National Library of Canada
Bibliothèque nationale du Canada

Canadian Theses Service
Service des thèses canadiennes

Ottawa, Canada
K1A 0N4

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

UNIVERSITY OF ALBERTA

FLUID FLOW AND THE BEHAVIOUR, ECOLOGY, AND MORPHOLOGY OF SUBIMAGINAL BLACK FLIES (DIPTERA: SIMULIIDAE)

by

Markus Eymann

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

Spring 1991

National Library of Canada
Bibliothèque nationale du Canada

Canadian Theses Service
Service des thèses canadiennes

Ottawa, Canada
K1A 0N4

ISBN 0-315-70153-6

UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: Markus Eymann

TITLE OF THESIS: Fluid flow and the behaviour, ecology, and morphology of subimaginal black flies (Diptera: Simuliidae)

DEGREE: Ph.D.

YEAR THIS DEGREE GRANTED: 1991

Permission is hereby granted to the UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduces without the author's written premission.

M. Eymann
(student's signature)

P.O. Box 521
(student's permanenet address)
Manitouwadge, Ont.
P0T 2C0

Date :

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Fluid flow and the behaviour, ecology, and morphology of subimaginal black flies (Diptera: Simuliidae) submitted by Markus Eymann in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

D A Craig

(Supervisor)

Date: 28 Sept 1990

ABSTRACT

Laboratory and field studies were used to investigate the effects of fluid flow on behaviour, ecology and morphology of subimaginal black flies.

Drag on a single larva of Simulium vittatum Zetterstedt was measured using a modified analogue ammeter. Average drag ranged from 2.70×10^{-5} Newtons at 10 cm/s to 4.24×10^{-4} N at 90 cm/s. This drag was considerably smaller than the force required to detach a dead larva from its substratum.

Characteristics of field microhabitats occupied by larvae of black flies were characterized by an attached boundary layer, and perhaps by accelerating flow. It is suggested that these characteristics of flow past microhabitats account for the contagious dispersion of larvae.

A group of filter-feeding larvae exhibit one of three dispersion patterns; spaced, clumped or banded. Dispersion pattern is affected by the velocity of water flowing past the group, and by action of non-fluid-flow factors such as species composition of the group.

In the laboratory, flow past groups of larvae exhibiting a spaced and a banded dispersion pattern was made visible by injection of a solution of methylene blue into the flow. Flow past a larva in a spaced dispersion pattern appeared to be less turbulent than flow past an isolated larva. Water flowing over a band of larvae appeared to accelerate and flow away from the substratum, as it approached the front of the band.

Flow patterns around structurally different cocoons and pupae of five species of Simulium Latreille were described. Three features of flow pattern common to all cocoons were; 1) a solenoidal vortex around the cocoon, 2) an upward flow anterior (downstream) to the cocoon, and 3) one or two pairs of spiral-shaped vortices, which either touch or envelop the gill filaments of the pupa. Proximity of vortices to the gill

filaments of all pupae suggests that these are associated with gaseous exchange at the gill filaments.

It is concluded that subimaginal black flies are well adapted to life in flowing water.

Acknowledgements

I would like to thank D. A. Craig my principle supervisor and the rest of my Advisory Committee; N. Rajaratnam, B. S. Heming, J. R. Spence, and H. F. Clifford for encouragement and supervision. J. J. H. Ciborowski kindly acted as the external examiner on my committee. N. Rajaratnam and P. Steffler were instrumental in clarifying my understanding of fluid flow.

I am thankful to D. A. Craig, B. S. Hemming, J. R. Spence, J. J. H. Ciborowski for critical review of drafts of all chapters. J. J. H. Ciborowski, S. M. Smith, and D. C. Currie reviewed chapter 3. J. J. H. Ciborowski and an anonymous reviewer made many suggestions, which greatly improved chapter 4. W. G. Friend and R. Tanner reviewed an earlier draft of Chapter 5. L. L. Osborne and B. Statzner greatly improved chapter 2.

I am indebted to the graduate students in the Department of Entomology, in particular J. O. Lacoursière, and D. C. Currie for many valuable and interesting discussions.

M. (Mac) Mcintyre was always willing to help with technical aspects of designing experiments, J. Scott provided frequent help with illustrations, and I. Everitt never failed to straighten out administrative messes.

Lastly I would like to express my thanks to K. G. Jardine for help with field work, staightening out my grammar, and for general moral support.

This study was supported by grant OGP-5753 National Sciences and Engineering Research Council of Canada to D. A. Craig, and by a Max and Marjorie Ward Scholarship and a grant-in-aid from the Boreal Institute for Northern Studies.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION

Subimaginal black flies are among the most conspicuous components of the benthic community of rivers and streams. Both adult and immature stages have been intensively studied because of the importance of adults as vectors of disease. Because larvae are lotic filter-feeders, they are concentrated in an easily definable habitat and are the easiest life stage to control. As a result, considerable attention has been paid to the filter-feeding ecology of larval black flies, in the hope that this knowledge would lead to a more efficient formulation of black fly larvicide. Our present knowledge of the economic importance and filter-feeding ecology of larval black flies is briefly reviewed in the first part of this chapter. The principles of fluid flow that pertain directly to black fly larval ecology are reviewed in the second part. In the final part a brief overview of studies that have examined the relationship between flow and benthic organisms is presented.

1) Economic importance

The economic importance of black flies stems from their habits of, 1) blood feeding on humans and domestic animals, and 2) blood feeding more than once in their life, making them potential vectors for disease-causing organisms.

In many areas of Canada, such as parts of the Canadian Shield, the large numbers of anthropophilic black flies may be the primary factor inhibiting the development of a tourist industry. Alternatively, black flies may be regarded as protecting these wilderness areas from the ravages of tourism.

In northern Alberta, black flies of the morphospecies Simulium arcticum Malloch often feed on cattle in large numbers. Their combined activities can reduce weight gain and milk production and can even lead to death of cattle (Fredeen 1969). Considerable resources have been directed at alleviating this problem (Charnetski and Haufe 1981), although success has been limited. This may be largely due to the large number of streams in which the pest species may be breeding, and because of uncertainty about the identity of the pest species. It is not clear which of the S. arcticum sibling species are the major pests.

By far the most serious economic impact of black flies occurs in areas where they act as vectors for human disease. The most important disease transmitted by black flies is river blindness or onchocerciasis, which is caused by a microfilarial worm Onchocerca volvulus Leukhart. This is a serious disease in extensive areas of Africa south of the Sahara Desert, where it is transmitted by members of the S. damnosum Theobald [complex] (Walsh et al. 1981), and in isolated regions of Central America, where it is transmitted by S. metallicum Bellardi [complex] and other species (Ogata 1981). There is a pilot project operated by The World Health Organization (WHO) intended to control onchocerciasis in Africa by controlling its vector (Walsh et al. 1981) by treatment of the larvae.

2) Life History

The larvae of most species of black flies are filter feeders. Those species that do not filter feed graze on periphyton. Filter-feeding species can also graze (Craig and Currie 1987).

Larvae possess a pair of fan-like, labral appendages which are used in filter feeding. The fans consist of a number of rays that are curved so that the fan takes on the shape of a shallow bowl. Each fan ray has a row of short hairs called microtrichia that project into the flow when the larva is filter feeding. To filter feed, a larvae engages the barbed hooks of its posterior proleg into a silk pad on the substratum. It attaches itself with its anal papillae directed upstream and its ventral surface facing the substratum, and rotates 90° to 180° to hold its labral fans into the current. The fans are alternatley adducted at irregular intervals and cleaned off with the mandibles and labrum (Chance 1970). During the cleaning process, the fans are placed into the mouth of the larva and coated in a mucosubstance produced by glands in the labrum (Ross and Craig 1980). This mucosubstance may increase the filtering efficiency of the fans.

The larvae of black flies are commonly found in a highly contagious dispersion (Hocking and Pickering 1954, Rühm 1970 (in Hart 1979)). Larvae on a stream bottom are found in groups separated by areas almost devoid of larvae. This patchy dispersion suggests resource patchiness. In this case the "resource" that is most likely to be patchy is water flow. Water flow can be considersed a resource because it drives water through the larval fans, enabling filter-feeding. The flow of water over a stream bed is very heterogeneous. Because some types of flow may be better suited to filter feeding by larvae than others, it is possible that areas of substratum with certain types of flow are more likely to be colonized than other areas. An alternative explanation for the patchy dispersion of larvae is that they are found in groups because of mutually beneficial alterations of flow by larvae in a group. These two hypotheses are not mutually exclusive.

Larvae within a group are not arranged randomly but occur in one of three dispersion patterns: 1) A spaced dispersion pattern, in which each larva keeps an area around itself clear of other larvae (Eymann and Friend 1988). 2) A clumped dispersion pattern, where each larva touches each of its immediate neighbours (Eymann and Friend 1988, Hart 1987, Wotton 1987). 3) A banded dispersion pattern, where larvae arrange themselves in bands that are perpendicular to the mean direction of flow (Brenner and Cupp 1980, Davies et al. 1962, Colbo 1987). These three dispersion patterns are desinct from one another and do not appear to be part of a continuum.

The pupae of black flies are found in the same water courses, sometimes even on the same surfaces, as the larvae. They resemble the pupae of other members of the superfamily Chironomoidea, except for a pair of conspicuous prothoracic gills, and a silken cocoon out of which the gills project. Although the pupae are not often dealt with in ecological studies, they have received considerable attention from taxonomists because they show more structural diversity than either the larvae or the adults. Most of this structural diversity is in the gills and the cocoons. Virtually nothing is known about pupal ecology. Details of the ecology of both the adults and larvae are reviewed in Laird (1981) and Kim and Merritt (1987).

3) Taxonomy

Crosskey (1987) recognized 1,461 nominal species and 23 genera belonging to the family Simuliidae world wide, with more then one half of the species belonging to the genus Simulium. Almost 200 species and 12 genera are represented in North America including Mexico.

A problem with ecological work on black flies is that many nominal species actually consist of a number of morphologically similar sibling species and are more precisely referred to as a "species complex". Members of a complex can often only be distinguished by cytological examination of the banding patterns on the polytene chromosomes of the larval salivary glands (Rothfels 1987). Sibling species are often referred to as a cytospecies. These cytospecies are believed to be reproductively isolated taxonomic units, and in some instances, have been shown to have ecologically different requirements (Adler and Kim 1984).

Most of the studies described in this thesis are comparative in nature and consider characteristics that are the same for several morphospecies. Also considered are morphological characteristics, many of which are the same or similar for all members of a species complex. Because there are few experts in North America capable of interpreting the banding patterns of salivary chromosomes, in most instances cytotypes were not determined. Exceptions were made for S. tuberosum [complex] in chapters 3 and 4, and S. venustum/verecundum [complex] in chapter 5 (Dr. P. H. Adler, Clemson Unbiversity, pers. commun.).

Fluid flow

Because subimaginal black flies live in an environment dominated by moving water, an understanding of fluid flow is essential to understanding many aspect of their interaction with the environment. It is particularly important for investigations of dispersion pattern, morphology, microhabitat occupation, and other aspects oof black fly biology that may be related to filter feeding.

1) Laminar flow, turbulent flow, and Reynolds number

Water flow falls into two distinct catergories, - laminar and turbulent. When flow is laminar, a small particle of neutral buoyancy suspended in the water will travel along a straight, predictable path. This is because when flow is laminar, the water behaves like a series of very thin sheets or laminae organized in a predictable way. A very thin sheet of water in contact with the surface is stationary relative to the surface, this is called the no-slip condition (Vogel 1981). The sheet of water immediately above it flows at some velocity; the next sheet flows at a somewhat higher velocity and so on.

When flow is turbulent the path of a neutrally buoyant particle becomes unpredictable; it can slow down, speed up, or change direction from one instant to the next. This erratic behaviour is the result of the complex structure of fully turbulent flow, which consists of eddies, within eddies, within eddies. The largest eddies are the size of the channel, and the smallest are a bit less than one mm. The size of the damllest eddies is determined by the viscosity of the water. Flows in nature, other than ground water flow are almost always turbulent. Exceptions are slow moving precipitation runoff and seepages less than 1 cm deep. Permanent streams or rivers are almost always turbulent, although a thin layer at the bottom of a water course close to a solid surface will always be laminar. The no-slip condition holds for turbulent as well as laminar flow.

Whether flow is laminar or turbulent is determined by a number of parameters; the velocity of flow (V), the "characteristic size" of the flow (l), the density (ρ), and viscosity of the fluid (μ). These parameters do not have to be considered separately because they can be combined into a single dimensionless parameter called a Reynolds number, represented by the equation $R_e=(lV\rho)/\mu$. This number is the ratio of inertial (l,V, and ρ) to viscous (μ) forces. When inertial forces dominate the flow, R_e is high and flow is turbulent. When viscous forces dominate the flow, R_e is low and flow is laminar. For most open channel flows R_e is "high" if it is >2,000.

The values of most of the parameters used in calculating R_e can be easily determined. The characteristic size (l), however, can present problems. When characterizing flow in a circular pipe, l is simply the diameter of the pipe. When characterizing a boundary layer on a plate, l can be the distance from the leading edge of the plate, or the thickness of the boundary layer. For flow past a symmetrical object such as a cylinder that is perpendicular to the mean direction of flow, l is the diameter of the object. For flow past an irregularly shaped object, l is somewhat more difficult to define. For a black fly larva, which is an elongate object at some angle to the substratum, several alternatives present themselves (Fig. 1); A) the length of the larva, B) the diameter of the larva, C) the greatest distance above the substratum in a direction perpendicular to the substratum, or D) the length of the larva in plan view. The first two options measure inherent properties of the larva, but do not consider the orientation of the larva relative to the flow. The second two options add information about the orientation of the larva relative to the flow, because they take into account the angle of the larvae to the substratum. Probably the best measure of l on a filter-feeding larvae of a black fly is E) (Fig. 1), the longest distance along the mean direction of flow when the larva is viewed from the side. This measure changes with the angle of the larva to the flow and considers the dimension that is most likely to influence the pattern of flow past a larva.

2) The principle of continuity

When water flows through a reach of a channel, the mass discharge at the downstream part of the reach must equal the mass discharge at the upstream part, provided that no water is removed from or added to the channel along the reach. Because mass discharge equals the product of cross-sectional area (a), velocity (V), and density (ρ), $a_1V_1\rho_1=a_2V_2\rho_2$ where the subscripts refer to the upstream and downstream part of the reach of the channel. Because density of water in open channel flow can be assumed to remain constant, $a_1V_1=a_2V_2$. Consequently, if cross-sectional area at the downstream station is less than at the upstream station, velocity must increase. If the reduction in cross-sectional area is caused by an object projecting from the bottom of the channel or suspended in the flow, most of the increase in velocity takes place near the object.

It is sometimes useful to describe open channel flow with a dimensionless ratio called a Froude number (F). $F=V/\sqrt{gh}$ where; $g=9.81\ m/s^2$ and h=depth (m) of the flow. The Froude number is a ratio of inertial to gravitational forces. In flows where inertial forces dominate, $F>1$ and flow is referred to as supercritical. In flows where gravitation forces dominate, $F<1$ and flow is referred to as subcritical. When $F=1$ neither of the forces dominate and flow is referred to as critical.

3) Boundary layers and boundary layer separation

When water flows past any solid surface a thin layer of water close to the surface flows at a lower velocity than the rest of the water. This is called the boundary layer. Within the boundary layer velocity is not constant, but is zero at the substratum and increases with distance from the substratum. The flow outside the boundary layer is called free-stream flow. The velocity outside the boundary layer is called the free-stream velocity or the mainstream velocity. Theory predicts that free stream velocity will be reached at infinity, therefore the boundary layer is considered to be the distance from the surface to the point at which some percentage of free stream velocity is reached. This percentage is conventionaly 99% in engineering problems, it may be 90% in biological applications. A boundary layer is present in all flows over a surface, no matter what the velocity of flow or the material of the surface.

A boundary layer may be laminar or turbulent. A turbulent boundary layer is less turbulent than the free stream flow, because of the effect of the substratum. Within a turbulent boundary layer, there exists a thin layer close to the substratum where flow is laminar, called the viscous sublayer. A boundary layer may be laminar even though the free-stream flow is turbulent.

A boundary layer can be thought of as being attached to the surface over which it flows. Under certain conditions, it will separate from the surface; it may then reattach or remain separated. If the Reynolds number is high enough the boundary layer will separate as it flows over any object suspended in the water or projecting out of the substratum into the water. Separation commonly happens at the downstream face of an object. Because of the principle of continuity, water slows down as it flows around the downstream face of an object. Where water slows down pressure increases, therefore the downstream face is an area of higher pressure. Water cannot flow from an area of low pressure to an area of high pressure, consequently, it separates from the rock and forms a wake. This wake can take several forms; attached vortices, vortices that are shed at regular intervals, or a fully turbulent wake. If the object is streamlined, as in the case of a fish or an airplane wing, separation may be delayed or even prevented. In the case of a bluff (non-streamlined) body, separation can occur at low Re. When there is a sharp angle delineating the downstream face of an object, separation takes place at this angle. Otherwise the site of separation is difficult to predict.

4) Drag and coefficient of drag (C_D).

Benthic organisms have to deal with drag induced by water flowing past them. Drag is the force applied to an object by fluid flowing past it. Drag acts in the direction of flow. The object applies an equal and opposite force to the fluid. There are two types of drag; friction drag and form drag. Friction drag has its origins in the internal friction of the water in the boundary layer of the object. The force required to slow down the water in the boundary layer is proportional to the force of the friction drag. Form drag is the drag associated with boundary layer separation and wake formation. The relative importance of form and friction drag is determined by the shape of the object and its Re. For a given shape, the importance of form drag increases with Re. At a given Re, a bluff-body will experience more form drag than a streamlined body.

Drag can be expressed as a dimensionless ratio called the coefficient of drag (C_D), which is defined by $C_D=D/(0.5\rho V^2S)$ where; D=drag (N), ρ=density, S=area, V=free-stream velocity. The area S can be the area of the wetted surface or the plan form surface, but more commonly, it is the frontal area; the area taken up by the object when viewed from directly upstream. C_D allows comparison of objects of different sizes and shapes, especially when C_D is calculated for a known Re or series of Re's.

Life in flowing water

Water resembles air in that both are Newtonian fluids. An object of a given shape will induce the same flow pattern in air as in water provided that the Reynolds numbers are the same. Water differs from air in that it is many orders of magnitude higher density and dynamic viscousity. An object of a given size moving at a given velocity will have a Re that is about one order of magnitude higher when it is in water than when it is in air (Vogel 1981). The difference in Re results in an approximately equivalent difference in drag. The differences in density and viscosity between the two fluids have other important biological consequences. These are discussed below.

1) Filter feeding

The difference in density between air and water has important consequences to filter feeders. Most living things consist primarily of water, consequently they are close to neutral buoyancy in water. When an organism is very small (<0.5 mm), the viscosity of water together with the neutral buoyancy of the organism will tend to keep the organism in suspension. This is also true for particles of detritus that are of biological origin. Since both small particles of detritus and small living organisms are potential food for filter feeders, water is well suited for this type of feeding. The same detritus particles in air would fall out of suspension much more rapidly, therefore filter feeding is much less common in air.

Filter-feeding organisms can be classified in several ways with the simplest being to categorize them as active or passive. Active filter feeders create their own current, and commonly live in still water, they include larvae of mosquitoes, most filter-feeding microcrustaceans, sponges, and bivalves. Passive filter feeders use an ambient current and live in rivers and streams, they include larvae of Simuliidae, Hydropsychidae, some Chironomidae and some Ephemeroptera. The distinction between active and passive is not always clear because some passive filter feeders, such as larvae of black flies (Ciborowski and Craig 1989) are known to form groups which appear to alter flow in ways that benefit most members of the group. Many active filter feeders such as bivalves and sponges, rely on ambient currents to replace recently filtered water. Despite this, it is still useful to distinguish between active and passive filter feeders, because an active filter feeder probably has to expend far more energy to process a given volume of water than does a passive filter feeder.

2) Drag

Drag on an object is approximately one order of magnitude higher in water than in air, all other things being equal. Consequently, resistance to drag is more important to an organism living in water than one living in air. Wainwright and Dillon (1969) showed that the blades of seafans (Gorgonia sp.) orient perpendicularly to the current to minimize drag-induced torque on the stem. Smith and Dartnall (1980) working with larvae of Psephenidae, or water penny beetles, which are commonly found on rocks in fast water showed that they use boundary layer suction to reduce drag.

Thesis objectives

The purpose of this thesis is to investigate the effects of fluid flow on the behaviour, ecology, and morphology of subimaginal black flies, with special emphasis on the dispersion patterns of larvae. Because of the complexity and heterogeneity of flow in an open channel and, because flow patterns are normally invisible, considerable gaps exist in our knowledge of the effects of flow on benthic stream organisms, particularly immature black flies. In this thesis I will try to fill in some of these gaps. This thesis is presented as a series of papers ready for publication. Chapters 2-6 are concerned with larvae and chapter 7 is concerned with pupae.

Chapter 2 deals with drag on individual larvae of S. vittatum and compares this drag to the strength of attachment of a larva to the substratum. I show that the strength of attachment was much greater than the drag, suggesting that behaviours of larval black flies are not likely to be a mechanism for reduction of drag. Chapter 2 has already been published in the Journal of the North American Benthological Society.

Chapters 3 and 4 are comparative studies that examine the effects of fluid flow and other factors on gross behavioural patterns of a number of black fly species. Chapter 3 deals with the effects of flow on microhabitat occupation. I try to determine whether the highly contagious dispersion of larvae of black flies is a result of settlement on substrata with a special type of flow, or a tendency to settle near other larvae that permit induction of mutually beneficial flow. Chapter 3 shows that the microhabitats occupied by black flies are characterized by an attached boundary layer, and possibly by acceleration of water. This supports the hypothesis that the contagious dispersion exhibited by larvae is a result of settlement of substrata with special types of flow. Chapter 3 is unsubmitted. Chapter 4 deals with the effects of flow on dispersion patterns. Velocity of flow past a microhabitat appears to be the only fluid flow parameter affecting dispersion pattern. However, non-fluid-flow factors such as the species composition of a group may also influence dispersion pattern. Chapter 4 is unsubmitted.

In chapter 5, I describe a population of larval black flies that consisted of two species that exhibit different dispersion patterns when they co-occur than when they are found in a group consisting of a single species. It is shown that the species that constitutes the majority of individuals in a group determines the dispersion pattern of that group and that water velocity appears to affect this relationship. Chapter 5 has been submitted to Aquatic Insects.

In chapter 6, I describe the flow around spaced and around banded groups of larval black flies. Water appears to become less turbulent as it flows between pairs of spaced larvae, and water is shown to accelerate as it flows over a band of larvae. Chapter 6 is unsubmitted.

In chapter 7, I describe the flow around the pupae of five morphologically distinct species of black flies. The flow patterns around all five species are characterized by a solenoidal vortex and a pair of downstream vortices as predicted from studies of other bluff bodies in boundary layers. The downstream vortices always either touch or engulf the gills of the pupae, and may be important to respiration. Chapter 7 has been submitted to Hydrobiologia.

In chapter 8 I present general conclusions

References Cited

Adler, P. H., and K. C. Kim. 1984. Ecological characterization of two sibling species, IIIL-1 and IS-7, in the Simulium vittatum complex (Diptera: Simuliidae). Can. J. Zool. 62: 1308-1315.

Brenner, R. J., and E. W. Cupp. 1980. Rearing black flies (Diptera: Simuliidae) in a closed system of water circulation. Tropenmed. Parasit. 31: 247-258.

Chance M. M. 1970. The functional morphology of the mouthparts of blackfly larvae (Diptera: Simuliidae). Quaest. Entomol. 6: 245-284.

Charnetski, W. A., and W. O. Haufe 1981. Control of Simulium arcticum Mallock in northern Alberta, Canada. In Blackflies: The future for biological methods in integrated control. Edited by M. Laird. Academic Press. Toronto.

Ciborowski, J. J. H., and D. A. Craig. 1989. Factors influencing dispersion of larval black flies (Diptera: Simuliidae): effects of current velocity and food concentration. Can. J. Fish. Aquat. Sci. 46: 1329-1341.

Colbo, M. H. 1987. Problems in estimating black fly populations in their aquatic stages. In Black flies: Ecology, Population Management, and Annotated World List. Edited by K. C. Kim and R. W. Merritt. The Pennsylvania State University. University Park, PA.

Craig, D. A., and D. C. Currie 1987. Feeding strategies of larval black flies. In: Black flies: Ecology, Population Management, and Annotated World List. Edited by K. C. Kim and R. W. Merritt. The Pennsylvania State University. University Park, PA.

Crosskey, R. W. 1987. An annotated checklist of the world black flies (Diptera: Simuliidae). In: Black flies: Ecology, Population Management, and Annotated World List. Edited by K. C. Kim and R. W. Merritt. The Pennsylvania State University. University Park, PA.

Davies, D. M., B. V. Peterson, and D. M. Wood. 1962. The black flies (Diptera: Simuliidae) of Ontario. Part I. Adult identification and distribution with descriptions of six new species. Proc. Entomol. Soc. Ont. 92: 70-154.

Eymann, M., and W. G. Friend. 1988. Behaviors of larvae of the black flies Simulium vittatum and S. decorum (Diptera: Simuliidae) associated with establishing and maintaining dispersion patterns on natural and artificial substrates. J. Insect Behavior, 1: 169-186.

Fredeen F. J. H. 1969. Outbreaks of the black fly Simulium arcticum Malloch in Alberta. Quaest. Entomol. 5: 341-372.

Hart, D. D., 1979. Patchiness and ecological organization: experimental studies within stream benthic communities. Ph. D. thesis, University of California, Davis.

Hart, D. D. 1987. Processes and patterns of competition in larval black flies. In Black flies: Ecology, Population Management, and Annotated World List. Edited by K. C. Kim and R. W. Merritt. The Pennsylvania State University. University Park, PA.

Hocking, B., and L. R. Pickering. 1954. Observations on the bionomics of some northern species of Simuliidae (Diptera). Can. J. Zool. 32: 99-119.

Kim, K. C., and R. W. Merritt (eds.). 1987. Black flies: Ecology, Population Management, and Annotated World List. The Pennsylvania State University. University Park, PA.

Laird, M. (ed.). 1981. Blackflies: The future for biological methods in integrated control. Academic Press. Toronto.

Ogata, K. 1981. Preliminary report on Japan-Guatemala onchocerciasis control pilot project. In Blackflies: The future for biological methods in integrated control. Edited by M. Laird. Academic Press. Toronto.

Ross, D. H., and D. A. Craig. 1980. Mechanisms of fine particle capture by larval black flies (Diptera: Simuliidae). Can. J. Zool. 58: 1186-1192.

Rothfels, K. H. 1987. Cytological approaches to black fly taxonomy. In Black flies: Ecology, Population Management, and Annotated World List. Edited by K. C. Kim and R. W. Merritt. The Pennsylvania State University. University Park, PA.

Rühm, W., 1970. Zur dipersion der larvenstadien und des puppentadiums von Boophthora erythrocephala de Geer (Simuliidae). Z. Angew. Entomol. 6: 311-321.

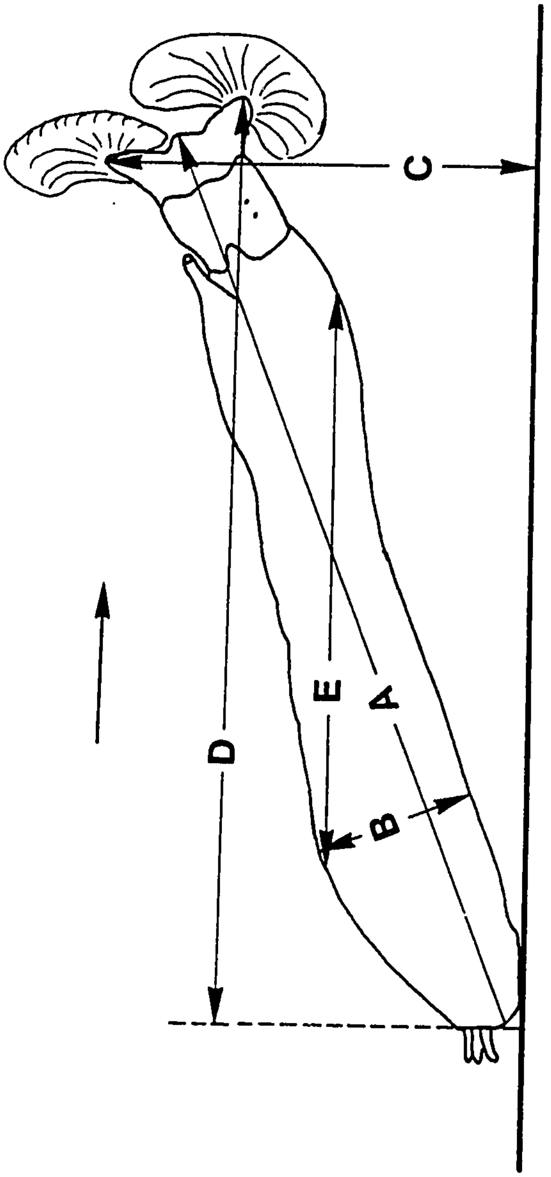
Smith, J. A., and A. J. Dartnall. 1980. Boundary layer control by water pennies (Coleoptera: Psephenidae). Aquatic Insects 2: 65-72.

Wainwright, S. A., and J. R. Dillon. 1969. On the orientation of sea fans (Genus Gorgonia). Biol. Bull. 136: 130-139.

Walsh, J. F., J. B. Davies, and B. Cliff. 1981. World Health Organization control programme in the Volta River basin. In Blackflies: The future for biological methods in integrated control. Edited by M. Laird. Academic Press. Toronto.

