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Cross-phyletic patterns of particle selection by deposit feeders

by Robert F. L. Self[1] and Peter A. Jumars[1]

ABSTRACT

In controlled laboratory experiments using a wide array of exotic sediments of known characteristics (glass and plastic beads) we studied the mechanical, evolutionarily-fixed component of particle selection for ingestion in 5 surface and 6 subsurface deposit feeders, from 3 phyla (Annelida, Mollusca and Arthropoda). Three species were nonselective within all or part of the 3-324 μm particle size range tested, while the remaining 8 species exhibited unimodal patterns of size selection, peaking near 6 μm. In addition, the surface deposit feeders displayed a strong preference for particles of low specific gravity. Particle selection in tube construction by the polychaetes followed similar but weaker trends. Initial particle gathering into the mantle cavities of the bivalves by inertial suction or adhesion to mucus-covered appendages appeared nonselective.

1. Introduction

Iteration between theory and observation is the surest way to advance scientific understanding (Box, 1976). A major but rarely articulated stumbling block to gaining such understanding of deposit feeding is the difficulty in resolving those aspects of the process that are fixed evolutionarily from those that are under behavioral control. Extant foraging theory applies only to the latter; it is nonsensical to predict and test what an individual ought to do, if that behavior either lies beyond its abilities or has no alternative (cf. assumptions underlying optimal foraging, Townsend and Hughes, 1981, p. 107). Theories directed specifically at what deposit feeders do or should do (Levinton and Lopez, 1977; Taghon *et al.,* 1978; Cammen, 1980; Taghon, 1981; Miller *et al.,* 1984; Penry and Jumars, 1987) have focussed primarily on particle selection, ingestion rate and digestion. For deposit feeders in particular and microphages in general, however, the extent to which these aspects of foraging are under behavioral control is still poorly known, making interpretations of experiments and of other observations ambiguous.

Interpretation is clearest where this ambiguity has been removed in one of two ways. The most obvious means is to focus on the level of the individual and to demonstrate behavioral plasticity, for example, with respect to predictions of increasing feeding rate

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with increasing food quality (Taghon and Jumars, 1984). A less obvious way to remove the ambiguity is to make comparisons and contrasts well outside the range of behavioral plasticity of individuals, so that any such plasticity becomes weak "noise" incapable of obscuring a strong, *nonbehavioral* "signal." For example, Cammen (1980) compares feeding rate among 19 species of deposit feeders across a thousand-fold range in organic content of ingested food. Ambiguity is removed by far exceeding the range of organic content likely to be experienced by any one individual, namely by focussing on pattern among, rather than within, species. The interpretation is clear when controlled for temperature and corrected for body size: mass specific (g sediment g^{-1} of flesh) feeding rates are faster in species that have evolved on substrates of lower organic content, balancing in such a way as to provide similar rates of organic matter ingestion (g organic matter g^{-1} of flesh s^{-1}) across the entire spectrum of species and environments. Cammen's (1980) data analysis thus effectively isolates the evolution-arily-fixed, nonbehavioral component of the relation between feeding rate and sediment organic content. The two approaches together give much more information than either alone. Cammen's (1980) review gives an among-species, among-environment context in which to view and evaluate individual behaviors, but his data do not bear on individual behaviors. Taghon and Jumars' (1984) data deal expressly with individual behaviors but do not bear on patterns of organic matter intake among species and among environments.

Uncertainty about degree of behavioral flexibility is particularly acute in attempting to generalize about particle selection by deposit feeders. Experiments demonstrate the existence of some behavioral flexibility to change selective patterns among particles (Taghon, 1982), but the mechanisms of selection are mechanically complex (e.g., Jumars *et al.,* 1982; Miller, 1984), and the range of behavioral flexibility in particle selection remains questionable (Jumars *et al.,* 1982; Whitlatch and Weinberg, 1982). At particle ingestion rates of 20 Hz (Miller, 1984) or more, characteristic of deposit feeders, the degree of passive mechanical versus active behavioral selection is exceedingly difficult to resolve. Further, it is not clear to us that a literature review and summary analogous to Cammen's could be applied to shed much light on the inherently multivariate process of particle selection.

Therefore, we pursued an alternate means of obtaining among-species contrasts freed, as much as possible, from effects of individual behavioral plasticity. The approach is experimental and involves the removal of food-value differences, and hence food-value cues for selection, among the particles. Specifically, no food value was contained in the particles for which size and specific gravity selection were evaluated, but organic matter sufficient to produce ingestion was contained in the background "carrier" for these particles. What we hoped to resolve was the pattern of passive mechanical selection for particle size and specific gravity among species--the evolu-tionarily-ingrained norm from which to evaluate behavioral deviations. In a sense, this norm represents the null hypothesis against which to resolve behaviorally-based

Table 1. Array of species used in particle selection experiments.

Species	Size Measure	Median Size	Feeding Time (hr)	"Foregut" Location
Surface deposit-feeders				
Pseudopolydora kempi japonica	volume (mm³)	0.31	2.5–4	setiger 9–20 (midgut)
Hobsonia florida	volume (mm³)	0.34	1.5–3	anterior of gut diverticulum
Owenia fusiformis	volume (mm³)	16.00	6	anterior of 5th setiger
Macoma balthica	shell length (mm)	5.50	2–7	esophagus and stomach
Corophium salmonis	length of second segment of fourth pereopod (mm)	0.71	2–4	whole gut
Subsurface deposit-feeders				
Yoldia scissurata	shell length (mm)	18.00	22	esophagus
Barantolla americana	volume (mm³)	0.21	22	whole gut
Capitella cf. *capitata*	volume (mm³)	0.25	22	whole gut
Sternaspis scutata	volume (mm³)	97.00	13–26.5	esophagus
Axiothella rubrocincta	volume (mm³)	146.00	22–26.5	setiger 2–6
Abarenicola pacifica	volume (mm³)	315.00	19–21.5	setiger 2–6

selection when food value is contained in one particle type. We found a surprising degree of concordance among taxa. Despite radically different food-gathering and ingesting mechanisms, nearly all 11 species surveyed (including molluscs, polychaetes and a crustacean) demonstrated peak selectivity for particles roughly 6 µm in diameter (rather than a monotonic change in selectivity with particle size), suggesting cross-phyletic evolutionary constraints as strong and pervasive as those revealed by Cammen (1980).

2. Methods and materials

a. Species investigated. Our primary criteria for use of deposit feeders were availability and demonstrated capability for maintenance of the animal in the laboratory. A secondary consideration was comparatively small size, minimizing the volume of expensive particles needed for the numerous experimental trials per species. The surface deposit feeders studied were *Owenia fusiformis, Pseudopolydora kempi japonica, Macoma balthica, Macoma nasuta* and *Corophium salmonis*, in addition to *Hobsonia florida* (preliminary analysis of *H. florida* data reported in Jumars, *et al.*, 1982). The subsurface deposit feeders studied were *Yoldia scissurata, Sternaspis scutata, Abarenicola pacifica, Capitella* cf. *capitata, Barantolla americana*, and *Axiothella rubrocincta* (Table 1). We recognize the possibility that all of the species

classified as subsurface deposit feeders may in the field derive some of their nutritional needs from surface deposits, but food gathering and ingestion in our experiments occurred below the surface, consistent with our classification. For brevity, most original observations of polychaete feeding behavior are not cited below; we direct the interested reader to Fauchald and Jumars' (1979) review for such documentation.

Hobsonia florida is a multi-tentaculate ampharetid polychaete that occupies a robust tube and inhabits tidal sand- and mudflat, estuarine environments. Animals extend their tentacles from the tube opening and forage over a cardioid-shaped area, showing strongest selection for lighter (in weight) and smaller particles, down to a size range of roughly 14 μm, below which selectivity again decreases (Self and Jumars, 1978; Jumars *et al.,* 1982; Taghon, 1982). It shows a moderate ability to select among particles on the basis of organic coatings (Taghon, 1982), though the mechanism may be mechanical, behavioral, or a combination of both (Jumars *et al.,* 1982).

