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Role of particle wettability in capture by a suspension-feeding crab (*Emerita talpoida*)

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Abstract Suspension feeders sometimes depend on adhesion between particle and collector to capture food. If food particles have different adhesive properties than other particles, food could be passively selected by adhesive mechanisms. In this regard, the effect of particle wettability on adhesion to artificial and natural collectors was studied. First, the adhesion of glass particles to artificial collectors, both varying in wettability, was assessed to determine if wettability influenced adhesion in seawater. The adhesive force between glass particles and artificial collectors was measured by increasing the force pulling particles away from the collector until 50% of the particles fell off the collector. Adhesion increased as particle wettability decreased. Next, glass particles were used to determine if the antennal collector of the suspension-feeding mole crab *Emerita talpoida* captured particles based on particle wettability. 0.5 to 10 and 15 to 25 μm particles were suspended in a recirculating flow tank filled with seawater, and ablated antennae were exposed to this flow, after which the captured particles were counted. Results for the 0.5 to 10 μm particles confirmed predictions based on results from artificial collectors; particle capture increased as particle wettability decreased. The 15 to 25 μm particles may have been captured by sieving, and consequently did not follow predictions based on adhesion. Passive selection of particles based upon wettability differences can occur.

Introduction

While feeding, suspension-feeding animals encounter a wide range of particles varying in size, shape, density, motility, nutritional quality and toxicity. Many suspension-feeding animals select among particles. Some avoid eating harmful (Fiedler 1982; Huntley et al. 1986; Turriff et al. 1995), less nutritious (Paffenhöfer and Van Sant 1985; Houde and Roman 1987; Cowles et al. 1988; Butler et al. 1989), or inorganic (Kirk 1991) particles. While the mechanism of particle selection is not known in many cases, the presence of chemoreceptors on copepod mouthparts (Friedman and Strickler 1975) and the enhancing effect of algal exudates on filtering and ingestion rates (Poulet and Oullet 1982; Gill and Poulet 1988; Ward et al. 1992) indicate that an active method involving chemoreception is used by some animals to select particles. However, the results of other particle-selection experiments suggest that passive methods of selection may also be used (Shumway et al. 1985; Butler et al. 1989).

Passive methods of selection may result from an inability to manipulate particles of certain sizes, textures or shapes, differences in encounter rate among particles, or differences in retention efficiency among particles. Size selection, in particular, is frequently attributed to passive mechanisms. Animals are limited to particles they can fit inside their mouth or phagocytose (Fenchel 1980), and suspension feeders that sieve are limited to particles that fail to pass through their filter.

Suspension feeders that rely on adhesion between the particle and collector to catch particles can also passively select particles by size. Due to a greater encounter rate of large particles, animals sometimes capture more large particles than smaller ones; Shimeta (1996) found that a suspension-feeding polychaete caught proportionately more larger beads than smaller ones, and LaBarbera (1984) documented similar results with a brittlestar. However, as particle size increases, drag on the particle increases and the adhesion between particle and collector may be too weak to retain the particle. For example, small suspension-feeding worms caught proportionately more smaller beads at high flow-velocities because their smaller palps had too little contact area to capture large particles at high flow-velocities (Shimeta

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1996). Particle size is not the only basis for passive particle selection. Both the electrostatic charge of particles (LaBarbera 1978; Gerritsen and Porter 1982) and wettability (Gerritsen and Porter 1982) have been implicated as factors affecting adhesion between particle and collector.

If charge and wettability affect adhesion between particle and collector, selection among particles based on stickiness could occur if such chemical differences exist among particles. This study focused on the role of particle wettability in adhesion to determine if it is a viable basis for particle selection.

Materials and methods

Particles

Silica particles in four size ranges (10 to 40, 40 to 63, 63 to 90, 125 to 200 μm; size-graded by Sigma Chemical Co.) were used in adhesion tests with artificial collectors, and two size ranges (0.5 to 10, 15 to 25 μm) were used in capture experiments with mole crab (*Emerita talpoida*) collectors. Particles looked like shards of broken glass. All particles were treated with silanes to alter surface wettability.

Silanes are compounds in which one or more organic groups (*R*) are bound to an atom of silicon (Si): $R_n SiX_{(4-n)}$ (Streitwieser and Heathcock 1985). *X* is a hydrolyzable group that undergoes hydrolysis to form a reactive silanol group which then hydrogen-bonds to other silanol groups, including those on the surface of glass (Arkles 1977). After a stable, covalent siloxane linkage is formed by dehydration, the *R* groups become the outermost surface (Arkles 1977). The nature of the *R* groups determines the wettability of this new surface (Baier et al. 1968). For example, if *R* groups are fluorocarbons, the surface resembles Teflon and has a very low wettability; if *R* groups are charged, the surface has a high wettability.

Silanization procedures were similar to those used by Roberts et al. (1991). Particles were first cleaned of all organic matter by heating them for 4 h at 500 °C. After cooling to 100 °C, the particles were removed from the 500 °C furnace and kept in a drying oven at 100 to 105 °C until use. Particles were removed from the drying oven immediately prior to silanization.

Each size range of particles was treated with separate silane solutions. Silanization procedures are listed in Table 1 along with the surfaces treated by each silane. After silanization, each surface was rinsed twice with solvent, air-dried in a fume hood, and finally dried at 100 to 105 °C for 30 min to stabilize the siloxane linkage. Particles were kept in an oven at 100 to 105 °C until use. Since the surfaces oxidize over time, and surface chemistry alters, particles were used within a few weeks after silanization. In addition to silanized particles, baked particles were also used in experiments with natural and artificial collectors.

Artificial collector surfaces

Artificial collector surfaces were made from glass coverslips (Fisher Scientific, 12-541B microscope coverglass). All six surfaces except one were baked at 500 °C for 4 h prior to further treatment or use. When coverslips are baked, the coating is oxidized and the resulting surface is composed of hydroxyl groups and is highly wettable. Four of the five baked coverslips were treated with silanes (Table 1). Unheated coverslips were coated by the manufacturer with an unknown substance that gives it a wettability similar to surfaces treated with trimethylchlorosilane.

