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Mechanisms and fluid mechanical aspects of filter-feeding in blackfly larvae (Diptera:Simuliidae) and mayfly nymphs (Ephemeroptera:Oligoneuriidae)

by

Stephen Aki Braimah

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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ABSTRACT

Nymphs of *Isonychia campestris* McDunnough and larvae of *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 (i.e. 0.5µm - 5.7µm) particles.

It is shown that direct interception and diffusive and/or motile-particle deposition are mechanisms by which smaller particles reach filter surface. The latter mechanism is a better predictor of size distribution of such small particles which were caught and consumed by both insects. Adhesion of particles is probably by electrostatic attraction/surface chemical effects.

A density gradient technique used to recover particles from guts of insects eliminated natural faecal materials and enabled counts of total number of particles consumed by each insect.

Fluid mechanical aspects of the study indicate that filter feeding in immatures of both insects is characterized by low Reynolds number (*Re*) (i.e. *Re* = 0.02 - 3.9). Gradients of velocity in the boundary layer around rays of scaled-up models of portions of filters, towed through Canola oil, revealed that capture of small particles occurs in the viscous boundary layer closest to the ray. Adhesion of such small particles is enhanced by their neutral

bouyancy which increases the transit time in the filters.

Boundary layer thickness around scaled-up models showed that there was very little flow between adjacent rays of filters of larvae of *S. bivittatum* up to *Re* value of 0.49 (real life equivalent of 10.0 cm/sec) and *Re* of 1.39 (17.5 cm/sec) for nymphs of *I. campestris*. Microtrichia of *S. bivittatum* functioned as a solid wall with no flow between adjacent microtrichia up to *Re* of 3.98 (80.0 cm/sec) and for *I. campestris* up to *Re* of 7.79 (100.0 cm /sec). Inability of both insects to capture particles efficiently at low velocities of 3.5 - 4.2 cm/sec is attributed to the lack of suitable currents. High form drag on filters and other parts of the insects and decreased boundary layer thickness account for low retention efficiency at high velocities of 35.0 - 47.0 cm/sec.

It is suggested that aggregation in both insects may be a behavioural adaptation for optimizing foraging.

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Dr. B.C. Kondratieff of Virginia Polytechnic Institute and State University, identified nymphs of *I. campestris* McD. D.C. Currie assisted in identifying larva of *S. bivittatum* Mall. Several of my colleagues helped in editing the text on computer. I am particularly thankful to D.R. Maddison for his patience and time in teaching me how to use the computer and for help in writing most of my programs.

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1. INTRODUCTION

The importance of filter feeding as a dominant process of primary consumption in freshwater and marine environments is well known. It has served as motivation for numerous studies on structure, filtration mechanisms and efficiency of filters used to capture particles. Information from such studies have been used to estimate type and amount of seston processed by filter feeders in order 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, 1968b; Paffenhoffer and Strickland, 1970; Vogel, 1974, 1976, 1977, 1978a, 1978b; Strathman et al. 1972; Strathman, 1973; Reiswig, 1971b, 1975b) have dealt with mechanisms of filter feeding in taxonomically diverse marine organisms. Filter feeding in freshwater environments is known from different groups (Merrit and Cummings, 1978; Wallace and Merrit, 1980). Phylogenetic studies of extant superfamilies of mayflies (MaCarfferty and Edmunds, 1979) and other studies on blackflies (Puri, 1925; Fortner, 1937; Grenier, 1949; Crosskey, 1960; Craig, 1969; Wood, 1978) support the suggestion of Resh and Solem (1978), Wallace and Merrit (1980) that filter feeding evolved independently several times in freshwater macroinvertebrates.

Wallace (1975), Wallace and Sherberger (1975), Malas and Wallace (1977) Wallace et al. (1977) report on filtering mechanisms in net-spinning caddisflies. Wallace and O'Hop (1979) gave information on mechanisms of fine particle capture in mayflies *Isonychia* spp. Gallep (1974), Gallep and Hasler (1975) discussed filtering mechanisms in the caddisflies, *Brachycentrus americanus* Banks and *Brachycentrus* spp.

Filter feeding mechanisms of larval blackflies have received more attention due to the pest status of this dipteran. Chance (1970) reviewed much of the work on structure and function of cephalic fans (Figure 1) of larval blackflies and associated mouthparts. Craig (1974, 1977) presented studies of morphology, development and related functions of simuliid mouthparts. Chance (1977) reviewed feeding behaviour of some blackfly larvae. This review and other publications (Freeden, 1964; Wotton, 1976, 1977, 1978b, 1980, 1982; Carlsson et al, 1977; Wallace and O'Hop, 1979; Ross and Craig 1980; Craig and Chance, 1982) show that larvae of blackflies and nymphs of *Isonychia* spp can ingest particles in the size class of 0.091 to 350.0μm. Wotton (1978b) reported that over 80% of all particles ingested by *Metacnephia tredecimatum* Edwards in a Swedish lake-outlet were less than 2.0μm in diameter. Other studies (Wotton, 1977; Kurtak, 1979) found that 50% of particles ingested by blackfly larvae were less than 1.0μm in diameter. Merrit et al. (1982) found that the majority of particles in the guts of blackfly larvae to be less than 0.5μm. Hamilton (1979) gave size distribution of particles consumed by some ephemeropteran nymphs. Wallace and O'Hop (1979) reported a range of coarse particulate organic matter (CPOM), and fine particulate organic matter (FPOM) in the gut of *Isonychia* species found in some streams in southeastern U.S.A. They proposed that nymphs of this mayfly are capable of capturing particles as small as 0.021 - 1.0μm based on measurement of spaces between adjacent rays.

Despite the large amount of information on structure of filters and size of particles they ingest, mechanisms by which filtering takes place in larval blackflies, caddisflies and nymphs of mayflies have been attributed generally to direct sieving. The lack of information on other mechanisms was mostly due to difficulties involved in flow visualization because of the small size of filters. The function of filters as mechanical sieves was demonstrated for larval blackflies by Noel-Buxton (1956), Kershaw et al. (1965, 1968), Chance (1970), Kurtak (1973, 1978). Gallep (1974), Gallep and Hasler (975) showed that filters of larval caddisflies can behave as sieves. Wallace and O'Hop (1979 demonstrated sieving capability of filters of nymphs of *Isonychia* species.

An early sieving model was proposed by Alder and Hancock (1852) and predicts that all particles smaller than pores between filtering rays will not be captured, however, Wallengren (1905) proposed that particles smaller than pore spaces could be captured when they collide and adhere to sticky substances on individual fibers.

Rubenstein and Koehl (1977) combined the concept of Wallengren (1905) with hydrodynamic principles and they proposed that in addition to sieving, it is possible that most biological filters may capture particles by five mechanisms, namely;

1. Direct interception (N_{di}):

When the center of a massless particle following a streamline comes within one particle radius ($d_p/2$) of a filter it will contact the fiber and be captured. The intensity of direct interception can be expressed by the dimensionless index:

$$N_{di} = d_p/d_f \quad \ldots\ldots\ldots\ldots\ldots (1)$$

where d_p = diameter of particle, d_f = diameter of fiber.

2. Inertial impaction (N_{ii}):

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 streamline. Such particles are intercepted by the fiber if they pass within one particle radius of the fiber. The following index describes the intensity of deposition by inertial impaction:

$$N_{ii} = [(\rho_p - \rho_m)d_p^2 V_0]/18\mu d_f \ldots\ldots(2)$$

where ρ_m = density of the medium, ρ_p =density of a particle.

μ = dynamic viscosity of the medium.

V_0 = velocity upstream away from effect of the filters.

3. Gravitional deposition (N_{gd}):

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. The dimensionless index expressing the intensity of particle capture due to gravitation is:

$$N_{gd} = V_g/V_0 \ldots\ldots(3)$$

where $V_0 = [d_p^2 g(\rho_p - \rho_m)]/18\mu$

V_0 = settling velocity of a particle

Other terms as defined above.

4. Diffusion or motile-particle deposition (N_{dd}):

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. The intensity of capture due to the motion of particles out of the streamline is:

$$N_{dd} = KT/d_p[1/3\pi\mu V_0 d_f] \ldots\ldots\ldots(4)$$

K = Boltzman's constant.

T = absolute temperature.

Other terms as defined above.

5. Electrostatic attraction (N_{ee}):

If the particle and fiber are of opposite electrical charge the particle can be attracted to the fiber and captured. The intensity of capture due to this mechanism is:

$$N_{ee} = 4Qq/(3\pi\mu d_p d_f V_0) \ldots\ldots\ldots (5)$$

Q = charge per unit length of filter.

q = charge of a particle.

Other terms as defined above.

A basic assumption of the Rubenstien-Koehl model is the presence of mucus or sticky substances to which particles could adhere. It is assumed also that there is 100% collection efficiency of all particles which contact the surface of filters. A third assumption is that surface of filters remain clean after particle ingestion and pores between adjacent rays do not become clogged. A fourth assumption (specifically for direct interception) is that $a_f >> a_p$ (a_f is fiber radius, a_p is particle radius). Two more assumptions (specifically for diffusive deposition) are that boundary layers are thin and that the velocity term characterizing mass transfer of particles in the filters of insects is similar to that for an isolated sphere. Jørgensen (1966), Strathman et al. (1972), Strathman (1973, 1975), Strathman and Bonar (1976), Strathman and Leise (1979) have shown that most marine suspension feeders coat their filters with mucus. Presence of mucosubstances on filters was demonstrated first for insects in freshwater environments in larval blackflies (Ross and C [illegible] 1980). Although no mucosubstance secreting organs have yet been identified in other freshwater insect except mosquitoes, possibly other secretions such as their saliva could help in particle capture.

Mechanisms of particle capture suggested by Rubenstein and Koehl (1977) were originally derived for gas-borne particles and the authors showed as a first approximation that the mechanisms may be important in liquid environments. Spielman and Goren (1970), Spielman and Fitzpatrick (1973), Chang (1973), Goren (1979), Spielman (1977), Schrijver et al. (1981) extended these mechanisms for liquid systems to include hydrodynamic interactions (Hamaker, 1937; Charles and Mason, 1960; Hamza and MacDonald, 1981) between particle and collector. This interaction is attributed to the continuum description of fluid motion with no-slip at both collector and particle surfaces. This condition causes infinitesimally slow drainage of fluid from the gap between the collector and particle as they approach each other under a finite force and tends to oppose contact. However, the action of attractive London-van de Waals forces become strong at such close distances and overcomes the interaction. Results of those studies have led to modifications which show general applicability of the

Rubenstein-Koehl model to liquid systems.

1. Direct interception:

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

$$\eta_{dI} = 2A_F(r_p/r_B)^2 \int (N_{Ad}, r_p/\lambda) \ldots\ldots\ldots (6)$$

where λ is the wavelength of the hydrodynamic retardation function (typically on the order of 10^{-5} cm) and N_{Ad} is the dimensioness adhesion number:

$$N_{Ad} = Qr.^2/9\pi\mu A_F U r_p{}^4 \ldots\ldots\ldots (7)$$

Briefly, the value of the adhesion number (N_{Ad}) depends on the ratio of London-van de Waals attractive forces and hydrodynamic retardation forces. LaBarbera (1984) showed that suspension feeding is 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.

2. Inertial impaction:

The extended theory (Spielman, 1977 does not consider inertial impaction to be important in liquid systems because of the low value of the Stokes number for most liquid suspended particles. Spielman's finding is at variance to that of Silvester (1983) who based his calculations of Stokes number of suspended particles on density of particles (i.e ρ_p) alone instead of buoyant density (i.e. $\rho_p - \rho_m$).

3. Gravitational deposition:

The dimensioness index of capture efficiency is replaced by efficiency of capture (η) and is given by Yao et al. (1971) as:

$$\eta = (\rho_{p} - \rho_{m}) g d_{p}^{2} / 18 \mu V_{0} \ldots\ldots\ldots (8)$$

4. Diffusion or motile-particle deposition:

The efficiency of diffusive deposition is given as:

$$\eta = 3.64 A_{f}^{1/3} Pe^{-2/3} \ldots\ldots (9)$$

(Spielman, 1977; Schrijver, 198[illegible]; LaBarbera, 1984)

where Pe is the Peclet number represented by: $2r_{f}U/D$

D is the Brownian diffusion coefficient represented by:

$$D = KT / 6\pi\mu r_{p} \ldots\ldots\ldots\ldots (10)$$

K and T as defined in equation 4.

5. Electrostatic attraction:

Gerritsen and Porter (1982) suggested that surface chemistry of filters and particles could account for particle adhesion at low velocities in *Daphnia magna* and other filter feeders which do not coat their filters with mucus. Thus, they expanded and redefined the Rubenstein-Koehl model of electrostatic attraction to include chemical interactions such as ionic or hydrophobic-hydrophilic effects. Lewin (1984) suggested that some microorganisms (i.e. bacteria) may be able to manipulate adhesion molecules in the flagella to enhance attachment to surfaces in liquid systems. LaBarbera (1978) showed that the presence of mucus on the tube feet of *Ophiopholis aculeata* (L) enabled it to capture more particle possessing specific charges and concluded that electrostatic attraction as defined by the Rubenstein-Koehl model is the predominant mechanism of particle adhesion in this organism.

LaBarbera (1984) showed general applicability of the extended model 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 for particle capture in *Simulium vitattum* Zett.,*Prosimulium mixtum fuscum* Syme and Davies and *Stegopterna mutata* (Malloch). They proposed that the former mechanism may be the predominant mode of fine particle capture. 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 proposed that the mechanism of inertial impaction could be more important for large particles (eg.>100μm) at high velocities. Silvester (1983) suggested that inertial impaction and direct interception are important in particle capture by some species of net-spinning caddisflies. His conclusion on the importance of inertial impaction is at variance to most other studies (i.e. Strathmann, 1971; Fenchel, 1980; LaBarbera, 1984) and requires further investigation.

Principles of fluid mechanics and aquatic insects.

The application of fluid mechanical principles to the study of aquatic insects have been useful in understanding the relation between various structures and the functions they perform. Hydrodynamics of swimming in water beetles, *Acilius* and *Dytiscus* was studied by Nachtigall(1960) and Nachtigall and Bilo (1965). Ambühl (1959) provided information on the effect of boundary layer thickness on the adaptations of freshwater insects to velocity. Bournand (1963) used a hydrodynamic approach to study the effect of current velocity on trichopteran larvae. Decamps et al. (1975) studied the microdistribution of simuliid larvae by hydrodynamic analysis. Smith and Dartnall (1980) demontrated that boundary layer control by psephenid larvae is an active compensating process against being swept off the substrate. Statzner and Holm (1982) used laser doppler anemometry to study distribution of velocity around nymphs of the mayfly *Ecdyonurus venosus* and showed that hydrodynamic lift was greatest on the thoracic segment of the body. They suggested that dorsoventral flatness (Ambühl, 1959) is not as important as the position of appendages on the thoracic segments in preventing nymphs from being swept away by the current.

Principles of fluid mechanics and filter feeding.

Filter feeding involves processing water, retention of particles on filters and transfer of retained particles to the mouth. Principles of fluid mechanics are exploited to achieve each of the three phases of feeding.

A review of suspension feeding in flagellates, ciliates, sponges, copepods, bivalves and ascidians (Jørgensen, 1983) and other studies O'Neil (1978), Koehl and Strickler (1981), Koehl (1982), Vogel (1981), Carey (1983), Gerritsen and Porter (1982) Porter et al. (1983), LaBarbera (1984) showed that viscous forces play a more important role particle capture in aquatic invertebrates than was previously realized. Craig and Chance (1982) showed that water flow through cephalic fans of *S. vittatum* larvae is laminar at a velocity of 20 cm/sec. A summary of hydrodynamic principles that are relevant to filter feeding in simuliid larvae and ephemeropteran nymphs is outlined below.

Regimes of flow:

In moving fluids two types of flow, laminar and turbulent may occur. Flow is laminar in situations where layers of fluid in different velocity gradients move downstream in smooth trajectories and all fluid particles move in parallel layers. In turbulent flow, the fluid particles move in an irregular manner though the net direction of flow is downstream. The transition from laminar to turbulent flow occurs in a zone that is characterized by both types of flow. The reasons for the breakdown of laminar to turbulent flow are poorly understood. An important reason for the paucity of information is that the mathematical equations that describe fluid flow defy solutions outside the smooth laminar flow zone.

Reynolds Number:

Reynolds number (*Re*) quantifies the relative importance of inertial (fluid momentum) forces and viscous (fluid stickiness) forces. *Re* indicates only the order of magnitude of the two forces. The units of force cancel out making *Re* a dimensionless number.

$Re = VL\rho/\mu$ (Vogel, 1981)......(11)

where V = velocity upstream and removed from the effect of the fiber.

L = characteristic length dimension.

ρ = density of fluid medium.

μ = dynamic viscosity of medium.

The ratio of μ/ρ is called kinematic viscosity (γ).

In a given flow, different representatives of the characteristic length dimension (L) and velocities (V) of flow may be chosen for and in defining *Re* , hence different values for the number. In comparing flow systems with *Re* similarly defined, the system with the lower *Re* value has a more pronounced viscous effect. Flow is usually laminar at

Re less than 2000 and turbulent at Re greater than 10,000, for circular pipes (Reynolds, 1883). Transition to turbulent flow occurs between *Re* values of 2000 and 10,000. Generally, *Re* at the zone of transition is a function of stability of flow, dimensions and texture of the object.

Flow at very low *Re* values (i.e. Re less than 1) is characterized by large viscous forces, inertial forces being negligible (Fung, 1969) and flow is typically laminar and reversible. Detailed fluid mechanics of flow dominated by viscous forces is given by Happel and Brenner (1965). Typical values of *Re* for some flagellate protozoa which live in such peculiar but ordered environments have been calculated by Purcell (1977).

Velocity gradients and boundary layers:

There is no slip (i.e. no relative motion) between a surface and the fluid layer immediately adjacent to it. This condition of flow creates a gradient of velocity near the surface due to slowing down of subsequent layers of fluid. Velocity changes from zero at the surface to that of free stream flow some distance away. The thickness of the boundary layer (δ), or the regions of the fluid to which the viscous effect extends, is arbitrarily assumed to be the distance from the surface where the velocity has increased to at least 99% of the free stream flow (Schlichting, 1960). Although, 99% is the most commonly used figure some authors (Streeter and Wylie, 1979) use 90%. Vogel (1981) pointed out that the outer limit depends on the function for which one is invoking a boundary layer, and suggests that 90% propbably has more biological significance.

Re less than 1:

Flow within a boundary layer may be laminar, transitional or turbulent depending on the magnitude of the *Re*. At very low *Re* values the boundary layer thickness δ is represented by:

$$\delta = d/Re^{1/2} \text{ (Fung, 1969)} \ldots\ldots\ldots\ldots (12)$$

where d = diameter of object.

Re = Reynolds number.

δ = thickness of boundary layer.