Owenia fusiformis, an oweniid polychaete, can feed on particles either from suspension or from the sediment surface. The species is a common intertidal and shallow subtidal inhabitant of sand and gravel beaches. *Owenia* has a crown of short (3 mm), frilled, ciliated tentacles with which it gathers particles for tube building and ingestion (Dales, 1957). In the surface deposit-feeding mode *O. fusiformis* extends the tentacular crown barely beyond the tube opening. Individuals bend over and pat the sediment surface with the crown, and then straighten up while particles are passed to the mouth or rejected. *O. fusiformis* is known to be strongly selective of flattened grains in its tube building (Fager, 1964), but selectivity in feeding has not been examined.

Pseudopolydora kempi japonica is a bi-tentaculate, facultatively (Taghon *et al.,* 1980) surface deposit-feeding, spionid polychaete. The animal's tube opening, from which the tentacles (palps) extend, is usually built a few millimeters above the sediment surface. The long (up to 6 cm), muscular tentacles sweep out a circular feeding area (Miller and Jumars, 1986). Particles are transported toward the mouth on the tentacles along a ciliated, mucus-covered groove. Selection has been demonstrated on the basis of particle size, specific gravity, surface texture, and organic coating (Self and Jumars, 1978; Jumars *et al.,* 1982; Taghon, 1982).

Macoma nasuta and *M. balthica* are tellinid bivalves. These species inhabit sand- or mudflat areas. They burrow below the sediment surface and feed upon surface deposits through a long, muscular siphon. Potential food is sucked down the inhalant siphon into the mantle cavity where sorting occurs on the ctenidia and palps. Selection for particles of smaller size, lower specific gravity, and higher organic content results (Hylleberg and Gallucci, 1975).

Corophium salmonis is a gammaridean amphipod. Individuals at our collection site often occupy abandoned tubes of *H. florida* and *P. kempi japonica.* In its surface deposit-feeding mode the animal initially excavates a volume of sediment at one end of its tube with a scraping action of the second antennae; after withdrawing into its tube

with the second antennae grasping the sediment aggregate, particles are manipulated by the mouthparts. Previous observations (Miller, 1984, Fig. 4) suggest a selectivity peak around 10 μm and strong selection on the basis of organic coating (Taghon, 1982).

Yoldia scissurata, a burrowing protobranch bivalve, feeds by extending two mucus-covered, ciliated tentacles (palp proboscides) into surrounding sediment. Material is transported back along these tentacles to the mantle cavity, where the ctendia and labial palps further process the material (Purchon, 1977). Particle sorting occurs on all three structures, the finest particles tending to be accepted for ingestion (Stasek, 1965).

Sternaspis scutata, the "mud owl," is a cosmopolitan species found in shallow subtidal to deep-sea muds. Feeding methods in this polychaete family have not been described, but members have been assumed to deposit-feed. Our observations corroborate this assumption. The animal is able to evert half its body length, but the anatomical apparatus that allows this eversion and inversion has not been described. The anteriormost setigers bear large, stout setae (paleae) which may act both as anchors in the sediment while burrowing and as means for capturing, crushing and disaggregating food. A separately eversible pharynx is not obvious when animals are dissected.

Abarenicola pacifica, a lugworm, occupies a U-shaped burrow within sandflats. Ingestion of sediment takes place below the sediment surface and can cause the surface layer to cave in, forming a funnel-shaped depression. Material is ingested by inversion of the mucus- and papillae-covered pharynx. Observations by Hylleberg (1975) suggest that *A. pacifica* can select particles based on size.

Capitella cf. *capitata* and *Barantolla americana* are members of the polychaete family Capitellidae and have similar feeding methods and habitats. Family members generally feed, usually but not always head downward, by everting a papillose, sac-like pharynx, but little is published on their particle selectivity. A related species, *Heteromastus filiformis,* shows preference for smaller particles in natural mixtures (Cadée, 1979).

Axiothella rubrocincta is a bamboo worm or maldanid polychaete. Its feeding ecology has been described in detail by Kudenov (1982). Individuals in his population occupy U-shaped tubes of agglutinated sediment and form a feeding funnel, but individuals in the population we studied (Wilson, 1983) feed head downward in a straight tube and produce no depression. Otherwise, Kudenov's (1982) observations appear equally well to apply to our specimens. Individuals apress a mucus-coated, eversible pharynx to sediments in the feeding space. Sediment is entrained and transported via ciliary currents and pharyngeal inversion to the gut.

b. Selectivity experiments. Species of surface deposit feeders (Table 1) were collected then transported to the Friday Harbor Marine Laboratory, San Juan Island, Washing-

Table 2. Physical characteristics of beads used in particle selection experiments.

Size (μm) 80% within range	Geometric mean (μm)	Composition	Refractive index	Specific gravity	Log_{10} wt in water (g cm s^{-2})
3	3	Polystyrene	opaque	1.23	−8.67
5.2	5.2	Polystyrene	1.59	1.06	−8.70
7.3	7.3	Polystyrene	1.59	1.06	−8.26
8.6	8.6	Polystyrene	1.59	1.06	−8.04
9	9	Polystyrene	opaque	1.23	−7.24
13.5	13.5	Polystyrene	1.59	1.06	−7.46
15	15	Polystyrene	opaque	1.23	−6.57
15.4	15.4	Polystyrene	1.59	1.06	−7.28
22.2	22.2	Polystyrene	1.59	1.06	−6.81
25.4	25.4	Polystyrene	1.59	1.06	−6.63
35	35	Polystyrene	1.59	1.06	−6.21
*44–62	52	Glass	1.51	2.42	−3.99
44–62	52	Glass	1.65	2.99	−3.97
44–62	52	Glass	1.91	3.99	−3.79
50	50	Polystyrene	1.59	1.06	−5.75
50	50	Polystyrene	opaque	1.23	−5.00
55.6	55.6	Polystyrene	opaque	1.23	−4.86
105–125	115	Polystyrene	1.59	1.06	−4.66
†74–105	88	Glass	1.51	2.42	−3.31
110–149	125	Glass	1.51	2.42	−2.98
110–149	125	Glass	1.65	2.99	−2.83
110–149	125	Glass	1.91	3.99	−2.65
149–210	177	Glass	1.51	2.42	−2.52
177–210	193	Glass	1.65	2.99	−2.14
177–250	210	Glass	1.51	2.42	−2.18
250–350	296	Glass	1.51	2.42	−1.73
297–354	324	Glass	1.91	3.99	−1.29
600–700	648	Polystyrene	1.59	1.06	−2.41

Control particle type in experiments with *P. kempi japonica* (†) and all other species (*).

ton and placed in seawater tables (11–15°C). Methods and materials followed closely the "Empirical description of selectivity" section in Jumars *et al.* (1982). Briefly, one bead type (control bead) was paired in separate trials with numerous other bead types (test beads) such that the mixture would contain equal numbers of control and test beads (estimated from subsamples, Table 2). This bead mixture, in turn, was combined with an equal volume of commercially available, fine-grained (120-mesh, 125-μm median grain size) olivine sand (Northwest Olivine Co.) and a 0.5% by weight amount of Tetramin® fish-food flakes, mixed together as a paste with a small volume of seawater. A control glass bead with a geometric mean diameter of 88 μm and a specific gravity of 2.42 was used in the bead mixtures fed upon by *P. kempi japonica* in the March experiment (Table 2); all other experiments used 52-μm, 2.42 specific gravity, glass beads as the internal control against which relative selection was measured

(Table 2). The 48 mm diameter × 8.5 mm deep petri dishes (4 ml total volume) used as feeding containers for the smaller surface deposit feeders were of insufficient depth for *O. fusiformis*. Individuals were established in a plastic container of olivine 11 cm deep × 25 cm × 25 cm for 2 wk before use. For this species, the bead mixture paste was spread onto the sand surface with a spatula over an area where at least 5 individuals were located. The resulting depth of the bead mixture was 0.5 cm. *O. fusiformis* had little trouble regaining the surface and resumed feeding within an hour.

