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THE UNIVERSITY OF ALBERTA

SUSPENSION-FEEDING BEHAVIOUR OF BLACK FLY LARVAE (DIPTERA: SIMULIIDAE): HYDRODYNAMICAL PERSPECTIVES

by

Jean O. Lacoursière

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

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FRONTISPIECE

Larva of *Simulium vittatum* Zett. filter-feeding on resuspended dye particles

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certity that they have read, and recommended to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled SUSPENSION-FEEDING BEHAVIOUR OF BLACK FLY LARVAE (DIPTERA: SIMULIIDAE): HYDRODYNAMICAL PERSPECTIVES submitted by JEAN O. LACOURSIERE in partial fulfilment of the requirements for the degree of DOCTOR OF PHILISOPHY.

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Supervisor

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External Examiner

Date 23-XI-89

DEDICATION

Je dédie cette thèse à mes parents, Jacques Lacoursière et Monique Dubois pour leurs constant support, encouragements et amour.

ABSTRACT

Hydrodynamics of suspension feeding and concurrent microenvironment selection by aquatic larvae of the black fly *Simulium vittatum* Zett. are investigated under laboratory conditions, and a compact and versatile flume for studying influence of hydrodynamical factors on benthic invertebrate behaviour is described.

Detailed study of the suspension-feeding stance and examination of water flow through filtering appendages (*i.e.*, labral fans) demonstrate that change in body deflection with increasing water velocity is most likely passive. However, overall feeding stance is the outcome of active feedback between flow forces and behavioural reactions to maintain the fans at optimal filtering position. Unexpectedly, labral-fans react to velocity increases with structural reconfiguration resulting in aperture expansion. An increasing fraction of the water directly approaching the fan aperture flows around its perimeter as velocity decreases; no flow through the fans is observed below 2.5 cm/s, and fluid transmissivity never exceeds 30-35%, even at flows up to 50 cm/s. Calculations of suspension-feeding efficiency are reformulated to reflect labral fan transmissivity and behavioural components of the feeding process. Accordingly, *S. vittatum* larvae are shown to be *ca.* 4 to 26 times more efficient at suspension feeding than previously assessed.

Larvae did not assume stances nor select positions along the flat substrate demonstrating any significant response to changing boundary layer thickness, leading me to reject the hypothesis that simuliid larvae hide entirely in the boundary layer to reduce direct influence of the mainstream current. Contrary to general belief, larvae do not necessarily seek maximum velocity in a longitudinal velocity gradient. Larvae preferably gather along the separation zone where the thin boundary layer detaches from the curved substrate's surface. Larvae always avoid zones of maximum surface shear stress. Larval reaction to changes in flow conditions is immediate, and it is suggested that larvae scan the

velocity profile at the substrate to cue on a sharp difference experienced between the abdomen and labral fan level, hence maximizing particle-flux through the fans while minimizing drag forces on the bulbous portion of the body. Scaling microdistribution studies to the organismal level enables isolation of the proximal factors affecting formation of local assemblages.

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I express my deepest gratitude to Douglas A. Craig, mentor and friend, for his constant and valuable support, encouragement, and advice throughout my tenure at the University of Alberta.

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1. INTRODUCTION

Black fly larvae (Diptera: Simuliidae) are among the most conspicuous and easily recognizable inhabitants of lotic ecosystems. Readily distinguishable from most other benthic invertebrates by an elegant pair of hemispherical labral fans used in feeding, simuliid larvae are predominantly suspension feeders (collector-filterers, *sensu* Cummins 1973) although other feeding modes such as scraping, collector-gathering, and predation have been observed (see Currie and Craig 1987 for review). Simuliid larvae are found almost exclusively in flowing water, from frigid meltwater seepages to large, tepid tannin-stained rivers. A basic requirement for the majority of species, is that the water in which they live must flow, even if imperceptibly, in one direction to carry suspended food particles through the labral fans (located dorsolaterally on the head). After selecting a feeding site, larvae firmly attach themselves on the substratum by a posteroventral circlet of hooks, where, while leaning with the current, they longitudinally rotate their body between 90° and 180° to expose the adoral (concave) side of their fans to the flow. Material captured by the fans is transferred to the mouth via mandibular and maxillary brushes, as the fans are alternately closed and the apical portion of the rays inserted into the cibarium. Detailed accounts of structure and functional morphology of the labral fans are given in reviews by Colbo and Wotton (1981), and Craig and Chance (1982).

Larvae often display strikingly nonrandom dispersion patterns detectable at several levels of resolution. Within an outlet system, density of simuliid larvae is maximal immediately below the lake, and decreases with downstream distance (Lewis and Bennett

1975, Sheldon and Oswood 1977, Carlsson *et al.* 1977, Back and Harper 1979,). The abrupt decline in abundance is usually explained by the disappearance of planktonic particles arising from the lake (Maciolek and Tunzi 1967, Carlsson *et al.* 1977, Wotton 1979). Within a stream reach, black fly larvae most commonly aggregated in zones of high flow (*i.e.*, riffles), and are conspicuously absent from zones with low velocities (*i.e.*, pools). Such distributions have recently been correlated to various hydraulic indicies indicative of the tractive forces acting on the streambed (*e.g.* indicies relating water velocity, water depth, water and streambed slopes, as well as size, nature and roughness of the substrate) (see reviews in Statzner 1981, Osborne and Herricks 1983, Wetmore 1987, and Statzner *et al.* 1988). At the substrate level, individuals on a single element (*eg*., rocks, branches) may be randomly arranged, or may be observed to form dense, contiguous aggregates (Wotton 1982, Eymann 1985), in reticulate patterns (Hocking and Pickering 1954) or to form disjointed parallel bands aligned normal to the flow direction (Twinn *et al.* 1948, Colbo 1987). At a finer scale, black fly larvae may be organized into arrays of quasi-uniformly spaced individuals, each surrounded by small unoccupied areas (Harding and Colbo 1981, Eymann 1985). Principally at the latter two scales, patterns can be transitory (Gersabeck and Merritt 1979), varying with change in local water velocity, or persisting for the duration of a larval generation (Colbo 1979). Despite early works by Ambühl (1959), Décamps *et al.* (1975) and more recently by Chance and Craig (1986), and Eymann (1988), flow characteristic (*i.e.*, summary of three-dimensional flow patterns and flow forces) at the organismal level is still not well understood, and the proximate mechanisms (*i.e.*, the cause-and-effect relationships) by which flow affects formation of local assemblages still elude characterization.

Larval black flies are dominant members of many lotic ecosystems, where under certain conditions some species can pack themselves tightly together on the stream bed and form mats with densities as high as 10^6 individuals/m^2 (Wotton 1987). In general, the rôle of black fly larvae in aquatic ecosystems is believed to be largely qualitative (Cummins 1987); *i.e.*, as collector-gatherers, simuliid larvae mainly change detrital particle sizes from the ultrafine transported organic matter (UTOM: 0.45 - 50μm), to fine particulate organic matter sizes (FPOM: 50μm - 1mm) more readily available to other organisms (*i.e.* by production of fecal pellets). Although black fly larvae can undoubtedly influence stream seston dynamics (Sheldon and Oswood 1977, Wallace *et al.* 1982), their rôle is still considered minor in most situations (*e.g.* Merritt *et al.* 1984, Cummins 1987). Recently however, experimental studies involving eradication of simuliid larvae through use of a highly selective toxin (produced by the bacterium *Bacillus thuringiensis israelensis*), showed that black fly larvae can reduce seston flux by 32 - 55% over a 40-m stream section (Morin *et al.* 1988), supporting earlier studies by Maciolek and Tunzi (1967), Ladle *et al.* (1972), and Voshell (1985).

It is generally suggested that only a small fraction of the particles passing through the labral fans of simuliid larvae are actually captured and ingested. Kurtak (1973, 1978), Chance (1977), Wotton (1978), Colbo and Wotton (1981), Schröder (1980a,b, 1981b), Hart and Latta (1986) and others have calculated suspension-feeding efficiencies of black fly larvae ranging from < 0.01 to 12% for particle sizes studied. Schröder (1981a) collated literature values of assimilation efficiency of simuliid larvae and reported efficiencies ranging from 1.8 to 79% depending on the food particle type, but assimilation efficiencies reported are usually in the lower part of this range (Wotton 1978, McCullough *et al.* 1979, Morin *et al.* 1988). These low estimates of particle capture and assimilation efficiencies have contributed to the general perception that simuliid larvae account for little qualitative or quantitative impact on stream seston dynamics.

Efficiency of particle capture by black fly larvae has been defined traditionally as the ratio of the number of particles ingested per unit time to the total number of particles delivered to the labral fans during the same time interval. Although the underlying concept defining particle capture efficiency by black fly larvae is correct, application of hydrodynamic principles (Silvester 1983, Cheer and Koehl 1987a,b) indicates that the corollary associated with the actual methods of calculating the number of offered particles is unsuitable. Methods used to estimate number of particles offered to a filter-feeding larva, incorrectly assume that all water approaching the effective fan aperture from far upstream passes through the fans (*i.e.*, is processed). Even though recent studies on the fluid mechanical aspects of suspension-feeding in black fly larvae (Braimah 1985, 1987a,b), and on the complex feedback interactions between fluid, body shape and behaviour (*i.e.*, behavioural hydrodynamics *sensu* Craig 1989) have demonstrated that hydrodynamic phenomena play a major rôle in shaping black fly larva behaviours (Craig and Chance 1982, Chance and Craig 1986, Craig and Galloway 1987, Eymann 1988, pers. com), fluid transmissivity of the labral fans has never been directly assessed. Consequently, the real volume of water (hence the number of offered particles) passing through labral fans of black fly larvae is still unknown.

Black flies have been intensively studied from many perspectives (*i.e.*, ecological, taxonomic, biochemical, cytogenetic, and control) because of their economic and medical importance. Adult females of most species feed on blood and can cause allergic, often painful reactions to the host. Large outbreaks may consequently cause enormous distress to humans and livestock, resulting in considerable reduction in outdoor recreational activities and annual economic losses in production and control costs of beef and dairy cattle (Laird 1981, National Research Council Canada 1982, Fredeen 1984, 1985, Kim and Merritt 1987). Black flies are also serious vectors of disease agents, second only to mosquitoes and ticks (Kim and Merritt 1987). Although black flies are not generally incriminated as specific disease vectors for humans in Canada, in other areas, particularly West Africa, medical problems for humans are severe enough to warrant massive control actions. Pathogen transmission, reduction in productivity, as well as mortality have been documented in livestock and wildlife throughout Canada (National Research Council Canada 1982). Contact insecticides have been used on all developmental stages of black flies, but spectacularly successful control has been achieved by use of particulate chemical or biological compounds against the suspension-feeding larval stages (see review in Laird 1981, and Kim and Merritt 1987).

Much of the research on larval black flies has been aimed at their suppression. Growing environmental concerns regarding the increasing use of insecticides in flowing-water environments however, has led to research of more efficient and selective pesticide formulations more in tune with the "target's" behaviours (*i.e.*, ingested particle sizes, feeding behaviour, and microhabitat selection). Further, the possibility of negative impacts on nutrient spiralling[1] induced by sustained suppression of elements otherwise present in the ecosystem, has also triggered more fundamental research about the rôle of suspension-feeders (and other functional groups, *sensu* Cummins 1973) in lotic ecosystems.

It appears that suspension-feeding efficiency of simuliid larvae is central to adult reproductive success, because food availability at the larval stage can influence survivorship of the pupal stage (Brenner and Cup 1980), as well as size and fecundity (Colbo and Porter 1979, 1981) and mating success (Simmons and Edman 1981) of adults. Consequently, the basic premise of my research is that selection should have favoured morphologies and behaviours that maximizes the flow of water through the feeding structures, and minimizes drag forces acting on supporting structures (*i.e.* the larval body).

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[1] Nutrient Spiralling Concept: A nutrient atom is consider to have completed a cycle when it returns to the water in a dissolved form available for reutilization (water phase), after being biotically removed from the fluid (particulate phase) and passed through the food chain (consumer phase). Nutrients in a flowing-water system do not cycle in place, but are continuously displaced downstream as they complete a cycle, so that the path of the nutrient describes an imaginary spiral. The shorter the spiralling length, the more efficiently the nutrient is utilized, i.e. the more times the nutrient atom is recycled within a given stream reach (Webster 1975, Newbold *et al.* 1981).

It is this dual concern that inspired the present research. I therefore have focused on the two major gaps in knowledge of Simuliidae, common to both concerns: 1) What is the transmissivity of a labral fan (*i.e.* how much water is really filtered) ?, and 2) What are the hydrodynamical conditions influencing the formation of local assemblages of suspension-feeding larvae (*i.e.*, what are larvae cueing on) ? This thesis is presented as a series of papers.

In Chapter II, I present the design of a compact, versatile flume for study of the influence of hydrodynamical factors on the behaviour of benthic invertebrates. A specially designed diffuser, composed of an adjustable array of small horizontal rods, controls the pressure head in the return portion of the water-circulating system, thereby tailoring the velocity profile at the entrance of the testing-section. This adjustable diffuser facilitates creation of tailored flow conditions (*e.g.* zone of high shear stress, adjustable velocity gradient, and turbulence level), to which a group or single organism can be selectively exposed. The principal objective was to create an inexpensive desk-top version of larger, more bulky systems, without sacrificing performance and versatility.

In Chapter III, I produced a detailed analysis of the suspension-feeding stance of *Simulium vittatum* Zett. larvae and investigated the water flow through their labral fans (*i.e.*, transmissivity). I report that, labral fans of *S. vittatum* larvae unexpectedly react to velocity increases with structural reconfiguration resulting in aperture expansion, and that only a small fraction of the water directly approaching the fan aperture flows through them. Consequently, calculation of suspension-feeding efficiency is reformulated to reflect labral fan transmissivity and behavioural components of the feeding process.

In Chapter IV, I designed an experimental procedure by which the effects of hydraulic conditions can be evaluated for mobile suspension-feeding organisms such as black fly larvae. Hydrodynamics relevant to the micro-hydraulic events forming the

environment of benthic rheophilic organisms are presented. I report that contrary to general belief, simuliid larvae do not typically hide entirely in the boundary layer to reduce direct influence of the mainstream current, nor do they necessarily seek maximum velocity in a longitudinal velocity gradient. Larval reaction to hydraulic changes is immediate, and I suggest that *Simulium vittatum* larvae scan the velocity profile at the substrate to cue on a rapid velocity difference between the abdomen and labral fan level as part of the selection process of a suspension-feeding microsite; hence maximizing particle-flux through the labral fans while minimizing drag forces on the bulbous portion of the body.

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2. A SMALL FLUME FOR STUDY OF THE INFLUENCE OF HYDRODYNAMICAL FACTORS ON BENTHIC INVERTEBRATE BEHAVIOUR[1]

2.1 SYNOPSIS

A compact, versatile flume for study of the influence of hydrodynamical factors on the behaviour of benthic invertebrates is described. A range of of lotic micro-environments can be simulated under controlled and replicable conditions, by tailoring the velocity profile at the entrance of the testing-section. A specially designed diffuser, composed of an adjustable array of small horizontal rods, controls the pressure head in the return portion of the water-circulating system, thereby establishing the desired velocity profile. Because of the design and location of the diffuser, stable water velocities were achieved to a maximum of 81.5 ± 0.6 cm/s, with a coefficient of variation (turbulence estimate) of 0.8%. This adjustable diffuser facilitates creation of tailored flow conditions (*e.g.* zone of high shear stress, adjustable velocity gradient, and turbulence level), to which group or single organism can be selectively exposed. Simultaneous observations of flow and organism behaviours are realized through standard flow visualization techniques. Compact (72 cm long x 22 cm high x 10 cm wide; 10 litre) and easily transportable, this flume presents an inexpensive desk-top version of larger, more bulky systems, without sacrificing performance and versatility.

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[1] An earlier version of this chapter has been accepted for publication by the Journal of the North American Benthological Society, October 9th 1989

2.2 INTRODUCTION

Water movement is the dominant physical feature of lotic ecosystems, and yet, hydrodynamical factors remains among the least understood environmental variables affecting stream benthic invertebrates (Davis 1986; Nowell and Jumars 1984; Statzner 1981, 1987, Statzner et al.1988). Historically, ecologists working in lentic and especially marine environments have focused on the role played by hydrodynamics and flow forces in their respective ecosystems (Statzner et al. 1988), but surprisingly, stream ecologists have generally ignored the influence of those same parameters. Scarcity of research in hydrodynamics of lotic benthic organisms was probably due to the difficulties inherent in dealing with high velocities, but also perhaps to the powerful influence of Macan (1962,1974) who was not convinced that velocity *per se* could determine benthic organism distributions. Nevertheless, many works do correlate distribution and densities of benthic stream invertebrates with velocity alone, or in combination with water depth and physical characteristics of the streambed (see reviews in Brown and Brown 1984, Gore 1978, Hynes 1970, Macan 1962, Statzner 1981, Statzner et al. 1988). But, it is only recently that stream ecologists have attempted to combine various characteristics of flow, rather than consider only discharge or mean current velocities ("hydraulic stream ecology" *sensu* Statzner et al. 1988). Yet, because flow characteristics (*i.e.*, summary of three-dimensional flow patterns and flow forces) at the organism level is still poorly understood, the mechanisms by which flow locally affects lotic invertebrates still elude characterization. The physical consequences of living in a medium such as flowing water have been discussed by Vogel (1981), Lugt (1983), Koehl (1982, 1984), Nowell and Jumars (1984), Davis (1986) and Sylvester and Sleigh (1985). Despite very early works by Clemens (1917) and Von Gelei (1928), little has been done on lotic benthic invertebrates since Ambühl (1959, 1961) showed how bottom dwellers might use the boundary-layer to escape from the forces engendered by the mainstream velocity. Similar fundamental research was done by Trivellato and Décamps (1968) and later by Décamps et al. (1975), who attempted to relate black fly (Diptera; Simuliidae) larvae distribution to various flow parameters. Lately however, hydrodynamic parameters (such as boundary-layer thickness, boundary-layer separation, solenoidal and paired vortices, and shear stress forces) have been shown experimentally to play a major rôle in shaping the behaviour of lotic organisms (Braimah 1987a,b, Craig & Galloway 1987, Craig et al. 1988, Eymann 1988, pers. com, Soluk and Craig 1988); in studies oriented to the complex "feedback interactions between fluid and organism behaviours", in an approach refered to as "behavioural hydrodynamics" (*sensu* Craig 1989[2]).

To isolate mechanisms by which flow locally affects inhabitants of the benthic community, more detailed descriptions of the three-dimensional flow patterns around living organisms are required. However, since flow characteristics and complexity can change drastically over just a few millimetres, or over a few milliseconds, exhaustive analysis of flow patterns can be very difficult, if not impossible, under field conditions. The purpose of a flume, or flow tank, is not only to simulate the essential aspects of field conditions near or around the substrate, but also to simplify them so that the flow characteristics can be measured and summarized in their component parts (*i.e.*, see Nowell and Jumars 1984; Silvester and Sleigh 1985; and Vogel 1981, 1988 for reviews). Only then can the complex interactions between an organism's behaviour and its immediate

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[2] The expression "behavioural hydrodynamics" was introduced by D. A. Craig at the 37th annual meeting of the North American Benthological Society, Guelph (Ontario), Canada, 1989.

hydrodynamical milieux, be truly studied. Sedimentary geologists and civil engineers have used flumes for more than a century in an effort to examine modes and rates of sediment transport. In most common designs, water is allowed to flow between two tanks through a long horizontal trough; after falling into a downstream reservoir, the water is then pumped back into a large upstream storage tank. This design can produce flows of great temporal and spatial uniformity, but suffers from several practical disadvantages for the biologist; *i.e.*, extensive power consumption associated with high water velocity, increased water temperature through mechanical pumping, large total volume (storage tank) necessary to attenuate turbulence induced by pumping. Some engineering considerations and construction techniques in designing laboratory flumes have been summarized by Williams (1971), Vogel (1981) and Nowell and Jumars (1987). Extensive use of flumes in benthic stream studies had however to wait until a smaller, more specific and appealing design was introduced to the stream ecologist community by Vogel and LaBarbera (1978). The substance of their design is the elimination of the downstream waterfall and the use of an approximately constant cross-sectional area for the entire re-circulating circuit. To provide easy access to the test-area, and minimize air-water interface (surface waves are a nuisance), the return portion of the circuit is enclosed and located beneath the test-section. Since no great pressure head is required to move the water (*i.e.*, low water volume and neglectable system height), a relatively slowly revolving axial propeller provides adequate flow velocities with relatively little turbulence, which reduces power requirements, needs for large water volume and cooling systems (Vogel and LaBarbera 1978, Vogel 1981). Creation of a velocity gradient of zero (smooth, uniform flow) at the testing-section entrance is the major goal of most flume designs. However, from head-waters to mouth, stream ecologists have to face great diversity of habitats, each of them associated with their flow complexity. Behavioural hydrodynamic research could therefore benefit from a smaller system allowing work at very different, but well defined and controllable conditions (*i.e.*, from slowly developing boundary-layer, to zones of high shear stress, steep velocity gradients, and high turbulence) over a wide variety of substrates; this without any compromise on the overall size of the system. However, reduction in flume volume is generally associated with an increase in turbulence, due to strong circulation induced by abrupt curvature of the return section and length reduction of the settling section (zone between the return section and the test area where turbulence subside).

This paper[3] describes a small flume, originally designed for observation of filter-feeding responses of black fly larvae (Diptera: Simuliidae) to changes in flow conditions. Similar in principle to the recirculating channel of Vogel and LaBarbera (1978), this system uses a specially designed diffuser for differential control of the pressure head in the return portion of the circuit to establish the desired velocity profiles at low turbulence levels. More compact and easily transportable, this flume presents an inexpensive desk-top version of larger, more bulky systems, without sacrificing performance and versatility.

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[3] In the present study, this flume was used for the analysis of the fluid transmissivity of the filtering-appendages of *Simulium vittatum* larvae (*i.e.*, Chapter 3).

2.3 MATERIALS AND METHODS

2.3.1 Velocity sampling and flow visualization methods Water velocities were monitored at 2.5 cm downstream of the adjustable diffuser, and in the centre of the testing-section (35 cm downstream of the adjustable diffuser), with portable velocity meters (Novonics Kent Miniflow 265 & 422, Nixon Instrumentation Ltd.) using a 1.0 cm diameter, five-bladed rotor mounted on jewel bearings (free-propeller probe # 649 s/l). Velocities were sampled every 0.5 cm, at frequencies of 28 to 280 Hz for periods up to 60 sec, with an APPLESCOPE-D2 system (RC Electronics Inc., 7265 Tuolumne St., Goleta, CA93117, USA) on an Apple II+ personal computer. A digitized version of the ouptut (*i.e.*, current signal proportional to the water velocity) was analysed for sample statistics (*i.e.*, mean velocities, standard deviations and coefficients of variation) on an Apple II+ personal computer using a short Basic™ program (modified from J. Ciborowski, University of Windsor, Ontario, Canada).

Fluorescent pigments (A-11 Arora pink; Day-Glo Color Corp., Cleveland, Ohio, U.S.A.) and aluminium flakes were used in standard flow visualization techniques (Merzkirch 1987, Vogel 1981).

2.3.2 Description of the Apparatus The apparatus is essentially a recirculating system of constant width, similar in principle to the standing-water channel of Vogel and LaBarbera (1978) (Fig. 1). To facilitate cleaning and accessibility to the different parts, the flume is composed of three major components (Fig. 2): the reservoir (T) and two end modules -- the return (R) and the driving (D) modules. The principal material used is clear Plexiglas®, and the parts are screwed and/or glued together with dichloroethylene (other solvents, epoxy, or silicone rubber may also be used).

2.3.2.1 Reservoir. The dimensions of this component were dictated partially by the cross-sectional area of the test-section, the distance between the test-section and the outflow of the return portion of the circuit, and the desired volume of 10 litres. As a general rule, longer troughs give smoother flows than shorter ones. However, boundary-layers can develop just as quickly on the side of the trough as on the bed, bringing nonuniformity of velocity (*i.e.*, secondary -- non-downstream circulation along the corners) across the length of the working section; conversely, other nonuniformities (*i.e.*, turbulence) become substantial with smaller length (Nowell and Jumars 1987, Vogel and LaBarbera 1978, Vogel 1981). As seen in fig. 2, the reservoir (made of 5.8 mm (1/4 inch) thick clear Plexiglas®) is asymmetrically divided into an upper trough (open-channel) of 90 cm^2 cross-sectional area and a closed return section of half this size, by a divider (**d**; 5 pieces of 5.8 mm Plexiglas®). Glass windows (to minimize optical distortion) are embedded in the three walls of the test-section to maintain smoothness of the inside-walls, and create an observation chamber (testing-section; **ts**). Viewing through the bottom glass is allowed by a 45° angled mirror (**m**) inserted in the divider through an opening in the side of the flume. To ensure constant conduit diameter throughout the system, the inside wall of both ends of the reservoir are reduced to a thickness of 2.9 mm (1/8")(dotted line in fig. 2) -- which allows the driving (D) and return (R) modules to slide in position and yet maintain wall continuity (smoothness) throughout the entire circuit. To counteract part of any circular component of the flow induced by the propeller rotation, streamlined baffles (**b**; 2.9 mm thick Plexiglas® wing-shaped plate) are placed parallel to the flow in the return section. Three cross-beams placed at the top of the open channel add strength to the reservoir, and provision can be made for a drain valve in the bottom of the return portion of the reservoir (not shown on diagram) to facilitate water changes without disturbing the organisms.

2.3.2.2 Driving module. To allow maximum distance for fan-induced turbulence to subside, the driving module (made of 2.9 mm thick clear Plexiglas®) is placed at the downstream end of the trough (Figs. 1, 2). To improve performance and minimize vortex formation and entrained air bubbles, the propellers are housed well below the water surface in the bottom part of a cylindrical conduit (Fig. 3 C; 50 mm section of a 82 mm internal diameter (ID) Plexiglas® cylinder), and a circular collimator (cc; plastic light diffuser: grid of 13 x 13 mm openings with upstream and downstream sides honed to sharp edges) is fitted on top of it. To take full advantage of the blade width of large propellers, the length of the blades (p; 100 mm model airplane plastic propeller) is reduced to fit the inside diameter of the cylindrical conduit. The two propellers are held one over the other in a "+" position on a stainless steel shaft (7 mm outside diameter (OD), 82 mm long) by lock pins passing through the propeller hub and the shaft. The propeller shaft is housed in a Teflon® bearing (tb; 20 mm high; 15 mm OD, 7.2 mm ID at 10 mm deep) held centered in the lower part of the cylinder by four short streamlined pieces of Plexiglas® (pb; 20 mm by 33.5 mm, 2.9 mm thick with upstream and downstream sides honed to sharp edges), which also serve as baffles to counteract the circular component of the flow induced by the propellers rotation. To reduce abruptness of the corners which would increase turbulence and ensure smoothness of flow, a curved deflector plate (cd1; Plexiglas® 1.4 mm thick, radius of 10 cm) is placed in the intake area over the propellers, and a half-hemispherical shaped deflector (cd2; carved Plexiglas® block, 5 cm thick) fills the outlet section (Fig. 2; 3 C). The propeller shaft emerges through the deflecting plate and the top of the driving module, through a short shaft pipe (ps; Plexiglas® tube, 7.2 mm ID, 15 mm OD). The two propellers are driven by a Bodine® shunt-wound 1/50 HP

115VDC motor (type NSH-12) regulated by a Minarik® feedback adjustable speed control (Model SL-15), ensuring propeller rotation speed stability. The motor is mounted on a stand (**ms**) sitting tightly on top of the driving module. The motor shaft is coupled with the propeller shaft by a short piece of flexible Tygon® tubing, secured by two hose-clips.

2.3.2.3 **Return module.** To ensure a progressive deceleration of the water as it returns to the open channel (the velocity in the return section is twice the velocity in the trough since the continuity principle dictates that a reduction in cross-section area (S) has to be compensated by an increase in velocity (U) to keep the discharge (Q) constant; *i.e.*, $Q = S_1U_1 = S_2U_2$) the return module is a conduit of regularly expanding cross-section. As seen in fig. 2 and 3A, the outer wall of the conduit is a curved deflector plate (**df**; Plexiglas® 1.4 mm thick of expanding radius, r), and the inner core is a hemispherical divider (**dfh**; half 50 mm OD Plexiglas® cylinder and a frontal plate).

2.3.2.4 **Adjustable diffuser.** The flow conditions at the trough entrance are critical to the development of the flow characteristics generated in the test-section of the flume. As stated by Nowell and Jumars (1987), "the problem can be viewed as getting the flow to 'forget' its recent history". Because the water exiting the return-module have strong circulation from going around the steep curve of the module (centrifugal force), a porous obstruction is fitted into the module exit-frame to differentially diffuse flow irregularities over the entire height of the water column. This adjustable diffuser (**ad**) (Fig. 2; 3 B) is designed to selectively increase resistance to the flow where needed, *i.e.*, to pre-shape the desired velocity profile. The diffuser is made of an array of 70 horizontal rods (**hr**; 87 mm long, 3 mm OD Plexiglas® rods) held in place through holes in two streamlined plates (**dp**; 23 mm by 100 mm, 2.9 mm thick Plexiglas® plate with upstream and downstream sides honed to sharp beveled-edges) fitted to the curvature of the exit-opening of the return-module. The holes (3 mm ID) are in a 17:18:17:18 arrangement, each hole being centered on the vertices of an equilateral triangle of 5.5 mm side lengths. This arrangement ensures that water cannot flow through the diffuser in a straight path when two sets of rods are placed in adjacent rows; differential resistance is therefore created as more rods are selectively added to the diffuser.

2.3.2.5 Collimators. To dampen any remaining large-scale turbulence (non-downstream flow) at the exit of the adjustable diffuser, a fixed collimator[4] (fc; 18 mm thick, plastic grid commercially used as filters for fluorescent lighting fixtures, 13 mm^2 openings) is placed immediately against the diffuser (under the upstream cross-beam of the reservoir). Since several short spaced collimators provide better smoothing of flow then a single long one of same overall resistance, a movable collimator (mc; 11 mm thick) of the same nature is positioned about 5 cm downstream (Fig. 1). Upstream and downstream sides of the collimators are honed to sharp edges (streamlined) to minimize turbulence.

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[4] By analogy to the optical apparatus producing parallel rays of light, any arrangment of slits or apertures which limits a stream of particles to a beam in which all the particles move in the same, or nearly the same, direction is called a collimator.

2.4 RESULTS AND DISCUSSIONS

What specific characteristics of fluid motion are needed depend on the question we are trying to answer, and how well that question can be answered is determined by how well we can tailor flow profiles in our flume to match the field situations. The adjustable diffuser has been developed in order to pre-shape the flow at the trough entrance. Empirical tests are necessary to determined the optimum rod configuration corresponding to the velocity profile sought for the test-section entrance. We suggest to start with the full complement of rods, and systematically remove them to adjust the resistance to the flow; fine tuning of the profile can be achieved by use of thinner rectangular rods (by removing the top and bottom third of the rod; Fig 4 A). Figure 4 shows velocity profiles in mid-width position, immediately downstream of the adjustable diffuser (2.5 cm) and in the middle of the test-section (35.5 cm), associated with two different diffuser configurations. Diffuser configuration (A) selectively increases resistance to the flow in the upper- and mid-height sections of the return-module outlet (where velocity is maximum) creating an homogeneous pressure head on the downstream side of the diffuser (fig. 5 A). Consequently, a zero velocity gradient of average speed of 30.0 ± 0.2 cm/s is generated throughout the entire water column of the test-section entrance, with the exception of the upper- and lower-most part where air- and solid-interface respectively affect the flow (fig. 4; 5 B). Diffuser configuration (B) generates a profile of maximum velocity of 64.0 ± 0.5 cm/s at mid-height (six fold faster than the velocities at the outer limits), by selectively increasing resistance to the flow in the upper- and lower-sections of the return-module outlet (fig. 4; 5 C, D). Diffuser configurations of type A are only suitable for a single flow rate, due to variation in flow circulation in the return-module associated with velocity changes. Therefore, the number and size of the rods, as well as the number of rows, has to be adjusted to fit new velocities. Diffuser configuration of type B is suitable to generate any vertical (symmetrical) velocity gradient field (convenient for velocity preference experiments).

For steady flows, it is generally held that at a certain distance downstream from the collimators, the turbulence in the open-channel becomes isotropic (*i.e.*, one in which the mean oscillations in the three spacial components are equal; Schlichting 1987), as shown in the test-section by photographic analysis of aluminium dust trajectories. Consequently, approximation of turbulence intensity can be simplified, by considering only velocity oscillations in the downstream direction. The expression of a sample variability relative to its mean (*Coefficient of variation = (standard deviation / sample mean) x 100*) can therefore be used as a good approximation of turbulence intensity (**Tu**):

$$\mathbf{Tu}\,(\%) = \frac{\sigma}{U_x}\,100 \qquad \text{(Eg. 1)}$$

where U_x is the mean velocity of the downstream velocity component, and σ its standard deviation) (Evers 1983, Granger 1985, Schlichting 1987). Because of the design and location of the adjustable diffuser, generated turbulence intensities between 0.5% and 12% were recorded. The maximum velocity achieved with the described design was 81.5 ± 0.6 cm/s, generated with a coefficient of variation (turbulence estimate) of 0.8%. Our assessments of turbulence intensity are certainly underestimated, since it can be argued that the velocity sampler (1.0 cm diameter free-propeller probe) used does not have adequate frequency response[5] for subtle flow variations (*i.e.*, the momentum of the nylon propeller does not allow detection of high frequency fluctuations -- higher than about 5 Hz). Nevertheless, free-propeller velocity meters are among the most commonly used current flowmeter systems under field conditions. Until portable and simple flowmeters are available with more sensitive velocity and turbulence readings under field conditions, the free-propeller velocity meters combined with continuous sampling recorder systems, are most adequate tools for comparative work. Studies suggest that flow is fully turbulent in lotic environment (Smith 1975, Leopold et al. 1964), but little work has been done to determined the turbulence frequencies (abiotic or biotic in origin) of biological significance and their influence on the behaviour of lotic invertebrates. Such an endeavour would required more sensitive and complex techniques such as Laser Doppler Anemometry (Statzner and Holm 1982).

Investigations covering filter-feeding efficiency, micro-habitat selection, and calculation of flow forces on benthic invertebrates such as black fly, mayfly, and net-spinning caddisfly immatures have been executed in our laboratories using this flume design (Eymann 1988, pers. com.; Lacoursière unpub. data; Soluk and Craig pers. com.). Artificial substrates such as flat plates and cylinders (perpendicular or angled to the flow direction), as well as natural coarse (gravel) and soft-deformable (sand) substrates were used in these experiments (Fig. 6). Soft-deformable substrate requires the use of a tray (hollowed out, 2.25 cm thick Plexiglas® plate with the upstream side honed to a sharp edge; Fig. 6 B) fitting on the floor of the open channel to restrict the substrate to the testing area. Since every measurement in a flow tank involves the imposition of a wall somewhere near the tested object (obstruction), care should be given in selecting the size and position of the subject and/or substrate into the test-area, to avoid wall effects (*i.e.*,

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[5] The exact frequency response of the 1.0 cm diameter free-propeller, low velocity probe (649 s/l) is not available. However, technical information from Nixon Instrumentation Ltd. indicate that 200 milli-seconds are necessary to detect an "instantaneous" two-fold velocity change.

interaction between circulation patterns induced by the object and the sidewall). Boundary-layers can develop just as quickly on the side of the trough as on the bed, if their roughness is similar. Hence, assuming laminar flow conditions in the boundary-layer, the thickness of the boundary-layer (δ) in midpoint of each wall of the test-section entrance (at 20.0 cm from the second collimator) would be about 1.0 cm, for a mean cross-sectional velocity (U_∞) of 5 cm/s --*i.e.*, slowest conditions tested, since:

$$\delta \approx 5\sqrt{\frac{\nu\, x}{U_\infty}} \qquad \text{(Eq. 2.2)}$$

(Schlichting, 1987) where x is the length downstream from the formation point of the boundary-layer, and ν the kinematic viscosity of fresh water at 18°C). When turbulent conditions arise in a boundary-layer, turbulences increase momentum exchange between the slower fluid layers near the surface of the substrate and the faster layers away from it; creating a steeper velocity gradient than those in laminar flow (Schlichting, 1987). Generally speaking, the thickness of a turbulent boundary-layer is larger than that of a laminar boundary-layer owing to the greater energy losses in the former (Schlichting, 1987). Thus, the anticipated boundary-layer thickness at the test-section entrance becomes approximatively 1.2 cm since:

$$\delta \approx 0.376\, x \left(\frac{U_\infty x}{\nu}\right)^{-0.2} \qquad \text{(Eq. 2.3)}$$

(Schlichting, 1987) under the same mean cross-sectional velocity condition. Over an hydrodymamically smooth surface, transition from laminar to turbulent flow conditions in the boundary-layer occurs when the local Reynolds number (Re_x):

$$Re_x = \frac{U_\infty x}{\nu} \qquad \text{(Eq. 2.4)}$$

exceeds approximatively 5 x 10^5 (Vogel 1981). This number can only be a guideline because it is chiefly the boundary condition (*i.e.*, solid - fluid interface), namely the roughness of the substrate which determines the onset of turbulence for any imposed velocity (Schlichting, 1987; Vogel 1981; Nowell and Jumars 1984, 1987). Although flow in lotic environment is considered fully turbulent (Hynes 1970), a turbulent flow away from the boundary layer provides no indication of whether the boundary-layer itself will be turbulent. Indeed, growing laminar boundary-layers have been frequently observed in fully turbulent streams (Eymann, pers. com; Lacoursière, unpub. data), though it is believed that boundary-layers over natural sediment surfaces are virtually always turbulent (Nowell and Jumars 1984, 1987). Qualitatively, simple dye studies or other visualization techniques can reveal the two distinct conditions.