Turbulent boundary layers occur at *Re* >500,000 and are comparatively thicker than laminar boundary layers. The thickness of a turbulent boundary layer is given as:

$$\delta = 0.38d/Re^{1/5} \text{ (Vogel, 1981)} \ldots\ldots\ldots\ldots (13)$$

A no-slip condition exits even at very high *Re*, thus within the turbulent boundary layer flow remains laminar in the layer of fluid immediately adjacent to the surface. This region is known as the laminar or viscous sublayer. The thickness of the viscous sublayer δ is given as:

$$\delta = 11.5\gamma/V_F{}^{1/2} \text{ (Francis, 1975)} \ldots\ldots (14)$$

where V_F = shear velocity at the object.

γ = kinematic viscocity

Drag in fluid flow:

Drag is defined as the rate of removal of momentum from a moving fluid by an immersed body (Vogel, 1981). By means of momentum theorem, it is possible to relate the change in momentum to the total resistance which the body exerts on the fluid to cause this reduction in velocity. The drag experienced by the body is represented by:

Drag $= \rho \int U_1 \cdot (U_o - U_1)\Delta S$ (Vogel, 1981).......(15)

where ρ = density of fluid at experimental temperature.

U_0 = velocity upstream from object.

U_1 = velocity at the downstream region (i.e. in the wake of object).

ΔS = area of object.

The physical dimensions of the body and conditions of flow cause it to experience two kinds of drag force.

Frictional drag:

Frictional drag is caused by interlamellar stickiness of fluids i.e. no-slip which creates a shear region in a fluid near a surface (Koehl, 1982). Frictional drag is important and predominant in more viscous flow. The magnitude of frictional drag depends on the amount of surface a body exposes to flow and also the texture of the body.

Pressure drag:

Pressure drag occurs due to the separation of the boundary layer from the surface. Separation is caused by differences in dynamic pressure on the front and on the rear part of the surface. Energy used to accelerate fluid past the surface is not returned to it in the slower flow near its rear (Shapiro, 1961). The excess energy forms vortices in the wake. The magnitude of pressure drag depends mostly on shape of the object.

Drag coefficient (C_d):

Drag coefficient is the dimensionless index that expresses the magnitude of drag force encounted by a submerged object (Li and Lam, 1964). C_d is represented by:

$C_d = 2D_f/A\rho V^2$ (Li and Lam, 1964)....(16)

where D_f = drag force.

A = wettable surface area.

ρ = density of medium.

V = speed of movement of object or of fluid flow past it.

C_d as defined in the equation above is the total drag on the body i.e. C_d = C/friction + C/pressure.

For a laminar boundary layer:

C/friction = $1.33/Re^{1/2}$ (Francis, 1975).........(17)

For a turbulent boundary layer:

C/friction = $0.072/Re^{1/5}$ (Francis, 1975).........(18)

For a transitional boundary layer:

C/friction = $0.072/Re^{1/5} - 1700/Re$ (Francis, 1975).....(19)

C/pressure is a high *Re* phenomenon and it is represented by:

$$C/pressure = C/friction(1 + 1.5((d/l)^3)^{1/2} + 7(d/l)^3)$$

(Webb, 1974).................................(20)

where l = length of the body

d = maximum diameter of the body

Equations 18, 19 and 20 are not applicable to filters of blackfly larvae and mayfly nymphs.

Modelling and Reynolds Number:

Scaled-up or scaled-down models which are geometrically similar to real life forms facilitate flow visualization and make it easier to study fluid mechanical principles. A principle required for constructing models is to maintain equality of *Re* for both situations. If the Reynolds number for two systems are the same then there is similarity in the streamlines pattern in the model and prototype and both have equal drag coefficient i.e. dynamic similarity (Fung, 1969). For example to work on small objects i.e. filters of larvae of *S. bivittatum* and nymphs of *I. campestris* large models can be constructed and tested in a highly viscous medium. It is important to remember to vary velocity and kinematic viscosity to ensure equality of Re.

Models have been of great help to aerodynamicists and hydrodynamicists. Wu et al. (1975) and Vogel (1981) are good sources for biological investigations which used models. Gerritsen and Porter (1982) used scaled-up model made with

110μm mesh plankton netting oscillated in glycerin to study boundary layer thickness at the filtering setules on the appendage of *Daphnia magna*. Silvester (1983) used nylon thread to study pressure drop across trichopteran filter nets by calculating changes in velocity of water flow through them.

Information given above on fluid mechanical principles and practices served as background for the investigation of hydrodynamics of filter feeding in larvae of *S. bivittatum* and nymphs of *I. campestris*.

The objectives of this study were: 1. to determine the extent to which incorporation of hydrodynamic retardation forces (Spielman, 1977; LaBarbera, 1984) and other modifications (Gerritsen and Porter, 1982) of the Rubenstien-Koehl model apply to particle capture and retention in passive filter feeding insects in freshwater environments. 2. to use scaled-up models to study fluid mechanical principles that are exploited in processing water for food. 3. to suggest the biological importance of these principles.

2. MATERIALS AND METHODS

2.1 Collection and maintainance of nymphs of *I. campestris*, and larvae of *S. bivittatum*

Mature larvae of *S. bivittatum* with well developed gill histoblasts, and nymphs of *I. campestris* with rudimentary wing pads were collected from Milk River near Writing-On-Stone Provincial Park, Southern Alberta (49° 00N, 110° 33W). Water from Milk River was used to maintain live specimens in a laboratory stream designed after Corkum and Pointing (1977). A Variac control on the motor was used to regulate flow. Temperature was maintained at that of the Milk River (18°C) with a refrigerating unit.

2.2 Flow tank and feeding experiments

Prior to being fed a suspension of monodispersed, polystyrene particles (Analychem Corporation Ltd. Markham, Ontario) insects were starved for 12 hours 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 (Figure 11). Thin rubber tubings (0.5 mm) thick with a 0.5 cm pore size were used to construct collimators instead of plastic straws mentioned in the original design since the former withstood higher water velocities. Another collimator was inserted above the propeller to reduce turbulence. Vortices induced by the propeller were eliminated by inserting a partly curved plexiglass fairing in the lower return conduit (Figure 11). This is an addition to the original model to improve and increase overall flow. 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 (Figure 11). An attachment site for the ephemeropteran nymphs and simuliid larvae was made from thin (1.0 mm^2) pieces of balsam wood. Seven pieces were cut long enough to fit the internal diameter of the trough. Seven other pieces were cut long enough to project 1.5 cm above the level of water in the trough. Vertical and horizontal pieces were glued together to form 1.0 cm openings. Two such grids (A & B) were placed 16.0 cm apart in the tank and each 22.0 cm from the end of the trough (Figure 11). Simuliid larvae were introduced into the trough with a soft brush. Larvae usually spin an anchor line of silk onto the fine hairs of the brush when first introduced. They then drift in the current until they get to the balsam wood, attach 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 attach with their meso- and metathoracic legs.

2.3 Measurement of velocity at which insects fed

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

2.4 Concentration of polystyrene particles in the feeding suspension

Five different sizes of polystyrene particles having diameters of $0.5\pm0.006\mu m$, $1.2\pm0.017\mu m$, $5.7\pm1.5\mu m$, $25.7\pm5.8\mu m$, $90.7\pm17.7\mu m$ were added to three liters of filtered distilled water for each experiment in 1981 and a sixth size of $50.1\pm20.0\mu m$ was added in 1982. The number of particles, in each size class, per ml (Tables 1, 2) were determined using:

$$\text{Number of particles/ml} = A \times 24 \times 10^{12}/4 \times \phi^2 \times \rho \quad \ldots\ldots(21)$$

(Polysciences Inc. 1980).

A = grams per ml of polymer in latex.
ϕ = diameter in (μm) of monodispered latex.
ρ = density of polymer as grams per ml.

The number of each size class of particle in the feeding suspension was confirmed with a Model TA II Coulter Counter. The mixture of polystyrene particles was sonicated for 1.0 minute before it was added to the flow tank. Sedimentation and aggregation of particles were reduced by the rotating motion of the propeller fan which served as stirring rod. Each insect was labelled according to site of feeding (Appendix 3) and any changes in position were monitored and recorded. Insects were allowed to feed for 45 minutes in 1981 and for 30 minutes in 1982.

2.5 Concentration of particles available to insects at different times and velocities

Three (2 ml) replicate samples of the feeding suspension were collected at 10 minutes intervals at different velocities, in a separate experiment without mayfly nymphs or blackfly larvae, to determine the concentration of each size class of polystyrene particles in the feeding suspension over time (Figure 13).

2.6 Recovery of polystyrene particles from the gut of insects

At the end of each feeding test insects were collected and stored in 95% alcohol in labelled plastic vials. Head fans of the blackfly larvae and forelegs of the ephemeropteran nymphs were removed and stored. The rest of the insect was dissolved over 12 hours in 0.25 ml of 6% NaOCl which had been filtered through 0.22µm, 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. Clean monodispersed particles were recovered from the mixture through a density gradient centrifugation process.

2.6.1 Density gradient and particle sedimentation

Percoll (Pharmacia Fine Chermicals; 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 1.5M NaCl. This stock solution was mixed with 0.15M NaCl to make a series of 3 ml experimental samples. Three microliters each of a suspension of 9 differently coloured Density Marker Beads (Pharmacia Fine Chemicals; Dorval, Quebec) were soaked in 6% Sodium hypochlorite (NaOCl) for 12 hours prior to being added to the samples in 4 ml capacity, Autoclear Polycarbonate Centrifuge Tubes(Damon/IEC Division,Needham Hts., Mass). The tubes were capped, inverted several times and centrifuged at 20,200 gav. for 30 minutes 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 (Figure 12). The 40% density layer was selected since marker beads with corresponding density (1.05/gm) to polystyrene particles lay in a region with maximum separation from bordering gradients. Portions (3 ml) of the 40% layer were then centrifuged at 20,200 gav. for 30 minutes 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 gav. for 45 minutes to separate the particles and insect remains at their iso-pynic densities. (i.e the particles and insect remains will sediment to an equilibrium position in the gradient where the gradient density is equal to the density of particle or insect remains). Polystyrene particles do not have the same density as insect remains, thus both separate. Clean Pasteur pipettes were used to collect particles. Cleanliness of particles, after recovery was checked with a Scanning Electron Microscope. Particles were then transfered to clean triple-filtered Isoton (Coulter Electronics Ltd., Vancouver, B.C) in 2 ml capacity vials for sizing and counting with a Model TA II Coulter Counter.

2.6.2 Determination of size and number of particles consumed by each insect

Size and number of particles consumed by individual insects were determined with the Coulter Counter. Theory of electronic particle sensing is based on changes in resistance between two electrodes on either side of a changeable aperture through which particles suspended in an electrically conductive liquid are forced. The change in resistance produces a voltage of short duration which has a magnitude proportional to particle size. The series of pulses is then electronically scaled, counted and sized.

Briefly, an aperture will accurately measure particles having diameters between 2% and 40% of its diameter. For example, a 50µm aperture will accurately measure particles having diameters from 1.0µm to 20µm. Since the insects were fed suspension of particles having diameters of 0.5±0.006µm, 1.2±0.017µm, 5.7±1.5µm, 25.7±5.8µm, 50.1±20.1µm, 90.7±17.7µm, 50µm and 280µm apertures were used. Data from the 50µm aperture was extrapolated to give values for 0.5µm particles using the method of Eckhoff (1966). Contents of the 2 ml vials with recovered polystyrene particles were added to 48ml of triple-filtered Isoton to make a 50 ml sample. The samples were then divided into 25 ml portions and each portion was made up to 50 ml with triple-filtered Isoton. One portion was filtered through a 15µm nylon mesh (Thompson and Co., Montreal, Quebec). This portion was used in the 50µm aperture and the unfiltered portion in the 280µm aperture. The number of particles in 20 ml protions was determined and back-calculated to give total counts per insect. Readers should consult the reference manual for Coulter Counter Model TA II for more information on technique and procedure for multi-aperture analysis.

2.7 Scanning Electron Micrographs of filters of simuliid larvae and ephemeropteran nymphs

Cephalic fans of simuliid larvae and forelegs of the ephemeropteran nypmhs were prepared for SEM studies after the method of Ross and Craig (1979). Diameter and length of microtrichia, number of microtrichia per ray, number of rays per fan and per foreleg and number of rows of ray per segment of foreleg were measured from photomicrographs.

2.8 Scaled-Up Models of portions of filters

Scaled-up models of portions of cephalic fans of larvae of *S. bivittatum* (Figure 2) and rays on the forelegs of nymphs of *I. campestris* (Figure 7) were made with plexiglass and metal pins. The width and length of plexiglass and metal pins were increased by a factor of 2500 - 3000. Plexiglass and metal pins represent ray and microtrichia respectively. Relative shape, orientation and dimension of each scaled-up model were determined from SEM·photomicrographs of the original structure.

2.8.1 Towing experiments

The models were towed through Canola oil at various velocities (Tables 2 & 6) by a gear-reduced type NSH-12 Fractional Horsepower motor (Bodine, Electric Co.Chicago, Illinios) attached to a model SL 15 Minarik feed-back control (Minarik Electric Co., Los Angeles, California). A trolly to which the models were attached was mounted on two linear bearings and pulled along two parallel case-hardened steel bars by a string pulley (Figure 15). This arrangement reduced vibration to the models and improved flow visualization. Electrically controlled start-stop contacts were used to maintain a fixed distance of 68.0 cm travelled by each model. The oil was cooled to 10°C to achieve the desired dynamic viscosity of 143.0 centipoise. Size classes of large polystyrene particles to represent 0.5μm, and 1.2μm particles were added to the oil. These particles were kept in suspension by stirring. An interval of 30 seconds was required between each experiment to allow turbulence created by stirring to subside. Reynolds number (*Re*), boundary layer thickness (δ) and drag coefficient (C_d) were calculated for each model at various velocities (Tables 3 & 6). These values were compared to that for live ephemeropteran nymphs (Table 5) and simuliid larvae (Table 4) by invoking the principle of dynamic similarity (Fung, 1969; Francis, 1975; Vogel, 1981; Koehl and Strickler, 1982). Observations were recorded with a Panasonic video camera with a Micro-Nikkor 105 mm lens. Frame-by-frame analysis of the tape was made with Sony Automatic Editing Unit, RM-440.

2.8.2 Boundary layer around models

Pictures of polystyrene particles in different velocity gradients (Fig[illegible]s 16i, ii, iii) in the laminar boundary layer around each ray were taken from the video monitor. The editing unit was switched to manual mode so that the time interval between successive photographs could be controlled. Two fields of interlacing scan lines make up one TV frame i.e. 1 field is equal to 1/60sec. Photographs were taken with a Canon A1 camera with a 80-210 mm macro zoom lens and a 2X Tameron converto Tri-X film rated at ISO 800 was used. Exposure was 1/8th of a second at F4.

The distance and velocity of polystyrene particles from the surface of some rays and microtrichia (Table 7) were approximated using:

$$\delta U_x \cdot \delta y = 0.32U^{3/2}\rho_c^{1/2}X^{-1/2}\mu_c^{-1/2} \ldots\ldots (22)$$

(Vogel, 1981)

where δU_x = change in velocity along microtrichia and ray.

δy = change in thickness of boundary layer.

X = distance downstream from leading edge of microtrichia and associated ray.

U = Free stream velocity.

ρ_c = Density of Canola oil.

μ_c = Dynamic viscosity of Canola oil.

3. CALCULATIONS AND RESULTS

3.1 Mechanisms of particle capture

In order to determine the mechanisms which were operative, collection efficiency of the filters by each mechanism was calculated. Relative efficiencies were used 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 (Figure 13) was used to predict distribution of size classes that should have been caught. Such distributions were compared to those actually caught by the insects. (Figures 17 - 27).

3.1.1 Direct Interception

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

$$\eta_{di} \propto (r_p / r_f^{2})^{2.3} \ldots\ldots (23)$$

and predicted relative capture efficiency due to direct interception for situations where the adhesion number is large (i.e. neglegible retardation forces). Note (Figures 17 -27) that this mechanism should theoretically predominate for capture of particles greater than 1.0μm, however, experimental results showed lower efficiency. For 1.0μm particles, agreement between experimental results and theoretical prediction is closer at lower velocities of 4 - 18 cm/sec for *I. campestris* and velocities of 4 - 28 cm/sec for *S. bivittatum*

3.1.2 Inertial Impaction

This mechanism was not tested because insects were not fed large, dense particles.

3.1.3 Diffusion or motile-particle deposition

The equation for diffusive deposition was simplified to:

$$\eta \alpha (r_{\rho} r_{f})^{-2\ 3} \ldots\ldots\ldots (24)$$

and predicts relative capture efficiency due to diffusive deposition. The overall close agreement between theory and observation, especially at high velocities (Figures.17-27) show that this model is a good predictor of size distribution of smaller particles captured by both insects.

3.1.4 Gravitational deposition

The parallel orientation of filters of both insects to flow and the velocities used make this mechanism non applicable to the simuliid larva. It is of low applicability perhaps, in the ephemeropteran nymph.

3.1.5 Electrostatic attraction

Surface properties of filters and polystyrene particles and chemical nature of mucosubstanses or sticky substances which contribute to adhesion of particles were not studied.

3.2 Availability of particles in suspension

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

$$C_0 = C_1 e^{-kt} \quad \text{Coughlan (1969).....(21)}$$

where C_0 = concentration at time t

C_1 = initial concentration

k = decay rate (i.e. rate of sedimentation)

Note (Figure 13) that sedimentation of large particles (i.e. >20μm) was substantial at low velocities. Most of the particles in all size classes were in suspension at all times at velocities above 28 cm/sec.

3.3 Aspects of feeding biology

Aspects of feeding biology of both insects were studied with histograms of mean number of each size class of polystyrene particles in the guts at various velocities (Figures 28 - 35).

3.3.1 *I. campestris* and *S. bivittatum*

The large size and greater number of filtering elements of nymphs of *I. campestris* enabled them to consume more of each size class of particles in the feeding suspension than larvae of *S. bivittatum* at all velocities. Number of the smaller size classes of particles consumed, decreased with increasing velocity in both insects. Fewer insects fed at velocities below 5.0 cm/sec and above 40.0 cm/sec. Capture efficiency of particles in the smaller size classes (i.e.

0.5μm to 5.7μm) was higher than for larger particles (i.e > 20μm) at all velocities (Figures 28 - 35).

3.3.2 One-way analysis of variance (Anova)

Anova was used to test for differences in the number of 0.5±0.006 - 5.7±1.5μm polystyrene particle consumed at different velocities (Tables 8-11). Scheffe's test (Kleinbaum and Kupper,1978) was used to make pairwise and contrast other than pairwise comparisons. Any two means not underscored by the same thick or dotted line are significantly different (P>0.05). Any two means underscored by the same thick line are not significantly different (P>0.05). Those underscored by the same dotted line are not significantly different (P>0.05) but they have wide contrast intervals i.e. evidence for difference.

3.3.2.1 *S. bivittatum*

There was significant difference (P>0.05) in the number of particles consumed at low velocities of 5.0 - 10.0 cm/sec and high velocites of 35.0 - 47.0 cm/sec for particles in the size class of 0.5μm - 5.7μm (Figures 28 and 29). Pairwise comparision with Scheffe's method show that there is significant difference (P>0.05) in the number of 0.5μm and 1.2μm particles consumed at 5.0 cm/sec and at velocities of 8.0 - 10.5 cm/sec (Table 9). A velocity range of 5.0 - 22.0 cm/sec enhances particle capture for the simuliid larvae (Figures 28 - 31). A significantly different

($P>0.05$) number of particles were consumed over this range of velocity than at all other higher velocities of 25.0 - 47.0 cm/sec combined.

