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THE MECHANISMS OF FILTER FEEDING:  
SOME THEORETICAL CONSIDERATIONS

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Despite a wealth of information on the structure of biological filters, the retention of particles by these filters, and the rates and metabolic costs of water transport through them (Jørgensen 1955, 1966, 1975*a*), the mechanisms by which this filtering takes place are poorly understood.

A review of the literature on filter feeding reveals that biologists generally assume that filters act as sieves. Originally proposed by Alder and Hancock (1851, in Dral 1967), the sieve theory of filtration states that the filtering apparatus removes only those particles too large to pass through the pores of its filtering mesh (fig. 1, *B* and *H*). However, Wallengren (1905, in Dral 1967) proposed that even particles smaller than the mesh size could be captured by suspension feeders simply by striking and adhering to the sticky structural elements of the filtering apparatus. We believe that Wallengren's basic concept, when coupled with hydrodynamic principles appropriate to the morphology and ecology of aquatic organisms, can serve as the foundation of an expanded theory of the mechanisms of filter feeding.

Filtration is the separation of particles from fluids by the use of porous media. Sieving is only one of several mechanisms by which filters remove particles from a fluid, and sieves suffer from high clogging rates and excessively high resistance to the flow of fluid through them (Chen 1955). To remove particulate matter from gases, industrial engineers have developed filtering devices in which the pores are several orders of magnitude larger than the particles which are trapped. By developing theories which consider several mechanisms of particle capture in addition to sieving, engineers have been successful in predicting the effectiveness of particle removal by these filters. We believe that this theory of filtration can be applied to biological filters.

This paper will enumerate the basic mechanisms by which any filter, biological or man made, can remove particles from fluids and the variables on which the effectiveness of each mechanism depends. It will provide insights for those investigating such areas as the efficiency of various modes of filter feeding and the mechanisms of size-selective suspension feeding.

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Filters can be characterized as fiber or pore filters. We will first discuss the mechanisms by which particles are captured by individual fibers and pores. Then we will examine the collecting properties of entire filters. Finally we will speculate on the biological implications of this theory.

#### THE THEORY

Three elements are involved in any filtration system: the dispersed particles, the fluid medium, and the filter. By characterizing each of these elements, it is possible to predict the manner by which particles are captured.

The equations were derived from aerosol particles; thus they are valid for particles with radii between  $10^{-7}$  and  $10^{-1}$  cm (Fuchs 1964) and with low settling velocities in the fluid, and for flow situations where particle motion is dominated by viscous forces ( $Re < 1$ ) (Hidy and Brock 1970). Particles are assumed to be spherical and to adhere to the filter upon contact. The ways in which biological particles and filters deviate from these assumptions and the impact of such deviations on the predictions of the theory will be discussed later.

#### *Capture by a Single Fiber*

The first step in characterizing the mechanisms of particle capture by a single fiber entails describing the velocity field surrounding the fiber. Although this can be done mathematically (Chen 1955; Pich 1966), it is sufficient for our purposes to describe the velocity field graphically using streamlines as indicators of flow direction (fig. 1, *A*). It is assumed that the solitary fiber is cylindrical and oriented with its long axis normal to the direction of flow. The velocity upstream from such a fiber can be characterized by a series of parallel streamlines. At a specific point, determined by the fiber diameter as well as the velocity, viscosity, and density of the fluid, the streamlines begin to diverge around the fiber. Downstream the streamlines again converge and run parallel to each other. We assume that the particles do not affect the flow pattern.

There are five mechanisms by which a fiber can remove dispersed particles from this velocity field: (1) direct interception, (2) inertial impaction, (3) gravitational deposition, (4) diffusion or motile-particle deposition, and (5) electrostatic attraction. If the system can be characterized with respect to the particles (size, shape, mass, charge), the fluid medium (velocity, viscosity, density, temperature), and the fiber (thickness, orientation, charge), each mechanism can be expressed in terms of a dimensionless index. Thus one can compare the magnitudes of these parameters and so determine the relative importance of each mechanism of particle capture (Ranz and Wang 1952; Pich 1966).