Nowell and Jumars (1984) give as general rules, that any object or group of objects should not occupied more than 25% of the channel width (to avoid flow blockage, where the fluid has greater tendency to go over rather than around the objects, compared to comparable field situation without the sidewalls), or more than 35% of the flow depth (the flow field can be strongly affected by induced deflection of the free surface in the flume) to ensure similarity in flow patterns between flume and field situations. Hence, cross-sectional area of the test-section, as well as position and size of the observed organisms should always be mentioned in reporting behavioural hydrodynamic studies.

2.4 CONCLUSIONS

The distinct advantage of this flume design lies in the devlopment of the adjustable diffuser, that, not only tailors velocity profiles at the test-section entrance, but also allows flume-volume reduction without sacrificing performance and versatility. Combination of diffuser and substrate (natural or artificial) configurations can simulate a large range of lotic micro-environments under controlled and replicable conditions. Because of its short open-channel length, this flume is however totally unsuited for work requiring fully grown boundary-layer. Nevertheless, flow throughout the greater part of running water systems is turbulent, *i.e.*, chaotic, and any major variation in flow directionality and intensity is more likely to disrupt boundary-layer growth; conversely, fully developed boundary-layers would be found in larger systems and slow moving pools.

In addition, because of its small size and its design simplicity (easy to build), this system is also suitable for experiments requiring control of particle flux. Consequently, an array of these small units can easily form a bioassay complex, allowing simultaneous replication of experiments under controlled flow conditions, in a relatively confined laboratory area. Furthermore, since the motor, the controls and the accessories can be placed inside the trough, this self-contained system is easily transportable and is presented as an inexpensive desk-top version of larger, more bulky systems.

The importance of flow to the ecology of lotic benthic communities is unquestionable. Recent works indicate that stream communities maybe more physically than biologically controlled systems (Reice 1985, Statzner 1987). Flumes will find an expanding rôle in linking organismic responses to a more comprehensive treatment of the physical environment. Undoubtedly, benthic flow environments are difficult to describe and quantify, but future progress in stream ecology depends upon biologists' abilities to understand and describe benthic flow regimes. Single velocity measurements are no longer acceptable in benthic studies.

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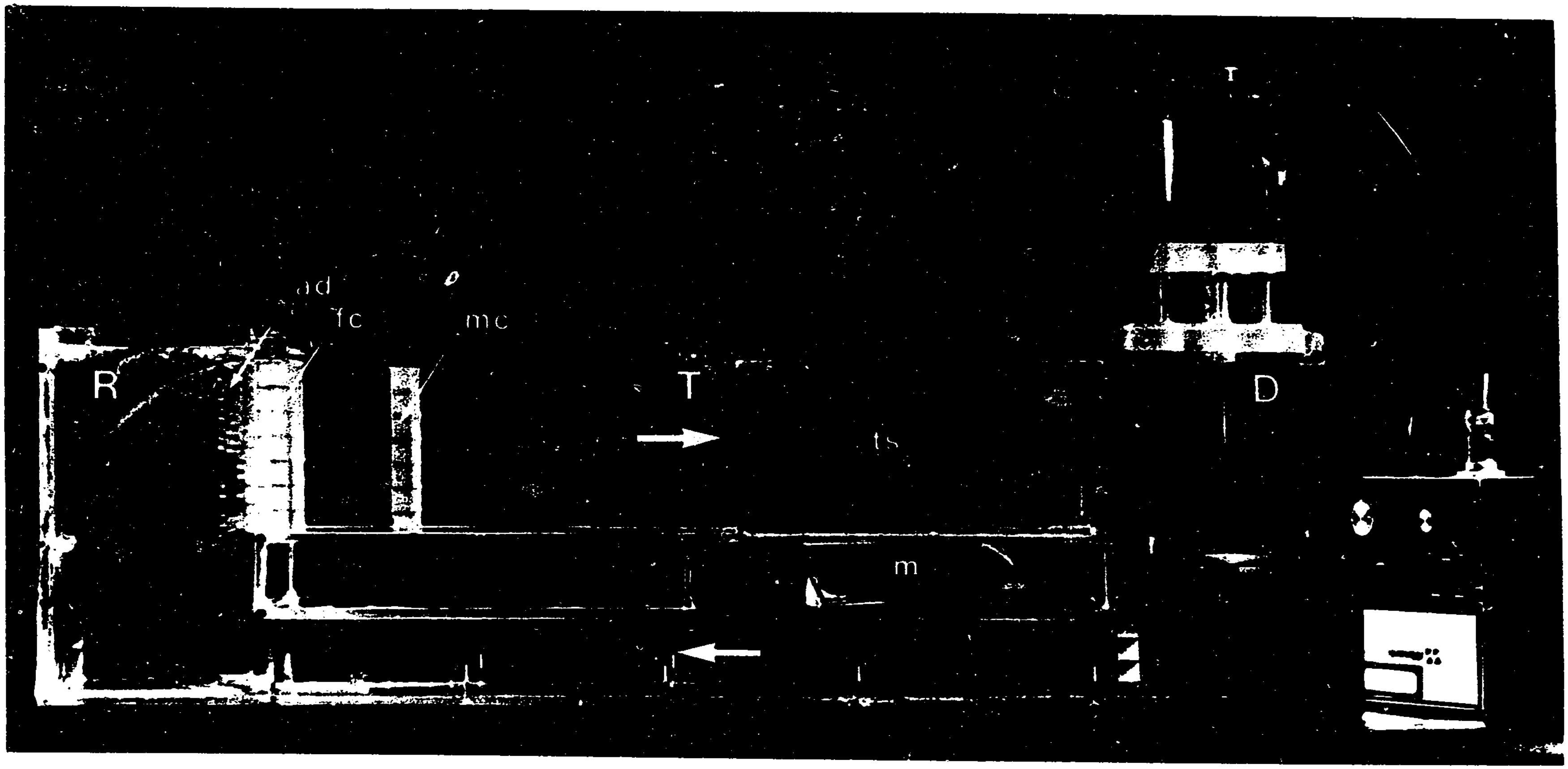
Fig. 1 Compact flume for behavioural hydrodynamic studies of benthic invertebrates; 10 Liters volume. General view, **T**, reservoir; **D**, driving module; **R**, return module; **ad**, adjustable diffuser; **fc**, fixed collimator; **m**, mirror; **mc**, movable collimator; **ts**, testing-section.


ad
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mc
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T
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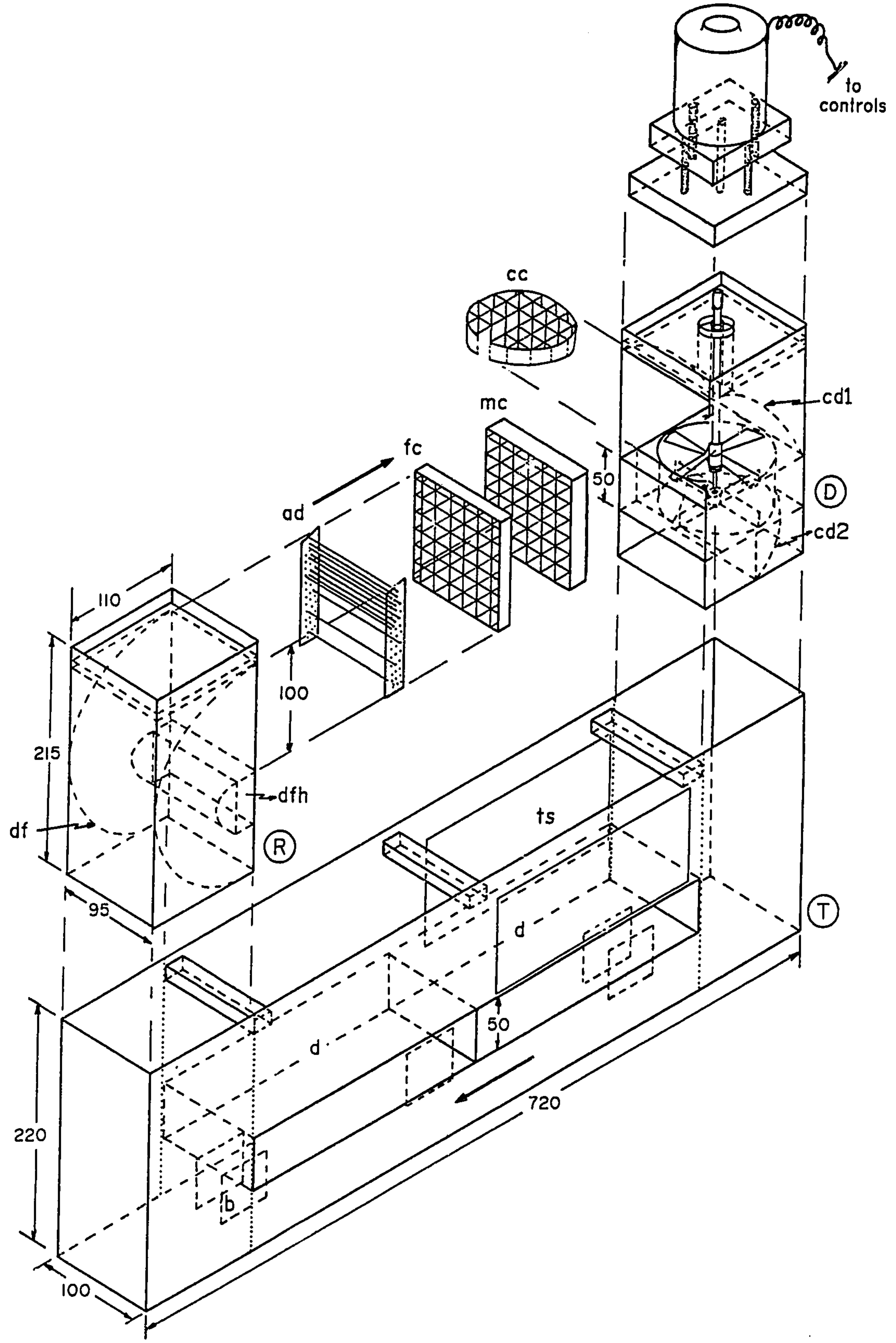
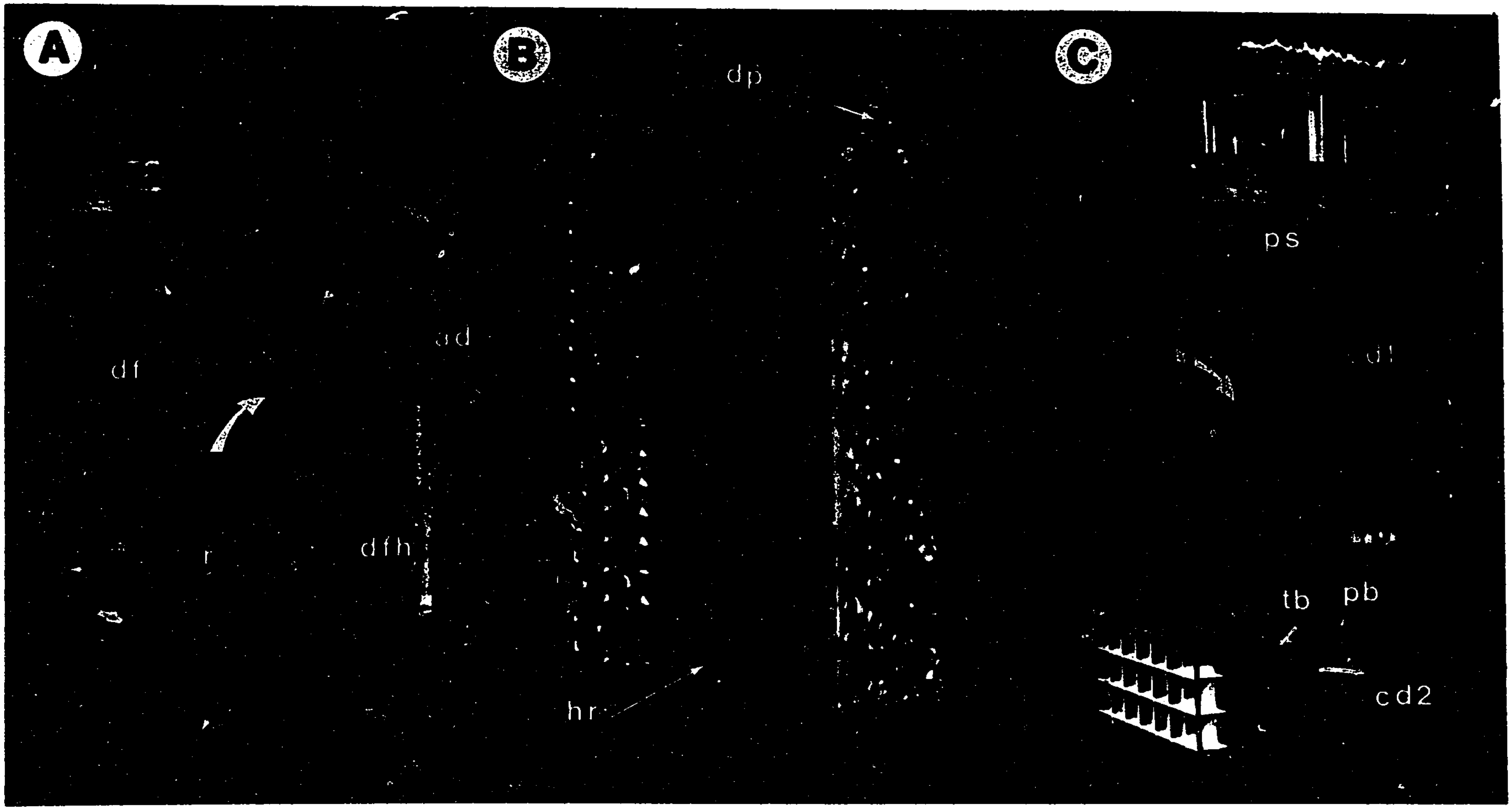
D
m

Fig. 2 Exploded diagram of the flume showing mesurements (mm) and other details: **T**, reservoir; **D**, driving module; **R**, return module; **ad**, adjustable diffuser; **b**, baffles; **cc**, circular collimator; **cd1**, intake curved deflector; **cd2**, outlet curved deflector; **d**, divider; **df**, deflector plate; **dfh**, hemispherical deflector; **fc**, fixed collimator; **mc**, movable collimator; **ts**, test section.



to controls
cc
cd1
mc
fc
50
D
ad
cd2
110
100
215
dfh
df
R
ts
95
T
d
d
50
220
720
b
100

Fig. 3 Fulme major components. A) Return module: **ad**, adjustable diffuser; **df**, deflector plate; **dfh**, hemispherical deflector; **r**, expanding radius. **B**) Adjustable diffuser: **dp**, deflector frame plate, **hr**, horizontal rods. C) Driving module: **cd1**, intake curved deflector; **cd2**, outlet curved deflector; **ms**, motor stand; **p**, propeller; **pb**, propeller baffles, **ps**, propeller shaft pipe; **tb**, Teflon® bering.


A
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cd1
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pb
cd2

Fig. 4 Adjustable diffuser configurations and associated velocity profiles. Each data point forming the velocity profiles is represented by an average velocity ± its standard deviation. The filled circles represent rods, lined circles represent smaller rectangular rods, and hollow circles represent empty holes in the diffuser frame plate.

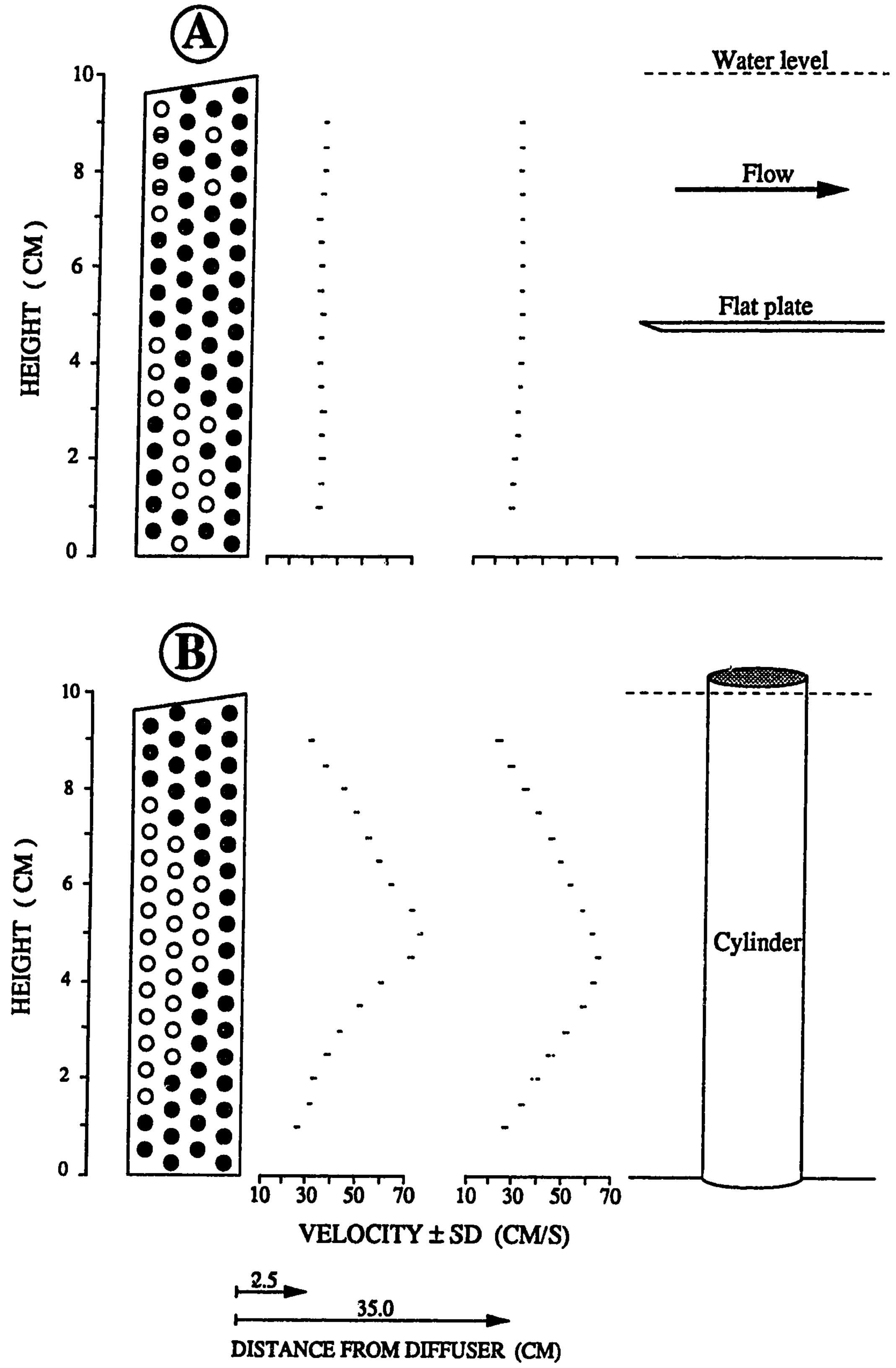

A
B
10
8
6
4
2
0
HEIGHT (CM)
Water level
Flow
Flat plate
Cylinder
10
30
50
70
VELOCITY ± SD (CM/S)
2.5
35.0
DISTANCE FROM DIFFUSER (CM)

Fig. 5 Flow visualization (Arora pink Day-Glow™ fluorescent pigments) of the velocity profile (*i.e.*, envelope of arrival time) at the open-channel entrance (**A**,**C**) and testing-section entrance (**B**,**D**) for two collimator configurations (Fig. 4): **ab**, adjustable diffuser; **ts**, testing-section. The fluorescent pigments were injected in the entrance of the driving module.

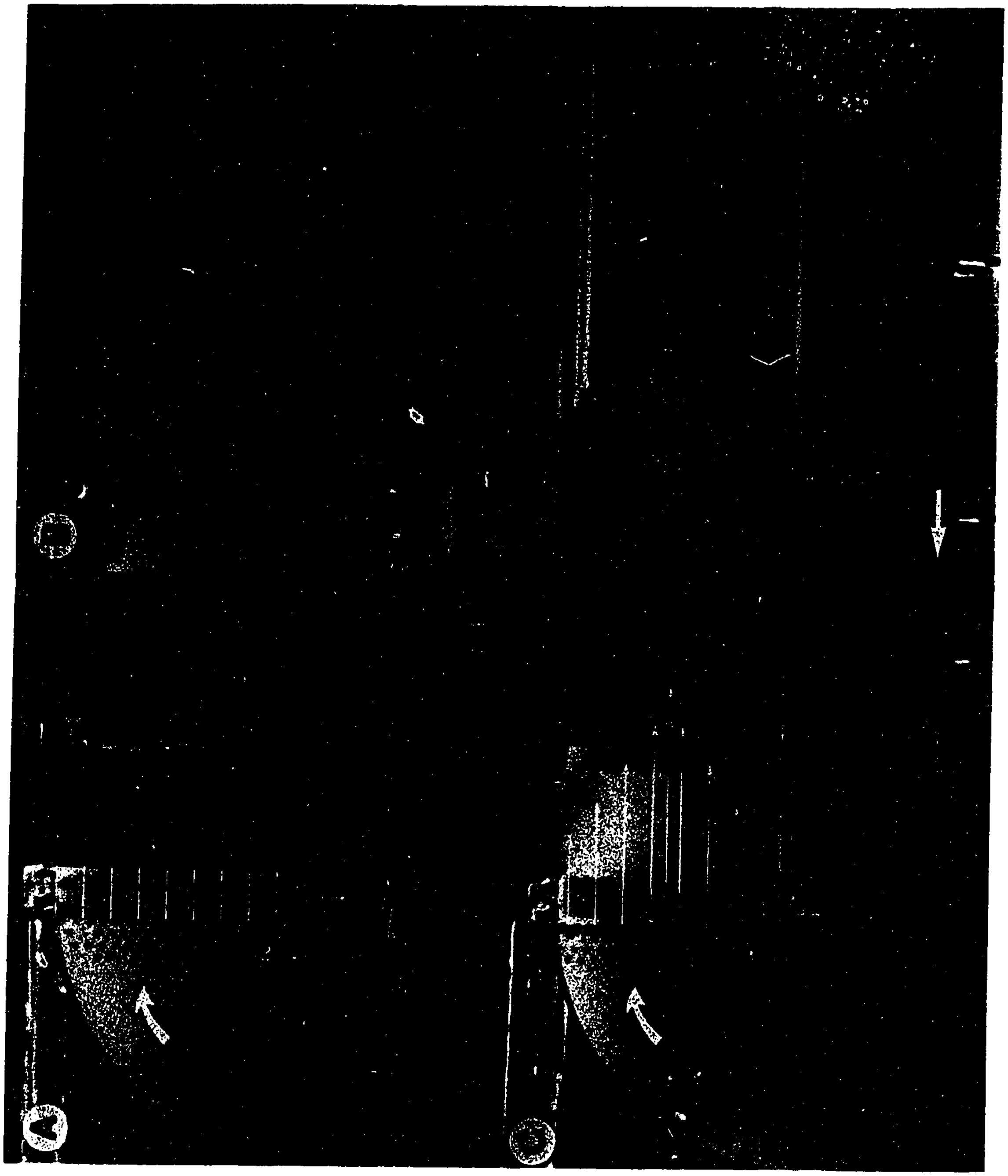
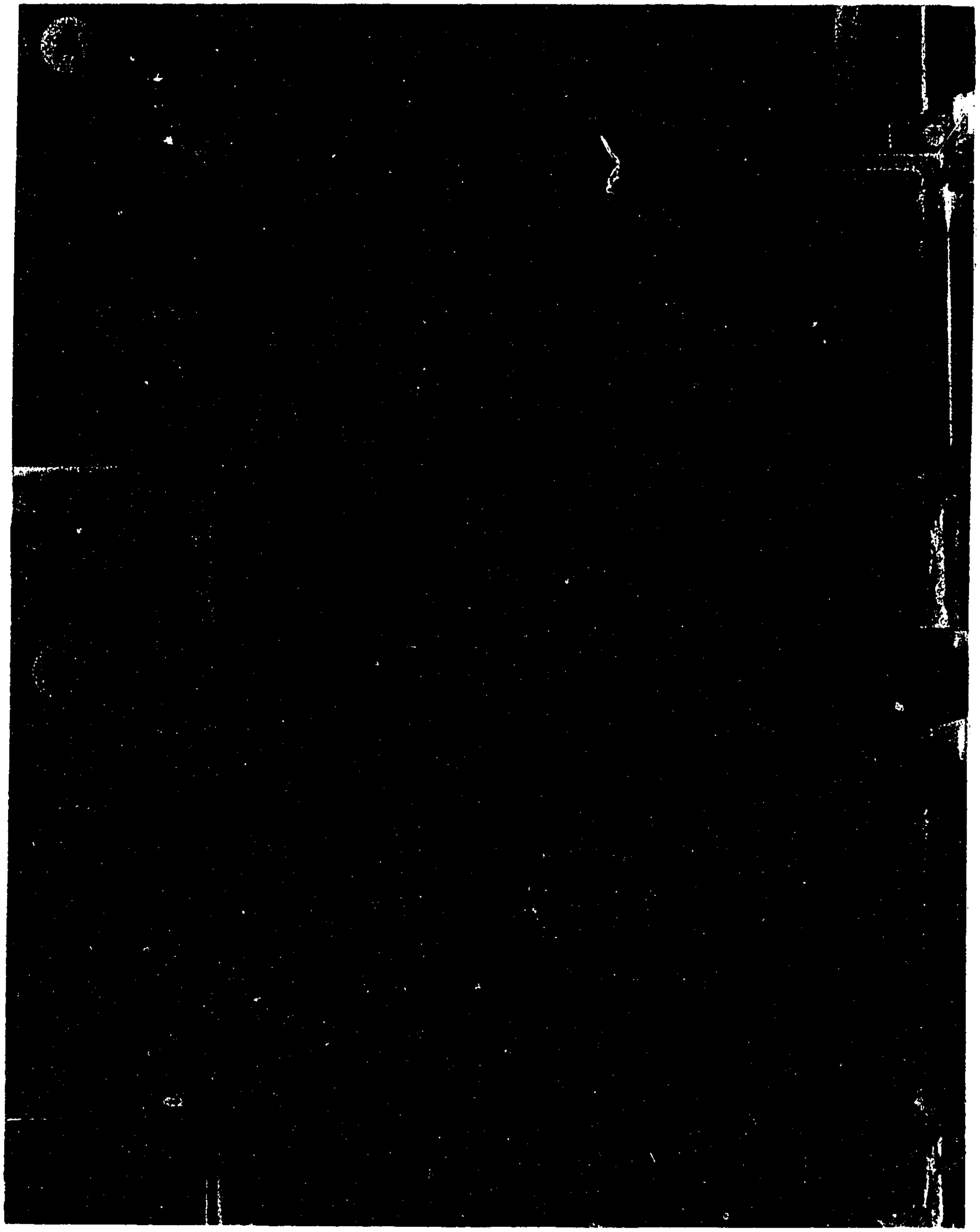


Fig. 6 Artificial and natural substrates in testing-section. **A)** Flat-plate with beveled upstream-edge: **fp**, flat plate; **m**, mirror; **ts**, testing-section. **B)** Soft deformable-substrate: **sds**, soft deformable-substrate (sand); **t**, tray; **ts**, testing-section.



3. Fluid transmissivity and filtering efficiency of labral fans of black fly larvae (Diptera: Simuliidae): Hydrodynamical, morphological and behavioural aspects

3.1 SYNOPSIS

The feeding mechanism of simuliid larvae is further elucidated by detailed study of the suspension-feeding stance of *Simulium vittatum* Zett. and examination of the water flow through their filtering appendages (*i.e.*, labral fans). Although change in body deflection with increasing water velocity is most likely passive (follows concurrent rise in flow forces), overall feeding stance is the outcome of an active feedback process between flow forces and behavioural reactions, to maintain the fans at optimal filtering position. Fans of *S. vittatum* larvae react unexpectedly to velocity increases with structural reconfiguration resulting in aperture expansion. An increasing fraction of the water directly approaching the fan aperture flows around its perimeter as velocity decreases; no flow through the fans is observed below 2.5 cm/s, and fluid transmissivity never exceeds 30-35%, even at velocities up to 50 cm/s. Calculations of suspension-feeding efficiency are reformulated to reflect labral fan transmissivity and behavioural components of the feeding process. Accordingly, *S. vittatum* larvae are shown to be 4 to 26 times more efficient at suspension feeding than previously assessed and correction factors are proposed.

The observed relationships are analysed with respect to concomitant changes in flow forces and known feeding behaviours of black fly larvae. The implications of such relationships are discussed with respect to suspension-feeding efficiency assessments.

3.2 INTRODUCTION

Black fly larvae (Diptera: Simuliidae) are among the most conspicuous and easily recognizable inhabitants of lotic ecosystems. Readily distinguished from most other benthic invertebrates by an elegant pair of hemispherical labral fans used in feeding (Fig.1), simuliid larvae are predominantly suspension feeders (collector-filterers, *sensu* Cummins 1973) although other mode of feeding such as scraping, collector-gathering, and predation have been observed (see Currie and Craig 1987 for review). As passive suspension feeders, black fly larvae rely on water flow to deliver food items to their fans. Firmly attached on the substratum by a posteroventral circlet of hooks, the larvae lean with the current and longitudinally rotate their body between 90° and 180° to expose the adoral (concave) side of their fans to the flow. The method of attachment and general orientation of simuliid larvae to the flow are well described (Barr 1984, Colbo and Wotton 1981, Chance and Craig 1986, Craig and Galloway 1987 and others), and more detailed accounts of the filter-feeding stance (*i.e.*, angles of the different body parts to the flow direction) are reported by Fortner (1937) and Schröder (1987a). Typically, as current velocity increases, larvae progressively lean with the flow, which brings the head and fans closer to the substrate. This change in feeding stance has been considered to be passive (Grenier 1949, Maitland and Penny 1967), although Kurtak (1973) and Schröder (1987a) reported differences in stance between different species exposed to similar velocities. Material captured by the fans is transferred to the mouth via mandibular and maxillary brushes, when the fans are alternately closed and the apical portion of the rays inserted into the cibarium (see Craig and Chance 1982 for review). Current velocity and particle concentration are the major components of food availability; velocity establishing the rate (*i.e.*, particle flux) at which food particles flow past the fans (Chance 1977). Kurtak (1973, 1978), Chance (1977), Schröder (1980a, 1981) and Thompson (1987b) described a decrease in efficiency of ingestion as velocity increases, whereas Lacey and Mulla (1979), and Braimah (1985, 1987b) established a curvilinear relationship between ingestion rate and water velocity, with ingestion increasing up to an optimum velocity and then decreasing. Kurtak (1978), Lacey and Mulla (1979), and Schröder (1980a) similarly found that ingestion rates reach a plateau at high food concentrations, and may decline beyond a certain concentration (Hart and Latta 1986). Other factors such as water temperature, water-borne stimulants and level of starvation also influence ingestion rates through changes in frequency of labral fan movements (*i.e.*, the labral fan flick rate, *sensu* Chance 1970; a principal component of particle handling process) (Biggs 1985, Hart and Latta 1986, Schröder 1980b). Since simuliid larvae inhabit a medium that simultaneously delivers food items to, as well as exerting forces on them, it can be hypothesized "that larvae attempt to maximize the difference between benefit and cost of a particular site by achieving water flow around the body and through the fans for maximum filtration efficiency while keeping energetic cost such as drag, as low as possible" (Craig and Galloway 1987). Study of the complex feedback interactions between fluid, body shape and particularly behaviour of the organism (behavioural hydrodynamics *sensu* Craig 1989) have recently demonstrated that hydrodynamic phenomena (*eg.*, boundary-layer thickness, boundary layer separation, solenoidal and paired vortices, and shear stress forces) play a major rôle in shaping the behaviour of black fly larvae (Craig and Chance 1982, Chance and Craig 1986, Craig and Galloway 1987, Eymann 1988, pers. com) and other suspension-feeding benthic invertebrates (Craig et al. 1989, Soluk and Craig 1988, Ciborowski and Craig 1989, Craig 1989, Lacoursière unpubl. data).

In general, the rôle of black fly larvae in aquatic ecosystems is believed to be largely qualitative (Cummins 1987); *i.e.*, as collector-gatherers mainly changing detrital particle sizes from the ultrafine transported organic matter (UTOM: 0.45 - 50μm), to fine particulate organic matter sizes (FPOM: 50μm - 1mm) more readily available to other organisms (*i.e.* by production of fecal pellets). Although black fly larvae can undoubtedly influence stream seston dynamics (Sheldon and Oswood 1977, Wallace et al. 1982), their rôle is still considered minor in most situations by some (*eg.*, Merritt *et al.* 1984, Cummins 1987). But, recent definitive studies involving eradication of simuliid larvae through use of a highly selective toxin (produced by the bacterium *Bacillus thuringiensis israelensis*), directly showed that black fly larvae reduce seston flux by 32 - 55% over a 40-m stream section (Morin et al. 1988), supporting earlier studies by Maciolek and Tunzi (1968), Ladle et al. (1972), and Voshell (1985).

It is generally suggested that only a small fraction of the particles passing through the labral fans of simuliid larvae are actually captured and ingested. Kurtak (1973, 1978), Chance (1977), Wotton (1978), Colbo and Wotton (1981), Schröder (1980a,b, 1981), Hart and Latta (1986) and others have calculated suspension-feeding efficiencies of black fly larvae ranging from < 0.01 to 12% for particle sizes studied. These low estimates of particle capture efficiency may have given the general perception that simuliid larvae account for little quantitative impact on stream seston dynamics. However, application of hydrodynamic principles indicates that the basic assumptions used in defining the efficiency of particle capture by simuliid larvae are not all appropriate.

Efficiency of particle capture by black fly larvae ($E_{(\%)}$; *i.e.*, suspension-feeding efficiency) has traditionally been defined as the ratio of the number of particles ingested per unit time to the total number of particles delivered to the labral fans during the same time interval:

$$E_{(\%)} = \frac{\text{number of particles ingested}}{\text{number of particles offered}} \quad 100 \qquad \text{(Eq. 3.1)}$$

(Kurtak 1973). Gut loading and intestinal transit time are clearly established for some species (review in Colbo and Wotton 1981, Elsen 1987), and reliable methods for estimating the amount of food ingested by larvae are also well described (Dadd 1968, Chance 1977, Wotton 1978, Ladle and Hansford 1981, Hart and Latta 1986). However, evaluation of the number of particles offered to a filter-feeding larva is not as straight forward.