3.3.2.2 *I. campestris*

There was significance difference ($P>0.05$) in the number of 0.5µm and 1.24µm particles consumed at low velocities of 3.5 - 5.5 cm/sec and high velocities of 30.0 - 45.0 cm/sec (Figure 32, Table 8). There was no significant difference ($P>0.05$) in the number of particles in the size class of 5.7µm - 90.7µm except for 5.7µm in 1982.

Pairwise comparision with Scheffe's method show that there is significant difference ($P>0.05$) in the number of 0.5µm particles consumed at 4.0 cm/sec and those consumed at 9.0 cm/sec (Figure 32 - 35). A velocity range of 3.5 - 20.0 cm/sec enhance particle capture in the ephemeropteran nymphs. A significantly different ($P>0.05$) number of particles were consumed over this range of velocity than at all other higher velocities of 27.0 - 45.0 cm/sec combined. More nymphs of *I. campestris* fed over a lower range of velocity (3.4 - 5.5 cm/sec) than did larvae of *S. bivittatum* (Appendix 1).

3.4 Fluid mechanical principles and practices relevant to particle capture in both insects

3.4.1 Drag

Drag on the models of portion of filters of nymphs of *I. campestris* (Figure 7) and cephalic fans (Figure 2) of *S. bivittatum* was calculated using the formula of Vogel (1981) given in the introductory section (i.e.):

$$\text{Drag} = \rho \int U_1 \ (U_0 - U_1) \Delta S \ ....(25)(\text{Vogel, } 1981)$$

The area of model of cephalic fan of the insects was calculated using a modified form of I in:

$$\Delta S = R \times (A + (I \times M)).......(26)$$

(Ross and Craig, 1980)

I = area of curved surface of microtrichia was used due to arrangement (i.e. $I = r\ (r^2 + h^2)^{1/2}$). r = radius, h = height (i.e. length of microtrichia).

where R= average number of rays per fan or foreleg.

M= average number of microtrichia per ray.

A= average surface area of both sides of a fan ray.

Area of rays on each row of the forelegs of nymphs of *I. campestris* was calculated using:

$$\Delta S = R \times (A + (I_1 \times M) + (I_2 \times M)).......(27)$$

I_1=average area for first row of rays; I_2 for second row of rays.

Estimates of U_1 were based on velocity of particles in the region behind rays. Results of these calculations indicate that drag on the filters of nymphs of *I. campestris* was greater than on the cephalic fans of larvae of *S. bivittatum* at all current velocities (Table 12). Thus, nymphs of this ephemeropteran were observed to move to the boundary layer at the side of the flow tank before larvae of *S. bivittatum*. Nymphs have a higher relative increase in drag on filters from low to high velocities. There was a 6-fold increase for larvae of *S. bivittatum* and a 40-fold increase for nymphs of *I. campestris* (Table 12). The latter increase is due to the greater number of rays on the forelegs and also the double row of rays on the tibia and tarsus and triple-row on the upper part of the femur closer to the mesothorax (Figures 6 and 10).

3.4.2 Drag Coefficient (Cd)

Drag coefficient(C_d) was calculated using:

$$C_d = 1.33/Re^{1/2} \ldots\ldots (28)$$

Calculated values of C_d in this study at *Re* less than 1.0 are relative values for these odd shapes. Under this condition of flow the inertia term in the Navier-Stokes equation can be neglected (Fung, 1969). Limits of the boundary layer (i.e. region of the water in which the effect of viscosity is felt) become difficult to define due to creeping motion and the curious phenomenon of reversal of flow. Tomotika and Aoi (1953) gave solutions of C_d for different shapes and their orientation for creeping flow.

3.4.3 Reynolds number (Re)

Reynolds number for filters of nymphs of *I. campestris* and larvae of *S. bivittatum* were calculated using:

$$Re = \rho VL/\mu \text{.......(29)}$$

where ρ, V, L, and μ are as defined in the introduction. Particle capture by microtrichia and rays of live larvae of *S. bivittatum* (Table 4) and nymphs of *I. campestris* (Table 5) occur at low *Re* values of 0.02 - 3.2. The lowest *Re* value for the models (Tables 3 and 6) was not as low as the lowest *Re* for live insects, but a higher *Re* was obtained with models. The range of overlap of *Re* values was wide enough to enable comparison of flow patterns between models and live insects at *Re* values of 0.07 - 2.11 for larvae of *S. bivittatum* and *Re* values of 0.07 - 3.24 for nymphs of *I. campestris*.

3.4.4 Boundary layer (δ)

Thickness of the boundary layer around rays was calculated using:

$$\delta = d/Re^{1/2} \text{ (Fung, 1969)........(30)}$$

Boundary layer thickness around each microtrichium, of live larvae *S. bivittatum*, even at maximum velocity of 47.0 cm/sec, extended 1.3μm - 1.5μm i.e. to the fifth micritrichium away from it. Models indicate that boundary layer thickness around each microtrichium (i.e. metal pins) extended only to the next microtrichium at *Re* value of 3.98 which is a real life equivalent of 80.2 cm/sec . Boundary layer thickness around each microtrichium in the first row of models of rays of nymphs of *I. campestris* extended to the third microtrichium at maximum *Re* value of 7.97. This is equivalent to a velocity of 100.0 cm/sec for live nymphs. Values of boundary layer thickness show that microtrichia of larvae of *S. bivittatum* and nymphs of *I. campestris* behaved as a solid wall with no flow between individual microtrichium. Distance between adjacent rays and thickness of the boundary layer around each ray indicate that there was very little flow between rays up to *Re* values of 0.49 for larvae of *S. bivittatum* and *Re* values up to 1.39 for rays on the first row of filters of nymphs of *I. campestris*. Calculations indicate that the thickness of the boundary layer is about 28 - 33% the diameter of ray at the maximum velocity of 80.0 cm/sec for live larvae of the simuliid. At the maximum velocity of 100.0 cm/sec for the ephemeropteran nymphs, boundary layer thickness is about 35 - 38% the diameter of the ray for rays in the first row and it is about 39 - 46% the diameter of the ray for the second row of rays due to reduction in velocity and concomitant reduction in *Re* value.

4. PATTERN OF FLOW AROUND MODELS

Much of the observations described in this section are recorded on video tape which is submitted with this thesis. These descriptions are presented as an interpretation and aid to the visual record.

4.1 Flow pattern at Re<1 (Real life equivalent of 20.0cm/sec .)

4.1.1 *S. bivittatum*

Generally, there was very little flow through adjacent rays. Flow was dominated by viscous forces causing reversal of flow. Polystyrene particles travelled with the models in the very thick viscous boundary layer that surrounded rays and microtrichia. Large particles in the viscous layer sedimented. At the end of each towing run there were more smaller particles than large ones on the ray and microtrichia (See also Figures 16i, ii, iii).

4.1.2 *I. campestris*

Pattern of flow observed was similar to that of larvae of *S. bivittatum*. When there was very little flow through the first row of rays it was observed that particles entered the viscous boundary zone between the first and second rows of rays and moved with it. Larger particles in this zone were observed to sediment. Number and size of polystyrene particles captured by ray and microtrichia on the first and second rows of rays at the end of each towing run was similar to that observed for larvae of *S. bivittatum*. Rays in the first row had more particles than rays in the second row.

4.2 Pattern of flow at $1<Re<8$ (Real life equivalent of 30.0 - 100.0 cm/sec)

4.2.1 *S. bivittatum*, ($1<Re<4$) (Real life eqiuvalent of 30.0 - 80.0cm/sec)

The effect of viscous forces decreased considerably above *Re* of 1.0, although it was still noticeable up to *Re* value of 1.5. The viscous boundary layer around each ray was reduced and there was flow through adjacent rays. There was a general increase in velocity gradients around each ray and microtrichia and particles in faster gradients were observed to overtake slower moving particles nearer the rays and microtrichia (Figures 16i, ii, iii). The effect of viscous forces decreased even further around *Re* of 3, producing thinner boundary layers and faster flow through adjacent rays. Sedimentation rate of large particles also decreased. There were more smaller particles on the rays and microtrichia even at the maximum *Re* of about 4.0.

4.2.2 *I. campestris*, ($1<Re<8$) (Real life equivalent of 17.5 - 100.0cm/sec)

Patterns of flow observed at Re>1 for rays on the first row were similar to that of cephalic fan of simuliid larvae except that viscous forces were still noticeable at *Re* value of 2.0. There was flow through rays on the second row which was operating at *Re* of 0.7 (Table 5). The dead zone in between the first and second row of rays (Figure 14) was observed to become mobile at *Re* of 3.0, but sedimentation of large particles continued. There was considerable decrease in the effect of viscous forces on this zone at *Re* of 5.0, producing faster velocity gradients(i.e. thinner boundary layers) and a decrease in the sedimentation rate of large particles. The trend of particle deposition on rays and microtrichia was similar to that observed at *Re* >1. Number of particles captured at higher *Re* were less than at *Re* less than 1.

5. DISCUSSION

5.1 Determination of size and number of particles consumed by both insects

The density gradient centrifugation technique used to recover particles from gut of insects makes it possible to determine total number of particles consumed by each insect. It eliminates the problem of identifying synthetic particles in the presence of natural faecal materials (Figure 5). The solution of NaOCl can dissolve mucosubstance or derivatives of it and other sticky secretions . Thus, tendency of particles to stick together is greatly reduced. The fast and highly accurate electronic method of particle sizing and counting reduces error that is inherent in two-dimensional photographic methods. The large number of particles reported in this study compared to most previous studies (Shapas and Hilsenhoff 1976; Coffman et al. 1971; Kurtak, 1978, 1979; Wallace and O'Hop, 1979; Schröder, 1980) is due to the differences in the technique of counting.

5.2 Mechanisms of particle capture

Particle capture by the filters of nymphs of *I. campestris* and larvae of *S. bivittatum* occur over a range of low Reynolds number, in which flows are characterized by partial and total viscous forces. A significant number of polystyrene particles smaller than spaces between adjacent rays were consumed at all velocities. Thus, in addition to sieving, filters of both insects capture particles by direct interception and diffusive and/or motile-particle deposition. Gravitational deposition may be operative at the second and third rows of rays in nymphs of *I. campestris* based on observations in models.

5.2.1 Direct interception

The discrepancies i.e. lower efficiency of observations compared to predicted efficiency of model (Figures 17 - 27) are due possibly to violations of certain assumptions of the models. The assumption that there is 100% collection efficiency of all particles which contact the surface of filters is unrealistic. Information is needed on the surface properties of particles and filters and/or sticky substances used to coat filters. Future studies should focus on these aspects. It should also be pointed out that particles larger than 2.0µm and 5.0µm violate the assumption that $a_f >> a_p$ for *S. bivittatum* and *I. campestris* respectively. (a_f is filter radius and a_p is particle radius). The later violation disturbs the flow field near filters by distorting the area of capture envelope and could have decreased capture of such particles substantially. Sedimentation of large particles (Figure 13) also decreased filter efficiency for such particles, at low velocities. 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 zoo-, phyto-, bacterioplankton.

5.2.2 Diffusive or motile-particle deposition

The model for diffusive and/or motile-particle deposition gives an overall better prediction of the size distribution of smaller particles captured by both insects (Figures 17 - 27). Possible causes for the observed discrepancies between theoretical prediction and experimental result are due to violation of the assumption of 100% collection efficiency. It is also 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 capture by this mechanism. Also the assumption of a thin boundary layer is violated, especially at low velocities and this may have resulted in larger discrepancies between predictions and observations at such low velocities. Note that both theoretical and experimental results indicate motile-particle deposition of particles which are too large (i.e 25.0μm) to exhibit significant Brownian motion (Figures 17-27). However, this may be the result of filters of both insects which tend to sway and vibrate, especially at high velocities. Such movements i.e.

external forces (Fuch, 1964; Patlak, 1953) will cause particles to follow a random path and increase collision between such particles and filters.

In addition, the motile ability of most zoo-, phyto-, and bacterioplankton contributes to capture of these organisms by this mechanism and probably account for the abundance of such organisms in guts of filters feeders in natural environments. The above suggestion needs further investigation.

Similarity in size distribution of particles reported in this study, and field studies on particle sizes in guts of larvae of blackflies (Wotton, 1977, 1978b, 1980; Carlsson et al, 1977; Kurtak, 1979; Merrit et al. 1982) and nymphs of *Isonychia* species (Wallace and O'Hop, 1979;) suggest that these two mechanisms are operative and important in natural habitats of both insects.

5.2.3 Inertial impaction

Speilman (1977) suggested that this mechanism is not very important for liquid-borne particles because of the small Stokes number of suspended particles in liquid systems. There is a controversy in the literature on the use of bouyant density (i.e. $\rho_p - \rho_m$) to calculate Stokes number of suspended particles. (ρ_p is particle density and ρ_m is density of medium). Silvester (1983) based his calculation Stokes number on (ρ_p) alone for particles >50.0µm and [illegible] that this mechanism becomes important for particle capture by some species of net-spinning caddisflies. LaBarbera (1984) suggested that this mechanism could be important for aquatic organisms which feed on relatively large, dense particles in very high flow velocities. Ross and Craig (1980) showed theoretically that this could be true for larvae of blackflies. Thus, capture of large, dense particles is possible by this mechanism in the insects studied, but it was not analysed since insects were not fed large, dense particles. There is need for more investigation in this area of aquatic filter feeding.

5.2.4 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 should be greater than the velocity vector to enable substantial sedimentatiuon. Gravitational deposition is of no importance in particle capture in immature stages of the 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.

5.2.5 Electrostatic attraction/Surface chemical effects

The expanded form of this mechanism by Gerritsen and Porter (1982) [illegible] include surface chemical properties of particles and the collector, and the suggestion of Lewin (1984) that microorganisms (e.g. bacteria) can shuffle adhesion molecules in the flagella to enhance attachment to surfaces show that this mechanism may play a more important role in particle adhesion than previously realised in suspension feeding macroinvertebrates. When particles reach the surface of the filter by one or more of the four mechanisms they may become attached to it by this mechanism. Low *Re* values at which filters operated enhance adhesion of particles to filters due to differences in charge caused by chemical properties and hydrophobic/hydrophilic effects. This aspect of suspension feeding deserves more attention and future studies should endeavour to report adhesive characteristics of filters and particles they capture.

5.3 Structure of filters and particle capture

5.3.1 *S. bivittatum*

The structure and orientation of microtrichia on the rays of *S. bivittatum* are shown in Figures 3 and 4. Larvae of this species filter by presenting mucosubstance-coated microtrichia to currents. It has been suggested (Ross and Craig, 1980) that the mucosubstances may be negatively charged. It is also possible that these substances change the surface chemistry of microtrichia to increase and improve adhesion between them and particles captured from suspension. The slimy nature of mucus may also reduce drag on the filters, as suggested to occur in fish (Hoyt, 1975). The plane of orientation of microtrichia is parallel to flow (Figure 3). The thickness of the boundary layer (Tables 3 & 4) is such that they behaved as a solid wall with no flow between them. The boundary layer around microtrichia is 1.5μm thick at the maximum *Re* of 2.11 (real velocity equivalent of 42.0cm/sec). Any tendency to collapse is reduced by close packing and a thickened base. Parallel filter orientation and arrangement reduces drag (Spielman, 1977; Vogel, 1981), but it also reduces capture efficiency due to the surface area exposed to flow. Different arrangement and dimensions of filters may also affect the pattern of flow around them.

5.3.2 *I. campestris*

The double-row of rays on the tibia and tarsus and triple-row on the part of the femur closer to the trochanter (Figures 6 and 10) create a zone of little or no flow in the area immediately in front of the second and third rows of microtrichia (Figure 14) due to overlap of boundary layers. Scaled-up models of portion of the filters show that this zone of overlap exists up to *Re* of about 3.0. This arrangement also increases the amount of surface exposed to flow with a consequent increase in drag which may restrict nymphs to slower currents. The second and third rows of microtrichia are operating at highly reduced Re's compared to rays in the first row.

Although no mucosubstance secreting organ is known from mayflies observations from this study, Figure 10, suggests that nymphs of *I. campestris* coat their microtrichia with substances that enhance particle capture. A possible source of this substance is their saliva or other secretions in the mouth. Properties of this substance may be similar to those shown for *S. vittatum* Mall. (Ross and Craig, 1980) and those suggested for larvae of *S. bivittatum*.

5.4 Aspects of biology of particle consumption

5.4.1 Velocity and particle consumption

Larvae of *S. bivittatum* will filter feed at velocities between 5.0 - 30.0 cm/sec. Tolerance limits of velocity are known from studies on other blackflies (Grenier, 1949; Phillipson, 1956, 1957; Wu, 1931; Harrod, 1965; Carlsson, 1962; Trivellato and Decamps, 1968; Kurtak, 1973, 1978; Decamps et al. 1975; Gersabeck and Merrit, 1979; Schroder, 1983). Nymphs of *I. campestris* prefer to filter feed at velocities between 3.0 - 25.0 cm/sec. Tolerance limits of water velocity have been reported for some mayfly species (Minshall and Winger, 1968; Minshall and Minshall, 1977).

Particle capture mechanisms which are operative are enhanced over a range of velocity of 8.2 - 10.5 cm/sec for both insects. Pairwise comparision and contrast indicate that the number of particles consumed in this range of velocity is significantly ($P>0.05$) higher than at lower and higher velocities outside this range (Figures 30-37).

5.4.1.1 *S. bivittatum*

Maximum consumption of polystyrene particles by larvae of *S. bivittatum* occured at velocities lower (i.e. lower Re) than larvae usually encounter in their natural environment. Immature stages of this species are usually found in irrigation canals and large rivers in the southern Parkland and Prairie Ecoregions of Alberta. They were collected mostly on trailing vegetation and submerged twigs where velocities range from 20.0 - 30.0 cm/sec. In experiments, number of particles consumed at these velocities is about one quarter of the number consumed at velocity between 8.0 - 10.0 cm/sec.

Conditions of flow (i.e. increased boundary layer, reversal of flow) around filters at velocities less than 5.0 cm/sec would favour particle capture by the mechanisms of diffusive deposition and direct interception, but the majority of larvae were observed to detach from feeding sites in the flow tank at that velocity and spent most of the time drifting in search of more suitable currents to feed in. It has been suggested (Vogel, 1981), and demonstrated in this study (i.e. flow visualization with scaled-up models) that thick boundary layers of filters cause deflection of edible particles. At velocities above 35.0 cm/sec the 6-fold increase in drag on filters and on the whole larval body becomes more than larvae will tolerate. Larvae therefore either drifted or moved to slower velocities at the sidewall of the flow tank. Although, there is no significant difference ($P>0.05$) in the number of polystyrene particles consumed at velocities above 35.0 cm/sec (i.e. 35.0 - 47.0 cm/sec) contrast intervals between the number of particles consumed show a decreasing trend with increasing velocity. This might be due to considerable decrease in thickness of boundary layer at such high velocities. It has been suggested (Chance, 1977) that this decrease in thickness of boundary layer offers less protection to blackfly larvae.