*Direct interception.*—When the center of a massless particle following a streamline comes within one particle radius ( $d_p/2$ ) of a fiber it will contact the fiber and be captured (fig. 1, *C*). (A listing of the notations appears in the Appendix.) The intensity of direct interception can be expressed by the

## KEY:

- ⊙ = crosssection of fiber
- = particle
- ▨ = longitudinal section of pore
- = streamline
- ..... = path of particle

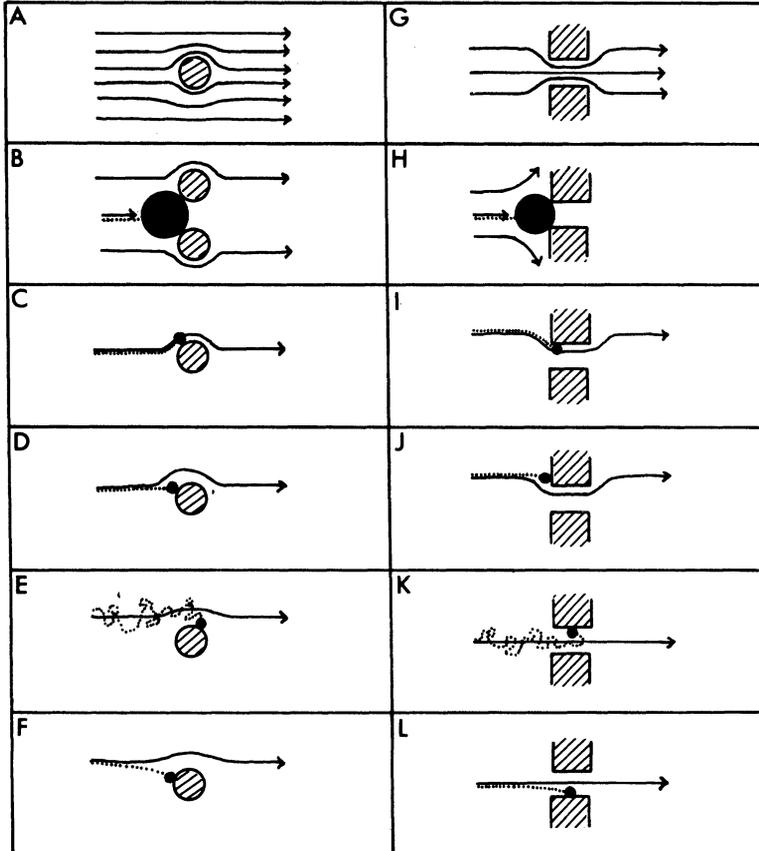


FIG. 1.—Diagrams of: *A*, flow around a fiber; *G*, flow through a pore; *B* and *H*, sieving; *C* and *I*, direct interception; *D* and *J*, inertial impaction; *E* and *K*, motile-particle deposition; *F* and *L*, gravitational deposition.

dimensionless index:  $N_{Rf} = d_p/d_f$  (Pich 1966). Thus for a given fiber diameter, the intensity of capture by direct interception depends only upon the size of the particle.

*Inertial impaction.*—Particles with mass tend to follow streamlines until the fluid is diverted and accelerated as it passes around the fiber. Then, due to their own inertia, the particles tend to deviate from the streamlines. Such particles are intercepted by the fiber if they pass within one particle radius of the fiber

(fig. 1, *D*). The following index describes the intensity of deposition by inertial impaction:  $N_{If} = [(\rho_p - \rho_m)d_p^2 V_o]/18\mu d_f$  (after Fuchs 1964). This index is the ratio of the stop distance (the distance the particle would travel before being stopped by fluid resistance) to the fiber diameter. Thus a small increase in particle diameter would lead to a large increase in the intensity of inertial deposition; increasing velocity would also increase the intensity of inertial deposition.

*Gravitational deposition.*—Particles denser than the fluid in which they are dispersed tend to sink. If a particle falls within one particle radius of the fiber, it will be intercepted (fig. 1, *F*).

The dimensionless index expressing the intensity of particle capture due to gravitational sedimentation is:  $N_{Gf} = v_g/V_o$  (Chen 1955), where  $v_g$  is the settling velocity of the particle,  $v_g = [d_p^2 g(\rho_p - \rho_m)]/18\mu$ . This index represents the ratio of the settling velocity of the particle to the upstream velocity of the fluid. As in inertial impaction, the intensity of capture due to gravitational deposition increases with the square of particle diameter, but it decreases with increasing velocity.

