

Mechanisms of filter feeding in immature *Simulium bivittatum* Malloch (Diptera: Simuliidae) and *Isonychia campestris* McDunnough (Ephemeroptera: Oligoneuriidae)

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Immatures of *Isonychia campestris* McDunnough and *Simulium bivittatum* Malloch, fed mixtures of six size classes of polystyrene particles, captured particles that were smaller than the pore spaces between filtering structures more efficiently than was expected if filters functioned only as mechanical sieves. Capture efficiency was highest for the smallest (0.5-5.7 μm) particles. Relative efficiencies of filters for capturing suspended particles by four aerosol filtration mechanisms show that interception and diffusive deposition are mechanisms by which smaller particles reach the filter surface. The latter mechanism is a better predictor of size distribution of 0.5- to 5.7-μm particles captured by both insects. Adhesion of particles to filtering structures is probably by hydrophilic-hydrophobic or ionic interaction between particles and filters.

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Les larves d'*Isonychia campestris* McDunnough et de *Simulium bivittatum* Malloch nourries de mélanges de particules de polystyrène de six classes de taille différentes sont capables de capturer des particules plus petites que les pores qui séparent les structures de filtration, plus efficacement que prévu selon l'hypothèse qui suppose que les filtres fonctionnent simplement comme des passoires mécaniques. C'est dans le cas des particules les plus petites (0,5-5,7 μm) que l'efficacité de capture est la plus grande. L'efficacité relative des filtres dans la capture de particules en suspension par quatre mécanismes de filtration en aérosols démontre que les petites particules peuvent atteindre la surface des filtres par des mécanismes d'interception et d'accumulation par diffusion. C'est ce dernier mécanisme qui peut le mieux expliquer la répartition des particules de 0,5-5,7 μm telle qu'elle se fait chez les deux insectes. L'adhérence des particules aux structures filtrantes se fait probablement par interaction hydrophile-hydrophobe ou ionique entre les particules et les filtres.

[Traduit par la revue]

Introduction

The importance of filter feeding as a dominant process of primary consumption in freshwater and marine environments has served as motivation for numerous studies on structure, mechanisms, and efficiency of filters used to capture particles. Information from such studies has been used to estimate type and amount of seston processed by filter feeders to determine their importance as primary consumers. Jørgensen (1949, 1966, 1975, 1976) presented information on various structures used for filter feeding and metabolic costs associated with water transport through them, in many marine filter feeders. Several other studies (Bullivant 1968; Paffenhöffer and Strickland 1970; Vogel 1974, 1976, 1977, 1978a, 1978b, 1981; Strathmann et al. 1972; Strathmann 1973; Reisswig 1971, 1975) have dealt with mechanisms of filter feeding in taxonomically diverse marine organisms. Filter feeding in freshwater environments is known from different groups (Merritt and Cummins 1978; Wallace and Merritt 1980). Wallace and O'Hop (1979) gave information on mechanisms of fine particle capture in mayflies, *Isonychia* spp. Chance (1970) studied the structure and function of labral fans (Fig. 1) and associated mouthparts of larval black flies. This study and other publications (Clemens 1917; Fredeen 1964; Coffman et al. 1971; Wotton 1976, 1977, 1978, 1980, 1982; Shapas and Hilsenhoff 1976; Carlsson et al. 1977; Wallace and O'Hop 1979; Schröder 1980; Ross and Craig 1980; Craig and Chance 1982) show that larvae of black flies and nymphs of *Isonychia* spp. can ingest particles in the size class of 0.091 to 350.0 μm.

Despite the large amount of information on structure of filters and the size of particles they capture, the mechanism by

which filtering takes place in larval black flies and in nymphs of mayflies has been attributed generally to direct sieving. The function of filters as mechanical sieves was demonstrated for larval black flies by Noel-Buxton (1956), Kershaw et al. (1965, 1968), Chance (1970), and Kurtak (1973, 1978, 1979). Wallace and O'Hop (1979) demonstrated sieving capability of filters (Fig. 2) of nymphs of *Isonychia* species.

Rubenstein and Koehl (1977) proposed that in addition to sieving, it is possible that four other filtration mechanisms may be operative in filter feeding animals. These mechanisms are as follows.

Direct interception

A neutrally buoyant particle following a streamline that comes within one particle radius of a filter will contact the filter and be captured (Fig. 3, case A).

Spielman (1977) showed by numerical calculations that the efficiency of particle capture (η) for interception is:

$$[1] \quad \eta = 2A_F(r_p/r_f)^2 \int (N_{Ad}, r_p/\lambda)$$

where r_p = radius of particle; r_f = average radius of one ray in the filter-feeding structure; A_F = the pattern of streamlines; λ is the wavelength of the hydrodynamic retardation function (typically on the order of 10^{-5} cm); and N_{Ad} is the dimensionless adhesion number represented by:

$$[2] \quad N_{Ad} = Qr_f^2/9\pi\mu A_F U(r_p)^4$$

where Q = the Hamaker constant; μ = dynamic viscosity of the medium; and U = free stream velocity. Briefly, the value of the adhesion number (N_{Ad}) depends on the ratio of London-van der Waals attractive forces and hydrodynamic retardation forces. LaBarbera (1984) showed that suspension feeding is