Some modifications were necessary for the subsurface deposit feeders as well. Pre-tests using a mixture of beads and olivine sand with *Axiothella rubrocincta* were unsuccessful. A bead mix:False Bay sand (500 μm sieved) ratio of 1:7 by volume proved satisfactory and gave adequate numbers of beads (20–100) in individual guts and numbers of individuals (3–5) with beads in their guts. Larger feeding containers were also required in order to provide an adequate depth (6 cm) for their natural feeding posture. Consequently, a larger volume of the bead mixture/False Bay sand (104 ml) had to be used. The feeding containers were constructed by gluing plastic tubing 4.7 cm in diameter by 6 cm onto a bottom plate. The bottom plate consisted of plastic screen material (50–100 μm mesh size) overlying a flat plastic plate 6.5 mm thick, through which numerous small holes (6.5 mm) had been bored. These structures were raised above the floor of the water table about 2 cm by another piece of tubing perforated with four slits spaced around the perimeter. They retained the experimental mixture yet allowed flushing of water through the sediments.

After an appropriate feeding period (Table 1) experimental animals were fixed in 20% formalin then preserved in 80% ethanol to await gut and mantle (bivalves) analysis. The length of the major axis of the shell for the bivalves *M. balthica* and *Y. scissurata*, and the length of the second segment of the fourth pereopod for *C. salmonis* were used as estimates of animal size. We followed the methods of Self and Jumars (1978) and estimated animal size of the polychaetes by calculating animal volume (Table 1). The projected areas of camera-lucida tracings of representative individuals were determined with manual and automated planimeters. The projected area was then used to compute volume assuming cylindrical or hemispherical shapes. The procedures described in Self and Jumars (1978) were also used to assess the relative proportions of each bead type from foregut (Table 1) and ambient sediment samples. Beads were distinguished by size, refractive index, transparency, or a combination of these differences (Table 2).

Information about a species' selectivity for particles used for tube construction or burrow lining was also collected for 6 of the 8 polychaete species. *Sternaspis scutata* did not build a tube or lining, and *Owenia fusiformis'* selective abilities were evaluated in a longer-term experiment. We removed a piece of the tube or burrow lining from the outer body of individuals used in the gut selection experiments, dissolving the mucous matrix by submersion in 30% hydrogen peroxide for a few minutes (repeating if needed), then determining bead proportions as described above.

O. fusiformis required much more time to add material to its tube than we allowed

for evaluation of particle selection with ingested material. Another experiment was performed which would evaluate *Owenia's* reported ability to select particles according to shape. Angular glass particles (Potters Industries, Canby, Oregon) of specific gravity 2.42 and size 297–420 μm were cleaned then shaken through nested 500-μm and 300-μm sieves. Particles retained on the 300 μm sieve were mixed, by equal numbers, with spherical glass beads (Cataphote Division, Ferro Corp., Jackson, Mississippi) of equal specific gravity, size range, and preparation. Ten individual angular and spherical particles from the mixture were also weighed with a Cahn 25 Electrobalance® to further insure that shape was the sole variable differentiating the particle types. The glass particle mixture was combined with an equal volume of olivine sand, then spread as a seawater paste over the tube openings of individuals which had acclimated in a deep sediment container in a seawater table for 2 d. Ten ambient samples were taken. Anterior portions of the tubes, composed of newly added material, were severed after 6, 8, and 10 d, then preserved in 80% ethanol.

To gain information about particle selection by siphon-feeding bivalves at the initial stage of particle capture, *Macoma nasuta* individuals were collected from False Bay, San Juan Island, Washington and acclimated in water tables in the laboratory. A mixture was prepared as described above, with 52-μm diameter (specific gravity 2.99) and 125 μm (specific gravity 3.99) beads. The mixture was spread in the foraging areas of individual *M. nasuta* as a seawater paste, samples taken to determine ambient bead proportions, and the area continuously observed. An individual was recovered from the sediment, its mantle cavity punctured, then fixed in 20% formalin, after it was observed feeding on the glass bead mixture for approximately 5 min. The proportions of the two glass bead types from the mantle cavity and ambient samples were then determined as described above.

c. Statistical procedures. Strength of selection for a particle type was quantified as $\log_{10}$ of the odds ratio (Fleiss, 1973; Cock, 1978; Gabriel, 1979; Jumars *et al.*, 1982; Miller, 1984). The odds ratio is calculated as:

$$\frac{T_g C_a}{C_g T_a}, \text{ where}$$

T_g = estimated proportion of test beads in a gut; C_g = estimated proportion of control beads in a gut, and $T_g + C_g = 1$; T_a = estimated proportion of test beads in the ambient particle mixture; C_a = estimated proportion of control beads in the ambient particle mixture, and $T_a + C_a = 1$.

The statistical problem was to quantify the *pattern* of selectivity as measured by the log odds ratio, the dependent variable, with respect to the independent variables, $\log_{10}$ (geometric) mean test particle diameter and test particle specific gravity (Table 2). The null hypothesis was that selectivity was independent of test bead physical characteristics. The alternative hypotheses were that the variables (or their correlates)

were dependent and that the nature of the dependence was unique to each species. Perusal of the plotted data and previous work on particle selection by deposit feeders (e.g., Levinton, 1979; Jumars, *et al.,* 1982; Miller, 1984) suggested two alternative relations, linear and curvilinear, between selectivity and particle size. We had no *a priori* predictions about the specific mathematical representation of the curved line; the apparent parabolic shape of most of the scattergrams suggested the quadratic equation would be a simple and easily tested alternative to a linear association. The results of Self and Jumars (1978) suggested particle specific gravity as a variable upon which deposit-feeders' selectivity depends. Multiple regression (Nie *et al.,* 1975) and analysis of variance (Box *et al.,* 1978, pp. 473–483) procedures were applied to the data in which treatments were the particular paired bead mixtures to which two or more individuals were assigned. The relative proportions of control and test particles ingested by an individual, its response to that paired bead mixture, and quantified as the log of the odds ratio are the treatment effects. The method of least squares was used to determine the values of the coefficients *a, b, c,* and *d* in the linear,

log(odds ratio) = *a* + *b* log(geometric mean test particle diameter) + *E*; curvilinear,

log(odds ratio) = *a* + *b* log(geometric mean test particle diameter) +
            c (log(geometric mean test particle diameter))² + *E*;

and, multiple curvilinear,

log(odds ratio) = *a* + *b* log(geometric mean test particle diameter) +
            c (log(geometric mean test particle diameter))² +
            d (test particle specific gravity) + *E*;

models, where E = residual error. The models were assessed stepwise from simplest (linear) to most complex (multiple curvilinear). If the more complex model increased the explained sum of squares a significant amount as determined by the magnitude of the appropriate F ratio (model mean square : experimental error mean square), it was judged the best model for that species. Residuals (observed minus expected based on "best model") were then plotted against expected log odds ratio, log diameter, specific gravity and animal size to evaluate model assumptions of independently and randomly distributed residuals.

