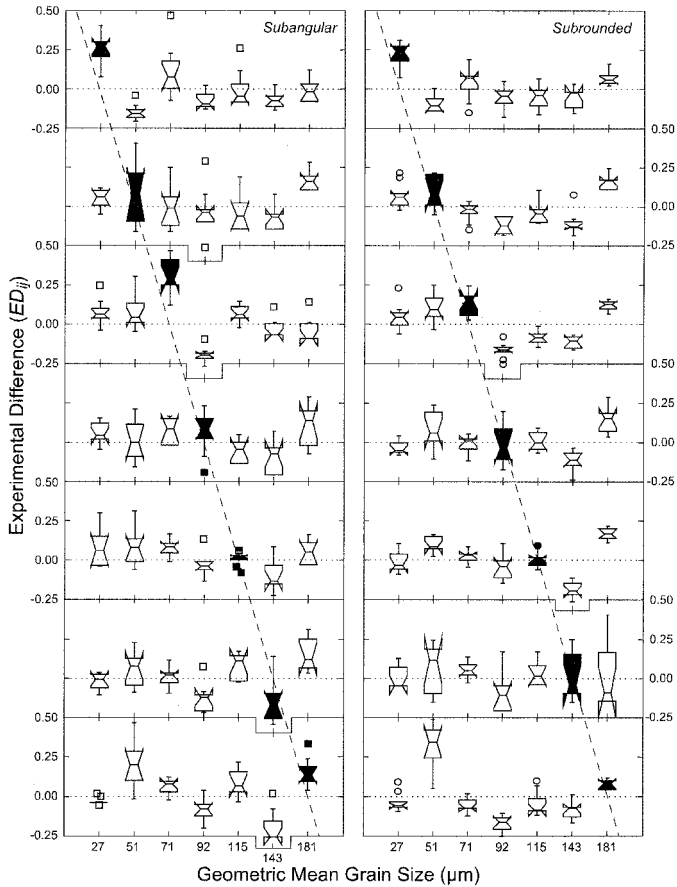


Figure 3. Notched box-and-whiskerplots (McGill *et al.*, 1978) of the experimental difference, ED_{ij} (between experiment and control without bacterial coatings) versus geometric mean grain size for subangular (left panels) and subrounded (right panels) grains for the 1986 data. “Jogs” in the abscissa keep points in the panel where they belong. Units on the ordinate alternate from the left side to the right of the figure to avoid ambiguity, as the appropriate unit differs between vertically adjacent panels where the panels meet. Filled symbols indicate the size class that was bacterially coated in the experiment, the narrowed waist of the “notch” spans the 95% confidence limits of the median, and the “bel” at the waist is that median. The longest horizontal lines in each symbol mark the 25th and 75th percentiles of the sample, and the isolated circles and squares are outliers > 1.5 times the interquartile range away from the top or the bottom of the box. Dashed lines indicate the slope expected if ED_{ij} stayed constant from one grain size to the next as the coated grain size shifts upward. They are drawn through the position of zero experimental difference so that one can see that the treatment effect (filled symbols) does not stay constant, but decreases for larger grains. Grain size is plotted ordinally to allow interpretation of this slope and to space the symbols horizontally; equal distances along the abscissa are not equal differences in size.

subrounded grains. Subangular grains will have more surface area than subrounded ones, even when the volumes of the particles are kept the same. In adhesion, however, contact area is key, and the subangular grains will on average have a smaller radius of curvature, which on average may lead to a smaller contact area. Conversely, they also have more grain surfaces that are flat, and so might present good attachment surfaces despite this argument about average curvature. An interesting second-order effect is the newly discovered tendency of less spherical particles to pack more tightly (Donev *et al.*, 2004), potentially influencing contact probabilities. Because we measured the second major axis, our subangular grains probably have more volume and weight than our angular grains of the same nominal size. Bacteria-coated grains may further compound the difficulty of lifting them by adhering to adjacent grains, a problem that should become more severe as particles approach a size that causes failure of retention. Comparison of the displacement of the filled symbols from the dashed lines of Figure 3 shows a diminishing effect of bacterial coating as grain size increases, likely caused by such adhesive failure.