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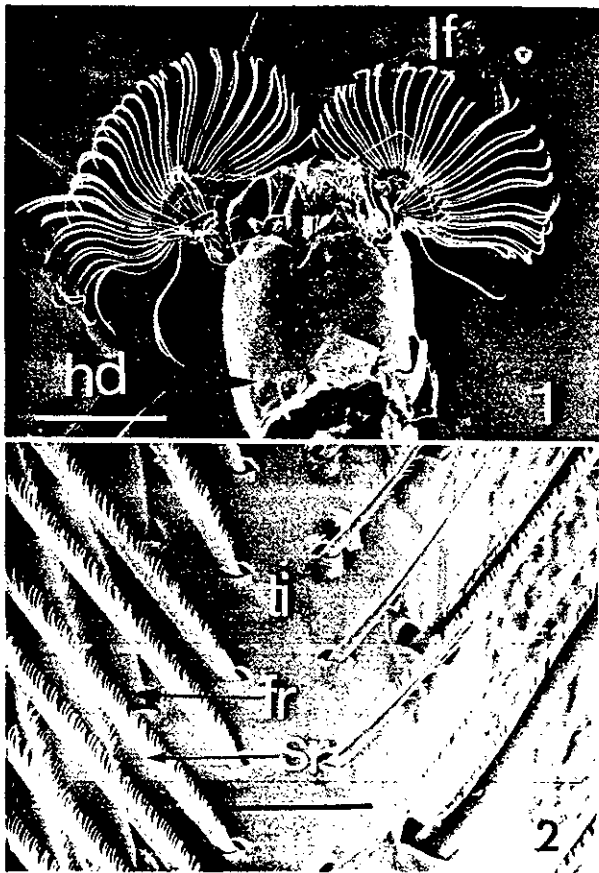


FIG. 1. Labral fans of *S. bivittatum*. Scale bar = 250 μm . FIG. 2. First and second rows of rays of foretibia of *I. campestris*. Scale bar = 25 μm . *fr*, first row; *hd*, head; *lf*, labral fans; *sr*, second row; *ti*, tibia.

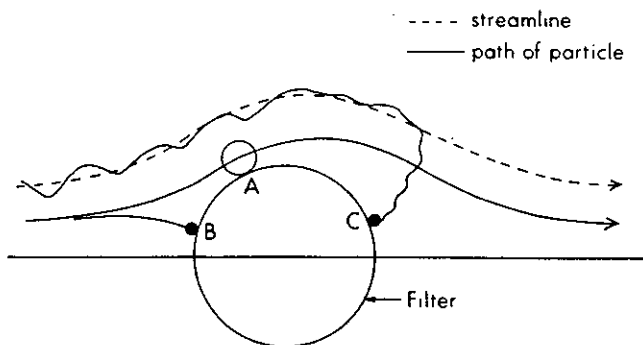


FIG. 3. Mechanisms of particle transport to filter-feeding structures. A, direct interception; B, inertial, gravitational impact; C, diffusion deposition.

characterized by large adhesion number (i.e., large attractive forces, so hydrodynamic retardation is negligible). Information on other ratios of the two forces and details are included in LaBarbera's paper.

Inertial impaction

This mechanism assumes that particles denser than fluid in which they are dispersed follow streamlines until the fluid is diverted and accelerated as it passes around the filter. The inertia of the particles causes them to deviate from the streamline and they are captured if they pass within one particle radius of the filter (Fig. 3, case B). The efficiency of particle capture (η) for inertial impaction is given as:

$$[3] \quad \eta = [(\rho_p - \rho_m)d_p^2U]/18\mu d_f \quad (\text{Fuchs 1964})$$

where ρ_m = density of the medium; ρ_p = density of a particle; μ = dynamic viscosity of the medium; d_p = diameter of particle; d_f = average diameter of one ray in the filter feeding structure; and U = free stream velocity.

Gravitational deposition

This mechanism is similar to inertial impaction except that deviation of particles from the streamline is caused by the influence of the gravitational vector when it is greater than the combined effect of the fluid drag and the velocity vector on the particle. The efficiency of particle capture (η) for gravitational deposition is given as:

$$[4] \quad \eta = [gd_p^2(\rho_p - \rho_m)]/18\mu U \quad (\text{Yao et al. 1971})$$

where g = acceleration due to gravity (other terms as defined above).

Diffusion or motile-particle deposition

Small particles in suspension exhibit random motion caused by collision with molecules of the suspending medium, resulting in deviations in the paths of these particles (Fig. 3, case C). Such particles are captured when they contact the surface of the filter. The filter is "a region of zero concentration" (LaBarbera 1984), hence the term diffusion applied to this mechanism. The efficiency of diffusive deposition is given as:

$$[5] \quad \eta = 3.64A_F^{1/3}Pe^{-2/3}$$

(Spielman 1977; Schrijver et al. 1981; LaBarbera 1984)

where Pe is the Peclet number represented by $2r_fU/D$. D is the Brownian diffusion coefficient represented by:

$$[6] \quad D = KT/6\pi\mu r_p$$

where K = Boltzmann constant, and T = absolute temperature ($^\circ\text{K}$).

Adhesion of particles to filters

A basic assumption of the Rubenstein-Koehl models is the presence of mucus or sticky substances to which all particles contacting the surface of filters adhere. Jørgensen (1966), Strathmann et al. (1972), Strathmann (1973, 1975), Strathmann and Bonar (1976), and Strathmann and Leise (1979) have shown that most marine suspension feeders coat their filters with mucus. LaBarbera (1978) showed that the presence of mucus on the tube feet of *Ophiopholis aculeata* (L.) enabled it to capture more particles possessing specific charges. Presence of mucosubstances on filters was demonstrated for insects in freshwater environments in larval black flies (Ross and Craig 1980). Gerritsen and Porter (1982) showed that in the absence of mucosubstances (mucus), surface chemical interactions, such as hydrophobic-hydrophilic or ionic interaction between filters and particles, could account for particle adhesion at low velocities in *Daphnia magna* Straus and suggested that these interactions may be operative in other suspension feeders that do not coat their filters with mucus.

