

MECHANICS OF PARTICLE SELECTION BY TENTACULATE DEPOSIT-FEEDERS¹

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Abstract: A variety of experiments with glass and plastic beads covering a wide range of particle sizes and weights are used to develop a two-step, stochastic model of particle selection by deposit-feeders. These experiments include measurements of selectivity as a function of transport distance along a terebellid (polychaete) tentacle, of the degree to which a food source can be depleted of the preferred particle type by a terebellid, of selectivity by spionids (polychaetes) having lost their tentacles, of selectivity by an ampharetid (polychaete) as a function of available particle types, and of "selectivity" by adhesive-coated microscope slides. A large component of mechanical selection is seen to be achieved at the point of particle pick-up.

The first step of the heuristic model is particle contact by the tentacle. By appealing to the Delesse principle and to the results with adhesive-coated slides, the probability of particle contact is shown to be a function of particle size. On a per-particle basis, larger particles have a higher probability of being contacted by a tentacle than do smaller ones. The second step is the retention of the particle given that it has been contacted. It is suggested that the conditional (i.e., given contact) probability of such retention is a function of the adhesive strength of the mucus found on the tentacle and that it will depend on both particle weight per unit surface area and particle surface characteristics. In general, the conditional probability of retention will be a decreasing function of submerged particle weight per unit surface area. An important deduction from this model is that size-selection in tentaculate deposit-feeders need have no morphological correlates; the lower the adhesive strength of the mucus, the greater will be the animal's selectivity for smaller, lighter particles.

INTRODUCTION

In part because of greater fisheries interest, suspension-feeders have been studied far more extensively (e.g., Jørgensen, 1966) than have deposit-feeders. Even so, much of what is known about the process of suspension-feeding is empirical and descriptive, with remarkably little analytic knowledge of the fluid and solid mechanics of particle selection and rejection. An outstanding exception to this generalization is the recent theoretical work of Rubenstein & Koehl (1977), together with the experimental efforts that it has stimulated (e.g., LaBarbara, 1978). Major gaps in theoretical description and analytic ability remain, however, in the important low Reynolds number situations of copepod "filtration" (Koehl, pers. comm.) and ciliary suspension-feeding (Jørgensen, 1981).

At present, students of the deposit-feeding guild are in a similar but perhaps even

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more disadvantaged position. A substantial number of descriptive or empirical studies of particle selection have been carried out (e.g.: Goodbody, 1960; George, 1964; Gordon, 1966; Odum, 1968; Hughes, 1973, 1975, 1979; Meadows & Bird, 1974; Whitlatch, 1974, 1980; Fenchel *et al.*, 1975; Hylleberg & Gallucci, 1975; Tietjen & Lee, 1975; Cadée, 1976; Ching, 1977; Kikuchi & Kurihara, 1977; Powell, 1977; Ghiold, 1979; Kunze & Anderson, 1979; Levinton, 1980; Lopez & Kofoed, 1980; Marais, 1980; Scheibling, 1980; Sloan & von Bodungen, 1980; Tevesz *et al.*, 1980; Curtis & Hurd, 1981; Shick *et al.*, 1981). The lack of mechanistic models of deposit-feeding, however, makes it difficult to generalize from studied species to unstudied ones and to distinguish what a species actively selects for ingestion from what the mechanical limitations of its selection mechanism(s) constrain it to ingest. The latter distinction is crucial in the testing of optimal foraging theory for deposit-feeders (Taghon *et al.*, 1978; Hughes, 1980), and empirically substantiated constraints on selection already have required modification of the theory (Taghon, 1981). Contrary to the most basic predictions of optimal foraging theory developed for macrophages (Pyke *et al.*, 1977), deposit-feeders do not succeed in ingesting only the items of presumed highest food value (e.g., Whitlatch, 1974).

We elected to build upon our earlier results and methodologies (Self & Jumars, 1978) in order to analyze the mechanics of tentaculate deposit-feeding and, hopefully, to stimulate thought toward a general theory of deposit-feeding mechanics. Just as the development of suspension-feeding mechanics drew upon the seemingly exotic field of aerosol filtration theory (Rubenstein & Koehl, 1977), we will resort to sediment transport theory (Graf, 1971; Yalin, 1972; Middleton & Southard, 1978) and the theory of cellular adhesion to develop some of our concepts of deposit-feeder selectivity. First, however, we will (1) review what can be inferred of mechanics from past observations, (2) present our initial hypothesis concerning the mechanism, and (3) describe the experiments and observations that led us successfully to discredit this hypothesis and to formulate a new stochastic model of the tentaculate deposit-feeding process.

What kinds of particles are selected by tentaculate deposit-feeders and what insights does the pattern of "preference" offer into the mechanism(s) of selection? Particle size is the variable that has achieved the most attention in the above-listed and other studies. As reviewed and found by Taghon (1982), the clear majority show selection for smaller particles. A few studies (e.g., George, 1964) suggest that little selection occurs in some species (though such demonstrations are plagued by the statistical difficulty that acceptance of the null hypothesis of no selection may be the result of either no real selection or of small sample size and weak tests). Even fewer studies succeed in demonstrating selection for larger particles (e.g., Whitlatch, 1974), but these few studies are important in suggesting that any truly general mechanistic interpretation of tentaculate deposit feeding must include a means of selection for larger particles.

In retrospect, our initial hypothesis was insufficiently ambitious or general to include the latter possibility in any explicit way. The much more limited observations of Self & Jumars (1978) also indicated that the sought after mechanism(s) would be capable

of selectively retaining the lighter (in weight) and the rougher (in small-scale surface texture) of similarly sized particles.

We (unpubl. obs.) and others (e.g., Aller & Yingst, 1978) had observed that rejected particles may build up around tube or burrow openings of tentaculate deposit-feeders, at least during periods of little hydraulic sediment transport. Casual microscopic observations of *Hobsonia florida*, coupled with higher apparent selection in larger individuals of the species (Self & Jumars, 1978), led us to suspect that perhaps a major part of the selection process in tentaculate deposit-feeders might be accomplished via selective loss of particles from the tentacles during transport of particles to the mouth, suggesting a key selective role for the tentacles themselves. At least for part of their paths along tentacles and toward the mouth, entrained particles usually travel (e.g., Fig. 1 of the ampharetid polychaete *H. florida* in Fauchald & Jumars, 1979) suspended by mucus between tentacle and bed. From this precarious position, it is not difficult to imagine the selective loss of larger, heavier and smoother particles. Furthermore, barring doubts expressed by MacGinitie (1941) about experimental artifacts, this selective loss mechanism during particle transport would have an analog in eulamelibranch bivalves (Allen, 1958).

Several predictions arose from this hypothetical selection mechanism. The first prediction was that selectivity would increase with the distance (along a tentacle) that particles were transported (longer transport distances allowing a greater degree of selective loss); it seemed logical that larger, heavier and smoother particles would be the more readily lost from the tentacle during transport. A second (corollary) prediction was that tentaculate deposit-feeders which were prevented from transporting food particles for any substantial distance along a tentacle would show relatively little selectivity. Yet a third prediction was that enhanced shear in the flow to which the tentacles were exposed would, by increasing (selective) loss of particles from the tentacles, increase selectivity. Finally, a fourth prediction was that deposit-feeders which had lost their tentacles would also have lost much of their selective abilities. We set about to test these predictions.

We succeeded in soundly discrediting the preliminary model of selective loss from the ciliary transport tracts as the only major mechanism of selection. Evidence from our initial experiments suggested selection at the initial point of sediment pick-up but was insufficient to allow us to infer the mechanism responsible. Consequently, we extended our experiments to a broader range of particle sizes and weights to view the results of selection nearer to the extremes of these variables (but still within the animal's ingestible range). This extension and a crude analog model of tentacles suggested a mechanically selective process which proves consistent not only with our own experiments but also with the earlier, seemingly conflicting, literature cited above.

Before we proceed much further, we should point out that tentaculate deposit-feeders do have other feeding modes and other selection mechanisms than the microphagous, deposit-feeding ones upon which we have chosen to concentrate. *Pygospio elegans* (Fauchald & Jumars, 1979, Fig. 22; Dauer *et al.*, 1981) and *Pseudopolydora kemp*

japonica (pers. obs.), for example, can reject groups of particles or relatively large single particles via a ciliated midventral cleft of the lower lip. The criteria used in rejection are as yet unknown, but the number of particles following this route is insufficient to account for the selection described below. Both species are capable also of suspension feeding (Taghon *et al.*, 1980). *P. kempji japonica*, as documented in a film by E. D. Gallagher (Department of Oceanography, University of Washington), furthermore can switch abruptly to a decidedly macrophagous, predatory mode. E. D. Gallagher has recorded several sequences of juvenile *Corophium salmonis* (Amphipoda) entrapped by swimming into the mucus of one tentacle, manipulated with a coordinated effort of both tentacles until the *C. salmonis* is oriented "end on", and then swallowed whole. One of us (P.A.J.) has seen similar raptorial sequences with ostracods as prey for *Pygospio elegans*. We do not argue that these alternate feeding modes are unimportant either energetically or in terms of their implications for community structure (cf. Feller *et al.*, 1979). We simply point out that the tentaculate species we discuss do often engage in microphagous deposit-feeding and that mechanical processes are involved – otherwise the animals would show no relative preferences among cleaned glass and plastic beads of varying sizes and specific gravities.