Mole crab collectors

Mole crabs use a pair of second antennae to collect food particles. The two antennal filters of *Emerita talpoida* are composed of long plumose flagella, 2 to 2.5 cm in an adult female (Fig. 1a). The entire length of the ventral side of each flagellum is covered with duplicate sets of four rows of setae which are, in turn, covered with shorter setules (Snodgrass 1952). The exteriormost setae are the longest, at about 2 to 3 mm, and vary in diameter from 13 to 21 μm. I could not precisely measure the length of the second pair of setae, but Snodgrass showed them as about two-thirds the length of the first pair, or 1 to 2 mm. They varied from 21 to 25 μm in diameter. The third and fourth pairs of setae are very short (< 400 μm: approximated from Snodgrass 1952), and are probably not involved in food collection (Snodgrass 1952).

As measured by a light microscope at 100×, the exteriormost setae are covered with fine, cylindrical setules (Fig. 1b) that are ~ 200 μm long and 3 to 4 μm wide. They are separated by 10 to 20 μm. The second pair of setae are covered with shorter, flat setules ~ 60 μm long and 4 to 8 μm wide. Spaces between these setules range from 10 to 50 μm.

The particles used in capture experiments (0.5 to 10 μm and 15 to 25 μm) were smaller than most pore spaces in the antennae. 15 to 25 μm particles were placed on the antennae and most appeared smaller than the spaces between the setae.

Flow patterns through the collector varied between the two flow speeds tested. At 4 cm s^{-1}, fluid only passed through the outer edges of the collector, while at 33 cm s^{-1} fluid passed through all sections of the collector. No tangential movement of water along the ventral, upstream side of the collector was detected, but vortices on the dorsal, downstream side were present at both flow speeds.

The particle collectors of the mole crab were removed immediately prior to an experiment by grasping the elongate segment below the collecting segments and pulling. This caused the

Table 1 Silanization procedures used for altering wettability of glass particles and coverslips

Treatment	(Abbreviation)	Solvent	% silane	Reaction time	Surfaced treated
Tridecafluoro-1,1,2,2-tetrahydrooctyltrichlorosilane	(TDF)	methylene chloride	1	1 h	10–40, 40–63, 63–90, 125–200 μm particles; coverslips
Dimethyldichlorosilane	(DMS)	methylene chloride	1	1 h	0.5–10 μm
Trimethylchlorosilane	(TMS)	methylene chloride	1	1 h	0.5–10, 15–25 μm particles; coverslips
Aminopropyltrimethoxysilane	(APS)	95% ethanol	2	15–30 min	0.5–10 μm
Diphenyldichlorosilane	(DPS)	methylene chloride	1	1 h	0.5–10, 10–40, 40–63, 63–90, 125–200 μm

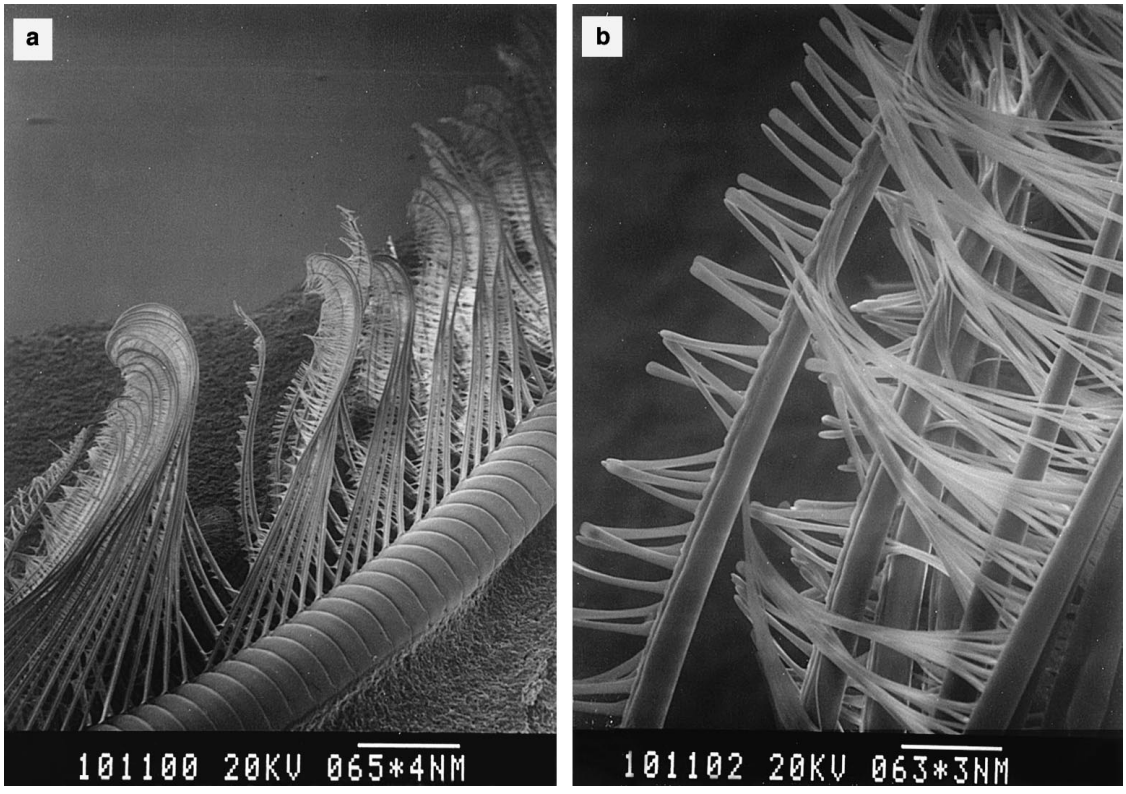

Fig. 1 *Emerita talpoida*. **a** SEM micrograph of second antenna: largest cylinder is terminal flagellum of the structure; next largest cylinders are setae, and attached to these are setules. **b** SEM micrograph of first and second pairs of setae; long, slender setules on right belong to first pair of setae, short, wide setules on left belong to second pair

antenna to separate from the mole crab at the junction between the coxopodite (the most basal segment of the antenna) and the body.