The smallest grains were eaten in the experiments to a greater extent than in the controls when food-coated grains were smaller than 92 μm (Fig. 3), and in subangular grains this effect extended to food-coated grain sizes of 115 μm . We suspect that at least some of this effect comes from adhesion of the smallest grains to the bacterially coated ones.

Although the data demonstrate that *P. kempfi japonica* succeeds for most combinations of grain sizes and shapes in ingesting selectively the bacteria-covered grain size (Fig. 3), they are ambiguous in their support of adjusted adhesive strength as the mechanism responsible. Consistent with such adjustment is the frequent selection of smaller grains in addition to the food-containing size class. This phenomenon appears rarer when larger grain sizes contain bacteria, but this rarity may be artifactual. Selection of one grain size must be at the expense of other grain sizes. Therefore, as food value gets shifted further up to the larger size classes, it becomes less likely and eventually impossible to observe a positive experimental difference on all of the size classes below the one that contains food.

Moreover, the bacterial stickiness argument and the tentacle mucus adjustment mechanism are neither mutually exclusive nor exhaustive explanations of the results. Another possibility is that the animal uses chemosensory cilia on its tentacles (Dauer *et al.*, 1981; Jumars *et al.*, 1982) to locate randomly produced concentrations of the food-rich size fraction, spending more time feeding there. J. Grebmeier (personal communication) has performed experiments showing that when only one-half of the feeding circle contains food value *P. kempfi japonica* spends the majority of its time with palps in that sector. Chemosensing also changes the way that palps are deployed and the intensity of feeding (Ferner and Jumars, 1999). A further alternative is chemical sensing after the grains are entrained, with selection accomplished via post-capture rejection. Although we have on occasion observed *P. kempfi japonica* to reject individual grains, post-capture rejection is rare in this species and usually is directed at groups of grains on one palp, where it is accomplished simply by reversing the ciliary beat and running the bolus off the distal end of the palp. Our extensive qualitative observations showed no indication that size-selective

post-capture rejection occurred. Other spionid species (Dauer *et al.*, 1981; Shimeta and Koehl, 1997; Self and Jumars, personal observations) may exhibit considerably more post-capture rejection.

c. Experiments with restricted size classes and glass beads

We next repeated the initial experiment with sediment comprising only three, nonoverlapping size classes (4–34, 63–80 and 125–163 μm). This simplified grain-size array also allowed us to suggest *a priori* a strict ordering of particle size preference that would be expected if adhesive strength were adjusted as the mechanism for achieving selection (cf. “Methods and Materials”). With the food value in small beads, one would expect a weak mucus incapable of retaining large and most medium particles. With the food value in the medium grain size, the glue should be strong enough to hold both medium and small particles, but the former should be encountered more frequently due to their larger size. With the food value in the largest size class, the glue must be strong enough to retain all sizes, so the order of preference should be based strictly on encounter frequency.

The results of this analysis in general (Table 3 and Fig. 4) support the *a priori* alternatives, although they also would support some other interpretations (the *a posteriori* alternatives of Table 3). Only in the case of food value on medium-sized, subrounded grains does the *P* value fall short of our conservative rejection criterion. Once again ANOVA results show significant effects of food value and size on particle selection, but in this case no significant effect of shape (analysis not shown).

As a further test we included glass beads of two sizes in a supplemental experiment. The treatments included no food value in any size class, food value in only the smallest and food value in only the largest. Because of the small effect of shape in earlier results, and in order to increase the power of the test by including more particles, we chose to drop the shape distinction for this experiment. Shifting food value to the largest size class should shift selection toward the larger glass beads if this selection is accomplished purely by changing strength of the adhesive. We saw the expected effects of food value on selection of the coated grains (Fig. 5). Although there were significant differences in residual retention of the small glass beads and the large glass beads (Wilcoxon signed ranks test, $P < 0.05$) between each pair of the three treatments, the direction of those shifts (Fig. 5) is not consistent with the idea that the animal is changing its mucus strength to achieve selection for the food-coated size class. Rather, the small but significant differences are most likely due to the adhesive effects of the bacterial coating itself. The fewest small beads are retained in the absence of any bacterial coatings. When the smaller grains are coated with bacteria, a few small glass beads apparently are trapped in the bacterial matrix. Because we kept number of particles per unit of volume constant, the treatment including larger coated grains also included more bacterial exopolymer, and the most small grains were brought along when large grains were ingested preferentially in that treatment. Selection of larger beads is the mirror image of these results with small grains simply because increased selection of small beads is at the expense of large beads.