*Diffusion or motile-particle deposition.*—Very small particles display random Brownian motion as they collide with molecules of the surrounding medium. As a result, the trajectories of these particles deviate from the streamlines. If a random movement brings the center of the particle to within one particle radius of the fiber, it will be captured (fig. 1, *E*). Although many biological particles are too large to display true diffusion, locomotory movements causing their trajectories to deviate from the streamlines will change their probability of capture in an analogous manner. The dimensionless index expressing the intensity of capture due to the motion of particles out of the streamline is:  $N_{Mf} = D/(V_o d_f)$  (Pich 1966), where  $D$  is the diffusion coefficient,  $D = KT/(3\pi\mu d_p)$ . Rearranging, the dimensionless index becomes

$$N_{Mf} = \frac{KT}{d_p} \left( \frac{1}{3\pi\mu V_o d_f} \right).$$

A decrease in velocity increases the time during which particle motion can take place in the vicinity of the fiber, thus increasing the probability of contact. Decreasing the viscosity of the fluid will increase the rate of particle movement relative to the fluid, thus enhancing the probability of particle capture.

For particles undergoing Brownian motion the intensity of diffusive deposition is directly proportional to the Boltzmann constant and the absolute temperature and inversely proportional to the particle diameter. For motile biological particles, an analogous expression for  $KT/d_p$ , which has the units of force, must be determined experimentally for each situation. Because force is a vector, this expression allows for directional as well as random swimming.

*Electrostatic attraction.*—If the particle and fiber are of opposite electrical charge the particle can be attracted to the fiber and captured. One dimensionless index describing the intensity of electrostatic deposition is:  $N_{Ef} = 4Qq/(3\pi\mu d_p d_f V_o)$  (Pich 1966). Increasing the attractive force between the fiber and the particle by increasing the charge of either will increase the intensity of

electrostatic deposition. As for diffusive deposition, the intensity of electrostatic deposition is inversely proportional to the particle diameter and the fiber diameter and to the fluid velocity and viscosity. In seawater, a medium containing many ions, it is hard to imagine that this mechanism plays a significant role in attracting particles to a filter. Although we will not discuss this mechanism further, it may play a role in freshwater systems.

#### *Capture by a Single Pore*

Similar dimensionless indexes have been developed for the capture of particles by a straight tube of circular cross-section parallel to the direction of flow in a membrane which is oriented normal to the flow. The pattern of flow through such a pore is illustrated in figure 1, *G*.

*Direct interception.*—The dimensionless index expressing the intensity of capture due to direct interception of particles by a pore (fig. 1, *I*) is:  $N_{Rp} = d_p/d_c$  (Pich 1966). Thus larger particles and smaller pores will increase the intensity of direct interception.

*Inertial impaction.*—Particles are captured on the surface of a pore filter by inertial impaction (fig. 1, *J*), the intensity of which is depicted by the index:  $N_{Ip} = [(\rho_p - \rho_m)d_p^2 V_o]/(18\mu d_c)$  (after Pich 1966). The intensity of inertial impaction increases with increasing velocity, relative particle density, or particle size, and with decreasing pore diameter. If a pore is not straight, then inertial impaction could also occur within the capillary wherever the fluid is accelerated in a new direction.

*Gravitational deposition.*—The dimensionless index expressing the intensity of gravitational deposition of particles in a horizontal pore (fig. 1, *K*) is:  $N_{Gp} = 3v_g L/4d_c V_c$  (Pich 1966). Gravitational deposition is enhanced by low fluid velocities in long, narrow pores, and its intensity increases as the square of particle diameter.

*Diffusion or motile-particle deposition.*—Particles moving out of the streamlines within the pore may touch the wall of the pore and be captured (fig. 1, *L*). The index expressing the intensity of this mechanism of particle capture by pores is:  $N_{Mp} = (2DL)/d_c^2 V_c$  (Pich 1966). A decrease in pore diameter can greatly increase particle collection by this mechanism. The longer the pore, the slower the velocity through it, or the higher the diffusion coefficient of the particle, the more important is this mode of particle collection.

#### *Efficiency of Particle Capture*

Filtering efficiency is defined by engineers as the ratio of the number of particles striking a filtering element (a fiber or the walls of a pore) to the number which would strike it if the streamlines were not diverted by it (Dorman 1966). Various expressions for the efficiency of particle capture by each mechanism discussed above have been empirically determined for fibers as well as pores. Efficiency is always a function of the dimensionless index that expresses the intensity of capture by that mechanism. Because this paper is a general state-

ment of the mechanisms of particle capture and their dependence on measurable physical variables, we feel that the dimensionless parameters serve this purpose better than the more complicated efficiency equations which contain numerous empirically derived terms. In specific cases, however, biologists may choose to derive their own filtering efficiency equations.