Although larvae of some blackflies evolved to prefer faster velocities with reduced boundary layer and faster velocity gradients around their body, larvae of some species of blackflies 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. Filters of such larvae might function as gravel/sand filters thus, large particles will be captured as they sediment. Diffusive and/or motile-particle deposition and direct interception might be operative in the current generated as cephalic fans adduct and abduct. Thus, feeding may be possible at Re 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 blackfly larvae. Work is needed on larvae that inhabit still or slow flowing water.

In nature, the actual regime of velocities at which some blackfly larvae capture suspended particles is virtually unmeasurable 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 betwee[illegible]ighbouring larvae as known in fish schooling (Weihs, 1975), in sand dollars (O'Neil, 1978) and polycheates (Carey, 1983) and may produce slower velocities and enhance laminar flow through cephalic fans. The latter condition enhances efficiency of particle capture.

5.4.1.2 *I. campestris*

The velocity range of 7.5 - 10.5 cm/sec at which maximum consumption of polystyrene particles occured in the nymphs of *I. campestris* in this study is about the same as in their natural environment. Nymphs of this species were usually collected among twigs and under stones that were located at the sides and bottom of Milk river where velocities are relatively slow. Free stream velocity is seldom encounted by nymphs. Capture of suspended particles occurs at low velocities in the shelter of the boundary layer around stones and twigs. Nymphs that were released into faster flow in laboratory and field experiments were observed to swim vigorously to twigs and wooden debris. They are able to capture particles at lower velocities than larvae of *S. bivittatum* perhaps because, rapid movements of their respiratory gills accelerate water over the body to prevent the build up of oxygen defficient water around nymphs as known in *Ephemera simulans* and *Hexagenia limbata* (Ericksen, 1963). Although a large percentage (60% in 1981 and 70% in 1982) of nymphs fed at velocities between 3.5 - 5.5 cm/sec, nymphs spent most of the time swimming around in search of suitable currents to feed in, hence the low number of particles consumed. At velocities above the upper tolerance limit of 30.0 cm/sec the estimated 40-fold increase in drag on filters and on the whole nymph is more than nymphs will tolerate. To minimize the increase in drag especially on the body, nymphs moved to the boundary layer at the sidewall of the flow tank. Although there was no significant difference ($P>0.05$) in the number of polystyrene particles consumed at velocities between

35.0 - 45.0 cm/sec, contrast intervals between them show a decreasing trend with increasing velocity. This might be due to considerable decrease in thickness of boundary layer around filters at such high velocities.

[illegible]phs of *I. campestris* utilize resources in the sl[illegible] velocities of the stream than larvae of *S. bivittatum*. There is no temporal difference in the occurence of nymphs of *I. campestris* and larvae of *S. bivittatum* in Milk river. Fine particulate organic matter(FPOM) and dissolved organic matter (DOM) may not be limiting factors in freshwater environments (Wallace et al. 1977; Wallace and Merrit, 1980; Malas and Wallace, 1977) although substrate could be limiting. Based on these studies, there may not be competition for (FPOM) and (DOM) between the two insects. The pattern of distribution with the majority of nymphs of *I. campestris* in slower currents may contribute in decreasing the amount of FPOM and DOM that is lost from downstream reaches of the river and improves overall energy utilization by downstream communities as suggested by Vannote et al. (1980).

6. BIOLOGICAL IMPORTANCE

Fluid mechanical properties such as Reynolds number, boundary layer thickness, and drag that are exploited by immature stages of both insects and the adhesive characteristics of filters will determine amount and type of food consumed. Immature stages of both insects are found in nature at velocities between 10.0 - 30.0 cm/sec which enhances collision between filters and particles through the mechanisms of interception and diffusive and/or motile-particle deposition. Suspended FPOM and DOM will reach the surface of filters mostly by the latter mechanism. The motile ability of zoo-, phyto-, and bacterioplankton will increase efficiency of this mechanism in natural environments. Particles probably become attached to the surface of filters by electrostatic attraction/surface chemical properties. In addition, microorganisms (e.g. bacteria) may have the capabilty of genetic manipulation of adhesion molecules in the flagella to enhance adhesion to surfaces (Lewin, 1984). The attachment efficiency, Ea, is a function of surface properties of filters and food particle and resident time of particles near filters, thus it is enhanced by slow flows (i.e. thick boundary layers) and opposite charges and motility around filters. Isolated larvae of *S. bivittatum* and nymphs of *I. campestris* which inhabit slower sections of the river and members of aggregates which are not exposed to free stream flow will have higher Ea values (i.e. capture more particles that enter the collision envelope). Larvae of *S. bivittatum* and nymphs of *I. campestris* in faster velocities, compensate for the decrease in Ea by processing larger volumes of water per unit time whilst experiencing higher drag. Availability of large seston, particularly faecal materials to downstream communities is increased (Wotton, 1980) and this increases the probability of collision between particles and filters of such communities. Wotton (1980) showed that feeding on large particles is a more economic strategy than feeding on small particles due to the smaller volume of water processed per unit food intake. It appears that feeding on large particles is an excellent means of optimizing foraging in both insects, however, availability of large seston to filter feeders is low at both low and high velocities. At slow velocities, large particles sediment faster and are seldom available for capture. At high velocities inertia of large particles increases only if they are very dense because they are suspended in a dense medium and they tend to follow the streamline and only seldom enter the collision envelope around filters to be captured. Resident time of such large particles near filters is also short. Aggregation of filter feeders may be a behavioural adaptation for optimizing foraging.

In summary, most of the objectives of this study were achieved. Results indicate that the modifications (Spielman, 1977; Gerritsen and Porter, 1982) to the theoretical models of the Rubenstein-Koehl model are justified and necessary in liquid systems. Recent suggestions by Lewin (1984) that microorganisms (e.g. bacteria) may have the capabilty of genetically manipulating adhesion molecules in their flagella to enhance adhesion to surfaces in liquid systems reveal much about the hydro-chemical forces and genetic manipulations that are involved in adhesion of particles to surfaces. There is need for studies on filtering efficiency of filters of insects using particles with different charges after the method of LaBarbera (1978). Such studies will contribute to better understanding of nature and properties of substances that enhance particle retention by filters. Information is also needed on velocity terms and streamline patterns for filters of insects in order to calcualate absolute efficiencies.

Scaled-up models enhance flow visualization around filters and are also useful in elucidating fluid mechanical principles such as boundary layer (δ), Reynolds number (*Re*) and coefficient of drag (C_d) which are exploited in processing water for particles.

Suggestions on biological importance of filter feeding were not tested and are at best speculation based on other past studies. These suggestions are nevertheless testable and should form part of future study on biology of filter feeding.

7. FIGURES

Figures 1 to 5. Filtering structure of larvae of the blackfly.

Figure 1. Cephalic fans of *S. bivittatum*. Bar scale = 250μm.

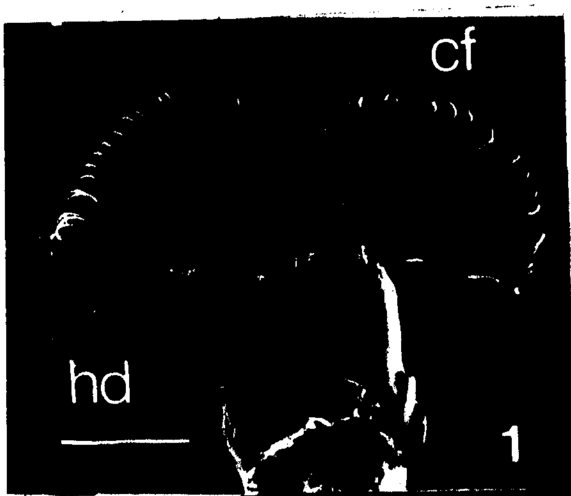
Figure 2. Scaled-up model of portion of three rays of *S. bivittatum*. Bar scale = 2 cm.

Figure 3. Frontal view showing orientation of ray and microtrichia to flow. Bar scale = 2μm.

Figure 4. Lateral view of rays of *S. bivittatum*. Bar scale = 25μm.

Figure 5. Mixture of polystyrene particles and natural faecal materials showing some diatoms from gut of *S. bivittatum*. Bar scale = 5μm.

cf, cephalic fan; di, diatom; hd, head; m, microtrichia; po, polystyrene particle; r, ray.



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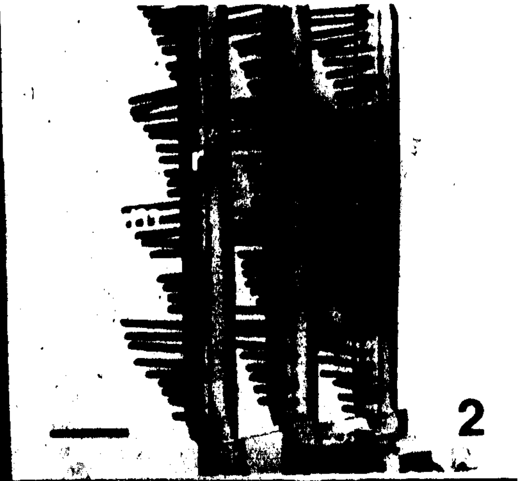

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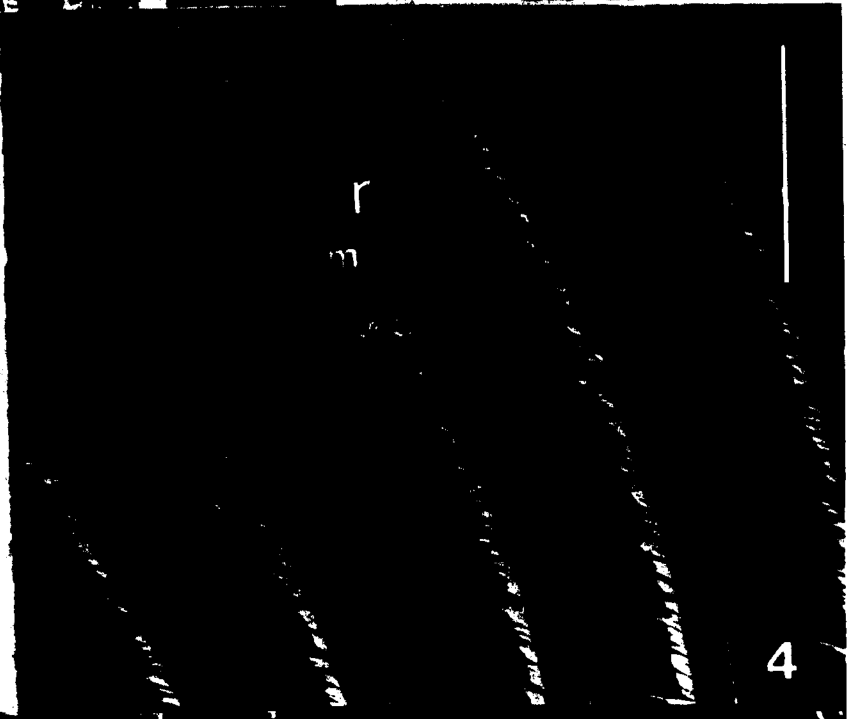

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Figures 6 to 10. Filtering structure of nymph of the mayfly.

Figure 6. First and second rows of rays on foretibia of *I. campestris*. Bar scale = 25μm.

Figure 7. Scaled-up model of portion of two rays on first and second rows of rays on foretibia of *I. campestris*. Bar scale = 2 cm.

Figure 8. Frontal view showing orientation of ray and microtrichia to flow in *I. campestris*. Bar scale = 4μm.

Figure 9. Polystyrene particles caught by secretions on microtrichia and rays of filters of *I. campestris*. Bar scale = 2μm.

Figure 10. First, second and third rows of rays on forefemur of *I. campestris*. Bar scale = 40μm.

fe, femur; fr, first row; lm, lateral microtrichia; m, microtrichia; po, polystyrene particle; r, ray; sr, second row; ti tibia; tr, third row.


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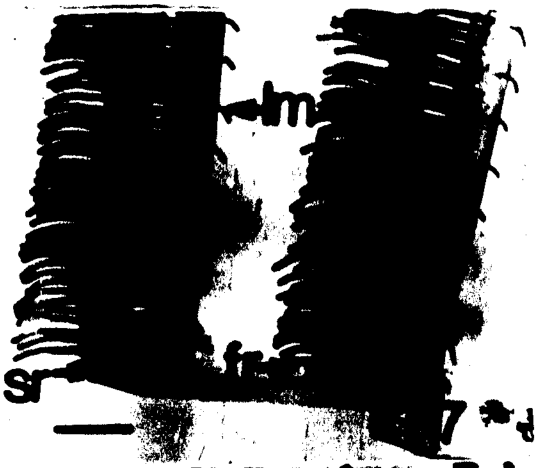
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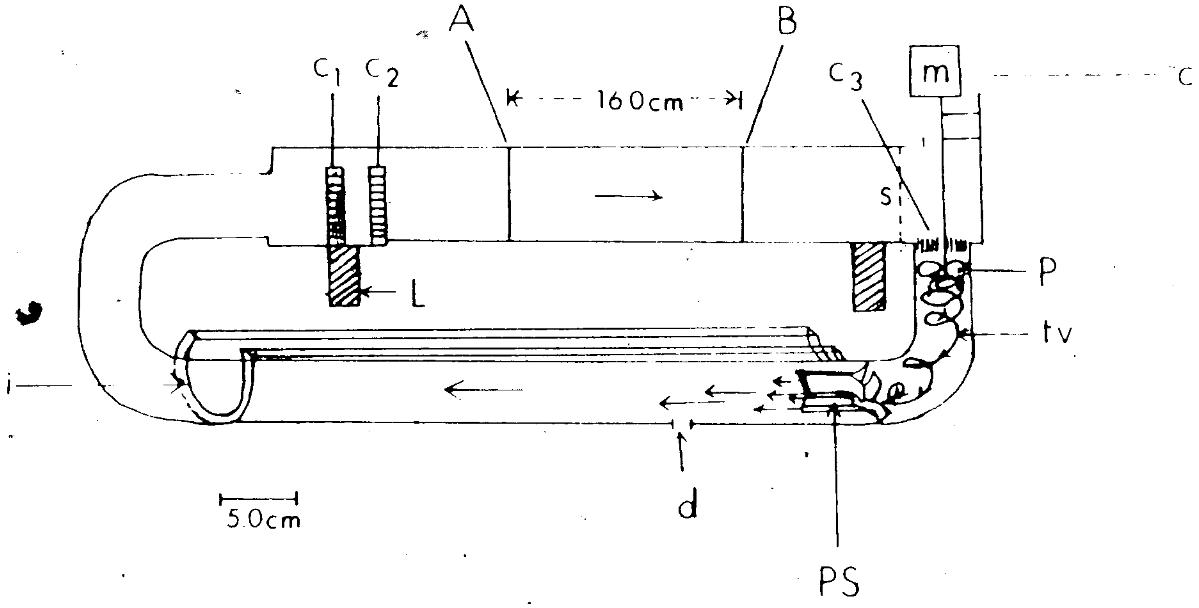

Figure 11. Flow tank. -A,B,-feeding positions; c-feedback control to motor (m); c_1, c_2, c_3-collimator; d-drain; i-bottom part of ice container. Top cover not illustrated. L-support for tank; p-propeller PS-plexiglass structure for minimizing turbulence (tv) generated by propeller; s-screen.

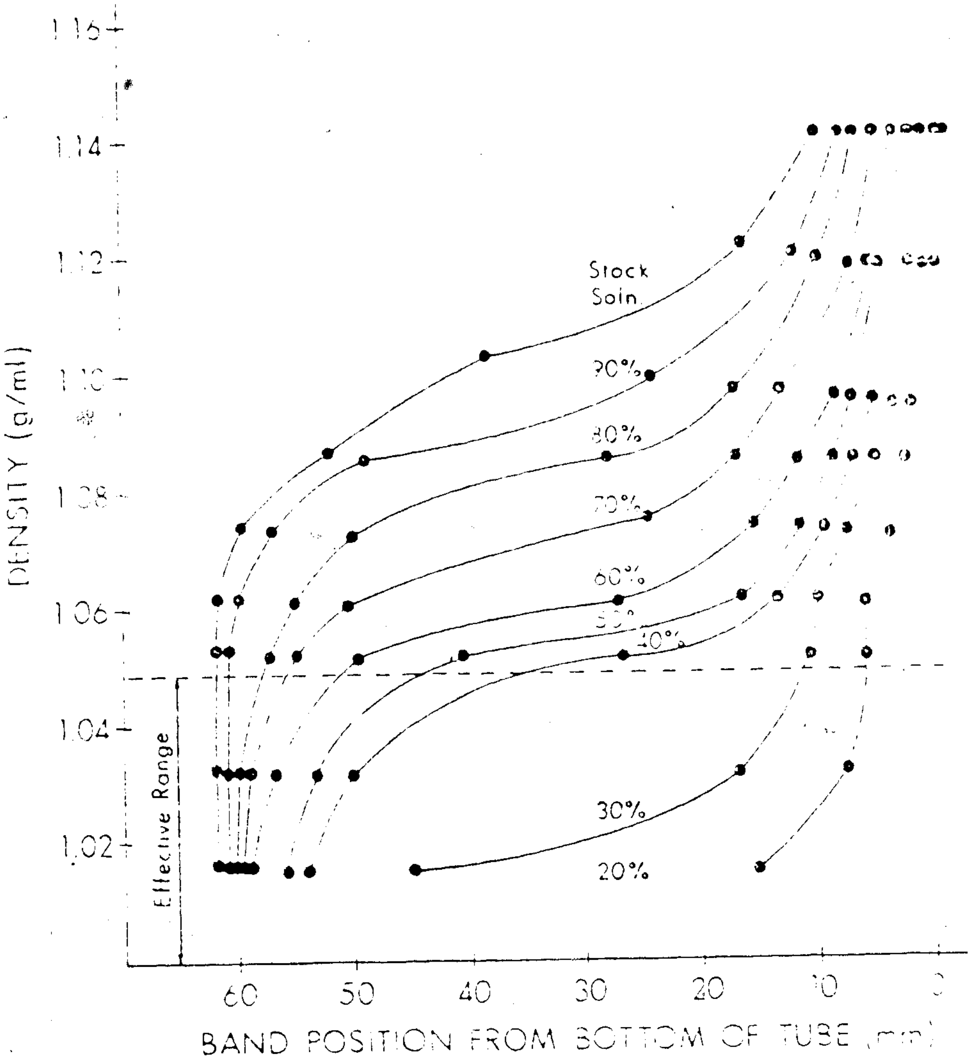

Figure 1 Density gradients position in solution of iso-osmotic Percoll in 0.15M NaCl plus 0.25 ml of 6% NaCCl.