Table 3. Nonparametric test of predicted order (Sarris and Wilkening, 1977) on the particle selectivity pattern of *P. kempji japonica* in the summer 1987 experiments with shifting food value. S, M and L stand, respectively for the small, medium and large particles. Subscripts are 0 for null hypotheses and *a* for alternatives. Primes (apostrophes) denote *a posteriori* hypotheses of interest upon inspection of the results. Because of multiple testing, only $P < 0.0025$ can be considered significant at an overall α level of 0.05 (cf. "Materials and Methods").

Bacterially coated size range (μm)	Shape	Hypotheses	<i>P</i>
4–34 = S	Subangular	$H_0: S \leq M \leq L$ $H_a: S > M > L$	<0.0001
		$H'_0: S \leq L \leq M$ $H'_a: S > L > M$	0.054
	Subrounded	$H_0: S \leq M \leq L$ $H_a: S > M > L$	0.0014
		$H'_0: S \leq L \leq M$ $H'_a: S > L > M$	0.0003
63–80 = M	Subangular	$H_0: M \leq S \leq L$ $H_a: M > S > L$	0.0014
		$H'_0: M \leq L \leq S$ $H'_a: M > L > S$	0.0014
	Subrounded	$H_0: M \leq S \leq L$ $H_a: M > S > L$	0.054
		$H'_0: M \leq L \leq S$ $H'_a: M > L > S$	0.0014
125–163 = L	Subangular	$H_0: L \leq M \leq S$ $H_a: L > M > S$	<0.0001
		$H_0: L \leq M \leq S$ $H_a: L > M > S$	<0.0001
	Subrounded	$H'_0: L \leq S \leq M$ $H'_a: L > S > M$	0.0014

d. Analog model

Results with the analog model (Fig. 6) confirm an effect of the bacterial coating on adhesive properties of grains. A larger force applied to the glass slide reduces the effect of the bacterial adhesive on particle selection because the petroleum jelly coating penetrates the bed further and is very efficient at retaining grains (cf. Jumars *et al.*, 1982). A very thick coating and a heavy pressure (causing the jelly to penetrate the surficial layer of grains) should act to reduce or eliminate bias toward more frequent contact of larger particles. We do not mean to imply a good match between petroleum jelly and the natural adhesives used by *P. kempji japonica*. Rather, this analog experiment serves to demonstrate that surface