#### *Combination of Mechanisms of Particle Capture*

Up to this point we have discussed each mechanism of particle capture as acting independently. Some interesting ramifications arise, however, from considering the simultaneous action of several mechanisms. One of the consequences of this action is that a filtering element differentially captures particles of different sizes. As particle size is reduced, collection by diffusion deposition is enhanced. As particle size is increased, a filtering element's ability to collect particles by inertial deposition, gravitational sedimentation, and direct interception is improved. As a result there is an intermediate range of particle sizes for which the intensity of capture by the simultaneous action of all mechanisms reaches a minimum. This minimum occurs at smaller particle sizes as velocity is increased and fiber diameter is decreased.

Similarly, for a given size of particle, the capturing ability of a filtering element depends upon velocity. As velocity is decreased, motile-particle and gravitational deposition are enhanced; as velocity is increased inertial impaction of particles is improved (fig. 2). Thus, for a given size of particle there is an intermediate range of velocities for which the intensity of capture by the simultaneous action of all mechanisms reaches a minimum.

Therefore, for any given particle size and velocity, only one or two of the filtration mechanisms listed above will play a significant role in particle capture by a fiber or a pore. The main mechanism for a given filtration situation is that having the largest dimensionless index; the other mechanisms may be ignored as a first approximation (Pich 1966).

#### *Capture by Whole Filters*

In deriving the equations to describe the various modes of particle collection by entire filters rather than isolated filtering elements, two approaches have been used. One approach, which is used for dense filters (small  $h/d_f$ ), models the filter as a collection of capillaries. The other approach, which is used for porous filters (large  $h/d_f$ ), models the filter as a collection of fibers. The expressions derived using either approach "should not be regarded as even roughly quantitative; they can only serve to give some initial guidance as to the way in which . . . filters act" (Fuchs 1964, p. 214). We will therefore only discuss them qualitatively.

Because the flow pattern around a fiber is changed by the presence of neighboring fibers, the intensity of particle collection of a fiber in a filter is different from that of an isolated fiber. As the volume fraction ( $\alpha$ ) of fibers in a filter

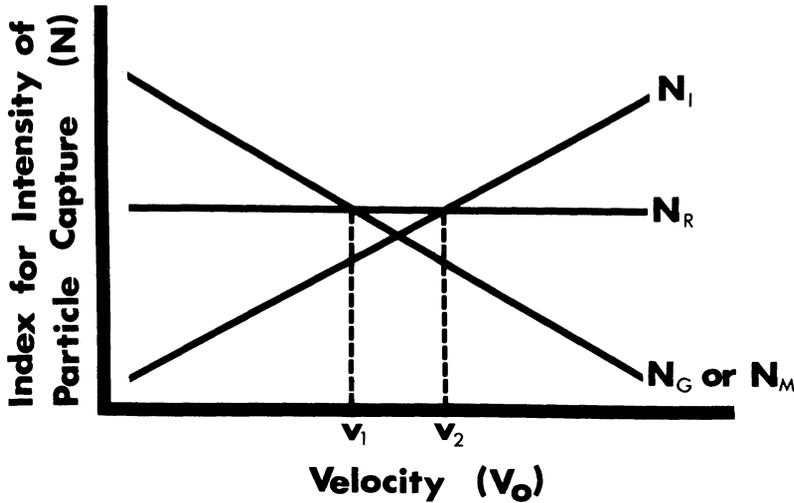


FIG. 2.—Hypothetical effect of velocity ( $V_0$ ) on the intensity of particle capture ( $N$ ) for a given fiber ( $d_f$ ), particle ( $d_p$ ,  $\rho_p$ ) and fluid medium ( $\rho_m$ ,  $\mu$ ,  $T$ ). At velocities greater than  $V_2$  inertial impaction is the mode of particle capture with the largest index ( $N_I$ ) and is thus the most important mode. At velocities between  $V_1$  and  $V_2$  direct interception (index  $N_R$ ) predominates, and at velocities lower than  $V_1$  gravitational deposition (index  $N_G$ ) or motile-particle deposition (index  $N_M$ ) is the main mode of particle capture. Whether gravitational or motile-particle deposition predominates at low velocities depends upon the particle density and motility.

increases, the streamlines around a fiber are compressed. This increases collection by direct interception because more particles approach the fiber at the critical distance  $d_p/2$ . Since increasing  $\alpha$  increases the velocity of flow in the filter as well as the curvative of the streamlines, collection of particles by inertial impaction also increases. The increase in velocity decreases motile-particle deposition by reducing the time available for "diffusion." Considering all these factors together, the total collection intensity of a fiber in a filter increases as  $\alpha$ , the fiber volume fraction, of the filter is increased (Chen 1955; Fuchs 1964; Dorman 1966).