Most mole crabs were collected from Atlantic Beach, North Carolina (76° 46′ 12″ W; 34° 42′ N), but occasionally also from Topsail Beach (77° 33′ 36″ W; 34° 25′ 48″ N) when the pumping of dredge spoils onto Atlantic Beach buried the crabs. Crabs used for experiments with 15 to 25 μm particles were collected in Sarasota, Florida (82° 31′ 12″ W; 27° 15′ 36″ N). Mole crabs were transported to the Duke University Marine Laboratory and kept in flow-through seawater tanks partly filled with sand for the crabs to bury themselves in. The crabs could be maintained in the laboratory for several months.

Measuring wettability

Wettability of the silanized particles and coverslips was measured with the "standard harmonic mean" (SHM) method (Gerhart et al. 1992). The SHM method is similar to contact-angle analysis in that drops of different solutions are used to measure wettability, but it differs in that the width of the drop on the surface is measured rather than the contact angle. Results from this method strongly correlate with the combined polar components (γ^P) of wettability that are obtained through contact-angle analysis (Gerhart et al. 1992).

The solutions used in the wettability analysis consisted of a series of HPLC-grade water and HPLC-grade methanol mixtures in the following volume percentages of water: 100, 80, 60, 40, 30, 20, 10 and 0%. Starting with the 100% water solution, 25 μl drops were placed on previously unwetted surfaces on coverslips, and drop width was measured to the nearest millimeter. When a drop from a solution measured ≥20 mm, a value of 20 was assigned to it and all the remaining solutions with smaller water percentages. A single measure of wettability (SHM), scaled from 0 to 100, was calculated from the eight recorded drop widths by computing a standardized harmonic mean with the following equation:

$$\frac{\left[\left(\frac{8}{1/W_{100}+1/W_{80}+1/W_{60}+1/W_{40}+1/W_{30}+1/W_{20}+1/W_{10}+1/W_0}\right)-4\,\text{mm}\right]}{16\,\text{mm}}\times 100, \quad (1)$$

where W_n = drop width in millimeters at n% water, 8 = number of solutions used, 4 = minimum possible drop width in millimeters, and 16 = maximum range of drop sizes in millimeters. The SHM value is dimensionless.

Measurements could not be performed directly on the particles, so wettability was measured on three glass coverslips treated with the same silane solution as the particles. Measurements were performed on three different coverslips and the results were averaged (Table 2). Artificial collector wettability was measured directly on the collector surface. The results from three surfaces were averaged (Table 2).

Particles and collectors were given names (see Tables 1 and 2) beginning with an abbreviation of the silane used in production and ending with its wettability. For example, particles treated with dimethyldichlorosilane and resulting in a wettability of 13 are designated DMS-13.

The wettability of the mole crab collector was also measured, but not with the SHM method. When a hydrophilic object extends across the air–water interface, the water around the object will move up it just as water moves up the side of a hydrophilic cylinder to form a meniscus. When a hydrophobic object is in the air–water interface, the water fails to spread up the object. By inserting a dry mole crab collector into the interface and determining the spread of water up the collector, the wettability of the collector could be determined. No number was recorded; the collector was simply considered either hydrophilic or hydrophobic. Setae from the entire length of the collector were observed and categorized in this way under a dissecting microscope. Water spread up the sides of all setae tested, indicating that all the setae were hydrophilic.

Table 2 Wettability and standard error of particles and artificial collectors measured with the SHM (standard harmonic mean) method; lowest possible wettability = 0, highest possible wettability = 100 (*TDF* tridecafluoro-1,1,2,2-tetrahydrooctyltrichlorosilane; *DMS* dimethyldichlorosilane; *TMS* trimethylchlorosilane; *UGL* untreated, unheated glass; *APS* aminopropyltrimethoxysilane; *DPS* diphenyldichlorosilane; *GL* untreated, heated glass

Surface	Treatment						
	TDF	DMS	TMS	UGL	APS	DPS	GL
Particles							
0.5–10 μm	–	12 ± 0.34	23 ± 2.1	–	59 ± 1.1	65 ± 2.1	94 ± 1.3
15–25 μm	11 ± 0.32	–	39 ± 0.72	–	–	–	100 ± 0.0
10–40 μm	11 ± 0.32	–	–	–	–	73 ± 2.0	98 ± 1.7
40–63 μm	10 ± 0.46	–	–	–	–	53 ± 4.2	98 ± 1.7
63–90 μm	10 ± 0.33	–	–	–	–	52 ± 1.9	98 ± 1.7
125–200 μm	10 ± 0.33	–	–	–	–	44 ± 4.3	98 ± 1.7
Collectors	10 ± 0.25	13 ± 0.26	24 ± 1.2	21 ± 0.67	–	49 ± 1.5	98 ± 1.7

Measuring adhesion to artificial collectors

Particle adhesion to artificial collector surfaces was measured in an adhesion chamber similar to the one described in Johnson and Azetsu-Scott (1995). The device held a 7 mm i.d. o-ring between two coverslips, creating a 2 mm-thick watertight chamber inside the o-ring. One of the coverslips was the artificial collector surface.

Adhesion was determined by placing a drop of particle suspension onto the collector surface inside the o-ring. Particles were suspended in 100 kdaltons (kd) filtered seawater, and particle concentration was low enough to keep most particles from touching each other on the collecting surface. Particles in suspension settled onto the collector surface within seconds. When water completely filled the space within the o-ring, another coverslip was clamped down on the o-ring to create a water-filled, airtight chamber.

The 100 to 300 particles resting on the surface within the water-filled chamber were counted and then the entire device was gently inverted. Particles whose adhesive and buoyant forces counterbalanced or exceeded the weight of the particle remained stuck to the collector surface while the others fell off. The number of particles that remained on the collector surface was counted and divided by the original number to get the fraction of adhering particles. Particle adhesion was tested on most combinations of particle-and collector-surface wettabilities. Size ranges of the particles was increased to create greater weights. 10 to 40, 40 to 63, 63 to 90, and 125 to 200 μm size ranges were tested. Adhesion of the smallest particles (10 to 40 μm) was not measured on DMS-13, TMS-23 and DPS-50 collector surfaces because adhesion to similarly wettable surfaces was near 100%.