Wotton, R. S. 1987. The ecology of lake-outlet black flies. In Black flies: Ecology, Population Management, and Annotated World List. Edited by K. C. Kim and R. W. Merritt. The Pennsylvania State University. University Park, PA.

Figure 1. Diagram of filter-feeding larva of S. vittatum illustrating different ways of measuring the characteristic length (l) used in calculating Reynolds number. Letters A to E represent ways of measuring l. Arrow indicates direction of flow.


C
D
E
A
B

2. DRAG ON SINGLE LARVAE OF THE BLACK FLY SIMULIUM VITTATUM (DIPTERA: SIMULIIDAE) IN A THIN, GROWING BOUNDARY LAYER

Introduction

The larvae of most species of black flies live attached to solid substrata in flowing water where they feed on suspended particles captured with labral fans. Larvae require an ambient flow because they lack a mechanism for propelling water through their fans (Colbo and Wotton 1981). An unavoidable consequence of flow around a larva is drag: a force imparted in the mean direction of flow on a submerged object by fluid flowing around it. If drag becomes stronger than the larva's attachment to the substratum, the larva may be pulled off the substratum and lose its ability to filter-feed. Consequently, selection for morphological and behavioural modifications that reduce drag, especially at higher velocities, should occur. Drag on a passive filter such as the labral fans, however, cannot be reduced without a loss of filtering efficiency (Vogel 1981). The drag on a larva is therefore a compromise between minimizing the danger of being pulled off of the substratum and maximizing filter-feeding efficiency.

The only measurement of drag on a black fly larva reported in the literature, is reported by Braimah (1987), who reported an estimated drag of 2.20×10^{-4} N on fans of a larva of Simulium bivittatum at 6 cm/s based on the difference in velocity just upstream and just downstream of the fans. In this chapter, I describe a method for measuring drag on an individual larva. Drag on individual larvae of Simulium vittatum filter feeding on a thin, vertical support was measured for water velocities of 10-90 cm/s. This method simulates a field situation in which a larva is attached to the tip of a small twig projecting into the free-stream. Drag was also measured on larvae attached to a piece of cover slip. Comparisons of drag on larvae with labral filtering fans abducted and with fans adducted were made to determine what portion of total drag was a consequence of the fans. Coefficient of drag (C_D) was calculated from the above results and compared to C_D reported in the engineering literature.

Probing is a class of behaviours that involves a cessation of feeding, retraction of fans and bending of the body so that the head can be moved over the substratum (Eymann and Friend 1988). Probing is sometimes called "avoidance behaviour" because it is believed to reduce drag on the larva by moving it into the slower flow of the boundary layer (Chance and Craig 1986). Alternatively, probing may be a means of obtaining information about the immediate environment of the larva. Drag on probing larvae was measured and compared to drag on filter-feeding larvae. If probing is a mechanism for reducing drag a probing larva should have a lower drag than a feeding larva.

A filter-feeding larva is attached to the substratum by a circle of hooks on its posterior proleg which is engaged in a silk pad (Barr 1984). The strength of larval attachment to its silk pad was measured and compared to drag. Extrapolations based on the measurements of drag were used to estimate the water velocity that would result in a drag equal to the strength of the larva's attachment to the substratum

Methods

Figure 1 shows the apparatus used to measure drag. An analogue ammeter was dismantled until the needle was exposed. This ammeter functioned as a linear, electromechanical transducer (Vogel and Chapman 1966). A section of 2.5 mm aluminum wire was ground down to a 1.5x0.8 mm ovoid shape and attached to the ammeter needle with epoxy glue. An ovoid shape was chosen because its low C° (Hoerner 1965) made the instrument more sensitive to drag on an attached larva. The dismantled ammeter was mounted, with the needle and the ovoid wire pointing down, on a clamp attached to a vertical rack and pinion on a retort stand. One terminal of the ammeter was connected to the positive terminal of a variable voltage power supply by way of a 10 kΩ resistor. The negative terminal of the power supply was connected to a digital ammeter which, in turn, was connected to the remaining terminal of the analogue ammeter.

The rack and pinion was used to lower the wire 0.35 cm into the water 2.5 cm from the wall of a flow tank, built according to a design by Vogel and LaBarbera (1978) and modified by J. O. Lacoursière (University of Alberta, personal communication). At 2.5 cm from the wall, the wire was outside the 0.5 cm thick boundary layer at 25 cm/s (unpublished data). At higher velocities the boundary layer will be even thinner (Schlichting 1968). The wire was orientated with the long axis of the ovoid parallel to the mean direction of flow. Two collimators were placed in the flow tank to reduce turbulence (Fig. 1). The wire was 30 cm downstream of the second collimator. The water in the flow tank was driven by dual propellers, their velocity being adjusted with a Minarik® rheostat. The water was kept at room temperature which was approximately 20°C. The Reynolds number of the flow tank was 1×10^4 to 8×10^4 in the range of velocities used in this study. The characteristic length used to calculate Reynolds number of the flow tank was the width of the tank (9 cm).

Flowing water pushed the wire in the direction of flow. Electricity running through the analogue ammeter moved the wire in the other direction. The electrical output of the power supply was manually adjusted until the wire was vertical. A vertical line on the body of the ammeter was used to zero the wire. The electrical output required to keep the wire vertical was measured in amperes with the digital ammeter. As water velocity was increased, the amperage required to return the wire to a vertical position increased as well. Amperage was therefore a measure of the force required to keep the wire vertical. This apparatus works on a similar principle to an apparatus used by Bournaud (1963) to measure drag on the caddisfly larva Micropterna testacea (Limnophilidae). His apparatus differed from the one reported here because it used weights on a lever to return the wire to vertical and, because he measured forces almost 10 times larger then the ones reported here.

Amperage was converted to units of force (Newtons) by measuring the amperage required to resist a known force. To do this the analogue ammeter was rotated 90° on the clamp and the electrical output was increased until the wire was horizontal. Amperage was recorded at this point. A 1 mg weight was suspended from the wire; the amperage required to return the wire to horizontal was recorded and subtracted from the first reading to give the amperage required to produce 9.81×10^{-6} N of force. This procedure was repeated with 19 combinations of weights up to 24 mg (2.35×10^{-4} N). This was done in the air. The accuracy of the weights was confirmed with an analytical balance. The regression equation for amperage (I), in milliamps, against force (F), in $N \times 10^{-5}$ was $F=0.770I+0.00153$ ($N=20$, $R^2=0.99$). This equation was used to convert experimental results in amperes to Newtons. Because of the high coefficient of correlation of these measurements, and because an ammeter responds in a linear manner (Vogel and Chapman 1966), this equation was assumed to hold over the entire range of drag measurements.

The drag on the wire submerged 0.35 cm (indicated by a mark on the wire) into the water in the flow tank, was measured at several velocities between 10 and 90 cm/s. Water velocity was measured every time drag was measured. This measurement was done with a propeller type Kent Miniflow® flowmeter which was positioned on the opposite side of the flow tank, 2.5 cm from the wall and just far enough under water to submerge the propeller. The output from the flowmeter was fed directly into an Apple II Plus computer which took 1000 velocity measurements at 0.036 s intervals and calculated their mean and standard deviation. Regression analysis was performed on these data, with velocity as the independent variable and drag as the dependent variable, using the Regression program of SPSSx (Statistical Package for Social Sciences 1986).

A single larva of S. vittatum was gently sucked up in a plastic eyedropper, and allowed to loop out onto one face of the wire in still water. The propeller of the flow tank was turned on. When the larva started to "flick" its labral fans it was assumed to be filter feeding. No attempt was made to control the location of attachment of the larva to the wire. Drag on the wire with the attached larva was measured in the same way as for the wire alone. This procedure was repeated at various velocities, with nine larvae, all approximately 6 mm long. Regression analysis was done using velocity as the independent variable and drag as the dependent variable from each larva as well as for the pooled data for all larvae. Drag on a larva plus the wire for velocities from 10-90 cm/s was calculated at 10 cm/s intervals using the regression equation for the pooled data. These values were subtracted from the drag on the bare wire, calculated at the same velocities to give an estimate of the drag on a black fly larva itself.

Drag on the black fly larva and on the wire may have an interactive component, i.e., drag on the wire or the larva may be altered by the larva's proximity to the wire. To test for the importance of this effect, the experiment was repeated on a support with a different shape - a 4x4 mm piece of microscope cover slip. The piece of cover slip was attached to the downstream edge of the ovoid wire with epoxy glue. It was attached so that the coverslip was parallel to the mean direction of flow and the bottom of the cover slip was flush with the bottom of the wire. The drag on the wire plus the coverslip was measured at different velocities. A single black fly larva was allowed to attach itself to the coverslip. Drag was measured on three larvae (one at a time), all approximately 6 mm long. Regression analysis was performed as before.

The coefficient of drag (a dimensionless form of the drag measure) was calculated using the equation:

$C_D=D/(0.5\rho U^2S)$ Gerhart and Gross (1985)

where: C_D=coefficient of drag, ρ=density of water (998 kg/m^3 at 20°C), S=frontal area, U=mean free-stream velocity. Frontal area was measured by placing a prism, which bent the light 90°, directly downstream of a filter-feeding larva, then photographing the larva through the side of the flow tank and measuring the area of the larva on the photograph. C_D was ploted against Reynolds number, which was calculated using the equation:

$R_e=(Ul)/v$ Gerhart and Gross (1985)

where: R_e=Reynolds number, l=characteristic length, v=kinematic viscosity (1.0×10^{-6} m^2/s at 20°C_D). Characteristic length was the longest dimension parallel to the direction of flow.

To determine the portion of total drag due to the fans, drag was measured on the same larva at the same velocity with its fans abducted and with its fans adducted. A larva was induced to adduct its fans by a single, gentle tap on the ammeter. Drag on the larva with adducted fans was subtracted from drag on the larva with abducted fans. The difference was assumed to equal the drag on the fans. Drag on fans was measured using two larvae (one at a time) on the wire. A regression analysis with drag on the fans as the dependent variable and water velocity as the independent variable was performed.

Probing may increase drag by increasing the larva's frontal area (Hoerner 1965), or it may decrease drag by bringing more of the larva into the slow flowing boundary layer (Chance and Craig 1986). To determine the effect of probing on drag, drag was measured on probing larvae. Because probing could not be easily induced, these measurements had to be taken when a larva probed spontaneously. Consequently there was a low sample size, and high variability. Therefore regression analysis was not performed although the results are shown graphically, and a paired t-test was used to test for differences between the drag on probing and filter-feeding larvae.

The strength of a larva's attachment to the substratum was measured in the field. Late instar, approximately 6 mm larvae that were attached to trailing vegetation close to the surface of the river were selected. Water velocity at the location of the larva was measured with a Model PVM-2® (Montedero Whitney Inc.) flowmeter. Approximately one litre of boiling water was rapidly poured over the selected larva, killing it so quickly that it did not detach itself. The piece of vegetation with the attached, dead larva was removed from the river and fastened horizontally to two alligator clips on a retort stand which was kept on a plastic tarpaulin on the river bank. An 8 mg wire clip was attached to the larva just behind the head. Small weights were hung from the clip, causing the larva to hang perpendicular to the piece of vegetation. The size of the weights was increased in 100 mg increments until the larva was pulled off of the vegetation. This was repeated with 11 larvae. This experiment assumed that the strength of the attachment is the same for a dead larva as for a living one, and that boiling water had a negligible effect on strength of the attachment.

Results

The relationship between water velocity and drag for the ovoid wire and for the ovoid wire plus one of the nine single, filter-feeding larvae shows a discontinuity at approximately 30 cm/s (Fig. 2). Consequently two regression equations were calculated; one for data <30 cm/s and one for data >30 cm/s. For the wire by itself, these equations were:

$D=0.0011U^2-0.075$ (N=13, $R^2=0.86$) for $U<30$ cm/s, and

$D=0.00072U^2+1.25$ (N=52, $R^2=0.98$) for $U>0.30$ cm/s

where U=mean free-stream water velocity in cm/s and D=drag force in $N \times 10^{-4}$.

Because no significant differences in the slopes of the regression equations were found between any pair of larvae, the data for all nine larvae were pooled. For the wire plus a single, filter-feeding larva the equations were;

$D=0.0022U^2+0.15$ (N=67, $R^2=0.86$) for $U<30$ cm/s, and

$D=0.0011U^2+2.52$ (N=191, $R^2=0.88$) for $U>30$cm/s.

The slopes of the equations for the wire with and without a larva were significantly different at both ranges of velocities ($p<0.01$). The relationship between water velocity and an estimate of drag on a black fly larva by itself, based on the difference between the drag on the wire and the drag on the wire plus an attached larva, is represented by

$D=0.044U-0.053$ (N=10, $R^2=0.99$).

The data for the cover slip and for the cover slip with one of the three single, filter-feeding larvae did not show any discontinuity (Fig. 3). Consequently only one pair of curvilinear regression equations was calculated:

$D=0.0036U^2+0.027U+0.62$ (N=67,$R^2=0.99$) for the cover slip alone, and

$D=0.0044U^2+0.0090U+1.62$ (N=160,$R^2=0.97$) for the cover slip plus a larva.

The coefficients of this pair of equations are not significantly different at the 0.95 α level. The relationship between water velocity and an estimate of the drag on a black fly larva by itself, based on the difference between the drag on the cover slip and the drag on the cover slip plus an attached larva, is represented by

$D=0.053U-0.12$ (N=9, $R^2=0.94$).

The slope of this equation is not significantly different from the regression equation obtained for drag on a larva on the wire ($p>0.1$).

The relationship between water velocity and difference in drag on a larva with its fans adducted, subtracted from drag on the same larva with its fans abducted, is represented by

$D=0.035U-0.31$ (N=31, $R^2=0.95$) (Fig. 4).

The effect of Reynolds number on coefficient of drag for a larva on the wire and for a larva on the cover slip is shown in a log-log plot in Figure 5. The coefficient of drag on a larva after the effect of drag on the fans was subtracted is also shown. C_D for $R_e<2{,}000$ (corresponding to $U<30$ cm/s) remains relatively constant as R_e changes, at $R_e>2{,}000$ however, C_D decreases as R_e increases.

The relationship between water velocity and the difference in drag on a larva when it is probing and when it is filter feeding is shown in Figure 6. Drag on probing a larva was significantly higher than drag on a filter-feeding larva according to a paired t-test ($p<0.05$).

The force required to remove a dead larva from its attachment was 1.2×10^{-2} $\pm2.4\times10^{-3}$ N (mean±standard error) (N=11). The range was 4.9×10^{-3} N to 2.8×10^{-2} N. This corresponds to a range of 0.5-2.8 grams. Water velocity near the collected larvae ranged from 15-30 cm/s. None of the larvae had silk in the hooks of their posterior proleg. The mean size of the larvae was 6.1±0.30mm. No correlation could be found between strength of attachment and the size of the larvae.

Discussion

When two submerged objects are in close proximity to each other, the combined drag on both objects together (D_{1+2}) may be greater than or less than the sum of the drag on each object in isolation (D_1+D_2). The difference between the two is called the interference drag (ΔD) (Hoerner, 1965). Because drag on a larva was obtained by subtracting drag on the larva on a support from drag on the support by itself, this method assumes that interference drag is zero.

As a partial test of this assumption drag was measured for larvae on the ovoid wire and on the cover slip. There was no significant difference between the slopes of the regression equations for water velocity against drag on larvae attached to either support. This suggests that interference drag is small in this system.

The discontinuity seen in the relationship between water velocity and drag on the wire at approximately 30 cm/s (Fig. 2) can probably be explained by a change in the type of wake. Drag can be thought of as a transfer of momentum from the submerged body to the fluid (Hoerner 1965). The change in the momentum of the fluid is manifested as an increase in turbulence and a decrease in velocity of the fluid in the wake. A sudden change in the volume or in the type of flow in the wake will therefore result in a sudden change in the magnitude of the drag. One such change in the wake happens at R_e=40 for a circular cylinder (Hoerner 1965, Vogel 1981). Here, it happened at 30 cm/s where R_e (wire) was relatively high (450). This may be because the ovoid wire was more streamlined than a cylinder (Hoerner 1965). Although no discontinuity was seen in the cover slip data the total range of forces was much higher in this system and may have masked this effect.

Black fly larvae are non-rigid bodies. However most research of drag has been done with rigid bodies (Hoerner 1965). Consequently, C_D and its relationship with R_e (Fig. 5) may have a different significance for larvae of black flies than for rigid bodies. This difference may exist because a non-rigid body is able to respond to pressure differences by changing shape.

C_D for a black fly larva decreased as R_e increased when $R_e > 2{,}000$ (Fig. 5). A similar response is seen for circular cylinders and other bluff (non-streamlined) bodies (Hoerner 1965). At $200 < R_e < 2{,}000$, however, C_D for a black fly larva remained relatively constant whereas C_D for a bluff body exhibits a decrease as R_e increases. At these lower R_e's a larva changes its angle to the mean direction of flow as velocity changes. Consequently its frontal area (see above equation for C_D) also changes. At 10 cm/s ($R_e=200$) the larva was bent away from the support and its frontal area was approximately 3 mm^2. As R_e and water velocity increases, frontal area decreases until, at 30 cm/s ($R_e=2{,}000$), the larva is parallel to the mean direction of flow and frontal area is approximately 1 mm^2. At lower R_e's, therefore the changes in frontal area keep C_D more or less constant. At velocities above 30 cm/s frontal area does not change, in agreement with data reported by Chance and Craig (1986) for S. vittatum.

Comparison of Figure 2 and Figure 4 shows that, at low velocities, drag on the fans accounts for almost one half of the total drag on the larva. This high drag on the fans has two possible explanations: 1) the fans are outside of the boundary layer (Chance and Craig 1986) and, therefore, in faster flowing water than the body of the larva, and 2) the fans are cup-shaped with the concave face pointing upstream, and this shape has a high C_D for a given R_e compared to other bluff bodies (Hoerner 1965). Craig and Chance (1982) reported paired eddies downstream from the fans. These eddies disappeared when the fans were retracted. The formation of these eddies represents a transfer of momentum from the fans to the water, the transfer being manifested as drag on the fans. Such eddies are therefore consistent with a high C_D on the fans.

Braimah (1987) reported a drag of 2.20×10^{-4} N on the fans of S. bivittatum at 6 cm/s. In the present study larvae did not feed at velocities below 10 cm/s. Consequently, drag was not measured at lower velocities. Extrapolation based on the regression equations reported here results in drag on fans of 2.1×10^{-5} N at 6 cm/s. This is more than an order of magnitude less than the results of Braimah (1987). This difference may be a consequence of the different species studied, or of the different methods employed.

Drag on the fans, which can be thought of as small irregularities in the shape of the larva, should account for a progressively larger portion of total drag as velocity increases (Vogel 1981). The linear relationship between drag on the fans and velocity (Fig. 4) shows that this is not the case. This suggests that the larva compensates for the higher drag on the fans at higher velocities, perhaps by changing the angle of the fans to the mean direction of flow as reported by Schröder (1987) in six species of mid-European simuliids.

Drag was higher on a probing larva than on a feeding larva (Fig. 6) probably because a probing larva has a higher frontal area than a feeding larva. Apparently, the reduced velocity of the water in the boundary layer does not compensate for the increase in frontal area. This is contrary to the suggestion by Chance (1970) and Chance and Craig (1986) who reasoned that a probing larva moves its body deeper into the boundary layer, thus reducing drag. It follows, then, that probing serves some function other than reduction of drag. Perhaps it provides the larva with information about its environment, such as the location of nearby neighbours or predators. However, it should be noted that the boundary layer was relatively thin on a support as small as the ovoid wire. In a thicker boundary layer, probing may indeed reduce drag.

The high variance in drag on probing larvae (Fig. 6), is likely a consequence of individual differences in probing. The higher incidence of probing at higher velocities (Fig. 6) may be an artifact of the design of the experiment. Because of turbulence, the surface of the water rose and fell. At higher velocities, where turbulence was higher, the water surface occasionally touched the larva, and this stimulus was often enough to induce probing.

The lowest force required to remove a larva from its attachment ($4.9\mathrm{x}10^{-3}$ N) was higher than the highest drag measured ($4.5\mathrm{x}10^{-4}$ N). This suggests that for the range of velocities investigated in this experiment, drag is not strong enough to pull larvae off the substratum. Extrapolation based on data from larvae on the ovoid wire shows that water velocity would have to be 1,100 cm/s for drag to equal the minimum strength of attachment measured, and 2,700 cm/s for drag to equal the mean strength of attachment of a larva to the substratum. Extrapolation based on data from larvae on the cover slip shows that the water velocity would have to be 3,300 cm/s for drag to equal the minimum strength of attachment and 8,300 cm/s for drag to equal the mean strength of attachment of a larva to the substratum. Although these velocities are based on extrapolation, and therefore subject to error, it is noteworthy that they are at least an order of magnitude higher than the velocities at which the larvae of common North American black flies are found (8-162 cm/s) (Colbo 1979, Kurtak 1978, Lewis and Bennett 1975). Under most field conditions, larvae are found in more developed and thicker boundary layers than in this experiment. Consequently, drag that they experience will be even lower than the drag measurements reported here.

This chapter reports a simple method for measuring drag on a black fly larva; it can be adapted to any rheophilic organism that will attach itself to an appropriate support. This method most closely approximates conditions on the tips of twigs extending into the free-stream flow. The results should be applied to other field situations with caution because hydrodynamic conditions may differ considerably under different situations. Drag, at equivalent velocities, at the bottoms of rivers and streams should be lower than the drag reported here because of a thicker boundary layer. Larvae are not likely to be pulled off of the substratum under common field conditions.

Literature cited

Barr, W. B. 1984. Prolegs and attachment of Simulium vittatum (sibling IS-7) (Diptera: Simuliidae) larvae. Canadian Journal of Zoology 62:1355-1362.

Bournaud, M. 1963. Le courant, facteur écologique et éthologique de la vie aquatique. Hydrobiologia 21:125-165.

Braimah, S. A. 1987. Pattern of flow around filter-feeding structure of immature Simulium bivittatum Malloch (Diptera: Simuliidae) and Isonychia campestris McDunnough (Ephemeroptera: Oligoneuriidae). Canadian Journal of Zoology 65:514-521.

Chance, M. M. 1970. The functional morphology of the mouthparts of the blackfly larvae (Diptera: Simuliidae). Quaestiones Entomologicae 6:245-284.

Chance, M. M., and D. A. Craig. 1986. Hydrodynamics and behaviour of Simuliidae larvae (Diptera). Canadian Journal of Zoology 64:1295-1309.

Colbo, M. H. 1979. Distribution of winter-developing Simuliidae (Diptera), in Eastern Newfoundland. Canadian Journal of Zoology 57:2143-2152.

Colbo, M. H., and R. S. Wotton. 1981. Preimaginal black fly bionomics. Pages 209-226 in M. Laird (editor). Black flies: The Future of Biological Methods in Integrated Control. Academic Press, Toronto.

Craig, D. A., and M. M. Chance. 1982. Filter feeding in larvae of Simuliidae (Diptera: Culicomorpha) aspects of functional morphology and hydrodynamics. Canadian Journal of Zoology 60:712-724.

Eymann, M., and W. G. Friend. 1988. The behaviours of the Black fly larvae Simulium vittatum and S. decorum (Diptera:Simuliidae) associated with establishing and maintaining dispersion patterns on natural and artificial substrate. Journal of Insect Behaviour 1:169-186.

Gerhart, P. M., and R. J. Gross. 1985. Fundamentals of Fluid Mechanics. Addison-Wesley Publishing Co., Don Mills, Ontario.

Hoerner, S. F. 1965. Practical information on aerodynamic drag and hydrodynamic resistance. Published by the author (S. F. Hoerner).

Kurtak, D. C. 1978. Efficiency of filter feeding of black fly larvae (Diptera:Simuliidae). Canadian Journal of Zoology 56:1608-1623.

Lewis, D. J., and G. F. Bennett. 1975. The blackflies (Diptera: Simuliidae) of insular Newfoundland. III. Factors affecting the distribution and migration of larval simuliids in small streams on the Avalon Peninsula. Canadian Journal of Zoology 53:114-123.

Schlichting, H. 1986. Boundary-Layer Theory. (Sixth Ed.) Translated by J. Kestin. McGraw-Hill Book Co. Toronto.

Schröder, P. 1987. Der Anstellwinkel filtrierender Kriebelmuckenlarven (Dipt.,Simuliidae) zur Strömungsrichtung. Archiv für Hydrobiologie, Supplement 77 1:39-49.

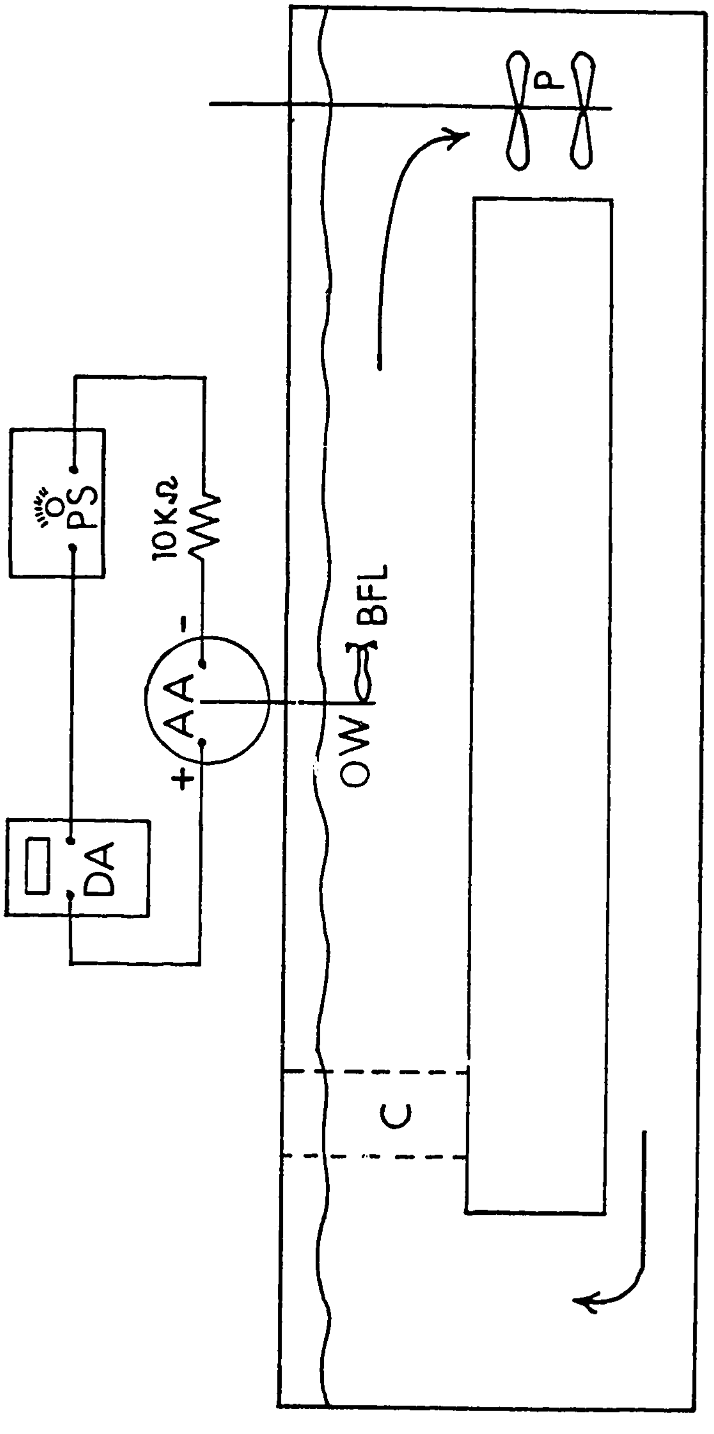
Statistical Package for Social Sciences. 1986. SPSSx User's Guide. SPSS Inc, Toronto.

Vogel, S. 1981. Life in Moving Fluids: The Physical Biology of Flow. Princeton University Press, Princeton.

Vogel, S. and R. D. Chapman. 1966. Force measurements with d' arsonval galvanometers. Review of Scientific Instruments 43:520.