MATERIAL AND METHODS

SELECTIVITY-VERSUS-DISTANCE EXPERIMENT

To test explicitly the dependence of selectivity on transport distance along a tentacle, we placed a mixture of two glass bead types in known proportions (determined microscopically from subsamples) at various distances from the tube openings of individual *Thelepus crispus* Johnson (Terebellidae). We used *T. crispus* (collected from the intertidal zone of Garrison Bay, San Juan Island, Washington) in place of *Hobsonia florida* because of the great extensibility of terebellid tentacles (Dales, 1955), making them ideal animals with which to test our hypothesis of increasing selectivity with transport distance along a tentacle. First, a bed of subangular gravel about three grain layers thick from the intertidal zone of Friday Harbor Laboratories (FHL), San Juan Island, Washington (median grain size = 6 mm) was laid in a plastic silverware separator. Next, a terebellid in its natural tube was placed in each of the four compartments of the silverware separator (submerged in a sea-water table at FHL) and allowed to acclimate. After the sea-water inflow was turned off to eliminate major flow effects, a microscope cover slip (22 × 56 mm), to which an aliquot of a moistened bead mixture (with ground Tetramin added to enhance the palatability of the beads – as was done in all the experiments with live animals below) had been frozen, was placed at a measured distance from the terebellid's anterior tube opening. The silverware separator, with its smooth, vertical walls, tended to steer the probing tentacles toward the microscope slide and thus to ensure that sufficient quantities of the bead mixture were ingested to allow meaningful analysis. Feeding was allowed to continue for 4 h after the

first tentacle reached the bead mixture, then the animals were fixed in formalin, their body volumes measured, and their foregut contents dissected out for analysis of the ingested bead proportions (as per the methods of Self & Jumars, 1978).

DEPLETION EXPERIMENT

In a complementary experiment, a number of *Thelepus crispus* individuals (again in their tubes) were placed individually with their anterior tube openings directly overlying Petri dishes of beads in a sea-water table with the flow turned off. Twelve samples of the starting bead mixture were then taken. Feeding was allowed to continue until approximately half of the total bead mixture had been ingested, ranging in time from 7 to 13 h. The dish and animal were then retrieved for analysis of gut and residual bead proportions.

FLOW SENSITIVITY EXPERIMENTS

Because all flow effects (unrealistically) were eliminated from the above experiments, controlled flow was included in the next series. All these flows were produced in the 2.5-m long flume described by Nowell *et al.* (1981). The flow experiments were conducted with four polychaete species, *T. crispus* (collected from the intertidal zone of Garrison Bay, San Juan Island, Washington), *Hobsonia florida* (Hartman) (from the Skagit River mudflat, Puget Sound, Washington), *Pseudopolydora kempji japonica* Imajima & Hartman and *Pygospio elegans* Claparède (both from False bay, San Juan Island, Washington). The "no flow" controls were located in water tables, the polychaetes (*Hobsonia florida*, *Pseudopolydora kempji japonica*, *Pygospio elegans*) being placed in large plastic containers with a sediment bed. Four bead types were mixed and presented to the animals. Three were made of glass, 44–62 μm diameter (geometric mean diameter 52 μm), but differing in specific gravity (Table I). The fourth bead type was made from polystyrene, with a mean diameter of 50 μm and a specific gravity of 1.06 (Table I).

For experiments with individual *Thelepus crispus*, no substratum was added to the Plexiglas bottom of the flume, and all individuals were placed 10 to 20 cm upstream of the removable core box (which in these experiments was replaced with a smooth acrylic plate to minimize alterations of the boundary layer flow). Aliquots of the moistened bead mixture were placed on 22-mm square cover slips and frozen. Estimates of the bead proportions were made from microscopic examination of subsamples of the bead mixture. The frozen paste and cover slip were placed 4 cm downstream from *T. crispus* individuals. Flow was then increased and water depth was noted; bed shear velocity (u_*) was calculated from near-bed velocity profiles. Velocities are reported in terms of a bed shear velocity because this variable is used routinely in computations of particle motion and sediment transport. Water temperature and density were monitored during the *T. crispus* experiments; but because the range of variation of these measurements was so small (0.3 °C and 0.001 $\text{g} \cdot \text{cm}^{-3}$), they were discontinued. After

a 1- to 2-h feeding period, *T. crispus* individuals were removed from the flume and fixed in 20% formalin, then preserved in 80% ethanol for gut content analysis.

TABLE I

Bead types used in experiments: polystyrene, $\rho = 1.23$ beads from 3M Company, Nuclear Products Dept.; polystyrene, $\rho = 1.06$ beads from Particle Information Services, Inc.; glass beads from Cataphote Division, Ferro Corp.; X, bead types used; C, control bead in paired experiments, cf. Fig. 7.

Size range (μm)	Geometric mean (μm)	Composition	Refractive index	Specific gravity	Log 10 wt in water ($\text{g} \cdot \text{cm}^{-1} \cdot \text{s}^{-2}$)	9/79 Expt. 1	3/80 Expt. 2
3	3	Polystyrene	opaque	1.23	-8.55	X	
5.2	5.2	Polystyrene	1.59	1.06	-8.60	X	X
7.3	7.3	Polystyrene	1.59	1.06	-8.16	X	
8.6	8.6	Polystyrene	1.59	1.06	-7.95		X
9	9	Polystyrene	opaque	1.23	-7.12	X	X
13.5	13.5	Polystyrene	1.59	1.06	-7.36		X
15.0	15.0	Polystyrene	opaque	1.23	-6.45	X	X
15.4	15.4	Polystyrene	1.59	1.06	-7.19	X	X
22.2	22.2	Polystyrene	1.59	1.06	-6.71	X	X
25.4	25.4	Polystyrene	1.59	1.06	-6.54	X	X
35.0	35.0	Polystyrene	1.59	1.06	-6.12	X	X
44-62	52	Glass	1.51	2.42	-3.99	C	X
44-62	52	Glass	1.65	2.99	-3.85	X	X
44-62	52	Glass	1.91	3.99	-3.66	X	X
50	50	Polystyrene	1.59	1.06	-5.65	X	X
50	50	Polystyrene	opaque	1.23	-4.88	X	
55.6	55.6	Polystyrene	opaque	1.23	-4.74		X
105-125	115	Polystyrene	1.59	1.06	-4.57	X	X
74-105	88	Glass	1.51	2.42	-3.31		C
110-149	125	Glass	1.51	2.42	-2.82	X	X
110-149	125	Glass	1.65	2.99	-2.68		X
110-149	125	Glass	1.91	3.99	-2.50		X
149-210	177	Glass	1.51	2.42	-2.40	X	
149-210	177	Glass	1.65	2.99	-2.25	X	
290-420	349	Glass	1.51	2.42	-1.51	X	
310-350	329	Polystyrene	1.59	1.06	-3.20	X	
600-700	648	Polystyrene	1.59	1.06	-2.32	X	

Hobsonia florida and the spionids *Pseudopolydora kempii japonica* and *Pygospio elegans* were placed in natural sediment in either the removable core box of the flume (experiment) or large plastic containers in sea-water tables (control) and allowed to acclimate for 2 h. After mixing the 52- μm glass bead types of specific gravities 2.42 and 3.99 in approximately equal proportions and adding sufficient water to form a paste, the bead mixture was spread on fiberglass window screen material overlying aluminum foil to achieve a uniform layer of $\approx 1\text{-mm}$ thickness. The paste was then frozen onto the screening, assuring a layer of uniform thickness when placed on the substratum. The water melted as soon as the screens were in place, and the beads dropped off onto the

substratum. After removal of the screening, samples of the bead mixture were taken with a microspatula from the flume box and plastic containers in the water tables, to allow estimation of the ambient bead proportions (i.e., bead proportions actually provided to the animals). Next, the flume was slowly filled with sea water and flow velocity increased while the containers in the water table ("no flow" control) were also slowly filled with sea water. Either "high flow" ($0.4 < u_* < 1.2 \text{ cm} \cdot \text{s}^{-1}$) or "low flow" ($u_* < 0.1 \text{ cm} \cdot \text{s}^{-1}$) were provided in a 3–5 cm flow depth. At the end of the 1- to 3-h feeding time, the animals were collected, separated from the sediment with a 350- μm sieve, fixed in 20% formalin, and preserved in 80% ethanol for gut content analysis.

PALP REMOVAL EXPERIMENT

Spionid polychaetes of some species routinely lose their feeding palps (tentacles) when disturbed, without apparent loss of their ability to ingest sediment particles. This observation suggested an experiment with the spionid *P. elegans* to evaluate the selective abilities of individuals lacking their feeding palps. *P. elegans* individuals from False Bay, San Juan Island, Washington, were sorted from sediments. Approximately 20 individuals were removed from their tubes and the dehiscent feeding palps removed. These and 20 other individuals with tentacles intact were placed in separate dishes of natural sediment (from False Bay) and allowed to acclimate in a water table for 1 h. A 1-mm thick layer of a 44–62 μm glass bead mixture, of specific gravities 2.42 and 3.99, was placed on the substratum, using the procedures described in the flow experiment series. After a 2-h feeding period, surface sediment samples were taken. The animals were then separated from the sediment, fixed in 20% formalin, and preserved in 80% ethanol.