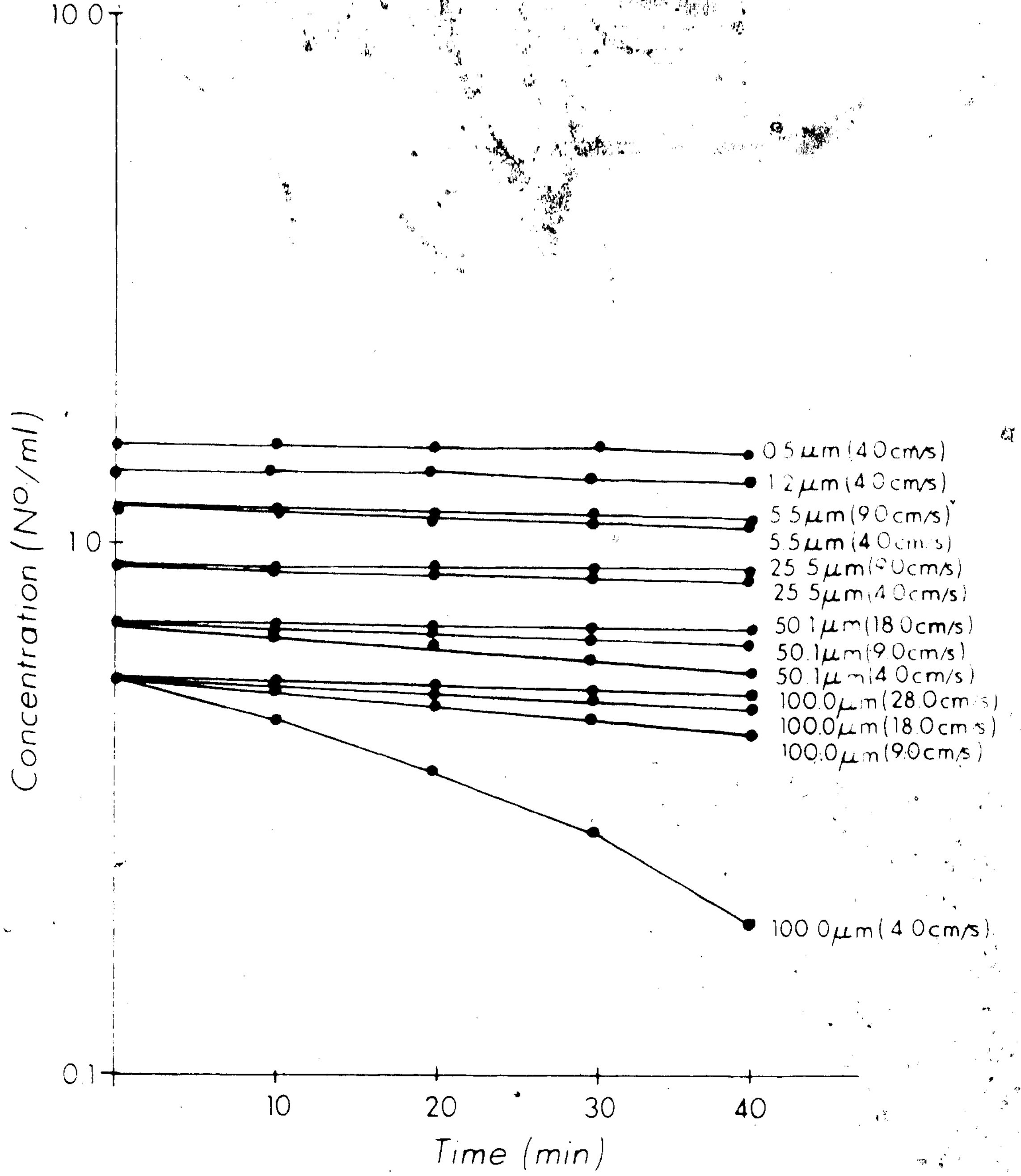

Figure 13. Concentration of different size particles of polystyrene in feeding suspension at different velocities with time.

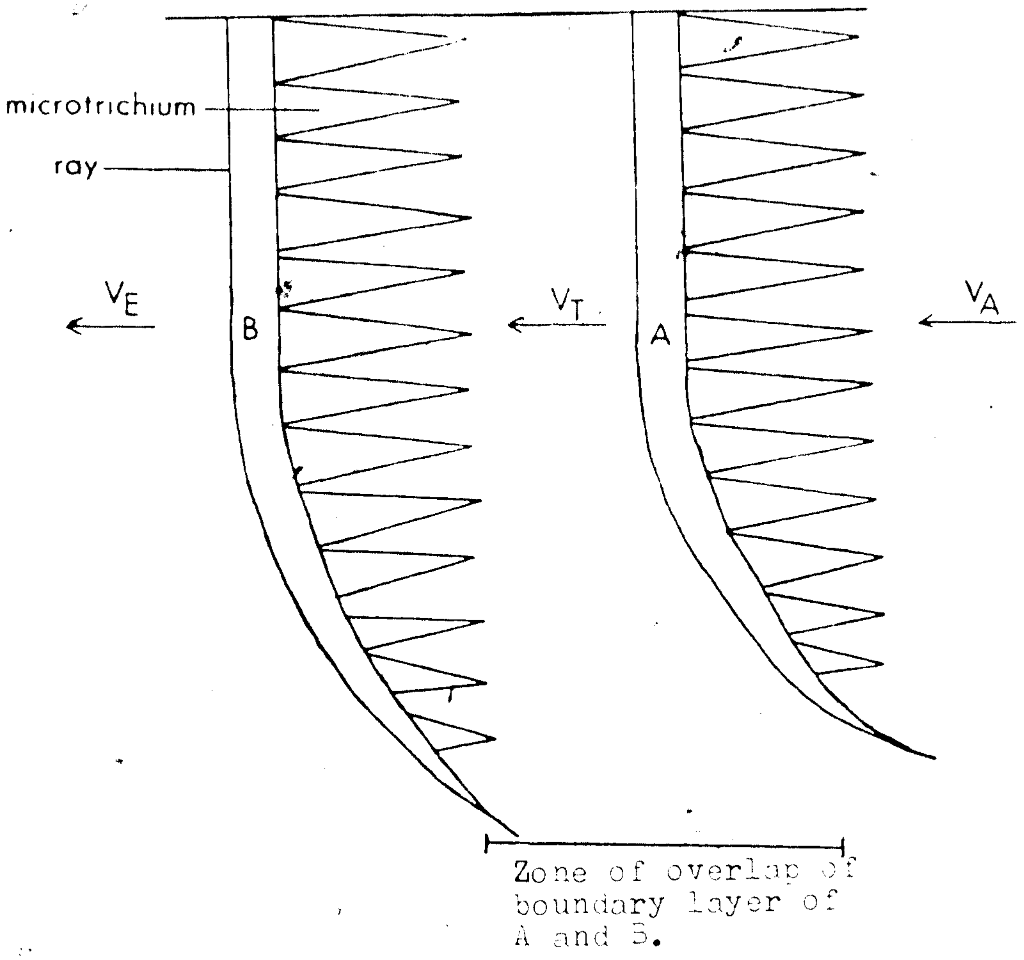

Figure 14. Diagramatic representation of orientation and arrangement of ray and microtrichia in *I. campestris* McD. V_A is velocity at the first set of microtrichia. V_T is the velocity in the zone behind A. The rate of flow in this zone is slowed and disturbed by A. There is no flow in this zone up to Re value of 2.5 due to overlap of boundary layer of adjacent rays. V_E is velocity in the zone behind ray B.

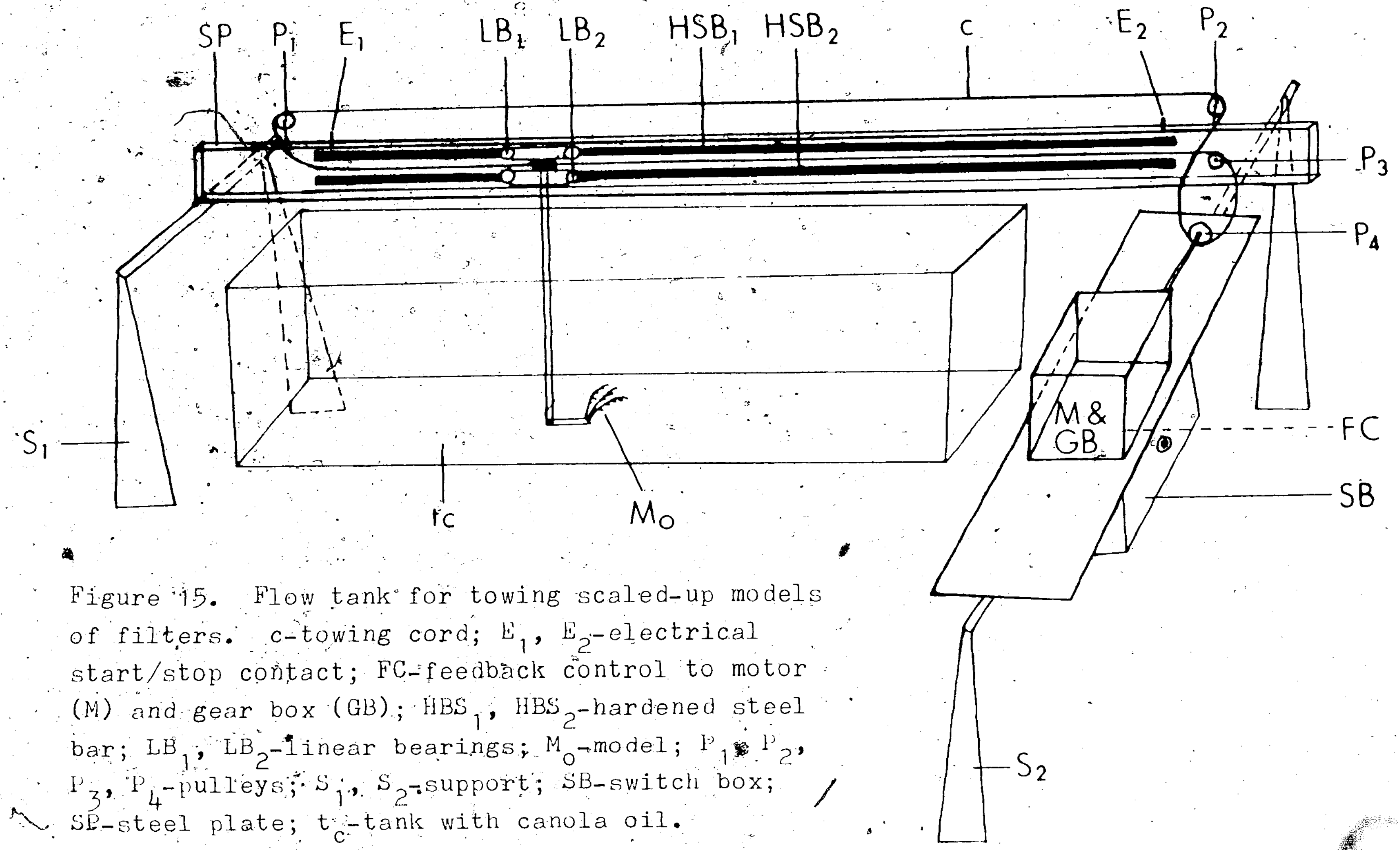

Figure 15. Flow tank for towing scaled-up models of filters. c-towing cord; E_1, E_2-electrical start/stop contact; FC-feedback control to motor (M) and gear box (GB); HBS_1, HBS_2-hardened steel bar; LB_1, LB_2-linear bearings; M_o-model; P_1, P_2, P_3, P_4-pulleys; S_1, S_2-support; SB-switch box; SP-steel plate; t_c-tank with canola oil.

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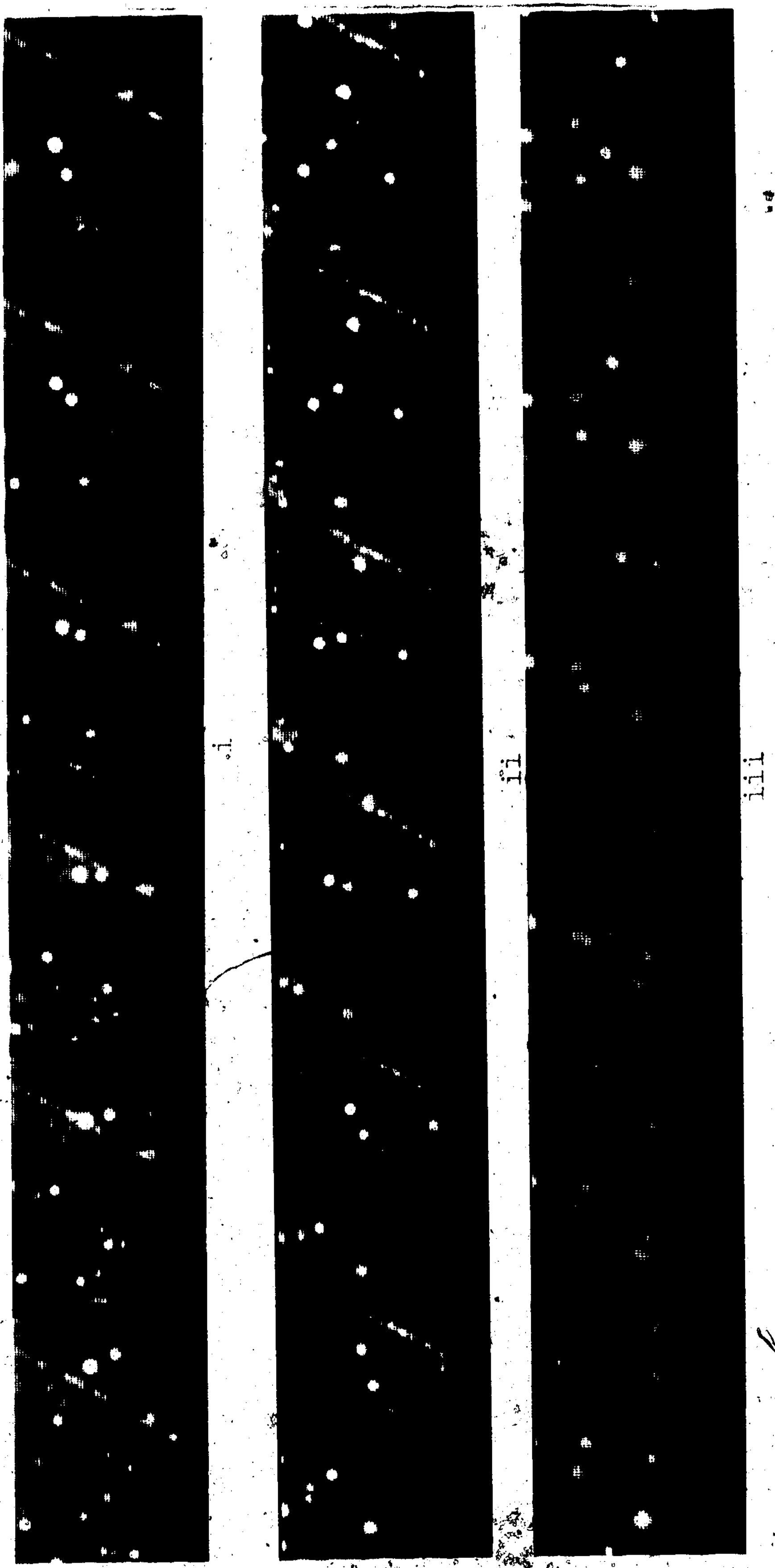
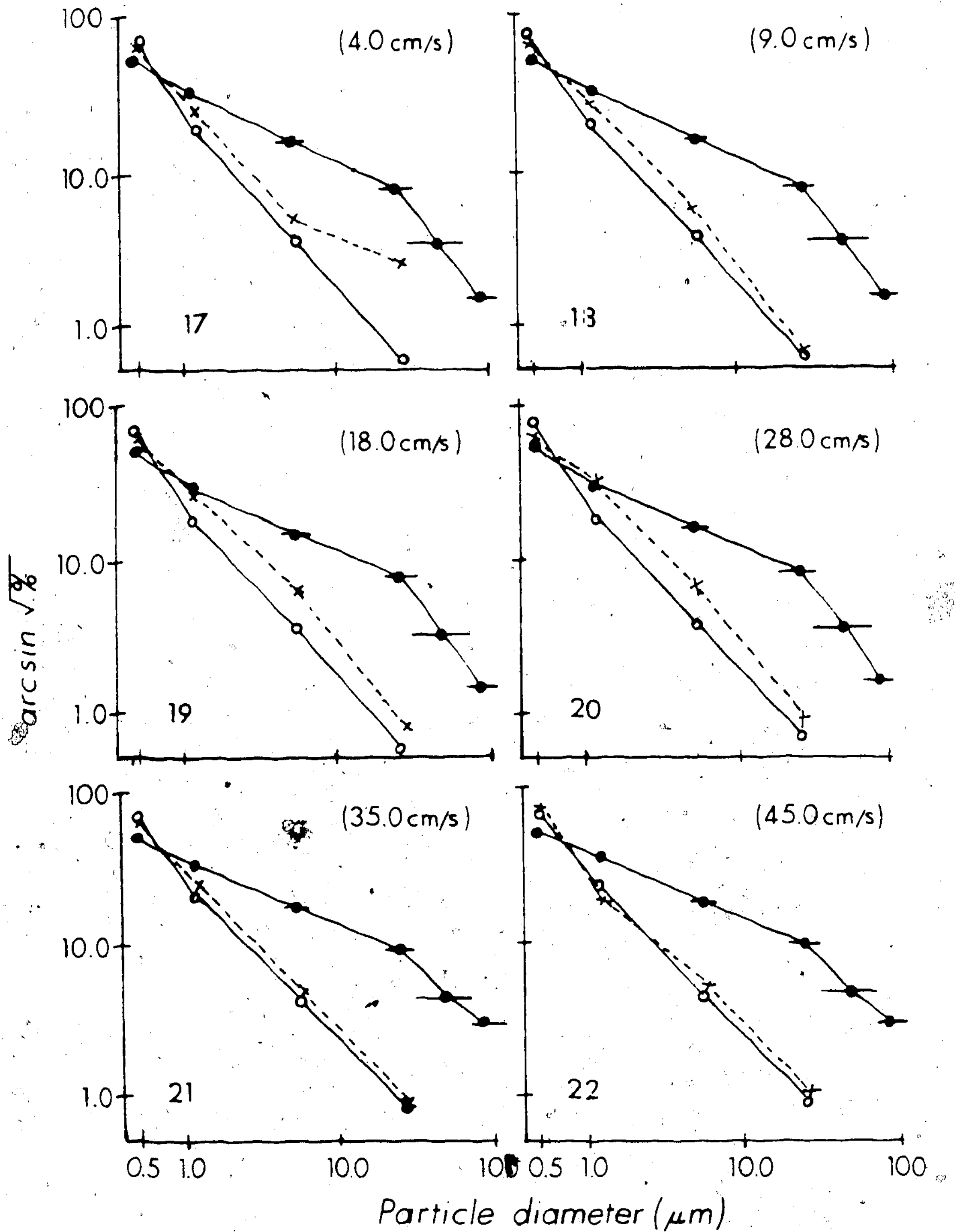
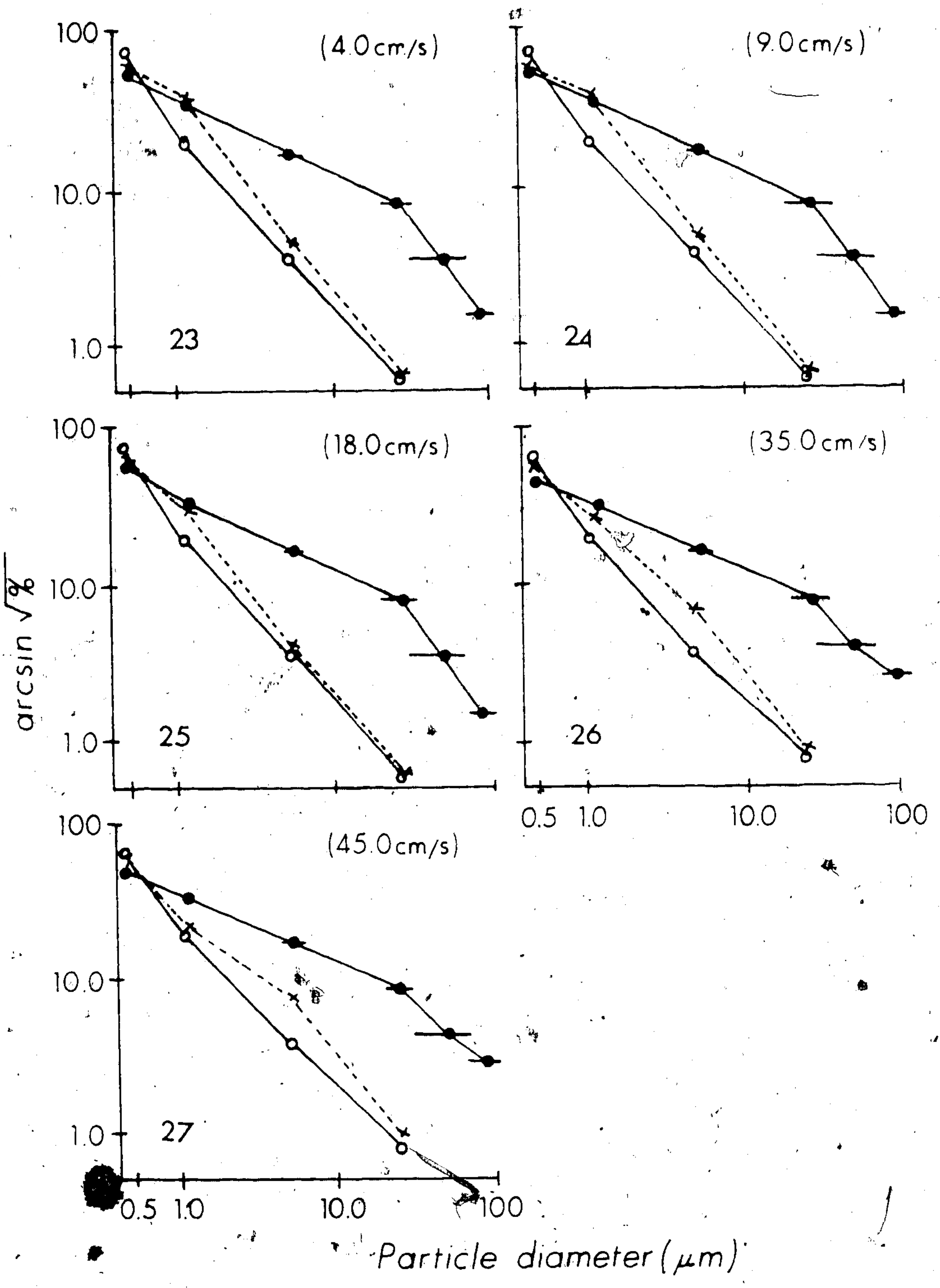