A second assumption is that the surface of filters remain clean after particle ingestion and pores between adjacent rays do not become clogged. A third assumption (specifically for direct interception) is that $r_f \gg r_p$. Two more assumptions made by Spielman (1977) (specifically for diffusive deposition) are that the boundary layer around filters is thin and that the velocity term characterizing mass transfer of particles in

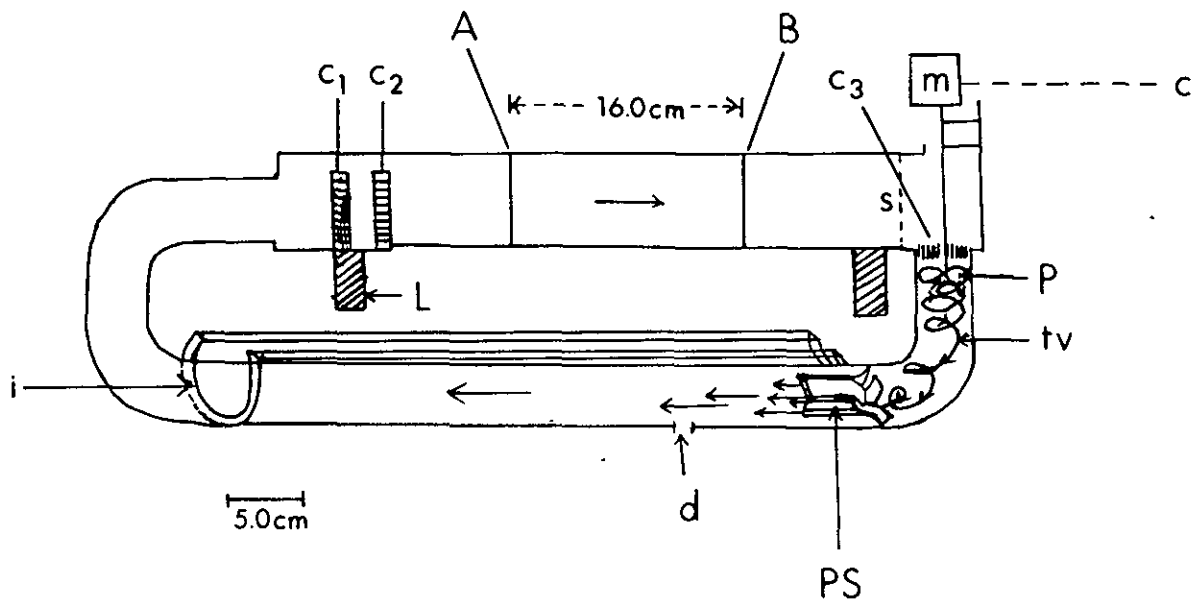


FIG. 4. Flow tank. A, B, feeding positions; *c*, feedback control to motor (*m*); *c*₁, *c*₂, *c*₃, collimator; *d*, drain; *i*, bottom part of ice container (top part not illustrated); *L*, support for tank; *p*, propeller; PS, Plexiglas structure for minimizing turbulence (*tv*) generated by propeller; *s*, screen.

the filters of insects is similar to that for an isolated sphere. These assumptions are addressed later in this paper.

LaBarbera (1984) showed the general applicability of these models to aquatic systems and demonstrated the importance of direct interception as the predominant mechanism of collision between particles and filters in *O. aculeata*. Ross and Craig (1980) proposed that the mechanisms of direct interception and inertial impaction are important filtration mechanisms in *Simulium vittatum* Zett., *Prosimulium mixtum/fuscum* Syme and Davies, and *Stegopterna mutata* (Malloch). Ross and Craig (1980) suggested that direct interception may be the predominant mode of fine particle capture. R. S. Wotton (personal communication in Ross and Craig 1980) suggested that colloidal particles and dissolved organic matter (DOM) adhere to mucosubstance from pockets of still or slow-moving water formed around the microtrichia. They also considered inertial impaction important for large particles (e.g., >100 μm) at high velocities. Silvester (1983) suggested that inertial impaction and direct interception are important in particle capture by some species of net-spinning caddisflies. Apart from the work of LaBarbera (1978, 1984) on an active suspension-feeding echinoderm, the theoretical models have not been tested experimentally on other suspension-feeding animals.

The objective of this study is to determine the extent to which the Rubenstein-Koehl models and extensions to them (Spielman 1977; Gerritsen and Porter 1982; LaBarbera 1984) apply to particle transport and capture in passive filter-feeding insects in freshwater environments.

Materials and methods

Collection and maintenance of nymphs of *Isonychia campestris* and larvae of *Simulium bivittatum*

Mature larvae of *Simulium bivittatum* and nymphs of *Isonychia campestris* were collected from Milk River near Writing-On-Stone Provincial Park, southern Alberta (49°00' N, 110°33' W), Canada. Water from Milk River was used to maintain live specimens in a laboratory stream designed after Corkum and Pointing (1979). Temperature was maintained at that of the Milk River (18°C) with a refrigerating unit.

Flow tank and feeding experiments

Before being fed a suspension of monodisperse polystyrene particles (Analychem Corporation Ltd., Markham, Ontario) insects were starved for 12 h in filtered distilled water in a flow tank designed after Vogel and LaBarbera (1978). The flow tank had a trough with length to width ratio of 10 (Fig. 4). Vortices induced by the propeller were eliminated by inserting a partly curved Plexiglas fairing in the lower return conduit (Fig. 4). The propeller shaft was driven by a type NSH-12 Fractional Horsepower motor (Bodine Electric Co., Chicago, Illinois) with a model SL 15 Minarik feedback control (Minarik Electric Co., Los Angeles, California). Water temperature was kept at 20°C by ice in a container designed to fit around the lower return conduit (Fig. 4). A 1.0-cm² grid made from thin (1.0-mm²) pieces of balsam wood served as site of attachment for both insects. Two such grids (A and B) were placed 16.0 cm apart in the tank and each 22.0 cm from the end of the trough (Fig. 4). Simuliid larvae were introduced into the trough with a soft brush. Larvae usually spun an anchor line of silk onto the fine hairs of the brush when first introduced. They then drifted in the current until they reached the balsam wood, attached to it with their posterior proleg, and cut the anchor line off. Ephemeropteran nymphs were introduced into the flow tank near the balsam wood. They swam to it and attached with mesothoracic and metathoracic legs.

Measurement of velocity at which insects fed

Different settings of the feedback control of the motor were used for each experiment. The range of velocity at which each of the insects fed was later measured with a Novonics Stream Flow model 403 velocity meter, accurate to within 1% (Nixon Instrumentation Ltd., Cheltenham, England).