EMPIRICAL DESCRIPTION OF SELECTIVITY

To quantify the selectivity of *Hobsonia florida*, we paired one bead type (control bead) with numerous other bead types (test beads), then determined the animals' selectivity given the respective proportions in that mixture (estimated from subsamples). Two complete runs were made in which two different control beads were used. In the September 1979 experiment, the control glass bead used had a geometric mean diameter of 52 μm and a specific gravity of 2.42; in March 1980, a slightly larger control glass bead of 88 μm , specific gravity 2.42, was used (test beads paired with control beads for each experiment noted in Table I). The mixtures were prepared in such a way as to achieve (1) approximately equal numbers of the control and test beads, (2) equal volumes of the bead mixture and a commercially available fine-grained (120-mesh, 125 μm) quartz sand (Northwest Olivine Co.), and (3) total volume of 4 ml in the 48 \times 8.5 mm Petri dishes used as feeding containers. In addition, a 0.5% by weight amount of Tetramin was mixed in. Each composite was blended with sea water until pasty. After gentle submersion of the feeding containers in the sea-water tables, 10 individuals of *H. florida*, in their tubes, were placed on the mixtures' surfaces. Feeding times

ranged from 1.5 to 3 h; 10 surface sediment samples were then taken with a microspatula and stored for analysis. Animals, many of which had added to their tubes from the bead mixture, were recovered and fixed in 20% formalin. After fixation, the worms were inspected to see if at least five individuals had ingested beads. If fewer than this number contained beads in their foreguts, feeding on that bead mixture was repeated. Preservation in 80% ethanol followed.

Methods of assessment of the relative proportions of each bead type from the guts and ambient sediment samples followed the procedures described in Self & Jumars (1978). Foregut samples from *Thelepus crispus* individuals were obtained from a region anterior to setiger 6. Beads were distinguished by size, refractive index, transparency ($\rho = 1.23$, polystyrene beads being opaque), or a combination of these differences.

ANALOG MODELS

Additional experiments were conducted to explore hypothetical mechanisms of particle selection. Three analogs of feeding tentacles were employed. (1) A flat, rigid, adhesive surface (two-sided adhesive tape attached to a glass slide), (2) a thin (0.1 mm), and (3) a thick (1 mm), flat, adhesive surface (Vaseline petroleum jelly attached to a glass slide). In addition, we investigated the effect of application pressure by placing metal bolts of two weights (weights in water 80.8 g and 34.4 g) on the slides. A bead mixture (88 μm , $\rho = 2.42$, with 15.4 μm , $\rho = 1.06$) previously employed in the *Hobsonia florida* selection experiment was used in this series. The ambient surface bead proportions had been determined previously.

A glass microscope slide, 3.5 \times 2.5 cm \times 1 mm, was used for all the flat surface treatments. Two-sided adhesive tape was attached to the slide; then a 3-mm strip was cut away from the periphery with a razor blade to minimize edge effects. For the petroleum jelly treatments, the slide was heated in a glass Petri dish. The jelly was then placed on the slide and allowed to melt, covering the slide surface to the desired thickness. Borders were trimmed after the jelly had solidified, again to minimize edge effects.

Petri dishes containing the bead mixtures were submerged under 8 cm of fresh water in a plastic container. The slide was then placed gently onto the mixture's surface and one of the weights placed on top of the slide. After ≈ 30 s, the weight was removed from the slide, and the slide lifted off the sediment surface and out of the water bath for sampling of the adhering beads. Ten strips of tape were individually cut away from the slide with a razor blade and bead proportions determined. Adhesion of particles to the tape appeared strong; particles remained attached even after being disturbed by the passing razor blade. Sampling of the petroleum jelly slides entailed removal of the jelly and adherent particles from 10 locations (away from the borders) with a microspatula, then melting these subsamples onto slides for determination of bead proportions.

STATISTICAL PROCEDURES

Standard nonparametric statistics (Tate & Clelland, 1957; Hollander & Wolfe, 1973) were employed for hypothesis testing. In addition, a novel, unbiased technique (Cleveland, 1979) for smoothing two-dimensional scatter plots was used in those experiments where the volume of data required such a procedure. This procedure is a new and valuable means for smoothing data which are not collected at regular intervals along the abscissa.

Selectivity was quantified as the logarithm (base 10, hereafter denoted simply as "log") of the odds ratio (Gabriel, 1979). The odds ratio (equivalent to method 4 of Cock, 1978) is calculated as:

$$\frac{P_1 q_2}{P_2 q_1},$$

where P_1 = proportion of diet comprised by a given particle type; q_1 = proportion of diet comprised by all other assayed particle types, and $P_1 + q_1 = 1$; P_2 = proportion of ambient particle mixture comprised by the given particle type; q_2 = proportion of ambient particle mixture comprised by all other assayed particle types, and $P_2 + q_2 = 1$.

The log of the odds ratio has the attributes that wide ranges of preference may be accommodated in a single figure and that interpretation is straightforward. For example, if the log of the odds ratio equals 2, 99 beads of the experimental type (P) are taken for every control bead (q); with the log of the odds ratio equal to 3, the odds are 999 : 1. Obviously, if $\approx 10^2$ beads are counted (as done here because of limits in gut volume), an odds ratio as high as 3 can never be realized. Comparable information is more difficult to extract from other indices of electivity (Cock, 1978).

RESULTS AND DISCUSSION

SELECTIVITY-VERSUS-DISTANCE EXPERIMENT

The slope (if not the intercept) of the curve in Fig. 1 is in accord with the prediction of increasing selectivity for lighter beads with increasing transport distance along the tentacle, and the fit is amazingly good. Closer examination, however, reveals several problems with the facile interpretation of increasing selectivity as a function of increasing distance of transport. Analysis of residuals suggests that most of the remaining scatter ($P = 0.063$ in a stepwise linear regression) can be explained as a function of animal size (volume), larger animals showing apparently *lower* selectivity. Another result barring straightforward interpretation according to our a priori hypothesis invoking loss of the less preferred particle during transport along a tentacle is the fact that the intercept of the curve does not correspond with the bead proportions in the starting mixture.

A more parsimonious and consistent (with subsequent experiments as well) alternative explanation of these results, unfortunately, is that the surficial layer of the bead

source gradually, over the 4-h experiment, is depleted of the preferred lighter bead type. The larger the animal and the shorter the distance to the bead source, the greater is the

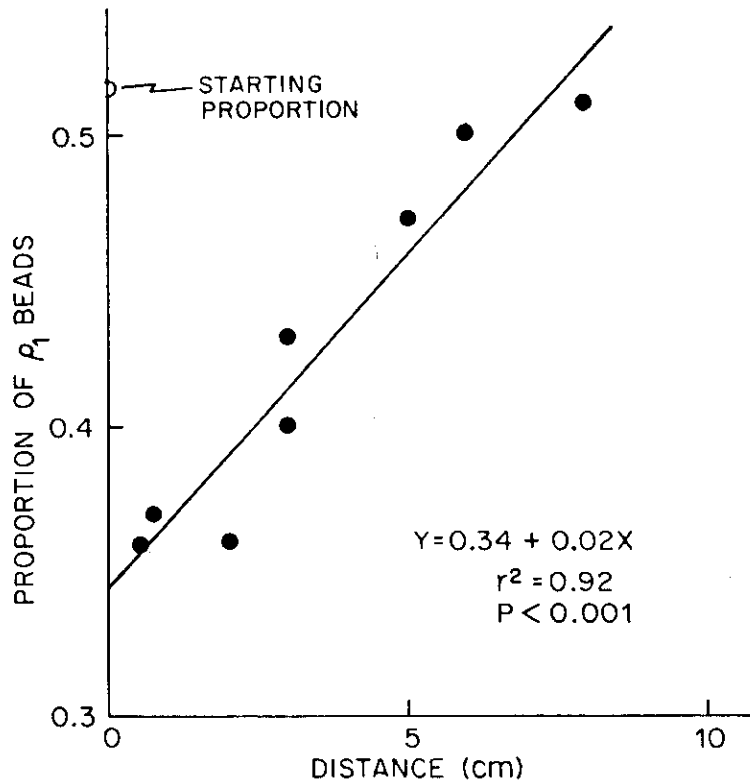


Fig. 1. Proportions of glass beads having the lower specific gravity (ρ_1) found in the foreguts of *Thelepus crispus* (Polychaeta, Terebellidae) placed at various distances from identical starting mixtures ($\rho_1 = 2.99$, $\rho_2 = 3.99$; $\mu_1 = \mu_2 = 52 \mu\text{m}$): animal sizes were randomized to avoid potentially confounding the effects of animal size and distance to food source; flow was minimized in this experiment.

alteration of the bead mixture remaining on the slide. Implicit in this interpretation is the idea that selection occurs at the point where material initially is gathered onto the tentacle, most often near the tentacle tip (Dales, 1955, and pers. obs.).

DEPLETION EXPERIMENT

A straightforward test of the ability to select at the point of pick-up is the depletion experiment. The results (Fig. 2) show that in the mixture of four different particles of similar sizes but differing specific gravities, depletion of the preferred (lighter in weight) particles does occur. These results do not negate the possibility of sorting during transport along a tentacle, but they do show that substantial selection can occur without such transport, presumably at the point of pick-up (no rejection having been observed).