   If the pattern of preference with respect to particle size or particle submersed weight (the simplest combination of size and specific gravity) turned out to be unimodal, then the diameter and standard error of the most strongly preferred test particle (maximum log odds ratio) was determined. Differentiating the quadratic equation with respect to log test particle diameter, setting the derivative equal to zero, then solving for log test particle diameter, gives an estimate of the preferred particle size. The solution is: $\log_{10}$ (preferred particle size) = $-1/2(b/c)$. The variance (S_{pd}^2) about the estimate was calculated using error propagation techniques (Gore, 1952) where, $S_{pd}^2 = S_b^2/4c^2 +$
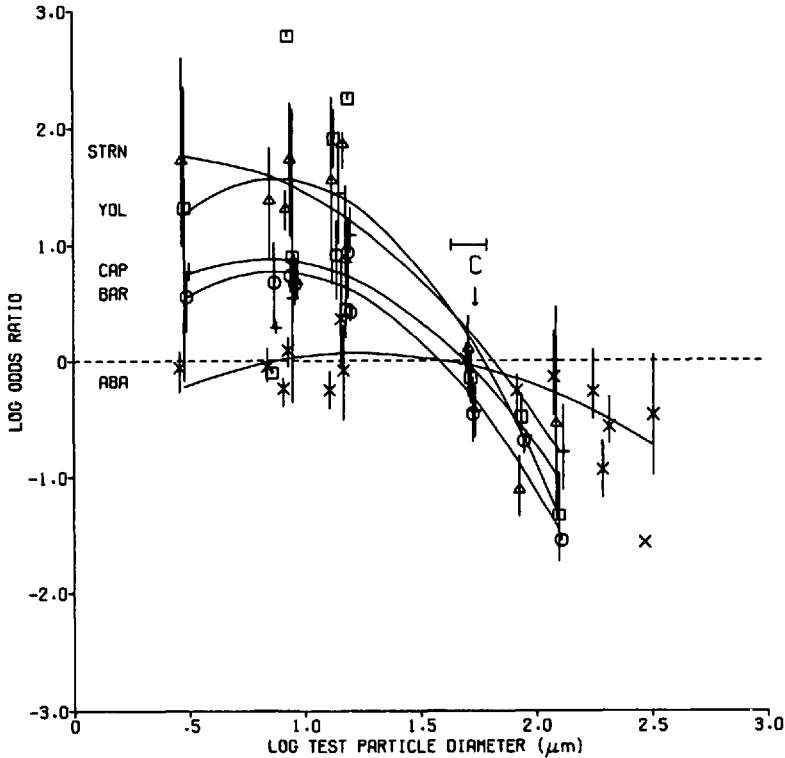
Figure 1. Particle preference (mean ± range $\log_{10}$ of the odds ratio) exhibited by *Sternaspis scutata* (△), *Yoldia scissurata* (□), *Barantolla americana* (○), *Capitella* cf. *capitata* (+), and *Abarenicola pacifica* (×) plotted against $\log_{10}$ of the diameter of particles mixed with 52-μm, $\rho = 2.42$ control beads (C) of size range (⊢——⊣). Curved line based on least squares fit assuming a second degree polynomial model.

$S_c^2 b^2/4c^4$, in which S_b and S_c are the standard errors of the coefficients b and c. An identical sequence of calculations was used when solving for the most strongly preferred particle weight based on a curvilinear regression of log odds ratio against log particle submersed weight. The preferred particle diameter, expressed for a particle having a specific gravity equivalent to that of quartz (2.65), was then calculated.

We employed nonparametric statistical procedures (Hollander and Wolfe, 1973) when testing for differences between population medians.

3. Results and discussion

The patterns of particle preference for ingested material exhibited by 9 of the 11 species studied suggested that selectivity was a unimodal function of test particle diameter (Figs. 1, 2a, 3a). Positive values of the log odds ratio indicate preference for test particles over the control particles. Negative log odds ratio values indicate
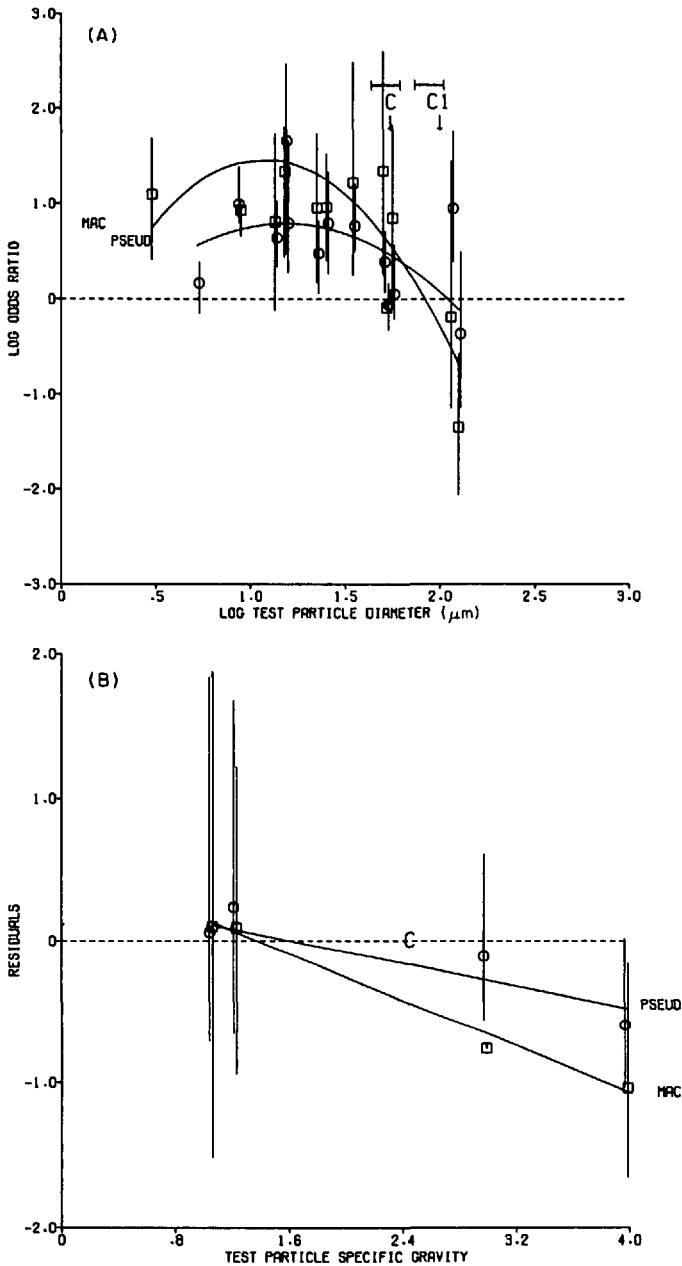
Figure 2. (a) Particle preference (mean ± range log₁₀ of the odds ratio) exhibited by *Macoma balthica* (▢) and *Pseudopolydora kempi japonica* (○) plotted against log₁₀ of the diameter of particles mixed with 52-μm (C) and 88-μm (Cl, *P. kempi japonica* only) control beads of size range (⊢——⊣). Curved line based on least squares fit assuming a second degree polynomial model. (b) Residual particle preference (mean ± range of observed log₁₀ of the odds ratio minus expected log₁₀ of the odds ratio assuming a second degree polynomial model) for *M. balthica* (▢) and *P. kempi japonica* (○) and plotted against specific gravity of particles mixed with $\rho = 2.24$ control beads (C). Straight line based on least squares fit of linear portion of multiple curvilinear model.
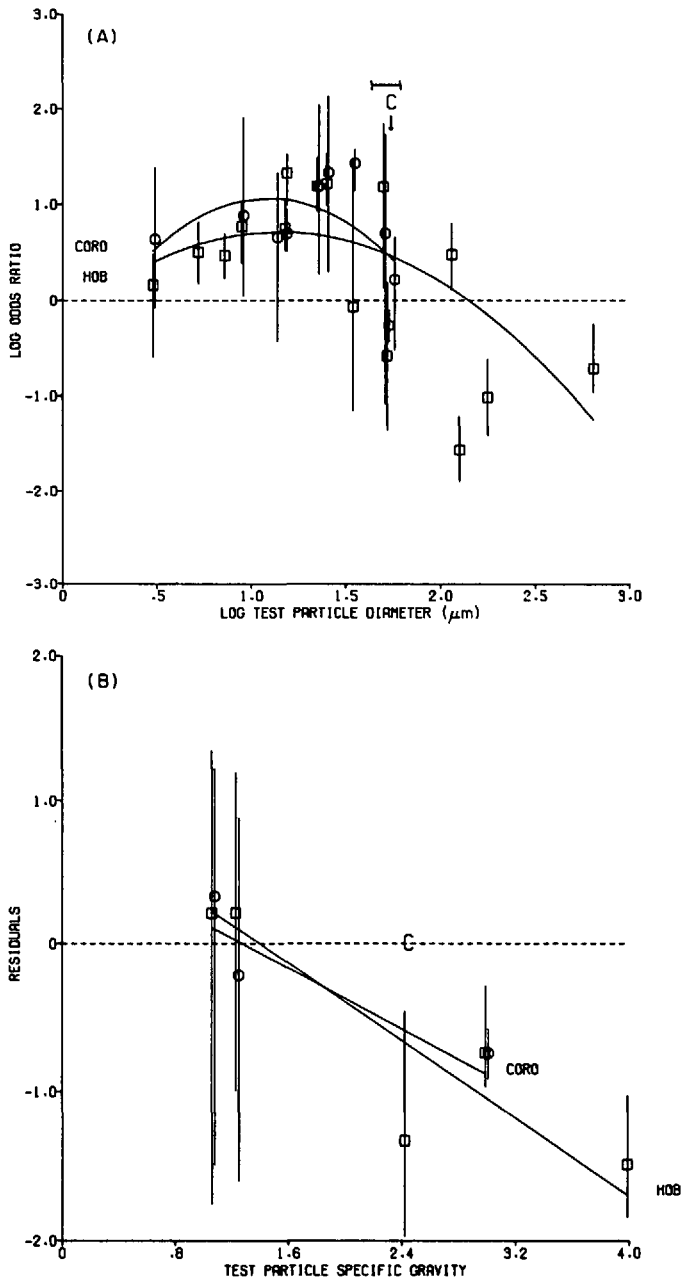
Figure 3. (a) Particle preference (mean ± range $\log_{10}$ of the odds ratio) exhibited by *Hobsonia florida* (▣) and *Corophium salmonis* (○) plotted against $\log_{10}$ of the diameter of particles mixed with 52-μm control beads (C) of size range (⊢——⊣). Curved line based on least squares fit assuming a second degree polynomial model. (b) Residual particle preference (mean ± range of observed $\log_{10}$ of the odds ratio minus expected $\log_{10}$ of the odds ratio assuming a second degree polynomial model) for *H. florida* (▣) and *C. salmonis* (○) plotted against specific gravity of particles mixed with $\rho = 2.42$ control beads (C). Straight line based on least squares fit of linear portion of multiple curvilinear model.