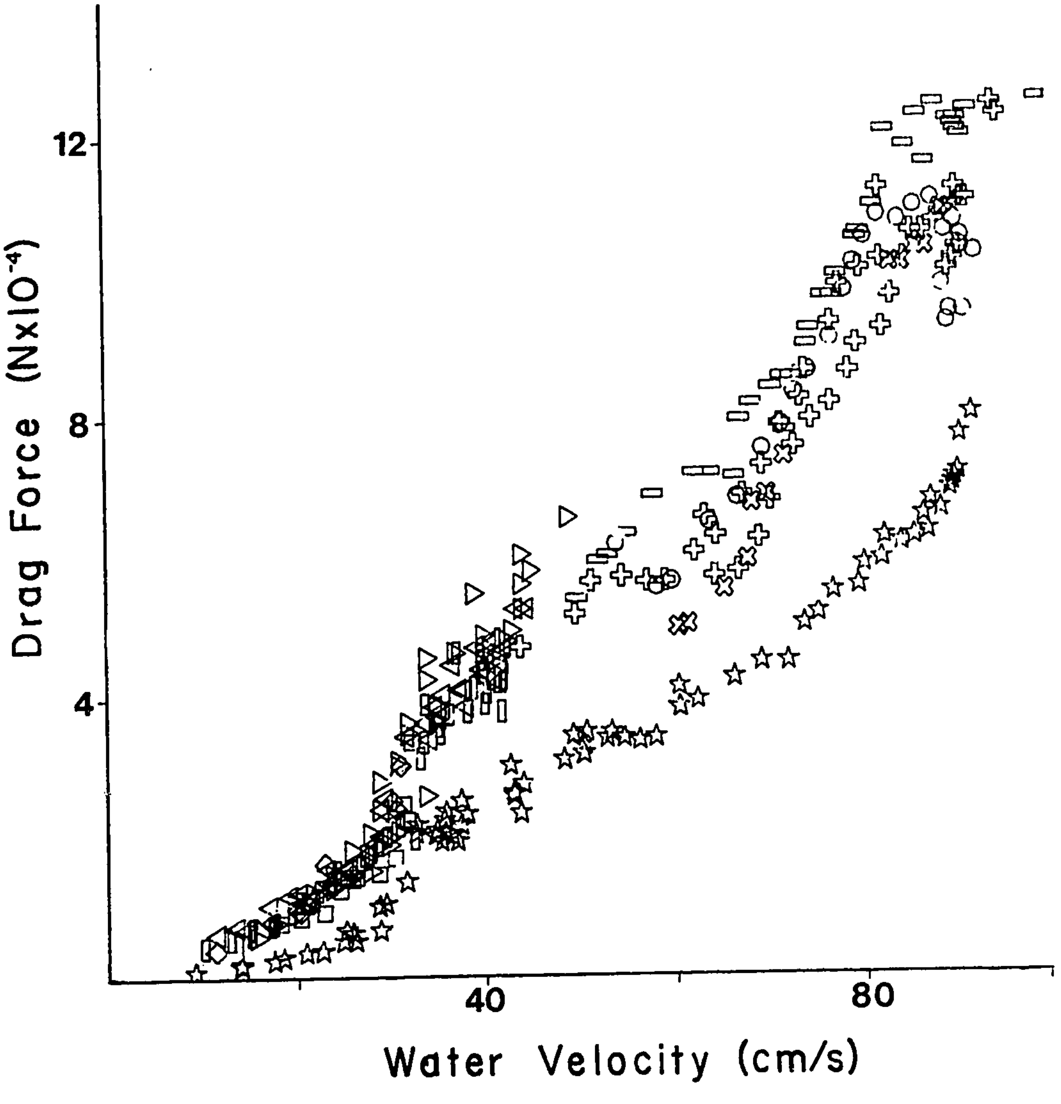
Vogel, S. and M. LaBarbera. 1978. Simple flow tanks for research and teaching. Bioscience 28:638-643.

Figure 1. Schematic representation of apparatus used to measure drag on a single larva of S. vittatum. AA=analogue ammeter, OW=ovoid wire, BFL=black fly larva, C=collimators, DA=digital ammeter, P=propellers, PS=power supply. Arrows show direction of flow.



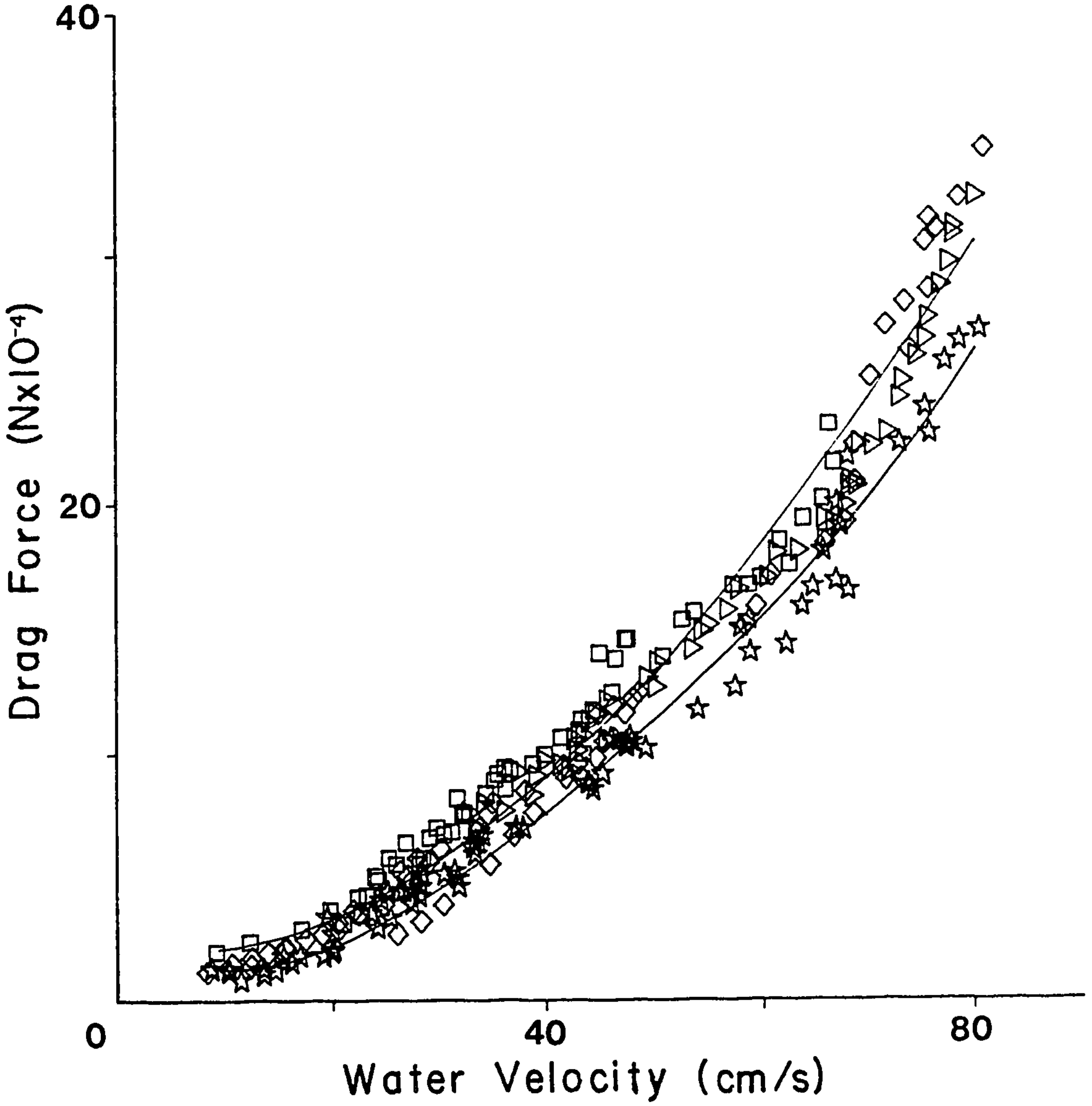
DA
+
AA
-
PS
10 KΩ
OW
BFL
P
C

Figure 2. Drag force on an ovoid wire by itself (stars) and with one of nine, different, filter-feeding larvae of S. vittatum attached to it (each symbol type represents data from one larva).



Drag Force (Nx10^{-4})
12
8
4
40
80
Water Velocity (cm/s)

Figure 3. Drag force on a piece of cover slip by itself (stars) and with one of three, different, filter-feeding larvae of S. vittatum attached to it (each symbol type represents data from one larva).



40
20
0
40
80
Drag Force (Nx10⁻⁴)
Water Velocity (cm/s)

Figure 4. Drag on the labral fans of a larva of S. vittatum, calculated by subtracting drag on a larva with its fans adducted from drag on the same larva with its fans abducted at the same velocity (each symbol type represents data from one larva).

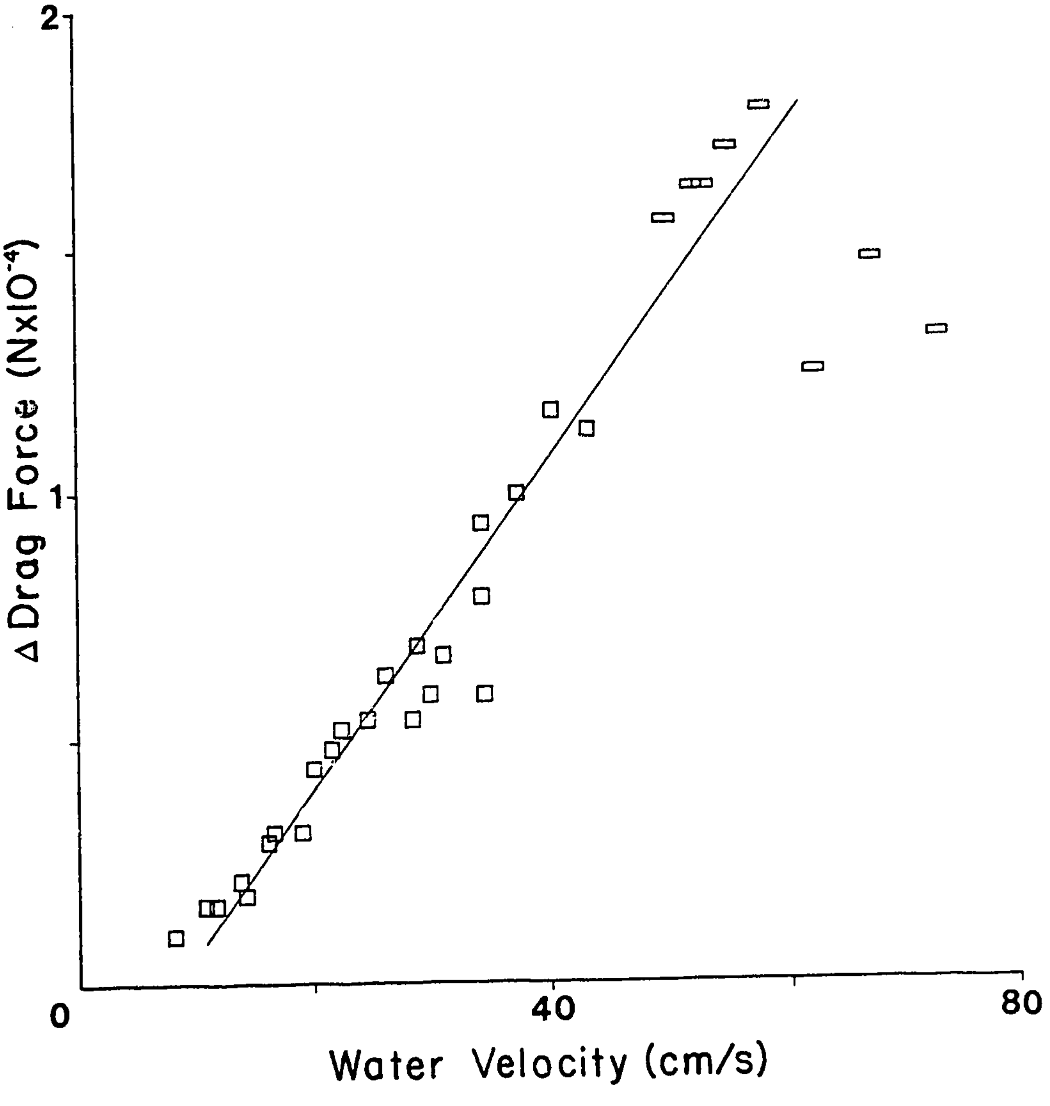

2
1
0
40
80
Δ Drag Force (Nx10^{-4})
Water Velocity (cm/s)

Figure 5. Coefficient of drag on a larva of S. vittatum as a function of Reynolds number: Squares represent filter-feeding larvae, circles represent larvae with adducted labral fans. Solid lines represent larvae on the ovoid wire, broken lines represent larvae on a piece of cover slip.

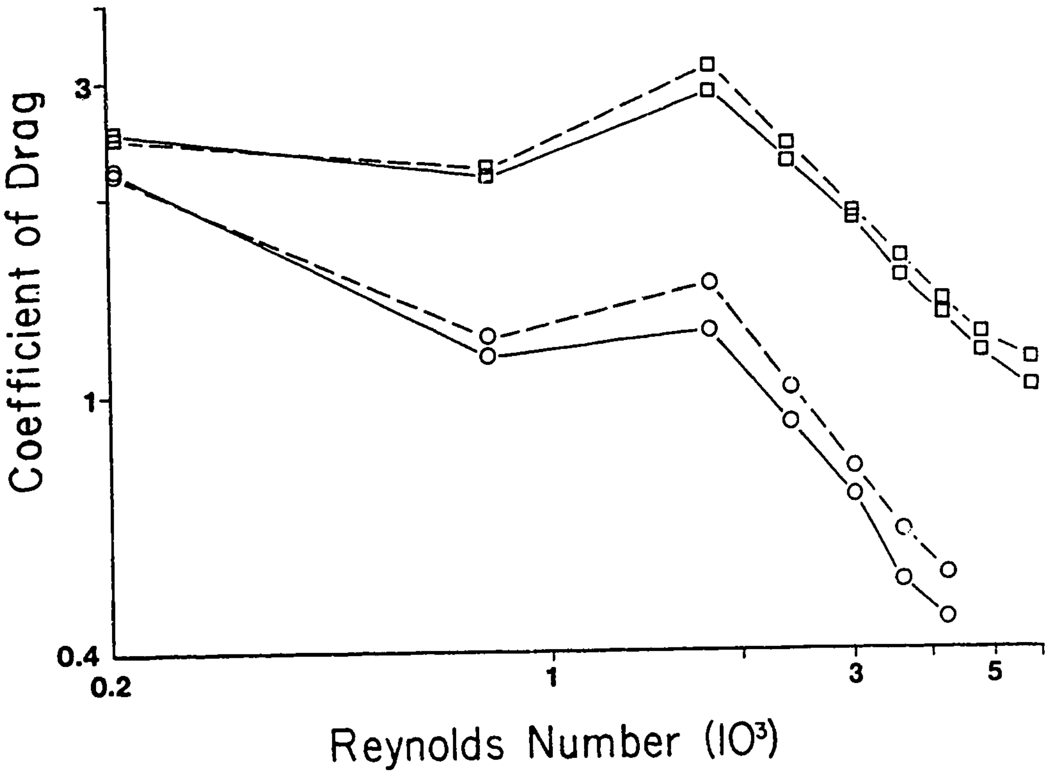
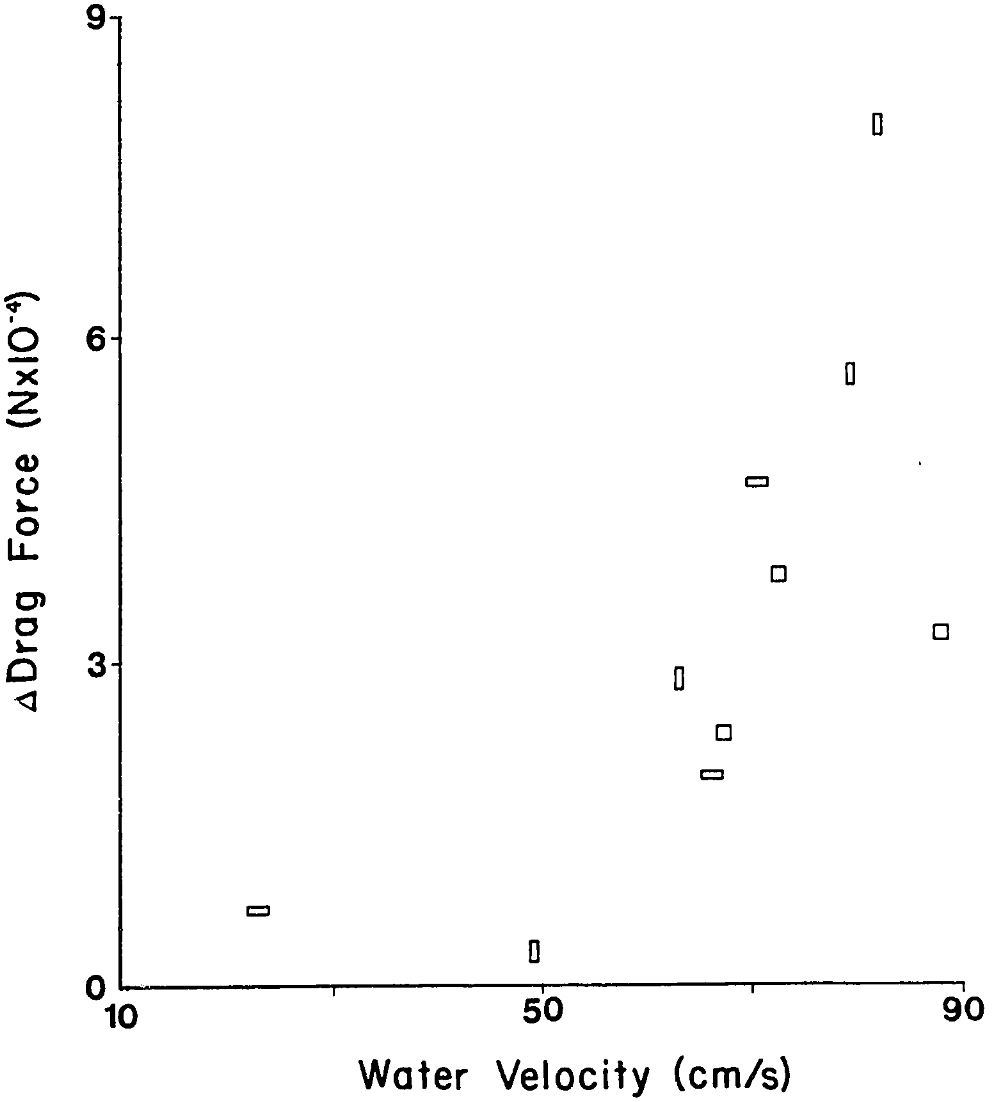

Coefficient of Drag
3
1
0.4
0.2
1
3
5
Reynolds Number (IO³)

Figure 6. The drag on a probing larva of S. vittatum. subtracted from drag on the same larva when it is filter feeding at the same velocity (each symbol type represent data from one larva).


9
6
3
0
ΔDrag Force (Nx10^{-4})
10
50
90
Water Velocity (cm/s)

3. FLUID FLOW PAST MICROHABITATS OCCUPIED BY LARVAE OF BLACK FLIES (DIPERTA: SIMULIIDAE)

Introduction

The larvae of most species of black flies are filter feeders that live attached to submerged substrata in rivers and streams. As a result of the current of the river or stream, water flows through the labral fans of the larvae. The labral fans capture suspended particles that are then ingested. It has often been noted that, on the scale of a stream reach, the larvae of black flies exhibit a highly contagious dispersion (Hocking and Pickering 1954, Décamps et al. 1975, Hart 1986). It is not known whether this is a result of patchiness of a resource in the habitat, or results from larvae forming groups that induce mutually beneficial flow, as suggested by Chance and Craig (1986).

Filter-feeding efficiency of larval black flies is important, because food intake by larvae affects several biological parameters related to the reproductive success of adults. Food availability at the larval stage affects the size and fecundity of adults of Simulium vittatum [complex] Zetterstedt and S. verecundum [complex] Stone and Jamnback (Colbo and Porter 1979, 1981), the mating success of S. decorum [complex] Walker (Simmons and Edman 1981) and the survivorship of pupae of S. pictipes Hagen (Brenner and Cupp 1980). This suggests that the selection of microhabitats that enhanc filter-feeding efficiency may have a selective advantage to the larvae.

The beds of most rivers and streams have a complex topography because of the presence of totally or partially submerged rocks, logs or aquatic vegetation. Such topography results in water flow that is highly variable, sometimes changing direction over a distance of less than 1 cm. Because of this complexity, some parts of the river or stream bed may be better suited than others for filter feeding by larvae of black flies. These variable flow conditions represent a kind of resource patchiness, that may influence filter-feeding efficiency. It can therefore be predicted that certain flow conditions characterize most or all microhabitats colonized by larval black flies.

The literature does not support this prediction as there are many contradictions about the hydrodynamic characteristics of microhabitats colonized by larval black flies as the following summary illustrates.

The flow parameter most commonly invoked to explain microhabitat occupation by larval black flies is water velocity. In temperate North America, larvae have been found in flow velocities ranging from <1 cm $\cdot$ s^{-1} for *Simulium* sp. (Osborne et al. 1985) to 165 cm $\cdot$ s^{-1} for larvae of *Prosimulium* *mixtum*/*fuscum* [complex] Syme and Davies (Lewis and Bennett 1975). Wetmore (1987) showed that larvae of *S*. *vittatum* were found in microhabitats with velocities higher than those of randomly selected microhabitats. Décamps et al. (1975) reported that larvae of *S*. *variegatum* Meigen (as *Odagamia* *variegata* Meigen), and *S*. *argyrentum* Meigen (as *O*. *obreptans* Edwards) occupied the highest velocity region in a longitudinal velocity gradient on a rock on the stream bed. Therefore, larvae of black flies can be found in microhabitats with a wide range of water velocities, but they are more common in microhabitats with high water velocities relative to the range of velocities in a particular habitat.

In contrast, laboratory experiments by Braimah (1987) showed that the highest feeding efficiency for larvae of *S*. *bivittatum* Malloch, at the particle sizes studied, was at 10-25 cm $\cdot$ s^{-1}. Kurtak (1978) reported that, of larvae of nine species studied in the laboratory, those of only one species (*S*. *jenningsi* [complex] Malloch) filter fed most efficiently at 70 cm • s^{-1}, the remaining eight species were more efficient at 50 or 30 cm • s^{-1}. This suggests that one or more variables acting in the field were not reproduced in the laboratory studies.

Water velocity at any point in a river or stream has a mean magnitude and direction. When flow is turbulent, small unpredictable fluctuations in magnitude and direction are superimposed onto the flow. Intuitively, turbulence can be thought of as the "mixing ability" of the flow. The more turbulent the flow the faster another fluid added to the flow will mix with the surrounding fluid.

Literature dealing with the relationship between microhabitat occupation and turbulence is contradictory. Craig and Chance (1982) concluded that the structure and feeding behaviour of larvae of S. vittatum minimizes turbulence of flow past the body and head. Maitland and Penney (1967), who worked with larvae of many species of black flies, and Osborne et al. (1985) reported finding larvae in places where turbulence was low. However, Kurtak (1978) stated that larvae of S. parnassum Malloch in laboratory experiments ingested suspended particles more rapidly when in a region of turbulent flow. Brenner and Cupp (1980) stated that larvae of S. pictipes, S. vittatum, and S. decorum in rearing troughs tended to occupy baffles, where they believed flow was more turbulent. Only Craig and Chance (1982) and Osborne et al. (1985) explained how turbulence was estimated.

There is more agreement about the relationship between microhabitat occupation and the angle of the substratum relative to direction of flow. Hocking and Pickering (1954), Maitland and Penney (1967) and Décamps et al. (1975) reported that the densest colonies of larvae were found on surfaces that were perpendicular, or almost perpendicular to the mean direction of flow. Brenner and Cupp (1980) who made similar observations in the laboratory, report that larvae of black flies in a rearing trough selectively occupied baffles that were facing into the flow.

The boundary layer is a thin layer of water close to a substratum that flows more slowly than the rest of the fluid. An attached boundary layer is literally attached to its substratum. Under certain conditions such as those found at the downstream portion of an immersed rock or log, the boundary layer will separate from the substratum. If a boundary layer remains separated it will form a wake which may take the form of an attached vortex or vortex pair, vortices shed at regular intervals, or a fully turbulent wake (Schlichting 1979). The latter is the most common type of wake found in habitats in which larvae of black flies are found. Décamps et al. (1975) reported finding no larvae downstream of the line of separation of the boundary layer from a rock.

Craig and Galloway (1987) have hypothesized that Froude number (F) (Vogel 1981, Newbury 1984, Craig 1987) may affect microhabitat occupation. Flow is termed subcritical, critical, or supercritical when $F<1$, $F=1$, and $F>1$ respectively. Froude number is a ratio of inertial to gravitational forces. When F increases as water flows over an obstacle, cells of turbulence are stretched out. The stretching of cells of turbulence reduces the level of turbulence of the flow (Craig and Galloway 1987). Wetmore (1987) showed that larvae of S. vittatum occupied microhabitats with a higher Froude number than were available at random.

In this chapter I looked for flow characteristics that are common to microhabitats occupied by filter-feeding larvae of black flies of several species in the field. Because I was interested in observing as many aspects of the flow at once as possible, my primary technique was to make the flow visible by injecting dye.

Materials and Methods

Because larvae of black flies are commonly found in a contagious dispersion, they are often found in aggregates, which will be termed groups in this thesis. Further, the area of substratum occupied by such a group will be termed a microhabitat.

Two hundred microhabitats, each occupied by a group of black fly larvae at 30 sites in Alberta and British Columbia, Canada (Fig. 1, Table 1) were examined. These sites were primarily small streams (<1 m wide) to small rivers (<5 m wide) because larvae in larger rivers were not accessible in situ without specialized equipment.

The following procedure was used to select sites. A map was consulted to find a road which traversed many streams. These roads were followed until a bridge or culvert was encountered. If running water was present under the bridge, or in the culvert, it was investigated for the presence of larval black flies. When a microhabitat occupied by a group of black fly larvae was found, flow past the microhabitat was characterized, and the larvae were collected into Carnoy's solution (3 ethanol (98%): 1 acetic acid) for later identification in the laboratory. From 1 to 46 microhabitats were sampled at each site depending on the number of groups of larvae found, and the diversity of dispersion patterns (Eymann 1985, chapter 3) exhibited by the larvae. Morphologically distinct species or species groups were identified using taxonomic keys of Currie (1986) and Hall (1974). The classification system of Crosskey (1987) was used.

Water velocity, 1-2 cm above a group of larvae, was measured with an electromagnetic flow meter (Model PVM-2, Montedoro-Whitney Inc.). The depth of water above the larvae was measured with a ruler. A pencil was placed into the water and the behaviour of ripples around it were observed to determine whether flow was subcritical, critical, or supercritical (Newbury 1984, Craig 1987). Froude number was calculated from the depth and velocity at each site using the formula: $F=U/\sqrt{gl}$ (Vogel 1981) where; F=Froude number, U=velocity, g=acceleration due to gravity, and l=depth.

To make flow patterns visible, a syringe with a 12 cm long, 1 mm diameter needle was used to inject a 0.05 % (by weight) solution of methylene blue into the flow (Rühm and Pegel 1986). To minimize the effect of the syringe needle on local flow conditions, the needle was placed on the substratum, perpendicular to the direction of flow. With the tip of the needle close to the substratum, and with the opening directed downstream, th [illegible] injected as slowly as possible. The behaviour of the resulting dye plu [illegible] information about the flow, showing whether the boundary layer wa [illegible] g. 2A) (provided that the boundary layer was thicker than the diameter of the needle), or turbulent (Fig. 2B); and whether the boundary layer was attached to the substratum (Fig. 2A-B) or separated (Fig. 2C-E). The flow parameters discussed in this chapter are described in detail by Schlichting (1979), Vogel (1981), and Van Dyke (1982).

This approach only considers the conditions at the time measurements were made and not those at the time the microhabitat was first colonized, or over the time between colonization and when measurements were taken. However, larvae of black flies will respond to some changes in flow conditions by leaving a microhabitat within a day in the field (chapter 5), and within hours in the laboratory (Lacoursière 1989). Consequently, the flow characteristics described here are those which did not induce larvae to leave the microhabitat.

Results

Larvae were found at velocities ranging from 10-210 $cm \cdot s^{-1}$; the mean velocities for a given species at a given site fell between 23 and 120 $cm \cdot s^{-1}$. Larvae of most species were found in a wide range of velocities and the ranges of most of the species studied showed considerable overlap (Fig. 3). This agrees with results of other studies (e.g. Harrod 1965, Lewis and Bennett 1975).

Laminar mainstream flow is rare in rivers and streams (Craig 1987) and no examples were found. However, laminar boundary layers were found, especially on logs or rocks that projected out of the boundary layer of the stream bed, and into the mainstream flow. At four sites larvae were found in laminar boundary layers. At three of these sites comparisons with groups of larvae in turbulent boundary layers were possible. The larvae found at the three sites were: 1) One *S. piperi* Dyar and Shannon and seven *S. tuberosum* [complex] Lundström (cytotype FG) larvae occupied a rock with a laminar boundary layer and a water velocity of 55 $cm \cdot s^{-1}$. A neighbouring rock with a turbulent boundary layer and water velocity of 60 $cm \cdot s^{-1}$ had two *S. piperi* and 11 *S. tuberosum* larvae. 2) A group of larvae of *S. venustum/verecundum* [complex] on the inside of a culvert was at the transition from a laminar to a turbulent boundary layer, so that some individuals were in a laminar boundary layer and some in a turbulent boundary layer. No difference could be seen between the two parts of the group of larvae. Water velocity could not be measured because the water was too shallow for the velocity probe. 3) A group of *S. hunteri* Malloch was found on a rock with a laminar boundary layer in a stream with a main stream velocity of 30 $cm \cdot s^{-1}$. In other streams *S. hunteri* was found in turbulent boundary layers. These data show that larvae of at least three morphological species of black flies can occupy microhabitats with either type of boundary layer.

A group of *S. transiens* Rubtsov larvae was found in a laminar boundary layer on a 1.5 cm diameter branch that projected into the main stream flow. Water flowed past this branch with a main stream velocity of 23 cm $\cdot$ s^{-1}. Comparison to other sites was not possible because these were the only larvae of *S. transiens* found.

No larvae of any species were found downstream of the line of separation (l. s.) that constitutes the beginning of the formation of a fully turbulent wake (Fig. 4 w). The larvae of eight species (*C. dacotensis*, *S. transiens*, *S. virgatum* [complex] Coquillet, *S. canadense* Hearle, *S. tuberosum*, *S. piperi*, *S. vittatum*, *S. venustum/verecundum*) were found occupying at least one microhabitat with separation leading to development of a fully turbulent wake. Areas where the boundary layer separated and then reattached a small distance downstream, leaving a flat, disk-shaped region of recirculating flow (Fig. 4 r. f.) were also free of larvae. The larvae of five species (*S. arcticum* [complex] Malloch, *S. tuberosum*, *S. piperi*, *S. virgatum*, *S. canadense*) were found on substrata that exhibited this type of separation. None of these larvae were found in the region of recirculating flow. One exception was found where the region of recirculating flow was large (3.5 cm in diameter), and almost circular in cross-section; this region was occupied by 12 larvae of *S. venustum/verecundum*. Regions of recirculating flow were easily recognized because, when dye was injected into them, the dye spread out, colouring the entire volume. Substrata with attached boundary layers, but unoccupied by larvae were found in some of the habitats investigated.