Concentration of polystyrene particles in the feeding suspension

Six different sizes of polystyrene particles having diameters of 0.5 ± 0.006 , 1.2 ± 0.017 , 5.7 ± 1.5 , 25.7 ± 0.8 , 50.1 ± 20.0 , and 90.7 ± 17.7 μm were added to 3 L of filtered distilled water for each experiment. The number of particles in each size class per millilitre (Table 1) were determined using the following formula.

$$[7] \quad \text{No./mL} = (A \times 24 \times 10^{12}) / (4 \times \phi^3 \times \rho)$$

(Polysciences Inc. 1980)

where *A* = g/mL of polymer in latex; ϕ = diameter in μm of monodisperse latex; and ρ = density of polymer as g/mL.

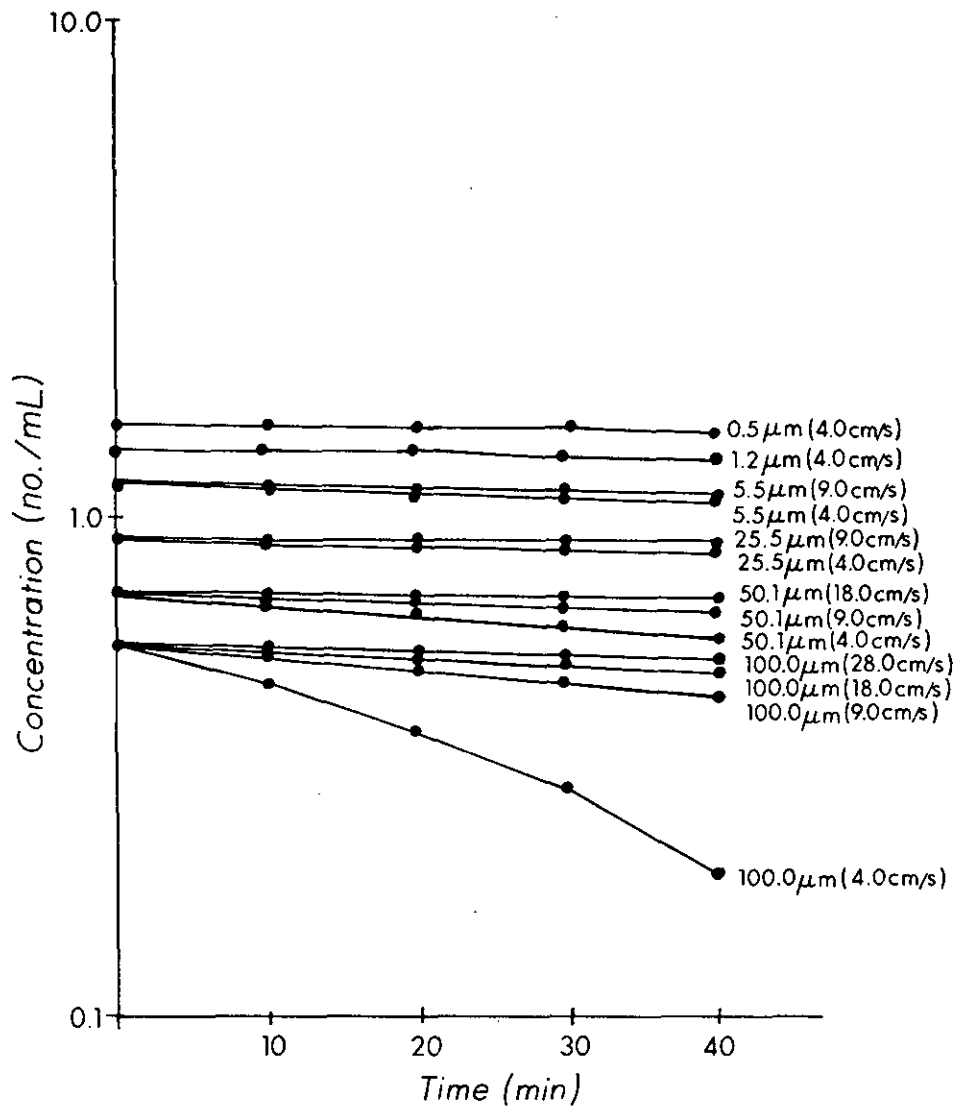


FIG. 5. Changes in concentration of different size polystyrene particles in feeding suspension at different velocities.

TABLE 1. Concentration and expected proportions of polystyrene particles of six size classes in feeding suspension (SD is given in parentheses)

Particle diameter (μm)	Concentration of particles (no./mL)	Replicates (N)	Expected proportion (arcsin √%, degrees)
0.5 (0.006)	4.1×10^6 (0.9×10^5)	5	60.33
1.2 (0.016)	1.2×10^6 (1.0×10^5)	5	27.97
5.5 (1.7)	1.2×10^5 (0.5×10^4)	5	8.53
25.7 (5.8)	1.1×10^4 (1.0×10^3)	5	2.43
50.1 (20.1)	1.4×10^3 (1.1×10^2)	5	0.81
90.7 (17.7)	3.0×10^2 (4.8×10^1)	5	0.57

The number of each size class of particles in the feeding suspension was confirmed with a model TA II Coulter Counter. The counts were corrected for coincident particle passages (i.e., doublets, triplets, etc.). The mixture of polystyrene particles was sonicated for 1.0 min before it was added to the flow tank. Sedimentation and aggregation of particles was reduced by the rotating motion of the propeller shaft which served as a stirring rod. Each insect was labelled according to

site of feeding and any changes in position were monitored and recorded. Insects were allowed to feed for 30 min.

Concentration of particles available to insects at different times and velocities was determined by collecting three 2-mL replicate samples of the feeding suspension at 10-min intervals at various velocities (Fig. 5).

The rate at which particles settled out of suspension was calculated using the following equation:

$$[8] \quad C_0 = C_1 e^{-kt} \quad (\text{Coughlan 1969})$$

where C_0 = concentration at time t ; C_1 = initial concentration; and k = decay rate (i.e., rate of sedimentation).