Calculating adhesive force between particle and collector

Adhesive force between the particle and the collector (F_a) was calculated from the detachment force (F_d), the force pulling the particle away from the collector surface, when 50% of the particles adhered to the collector. The detachment force is the difference between the weight of the particle (F_g) and the force due to buoyancy (F_b):

$$F_d = F_g - F_b \quad . \tag{2}$$

The weight of a particle is simply the product of its mass and the acceleration due to gravity:

$$F_g = \mathrm{mg} \quad . \tag{3a}$$

When 50% of the particles remain stuck to the collector surface, the forces on the average particle – gravity (F_g), adhesion (F_a) and buoyancy (F_b) – balance each other, so

$$F_g = F_a + F_b \quad , \tag{3b}$$

and thus

$$F_a = F_{d50} \quad . \tag{4}$$

The detachment force at 50% adhesion (F_{d50}) was determined from graphs of adhesion percentage and detachment force. Because ranges of particle sizes were used to measure adhesion rather than discrete sizes, an average particle mass was calculated for each size range before calculating the detachment force.

The average particle mass was determined by suspending a known mass of particles in a known volume of water. After mixing the solution to distribute particles evenly throughout the water, small samples ranging from 8 to 25 μl were removed for particle counting. All particles were counted under a 100× on a compound light microscope. Eight samples were counted, and the average was used to calculate the mass per particle. Substituting this value into Eq. (3a) gives the average weight of a particle.

Buoyancy of an average particle (F_b) was calculated as:

$$F_b = \rho_{\mathrm{water}} g V \quad . \tag{5}$$

Particle volume was calculated from the mass of an average particle using a particle density for glass of 2600 kg m^{-3} (Weast and Astle 1980). Seawater density (ρ_{water}) at 35‰S and 20 °C was 1024 kg m^{-3} (Vogel 1994).

Measuring capture of particles by *Emerita talpoida* collectors

To determine particle-capture differences due to particle wettability, particles were suspended in a flowtank and mole crab antennae were exposed to this flow. Particles captured by the antennae were counted after removal from the flow tank.

A small, recirculating flow tank, similar to the design outlined in Vogel and LaBarbera (1978), was constructed for particle-capture experiments. The working section was made of 1 cm-thick Plexiglas and measured internally 10 cm wide, 68 cm long and 13 cm high. Entrance and exit holes were 7.6 cm in diameter and were cut from the vertical ends of the working section: 3″ (7.6 cm) Schedule 40 PVC pipe was connected to the entrance and exit holes and completed the loop. A shaft with a 2.5″ (6.4 cm) plastic propeller was inserted into the vertical section of pipe, near the downstream end of the working section, through a three-way PVC elbow. Reinforced nylon pulleys (Small Parts, Inc., Miami Lakes, Florida) were mounted on the propeller shaft and the motor shaft to drive the propeller. Pulleys were connected with round, polycord belting (Small Parts Inc.). The speed of the water was controlled with a combination of a 1/15 hp motor (CM31D17NZIB: Leeson Electric Corp., Grafton, Wisconsin) with a speed control MM21211A: Minarik Electric Co., Glendale, California), and by changes of the gear ratio of the pulleys. A flow straightener, made from 2.5 cm-long sections of 0.6 cm diam soda straws glued together in a 10 × 10 × 5 cm Plexiglas support, was 20 to 25 cm upstream of the antennae and 9.5 cm downstream of the working-section entrance.

Flow speed was calculated from the distance traveled by a 4.0% aqueous solution of Evans Blue dye in the working section of the tank divided by the time to travel that distance. Speed was measured at the depth of the mole crab collectors. Results from five replicates were averaged together. Two speeds were used in the experiments, 4 ± 0.5, and 33 ± 3.3 SD cm s^{-1}. Flow-tank speeds were chosen, in part, to reflect backwash speeds on a North Carolina beach with a slope of 0.1. Backwash speeds ranged from 0.38 to 1.1 m s^{-1} when measured by the movement of positively buoyant plastic beads over 10 to 30 cm of beach (Ellers 1995). The flow-tank speed of 33 cm s^{-1} was chosen to reflect the lower part of this range. The flow-tank speed of 4 cm s^{-1} was chosen to determine if a still slower speed was more likely to result in differential adhesion, and because *Emerita talpoida* inhabit the lower energy portions of the beach (Bowman and Dolan 1985).

Particles of different wettability were suspended in the flow tank separately. The flow tank was filled with 14 liters of 5 μm-filtered seawater before the particles were added. Before introducing the particles into the flow tank, particles were mixed with ≃7 ml of 95% ethanol to reduce particle clumping. This solution was mixed into the flow tank while the water velocity was ≃30 cm s^{-1} by pipetting it beneath the water surface in the part of the working section closest to the propeller. The percentage of ethanol in the flow tank after mixing was <0.05% by volume. For the 0.5 to 10 μm particles, seawater was filtered to remove particles and molecules >100 kd. One gram of 0.5 to 10 μm particles was added to the flow tank for the 4 cm s^{-1} experiments, while 0.5 g was added for the 33 cm s^{-1} experiments. For the 15 to 25 μm particles, water was filtered to remove particles greater than a few micrometers. 0.3 g was added for the 4 cm s^{-1} experiments, and 0.1 was added for the 33 cm s^{-1} experiments. After the entire solution had been added and mixed thoroughly in the flow tank, the water velocity was adjusted to either 4 or 33 cm s^{-1} and crab collectors were exposed to the particle-laden flow.

Antennae, removed from the crab immediately prior to each experiment, were first placed in a 0.5 ml microcentrifuge tube filled with filtered water. The tube was covered and submerged underwater to prevent the antenna from picking up particles trapped in the air–water interface. Upon removal of the antenna, it was positioned in the particle-laden flow tank with the long axis normal to flow at approximately one-third depth in the working section, halfway between the two sidewalls and 20 to 25 cm downstream of the flow-straightener. By grasping the antenna at the third antennal segment with tweezers, the antenna extended from a semi-circular shape to a rigid, straightened shape. The antenna was held in this manner during immersion in the flow tank. The ventral side of the antenna faced upstream in a position similar to the way crabs hold the antennae in flow. With the 0.5 to 10 μm particles, antennae were held in flow for 2 min at 4 cm s^{-1}, and 20 and 40 s at 33 cm s^{-1}. With the 15 to 25 μm particles, antennae were held in flow for 5 s at both 4 and 33 cm s^{-1}.