Kurtak (1973) was the first to define the number of offered particles as the number of particles passing through the cross-sectional (normal to the flow) area of both fans per unit time (*i.e.*, fan aperture), with deviation of the fans from the vertical position allowed to act as a variable. However, as water velocity increases, progressive deflection of the larvae and concomitant changes in labral fan stance significantly reduces the "**effective fan aperture**" (*i.e.*, fan area projected on an axis normal to the flow direction; refered to earlier as "**effective catchment area**[1]" by Schröder 1987a,b) exposed to the flow (Schröder 1981, Chance and Craig 1986). Taking this into account, Schröder (1987b) re-assessed previously published ingestion efficiencies, and calculated increases of some 95 fold (*e.g.* 0.79% to 75.48%) concomitant with the decrease in the estimated number of offered particles. Although the underlying concept defining particle capture efficiency (Eq. 3.1) by black fly larvae is correct, the present methods of calculating the number of offered particles is inaccurate because both Kurtak's (1978) and Schröder's (1987a,b)

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[1] The term "**effective catchment area**" used by Schröder (1987a,b) to defined the vertical (perpendicular to flow direction) projection of the labral-fan aperture, is more descriptive of the total area of filter medium (*i.e.*, ratio of the total cuticle surface area of the rays and microtrichia, to the curved "hemi-ellipsoidal" surface area of the labral-fan) exposed to flow and usable for its intended purpose (*sensu* "effective filter" defined in the Filtration Dictionary of the Filtration Society 1975). I therefore refer to the projection of the labral fan aperture normal to the flow direction as the "**effective fan aperture**".

methods incorrectly assume that all water approaching the effective fan aperture from far upstream passes through the fans.

The traditional definition of efficiency of particle capture by black fly larvae, as stated by Kurtak (1973) and Schröder (1987a,b), is essentially derived from the basic standard engineering definition of filter efficiency:

$$E_{(\%)} = 1 - \frac{\text{number of emergent particles}}{\text{number of incident particles}}\ 100 \qquad \text{(Eq.3.2)}$$

(Warring 1981); which was formulated for filters incorporated in closed systems (*i.e.*, systems in which all fluid is driven through the filter by vacuum or pressure, to conteract the pressure drop[2] associated with the fluid moving through any porous structure). However, the pressure drop through a filter in open flow (*e.g.*, filter of finite dimension positioned in the centre of a flow field) can cause most of the fluid to divert around it; making the volume flow through the filtering structure a small fraction of the anticipated volume flow. The Continuity Principle dictates that, assuming fluid incompressibility, the product of cross-sectional areas (*S*) and average velocities (*U*) normal to the plane of that area (*i.e.*, $\text{Volume} = S_1U_1 = S_2U_2 = S_xU_x \ldots$), is the same anywhere between rigid walls or flow streamlines[3] (White 1986). Consequently, as water spills around the filter's perimeter, flow speed through the structure is a small fraction of the bulk flow speed (Silvester 1983). Particle capture efficiencies derived from theory always relate to the volume of fluid which is actually processed by the filter; whereas previously published suspension-feeding efficiencies of black fly larvae are inaccurately expressed in terms of an anticipated volume of fluid approaching the effective fan aperture from far upstream.

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[2] $\Delta p = p_2 - p_1$; where p_1 and p_2 are the pressures on each side of the filtering structure.

[3] In an open flow field (under steady laminar condition) streamlines (*i.e.*, line everywhere tangent to the instantaneous velocity vectors of a fluid "particle"), are analogs to rigid walls of pipes (Vogel 1981). Mapped this way, the fluid is automatically prohibited from crossing the lines forming the streamtube (*i.e.*, summation of the streamlines in a closed pattern), so that if a pair of lines diverges, the fluid must be slowing down; if a pair converges, the fluid is accelerating. In short, under these conditions the streamlines can be considered walls of a pipe.

Silvester (1983) and Cheer and Koehl (1987a,b) mathematically explored flow through fibrous biological filters in open flow field. Flow rates through rectangular-mesh nets constructed by suspension-feeding caddis-fly (Trichoptera) larvae, and concomitant efficiencies of particle capture due to the different mechanisms of filter action (*i.e.*, direct interception and diffusional deposition, *sensu* Rubenstein and Koehl 1977) were assessed in terms of the flow from far upstream approaching the mouth of the filter system (Sylvester 1983). Cheer and Koehl's (1987a) model examined general fluid movement through fibrous biological filters of finite width, to explore which aspects of morphology and relative fluid motion are important to flow through the filter. Cheer and Koehl (1987b) further evaluated several models of fluid flow through feather-like filters by comparing their predictions with observational data (male moth antenna and black fly larvae labral fans). Their studies clearly demonstrate that flow through such structures can be much slower than velocities far upstream from them. In developing their model, Cheer and Koehl (1987a) elegantly showed that the finest elements (*i.e.*, small projections) of the filtering structure are the structural features with the greatest effect on "**transmission**" (*i.e.*, the ratio of the volume of fluid actually moving through the filter to the volume that would have moved through an area equal to the filter aperture during the same time; refered to as "**leakiness**[4]" by Cheer and Koehl 1987a,b), and that water velocity as well as the general structure of such filters can be critical in determining their performance. To further illustrate the influence of small hairs and larger bristles on the portion of fluid flowing through a filtering structure, Cheer and Koehl (1987b) established that, for an upstream water velocity of 18 cm/s, fluid transmission through *Simulium*

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[4] Cheer and Koehl (1987a) refer to **leakiness** as "the best measure of the degree to which the appendage operates as a rake vs. as a paddle". Alhough the words "**leakiness**" and "**transmission**" are very similar (Oxford English Dictionary), there are substantial connotations of "waste / lost" to the term "**leakiness**". Consequently, the term "**transmission**" (*i.e.*, to go through; O.E.D.) was chosen to represent the ratio of the volume of fluid actually moving through the filter to the volume that would have moved through an area equal to the filter aperture during the same time, since the amount of particle-laden fluid processed by the filter is the primary concern in filtration process (in contrast to what is "escaping" around it).

vittatum labral fans would be 92% if the fan was composed only of rays, and reduced to only 7.8% if microtrichia were added laterally on each rays. To corroborate their findings, they subsequently compared the last estimate (*i.e.*, 7.8%), to a transmission[5] of 10 - 12.5% calculated from Craig and Chance's (1982) observation: "Water velocity can be reduced in the order of 8 - 10 times as a result of flow through the cephalic fans". This comparison should however be considered with caution since microtrichia of *S. vittatum* primary fans are borne on the upstream side of the curved rays (*i.e.*, pointing into the flow) (Fig. 2). Moreover, reanalyses of Craig and Chance's composite diagram of the paths followed by tracer particles flowing through a fan (Craig and Chance 1982; their Fig. 8, particle #2, #3, and #6), show, contrary to their estimate of 8 - 10 times, that the average velocity reduction was more in the order of only 3 to 5 times; producing an average transmission of *ca.* 25%. Nevertheless, that Cheer and Koehl's model (1987a) yielded predictions of the same order of magnitude (compared to the other models tested) as Craig and Chance's observations (1982), shows that their simple 2-D approximation of the flow through a simuliid labral fan (which is actually a much more complicated 3-D structure) has probably included the physical factors of most importance in determining transmission. Microtrichia and rays of *Simulium vittatum* larvae exposed to velocities of 3.6 - 42.6 cm/s, operate at Reynolds numbers[6] (*Re*) between *ca.* 0.04 - 0.42 and 0.17 - 2.11 respectively (Braimah 1985, 1987b). At these low Reynolds Number, changes in

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[5] Following Continuity Principle, since the same area (*i.e.*, effective fan aperture) is used in calculation of both volumes (*i.e.*, the volume of water filtered and the volume of water approaching the effective fan aperture from far upstream), transmission can therefore be expressed as the ratio of the velocities (*i.e.*, U_g / U_0; where U_g is the velocity through the filter, and U_0 is the velocity far upstream from the filter) (Cheer and Koehl 1987b).

[6] Dimensionless number representing the ratio of inertial forces to viscous forces:

$$Re = \frac{U l \rho}{\mu} \qquad \text{(Eq. 3.3)}$$

where U is the relative velocity of the object to the flow, l is a characteristic linear dimension, ρ is the fluid density, and μ the dynamic viscosity of the fluid ($\mu \ / \ \rho = \nu$, the kinematic viscosity)(White 1986). At low *Re*, viscous forces predominate and laminar flow results; high *Re* characterizes turbulent flow.

cross-sectional shape of the ray-microtrichia complex may have the same effect as a change in apparent diameter; *i.e.*, microtrichia perpendicular to flow direction (Koehl pers. com.).

Dish-shape fans with the concave side facing the flow are predominant on suspension-feeding organisms in unidirectional currents, in contrast to flat-shaped fans in oscillating-multidirectional flow, and may maximize particle capture (Warner 1977). Since water velocity and particle availability are closely related, species- and instar-specific structural differences of labral fans (*i.e.*, form, size and relative number of microtrichia-ray complex controlling the general shape of the labral fan) in relation to water flow, may account for differences in capture efficiencies of different particule types (Kurtak 1978, Schröder 1987b, Thompson 1987a, and others) and specific flow microhabitat preferences (Philipson 1956, Kurtak 1978, Gersabeck and Merritt 1979).

Labral fans of *Simulium vittatum* larvae consist of a basal stem (S) with an apical semicircular array of long, curved rays (r_1) bearing a single row of microtrichia (m) on their inner-curved surface (*i.e.*, facing the flow), namely the primary fan (F_1) (Fig, 2a,b). A second group of finer rays (r_2) refered to as the secondary fan (F_2) are deployed on the medio-basal portion of the stem (Fig. 2a) and believed to deflect flow into the primary fan, keeping the basal spaces between the primary rays free of particles (see Chance 1970, and Craig 1974 for review of labral fan morphology). The rays and microtrichia are coated with a mucosubstance, which is thought to increase adhesion of intercepted particles (Ross and Craig 1980).

The basic principle underlying flow through a fibrous obstruction, considers flow circulation around each element of the filtering structure (Silvester 1983, Cheer and Koehl 1987a,b). Whenever a viscous fluid flows over a solid surface, the layer of fluid in contact with the surface sticks to it and a velocity gradient develops (*i.e.*, arising through subsequent deceleration of adjacent fluid layers[7] due to the influence of fluid viscosity) between the solid surface and the freestream flow (Vogel 1981, White 1986). The lower the *Re* (*i.e.*, the smaller the object, or the slower the relative velocity at fixed kinematic viscosity) the more gentle is this velocity gradient and the thicker, with respect to the dimensions of the object, is the zone of fluid out to which the viscous effect extends. As mathematically demonstrated by Cheer and Koehl (1987b), the amount of fluid slowed down around each ray-micritrichia complex is the driving phenomenon controlling flow through the labral fans of simuliid larvae (Fig. 2b). Invoking the principle of dynamic similarity[8] (Schlichting 1987, Vogel 1981, White 1986), Braimah (1985, 1987a,b) calculated from a scaled-up model of portion of a labral fan, the thickness of the shear gradient layer[9] surrounding rays and microtrichia of *Simulium bivittatum* Malloch larvae. Distance between adjacent rays and thickness of the shear gradient layer around each ray-microtrichia complex indicated that there is little or no flow between rays up to velocities of about 9.8 cm/s. From Braimah's calculated shear gradient layer thickness for rays and microtrichia of live larvae and scaled-up models (his tables 3 and 4; 1985), it can be estimated, given a 25µm wide gap between adjacent rays (Braimah 1987a), that shear gradient layers occupy almost the entire gap (*ca.* 97%) at velocity of *ca.* 3.6 cm/s, and the

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[7] Although uniform fluids do not partition in layers, the term "layers" is herein used to facilitate visualization of the processes

[8] Flow about geometrically similar bodies (different linear dimensions) immersed in different fluid moving at different velocities are similar, if at all geometrically similar points, the forces (inertial and viscous) acting on a fluid particle bear a <u>fixed ratio</u> at every instant of time (Vogel 1981, White 1986). In short, equality of Reynolds number for two flows means that the physical character of the flows will be the same:

$$Re_m = Re_l = \frac{U_m l_m}{v_m} = \frac{U_l l_l}{v_l} \qquad \text{(Eq. 3.4)}$$

where Re is the Reynolds Number; U_m, the velocity of the model, l_m, the characteristic length of the model, v_m, the kinematic viscosity of the fluid surrounding the model, U_l, the velocity of the water approaching the larval ray-microtrichia complex, l_m, the characteristic length of the larval ray-microtrichia complex, and v_m, the kinematic viscosity of the water.

[9] The shear gradient layer thickness is defined as the distance normal to the surface of the microtrichia or ray, which is required for the local velocity to reach 99% (Vogel 1981, White 1986) of the ambient flow velocity (*i.e.*, flow upstream from the rays).

zone of viscous effect rapidly decreases as velocity increases (*ca.* 57% at 10 cm/s; 43% at 20 cm/s; 35% at 30 cm/s) to eventually stabilize at ambient velocities (*i.e.*, velocity through the labral fans) above 30 cm/s (*ca.* 28% at 40 cm/s). That is, the pressure drop produced by the structure and surrounding shear gradient layers can cause most of the fluid approaching the labral fan from far upstream to divert around its perimeter if mainstream velocity is below a certain value.

Knowledge of the different components involved in the filtering processes of suspension-feeding of simuliid larvae is still fragmentary. Although relationships between components of the particle handling process and ingestion rates have been examined, particle capture efficiency has yet to be experimentally explored. Accurate calculations of the amount of water processed by the labral fans will help to quantify more precisely the rôle played by black fly larvae in the transport and processing of suspended material in running water systems (*i.e.*, nutrient spiralling *sensu* Webster 1975). These data could also be incorporated in models used to determine the lethal dosage of particulate insecticide formulations, increasing accuracy and thus minimizing operational costs and impact on nontarget species.

The goal of this study was to assess the flow transmissivity of the labral fans of mature *Simulium vittatum* Zett. larvae, in relation to increasing freestream velocity and concurrent labral fan deflection. Labral fan aperture size and deflection angle, the two components of effective fan aperture, were analysed relative to water velocity changes. I also examined in detail the progressive deflection of the body regions as freestream velocity increases, which establishes the overall suspension-feeding stance. The observed relationships are analysed with respect to concomitant changes in flow forces and known feeding behaviours of black fly larvae. The implications of such relationships are discussed with respect to assessment of suspension-feeding efficiencies.

3.3 MATERIAL AND METHODS

Simulium vittatum Zett. larvae were collected from Pyramid Lake outlet (Alberta; 52° 55' North, 118° 06' West) during the months of February and March, and kept in the laboratory at temperatures of*ca.* 2-4°C and light regime of*ca.* 16hr dark and 8 hours light using the short-term maintenance system described by Lacoursière and Boisvert (1987). All experiments were conducted at constant flow velocities (coefficient of variation of less than 1%), in a small recirculating flume described in detail by Lacoursière (1989). Water velocities were monitored with a portable velocity meter (Novonics Kent Miniflow 265 & 422, Nixon Instrumentation Ltd.) using a 1.0 cm diameter, five-bladed rotor mounted on jewel bearings (free-propeller probe # 649 s/l). Velocities were sampled at frequencies of 28 to 280 Hz for periods up to 60 sec, with an APPLESCOPE-D2 system (RC Electronics Inc., 7265 Tuolumne St., Goleta, CA93117, USA) on an Apple II+ personal computer. A digitized version of the output (*i.e.*, current signal proportional to the water velocity) was analysed for sample statistics (*i.e.*, mean velocities, standard deviations and coefficients of variation) on an Apple II+ personal computer using a short Basic™ program (modified from J.J.H. Ciborowski, University of Windsor, Ontario, Canada). Observations were recorded with a JVC® colour Video Camera (model no. GX-S700U), and a Panasonic VHS Omnivision II Video Cassette Recorder (model no. AG-6200. EIA Standard: 30 frames/sec) connected to a Panasonic Time-Date Generator (model no. WJ-810). Micro-Nikkor® 55-mm (f/3.5) and Carl Zeiss Luminar® 25-mm (f/3.5) & 40-mm (f/4.5) lenses were used in conjunction with extension tubes, and C-mount adaptors to produce magnifications of 10 to 96 fold. Measurements were taken with a vernier caliper and a protractor, from a JVC® Video Monitor flat-screen (model no. TM-R9U), using frame-by-frame analysis (Panasonic Remote Search Controller NV-A505). Measurements from the monitor were calibrated by recording the vernier caliper at all magnifications. Illumination was provided by fibre optic lights (Intralux® 6000, Volpi, Zürich), and an auxiliary UV-light source (General Electric co., # F1518-BL fluorescent tube) was used to increase tracer fluorescence (fluorescein sodium in aqueous solution). Back lighting and lateral lighting provided adequate contrast between specimens and backgrounds.

Larval suspension-feeding stance (*i.e.*, labral fan, cephalic, thoracic, and abdominal deflection angles; longitudinal body rotation and body yaw) and changes in labral fan aperture size in relation to water velocity increase, were studied using unfiltered stream water at temperature of*ca.* 2-4°C. About 30 larvae (6th and 7th instar) were placed in a flume on the upper surface of a flat-plate (with a beveled upstream edge) held parallel to the flow direction (in the centre of the test-section), and allowed to acclimate for 12-16 hours. Subsequent acclimatation periods of 5 min followed each velocity change. Deflection angle and fan aperture measurements were taken on at least 15 larvae, with 20 measurements per larva, per velocity (*ca.* 5 measurements s^{-1} of recording; every other second recorded was analyzed over a total recorded period of 7s). High-plant-content fish food (Tetra®, Federal Republic of Germany) and yeast (Engedura, Edward Agencies, Winnipeg, Canada) were added in small quantities (0.005-0.1g dry weight per litre) following larval transfer to the flume, to stimulate suspension-feeding.

Cephalic (C°), thoracic (T°), and abdominal (A°) deflection angles are defined as the deviation of the medial portion of the structure from the vertical axis intersecting the first upstream segment of the structure (*i.e.*, perpendicular to the flow at 0° deflection), and longitudinal body rotation (R°) is defined as the deviation from the position where the entire length of the ventral nerve cord and ganglia (visible through the ventral abdominal and thoracic wall) are facing the substrate (Fig.1a, 3). Overall deflection (D°) is defined as the deviation from the vertical axis originating at the attachment site, of the first thoracic segment closest to the substrate (*i.e.*, first thoracic segment in contact with the substrate at maximum deflection of 90°). Abdominal and thoracic yaw angles are defined as the deviation from the plane defined by the flow direction (observed through the transparent substrate via a 45° angled mirror; Lacoursière 1989). Labral fan deflection angle (θ) is defined as the deviation from the vertical axis (*i.e.*, position perpendicular to the flow direction which would yield maximum cross-section of the filtered water column), of the plane outlined by the labral fan aperture (d_x) (Figs. 1b, 3, 4). Since *Simulium vittatum* larvae demonstrate little labral fan yaw (*i.e.*, deviation from the horizontal axis), angle variation is allow to act as a variable.

Labral fan aperture[10] (d_x) is defined as the distance between the apex of opposite rays, taken at midfan width (*sensu* Chance 1970) (Fig. 1b, 4). To compensate for variations in aperture size inherent to individuals and larval stages, the standardized labral fan aperture increase (A_i) is expressed as:

$$A_i = \frac{d_x}{d_{min}} 100 \qquad \text{(Eq. 3.5)}$$

where d_x is the diameter of the fan observed at a flow velocity U_x, and d_{min} is the fan diameter observed at the lowest velocity tested for that fan.

Study of flow through the labral fan of dead larvae in relation to water velocity increase was conducted at room temperature (*ca.* 18°C) using dechlorinated tap water

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[10] Although the rays cover an angle of 200 - 250° when fully deployed (Chance 1970), changes in area (*i.e.*, aperture) are expressed as ratios of the different diameters (distance between apex of opposite rays), since only variations (in contrast to estimations *per se*) in the two components (area and velocity) that define the volume of water filtered by a labral-fan are considered in this study.

filtered to remove all particles (> 0.45μm). Black fly larvae (6th and 7th instar) killed rapidly in Carnoy's solution (3:1 solution of 98% ethanol and glacial acetic acid), display fully abducted labral fans. Larvae were kept in fresh Carnoy's solution for at least a week before being carefully selected for complete expansion of both labral fans to correspond to the aperture measurements observed on live specimens suspension feeding at low flow velocities (*ca.* 5-10 cm/s). A single fixed larva was suspended (upside down in the centre of the flume testing-section) by the tip of the abdomen, using an extremely fine point, self-closing Microdissection Forceps (# 14 W 1011, Ward's Natural Sciences Ltd., Mississauga, Ontario, Canada) mounted on translation stages to allow multi-directional motion. Larvae were positioned facing the flow direction, and their angle adjusted to tilt the labral fans (hereafter refered as "static fans", in contrast to the "dynamic" fans of actively filter-feeding larvae) into pre-selected angles (between -30° and +30°). Flow patterns were visualized by injecting an aqueous solution of Fluorescein sodium dye through a micropipet (0.5 mm outside diameter) firmly positioned on a rack-and-pinion micro-manipulator, upstream of the fully abducted labral fans.

The effective fan aperture (EFA_x) is defined as the area horizontally projected on a plane perpendicular to the flow direction (*i.e.*, incorporating fan aperture increase and deflection). Given that we are more interrested in changes of fan aperture[10], the effective fan aperture can be represented by its diameter only, and can be expressed consequently as:

$$EFAd_x = d_x \cos\theta \qquad \text{(Eq. 3.6)}$$

where d_x is the fan diameter observed at water velocity U_x, $EFAd_x$ is the corresponding diameter of the effective fan aperture, and θ is the deflection angle. The standardized effective fan aperture variation (Δ EFA) is defined as:

$$\Delta\, \mathbf{EFA}_{(\%)} = \left(\frac{\mathbf{EFAd_x}}{\mathbf{EFAd_{min}}} - 1\right) 100 \qquad \text{(Eq. 3.7)}$$

where $\mathbf{EFAd_{min}}$ is the diameter of the effective fan aperture estimated at the lowest velocity tested for this fan.

The transmission coefficient (e_t) is defined as the ratio of the volume of water actually passing through a labral fan (*i.e.*, $EFA_x\ U'_x$), to the volume that would have passed through an area equal to its effective fan aperture (*i.e.*, the reference volume: $EFA_x\ U_x$) for the same unit time (Fig. 4). By the Continuity Principle, a thin streak of tracer-dye injected upstream of a labral fan should be deflected (*i.e.*, following the diverging streamlines) as the water decelerates upon approaching the effective fan aperture. Consequently,

$$\mathbf{EFA_x\, U'_x = STA_x\, U_x} \qquad \text{(Eq. 3.8)}$$

where EFA_x is the effective fan aperture, U'_x the ambient velocity through the labral fan, STA_x the cross-sectional area of the filtered streamtube, and U_x the mainstream velocity.

The diameter of the streamtube (STd_x) was found by determining, with a stream of dye, the diverging streamlines (*i.e.*, streaklines: instantaneous photograph of a stream of dye) that made contact with the top and bottom edges of the fan perimeter (Fig. 4). The volume of water approaching the labral fan from far upstream (volume that would have passed through an area equal to its effective fan aperture) is equal to the product of the EFA_x and the mainstream velocity (U_x). Consequently, since the effective fan aperture is represented by its diameter only, and the mainstream velocity (U_x) is used in estimating both volumes (*i.e.*, the volume of water filtered and the volume of water approaching the effective fan aperture from far upstream), the transmission coefficient can be expressed as:

$$e_t = \frac{U_x \, STA_x}{U_x \, EFA_x} \propto \frac{STA_x}{EFA_x} \propto \frac{STd_x}{EFAd_x} \qquad \text{(Eq. 3.9)}$$

where $EFAd_x$ is the diameter of the effective fan aperture. A maximum transmission coefficient of "1" (*i.e.*, 100%) implies that all water approaching the effective fan aperture from far upstream passes through the labral fans. The transmission coefficient of static fans was estimated for labral fan deflection of ± 30°, and mainstream velocities between 2.5 and 70 cm/s.

Assessment of the initial non-linear regression equations are based on procedures delineated by Jensen (1984) for development of structured regression hypotheses, and these were subsequently tested and adjusted through a best-fit analysis (least squares method) executed with the non-linear regression module of SYSTAT™ (Systat, Inc., Illinois, USA) on a Macintosh™ (Apple computer Inc.) personal computer. Figure 11a was generated using the "Smooth = Local" function of the Graph™ module of SYSTAT™ (Systat, Inc., Illinois, USA), which produces a locally weighted (*i.e.*, every patch on the surface requires four weighted multiple regressions on the points) three dimensional surface. Other graphics were generated using Cricket Graph™ (Cricket Software Inc., Philadelphia, USA), and MacDraw II™ (Apple computer Inc.) softwares.

3.4 RESULTS AND DISCUSSION

3.4.1 Suspension-feeding stance. As mainstream velocity increases *Simulium vittatum* larvae lean progressively with the flow bringing the head and the labral fans in proximity to the substrate. Changes in angles of deflection (*i.e.*, abdominal, thoracic, and cephalic) and yaw appear to be passive, since larvae in a group oscillate together as velocity is altered rapidly. Further, the overall angle of deflection of dead larvae still anchored to the substrate changes similarly with velocity (Grenier 1949, Chance 1977, pers. observations). Analysis of abdominal, thoracic, cephalic and overall deflections, and longitudinal body rotation[11] however, shows that larvae of the same size exhibit a wide variety of postures at water velocities of 5 - 15 cm/s (Fig. 5). In that velocity range, larvae can stand vertically into the flow (body rotation of *ca.* 180°, and almost no thoracic deflection) or lie on their side with their thorax almost in contact with the substrate (body rotation of *ca.* 90° and thoracic deflection of *ca.* 90°). High abdominal and thoracic yaw angles are usually associated with low body rotation (which is always higher than 90°) and cephalic deflection. Some larvae have been observed filter feeding on their back (body rotation of *ca.* 180°, thoracic deflection of *ca.* 90°, and little cephalic deflection), but on average *Simulium vittatum* larvae exposed to low velocities (5 - 15 cm/s) reach high into

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[11] Technical difficulties prevented accurate analysies of changes in yaw angles (abdominal and thoracic) with velocity increases. However, qualitative observations suggest that the relations to velocity increases are similar to all the other angles studied (*i.e.*, variability decreases as the water velocity approaches 25-30 cm/s).

the flow to present the maximum fan aperture to the particle-laden fluid. Larvae do not usually remain in low velocity currents. Suspension-feeding stance is readily modified following even small disruptions (*eg*. contact with neighbours, vibrations or shadows); consequently greater time is spent probing (*sensu* Eymann and Friend 1988) and moving along the substrate as velocity decreases toward 5 cm/s. Such movement was also observed by Wotton (1985) on *Simulium noelleri* larvae, and Chance and Craig (1986) on *S. vittatum* larvae.

As mainstream velocity increases (> 15 cm/s), suspension-feeding stance becomes less variable among larvae and they demonstrate more tolerance to disruptions. While abdomen, thorax and head are brought closer to a horizontal angle, longitudinal body rotation increases simultaneously toward 180° (*i.e.*, maximum roll) to keep the labral fans from colliding with the substrate[12] (hampering full deployment of the rays). Significant decrease in angle variability of all body-sections as water velocity increases to *ca*. 25 - 30 cm/s, suggests that ability to assume diverse stances is strongly impeded by increasing velocity and associated flow forces. These observations are congruent with the relationship observed between water velocity and drag forces acting on a single filter-feeding larva of *Simulium vittatum* (Eymann 1988). Drag increases progressively as velocity reaches *ca*. 25 - 30 cm/s, increases suddenly *ca*. 1.8 fold between 30 - 35 cm/s, and then subsequently shows progressive increase with velocity (Eymann 1988). At high *Re*, drag forces acting on an object are directly influenced by the extent of the frontal area exposed to the flow (*i.e.*, maximum projection of the object onto a plane perpendicular to the downstream direction), and the square of the object speed (*i.e.*, U^2) relative to the fluid (Vogel 1981, White 1986). Since the frontal area of *Simulium vittatum* larvae exposed to the flow does not change significantly above velocities of about 30 cm/s

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[12] Although very uncommon, larvae of *Simulium vittatum* have been observed laying on the substrate with their prothoracic leg anchored into a silk pad, filter-feeding with both labral fans alternately abducted in mainstream velocities between 0 and 60 cm/s (laboratory conditions) (personal observations).

(Chance and Craig 1986, Eymann 1988), Eymann (1988) suggested that changes in three-dimensional flow patterns surrounding a larva as velocity reaches 30 cm/s were the result of an abrupt variation in the rate of increase of the flow forces acting on the organism. The significant decrease in angle variability of all body-sections as water velocity increases to 25 - 30 cm/s is consistant with this hypothesis, but also suggests a combined behavioural influence (see section 3.4.2).

The overall body deflection of *Simulium vittatum* larvae increases rapidly up to approximately 79° as velocity reaches 35 cm/s, after which it increases more slowly to *ca.* 84° at maximum velocity investigated (50 cm/s). Comparable maximum overall deflection angles[13] (*ca.* 78°) were also observed by Chance and Craig (1986) on *S. vittatum* larvae as velocity reached 70 cm/s. Similarly, Fortner (1937) and Schröder (1987a) established in more detail, for different simuliid species, comparable relationships between deflection angles of the different body-sections and mainstream velocity.

While thoracic deflection demonstrates the highest plasticity, variation in abdominal deflection angle is relatively limited and probably reflects the influence of the posterior abdominal shape of the larva (*i.e.*, bulginess of segments 5-8 and relative position of the posteroventral circlet of hooks on the last abdominal segment). *Simulium vittatum* larvae exhibit a minimum abdominal deflection of 42°, standing in velocity of 5 cm/s; whereas the maximum deflection angle of 75° is attained as velocity reaches *ca.* 35 cm/s (Fig. 5). Larvae of other simuliid species differ in shape from that of *Simulium vittatum*, and one should expect differences in medians and range of abdominal deflection angles associated with larvae inhabiting habitats with different flow characteristics. Such comparison to other species is only partially achievable since detailed information about

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[13] Chance and Craig's (1986) deflection angle is defined as the deviation from the vertical axis intercepting the attachment point, of the median longitudinal axis of the body (*i.e.*, from the attachment point to the centre of the cephalic capsule). Consequently, the achievable maximum deflection is ca. 85° (*i.e.*, ca. 5° to account for half the thickness of the body).

body shape is usually not given. However, from Schröder's (1987a) data, significant ($P < 0.05$) differences between the average minimum abdominal deflection angles (observed at the lowest velocity of 5 cm/s) of some European black fly species can be made. Further, *Simulium vittatum* larvae can stand into the flow at angles 10 to 13° closer to the vertical than some of the European species ($P < 0.002$) at velocities of 5 cm/s. Since velocity ranges covered by Schröder (1987a) did not extend far enough to establish either the full deflection ranges or the maximum deflection angles of each species, further comparisons are impossible. Nevertheless, I hypothesize that larvae inhabiting swift flows will have a posterior abdominal shape allowing a more acute angle with the substrate (*i.e.*, thinner, less bulbous posterior end) than larvae of species found in slower flow.

In short, deflection (*per se*) is most likely passive (*i.e.*, follows concomitant increase in flow forces; Eymann 1988), but control of the overall suspension-feeding stance is an active process most likely maintaining the filtering appendages in adequate flows.

3.4.2 Labral fan deflection. As mainstream velocity increases, labral fans of black fly larvae lean progressively with the flow following two distinct sequences separated by a zone of transition at *ca.* 30 cm/s (Fig. 6). Little or no deflection was observed at velocities below 10 cm/s, and in consequence the fans are positioned dominantly perpendicular to the flow. As velocity increases, fans deflect gradually from the vertical position to stabilize at *ca.* 15° at velocities of 25 - 30 cm/s, following a curvilinear relationship estimated as:

$$\theta = -0.34 - 0.5\,U_x + 0.0985\,U_x^2 - 0.0022\,U_x^3 \qquad \text{(Eq.3.10)}$$

($5 < U_x < 30$ cm/s; $n = 25$, $r^2 = 0.97$). Further increases in velocity quickly induce a sharp increase in fan deflection until it asymptotically approaches angles between 30 to 35° at velocities of 45 - 50 cm/s, following a curvilinear relationship estimated as:

$$\theta = -268.1 + 17.39\,U_x - 0.33\,U_x^2 + 0.0021\,U_x^3 \qquad \text{(Eq.3.11)}$$

($30 < U_x < 50$ cm/s; $n = 25$, $r^2 = 0.96$).

Correlations between labral fan position and water velocity are well documented for larvae of a few black fly species (Fortner 1937, Schröder 1987a). In most cases, the relationships are asymptotic in nature (*i.e.*, fans progressively deflect toward a certain limit angle, as free-stream velocity increases), even though according to Schröder (1987a) some species show no special orientation of their fans to the current. Although velocity ranges were similar to those tested in this study, no discontinuity in the relationships is indicated by these authors. However, reanalysis of data about the deflection of *Simulium cryophylum* labral fans with increasing water velocity, given by Schröder[14] (1987a; his table 2, page 43), clearly demonstrate a sharp discontinuity in the rate of deflection as water velocity approaches 30 cm/s (Fig. 6). By subtracting drag on a larva with its fans adducted, from drag on the same larva with its fan abducted, Eymann (1988) estimated drag on labral fans to be directly proportional to water velocity (*i.e.*, linear relationship). However, in light of the new findings presented here, the same data set[15] (Eymann 1988, his figure 4) was reanalyzed (Eymann pers. com.), and a discontinuity in the relationship between drag forces on labral fans and water velocity was shown when velocities reached

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[14] *Simulium cryophylum* was selected from Schröder's data set for the broad velocity range covered in the experiment.

[15] Analysies were made on only one of the two larva used by Eymann (1988). A curvilinear relationship between water velocity and labral fan deflection was shown for water velocities between 5 and 30 cm/s only; insufficient data points beyond this velocity range did not allow further analysies.

approximately 30 cm/s (Fig. 6). This strong positive correlation between deflection of the labral fans and drag forces acting on them, would initially suggest that deflection of the filtering apparatus from the vertical stance is strictly passive in nature (*i.e.*, controlled by the flow forces). Examination of the same relationship within the overall feeding-stance context however, shows differently (see below).

While abdomen and thorax make progressive contact with the substrate as mainstream velocity rises to 25-30 cm/s, the relative angle between head and thorax increases rapidly as the angle between labral fans and head decreases (Fig. 7b). In contrast to the rapid increase in labral fan deflection angle that should result from a rapid increase in head deflection toward the substrate, the labral fans are maintained actively at a lesser degree of deflection through a compensatory reduction in head-labral fan angle. Sharp decrease in relative angle between the head and the thorax (Fig. 7b), combined with a longitudinal rotation of the body of about 180°, probably positions the labral fans away from possible turbulence, originating from interference flow between the lower body parts and the substrate, to re-expose them to the mainstream flow. Consequently, as labral fans protrude into the flow, drag forces acting on them probably account for a large portion of the increase in overall drag as observed by Eymann (1988) at velocities *ca.* 30 cm/s. From Eymann's (1988) equations that relate drag forces on an ovoid wire by itself to one of nine different filter-feeding larvae of *Simulium vittatum* attached to it, I calculated the increase in drag[16] on a filter-feeding larva to be approximately 0.52 x 10^{-4} Newton as the velocity rises from 30 to 35 cm/s. It therefore appears that *ca.* 60% (0.32 x 10^{-4} Newton[17]) of the change in overall drag of a filter-feeding larva can be accounted for by the abducted labral fans. Although the abrupt changes in angles between adjacent body parts (*i.e.*, relative angles) observed as velocity approaches 25-30 cm/s (Fig. 7a, b) are

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[16] Drag on a black fly larva was calculated by substracting the drag on the ovoid wire from the overall drag on larva plus wire.

[17] From figure 4.

consistant with Eymann's (1988) hypothesis of a sudden shift in three-dimensional flow patterns surrounding a larva as velocity reaches *ca.* 30 cm/s, they also suggest that the angle at which the labral fans are held in relation to the head, and consequently against the flow, is under active control. Positioning (*i.e.*, resisting to flow forces) of the labral fan is most likely controlled by the powerful fan-flexing muscle (posterior frontolabral muscle 61 in the nomenclature of Craig 1974) attached to the torma of the fan base in *Simulium* larvae. As a result of these observations, the overall stance of a filter-feeding larva can consequently be seen as the outcome of a feedback system between flow forces and behavioural reaction (Fig. 8).

As the three-dimensional flow around the larva is modified through variation in velocity or flow disturbances and behavioural responses, flow forces shift accordingly, and biomechanical changes are imposed on the larval body. In response to these changes, larvae may or may not choose to rectify their stance in order to (most likely) optimize suspension-feeding. Moreover, it is probably more energetically costly to close the labral fans and stand against the flow as the water velocity gradually increases, and past a certain threshold (30 cm/s for *Simulium vittatum*) more sound for the larvae to simply "go with the flow" and assume a more streamlined stance. Further studies involving oxygen consumption under set food flux (*i.e.*, the product of particle concentration and water velocity) and hydrodynamic flow conditions are required to elucidate the energetic costs of life in lotic environments.