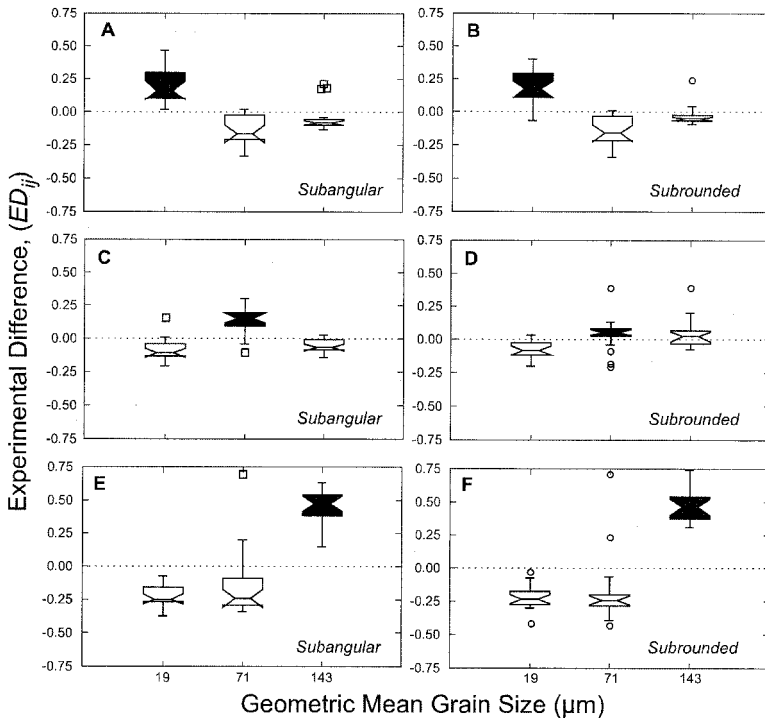


Figure 4. Notched box-and-whisker plots (McGill *et al.*, 1978; see caption of Fig. 3 herein) of the experimental difference, ED_{ij} (between experiment and control without bacterial coatings) versus geometric mean grain size for subangular (left panels), and subrounded (right panels) grains for the 1987 data. Filled symbols indicate the size class that was bacterially coated in the experiment. In each case the worms succeeded in selecting significantly more of the coated grains. Grain size is plotted ordinally in order to space out the symbols.

properties of the particles can affect retention without any active behavioral control on the part of the animal. The fact that the direction of the effect is the same for petroleum jelly and for the animal does suggest, however, that hydrophobic surface interactions may also be involved in the animal's selection ability, as has been observed in the mole crab, *Emerita talpoida* (Conova, 1999).

e. Broader implications

The most parsimonious explanation of our results is that the strength of the adhesive secreted on the palps stays fixed. We warn the reader, however, that our absence of convincing evidence of an adjustment in adhesive strength cannot be taken as evidence of absence of this capability either in this species under other circumstances or in other species. Our results clearly reveal a role of bacterial coatings in affecting the probability of adhesive retention by *P. kempii japonica*. They thus suggest that choice of larger particles

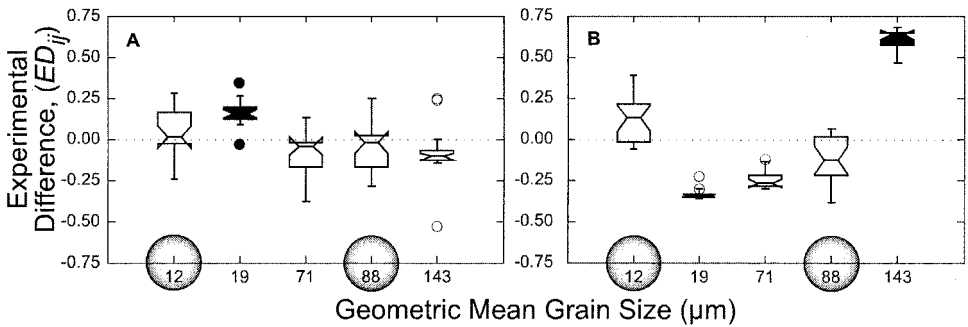


Figure 5. Notched box-and-whisker plots (McGill *et al.*, 1978; see caption of Fig. 3 herein) of the experimental difference, ED_{ij} (between experiment and control without bacterial coatings) versus geometric mean grain size for a mixture of three grain sizes and two sizes of glass beads (the latter indicated by circles on the abscissa). Unlike previous plots, grain shapes were combined to increase statistical power of the analysis of these separate 1987 experiments. Filled symbols indicate the size class that was bacterially coated in each experiment (A, 19 μm ; B, 143 μm). If selection for coated grains was achieved by change in adhesive or tensile strength of the mucus, one would expect a shift from A to B toward greater selection of the 88- μm beads, but no such shift was observed.

by *Pectinaria gouldii* (Whitlatch, 1974; Whitlatch and Weinberg, 1982) may be explained either by improved retention of organically coated grains or by the presence of a very strong adhesive on the animal's tentacles (or, more likely by evolutionary convergence of the two mechanisms). Several of the instances of selection demonstrated by Taghon (1982) may also have been effected through improved adhesion to protein-coated glass beads versus clean ones. If worms simply ingest most of the retained particles, this improved retention could also explain at least part of the greater feeding rate observed on coated beads (Taghon and Jumars, 1984). A broad diversity of deposit feeders, including polychaetes, hydrobiid snails, protobranch bivalves, echiurans, sipunculans, holothuroids, echinoids, asteroids and enteropneusts uses adhesive means of particle collection and thus may have similar interactions with food-coated particles.