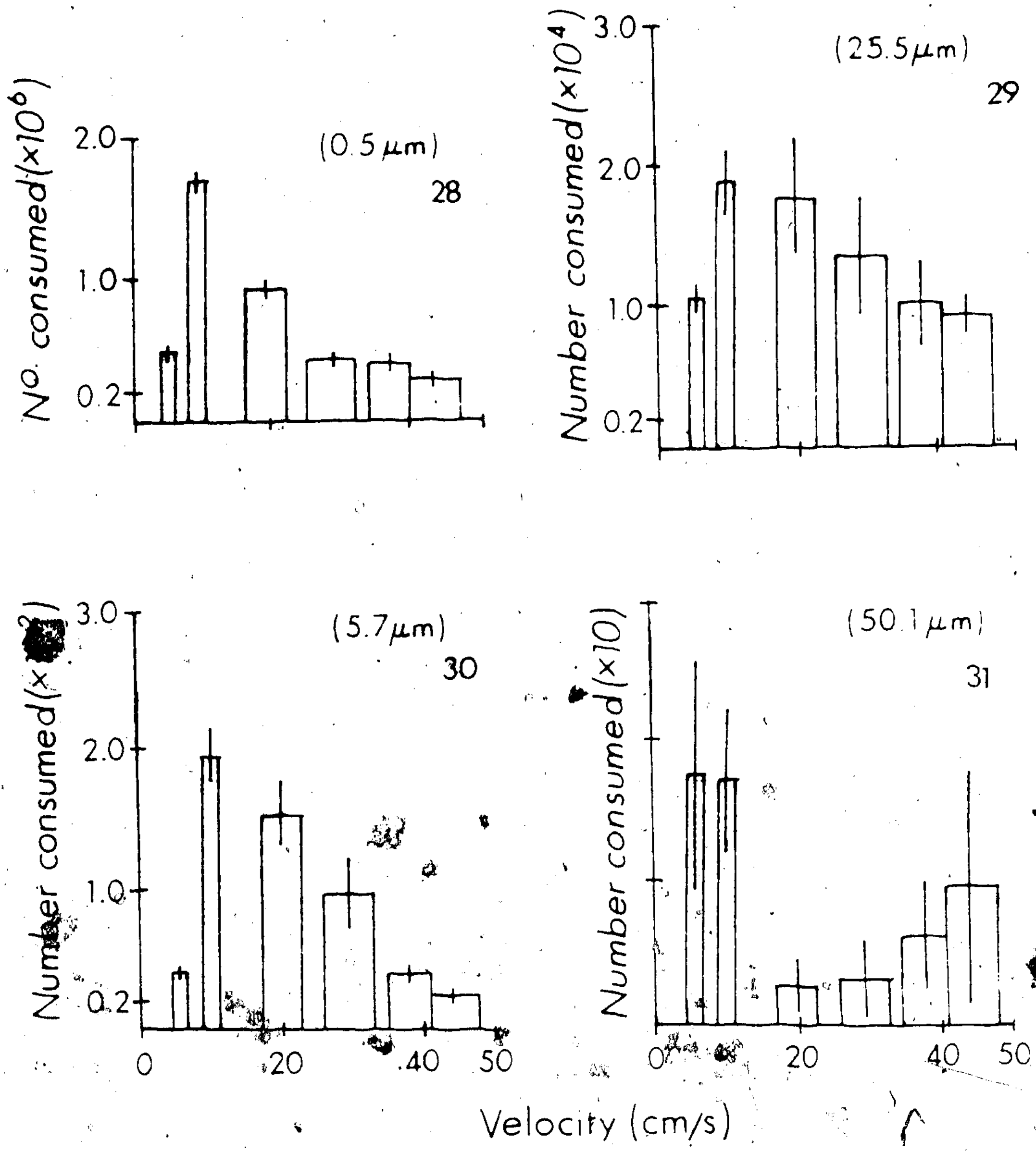
Figures 16i, ii, iii. Sequence of photographs (from TV monitor) of polystyrene particles in boundary layer around scaled-up model of filter of *Simulium bivittatum* Malloch. Arrows indicate direction of motion of particles in different velocity gradients (see Table 7). Particles 16iiie and 16iiih have adhered to the filter and travelled with it in successive frames. Bar scale = 1.0cm.



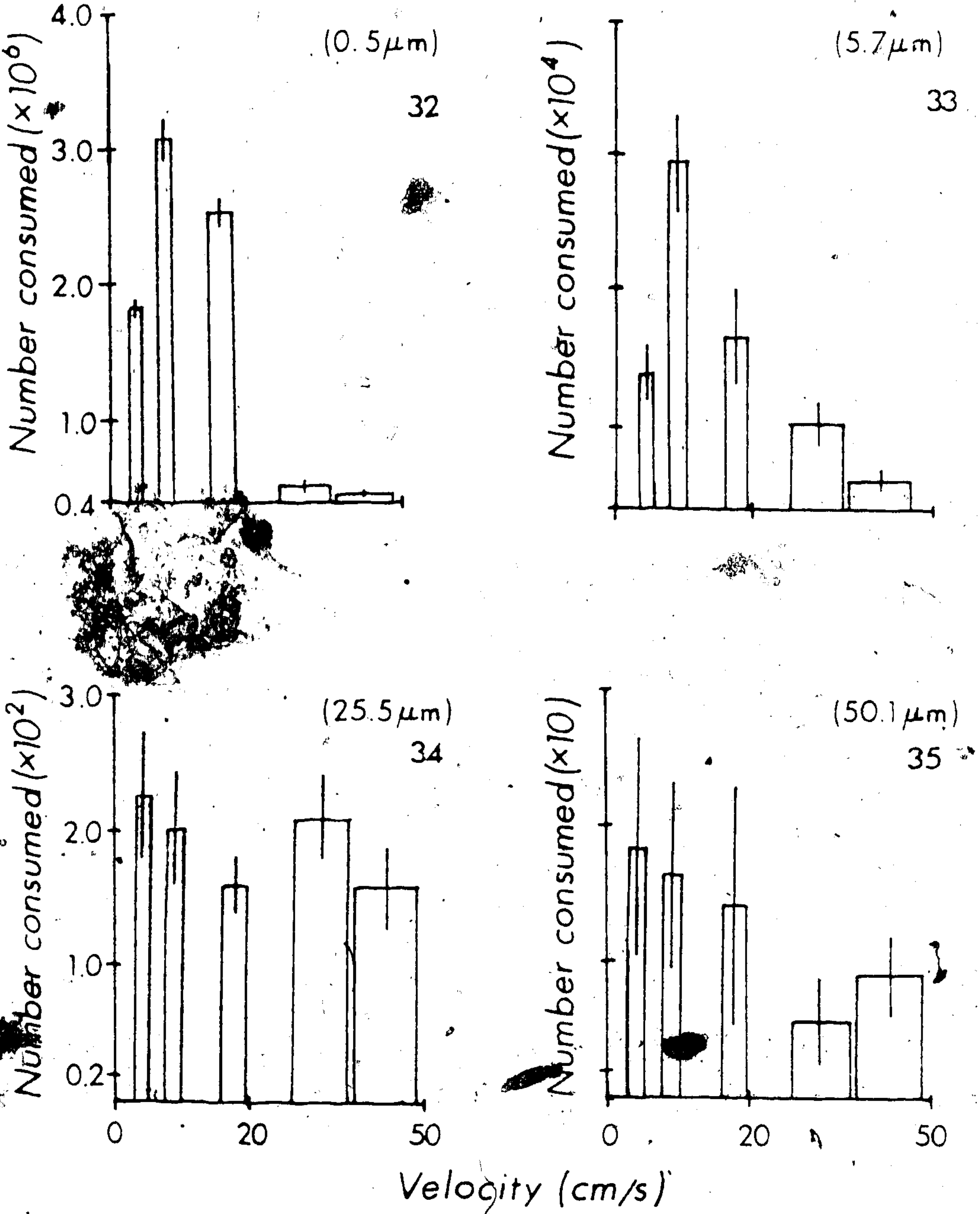
Figures 17-22. Predicted size distribution of polystyrene particles that should be caught by larvae of *S. bivittatum* based on a model of direct interception (•) and diffusive deposition (o) and observed size distribution (x) at various velocities. (——●—— —SD for particle size supplied by manufacturer).



Figures 23-27. Predicted size distribution of polystyrene particles that should be caught by nymphs of I. campestris based on a model of direct interception (●) and diffusive (o) and observed size distribution (x). (—●— —SD for particle size supplied by manufacturer).



Figures 28-31. Mean number of selected polystyrene particles sizes consumed by S. bivittatum at different velocities (1982). Feeding time = 30 minutes. Vertical bar = ± 1SD.



Figures 32-35. Mean number of selected polystyrene particles sizes consumed by I. campestris at different velocities (1982). Feeding time = 30 minutes. Vertical bar = ± 1SD.

8. TABLES

Table 1. Concentration and expected proportions of polystyrene particles, of five size classes, in feeding suspension (1981). (Number in parenthesis is ±1 SD)

Particle diameter +1SD (μm)	Concentration of particles(No/ml). ±1SD	N	Expected proportion (degrees)
0.5±0.006	4.4×10^{6} (1.6×10^{5})	5	60.23
1.2±0.016	1.0×10^{6} (9.2×10^{4})	5	25.19
5.5±1.7	1.1×10^{5} (0.6×10^{4})	5	8.12
25.7±5.8	1.0×10^{4} (1.1×10^{3})	5	2.44
90.7±17.7	2.7×10^{2} (5.6×10^{1})	5	0.40

Table 2. Concentration and expected proportions of polystyrene particles, of six size classes, in feeding suspension (1982). (Number in parenthesis is ±1 SD)

Particle diameter +1SD (μm)	Concentration of particles(No/ml). ±1SD	N	Expected proportion (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	[illegible]
5.5±1.7	4.2×10^{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

Table 3. Velocity, Reynolds number (Re), Boundary layer thickness and Coefficient of drag (Cd) for scaled-up model of portion of cephalic fans of S. vittatum Malloch (First number in parenthesis is ±1 SD; second is the number of replicates)

Velocity (cm/sec)	Reynolds Number (Re)		Thickness of boundary layer (cm)		Coefficient of drag for Ray (Cd)
	Ray	Microtrichia	Ray	Microtrichia	
0.54(0.02,5)	0.35(0.02)	0.07(0.004)	1.90(0.07)	0.76(0.02)	2.25(0.09)
0.69(0.01,3)	0.45(0.01)	0.09(0.002)	1.61(0.02)	0.67(0.01)	1.98(0.03)
0.85(0.01,3)	0.55(0.01)	0.11(0.002)	1.50(0.02)	0.60(0.008)	1.79(0.02)
1.62(0.01,3)	1.04(0.01)	0.21(0.002)	1.10(0.02)	0.44(0.004)	1.30(0.01)
2.43(0.02,3)	1.56(0.02)	0.31(0.004)	0.88(0.01)	0.36(0.004)	1.06(0.01)
3.24(0.02,2)	2.08(0.02)	0.42(0.004)	0.76(0.001)	0.31(0.002)	0.92(0.01)
4.00(0.01,2)	2.58(0.02)	0.52(0.002)	0.68(0.002)	0.28(0.001)	0.83(0.002)
5.23(0.02,2)	3.37(0.02)	0.67(0.02)	0.60(0.002)	0.24(0.001)	0.73(0.003)
5.67(0.04,3)	3.65(0.04)	0.73(0.04)	0.58(0.005)	0.23(0.01)	0.70(0.001)
6.18(0.01,2)	3.98(0.01)	0.79(0.01)	0.55(0.002)	0.23(0.002)	0.67(0.001)

Table 1. Velocity, Reynolds number (Re), Boundary layer thickness and Coefficient of drag (Cd) for cephalic fans of *S. bivittatum* Malloch (First number in parenthesis is ±1 SD; second is the number of replicates)

Velocity	Reynolds Number (Re)		Thickness of boundary layer (µm)		Coefficient of drag for Ray (Cd)
(cm/sec)	Ray	Microtrichia	Ray	Microtrichia	
3.6(0.28,8)	0.17(0.01)	0.04(0.003)	12.42(0.19)	5.00(0.26)	3.22(0.14)
8.3(0.30,8)	0.41(0.02)	0.08(0.003)	7.81(0.28)	3.54(0.10)	2.08(0.07)
9.8(0.58,9)	0.49(0.03)	0.10(0.006)	7.14(0.31)	3.16(0.13)	1.90(0.08)
17.9(2.35,18)	0.88(0.11)	0.22(0.02)	5.33(0.47)	2.12(0.11)	1.44(0.11)
31.6(2.89,14)	1.57(0.14)	0.31(0.03)	3.99(0.25)	1.79(0.13)	1.06(0.06)
42.6(2.82,12)	2.11(0.15)	0.42(0.03)	3.14(0.17)	1.54(0.07)	0.92(0.05)

Table 5. Velocity, Reynolds number (Re), Boundary layer thickness and Coefficient of drag (Cd) for first row of filtering rays of I. campestris McDunnough (First number in parenthesis is ±1 SD; second is the number of replicates)

Velocity (cm/sec)	Reynolds Number (Re)		Thickness of boundary layer (um)		Coefficient of drag for Ra. (Cd)
	Ray	Microtrichia	Ray	Microtrichia	
3.4(0.14,6)	0.27(0.02)	0.02(0.001)	15.53(0.82)	4.73(0.17)	2.56(0.13)
8.2(0.20,6)	0.66(0.02)	0.06(0.002)	9.93(0.21)	2.74(0.06)	1.64(0.04)
9.6(0.46,7)	0.77(0.05)	0.06(0.004)	9.19(0.42)	2.73(0.13)	1.52(0.08)
17.4(1.8,16)	1.39(0.20)	0.12(0.02)	6.81(0.71)	1.93(0.14)	1.13(0.12)
30.2(1.9,10)	2.42(0.22)	0.20(0.02)	5.19(0.33)	1.50(0.11)	0.85(0.06)
40.5(1.0,7)	3.24(0.11)	0.30(0.01)	4.18(0.11)	1.22(0.03)	0.74(0.02)

Table 6. Velocity, Reynolds number (Re), Boundary layer thickness and coefficient of drag (Cd) for scaled up model of portion of filtering ra[illegible] [illegible] McDunnough (First number in parenthesis is ±1 SD; second is the number of replicates)

Velocity (cm/sec)	Reynolds Number Re: Ray	Reynolds Number Re: Microchia	Thickness of boundary layer (cm): Ray	Thickness of boundary layer (cm): Microchia	Coefficient of drag for Ray (Cd)
					First row
0.54(0.02,5)	0.70(0.01)	[illegible](0.004)	2.15(0.09)	0.76(0.02)	1.58(0.06)
0.69(0.01,5)	0.89(0.01)	0.09(0.002)	1.91(0.01)	0.67(0.01)	1.40(0.01)
0.85(0.01,5)	1.09(0.02)	0.11(0.002)	1.72(0.02)	0.60(0.008)	1.27(0.02)
1.62(0.01,5)	2.08(0.02)	0.21(0.002)	1.25(0.01)	0.44(0.004)	0.92(0.01)
2.43(0.02,5)	3.13(0.04)	0.31(0.004)	1.02(0.01)	0.36(0.004)	0.75(0.[illegible])
3.24(0.02,3)	4.17(0.04)	0.42(0.004)	0.88(0.01)	0.31(0.002)	0.65(0.003)
4.00(0.01,3)	5.16(0.02)	0.52(0.002)	0.79(0.002)	0.28(0.001)	0.58(0.002)
5.23(0.02,3)	6.75(0.[illegible]1)	0.67(0.02)	0.69(0.002)	0.24(0.001)	0.51(0.002)
5.67(0.01,3)	7.32(0.06)	0.73(0.04)	0.61(0.04)	0.23(0.01)	0.49(0.003)
6.18(0.01,3)	7.97(0.02)	0.79(0.01)	0.61(0.001)	0.23(0.002)	0.47(0.003)
					Second row
0.00	0.00	0.00	very thick	very thick	0.00
0.00	0.00	0.00	very thick	very thick	0.00
0.00	0.00	0.00	very thick	very thick	0.00
0.54(0.01)	0.70(0.06)	0.07(0.01)	2.15(0.03)	0.76(0.01)	1.59(0.01)
1.21(0.02)	1.60(0.01)	0.16(0.02)	1.12(0.02)	0.52(0.02)	1.05(0.02)
1.67(0.01)	2.15(0.02)	0.22(0.01)	1.23(0.01)	0.43(0.04)	0.91(0.004)
2.86(0.01)	3.69(0.02)	0.37(0.01)	0.91(0.002)	0.33(0.01)	0.69(0.02)
4.07(0.002)	5.25(0.01)	0.53(0.02)	0.79(0.01)	0.27(0.02)	0.58(0.002)
4.41(0.01)	5.69(0.02)	0.57(0.02)	[illegible]	0.26(0.02)	0.56(0.02)
5.30(0.02)	6.84(0.01)	0.68(0.01)	[illegible]	0.24(0.02)	0.51(0.02)