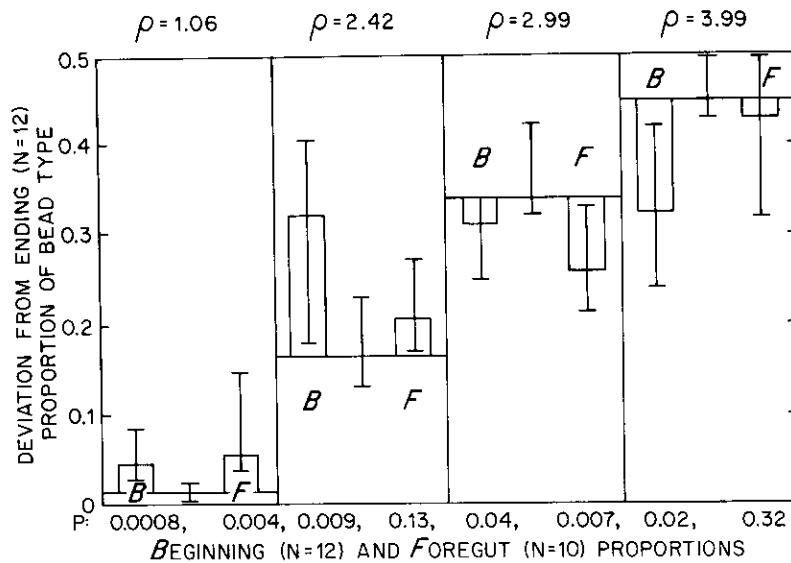


Fig. 2. Median proportions of 50- μ m to 52- μ m beads of various specific gravities (ρ) from the before (B) and after (horizontal line) feeding bead mixtures, and *Thelepus crispus* foreguts (F); error bars, 95% nonparametric confidence limits of medians; P, two-tailed Mann-Whitney U probability that before-versus-after and foregut-versus-after proportions were drawn from distributions having the same median; N, number of samples of the bead mixture or foreguts analyzed.

FLOW SENSITIVITY EXPERIMENT

If passive loss of less preferred particles during transport along a tentacle were a major factor in selectivity, one would expect increasing loss to enhance this selectivity. No such enhancement is evident in *Thelepus crispus* (Fig. 3), *Hobsonia florida* (Fig. 4), *Pseudopolydora kempji japonica* (Fig. 4), or *Pygospio elegans* (Fig. 4), exposed to fluid shears produced by heightened flow velocities. With each species studied, the proportion of individuals successfully feeding (i.e., containing enough beads in the foregut to allow a quantitative analysis) decreased at increased shear velocities. The apparently lower selectivity for the beads of lowest specific gravity at high shears in *Thelepus crispus* (Fig. 3) is an artifact. This shear velocity is just below that required to erode the lightest glass beads ($\rho = 2.42$); winnowing of the plastic ($\rho = 1.06$) beads was apparent during the run.

These data do not preclude effects of increased fluid shear on selectivity. The transport along the tentacles of larger particles with correspondingly greater drag certainly would be impeded by enhanced flow velocity (Taghon, 1982). The present experiments, however, suffice to demonstrate that, within the experimental size class of particles, loss of particles from the tentacles is not a major source of apparent selective ability. Again, the results are consistent with the idea that a major component of selection occurs at the point of particle pick-up.

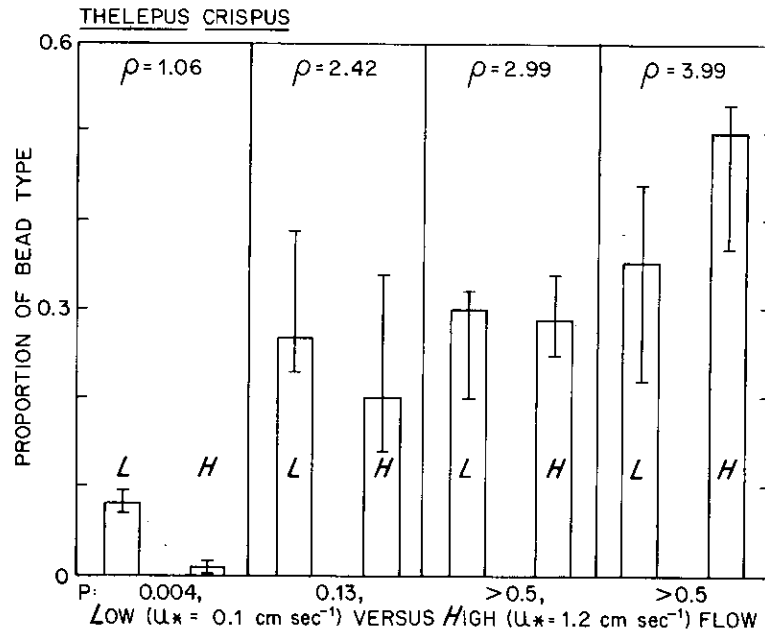


Fig. 3. Median proportions of 50- μm to 52- μm beads of various specific gravities (ρ) in the foreguts of *Thelepus crispus* individuals subjected to high and low flow conditions: error bars, 97% nonparametric confidence limits of medians; P , two-tailed Mann-Whitney U probability that foregut proportions were drawn from distributions having the same median.

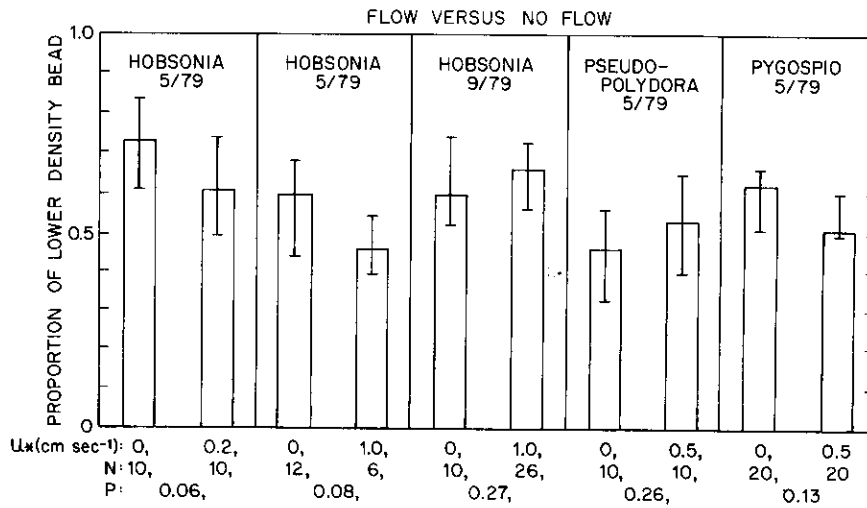


Fig. 4. Median proportions of 52- μm glass beads having the lower specific gravity in the foreguts (*Hobsonia*) or midguts (spionids) of animals in various flow regimes: error bars are 95% nonparametric confidence limits of medians; u_* , boundary shear stress; N , number of foreguts or midguts analyzed; P , two-tailed Mann-Whitney U probability that gut proportions were drawn from distributions having the same median.

Neither the terebellid (*T. crispus*) nor the ampharetid (*Hobsonia florida*) appears able to deal effectively with high flows or with particles in transport. Tentacles in both these species trail passively downstream at the higher flow velocities, and the animals frequently withdraw into their tubes instead of remaining exposed to the buffeting of near-bed turbulence. As opposed to the two spionids (Taghon *et al.*, 1980), neither of these terebellimorph polychaetes appears to have the musculature or other devices (e.g., the flow-baffling tube cap in the terebellid *Lanice conchilega*) needed to actively capture and retain material in bedload or suspended load transport.

PALP REMOVAL EXPERIMENT

The palp removal experiment shows most clearly (Fig. 5) that transport along a tentacle is unnecessary for selection to occur. Animals without palps feed by apressing

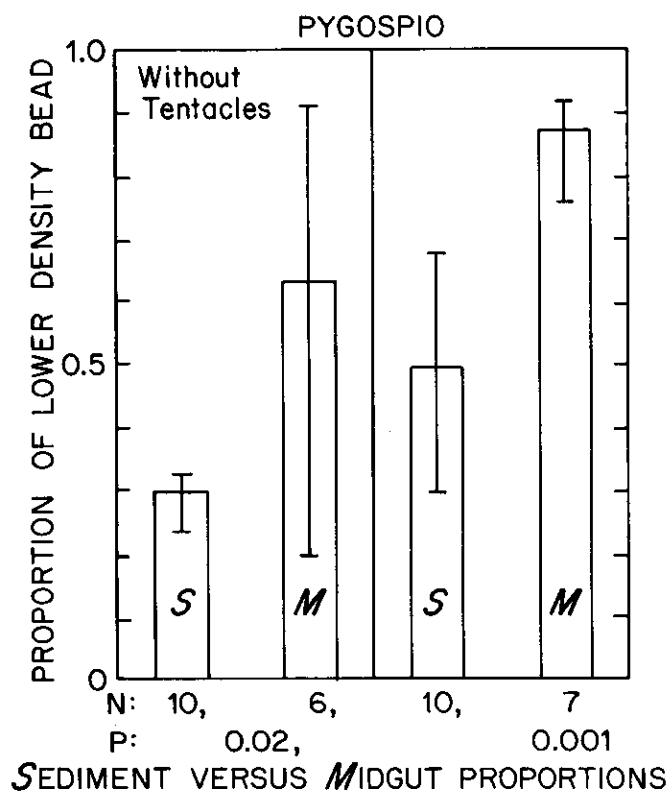


Fig. 5. Median proportions of 52- μ m glass beads having the lower specific gravity from sediment samples (S) and animal midguts (M); N, number of sediment samples or midguts analyzed; P, two-tailed probability that sediment and midgut proportions were drawn from distributions having the same median; error bars are 97% nonparametric confidence limits of medians.

their everted pharynges to the sediments and then retracting the sediment-coated pharynges. Therefore, these results are quite direct evidence of selection at the initial point of pick-up. The value of the dehiscent tentacles may not immediately be apparent from the figure; they decrease variability in selective ability (error bars in Fig. 5), increase the effective feeding radius, and decrease the probability of mortal contact with predators (Woodin, in prep.).