Froude number (F), as indicated by the behaviour of ripples around a partially submerged pencil (Newbury 1984, Craig 1987), was a good predictor of presence of larval black flies in some situations, but not in others. A mixed group of larvae of *S. vittatum*, *S. tuberosum*, and *S. piperi* was found on a rock where flow went from critical to supercritical. The upstream edge of this group of larvae corresponded to the transitions from critical to supercritical flow, so that of the larvae were in supercritical flow. However, the larvae of black flies belonging to the species examined in the course of this study do not appear to be restricted to any one type of flow because larvae of each of the following species; S. canadense, S. decorum, S. piperi, S. tuberosum, S. venustum/verecundum, S. vittatum, and S. virgatum, were found in subcritical, critical, and supercritical flow (Table 2). In table 2 S. tuberosum is subdivided according to the cytotype of the larvae (Mason 1982). Of those species found in only one or two types of flow (P. onycodactylum Dyar and Shannon, S. arcticum, S. hunteri, and S. transiens), five or fewer groups of larvae were found, suggesting that they may be found in other types of flow if more groups had been examined.

The mean calculated Froude number was above one for all species except S. transiens (Table 2). Froude number for a single microhabitat ranged from 0.18 to 6.3.

Discussion

Larvae of most species of black flies investigated occupied microhabitats with a wide range of water velocities. The slowest water velocity past a microhabitat occupied by larval black flies was 10 $cm \cdot s^{-1}$. Even slower velocities have been reported in the literature (Osborne et al. 1985). It appears that, as long as water velocity is high enough that water flows through the labral fans, a microhabitat can be occupied by larvae. The velocity of water flowing past substrata occupied by black fly larvae is not consistent from one species or habitat to the next, and is highly variable even within a species. Consequently, it alone is not likely to account for the contagious dispersion exhibited by larvae of black flies.

Velocity measurements alone provide no information about the boundary layer of the substratum occupied by these larvae. However, laboratory studies of S. vittatum (Chance and Craig 1986) have shown that larvae are found in a thin boundary layer. More recent studies on larvae of S. vittatum (Lacoursière 1989) have shown that the labral fans and sometimes the head and thorax of larvae project out of the boundary layer into the main stream flow. Therefore, the velocity measurements reported in Fig. 3 probably reflect the velocities to which the labral fans, and perhaps the more anterior part of the larvae were subjected.

The only flow parameter that characterized all 200 substrata occupied by larvae of black flies was the presence of an attached boundary layer. This agrees with results reported by Décamps et al. (1975). Furthermore, larvae were almost never found on substrata with separated boundary layers. It was often possible to anticipate the location of boundary layer separation from the abrupt end to a group of larvae at the downstream part of a rock.

There are two types of separated boundary layers (Fig. 4). The first involves a boundary layer that separates because of a small irregularity on the substratum, then reattaches at some distance downstream after flowing over an area of recirculating flow (c. f. Figs. 33, 35, 36 in Van Dyke 1982). A larva in a small area of recirculating flow will be exposed to water flowing in a different direction at its anterior end than at its posterior end. This kind of flow will probably interfere with the system of vortices described by Chance and Craig (1986), consequently affecting the larva's ability to filter-feed. In rivers and streams in which most rocks have been worn smooth by erosion, such areas are probably rare enough that they do not significantly reduce the amount of substratum available for occupation. If the area of recirculating flow is larger than twice the larval body length interference with the vortex system of the larva may not be a problem. Only one such large area of recirculating flow was found, and it was occupied by larvae of S. venustum/verecundum.

In the second type of separation, the boundary layer does not reattach, but curls and breaks up to become incorporated into a wake that is more turbulent and slower than the surrounding flow (Van Dyke 1982). This high level of turbulence downstream from separation is apparent at the surface of the rock; if dye is injected into the flow from a needle touching the rock the dye plume will behave erratically, changing direction at irregular intervals lasting a few seconds (Fig. 2C), or the dye plume may mix rapidly into the wake (Fig. 2D). This contrasts sharply with the uniform behaviour of a dye plume injected near the surface of the rock, but upstream of separation (Fig. 2E). The high level of turbulence in a wake will buffet a larva, probably interfering with its ability to filter-feed.

The observation that larval black flies avoid regions of high turbulence such as wakes, combined with the observation that larvae occupy substrata that face into the flow (Hocking and Pickering 1954, Maitland and Penney 1967, Décamps et al. 1975, Brenner and Cupp 1980) suggests that accelerating flow may be an important factor in microhabitat occupation. As water flows past a surface that faces into the current, it must accelerate because of the principle of continuity (Vogel 1981). One effect of acceleration on two-dimensional, turbulent, boundary layers is the disappearance of large eddies followed by the decay of turbulence (Badri Narayanan and Ramjee 1969). Decay of turbulence also takes place in accelerating potential flow. This principle is commonly employed in the design of wind tunnels where it is used to reduce the turbulence at the working section (Pope 1954). Larvae in accelerated flow on a surface facing into the current will therefore be subjected to less turbulence, and consequently less buffeting than larvae in unaccelerated flow.

The apparent contradiction between the results of observations made in the field which showed that larvae occupy high velocity microhabitats (Décamps et al. 1975, Wetmore 1987), and the results of experiments run in the laboratory that showed that larvae are more efficient at filter feeding at lower or intermediate velocities (Kurtak 1978, Braimah 1987) may be resolvable if the effects of acceleration are considered. In most laboratory flumes, both acceleration and turbulence are kept to a minimum because accelerating flow, or too much variance in velocity, makes results difficult to interpret. In rivers and streams where larval black flies are found, areas of high water velocity are usually also areas of accelerating flow, and consequently, areas of reduced turbulence. Therefore it may be inappropriate to compare results of laboratory experiments that vary only in velocity, to field observations where velocity varies with other parameters such as acceleration and turbulence.

In some instances, groups of larvae on a rock appeared to distribute themselves according to whether flow was subcritical, critical, or supercritical; however, most species were found in microhabitats characterized by all three types of flow (Table 2). Changes in flow from subcritical to critical to supercritical are a result of acceleration of flow (Newbury 1984). This acceleration results in a reduction in turbulence in critical and supercritical flows (Craig and Galloway 1987). In those instances where larvae appear to distribute themselves according to whether flow is subcritical, critical, or supercritical, the larvae may, in fact, be distributing themselves according to whether or not flow is accelerating. However in many instances, when water is forced to accelerate, flow remains subcritical because it is either so slow, or so deep, that acceleration will not cause a change in the type of flow. Consequently, the response to critical and supercritical flow is not consistent.

The mean Froude number for larvae of most species of black flies studied was close to 1.5 (Table 2), suggesting that these larvae were more common in microhabitats with shallow, rapid flow. This is consistent with the hypothesis that microhabitats occupied by larvae of black flies are characterized by accelerated flow.

Larvae of several species of black flies (S. tuberosum, S. venustum/verecundum, and S. piperi) were found in both laminar and turbulent boundary layers in the same river or stream. Although conclusions should be drawn with caution because of the limited quantity of data, it appears that the probability of larvae occupying a substratum is the same whether that substratum has a laminar or a turbulent boundary layer.

Larvae of S. transiens and S. hunteri occupied substrata with laminar boundary layers. However, it was not possible to compare these groups of larvae to other groups of the same species in the same stream in a turbulent boundary layer. Larvae of other species may have been in laminar boundary layers that were thinner than the diameter of the syringe needle and therefore not observed. Laminar boundary layers are more commonly found on substrata that project into the main stream flow, because such substrata have their own boundary layer independent of that of the bed of the river or stream.

Although both a wake and a boundary layer can be turbulent, the turbulence can have different effects on black fly larvae. The vortices, or cells of turbulence are generally contained in, and are no larger than the boundary layer (c. f. Figs. 158, 162, 163 in Van Dyke 1982) or the wake (c. f. Figs. 55, 57, 71 in Van Dyke 1982). Since the wake of a rock is generally several times larger than the boundary layer of a rock, the largest vortices in the wake are several times larger than the largest vortices in its boundary layer. The large vortices in the wake account for the erratic behaviour of the dye plume downstream of separation. These vortices will buffet a larva around by as much as 180°, likely interfering with its filter-feeding activity. In contrast, buffeting in a turbulent boundary layer will be less severe because of smaller vortices.

The net-spinning larvae of Hydropsyche Pictet (Trichoptera: Hydropsychidae) occupy microhabitats characterized by separated boundary layers (Osborne and Herricks 1987). The larvae of Brachycentrus occidentalis Banks (Trichoptera: Brachycentridae), which do not spin webs but filter feed with modified middle and hind legs, are most commonly found on the crests of rocks (Wetmore 1987) where the boundary layer is attached. It appears that lotic filter feeders that use modified appendages have different microhabitat requirements than lotic filter feeders that use silken nets. It would be interesting to see if this generalization can be applied to other taxa of lotic filter feeders.

The contagious dispersion commonly exhibited by larvae of black flies can be, at least partly, attributed to the heterogeneity of flow over a river bed. A microhabitat occupied by larval black flies appears to be characterized by the following flow properties, 1) a high enough flow velocity that water will be forced through the labral fans, 2) an attached boundary layer that, according to Chance and Craig (1986) and Lacoursière (1989), should be thinner than the height of the black fly larva, and 3) accelerating flow, which reduces turbulence. These suggestions are consistent with the hypothesis that the contagious dispersion exhibited by larval black flies is a response to an underlying patchiness in the types of flow in the stream bed.

References

Badri Narayanan, M. A., and V. Ramjee. 1969. On the criteria for reverse transition in a two-dimensional boundary layer flow. J. Fluid Mech. 35: 225-241.

Braimah, S. A. 1987. The influence of water velocity on particle capture by the labral fans of larvae of Simulium bivittatum Malloch (Diptera: Simuliidae). Can. J. Zool. 65: 2395-2399

Brenner, R. J., and E. W. Cupp. 1980. Rearing black flies (Diptera: Simuliidae) in a closed system of water circulation. Tropenmed. Parasit. 31: 247-258.

Chance, M. M., and D. A. Craig. 1986. Hydrodynamics and behaviour of Simuliidae larvae (Diptera). Can. J. Zool. 64: 1295-1309.

Colbo, M. H., and G. N. Porter. 1979. Effects of the food supply on the life history of Simuliidae (Diptera). Can. J. Zool. 57: 301-306.

Colbo, M. H., and G. N. Porter. 1981. The interaction of rearing temperature and food supply on the life history of two species of Simuliidae (Diptera). Can. J. Zool. 59: 158-163.

Craig, D. A. 1987. Some of what you should know about water or, K.I.S.S.* for hydrodynamics (*Keeping It Stupidly Simple). Bull. N. Am. Benthol. Soc. 4(2): 178-182.

Craig, D. A., and M. M. Chance. 1982. Filter feeding in larvae of Simuliidae (Diptera: Culicomorpha): aspects of functional morphology and hydrodynamics. Can. J. Zool. 60: 712-724.

Craig, D. A., and M. M. Galloway. 1987. Hydrodynamics of larval black flies. p. 171-185. In K. C. Kim and R. W. Merritt [ed.]. Black flies: Ecology, Population Management, and Annotated World List. The Pennsylvania State University. University Park, PA.

Crosskey, R. W. 1987. An annotated checklist of the world black flies (Diptera: Simuliidae). In: Black flies: Ecology, Population Management, and Annotated World List. (K. C. Kim and R. W. Merritt ed.). The Pennsylvania State University. University Park.

Currie, D. C. 1986. An annotated list of and keys to the immature black flies of Alberta (Diptera: Simuliidae). Mem. entomol. Soc. Can. 134.

Décamps, H., G. Larrouy, and D. Trivellato. 1975. Approche hydrodynamique de la microdistribution d'invertébrés benthiques en eau courante. Annls. Limnol. 11(1): 79-100.

Eymann, M. 1985. The behaviours of the blackfly larvae *Simulium vittatum* and *S. decorum* (Diptera:Simuliidae) associated with establishing and maintaining dispersion patterns on natural and artificial substrate. M. Sc. Thesis. University of Toronto.

Hall, F. 1974. A key to the *Simulium* larvae of southern California (Diptera: Simuliidae). California Vector News 21: 65-71.

Harrod. J. J., 1965. Effect of current speed on the cephalic fans of larva of *Simulium ornatum* var. *nitidifrons* Edwards (Diptera: Simuliidae). Hydrobiologia. 26: 8-12.

Hart. D. D. 1986. The adaptive significance of territoriality in filter-feeding larval blackflies (Diptera: Simuliidae). Oikos 46: 88-92.

Hocking, B., and L. R. Pickering. 1954. Observations on the bionomics of some northern species of Simuliidae (Diptera). Can. J. Zool. 32: 99-119.

Kurtak, D. C., 1978. Efficiency of filter-feeding of black fly larvae (Diptera: Simuliidae). Can. J. Zool. 56: 1608-1623.

Lacoursière, J. O. 1989. Suspension-feeding behaviour of black fly larvae (Diptera: Simuliidae): Hydrological perspectives. University of Alberta. Ph. D. Thesis.

Lewis, D. J., and G. F. Bennett. 1975. The blackflies (Diptera: Simuliidae) of insular Newfoundland. III. Factors affecting the distribution and migration of larval simuliids in small streams on the Avalon Peninsula. Can. J. Zool. 53: 114-123.

Maitland, P. S., and M. M. Penney. 1967. The ecology of the Simuliidae in a Scottish river. J. Anim. Ecol. 36: 179-206.

Mason, G. F. 1982. Cytological studies of sibling species of Simulium tuberosum (Lundström) (Diptera: Simuliidae). Can. J. Zool. 60: 292-303.

Newbury, R. W. 1984. Hydrologic determinants of aquatic insect habitats. p. 323-357. In V. H. Resh and D. M. Rosenberg [ed.]. The Ecology of Aquatic Insects. Praeger Publishers. Toronto, Ont.

Osborne, L. L., E. E. Herricks, and V. Alvian. 1985. Characterization of benthic microhabitat: An experimental system for aquatic insects. Hydrobiologia. 123: 153-160.

Osborne, L. L., and E. E. Herricks. 1987. Microhabitat characteristics of Hydropsyche (Trichoptera: Hydropsychidae) and the importance of body size. J. N. Am. Benthol. Soc. 6(2): 115-124.

Pope, A. 1954. Wind-tunnel Testing. John Wiley and Sons, Inc. New York, NY. 511 p.

Rühm, W., and M. Pegel. 1986. Die Substratbesiedlung durch Kriebelmückenlarven und -puppen (Simuliidae, Dipt.). Arch. Hydrobiol. 107(1): 75-87.

Schlichting, H. 1979. Boundary-Layer Theory. McGraw-Hill Book Company. Toronto, Ont. 817 p.

Simmons, K. R., and J. D. Edman. 1981. Sustained occupation of the black fly Simulium decorum Walker (Diptera: Simuliidae). Can. J. Zool. 59: 1-7.

Van Dyke, M. 1982. An Album of Fluid Motion. The Parabolic Press. Stanford, CA. 176 p.

Vogel, S. 1981. Life in Moving Fluids: The Physical Biology of Flow. Princeton University Press. Princeton, NJ. 352 p.

Wetmore, S. H. 1987. Characterizing the hydraulic habitat of a passive filter feeder, Brachycentrus occidentalis (Banks). M. Sc. Thesis. Univ. Toronto, Ont. 92 p.

Table 1. Sites from which larvae of black flies were collected. Refer to Fig. 1 for location on map.

Site	Location	Date	Number of Microhabitats
1	Jackob Ck. Alta. on Hyw. 1A (51°12'N 114°49'W)	9 July 1987	2
2	Old Fort Ck. Alta. on Hwy. 1A (51°09'N 115°03'W)	9 July 1987	1
3	Sherbrooke Ck. BC on Hyw. 1 (51°26'N 116°23'W)	9 July 1987	1
4	Hospital Ck. BC on Hwy. 1 (51°18'N 116°57'W)	10 July 1987	2
5	Tangier R. BC on Hwy. 1 (51°07'N 117°51'W)	10 July 1987	3
6	American Ck. (=Texas Ck.) BC on Hyw. 1 (49°21'N 121°25'W)	24 July 1987	1
7	Sclufield Ck. BC on Hwy. 99 (49°24'N 123°15'W)	22 July 1987	3
8	Lyall Ck. on Saturna Is. BC (48°47'N 123°10'W)	14 July 1987	4
9	Chemainus R. BC (48°46'N 123°56'W)	19 July 1987	5
10a	Skutz Falls on Cowichun R. BC (48°47'N 123°52'W)	19 July 1987	46
10b	Skutz Falls on Cowichun R. BC (48°47'N 123°52'W)	11 July 1988	21
11	North Nanaimo R. BC on Nanaimo L. Rd. (49°06'N 124°08'W)	16 July 1987	4
12	Tsolum R. BC on Bay Main Rd. (49°47'N 125°14'W)	17 July 1987	3
13	Browns R. BC on Bay Main Rd. (49°41'N 125°06'W)	17 July 1987	1
14	Fifty seven Ck. BC on Big Bar L. Rd. (51°15'N 121°42'W)	18 July 1987	3
15	unnamed Trib. of Big Bar L. on Big Bar L. Rd. (51°17'N 121°45'W)	28 July 1987	2
16	unnamed Ck. of site 15 - 2 km downst. (51°18'N 121°45'W)	28 July 1987	9
17	Big Bar Ck. BC on Big Bar L. Rd. (51°20'N 121°52'W)	29 July 1987	2
18	Meason Ck. BC north of Dog Ck. (51°47'N 122°18'W)	30 July 1987	2
19	unnamed Ck. just south of Williams L. BC on Bella Coola Hyw. (52°05'N 122°10'W)	3 Aug. 1987	2
20	Chilanko R. BC on Bella Coola Hyw. (53°48'N 122°59'W)	3 Aug. 1987	2
21	Alexis Ck. BC on Bella Coola Hyw. (52°05'N 123°18'W)	3 Aug. 1987	3
22	Narcosli Ck. BC south of Quesnel (52°49'N 121°29'W)	4 Aug. 1987	2
23	Cottonwood R. BC 10 km north of Quesnel (53°10'N 122°29'W)	4 Aug. 1987	1
24	unnamed Ck. north of Fox Ck. Alta. on Hwy. 43 (54°25'N 116°55'W)	8 Aug. 1989	1
25	Two Ck. Alta. on Hwy. 43 (54°15'N 116°20'W)	8 Aug. 1989	5
26	Swan R. Alta. on Hwy. 2 (55°18'N 115°25'W)	20 June 1987	1
27a	Driftwood R. east of Slave L. (55°15'N 114°14'W)	17 June 1986	9
27b	Driftwood R. east of Slave L. (55°15'N 114°14'W)	20 June 1986	6
28	Driftwood R. ca. 100 m upstream of site 27	20 June 1986	6
29	Whitemud Ck. on 23 Ave. Edmonton Alta. (53°28'N 113°32'W)	20 Aug. 1988	20
30	Norris Ck. Alta. on Hwy. 16 (53°34'N 112°42'W)	8 May 1987	31

Table 2: The Froude number ($\bar{x}$±S. E.(n)), and the ratio of the number of groups of larvae found in microhabitats with subcritical, critical, or supercritical (SB:C:SP) flow.

Species	Froude number	SB:C:SP
P. onycodactylum	1.7(3)	0:1:2
S. arcticum	1.5(3)	2:0:1
S. canadense	1.6±0.1(56)	13:9:34
S. decorum	2.6±0.9(4)	1:1:3
S. hunteri	2.3(3)	2:0:3
S. piperi	1.6±0.1(19)	6:6:7

Species	Froude number	SB:C:SP
S. transiens	0.37(1)	1:0:0
S. tuberosum (FG)[a]	1.6±0.1(20)	3:8:9
(AB)[a]	1.4±0.3(8)	3:1:4
S. venustum/ verecundum	1.3±.2(12)	6:5:5
S. vittatum	1.6±0.2(12)	3:4:5
S. virgatum	1.6±0.1(25)	1:1:23

[a] Letters in parentheses indicate cytotype.

Figure 1. Map of southern portion of Alberta and British Columbia showing the location of field sites investigated in the course of this study.

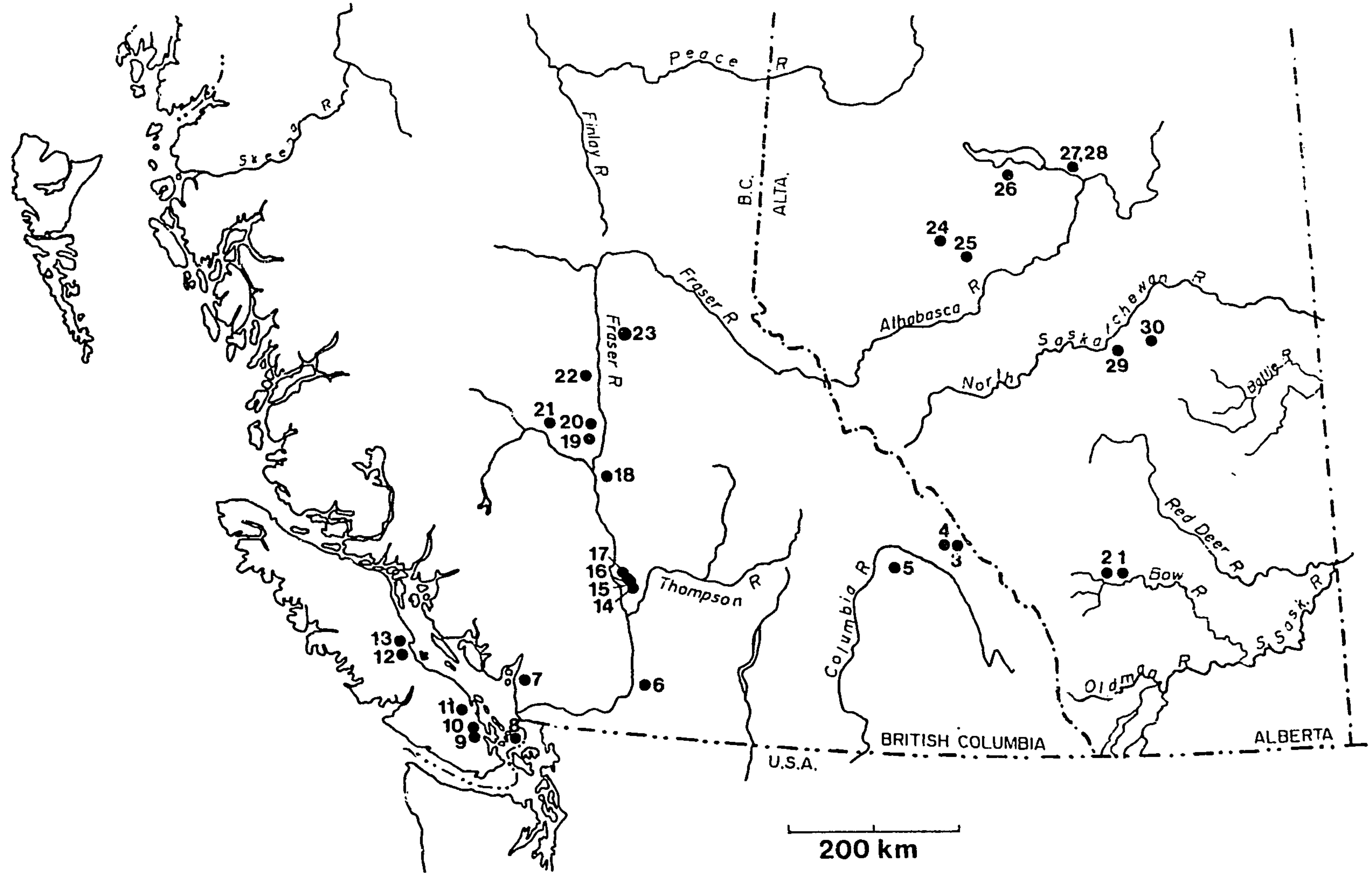

Peace R
Finlay R
Skeena R
B.C.
ALTA.
Fraser R
Fraser R
Athabasca R
North Saskatchewan R
Battle R
Red Deer R
Bow R
S. Sask. R
Oldman R
Thompson R
Columbia R
BRITISH COLUMBIA
ALBERTA
U.S.A.
200 km
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27,28
29
30

Figure 2. The appearance of plumes of methylene blue (p., stippled area) injected into the flow from a syringe needle (s. n.) under various flow conditions. a) Plume injected into laminar flow; width of plume increases slowly, boundary between plume and water is well defined. b) Plume injected into turbulent flow; width of plume increases rapidly, boundary between plume and water not well defined due to mixing action of turbulent flow. c) Plan view of methylene blue injected into a low-Reynolds-number wake, downstream of the line of separation (l. s.). Plume changes shape many times in a period of a few seconds. The three plume shapes shown are examples of what may be observed. d) Plan view of methylene blue injected into the wake of a rock at high Reynolds number. Plume moves upstream to the line of separation then flows downstream. Plume widens rapidly often colouring the entire wake. e) Cross-section of a rock showing the behaviour of a plume upstream and downstream of the line of separation. Upstream of separation the plume follows the boundary layer until separation. Downstream of separation the plume flows upstream to the line of separation then changes direction, flowing downstream. Arrows indicate direction of flow.

