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Mechanisms of particle selection by tentaculate suspension feeders during encounter, retention, and handling

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Abstract

Selection among food particles can occur during any of the successive steps in suspension feeding: particle encounter, retention, and handling. We made predictions for mechanical particle-size selection in encounter and retention by tentaculate suspension feeders (e.g., polychaetes, cnidarians, and echinoderms), and we measured concurrent selection during each step in feeding for two species of spionid polychaetes (*Pseudopolydora paucibranchiata* Okuda and *Pseudopolydora kempi japonica* Imajima and Hartman). In flume experiments we measured selection between two sizes of plastic beads was measured in flume experiments using video analyses of encounter and retention, and we determined handling selection by subsequent examination of gut contents. Encounter was strongly biased toward large particles, as predicted for the physical mechanism of direct interception. In contrast, retention was often biased toward small particles, as predicted by a model of the balance of forces on an encountered particle (i.e., an adhesive force which promotes retention vs. drag and lift forces which may cause particle loss). Handling was also biased toward small particles, apparently by active rejection of large particles. Flow speed and palp width affected selection only during particle retention. As predicted by the retention model, the retention bias toward smaller particles was stronger at higher flow speed and for worms with narrower palps. Retention mechanics alone thereby resulted in small worms ingesting relatively fewer large particles (and more small particles) in fast flow than they did in slow flow. Furthermore, in fast flow small worms ingested relatively fewer large particles than did larger worms. Given the wide range of particle sizes and types available in the field, retention mechanics can directly influence feeding ecology by placing constraints of flow speed and appendage size on the diet obtainable by tentaculate suspension feeders.

Keywords: Particle selection; *Pseudopolydora kempi japonica*; *Pseudopolydora paucibranchiata*; Spionid polychaete; Suspension feeding; Tentacle

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1. Introduction

Suspension feeding is a multi-step process, with the possibility of passive mechanical selection or active behavioral selection among food particles occurring at several stages prior to ingestion. A wide variety of potential food items is available in suspension, and selection among them has numerous implications for animal nutrition and food-web dynamics (e.g., Jørgensen, 1966; Sebens and Koehl, 1984; Kiefer and Berwald, 1992). Potential selection criteria include particle size, shape, specific gravity, stickiness, and taste. In order to understand and to predict how selection depends on factors such as particle characteristics, animal morphologies, and flow environments, passive-mechanical and behavioral mechanisms operating during the separate steps in particle capture and handling must be elucidated.

The first step in suspension feeding is particle encounter (Fig. 1). A suspended particle contacts the capture device (e.g., tentacle) by one of several mechanisms: direct interception, inertial impaction, diffusional encounter, or gravitational deposition (Rubenstein and Koehl, 1977). These mechanisms depend on the small-scale fluid and particle dynamics near the particle-capturing structure (reviewed by Shimeta and Jumars, 1991). The second step in suspension feeding is particle retention, which is required for successful capture of an encountered particle. Although some retention mechanisms, such as trapping particles against a sieve structure or securing particles with nematocysts, have been studied extensively, other retention mechanisms, such as mucous adhesion or surface electrostatics, have received less attention (Shimeta and Jumars,

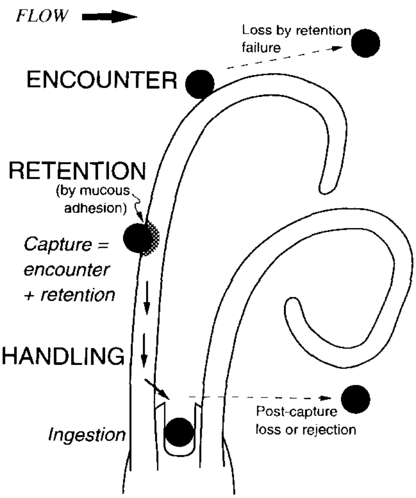

Fig. 1. Component steps in suspension feeding, illustrated for a bitentaculate spionid polychaete. A particle is encountered, then either lost or retained (i.e. captured, depending on a retention mechanism such as mucous adhesion), and finally handled until it is either ingested, rejected, or lost. Shading around the captured particle represents the mucous bond.

1991). The third step in suspension feeding is particle handling, i.e., transport to the mouth by mechanisms such as ciliary beating or motion of the particle-capturing appendage. During post-capture handling, both physical and behavioral mechanisms can determine whether a captured particle is ingested or lost. These mechanisms can include passive mechanical loss due to strong flow forces or sorting limitations, and active behavioral rejection of unwanted particles.

The ingested spectrum of food particles can differ from that available in suspension because of selection during encounter, retention, and/or handling, but no previous study has quantified all of these stages in feeding. Most predictions of mechanical selection by suspension feeders derive from the particle-size dependency in encounter models. However, few tests of models have involved measurement of true particle encounter. More often, particle capture or ingestion has been measured, and the steps of retention and handling have been assumed to involve no losses of particles (reviewed by Shimeta and Jumars, 1991). Several investigators have suggested that reduced capture or ingestion rates in high velocities are caused by strong drag forces that limit particle retention (e.g., Rubenstein and Koehl, 1977; Patterson, 1984; Okamura, 1984, 1985; McFadden, 1986), but this hypothesis has not been verified with quantitative measures of retention efficiencies. Examples of studies that have considered some of the component steps in suspension feeding include that of Appelmans (1994), who investigated particle selection in both capture and handling by an echinoderm larva, and that of Leonard et al. (1988), who separated encounter from retention in their analysis of particle capture by a crinoid. An analogous dissection of the component mechanisms of selection in tentaculate deposit feeding was introduced by Jumars et al. (1982). Taghon (1982) suggested that drag forces in strong flow might shift the deposit-feeding selectivity of spionid polychaetes to smaller particles, which is a hypothesis similar to the one we present below for particle retention by suspension feeders.

We modeled passive mechanical selection based on particle size by tentaculate suspension feeders, emphasizing influences of ambient flow speed and tentacle size on selectivity. By ‘tentaculate suspension feeder’ we mean an animal that captures suspended particles on one or more cylindrical structures that do not allow trapping against a sieve, and that depends primarily on ambient flow to produce a particle flux to these structures. Tentaculate suspension feeders thereby include, e.g., various polychaetes, cnidarians, and echinoderms. Our use of the term ‘tentacle’ includes structures otherwise referred to as, e.g., tentacles, palps, tube feet, and even mucous threads. We focused on particle size because it often relates to food value; e.g. caloric content generally scales with volume among organic particles, and with surface area among organically coated mineral grains. We tested our predictions by measuring selectivity in each step of feeding using two species of spionid polychaetes. Spionids are widely distributed and abundant worms that suspension and deposit feed with a pair of mucus-coated palps (e.g., Taghon et al., 1980; Dauer et al., 1981). Shimeta (1996) found that particle size-selective ingestion by the spionid *Pseudopolydora paucibranchiata* varied with ambient flow speed and animal size in both feeding modes, and he suggested that mechanisms of particle capture on the palps were responsible for the observed patterns of selectivity. Our model predictions and experiments provide a general framework for interpreting such selective suspension feeding.

2. Theory and predictions

2.1. Particle encounter

We predicted that encounter is biased toward larger particles. As explained below, however, we were unable to predict whether the strength of this bias varies with velocity and tentacle size; our null hypothesis was that selective encounter is independent of these variables. We treated only encounter by direct interception, which is considered the predominant mechanism for most non-motile food particles (Shimeta and Jumars, 1991). Our predictions might not apply to those animals and/or situations in which ciliary currents around tentacles (e.g., Mayer, 1994), or responses of cilia to approaching particles (e.g., Strathmann, 1987), influence interception.

Encounter by direct interception occurs when a particle follows a streamline that brings its center within one particle radius of a tentacle (Rubenstein and Koehl, 1977). The particle radius (r_p) itself defines the limiting streamline for contact. Therefore, the volume of water from which particles are encountered (and hence, the encounter rate, E) is directly related to particle size, i.e., $E \propto r_p^n$, where $n > 0$. Encounter is thus biased toward larger particles, and the strength of the bias depends on the exponent, n. Rubenstein and Koehl (1977), Shimeta and Jumars (1991) and Shimeta (1993) gave analytical models for the rate and efficiency of direct interception of spherical particles when both the tentacle Reynolds number (Re_t) and the ratio of particle radius to tentacle radius (r_p/r_t) are less than 0.1 ($Re_t = 2\ r_t\ U/\nu$, where U is free-stream velocity and ν = kinematic viscosity = 0.01 cm^2 s^{-1}). However, many tentaculate suspension feeders (e.g., polychaetes, ophiuroids, crinoids, holothuroids, sea anemones, corals, sea pens) experience $Re_t \geq 1$ because they feed at relatively high velocities with relatively large tentacles, or they experience $r_p/r_t \geq 1$ because they encounter relatively large particles (Shimeta and Jumars, 1991). Increasing Re_t above 0.1 can strengthen the r_p-dependence of encounter rate by enhancing streamline compression around the tentacle (Shimeta and Jumars, 1991). However, increasing r_p/r_t above 0.1 can reduce the r_p-dependence by creating interference to contact that is stronger for larger particles due to interaction between flow fields around the tentacle and the particle (cf. Davies, 1973). Therefore, we determined experimentally the strength of the encounter bias for large particles, as well as its dependence on velocity and tentacle diameter.

2.2. Particle retention

We made the following predictions, each derived below from a model of retention mechanics for an isolated tentacle, where trapping against a sieve cannot occur. First, smaller particles are preferentially retained over larger particles, except when all particles being compared are much smaller than the tentacle diameter. Second, the retention bias toward smaller particles is stronger for narrower tentacles than it is for wider tentacles, except when all tentacles being compared are much larger than the particles. Third, the efficiency of retention (i.e., proportion of encountered particles that are captured) is inversely related to velocity. Fourth, the retention bias toward smaller particles is stronger in faster flow than it is in slower flow. We refer to mucous adhesion throughout this analysis because it is important in retention for a variety of polychaetes, echinoderms, and some cnidarians (e.g., Jørgensen, 1966; Pentreath, 1970; Lewis and Price, 1975; Jumars et al., 1982; Sebens and Koehl, 1984; Lahaye and Jangoux, 1985). Nematocysts (e.g., Mariscal, 1974; Conklin and Mariscal, 1976) and possibly surface electrostatics (e.g., LaBarbera, 1978) are important retention mechanisms for some tentaculate suspension feeders, and our qualitative predictions should apply to these cases as well.