After exposing the antenna to the flow, it was removed from the flow tank by placing it in a 0.5 ml polypropylene microcentrifuge tube filled with 100 kd-filtered seawater that had been submerged in the working section of the flow tank. The tube opening was covered to prevent the antenna from picking up particles trapped in the air–water interface. The tube was then shaken for 15 s on a vortexing machine to shake the particles off the antenna. With the 0.5 to 10 μm particles, the antenna was removed from the tube with forceps, and particles in the tube were counted by measuring absorbance of the solution with a spectrophotometer (Beckman DU 640) with a pathlength of 1 cm. Each absorbance reading took 0.5 s. The wavelength used in measuring absorbance depended on the particle type, DMS-13, TMS-23, and APS-59 were measured at 325 nm; DPS-65 at 367 nm; and GL-93 at 375 nm. Absorbance measurements were transformed to particle concentrations with the standard curves obtained for each particle type. All standard curves were linear in the range tested, with increasing concentrations resulting in increasing absorbances. Results of the experiments are presented as total number of particles captured. Three tests were conducted for each particle type. Each particle-capture test consisted of a new supply of seawater, particles and ten antennae. The results from the ten antennae were averaged.

Because particles may adhere to the antennae with different strengths, vortexing the tubes to shake particles off the antennae may not remove all particle types equally. For example, if DMS-13 particles adhere very strongly to the antenna and vortexing does not remove most of these particles, a low absorbance would be recorded. To test whether vortexing was sufficient to remove most of the particles from the antenna, or whether there were differences in the amount of removal, antennae from one test at 4 cm s^{-1} were placed into glass test tubes after vortexing and burned in a furnace at 500 °C for 24 h. After cooling, the remaining inorganic pieces and any calcium carbonate were dissolved in 0.5 ml of 6 *M* HCl, leaving behind any remaining glass particles. Absorbances of these HCl solutions of DMS-13, TMS-23, DPS-65 and GL-93 particles were compared for any differences at 204, 301, 326, and 464 nm, respectively, with a Beckman DU 640 spectrophotometer at a 1 cm pathlength. Absorbances from control solutions containing antennae only were substracted from the experimental absorbances and the result was converted to a concentration with the slope of each wettability's standard curve. An ANOVA failed to reveal removal differences among particle types (ANOVA: $F_{3,27} = 0.193$, $p = 0.9$), indicating that the same number of particles remained stuck to the antennae after vortexing, regardless of wettability. Therefore, the data collected is an accurate reflection of the number of particles actually captured, although it underestimates capture by one-half to two-thirds.

0.5 to 10 μm particles were also tested to determine if clumping differences among particles types existed. Particles were mixed in filtered seawater and at the same concentration used in the 4 cm s^{-1} experiments. Samples of these suspensions were placed on a microscope slide and observed at 1000× with an oil immersion objective. The percentage of particles and particle clumps <1.4 μm, between 1.4 and 7.0 μm, and >7.0 μm was determined. This procedure was repeated three times with particles of all 5 wettabilities. An ANOVA failed to reveal any significant differences in the size distribution of particles (<1.4 μm: $F_{4,10} = 0.567$, $p > 0.05$; 1.4 to 7.0 μm: $F_{4,10} = 0.069$, $p > 0.05$; >7 μm: $F_{4,10} = 2.906$, $p > 0.05$).

The 15 to 25 μm particles were counted by removing a water sample from the microcentrifuge tube, placing it in a hemacytometer, and averaging the counts from three 0.1 μl fields. Twenty antennae were tested for each different particle type. Because the 15 to 25 μm particles were heavier than the 0.5 to 10 mm particles, vortexing of the 15 to 25 μm particles was assumed to be sufficient and without bias according to particle type. They also did not form clumps.

Results

Particle adhesion to artificial collectors

In general, as particle and collector wettability increased, adhesion declined. The percentage of particles remaining stuck to the artificial collector decreased as both particle and collector wettability increased (Fig. 2) and, consequently, so did the adhesive force between particle and collector (Table 3).

While adhesion generally declined as wettability increased, wettability affected adhesion most between 0.37 and 9.0 nN where there were large differences in adhesion percentage. At the lowest force tested, 0.0025 nN, all particles stuck to all coverslips, regardless of wettability, with adhesion percentages >90%. At 0.37 nN, adhesion percentage ranged from 99 to 50%. At 2.3 and 9.0 nN, the largest differences in adhesion percentages were ≃90%.

When compared among particles on the same coverslip, however, particle wettability sometimes had little affect on adhesion. This occurred at the highest forces, 2.3 and 9.0 nN, on highly wettable coverslips. No statistically significant differences in particle adhesion were found on GL-98 coverslips at 2.3 and 9.0 nN (Kruskal–Wallis $H = 3.232$, $p = 0.199$; and $H = 1.274$, $p = 0.529$) and on DPS-49 coverslips at 9.0 nN (Kruskal–Wallis: $H = 0.801$, $p = 0.670$).

Capture of 0.5 to 10 μm particles by *Emerita talpoida*

Differences in capture rates among the particles of five different wettabilities were evident at both 4 and 33 cm s^{-1}. At 4 cm s^{-1}, particle wettability was negatively correlated with capture rate (Fig. 3a; $r^2 = 0.84$, $p < 0.05$). At 33 cm s^{-1}, particle wettability was also negatively correlated with capture rate at both exposure times, but capture rate declined at an exponential rather than a linear rate (Fig. 3b; 20 s: $r^2 = 0.99$, $p = 0.007$; 40 s: $r^2 = 0.99$, $p = 0.0016$). Data from both exposure times were fitted with an exponential function, $f(x) = a \cdot \exp(b/(x + c))$, using "Sigmaplot 4.0 for Windows."

Capture of 15 to 25 μm particles

No differences in capture rate among the particles of five different wettabilities were found at either 4 or 33 cm s^{-1} (Fig. 4).