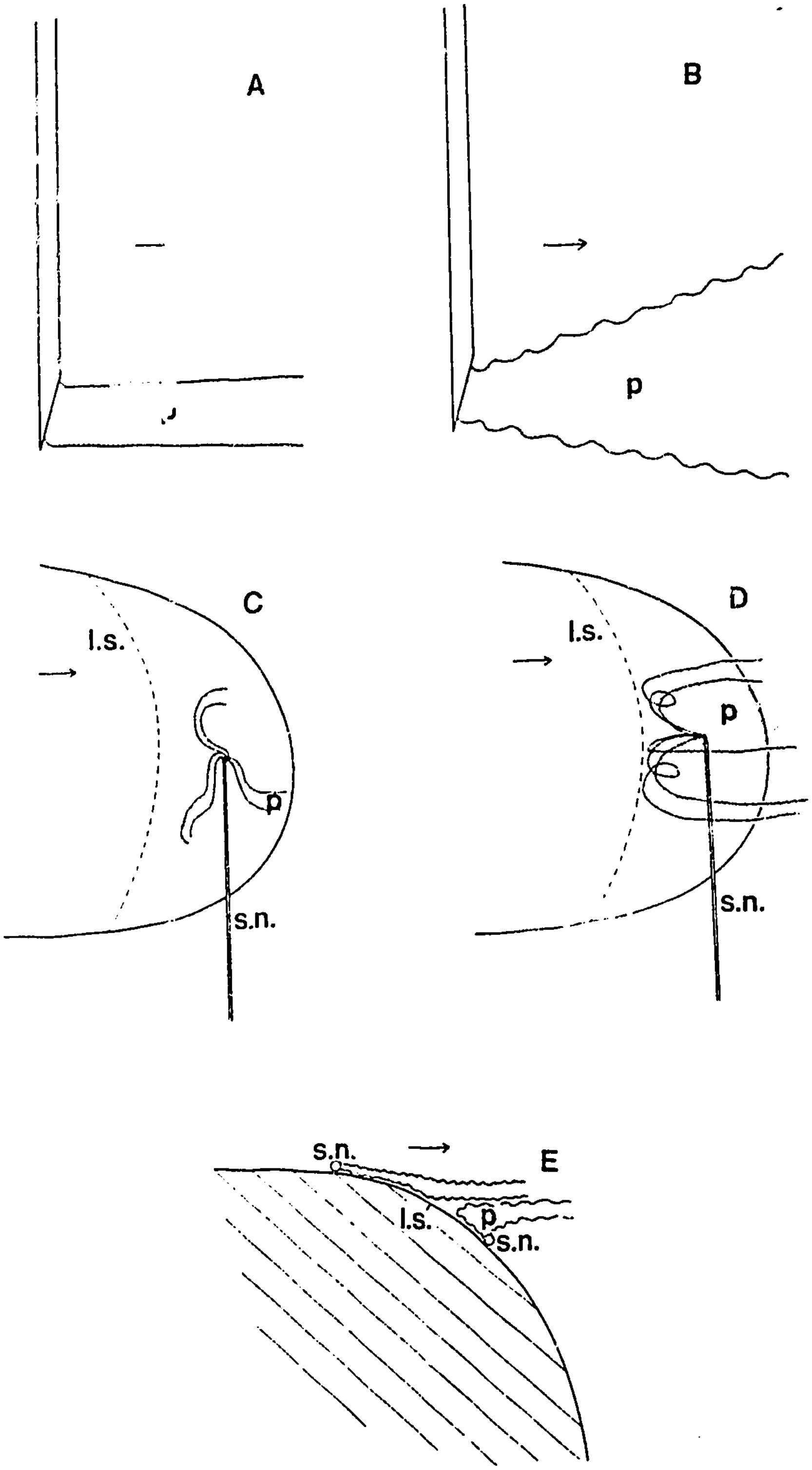
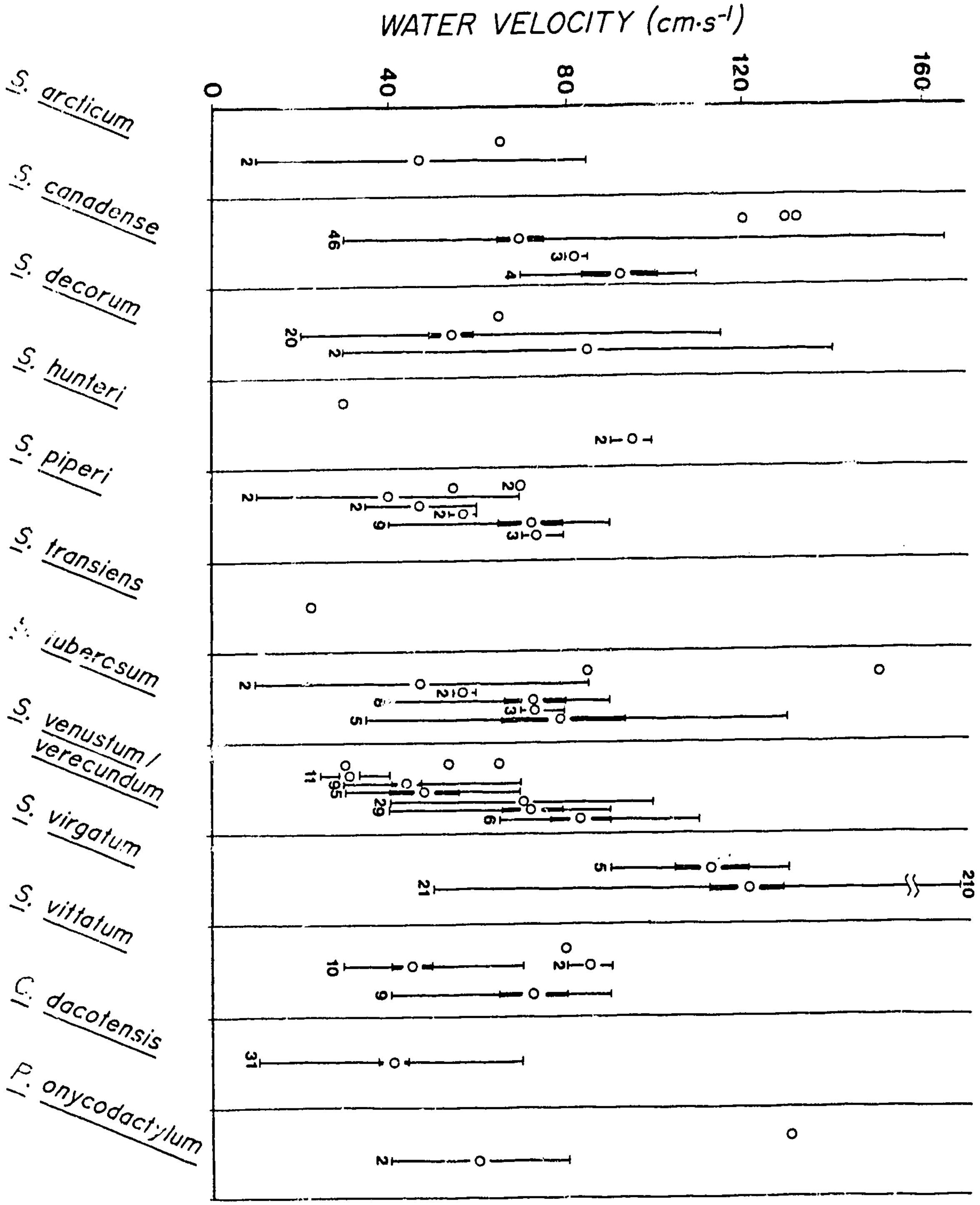
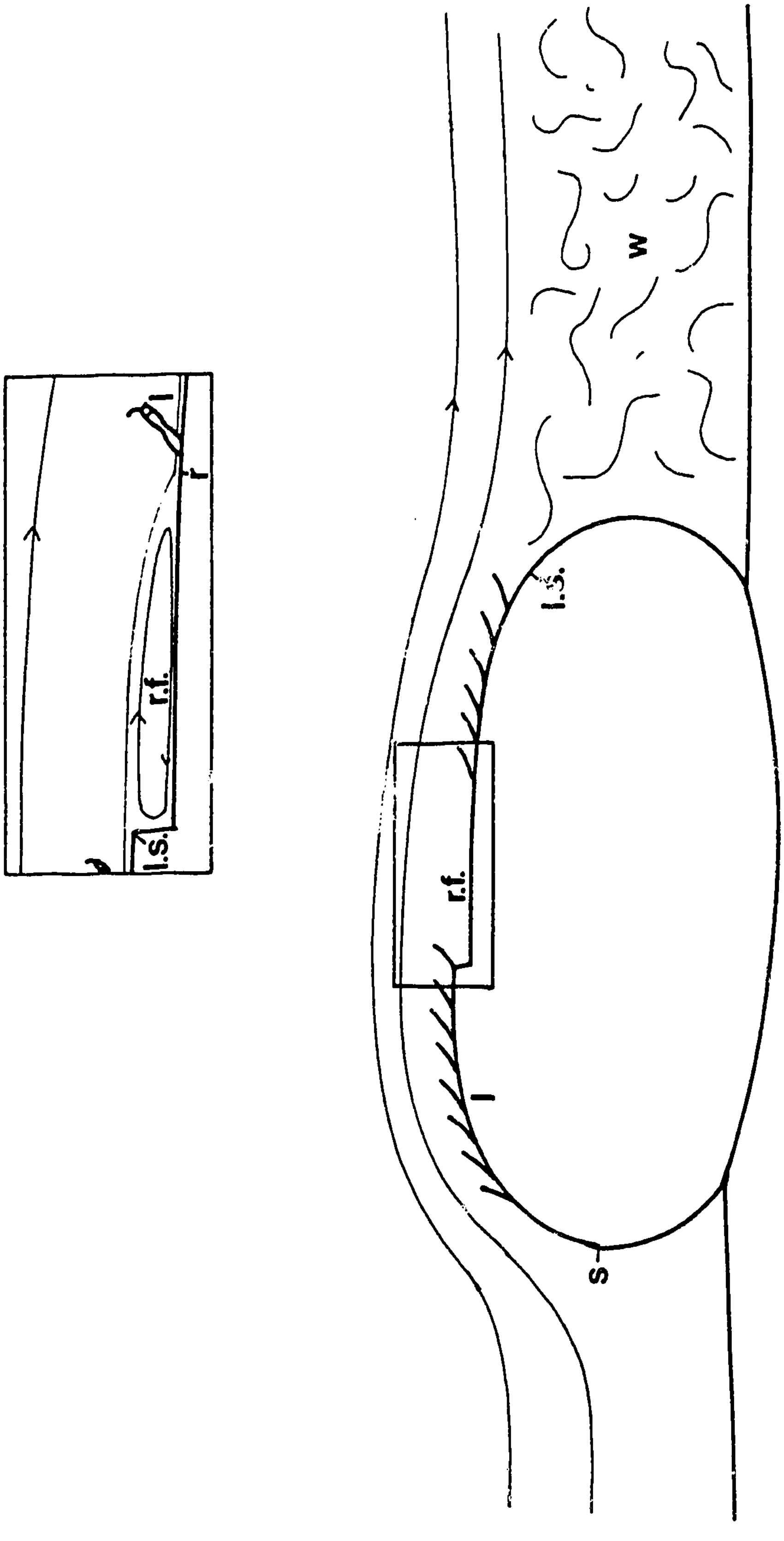

A
p
B
p
C
l.s.
p
s.n.
D
l.s.
p
s.n.
E
s.n.
l.s.
p
s.n.

Figure 3. The mean velocity of water flowing past microhabitats occupied by larvae of a species of black fly at a site. Each circle is a mean velocity for that species at one site. The large thin bars indicate the range, small thicker bars indicate standard error. Numbers indicate sample size. When no error bars are shown, water velocity past only one microhabitat was measured at that site.



WATER VELOCITY (cm·s⁻¹)
0
40
80
120
160
S. arcticum
S. canadense
S. decorum
S. hunteri
S. piperi
S. transiens
S. tuberosum
S. venustum / verecundum
S. virgatum
S. vittatum
C. dacotensis
P. onycodactylum
2
46
3
4
20
2
2
2
2
2
2
9
3
2
2
6
3
5
11
195
29
6
5
21
210
10
2
9
31
2

Figure 4. Schematic hypothetical cross section of a typical rock, completely submerged and occupied by black fly larvae (l). Two types of boundary layer separation are shown; 1) separation of the boundary layer caused by a small irregularity in the rock. The separated boundary layer flows over a region of recirculating flow (r. f.) and reattachs (r.) further downstream. 2) Separation of the boundary layer at the downstream end of a rock followed by wake (w) formation. Insert shows enlargement of area of recirculating flow. Note absence of larvae where the boundary layer has separated. s. - stagnation point.


l
r
r.f.
l.s.
w
l.s.
r.f.
l
s

4. HYDRODYNAMIC AND BIOTIC FACTORS AFFECTING DISPERSION PATTERNS OF LARVAE OF BLACK FLIES (DIPERA: SIMULIIDAE) IN THE FIELD

Introduction

The larvae of most species of black flies are filter feeders that live attached to the substratum of rivers and streams. The larvae distribute themselves over the substrata of such water courses in characteristic patterns. Different patterns are apparent depending on the scale at which the larvae are being observed. When observed on the scale of a riffle, larvae are commonly found in a contagious dispersion, with certain parts of a riffle colonized by discrete groups of larvae while ring areas are devoid of larvae (Hocking and Pickering 1954, Rühm 1970 (in 979)).

The larvae in a group can exhibit one of three dispersion patterns:

1) A spaced dispersion pattern, in which each larva has an area around itself devoid of other larvae (Eymann and Friend 1988). Spaced dispersion patterns have been studied statistically by Colbo (1979), who used the chi-squared statistic to analyze dispersion patterns of larvae of Prosimulium mixtum Syme and Davies, and by Hart (1987) who used the variance:mean ratio to analyze that of larvae of Simulium aureum [complex] Fries. In both cases, statistically significant uniform dispersion was found. A method of computer analysis of spaced dispersion patterns is described in Eymann et al. (1987).

2) A clumped dispersion pattern, where each larva touches each of its immediate neighbours (Eymann and Friend 1988, Wotton 1987).

3) A banded dispersion pattern, where the larvae arrange themselves in bands that are perpendicular to the mean direction of flow. Banded dispersion patterns have been exhibited in the laboratory by larvae of *Cnephia dacotensis* (Dyar and Shannon) (Brenner and Cupp 1980) and *C. ornithophilia* (Davies *et al.* 1962) (Colbo 1987).

Many papers, focused on other aspects of black fly larval biology, have mentioned dispersion patterns. A small number of papers dealt with the behaviours associated with dispersion patterns (Hart 1986, Eymann and Friend 1988, Hart 1987), and about the benefits a spaced dispersion pattern convey to larvae within a group exhibiting a spaced dispersion pattern (Ciborowski and Craig 1989). However, as far as I know none has examined and compared the dispersion patterns exhibited by larvae of several species under field conditions. In this chapter, I describe the dispersion patterns exhibited by larvae of 11 morphospecies of black flies under various flow conditions in field situations. I found that species of black flies could be assigned to groups depending on the dispersion patterns exhibited by their larvae. Consequently, I looked for other biological characteristics that species in each group had in common. One of these was body form, a variable that has been used in taxonomic works on larvae of black flies (e. g. Davies *et al.* 1962). I also considered life history characteristics reported in the literature in light of different dispersion patterns. The aim was to generate hypotheses about the ecological significance of the dispersion patterns observed.

Methods and Materials

Populations of larval black flies in 29 streams and rivers in Alberta and British Columbia, Canada were examined. This includes all of the sites reported in chapter 3 except site three (Sherbrooke Ck. BC). At each site, the dispersion patterns exhibited by groups of larvae were noted. Flow velocity and depth were measured, and separation and turbulence of the boundary layer was determined as in chapter 3. Larvae were collected into Carnoy's solution (3 ethyl alcohol: 1 acetic acid) and identified to morphological species using Currie (1986), and Hall (1974). The classification of Crosskey (1987) was followed. S. venustum [complex] Say and S. verecundum [complex] Lundström cannot be distinguished in the larval stage, except through examination of the polytene chromosomes; consequently they will be referred to as S. venustum/verecundum. If more than one type of dispersion pattern was seen in one stream reach, measurements of flow past at least seven groups exhibiting each of the dispersion patterns were made. Because these measurements were made on groups in the same reach, they allowed comparison of flow past groups of larvae exhibiting different dispersion patterns under conditions where temperature, water chemistry, quantity and quality of seston, and often species of larvae were constant. The 11 species investigated were divided into three categories based on the dispersion patterns they exhibitied.

To quantify the body forms of larvae, widths of abdominal segments four to nine, and total body lengths were measured with an eyepiece micrometer on a Wild M3 dissecting microscope at 6.4X or 16X magnification. The segment width:body length ratio was then calculated. This was repeated for 10 specimens of each morphospecies examined in the field. Specimens with pale, but fully developed gill histoblasts were used since such specimens represent final instar larvae. Mean segment width:body length ratios for each of the morphospecies were subjected to cluster analysis. It was predicted that the categories based on body form would be similar to the categories based on dispersion pattern.

For the purpose of cluster analysis, each segment was treated as a dimension. The euclidean distance metric was used. The clusters were joined using single and complete linkage methods. Because no one linkage method has been shown to be preferable to the others (Everitt 1980), two linkage methods were used, and those clusters that appeared in both methods were considered more likely to reflect real clusters in the data. This analysis was done on a Macintosh SE® computer using Systat® statistical software. The results of the cluster analysis were interpreted in light of dispersion patterns exhibited by each species and life history information available in the literature.

Results

Ten of the morphospecies of black flies studied could be assigned to one of three categories, based on the dispersion pattern exhibited by their larvae when found in groups consisting of a single species. A group of larvae was treated as a group consisting of a single species if one morphospecies made up >95% of the group, because it was considered unlikely that a species making up < 5% of a group could affect the group's dispersion pattern.

"Bander-clumpers", exhibited a banded dispersion pattern when found in lower velocity microhabitats, and a clumped dispersion pattern in higher velocity microhabitats (Table 1). This category includes the larvae of *S. decorum* Walker, and *C. dacotensis*. In a flume described by Lacoursière (1990), the dispersion pattern of a group of *C. dacotensis* larvae could be manipulated by changing the flow velocity. The larvae established a banded dispersion pattern at a mean (± S. E.) water velocity of 31± 4.8 cm/s (this experiment was repeated six times). When the water velocity was increased, the larvae reorganized themselves into clumps within 24 hours. This was done twice; in one instance the water velocity was increased from 28 cm/s to 45 cm/s, and in another, from 42 cm/s to 79 cm/s. Only freshly collected larvae of *C. dacotensis* consistently exhibited banded or clumped dispersion patterns in the laboratory. After two to three days in the flume, the larvae would exhibit only a spaced dispersion pattern. Groups consisting primarily of *C. dacotensis* were never seen in a spaced dispersion pattern in the field, despite extensive observations of this species during the course of this and related studies (chapter 5).

"Spacers" included those species with larvae that were found exhibiting only a spaced dispersion pattern (Table 2). These included *P. onycodactylum* [complex] Dyar and Shannon, *S. hunteri* Mallock, *S. piperi* Say, *S. transiens* Rubtsov, *S. tuberosum*, *S. venustum/verecundum*. Most groups consisting of a combination of two or more of these species also exhibited a spaced dispersion pattern (Table 3). Groups consisting of more than one species of spacers often included larvae of *S. vittatum* (Table 3). Groups of larvae exhibiting a spaced dispersion pattern were more commonly encountered than groups exhibiting any other dispersion pattern. Twenty-seven of the 29 sites investigated (93 %) had some spaced larvae, and 23 (79 %) had no groups of larvae that exhibited any other dispersion pattern.

"Spacer-clumpers" were larvae that exhibited a spaced dispersion pattern when found in microhabitats characterized by lower water velocities, and a clumped dispersion pattern in microhabitats characterized by higher water velocities (Table 4). These included larvae of *S. virgatum* [complex] Coquillett and *S. canadense* Hearle which were found in large numbers in habitats characterized by fast flowing water (Mohsen and Mulla 1982). A population consisting of *S. venustum/verecundum* and *S. vittatum*, with a mean of 70 % *S. vittatum*, also exhibited both spaced and clumped dispersion patterns (Table 4). In this instance, no relationship could be found between dispersion pattern and either the species ratio or any of the flow parameters measured. The dispersion patterns exhibited by these larvae were "untidy"; for example, small groups of clumped larvae could be found within a larger group of larvae exhibiting a spaced dispersion pattern.

Larvae of *S. vittatum* did not fit into any of the three categories described above because they exhibited all three dispersion patterns. They were found banded as first instar larvae in the laboratory, clumped near a lake outlet in Ontario (Eymann 1985), and spaced in the field both in groups consisting of a single species (Table 2) and in groups consisting of more than one species with spacers (Table 3).

The ratios of segment width:body length for larval abdominal segments four to nine are graphically represented in Figure 1. The larvae of the species represented could be divided into three categories: 1) Those in which abdominal segment seven was the thickest part of the abdomen, but not thick enough to result in a prominent bulge (Fig. 1a). This category included the larvae that exhibit banded or clumped dispersion patterns when found in groups consisting of a single species, plus the larvae of *S. vittatum*. 2) Those species in which abdominal segment seven was the thickest part of the abdomen, resulting in a prominent bulge (Fig. 1b), these included the spacers. 3) Larvae of *S. virgatum* and *S. canadense*, which had an abdomen that gradually thickened from segment four to eight (Fig. 1c). Larvae of these species exhibited spaced or clumped dispersion patterns when found in groups consisting of a single species.

Cluster analysis using euclidean distance and single linkage methods produced results that agree with the above interpretation, except that larvae of *S. transiens*, which were found in spaced dispersion patterns, separated into their own cluster (Fig. 2a). Examination of Figure 1b shows that each of the segments of *S. transiens* was thicker than the corresponding segment in the other spacers. Consequently this species may represent a fourth body form. When the complete linkage method was used, a similar interpretation resulted except that the larvae of *S. venustum/verecundum* and *S. tuberosum* split off from the other spacing species (Fig. 2b).

Discussion

The species with larvae exhibiting banded and clumped dispersion patterns, S. decorum, and C. dacotensis, tend to be associated with impoundment outlets (Table 5). Larvae of S. decorum are found almost exclusively on beaver dams and small man-made dams (Currie 1986). Larvae of C. dacotensis, although not as closely associated with impoundment outlets as S. decorum, were commonly found closer to impoundment outlets than larvae of spacing species of black flies (Davies et al. 1962, Wotton 1987). It has often been reported that the number and production of filter feeders, including larvae of black flies (Carlsson et al. 1977, Wotton 1987), filter-feeding larvae of caddisflies (Oswood 1978, Parker and Voshell 1983, Richardson 1984, Mackay and Waters 1986), was higher at an impoundment outlet than at other parts of a river or stream. This has commonly been attributed to the greater nutritional quality of seston at impoundment outlets. Parker and Voshell (1983) attributed the higher production of caddisfly larvae downstream of a lake in Virginia, USA to an increase in the amount of zooplankton in the seston at the lake outlet. Richardson (1984) showed that when Neureclepsis bimaculata (L.) were fed seston from the outlet of a lake in Alberta, Canada they grew faster than when they were fed seston from 17 km downstream of the lake outlet. He also showed that a small impoundment in a river resulted in a significant decrease in the amount of inorganic seston in the water. Therefore, larvae of black flies tending to be associated with impoundment outlets may benefit from the higher nutritional content of seston that is flowing out of such an impoundment.

The higher nutritional quality of seston at an impoundment outlet may reduce the benefit of feeding facilitation caused by a spaced dispersion pattern, because feeding facilitation was only apparent at low food levels (Ciborowski and Craig

1989).There is a cost to establishing a spaced dispersion pattern; the energy expended in behaviours such as probing and fencing that lead to the establishment of such a dispersion pattern (Eymann and Fiend 1988). Consequently, the costs of establishing a spaced dispersion pattern may not outweigh the benefits at a lake outlet.

Larvae of C. dacotensis exhibited clumped dispersion patterns when found in microhabitats where the average water velocity was 50-60 cm/s (Table 1). According to Kurtak (1978), C. dacotensis filter-feeds more efficiently at 50 cm/s than at 30 or 70 cm/s. It appears, therefore, that this species forms clumps at water velocities the same as or higher than those at which its filter feeding is most efficient. This suggests that these larvae establish clumped dispersion patterns in microhabitats where flow conditions are particularly well suited for them.

Larvae of C. dacotensis exhibited bands when found in microhabitats with lower water velocities (x=28-31 cm/s) (Table 1). Water accelerates as it flows over an obstacle like a band because of the principle of continuity (Vogel 1981). This increases the velocity of the water flowing through the fans (chapter 6). Because larvae of C. dacotensis appear to filter-feed more efficiently at 50 cm/s than at 30 cm/s (Kurtak 1978), this acceleration may increase the feeding efficiency of larvae of this species. The smaller bulge at segment seven of bander-clumpers (Fig. 1a) would enable more larvae of these species than spacers to pack into a known area, if the larvae were of the same length. This reduces the spaces between the larvae in bands, thereby increasing the acceleration needed for the water to flow over the bands.

Since larvae of S. vittatum exhibited all three dispersion patterns, it could not be placed into any of the categories based on dispersion pattern. They do, however, have a body form similar to that of bander-clumpers (Fig. 1a, 2a and b) and, like them, can be found near impoundment outlets (Currie 1986, Wotton 1987). Therefore, the larvae of S. vittatum were more like the bander-clumpers than any of the other categories of larvae. Members of the S. vittatum complex are widespread across North America (Currie 1986) and are capable of living in habitats not commonly colonized by other species (Burger 1987). This broad geographical distribution, and tolerance of marginal habitats may be related to its apparent lack of specialization in dispersion pattern.

Species with larvae found near impoundment outlets had either strictly autogenous adults as in C. dacotensis, or adults that were autogenous for the first gonotrophic cycle as in S. decorum and S. vittatum (Wotton 1987). This is consistent with the hypothesis that these larvae occur near impoundment outlets because such habitats provide a rich food source. This abundance of food allows the larvae to store enough nutrients that the adults can produce at least one batch of eggs without taking a blood meal (Anderson 1987).

Simulium noelleri Friedrichs, a European species related to S. decorum, is also a clumper (Wotton 1987) found near impoundment outlets (Burger 1987), and is also autogenous for its first gonotrophic cycle (Wotton 1987). Cnephia ornithophilia is a impoundment outlet species (Colbo 1979) with larvae that are known to form bands in the laboratory (Colbo 1987), and clumps in the field (Harding and Colbo 1981). However, its adults are anautogenous (Cupp and Gordon 1983).

The larvae of six of the species studied were found only in spaced dispersion patterns within groups consisting of a single species (Table 2). When found in groups consisting of more than one species, they also exhibited a spaced dispersion pattern (Table 3). Most spacers were found in reaches of streams or rivers not associated with outlets of impoundments (Table 5). One exception to this rule was S. piperi which, according to Currie (1987), was found at outlets to mountain beaver ponds. My observations confirm this; four of seven sites at which S. piperi was collected were outlets to small impoundments, such as beavers ponds (2 sites), artificial ponds (1 site), or pools created by roads (1 site).

Larvae exhibiting a spaced dispersion pattern, except S. piperi, lived away from impoundment outlets (Table 5) where the seston may have a lower nutritional content (Parker and Voshell 1983, Richardson 1984). Because feeding facilitation induced by a spaced dispersion pattern is apparent at low food levels (Ciborowski and Craig 1989), spacing will be more likely to benefit these larvae than those found near impoundment outlets. Because large parts of most rivers and streams did not constitute impoundment outlets, there was probably more substratum available for colonization by these species than is available for the bander-clumpers. Consequently, intraspecific competition for substratum may be lower, reducing the cost of establishing a spaced dispersion pattern.

When different linkage methods were used in the cluster analysis, the only species that did not cluster in the same way each time were the spacers (Figs. 2 a,b). This suggests that there was more variance in body form within this category than in the other two categories. It is possible that the larvae of some of these species may exhibit other dispersion patterns under conditions not observed during the course of this study. Clearly, this was the most heterogenous of the categories studied.

Cluster analysis showed the body form of S. transiens to differ from those of the other spacers. The body of this species was thickened at segment seven like the body of the other spacers, but for each segment, the segment width:body length ratio was larger (Fig. 1b). Larvae of S. transiens differ from those of other spacing species in that they were found commonly in medium to large sized rivers (Currie 1986), while the other spacers observed in this study were found commonly in smaller streams. Because only one group of S. transiens was found in this study, it is possible that this species may exhibit other dispersion patterns under different conditions.

Of the five morphospecies of black fly with spacing larvae and similar larval body form, four are known to have blood-feeding adults, and two to have obligate anautogenous adults (Table 5). This is consistent with the hypothesis that such larvae occurr in habitats where nutritional quality of the seston was lower, such that they are not able to store enough nutrients as larvae for the adults to produce eggs without a bloodmeal. Gordon and Cupp (1980) reported that cytotype ACgB of S. venustum is autogenous for the first gonotrophic cycle. However, this cytotype was probably not encountered in this study because it is not known from western Canada (Rothfels 1981).

S. canadense and S. virgatum have larvae that exhibit spaced or clumped dispersion patterns (Table 4). Although these species have been assigned to different subgenera (Crosskey 1987), they have been shown to be closely related to each other based on cytological evidence (Rothfels 1979). They are specialized for fast water habitats such as rapids and waterfalls (Mohsen and Mulla 1982). The benefits of specialization for life in fast water habitats are not as clear as those of specialization for impoundment outlets. It may be a way of avoiding competition from larvae of other species of black flies not living in fast water. Alternatively, fast water may sweep away predators that would be able to persist in slower water. Another species that may belong to this group according to cytological evidence is S. longistylatum Shewell (Rothfels 1979). Larvae of this species are also found near water falls (Cupp and Gordon 1983) and occurs on rocks in such high densities that they give the rocks a "moss-like appearance" (Davies et al. 1962).

Larvae of S. canadense and S. virgatum may form clumps in microhabitats characterized by higher water velocities to raise the boundary layer. The heads of larvae in a clump act like a new surface, above the surface of the substratum. The boundary layer will be attached to this new surface, rather than to that of the substratum. Consequently, the boundary layer will be higher above the substratum than it would be if the clump were not there. The fans of larvae in clumps may, therefore, be inside the boundary layer where flow is slower than in the mainstream. The bodies of larvae in clumps will certainly be protected from the full force of the flow. While the resulting reduction in drag is not likely to be important (Eymann 1988), protection from buffeting may be.

Body form of spacer-clumpers differs from that of the other species examined in this study, in that segment eight rather than seven is the thickest part of the abdomen (Fig. 1c). This adaptation has been noted by other authors (Burger 1987). They also form a cluster separate from the other species that is not affected by the linkage method used (Fig 2 a, b). This body form may adapt them for for forming clumps; swelling on the ventral surface of the abdomen, anterior to the posterior proleg, may make the upright posture, characteristic of larvae in clumps, easier to achieve.

The larvae of S. exasperans Craig and S. tahitiense Craig, two species of Tahitian black flies, have a body form similar to that of the spacer-clumpers (S. canadense and S. virgatum). Larvae of both these species were found in clumps in larger rivers; often in the same group (Craig pers. comm.). The larvae of two other species of Tahitian black flies, S. malardei Craig and S. lotii Craig, were not found in clumps and had a body form more typical of spacers. Craig (1987) also described a fifth body form, characteristic of the oviceps (Edwards) species group which appeared to be specialized for thin, high velocity sheets of water undergoing laminar flow. Figure 3 illustrates the relationships I postulate among factors acting on the dispersion patterns exhibited by groups of larval black flies. Arrows indicate the direction of the putative cause and effect relationship between two factors; a broken line, a weak relationship, and a question mark, an uncertain relationship. Starting at the top of the figure, the oviposition behaviour of the female determines the habitat occupied by the larvae. For example, larvae can occupy an impoundment outlet only if the eggs from which they hatched were deposited near an outlet. Habitat occupation affects microhabitat occupation, but only to the extent that a larva cannot occupy a microhabitat that is not present in its habitat. The microhabitat occupied by a larva is probably the most important factor in determining the nature of flow past the larva (chapter 3). Conversely, the nature of flow may determine whether a larva will stay where it is (Lacoursière 1989). The nature of flow past a group of larvae affects their dispersion pattern in at least some species of black flies. The nutritional quality of the seston ingested by a larva may be at least partly determined by the distance of that larva from an impoundment outlet (Parker and Voshell 1983, Richardson 1984). This distance is determined by both the oviposition behaviour of the female and the habitat occupation behaviour of the larvae. The nutritional quality of the seston appears to affect the dispersion pattern of the larvae, because larvae of species living near impoundment outlets exhibit different dispersion patterns than those of species not specialized in this way. The species of the black fly affects its oviposition behaviour, (Golini and Davies 1987), habitat colonization, and dispersion pattern, and to a lesser extent, its microhabitat colonization.

The dispersion pattern exhibited by a group of larvae is determined by a complex interaction of a number of factors, the most important of which are the species composition of the group, and the velocity of water flowing past the group, and possibly the nutritional quality of the seston in the water.

References

Anderson, J. R. 1987. Reproductive strategies and gonotrophic cycles of black flies. In Black flies: Ecology, Population Management, and Annotated World List. Edited by K. C. Kim and R. W. Merritt. The Pennsylvania State University. University Park, PA.

Brenner, R. J., and E. W. Cupp. 1980. Rearing black flies (Diptera: Simuliidae) in a closed system of water circulation. Tropenmed. Parasit. **31**: 247-258.