Retention of a particle encountered on an isolated tentacle requires the force promoting adhesion to equal or exceed the sum of the forces resisting adhesion:

$$F_{\mathrm{A}} \geq F_{\mathrm{D}} + F_{\mathrm{L}} + F_{\mathrm{G}}, \tag{1}$$

where F_{A}, F_{D}, F_{L}, and F_{G} are the adhesive, drag, lift and gravitational forces on the particle, respectively. This force balance assumes (1) that prey are not live, or at least not able to exert a significant struggling force against retention, (2) that gravity resists retention, requiring either that the tentacle is oriented vertically or that the particle is not encountered exactly on the top of the tentacle, and (3) that the drag force (oriented downstream) acts in a direction away from the tentacle, requiring that the particle is encountered at any position other than at the center of the upstream side of the tentacle. Indeed, most particles are not encountered along the center, stagnation streamline (Shimeta and Jumars, 1991). The forces can be parameterized for spherical particles and substituted into Eq. (1) as follows:

$$\sigma_{\mathrm{B}} A_{\mathrm{C}} \geq 0.5 \rho C_{\mathrm{D}} \langle u^2 \rangle A_{\mathrm{p}} + 0.5 \rho C_{\mathrm{L}} \langle u^2 \rangle A_{\mathrm{p}} + (\rho_{\mathrm{p}} - \rho) g V_{\mathrm{p}}, \tag{2}$$

where σ_{B} is the breaking stress of the particle-tentacle bond, A_{C} is the area of contact made between the particle and tentacle, C_{D} and C_{L} are the drag and lift coefficients, $\langle u^2 \rangle$ is the average of the squared local velocity over the particle, A_{p} is the exposed cross-sectional area of the particle, ρ_{p} and ρ are the particle and fluid densities, g is the gravitational acceleration, and V_{p} is the particle volume. Particle retention can be quantified as the retention efficiency, R = proportion of encountered particles that are captured.

The gravitational force is generally insignificant relative to the drag and lift forces for most particles under typical feeding conditions. Of the examples in Fig. 2a, only very large organic particles (e.g., larvae) and mineral grains of coarse-silt or larger size can reach $F_{\mathrm{G}} > 0.1\ [F_{\mathrm{D}} + F_{\mathrm{L}}]$, and only in very slow flows ($\leq$order 1 cm s^{-1}). Organic particles (e.g. algal cells) often experience a greater applied force than do denser but smaller mineral grains (Fig. 2b), because of the greater contribution of the drag and lift forces relative to the gravitational force, thus favoring retention of the denser particles. F_{G} can be important for selective retention among similarly sized particles that differ greatly in specific gravity (e.g., a mineral grain and an algal cell), but again only in very slow flows (Fig. 2b). For the sake of clarity in our presentation we assume $F_{\mathrm{G}} = 0$ (although we consider the implications of specific gravity where they might be important). Therefore, retention requires

$$\sigma_B A_C \geq 0.5 \rho \langle u^2 \rangle A_p (C_D + C_L). \tag{3}$$

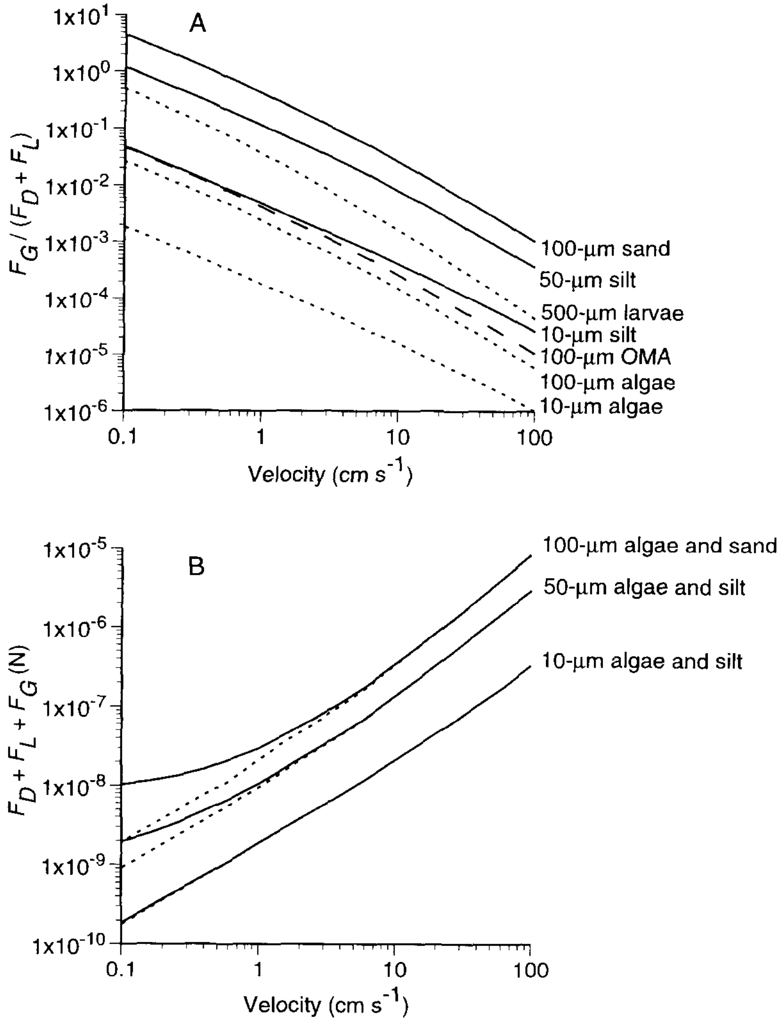

Fig. 2. Calculated(Eq. (2)) drag (F_D), lift (F_L), and gravitational (F_G) forces resisting retention of encountered, spherical particles. Dotted lines represent organic particles, dashed line indicates organic–mineral aggregates (OMA), and solid lines are mineral grains. Values of (ρ_p-rρ) are taken from Gibbs (1985) for OMA, Jackson (1989) for algal cells, Butman (1986) for larva, and $\rho_p-\rho=1.63$ for mineral grains. (A) illustrates the contribution of F_G relative to F_D and F_L. (B) illustrates the influence of particle specific gravity on the sum of forces experienced by particles of similar size (algae and mineral grains).

Our first two predictions concerning selective retention were derived from a qualitative argument considering the dependence of contact area, A_C, on relative sizes of the particle (r_p) and tentacle (r_t). Particles that are much smaller than the tentacle can be well-embedded in mucus upon contact (Fig. 3a). (Tentacle compliance that allows the surface to wrap at least partially around the particle can create a similar effect.) In the

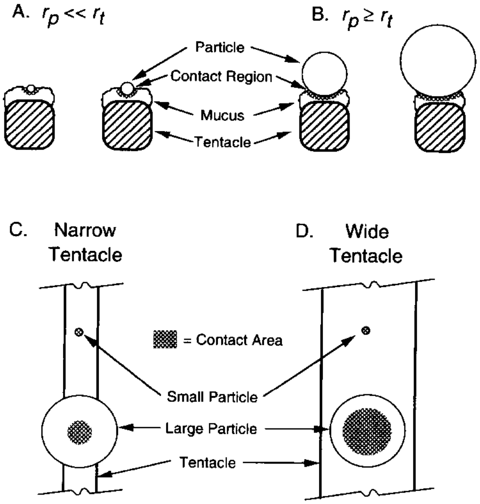

Fig. 3. Contact-area relations between a particle and a tentacle, drawn for mucous retention as an example. Shading represents mucous bond. (A), (B) cross-sectional views through tentacle, coated with mucus on upper surface; r_p and r_t are the radius of the particle and tentacle, respectively. Smaller particles should be retained preferentially over larger particles in case (B). (C),(D) frontal views of tentacle, with mucous bonds visible through particles. The retention bias toward smaller particles should be stronger in case (C) than in case (D).

limit of $r_p << r_t$, particles of different sizes should have a contact area that varies approximately in direct proportion with their surface area ($\propto r_p^2$). In contrast, when the particle size is similar to or larger than that of the tentacle, contact area cannot remain proportional to particle area (Fig. 3b).

The first prediction was therefore that smaller particles are preferentially retained over larger particles, except among particles that are all much smaller than the tentacle diameter. In the latter case ($r_p << r_t$, Fig. 3a), A_C and thus the adhesive force rise at least as rapidly with particle size (approximately $\propto r_p^2$) as do the drag and lift forces. We say 'at least' because, although F_D and F_L depend directly on particle cross-sectional area (A_p), they in fact have functions that are weaker than r_p^2, due to the inverse dependence of the drag and lift coefficients (C_D and C_L) on r_p. For the relevant range of particle Reynolds number, C_D varies from $\propto r_p^{-1.0}$ to ca. $\propto r_p^{-0.4}$ as velocity and/or particle size increase (Vogel, 1994); C_L for hemispheres against a boundary has the same functionality as C_D (Chepil, 1958). In contrast, among particles that are roughly similar to or larger than the size of the tentacle, contact area does not maintain proportionality with particle area (Fig. 3b), and at some point A_C becomes a weaker function of r_p than are the drag and lift forces. The result is that retention is increasingly likely to fail as particle size increases, and thus smaller particles are preferentially retained. (Note that if the gravitational force (F_G) is important, as for very large or dense particles in slow flow (cf. Fig. 2), the retention bias toward small particles can be even stronger, because the sum of forces resisting retention (Eq. (2)) then scales with r_p^3.)

Our second prediction, a corollary to the first, was that variation in tentacle diameter should have virtually no effect on retention if r_t is consistently $>>r_p$; otherwise, the narrower the tentacle, the stronger the bias toward retaining small particles. Tentacles of two different widths can create the same contact area with a small particle that in each case satisfies the condition $r_p<<r_t$ (Fig. 3c, d), and thus they have similar retention efficiency. In contacting a much larger particle, however, the smaller tentacle can have poorer retention than the larger tentacle because of a reduced contact area (Fig. 3c). The retention bias toward smaller particles is therefore stronger among narrower tentacles than it is among wider tentacles.

The third and fourth predictions resulted from the velocity dependence of the drag and lift forces (Eq. (3)). Because these forces increase with velocity, while the adhesive force is independent of velocity, we predicted that retention efficiency falls as velocity rises. Furthermore, we predicted that the bias toward retaining smaller particles increases at higher velocities due to the nonlinearities in the drag and lift forces with respect to velocity and particle size. Larger particles experience a greater increase in (F_D+F_L) in response to rising velocity than do smaller particles. Using our experimental conditions as an example, an increase in velocity from 1.3 to 9.1 cm s^{-1} caused (F_D+F_L) on 80 μm spheres to rise by 1.9×10^{-7} N (or by a factor of 9.8*x*), while (F_D+F_L) on 33 μm spheres rose by only 6.2×10^{-8} N (or by a factor of 8.5*x*). Because adhesive failure depends on the applied force exceeding a threshold corresponding to the adhesive force, the absolute rise in (F_D+F_L) is of more importance than the proportional rise.

2.3. Particle handling

Tentaculate suspension feeders from many phyla display selectivity during post-capture handling, which might be passive and/or active (e.g., Pentreath, 1970; Winston, 1978; Dauer, 1984, 1985; Holland et al., 1986), and little information is available on the role of particle size per se (except, e.g., Nicol, 1930; Bonar, 1972). We therefore made no predictions regarding handling selection based on particle size.