The fluid medium in which particles are suspended must be moved through a filter if the particles are to be caught, hence the resistance of a filter to fluid flow is as important a consideration as its intensity of particle collection. The expressions which have been derived for the resistance to fluid flow of filters of various geometries are reviewed in Chen (1955), Fuchs (1964), and Pich (1966). For dense filters the resistance equations have been derived from Poiseuille's equation for the pressure ( $\Delta P$ ) needed to drive a fluid through a pipe when flow is laminar:  $\Delta p = 8\mu L\omega/\pi(d_c/2)^4$ . For porous filters the resistance equations have been derived from the equation for the drag ( $F$ ) on a cylinder in laminar flow:  $F = C\mu d_f V$ . The resistance of a filter to fluid flow increases as the velocity and viscosity of the fluid and the thickness of the filter increase. The

resistance is directly proportional to the volume fraction of fibers ( $\alpha$ ) and to the diameter of the fibers. Thus the factors which affect the intensity of particle collection of a filter also affect the resistance of that filter to fluid flow.

We have thus far discussed only filters with fibers oriented normal to the direction of flow. Clearly not all biological filters have such a geometry. A theoretical consideration by Spielman and Goren (1968) of the effects of certain fiber orientations on filter behavior indicates that the intensity of particle capture and the resistance of a filter are both greater for fibers randomly arranged in planes perpendicular to the direction of flow than for fibers in a three-dimensional random arrangement. Particle capture and filter resistance, in turn, are lower for fibers randomly arranged in planes parallel to the direction of flow and lowest for fibers arranged parallel to the flow.

The other assumptions of filtration theory, that particles are spherical and that all particles adhere upon contact, can be relaxed without altering the general trends indicated by the equations we have presented. The likelihood of a particle adhering to a filter depends upon such factors as the flow velocity and the surface nature (e.g., charge, mucus, protrusions) of the particle and filter. Functions which correct for imperfect adhesion can be empirically derived for particular filtering situations and can be applied to the dimensionless indexes. Similarly, empirically derived functions accounting for the fact that non-spherical particles are more likely to be captured than spherical (Dickey and Bryden 1946) can be applied to the dimensionless indexes. In either case, the basic trends indicated by the equations will not be changed.

Up to this point we have been discussing the performance of filters before particles have accumulated on them (stationary filtration). The build-up of particles on a filter results in structural changes in the filter which alter its collection abilities as well as its resistance to flow. The secondary processes to be considered in nonstationary filtration include the loss of particles from the filter during the course of further filtration, the deposition of particles on each other, and the clogging of the filter. Accumulated particles can themselves act as filters, thereby increasing the particle-capturing ability of the filter while at the same time increasing its resistance to flow. As filtering proceeds, the intensity of particle collection usually increases before large changes in resistance occur due to clogging.

Because organisms constantly remove captured particles from their filters, biological filtration can be considered as stationary as a first approximation. However, consideration of secondary processes reveals that one of the means by which an animal can alter the properties of its filter (to feed on particles of a different size or to feed in a different flow velocity, e.g.) is to change the rate at which it cleans off its filter. It also points out the importance of studying the mechanisms by which particles adhere to biological filters.

#### BIOLOGICAL IMPLICATIONS

The filtration theory presented above is only qualitatively valid for biological filters. We present this theory in order to enumerate the mechanisms by which

filtration can take place and to illustrate how their effectiveness depends on certain measurable characteristics of the filter, the particles, and the flow.

The theory illustrates that filter feeders need not be restricted to sieving in order to catch particles. The sieve theory implies 100% capture of particles larger than the pore size and 0% of those smaller (Pich 1966). A decreasing percentage capture of smaller particles, as found for mussels (Jørgensen 1975*b*), oysters (Haven and Morales-Alamo 1970), scallops (Vahl 1972), and copepods (Hargrave and Geen 1970; Nival and Nival 1976), is consistent with the expanded theory we have presented.