Burger, J. F. 1987. Specialized habitat selection by black flies. In Black flies: Ecology, Population Management, and Annotated World List. The Pennsylvania State University. Edited by K. C. Kim and R. W. Merritt. University Park, PA.

Carlsson, M., L. M. Nilsson, Bj. Svensson, S. Ulfstrand, and R. S. Wotton. 1977. Lacustrine seston and other factors influencing the blackflies (Diptera: Simuliidae) inhabiting lake outlets in Swedish Lapland. Oikos, **29**: 229-238.

Ciborowski, J. J. H., and D. A. Craig. 1989. Factors influencing dispersion of larval black flies (Diptera: Simuliidae): effects of current velocity and food concentration. Can. J. Fish. Aquat. Sci. **46**: 1329-1341.

Colbo, M. H. 1979. Distribution of winter-developing Simuliidae (Diptera), in eastern Newfoundland. Can. J. Zool. **57**: 2143-2152.

Colbo, M. H. 1987. Problems in estimating black fly populations in their aquatic stages. In Black flies: Ecology, Population Management, and Annotated World List. Edited by K. C. Kim and R. W. Merritt. The Pennsylvania State University. University Park, PA.

Craig, D. A. 1987. A taxonomic account of the black flies (Diptera: Simuliidae) of the Society Islands - Tahiti, Moorea and Raiatea. Quaest. Entomol. **23**: 372-429.

Crosskey, R. W. 1987. An annotated checklist of the world black flies (Diptera: Simuliidae). In: Black flies: Ecology, Population Management, and Annotated World List. Edited by K. C. Kim and R. W. Merritt. The Pennsylvania State University. University Park, PA.

Cupp, E. W., and A. E. Gordon. 1983. Notes on the systematics, distribution, and bionomics of black flies (Diptera: Simuliidae) in the northeastern United States. Search: Agriculture, **25**.

Currie, D. C. 1986. An annotated list of and keys to the immature black flies of Alberta (Diptera: Simuliidae). Mem. entomol. Soc. Can. **134**.

Davies, D. M., B. V. Peterson, and D. M. Wood. 1962. The black flies (Diptera: Simuliidae) of Ontario. Part I. Adult identification and distribution with descriptions of six new species. Proc. Entomol. Soc. Ont. **92**: 70-154.

Everitt, B. 1980. Cluster Analysis (2nd. ed.). Halsted press (Division of John Wiley and Sons). N. Y.

Eymann, M. 1985. The behaviours of the blackfly larvae Simulium vittatum and S. decorum (Diptera:Simuliidae) associated with establishing and maintaining dispersion patterns on natural and artificial substrate. M. Sc. thesis, University of Toronto, Toronto.

Eymann, M. 1988. Drag on single larvae of the black fly Simulium vittatum (Diptera: Simuliidae) in a thin, growing boundary layer. J. N. Am. Benthol. Soc. 7: 109-116.

Eymann, M., and W. G. Friend. 1988. Behaviors of larvae of the black flies Simulium vittatum and S. decorum (Diptera: Simuliidae) associated with establishing and maintaining dispersion patterns on natural and artificial substrates. J. Insect Behavior, **1**: 169-186.

Eymann, M., J. M. Schmidt, and W. G. Friend. 1987. Computer analysis of polarized spacing patterns with special reference to the larvae of the black fly, Simulium vittatum. Can. J. Zool. **65**: 602-604.

Golini, V. I., and D. M. Davies. 1987. Oviposition of black flies. In Black flies: Ecology, Population Management, and Annotated World List. Edited by K. C. Kim and R. W. Merritt. The Pennsylvania State University. University Park, PA.

Gordon, A. E., and E. W. Cupp. 1980. The limnological factors associated with cytotypes of the Simulium (Simulium) venustum/verecundum complex (Diptera: Simuliidae) in New York state. Can. J. Zool. **58**: 973-981.

Hall, F. 1972. Observations on black flies of the genus Simulium in Los Angeles County, California. Vector News, **19**: 53-58.

Hall, F. 1974. A key to the Simulium larvae of southern California (Diptera: Simuliidae). California. Vector News, **21**: 65-71.

Harding, J., and M. H. Colbo. 1981. Competition for attachment sites between larvae of Simuliidae (Diptera). Can. Entomol. **113**: 761-763.

Hart, D. D., 1979. Patchiness and ecological organization: experimental studies within stream benthic communities. Ph. D. thesis, University of California, Davis.

Hart, D. D. 1986. The adaptive significance of territoriality in filter-feeding larval blackflies (Diptera: Simuliidae). Oikos, **46**: 88-92.

Hart, D. D. 1987. Processes and patterns of competition in larval black flies. In Black flies: Ecology, Population Management, and Annotated World List. Edited by K. C. Kim and R. W. Merritt. The Pennsylvania State University. University Park, PA.

Hearle, E. 1929. A remarkable Simuliid pupa Notes on Simulium virgatum in British Columbia. Proc. B. C. Entomol. Soc. **26**: 48-54.

Hocking, B., and L. R. Pickering. 1954. Observations on the bionomics of some northern species of Simuliidae (Diptera). Can. J. Zool. **32**: 99-119.

Kurtak, D. C. 1978. Efficiency of filter-feeding of black fly larvae (Diptera: Simuliidae). Can. J. Zool. **56**: 1608-1623.

Lacoursière, J. O. 1989. Suspension-feeding behaviour of black fly larvae (Diptera: Simuliidae) : Hydrological perspectives. Ph. D. thesis, University of Alberta, Edmonton.

Lacoursière, J. O. 1990. A small flume for study of the influence of hydrodynamical factors in benthic invertebrate behaviour. J. N. Am. Benthol. Soc. **9**: in press.

Mackay, R. J., and T. F. Waters. 1986. Effects of small impoundments on Hydopsychid caddisfly production in Valley Creek, Minnesota. Ecology, **67**: 1680-1686.

Mohsen, Z. H., and M. S. Mulla. 1982. The ecology of black flies (Diptera: Simuliidae) in some southern California streams. J. Med. Entomol. **19**: 72-85.

Muhammad, L. A. 1987. A cytological description of Simulium virgatum Coquillett and related species. M. Sc. thesis, Sul Ross State University, Alpine.

Oswood, M. V. 1978. Abundance patterns of filter-feeding caddisflies (Trichoptera:Hydropsychidae) and seston in a Montana (U.S.A.) lake outlet. Hydrobiol. **63**: 177-183.

Parker, C. R., and J. R. Voshell. 1983. Production of filter-feeding Trichoptera in an impounded and a free-flowing river. Can. J. Zool. **61**: 70-87.

Richardson, J. S. 1984. Effects of seston quality on the growth of a lake-outlet filter feeder. Oikos, **43**: 386-390.

Rothfels, K. 1979. Cytotaxonomy of black flies (Simuliidae). Ann. Rev. Entomol. **24**: 507-539.

Rothfels, K. 1981. Cytotaxonomy: principles and their application to some northern species-complexes in *Simulium*. *In* Blackflies: The Future for Biological Methods in Integrated Control. *Edited by* M. Laird. Academic Press. Toronto.

Rühm, W., 1970. Zur dipersion der larvenstadien und des puppentadiums von *Boophthora erythrocephala* de Geer (Simuliidae). Z. Angew. Entomol. **6**: 311-321.

Vogel, S. 1981. Life in Moving Fluids: The Physical Biology of Flow. Princeton University Press. Princeton, NJ.

Wotton, R. S. 1987. The ecology of lake-outlet black flies. *In* Black flies: Ecology, Population Management, and Annotated World List. *Edited by* K. C. Kim and R. W. Merritt. The Pennsylvania State University. University Park, PA.

Table 1. Water velocity (cm/s) (x±S.E.(n)) past groups of larvae of black flies that exhibited banded and clumped dispersion patterns.

	Species		
	C. dacotensis (1987)	*C. dacotensis* (1988)	*S. decorum*
Banded	28.4±2.2 $(18)_{a,I}$	30.9±1.8 $(11)_{a,I}$	35.0±2.1 $(11)_{a,I}$
Clumped	60.8±4.2 $(12)_{ab,II}$	50.7±2.5 $(7)_{a,II}$	73.3±5.8 $(12)_{b,II}$

Different Roman numerals denote significant differences in columns (∞=0.05).

Different letters denote significant differences in rows (∞=0.05).

Table 2. Water velocities past groups of larvae of black flies exhibiting a spaced dispersion pattern, and consisting of a single species.

Species	Velocity (cm/s) (x±S. E. (n))
P. onycodactylum	40-80 (2)
S. hunteri	30-90 (2)
S. piperi	43.8±13.4 (4)
S. transiens	23 (1)
S. tuberosum	86.0±11.0 (10)
S. venustum/ verecundum	54.5±5.4 (23)
S. vittatum	80 (1)

Table 3. Water velocity past groups of larvae of black flies exhibiting spaced dispersion pattern, and consisting of more than one species.

Species in group	Velocity (cm/s) (x±S. E. (n))
S. piperi S. tuberosum	67.0±4.4(5)
S. piperi S. hunteri	35(1)
S. venustum/verecundum S. vittatum	15(1)
S. venustum/verecundum S. decorum S. vittatum	85(1)
S. venustum/verecundum S. vittatum S. tuberosum S. piperi	72.2±6.7(9)
S. venustum/verecundum S. decorum	30(1)
S. venustum/verecundum S. tuberosum	67.1±8.2(7)

Table 4. Water velocity (cm/s) (x±S.E.(n)) past groups of larvae of black flies that exhibited spaced and clumped dispersion patterns.

	Species		
	S. canadense	*S. virgatum*	*S. venustum/verecundum* and *S. vittatum*
Spaced	57.0±3.5 $(22)_{b,I}$	95.8±7.6 $(12)_{c,I}$	38.3±4.2 $(20)_{a,I}$
Clumped	96.5±5.5 $(24)_{b,II}$	152.8±2.7 $(9)_{c,II}$	41.7±3.1 $(20)_{a,I}$

Different Roman numerals denote significant differences in columns (∞=0.05).

Different letters denote significant differences in rows (∞=0.05).

Table 5. Dispersion patterns and body forms of larvae of black flies compared to life history parameters reported in the literature.

Species	Dispersion pattern	Body form	Habitat	Autogeny	Number of cytotypes
S. vittatum	banded/ clumped/ spaced	type1	lake outlet (C,W)	autogenous 1st gonotropic cycle (W)	2(C)
S. decorum	banded/ clumped	"	beaver pond, lake outlet (W,C)	" (W)	3(C)
C. dacotensis	"	"	lake outlet, (D) rich streams (C)	autogenous (W)	---
S. tuberosum	spaced	type 2	small streams, medium R. (C)	anautogenous (C&G)	9 holarctic (C)
S. piperi	"	"	small montane streams, beaver pond outlet (C)	---	---
S. venustum/ verecundum	"	"	small streams, medium R. (C)*	anautogenous (C&G)	14(C)
S. hunteri	"	"	small, medium streams (C)	(blood feed) (C)	---
P. onycodactylum	"	"	small stream, small rivers (C)	(may be ornithophilic) (C)	11(C)
S. transiens	"	type 3	medium, large R. (C)	(man biter in USSR)	---
S. virgatum	spaced/ clumped	type 4	waterfalls, rapids (M&M)	(will bite horse)(H_1)	7(M)
S. canadense	"	"	"	(may bite horse)(H_2)	---

**S. venustum* (ACgB) found at lake outlets (Burger 1987).

(C) Currie 1986, (C&G) Cupp and Gordon 1984, (D) Davies 1962, (H_1) Hall 1972, (H_2) Hearle 1929, (M&M) Mohsen and Mulla 1982, (M) Muhamad 1987, (W) Wotton 1987.

Figure 1. Diagrammatic representation of the body forms of larval black flies. Each species is represented by an average of 10 larvae with pale but fully developed gill histoblasts. The height of each symbol represents the ratio of segment width:body length for each segment from four to nine. Segment nine was measured at the posterior proleg. a) Larvae exhibiting a banded dispersion pattern at lower water velocity microhabitats, and a clumped dispersion pattern at higher water velocity microhabitats plus larvae of S. vittatum, illustrating type 1 body forms. b) Larvae exhibiting a spaced dispersion pattern, illustrating types 2 and 3 body forms. c) Larvae exhibiting a spaced dispersion pattern at lower water velocity microhabitats, and a clumped dispersion patterns at higher water velocity microhabitats, illustrating type 4 body forms.

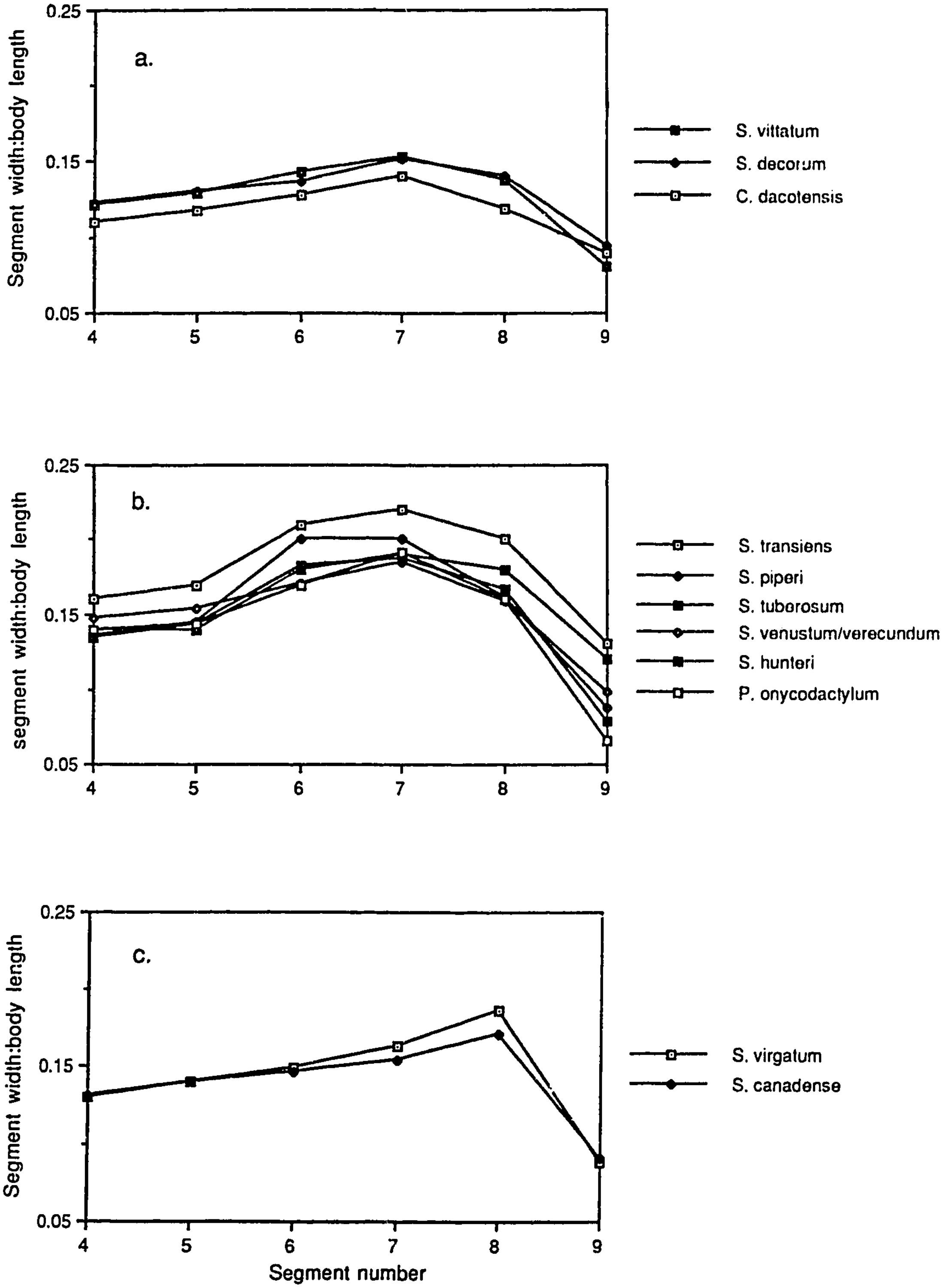
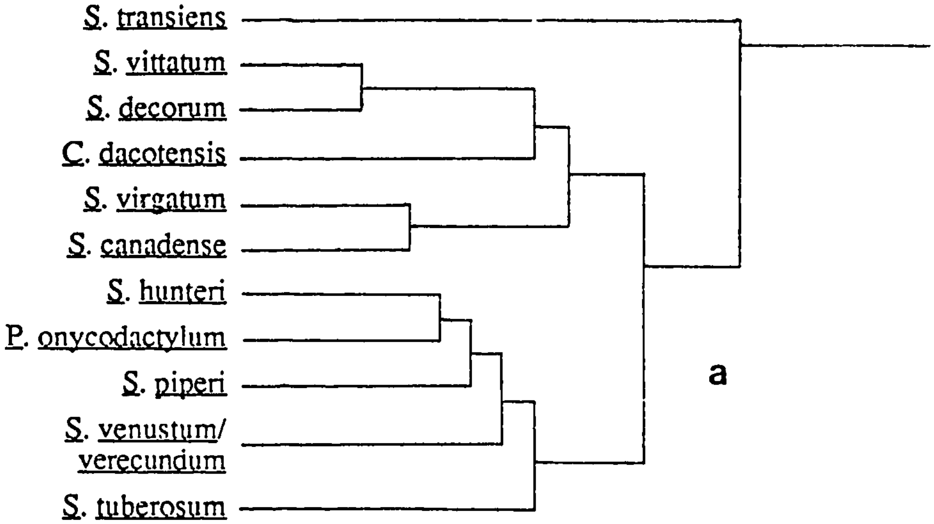
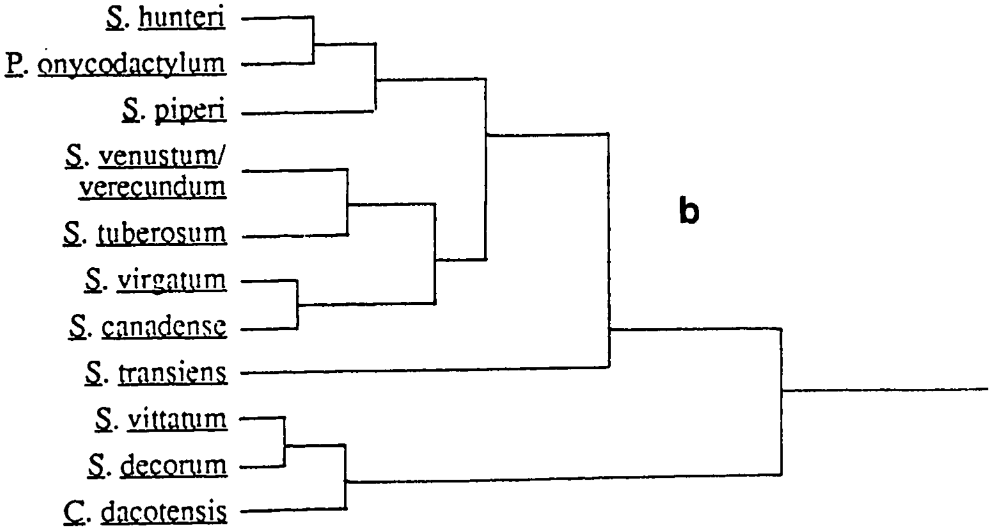
a.
0.25
0.15
0.05
Segment width:body length
4
5
6
7
8
9
S. vittatum
S. decorum
C. dacotensis
b.
0.25
0.15
0.05
segment width:body length
4
5
6
7
8
9
S. transiens
S. piperi
S. tuberosum
S. venustum/verecundum
S. hunteri
P. onycodactylum
c.
0.25
0.15
0.05
Segment width:body length
4
5
6
7
8
9
Segment number
S. virgatum
S. canadense

Figure 2. The results of cluster analysis on the body forms of larvae of black flies, using the Euclidian distance metric. The segments were used as the dimensions. a) Single linkage (nearest neighbour) method. b) Complete linkage (farthest neighbour) method.



S. transiens
S. vittatum
S. decorum
C. dacotensis
S. virgatum
S. canadense
S. hunteri
P. onycodactylum
S. piperi
S. venustum/ verecundum
S. tuberosum

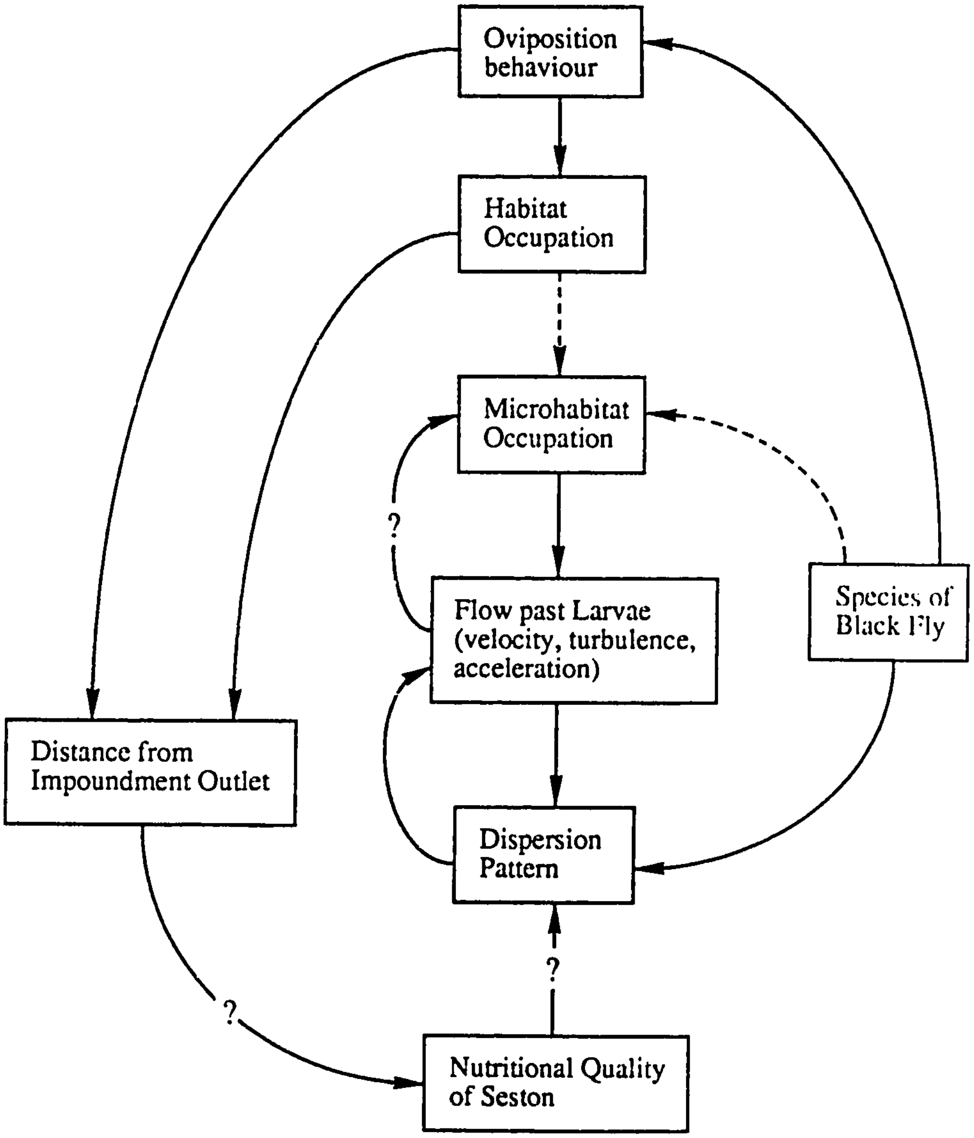
a



S. hunteri
P. onycodactylum
S. piperi
S. venustum/ verecundum
S. tuberosum
S. virgatum
S. canadense
S. transiens
S. vittatum
S. decorum
C. dacotensis

b

Figure 3. Flow chart showing relationships among the factors affecting dispersion pattern of a group of larval black flies. Arrows indicate direction of the putative cause and affect relationship, broken lines, a weak relationship, and question marks, a hypothetical relationship.


Oviposition behaviour
Habitat Occupation
Microhabitat Occupation
?
Flow past Larvae (velocity, turbulence, acceleration)
Species of Black Fly
Distance from Impoundment Outlet
Dispersion Pattern
?
?
Nutritional Quality of Seston

5. DISPERSION PATTERNS EXHIBITED BY LARVAE OF THE BLACK FLIES CNEPHIA DACOTENSIS AND SIMULIUM ROSTRATUM (DIPTERA: SIMULIIDAE)

Introduction

Larvae of most species of black flies are found attached to the substratum of rivers and streams, where they filter suspended food with their labral fans. They commonly occur in well defined groups, which appear to be constrained by the flow properties of the microhabitat (chapter 3). Within these groups, larvae arrange themselves into one of three dispersion patterns: 1) spaced, where each larva keeps an area around itself free of other larvae (Hart, 1986; Eymann and Friend, 1988); 2) clumped, where each larva is touching each of its immediate neighbours (Colbo and Moorhouse, 1979; Eymann and Friend, 1988); and 3) banded, where larvae form bands perpendicular to the mean direction of flow. Banded dispersion patterns in laboratory flumes are described by Brenner and Cupp (1980) and by Colbo (1987). The dispersion pattern exhibited by a group of larvae consisting of a single species is affected by species and by velocity of water flowing past the group (chapter 4). It is not known how two species exhibiting different dispersion patterns interact if present in the same stream reach.

In the field, groups of larvae of the Simulium rostratum (Lundström) exhibit spaced dispersion patterns (chapter 4). While those of Cnephia dacotensis (Dyar and Shannon) commonly exhibit a banded dispersion pattern at lower velocities and a clumped dispersion pattern at higher velocities (chapter 4). Larvae of C. dacotensis are not known to exhibit a spaced dispersion pattern.

In this chapter, the dispersion patterns exhibited by a population consisting of S. rostratum, a member of the S. venustum/verecundum species group and C. dacotensis are described. The banded dispersion pattern of C. dacotensis is described.

Material and Methods

This work was carried out in Norris Creek, a second order stream flowing through farmland approximately 50 km east of Edmonton, Alberta, Canada.

Bands of C. dacotensis larvae were studied during May, 1987. To test the hypothesis that the location of bands reflects some underlying property of the substratum, the following experiment was performed: Twelve 15x20 cm plexiglass plates were placed on the stream bottom with the downstream end of the plate lower than the upstream end so that the upper face was at a 10-20° angle to the mean direction of flow. The plates had a 2x2 cm grid drawn on them with a waterproof felt pen. Before they were placed in the stream, the plates were each attached to a rock with silicone sealant, to anchor them to the stream bottom.

Three days later, when bands of larvae of C. dacotensis had established themselves on the plates, their positions were recorded on a diagram. Seven plates were not colonized because they became entangled in mats of filamentous algae. From four of the remaining five plates one half, to one and one half bands were removed, while one plate was left undisturbed. The positions of the bands were recorded the following day. As a control, bands were left undisturbed and their positions again recorded the following day. Positions of bands of larvae on four rocks were monitored over a two day period. If bands on plates or rocks changed position from day to day, the hypothesis that the location of bands reflects some underlying property of the substratum is falsified. Approximately 5 hours were spent directly observing larval behaviour in and between bands.

A population of black fly larvae consisting of a mixture of C. dacotensis and S. rostratum was found in Norris Creek, on 13 May, 1988. Most larvae occurred on rounded, well eroded rocks. These larvae were either spaced or clumped, but none showed a banded dispersion pattern. Ten groups of larvae exhibiting a spaced dispersion pattern and 10 exhibiting a clumped dispersion pattern were selected for further investigation. Water velocity was measured 1 to 2 cm above each group of larvae using a electromagnetic flow meter (Model PVM-2, Montodoro Whitney Inc.). A sample of larvae from each group was fixed in Carnoy's solution (3 ethanol:1 acetic acid), for cytological determination. If a group of larvae was small (<100 individuals), the entire group was collected; if larger, approximately 100 larvae from one part of the group were collected. This method of collection assumed that larvae of the two species of black flies were evenly distributed within the group. Larvae were taken to the laboratory, identified to morphospecies (Currie 1986) and counted, and larvae of S. rostratum were identified to cytospecies.

T-tests were used to test for difference in mean water velocities and mean percent C. dacotensis in the groups. Percentages were arcsine, square-root transformed before being subjected to the t-test.

Results

An example of a plexiglass plate from which larvae of C. dacotensis had been removed is shown in Figure 1. One and one half bands, indicated by brackets (Fig. 1a), were removed on day one. On day two (Fig. 1b), the part of the plate that was cleared of larvae had been recolonized and the position of all bands had changed. This is similar to results obtained on the other three plates from which bands were removed. Figure 2 shows the plate from which no larvae were removed. The position of bands changed from day one (Fig. 2a) to day two (Fig. 2b). On day three, the arrangement of the bands on the five plates was again different. Two of the plates had almost no larvae left on them because they were in the wake of a log that had settled upstream.

The arrangement of bands (B) on rocks that were part of the stream bottom also changed over a 24 hour period as the example in Figure 3 shows. The bands on the rock in Figure 3a were arranged in an arch around the stagnation point (SP). Injection of dye into the flow showed that the water flowed over the rock, away from the stagnation point, in a fan-like manner (arrows). The arcs were so arranged that a tangent to the arc at any point was perpendicular to the mean direction of flow at that point. Figure 3b shows the same rock 24 hours later. Part of the rock was exposed (E) because of a drop in the water level. In Figure 3a and 3b the larvae at either side exhibited a clumped dispersion pattern (C).