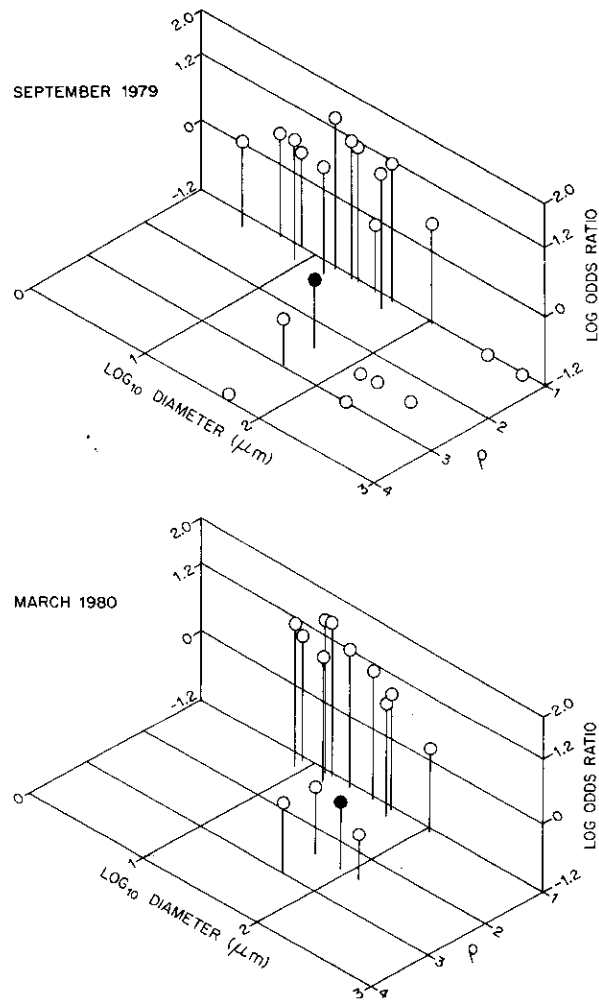


Fig. 6. Median values of particle preference (log of the odds ratio) by *Hobsonia florida* versus log of the diameter and specific gravity (ρ) of beads mixed with 52- μm , $\rho = 2.42$ (September 1979) or 88- μm , $\rho = 2.42$ (March 1980) control beads (darkened circles): 1 to 12 foreguts and 10 surface samples per bead mixture were analyzed.

EMPIRICAL DESCRIPTION OF SELECTIVITY

Selection does occur, then, at least at the point of pick-up. On the basis of a limited variety of experimental particles, Self & Jumars (1978) suggested that a single resource axis (i.e., particle size) was insufficient to characterize selectivity and that both particle size and particle weight (specific gravity) are involved in the mechanics of particle selection by tentaculate deposit-feeders. Experiments with a wider variety of particles (Fig. 6) bear out this assertion. The general tendency is for increasing preference with decreasing specific gravity and decreasing particle diameter, but (cf. Fig. 6) the trend may be reversed for the smallest particles. Two-dimensional plots (Fig. 7) show more clearly that selectivity is a monotonic function neither of particle size nor of particle weight (the most obvious function of both size and specific gravity). The frequency of filled guts also decreases (Fig. 7) with increasing mean particle size of the bead mixture,

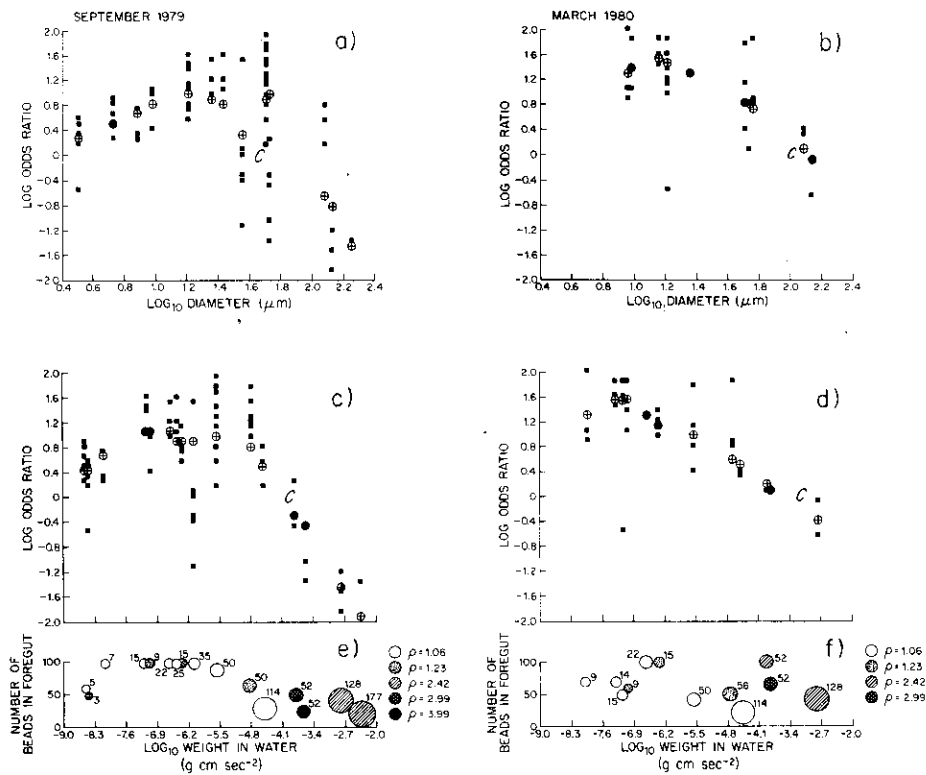


Fig. 7. Particle preference (log of the odds ratio) by *Hobsonia florida* plotted against log of the diameter (a, b) and log of the particle weight (c, d) in sea water of beads mixed with 52- μm , $\rho = 2.42$ (September 1979, a, c) or 88- μm , $\rho = 2.42$ (March 1980, b, d) control beads (C); ■, particle preference by *H. florida* individuals; ⊕, results of unbiased smoothing technique; median number of beads in foregut (maximum counted were 100) plotted against log of the particle weight in sea water in e, Sept. 1979 and f, March 1980; particle sizes (in μm) are indicated in the two lower graphs.

and, as might be expected, there appears to be a size cut-off above which particle ingestion ceases irrespective of particle weight.

ANALOG MODELS

In an effort to understand whether selection of the above-described type would result from any arbitrary geometry of collection apparatus and any adhesive, we performed simple experiments with adhesive-coated slides. Selectivity by the slides was precisely opposite in direction (Fig. 8) to the general trend in *Hobsonia florida*. Observations

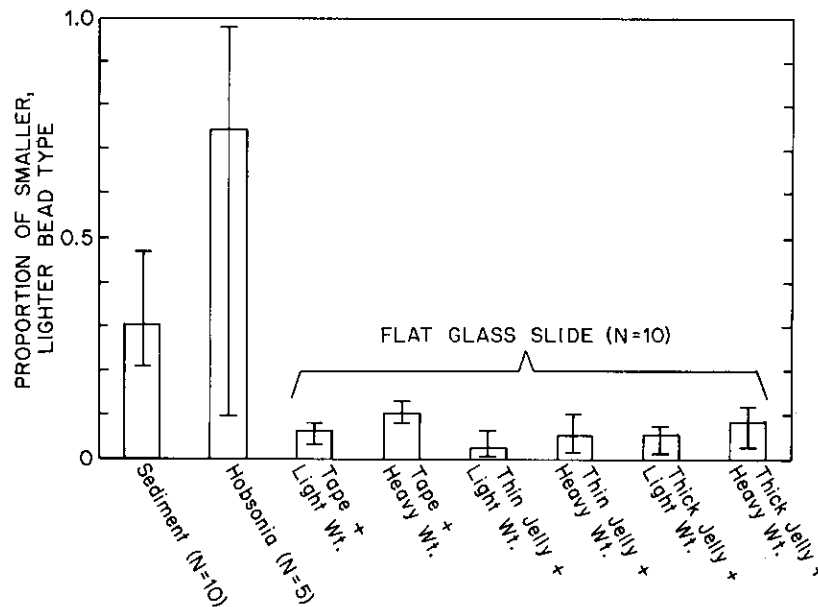


Fig. 8. Particle preference of *Hobsonia florida* compared to adhesive-coated glass slides: the bead mixture consisted of 88- μm , $\rho = 2.42$ and 15.4- μm , $\rho = 1.06$ beads.

through a dissecting microscope suggested that, once contacted by the adhesive, very few particles dropped from the slide. Despite the small number of replicates (10 per treatment), two-way analysis of variance (suitably arcsine transformed cf. Sokal & Rohlf, 1969) revealed a barely significant difference ($P \cong 0.04$) among the three adhesives and a strong difference ($P \cong 0.001$) between the two applied weights in the proportion of smaller particles retained. No statistical interaction effect was found ($P \cong 0.93$). Tentacle geometry, behavior in tentacle deployment (e.g., pressure applied), and/or adhesive character (including thickness) must account for the disparity between our analogs and real tentacle feeders.

HEURISTIC MODEL

If indeed few particles were lost, why did the adhesive-coated slides show such strong bias toward the larger particles? The principles of stereology (Underwood, 1968) provide a ready qualitative answer and a crude quantitative approximation, but one that apparently is satisfactory to first order. We determine relative bead proportions (by number) in the ambient sediments by randomly sampling volumes of the mixture (p. 54). Suppose that the mixture were embedded in epoxy and thin sectioned. In what numerical ratio would beads be encountered (or "transected," in the jargon of stereology)? The Delesse principle (Weibel, 1963) provides a ready answer.