3.4.3 Labral fan reconfiguration. Although never observed previously, I discovered that labral fans of black fly larvae adjust to flow velocity changes by way of structural reconfiguration. Increases in labral fan aperture of nearly 20% were observed for both suspension-feeding larvae and static fans (Fig. 9). Qualitative observations revealed that, in both situations, fan aperture increase is primarily a consequence of progressive motion of the ray bases at their attachment to the fan stem; whether it is the result of cuticular distortion of the ray bases, or a simple hinge motion of the articulation, is unresolved at this point (see Chance 1970, Craig 1974, and Davies 1974 for review of labral fan structures). The relation between flow velocity and labral fan aperture increase differ for static fans and dynamic fans (Fig.9). In both situations, labral fans show little or no variation in aperture at flow velocities < 5 - 8 cm/s. For the static fans, successive increments in flow velocity induce progressive increase of the fan aperture, as seen by the gentle curvilinear relationship displayed between aperture increase (A_i) and flow velocity (U_x):

$$A_i = 0.69 + 0.0539\,U_x + 0.0055\,U_x^2 \qquad \text{(Eq. 3.12)}$$

($0 < U_x < 55$ cm/s; $n = 28$, $r^2 = 0.78$). This progressive opening of static labral fans most likely reflects the gradual increase in flow forces on the whole filtering structure, as suggested by similarity to the relationship between velocity and drag forces on a bluff body (*i.e.*, object not having a streamlined profile), where it is commonly postulated that for such a shape, drag is proportional to the square of the velocity (Vogel 1981, White 1986). Qualitative observations showed that further increase in flow velocity (> 55 cm/s), induced significant deformation of ray shape (*i.e.*, decrease in ray curvature), principally near the tip of the rays. Preliminary examination suggests that deformation is not permanent, since no significant difference in fan aperture was observed on labral fans consecutively exposed to extreme increases and decreases in water velocities. Because structural deformation of the primary rays is associated with ray wobbling and fan oscillation, which ultimately induces fan collapse, aperture increases observed at velocities greater than 55 cm/s are considered unreliable. It is doubtful that such an extreme situation (fans held perpendicular to the flow direction at high flow velocities) arises under natural conditions, since labral fans of suspension-feeding larvae are of course free to deflect into the flow.

Conversely, dynamic labral fans displayed rapid aperture expansion as water velocity increased progressively from 10 cm/s to 25-30 cm/s, as described by the following relationship:

$$A_l = 1.23 - 0.74\,U_x + 0.1\,U_x^2 - 0.0021\,U_x^3 \qquad \text{(Eq. 3.13)}$$

($0 < U_x < 30$ cm/s; $n = 18$, $r^2 = 0.97$), where aperture increase[18] stabilized near 20% .

Like the relation between dynamic fan deflection and water velocity, aperture increase of dynamic fans displays a strong correlation with flow forces acting on the filtering apparatus (*i.e.*, drag estimated by Eymann 1988; Fig. 6). Such congruence, suggests passive deformation (*i.e.*, aperture increase) of the labral fans as water velocity increases. There is no muscle responsible for the abduction (unflexing) of the fan (Craig 1974, Davies 1974). Therefore, the marked departure from the relationship between water velocity and aperture increase previously established for static fans, most likely reflects the difference in the type of flow passing through the dynamic fans (*i.e.*, possible flow deflection toward the fans, induced by the flow interraction between flow patterns above the substrate surface and around the larval body). However, although blood-pressure change alone cannot fully account for the abduction mechanism (storage of elastic energy and maintenance of blood-pressure in the base of the fan base are necessary in fan abduction), increase in absolute blood-pressure should not be discarded as a mechanism by which overall fan aperture could be controlled.

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[18] Because observation of individual ray curvature were done at the limit of visual resolution, increased fan oscillations associated with higher velocities, prevented accurate measurements of the fan aperture past velocities of 30 cm/s.

3.4.4 Effective fan aperture (EFA). The effective fan aperture (EFA_x) presented to the flow changes as labral fan aperture (d_x) and angle of deflection (θ) adjust to increased water velocity (U_x) (Fig. 10). Contrary to Schröder (1980a, 1987b) who assumed that effective fan aperture slowly decreases as velocity increases, the effective fan aperture of a *Simulium vittatum* larva actually increases as water velocity reaches 30 cm/s. The present work shows that within the velocity range *ca.* 5-30 cm/s, increases in labral fan aperture diameter offsets the loss in effective fan area caused by deflection alone. Lack of data for water velocities higher than 30 cm/s, prevents reliable estimates of further effective fan aperture changes. Nevertheless, if one assumes that fan aperture remains constant past velocities of 30 cm/s, a decrease in effective fan aperture should be expected. However, as suggested by the increase in drag on the labral fans as velocity increases past 30 cm/s (Fig. 6, Eq. 3.10), decline in effective fan aperture would be less acute as the fan would open further with additional velocity increases (Fig. 10). Consequently, once a particular velocity is reached, further increase in velocity reduces the effective fan aperture exposed to the flow, and the concommitant increase in volume of filtered water. This later observation probably accounts in part for the decrease in feeding efficacy observed by Lacey and Mulla (1979) on *Simulium vittatum* larvae at velocities > 40 cm/s, and by Braimah (1985, 1987b) on *S. bivittatum* as velocity reached 15-25 cm/s. Although these findings disagree with Chance (1977) who showed a decline in feeding efficacy of *S. vittatum* larvae as velocity decreased (velocity range studied: 3.7 - 34.8 cm/s), they are consistent with Kurtak's (1973, 1978) observations on *S. vittatum* larvae, which showed a decrease in feeding efficacy as velocity increased from beyond a water velocity of 30 cm/s. Since Kurtak (1973, 1978) only covered a range of experimental velocities between 30 and 70 cm/s, he probably only observed the declining portion of the relationship. In light of the new findings presented here, Schröder's (1987b) re-assessments of previously published filter-feeding efficiencies accounting for reduction in EFA caused by labral fan deflection (*e.g.* 95 fold increase; 0.79% to 75.48%) are probably over-estimates, since for those species, increases in labral fan aperture might also offset the loss in effective fan area caused by deflection. Concurrent increase in labral fan aperture and deflection angle therefore directly governs the reference volume (*i.e.*, volume of water approaching the effective fan aperture from far upstream) critical in assessing fluid transmission, hence particle-flux and particle capture efficiency.

3.4.5 Fluid transmission through "static" labral fans. To my knowledge, this is the first time deflection of a dye streakline (hence the continuity principle) is used to define the volume of water filtered by a biological filter.

As mainstream velocity increases, a larger portion of water approaching the effective fan aperture from upstream passes through the labral fans (*i.e.*, filtered cross section of the water column increases with velocity) (Fig. 11a). At low velocities (5 - 10 cm/s), most of the incoming water is deflected around the perimeter of the static labral fan (Fig. 1b) leading to low coefficients of transmission (0.04 - 0.24). As water velocity increases, fluid transmission through the static labral fan rises with maximum increases observed at deflection angles between -5° and +15°. When held against the flow, static labral fans exposed to free-stream velocities exceeding 55 - 65 cm/s, exhibited increasing ray wobbling followed by fan collapse, inducing unpredictable leaps in transmission. Thus for *Simulium vittatum*, transmission coefficients are unreliable for this range of velocities and deflection angles. Within the velocity range analysed (5 - 70 cm/s), the transmission coefficients of *S. vittatum* static labral fans never exceeded values of 0.5.

It has been shown earlier that dynamic and static labral fans demonstrate different responses (*i.e.*, fan aperture) to identical mainstream velocities. These dissimilarities are most likely the result of behavioural and biomechanical reactions to dynamically induced flow patterns around the larval body. Consequently, direct assessment of the transmissivity of a static labral fan not only delineates the basic flow through such porous structure, but also provides a "base-line transmissivity" (*i.e.*, related to structural limitations) to which velocity preferences of living simuliid larvae can be contrasted.

Velocity preference of black fly larvae is species-specific, and the range extremes are usually marked by failure to extend the labral fans (Kurtak 1973). *S. vittatum* larvae have been reported from a wide variety of habitats ranging in current velocities from 3 to 152 cm/s (Fredeen and Shemanchuck 1960, Williams and Hynes 1976, Chance 1977, Colbo 1979), but these larvae typically dwell in currents between 20 and 40 cm/s; generally avoiding velocities faster than 70 cm/s (Kurtak 1973). The slowest recorded velocity in which larvae of *S. vittatum* exhibit filter-feeding under experimental conditions is 3.7 ± 0.9 cm/s (Chance 1977). It was initially suggested that a minimum current velocity was necessary to hold the labral fans open for long periods to enable feeding (Zahar 1951, Harrod 1965). However, movements of the fans (*i.e.*, abduction and adduction) were subsequently shown to be independent of the current speed, and are probably controlled by the combined action of haemodynamic pressure (Wood *et al.* 1962; Chance 1970) and energy stored in the cuticle of the fans (Davies 1974, Craig and Chance 1982). However, as inferred by the small transmission coefficients observed for static labral fans of *S. vittatum* larvae at low velocities (0.04 - 0.17, respectively at 1.0 - 3.5 cm/s), and the concomitant thickness of shear gradient layers surrounding each ray-microtrichia complex (Braimah 1985, 1987a; shear gradient layers occupy about 97% of the gap between adjacent rays at velocity of 3.6 cm/s for *Simulium bivittatum* larvae), low fluid transmissivity of filtration appendages is the most likely limiting factor in slow velocity habitat exploitation rather than minimum velocity requirements to hold the labral fans open. Conversely, proper deployment of the labral fans may be impeded in flows at the upper extreme of the velocity range. Cessation of suspension-feeding activity has been noted for *Cnephia mutata* larvae following several failed attempts to adequately deploy their labral fans near the upper velocity (*ca.* 60 cm/s) for that species (Kurtak 1973). Observations on structural failure of static labral fans of *S. vittatum* at velocities of 55-65 cm/s (when held against flow) indicates a strong link between structural resilience of the filtering appendages and flow forces inherent at the upper [illegible] extreme of the species feeding range (*S. vittatum* usually do not occur in velocities greater than 70 cm/s; Kurtak 1973, Colbo 1979). Since Eymann (1988) elegantly demonstrated that drag forces necessary to remove larvae of *S. vittatum* from their attachments would result only from velocities in excess of 11 - 27 m/s, the upper extreme velocity preference for a species is most likely delineated by velocities suitable for suspension-feeding processes (*i.e.*, sufficient flow through fully deployed fans) rather than attachment or locomotion failure. These observations strongly suggest that reports of the presence of *S. vittatum* larvae suspension-feeding at velocities well exceeding 100 cm/s (maximum velocity for attachment under extreme conditions; Kurtak 1973) should be examined with caution, since is is most likely [illegible] larvae were in a microhabitat not detected by the sampling instruments or procedures.

3.4.6 Fluid transmission through "dynamic" labral fans. As mainstream velocity increases, labral fans of live black fly larvae progressively lean with the flow. Consequently, the relationship between mainstream velocity and observed (*i.e.*, natural) deflection angles of dynamic labral fans (from Fig. 6) was overlayed on the three-dimensional representation of the static labral fans transmissivity (Fig. 11a), and a lateral projection of this line, along the e_t-U_x axies, gives an approximation of the base-line transmissivity (*i.e.*, related to structure only) of suspension-feeding labral fans of *S. vittatum* larvae associated with the natural deflection angles of the labral fans (Fig 11b). As mainstream velocity increases to *ca.* 20 cm/s, the transmission coefficients of dynamic labral fans would reach a maximum of *ca.* 0.3. Further velocity increases (20 to 55 cm/s) would appear to produce little or no significant change in transmissivity because of progressive labral fan deflection (Fig. 11b). Because flow through dynamic and static labral fans differ when exposed to the same mainstream velocity, the real transmission coefficients of a suspension-feeding labral fan are consequently expected to fluctuate around the base-line transmissivity previously defined. As suggested by larger apertures observed for dynamic labral fans exposed to mainstream velocities faster than 10 cm/s (*cf.* Fig. 9), concomitant increases in gap size between adjacent rays should raise transmissivity at low velocity (10 - 15 cm/s). Active control of labral fan aperture (as opposed to strictly passive reaction) would be a useful behavioural adaptation to increase transmissivity without reducing the effective catchment area (*i.e.*, number of rays and microtrichia) for filtering at low velocity, and would be consistent with the underlying assumption that behaviour altering larval stance is mainly related to maximizing water flow through the filtering appendages (Craig and Chance 1982, Craig and Galloway 1987, Kurtak 1973, 1978).

A transmission coefficient of *ca.* 0.29 estimated for a dynamic labral fan of *S. vittatum* larvae exposed to a mainstream velocity of 18 cm/s (Fig. 11b) is similar to the average transmission coefficient of *ca.*25% recalculated from Craig and Chance's data (1982; their Fig. 8, particles #2, #3, and #6) for actively filter-feeding larvae of *S. vittatum*. As expected from the configuration of the ray-microtrichia complex (*i.e.*, microtrichia on the upstream side) both estimates are higher than the transmissivity of 7.8% predicted by Cheer and Koehl's model (1987b) for the same species (but with the microtrichia set laterally on the rays) and flow velocity. It therefore appears that at such low Reynolds numbers, changes in cross-sectional shape of the ray-microtrichia complex (*i.e.*, chord to maximum thickness ratio of 8:1 for *S. vittatum*) may have a similar effect as change in apparent diameter (*i.e.*, microtrichia perpendicular to flow direction). Prediction accuracy of models such as Silverter's and Cheer and Koehl's, could probably be improved by exploring the specific effects of cross-sectional shape (*e.g.* round *vs.* ellipsoid-shape) of filtering fibbers and overall form of the filtering structure (*e.g.* dish-shape *vs.* flat-shape) on transmissivity.

3.4.7 Suspension-feeding efficiency. Suspension-feeding efficiency of simuliid larvae is defined as the ratio of number of particles ingested per unit time to the total number of particles delivered to the labral fans during the same time interval. The number of particles present in the gut of a suspension-feeding black fly larva is influenced by particle availability in the water column, but is directly controlled by the filtering efficiency of the fans (*i.e.*, filter performance) and by the different behavioural components of the suspension-feeding process. To adequately depict flow through a filter, the performance of a structure such as a labral fan has to be defined by both the efficacy of particle capture *per se* of the structure, and its fluid transmissivity (Sylvester 1973, Cheer and Koehl 1987a,b). Black fly larvae do not spend 100% of their time suspension-feeding (Chance 1977, unpubl. data by Hart and Maloney in Hart and Latta 1986, Thompson 1987b, Schröder 1988), and both fans are fully exposed to the flow for only a portion of that period (Kurtak 1973, Craig and Chance 1982, Lacey and Lacey 1983, Biggs 1985). The total time a fan is exposed to the flow is proportional to its flick rate (*sensu* Chance 1977) and the average time it is kept extended. Additionally, particles trapped by the rays and microtrichia may not all be ingested because of mandibular and labral brushes fail to reach all of the labral fan area (Craig 1977), and particles are lost during transfer to the oesophagus. Taking into account such a chain of events (Fig. 12a), the number of particles found in the gut ($\#_g$) of a suspension-feeding black fly larva can be succinctly defined as:

$$\#_g = \overline{C}_w\, \overline{U}_\infty\, 2\,EFA\; e_t\, e_f\, t_{sf}\, t_{abd}\, e_h \qquad \text{(Eq. 3.14)}$$

where $\overline{C}_w$ is the average particle concentration in the water column, $\overline{U}_\infty$ is the average mainstream velocity, EFA is the effective fan aperture, e_t is the transmission coefficient of the labral fan, e_f is the particle capture efficacy (*per se*) of the labral fan, t_{sf} is the time portion spent filtering, t_{abd} is the average portion of time the labral fans stay fully abducted (related to the number of fan abductions and the average duration of an abduction per unit time), and e_h is the efficiency of the particle transfer to the oesophagus.

Assuming suspension-feeding is the only mode of feeding of a black fly larva, the number of particles present in its gut is solely dependant on the particle availability in the water column, and the larva suspension-feeding efficiency (E_{sf}), such that:

$$E_{sf}\, \overline{C}_w\, \overline{U}_\infty = \#_g = \overline{C}_w\, \overline{U}_\infty\, 2\,EFA\; e_t\, e_f\, t_{sf}\, t_{abd}\, e_h \qquad \text{(Eq. 3.15).}$$

From this equation, we can therefore discern that suspension-feeding efficiency is linked to three major components (Fig 12b), the efficiency of filtration ($E_{sf} = 2EFA\ e_t\ e_f$) which is dependant on the filter ability (*i.e.*, both labral fans) to change aperture with flow (2EFA, *i.e.*, filter plasticity) and the filter performance ($e_t\ e_f$), the continuity element ($t_{sf}\ t_{abd}$), and the handling efficiency (e_h). Behavioural components (*i.e.*, continuity element and handling efficiency) have been shown experimentally to be dependant on parameters such as water velocity and temperature, particle size, type (phagostimulant property) and concentration, as well as physiological level of satiation (Schröder 1980b, Biggs 1985, Hart and Latta 1986, unpubl. data by Hart and Maloney in Hart and Latta 1986, Thompson 1987b). Similarly, the engineered component (in contrast to behavioural) of suspension-feeding efficiency, the filter efficiency[19] (E_f) (*i.e.*, filter plasticity and performance), has been shown experimentally and mathematically to be dependant of

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[19] For simplicity of the equation, an assumption is made that the effective fan aperture (EFA) is under no, or relatively little, behavioural influence compared to the passive response to flow forces.

parameters such as water velocity, filter orientation to the flow, and diameter and spacing of the fibres of the filter (Sylvester 1973, Warner 1977, Cheer and Koehl 1987a,b, this study). Consequently, as all components of the process controling the number of particles present in the gut of a suspension-feeding larva are experimentally defined relative to a designated set of parameters, the ratio:

$$\frac{\text{Observed number of ingested particles}}{\overline{C}_w\ \overline{U}_\infty\ 2\,EFA\ e_t\ e_f\ t_{sf}\ t_{abd}\ e_h} \approx \xrightarrow[\text{lim}]{} 1 \qquad \text{(Eq. 3.16)}$$

Therefore, equation 3.14 is a testable hypothesis about the parameters influencing suspension- feeding efficiency.

The total number of particles delivered to the labral fans is influenced by particle availability in the water column, but is directly controlled by the time the fans are actually abducted into the flow, as well as the fan aperture and transmissivity. Consequently, assuming that black fly larvae rely totally on filtration to feed, suspension-feeding efficiency (E_{sf}) of a black fly larva can therefore be defined as:

$$E_{sf} = \frac{\text{Observed number of ingested particles}}{\overline{C}_w\ \overline{U}_\infty\ 2\,EFA\ e_t\ t_{sf}\ t_{abd}} \qquad \text{(Eq. 3.17)}$$

the ratio of the number of particles ingested per unit time to the total number of particles actually delivered to the abducted labral fans during the same time interval.

To depict adequately the flow through the labral fans, the performance of the filtering structure is defined by both its efficacy of particle capture and fluid transmissivity (*i.e.*, e_t e_f). Therefore, at fixed filter aperture, a structure catching every particle passing through it, but so dense that very little water moves through can have the same performance as a filter that permits high flow rate, but only captures a small fraction of the particles that move through its aperture. It can therefore be hypothesized that species inhabiting different microhabitats (*e.g.*, different ranges in water velocity, particle size and concentration), should have filter configurations which maximize filtering performance (consequently suspension-feeding efficiency) by achieving the optimum balance between the particle capture efficacy and transmissivity. It is commonly believed that size and strength of the labral fan rays are related to flow and/or food abondance (Fortner 1937, Grenier 1949, Carlsson 1962, and Currie and Craig 1987). In general, larvae inhabiting fast-flowing water have smaller (relative to cephalic capsule size) and more robust fan rays, whereas relatively larger more delicate fans are more characteristic of larvae in slow-flowing waters. As more definite information on the mode of feeding, microhabitat preferences (*e.g.*, different range in water velocity, particle size and concentration), and associated structural configurations of the labral fans of various simuliid species become available, filter performance assessment could prove to be an objective method in comparative study of suspension feeding organisms.

Despite the abundance of information on structure of biological filters such as simuliid labral fans, the particle capture efficacy of these filters and the mechanisms by which this filtering take place are poorly understood (*e.g.* only study on simuliid larvae by Braimah 1985, 1987a, b). Consequently, assessment of the filtering efficacy (e_f) of a labral fan (through Eq. 3.16), will give more insight into the hydrodynamics of particle retention and the relative importance of its different components (*i.e.*, direct interception, inertial impaction, gravitational deposition, motile-particle deposition, and sieving; *sensu* Rubenstein and Koehl 1977).

Although most simuliid species are predominantly suspension-feeders, other feeding modes such as scraping, collector-gathering, and predation have been observed (see Currie and Craig 1987 for review). Consequently, the overall feeding efficiency (E_F) of any simuliid larva can ultimately be defined as:

$$E_F = t_{sf}E_{sf} + t_gE_g + t_{df}E_{df} + t_pE_p \qquad \text{(Eq. 3.18)}$$

where t_{sf} is the time portion spent suspension-feeding, E_{sf} is the suspension-feeding efficiency, t_g is the time portion spent grazing, E_g is the grazing efficiency, t_{df} is the time portion depositing-feeding, E_{df} is the deposition-feeding efficiency, t_p is the time portion spent predating, and E_p is the pedation efficiency. It should be possible to specify the time allocation of the feeding process, such as: $t_{sf} + t_g + t_{df} + t_p = 1 - t_0$ (where t_0 is the time portion spent not feeding, *e.g.* grooming).

3.4.8 Correction factor for published suspension-feeding efficiencies.

Suspension feeding efficiency derived from theory relates to the volume of fluid which is actually processed by the filtering structure (Eq. 3.17); whereas previously published suspension-feeding efficiencies of black fly larvae are expressed in terms of an anticipated volume of fluid approaching the effective fan aperture from far upstream. Consequently to adjust for variation in volume inherent to filter flexibility and transmissivity, and filtering continuity (*i.e.*, continuity element), the basic equation defining particle capture efficiency (cf. Eq. 3.1) accordingly becomes:

$$E_{sf}(\%) = \left(\frac{\text{number of ingested particles}}{\text{number of particles offered}_{FA}}\right) \left(\frac{1 - \Delta EFA}{e_t\ t_{sf}\ t_{abd}}\right) 100 \qquad \text{(Eq. 3.19)}$$

where the first component of the equation is the suspension feeding efficiency as calculated from Kurtak's (1973) equation (Eq. 3.1; *i.e.*, using a fixed fan aperture), and the second component is the correction factor.

Assuming ΔEFA of *ca.* 0.15 (Fig. 10), e_t of *ca.* 0.3 (Fig. 11b; defined for dynamic labral fans), t_{sf} and t_{abd} of *ca.* 0.85 and 0.78 respectively (pers. observations[20]) estimated for *S. vittatum* larvae exposed to particle free water (filtered stream water, < 0.45μm) at mainstream velocity of *ca.* 30 cm/s, it can be anticipated that larvae of *S. vittatum* are at least *ca.* 4.4 times more efficient at suspension-feeding than previously assessed. From Kurtak's (1973, his tables VII, and VIII) suspension-feeding efficiencies calculated for larvae of *S. vittatum* exposed to different particles sizes at mainstream velocity of 30 cm/s, the efficiency range originally assessed as 0.009 - 7.0%, become *ca.* 0.04 - 30.8%. The magnitude of the correction factor increases as mainstream velocity declines toward the lower extreme of the velocity range (*e.g.* correction factor of *ca.* 26.2 fold at mainstream velocity of *ca.* 5 cm/s; ΔEFA, e_t, t_{sf} and t_{abd} of 0.0, 0.05, 0.91 and 0.83 respectively)

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[20] values concurrent with Schröder (1988).

3.5 CONCLUSIONS

As predicted by mathematical models (Silvester 1983, Cheer and Koehl 1987a,b), only a fraction of the particle-laden water approaching the labral fan aperture is actually filtered; an increasing fraction flows around the labral fan perimeter as mainstream velocity decreases. Although the underlying concept defining published particle capture efficiencies of black fly larvae was correct (*i.e.*, Eq. 3.1), low fluid transmissivity through labral fans observed in this study demonstrated conclusively that simuliid larvae are more efficient at suspension feeding than previously assessed. I proposed that this feature is a critical aspect of habitat use for simuliid larvae, low fluid transmissivity of the filtration appendages is one of the most likely limiting factor in slow velocity habitat exploitation. My results additionaly suggest that occupation of high velocity habitats is limited by disruption of filtering structure integrity, rather than attachment or locomotion failure as has been previously speculated. Gut content reflects obviously the feeding behaviour of an organism as a whole, rather than just the efficacy of its filter system.

More realistic assessment of the volume of particle-laden water processed by suspension-feeding larvae will not only enhance precision in estimates of suspension-feeding efficiency, but also allows assessment of the performance of the filtering appendage (*i.e.*, balance between particle capture efficacy *per se* of the labral fans and its transmissivity). Despite the abundance of information on structure of biological filters such as simuliid labral fans, particle capture efficacy of these filters and the mechanisms by which this filtering take place are poorly understood. Assessment of the filtering efficacy (e_f) of a labral fan (through Eq. 3.16), will give more insight into the hydrodynamics of particle retention and the relative importance of its different components (*i.e.*, direct interception, inertial impaction, gravitational deposition, motile-particle deposition, and sieving; *sensu* Rubenstein and Koehl 1977)

Detailed analysis of the suspension-feeding stance demonstrated that although change in body deflection with increasing water velocity is probably passive, overall feeding stance is the outcome of a dynamic feedback process between flow forces and behavioural reactions, to actively maintain the labral fans at optimal filtering position. Energetic costs of standing against the flow probably increase as the water velocity increases, and past a certain threshold (*ca.* 30 cm/s for *S. vittatum*) it may be more efficient for the larvae to simply "go with the flow" and assume a more streamlined stance.

Shape of impressively preserved upper Cretaceous fossil simuliid larvae (Riek 1970) is still unaltered today in some extant simuliid larvae, so it can be assumed that black fly larvae have dealt with the same forces for at least the last 135 millions years. Hence, understanding the influence of flow forces gives unique insights on the evolutionary pressure leading to considerable inter-specific variation in posterior abdominal shape and labral fan structures, associated with colonization of different flow environments. Larvae of other simuliid species that differ in shape from that of *Simulium vittatum* Zett. should be examined to see if differences in flow patterns around the body and through the labral fans correlate with differences in larval stance, feeding behaviour (*e.g.*, aberrant behaviour of Tahitian simuliid larvae living in a water-film but lacking longitudinal rotation of the body; Craig personal communication) and suspension-feeding efficiency (labral fans performance, *i.e.*, balance between particle capture efficacy *per se* and transmissivity). To quote Craig and Chance (1987): "Simuliid larval feeding can no longer be considered a passive affair !"

Observations made here for simuliid larvae may have relevance to other filter-feeding insects. In short, in light of the apparent association between body and labral fan structures and choice of flow environment, compounded to the possibility of selectively removing them from a chosen lotic system (Back *et al.* 1985, Morin *et al.* 1988), black fly larvae are ideal candidates for development and assessment of conceptual models evaluating the impact of suspension-feeding organism populations on nutrient dynamics.

There is little doubt that hydrodynamic phenomena play a major rôle in shaping structure and behaviour of black fly larvae. Overlooked for too long, flow conditions prevailing at the larval scale are probably among the most important environmental variables involved in the ecology of immature similiids.

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Fig. 1 Suspension-feeding larva of *Simulium vittatum* Zett. A) Larval feeding stance and upper-vortex interception by the right labral fan (*i.e.*, larva facing the reader, longitudinal body rotation of *ca.* 90°) at water velocity of 15 cm/s: LF, labral fan; V_u, upper-vortex. B) Dye streakline diverted to the perimeter of a "static" fan (*i.e.*, dead larva) at water velocity of *ca.* 10 cm/s: θ, labral fan deflection angle; **EFA**, effective fan aperture; **LF**, labral fan; **P**, abdominal proleg; S_d, dye streakline.

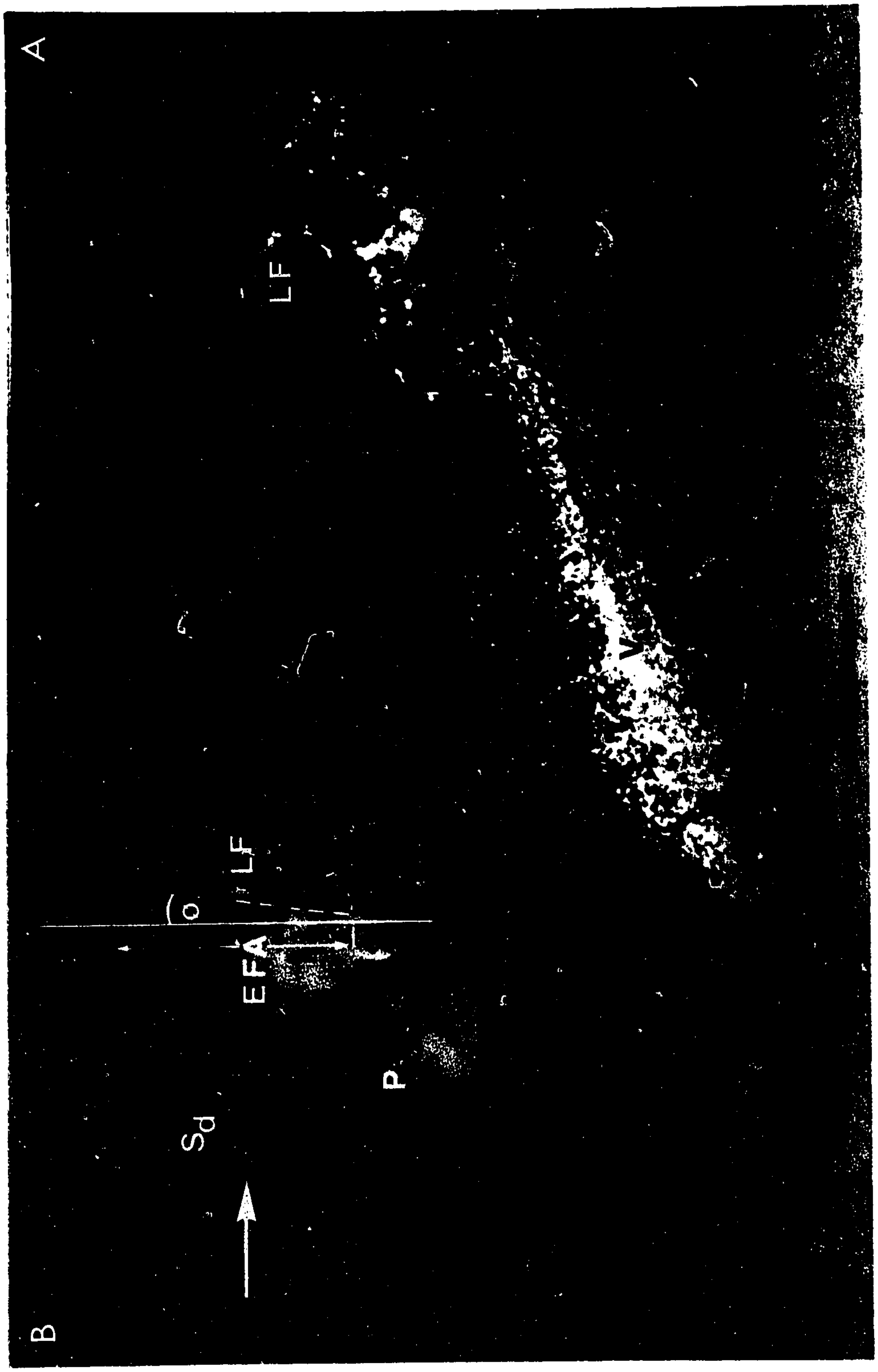
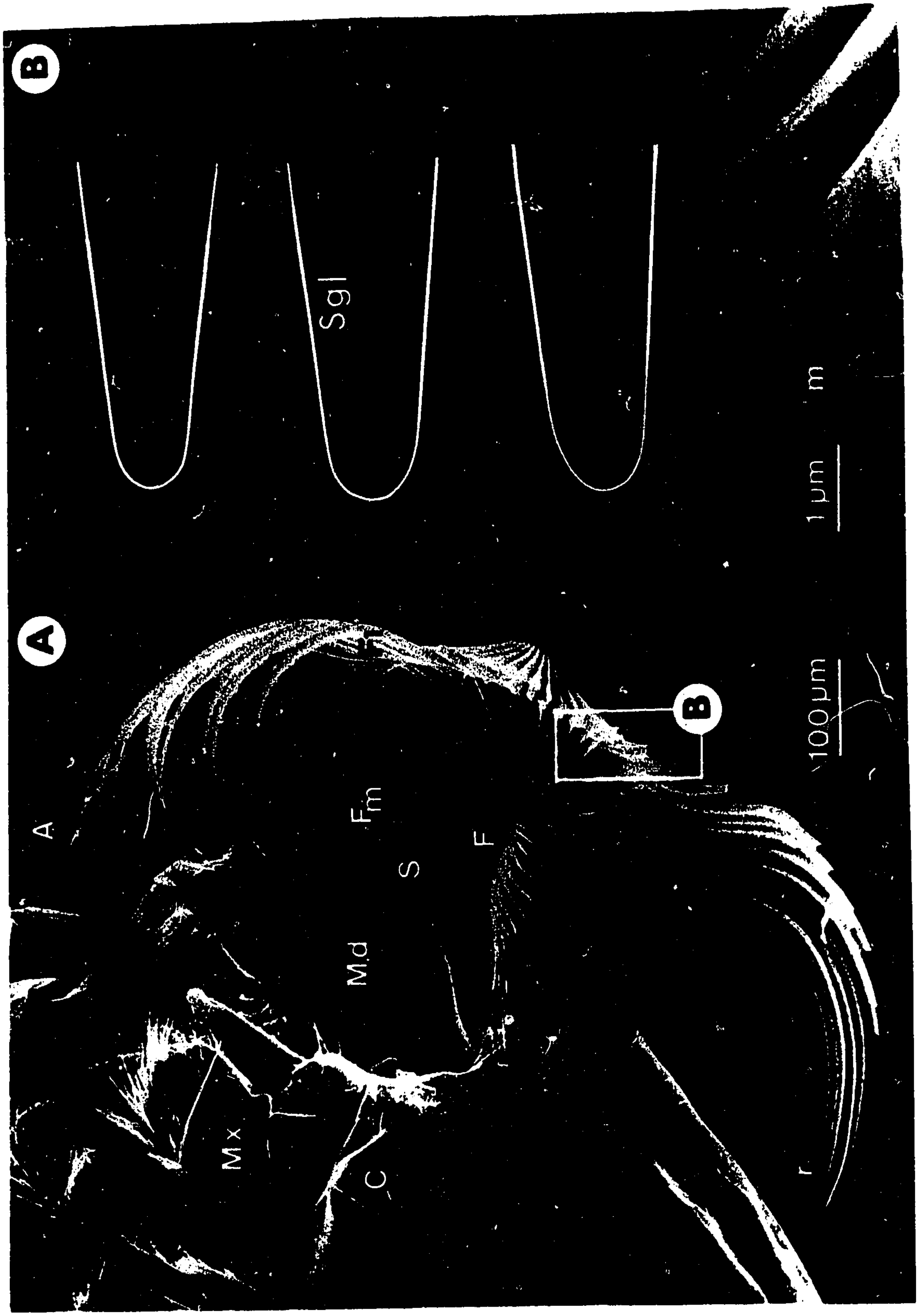

A
LF
V
LF
O
EFA
P
Sd
B

Fig. 2 Scanning Electron Micrograph of *Simulium vittatum* Zett. larval head. **A)** Lateral view of the cephalic capsule and a partially cut labral fan (*i.e.*, apical portion of some primary rays removed): **A**, antenna; **C**, cephalic capsule; $\mathbf{F_1}$, primary fan; $\mathbf{F_2}$, secondary fan; $\mathbf{F_m}$, medial fan; **Md**, mandible; **Mx**, maxillary; $\mathbf{r_1}$, primary ray; **S**, labral fan stem. **B)** Cross-section of ray-microtrichia complex: **m**, microtrichia; $\mathbf{r_1}$, primary ray; **Sgl**, diagrammatic representation of shear gradient layers (*i.e.*, zone of viscous effect) (not to scale).