Observations of larvae of C. dacotensis in undisturbed groups consisting of a single species showed that most larvae were either in bands or in clumps. The bands were two to three larvae thick and up to 30 cm long. The mean and standard error of distance between bands was 1.9±0.16 cm (n=18). Those larvae that were between bands were almost always probing or looping (sensu Eymann and Friend, 1988). Of eight looping larvae watched until they stopped, seven stopped when they encountered a band. The other larva stopped looping and started to filter-feed when it had looped onto the top of a small clump of filamentous algae that was higher than the surrounding substratum. The larvae in bands were perpendicular to the substratum, except when the water flowing over them was so shallow that a perpendicular posture was impossible to achieve.

Cytological examination of larvae belonging to the *S. venustum/verecundum* species group indicated that they were *S. rostratum* (=*S. verecundum* ACD)(P. H. Adler pers. commun.). When larval *C. dacotensis* were found together with those of *S. rostratum*, the banded dispersion pattern was no longer apparent; instead, spaced and clumped dispersion patterns were observed. Figure 4 shows the relationships among velocity, percent *C. dacotensis* and dispersion pattern for the groups of larvae investigated. Groups of larvae exhibiting a spaced dispersion pattern (circles) were found at significantly lower velocities (x±S.E.=46.5±4.6 cm s^{-1} (n=10)) than groups of larvae exhibiting clumped dispersion pattern (triangles) (78.5±5.2 cm s^{-1} (n=10)) ($p<0.01$). The percent *C. dacotensis* in groups of larvae exhibiting a spaced dispersion pattern was significantly lower (x=14.9% x±S.E.=(11.9, 18.1)) than in groups of larvae exhibiting a clumped dispersion pattern (x=80.5% x±S.E.=(72.3, 87.6)) ($p<0.001$).

Discussion

Bands of larvae of C. dacotensis on both natural and artificial substrata exhibit considerable mobility, changing position from one day to the next (Figs. 1-3).The mobility of bands shows that their arrangement is not a direct result of the shape of the underlying substratum. Colbo (1979) reported a similar mobility of groups of larvae of Prosimulium mixtum Syme and Davies [complex] and Stegopterna mutata (Malloch) [complex] exhibiting spaced dispersion patterns. He showed that these larvae shifted position over several days, presumably in response to changes in flow patterns.

C. dacotensis was the first species of larval black fly to appear in Norris Creek in the spring of 1988 (personal observation). They were present in large numbers, over most of the available substratum in bands or clumps. Larvae of S. rostratum later appeared in this already densely-populated stream.

The dispersion patterns exhibited by groups consisting of both C. dacotensis and S. rostratum varied both with water velocity and with proportion of C. dacotensis (Fig. 4). Consequently, it is not possible to determine which of these factors resulted in the observed dispersion patterns from the data presented here. However, Eymann (Chapter 4) has reported that groups of larvae of only C. dacotensis have never been observed in a spaced dispersion pattern. Groups of larvae of only S. venustum/verecundum, the species complex to which S. rostratum belongs, were found in a spaced dispersion pattern (chapter 4). In this study, groups consisting of both S. rostratum and C. dacotensis exhibited a dispersion pattern characteristic of either one or the other of the species in the group. Therefore, presence of another species apparently induces dispersion patterns that each species does not exhibit by itself. This relationship between species composition of a group and dispersion pattern appears to be affected by water velocity.

Groups of black fly larvae consisting of both species and exhibiting a spaced dispersion pattern consisted of >50% *S. rostratum* in all but one case (Fig. 4). This suggests that the spacing larvae, *S. rostratum* prevented the non-spacing *C. dacotensis* from forming bands or clumps. Larvae of *S. vittatum* establish spaced dispersion patterns by preventing neighbouring larvae from making a silk pad near them (Eymann and Friend 1988). A similar behaviour by *S. rostratum* probably prevented *C. dacotensis* from banding or clumping.

Groups of larvae consisting of both species and exhibiting a clumped dispersion pattern consisted of >50% *C. dacotensis* (Fig. 4). Presumably, because of their low numbers, larvae of *S. rostratum* were not able to prevent larvae of *C. dacotensis* from making a silk pad near them. The larvae of *S. rostratum* may have then habituated to being in a clump of *C. dacotensis* larvae.

Harding and Colbo (1981) investigated interactions between a banding-clumping species *C. ornithophilia* Davies et al., and a spacing species *P. mixtum*. They reported that the banding-clumping species tended to displace the spacing species. No direct evidence of displacement of larvae of one species by larvae of another was observed in the present study.

The present data show that the positions of bands of larvae of *C. dacotensis* on the substratum can change from day to day. In a population consisting of both bander-clumpers (*C. dacotensis*) and spacers (*S. rostratum*), the dispersion pattern exhibited by a group is apparently the dispersion pattern of the most common species in the group.

References

Brenner, R. J., and E. W. Cupp. 1980: Rearing black flies (Diptera: Simuliidae) in a closed system of water circulation. - Tropenmed. Parasit. 31: 247-258.

Colbo, M. H. 1979: Distribution of winter-developing Simuliidae (Diptera), in Eastern Newfoundland. - Can. J. Zool. 57: 2143-2152.

Colbo, M. H. 1987: Problems in estimating black fly populations in their aquatic stages. Pages 77-89. in K. C. Kim and R. W. Merritt (eds.). Black flies: Ecology, Population Management and Annotated World List. - Pennsylvania State University. University Park.

Colbo, M. H., and D. E. Moorhouse. 1979: The ecology of pre-imaginal Simuliidae (Diptera) in South-east Queensland, Australia. Hydrobiol. - 63: 63-79.

Currie, D. C. 1986: An annotated list of and keys to the immature black flies of Alberta (Diptera:Simuliidae). - Mem. Entomol. Soc. Can. 134.

Eymann, M., and W. G. Friend. 1988: Behaviors of larvae of the black flies Simulium vittatum and S. decorum (Diptera: Simuliidae) associated with establishing and maintaining dispersion patterns on natural and artificial substrates. - J. Insect Behavior. 1: 169-186.

Harding, J., and M. H. Colbo. 1981: Competition for attachment sites between larvae of Simuliidae (Diptera). - Can. Entomol. 113:761-763

Hart, D. D. 1986: The adaptive significance of territoriality in filter-feeding larval blackflies (Diptera: Simuliidae). - Oikos. 46: 88-92.

Figure 1. Schematic representation of a group of larvae of C. dacotensis exhibiting a banded dispersion pattern on the downstream portion of a 15x20 cm plexiglass plate. (a) Larvae indicated by brackets were removed; (b) same plate 24 hours later. Water velocity was 25 cm s^{-1}. Arrow indicates direction of flow.

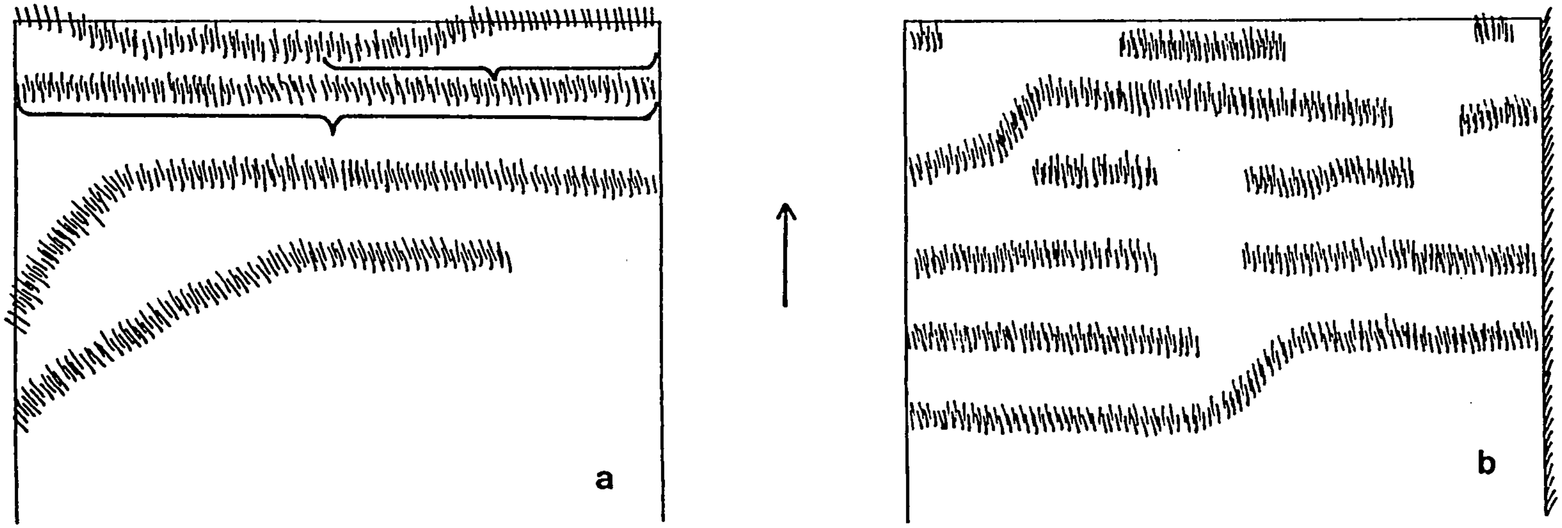

a
b

Figure 2. A group of larvae of C. dacotensis exhibiting a banded dispersion pattern on the downstream portion of a 15x20 cm plexiglass plate. (a) No larvae removed; (b) same plate 24 hours later. Water velocity was 12 cm s^{-1} on day one and 22 cm s^{-1} on day two. Arrow indicates direction of flow.

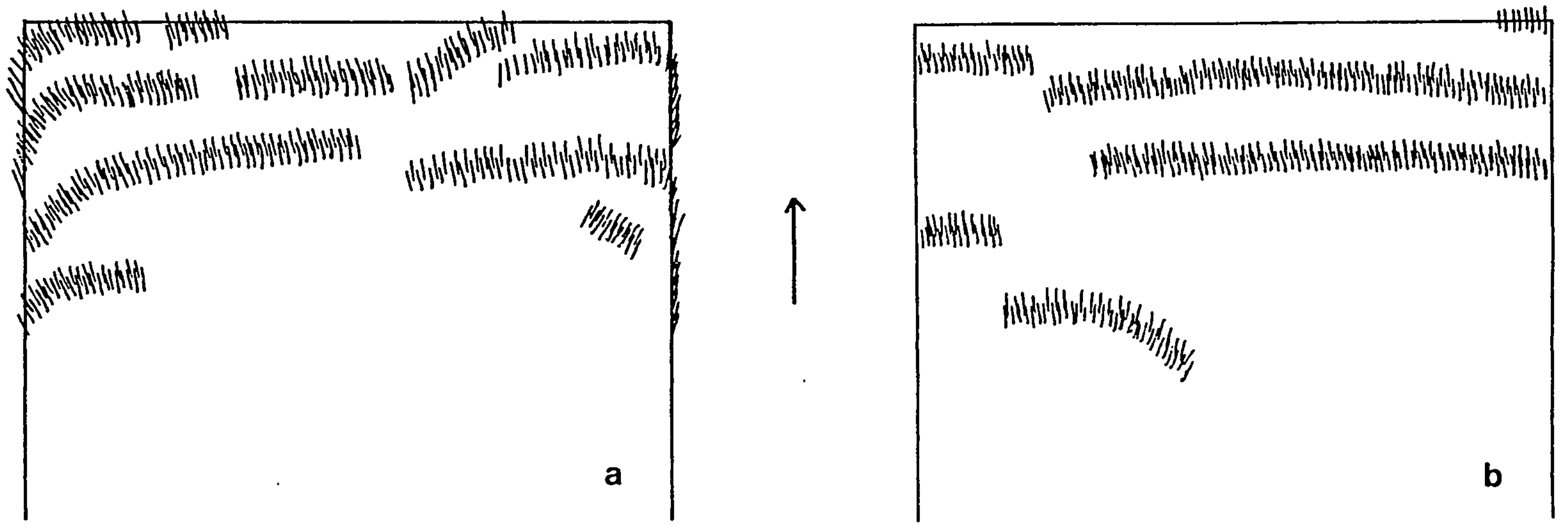

a
b

Figure 3. A group of larvae of C. dacotensis exhibiting a banded dispersion pattern (B) on a rock on a stream bottom. Larvae on either side of the rock (C) exhibit a clumped dispersion pattern. SP = stagnation point. Arrows indicate direction of flow. (a) Arrangement of larvae on day one. Velocity over middle of rock was 40 cm s^{-1}. (b) Arrangement of larvae 24 hours later. Drop in water level exposed area E. Water velocity was 38 cm s^{-1}.

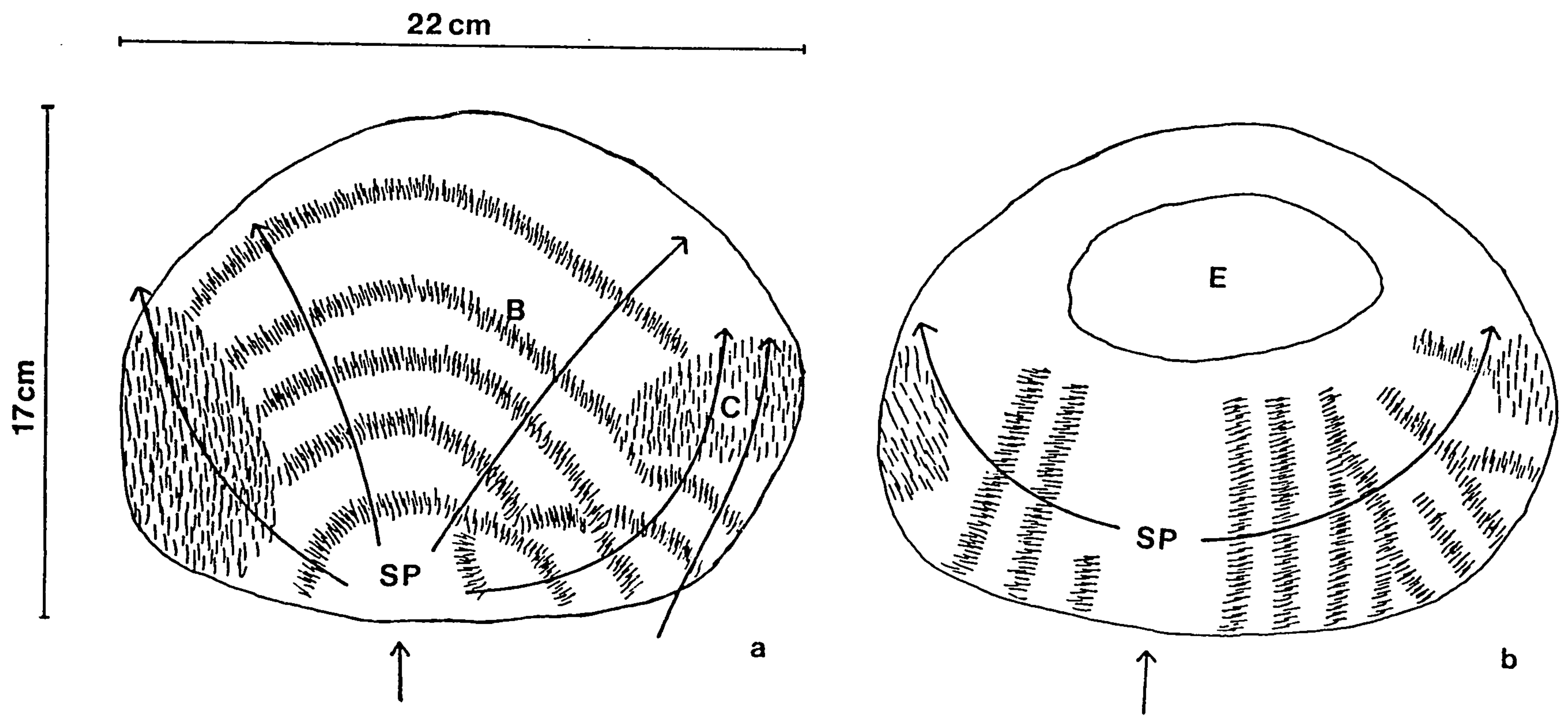
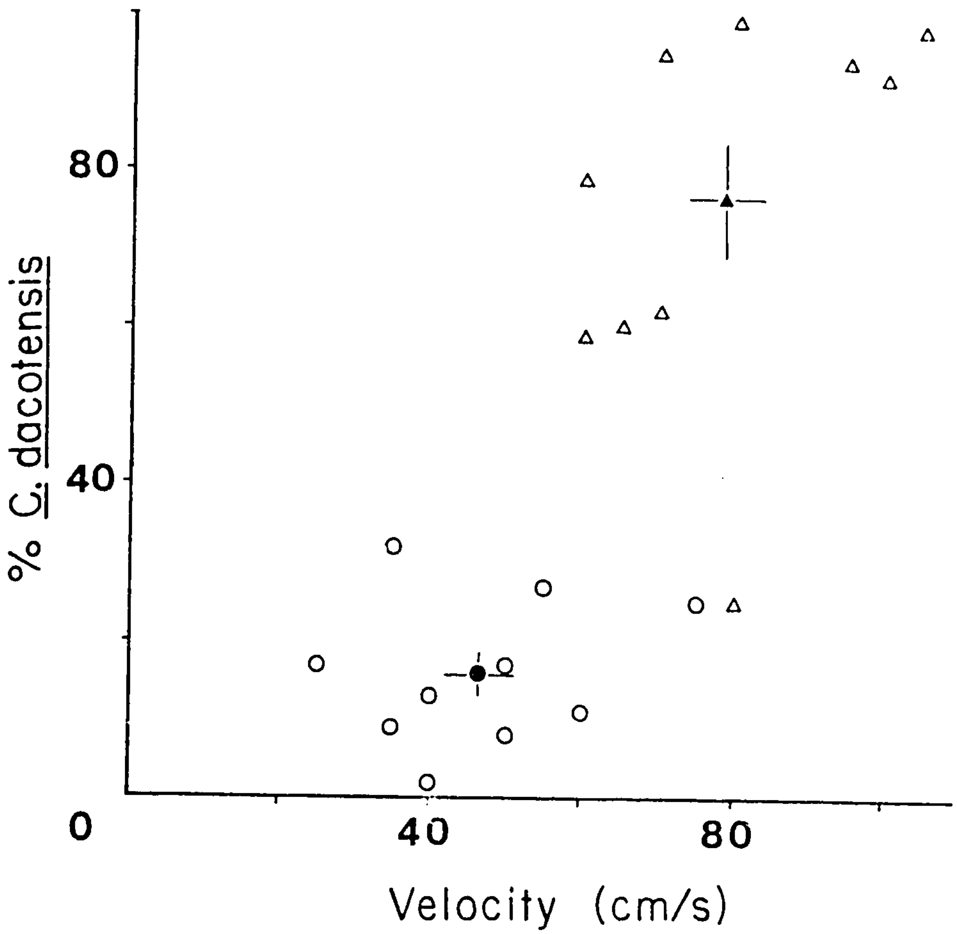

22 cm
17cm
B
C
SP
a
E
SP
b

Figure 4. The relationships among water velocity, percent C. dacotensis, and dispersion patterns exhibited by a mixed population of larvae of C. dacotensis and S. rostratum. Circles represent groups of larvae exhibiting a spaced dispersion pattern and triangles, groups of larvae exhibiting a clumped dispersion pattern. No banded dispersion patterns were observed. The solid symbols represent the means and the error bars, standard errors.


% C. dacotensis
80
40
0
40
80
Velocity (cm/s)

6. FLOW PATTERNS AROUND GROUPS OF SPACED AND BANDED LARVAE OF BLACK FLIES (DIPTERA: SIMULIIDAE)

Introduction

The larvae of most species of black flies are filter feeders that live attached to the substratum of rivers and streams. These larvae are often found in a contagious dispersion (Hocking and Pickering 1954, Décamps et al. 1975, Hart 1986). In a reach of a river or stream, larvae often occur in well defined groups, sometimes separated by distances of several meters. The larvae in a group are commonly arranged in one of three dispersion patterns; 1) spaced, where each larva keeps an area around itself clear of other larvae (Hart 1987, Eymann and Friend 1988), 2) clumped, where each larva is touching each of its nearest neighbours (Hart 1987, Wotton 1987, Eymann and Friend 1988), or 3) banded where the larvae arrange themselves in bands perpendicular to the mean direction of flow (Colbo 1987). The dispersion pattern exhibited by a group of larvae varies with the species composition of the group, and some species exhibit more than one dispersion pattern. The dispersion pattern exhibited by these species appears to depend on the velocity of water flowing past their microhabitat (chapter 4).

Flow past isolated larvae of Simulium vittatum Zetterstedt [complex] at 15 cm/s was described by Chance and Craig (1986). A solenoidal vortex forms at the upstream end of the larva and bends around either side of it resulting in a U-shape. This commonly encountered flow pattern develops around an object in a boundary layer (Lugt 1983). The U-shape of the solenoidal vortex of filter-feeding larvae of black flies is modified by the shape and posture of the larvae. A larva attaches itself with its ventral side facing the substratum and twists its body along its logitudinal axis 90 - 180 ° so that the labral fans face into the flow. In those instances where the larva rotates 180°, it is approximately bilaterally symmetrical. In most instances the larva twists <180°, resulting in a concave (ca) and a convex (ce) side (Fig. 2) with a yaw toward the concave side (Chance and Craig 1986). The arm of the solenoidal vortex on the concave side flows underneath the larva and upwards through one of the fans, while the other arm flows under the first arm (Chance and Craig 1986).

The spaced dispersion pattern is most commonly encountered, and has been most studied (Hart 1987, Eymann et al. 1987). Ciborowski and Craig (1989) showed that, at low food availabilities, a larva of S. vittatum close to a neighbouring larva will ingest more food in a given period of time than will an isolated larva. They termed this phenomena feeding facilitation. The mechanism underlying feeding facilitation is not understood. However, because filter feeding is a flow phenomena (Rubenstein and Koehl 1977), it can be hypothesized that feeding facilitation is caused by flow modification induced by proximity of larvae to each other in a spaced dispersion pattern. In the first part of this chapter, I test this hypothesis by looking for changes in flow around larvae in a spaced dispersion pattern, compared to that around an isolated larva (Chance and Craig 1986). I also test the hypothesis that water becomes less turbulent as it flows between a pair of spaced larvae.

Larvae exhibiting a banded dispersion pattern arrange themselves in bands perpendicular to the mean direction of flow. Bands of Cnephia dacotensis Dyar and Shannon are up to 30 cm long, 0.5 cm (2-3 larvae) thick, and approximately 2 cm apart (chapter 5). Larvae in bands are commonly found in an upright posture, perpendicular to the substratum. Larvae of C. dacotensis filter-feed more efficiently at 50 cm/s than at 30 cm/s (Kurtak 1978). Because these larvae exhibit banded dispersion patterns when found in microhabitats with a flow velocity of <50 cm/s (chapter 4), it is hypothesized that bands of larvae force water to accelerate as it flows past them. This hypothesis is tested in the second part of this chapter.

Materials and Methods

To obtain a group of larvae in a spaced dispersion pattern, larvae of S. venustum/verecundum from Norris Creek, Alberta or S. vittatum from Sturgeon River, Alberta were placed on a flat, 9x9 cm, plexiglass plate in a flume (Lacoursière 1990) full of stream water. Velocity in the flume was set at 30-50 cm/s and left for 1-2 days so that the larvae had time to establish a dispersion pattern. Velocity was measured with a small propellor probe attached to a Nixon Streamflow 422 flow meter.

The hypothesis that a spaced dispersion pattern dampens the turbulence of water flowing between larvae was tested in the following experiment. Pairs of larvae of S. venustum/verecundum on the plexiglass plate in the flume with water velocity set at 30 cm/s, were selected for study. An index of turbulence was obtained for one larva in the pair by recording the maximum deflection of the head from far left to far right over a 30 s period. The neighbour of the larva for which buffeting had been measured was removed, and the buffeting of the larva was again measured. This was repeated with 11 pairs of larvae. Maximum deflection of the larval head observed over a 30 s period was divided by total body length to obtain a dimensionless ratio. This provided a measure of buffeting and an index of turbulence. The statistical significance of the difference in buffeting before and after removal of neighbouring larvae was determined by applying a paired t-test to arcsin square root transformed data. Means are reported with their standard errors.

To obtain a group of larvae in a banded dispersion pattern, larvae of S. decorum from Whitemud Creek, Albertawere placed on a 3.8 cm diameter, plexiglass half-cylinder, clamped to the side of the flume. A similar half-cylinder was clamped to the other side of the flume, leaving a 3 cm gap between the two. Water velocity between the cylinders was measured at 24 cm/s. Larvae were left for one day so they could establish a band.

Once a dispersion pattern was established, flow through the group was made visible by injecting a 0.05% (by weight) solution of methylene blue through a glass haemocyte pipet (chapter 7). The flow of dye through, or around, the group of larvae was recorded on video tape for later analysis.

To obtain a preliminary description of changes in flow patterns around a larva in a group exhibiting a spaced dispersion pattern, pairs of larvae were considered. To test the hypothesis that water accelerates as it flows over a band, dye was injected into the flow 4 mm upstream of the front of the band and 1 mm above the substratum. The height of the plume above the surface just upstream of the band was measured nine times and an average was calculated. This was repeated at 1 mm intervals above the surface of the half-cylinder to a maximum height of 8 mm. The distance between the plumes just upstream of the front of the band was calculated. The principle of continuity (Vogel 1981) says that if the plumes converge as they approach the band the water is accelerating.

Results and Discussion

Flow patterns around larvae exhibiting a spaced dispersion pattern

Flow around individual larvae in a group exhibiting a spaced dispersion pattern was similar to flow around an isolated larva, each larva having its own solenoidal vortex. However, some changes in flow pattern were apparent. Pairs of larvae were divided into three arbitrary configurations according to position of larvae relative to each other. Although each of these configurations differed in the effects it had on flow between larvae, these configurations represent regions along a continuum of possible configurations. A total of 22 pairs of larvae were observed.

In the first configuration, two larvae were side by side, the silk pads that the larvae used to attach themselves to the substratum, were separated by no more than 0.3 body lengths along the mean direction of flow (distance A in Fig. 1). Larvae in such a configuration were separated by 0.61±0.09 (n=5) body lengths in the direction perpendicular to the mean direction of flow (distance B in Fig. 1). In this configuration, both the solenoidal vortex (sv) and its downstream arms where similar to those reported by Chance and Craig (1986). Acceleration of water flowing between the solenoidal vortices could clearly be seen when a dye plume flowed between a pair of larvae in three of the five pairs of larvae. By dividing the width of the dye plume upstream of the pair of larvae by its width as it flowed between the larvae, an index of maximum acceleration could be obtained. The mean index of maximum acceleration for three pairs of larvae was 1.75. Chance and Craig (1986) estimated an index of acceleration between larval pairs of S. vittatum by dividing the distance between the middle of the anal papillae of two larvae by the distance between the solenoidal vortices of the the larvae. They obtained a mean index of acceleration of 4.7 for three pairs of larvae. The Chance and Craig (1986) index assumes that all water in the area between the anal papillae flows between the larvae. However, some of it may flow over the larvae and some may flow into the solenoidal vortex. The present index accounts for this possibility, but not for the possibility that the cross-sectional shape of the dye plume changes as it flows between the larvae. Consequently, it is an index of acceleration and not a direct measure.

In the second configuration, two larvae were side by side as in the first configuration, but the silk pad of one of the larvae was positioned 0.4 to 1 body length upstream of the other (Fig. 2). Mean distance between the silk pads of the two larvae, along the direction perpendicular to the mean direction of flow was 0.49±0.04 body lengths. Often several larvae were lined up in this configuration, resulting in a row of larvae that was oblique to the mean direction of flow. One arm of the solenoidal vortex always flowed underneath the larva, as reported in Chance and Craig (1986). When a larva was present downstream of the larva being observed, the arm that flowed under the larva (usl) was on the same side as the downstream larva (dsl). This was true whether the downstream larvae was on the concave (n=5) or the convex side (n=4) of the upstream larva.

In the third configuration, the larvae were arranged so that one larva was almost directly upstream of the other (Fig. 3). The downstream larva was to one side of the upstream larvae so that the wake of the upstream larva did not flow through the fans of the downstream larvae (Fig. 3). The angle at which water flowed toward the stagnation point of the downstream larva was shifted 28±3.3° (n=8) away from the mean direction of flow. This deflection was apparently caused by the presence of the upstream larva.

In all three configurations, the changes in flow pattern were subtle and changes appeared to differ for all three configurations. In fact, each larva had a solenoidal vortex that was similar to that described in Chance and Craig (1986). Possibly larvae in a spaced dispersion pattern were arranged in such a way as to minimize disturbance of the flow patterns by neighbouring larvae. This suggests that some parameter other than structure of the vortices, accounts for feeding-facilitation in larvae of black flies exhibiting a spaced dispersion pattern.

The mean buffeting of a larva before its neighbour was removed was 0.44±0.04 (n=11) body lengths, after its neighbour was removed it was 0.52±0.05 body lengths, the mean difference in buffeting being 0.08 body lengths. This difference was significant according to a paired t-test ($p<0.005$). Pairs of larvae in this experiment were side by side either staggered or not. In chapter 3, it is suggested that less turbulent flow may be an important characteristic of microhabitats occupied by larvae of black flies. Reduction in turbulence may be the mechanism by which spacing induces feeding facilitation.