Recovery of polystyrene particles from the guts of insects

At the end of each feeding test insects that fed at the same position were collected and stored in 95% alcohol. Heads with both labral fans of the black fly larvae and the forelegs of mayfly nymphs were removed and stored. The rest of each insect was dissolved for 12 h in 0.25 mL of 6% NaOCl which had been filtered through a 1.22-μm, type GS, Millipore filter of mixed cellulose acetate and cellulose nitrate. Polystyrene particles are inert to NaOCl and ethanol; thus their original size and shape remain unchanged by such a process. Clean monodisperse particles were recovered from the mixture through a density gradient centrifugation process.

Density gradient and particle sedimentation

Percoll (Pharmacia Fine Chemicals, Dorval, Quebec), a density gradient medium, was made iso-osmotic to physiological saline by adding 9 parts (v/v) of Percoll to 1 part of 1.5 M NaCl. This stock solution was mixed with 0.15 M NaCl to make a series of 3-mL experimental samples. Three microlitres each of suspensions of nine differently coloured density marker beads (Pharmacia Fine Chemicals, Dorval, Quebec) were soaked in 6% NaOCl for 12 h before being added to the samples in 4-mL Autoclear polycarbonate centrifuge tubes (Damon/IEC Division, Needham Heights, Massachusetts). The tubes were capped, inverted several times, and centrifuged at $20\,200 \times g$ (avg.) for 30 min in a model RC 2 B Sorvall centrifuge. The density of marker beads was plotted against the distance of the corresponding coloured bands (measured to the nearest 0.5 mm) from the bottom of the tube (Fig. 6). The 40% density layer was selected since marker beads with corresponding density (1.05 g/mL) to polystyrene particles lay in a region with maximum separation from bordering gradients. Portions (3 mL) of the 40% gradient were then centrifuged at $20\,200 \times g$ (avg.) for 30 min to form various gradients. The mixture of polystyrene particles and dissolved insects was carefully layered on top of the gradient. The tubes were centrifuged at $400 \times g$ (avg.) for 45 min to separate the particles and insect remains at their isopycnic densities (i.e., the particles and insect remains sediment to an equilibrium position in the gradient where the gradient density is equal to the density of particles or insect remains). Polystyrene particles do not have the same density as insect remains; thus they sediment to different levels of the density medium. Clean Pasteur pipettes were used to collect particles. Cleanliness of particles after recovery was checked with a scanning electron microscope. Particles were then transferred to clean triple-filtered Isoton (Coulter Electronics Ltd., Vancouver, British Columbia) in 2-mL capacity vials for sizing and counting with a model TA II Coulter Counter.

Calculations and results

Mechanisms of particle capture

To determine the filtration mechanisms that were operative, collection efficiency of the filters by each mechanism was calculated. Relative efficiencies were calculated after the method of LaBarbera (1984). All constants (A_F , Q , U , μ , K , T) cancel out and efficiencies are a function only of r_p and r_f . The distribution of particles in suspension at various velocities (Fig. 5) was used to predict distribution of size classes that should have been caught. Such distributions were compared with those that actually were caught by the insects (Figs. 7–17).

Direct interception

LaBarbera (1984) simplified the equation for efficiency of direct interception to

$$[9] \quad \eta \propto (r_p/r_f^2)^{2/3}$$

and predicted relative capture efficiency due to direct interception for situations where the adhesion number is large (i.e., negligible retardation forces). Note (Figs. 7–17) that this mechanism should theoretically predominate for capture of particles greater than $1.0 \mu\text{m}$; however, experimental results showed lower efficiency. For $1.0\text{-}\mu\text{m}$ particles, agreement between experimental results and theoretical prediction is closer at lower velocities, 4–18 cm/s for *I. campestris* (Figs. 13–17) and 4–28 cm/s for *S. bivittatum* (Figs. 7–12).

Inertial impaction

This mechanism was not tested because insects were not fed large, dense particles and very high velocities were not used.

Diffusion or motile-particle deposition

The equation for diffusive deposition was simplified to

$$[10] \quad \eta \propto (r_p r_f)^{-2/3}$$

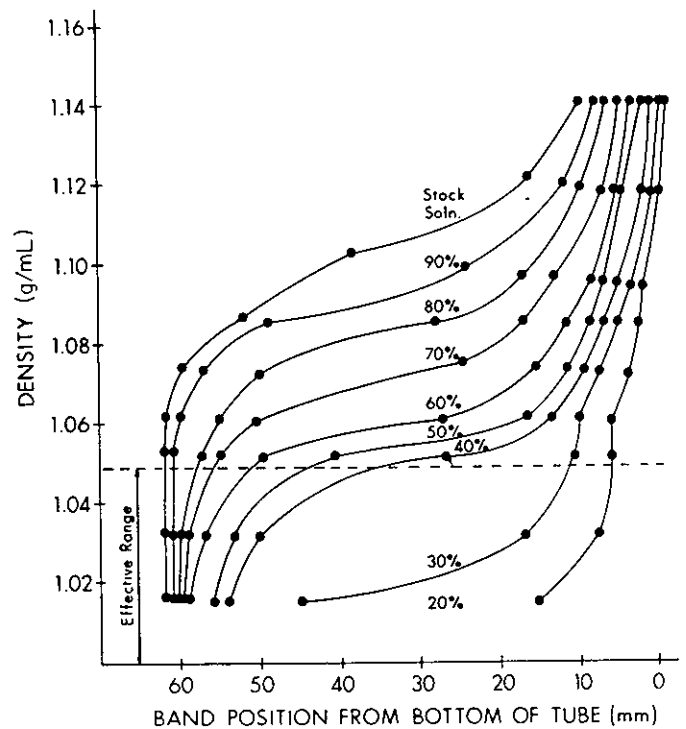


FIG. 6. Density gradient position in solution of iso-osmotic Percoll in 0.15 M NaCl plus 0.25 mL of 6% NaOCl.

and relative capture efficiency due to diffusive deposition was predicted. The overall close agreement between theory and observation, especially at high velocities (Figs. 7–17), shows that this model is a good predictor of size distribution of 0.5- to 5.7- μm particles captured by both insects.