A
B
A
Mx
C
Md
S
F
Fm
r
B
100 µm
Sgl
1 µm
m

Fig. 3 Schematic representation of larval suspension-feeding stance (deflection angles: **F°**, labral fan; **C°**, cephalic; **A°**, abdominal; **T°**, thoracic; **D°**, overall; and **R°**, longitudinal body rotation).

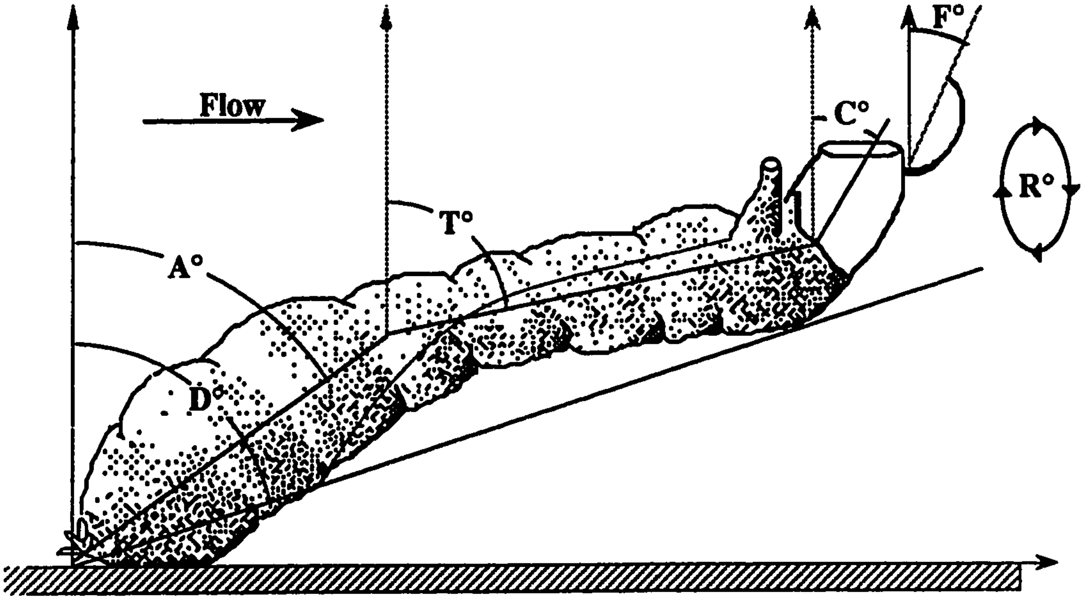

Flow
F°
C°
T°
A°
D°
R°

Fig. 4 Schematic representation of fluid flow through a black fly labral fan: $\mathbf{d_x}$, labral fan diameter; $\mathbf{EFA_x}$, Effective Fan Aperture; $\mathbf{EFAd_x}$, Effective Fan Aperture diameter; $\mathbf{STA_x}$, Streamtube cross-sectional area; $\mathbf{STd_x}$, Streamtube diameter; $\mathbf{U_x}$, free-stream water velocity; $\mathbf{U'_x}$, water velocity through the labral fan; θ, labral fan deflection angle.

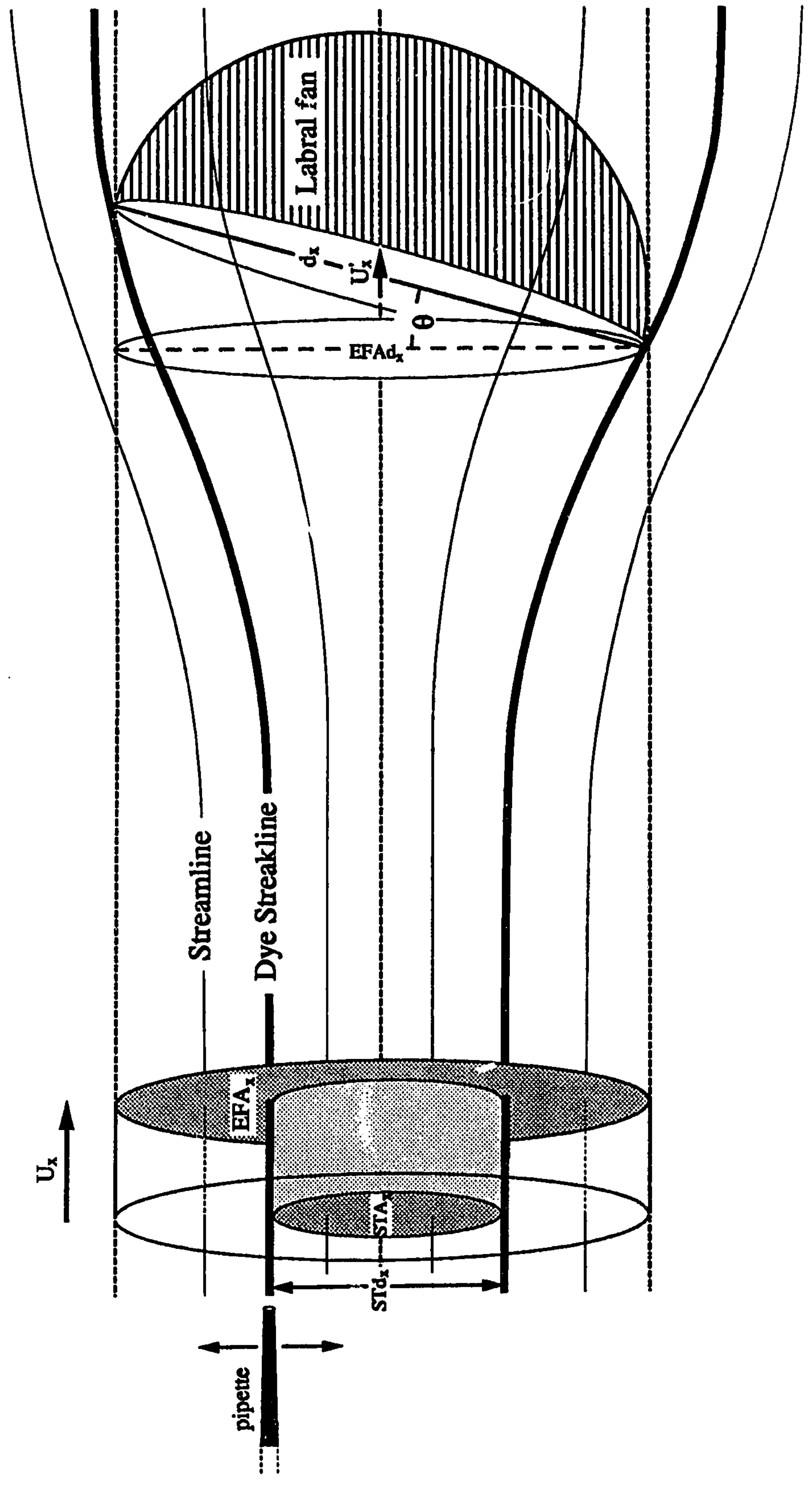

Labral fan
d_x
U'_x
θ
EFAd_x
Streamline
Dye Streakline
U_x
EFA_x
STA_x
STd_x
pipette

Fig. 5 Suspension-feeding stance of *Simulium vittatum* Zett. larvae. Analysis of influence of water velocity on deflection angles of body regions (deflection angles: **C°**, cephalic; **A°**, abdominal; **T°**, thoracic; **D°**, overall; and **R°**, longitudinal body rotation).

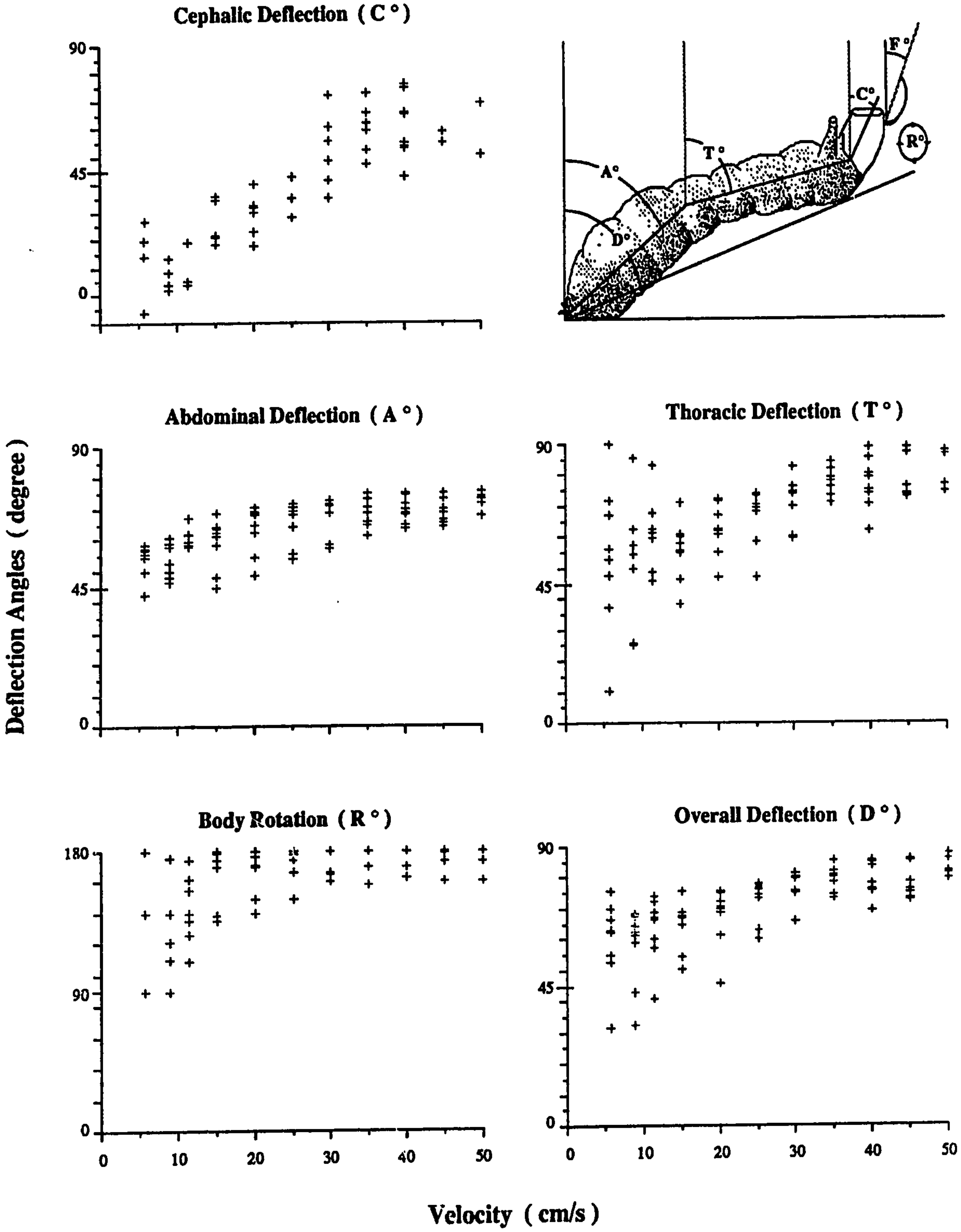

Cephalic Deflection (C °)
90
45
0
F°
C°
R°
T°
A°
D°
Abdominal Deflection (A °)
Thoracic Deflection (T °)
Deflection Angles (degree)
90
45
0
Body Rotation (R °)
Overall Deflection (D °)
180
90
0
0
10
20
30
40
50
Velocity (cm/s)

Fig. 6 Relation between the deflection angle (θ) of *Simulium vittatum* Zett. larvae labral fans and water velocity (U_x), in comparison to drag forces exerted on labral fans (as calculated from Eymann 1988). Vertical bars associated with the diamond symbol (data reanalyzed from Schröder 1987) represent standard deviation.

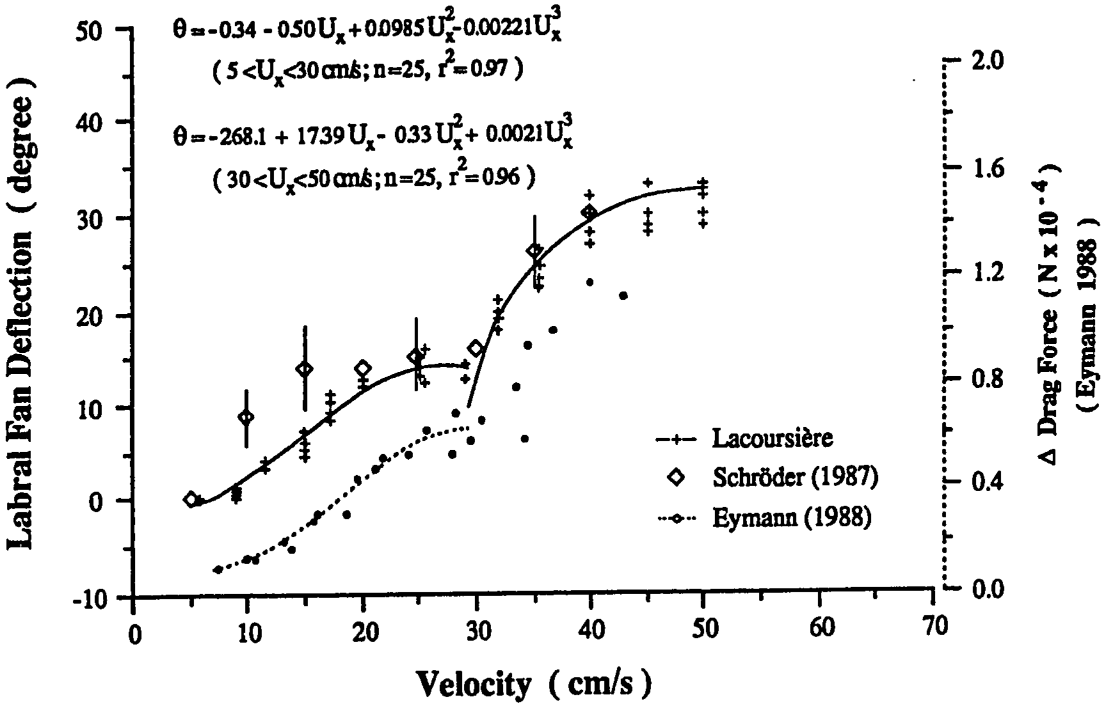

$\theta = -0.34 - 0.50U_x + 0.0985U_x^2 - 0.00221U_x^3$
$(5 < U_x < 30$ cm/s; $n = 25$, $r^2 = 0.97)$
$\theta = -268.1 + 17.39U_x - 0.33U_x^2 + 0.0021U_x^3$
$(30 < U_x < 50$ cm/s; $n = 25$, $r^2 = 0.96)$
Labral Fan Deflection (degree)
50
40
30
20
10
0
-10
0
10
20
30
40
50
60
70
Velocity (cm/s)
2.0
1.6
1.2
0.8
0.4
0.0
Δ Drag Force (N x 10⁻⁴)
(Eymann 1988)
Lacoursière
Schröder (1987)
Eymann (1988)

Fig. 7 Schematic representation of the suspension-feeding stance of *Simulium vittatum* Zett. larvae. A) Progressive deflection (average position, from Fig. 5) of the different body regions at various velocities. B) Relative angles between contiguous body regions with water velocity increase. The arrow points to the compensatory reduction in relative head-labral fan angle at the abrupt increase in cephalic deflection at 25 - 30 cm/s.

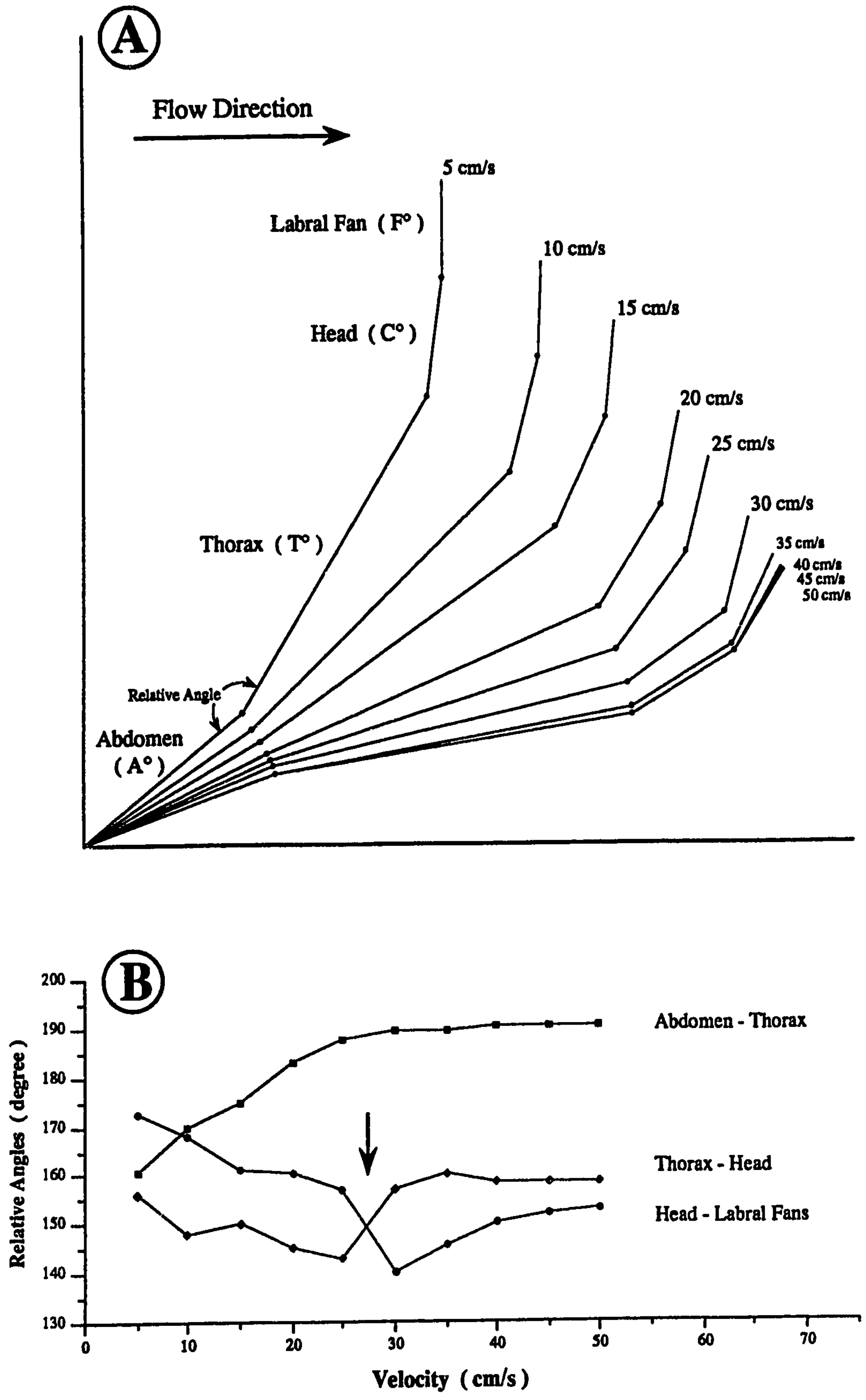

A
Flow Direction
5 cm/s
Labral Fan (F°)
10 cm/s
Head (C°)
15 cm/s
20 cm/s
25 cm/s
30 cm/s
Thorax (T°)
35 cm/s
40 cm/s
45 cm/s
50 cm/s
Relative Angle
Abdomen
(A°)
B
200
190
180
170
160
150
140
130
Relative Angles (degree)
Abdomen - Thorax
Thorax - Head
Head - Labral Fans
0
10
20
30
40
50
60
70
Velocity (cm/s)

Fig. 8 Simplified flow diagram of the feedback relationship between the overall suspension-feeding stance of a black fly larva and the flow forces generated by three-dimensional flow around the body.

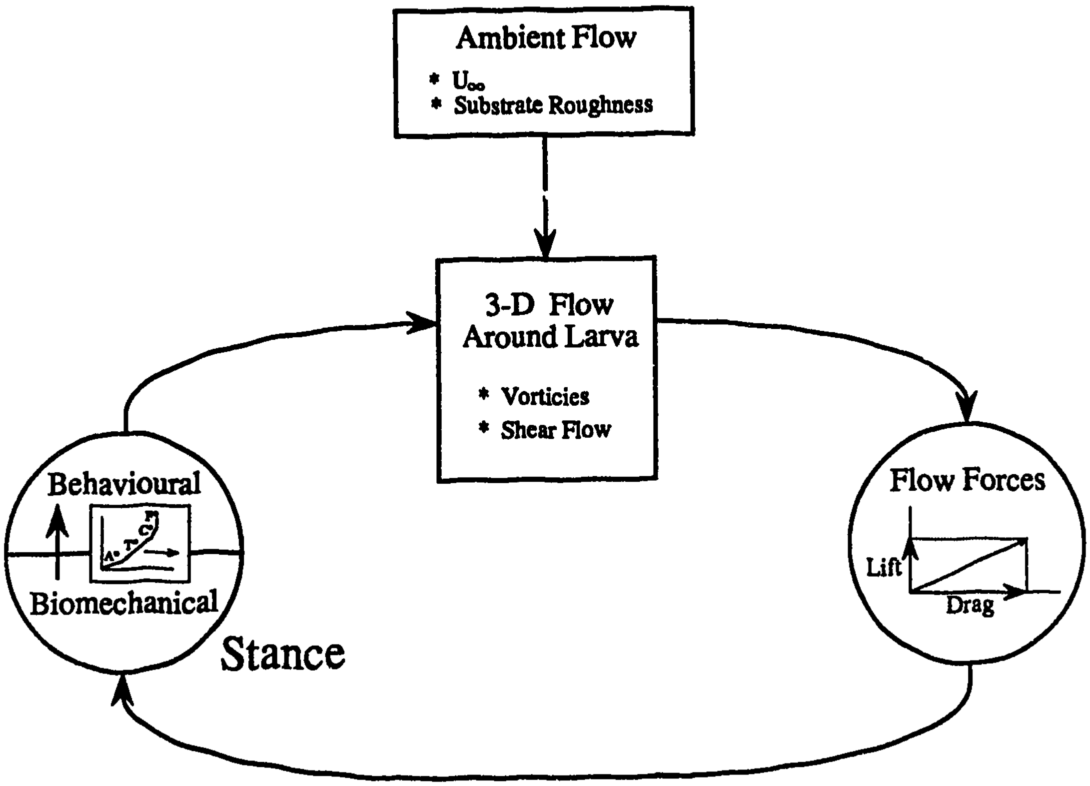

Ambient Flow
* U_∞
* Substrate Roughness
3-D Flow
Around Larva
* Vorticies
* Shear Flow
Flow Forces
Lift
Drag
Behavioural
A
T
C
F
Biomechanical
Stance

Fig. 9 Relationship between the aperture increase (A_i) of "static" (*i.e.*, dead larvae; solid line) and "dynamic" (*i.e.*, live larvae; broken line, vertical bars = standard deviation) labral fans of *Simulium vittatum* Zett. larvae and water velocity (U_x). Dotted line represents the portion of the relationship unreliable due to ray wobbling and fan collapse.

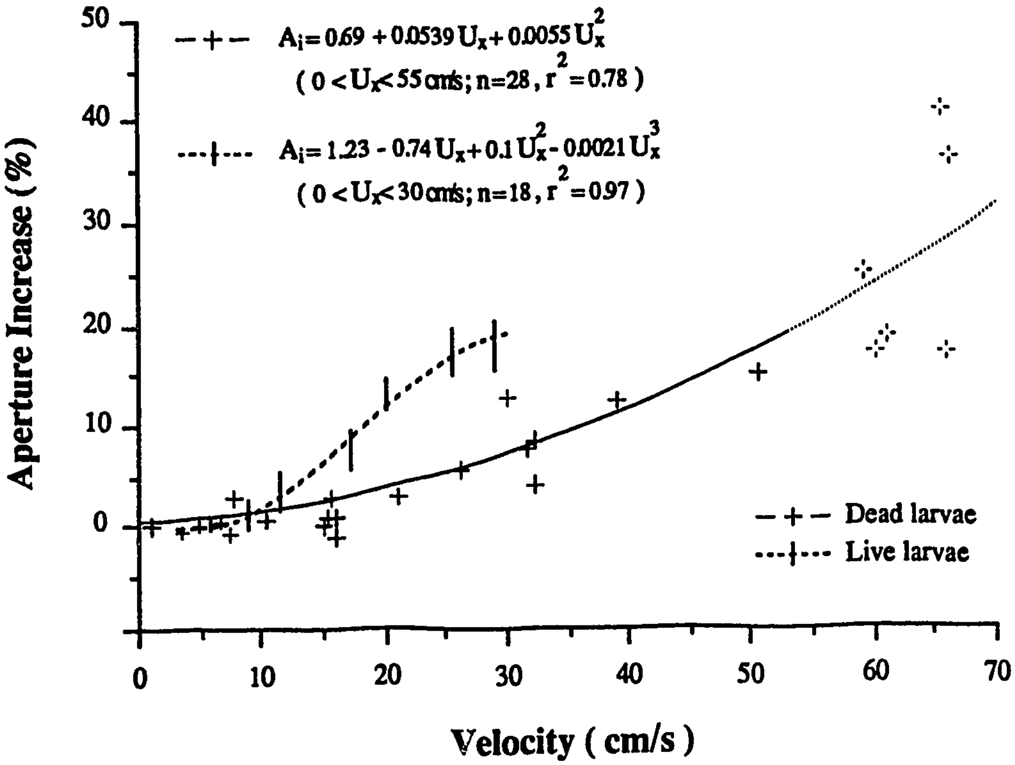

$A_i = 0.69 + 0.0539\,U_x + 0.0055\,U_x^2$
$(0 < U_x < 55\ \mathrm{cm/s};\ n=28,\ r^2=0.78)$
$A_i = 1.23 - 0.74\,U_x + 0.1\,U_x^2 - 0.0021\,U_x^3$
$(0 < U_x < 30\ \mathrm{cm/s};\ n=18,\ r^2=0.97)$
Dead larvae
Live larvae
Aperture Increase (%)
50
40
30
20
10
0
0
10
20
30
40
50
60
70
Velocity (cm/s)

Fig. 10 Variation of the standardized effective fan aperture (ΔEFA) of *Simulium vittatum* Zett. larvae, with water velocity increases. Relationships defined for the influence of both labral fan aperture increase and labral fan deflection (*i.e.*, $A_i + \theta$), or only labral fan deflection (*i.e.*, θ). Query (?) represents hypothesized relationships (lower-curve = if A_i stays constant beyond 30 cm/s; upper-curve = if A_i increases following a relationship similar to "drag on a labral fan vs. water velocity" relationship, *i.e.*, Eq. 10).

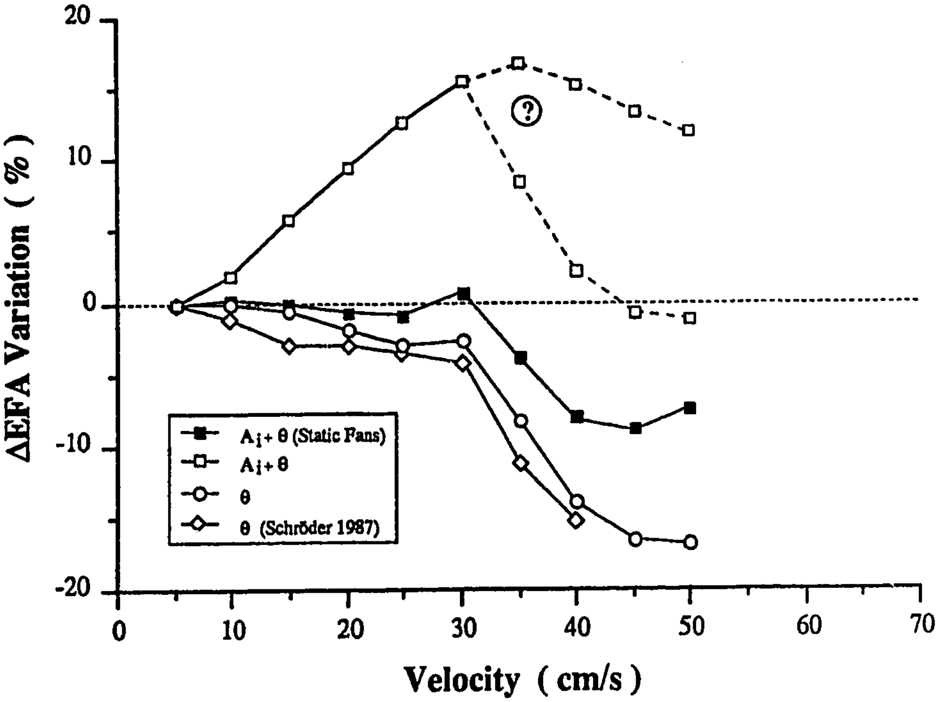

20
10
0
-10
-20
ΔEFA Variation (%)
0
10
20
30
40
50
60
70
Velocity (cm/s)
?
$A_i + \theta$ (Static Fans)
$A_i + \theta$
θ
θ (Schröder 1987)

Fig. 11 Base-line transmissivity of static and dynamic labral fans of *Simulium vittatum* Zett. larvae. A) Three-dimensional representation (true, localy-weighted three dimensional surface; *i.e.*, every patch on the surface required four weighted multiple regression on the point; SYGRAPH™) of the transmission coefficient (e_t) of "static" labral fans in relation to their angle of deflection (θ) and water velocity (U_x). Dotted region represent the unreliable portion of the relationship due to ray wobbling and fan collapse at high velocities. B) Base-line transmission coefficient of a dynamic labral fan in relation to velocity increase (bar represents range), established from lateral projection of the transect (line on the 3-D surface A; thickness represents range) representing the relationship between deflection angles of dynamic labral fans and mainstream velocity (from Fig. 6).

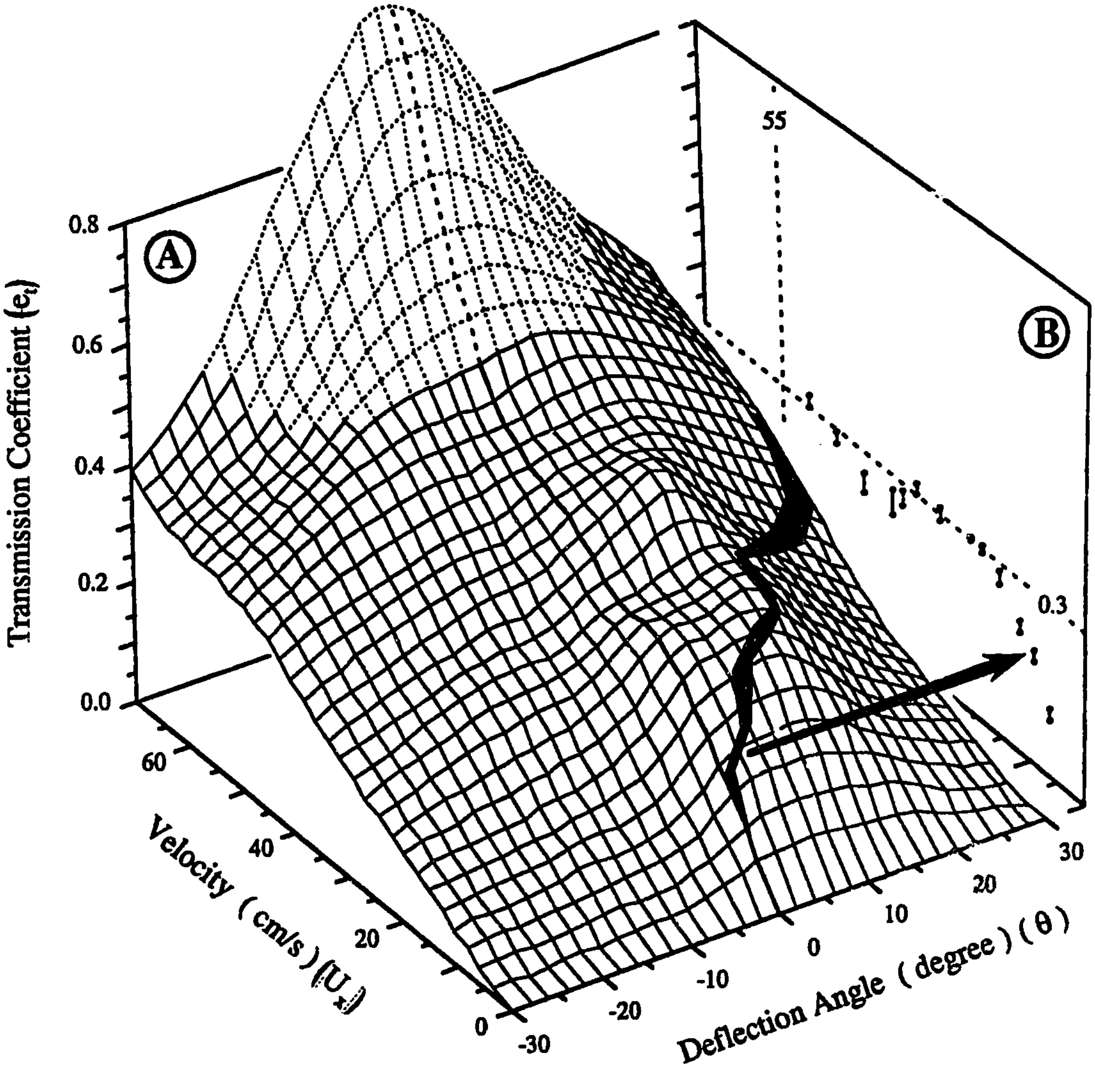
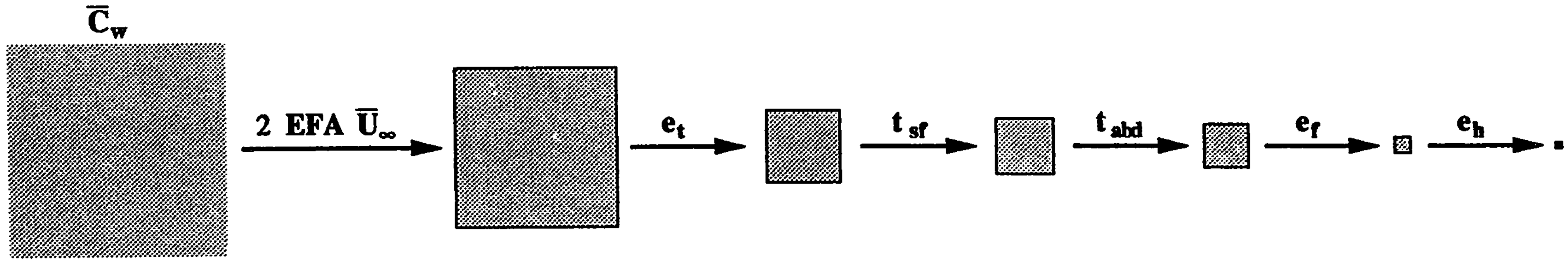

Transmission Coefficient (e_t)
0.8
0.6
0.4
0.2
0.0
A
B
55
0.3
60
40
20
0
Velocity (cm/s) (U_x)
-30
-20
-10
0
10
20
30
Deflection Angle (degree) (θ)

Fig. 12 Analysis of suspension-feeding efficiency ($\mathbf{E_{sf}}$) of simuliid larva **A)** Schematic representation of the chain of events leading to particle ingestion: $\overline{\mathbf{C}}_{\mathbf{w}}$, particle concentration in the water column; **EFA**, effective fan aperture; $\overline{\mathbf{U}}_{\infty}$, average mainstream velocity; $\mathbf{e_t}$, transmission coefficient; $\mathbf{t_{sf}}$, time portion spent feeding; $\mathbf{t_{abd}}$, time portion the fans are abducted; $\mathbf{e_f}$, particle capture efficacy of the filtering structure; $\mathbf{e_h}$, handling efficiency during particle transfer from the fans to the oesophagus, $\#_{\mathbf{g}}$, number of ingested particles. **B)** Equation relating the three major components defining suspension-feeding efficiency.