3. Materials and methods

3.1. Animal collection and maintenance

We collected the spionid polychaetes *Pseudopolydora paucibranchiata* Okuda from an intertidal fine-sand flat in Bodega Bay, CA, and *Pseudopolydora kempi japonica* Imajima and Hartman from an intertidal silty-sand flat at the Richmond Field Station (University of California) in San Francisco Bay, CA. Animals were sieved onto a 500 μm mesh screen in the field and brought to U.C. Berkeley, where they were kept in aerated sea water at 13°C. Worms were separated from their tubes and preliminary measures of palp width were made for each worm with an eyepiece micrometer under a dissecting microscope while they were anesthetized in 4% $MgCl_2$ in sea water. Plastic pipettor tips (0.75 cm widest i.d.), with the narrow end sealed, were filled with 250 μm sieved sediment from the collection sites and stored vertically. Each worm was placed on the sediment surface in a pipettor tip and was allowed to burrow and build a new tube. Worms in pipettor tips were kept submerged in trays of sea water from the Bodega Bay Marine Lab and fed a ground paste of Gerber® mixed cereal for one to four days before experiments were conducted.

3.2. Flume experiments

Experiments were run at 13°C in a recirculating flume as described by Shimeta (1996). The flume floor was clean, except for a 2 cm wide strip of 2 mm sand cemented near the channel entrance that ensured development of a turbulent boundary layer when the flume was run at low velocities. The flume was filled 4.3 cm deep with sea water passed through a 5 μm mesh filter bag. The working section of the flume included a removable Plexiglas plate with holes into which the pipettor tips containing individual worms fit snugly and were held flush with the flume floor. Worms were aligned in a single row parallel to the flow, separated from each other by 3.75 cm. This separation distance (ca. 37 worm-tube diameters) was sufficient to prevent the wake of a worm's tube from influencing the flow around a downstream neighbor (Nowell and Jumars, 1984).

We ran experiments with spherical polystyrene beads that were neutrally buoyant (specific gravity 1.02), which ensured that they were not available to the worms by deposit feeding. We purchased beads in two size classes, nominally 25–38 μm and 75–90 μm (SoloHill Labs, Inc.). These diameters fall within the range for particles in suspension in the field (e.g., algal cells, microzooplankters, detritus, mineral grains, and organic-mineral aggregates). Beads were rinsed with distilled water and wet-sieved between 15 and 45 μm Nitex screens (small bead-size class) or between 75 and 100 μm Nitex screens (large bead-size class) to eliminate any overlap in size ranges. The mean diameters in the two size classes, as measured under a dissecting microscope, were 33.2 μm (±6.0 μm s.e., $n = 54$) and 80.0 μm (±7.7 μm s.e., $n = 46$). When examining beads on videotapes or in experimental samples, all beads <60 μm were scored as 'small' and all beads ≥60 μm were scored as 'large.'

The two size classes of beads were added to the flume with 20 ml of filtrate from Gerber® mixed cereal (ground in sea water and passed through a 10 μm filter) to stimulate feeding. For determination of concentrations by microscope counts, the particle suspension was sampled repeatedly throughout experiments by withdrawing 40 ml isokinetically through a Pasteur pipette at 3 mm height in the working section of the flume using a peristaltic pump. The mean concentrations of small and large beads were 853 ml^{-1} (±81 ml^{-1} s.e., $n = 8$) and 722 ml^{-1} (±48 ml^{-1} s.e., $n = 8$), respectively. The mean proportion of the suspension composed of large beads was 0.46 (±0.02 s.e., $n = 8$). A size-frequency distribution from other experiments performed with this bead mixture is shown in Shimeta (1996).

Six worms of one species were placed in the flume at a time. Worms of both species held their palps in the water column to suspension feed almost exclusively throughout all experiments. Each worm was videotaped while feeding at constant flow velocity for at least 15 min. Videotapes were recorded on a Panasonic AG7350 SVHS VCR using a Watec WAT-902 CCD camera, a Nikon PB-6 extension bellows, and a Nikon Micro-Nikkor 105 mm macro lens. Lighting was provided overhead by a fiber-optic lamp

Table 1
Flow parameters calculated from suspended-bead trajectories

	P. paucibranchiata	
$U_{3\text{mm}}$ (cm s^{-1})	1.3±0.2	9.1±2.1
	(n=25)	(n=50)
u_* (cm s^{-1})	0.39	1.6
	P. kempi japonica	
$U_{3\text{mm}}$ (cm s^{-1})	1.8±0.1	7.4±1.9
	(n=20)	(n=40)
u_* (cm s^{-1})	0.66	1.3

$U_{3\text{mm}}$ = mean velocity 3 mm above the bed. u_* = shear velocity. Columns indicate treatments applied to each species.

covered by red acetate to prevent light avoidance by worms. Each *P. paucibranchiata* individual was videotaped at one of two velocity settings (Table 1), after which it was removed from the flume. The sealed end of the pipettor tip was cut off and the contents were rinsed with 20% formalin in sea water into a vial to preserve the worm for later analysis of beads that were ingested during videotaping. Too few individuals of *P. kempi japonica* were available to allow independent samples between velocity settings, so a single group of worms was videotaped at two different velocities (Table 1). After the high-velocity treatment the worms were removed and preserved for later analysis of beads ingested during that treatment.

3.3. Data analysis

We viewed videotapes on a Sony PVM-1341 Trinitron monitor. Flow parameters were measured from videotaped segments of the flowing particle suspension in the absence of worms, assuming that the neutral buoyancy of the beads made them adequate flow markers. Mean velocities were determined from measurements to the nearest mm of bead displacements over a 10-frame segment of videotape. Mean velocities are reported (Table 1) for 3 mm above the flume floor ($U_{3\text{mm}}$), which is the approximate height of the worms' palps (cf. Shimeta, 1996). Vertical profiles of mean velocity were used to calculate the shear velocity (u_*, a measure of bottom shear stress) from the slope of the best linear fit to the natural log of height vs. mean velocity (Nowell and Jumars, 1987).

Particle encounter and capture were quantified by frame-by-frame viewing of the videotapes of feeding. The magnification was such that the smallest beads (15 μm) appeared 2 mm in size on the monitor. Palp width for each worm was measured to the nearest mm on the monitor in the middle of the portion that was viewed, and this width measure was used in all data analyses. For each species, an encounter between a bead and a palp in the high-velocity treatment was defined to occur when a bead stopped, in contact with the palp, for at least two video frames (0.0333 s). In the low-velocity treatment for each species, the frame-number criterion for encounter was extended in proportion with the ratio of $U_{3\text{mm}}$ in the two treatments (Table 1). Thus, for *P. paucibranchiata*, the frame-number criterion at the low velocity was $(9.1/1.3)\times 2 = 14$

frames (0.233 s). For *P. kempi japonica*, the frame-number criterion at low velocity was $(7.4/1.8)\times 2=8$ frames (0.133 s). For each worm, the first 50 encounters were scored for bead size. A capture of a bead was defined to occur when an encountered bead began to move proximally along the surface of a palp, indicating that manipulative control of the bead had been achieved by the worm. For each worm, the first 50 captures were scored for bead size. The retention efficiency of each bead-size class was determined from the number of captures scored among the first 50 encounters.

To determine the numbers of beads of each size class that were ingested during videotaping, each fixed worm was retrieved from its tube, cleaned of any adhering beads under a dissecting microscope, and placed into a plastic microfuge tube containing chlorine bleach. After the body tissue was dissolved, the remaining bead sample from the gut was transferred to a Sedgwick–Rafter counting chamber and counted under a dissecting microscope. We assumed that all ingested beads were obtained by suspension feeding because the specific gravity reported for the beads matched that measured for the flume water (1.02), and beads did not accumulate on the flume floor during experiments. Only worms that had ingested at least 50 beads were included in statistical analyses of encounter, capture, retention, and ingestion. This arbitrary criterion was adopted to ensure that the particle suspension was acceptable to those individuals (cf. Hentschel, 1996; Shimeta, 1996), and for the ingestion data to at least match the sample sizes of 50 beads scored for encounter, capture, and retention.

We expressed the relative numbers of small and large beads in a sample (i.e., ambient suspension, or beads encountered, beads captured, or beads ingested by a worm) as the proportion of the sample composed of large beads (P_L, calculated as the number of large beads divided by the sum of the number of small and large beads). When compared between the successive steps in feeding, differences in this proportion reveal whether any selectivity between the bead sizes occurred during encounter, retention, or handling. Spearman's rank correlation coefficients were calculated with Systat 5.1 software. Significance values for the Spearman coefficients, as well as Wilcoxon rank sums (2-sample) and signed ranks (paired-sample) tests, were calculated following Conover (1980). Nonparametric linear regressions were calculated following Tate and Clelland (1957).

4. Results

4.1. General observations of feeding behavior

Measurements of ciliary-current velocities around the palps suggested that a passive mechanical process of direct interception was a valid first approximation for the particle-encounter mechanism. Following an extended period of suspension feeding by *P. paucibranchiata*, flow in the flume was stopped and palps remained vertical in the water column for several minutes, during which time we observed suspended beads to be occasionally entrained into a ciliary current. From videotaped sequences of these events, we measured the maximal particle velocity (among 5 measured particle trajectories) in the ciliary current to have a mean value of 0.13 cm s^{-1} (±0.01 s.e., $n=6$ worms), and there was no relation to palp size. To determine roughly whether this ciliary current was strong enough to influence particle trajectories in the presence of ambient flow, we compared it with calculations of velocity in the boundary layer around a cylinder normal to a flow. Using numerical solutions for flow at cylinder Re = 1, 2, 5, and 10 (Keller and Takami, 1966; Takami and Keller, 1969; Dennis and Chang, 1970), we calculated that the minimal velocity along the limiting trajectory for direct interception (i.e., one particle radius from the cylinder) ranged from 0.25 to 8.0 cm s^{-1} for parameter values corresponding to our particle diameters, palp diameters, and upstream flow velocities. Although we could not measure the ciliary current in the presence of ambient flow, nor did we look for ciliary-reversal responses to particles nearing the palps (cf. Strathmann, 1987), we concluded that the ciliary current had a minor influence on the trajectories of particles approaching the palps because its maximal velocity was at most only 0.02 to 0.5 times the calculated particle velocities in flow.

Mucous adhesion appeared to be the primary mechanism of particle retention for both species when feeding in flow. Dauer (1984, 1985) alternatively suggested, based on observing the spionids *Streblospio benedicti* and *Paraprionospio pinnata* in still water and examining excised palps, that particles were retained by being flicked onto the frontal groove of a palp by the latero-frontal cirri; mucus-bound particles were then transported in the frontal groove to the mouth. In contrast, we observed beads in flowing water to be contacted and retained either directly on the frontal groove or on the lateral surfaces of palps. Because beads caught on the sides of palps often remained there for several seconds or longer before being transferred to the frontal groove, we inferred that ciliary flicking was not required for initial particle retention. Rather, mucus was apparently responsible for their retention, as evidenced by the fact that, when retention failed, laterally encountered beads sometimes hung on briefly by a thread of mucus before fully breaking away.