Suppose a mixture of spherical bead types of varying size classes, and adopt the following notation:

Q_i = number of beads of the i th size class per unit volume V_T ;

n_i = number of transections of the i th size class per unit area in a random (thin) section through the unit volume V_T ;

V_i = volumetric fraction of bead type $i = Q_i v_i / V_T$;

d_i = diameter of the i th particle type;

v_i = individual volume of i th particle type.

According to the Delesse principle, the areal fraction of the i th particle type in a random thin section, on the average, will equal its volumetric fraction in the sampled volume. [A more general formulation, needed when particle shapes vary, can be found in Weibel (1963) or Underwood (1968).] Mathematically (as derived by Weibel, 1963), this relationship can be expressed as $(n_i)^{3/2} = Q_i (V_i)^{1/2}$. Algebraically it is then relatively easily derived that for particles of similar shape $(n_i/n_j) = (d_i Q_i / d_j Q_j)$. In words, the relative probability of transecting or contacting a bead of a given size is proportional to both its relative diameter and its relative abundance.

Imagine, now, a slide appressed to the surface of a volume of particles. Because of the surface relief not incorporated into the thin-section derivation above, the bias toward contacting larger particles will be even greater than that indicated by the Delesse principle, i.e., one would expect that

$$\frac{n_i}{n_j} < \frac{d_i Q_i}{d_j Q_j} \text{ for } d_i < d_j,$$

with the precise numerical value depending on details of grain packing (influenced by pressure applied to the slide). For the ambient sediments of Fig. 8,

$$\frac{d_i Q_i}{d_j Q_j} \cong \frac{15.4 (0.29)}{88 (0.71)} = 0.071.$$

With a thicker layer of adhesive impregnating the surface of the sediment or with greater applied pressure one would expect the bias toward larger particles to decrease. Given all these potential sources of variance, the fit of the analog model results (Fig. 8) to the Delesse prediction is surprising.

A flat microscope slide with a contact area much wider than the largest particle diameter under consideration was chosen to avoid an arbitrary tentacle width and curvature (i.e., in cross-section). As can be visualized readily, the smaller the radius of curvature (of the tentacle cross-sectional perimeter in contact with the sediment), the narrower the tentacle, and the shorter the actual segment upon which particle pick-up occurs, the greater will be the bias toward larger particles. As the extreme of sampling a volume with a line rather than a plane is approached, one would expect the bias to near (assuming $Q_i = Q_j$ and $d_i < d_j$) a factor of d_i^2/d_j^2 (Underwood, 1968). To some minor extent the bias may be counteracted by the rugosity or conformity of the tentacle to the sediment surface, but it is difficult to imagine how the direction of the bias, in terms of probability of contact, could be reversed.

How can selection in this model tentacle be reconciled with the observation of general "preference" for smaller, lighter particles in real animals (e.g., Figs. 6 and 7)? Pick-up in all the species utilized in this study is generally accomplished via a "patting" of the sediment surface by the mucus-coated distal portion of the tentacle. Not all contacted particles are picked up, but on what basis are particles selected at this initial point of contact? With clean particles, there are four possibilities given contact (Fig. 9).

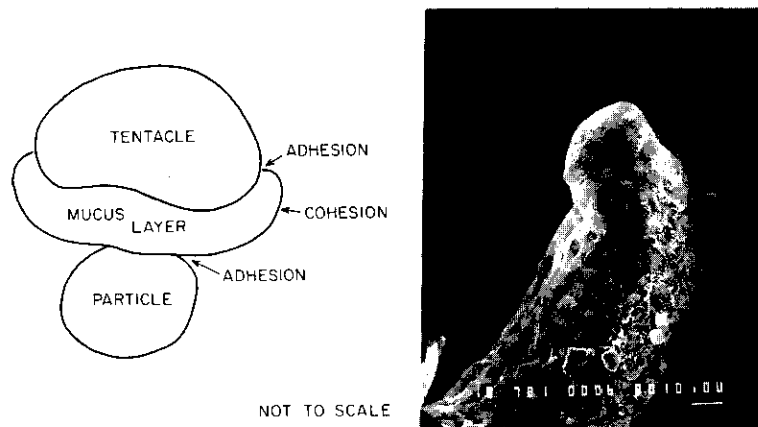


Fig. 9. Schematic representation of particle pick-up by a tentacle and scanning electron micrograph of *Hobsonia florida* tentacle (photographed by D. Miller, University of Washington, at the Friday Harbor Laboratories); bar in micrograph is 10 μm .

(1) The particle may be picked up; (2) the adhesive bond between mucus and the particle may break; (3) the adhesive bond between mucus and tentacle may break; or (4) cohesive bonds within the mucus may separate. Whichever failure mode obtains, the relevant first-order particle characteristic determining the probability of failure is the weight of the particle per unit surface area.

The present data offer no insight into which failure mode is dominant, but the data of Self & Jumars (1978) suggest that the adhesive bond between particle and mucus

is sensitive to surface texture (supporting possibility (2) above). Rough-surfaced particles were selected with greater frequency than were smooth-surfaced ones. Failure at this juncture would also act to minimize the amount of energy lost in the form of mucus. Even in the better studied suspension-feeding guild, little sorting of particles (as opposed to wholesale rejection of a bolus) has been observed after their entrapment in mucus (Foster-Smith, 1975; La Barbara, 1978); it is difficult to believe that such incorporation into a mucous matrix could facilitate the sorting process. Selection at the point of initial contact with a particle would minimize the energy expended as mechanical work, since the particle would neither be lifted nor moved. Given the rates at which deposit-feeders ingest material (Cammen, 1980; Taghon & Jumars, in prep.), this saving would be substantial. If the adhesion is similar in action to the adhesion of cells to surfaces, ionic charge of the surface, and more specific surface chemistry may be important in determining the strength of adhesion (Rappaport *et al.*, 1960; La Barbara, 1978; Grinnell, 1978). This prediction has been borne out recently by Taghon (1982), who has shown selection for glass beads to which protein has been covalently bonded. Whether the failure is adhesive or cohesive, larger particles and particles of higher specific gravity will have greater weight per unit surface area and thus will be less likely to be retained once they are contacted (Smith, 1980).

These considerations lead to a two-step, heuristic, stochastic model of selectivity in deposit-feeders. The first component is the probability of contacting a particle of a given type. Assuming either random or homogeneous distribution of bead types, the probability of contacting a particle will be strongly a function of particle size (Fig. 10). As per the Delesse principle, this probability depends very heavily on the size-frequency distribution of the available sediments – not just upon the characteristics of the particle type in question. It thus makes no sense to speak of an absolute selectivity for a given particle type out of the context of the particle milieu in which it is found. As per our earlier arguments, and contrary to the stochastic feeding model of Baumfalk (1979), larger particles will be contacted more frequently than their relative abundance would suggest. This argument is analogous with that used by Einstein (1950) in developing a “hiding factor” in his bedload transport equations. Smaller sediment grains are less likely to be entrained by a fluid flow to the extent that they are hidden from lift forces by larger grains.

The second step in our model of selection is the conditional probability that, once contacted, a particle will be picked up by the tentacle. In order to produce the pattern of selection observed (e.g., Fig. 7), this step must counteract the effect of particle size on probability of contact. The selection of smaller, lighter particles can be achieved via a controlled adhesive or cohesive strength in the mucus used to pick up particles (Fig. 10). The relevant particle variable here is (submerged) weight of the particle per its unit surface area, and this step in selection thus is independent of the ambient particle size-frequency and weight-frequency distributions. If the adhesive is perfect [$P(\text{pick-up}|\text{contact}) = 1$] for all particles in the mixture, this second step can be ignored.

Together, assuming particle specific gravity were kept constant, these two steps could lead easily to a unimodal curve of selectivity versus particle size (Fig. 10), as observed for *Hobsonia florida* (Fig. 7). Levinton (1979, Fig. 8) has produced a similar unimodal curve for the deposit-feeding snail, *Hydrobia*, but has not discussed the mechanics