Table 3. ANOVA results for multiple regression of log odds ratio against log test particle diameter, log test particle diameter squared and test particle specific gravity.

Source of Variation	Sum of Squares	d.f.	Mean Square	F	P
Sternaspis (Polychaeta)					
constant	18.21	1	18.21	37.16	<0.001
Regression model	35.02				
extra for linear	33.25	1	33.25	67.86	<0.001
extra for quadratic	1.73	1	1.73	3.53	0.092
extra for specific gravity	0.04	1	0.04	<1.	>0.25
Residuals	12.99	32			
lack of fit	7.55	21	0.36	<1.	>0.25
experimental error	5.44	11	0.49		
Total	66.22	36			
Yoldia (Bivalvia)					
constant	5.04	1	5.04	6.81	0.027
Regression model	41.75	3			
extra for linear	34.76	1	34.76	46.97	<0.001
extra for quadratic	6.61	1	6.61	8.93	0.015
extra for specific gravity	0.38	1	0.38	<1.	>0.25
Residuals	19.99	24			
lack of fit	12.56	14	0.90	1.22	>0.25
experimental error	7.43	10	0.74		
Total	66.78	28			
Barantolla (Polychaeta)					
constant	2.18	1	2.18	19.82	0.002
Regression model	13.00	3			
extra for linear	9.94	1	9.94	90.36	<0.001
extra for quadratic	2.95	1	2.95	26.82	<0.001
extra for specific gravity	0.11	1	0.11	1.	>0.25
Residuals	2.24	24			
lack of fit	1.12	14	0.08	<1.	>0.25
experimental error	1.12	10	0.11		
Total	17.42	28			
Capitella (Polychaeta)					
constant	1.99	1	1.99	12.44	0.013
Regression model	10.48	3			
extra for linear	7.79	1	7.79	48.69	<0.001
extra for quadratic	1.84	1	1.84	11.50	0.016
extra for specific gravity	0.85	1	0.85	5.31	0.062
Residuals	2.73	17			
lack of fit	1.80	11	0.16	1.00	>0.25
experimental error	0.93	6	0.16		
Total	15.20	21			

Table 3. (Continued)

Source of Variation	Sum of Squares	d.f.	Mean Square	F	P
Abarenicola (Polychaeta)					
constant	1.82	1	1.82	12.13	0.001
Regression model	3.06	3			
extra for linear	1.59	1	1.59	10.60	0.005
extra for quadratic	1.06	1	1.06	7.07	0.018
extra for specific gravity	0.41	1	0.41	2.73	0.130
Residuals	4.46	44			
lack of fit	1.83	27	0.07	<1.	>0.25
experimental error	2.63	17	0.15		
Total	9.34	48			

avoidance of test and preference for the control particle. A log odds ratio of zero indicates no preference. A curvilinear regression improved the fit (extra sum of squares for quadratic statistically significant at $P \le 0.05$) between log odds ratio and log test particle diameter for 7 of the 9 species (Tables 3–5). The improvement was less dramatic for *S. scutata* (Table 3, $P = 0.092$) and *C. salmonis* (Table 5, $P = 0.09$). The

Table 4. ANOVA results for multiple regression of log odds ratio against log test particle diameter, log test particle diameter squared and test particle specific gravity.

Source of Variation	Sum of Squares	d.f.	Mean Square	F	P
Macoma (Bivalvia)					
constant	25.18	1	25.18	27.08	<0.001
Regression model	37.95	3			
extra for linear	15.30	1	15.30	16.45	0.002
extra for quadratic	14.77	1	14.77	15.88	0.002
extra for specific gravity	7.88	1	7.88	8.47	0.013
Residuals	28.59	54			
lack of fit	16.53	41	0.40	<1.	>0.25
experimental error	12.06	13	0.93		
Total	91.72	58			
Pseudopolydora (Polychaeta)					
constant	16.87	1	16.87	45.59	<0.001
Regression model	11.53	3			
extra for linear	4.56	1	4.56	12.32	0.004
extra for quadratic	2.42	1	2.42	6.54	0.023
extra for specific gravity	4.55	1	4.55	12.30	0.004
Residuals	19.45	63			
lack of fit	14.29	49	0.29	<1.	>0.25
experimental error	5.16	14	0.37		
Total	47.85	67			

Table 5. ANOVA results for multiple regression of log odds ratio against log test particle diameter, log test particle diameter squared and test particle specific gravity.