Many suspension feeders have been shown to capture certain sizes of particles more effectively than others (Jørgensen 1975*a*). There has been considerable interest in the size-selective feeding of zooplankton (e.g., Harvey 1937; Mullen 1966; Parsons et al. 1967; Richman and Rogers 1969; Frost 1972; Lam and Frost 1976; Lehman 1976). We have enumerated which physical variables affect the intensity of capture by a filter of particles of various sizes. Boyd (1976) also suggests that the size selectivity of particle-feeders may be "a passive result of a mechanical feeding system" (p. 178), but he limits his considerations only to the sieving mechanism of particle capture and ignores the effect of velocity on particle-capture efficiency. According to sieve theory, an animal can change the size of particles on which it feeds only by changing the pore size of its filter. Our theory reveals several other means by which an organism could alter its diet. By changing the velocity of water passing through the filter, or by altering the diameter of adhesiveness of the filtering fibers, the range of particle sizes that can be captured most efficiently by the filter can be shifted. The theory also suggests that a given filter feeder is most effective at collecting the particles on which it feeds only in a certain range of velocities. Constant pumping or swimming rates for active filter feeders and specific positioning of the filter for passive filter feeders are adaptations which present their filters with the optimum flow velocities.

Filtration theory only deals with the mechanisms by which particles contact a filter feeder. The retention of particles by an animal's filter and the transport of particles from its filter to its mouth are obviously also very important in determining which particles it eats. Particle selection due to the physical characteristics of the filter and the particles should be distinguishable from particle selection due to the behavior of a filter feeder by comparison of filter and gut contents and by observation of particle ingestion and rejection.

The theory predicts that organisms of dissimilar sizes in unlike flow regimes will utilize different mechanisms for removing various types of suspended material from the water. According to the theory outlined above, the mechanism of particle capture being utilized by an animal is that mechanism having the largest dimensionless index (e.g., see fig. 2). We expect inertial impaction only to be an important mechanism for organisms feeding at high velocities on large or dense prey. Strathmann (1971, 1973) has argued that the velocities and the particle sizes and densities are too low for echinoderm larvae and lophophorates to be feeding by inertial impaction. We expect the motile-particle and gravitational deposition mechanisms of capture to be important only for organisms

feeding at low velocities. The latter mechanisms are probably important for those suspension feeders which pass slow currents over their feeding surfaces. Passive suspension feeders such as gorgonian corals (Leversee 1976) and zoanthids (Koehl 1977*a*, 1977*b*) that capture zooplankton swimming in eddies of slowly moving water may be utilizing the motile-particle mode of capture. Clearly the orb webs of spiders capture motile insects in this manner. Most biological filters and particles, however, probably fall into the intermediate size and velocity range where direct interception is the main mode of capture.

In order to test these predictions of which particle-capture mechanisms different filter feeders use, we searched the abundant literature on filter feeding for data to calculate the dimensionless indexes. Unfortunately we were able to find the necessary figures for only a few cases (table 1). The focus of most studies on filter feeding to date has not been the fluid mechanics of particle capture, hence the data gathered is inappropriate for our purposes here. For example, flow rates through filter feeders have typically been measured as the volume of water processed by one animal per unit of time, rather than as water velocity at the filter. Furthermore, because biologists generally consider filters as sieves, they have measured the spacings between fibers in filters rather than the diameters of the fibers. Similarly, biologists have often assessed pore diameters in filters by measuring the smallest sizes of particles captured. Although the sizes of particles captured by various filter feeders have been reported, the densities of the particles have not; we have used in our calculations density values reported for particles similar in type to those captured by the filter feeders. We have calculated the index for motile-particle deposition ( $N_M$ ) considering only Brownian motion because appropriate factors (analogous to  $KT/d_p$ ) for motile plankton have not yet been worked out. Even though the estimates of pertinent variables used in our calculations are crude, the predicted modes of particle capture seem to be consistent with the described paths of particles as they are captured by the animals listed in table 1. Because this paper enumerates the important variables that should be measured by those studying *how* aquatic animals feed on suspended material, we hope such measurements will be made in the future to allow more precise predictions and critical analyses of particle capture.