Gravitational deposition

The parallel orientation of rays and microtrichia of filtering structures of both insects to flow and the velocities used make this mechanism nonapplicable to simuliid larva, which live in fast-moving water. It is of perhaps low applicability at the second and third rows of rays of the mayfly nymphs.

Discussion

Determination of size and number of particles consumed by both insects

The density gradient centrifugation technique used to recover particles from guts of insects makes it possible to determine the total number of particles consumed by each insect. It eliminates the problem of identifying synthetic particles in the presence of natural faecal materials (Fig. 18). The solution of NaOCl can dissolve mucosubstance or derivatives of it and other sticky secretions; this reduces the tendency of particles to stick together (Fig. 19). Counts of aggregated particles (i.e., percentage coincident particle passages recorded by the Coulter Counter) in samples of feeding suspension showed that over 95% of the particles were monodisperse. Aggregation of particles (Fig. 19) occurred when the guts of insects were not dissolved in a solution of NaOCl.

Mechanisms of particle capture

Most particles caught and consumed by both insects at all velocities were smaller than the spaces between adjacent rays. Thus, in addition to direct sieving, particles reach the filters of both insects mostly by one or a combination of some of the four transport mechanisms.

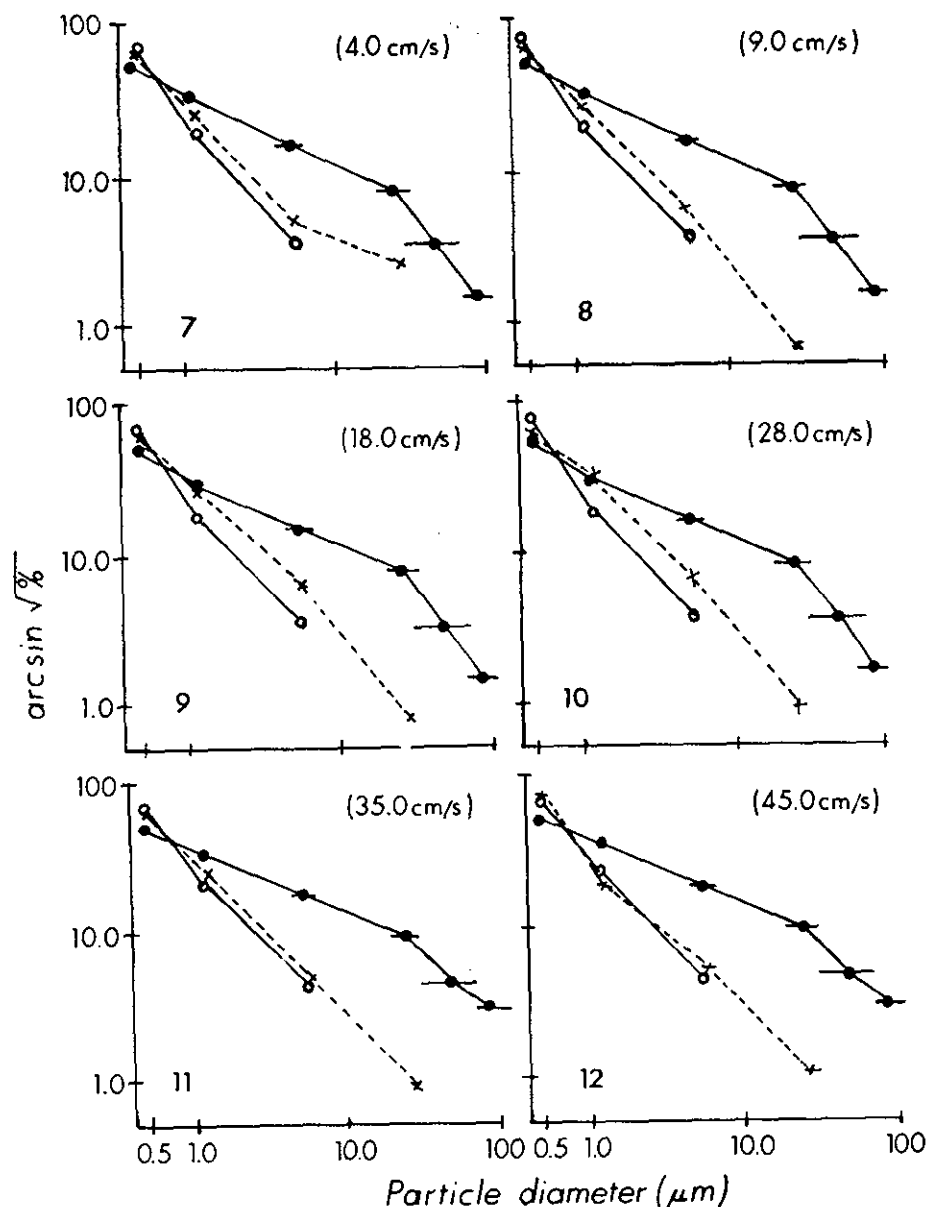


Fig. 7-12. Predicted size distribution of polystyrene particles that should be caught by larvae of *S. bivittatum* based on models of direct interception (●) and diffusion deposition (○) and observed size distribution (×) at various velocities. (Horizontal bar through solid circle means SD for particle size, supplied by manufacturer.)