Source of Variation	Sum of Squares	d.f.	Mean Square	F	P
Hobsonia (Polychaeta)					
constant	14.72	1	14.72	52.57	<0.001
Regression model	34.22	3			
extra for linear	7.49	1	7.49	26.75	<0.001
extra for quadratic	7.38	1	7.38	26.36	<0.001
extra for specific gravity	19.35	1	19.35	69.11	<0.001
Residuals	27.25	75			
lack of fit	22.50	58	0.39	1.39	>0.25
experimental error	4.75	17	0.28		
Total	76.19	79			
Corophium (Amphipoda)					
constant	23.85	1	23.85	33.59	<0.001
Regression model	5.66	3			
extra for linear	0.31	1	0.31	<1.	>0.25
extra for quadratic	2.44	1	2.44	3.44	0.09
extra for specific grafity	2.91	1	2.91	4.10	0.07
Residuals	19.42	39			
lack of fit	11.62	28	0.42	<1.	>0.25
experimental error	7.80	11	0.71		
Total	48.93	43			

52-μm diameter control particle approached the maximum size taken by *C. salmonis* (Miller, 1984). The consequence was poor resolution of the pattern of selectivity (significant portion of the variability of the log odds ratio explained by a constant, Table 5), but keeping the same control particle allowed among-species comparisons to be made. Miller (1984), using a 25-μm control particle mixed with test particles ranging from 5–53 μm also found a unimodal pattern of selectivity with respect to particle diameter. *S. scutata* ingested particles larger than the 52-μm control, and the precipitous decrease in the log odds ratio with increasing test particle diameter indicates adequate resolution (Fig. 1). We tentatively conclude that the pattern of selectivity is unimodal; particles smaller than 3 μm (our smallest test particle diameter), however, should be included in future experiments with *S. scutata* to remove ambiguity. *O. fusiformis* responded only to particle specific gravity, preferring particles of low density (Fig. 4, Table 6) irrespective of particle size. *A. rubrocincta* was the only species that apparently did not (statistically significantly) discriminate either particle size or density (Table 6) over the range of particles offered.

Since 11 regressions were performed we need to account for multiple testing. Using the Bonferroni *F* procedure (Huitema, 1980) we obtain an overall *P* level of 0.05 when the individual (for each species) experimentwise level is set at 0.005. Using this very
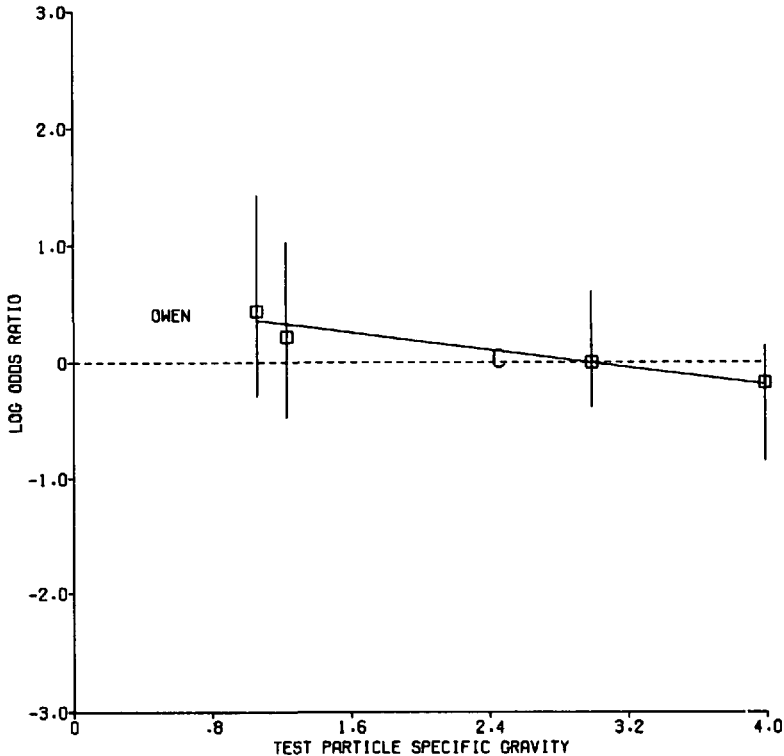
Figure 4. Particle preference (mean ± range $\log_{10}$ of the odds ratio) exhibited by *Owenia fusiformis* plotted against specific gravity of particles mixed with 52-μm, $\rho = 2.42$ control beads (C). Straight line based on least squares fit assuming a linear model.

conservative criterion, the explained variance is significantly increased by inclusion of log test particle diameter squared into the regression equation for *H. florida, M. balthica* and *B. americana. S. scutata, Y. scissurata, C.* cf. *capitata, A. pacifica* and *P. kempi japonica* demonstrate a strong linear dependence. Thus, the dependence of selectivity on particle size is justified. The form of the dependence (linear or curvilinear), however, depends upon which significance criterion is acceptable to the reader.

For some of the deposit feeders all of the variance of the log odds ratio was not explained by particle diameter alone. The residuals (observed log odds ratio minus estimated log odds ratio assuming dependence on particle diameter alone) of the curvilinear regressions are plotted as a function of test bead specific gravity (Figs. 2b, 3b). Addition of the independent variable test bead density to the quadratic equation with log test particle diameter significantly increases the explained sum of squares for the polychaetes *P. kempi japonica* and *H. florida,* and the bivalve *M. balthica* (Tables 4, 5). A weaker dependence of selectivity on particle density is

Table 6. ANOVA results for multiple regression of log odds ratio against log test particle diameter, log test particle diameter squared and test particle specific gravity.

Source of Variation	Sum of Squares	d.f.	Mean Square	F	P
Axiothella (Polychaeta)					
constant	0.58	1	0.58	2.23	0.18
Regression model	1.02	3			
extra for linear	0.19	1	0.19	<1.	>0.25
extra for quadratic	0.04	1	0.04	<1.	>0.25
extra for specific gravity	0.79	1	0.79	3.04	0.11
Residuals	6.44	33			
lack of fit	3.11	20	0.16	<1.	>0.25
experimental error	3.33	13	0.26		
Total	8.04	37			
Owenia (Polychaeta)					
constant	4.20	1	4.20	15.56	0.002
Regression model	5.73	3			
extra for linear	0.17	1	0.17	<1.	>0.25
extra for quadratic	0.0003	1	0.0003	<1.	>0.25
extra for specific gravity	5.56	1	5.56	20.59	<0.001
Residuals	8.99	65			
lack of fit	5.26	51	0.10	<1.	>0.25
experimental error	3.73	14	0.27		
Total	18.92	69			

exhibited by the surface deposit-feeding amphipod *C. salmonis* (Table 5). If the conservative Bonferroni *F* criterion is used, *P. kempi japonica, H. florida* and *O. fusiformis* display the strongest specific gravity selection ($P < 0.05$ overall). This result emphasizes the role that specific gravity (or its correlates, i.e., submersed particle weight and particle weight per unit of surface area) play in determining the particles ingested by all 5 species of surface deposit feeders. If particle selection were to be predicted on the basis of particle diameter alone without including specific gravity, selection for heavy particles of equivalent size would be overestimated for *Pseudopolydora, Macoma, Corophium, Hobsonia* and *Owenia*. Conversely, selection for low specific gravity particles would, on average, be underestimated.

The significance level of "extra for specific gravity" for *Corophium salmonis* (Table 5) is nearly equal to that for *Capitella* cf. *capitata* (Table 3). However, the slope of the regression line for *C.* cf. *capitata* was negative but shallow (-0.108) while the slope of the regression line for *C. salmonis* was negative and of comparable steepness (-0.513) to regression slopes for the other surface deposit-feeders. Unlike *C. salmonis,* for which we can draw upon earlier work (Taghon, 1982; Miller, 1984) to corroborate our conclusion of monotonic selection, more experiments are required to confirm or deny

Capitella's selectivity for less dense particles. We tentatively group it with the other subsurface deposit feeders, which appear insensitive to particle specific gravity *per se*, but show a strong size preference (Fig. 1, Table 3).