#### SUMMARY

We enumerate the five basic mechanisms by which any biological or man-made filter can remove particles from a fluid. These mechanisms are: (1) direct interception, (2) inertial impaction, (3) gravitational deposition, (4) motile-particle deposition, and (5) electrostatic attraction. For these mechanisms we present dimensionless indexes that indicate which measurable characteristics of the filter, the particles, and the flow affect the intensity of particle capture. By comparing the magnitudes of these indexes it is possible to determine the main mechanism a filter is using to capture particles. Awareness of these mechanisms and their interrelationships will provide insights for those investigating the efficiency of various modes of filter feeding and the mechanisms of size-selective suspension feeding.

TABLE 1  
 PREDICTIONS OF PROBABLE MODES OF PARTICLE CAPTURE  
 (Estimated Values of the Variables Are Based on Data Reported in the References Indicated by Superscript Letters)

Species and Type of Particle	$d_p$ (m)	$d_f$ (m)	$V_o$ (m/s)	$(\rho_p - \rho_m)$ (kg/m <sup>3</sup> )	$N_{Rf}$	$N_{If}$	$N_{Gf}$	$N_{Mf}$	Probable Modes of Capture
Echinoderm larvae:									
algal cells <sup>a</sup> .....	$5 \times 10^{-6a}$	$2 \times 10^{-7b}$	$2 \times 10^{-3a}$	20 <sup>c</sup>	25	$2.6 \times 10^{-4}$	$1.3 \times 10^{-4}$	$2.0 \times 10^{-4}$	direct interception
algal cells <sup>a</sup> .....	$10^{-4a}$	$2 \times 10^{-7b}$	$2 \times 10^{-3a}$	20 <sup>c</sup>	500	$10^{-1}$	$5.1 \times 10^{-2}$	$1.0 \times 10^{-5}$	direct interception
Brittle star ( <i>Ophiothrix fragilis</i> ):									
<i>Coccolithus huxleyi</i> <sup>d</sup> .....	$6.5 \times 10^{-6c}$	$10^{-4e}$	$2.5 \times 10^{-1d}$	180 <sup>c</sup>	$6.5 \times 10^{-2}$	$9.9 \times 10^{-4}$	$1.6 \times 10^{-5}$	$2.5 \times 10^{-9}$	direct interception
<i>Rhizosolenia stolterothii</i> <sup>d</sup> .....	$3.35 \times 10^{-5c}$	$10^{-4e}$	$2.5 \times 10^{-1d}$	20 <sup>c</sup>	$3.4 \times 10^{-1}$	$2.9 \times 10^{-3}$	$4.6 \times 10^{-5}$	$4.8 \times 10^{-10}$	direct interception
Bdelloid rotifer:									
green algae <sup>f</sup> .....	$2.0 \times 10^{-6f}$	$2 \times 10^{-7b}$	$1 \times 10^{-3f}$	70 <sup>g</sup>	10	$7.7 \times 10^{-5}$	$1.5 \times 10^{-4}$	$1.1 \times 10^{-3}$	direct interception
diatoms <sup>f</sup> .....	$2.0 \times 10^{-6f}$	$2 \times 10^{-7b}$	$1 \times 10^{-3f}$	150 <sup>g</sup>	10	$1.7 \times 10^{-4}$	$3.2 \times 10^{-4}$	$1.1 \times 10^{-3}$	direct interception
Sea anemone ( <i>Metridium senile</i> ):									
zooplankton <sup>h</sup> .....	$1.6 \times 10^{-3i}$	$10^{-3j}$	$2 \times 10^{-1h}$	6 <sup>k</sup>	1.6	$1.6 \times 10^{-1}$	$3.9 \times 10^{-2}$	$1.2 \times 10^{-12}$	direct interception
adult brine shrimp <sup>l</sup> .....	$5.0 \times 10^{-3i}$	$10^{-3j}$	$2 \times 10^{-1h}$	10 <sup>k</sup>	5	2.6	0.6	$4.0 \times 10^{-13}$	direct interception and inertial impaction
Sea anemone ( <i>Anthopleura elegantissima</i> ):									
zooplankton <sup>i</sup> .....	$1.8 \times 10^{-3i}$	$2 \times 10^{-3i}$	$1 \times 10^{-1m}$	6 <sup>k</sup>	0.9	$5.0 \times 10^{-2}$	$9.9 \times 10^{-2}$	$1.1 \times 10^{-12}$	direct interception
Zoanthid ( <i>Palythoa variabilis</i> ):									
crustacean parts <sup>j</sup> .....	$5.5 \times 10^{-3n}$	$1.0 \times 10^{-3n}$	$1 \times 10^{-2j}$	7.9 <sup>o</sup>	5.5	$1.2 \times 10^{-1}$	12.2	$7.3 \times 10^{-12}$	gravitational sedimentation
	$5.5 \times 10^{-3n}$	$1.0 \times 10^{-3n}$	$3 \times 10^{-1n}$	7.9 <sup>o</sup>	5.5	3.7	$4.1 \times 10^{-1}$	$2.4 \times 10^{-13}$	inertial impaction and direct interception
	$0.6 \times 10^{-3n}$	$1.0 \times 10^{-3n}$	$3 \times 10^{-1n}$	7.9 <sup>o</sup>	0.6	$4.4 \times 10^{-2}$	$4.8 \times 10^{-3}$	$2.2 \times 10^{-12}$	direct interception