Ⓐ



Ⓑ

$$E_{sf}\,\overline{C}_w\,\overline{U}_\infty = \#_g = \overline{C}_w\,\overline{U}_\infty\,\underbrace{2\,EFA\;e_t\;e_f}_{\text{filtering efficiency}}\,\underbrace{t_{sf}\,t_{abd}}_{\text{filtering continuity}}\,\underbrace{e_h}_{\text{handling efficiency}}$$

4. FLUID FLOW AND MICROHABITAT SELECTION BY LARVAE OF THE BLACK FLY *SIMULIUM VITTATUM* (DIPTERA: SIMULIIDAE) IN THE LABORATORY

4.1 SYNOPSIS

Positioning of *Simulium vittatum* Zett. larvae in a flume was studied at different mainstream velocities, on two substrates of different geometry: a thin flat plate parallel to the flow and a cylinder in crossflow. Larvae did not assume stances nor select positions along the flat substrate demonstrating any significant response to changing boundary layer thickness. Data consequently do not support the hypothesis that simuliid larvae typically totally hide in the boundary layer to reduce direct influence of the mainstream current. Contrary to general belief, larvae did not necessarily seek maximum velocity in a longitudinal velocity gradient. Larvae preferably gathered along the separation zone where the thin boundary layer detaches from the curved substrate's surface, but also remained along the stagnation line (*i.e.* leading point of the cylinder) if artificially positioned there. Larvae always avoided zones of maximum surface shear stress. Such micro-hydraulic events are dominant features of benthic rheophilic invertebrate environments. Scaling microdistribution studies to the organismal level can consequently help to isolate the proximal factors affecting formation of local assemblages.

Larval reaction to hydraulic changes is immediate, and it is suggested that *S. vittatum* larvae scan the velocity profile at the substrate to cue on a rapid velocity difference between the abdomen and labral fan level as part of selecting a suspension-feeding microsite. Thus they can maximize particle-flux through the labral fans and minimize drag forces on the bulbous portion of the body.

4.2 INTRODUCTION

Water movement is the dominant physical feature of lotic ecosystems, and hydrodynamical factors may simultaneously be the most important and least understood environmental variables affecting the ecology of stream benthic communities (Nowel and Jumars 1984, Davis 1986, Statzner 1981, 1987). Historically, ecologists working in lentic and especially marine environments have focused on the rôle played by hydrodynamics and flow forces in their respective ecosystems (Statzner *et al.* 1988), but surprisingly, stream ecologists have generally ignored hydrodynamic influences. Scarcity of research in hydrodynamics of lotic benthic organisms was probably due to the difficulties inherent in dealing with high velocities, but also perhaps, to the powerful influence of Macan (1962,1974) who was not convinced that velocity *per se* determined distribution of benthic organisms. Nevertheless, many authors have correlated distribution and densities of benthic stream invertebrates, including black fly larvae, with velocity alone or in combination with water depth and physical features of the streambed (*e.g.*, substrate size, nature and roughness) (see reviews in Brown and Brown 1984, Gore 1978, Hynes 1970, Macan 1962, Statzner 1981, Osborne and Herricks 1983, Statzner *et al.* 1988). Yet, because flow characteristic (*i.e.*, summarization of three-dimensional flow patterns and flow forces) at the organism level is still poorly understood, proximate mechanisms by which flow affects formation of local assemblages still elude characterization (Davis 1986; Nowel and Jumars 1984).

In 1949, Grenier wrote: "Je pense que si on pouvait évaluer la vitesse du courant à l'endroit même où se tient l'animal, on éprouverait des surprises comparables à celles qu'ont éprouvées les écologistes spécialisés dans l'étude des microclimats" (Grenier 1949). For stream ecologists, the "surprise" came as they realized the significance of a region of slower flow at the substrate's surface (*i.e.*, boundary layer; Prandtl 1929 *in* Schlichting 1987), in which benthic fauna could avoid the direct influence of the mainstream current (Ambühl 1959). Despite very early works by Clemens (1917) and Von Gelei (1928), flow environment at the organismal scale received very little attention from stream biologists between the fundamental work of Ambühl (1959) on a variety of benthic invertebrates, and that of Trivellato and Décamps (1968). Later Décamps *et al.* (1975) invoked more complex local hydraulic conditions and flow regimes to delineate microdistribution patterns of black fly larvae and pupae under natural and artificial settings. They observed very little influence of the laminar sub-layer (thin zone of laminar flow existing within the turbulant boundary layer, right at the substrate's surface) on the larval distribution, but influence of boundary layer (laminar or turbulent) thickness was unfortunately not discussed. They also reported that when exposed to a longitudinal velocity gradient over the substratum, larvae concentrated in a narrow band where velocity was maximal, often aggregating just upstream of "perturbations" induced by the "détachement de la lame" (*i.e.*, the boundary layer separation) (Décamps *et al.* 1975). More recently, Osborne and Herricks (1983, 1987) and Osborne *et al.* (1985) investigated streamflow and velocity as determinants of benthic insect distribution and community structure, and reported that under stream conditions, black fly larvae selected regions of an artificial substrate (hydraulically calibrated) where unidirectional, nearly laminar flow conditions occured, rather than regions subject to high turbulence and variable flow direction. Similarly, Wetmore (1987) demonstrated that *S. vittatum* larvae are found in microhabitats of significantly higher "shear stress" (*i.e.*, tractive force acting on the stream bed, defined as water "depth x slope x weight of water") and Froude number (*i.e.*, measure of the flow regime: sub-critical, critical, and super-critical), compared to the random distribution of these variables within a stream reach.

Statzner (1981) suggested that lack of research involving benthic micro-distribution and hydrological factors was due to difficulty in applying the theory of hydrodynamic phenomena to natural running waters due to the somewhat chaotic nature of the flow. At the organismal scale however, local flow conditions are often more consistent over a focused section along the substrate's surface, and the three-dimensional flow patterns (*i.e.*, micro-hydraulic events) about the resident living organisms can be more readily related to theoretical notions. Yet, chaotic motions of the overall water mass above the stream bed still render exhaustive analysis of flow patterns difficult under field conditions. The purpose of a flume, or flow tank, is consequently, not only to simulate the essential aspects of field conditions near or around the substrate, but also to simplify them so that the flow characteristics can be adequately measured and summarized in their component parts. Only then can the complex interactions between an organism's behaviour and its immediate hydrodynamical milieux, be truly studied. When presented simply, hydrodynamical parameters can provide valuable information about the environment surrounding an aquatic organism.

Flow patterns over and around surfaces of obstacles exposed to moving fluids have been studied by hydraulic and aeronautical engineers for many years. Relevant flow descriptions and associated formulae are commonly found only in publications which biologists are unlikely to encounter. However Ambühl (1959), Bournaud (1963), Trivellato and Décamps (1968), Statzner (1981), Vogel (1981), Nowell and Jumars

(1984), Silvester and Sleigh (1985) and Davis (1986) give exhaustive reviews of phenomena relevant to behaviours of organisms in lotic environments.

In any discussion concerned with the dynamic properties of fluid motion, both inertial and viscous effects must be considered. The ratio of these two effects is known as the Reynolds number (***Re***), and relates fluid density (ρ), viscosity (μ), and velocity (U), and the object's characteristic length (l, typically taken as the greatest length of the solid in the direction of the flow), in a dimentionless index:

$$\mathrm{Re} = \frac{\rho \, l \, U}{\mu} \qquad \text{(Eq. 1)}$$

It is not the dynamic viscosity (μ) or the density (ρ) which matter so much as their ratio, the kinematic viscosity (ν). While the conventional (*i.e.* dynamic) viscosity μ is a measure of the frictional resistance to flow of a fluid of density ρ, the kinematic viscosity can be seen as a measure of how likely the flow is to form vorticies (Vogel, 1981). If ***Re*** is much less than unity, flow is dominated by viscous forces, vorticies will be either nonexistant or non-sustained; viscous forces dictate the flow behaviour and the fluid momentum can almost be neglected. It is very important to understand that it is the value of the ***Re*** that dictates the character of the flow and not the value of the viscosity *per se* ; a tenfold increase in size (characteristic length) decreases relative viscous effects with precisely the same efficacy as a tenfold decrease in viscosity itself (Vogel 1981). If ***Re*** is much more than unity, inertial or momentum effects predominate, the immediate effect of viscosity may be neglected and the main fluid-bulk can be assumed to act as an invicid or ideal-fluid. If for biological-systems, small almost always means slow and large often means fast, then small creatures are living in a world dominated by viscous phenomena and large ones by inertial phenomena (Vogel 1981).

In a real situation such as water flowing past a fixed obstacle, both ideal and viscous-flow behaviour may be evident in different regions of the fluid. In the immediate vicinity of the surface of the obstacle, the fluid is stationary due to strong molecular forces sticking the first molecular layers of the fluid to the surface of the solid. The immediate corollary of the no-slip condition is that a velocity gradient is created as frictional forces between the slowly moving water particles and their neighbours above retard the motion of the fluid in a thin region near the surface of the solid, the boundary layer (Schlichting 1987). This region is defined as the region where shear stresses (*i.e.*, force per unit area acting parallel to the surface of the object) is predominant. Outside this layer, therefore, the shear stresses will be zero. There can be no sharp limit to the boundary layer, since there is obviously a continuous transition in the properties assumed by the fluid as one passes out from the boundary layer into the ideal fluid region (*i.e.*, region where presence of the surface of the solid does not affect the fluid behaviour). Nevertheless, it is convenient to define an arbitrary surface of demarcation between the two regions. By convention this is taken as the height from the solid's surface where the local flow speed (U_y) becomes a substantial fraction of the free-stream velocity (U_∞); 0.99 is the most commonly quoted fraction by mathematicians and engineers. However, for biological applications, 0.90 of the free-stream velocity seems to be a more practical measure of the transition from one flow regime to the other (Vogel 1981). The thickness (δ) of the boundary layer is measured out from the surface of the obstacle to the demarcation surface as defined above, and one can see that although δ may be defined precisely in mathematical terms, it still only describes the order of magnitude of a rather nebulous quantity (Vogel 1981, Silvester and Sleigh 1985).

The shape of the velocity profile in the boundary layer depends on flow properties (*e.g.* the flow Reynolds number, the background turbulence and accelerations), fluid properties (*e.g.* suspended sediment load), and boundary characteristics (*e.g.* the bed roughness and the cohesiveness of sediments). Velocity profiles have been measured for controlled laboratory flows and their characteristics have been determined theoretically under certain conditions. For the steady, uniform flow cases considered here (*i.e.*, a thin flat plate and a cylinder), the shapes of the velocity profiles are well known.

4.2.1 Fluid flow about a flat plate. For a thin flat plate oriented parallel to the direction of flow, a boundary layer starts to grow in the downstream direction from the leading edge, and its thickness δ increases continuously with distance (x) from this edge as an increasing quantities of fluid become affected by the viscous forces (Fig. 1). Shear stresses are consequently highest near the leading edge, decreasing continuously with distance from this edge (*i.e.*, velocity gradients are the steepest near the leading edge; Schlichting 1987). Boundary layer flow is laminar for $Re_x < 5 \times 10^5$ and turbulent for $Re_x > 2 \times 10^6$ (Schlichting 1987); where Re_x is the local Reynolds number associated with the distance from the leading edge (*i.e.*, characteristic length = x) (Schlichting 1987). For a laminar boundary layer, the thickness (δ) at any point along the plate can be calculated from the Basillus' solution:

$$\delta = \eta \sqrt{\frac{x\,\mu}{\rho\,U}} \qquad \text{(Eq. 2).}$$

where η is a variable function of the fraction of the mainstream velocity considered as the position of the boundary upper "limit" (*e.g.*, $\eta \approx 5.0$ for $0.99\ U_\infty$, $\eta \approx 3.4$ for $0.90\ U_\infty$; White 1986, Schlicting 1987). Consequently, increases in density or free-stream velocity thin the boundary layer while increases in viscosity and distance from the leading-edge thicken it. When the same equation is expressed in terms of Re_x, the result of this substitution shows that the relative thickness of the boundary layer depends solely on the Reynolds number (Vogel 1981):

$$\frac{\delta}{x} = \eta \, \mathrm{Re}_x^{-0.5} \qquad \text{(Eq. 3)}$$

Low Reynolds number consequently means relatively thick boundary layer. Laminar boundary layers are very stable in the downstream direction; any disturbance to the layer (*e.g.* caused by flow over a small bump) will be quickly dissipated by viscosity, restoring the velocity profile to the undisturbed state. Thus in laminar boundary layers, the flow is parallel to the bottom. When the shear near the bed is sufficiently large, turbulent eddies are generated as violent interchanges of microscopic momentum completely disrupt the orderly movement of the laminar flow otherwise present in this region, which mix lower-momentum fluid close to the bed with higher-momentum fluid away from the bed, *i.e.*, the flow patterns in the boundary layer become turbulent. Surface roughness or projections can also be responsible for momentum exchange in the fluid (Schlichting 1987). While the time-averaged flow velocity is in the horizontal axis, as in the laminar case, turbulent eddies have velocity components in all directions. So, in relation to boundary layer growth, the presence of even small free-stream turbulence increases momentum exchange between the slower water molecule near the surface of the substrate and the faster ones away from it. Consequently, the rate at which the boundary layer grows is increased: turbulent boundary layers exhibit a stronger velocity gradient than those in laminar flow (Schlichting 1987). Generally speaking, the thickness of a turbulent boundary layer is larger than that of a laminar boundary layer owing to the greater energy losses in the former (Schlichting 1987). Thus, for a turbulent boundary layer the equation expressing the thickness of a turbulent boundary layer (at $0.99\,U_\infty$) becomes:

$$\delta = 0.376\left(\frac{x\,\nu}{U_\infty}\right)^{0.2} = 0.376\,x\,\mathrm{Re}_x^{-0.2} \qquad \text{(Eq. 4)}$$

(Schlichting 1987, Vogel 1981). In practice, a boundary layer starts out as laminar near the leading edge, and then, the flow turns onto transitional flow and very shortly thereafter become turbulent somewhere downstream; where the particular location of the transition is dependant on Re_x (> 5×10^5) or more commonly on the Reynolds number of the boundary layer ($Re_\delta = U\delta / \nu > 1000$) (Silvester and Sleigh 1985). The turbulent boundary layer continues to grow in thickness, with a small region below it immediately at the solid surface called a viscous sublayer. In this sublayer, the flow is stable, just as in the laminar boundary layer. Descriptions of laminar and turbulent boundary layer can be found in White (1986), and Schlichting (1987).

Stream biologists should have a deep interest in the specific conditions within the boundary layer. Many organisms can spend most of their life partly or entirely within the boundary layers of either inanimate objects or of other organisms. For many organisms, free-stream velocity is something they may never encounter, but the distribution of the velocity in the gradient region may be a critical parameter in their existence (Vogel 1981). A laminar boundary layer and a laminar sublayer can be seen as semi-stagnant regions in which wastes are likely to accumulate and in which nutrients may be depleted, so they can represent a substantial barrier to diffusive exchange of heat or material (mainly the laminar sublayer), as well as a welcome refuge from the forces of the stream. A turbulent boundary layer can also provide a refuge but, being well-stirred, it provides much less of a barrier to transport (Vogel 1981).

Flow over a thin rigid flat plate is among the simplest hydraulic conditions to which benthic organisms can be subjected. However most natural substrates (disregarding thin substrates not covered by this study; *e.g.*, leaves and similar structures) bear curved surfaces over which water can accelerate and decelerate, producing complex flow patterns over the substrate's surface. Consequently, flow about a cylinder in crossflow was choosen for more realistic schematization of flow conditions over such surfaces.

4.2.2 Fluid flow about a cylinder in cross-flow. The flow patterns around a volumetric obstruction is more complicated because the velocities in the immediate vicinity of the object are not constant and equal to the mainstream velocity (U_∞), as assumed in the previous case. The cylinder is an obstruction that reduces the space available for the movement of the fluid. In a steady frictionless flow (*i.e.*, ideal fluid), the velocity of the fluid particle moving in the immediate vicinity of the cylinder, or its tangential velocity (U_ϕ) would theoritically be expected to correspond to:

$$U_\phi = 2\ U_\infty \sin \phi \qquad \text{(Eq. 5)}$$

where ϕ is the angle measured around the cylinder from the forward stagnation point (Schlichting 1987). Thus, following deceleration to a halt as it approaches the cylinder's most leading point (*i.e.*, forward stagnation where local velocity = 0), a fluid particle at the cylinder's surface would rapidly accelerate to $2U_\infty$ (at $\phi = 90°$) as it moves around the cylinder, to finally decelerate to zero at the rear stagnation point ($\phi = 180°$) before re-entering the main bulk-flow. In reality however, fluid viscosity induces an ever-present zone of shear stresses (*i.e.*, the boundary layer) near the surface which varies little in thickness with ϕ until, on approaching the zone in which the fluid begins to decelerate, the boundary layer becomes separated from the cylinder's surface (Vogel 1981, Silvester and Sleigh 1985, Schlichting 1987) (Fig.2). Then between the inner "limit" of the boundary layer and the cylinder's surface (where tangential velocity is greatly readuced) some backflow appears (Fig.2a), giving rise to vorticies in the wake behind the cylinder. The point at which the flow separates from the wall depends mainly on Reynolds number. At Re_d between about 10 and 40, the cylinder bears a pair of attached eddies on its rear. As Re_d further increases, the pattern is no longer stable, and the vorticies begin to alternately detach and propagate downstream in a vortex streets (*i.e.*, von Kármán's trail; see White 1986 and Schlichting 1987 for more details). Ultimately, the wake become turbulant and the point of separation of the boundary layer stabilizes at ϕ of *ca.* 82°. This configuration is maintained until Re_d reach *ca.* > 3 x 10^5, where the separation point moves back to *ca.* 120° (Silvester and Sleigh 1985, Schlichting 1987).

Definition of boundary layer thickness in this context is problematical, and to be consistent with the earlier discussion, should be defined as the distance from the cylinder surface where $U_\phi \approx 0.90\ (2U_\infty \sin \phi)$. Although technically correct, this gives the impression that, as in the case of the flat plate, organisms within the boundary layer are exposed to less velocity than in the mainstream flow, whereas in fact velocities are up to *ca.* 1.6 U_∞ as ϕ tends to 70° for the Re_d considered here (White 1974). It is convenient to express the variation in local velocity about the cylinder's surface as a ratio of the mainstream velocity (*i.e.*, U_ϕ/U_∞). Consequently, U_ϕ can be less than U_∞ notably near the forward stagnation point where ϕ tends to 0° and in the region of boundary layer separation (*i.e.*, $\phi \approx 82°$) (Fig. 3). Beyond the point of boundary layer separation, there is no steady-state boundary layer and velocity about the cylinder's surface fluctuate in intensity and direction due to vortex shedding. Location of the zone of maximum local velocity is mainly dependant upon the location of the boundary layer separation. Hence, the thickness δ of a boundary layer (defined by 0.90 U_ϕ) over the major part of the upstream portion of a cylindrical cylinder (*i.e.*, *ca.*, ± 45°) can be approximated from:

$$\frac{\delta}{a} \approx 1.4\left(\frac{2a\,U_\infty}{\nu}\right)^{-0.5} = 1.4\,Re_d^{-0.5} \qquad \text{(Eq. 6)}$$

where a is the cylinder's radius (Silvester and Sleigh 1985).

The tangential shear stress acting on the surface of a circular cylinder in crossflow is, as for any surface shear stress (τ_0), a function of the fluid viscosity and the rate of change in velocity (U_y) along an axis normal to the surface (y) (*i.e.*, velocity gradient at the wall):

$$\tau_0 \approx \mu\left(\frac{\partial U_y}{\partial y}\right) \quad \text{(Eq. 7)}$$

(Schlichting 1987). Consequently, the steeper the velocity gradient (*i.e.*, the more rapidly U_y varies from the surface), the higher the surface shear stress. For circular surfaces, it is more convenient to express τ_0 in the dimensionless form $\bar{\tau}$, defined as follow:

$$\bar{\tau} = \frac{2\tau_0}{\rho U_\infty}\sqrt{Re_d} \quad \text{(Eq. 8)}$$

(Zukauskas and Ziugzda 1985). In a laminar regime (*i.e.*, Re_d *ca.* $> 3 \times 10^5$), $\bar{\tau}$ reaches a maximum at $\phi \approx 55°$, and since tangential velocities at stagnation and separation points are equal to zero, the surface shear stress there is almost non-existant (*i.e.*, $\bar{\tau} \approx 0$) (Fig. 3). Beyond the point of boundary layer separation, there is no steady-state boundary layer, and the surface shear stress remains close to zero (*i.e.*, $\bar{\tau} \approx 0$) (Zukauskas and Ziugzda 1985). Consequently, the steeper the velocity gradient (*i.e.*, the higher τ_0), the lower the relative protection from the direct influence of mainstream velocity for the residing invertebrate.

Such micro-hydraulic events (*i.e.*, growing and fully developed boundary layer, laminar and turbulant boundary layer, boundary layer separation, stagnation points, and zone of high surface shear stress) are dominant features of benthic reophilic invertebrate environments. Hence, scaling microdistribution studies to the organismal level pursues

Ambühl's (1959) pioneer investigation into the influence of hydrodynamics on the ecology of benthic organisms. The ability to generalize (*i.e.*, schematize) and make direct comparisons between different investigations is one of the particular benefits of expressing environmental conditions (*i.e.*, micro-hydraulic events) in strict fluid dynamic terms.

Because of their relative mobility[1] and modes of feeding, black fly larvae are prime candidates in the development a conceptual model for evaluating the effects of hydrodynamics on the ecology of benthic organisms. As passive suspension-feeders, black fly larvae rely on water flow to deliver food items to their labral-fans. It appears that suspension-feeding efficiency of simuliid larvae is central to adult reproductive success, because food availability at the larval stage can influence survivorship of the pupal stage (Brenner and Cup 1980), the size and fecundity of the adults (Colbo and Porter 1979, 1981) and their mating success (Simmons and Edman 1981). Consequently, selection should have favoured morphologies and behaviours that maximize the flow of water through the feeding structures, and minimize drag forces acting on supporting structures (*i.e.* the larval body). After selecting a feeding-site, larvae firmly attached themselves on the substratum by a posteroventral circlet of hooks, where, while leaning with the current, they longitudinally rotate their body between 90° and 180° to expose the adoral (concave) side of their fans to the flow. Larvae often appear to display strikingly nonrandom dispersion patterns detectable at several levels of resolution. Individuals on a single substrate (*eg*., rocks, branches) may be randomly arranged, or may be observed forming dense, contiguous aggregates (Wotton 1982, Eymann 1985), in reticulate patterns (Hocking *et al.* 1954) or in disjoint parallel bands aligned normal to the flow direction

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[1] Larvae of black flies are capable of moving across the substratum by looping (Wu 1931, Barr 1984).

(Twinn *et al.* 1948, Colbo 1987). Patterns can be transitory (Gersabeck and Merritt 1979), varying with change in local water velocity, or persisting for the duration of a larval generation (Colbo 1979). As stipulated earlier, because flow characteristic (*i.e.*, summarization of three-dimensional flow patterns and flow forces) at the organism level is still poorly understood, proximate mechanisms by which flow affects formation of local assemblages still elude characterization.

This study is based on the premise that black fly larvae select a suspension-feeding location to maximize the difference between benefit and cost of that particular site, by achieving water flow around the body and through the fans for maximum filtration efficiency while keeping energetic cost such as drag, as low as possible. Consequently, to evaluate the effects of micro-hydraulic events on microhabitat selection and isolate the causative parameter (*i.e.*, the cue), black fly larvae were selectively exposed (*i.e.*, moved in and out) to different sections of a continuous array of defined hydrodynamic conditions.

Based partially on previously published information, and partly on personal field observations of local assemblages of simuliid larvae, I tested the following hypotheses:

A) Larvae will assume stance and position on a flat surface, in relation to the boundary layer thickness; *i.e.*, the larvae will migrate downstream from the plate's leading edge to stay within the boundary layer, as boundary layer thickness is sequentially decreased by mainstream velocity increases.

B) Within their velocity distribution range, larvae will select zones of maximum velocity along a longitudinal velocity gradient on a cylinder; and therefore will: **B$_1$**) be at 70° and/or between 70 and 80° (at maximum velocity, right before separation of the boundary layer) and **B$_2$**) avoid the stagnation zone.

C) Larvae will avoid zones of maximum surface shear stress.

4.3 MATERIAL AND METHODS

Experiments were conducted in September and October 1988 with late instar larvae (*i.e.*, larvae with visibly developed respiratory histoblasts) of *Simulium vittatum* Zetterstedt collected from Pyramid Lake outlet (52° 55' North, 118° 06' West), Alberta. Larvae were transported and kept in the laboratory at temperatures of 8-10°C and light regime of 12hr dark and 12 hours light, using the short-term maintenance system described by Lacoursière and Boisvert (1987). Experiments were performed within 4 - 5 days of larval collecting.

All experiments were conducted at constant flow velocities (coefficient of variation of less than 1%), in a 80 litres recirculatory flume (channel 15.5 cm wide x water depth 16.5 cm x 75 cm long; designed after Vogel and LaBarbera [1978]) containing aerated stream water, filtered to remove particles > 1μm diameter. Water temperature of 15°C ± 0.5 was kept constant with a refrigeration unit. Water temperature was taken into account for the kinematic viscosity when calculating *Re*'s.

Mainstream water velocities were monitored with a portable velocity meter (Novonics Kent Miniflow 265 & 422, Nixon Instrumentation Ltd.) using a 1.0 cm diameter, five-bladed rotor mounted on jewel bearings (free-propeller probe # 649 s/l). Velocities were sampled at frequencies of 28 to 280 Hz for periods up to 60 sec, with an APPLESCOPE-D2 card (RC Electronics Inc., 7265 Tuolumne St., Goleta, CA93117, USA) on an Apple II+ personal computer. A digitized version of the output (*i.e.*, current signal proportional to the water velocity) were analysed for sample statistics (*i.e.*, mean velocities, standard deviations and coefficients of variation) on an Apple II+ personal computer using a short Basic™ program (modified from J.J.H. Ciborowski, University of Windsor, Ontario, Canada).

Observations were recorded with a JVC® colour Video Camera (model no. GX-S700U), and a Panasonic VHS Omnivision II Video Cassette Recorder (model no. AG-6200. EIA Standard: 30 frames/sec) connected to a Panasonic Time-Date Generator (model no. WJ-810). Micro-Nikkor® 55-mm (f/3.5) and Carl Zeiss Luminar® 25-mm (f/3.5) & 40-mm (f/4.5) lenses were used in conjunction with extension tubes, and C-mount adaptors to produce magnifications of 10 to 96 fold. Measurements were taken with a vernier calliper and a protractor, from a JVC® Video Monitor flat-screen (model no. TM-R9U), using frame-by-frame analysis (Panasonic Remote Search Controller NV-A505). Measurements from the monitor were calibrated by recording the vernier calliper at all magnifications. A Nikkormat 35-mm camera and a Micro-Nikkor 50-mm lens were used for still photography. Kodak Tri-X film (ASA 400, push-developed to ASA 800) was used. Illumination was provided by fibre optic lights (Intralux® 6000, Volpi, Zürich), and an auxiliary halogen-light source (Smith-Vector Corp., Griffith, Indiana, U.S.A., Model 770) was used to increase tracer visibility.

Fluorescent pigments (A-11 Arora pink; Day-Glo Color Corp., Cleveland, Ohio, U.S.A.) methylene blue solution, and aluminium flakes were used in standard flow visualization techniques (Merzkirch 1987, Vogel 1981). Fluorescent pigments and methylene blue solutions were introduced through micropipettes of *ca.* 0.5 mm diameter, firmly mounted on a rack-and-pinion micro-manipulator for accurate positioning. Vertical lighting through an adjustable slit (on the top of the water channel), and back lighting provided adequate contrast between specimens and backgrounds.

The two artificial substrates (*i.e.*, flat plate and cylinder) were horizontally suspended at midheight of the water channel (Fig. 4). The flat plate (made of 2.9 mm (1/8 inch) thick clear Plexiglas®, 5 cm wide x 10 cm long; with upstream beveled-edge) was carefully positioned parallel to the flow, 8 cm beneath the water surface in midchannel, using a three-finger jaws Micro Clamp (# C6003-1, Canlab©) mounted on translation stages to allow multi-directional motion (Fig. 4a). The plate was marked with a squared grid of 120 5-mm^2 sections to facilitate location of the larvae. The cylindrical substrate (made of 3.7 cm diameter clear Plexiglas® rod, 14.5 cm long) was positioned perpendicular to the flow (*i.e.*, in crossflow), 7 cm beneath the water surface, in a thin frame locked onto the water channel bottom (Fig. 4b). The cylinder was held horizontally in the frame by two nylon screws centred at each extremity, which allowed smooth rotation. Rotation of the cylinder was achieved through alternate insertion of a stainless steel rod into a series of small holes on the cylinder surface (at *ca.* 2 mm from one of the cylinder extremity). As a result, a designated portion of the cylinder's surface bearing larvae could be selectively exposed to known hydrodynamical conditions. A 15 mm border along each extremity of the cylinder was coated with a thin film of silicon grease, to which black fly silk does not adhere; thus larval activity was restricted to the centre portion of the cylinder. The cylinder's surface was divided into 36 10°-segments; the division at the leading point of the cylinder was always refered to as 0° (*i.e.*, front stagnation point), whereas the diametrically opposed position was refered to as 180° (*i.e.*, rear stagnation point). Since larvae did not demonstrate any significant preferences for the top or bottom portion of the cylindrical substrate (*i.e.*, on each side of the plane delimited by the stagnation points), larval distribution frequencies over the top and bottom portion of the cylindrical substrate were pooled (*i.e.*, expressed for 18 10°-segments covering 180°). Front stagnation zone (ST_f), refers to the 0°-10° segment, maximum shear stress zone (τ_{max}) refers to the 50°-60° segment, maximum local velocity ($U\phi_{max}$) refers to the

60°-80° segments, zone of separation (SP) refers to the 80°-90° segment, and the wake zone (W) refers to the 90°-180° segments.

Velocity profiles over the surface of each artificial substrate were observed using still photographs of illuminated aluminium flakes. Water velocity was calculated using the flakes trajectory lengths, magnification of the image on the film, and camera shutter time. Thickness of the boundary layer over the flat plate, and local velocity some distance (*i.e.*, δ at 0.60 U_∞; see below) over the surface of the cylinder were assessed for general compliance with theoretical values.

Graphical manipulation of the numerical result of the Blasius solution for laminar layer flow over a flat plate (Granger 1985), indicates that the rate of changes in the velocity profile (*i.e.*, U_y / U_∞) is constant between.0.00U_∞ and 0.60U_∞, where it begins to increase exponentially; *i.e.*, the relationship between η and $f'(\eta)$ (*i.e.*, U_y / U_∞) goes from linear to exponential at *ca.* 0.60 U_∞. The height above the substrate surface where the rate in velocity reduction becomes minimum (*i.e.*, at *ca.* 0.60 U_∞) can therefore be selected to represent the depth within the boundary layer where protection from the mainstream velocity is foremost for organism such as simuliid larvae (*i.e.*, the local velocity is still high enough to ensure proper biological functions).

About 80 - 90 larvae (6th and 7th instar) were gently placed on the substrates with a fine paint brush, and allowed to acclimate for 24 hours at selected experimental velocities. High-plant-content fish food (Tetra®, Federal Republic of Germany) and yeast (Engedura, Edward Agencies, Winnipeg, Canada) were added in small quantities (0.005-0.1g dry weight per litre) following larval transfer to the flume, to stimulate suspension feeding. In assessing the influence of the boundary layer thickness on microsite selection, position of the larval head (*i.e.*, distance between the substrate and the geometrical centre of the cephalic capsule, and distance between the plate's leading edge and the vertical axis intersecting the geometrical centre of the cephalic capsule) was recorded for each larva at the end of the acclimatation period. The height of the cephalic capsule above the substrate surface (hence the position of the labral fans above the substrate) was consequently compared to the local thickness of the boundary layer. Distance of the larval head from the leading-edge of the substrate was used in calculations of local boundary layer thickness (*i.e.*, boundary layer thickness at the labral fan level). As mainstream velocity increases *S. vittatum* larvae progressively lean with the flow, which brings the head and the labral fans in proximity to the substrate. Consequently, the overall deflection of a larva is defined as the deviation from the vertical axis originating at the attachment site, of the first thoracic segment closest to the substrate (*i.e.*, first thoracic segment in contact with the substrate at maximum deflection of 90°). Mainstream velocities used to assessed the influence of boundary layer thickness on microsite selection, were in increments of 5 cm/s within a 5 - 50 cm/s velocity range.

Larval position (*i.e.*, position of the abdominal attachment site) along each of the 10°-segments of the cylindrical substrate was recorded at the end of each acclimatation period. To simulate an abrupt change in microsite hydraulic condition, the cylinder was rapidly rotated to expose the larvae to a different set of flow condition. The cylinder was either 1) rotated *ca.* 90° from separation point to stagnation point, 2) rotated *ca.* 50° from stagnation point to the zone of maximum shear stress, or 3) not rotated but exposed to a different water velocity. Mainstream velocities used were *ca.* 30 and 65 cm/s. Following continuous monitoring of larval reactions (*i.e.*, displacements and probing *sensu* Eymann and Friend 1988) during and immediately after treatments, position of the larvae were recorded every hour for the first 12h, and finally at 24 h.

Non-parametric statistical analyses were executed with Microsoft® EXCEL (Microsoft Corporation), and FASTAT™ (SYSTAT Inc., Illinois, USA) on a Macintosh™ (Apple computer Inc.) personal computer. Graphics were generated using

Cricket Graph™ (Cricket Software Inc., Philadelphia, USA), and MacDraw II™ (Apple computer Inc.) software.

4.4 RESULTS

Velocity distribution near the surface of the artificial substrates conformed to values predicted from theory. No significant ($p < 0.05$) differences between experimental and theoretical boundary layer thickness were observed along the thin flat substrate held parallel to the flow direction. Consequently, estimates of boundary layer thickness (δ) over the flate substrate refered to hereafter, are calculated from theory (*i.e.*, Eq. 2). Flow conditions within the boundary layers were always laminar in the first 80 mm of the flat plate.

Although very difficult to assess, local velocities *ca.* 1.0 mm from the cylinder's surface (*i.e.*, outside the boundary layer) measured at 70° from the stagnation point, were within ±10% of the velocities predicted by theory ($U_{\phi} \approx 1.6U_{\infty}$; Zukauskas and Ziugzda 1985). Boundary layers thickness (Eq. 6) were calculated as 0.25 and 0.16 mm for mainstream velocities of 30 and 65 cm/s respectively. Flow within the boundary layers was always laminar. As vorticies were shed alternately behind the cylinder, the stagnation point oscillated *ca.* ±3°, while the position of the boundary layer separation from the cylinder's surface was between 80° and 90° (exact location of separation was almost impossible to define).

4.4.1 Flat substrate parallel to the flow. Sixth and seventh instar larvae of *S. vittatum* Zett. exposed to flow velocities of 5 - 55 cm/s over a flat surface tended to gather on the upstream portion of the plate (0 - 3.5 cm). Although there was no strong correlation ($r^2 < 0.32$) between overall larval deflection and their attachment distance from the plate's leading edge, overall deflection angles observed at each velocity tended to decrease (*i.e.*, distance between the larval head and the substrate increased) with increasing distance from the plate's leading edge. Measures of distance of the larval head from the substrate in relation to boundary layer thickness show that *S. vittatum* larvae tend to keep their labral fans "outside" the boundary layer (Fig. 5a). About 85% of the data-points representing the position of the head are located over the iso-distance line (*i.e.*, where the head would meet the "edge" of the boundary layer) defined with the boundary layer thickness expressed as the distance from the substrate's surface where 0.90 of the mainstream velocity is observed; *ca.* 79% of the cases are above the iso-line if the boundary layer thickness is assessed as the distance from the substrate's surface where 0.99 of the mainstream velocity is observed. All data-points below the iso-distance line observed for boundary layer thickness between *ca.* 0.5 and 1.0 mm arise from a single larva with significantly shorter body length than the others (2.8 mm compared to the average of 4.2 ± 0.4 mm). Further, *ca.* 50% of the larvae had the bulbous portion of their abdomen (abdominal segments 5 - 8) partially protruding above the 0.90 boundary layer, while *ca.* 19% were below the 0.60 U_∞ boundary layer (Fig. 5b). Approximately 27 and 81% of the larvae were located in boundary layers of thickness less than 0.5 and 1.0 mm respectively. The average minimum height (calculated from mainstream velocities of 40 - 65 cm/s, where the abdomen is the closest to the substrate) of the 5th abdominal segment of *Simulium vittatum* Zett. larvae over the substrate's surface is *ca.* 0.62 ± 0.16 mm, and most likely reflects the influence of the bulgy posterior abdominal shape of the larvae and relative position of the posteroventral circlet of hooks on the last abdominal segment.