Discussion

Particle adhesion to artificial collectors

In general, the percentage of particles adhering to the artificial collectors declined as particle and collector wettability increased (Fig. 2). The physical basis for this result can be found in the Derjaquin–Landau–Verwey–Overbeek (DLVO) theory of colloid aggregation and a free-energy approach to adhesion. The DLVO theory predicts the aggregation of colloids by comparing the magnitude of van der Waals attractive energies to the electrical repulsive energies in the layer of ions surrounding the particles. The theory predicts stronger adhesion among low-wettability solids due to their

Fig. 2 Percentage of particles adhering to silanized coverslips at 0.0025, 0.37, 2.3, and 9.0 nN of force

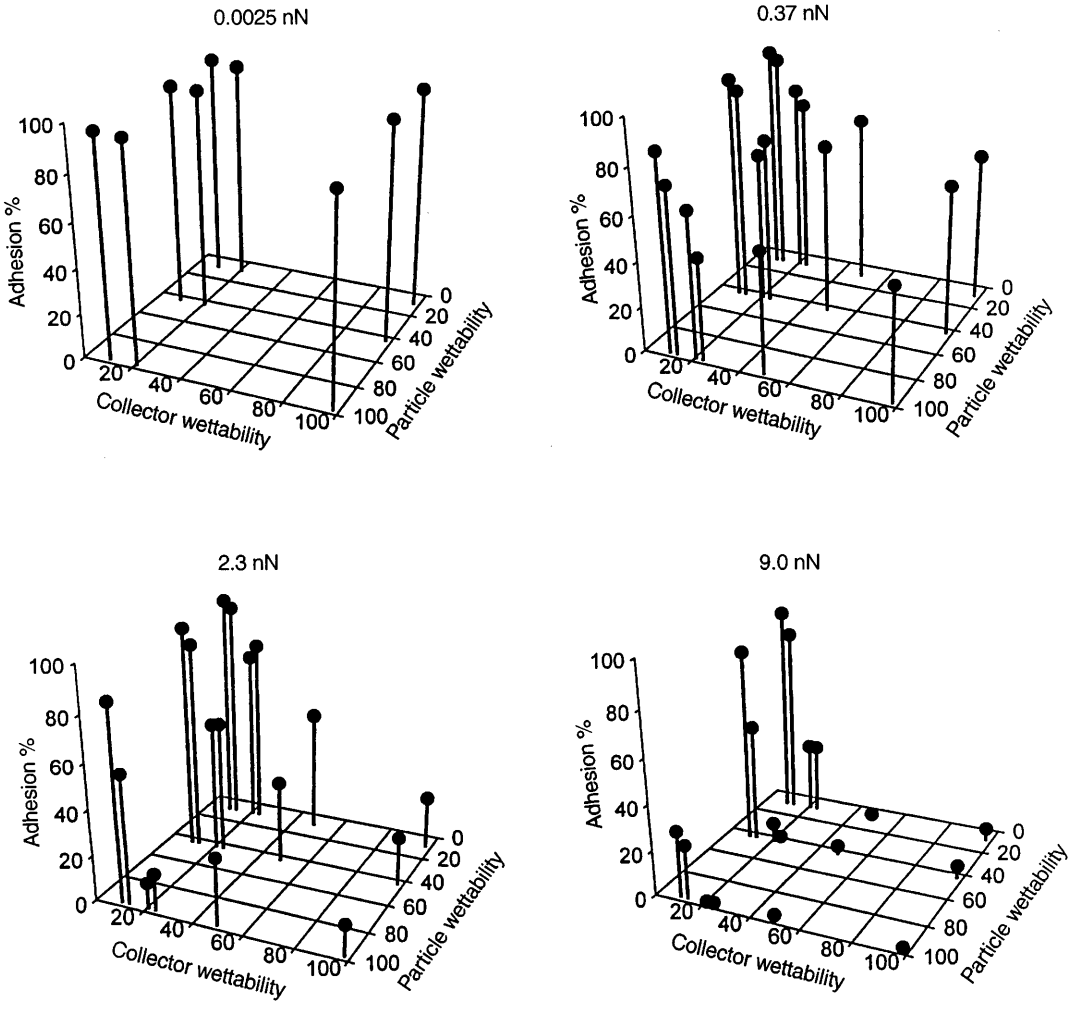

Table 3 Adhesive force, F_a (in nN) between particles and collectors (95% confidence intervals in parentheses)

Collector	Particle		
	TDF-10	DPS-50	GL-98
TDF-10	>9	>9	5 (4–8)
DMS-13	>9	>9	4 (2–6)
TMS-23	5 (3–9)	2 (0.3–3)	0.6 (0–2)
UGL-21	5 (4–7)	2 (0.7–3)	0.6 (0–3)
DPS-50	2 (1–2)	2 (1–2)	1 (0–2)
GL-98	1 (0–4)	1 (0–4)	0.4 (0–3)

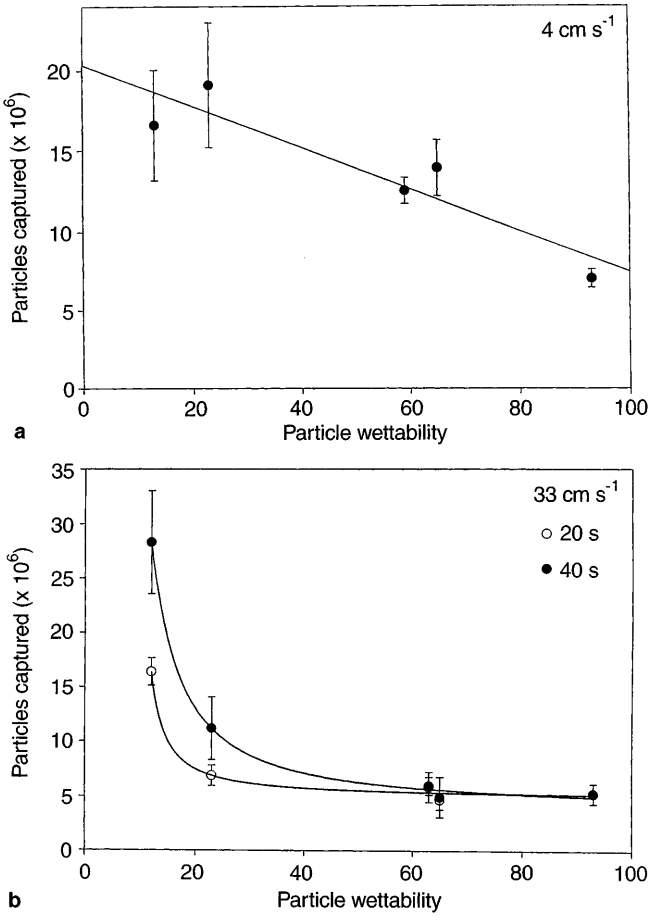

Fig. 3 *Emerita talpoida*. Number of 0.5 to 10 μm particles captured by second antenna during exposure to particle-laden flow in flow tank at 4 cm s^{-1} (**a**) and 33 cm s^{-1} (**b**)