SOURCES.—<sup>a</sup> Strathmann 1971; <sup>b</sup> DuPrav 1968; <sup>c</sup> Eppley et al. 1967; <sup>d</sup> Warner and Woodley 1975; <sup>e</sup> Woodley 1967; <sup>f</sup> Strathmann et al. 1972; <sup>g</sup> Hutchinson 1967; <sup>h</sup> Koehl 1977a; <sup>i</sup> Sebens 1977; <sup>j</sup> Koehl, unpublished data; <sup>k</sup> Gardnier 1933; <sup>l</sup> Sebens 1977, experimentally released prey; <sup>m</sup> Wainwright and Koehl 1976; <sup>n</sup> Koehl 1977b; <sup>o</sup> LaBarbera, personal communication.

NOTE.— $g = 9.807 \text{ m/s}^2$ ;  $\mu = 1.070 \times 10^{-3} \text{ N} \cdot \text{s/m}^2$  (34.84% seawater at 293°K);  $\mu = 1.005 \times 10^{-3} \text{ N} \cdot \text{s/m}^2$  (freshwater at 293°K);  $T = 293^\circ\text{K}$ ;  $K = 1.38 \times 10^{-23} \text{ J/}^\circ\text{K}$ .

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## APPENDIX

## NOTATIONS

$C$	= drag coefficient of a cylinder;
$D$	= diffusion coefficient = $(KT)/6\pi\mu(d_p/2)$ for Brownian motion;
$d, d_c, d_f, d_p$	= diameter; $d_c$ , of a pore; $d_f$ , of a fiber; $d_p$ , of a particle;
$F$	= drag force on a cylinder;
$g$	= acceleration due to gravity;
$h$	= distance between neighboring fibers in a filter;
$K$	= Boltzmann's constant;
$L$	= pore length;
$m$	= mass of a particle;
$N_{Ef}$	= index of electrostatic deposition for a fiber;
$N_G, N_{Gf}, N_{Gp}$	= index of gravitational deposition; $N_{Gf}$ , for a fiber, $N_{Gp}$ , for a pore;
$N_I, N_{If}, N_{Ip}$	= index of inertial impaction; $N_{If}$ , for a fiber; $N_{Ip}$ , for a pore;
$N_M, N_{Mf}, N_{Mp}$	= index of motile-particle or diffusion deposition; $N_{Mf}$ , for a fiber; $M_{Mp}$ , for a pore;
$N_R, N_{Rf}, N_{Rp}$	= index of direct interception; $N_{Rf}$ , for a fiber; $N_{Rp}$ , for a pore;
$Q$	= charge per unit length of fiber;
$q$	= charge of a particle;
$Re$	= Reynolds number = $\rho_m d_p V/\mu$ ;
$T$	= absolute temperature;
$V, V_c, V_o$	= velocity of a fluid; $V_c$ , in a pore; $V_o$ , upstream and removed from the effect of the fiber;
$v_g$	= settling velocity of a particle = $d_p^2 g(\rho_p - \rho_m)/18\mu$ ;
$\alpha$	= volume fraction of fibers in a filter;
$\Delta p$	= pressure needed to drive a fluid through a pipe;
$\mu$	= viscosity of the fluid;
$\rho, \rho_m, \rho_p$	= density; $\rho_m$ , of the fluid; $\rho_p$ , of a particle;
$\omega$	= rate (volume per unit time) a fluid is moving through a pore.

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