Table 7. Velocity of polystyrene particles in different gradients of velocity in boundary layer around scaled-up model of S. bivittatum

Figure	Velocity (cm/sec) ($\times 10^{-2}$)	Distance from filter (cm)
10ia	5.4	0.40
10ib	9.1	[illegible]
10iid	7.2	0.51
10iic	10.0	0.85
10iiie	0	0
10iii[illegible]	12.6	1.03
10iiig	15.3	1.28
10iiih	0	0

Table 10.8 Analysis of variance testing the effect of velocity on the number of [illegible] 5 [illegible] particles consumed by [illegible] (1981)

Particle Diameter (µm)	Velocity (cm/s) (3.1 – 20.0)*			(2[illegible] – 47.[illegible])*		ANOVA F
	Mean Number Consumed					
[illegible]	3.27	[illegible].69	1.91	[illegible]	[illegible].46	(>0.05)
[illegible]	1.44	.88	[illegible]	[illegible]	[illegible]	(>0.05)
[illegible]	3.12	[illegible]	[illegible]	[illegible]	.58	(>0.05)

Table [illegible] Analysis of variance testing the effect of velocity on the number [illegible] particles consumed by [illegible] (1981)

Particle Diameter (µm)	Velocity (cm/s) (3.1 – 20.0)*			(2[illegible] – 47.[illegible])*		ANOVA F
	Mean Number Consumed					
[illegible]	1.[illegible]	[illegible].13	2.68	[illegible]	[illegible]	(>0.05)
[illegible]	1.65	[illegible]	[illegible]	[illegible]	[illegible]	(>0.05)
[illegible]	1.21	.56	0.5[illegible]	[illegible]	[illegible]	(>0.05)

* Refer [illegible] appendix [illegible] 1

Table 10. Analysis of variance testing the effect of velocity on the number of 0.5 - 5.7 (um) particles consumed by S. *bivittatum* (1982)

Particle Diameter (um)	Velocity (cm/sec) (4.0 - 22.0)*			(25.0 - 47.0)*			ANOVA P
	Mean Number Consumed						
0.5±0.006	1.73	[illegible].98	0.51	[illegible]16	[illegible]14	[illegible].32	(>0.05)
1.24±0.016	1.61	3.0[illegible]	1.87*	1.27*	1.[illegible]	0.36	(>0.05)
5.7±1.5	2.01	1.57	0.79*	[illegible]11*	[illegible]12	[illegible].26	(>0.05)

Table 11. Analysis of variance testing the effect of velocity on the number of 0.5 - 5.7 (um) particles consumed by S. *bivittatum* (1981)

Particle Diameter (um)	Velocity (cm/sec) (4.0 - 22.0)*			(25.0 - 47.0)*			ANOVA P
	Mean Number Consumed						
0.5±0.006	2.20	1.38	0.67	[illegible].66	[illegible].57	[illegible].37	(>0.05)
1.24±0.016	6.33	4.2[illegible]	2.33	2.20	1.55	0.84	(>0.05)
5.7±1.5	1.30	3.18	1.11*	1.[illegible]2*	[illegible].90*	0.7[illegible]*	(>0.05)

* Refer to appendix 1

Table 12. Calculated drag for models of portion of the filtering structures of *I. campestris* McDunnough and *S. bivittatum* Malloch

Insect	Range of velocity (cm/sec)		Location of filtering structure	Drag
	Uo	U1		$(\times 10^{-\text{[illegible]}})$ N
I. campestris	0.80 - 0.90	0.40 - 0.45	Foreleg	9.20
I. campestris	6.00 - 6.20	4.00 - 4.65	Foreleg	380.10
S. bivittatum	0.80 - 0.85	0.30 - 0.35	Head	3.50
S. bivittatum	6.00 - 6.20	5.00 - 6.00	Head	22.0

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10. APPENDIX [illegible]

[illegible]

[illegible]	Number [illegible]				
[illegible]	[illegible] (0.6 × 10[illegible])	[illegible]	[illegible]	[illegible]	[illegible] (1.92)
[illegible]	[illegible] × 10[illegible] ([illegible] × 10[illegible])	[illegible]	[illegible]	3.10 × 10[illegible] (8.1 × 10[illegible])	[illegible]50 ([illegible])
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible] × 10 ([illegible] × 10[illegible])	[illegible]	[illegible]	[illegible] × 10[illegible] (9.1 × 10[illegible])	2.20 (1.78)
[illegible]	[illegible] × 10[illegible] ([illegible] 72 × 10[illegible])	[illegible]	[illegible]	[illegible] × 10[illegible] ([illegible] × 10[illegible])	[illegible]

Table 14 Mean number of polystyrene particles consumed by *I. campestris* McDunnough at different velocities (1982). (Number in parenthesis is ±1 SD)

Range of velocity (cm/sec)	N	Diameter of particle ±1 SD (um)					
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	50.1±20.1	90.7±17.7
		Number consumed					
3.4 - 5.5	7	1.94×10^6 (0.72×10^6)	0.76×10^5 (0.58×10^5)	1.44×10^3 (2.35×10^3)	2.27×10^2 (5.20×10^2)	1.86×10^1 (0.76×10^1)	0.71 (0.66)
8.0 - 10.5	9	3.27×10^6 (1.36×10^6)	1.44×10^5 (1.33×10^5)	3.12×10^3 (3.47×10^3)	2.03×10^2 (1.00×10^2)	1.67×10^1 (0.68×10^1)	0.55 (0.52)
16.5 - 20.0	8	2.69×10^6 (1.30×10^6)	0.88×10^5 (1.05×10^5)	1.73×10^3 (3.31×10^3)	1.61×10^2 (2.00×10^2)	1.44×10^1 (0.84×10^1)	1.50 (1.26)
27.0 - 35.0	7	0.51×10^6 (0.38×10^6)	0.12×10^5 (0.13×10^5)	1.04×10^3 (1.81×10^3)	2.11×10^2 (3.83×10^2)	0.57×10^1 (0.26×10^1)	0 (0)
36.0 - 45.0	5	0.44×10^6 (0.15×10^6)	0.07×10^5 (0.06×10^5)	0.58×10^3 (0.68×10^3)	1.60×10^2 (2.98×10^2)	0.90×10^1 (0.29×10^1)	2.00 (1.79)

Table 15 Mean number of polystyrene particles consumed by S. bivittatum Malloch at different velocities (1981) (Number in parenthesis is ±1 SD)

Range of velocity (cm sec)	N	Diameter of particle ±1 SD (um)				
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	90.7±17.7
		Number consumed				
1.0 - 5.8	1	0.67 × 10^4 (0.35×10^4)	2.33 × [illegible] (3.21×[illegible])	0.71 × [illegible] (1.13×[illegible])	1.95 × 10 (2.97 × 10)	0 (0)
8.3 - 10.5	8	2.20 × 10^4 (1.81×10^4)	6.33 × [illegible] (5.22×[illegible])	1.[illegible] × [illegible] ([illegible])	2.18 × 10 (3.85×10)	0 (0)
16.5 - 22.0	10	1.38 × 10^4 (0.85×10^4)	4.22 × [illegible] (4.48×[illegible])	1.27 × 10^4 (0.68×[illegible])	2.60 × 10 ([illegible]×10)	1.00 (0.94)
25.0 - 32.0	2	0.66 × 10^4 (0.64×10^4)	2.20 × [illegible] (4.24×[illegible])	1.[illegible] × [illegible] ([illegible].57×[illegible])	1.50 × [illegible] (5.66×10)	0 (0)
31.0 - 40.0	7	0.57 × 10^4 (0.75×10^4)	1.55 × 10 (2.43×10^4)	1.11 × 10^4 (1.10×10)	1.73 × [illegible] (3.72×10	0 (0)
40.0 - 50.0	1	0.37 × 10^4 (0.84×10^4)	0.84 × [illegible] (1.61×[illegible])	0.90 × [illegible] (5.52×[illegible]	2.35 × [illegible] ([illegible]×10)	0 (0)

Table 16. Mean number of polystyrene particles consumed by *S. vittatum* Malloch at different velocities (1982). (Number in parenthesis is ±1 SD)

Range of velocity (cm/sec)	N	Diameter of particle ±1 SD (µm)					
		0.5±0.006	1.2±0.016	[illegible]	25.7±5.8	50.1±20.1	90.7±17.7
		Number consumed					
4.0 - 6.0	5	0.51 × 10 (0.44×10)	1.27 × 10 (1.08×10^4)	0.4[illegible] × 10 (0.[illegible]×10)	1.07 × 10 (1.82×10)	1.80 × 10 (0.82×10)	0 (0)
8.0 - 10.5	9	1.73 × 10 (0.74×10)	4.61 × 10 (3.49×10^4)	2.[illegible] [illegible]	[illegible].94 × 10 ([illegible].84×10)	[illegible] × 10 (0.65×10)	1.11 (0.69)
16.5 - 22.0	9	0.98 × 10 (0.48×10)	3.09 × 10 (3.68×10^4)	[illegible] [illegible]	1.79 × 10 (4.15×10)	0.28 × 10 (0.18×10)	0 (0)
25.0 - 32.0	3	0.16 × 10 (0.23×10)	1.87 × 10 (0.72×10^4)	0.79 × 10 (2.19×10)	1.37 × 10 (3.84×10)	0.33 × 10 (0.27×10)	0 (0)
34.0 - 40.0	8	0.11 × 10 (0.15×10)	1.02 × 10 (1.08×10^4)	0.12 × 10 (0.16×10)	1.03 × 10 (2.77×10)	0.63 × 10 (0.39×10)	0.25 (0.23)
40.0 - 50.0	4	0.32 × 10 (0.14×10)	0.36 × 10 (0.25×10)	0.26 × 10 (0.37×10)	0.94 × 10 (1.37×10)	(1.00×10) (0.86×10)	0 (0)

11 APPENDIX 2

Table 17 Concentration (No/ml) of polystyrene particles available to insects after 10 minutes interval (Number in parenthesis is ±1SD)

Particle diameter (µm)±1 SD	Velocity (cm/sec)			
	[illegible]	8.0	18.0	28.0
	Particle concentration (No/ml)			
[illegible]	4.36x10[illegible] (0.23x10[illegible])	1.31x10[illegible] (0.18x10[illegible])	[illegible] [illegible]	[illegible] (0.23x10[illegible])
[illegible]	[illegible] (0.08x1[illegible])	1.06x10[illegible] (0.12x10[illegible])	[illegible] [illegible]	[illegible] [illegible]
[illegible]	[illegible] [illegible]	1.08x10[illegible] (0.13x10[illegible])	[illegible] [illegible]	[illegible] [illegible]
[illegible]	[illegible] [illegible]	9.67x10[illegible] (0.58x10[illegible])	[illegible] [illegible]	4.75x10[illegible] (0.56x10[illegible])
[illegible]	[illegible] [illegible]	[illegible] [illegible]	[illegible] [illegible]	[illegible] (0.26x10[illegible])
[illegible]	[illegible] [illegible]	[illegible] [illegible]	[illegible] [illegible]	[illegible] [illegible]

Table 18. Concentration (No/ml) of polystyrene particles available to insects after 20 minutes interval (Number in parenthesis is ±1SD)

Particle diameter (um)±1 SD	Velocity (cm/sec)			
	4.0	9.0	18.0	28.0
	Particle concentration (No/ml)			
0.5±0.006	4.28×10[illegible] (0.21×10[illegible])	4.34×10[illegible] (0.19×10[illegible])	1.[illegible]6×10[illegible] ([illegible]18×10[illegible])	4.28×10[illegible] (0.18×10[illegible])
1.2±0.106	9.46×10[illegible] (0.23×10[illegible])	9.65×10[illegible] (0.48×10[illegible])	[illegible]1×10[illegible] ([illegible]×10[illegible])	1.08×10[illegible] (0.12×10[illegible])
5.5±1.5	1.00×10[illegible] (0.10×10[illegible])	1.00×10[illegible] (0.11×10[illegible])	[illegible]1×10[illegible] ([illegible]2×10[illegible])	1.[illegible]5×10[illegible] (0.12×10[illegible])
25.7±5.8	8.52×10[illegible] (0.66×10[illegible])	9.05×10[illegible] (0.22×10[illegible])	[illegible]6[illegible]×10[illegible] ([illegible]0×10[illegible])	9.73×10[illegible] (0.60×10[illegible])
50.1±20.1	9.72×10[illegible] (0.60×10[illegible])	1.05×10[illegible] (0.10×10[illegible])	[illegible].25×10[illegible] ([illegible]18×10[illegible])	1.29×10[illegible] (0.23×10[illegible])
90.1±17.7	4.33×10[illegible] (0.28×10[illegible])	1.49×10[illegible] (0.37×10[illegible])	[illegible].98×10[illegible] ([illegible]36×10[illegible])	2.28×10[illegible] (0.29×10[illegible])

Table 19. Concentration (No/ml) of pol[illegible] particles available [illegible] after [illegible] interval (Number in parenthesis is ±1SD)

Particle diameter (um)±1 SD	Velocity, [illegible] 1.0	9.0	[illegible]	28.[illegible]
	Particle concentration [illegible]			
0.5±0.06	1.11×10[illegible] (0.17×10[illegible])	4.29×10[illegible] (0.19×10[illegible])	[illegible]	[illegible]
1.2±0.06	8.99×10[illegible] (0.56×10[illegible])	9.46×10[illegible] (0.33×10[illegible])	[illegible]	[illegible]
5.5±1.6	9.29×10[illegible] (0.28×10[illegible])	9.68×10[illegible] (0.69×10[illegible])	[illegible]	[illegible]
25.7±6.8	7.33×10[illegible] (0.44×10[illegible])	8.6[illegible]×10[illegible] (0.87×10[illegible])	[illegible]	[illegible]
50.1±20.1	6.85×10[illegible] (0.67×10[illegible])	9.16×10[illegible] (0.23×10[illegible])	[illegible]	[illegible]
90.1±17.[illegible]	1.71×10[illegible] (0.63×10[illegible])	3.28×10[illegible] (0.23×10[illegible])	[illegible]	[illegible]

Table 2[illegible]. Concentration (No/ml) of polystyrene particles available [illegible] after [illegible] minutes interval (Number in parenthesis is ±1SD)

Particle diameter (um)±1 SD	Velocity, [illegible]			
	4.0	9.[illegible]	18.[illegible]	28.[illegible]
	Particle concentration ([illegible])			
0.5±0.0[illegible]6	4.03×10[illegible] (0.14×10[illegible])	1.33×10[illegible] (0.26×10[illegible])	[illegible] ([illegible])	4.30×10[illegible] (0.25×10[illegible])
1.2±0.1[illegible]6	8.56×10[illegible] (0.12×10[illegible])	8.16×10[illegible] (0.39×10[illegible])	[illegible] ([illegible])	[illegible] ([illegible])
5.5±1.5	8.58×10[illegible] (0.10×10[illegible])	8.16×10[illegible] (0.[illegible])	[illegible] ([illegible])	[illegible] ([illegible])
25.7±5.8	6.37×10[illegible] (0.46×10[illegible])	8.18×10[illegible] (0.26×10[illegible])	[illegible] ([illegible]28×10[illegible])	9.68×10[illegible] (0.49×10[illegible])
50.1±20.1	4.78×10[illegible] (0.56×10[illegible])	7.96×10[illegible] (0.73×10[illegible])	[illegible] ([illegible])	[illegible] ([illegible]24×10[illegible])
90.1±17.7	[illegible].89 (0.69)	1.16×10[illegible] (0.19×10[illegible])	[illegible] ([illegible])	[illegible] ([illegible])

12. APPENDIX 3.

Table 21. Number of polystyrene particles, of five size classes, consumed by S. *bivittatum* Malloch (1981).

Larva number	Velocity (cm/sec)	Diameter of particles ±1 SD(μm)				
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	90.7±17.7
		Number consumed				
30 n	4.2	5.8×10^5	3.4×10^4	1.1×10^4	240	0
30 o	5.1	7.8×10^5	2.1×10^4	5.6×10	260	0
30 q	5.1	6.6×10^5	1.7×10^4	6.4×10^4	170	0
30 m	5.8	5.7×10^5	2.1×10^4	5.5×10^4	110	0

Table 22. Number of polystyrene particles, of five size classes, consumed by S. *bivittatum* Malloch (1981).

Larva number	Velocity (cm/sec)	Diameter of particles ±1 SD(μm)				
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	90.7±17.7
		Number consumed				
29 u	8.2	2.5×10^5	6.2×10^4	1.9×10^4	120	0
29 q	9.4	1.9×10^5	5.3×10^4	5.2×10^4	260	0
29 l	10.4	1.9×10^5	9.1×10^4	1.4×10^4	150	0
29 t	9.1	2.5×10^5	5.6×10^4	5.9×10^4	400	0
29 n	8.5	2.1×10^5	6.6×10^4	[illegible]	80	0
29 m	10.4	2.8×10^5	6.8×10^4	3.1×10^4	200	0
29 o	8.2	2.8×10^5	7.3×10^4	5.2×10^4	160	0
29 k	10.1	1.2×10^5	3.7×10^4	1.7×10^4	370	0

Table 23. Number of polystyrene particles, of five size classes, consumed by *S. bivittatum* Malloch (1981).

Larva number	Velocity (cm/sec)	Diameter of particles ±1 SD(um)				
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	90.7±17.7
		Number consumed				
27 x	19.5	1.4×10^5	2.9×10^5	4.3×10^4	540	10
27 v	19.5	1.1×10^6	6.4×10^5	3.3×10^4	70	0
27 r	19.5	1.4×10^6	4.3×10^5	2.5×10^4	430	0
27 m	16.5	1.6×10^5	4.8×10^5	4.4×10^4	50	0
27 n	16.5	1.1×10^5	3.9×10^5	2.8×10^4	130	0
27 q	22.0	9.4×10^6	2.4×10^5	3.2×10^4	210	0
27 y	16.5	1.8×10^6	6.4×10^5	5.6×10^4	70	0
27 o	16.5	1.2×10^6	2.9×10^5	1.7×10^4	90	0
27 u	19.5	1.2×10^6	2.8×10^5	9.8×10^4	820	0
27 l	16.5	1.8×10^5	5.4×10^5	5.1×10^4	190	0

Table 24. Number of polystyrene particles, of five size classes, consumed by *S. bivittatum* Malloch (1981).