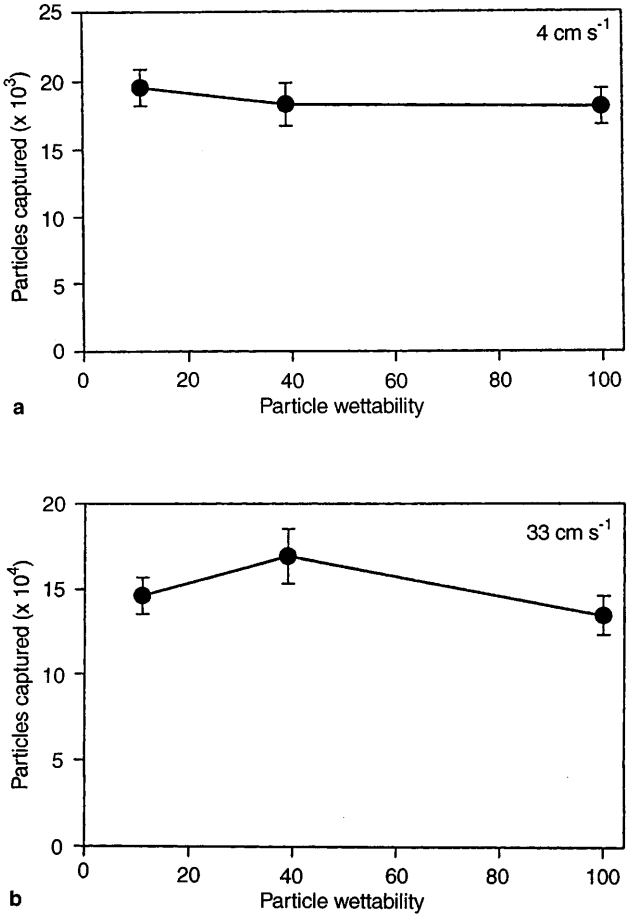

Fig. 4 *Emerita talpoida*. Number of 15 to 25 μm particles captured by second antenna at 4 and 33 cm s^{-1}

stronger van der Waals interactions (Marshall 1985; van Loosdrecht et al. 1990). The free-energy approach predicts greater adhesion between low-wettability solids because water between the surfaces is easily displaced from approaching hydrophobic surfaces (Rutter and Vincent 1980; Israelachvili and McGuiggan 1988). The results are also consistent with previous empirical results comparing particle adhesion on highly-wettable glass to lower-wettability polyester (Johnson and Azetsu-Scott 1995).

Adhesion depends not only on the wettability of the surfaces, but also on the physical forces tending to separate the two surfaces. In experiments in the adhesion chamber this force is gravity, but for a particle on a suspension feeder this force is a combination of gravity, drag and lift. The results from the adhesion chamber show that at very low forces (in this case 0.0025 nN), wettability has very little influence on adhesion – all particles stick (Fig. 2). Only at greater forces (0.37 through 9.0 nN) does an increase in particle and coverslip wettability cause adhesion to decline. At some even larger force, wettability will cease to have an effect on adhesion, and no particles will be able to adhere to the collector. The opportunity for passive particle selection based on wettability, therefore, is confined to an intermediate range of forces.

Some suspension feeders may in fact capture particles within this range of forces. The forces used in the artificial collector tests are similar to the calculated forces that 10 to 100 μm spherical particles would experience while retained on a collector exposed to local flows between 0.1 and 1 cm s^{-1} (Shimeta and Koehl 1997). This indicates that the forces involved in suspension feeding are neither too small (which would result in nearly perfect adhesion of all particles) nor too large for a passive particle-selection method based on wettability. Some organisms with collector flow-speeds in this range

include bivalve larvae (Gallager 1988) and daphnids (Gerritsen et al. 1988). At higher forces of 10^{-8} to 10^{-7} N – corresponding to a local flow of 10 cm s^{-1} (Shimeta and Koehl 1997) – particle wettability may also affect particle capture, since the adhesive forces between some particles and collectors exceed 10^{-8} N. Animals that suspension-feed at these velocities include black fly larvae (Craig and Chance 1982) and sea pens (Best 1988).

While the general trend of particle-to-artificial collector adhesion is one of decreasing adhesion with increasing surface wettability, from the point of view of a suspension feeder the most interesting part of this data is the effect of particle wettability on adhesion to any given collector. With this perspective, we can see that there were sharp declines in particle adhesion on some collectors and some minor declines on others. For example at 9.0 nN, adhesion to GL-98, which has a very high wettability, only fell from 6 to 2% as particle wettability rose, while adhesion to TDF-10 fell from 90 to 30%. To optimally discriminate among particles based on wettability at this force, suspension-feeding collectors may be non-wettable.

0.5 to 10 μm particle adhesion to mole crab (*Emerita talpoida*) antennae

Although there was a general decline in particle adhesion to artificial collectors as wettability increased, adhesion percentages to highly wettable collectors varied little with particle wettability. Adhesion percentages to an intermediate wettability collector (DPS-49) varied more greatly at intermediate detachment forces. Predictions of particle adhesion to the mole crab collector based on these results depend on knowing the collector's wettability. The mole crab antenna is wettable, but it is unknown whether it is highly wettable like GL-98 or more intermediate like DPS-49, since the surface roughness of the antenna prevented more precise measurement. An extremely high-wettability collector may not differentially capture particles, while a more intermediate collector may. The results from both flow speeds, showing that the antennae captured more non-wettable particles than wettable ones, indicate that the antennae probably have an intermediate wettability. It would also be unusual for an organic surface to have a wettability as high as inorganic glass, but the possibility that the model fails to predict adhesion to biological collectors cannot be ruled out entirely. Regardless of whether the mole crab results follow model predictions precisely, mole crabs are capable of passively selecting non-wettable particles over wettable ones between 4 and 33 cm s^{-1}.