Particle handling and rejection behavior were also similar in both species. Once a particle was captured, its subsequent loss during transport into the tube was extremely rare. Rejected particles were transported, singly or in small aggregates, out of the tube along the frontal groove of the palp; particles were then moved laterally out of the groove and were lost. We did not quantify particle rejection because it was sometimes difficult to distinguish between aggregates of rejected beads and small, loosely compacted fecal pellets, which were also released by a similar mechanism. Nonetheless, we inferred that differences between the captured and ingested proportions of beads of different sizes were the result of particle rejection.

4.2. *Pseudopolydora paucibranchiata*

When feeding in slowly flowing water ($U_{3mm} = 1.3$ cm s^{-1}), *P. paucibranchiata* showed no significant correlations between palp width and P_L (proportion of the sample composed of large beads) for either encounter, capture, or ingestion (Fig. 4a). P_L for encounter was always above the ambient P_L in suspension; thus, encounter was biased for large beads. The values of P_L for capture essentially overlap those for encounter, suggesting that there was no selective retention based on bead size. The net result is that capture was biased for large beads relative to their availability in suspension, and this

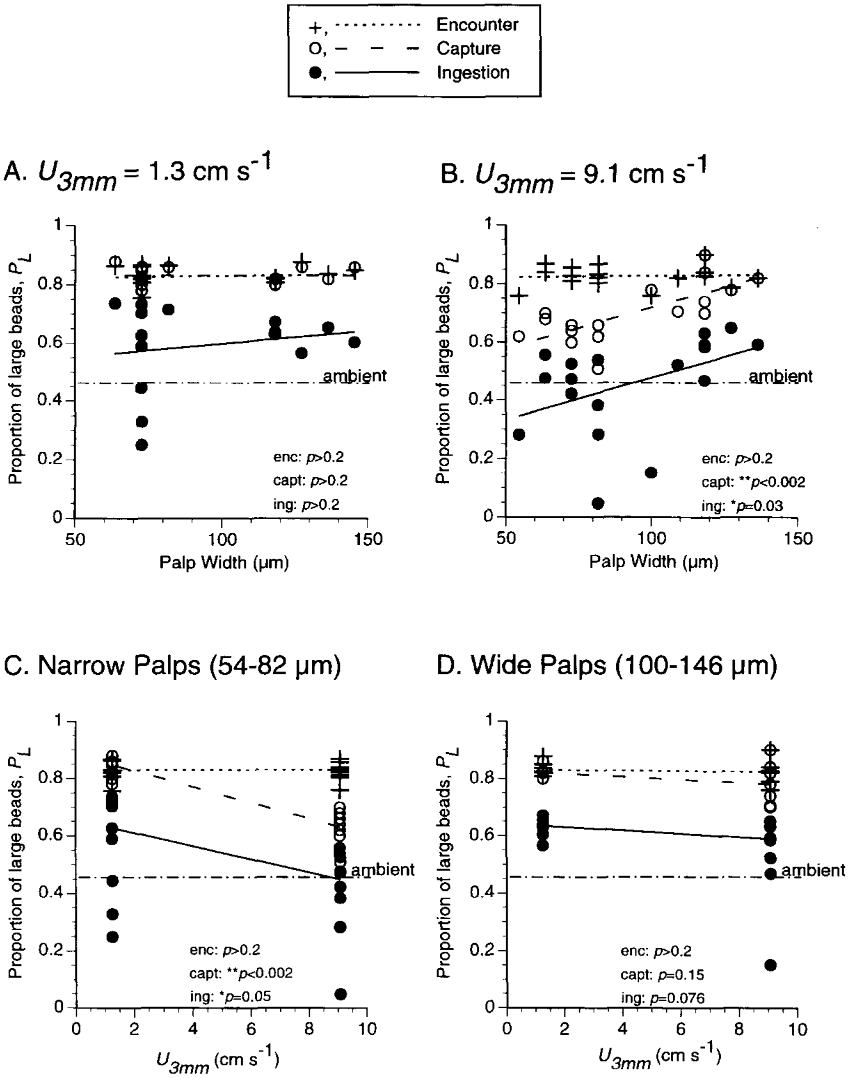

Fig. 4. Concurrent encounter, capture, and ingestion by *Pseudopolydora paucibranchiata*. Ordinates show the proportion of the sample composed of large beads (P_L). The dotted–dashed line indicates the proportion of the ambient suspension composed of large beads. Data aligned at a single palp width in A and B correspond to a single worm (although there is overlap where more than one worm of a single palp width was included). (A) lines through the data are nonparametric linear regressions meant only to aid the eye in seeing trends. Spearman rank correlation coefficients (r_s) are as follows ($n=15$; 2-tailed p values are shown on figure). Encounter $r_s=0.14$; capture $r_s=0.037$; ingestion $r_s=-0.068$. (B) lines are as in panel A; correlation coefficients are as follows ($n=18$). Encounter $r_s=-0.074$; capture $r_s=0.70$; ingestion $r_s=0.52$. (C) data for worms with narrow palps from panels A and B. Lines through the data connect medians between the two velocities. Two-tailed p values from Wilcoxon rank sums tests comparing medians are shown ($n=9$, 10). (D) data for worms with wide palps from panels A and B; lines are as in Panel C. Two-tailed p values from comparisons of medians are shown ($n=6$, 8).

bias was due to selection only at the step of encounter. Finally, the P_L values for ingestion were lower than those for capture, suggesting that large beads were preferentially rejected during post-capture handling. Nonetheless, the median P_L for ingestion was still higher than the ambient P_L ($p<0.005$), meaning that the net result of capture and ingestion was a bias for large beads eaten relative to their availability in suspension (although there were three worms with narrow palps that ingested a lower P_L than ambient; Fig. 4a).

Although the encountered P_L values still did not correlate with palp width in more rapidly flowing water ($U_{3mm}=9.1$ cm s^{-1}), both the captured P_L and the ingested P_L values showed significant positive correlation with palp width (Fig. 4b); i.e., worms with wider palps captured and ingested relatively more large beads (and fewer small beads) than did worms with narrower palps. As at the lower velocity, the encountered P_L values were above the ambient P_L for the suspension, indicating that encounter was biased for large beads. Furthermore, for nearly every worm the P_L values for capture were below those for encounter, suggesting that the retention step was biased for small beads; this bias was stronger for worms with narrower palps. Although the apparent retention bias for small beads partially offset the encounter bias for large beads, all of the P_L values for capture were above the ambient P_L in the suspension, meaning that there was a net bias for capture of large beads relative to their availability. As at the lower velocity, the P_L values for ingestion were lower than those for capture, suggesting that large beads were preferentially rejected during post-capture handling. The direct relationship between palp width and the P_L for ingestion paralleled the corresponding relationship with the captured P_L (tested below; Fig. 6), suggesting that the dependence of ingested P_L on palp width is produced entirely by the palp-width-dependent bias during particle retention.

We divided the experimental worms into two size classes according to palp width ('narrow palp' = 54–82 μm, and 'wide palp' = 100–146 μm) to test for an influence of velocity in each size class. The narrow-palp worms showed no difference between the P_L values for encounter at the two velocities, but the P_L values for capture and ingestion each dropped at the higher velocity (Fig. 4c). Therefore, the narrow-palp worms captured and ingested relatively fewer large beads (and more small beads) as the velocity rose. The median P_L for ingestion by narrow-palp worms was higher than the ambient P_L at 1.3 cm s^{-1} ($p=0.05$) but not at 9.1 cm s^{-1} ($p=0.23$); therefore, the combined process of capture and ingestion had a net bias for large beads relative to their availability at the low velocity, but it was nonselective at the high velocity. In contrast, the P_L values of wide-palp worms for encounter, capture, and ingestion each showed no significant difference between the two velocities (Fig. 4d). The median P_L for ingestion in this size class was greater than the ambient P_L ($p=0.007$), indicating that the combined process of capture and ingestion had a net bias for large beads relative to their availability.

Because there were no significant differences among the encountered P_L for different palp widths or at different velocities, we pooled the data for determining the functional dependence of encounter rate (E) on particle size (r_p). The exponent in the model, $E \propto r_p^n$, was calculated by using our data to solve the expression, $E_L/E_S=(C_L r_L/C_S r_S)^n$, where C = particle concentration and the subscripts 'L' and 'S' indicate the large and small beads, respectively. The mean value of the exponent was 2.00 (±0.27 s.e., $n=33$).

Retention efficiencies (R = proportion of encountered beads that were captured) for small and large beads (R_S and R_L, respectively) were measured directly by viewing individual encounter events. At the slow velocity ($U_{3mm} = 1.3$ cm s^{-1}) neither R_S nor R_L correlated with palp width (Fig. 5a). Furthermore, at 1.3 cm s^{-1} there was no significant difference between R_S and R_L for either the narrow-palp or the wide-palp worms (Fig. 5c, d), i.e., there was no retention bias at the low velocity. In contrast, in faster flow (9.1 cm s^{-1}), R_L was significantly lower than R_S for both size classes of worms (Fig. 5c, d), meaning that a retention bias for small beads appeared at this velocity. Note, however, that the retention bias among the wide-palp worms was apparently not strong enough to have caused a significant difference in the captured proportion of large beads between the two velocities (Fig. 4d). Indeed, the retention bias was stronger among the narrow-palp worms, as evidenced most clearly by the fact that at 9.1 cm s^{-1} R_L was positively correlated with palp width while R_S was independent of palp width (Fig. 5b). Finally, both the narrow-palp and the wide-palp worms showed significant reductions in both R_S and R_L at the higher velocity compared to the lower velocity (Fig. 5c, d).

Particle selection during post-capture handling is illustrated by plotting the ratio of the ingested P_L to the captured P_L (Fig. 6), thus indicating the extent to which handling alters the captured proportion of large beads. A value of 1.0 indicates that rejection of captured beads before ingestion was nonselective; values below 1.0 indicate that large beads were preferentially rejected. All worms at both velocities preferentially lost large beads (Fig. 6), as is evident on Fig. 4 by the fact that all P_L values for ingestion were lower than those for capture. The nonsignificant correlation coefficients in Fig. 6 reveal that the degree of this handling bias did not relate to palp width. Neither the narrow-palp nor the wide-palp worms showed a significant difference in handling bias between the two velocities ($p > 0.1$ for each). The mean value of ingested/captured P_L for the pooled data was 0.68 (±0.20 s.e., $n = 33$).

4.3. *Pseudopolydora kempi japonica*

Like *P. paucibranchiata*, *P. kempi japonica* feeding in slow flow ($U_{3mm} = 1.8$ cm s^{-1}) showed no significant correlations between palp width and P_L for either encounter or capture (Fig. 7a). All P_L values were above the ambient P_L in suspension; thus, encounter and net capture were both biased for large beads relative to their availability. However, the values of P_L for capture generally were slightly below the corresponding values for encounter ($p < 0.005$), suggesting a slight retention bias for small beads. For both species feeding in slow flow, the large-particle bias in capture was due to encounter.