The presence or absence of a specific-gravity response among the subsurface deposit feeders cannot be evaluated unambiguously with our present data because of a high correlation between specific gravity and particle diameter (Pearson product-moment correlation coefficient, $r = 0.8$). The large volume of sediments required for the subsurface deposit feeders coupled with the high cost of plastic beads made additional runs with large diameter (>50 μm) low specific gravity (1.06) polystyrene beads prohibitively expensive. Stepwise removal of that proportion of the variability of the dependent variable (log of the odds ratio), by one of the two correlated variables (log test particle diameter), by definition leaves little variability which can be explained by the second variable (test particle specific gravity). The result, in our experiments, is a decreased (perhaps artificially) *F*-ratio for the "extra for specific gravity" portion of the stepwise regression model (Table 3 and *Axiothella* in Table 6). The particles used for surface deposit feeders were chosen expressly to avoid high correlation between size and specific gravity and thus do not suffer from this ambiguity.

There did not appear to be any correlation between deviations from predicted log odds ratio and log particle diameter, particle specific gravity or animal size. Plots of residuals versus animal size for *Corophium salmonis* and residuals versus predicted log odds ratio, particle diameter and particle specific gravity for *Yoldia scissurata* (plots not shown for brevity), however, were "trumpet" shaped, indicating heteroscedasticity. The graph for *Corophium* indicates an unexplained, varying response by different sized individuals; populations of small individuals tended to have a sloppier selection mechanism than populations of larger individuals. The response of *Y. scissurata* varied with particle characteristics. Its selective mechanisms appear to perform more precisely when selecting between larger and more dense particles.

Granting the plausibility of the regression model assumptions and the unimodal patterns of selectivity, but keeping in mind the restrictions on interpretation of the *Y. scissurata* and *C. salmonis* data, we estimate the particle size at which peak selectivity should occur for subsurface deposit feeders directly from the selectivity versus particle size regression equations (Fig. 1). Estimates of the preferred particle size for the surface deposit feeders are based on the regression equation of selectivity versus particle weight-in-water (Fig. 5). The particle size or weight at which the regression curves cross the zero intercept serves as a coarse check on the validity of estimates based on the regression curves. As expected, the regression curves usually cross the zero preference (dashed) line within the particle size (Fig. 1) or weight (Fig. 5) range of the control particles; by definition no selection can occur if the control particle is paired with itself. The crossing points of the best-fit curves for *A. pacifica, B. americana* (Fig. 1), *P. kempi japonica* and *C. salmonis* (Fig. 5) are outside the nominal particle size ranges of the control beads (Table 2) by 5 μm or less, thus potentially contributing a small, systematic error to the estimates of the preferred
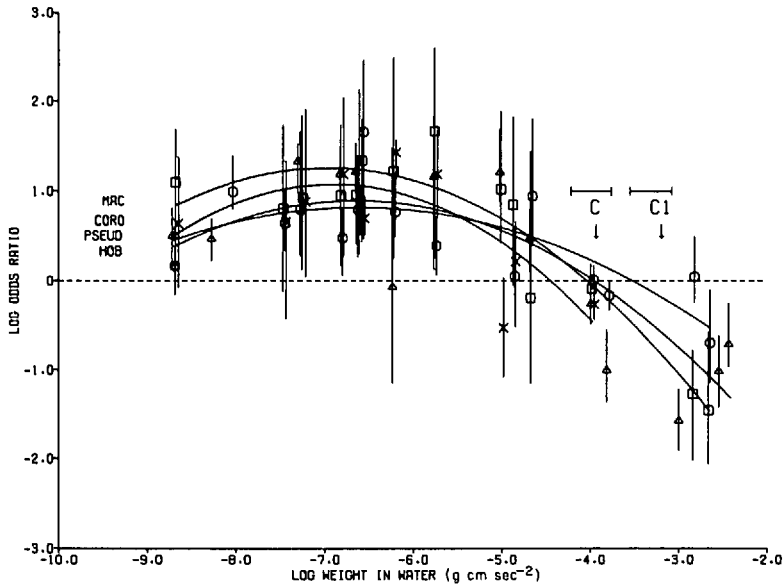
Figure 5. Particle preference (mean ± range $\log_{10}$ of the odds ratio) exhibited by *Macoma balthica* (□), *Corophium salmonis* (×), *Pseudopolydora kempi japonica* (○) and *Hobsonia florida* (△) plotted against $\log_{10}$ of the submersed weight of particles mixed with 52-μm (C) and 88-μm (Cl, *P. kempi japonica* only) control beads of weight range (⊢—⊣). Curved line based on least squares fit assuming a second degree polynomial model.

particle size. From Table 7 we see that the strength of the relationship between selectivity and particle characteristics varies among species. Further refinement of our *a posteriori* predictions of preferred particle diameter would require larger sample sizes for those species with r^2 values less than 0.70.

Table 7. Proportion of variance of the log odds ratio (r^2) explained by the variance of test particle diameter*, test particle specific gravity+ or test particle submersed weight#. N = sample size.

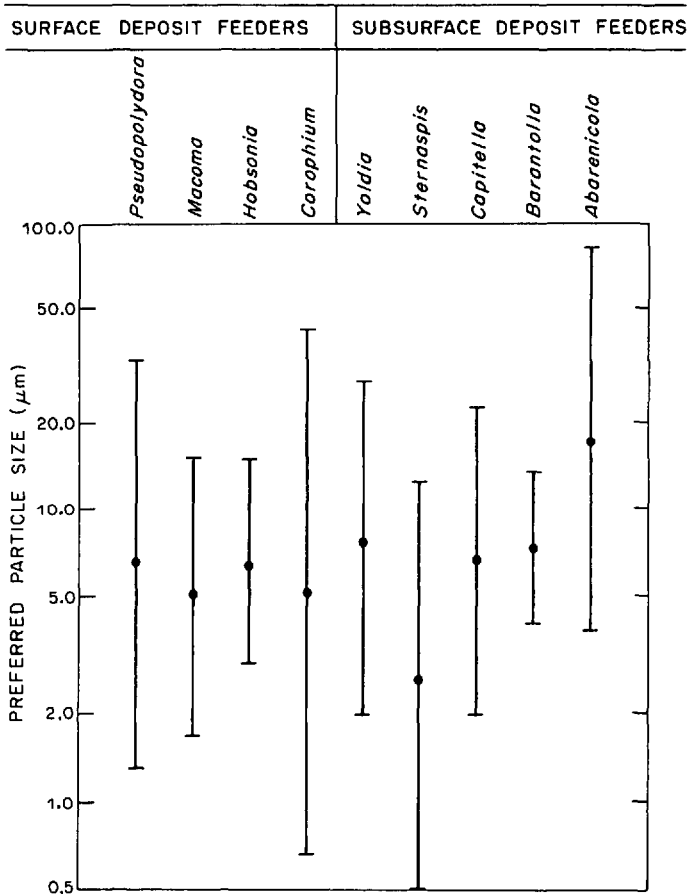| Species	N	r^2
Sternaspis scutata	36	0.73*
Yoldia scissurata	28	0.67*
Barantolla americana	31	0.85*
Capitella cf. *capitata*	21	0.73*
Abarenicola pacifica	48	0.32*
Macoma balthica	58	0.57#
Pseudopolydora kempi japonica	67	0.39#
Hobsonia florida	79	0.50#
Corophium salmonis	43	0.31#
Axiothella rubrocincta	37	0.14*
Owenia fusiformis	69	0.39+

Figure 6. Estimate of most highly preferred particle diameter ± 1 standard error (68% confidence limits) for surface (particle specific gravity of 2.65 assumed) and subsurface deposit feeders.