4.4.2 Cylindrical substrate perpendicular to the flow. Sixth and seventh instar larvae of *S. vittatum* placed on a cylinder perpendicular to flows of average velocities of *ca.* 30 and 65 cm/s, tended to gather along the zone of separation (*ca.* 80° - 90°), but also stayed along the stagnation line (*ca.* 0°) if cylinder rotation brought them there (Fig. 6). Conversely, larvae tended to avoid the zone of maximum shear stress (*ca.* 50° - 60°), and the zone immediately behind separation where vorticies are shed (> 100°). Larval distribution was significantly more delineated as velocity increases. At mainstream velocity of *ca.* 30 cm/s (*i.e.*, Reynolds number of the cylinder, $Re_d \approx 9,250$), large vorticies create a strong recirculation on the rear surface of the cylinder, making contact on the cylinder's surface at 120° - 150° and most likely creating a zone of high shear stresses. Larvae aggregated near the rear stagnation line (150° - 180°) while avoiding the zone of high shear stresses. As mainstream velocity increased to *ca.* 65 cm/s ($Re \approx 20,850$) smaller vorticies did not make contact with the cylinder surface, and were shed more rapidly, creating an oscillating flow over the rear surface where some larvae were evenly distributed.

As the cylinder was rotated *ca.* 50°, larvae from the stagnation line were exposed to a zone of increasing velocities and shear stresses on the upstream portion of the cylinder, while larvae from the separation zone were moved into the wake exposing them to a zone of higher shear (at $Re \approx 9,250$) or a zone of oscillating flow (at $Re \approx 20,850$). As a result, most larvae on the upstream portion of the cylinder moved toward the separation zone, looping past the zone of maximum surface shear stress (Figs. 7, 8). Principally at higher mainstream velocity, larvae moving directly downstream (*i.e.*, toward separation) turned abruptly to loop along the separation zone to rapidly anchor and start suspension-feeding. Conversely, after extensive probing (*sensu* Eymann and Friend 1988) some larvae (not already positioned at stagnation by rotation of the cylinder) moved toward the stagnation zone, and, as they made contact with it, also looped along to rapidly anchor and start suspension-feeding. Depending on mainstream velocity, larvae shifted into the cylinder's wake partly migrated back to separation (at *ca.* 65 cm/s), or toward the rear stagnation zone (at *ca.* 30 cm/s).

As the cylinder was rotated *ca.* 90°, larvae from the separation zone were shifted to the stagnation line. Most larvae at *ca.* 30 cm/s, and all larvae at *ca.* 65 cm/s stayed at stagnation, simply probing and looping to finally re-settle to filter-feed (Fig. 7, 8). Again, larvae avoided zones of high shear stresses, and depending on mainstream velocity the larvae shifted into the cylinder's wake partly migrated back to separation (at *ca.* 65 cm/s), or toward rear stagnation zone (at *ca.* 30 cm/s).

As mainstream velocity was rapidly decreased from 65 to 30 cm/s, some larvae retained their suspension-feeding posture, others demonstrated only short looping displacement around their original position, and as a result larval distribution along the stagnation and separation zone showed a more relaxed pattern (*i.e.*, greater distribution range on each side of the zones), while larvae on the rear surface of the cylinder migrated toward the rear stagnation zone (Fig. 7). Conversely, as mainstream velocity was rapidly increased from 30 to 65 cm/s, larval distribution along stagnation and separation zone tightened (*i.e.*, smaller distribution range on each side of the zones), while larvae on the rear surface of the cylinder migrate away from the rear stagnation zone (Fig. 8). In both cases, almost no larvae were observed in the zone of high shear stresses.

After displaying avoidance reaction (disturbed larvae cease feeding and rapidly pull themselves down to the substrate; *sensu* Chance and Craig 1986) as the cylinder was rotated, *S. vittatum* larvae immediately initiated probing and looping (Fig. 9a,b). Approximately 60% of all displacements observed during the first 60 minutes following cylinder rotations or water velocity changes were initiated during the first 5 min (Fig. 9a); and most followed treatments immediately (Fig. 9b). Although there were no significant differences in time spent looping ($P > 0.2$, $t = 1.008$, $\nu = 26$) and distance travelled ($P >$

0.2, $t = 1.231$, $v = 26$), between looping initiated within the first 5 min and the subsequent 55 min of the treatments (301 ± 391 sec and 50.9° ± 16.7° *vs*. 188 ± 152 sec and 43.2° ± 16.4° respectively), larvae initiating looping immediately after treatments tended to move for a longer time (time range: 30 - 1500 sec for looping initiated during the first 5 min compared to 0.75 - 540 sec for looping initiated during the subsequent 55 min). No marked differences between distance ranges travelled were observed (displacement lengths of 10° to 80° for looping initiated during the first 5 min compared to 10° to 60° for looping initiated during the subsequent 55 min). Throughout the experiments, approximately 1 - 1.5% of the larvae placed on the cylinder showed some sort of disruption (*i.e.*, probing and looping) over periods of 30 min; disruption sometimes lead to a single short displacement or a brief reaction of looping cascading through neighbouring larvae.

4.5 DISCUSSION

Movement of the surrounding water presents benthic organisms like black fly larvae with both benefits and problems. While flowing water provides them with a continuous supply of suspended food particles, it may increase the difficulty of maintaining contact with the local substrate. Consequently, suspension-feeding simuliid larvae should attempt to maximize the difference between benefit and cost of a particular site by adjusting their position and stance to keep water flow suitable for maximum filtration efficiency while keeping energetic cost, such as drag, as low as possible. Here, I discuss the hydrolic conditions to satisfy such requirements (*i.e.*, what are they cueing on ?).

Primary habitat selection by benthic suspension-feeding invertebrates such as black fly larvae is most likely influenced by micro-hydraulic events occurring at the substrate level, the scale presumably perceived by the organism itself. Detection of hydraulic changes by simuliid larvae is immediate, and primary relocation of *S. vittatum* Zett. larvae toward the new conditions is most often completed within 2 - 3 min of disruption; only a low level of background displacement activity (*ca.* 1 - 1.5% of population per 30 min.) were subsequently observed under my experimental conditions. This background movement has also been observed by Ciborowski and Craig (personal communication) who noted that typically <5% of *S. vittatum* larvae changed position on a flat plate during a 30 min interval when exposed to constant mainstream velocities. These concurrent observations suggest that gross patterns (*i.e.*, outcome of primary relocation) of organization toward local hydraulic conditions are most likely formed in the brief period following hydraulic changes, while later contacts among established larvae and invasions by single individuals dictate the more stable inter-larval positions (*i.e.*, dispersion pattern of an established group). Thus, as suggested by Ciborowski and Craig (1989), and Rühm and Pegel (1986) established patterns of larval distribution reflect both flow and food availability conditions. Eymann and Friend (1988) observed that larvae demonstrate more tolerance (*i.e.*, smaller distance between anchoring sites) toward neighbours if food is readily available.

Data from this study lead me to reject the hypothesis that simuliid larvae typically hide in boundary layers (and its associated gradient to zero current to the bottom) to remove themselves from the direct influence of the mainstream current. The majority (*ca.* 85%) of *S. vittatum* larvae maintained their labral fans well above the growing $0.90U_\infty$ boundary layer developing over the flat substrate, and 50% and 81% of the larvae also kept the bulbous part of their post-abdomen adjacent to or protruding from the 0.90 and 0.60 boundary layer, respectively. These results somewhat disagree with Chance and Craig's (1986) views (see also Craig and Galloway 1987), following Ambühl's (1956) suggestion, that simuliid larvae use the boundary layer to withdraw themselves entirely from the flow forces concurrent with mainstream velocities. Although they observed labral fans of *S. vittatum* larvae at, or just below, the 0.90 boundary layer - mainstream junction, their experiments were conducted in a fully developed boundary layer (most likely with an associated laminar sub-layer) and were not designed to assess the influence of boundary layer thickness on larval site-selection (Craig pers. com.). Further, I observed no downstream larval movements toward a thicker boundary layer as mainstream velocity was increased stepwise from 5 to 50 cm/s. Hence, the larvae did not migrate downstream from the plate's leading edge to stay within the boundary layer. As a result, a large portion of the larval body was exposed to the mainstream flow, and more than 62 and 80% of the larvae respectively were suspension-feeding in boundary layers less than 0.75 and 1.0 mm thick. Although a very weak correlation ($r^2 < 0.30$, $P = 0.007$) between overall larval deflection and their attachment distance from the plate's leading edge was observed, *S. vittatum* larvae do not assume stances nor select positions along the substrate demonstrating any significant response to changing boundary layer thickness. The trend in lower overall larval deflection as the distance from the plate's leading edge increases, most likely reflects the reduction in drag forces acting on the larvae as more of the body becomes surrounded by lower ambient velocities.

All larvae chose locations on the first 3.5 cm from the plate's leading-edge, which would most likely imply a preference toward zones of higher shear stress as indicated by Wetmore (1987) and Statzner (1981). This suggestion, however, is not supported by any of the distribution patterns observed on the surface of a cylindrical substrate, where larvae significantly avoid zones of maximum shear stress at velocities equivalent to those generated about the flat substrate. Few larvae (2.4% at 30 cm/s, 1.2% at 65 cm/s) were observed between the ±50° - 60° location on the cylinder's surface, where, because of the steepness of the velocity profile, no protection from the direct influence of the accelerating local flow is available at the larval scale. These result seems to contradict Wetmore (1987) who demonstrated that larvae of *S. vittatum* Zett. are found in microhabitats of significantly higher "shear stress" (defined as water "depth x slope x weight of water") than those present in randomly available microhabitats, and Statzner's (1981) investigation showing a weak relation between "hydraulic stress" (*i.e.*, combination of current velocity, water depth and substrate roughness) and microdistribution of benthic invertebrates in lotic systems. Such indicies, although powerful approximations of the tractive forces generated by flowing water on portions of the stream or river bed, seem not to adequately represent the micro-hydraulic conditions existing at the surface of a single substrate element (*i.e.*, at the larval level) and consequently may have little use in understanding proximal factors affecting formation of local assemblages of benthic invertebrates.

The incongruity between larval reaction toward surface shear stress above a flat and curved surface indicates that, although *S. vittatum* larvae can sustain high shear stresses (Eymann 1988), most larvae select another region if presented with a variety of hydraulic conditions. Flow over a thin, rigid, flat plate is among the simplest of hydraulic conditions to which benthic organisms can be subjected, and consequently this situation may not present essential cues present in natural environments. Simuliid larvae occur on a variety of substrates, including bedrock, boulders, smaller stones, vegetation, snags, and artificial substrates introduced into streams, most of which bear curved surfaces over which water can accelerate and decelerate, producing complex flow patterns about the substrate's surface. In swift lotic systems, boundary layers associated with each element of substrate colonized by black fly larvae, are mostly thin developing boundary layers that separate from the substrate's surface (Eymann personal communication, personal observations).

Contrary to expectations, larvae on the curved surface did not select primarily the zone of maximum velocity, but gathered predominantly where the boundary layer separates from the substrate's surface, or remained at the stagnation line (where local velocity is minimum). These results do not support Décamps *et al.* (1975) observations that, when exposed to a longitudinal velocity gradient over the substratum, larvae concentrate in a narrow band where velocity is maximal. Difference in distribution patterns on the frontal portion of the cylinder ($10° < \phi < 80°$) exposed to 30 and 65 cm/s suggest that *S. vittatum* larvae are more tolerant to local velocities of 20 - 60 cm/s. At higher velocities larvae mainly increase search for protective areas. These observations concur with reports that *S. vittatum* do not usually occur in velocities greater than 70 cm/s (Kurtak 1973, Colbo 1979), and that probability of structural failure of their labral fans increases as water velocity approaches 55-65 cm/s (Lacoursière, chapter 3.4.3). They also agree with Phillipson's (1956, 1957) demonstration of the species specific maximum velocity preference.

Although simuliid larvae have often been depicted aligned near or at the crest of a curved substrate (*eg*. Kurtak 1973, Décamps *et al.* 1975), this study is the first direct evidence for a micro-hydraulic event (*i.e.*, boundary layer separation) acting as causative agent of formation of simuliid assemblages. In the region of separation, rapid flow deceleration about the substrate's surface (*i.e.*, $\tau_0 \approx 0$) and subsequent backward flow create a lower region of little velocity, over which a region of faster flow circulates (*i.e.*, the lifted boundary layer) (Fig. 2). Consequently, larvae anchored in the region of boundary layer separation are more or less withdrawn from the full influence of the local velocities ($U_{\emptyset}$), while the filtering appendages can be kept in faster flows (Fig. 10). Boundary layer lifting from an original thickness of 0.16 mm at local velocity of *ca.* 100 cm/s (mainstream velocity of *ca.* 65 cm/s) offers relatively more protection to a *S. vittatum* larva (minimum height of the 5th abdominal segment over the substrate: *ca.* 0.62 ± 0.16 mm) than a boundary layer thickness of 0.25 mm at local velocity of *ca.* 50 cm/s (mainstream velocity of 30 cm/s); which could explain in part the tighter distributions along the separation line observed at higher mainstream velocity (65 cm/s). As mentioned by Ambühl (1959), organisms predominantly avoid the zone of dead water downstream of separation, where at the larval scale, flow is drastically reduced following a sharp edge inducing separation. Larvae anchored some distance (*i.e.*, 90°-110°) downstream of the boundary layer separation point, were predominantly members of a local clump (*sensu* Eymann 1985, Eymann and Friend 1988) also extending upstream of the separation zone. Although no direct flow measurements were executed within the larval clump, these observations strongly suggest that local changes in hydraulic conditions within and around the group can enhance further colonization. These laboratory results corroborate Eymann's (personal communication) observations of high concentrations of simuliid larvae in zones of boundary layer separation under natural conditions, pointing out that it was often possible to anticipate the location of separation from the abrupt end of a group of larvae on the downstream part of a rock, and some observations on flow modification induced by larval clumping. Both experimentations concur with the early observations of Décamps *et al.* (1975) on rocks showing high simuliid population just upstream of "perturbations" induced by the "détachement de la lame".

Conversely, it seems counter-intuitive that 15% of simuliid larvae selected the stagnation line as a suspension-feeding site, because local water velocities there are the lowest along an increasing longitudinal velocity gradient about the substrate's surface. But micro-hydraulic conditions at that location are surprisingly adequate for suspension-feeding. Because of the small diameter of the cylinder (37 mm) compared to the average larval length (4.2 ± 0.4 mm), larvae located on each side (≈ ± 2 - 3°) of the stagnation line were consequently exposed to a rapid increase in local velocity along their body length; hence labral fans were exposed to faster flows than the abdominal portion of the body. Approximately 90% of all larvae observed along the stagnation line were artificially positioned there by cylinder rotation. While movement toward the stagnation line was observed only when the cylinder was exposed to high mainstream velocity (24% immigration at 65 cm/s), 35% of the larvae left the stagnation line when the cylinder was exposed to low mainstream velocity (*ca.* 30 cm/s). These results suggest that, as for the boundary layer separation zone, the protection offered at the stagnation line is greater for larvae at higher velocities, and this explaines in part the tighter distribution pattern definition observed at higher mainstream velocity. It is common to find simuliid larvae covering the upstream portion of cylindrical substrates (*eg*. branches, logs), however observations of simuliid larvae aligned in a stagnation zone under natural conditions have yet to be reported. My results suggest that evidence for this should be sought in field situations.

As shown by larval distribution on the cylinder's surface swept by vorticies (*ca.* 20% of the larvae were located about the rear stagnation line at mainstream velocity of *ca.* 30 cm/s, and *ca.* 11% were covering the rear portion of the cylinder at the exception of the zone of rear stagnation at mainstream velocities of *ca.* 65 cm/s; Fig. 6), larvae readily colonized areas of recirculating flow if it was deep enough to ensure unidirectional flow over the entire larval body length, even if surface flow shifted in direction.

Although velocity profiles in the zones predominantly selected (stagnation and separation) and avoided (maximum surface shear stress) by *S. vittatum* larvae differ strongly, a common denominator emerges: in the zones of separation and stagnation, the labral fans are exposed to substantially higher velocities than the bulbous abdominal segments of the body, while in the zone of maximum surface shear stress no velocity differential is apparent at the larval scale (Fig. 10). This suggests that larvae are cueing on a steep velocity difference between the abdominal and cephalic (*i.e.*, labral fan) levels as part of selecting a suspension-feeding microsite. This criteria would maximize particle-flux through the labral fans and minimize drag forces on the bulbous portion of the larval body. This hypothesis may be related to the probing behaviours displayed by simuliid larvae (Eymann and Friend 1988), in which larvae move their heads up and down while moving them over the substrate in arcs around their attachment site. This probing could conceivably be used to scan of the local velocity profile. Simuliid larvae can detect changes in water velocity (or water acceleration) as demonstrated by the alternation of probing and looping motions of a larva moving directly toward the stagnation or separation zones, and by the sharp angle turn executed as either zone is encountered. Following some looping along separation or stagnation lines, larvae finally anchor and start suspension-feeding. Conversely, low larval occurrences in the zone of maximum surface shear stress, even in tolerable local velocities (*i.e.*, generated by mainstream velocity of 30 cm/s), may also be explained by my hypothesis as lack of suitable differences in velocity profile at the larval scale associated with that zone. Methods of cue detection are still largely the subject of speculation, and there is only circumstantial evidences for the involvement of particular sensory structures (*e.g.* stress receptors at the base of the labral fan rays Craig 1974), small mechano-receptive hairs on the larval body (Eymann, personal communication)).

Proximal hydraulic events influencing formation of local black fly assemblages operate unquestionably on the larval scale, and the shape of the velocity profile directly above the substrate surface may be the main determinant of suspension-feeding site suitability. Micro-hydraulic events such as boundary layer separations and zones of high surface shear stress cannot fully account for all distribution patterns within a stream reach, since substrates displaying identical hydraulic conditions are often left uncolonized while neighbouring ones are heavily populated. As passive suspension-feeders, black fly larvae rely on water flow to deliver food items to their labral-fans, hence behavioural response to micro-hydraulic events may be the major component of a more complex behavioural feedback-network including physiological (*e.g.*, water temperature, food availability; see Ross and Merritt 1987 for review) and bio-mechanical requirements (*e.g.* labral fan structural failure at high flow velocity, Lacoursière *section 3.4.3*). The results of my study support the hypothesis that black fly larvae select a suspension-feeding location that maximizes the difference between benefit and cost of that particular site, by achieving water flow around the body and through the fans for maximum filtration efficiency while keeping energetic cost such as drag, as low as possible

4.6 CONCLUSIONS

The importance of flow to the ecology of benthic organisms is unquestionable. Although many studies have documented the apparent adaptations or specializations of benthic invertebrates to life in fast-flowing waters, it is only recently that some of the theory and practical techniques of fluid mechanics have been applied in a more rigourous way. Micro-hydraulic events at the substrate surface are dominant features defining the immediate environment of rheophilic benthic invertebrates, and investigating the implications of hydrolic factors at the scale relevant to individual larvae contributes to understanding of the proximal factors affecting formation of local assemblages. Integration of hydrodynamical and behavioural feed-back studies in an approach refered to as "behavioural hydrodynamics" (*sensu* Craig 1989) is therefore a key step in defining proximal factors affecting local formations of benthic invertebrate assemblages. Future progress in stream ecology depends upon biologists' abilities to understand and describe benthic flow regimes. Single velocity measurements are no longer acceptable. In sum, there is a great deal that we cannot decipher about the ecology of lotic systems until we fully investigate the physical biology of flow.

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ig. 1 Schematic representation of flow and associated boundary layer velocity profiles over the surface of a thin flat plate parallel to the flow (not to scale): U_∞, average mainstream velocity; U_y, local velocity; δ, boundary layer thickness; x, distance from the plate's leading-edge; y, height above the substrate's surface.

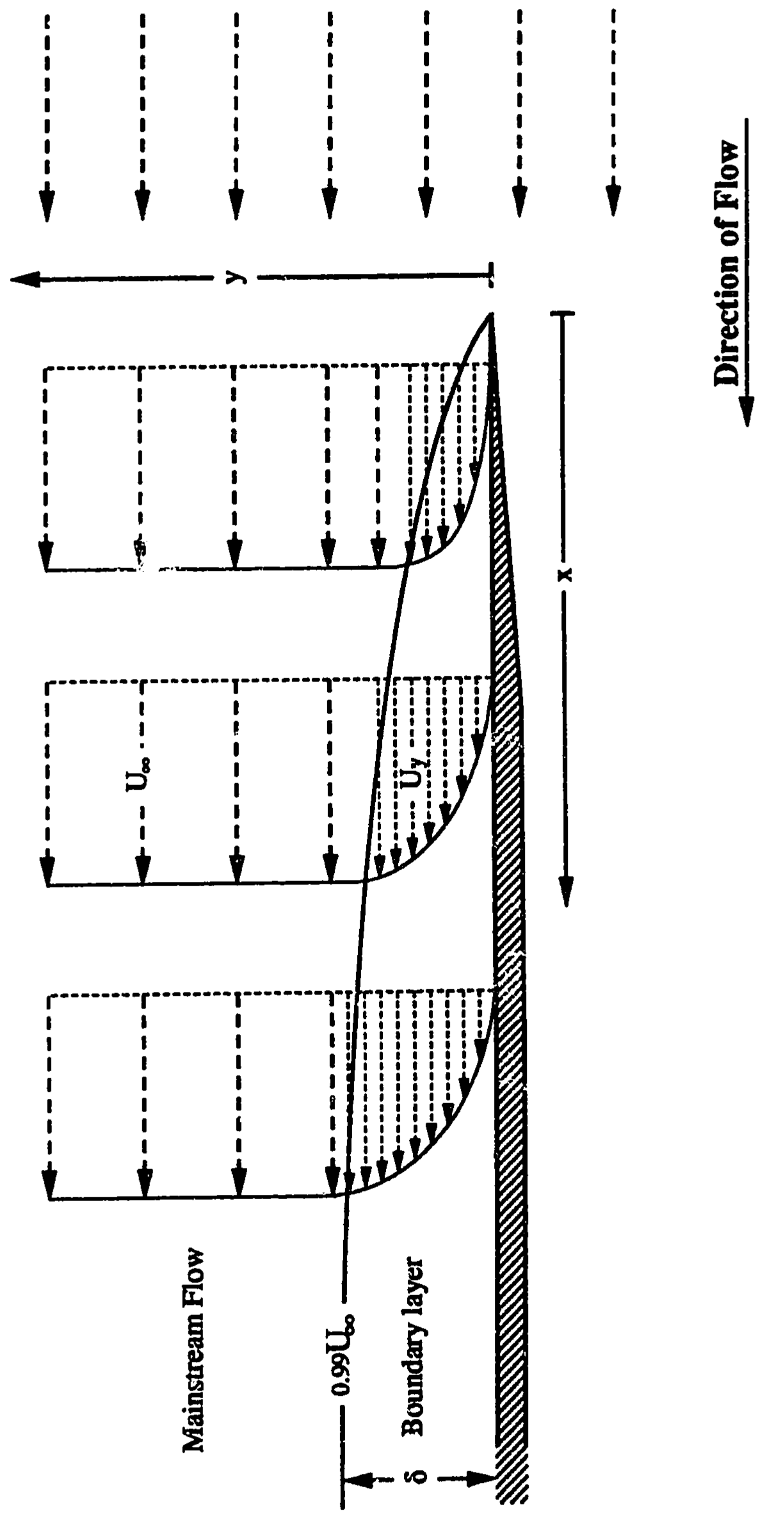

Direction of Flow
y
x
U∞
U_y
Mainstream Flow
0.99U∞
Boundary layer
δ

Fig. 2 Schematic representation of flow and associated velocity profiles about a cylinder in crossflow (not to scale): **Re_d**- Reynolds number (**U_∞ d** / ν; where **d** is the cylinder's diameter); **ø**, angle from the front stagnation point; **$U_ø$**, local velocity at angle ø; δ, boundary layer thickness. **A)** Flow at separation point. **B)** Flow in zone of maximum surface shear stress (τ_0): β, velocity gradient steepness. **C)** Flow at stagnation point.

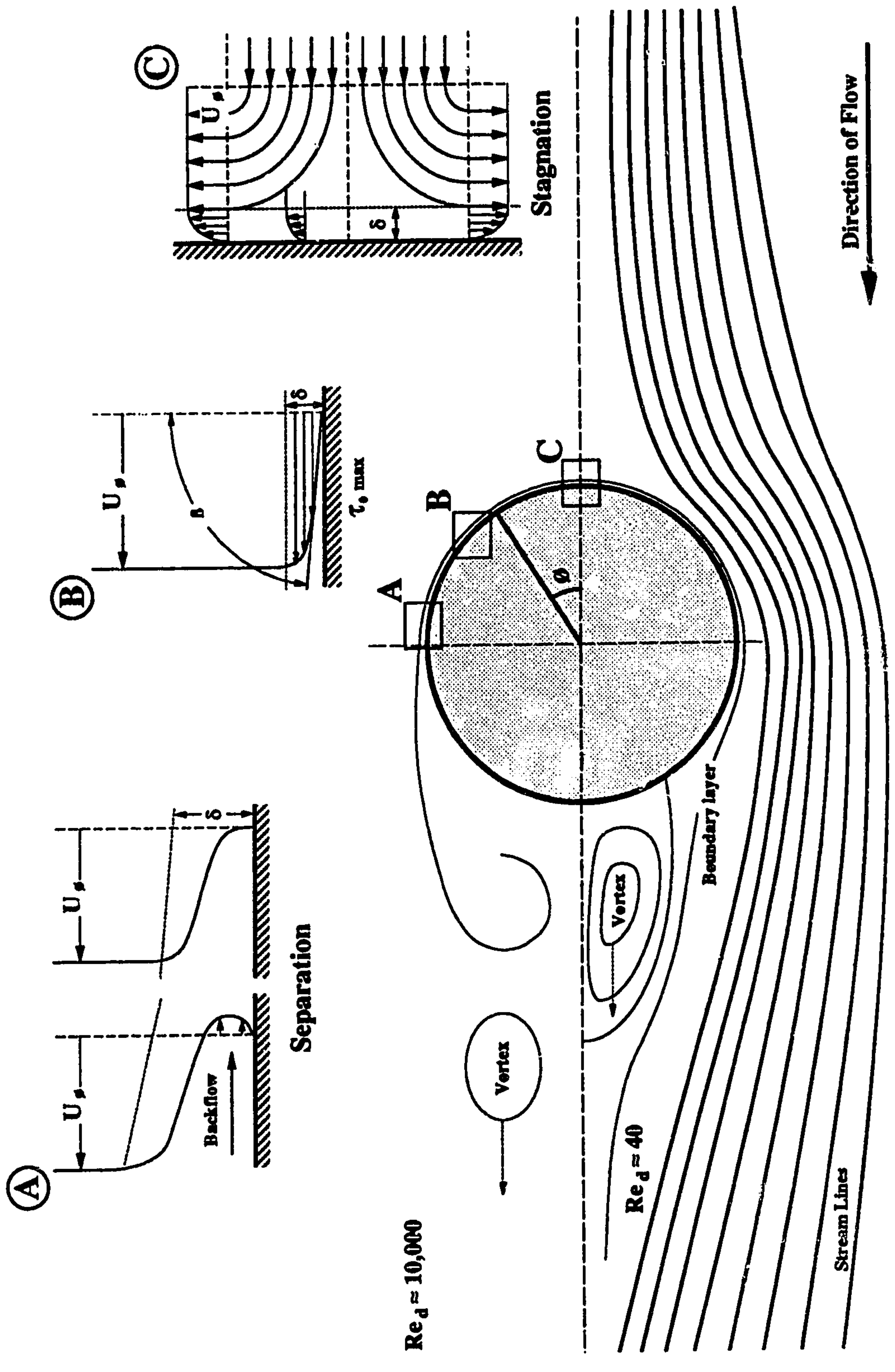

A
U_s
Backflow
δ
Separation
B
U_s
β
δ
τ_s max
C
U_s
δ
Stagnation
Direction of Flow
A
B
C
ø
Boundary layer
Vortex
Vertex
Vertex
Re_d ≈ 10,000
Re_d ≈ 40
Stream Lines

Fig. 3 Hydraulic conditions over the surface of a cylinder in crossflow: ø, angle from the front stagnation point; $U_ø$, local velocity at angle ø; U_∞, mainstream velocity; SP, separation zone; ST_f, front stagnation zone; τ_{max}, zone of maximum surface shear stress (τ_0); $\bar{\tau}$, Dimensionless Shear Stress index; W, cylinder's vortex sheet (*i.e.*, wake).

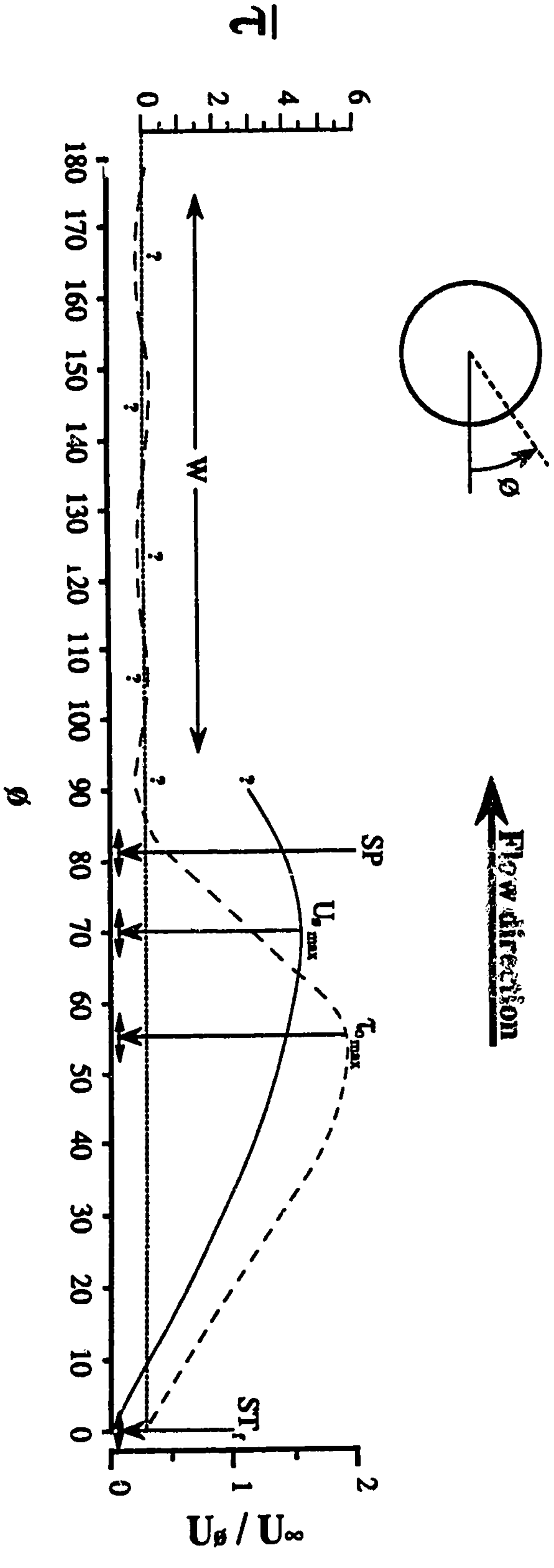

Flow direction
ø
SP
$U_{s\,max}$
$\tau_{s\,max}$
ST_r
W
?
$\bar{\tau}$
0
2
4
6
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
ø
0
1
2
Uø / U∞

Fig. 4 Artificial substrates of different geometry in the flume working section. **A)** Thin flat plate with beveled upstream-edge paralell to flow direction: **fp**, flat plate. **B)** Cylinder in crossflow: **c**, cylinder; **f**, frame; **s**, nylon screw; **h**, rotation hole.

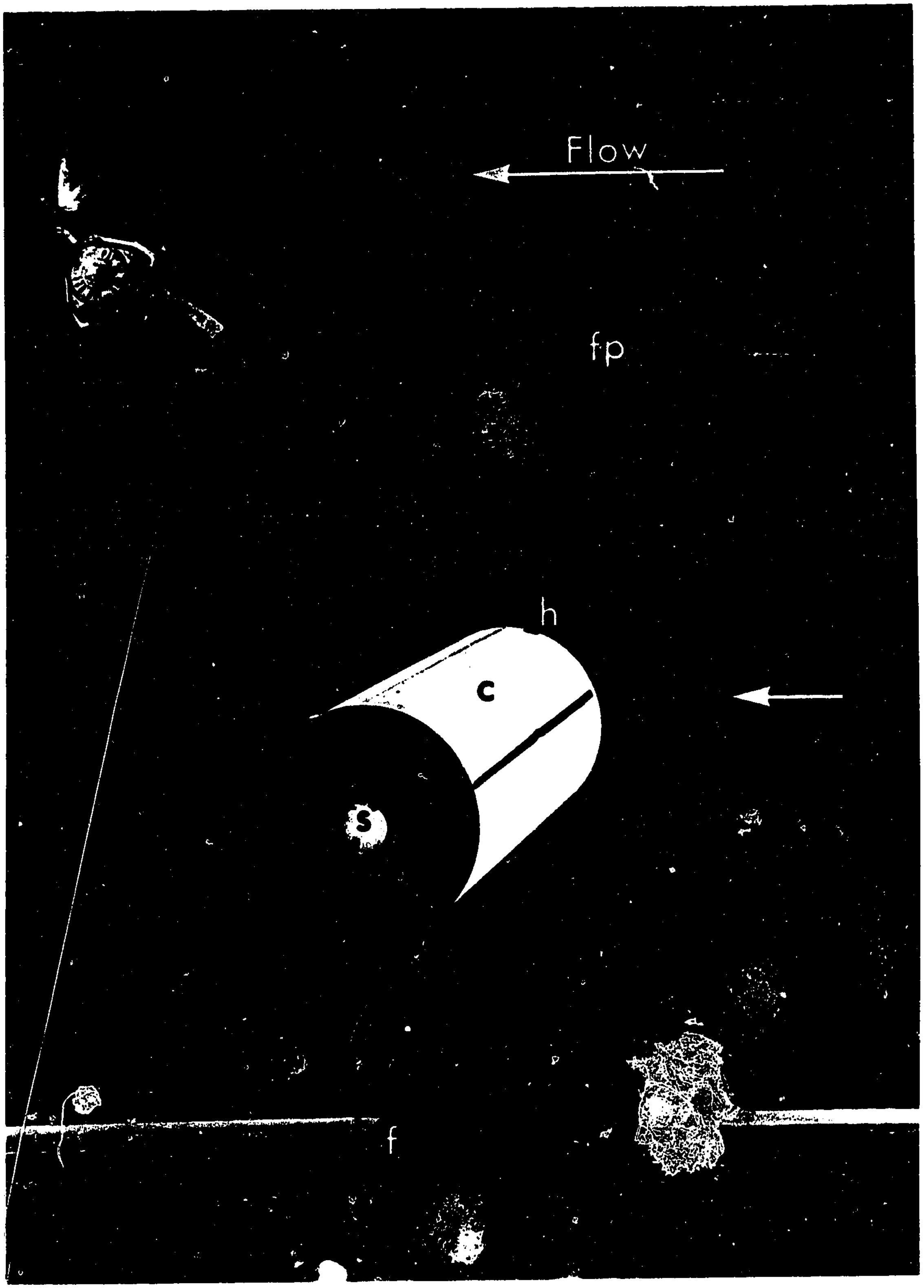

Flow
fp
h
c
s
f

Fig. 5 Stance of *Simulium vittatum* Zett. larvae in relation to calculated boundary layer thickness (δ: defined as the distances from the substrate's surface where 0.99, 0.90, and 0.60 of the mainstream velocity are present). **A)** Distance between the head and substrate surface in relation to boundary layer thickness. **B)** Distance between the 5th abdominal segment and the substrate surface in relation to boundary layer thickness.