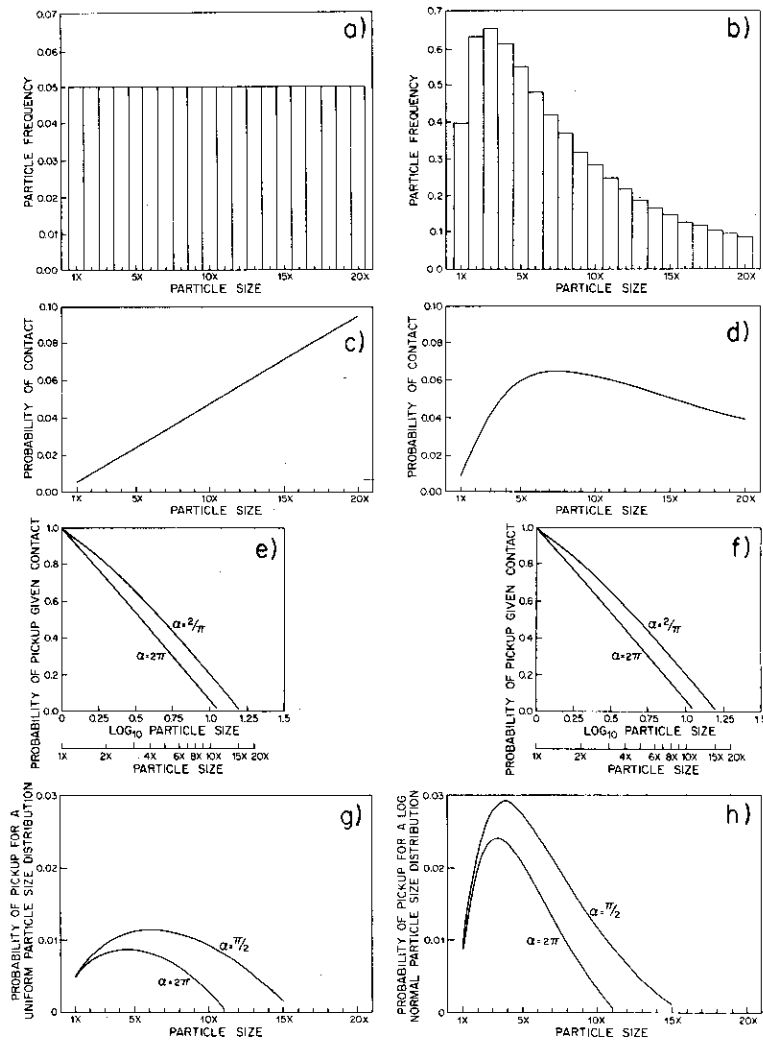


Fig. 10. Two-step model of selectivity by deposit-feeders from uniform and log-normal particle size-frequency distributions: the uniform particle size-frequency distribution, a, is generated by $F(d_i) = 1/20$, where $d_i = 1, 20$; the log-normal particle size frequency distribution, b, is generated by $F(d_i) = [d_i \sigma \sqrt{2\pi}]^{-1} e^{-\frac{1}{2} \left(\frac{\ln(d_i) - \mu}{\sigma} \right)^2}$, where $\mu = 0$, $\sigma^2 = 1$, and $d_i = 1, 20$; for c and d, $P(\text{contact}) = n_i / \sum n_i$, where $n_i = [F(d_i)] \times d_i$ and $d_i = 1, 20$; for e and f, $P(\text{pick-up} | \text{contact}) = \log[E(d_i)] - \log[E(1)] + 1$, where $E(d_i) = 1/(1 + \alpha d_i)$, $\alpha = \pi/2$ or 2π and $d_i = 1, 20$; for g and h, $P(\text{pick-up}) = P(\text{contact}) \times P(\text{pick-up} | \text{contact})$; parameterization of failure probability follows Davenport (1964).

whereby this pattern of selection is achieved. Furthermore, the *Hydrobia* curve may be complicated by changes in feeding behavior with changing particle size (Lopez & Kofoed, 1980).

Our model has several important implications both for resource partitioning among deposit feeders and for co-evolution in the predator-prey system of deposit-feeders and microbes. Differing adhesive strengths of mucus could produce differing particle preferences (Fig. 10), thus suggesting that morphological differences may be inadequate predictors of resource partitioning among species (Taghon, 1982). Can an individual alter or optimize its selective abilities by altering the adhesive strength of its mucus? Has the mucus on feeding tentacles evolved to adhere most effectively to bacteria-covered particles? Do sediment-dwelling bacteria have specific means (e.g., the glycocalyx described by Costerton *et al.*, 1978) of preventing such adhesion? Such questions demonstrate the value of this simple heuristic model and can be addressed readily in the laboratory.

LIMITATIONS OF THE MODEL

The Delesse principle, as applied above, offers only an approximate solution for the probability of contact. This probability may depend both on the relative size and morphology of the feeding appendage and on specific motions of the appendages during feeding (e.g., patting the sediment surface versus probing into it) as well as the characteristics of the adhesive. Furthermore, the probability of contact will be very sensitive to small-scale horizontal (i.e., within a feeding radius) and vertical variations (e.g., due to depletion of the preferred particle types or to physical grading) in grain-size and grain-weight distributions. More exact evaluation of the probability of contact will require kinematic analysis of feeding behavior and Monte Carlo simulation of particle-specific contact probabilities. Whitlatch (pers. comm.) has undertaken such kinematic analysis in concert with the development of more realistic models of particle contact by tentacles. We again repeat that our model includes neither the macrophagous feeding modes of some tentaculate "deposit" feeders nor any post-pick-up rejection mechanisms. Nor is it apparent that this model would be useful for deposit feeders employing a non-adhesive means of particle pick-up (e.g., tellinid bivalves or phoxocephalid amphipods).

It should also be made explicit that the above experimental results bear only upon non-cohesive sediments. If there are cohesive or adhesive bonds between particles, the probability of pick-up given contact depends also upon these inter-particle forces, not simply on individual particle characteristics. The added complexity is homologous with the added complexity of the initial motion problem in the hydraulic erosion of cohesive sediments. A force-balance model of the latter phenomenon can be found in Graf (1971, p. 324). Furthermore, a particle no longer need be contacted directly by the deposit feeder's mucus in order to be picked up. It is clear (e.g., Fig. 2 of Valiela *et al.*, 1979) that deposit-feeding mechanisms have evolved for dealing with cohesive sediments, but

just as hydraulic sediment transport theory begins with the simplest, non-cohesive sediment case, so begins our modeling of the deposit-feeding process.

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REFERENCES

- ALLEN, J. A., 1958. On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). *Philos. Trans. R. Soc. London, Ser. B*, Vol. 241, pp. 421-484.
- ALLER, R. C. & J. Y. YINGST, 1978. Biogeochemistry of tube-dwellings: a study of the sedentary polychaete *Amphitrite ornata* (Leidy). *J. Mar. Res.*, Vol. 36, pp. 201-254.
- BAUMFALK, Y. A., 1979. Heterogenous grain size distribution in tidal flat sediment caused by bioturbation activity of *Arenicola marina* (Polychaeta). *Neth. J. Sea Res.*, Vol. 13, pp. 428-440.
- CADEE, G. C., 1976. Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea. *Neth. J. Sea Res.*, Vol. 10, pp. 440-460.
- CAMMEN, L. M., 1980. Ingestion rate: an empirical model for aquatic deposit feeders and detritivores. *Oecologia (Berlin)*, Vol. 44, pp. 303-310.
- CHING, C. V., 1977. Studies on the small grey mullet *Liza malinoptera* (Valenciennes). *J. Fish Biol.*, Vol. 11, pp. 293-308.
- CLEVELAND, W. S., 1979. Robust locally weighted regression and smoothing scatter plots. *J. Am. Stat. Assoc.*, Vol. 74, pp. 829-836.
- COCK, J. M., 1978. The assessment of preference. *J. Anim. Ecol.*, Vol. 47, pp. 805-816.
- COSTERTON, J. W., G. G. GEESY & K.-J. CHENG, 1978. How bacteria stick. *Sci. Am.*, Vol. 238, pp. 86-95.
- CURTIS, L. A. & L. E. HURD, 1981. Nutrient procurement strategy of a deposit-feeding estuarine neogastropod, *Ilyanassa obsoleta*. *Estuarine Coastal Mar. Sci.*, Vol. 13, pp. 277-285.
- DALES, R. P., 1955. Feeding and digestion in terebellid polychaetes. *J. Mar. Biol. Assoc. U.K.*, Vol. 34, pp. 55-79.
- DAUER, D. M., C. A. MAYBURY & R. M. EWING, 1981. Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.*, Vol. 54, pp. 21-38.
- DAVENPORT, A. G., 1964. The buffeting of large superficial structures by atmospheric turbulence. *Ann. N. Y. Acad. Sci.*, Vol. 116, pp. 135-160.
- EINSTEIN, H. A., 1950. The bed-load function for sediment transportation in open channel flows. U.S. Dept. Agriculture Tech. Bull. 1026, 70 pp. (Reprinted as Appendix B in Shen, H. W., editor, 1972. *Sedimentation*. Fort Collins, Colorado.)
- FAUCHALD, K. & P. A. JUMARS, 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 16, pp. 193-284.
- FELLER, R. J., G. L. TAGHON, E. D. GALLAGHER, G. E. KENNY & P. A. JUMARS, 1979. Immunological methods for food web analysis in a soft-bottom benthic community. *Mar. Biol.*, Vol. 54, pp. 61-74.
- FENCHEL, T., L. H. KOFOED & A. LAPPALAINEN, 1975. Particle size-selection of two deposit feeders: the amphipod *Corophium volutator* and the prosobranch *Hydrobia ulvae*. *Mar. Biol.*, Vol. 30, pp. 119-128.
- FOSTER-SMITH, R. L., 1975. The role of mucus in the mechanism of feeding in three filter feeding bivalves. *Proc. Malacol. Soc. London*, Vol. 41, pp. 571-588.