Our *a posteriori* estimates of peak size selectivity for deposit feeders showing unimodal preference ranges from 3–17 μm (Fig. 6). The estimates are rather imprecise; all test particle sizes smaller than the control 50-μm particle are included in the 68% confidence limits. However, this size range is in accord with recently found patterns of attached bacterial abundance and organics adsorbed to mineral grains. Cammen (1982) finds increasing microbial and organic concentrations with decreasing particle size at 3 of 4 locations, examined in winter and summer. At the fourth location the trend holds for size fractions less than 50 μm. Deflaun and Mayer (1983) did not find bacteria colonizing any grains smaller than about 10 μm, but showed that the highest concentrations of organic carbon occurred in the 3-μm size fraction (their Fig. 4, pg. 879). For the surface deposit feeders, estimates of peak size selectivity are

dependent on the specific gravity of the material ingested. For, say, a specific gravity of 1.05 (organic aggregates, algal fragments, etc.) our estimates of the diameter at which peaked size selection occurs would be about 23 μm; about 4 times greater than the diameter assuming a particle density of 2.65 (Fig. 6).

Abarenicola pacifica did not show strong preference among particles smaller than about 50 μm (Fig. 1); below 50 μm the expected log odds ratio values are close to zero. For particle diameters greater than 50 μm, negative log odds ratio values indicate rejection of the test and preference for the control, 52-μm, bead. This result reaffirms the conclusions of Hylleberg (1975) who observed selection by *A. pacifica* for material passing an 80-μm sieve and Baumfalk (1979) who observed that the feces produced by the confamilial *Arenicola marina* consisted of finer material than the ambient sediments. On average, a population of *A. pacifica* will tend to select on the basis of particle diameter if given a choice between <52 μm and >52 μm particles, preferring the smaller particles. This species' discriminatory ability is severely depressed at smaller particle sizes in comparison to *C.* cf. *capitata* and *B. americana* which, although of smaller physical size, also evert a pharynx and ingest sediment adhering to it.

Axiothella rubrocincta and *Owenia fusiformis* were also nonselective for particle size, ingesting large and small particles equally (Table 6). These two species were the second and fourth ranked polychaetes, respectively, behind *A. pacifica* in terms of animal size (Table 1). Modeling deposit feeding in the context of optimality theory, Taghon *et al.* (1978) predict that the smallest particles should always be preferred. At low assimilation efficiencies, with short gut throughput times or with a relatively large gut to be kept full, however, large particles should also be taken to offset the energy cost of collecting more particles. Two sets of past observations of within-species gradients of particle size selectivity correlated with animal size are those of Whitlatch (1974), who observed that large individuals of *Pectinaria gouldii* have a larger mean particle size in their guts than smaller animals, and those of Taghon (1982), who in controlled experiments showed for 5 of 7 deposit-feeding species tested that the larger individuals of a species tended to be less selective for small particles than smaller individuals. Our data suggest that these trends may extend to among-species comparisons. Selectivity for smaller particles declines as the animal increases in size.

Whitlatch and Weinberg (1982) tested the hypothesis that particle selection for tube building rather than food quality could account for *Cistenides gouldii*'s preference for ingesting larger particles. The particle sizes cemented to *C. gouldii*'s tubes were very rare in the ambient sediments suggesting strong selectivity. But particles of the size commonly found in tubes were rare in animal guts, suggesting that the mechanisms of tube building and ingestion are independent processes. Particle selection for tube building or burrow lining by *P. kempi japonica, H. florida, A. pacifica, C.* cf. *capitata, B. americana* and *A. rubrocincta* tended to follow the same, albeit weaker, trends as for ingestion. (For brevity, we do not include plots and

ANOVA tables.) This result suggests similar mechanisms for selection of particles in tube construction and ingestion. In another experiment *Owenia fusiformis* exhibited an unqualified preference for angular over spherical glass particles for its tube (median proportion angular particles on tubes = 1.0, $N = 6$, median proportion angular particles in ambient mixture = 0.52, $N = 10$, $P < 0.001$, Mann-Whitney U test), comparable to *C. gouldii*'s preference for large rare particles. Differences in individual particle weights were not significant between the two particle types ($P > 0.50$, Mann-Whitney U test) so *Owenia*'s confirmed preference for lighter particles (Fig. 4, Table 6) could not have confounded the results. Further experiments are required to identify the mechanisms whereby *O. fusiformis* can be highly selective for large, angular (300 μm) and low specific gravity (1.05–1.23) particles but be nonselective for particle size *per se*.

Bivalves may have the most complex particle-sorting machinery of all the taxa we studied. We hoped that the contents of the mantle cavities of *Yoldia scissurata* and *Macoma balthica* would allow us to tease apart the contributions of the initial particle-gathering structures (palp proboscides in *Yoldia* and inhalant siphon in *Macoma*) to the exhibited selective abilities of the species (Figs. 1, 2). The relative proportions of test and control beads in the mantles of the bivalves were the results of at least two processes, gathering (capturing) sediment from the environment by either inertial suction (*Macoma balthica*) or adhesion to mucus-covered proboscides (*Yoldia scissurata*) and accumulation of pseudofecal material rejected by the ctenidial and palpal sorting mechanism. The mantle contents of *M. balthica* and *Y. scissurata* were not different from ambient bead proportions, but since the relative rates of sediment gathering and pseudofecal production were uncontrolled, the results are ambiguous. In the controlled experiments with *Macoma nasuta,* individuals were killed within 5 min of sucking up the paired bead mixture. Again there was no significant difference between mantle and ambient proportions (median proportion ambient 52-μm beads = 0.29, $N = 10$, median proportion mantle 52-μm beads = 0.30, $N = 9$, $P > 0.50$, Mann-Whitney U test). Hylleberg and Gallucci (1975) also concluded, and we concur, that sediment is indiscriminately sucked into the mantle cavity by *M. nasuta.*

Lastly, we must entertain the possibility of artifacts when dealing with exotic particles and unnatural particle mixtures. A concern in this instance is whether the particles smaller than about 10 μm are hidden from selection by falling into interstices in the sediment matrix. This hiding of particles would also operate within natural sediment mixtures, however, and it would seem that natural selection would operate to provide mechanisms for extracting finer particles if food value rewarded this evolutionary path. Further, and more specifically for our experimental setup, we did observe considerable variability among species. Varying patterns of preference with body size and lack of size preference in *O. fusiformis* are difficult to reconcile with an interpretation of overriding experimental artifact. Conversely, we do not assert that

identical patterns will be found with natural particles, only that dependence upon size and specific gravity are easiest to resolve when they can each be described by single, independent variables, i.e., one diameter and a single specific gravity. We caution the reader that for animals using adhesive mechanisms selectivity depends very heavily upon the mixture presented (Jumars *et al.,* 1982), and thus selectivity for a given particle depends critically upon the context of other particles with which that particle is presented.

4. Conclusions

Our results indicate a highly consistent pattern of selection among deposit feeders for particle size and specific gravity. We conclude that evolution has operated on radically different food-gathering mechanisms to arrive at remarkably consistent patterns of selectivity. Species with small body size show unimodal preference for particles in the size ranges with which most microbial biomass and organic content usually are associated. Surface deposit feeders in addition show selection for particles of lower specific gravities, with which a greater proportion of organic matter and less refractory organic matter is likely to be associated. At least one species of deposit feeder (*Owenia fusiformis*) appears to have specialized on specific gravity as a means of discriminating among particles, though the mechanism by which it can do so without also selecting for smaller particles is by no means clear. Reduced selectivity observed for species with greater body size is consistent with predictions from optimal foraging theory. The very fact that deposit feeders will ingest the clean glass beads upon which these conclusions are based and will select among them argues that selection in deposit feeders is best viewed as a stochastic process limited in the ability to discriminate by the rapid rates at which deposit feeders are constrained to operate. Conversely, our results do not negate the possibility of strong, behaviorally mediated selection (e.g., Taghon, 1982) for one particle type when high food value is associated with it alone. Instead, we believe that they represent a modest advance over the more naive null hypothesis of equally likely ingestion of particles of any size or specific gravity. Against this view of deposit feeder as machine adapted to average sediment conditions, behavioral flexibility can better be evaluated.

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