In faster flow (7.4 cm s^{-1}) *P. kempi japonica* again showed patterns very similar to those of *P. paucibranchiata* in faster flow. There was no correlation between palp width and the P_L values for encounter, and the encountered P_L was again above the ambient P_L for the suspension (Fig. 7b), indicating an encounter bias for large beads. In contrast, there were significant positive correlations between palp width and both the captured P_L and the ingested P_L. Worms with wider palps therefore captured and ingested relatively more large beads (and fewer small beads) than did worms with narrower palps. For most worms the P_L values for capture were below those for encounter, suggesting that

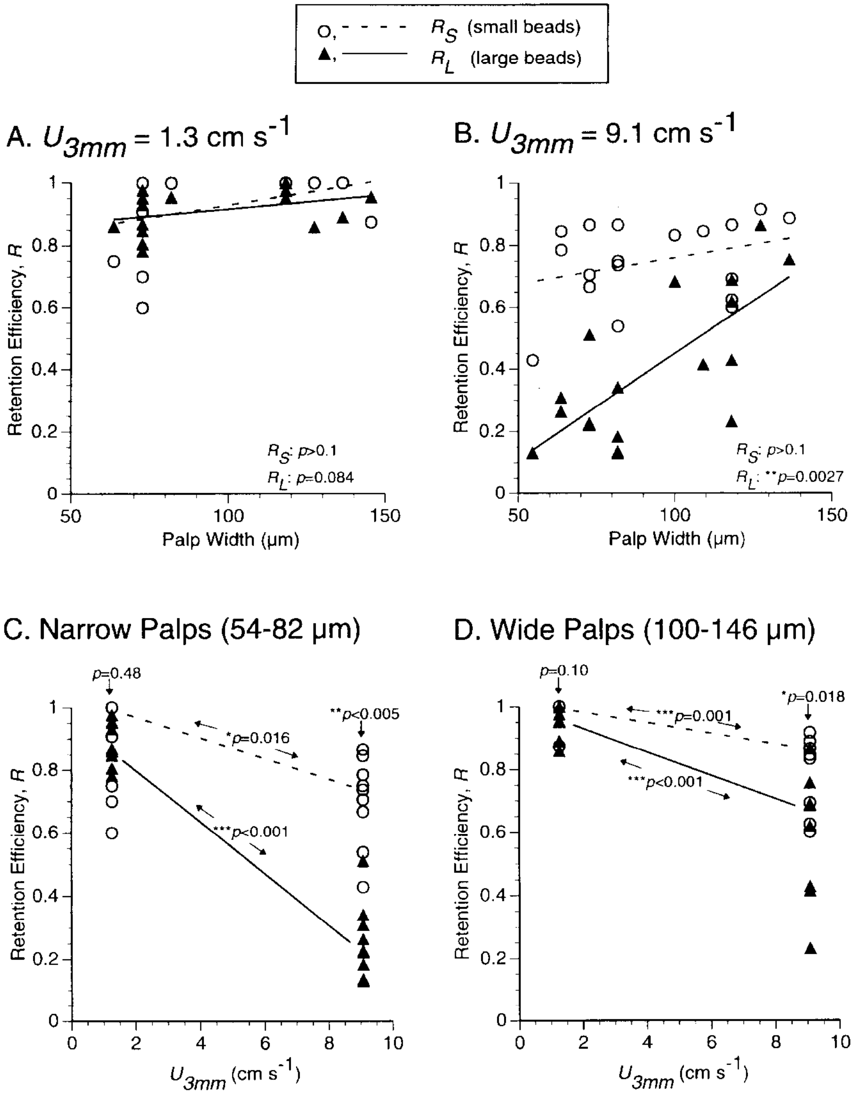

Fig. 5. Retention efficiencies of small and large beads (R_S and R_L) for *Pseudopolydora paucibranchiata*. R = number of captured beads divided by number of encountered beads. (A) lines through the data are nonparametric linear regressions meant only to aid the eye in seeing trends. Spearman rank correlation coefficients (r_s) are as follows ($n = 15$; one-tailed p values are shown on figure). R_S $r_s = 0.35$; R_L $r_s = 0.38$. (B) lines are as in panel A; correlation coefficients are as follows ($n = 18$). R_S $r_s = 0.31$; R_L $r_s = 0.65$. (C) retention efficiencies for worms with narrow palps from panels A and B. Lines through the data connect medians between the two velocities. One-tailed p values from Wilcoxon rank sums tests comparing medians are shown on the lines connecting medians ($n = 9$, 10). One-tailed p values from Wilcoxon signed ranks tests comparing R_S vs. R_L at a single velocity are shown above the data at each velocity ($n = 9$, 10). (D) retention efficiencies for worms with wide palps from panels A and B; lines are as in Panel C. One-tailed p values from comparisons of medians are shown on the lines connecting medians ($n = 6$, 8). One-tailed p values from comparisons of R_S vs. R_L at a single velocity are shown above the data at each velocity ($n = 6$, 8).

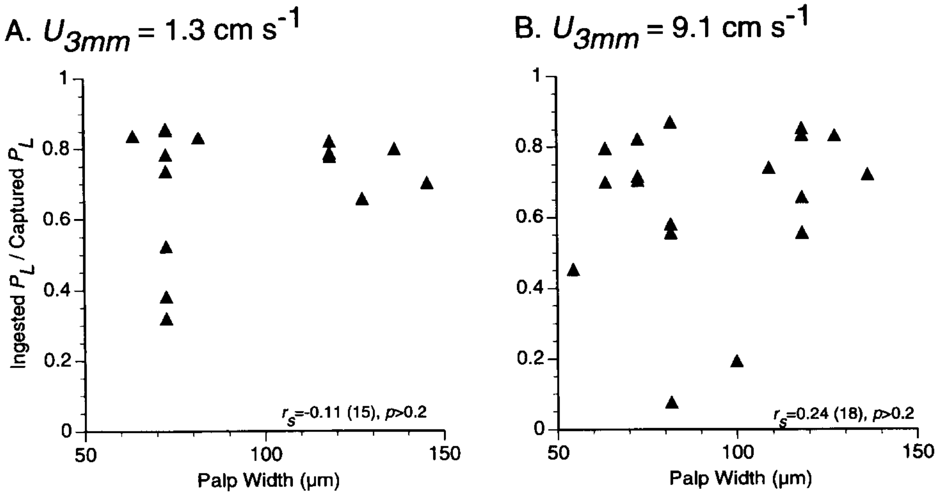

Fig. 6. Post-capture handling selection by *Pseudopolydora paucibranchiata*. Ordinates show the P_L for ingestion divided by the P_L for capture from data in Fig. 4. Values below 1.0 indicate preferential rejection of large beads. Spearman rank correlation coefficients (r_s) are shown with sample sizes and two-tailed p values.

retention was biased toward small beads; this bias was stronger for worms with narrower palps. Although the apparent retention bias toward small beads partially offset the encounter bias toward large beads, the P_L values for capture were above the ambient P_L of the suspension in all but one case (the worm with narrowest palps). Therefore, there was a net bias for capture of large beads relative to their availability. The P_L for ingestion was only measured after worms fed at 7.4 cm s^{-1} (Fig. 7b), and these values were consistently lower than the P_L for capture, suggesting that large beads were preferentially lost during post-capture handling as well. The capture and ingestion data are parallel (tested below; Fig. 9), indicating that the dependence of ingested P_L on palp width was produced entirely by the palp-width dependent bias during particle retention, as we observed for *P. paucibranchiata*.

We divided the experimental worms into two palp-width classes ('narrow palp' = 87–127 μm, and 'wide palp' = 136–200 μm) to test for an influence of velocity within each size class. In each palp-width class, there were two or three worms that were only videotaped in one of the two velocity treatments; these worms have been omitted from statistical tests that compare size classes between the two treatments, i.e. only the paired data were analyzed. The narrow-palp worms showed no difference between the P_L values for encounter at the two velocities, but the P_L values for capture dropped at the higher velocity (Fig. 7c). Therefore, as for *P. paucibranchiata*, the narrow-palp worms captured relatively fewer large beads (and more small beads) as the velocity rose. The median P_L for ingestion at 7.4 cm s^{-1} among narrow-palp *P. kempi japonica* was not different from the ambient P_L ($p = 0.40$), indicating that overall ingestion was nonselective relative to bead availability. In contrast, the wide-palp worms showed no difference between the two velocities in either the P_L values for encounter or the P_L