Our results, however, complicate the issue of size dependence of selection in natural sediments. Because we cleaned our sediments, Fig. 1A, B cannot be considered representative of size selection on natural sediments. If most natural coatings provide greater adhesion to the tentacle, then peak selection on natural grains will be shifted to even greater grain sizes than we observed for cleaned grains. Although we focus on mechanical issues, we do not deny the added value of chemosensory-mediated behaviors. Tentacles with a large aspect ratio (length/width cf. Ohta, 1984) provide an additional advantage in enabling worms to spend a greater fraction of their time feeding in locally enriched zones (well above grain scale) like those in the immediate vicinity of an animal tube under flow (Eckman and Nowell, 1984). Sticky appendages provide excellent means of rapid particle collection with moderate to strong bias toward food-containing fractions. The mechanism

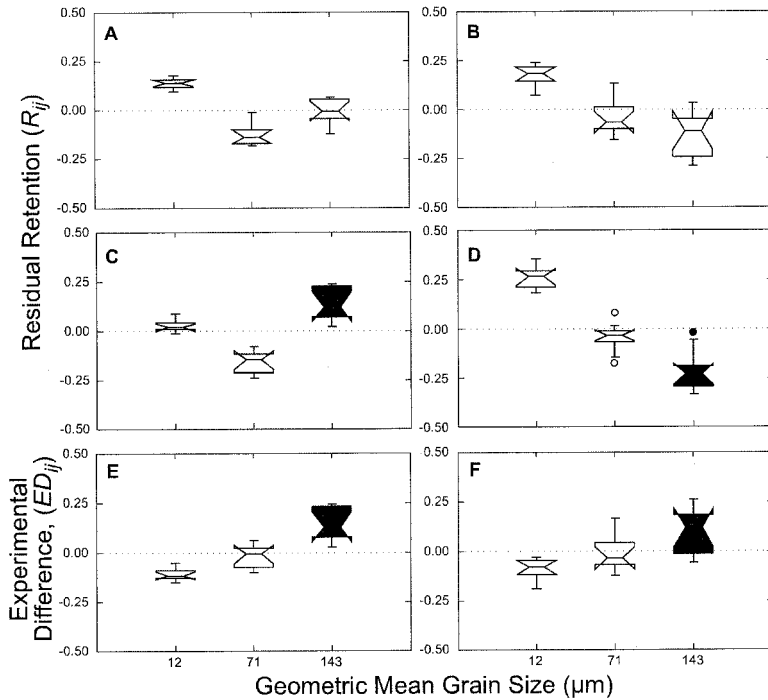


Figure 6. Notched box-and-whisker plots (McGill *et al.*, 1978; see caption of Fig. 3 herein) of the residual retention (R_{ij}) and experimental difference, ED_{ij} (between experiment and control without bacterial coatings), versus geometric mean grain size for a mixture of three grain sizes. Filled symbols indicate the size class that was bacterially coated (143 μm only). Left panels (A, C, D) are for the light weight, and right panels (B, D, F) for the heavy weight. A and B are controls without coatings, whereas C and D are their respective experimental contrasts, and E and F, respectively show the differences between the experiments and the medians of their respective controls. Unlike some previous plots, grain shapes were combined to increase the power of the analysis of these separate 1987 experiments, and these analog experiments were done with petroleum jelly-coated microscope slides set on the sediments with either light (left panels) or heavy (right panels) weights applied. Note the consistent selection by this hydrophobic adhesive for the bacterially coated grains (E, F) and decrease in selection for larger grains (A vs. B and C vs. D) when greater weight is applied.

is consistent with the rapid feeding rates and partial preference (Stephens and Krebs, 1986) seen in most deposit feeders (Jumars, 1993). The high scatter in selection on particles of natural shape, due to variation in both contact and retention that arises from variation in orientation, is surely an underlying reason for partial preference in deposit feeders.

Primary conclusions from our experiments thus are two. One is that—given equivalent specific gravity—adhesive-using deposit feeders will retain and ingest larger natural grains than glass beads. This conclusion may extend to other taxa that use adhesive mechanisms and have been studied using smooth-surfaced beads, e.g., the hydrobiids studied by

Levinton (1979). The other is that surface properties of grains provide a means for rapid mechanical selection of food-containing grains. No chemosensory evaluation of single grains is required to explain our results, and the particle-collecting machinery is elegantly biased toward collecting grains of high food value.

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