The differences in particle capture between the two flow speeds – the greater disparity in capture at the extremes of particle wettability and the relatively smaller capture of intermediate wettabilities at 33 cm s^{-1} – probably result from the increase in drag on the particles at the faster speed. As drag increases, particles with weaker adhesion will be captured less frequently and the differences in particle capture will increase, as they do when flow speed is increased from 4 to 33 cm s^{-1}.

15 to 25 μm particle adhesion to mole crab antennae

Unlike the 0.5 to 10 μm particles, particle wettability had no effect on capture of 15 to 25 μm particles by the mole crab antennae. It is possible that the particle size increase caused drag to increase to a point where adhesion efficiency of all particles was very low and that this resulted in equal numbers of captured particles. But it is also possible that the captured particles were collected by sieving rather than adhesive mechanisms. Even though the particles appeared to be smaller than the pore spaces in the antenna when they were placed together, the smallest pore spaces I measured were slightly smaller than the particles' diameter, suggesting that these small pore spaces may have captured most of the particles. Unfortunately I could not determine the location of particle capture since the antenna folded together after removal from the flow tank, and I cannot differentiate between these two possibilities.

Implications for suspension feeders

The ability of mole crab collectors to differentially capture some particles based on wettability raises the possibility that they may do so in their natural environment. A requirement for a passive-selection mechanism based on particle-wettability differences is a natural particle assemblage with a range of particle wettabilities. Currently there are no wettability measurements of phytoplankton, fecal pellets, or other aquatic particles other than bacteria. Wettability values for some of these bacteria are listed in Table 4, along with some non-biological surfaces for comparison.

While the values listed in Table 4 do not vary as widely as the non-biological surfaces, the measured differences in wettability among these bacteria do correlate with adhesive differences (Fattom and Shilo 1984; Busscher et al. 1984). More studies of phytoplankton and other particle wettabilities need to be made to further understand any role wettability may have in their capture and selection. However, measuring particle wettability is not very easy. The biphasic separation method, which measures the amount of particles remaining in the aqueous phase after mixing with hexadecane, may strip surface molecules from the cell surface and result in inaccurate wettability measurements. The more common contact-angle method requires cells to be layered on a flat surface, and this may also result in inaccurate measurement since the cells may produce different surface molecules when stuck to a substrate than when in suspension (Characklis and Cooksey 1983). The drying of cells before measurement and the surface roughness of the layer may also lead to inaccurate values with this method (Vrolijk et al. 1990).

Table 4 Wettability of aquatic biological surfaces. Results from two different methods are listed. Larger angles indicate greater hydrophobicity when contact angle is measured, while smaller percentages represent greater hydrophobicity when biphasic separation method is used. Values of highly wettable and non-wettable artificial surfaces are also listed for comparison

Method	Species	Result	Source
Contact angle	Two unidentified bacteria	20° 55°	Mozes et al. (1989)
	Escherichia coli	15°	van Loosdrect et al. (1990)
	Pseudomonas sp. 62	20°	
	Alcaligenes sp. 75	23°	
	Pseudomonas sp. 84	25°	
	Pseudomonas sp. 102	60°	
	Arthrobacter sp. 177	60°	
	Sulfonated polystyrene	24 ± 3°	Absolom et al. (1983)
	Fluorinated ethylene-propylene copolymer	110 ± 3°	
Biphasic separation	*Anabaena variabilis* (free-living)	100%	Fattom and Shilo (1984)
	Anabaena filiculoides (symbiotic)	30%	
	Phormidium sp. J-1	0%	
	Plectonema boryanum	100%	
	Vibrio proteolytica	50%	Paul and Jeffrey (1985)
	Phormidium sp. J-1	0–20%	Bar-Or et al. (1985)
	Phormidium sp. J-1 (incubated in darkness)	78%	
	0.5–10 μm TMS-23 particles	9%	Conova (unpublished data)
	0.5–10 μm GL-94 particles	66%	

It may be easier to measure the adhesive behavior of cells, as did Kiørboe and Hansen (1993) when they found stickiness differences among some phytoplankton.

Given that bacteria differ in wettability and adhesion, and phytoplankton differ in stickiness, it is possible that mole crabs and other suspension feeders passively select among particles based on wettability and adhesive variations. Mole crabs, in particular, live in an environment where they are subjected to numerous sand particles of which they are reported to ingest relatively little (Efford 1966). Capture results with the mole crabs indicate that they can avoid collecting these high-wettability inorganic particles even at low flow speeds. Large sand particles may also be too dense and associated with too much drag to be captured at speeds >25 cm s^{-1}, when the mole crab filter is oriented more parallel to the flow direction (Efford 1966) and water appears to pass over the antennae rather than through them. The ability of mole crabs to passively select among organic particles is less clear. Natural particle wettabilities are unknown, and mole crabs may not capture particles in nature at the same flow speeds tested in the laboratory. Peak backwash speeds range from 38 to 100 cm s^{-1} on a North Carolina beach (Ellers 1995), but it is not known at what speeds mole crabs actually feed. Bowman and Dolan (1985) found higher densities of mole crabs in more gently sloped sections of the beach, suggesting that they live in slower backwash; however, flow speed was not measured.

Mole crab collectors were used in these experiments primarily because they were large and easily obtainable in great quantities. Their ability to differentially capture particles based on wettability, as well as similar results with *Daphnia magna* (Gerritsen and Porter 1982), indicate that other suspension feeders may also have the same ability. A variety of different surface chemistries among particles and suspension-feeding appendages would allow greater precision in particle selection by differential adhesion, and finer division in resource partitioning among suspension feeders. Whether these animals actually select among particles with this mechanism in their natural environments or not will require further research and attention to the actual particle mixture and flow regimes surrounding the suspension feeders.

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