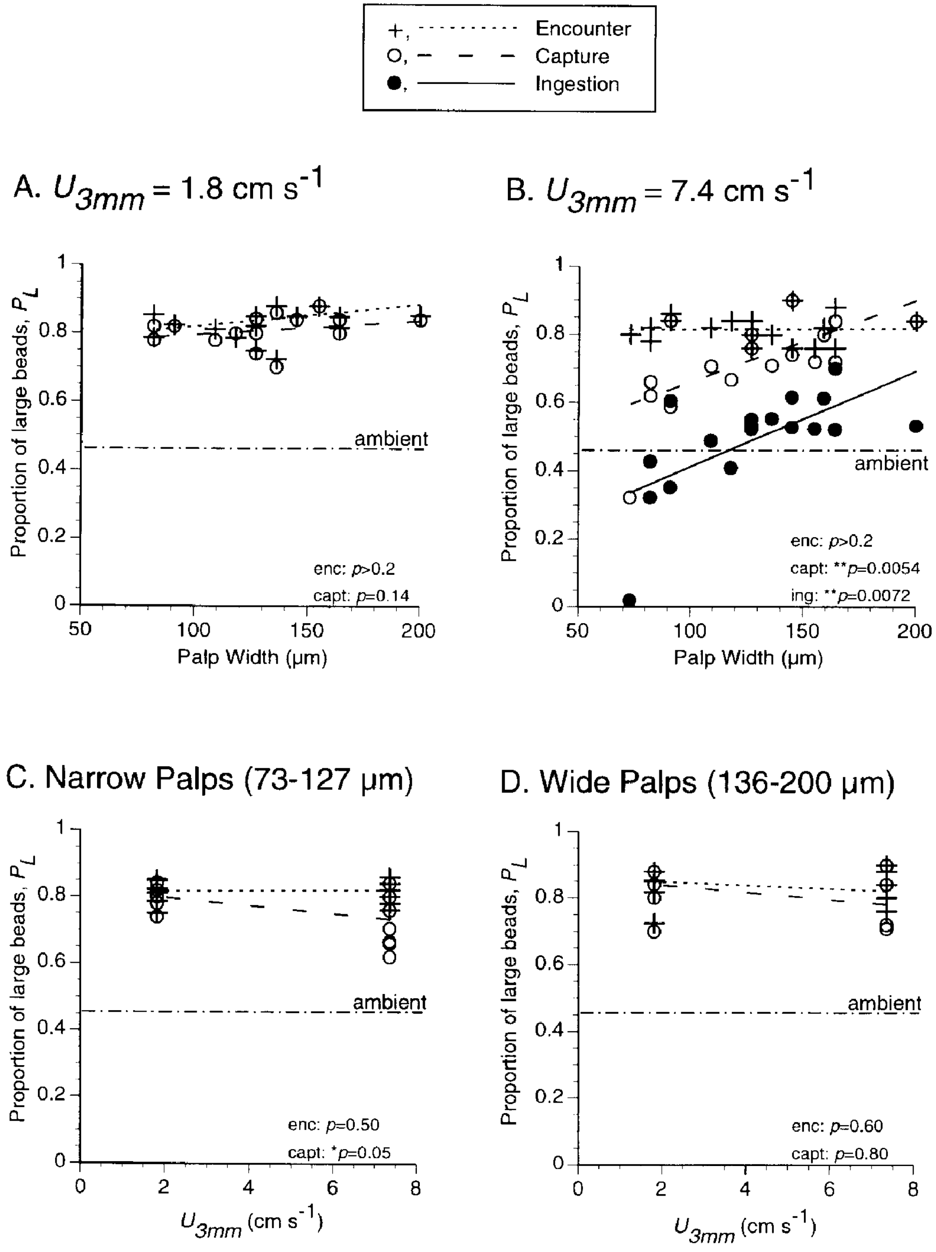

Fig. 7. Concurrent encounter, capture, and ingestion by *Pseudopolydora kempi japonica*. The format is as in Fig. 4. (A) correlation coefficients (r_s) are as follows ($n=15$). Encounter $r_s=0.31$; capture $r_s=0.41$. (B) correlation coefficients are as follows ($n=18$). Encounter $r_s=-0.0058$; capture $r_s=0.65$; ingestion $r_s=0.63$. (C) two-tailed p values from Wilcoxon signed ranks tests comparing medians are shown ($n=8$). (D) two-tailed p values from comparisons of medians are shown ($n=6$).

values for capture (Fig. 7d). As for *P. paucibranchiata*, the median P_L for ingestion among wide-palp *P. kempi japonica* in faster flow was significantly greater than the ambient P_L ($p<0.005$), showing that the combined process of capture and ingestion had a net bias for large beads relative to their availability in suspension.

Because the same worms were used in experiments at each velocity, we separately determined in each treatment the functional dependence of encounter rate on particle size. Calculating the exponent in the model, $E \propto r_p^n$, as we did above for *P. paucibranchiata*, we obtained at 1.8 cm s^{-1} a mean value of 1.95 (±0.34 s.e., $n=15$), and at 7.4 cm s^{-1} a mean of 1.90 (±0.34 s.e., $n=18$). There was no significant difference between either of these estimated exponents and that from the *P. paucibranchiata* data ($p=0.61$ using $U_{3mm}=1.8$ cm s^{-1} and $p=0.28$ using $U_{3mm}=7.4$ cm s^{-1} in *t*-tests).

Retention efficiencies (R_S and R_L) for *P. kempi japonica* feeding in slow flow (1.8 cm s^{-1}) showed no statistically significant correlations with palp width (Fig. 8a), as was observed for *P. paucibranchiata*. However, unlike *P. paucibranchiata* in slow flow, both palp-width classes of *P. kempi japonica* individuals feeding at 1.8 cm s^{-1} had significantly lower retention efficiencies for large beads than for small beads (Fig. 8c, d), i.e., the worms showed a bias for retention of small beads at the lower velocity. The strength of this bias, expressed as R_L/R_S, showed no correlation with palp width ($p>0.1$). Worms also showed a retention bias for small beads when feeding in faster flow (7.4 cm s^{-1}), with R_L significantly lower than R_S for both narrow-palp and wide-palp worms (Fig. 8c, d). R_S and R_L were each positively correlated with palp width at the higher velocity (Fig. 8b), but the relationship was clearly steeper for the large beads. The retention bias for small beads was therefore stronger for the narrow-palp worms; R_L/R_S was directly correlated with palp width (Spearman rank correlation coefficient $r_s=0.63$, $p=0.0036$). Finally, R_S and R_L both fell at the higher velocity for small-palp worms (Fig. 8c), but only R_L dropped for large-palp worms (Fig. 8d). Within both palp-width classes of worms, the retention bias for small beads strengthened at the higher velocity ($p<0.005$ for small-palp worms and $p=0.01$ for large-palp worms, testing R_L/R_S between the two velocities).

Particle selection during post-capture handling at 7.4 cm s^{-1} (Fig. 9) showed preferential rejection of large beads by all *P. kempi japonica* individuals tested, and, as for *P. paucibranchiata*, the strength of this handling bias did not relate to palp width. The mean value of ingested/captured P_L was 0.66 (±0.18 s.e., $n=18$), which was not significantly different from that for *P. paucibranchiata* ($p=0.20$).

5. Discussion

Particle-size selection occurred during each step in the suspension-feeding process of two species of spionid polychaetes. Large particles were selected during encounter; small particles were often selected during retention; and small particles were selected during handling. Particle retention was the only step in the feeding process that was affected by ambient flow speed or by the width of an animal's palps. Therefore, retention mechanics were ultimately responsible for the influences of flow speed and palp width on selective ingestion.

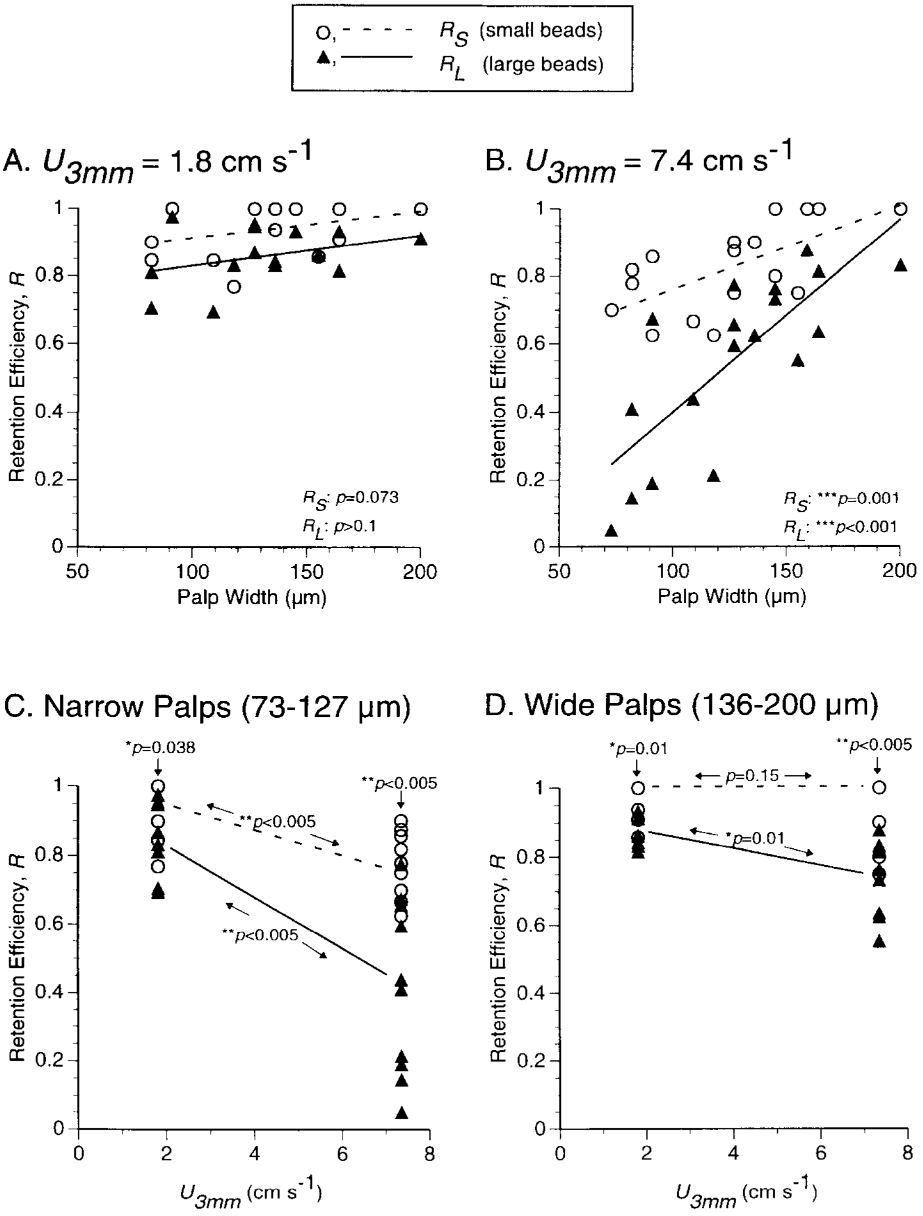

Fig. 8. Retention efficiencies of small and large beads (R_S and R_L) for *Pseudopolydora kempi japonica*. The format is as in Fig. 5. (A) correlation coefficients (r_s) are as follows ($n=15$). R_S $r_s=0.40$; R_L $r_s=0.28$. (B) correlation coefficients are as follows ($n=18$). R_S $r_s=0.69$; R_L $r_s=0.77$. (C) one-tailed p values from Wilcoxon signed ranks tests comparing medians are shown on the lines connecting medians ($n=8$). One-tailed p values from Wilcoxon signed ranks tests comparing R_S vs. R_L at a single velocity are shown above the data at each velocity ($n=8$, 10). (D) one-tailed p values from comparisons of medians are shown on the lines connecting medians ($n=6$). One-tailed p values from comparisons of R_S vs. R_L at a single velocity are shown above the data at each velocity ($n=7$, 8).

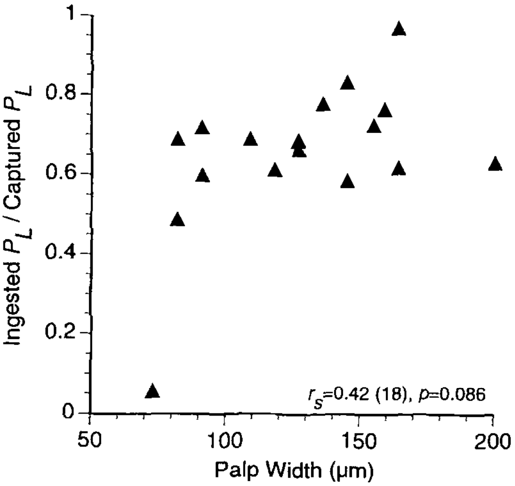

Fig. 9. Post-capture handling selection by *Pseudopolydora kempi japonica* at $U_{3\mathrm{mm}} = 7.4$ cm s^{-1}. Ordinate shows the P_L for ingestion divided by the P_L for capture from data in Fig. 7B. The Spearman rank correlation coefficient (r_s) is shown with sample size and two-tailed p value.