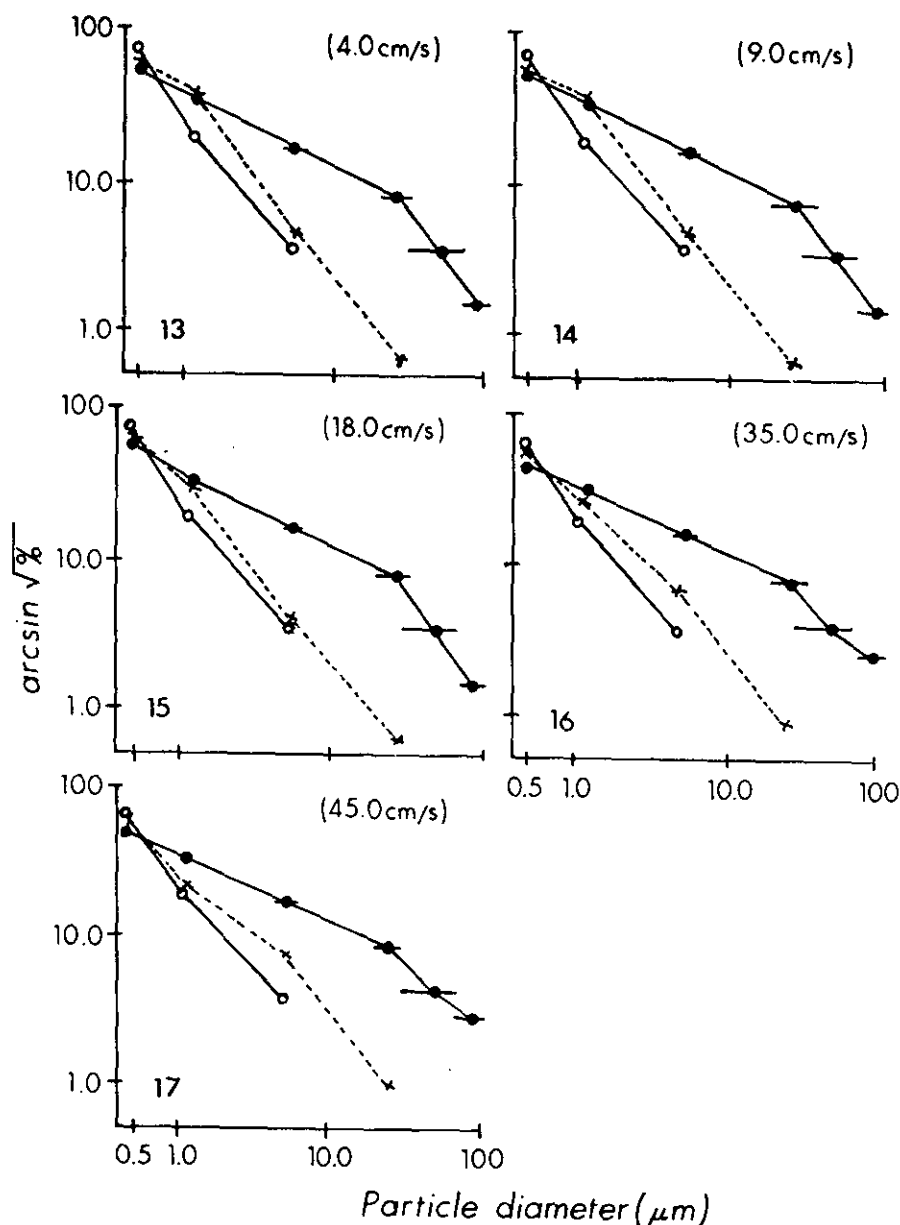
Direct interception

Lower observed efficiency compared with the predicted efficiency of models (Figs. 7-17) is due possibly to violation of the assumption that there is 100% collection efficiency of all particles that contact the surface of filters. Information is needed on the surface properties of particles and filters and (or) sticky substances used to coat filters. It should also be pointed out that particles larger than 2.0 and 5.0 μm violate the assumption that $r_p \gg r_f$ for *S. bivittatum* and *I. campestris*, respectively. The rate of adduction of the filters in both insects prevents clogging by particles, but the assumption that filters maintain a clean surface is probably unrealistic, especially under natural conditions, and needs further investigation. Surface properties of filters will probably affect type, number, and degree of adhesion of zooplankton, phytoplankton, and bacterioplankton.

Diffusive or motile-particle deposition

The model for diffusive deposition gives an overall better

prediction of the size distribution of 0.5- to 5.7- μm particles captured by both insects (Figs. 7-17). A possible cause for the observed discrepancies between theoretical prediction and experimental result is the violation of the assumption of 100% collection efficiency. The concentration gradient may not approach zero at the surface of filters and it is doubtful that filters maintain a clean surface. It is probably unrealistic to assume that the Stokes equation for the velocity terms describing mass transfer by diffusion about an isolated sphere can describe the mass transfer of particles in the filters of both insects. Future work should focus on this aspect of particle transport by this mechanism. Also the assumption of a thin boundary layer is violated, especially at low velocities (Brimah 1987) and this may have resulted in larger discrepancies between predictions and observations at such low velocities. Based on experimental data, this model is not operative in the capture of particles larger than 5.7 μm . The proportion of captured particles larger than 5.7 μm observed using this model is virtually zero at all



FIGS. 13-17. Predicted size distribution of polystyrene particles that should be caught by nymphs of *I. campestris* based on models of direct interception (●) and diffusion deposition (○) and observed size distribution (×) at various velocities. (Horizontal bar through solid circle represents SD for particle size, supplied by manufacturer.)

velocities (Figs. 7-17). Similar observations have been made by Schrijver et al. (1981) and Yao et al. (1971).

In nature it is possible for zooplankton and phytoplankton that are larger than $5.7 \mu\text{m}$ to reach the surface of filters of both insects by this mechanism if they are capable of active motion. Motion produced by flagella (external forces) (Fuchs 1964; Patlak 1953) may cause these organisms to follow a random path and make contact with the filter-feeding structures.

Similarity in size distribution of synthetic particles caught and consumed in this study and particles observed during field studies in guts of larvae of black flies (Wotton 1977, 1978, 1980; Carlsson et al. 1977; Kurtak 1979; Merritt et al. 1982) and nymphs of *Isonychia* species (Clemens 1917; Coffman et al. 1971; Shapas and Hilsenhoff 1976; Wallace and O'Hop 1979) suggest that this mechanism is operative and important in the natural habitats of both insects.