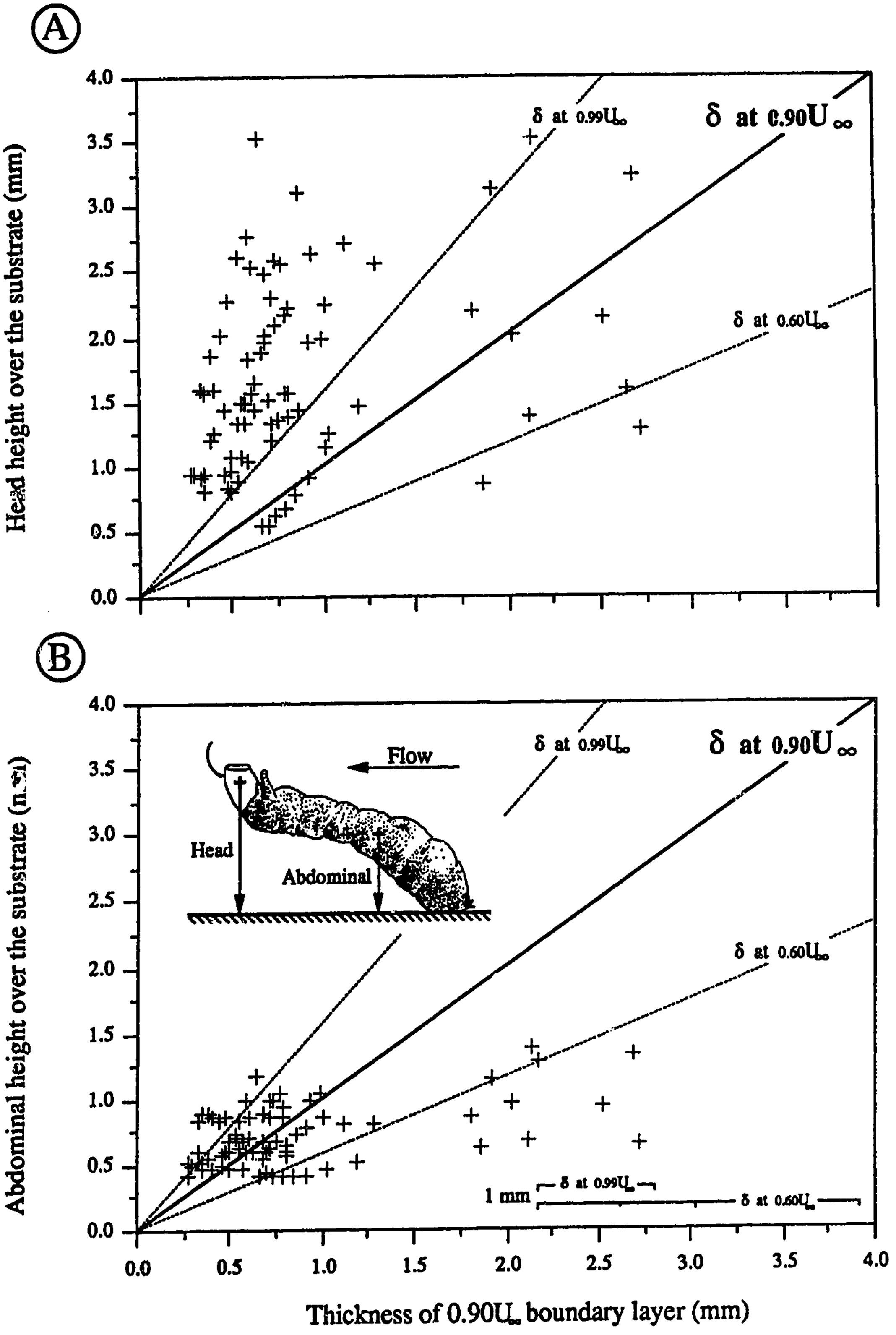

A
Head height over the substrate (mm)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
δ at 0.99U∞
δ at 0.90U∞
δ at 0.60U∞
B
Abdominal height over the substrate (mm)
Flow
Head
Abdominal
1 mm
δ at 0.99U∞
δ at 0.60U∞
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
Thickness of 0.90U∞ boundary layer (mm)

Fig. 6 Distribution of *Simulium vittatum* larvae on the surface of a cylinder in crossflow. A) Hydraulic conditions over the surface of a cylindrical cylinder in crossflow: ø, angle from the front stagnation point; $U_ø$, local velocity at angle ø; U_∞, mainstream velocity; SP, separation zone; ST_f, front stagnation zone; τ_{max}, zone of maximum surface shear stress (τ_0); $\bar{\tau}$, Dimensionless Shear Stress index, [illegible], cylinder's vortex sheet (*i.e.*, wake). B) Larval distribution on the surface of a circular cylinder exposed to an average mainstream velocity of 30.1 ± 0.8 cm/s: n, number of observations. C) Larval distribution on the surface of a circular cylinder exposed to an average mainstream velocity of 65.1 ± 1.1 cm/s.

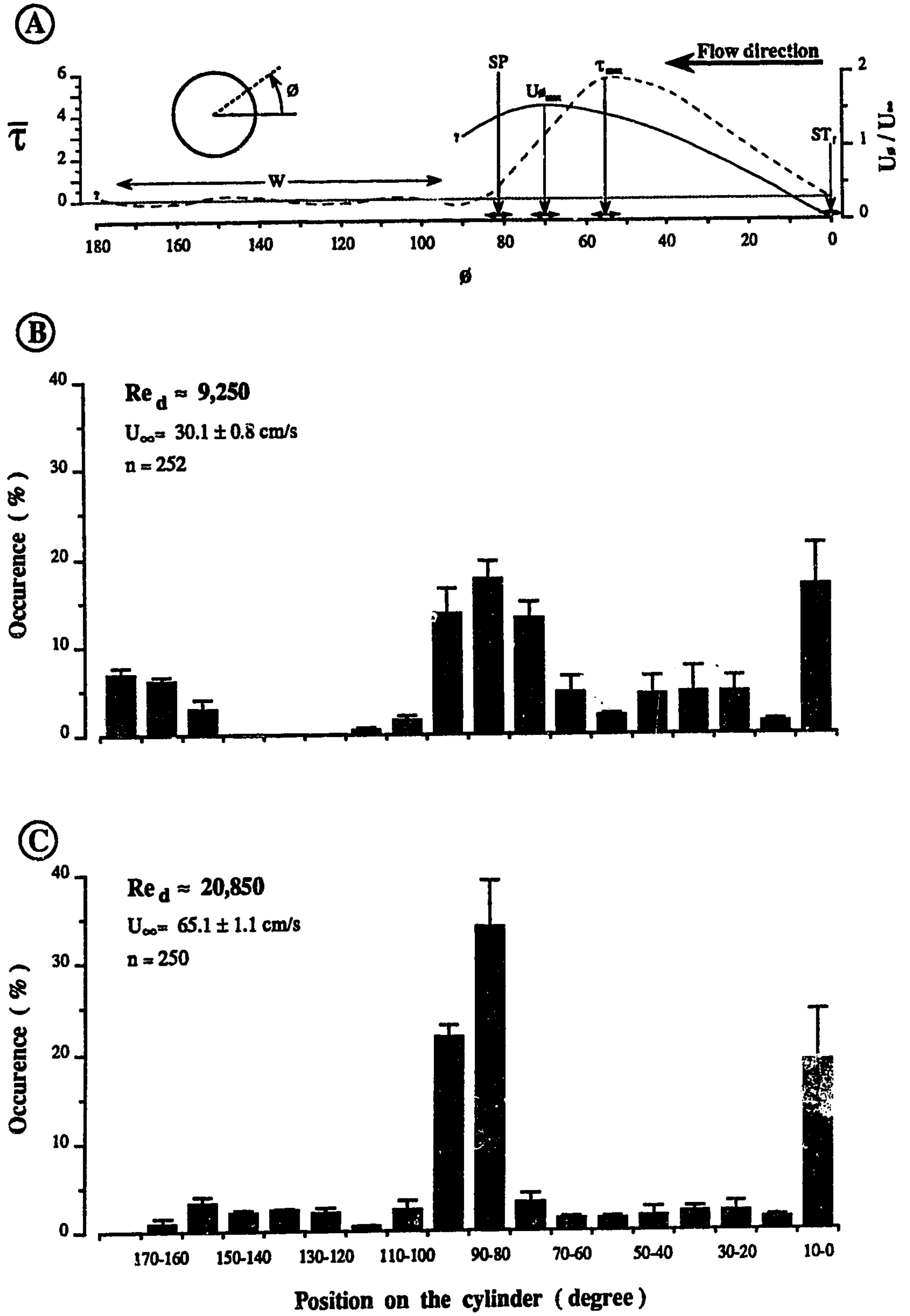

Ⓐ
Flow direction
$\bar{\tau}$
6
4
2
0
SP
$U_{\phi max}$
τ_{max}
ST
ø
W
?
2
1
0
U_ϕ / U_∞
180
160
140
120
100
80
60
40
20
0
ø
Ⓑ
$Re_d \approx 9,250$
$U_\infty = 30.1 \pm 0.8$ cm/s
n = 252
Occurence (%)
40
30
20
10
0
Ⓒ
$Re_d \approx 20,850$
$U_\infty = 65.1 \pm 1.1$ cm/s
n = 250
Occurence (%)
40
30
20
10
0
170-160
150-140
130-120
110-100
90-80
70-60
50-40
30-20
10-0
Position on the cylinder (degree)

Fig. 7 Distribution of *Simulium vittatum* larvae on the surface of a cylinder in crossflow following manipulation of hydraulic conditions at $Re_d \approx 9{,}250$. **A)** hydraulic conditions over the surface of a cylindrical cylinder in crossflow: **ø**, angle from the front stagnation point; $U_{ø}$, local velocity at angle ø; U_{∞}, mainstream velocity; **SP**, separation zone; ST_f, front stagnation zone; τ_{max}, zone of maximum surface shear stress (τ_0); $\bar{\tau}$, Dimensionless Shear Stress index; **W**, cylinder's vortex sheet (*i.e.*, wake); h, time (hours) following treatments. **B)** rotation of *ca.* 50° from stagnation point to the zone of maximum shear stress, **C)** rotation of *ca.* 90° from separation point to stagnation point, **D)** decrease in mainstream velocity from *ca.* 65 to 30 cm/s.

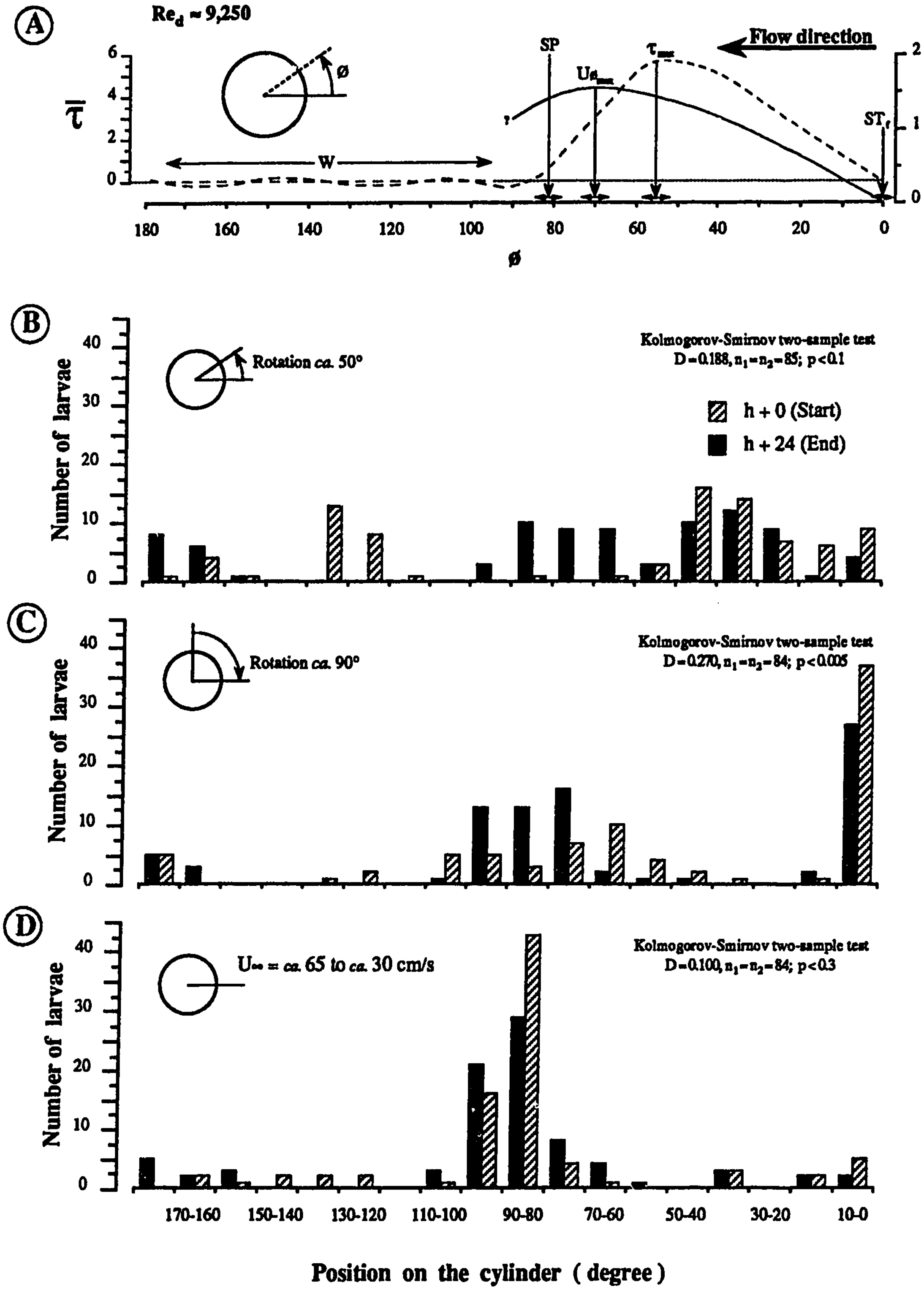

A
Re$_d$ ≈ 9,250
ø
SP
Uø$_{max}$
τ$_{max}$
Flow direction
τ
ST$_r$
W
6
4
2
0
τ̄
2
1
0
U$_ø$ / U$_∞$
180
160
140
120
100
80
60
40
20
0
ø
B
Rotation ca. 50°
Kolmogorov-Smirnov two-sample test
D = 0.188, n$_1$ = n$_2$ = 85; p < 0.1
▨ h + 0 (Start)
■ h + 24 (End)
Number of larvae
40
30
20
10
0
C
Rotation ca. 90°
Kolmogorov-Smirnov two-sample test
D = 0.270, n$_1$ = n$_2$ = 84; p < 0.005
Number of larvae
40
30
20
10
0
D
U$_∞$ = ca. 65 to ca. 30 cm/s
Kolmogorov-Smirnov two-sample test
D = 0.100, n$_1$ = n$_2$ = 84; p < 0.3
Number of larvae
40
30
20
10
0
170-160
150-140
130-120
110-100
90-80
70-60
50-40
30-20
10-0
Position on the cylinder (degree)

Fig. 8 Distribution of ***Simulium vittatum*** larvae on the surface of a cylinder in crossflow following manipulation of hydraulic conditions at $Re_d \approx 20{,}850$. **A)** hydraulic conditions over the surface of a cylindrical cylinder in crossflow: **ø**, angle from the front stagnation point; $U_{ø}$, local velocity at angle ø; U_∞, mainstream velocity; **SP**, separation zone; ST_f, front stagnation zone; τ_{max}, zone of maximum surface shear stress (τ_0); $\bar{\tau}$, Dimensionless Shear Stress index; **W**, cylinder's vortex sheet (*i.e.*, wake); h, time (hours) following treatments.. **B)** rotation of *ca.* 50° from stagnation point to the zone of maximum shear stress, **C)** rotation of *ca.* 90° from separation point to stagnation point, **D)** increase in mainstream velocity from *ca.* 30 to 65 cm/s.

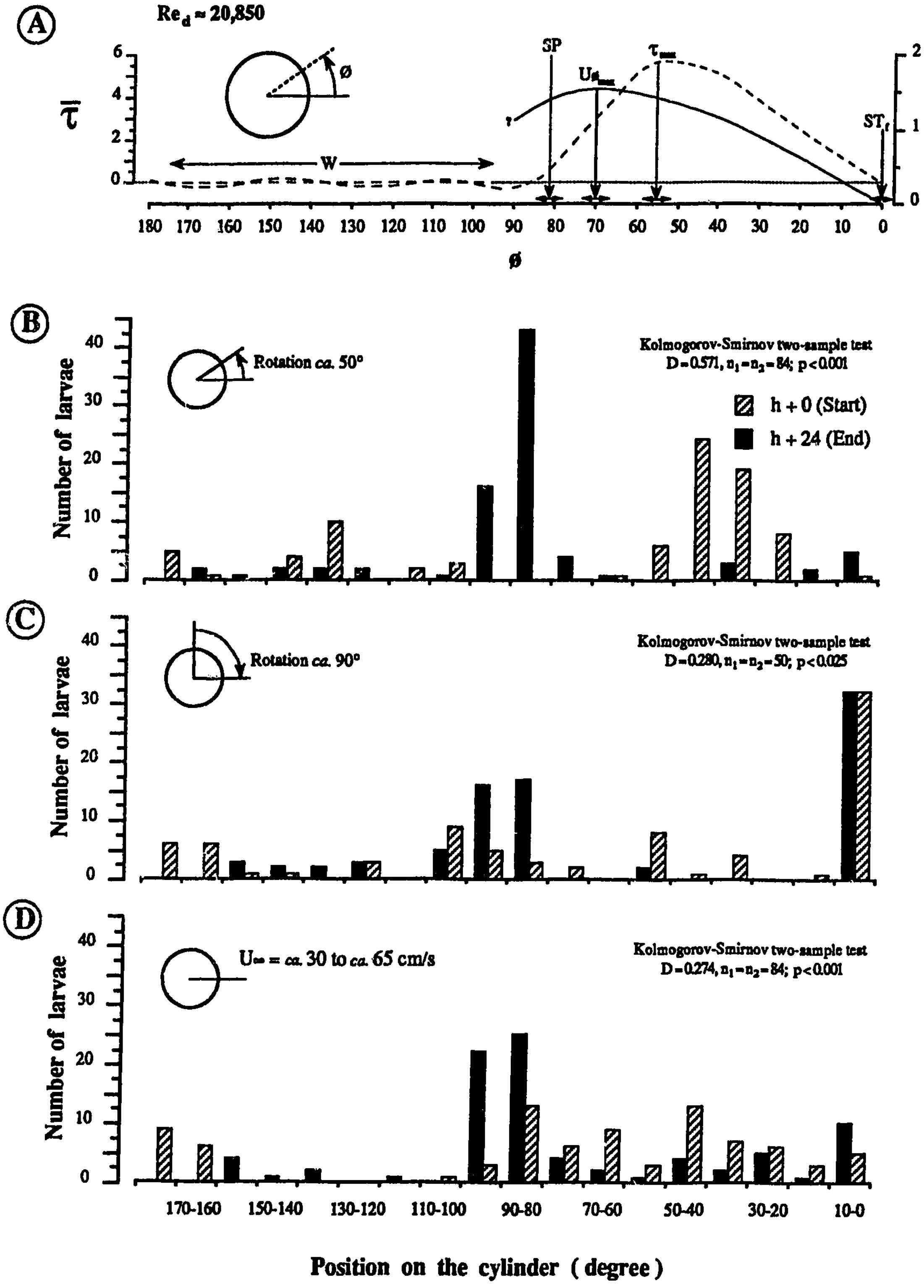
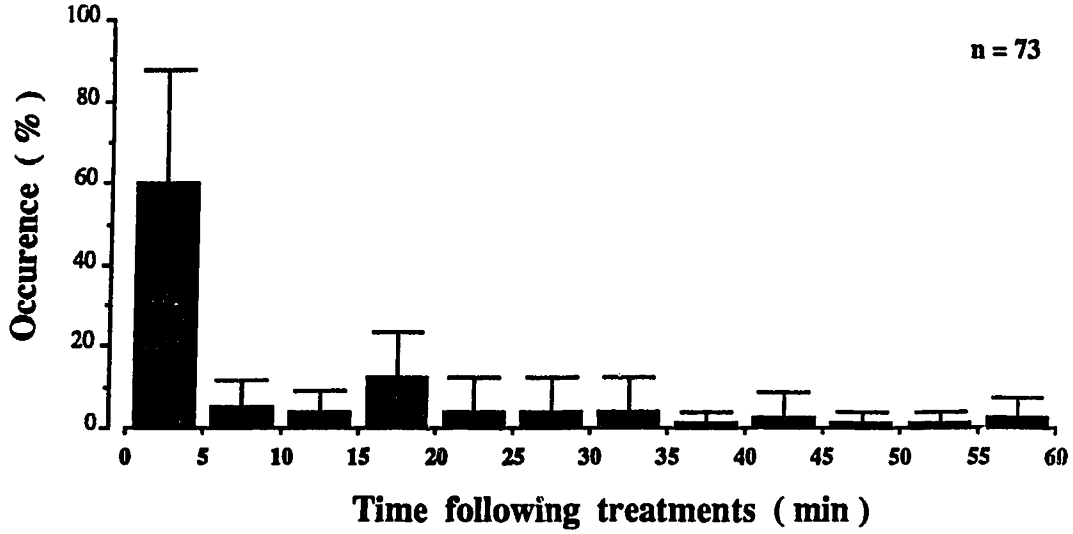

A
Re_d ≈ 20,850
τ
6
4
2
0
ø
W
SP
Uø_max
τ_max
ST_f
U_ø / U_∞
2
1
0
180 170 160 150 140 130 120 110 100 90 80 70 60 50 40 30 20 10 0
ø
B
Number of larvae
40
30
20
10
0
Rotation ca. 50°
Kolmogorov-Smirnov two-sample test
D=0.571, n1=n2=84; p<0.001
▨ h + 0 (Start)
■ h + 24 (End)
C
Number of larvae
40
30
20
10
0
Rotation ca. 90°
Kolmogorov-Smirnov two-sample test
D=0.280, n1=n2=50; p<0.025
D
Number of larvae
40
30
20
10
0
U∞ = ca. 30 to ca. 65 cm/s
Kolmogorov-Smirnov two-sample test
D=0.274, n1=n2=84; p<0.001
170-160 150-140 130-120 110-100 90-80 70-60 50-40 30-20 10-0
Position on the cylinder (degree)

Fig. 9 Displacement frequency of *Simulium vittatum* larvae following treatments: **n**, number of observations. **A)** Displacement during the first 60 min following treatments. **B)** Details of the displacement frequency of the first 5 min following treatments.

Ⓐ


n = 73
Occurence (%)
100
80
60
40
20
0
0
5
10
15
20
25
30
35
40
45
50
55
60
Time following treatments (min)

Ⓑ

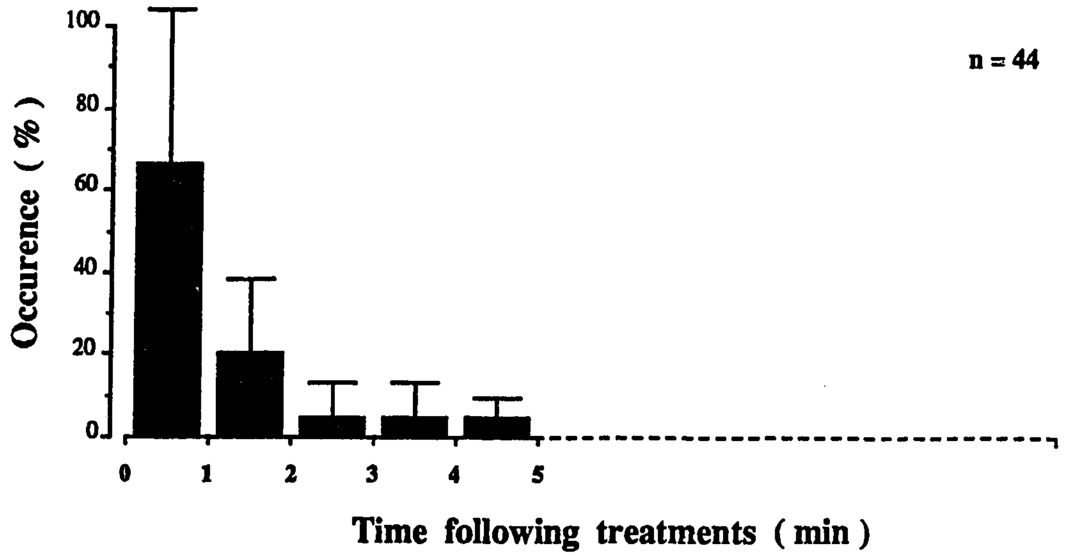
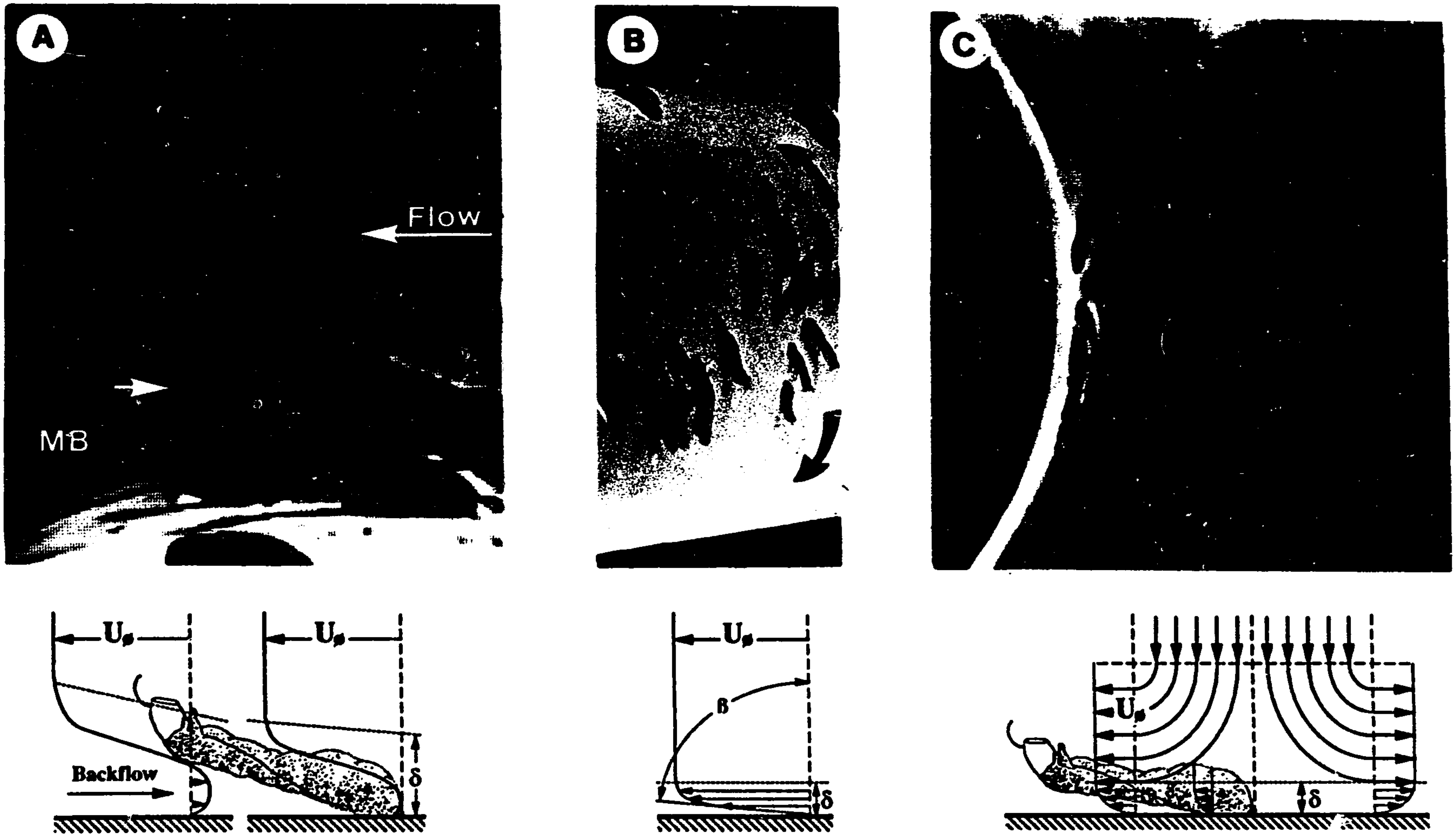

n = 44
Occurence (%)
100
80
60
40
20
0
0
1
2
3
4
5
Time following treatments (min)

Fig. 10 Flow profiles around a cylinder in crossflow, in relation to *Simulium vittatum* Zett. larvae exposed to three velocity profiles: U_ϕ, local velocity at angle ϕ from the front stagnation point;.δ, boundary layer thickness A) Larvae at separation point. B) Zone of maximum surface shear stress (τ_0): β, velocity gradient steepness. C) Larvae at stagnation point.



Separation

τ_0 max

Stagnation

5. GENERAL CONCLUSIONS

There is little doubt that hydrodynamic phenomena play a major rôle in shaping structure and behaviour of black fly larvae. Overlooked for too long, flow conditions prevailing at the larval scale are probably among the most important environmental variables effecting the ecology of immature similiids.

Micro-hydraulic events (*i.e.*, events of organismal scale) associated with the substrate surface are the dominant feature defining the immediate environment of rheophilic benthic invertebrates. This study is the first to demonstrate a conclusive cause-and-effect relationship between hydrodynamic phenomena and formation of local assemblages of simuliid larvae. Larval aggregation at zones of boundary layer separation and water stagnation, and larval avoidance of high surface shear stress zones have been associated with the shape of the velocity profile present in those regions (*i.e.*, larvae are found in regions offering maximum velocity difference between the abdomen and labral fan level; hence maximizing particle-flux through the labral fans while minimizing drag forces on the bulbous portion of the body). It is also the first time a *modus operandi* is advanced to tie previously described larval behaviours (*i.e.*, probing *sensu* Eymann and Friend 1988) and suspension-feeding microsite selection, suggesting that black fly larvae scan the velocity profile at the substrate to cue on a sharp velocity difference between the abdomen and labral fan level. Behavioural observations further suggested that changes in hydraulic conditions around and within a larval group enhance further colonization, enlarging the area over which the velocity profile is favourable. Consequently, I propose that gross patterns (*i.e.*, outcome of primary relocation) of organization toward local hydraulic conditions are most likely formed in the brief period following hydraulic changes, while later contacts among established larvae and invasions by single individuals dictate the more stable inter-larval positions (*i.e.*, dispersion pattern of an established group). This is congruent with conclusions from research by Ciborowski and Craig (1989). Positioning by black fly larvae within a group is a complex phenomenon involving both biotic (*eg*. food-particle concentration, agonistic interactions) and abiotic (*eg*. ambient flow) parameters (Hart 1986, 1987, Craig and Galloway 1987). Thus future studies must not only focus on three-dimensionel flow pattern description about individual and clustered larvae in relation to local water velocity, but should simultaneously assess the influence of food-particule availability on larval dispersal pattern adjustments. Optimal dispersion pattern of established group should be observed for the lower food-particle concentrations.

Characterization of the proximate mechanisms by which flow affects formation of local assemblages of black fly larvae, and delineation of incidental feeding modes not only bring unique insights in simuliid ecology, but also provide strong basis for interpretation and further enhancement of predictive models of specific relationships between the distribution of zoobenthos within a stream reach and the physical habitat (*eg*. Bovee and Milhous 1978, Gore and Judy 1981, Statzner 1981, Statzner *et al*. 1988). Although habitat selection by benthic invertebrates along stream reaches is influenced by the interractions of biotic and abiotic factors, more accurate knowledge of micro-habitat preferences based solely on physical variables can nonetheless lead to more sound suppression practices through more localized insecticide application in streams inhabited by pest simuliid species.

At a smaller scale, analysis of the flow through the labral fans revealed that, fans of simuliid larvae unexpectedly react to velocity increases with structural reconfiguration resulting in aperture expansion, and that as predicted by mathematical models (Silvester

1983, Cheer and Koehl 1987a,b) an increasing fraction of the water directly approaching the labral fan aperture flows around its perimeter as velocity decreases. Although the underlying concept defining published particle capture efficiencies of black fly larvae was correct (*i.e.*, Eq. 3.1), low transmissivity of the filtering appendages observed in this study conclusively demonstrated that simuliid larvae can be 4 to 26 times more efficient at suspension feeding than previously assessed. More realistic assessment of the volume of particle-laden water filtered by black fly larvae that reflects labral fan transmissivity and behavioural components of the feeding process, enhances precision in suspension-feeding efficiency assessments, and sets the ground for assessment of the particle capture efficacy *per se* (*i.e.*, from Eg. 3.15, 3.16). Subsequently, once capture efficacy *per se* and transmissivity of the labral fans are defined, the hydrodynamics of particle retention by the labral fan structures, and the relative importance of its different components (*i.e.*, direct interception, inertial impaction, gravitational deposition, motile-particle deposition, and sieving; *sensu* Rubenstein and Koehl 1977) can be properly assessed.

Detailed analysis of the suspension-feeding stance demonstrated that although change in body deflection with increasing water velocity is most likely passive (follows concurrent rise in flow forces), overall feeding stance is the outcome of an dynamic feedback process between flow forces and behavioural reactions, to actively maintain the labral fans at optimal filtering position. Shape of impressively preserved upper Cretaceous fossil simuliid larvae (Riek 1970) is the same as in some extant simuliid larvae, so it can be assumed that black fly larvae have dealt with the same forces for at least the last 135 millions years. However, recognition of the flow forces defining the "immediate" environment of reophilic benthic organisms brings new insights about the abiotic selective pressure acting on black fly speciation. Although overall simuliid body shape is more or less constant, considerable inter-specific variations in posterior abdominal shape and labral fan structures are encountered in different flow environments.

Larvae of other simuliid species which differ in shape from that of *Simulium vittatum* Zett. should be examined to see if differences in flow patterns around the body and through the labral fans correlate to differences in larval habitat preferences (*e.g.*, larval aggregation patterns seem species- and flow- specific; Eymann personal communication), feeding behaviour (*e.g.*, aberrant behaviour of Tahitian simuliid larvae living in a water-film but lacking longitudinal rotation of the body; Craig personal communication) and suspension-feeding efficiency (labral fans fitness, *i.e.*, balance between particle capture efficacy *per se* and transmissivity). To paraphrase Craig and Chance (1987): "Simuliid larval feeding can no longer be considered a passive affair !"

Observations made here for simuliid larvae may have relevance to other filter-feeding insects. For example, suspension-feeding larvae of *Hydropsyche* (Trichoptera), a net-spinning caddisfly, colonize microhabitats characterized by separated boundary layers (Osborne and Herricks 1987), but it is not known why they prefer such flow regimes. Is feeding-site selection (*i.e.*, local water velocities and particle availibility) of net-spinning caddisfly related to fluid transmissivity of the net ? Similarely, why do some net-spinning Trichoptera larvae form rows (Edington 1968) ?

It is clear that the scale on which an organism or process is examined can drastically change the perception of the controlling factors since, at different levels of resolution, different variables become dominant and different levels of generalization become suitable. We can no longer infer flow circulation around an organism according to its shape alone. Flow characteristics at the organism level must be measured and summarized in their component parts, only then can the complex interactions between an organism's behaviour and its immediate hydrodynamical milieux (*i.e.*, behavioural hydrodynamics) be truly studied. Undoubtedly, benthic flow environments are challenging to describe and quantify, but future progress in stream ecology depends upon clear understanding and accurate descriptions of benthic flow regimes. Single velocity measurements are no longer acceptable in benthic studies.

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BIOGRAPHY

The eldest of 4 children, I was born on August 12th 1958 in Shawinigan, a small industrial town situated on the St-Maurice river in the province of Québec (Eastern Canada). At the time, both parents had teaching positions. Around 1963, the family moved to Trois-Rivières, a larger town sited on the St-Laurent River (seaway). All my growing and learning, from kindergarten to Master Degree level was done in that rapidly expanding city. My interests toward all sciences was always present (by age 5, I was already part of archaeological expeditions in Northern Québec regions), and any query was met by an equal enthusiasm from my parents who, when in doubts of an answer, always directed me toward the proper sources. Water always played a major rôle in my life. During childhood, the family had easy access to a cabin on a lake fed by an extensive stream system. Training in aquatic sports, including scuba-diving and sailing, I grew familiar with that fluid surrounding, and interest rapidly expanded to all creatures connected to that world.

After three years of post-secondary education (C.E.G.E.P.) in Pure and Applied Sciences from the Collège Laflèche, I entered the Département de Chimie-Biologie of the Université du Québec à Trois-Rivières where I completed a Bachelor of Sciences degree in General Biology, and a Master of Sciences degree in Environmental Sciences. My major interest during those years was mainly in "killing" pest insects - namely black flies and mosquitoes, more than in their biology. Rapidly however, I realized that ecological and efficient control methods require knowledge of the target's habitus and behaviours. In pursue of that needed knowledge, I moved to Edmonton, a large city sited in the Western Canadian Prairies, to undertake a Doctoral degree where I became reunited with my early interested in the interaction between water flow and behaviour.