5.1. Particle encounter

We found that the first step in the suspension-feeding process, particle encounter, showed a consistent bias for large particles. Such an encounter bias is predicted for the mechanism of direct interception by models of the physical processes by which particles contact filters (e.g., Rubenstein and Koehl, 1977; Shimeta and Jumars, 1991; Shimeta, 1993). However, these models of direct interception cannot be applied quantitatively to our experiments because our tentacle Reynolds numbers ($Re_t = 0.7$ to 15) and ratios of particle-to-tentacle radius ($r_p/r_t = 0.2$ to 1.5) were higher than those assumed by the models ($Re_t < 0.1$, $r_p/r_t < 0.1$). We therefore determined empirically that encounter was proportional to $r_p^{1.9-2.0}$. Thus, for the range of Re_t and r_p/r_t we used, which are typical of many tentaculate suspension feeders (Shimeta and Jumars, 1991), a small increase in particle size leads to a large increase in encounter rate.

The size-selectivity of encounter was not affected by flow speed or palp width for the range of tentacle Reynolds numbers and particle sizes used in our experiments. Therefore, all worms in a population experiencing a similar range of velocities in the field should encounter particles from suspension with the same bias.

5.2. Particle retention

An encountered particle is retained by a tentacle if the adhesive force holding it to the tentacle is greater than the sum of the drag and lift forces tending to remove it. As predicted, we found that increases in ambient flow speed caused decreases in particle retention efficiency by spionid palps. Our data corroborate suggestions by other authors that retention efficiency is inversely related to velocity (e.g., Rubenstein and Koehl, 1977; Patterson, 1984; Okamura, 1984, 1985) and are similar to the results reported by McFadden (1986) for particle retention by a suspension-feeding soft coral. However, if lift and drag are very small relative to the adhesive force (e.g., if particles are much smaller than the tentacle, or if the ambient velocity is slow), then particle retention efficiency can be independent of flow speed. We found this to be the case only for the largest *P. kempi japonica* individuals when capturing the small particles. Similarly, Leonard et al. (1988) found retention to be independent of velocity for a suspension-feeding crinoid in slow flow (0.9–6.4 cm s^{-1}).

We also found that small particles were retained preferentially relative to large particles if the ambient flow was sufficiently fast, as predicted by considering the mechanics of retention. When the retention bias was present, the degree of selectivity was directly related to flow speed. Thus, flow speed in the habitat of such worms can determine whether and how strongly their particle retention is size-selective. Loudon (1990) also reported a retention efficiency bias towards small particles by caddisfly nets.

Also as predicted, we found that the bias toward retaining small particles was stronger for narrower palps than for wider palps. However, this effect was also mediated by flow speed, because it was only observed in the stronger flows. Thus, flow speed in the habitat can determine whether appendage sizes influence particle retention.

Selective retention can depend on particle characteristics other than size, e.g., shape, specific gravity, surface chemistry, and motility. A nonspherical particle (e.g., a pennate diatom encountered with its long axis parallel to that of the tentacle) can have a much larger contact area with the tentacle than does a sphere of equivalent volume. The surface texture of a particle can also influence how well it adheres to a tentacle (e.g., adhesion mechanisms discussed in Nachtigall, 1974; Kinloch, 1980). Indeed, deposit feeders (including spionids) that use mucus to adhere particles to their tentacles (as do many suspension feeders) show an apparent mechanical preference for rough particles over smooth ones (Self and Jumars, 1978). Although our retention model predicts that specific gravity is in most cases less important than particle size in determining selective retention (see Fig. 2), light particles might be less likely than heavy ones to be dropped by tentacles in very slow flow (<1 cm s^{-1} local to the tentacle). Preference for particles of low specific gravity has been documented for tentaculate deposit feeders (Jumars et al., 1982; Self and Jumars, 1988). Natural particles also vary widely in surface chemistry, and hence in their stickiness (e.g., phytoplankton cells, Kiørboe and Hansen, 1993). Suspension-feeding ophiuroids have been found to preferentially capture beads with surface charges relative to uncharged beads (LaBarbera, 1978), while tentaculate deposit feeders have been shown to select mechanically for mineral grains with organic coatings relative to clean grains (Taghon, 1982; Jumars, 1993). Motile particles (e.g., flagellated cells, zooplankton) differ by taxon and size in their ability to struggle against retention by suspension feeders. Struggling may enhance escape from some types of suspension feeders, whereas it may increase retention by others (e.g., prey struggling can induce nematocysts on cnidarian tentacles to fire).

Despite the variety of factors that can influence selective particle retention by tentaculate suspension feeders, the general effects due to ambient velocity and to particle and tentacle sizes should be similar to those we predicted and measured in this study.

Drag and lift forces increase with velocity, and the relative sizes of particle and tentacle can limit the contact area over which an adhesive bond can be formed (Fig. 3).

5.3. Particle handling

We found that spionids preferentially lost large particles, apparently by active rejection, after they were captured. The strength of handling selection was independent of both flow speed and palp width. We believe the rejection of large particles was due to behavioral preference rather than a passive mechanical obstruction to ingestion, because every worm had some large particles in its gut. Although post-capture rejection has been observed for spionids and other tentaculate suspension feeders (e.g., Pentreath, 1970; Winston, 1978; Dauer et al., 1981; Levin, 1981; Dauer, 1985; Holland et al., 1986), the rejection criteria have not been well documented. Passive, mechanical handling selection based on particle size has been observed (e.g., among sabellid polychaetes which use cilia to sort captured particles; Nicol, 1930; Bonar, 1972), but to our knowledge no tentaculate suspension feeder or tentaculate deposit feeder has previously been documented to reject particles actively by behavioral choice based only on particle size.

Because particle rejection during handling can depend on behavioral choice, simple physical models cannot predict selectivity during this step of feeding. Optimal foraging theory suggests that suspension feeders should preferentially ingest large particles because the caloric value of many suspended organic particles is directly related to their volume (Lehman, 1976; Shimeta, 1996). Our experimental particles had no food value, but the rejection of the large particles by suspension-feeding spionids is nonetheless surprising. The worms might have reacted to the plastic beads as though they were resuspended mineral grains, which generally have a nutritional value from surface films that scales to particle surface area rather than to volume. Optimal foraging theory for deposit feeders predicts preferential ingestion of small particles because of their relatively large ratio of surface area to volume (Taghon et al., 1978).

5.4. Net influences of flow speed and palp size on selective ingestion

Size-selection among ingested particles was the net result of passive mechanical selection during encounter and retention, and behavioral selection during handling. Flow speed and palp width only influenced selection during the retention phase, however. Therefore, although selection occurred at each step of the feeding process, the influences of flow speed and palp size on overall feeding selectivity (i.e., ingestion) were due exclusively to the mechanics of particle retention.

The net result of encounter, retention, and handling produced the following patterns of selective ingestion. Worms with narrow palps ingested relatively fewer large particles (and more small particles) in fast flow than they did in slow flow. Furthermore, in fast flow worms with narrow palps ingested relatively fewer large particles than did worms with wider palps. In general, the spionids ingested a greater proportion of large particles than was available in suspension. However, ingestion was nonselective for worms with the smallest palps at the highest velocity (probably because under these conditions the encounter bias for large particles was offset by the retention and handling biases for small particles). These effects of palp size and flow speed are similar to those measured during feeding experiments by Shimeta (1996).

The mechanics of particle retention may impose ontogenetic and environmental constraints on the feeding ecology of tentaculate suspension feeders like spionids. Because palp width and body size are directly correlated, juvenile spionids suspension feed on smaller particles when in strong flow compared to weak flow, and in strong flow juveniles suspension feed on smaller particles than do adults (Shimeta, 1996). When feeding on principally labile organic particles (e.g., algal cells, microzooplankters, detritus, and organic-rich aggregates), selectivity for smaller particles could result in a reduced caloric value of the diet on a per-particle basis. Variations in the flow environment could thereby have different effects for juveniles and adults as far as the caloric value of the food they can capture.

5.5. Comparisons with the mechanics of tentaculate deposit feeding

The mechanics of suspension feeding and deposit feeding with tentacles are similar in many ways, especially for animals like spionids that can feed in either mode. As in suspension feeding, contact between a deposit-feeding tentacle and particles on the substratum is biased toward large grains, while retention is biased toward small grains (Jumars et al., 1982). Taghon (1982) hypothesized that, in deposit feeding, drag forces in strong flow cause selective loss of large particles during post-capture transport to the mouth, which is a phenomenon analogous to the velocity effect on retention seen here in suspension feeding.

In contrast, the effect of tentacle width on selective encounter differs between suspension and deposit feeding. We measured no effect of palp width on the encounter bias toward large particles in suspension feeding, but the contact bias for large particles in deposit feeding is stronger on narrower tentacles than on wider tentacles (Hentschel, 1996). This difference can be understood by considering the encounter mechanics in each feeding mode. In suspension feeding by direct interception, encounter depends primarily on the size of a particle following a given streamline around the tentacle, while the tentacle width itself is relatively less important (Rubenstein and Koehl, 1977; Shimeta and Jumars, 1991; Shimeta, 1993). In contrast, tentacle width is more crucial in deposit feeding because contact depends directly on the surface area of the tentacle that is pressed onto the sediment. Models based on stereology predict a dependence of contact bias on tentacle width in deposit feeding (Whitlatch, 1989; Hentschel, 1996).

Retention mechanics in suspension feeding suggest by analogy the possible consequences of tentacle width for selective retention in deposit feeding. Narrower tentacles may preferentially retain smaller particles from deposits than do wider tentacles. This retention bias would counteract the contact bias toward large particles, which is stronger on narrow tentacles than on wide tentacles (Hentschel, 1996). The net result of these biases in contact and retention might explain why Hentschel (1996) found no net influence of palp width on selective ingestion by two spionid species deposit feeding in still water. However, Shimeta (1996) found that, when deposit feeding in strong flow, juvenile spionids ingested relatively fewer large particles than did adults. This influence of palp size could have been due to an even greater retention bias on the small palps induced by the faster flow.

5.6. Generality of model

Our experimental results for spionid particle selectivity during the encounter and retention stages of feeding agree with the predictions of simple mechanical models of idealized particles and tentacles, in spite of the morphological complexities of spionid palps (e.g., non-circular cross-sectional shape, ciliation). This finding suggests that the variables included in these simple models, such as particle and tentacle size, and hydrodynamic forces on particles, are fundamental determinants of suspension-feeding performance. Therefore, the mechanics of particle selection we have modeled and tested in this study should apply to a wide range of tentaculate suspension feeders (e.g., various polychaetes, echinoderms, and cnidarians), and may include those with retention mechanisms other than mucous adhesion (e.g., nematocysts). Although we believe that the fundamental variables we have modeled set the baseline constraints on selectivity by tentaculate suspension feeders, we also stress that experiments should be done with other taxa and with various types of natural particles to assess the extent to which morphology, retention mechanism, and behavior might mediate the ultimate influence of these mechanical constraints on feeding ecology.

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References

Appelmans, N., 1994. Sites of particle selection determined from observations of individual feeding larvae of the sand dollar *Dendraster excentricus*. *Limnol. Oceanogr.*, Vol. 39, pp. 404–411.