Inertial impaction

Speilman (1977) suggested that this mechanism is not very important for waterborne particles because of the small Stokes number of suspended particles in aquatic systems. Silvester (1983) based his calculation of Stokes number on density of suspended particles alone and showed that this mechanism is important for net-spinning caddisflies. His conclusion on the importance of inertial impaction is at variance with most other studies (i.e., Strathmann 1971; Fenchel 1980a, 1980b, 1980c; LaBarbera 1984) and requires further investigation.

LaBarbera (1984) suggested that this mechanism could be important for aquatic organisms that feed on relatively large, dense particles in very high flow velocities. He showed that the effect of this transport mechanism is weak but it can be detected in *O. aculeata*. Ross and Craig (1980) proposed that this mechanism may be important for transporting large particles

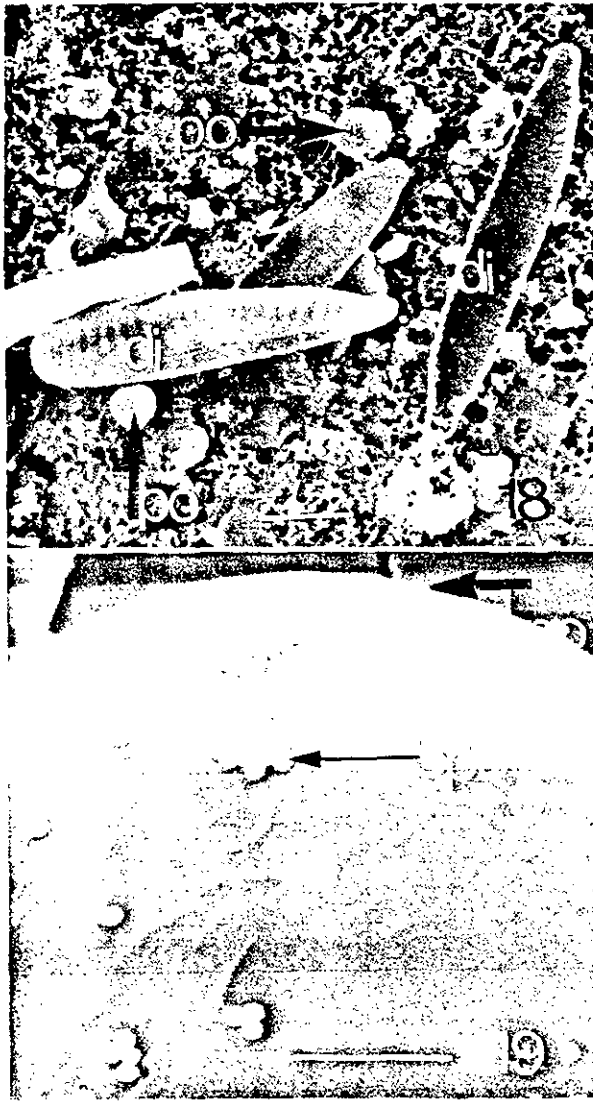


FIG. 18. Mixture of polystyrene particles and natural faecal materials showing some diatoms from gut of larvae of *S. bivittatum*. Scale bar = 5 μm . FIG. 19. Adhesion of several (0.5 μm) polystyrene particles to a large (20.0 μm) one. Scale bar = 4 μm . *di*, diatom; *L_{po}*, large polystyrene particle; *S_{po}*, small polystyrene particle; *po*, polystyrene particle.

(i.e., larger than 100 μm) to the filters of some black fly species that inhabit fast-flowing streams. The latter suggestion can be tested on larvae found in fast streams and further studies should focus on this aspect.

Gravitational deposition

The transit time of particles in the filter must be long for this mechanism to be effective (Speilman 1977; Gerritsen and Porter 1982). It is also necessary that the gravitational vector be greater than the combined effect of fluid drag and the velocity vector to enable sedimentation. Gravitational deposition is of no importance in particle capture in immature stages of simuliid larvae. It may, however, contribute minimally to capture of large particles at the second and third rows of rays on the filtering appendages in the ephemeropteran nymph where flow conditions favour sedimentation of large particles. The latter suggestion is substantiated by flow visualization with scaled-up models of filter-feeding structures (Braithmah 1987).

The low number of large particles caught by the filters indicates that this mechanism is of minor importance in particle transport in the ephemeropteran nymphs.

Phoretic black fly larvae and species that aggregate

Although larvae of some black flies prefer faster velocities of stream flow with reduced boundary layer and steep velocity gradients around their bodies, larvae of some species of black flies are found in phoretic associations with crabs, where they have to survive in still water for long periods of time while obtaining food (Hynes 1970; Raybould 1969; Raybould and Mhiddin 1978; Raybould et al. 1978). Gravitational deposition may contribute to capture of large particles in these larvae. The filters of such larvae might function as gravel and sand filters; thus, large particles will be captured as they sediment. Diffusive deposition and direct interception might be operative in the current generated as labral fans adduct and abduct. Thus, feeding may be possible at Reynolds numbers less than 1.0 in the world of "creeping motion" (Vogel 1981) to which such larvae are exposed. The inability of most species to survive in slow-moving water may be due to low oxygen content in such water. It has been shown (Wu 1931; Phillipson 1956, 1957) that low oxygen concentration of moving water affects the distribution of some species of black fly larvae. Work is needed on larvae that inhabit still or slow-flowing water.

In nature, the actual regime of velocities at which some black fly larvae capture suspended particles is virtually impossible to measure directly. Larvae of some species have a habit of aggregating on substrate so that some individuals are seldom exposed to free stream velocity. It is possible that such aggregates create hydrodynamic interactions between neighbouring larvae as known in fish schooling (Weihs 1975) and in sand dollars (O'Neil 1978) and polychaetes (Carey 1983); these interactions may produce slower velocities and enhance laminar flow through labral fans. Chance and Craig (1986) used scaled-up models of larvae and provided evidence that water flow around aggregates of *Simulium vittatum* Zett. is beneficial to feeding.

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