Larva number	Velocity (cm/sec)	0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	90.7±17.7
		Number consumed				
28 r	26.0	5.7×10^{5}	1.6×10^{5}	9.4×10^{4}	70	0
28 q	36.0	8.3×10^{5}	2.2×10^{5}	3.3×10^{4}	90	0
28 u	34.0	8.6×10^{5}	2.6×10^{5}	1.3×10^{4}	370	0
28 n	29.0	7.5×10^{5}	2.8×10^{5}	1.1×10^{4}	230	0
28 v	39.0	3.4×10^{5}	7.2×10^{5}	2.9×10^{4}	100	0

Table 25. Number of polystyrene particles, of five size classes, consumed by *S. bivittatum* Malloch (1981).

Larva number	Velocity (cm/sec)	0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	90.7±17.7
		Number consumed				
17 f	34.5	5.7×10^{5}	1.9×10^{5}	3.4×10^{4}	250	0
17 g	41.5	6.4×10^{5}	1.3×10^{5}	2.[illegible]$\times10^{4}$	610	0
17 c	40.0	5.9×10^{5}	1.3×10^{5}	5.3×10^{3}	80	0
17 a	40.0	3.4×10^{5}	1.0×10^{5}	1.7×10^{3}	190	0

Table 26. Number of polystyrene particles, of five size classes, consumed by *S. bivittatum* Malloch (1981).

Larva number	Velocity (cm/sec)	Diameter of particles ±1 SD(um)				
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	90.7±17.7
		Number consumed				
18 i	40.0	4.3×10⁵	1.1×10⁵	1.8×10⁴	130	0
18 j	45.0	3.8×10⁵	9.9×10⁴	2.9×10³	90	0
18 g	45.0	2.5×10⁵	5.2×10⁴	4.3×10³	70	0
18 h	47.0	2.1×10⁵	5.6×10⁴	1.7×10³	170	0

Table 27. Number of polystyrene particles, of five size classes, consumed by *I. campestris* McDunnough (1981)

Nymph number	Velocity (cm/sec)	Diam[illegible]es ±1 SD(um)				
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	90.7±17.7
		Number consumed				
30 d	5.4	2.7×10⁶	8.6×10⁵	4.3×10⁴	120	0
30 e	5.1	2.8×10⁶	1.0×10⁶	5.5×10⁵	500	0
30 f	4.8	2.9×10⁶	1.6×10⁶	5.8×10⁴	410	10
30 g	4.2	2.6×10⁶	1.3×10⁶	1.8×10⁴	200	0
30 i	3.8	2.5×10⁶	9.3×10⁵	3.9×10⁴	290	10
30 j	3.8	2.6×10⁶	8.0×10⁵	3.7×10⁴	260	0

Table 28. Number of polystyrene particles, of five size classes, consumed by I. campestris McDunnough (1981)

Nymph number	Velocity (cm/sec)	0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	~~90.7±17.7~~
		Number consumed				
29 g	8.8	4.4×10^6	1.9×10^5	8.2×10^4	800	0
29-a	9.8	1.6×10^6	1.2×10^5	6.9×10^4	250	0
29 b	9.1	3.9×10^6	1.1×10^5	1.1×10^4	50	0
29 i	8.5	3.6×10^6	1.2×10^5	6.6×10^4	410	0
29 h	8.8	4.5×10^6	1.9×10^5	4.7×10^4	250	10
29 j	8.2	1.9×10^6	1.2×10^5	8.2×10^4	590	10
29 f	7.8	3.4×10^6	3.3×10^5	3.6×10^4	160	0
29 d	9.8	1.8×10^6	1.4×10^5	5.6×10^4	130	0

Table 29. Number of polystyrene particles, of five size classes, consumed by *I. campestris* McDunnough (1981).

Nymph number	Velocity (cm/sec)	Diameter of particles ±1 SD(um)				
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	90.7±17.7
		Number consumed				
27 c	17.5	3.0×10^6	1.5×10^5	1.7×10^4	170	0
27 h	16.5	3.8×10^6	7.7×10^5	4.1×10^4	510	0
27 e	16.5	2.9×10^6	2.6×10^5	1.2×10^4	470	0
27 k	18.0	2.9×10^6	8.9×10^5	3.1×10^4	300	0
27 j	17.3	3.1×10^6	8.8×10	4.3×10^4	310	0
27 g	16.5	3.5×10^6	1.2×10^5	6.9×10^4	400	0
27 d	16.5	3.8×10^6	1.0×10	2.5×10^4	80	10
27 b	18.0	4.4×10^6	9.8×10^5	6.6×10^4	290	0

Table 30. Number of polystyrene particles, of five size classes, consumed by *I. campestris* McDunnough (1981).

Nymph number	Velocity (cm/sec)	Diameter of particles ±1 SD(um)				
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	90.7±17.7
		Number consumed				
28 h	39.0	6.7×10^5	1.3×10^5	3.2×10^3	110	0
28 k	34.5	3.1×10^5	8.9×10^4	5.4×10^3	190	10
28 g	32.0	5.2×10^5	1.0×10	5.5×10^3	220	0
28 a	36.0	6.6×10^5	1.6×10^5	5.2×10^3	210	0

Table 31. Number of polystyrene particles, of five size classes, consumed by *L. campestris* McDunnough (1981)

Nymph number	Velocity (cm/sec)	Diameter of particles ±1 SD(um)				
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	90.7±17.7
		Number consumed				
19 g	37.0	8.2×10^{5}	2.2×10^{5}	1.5×10^{3}	350	0
19 f	36.0	4.2×10^{5}	1.3×10[illegible]	6.3×10[illegible]	170	0
19 c	34.5	5.5×10[illegible]	1.7×10[illegible]	4.1×10^{4}	620	0
19 h	34.5	7.8×10[illegible]	1.5×10	1.0×10[illegible]	50	0

Table 32. Number of polystyrene particles, of five size classes, consumed by *L. campestris* McDunnough (1981)

Nymph number	Velocity (cm/sec)	Diameter of particles ±1 SD(um)				
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	90.7±17.7
		Number consumed				
20 c	37.0	4.0×10[illegible]	7.4×10[illegible]	4.9×10[illegible]	90	0
20 a	34.5	4.0×10[illegible]	1.2×10[illegible]	3.4×10[illegible]	40	0

Table 33. Number of polystyrene particles, of six size classes, consumed by *S. bivittatum* Malloch (1982).

Larva number	Velocity (cm/sec)	Diameter of particles ±1 SD(um)					
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	50.1±20.0	90.7±17.7
		Number consumed					
7 k	5.8	4.2×10^5	1.6×10^5	3.6×10[illegible]	1.7×10^2	20	0
7 m	4.8	5.5×10^5	1.2×10^5	4.5×10[illegible]	1.0×10^2	50	0
7 n	5.1	4.0×10^5	1.5×10^5	4.0×10[illegible]	1.3×10[illegible]	0	0
7 l	4.8	6.7×10^5	9.6×10^4	6.2×10[illegible]	5.0×10[illegible]	20	0
7 a	4.2	5.2×10^5	1.1×10^5	3.9×10[illegible]	8.5×10[illegible]	0	0

Table 3.4 Number of polystyrene particles, of six size classes, consumed by S. *bivittatum* Malloch (1982).

Larva number	Velocity (cm/sec)	Diameter of particles ±1 SD(µm)					
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	50.1±20.0	90.7±17.7
		Number consumed					
6 l	9.8	$1.7\times10^{\text{[illegible]}}$	4.8×10^{5}	$1.7\times10^{\text{[illegible]}}$	$2.5\times10^{\text{[illegible]}}$	10	0
6 f	9.8	$1.9\times10^{\text{[illegible]}}$	$4.1\times10^{\text{[illegible]}}$	$1.9\times10^{\text{[illegible]}}$	$1.6\times10^{\text{[illegible]}}$	5	5
6 m	9.6	$1.4\times10^{\text{[illegible]}}$	3.1×10^{5}	$2.6\times10^{\text{[illegible]}}$	$2.2\times10^{\text{[illegible]}}$	40	0
6 e	10.4	$1.5\times10^{\text{[illegible]}}$	4.7×10^{5}	$1.6\times10^{\text{[illegible]}}$	$6.3\times10^{\text{[illegible]}}$	5	0
6 i	10.4	$1.6\times10^{\text{[illegible]}}$	5.8×10^{5}	$1.3\times10^{\text{[illegible]}}$	$2.8\times10^{\text{[illegible]}}$	60	0
6 j	9.1	$1.8\times10^{\text{[illegible]}}$	$6.5\times10^{\text{[illegible]}}$	$2.1\times10^{\text{[illegible]}}$	$1.3\times10^{\text{[illegible]}}$	30	5
6 a	9.8	$2.0\times10^{\text{[illegible]}}$	3.9×10^{5}	$8.8\times10^{\text{[illegible]}}$	$3.1\times10^{\text{[illegible]}}$	10	0
6 c	8.5	$1.6\times10^{\text{[illegible]}}$	$5.2\times10^{\text{[illegible]}}$	$2.4\times10^{\text{[illegible]}}$	$2.1\times10^{\text{[illegible]}}$	0	0
6 g	8.5	$2.1\times10^{\text{[illegible]}}$	3.4×10^{5}	$3.6\times10^{\text{[illegible]}}$	$9.7\times10^{\text{[illegible]}}$	0	0

Table 35. Number of polystyrene particles, of six size classes, consumed by *S. bivittatum* Malloch (1982).

Larva number	Velocity (cm/sec)	Diameter of particles ±1 SD(um)					
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	50.1±20.0	90.7±17.7
		Number consumed					
5 j	19.5	9.3×10^5	4.3×10^5	9.8×10	1.8×10	0	0
5 h	22.0	8.5×10^5	4.6×10^5	7.8×10	8.5×10^2	0	0
5 r	16.5	9.2×10^5	3.7×10^5	1.2×10^4	7.0×10	0	0
5 g	18.0	1.3×10^6	3.1×10^5	2.2×10^4	8.5×10	15	0
5 e	22.0	9.7×10^5	2.3×10^5	1.1×10^4	1.7×10^2	0	0
5 i	19.5	9.2×10^5	9.7×10^4	1.6×10^4	2.5×10^2	0	0
5 m	16.5	1.2×10^6	2.8×10^5	2.4×10^4	1.5×10^2	0	0
5 d	16.5	9.5×10^5	2.1×10^5	1.8×10^4	8.0×10^2	10	0
5 k	16.5	8.4×10^5	3.9×10^5	2.1×10^4	2.4×10	0	0

Table 36. Number of polystyrene particles, of six size classes, consumed by *S. bivittatum* Malloch (1982).

Larva number	Velocity (cm/sec)	Diameter of particles ±1 SD(um)					
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	50.1±20.0	90.7±17.7
		Number consumed					
8 m	34.5	5.1×10[illegible]	8.0×10^{4}	4.3×10[illegible]	8.0×10[illegible]	30	0
8 l	32.0	4.0×10^{5}	[illegible]	5.1×10[illegible]	2.3×10[illegible]	10	0
8 f	29.0	4.7×10[illegible]	1.9×10^{5}	1.1×10[illegible]	8.0×10[illegible]	0	0
8 i	30.5	5.2×10[illegible]	1.7×10^{5}	4.6×10[illegible]	1.0×10[illegible]	0	0
8 n	34.5	4.3×10[illegible]	9.4×10^{4}	7.3×10[illegible]	2.0×10[illegible]	20	0
8 q	36.0	4.8×10[illegible]	9.6×10^{4}	3.9×10[illegible]	7.0×10[illegible]	0	0

Table 37. Number of polystyrene particles, of six size classes, consumed by *S. bivittatum* Malloch (1982).

Larva number	Velocity (cm/sec)	0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	50.1±20.0	90.7±17.7
		Diameter of particles ±1 SD(um)					
		Number consumed					
11 o	40.0	4.2×10	5.7×10^4	4.1×10	5.3×10	0	20
11 i	37.0	4.0×10	1.2×10^5	3.6×10	4.7×10	0	0
11 g	37.0	3.7×10	8.2×10^4	2.8×10	2.0×10	0	0
11 k	37.0	4.4×10	1.6×10^5	4.6×10	1.3×10	0	0

Table 38. Number of polystyrene particles, of six size classes, consumed by *S. bivittatum* Malloch (1982).

Larva number	Velocity (cm/sec)	0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	50.1±20.0	90.7±17.7
		Diameter of particles ±1 SD(um)					
		Number consumed					
12 l	39.0	4.6×10	1.3×10^5	3.0×10	4.5×10	0	0
12 p	41.0	3.2×10	3.9×10^4	3.7×10	1.4×10	40	0
12 e	41.5	3.7×10	4.1×10^4	2.9×10	8.0×10	0	0
12 k	47.0	2.9×10	2.8×10^4	1.8×10	8.5×10	0	0
12 i	47.0	3.1×10	3.6×10^4	2.1×10	6.9×10	0	0

Table 39. Number of polystyrene particles, of six size classes, consumed by [illegible]
McDonnough (1982)

Nymph number	Velocity (cm/sec)	Diameter of particles ±1 SD(μm)					
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	50.1±20.0	90.7±17.7
		Number consumed					
1 d	5.1	1.7×10[illegible]	6.0×10[illegible]	9.2×10[illegible]	1.8×10[illegible]	20	0
1 q	3.8	2.1×10[illegible]	8.3×10[illegible]	1.6×10[illegible]	1.8×10[illegible]	0	0
1 e	5.1	2.2×10[illegible]	1.0×10[illegible]	9.2×10[illegible]	1.[illegible]×10[illegible]	20	0
1 c	5.5	1.7×10[illegible]	5.7×10[illegible]	2.5×10[illegible]	1.1×10[illegible]	0	0
1 g	5.1	1.8×10[illegible]	7.4×10[illegible]	2.1×10[illegible]	1.8×10[illegible]	[illegible]	0
1 m	4.2	2.1×10[illegible]	5.8×10[illegible]	7.5×10[illegible]	3.5×10[illegible]	60	0
1 a	5.1	2.9×10[illegible]	9.4×10[illegible]	1.4×10[illegible]	2.7×10[illegible]	30	5

Table 40. Number of polystyrene particles, of six size classes, consumed by [illegible] McDunnough (1982)

Nymph number	Velocity (cm/sec)	Diameter of particles ±1 SD(um)					
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	5[illegible].1±20.0	90.7±17.[illegible]
		Number consumed					
3 a	8.5	3.2×10^{4}	8.9×10^{4}	8.6×10[illegible]	2.7×10	0	0
3 i	8.8	2.9×10[illegible]	9.5×10^{4}	3.1×10[illegible]	3.0×10	0	0
3 c	8.2	2.8×10^{4}	8.7×10^{4}	2.8×10^{3}	1.9×10	0	0
3 e	8.5	2.6×10^{4}	2.1×10[illegible]	4.1×10^{3}	2.2×10	0	0
3 f	8.5	3.2×10[illegible]	1.0×10[illegible]	3.4×10^{3}	1.3×10	5	0
3 j	8.8	3.9×10[illegible]	1.3×10[illegible]	4.4×10[illegible]	1.4×10	40	0
3 m	8.2	3.8×10^{4}	1.5×10[illegible]	1.2×10[illegible]	1.2×10	30	0
3 h	9.4	3.3×10[illegible]	9.1×10^{4}	2.3×10[illegible]	4.8×10	60	0
3 n	8.2	[illegible]	8.1×10^{4}	2.9×10[illegible]	9.6×10	15	5

Table 11 Number of polystyrene particles, of six size classes, consumed by *I. campestris* McDunnough (1982).

Nymph number	Velocity (cm/sec)	Diameter of particles ±1 SD(um) 0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	50.1±20.0	90.7±17.7
		Number consumed					
9 h	16.5	2.8×10^{6}	1.2×10^{5}	8.6×10^{4}	2.1×10^{2}	20	0
9 n	19.5	2.5×10^{6}	8.8×10^{5}	1.4×10^{5}	8.4×10^{3}	75	12
9 i	16.5	2.18×10^{7}	5.8×10^{5}	5.5×10^{4}	1.5×10^{2}	0	0
9 k	16.5	2.4×10^{6}	6.2×10^{5}	3.2×10^{4}	3.2×10^{2}	10	0
9 m	19.5	2.7×10^{6}	6.6×10^{5}	2.[illegible]$\times10^{4}$	5.1×10^{3}	5	0
9 e	18.0	3.0×10^{6}	8.2×10^{5}	8.1×10^{4}	1.6×10^{2}	0	0
9 j	16.5	3.4×10^{6}	1.5×10^{6}	2.8×10^{4}	1.0×10^{2}	5	0
9 d	18.0	2.6×10^{6}	7.9×10^{5}	1.7×10^{4}	2.1×10^{2}	0	0

Table 42. Number of polystyrene particles, of six size classes, consumed by *I. campestris* Malloch (1982).

Nymph number	Velocity (cm/sec)	Diameter of particles ±1,SD(um)					
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	50.1±20.0	90.7±17.7
		Number consumed					
10 b	30.5	6.9×10^5	1.5×10^5	1.6×10^4	2.6×10^2	0	0
10 g	32.0	4.6×10^5	8.6×10^4	4.1×10^3	1.7×10^2	0	0
10 a	32.0	5.4×10^5	1.2×10^5	5.0×10^3	7.7×10^2	0	0
10 f	27.5	5.7×10^5	6.5×10^4	1.0×10^4	[illegible]$.7\times10^2$	5	0
10 h	36.0	4.8×10^5	8.5×10^4	3.3×10^3	1.0×10^2	10	0

Table 43. Number of polystyrene particles, of six size classes, consumed by *I. campestris* Malloch (982).

Nymph number	Velocity (cm/sec)	Diameter of particles ±1 SD(um)					
		0.5+0.006	1.2±0.016	5.7+1.5	25.7±5.8	50.1±20.0	90.7±17.7
		Number consumed					
4 e	34.5	4.1×10^5	1.6×10^5	1.8×10^3	1.1×10^2	10	0
4 l	37.0	4.6×10^5	6.8×10^4	6.1×10^3	2.3×10^2	10	0
4 f	40.0	3.9×10^5	7.7×10^4	8.0×10^3	9.1×10^1	20	10
4 d	34.5	5.64×10^5	1.5×10^5	1.1×10^3	4.0×10^2	20	0

Table 44. umber of polystyrene particles, of six size classes, consumed by *I. campestris* Malloch (1982).

Nymph number	Velocity (cm/sec)	Diameter of particles ±1 SD(um)					
		0.5±0.006	1.2±0.016	5.7±1.5	25.7±5.8	50.1±20.0	90.7±17.7
		Number consumed					
2 a	37.0	4.3×10^5	6.6×10^4	6.0×10^3	2.5×10^2	0	0
2 b	34.5	3.7×10^5	1.1×10^5	8.9×10^3	1.9×10^2	5	0
2 e	39.0	4.5×10^5	4.2×10^4	5.5×10^3	1.3×10^2	5	0