Bonar, D.B., 1972. Feeding and tube construction in *Chone mollis* Bush (Polychaeta, Sabellidae). *J. Exp. Mar. Biol. Ecol.*, Vol. 9, pp. 1–18.

Butman, C.A., 1986. Larval settlement of soft-sediment invertebrates: some predictions based on an analysis of near-bottom velocity profiles. In, *Marine interfaces ecohydrodynamics*, edited by J.C.J. Nihoul, Elsevier Press, New York, pp. 487–513.

Chepil, W.S., 1958. The use of evenly spaced hemispheres to evaluate aerodynamic forces on a soil surface. *EOS (Trans. Am. Geophys. Union)*, Vol. 39, pp. 397–404.

Conklin, E.J. and R.N. Mariscal, 1976. Increase in nematocyst discharge in a sea anemone in response to mechanical stimulation. In, *Coelenterate ecology and behavior*, edited by G.O. Mackie, Plenum Press, New York, pp. 549–558.

Conover, W.J., 1980. *Practical nonparametric statistics*. John Wiley, New York, second edition, 493 pp.

Dauer, D.M., 1984. Functional morphology and feeding behavior of *Streblospio benedicti* (Polychaeta; Spionidae). In, *Proceedings of the first international polychaete conference, Sydney*, edited by P.A. Hutchings, The Linnean Society of New South Wales, pp. 418–429.

Dauer, D.M., 1985. Functional morphology and feeding behavior of *Paraprionospio pinnata* (Polychaeta: Spionidae). *Mar. Biol.*, Vol. 85, pp. 143–151.

Dauer, D.M., C.A. Maybury and 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.

Davies, C.N., 1973. *Air filtration*. Academic Press, London.

Dennis, S.C.R. and G.-Z. Chang, 1970. Numerical solutions for steady flow past a circular cylinder at Reynolds numbers up to 100. *J. Fluid Mech.*, Vol. 42, pp. 471–489.

Gibbs, R.J., 1985. Estuarine flocs: their size, settling velocity, and density, *J. Geophys. Res.*, Vol. 90, pp. 3249–3251.

Hentschel, B.T., 1996. Ontogenetic changes in particle-size selection by deposit-feeding spionid polychaetes: the influence of palp size on particle contact. *J. Exp. Mar. Biol. Ecol.*, in press.

Holland, N.D., J.R. Strickler and A.B. Leonard, 1986. Particle interception, transport and rejection by the feather star *Oligometra serripinna* (Echinodermata: Crinoidea), studied by frame analysis of videotapes. *Mar. Biol.*, Vol. 93, pp. 111–126.

Jackson, G.A., 1989. Simulation of bacterial attraction and adhesion to falling particles in an aquatic environment, *Limnol. Oceanogr.*, Vol. 34, pp. 514–530.

Jørgensen, C.B., 1966. *Biology of suspension feeding*. Pergammon Press, Oxford, 357 pp.

Jumars, P.A., 1993. Gourmands of mud: diet choice in deposit feeders. In, *Mechanisms of diet choice*, edited by R.N. Hughes, Blackwell Scientific, pp. 136–168.

Jumars, P.A., R.F.L. Self and A.R.M. Nowell, 1982. Mechanics of particle selection by tentaculate deposit-feeders. *J. Exp. Mar. Biol. Ecol.*, Vol. 64, pp. 47–70.

Keller, H.B. and H. Takami, 1966. Numerical studies of steady viscous flow about cylinders. In, *Numerical solutions of nonlinear differential equations*, edited by D. Greenspan, John Wiley and Sons, New York, pp. 115–140.

Kiefer, D.A. and J. Berwald, 1992. A random encounter model for the microbial planktonic community. *Limnol. Oceanogr.*, Vol. 37, pp. 457–467.

Kinloch, A., 1980. The science of adhesion. I. Surface and interfacial aspects. *J. Mat. Sci.*, Vol. 15, pp. 2141–2166.

Kiørboe, T. and J.L.S. Hansen, 1993. Phytoplankton aggregate formation: observations of patterns and mechanisms of cell sticking and the significance of exopolymeric material. *J. Plankton Res.*, Vol. 15, pp. 993–1018.

LaBarbera, M., 1978. Particle capture by a Pacific brittle star: experimental test of the aerosol suspension feeding model. *Science*, Vol. 201, pp. 1147–1149.

Lahaye, M.C. and M. Jangoux, 1985. Functional morphology of the podia and ambulacral grooves of the comatulid crinoid *Antedon bifida* (Echinodermata). *Mar. Biol.*, Vol. 86, pp. 307–318.

Lehman, J.T., 1976. The filter-feeder as an optimal forager, and the predicted shapes of feeding curves. *Limnol. Oceanogr.*, Vol. 21, pp. 501–516.

Leonard, A.B., J.R. Strickler and N.D. Holland, 1988. Effects of current speed on filtration during suspension feeding in *Oligometra serripinna* (Echinodermata: Crinoidea). *Mar. Biol.*, Vol. 97, pp. 111–125.

Levin, L.A., 1981. Dispersion, feeding behavior and competition in two spionid polychaetes. *J. Mar. Res.*, Vol. 39, pp. 99–117.

Lewis, J.B. and W.S. Price, 1975. Feeding mechanisms and feeding strategies of Atlantic reef corals. *J. Zool., London*, Vol. 176, pp. 527–544.

Loudon, C., 1990. Empirical test of filtration theory: particle capture by rectangular-mesh nets. *Limnol. Oceanogr.*, Vol. 35, pp. 143–148.

Mariscal, R.N., 1974. Nematocysts. In, *Coelenterate biology*, edited by L. Muscatine and H.M. Lenhoff, Academic Press, New York, pp. 129–178.

Mayer, S., 1994. Particle capture in the crown of the ciliary suspension feeding polychaete *Sabella penicillus*: videotape recordings and interpretations. *Mar. Biol.*, Vol. 119, pp. 571–582.

McFadden, C.S., 1986. Colony fission increases particle capture rates of a soft coral: advantages of being a small colony. *J. Exp. Mar. Biol. Ecol.*, Vol. 103, pp. 1–20.

Nachtigall, W., 1974. *Biological mechanisms of attachment.* Springer-Verlag, Berlin.

Nicol, E.A.T., 1930. The feeding mechanism, formation of the tube, and physiology of digestion in *Sabella pavonina. Trans. Roy. Soc. Edinburgh,* Vol. 56, pp. 537–598.

Nowell, A.R.M. and P.A. Jumars, 1984. Flow environments of aquatic benthos. *Annu. Rev. Ecol. Syst.,* Vol. 15, pp. 303–328.

Nowell, A.R.M. and P.A. Jumars, 1987. Flumes: theoretical and experimental considerations for simulation of benthic environments. *Oceanogr. Mar. Biol. Annu. Rev.,* Vol. 25, pp. 91–112.

Okamura, B., 1984. The effects of ambient flow velocity, colony size, and upstream colonies on the feeding success of bryozoa. I. *Bugula stolonifera* Ryland, an arborescent species. *J. Exp. Mar. Biol. Ecol.,* Vol. 83, pp. 179–193.

Okamura, B., 1985. The effects of ambient flow velocity, colony size, and upstream colonies on the feeding success of bryozoa. II. *Conopeum reticulum* (Linnaeus), an encrusting species, *J. Exp. Mar. Biol. Ecol.,* Vol. 89, pp. 69–80.

Patterson, M.R., 1984. Patterns of whole colony prey capture in the octocoral, *Alcyonium siderium. Biol. Bull.,* Vol. 167, pp. 613–629.

Pentreath, R.J., 1970. Feeding mechanisms and the functional morphology of podia and spines in some New Zealand ophuiroids (Echinodermata). *J. Zool., London,* Vol. 161, pp. 395–429.

Rubenstein, D.I. and M.A.R. Koehl, 1977. The mechanisms of filter feeding: some theoretical considerations. *Am. Nat.,* Vol. 111, pp. 981–994.

Sebens, K.P. and M.A.R. Koehl, 1984. Predation on zooplankton by the benthic anthozoans *Alcyonium siderium* (Alcyonacea) and *Metridium senile* (Actinaria) in the New England subtidal. *Mar. Biol.,* Vol. 81, pp. 255–271.

Self, R.F.L. and P.A. Jumars, 1978. New resource axes for deposit feeders? *J. Mar. Res.,* Vol. 36, pp. 627–641.

Self, R.F.L. and P.A. Jumars, 1988. Cross-phyletic patterns of particle selection by deposit feeders. *J. Mar. Res.,* Vol. 46, pp. 119–143.

Shimeta, J., 1993. Diffusional encounter of submicrometer particles and small cells by suspension feeders. *Limnol. Oceanogr.,* Vol. 38, pp. 456–465.

Shimeta, J., 1996. Particle-size selection by *Pseudopolydora paucibranchiata* (Polychaeta: Spionidae) in suspension feeding and in deposit feeding; influences of ontogeny and flow speed. *Mar. Biol.,* Vol. 126, pp. 479–488.

Shimeta, J. and P.A. Jumars, 1991. Physical mechanisms and rates of particle capture by suspension-feeders. *Oceanogr. Mar. Biol. Annu. Rev.,* Vol. 29, pp. 191–257.

Strathmann, R.R., 1987. Larval feeding. In, *Reproduction of marine invertebrates, Vol. IX,* edited by A.C. Giese, Boxwood Press, Pacific Grove, pp. 465–550.

Taghon, G.L., 1982. Optimal foraging by deposit-feeding invertebrates: roles of particle size and organic coating. *Oecologia,* Vol. 52, pp. 295–304.

Taghon, G.L., A.R.M. Nowell and P.A. Jumars, 1980. Induction of suspension feeding in spionid polychaetes by high particulate fluxes. *Science,* Vol. 210, pp. 562–564.

Taghon, G.L., R.F.L. Self and P.A. Jumars, 1978. Predicting particle selection by deposit feeders: a model and its implications. *Limnol. Oceanogr.,* Vol. 23, pp. 752–759.

Takami, H. and H.B. Keller, 1969. Steady two-dimensional viscous flow of an incompressible fluid past a circular cylinder. *Phys. Fluids,* Suppl. II, pp. II-51–II-56.

Tate, M.W. and R.C. Clelland, 1957. *Nonparametric and shortcut statistics.* Interstate Printers and Publishers, Danville.

Vogel, S., 1994. *Life in moving fluids: the physical biology of flow.* Princeton University Press, Princeton, second edition, 467 pp.

Whitlatch, R.B., 1989. On some mechanistic approaches to the study of deposit feeding in polychaetes. In, *Ecology of marine deposit feeders,* edited by G. Lopez, G. Taghon and J. Levinton, Springer-Verlag, New York, pp. 291–308.

Winston, J.E., 1978. Polypide morphology and feeding behavior in marine ectoprocts. *Bull. Mar. Sci.,* Vol. 28, pp. 1–31.