- GABRIEL, W. L., 1979. Statistics of selectivity. In, *Gutshop '78: fish food habits studied*, edited by S.J. Lipovsky & C. A. Simenstad (Proc. Second Pacific Northwest Technical Workshop), Washington Sea Grant, Univ. of Washington, Seattle, Washington, pp. 62-66.
- GEORGE, J. D., 1964. The life history of the cirratulid worm, *Cirriiformia tentaculata*, on an intertidal mudflat. *J. Mar. Biol. Assoc. U.K.*, Vol. 44, pp. 47-65.
- GHIOLD, J., 1979. Spine morphology and its significance in feeding and burrowing in the sand dollar *Mellita quinquesperforata* (Echinodermata: Echinodea). *Bull. Mar. Sci.*, Vol. 29, pp. 481-490.
- GOODBODY, I., 1960. The feeding mechanism in the sand dollar *Mellita sexiesperforata* (Leske). *Biol. Bull. (Woods Hole, Mass.)*, Vol. 119, pp. 80-86.
- GORDON, D. C., 1966. The effects of the deposit feeding polychaete *Pectinaria gouldii* on the intertidal sediments of Barnstable Harbor. *Limnol. Oceanogr.*, Vol. 11, pp. 327-332.
- GRAF, W. H., 1971. *Hydraulics of sediment transport*. McGraw-Hill Book Co., N.Y., 513 pp.
- GRINNELL, F., 1978. Cellular adhesiveness and extracellular substrata. *Int. Rev. Cytol.*, Vol. 53, pp. 65-144.
- HOLLANDER, M. & D. A. WOLFE, 1973. *Nonparametric statistical methods*. John Wiley & Sons, New York, N.Y., 503 pp.
- HUGHES, R. N., 1980. Optimal foraging theory in the marine context. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 18, pp. 423-481.
- HUGHES, T. G., 1973. Deposit feeding in *Abra tenuis* (Bivalvia: Tellinacea). *J. Zool.*, London, Vol. 171, pp. 499-512.
- HUGHES, T. G., 1975. The sorting of food particles by *Abra* sp. (Bivalvia: Tellinacea). *J. Exp. Mar. Biol. Ecol.*, Vol. 20, pp. 137-156.
- HUGHES, T. G., 1979. Mode of life and feeding in maldanid polychaetes from St. Margaret's Bay, Nova Scotia. *J. Fish. Res. Board Can.*, Vol. 36, pp. 1503-1507.
- HYLLEBERG, J. & V. F. GALLUCCI, 1975. Selectivity in feeding by the deposit-feeding bivalve *Macoma nasuta*. *Mar. Biol.*, Vol. 32, pp. 167-178.
- JØRGENSEN, C. B., 1966. *Biology of suspension feeding*. Pergamon Press, Oxford, 357 pp.
- JØRGENSEN, C. B., 1981. A hydro-mechanical principle for particle retention in *Mytilus edulis* and other ciliary suspension feeders. *Mar. Biol.*, Vol. 61, pp. 277-282.
- KIKUCHI, E. & Y. KURIHARA, 1977. In vitro studies on the effects of tubificids on the biological, chemical, and physical characteristics of submerged rice field soil and overlying water. *Oikos*, Vol. 29, pp. 348-356.
- KUNZE, J. & D. T. ANDERSON, 1979. Functional morphology of the mouthparts and gastric mill in the hermit crabs *Clibanarius taeniatus* (Milne Edwards), *Clibanarius virescens* (Krauss), *Paguristes squamosus* (McCulloch) and *Dardanus setifer* (Milne Edwards) (Anomura: Paguridae). *Aust. J. Mar. Freshwater Res.*, Vol. 30, pp. 683-722.
- LA BARBARA, M., 1978. Particle capture by a Pacific brittle star: experimental test of the aerosol suspension feeding model. *Science*, Vol. 201, pp. 1147-1149.
- LEVINTON, J. S., 1979. Deposit-feeders, their resources, and the study of resource limitation. In, *Ecological processes in coastal and marine systems*, edited by R. J. Livingston, Plenum Press, N.Y., pp. 117-141.
- LEVINTON, J. S., 1980. Particle feeding by deposit feeders: models, data, and a prospectus. In, *Marine benthic dynamics*, edited by K. R. Tenore & B. C. Coull, Univ. South Carolina Press, Columbia, pp. 423-439.
- LOPEZ, G. R. & L. K. KOFOED, 1980. Episammic browsing and deposit-feeding in mud snails (Hydrobiidae). *J. Mar. Res.*, Vol. 38, pp. 585-599.
- MACGINITIE, G. E., 1941. On the method of feeding of four pelecypods. *Biol. Bull. (Woods Hole, Mass.)*, Vol. 80, pp. 18-25.
- MARAIS, J. F. K., 1980. Aspects of food intake, food selection, and alimentary canal morphology of *Mugil cephalus* (Linnaeus, 1758 [sic]), *Liza tricuspidens* (Smith, 1846), *L. richardsoni* (Smith, 1846), and *L. dumerili* (Steindachner, 1869). *J. Exp. Mar. Biol. Ecol.*, Vol. 44, pp. 193-209.
- MEADOWS, P. S. & A. H. BIRD, 1974. Behaviour and local distribution of the fresh water oligochaete *Nais pardalis* (Piguet) (Family Naididae). *Hydrobiologia*, Vol. 44, pp. 265-275.
- MIDDLETON, G. V. & J. B. SOUTHARD, 1978. *Mechanics of sediment movement*. Lecture notes for short course no. 3, Eastern Section, Society of Economic Paleontologists and Mineralogists, 180 pp.
- NOWELL, A. R. M., P. A. JUMARS & J. E. ECKMAN, 1981. Effects of biological activity on the entrainment of marine sediments. *Mar. Geol.*, Vol. 42, pp. 133-153.
- ODUM, W. E., 1968. The ecological significance of fine particle selection by the striped mullet *Mugil cephalus*. *Limnol. Oceanogr.*, Vol. 13, pp. 92-98.
- POWELL, E. N., 1977. Particle size selection and sediment reworking in a funnel feeder, *Leptosynapta tenuis* (Holothuroidea, Synaptidae). *Int. Rev. Gesamten Hydrobiol.*, Vol. 62, pp. 385-408.

- PYKE, G.H., H.R. PULLIAM & E.L. CHARNOV, 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.*, Vol. 52, pp. 137-154.
- RAPPAPORT, C., J.P. POOLE & H.P. RAPPAPORT, 1960. Studies on properties of surfaces required for growth of mammalian cells in synthetic medium. *Exp. Cell Res.*, Vol. 20, pp. 465-510.
- RUBENSTEIN, D.I. & M.A.R. KOEHL, 1977. The mechanisms of filter feeding: some theoretical considerations. *Am. Nat.*, Vol. 111, pp. 981-994.
- SCHEIBLING, R.E., 1980. The microphagous feeding behavior of *Oreaster reticulatus* (Echinodermata: Asteroidea). *Mar. Behav. Physiol.*, Vol. 7, pp. 225-232.
- SELF, R.F.L. & P.A. JUMARS, 1978. New resource axes for deposit feeders? *J. Mar. Res.*, Vol. 36, pp. 627-641.
- SCHICK, J.M., K.C. EDWARDS & J.H. DEARBORN, 1981. Physiological ecology of the deposit-feeding sea star *Ctenodiscus crispatus*: ciliated surfaces and animal-sediment interactions. *Mar. Ecol. Progr. Ser.*, Vol. 5, pp. 165-184.
- SLOAN, N.A. & B. VON BODUNGEN, 1980. Distribution and feeding of the sea cucumber *Isostichopus badionotus* in relation to shelter and sediment criteria of the Bermuda platform. *Mar. Ecol. Progr. Ser.*, Vol. 2, pp. 257-264.
- SMITH, A.B., 1980. The structure, function, and evolution of tube feet and ambulacral pores in irregular echinoids. *Paleontology*, Vol. 23, pp. 29-83.
- SOKAL, R.R. & F.J. ROHLF, 1969. *Biometry*. W.H. Freeman & Co., San Francisco, 766 pp.
- TAGHON, G.L., 1981. Beyond selection: Optimal ingestion rate as a function of food value. *Am. Nat.*, Vol. 118, pp. 202-214.
- TAGHON, G.L., 1982. Optimal foraging by deposit-feeding invertebrates: roles of particle size and organic coating. *Oecologia (Berlin)*, Vol. 52, pp. 295-304.
- TAGHON, G.L., R.F.L. SELF & P.A. JUMARS, 1978. Predicting particle selection by deposit feeders: a model and its implications. *Limnol. Oceanogr.*, Vol. 23, pp. 752-759.
- TAGHON, G.L., A.R.M. NOWELL & P.A. JUMARS, 1980. Induction of suspension feeding in spionid polychaetes by high particulate fluxes. *Science*, Vol. 210, pp. 262-264.
- TATE, M.W. & R.C. CLELLAND, 1957. *Nonparametric and shortcut statistics*. Interstate Printers and Publishers, Inc., Danville, Illinois, 171 pp.
- TEVESZ, M.J.S., F.M. SOSTER & P.L. MCCALL, 1980. The effects of size-selective feeding by oligochaetes on the physical properties of river sediments. *J. Sediment. Petrol.*, Vol. 50, pp. 561-568.
- TIETJEN, J.H. & J.J. LEE, 1975. Axenic culture and uptake of dissolved organic substances by the marine nematode, *Rhabditis marina* (Bastian). *Cah. Biol. Mar.*, Vol. 16, pp. 685-694.
- UNDERWOOD, E.E., 1968. Stereology, or the quantitative evaluation of microstructures. *J. Microsc.*, Vol. 89, pp. 161-180.
- VALIELA, I., L. KOUMJIAN, T. SWAIN, J.M. TEAL & J.E. HOBBIIE, 1979. Cinnamic acid inhibition of detritus feeding. *Nature (London)*, Vol. 280, pp. 55-57.
- WEIBEL, E.R., 1963. Principles and methods for the morphometric study of the lung and other organs. *Lab. Invest.*, Vol. 12, pp. 131-155.
- WHITLATCH, R.B., 1974. Food-resource partitioning in the deposit feeding polychaete *Pectinaria gouldii*. *Biol. Bull.*, Vol. 147, pp. 227-235.
- WHITLATCH, R.B., 1980. Patterns of resource utilization and coexistence in marine intertidal deposit-feeding communities. *J. Mar. Res.*, Vol. 38, pp. 743-765.
- YALIN, M.S., 1972. *Mechanics of sediment transport*. Pergamon Press, N.Y., 290 pp.