The third configuration, in which one larva was almost directly upstream of the other, may not contribute to feeding facilitation. It appears to limit interference by preventing the wake of the upstream larva from flowing past the downstream larva. Figure 3 shows a thin plume of dye flowing away from the upstream larva past the downstream larva. This plume represents the von Karman trail (vKt) (Chance and Craig 1986) of the larva. The downstream larva is rotated only about 90° so that the von Karman trail of the upstream larva will flow past, not through its fans. This is consistent with the findings of Hart (1986) who showed that the presence of an upstream larva can reduce flick rates of a downstream larva, and that "aggressive" behaviours were more commonly directed against upstream neighbours than neighbours in any other direction.

Flow patterns around larvae exhibiting a banded dispersion pattern

The band, formed by larvae of C. dacotensis on the half-cylinder, was approximately two larvae thick. Because larvae in the band touched each other at the thickened posterior portion of their abdomens, individual larvae did not have their own solenoidal vortex. Consequently, the entire band can be thought of as a single obstacle to flow in analysis of flow patterns. Since the larvae only touched each other at the thickened bases of their abdomens, there were spaces between larvae at the upper part of the band, making it porous. This porosity was apparent when dye injected into the water a few mm in front of the band flowed between the larvae.

The most prominent feature of the flow pattern around a band, was a horizontal vortex (hv) downstream of the band (Fig. 4). The part of the downstream, horizontal vortex that flowed upward, formed a complex vertical vortex (vv). Some of the water that flowed through the band flowed into this vertical vortex. The vertical vortex and the water in front of the band both flowed upward, away from the substratum. This may account for the upright posture of these larvae. The presence of the horizontal vortex in the field was confirmed when dye was injected, with a syringe, into the flow just downstream of the band.

Water flowing over the band accelerated. This is predicted by the principle of continuity (Vogel 1981), and is confirmed in Figure 4, where the streamlines just upstream of the band were closer together than those 4 mm upstream of the band. Dividing the distance between streamlines 4 mm upstream of the band, by the distance between streamlines just upstream of the band, shows that the acceleration was approximately two fold. Water velocity between the two half-cylinders was 24 cm/s, therefore that just downstream of the band was approximately 50 cm/s. This acceleration resulted in faster flow and, consequently, in lower pressure at the upstream face of the band. This may further contribute to the upright posture of the larvae in the band. Acceleration also results in faster flow through the fans and may assist in filter feeding by banded larvae of C. dacotensis.

Both spaced and banded dispersion patterns resulted in significant alteration of flow, from that around an isolated larva. A spaced dispersion pattern resulted in reduced buffeting of larvae and is believed to reflect reduced turbulence. A banded dispersion pattern resulted in the replacement of the system of vortices around each larva with a larger system of vortices around the entire band. As water flowed over the band it accelerated, perhaps leading to more efficient filter feeding. Water both upstream and downstream of the band flowed upward, and the acceleration of water upstream of the band resulted in a low pressure region. These two factors appear to act together to cause an upright posture of the larvae. In both dispersion patterns, groups of larvae alter flow in ways that isolated larvae do not.

Literature Cited

Ciborowski, J. J. H., and D. A. Craig. 1989. Factors influencing dispersion of larval black flies (Diptera: Simuliidae): effects of current velocity and food concentration. Can. J. Fish. Aquat. Sci. 46: 1329-1341.

Chance, M. M., and D. A. Craig. 1986. Hydrodynamics and behaviour of Simuliidae larvae (Diptera). Can. J. Zool. 64: 1295-1309.

Colbo, M. H. 1987. Problems in estimating black fly populations in their aquatic stages. In K. C. Kim and R. W. Merritt [ed.]. Black flies: Ecology, Population Management, and Annotated World List. The Pennsylvania State University. University Park, PA.

Décamps, H., G. Larrouy, and D. Trivellato. 1975. Approche hydrodynamique de la microdistribution d'invertébrés benthiques en eau courante. Annls. Limnol. 11: 79-100.

Eymann, M. 1985. The behaviours of the blackfly larvae Simulium vittatum and S. decorum (Diptera:Simuliidae) associated with establishing and maintaining dispersion patterns on natural and artificial substrate. M. Sc. Thesis. University of Toronto.

Eymann, M., J. M. Schmidt, and W. G. Friend. 1987. Computer analysis of polarized spacing patterns with special reference to the larvae of the black fly, Simulium vittatum. Can. J. Zool. 65: 602-604.

Hart, D. D. 1986. The adaptive significance of territoriality in filter-feeding larval blackflies (Diptera: Simuliidae). Oikos, 46: 88-92.

Hart, D. D. 1987 Processes and patterns of competition in larval black flies. In K. C. Kim and R. W. Merritt [ed.]. Black flies: Ecology, Population Management, and Annotated World List. The Pennsylvania State University. University Park, PA.

Hocking, B., and L. R. Pickering. 1954. Observations on the bionomics of some northern species of Simuliidae (Diptera). Can. J. Zool. 32: 99-119.

Kurtak, D. C. 1978. Efficiency of filter-feeding of black fly larvae (Diptera: Simuliidae). Can. J. Zool. 56: 1608-1623.

Lacoursière, J. O., 1990. A small flume for study of the influence of hydrodynamical factors in benthic invertebrate behaviour. J. n. am. benthol. Soc. 9: in press.

Lugt, H. J. 1983. Vortex Flow in Nature and Technology. John Wiley and Sons. Toronto.

Rubenstein, D. I., and M. A. R. Koehl. 1977. The mechanisms of filter feeding: Some theoretical considerations. Am. Nat. 111: 981-994.

Vogel, S. 1981. Life in Moving Fluids: The Physical Biology of Flow. Princeton University Press. Princeton, NJ. 352 p.

Figure 1. Flow patterns around a pair of larval black flies exhibiting a spaced dispersion pattern in a side by side, non-staggered configuration. The stippled area around each larvae represents plumes of dye flowing around the outside of the solenoidal vortices (sv). The stippled area between the two larvae represents a plume of dye flowing between the larvae and exhibiting constriction due to acceleration. Free-stream velocity was 40 cm/s. Scale bar = one millimeter. The arrow indicates mean direction of flow.

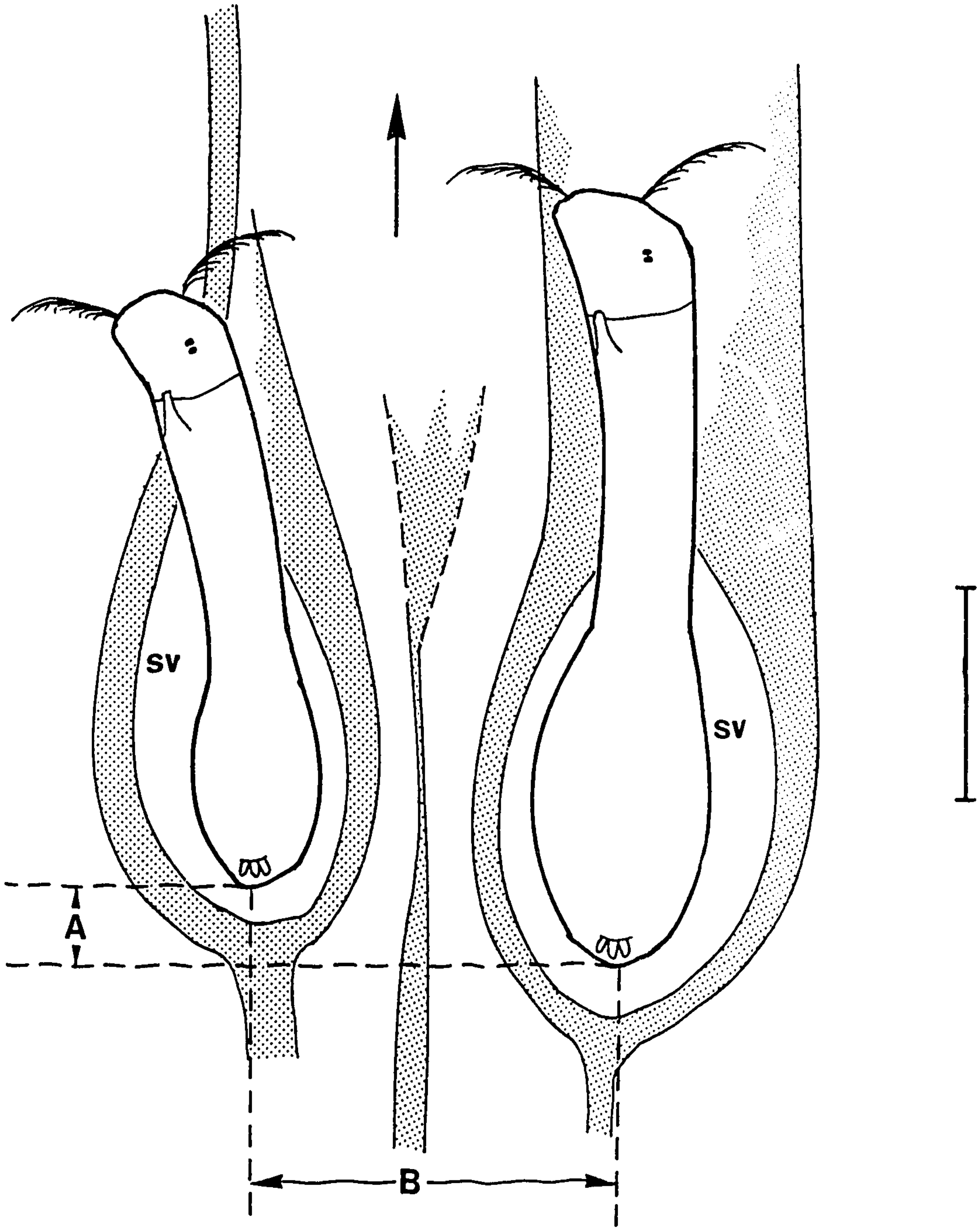

sv
sv
A
B

Figure 2. Flow patterns around a pair of larval black flies exhibiting a spaced dispersion pattern in a side by side, staggered configuration. The plume on the concave side (ca) of the upstream larva (usl) flows under the larva as does the plume flowing between the two larvae. Free-stream velocity was 53 cm/s. dsl - downstream larva, ce - convex side of larva. Other symbols as in figure 1.

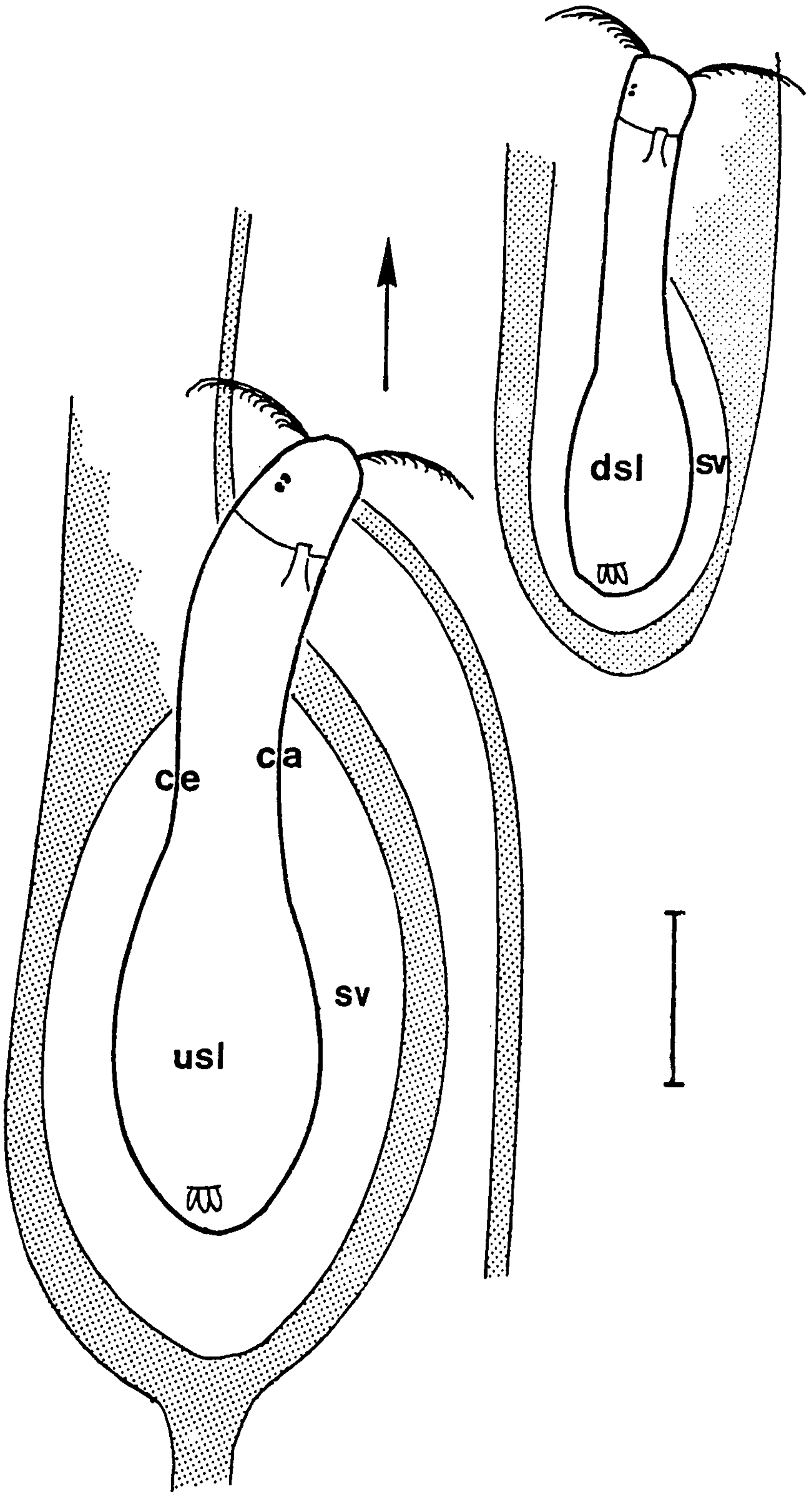

dsl
sv
ce
ca
sv
usl

Figure 3. Flow patterns around a pair of larval black flies exhibiting a spaced dispersion pattern in a configuration where one larva is almost directly upstream of the other. θ is the angle of deflection, from the mean direction of flow, of the water approaching the stagnation point (s) of the downstream larva. The von Karman trail (vKt) of the upstream larva just misses the downstream larva. Free-stream velocity was 40 cm/s. Other symbols as in Figure 1.

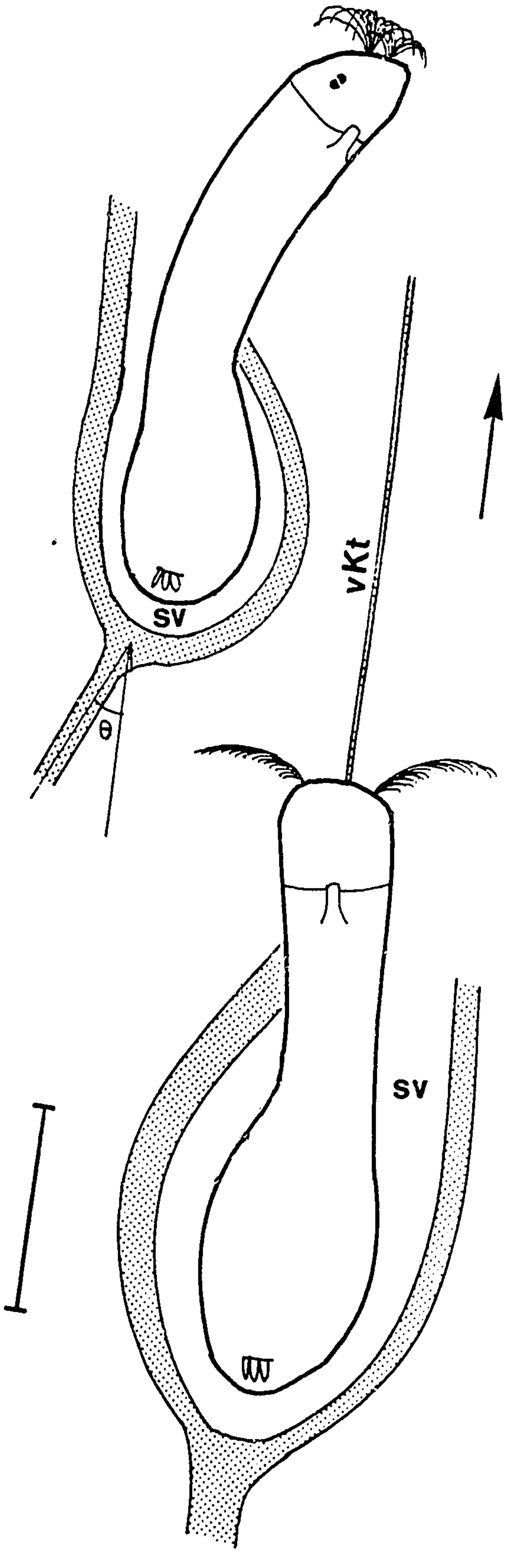
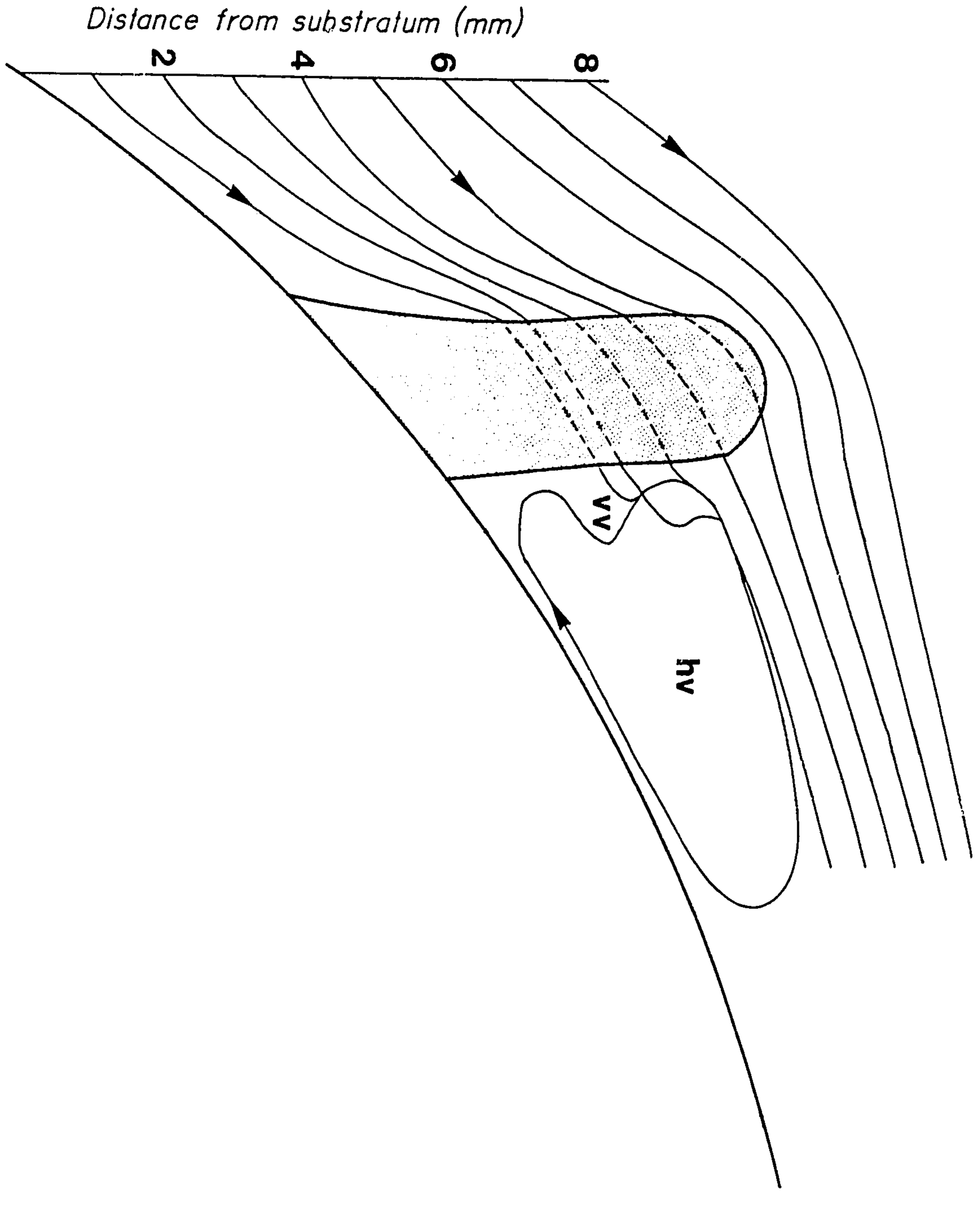

sv
vKt
θ
sv

Figure 4. A cross-section of a band of larvae of *C. dacotensis* that is two larvae thick (stippled area) on a half-cylinder showing the streamlines of water flowing past it. Those just upstream of the band are closer together than those four millimeters upstream, indicating that water accelerates as it approaches the band. A horizontal vortex (hv) downstream of the band represents slower flow and may act as a "cushion" lifting the band from the substratum. There is a vertical vortex (vv), within the horizontal vortex, just downstream of the band. Free-stream velocity above the band was 24 cm/s.


Distance from substratum (mm)
2
4
6
8
vv
hv

7. FLOW PATTERNS AROUND COCOONS AND PUPAE OF BLACK FLIES OF THE GENUS SIMULIUM (DIPTERA: SIMULIIDAE)

Introduction

Pupae of most species of black flies of the genus Simulium Latreille are contained in a silken cocoon that is attached to a hard surface submerged in the river or stream in which the larvae live (Currie 1986). In most species the posterior part of the cocoon is shaped like a longitudinally bisected ice cream cone with the pointed, posterior end directed upstream. The anterior part has a large opening through which plastron-covered gill filaments of the pupa project. This opening may be directed downstream, in which case the cocoons are called "slipper-shaped", or dorsally, in which case they are called "boot-shaped". In those species with "boot-shaped" cocoons, the gill filaments are surrounded by a collar of silk that extends beyond the pupal head. The collar may, or may not, have openings called fenestrae (Currie 1986). A cocoon is commonly oriented parallel to the current (Maitland & Penney 1967) suggesting that orientation and shape of the cocoon are adaptations to life in moving water.

The pupae of Simuliidae exhibit more structural diversity than larvae (Currie 1986), and are often much easier to identify. This difference in structural diversity between larvae and pupae within one family suggests that evolution of the two stages is driven by different kinds of selection. To compare the selective pressures acting on these two life stages we must compare the relationship of larvae and of pupae with their environment. While this relationship of larval black flies with the environment has been studied extensively (Kim & Merritt 1987), pupae have not enjoyed the same attention. As a first step towards understanding the relationship of black fly pupae with their environment, the flow patterns around pupae should be described, because flowing water is one of the dominant physical parameters acting on them.

In this chapter the results of a preliminary investigation describing the pattern of flow past cocoons, with pupae, of five species of black flies in the genus Simulium are presented. The species were selected because their cocoons and gill filaments differed from each other in shape.

Materials and Methods

Flow visualization experiments were performed in a 9x20x70 cm plexiglass flume (Lacoursière 1990). In the working section of the flume the water was 9 cm deep x10 cm wide in cross-section. Six to 12 cocoons with pupae of each species were attached 0.7 to 4.5 cm from the leading edge of a plexiglass plate, with dichloroethane, a solvent of plexiglass. The pupae used were of the species; S. arcticum, S. canadense, S. malyschevi, S. virgatum, and S. vittatum. They were obtained drom the collection of D. C. Currie. The 9x9 cm plate was bevelled along the lower face of its leading edge. Pupae were attached at varying distances from the leading edge to facilitate viewing from the side, and submerged 4 cm under the surface of the water, wedged between the walls of the flume. The plate was mounted at a 10° angle to the horizontal so that the downstream edge was higher than the upstream edge. This ensured that the surface of the plate with the attached pupae was facing into the current.

Current velocity in the flume was adjusted to 28±2 cm s^{-1}, velocity was measured just upstream of the plate with a propeller-type probe connected to a Nixon Streamflow 422 flow meter. A strong solution of methylene blue (0.05 % by volum) was injected into the flow near the pupa, through a glass capillary tube. This had been heated with a flame, drawn out as thin as possible, and bent to a 90° angle. The bent tube was attached to a micromanipulator so that its opening could be carefully positioned at various locations near the cocoon. The tube was connected to a syringe by a length of rubber tubing, and dye was injected into the flow by gently depressing the syringe plunger. Path of the dye plume past the cocoon was recorded using a JVC Highband Saticon camera with a 35 mm camera lens, and a Panasonic AG-6200 recorder. The dye plume was recorded from above and from the side. By repeatedly viewing the video tapes, the most common paths taken by water flowing past the cocoons could be described and recorded as line drawings.

For each species, the undisturbed 99% boundary layer thickness (d) and Reynolds number (Re) were calculated. Re was calculated using the equation $Re=(lu)/\upsilon$ (Vogel 1981) where: l=mean length of cocoon u=free-stream velocity, and υ=kinematic viscosity. Boundary layer thickness was calculated using the equation $d=5xRe_x^{-0.5}$ (Vogel) where: d=vertical distance from substratum at which velocity=99% of u, x= mean distance from the leading edge of the plate, and Re_x is Re of the boundary layer at x. A laminar boundary layer was assumed. Also calculated was k/d, where: k= height of the cocoon.

Results and Discussion

Figures 1-5 show schematic representations of flow patterns around cocoons. In each figure (A) shows the plan view and (B), the side view. Lines with arrows represent selected stream tubes (three-dimensional bundles of streamlines) that illustrate the most noteworthy features of the flow patterns. The stiplled areas represent the outer surface of the cocoons.

Figure 1 illustrates flow patterns around a pupa of Simulium vittatum Zetterstedt, having a collarless, "slipper-shaped" cocoon (Re=1,500, k/d=1.0). Water flows around the solenoidal vortex (sv) of the cocoon and forms a pair of small vortices near the substratum, under the gill filaments. These vortices flow upward, through the gill filaments, growing in width as they rise. When the vortices flow past the top of the cocoon they are swept downstream by water flowing over the cocoon. As the vortex bends downstream its stream tubes come closer together. According to the principle of continuity (Vogel 1981), when stream tubes converge, water is accelerating.

This cocoon shape is shared by pupae of many common, temperate species of black flies. Such pupae often occur on the downstream face of a rock, (Maitland & Penny 1967) a microhabitat having separated boundary layers. In such situations they are oriented in various directions (Maitland & Penney 1967, personal observations) reflecting the unpredictable and turbulent nature of the flow in these areas.

Cocoons of S. arcticum Malloch and S. virgatum Coquillet both have well developed collars with fenestrae (Re=1,450, k/d=1.4). The collar of S. arcticum (Fig. 2) has fenestrae on the anterior (af) and lateral (lf) regions. Water flowing past the cocoon of S. arcticum forms two pairs of vortices, one inside the collar (cv) and one outside (av), just downstream of the cocoon. The pair of vortices downstream of the cocoon formed from water that flowed around the sides of the solenoidal vortex. Vortices inside the collar form from water from two sources; 1) water flowing along the wall of the cocoon, then in through the lateral fenestrae, and 2) water from the anterior vortices that enters via the anterior fenestrae. Water exits the collar through the upper opening.

Gill filaments of S. arcticum are smaller than those of S. vittatum and are positioned close to the collar. This leaves an open space in the collar where the vortex pair can develop. Other S. arcticum cocoons have more fenestrae than the ones depicted (Currie 1986). The number and location of fenestrae may be a function of cytotype (Procunier & Shemanchuk 1983), or may be affected by flow conditions in the environment in which the pharate pupa has spun its cocoon.

S. virgatum (Fig. 3) spins cocoons with a collar with one lateral fenestrum (lf) on each side, and three posterior (upstream) fenestrae (pf) (Re=1,260, k/d=1.2). The lateral fenestrae may or may not be continuous with the upper opening of the collar. As with S. arcticum, two pairs of vortices are formed by water flowing past the cocoon, one inside the collar and one outside, just downstream of the cocoon. Unlike those of S. arcticum, the gill filaments of S. virgatum are arranged in a band across the collar with the inside pair of vortices anterior to the gill filaments. Water flows over the top of the upstream part of the cocoon, into the collar, through the posterior fenestrae and between the gill filaments. It may then flow out the lateral fenestrae or into the vortices inside the collar, eventually leaving either out the top of the collar, or out the lateral fenestrae. Unlike those of S. arcticum, the pair of vortices downstream of the cocoon do not contribute water to flow around the gills.

In the field (Chemainus River, B. C.), pupae of S. virgatum were often found arranged in clumps, in microhabitats with attached boundary layers, with all pupae oriented with their posterior ends directed upstream. Pupae were often found in clumps several cm across and free of larvae; these were often surrounded by large numbers of larvae.

S. malyschevi Dorogostaisky et al. shown in Figure 4, spins a cocoon with a small collar with extensive fenestration resulting in a "wicker-basket-like" appearance and a complex flow pattern (Re=840, k/d=0.90). Water flowing along the sides of the cocoon and along the outside of the solenoidal vortex (sv), forms a small pair of vortices downstream of the cocoon. The anterior vortex pair flows up over the lip of the collar where it enlarges to fill most of the space above it. Water also flows around the solenoidal vortex of the cocoon and upstream, between the anterior vortices, directly into a vortex above the collar. Water flows along the sides of the cocoon into the collar through the lateral fenestrae. Some of the water in the vortex above the collar may enter the collar, but the exchange of water between the collar and the vortex above it could not be seen clearly.

Water appears to leave the collar by flowing over its lateral and anterior lip. It is not known whether pupae of this species are more common in microhabitats with separated or unseparated boundary layers. Because of its smaller size, this pupa has a smaller Re and k/d than the other pupae investigated. This may account for some of the differences between flow patterns seen in this species and the other species.

Pupae of S. canadense Hearle (Fig. 5) have no collar on their cocoons, but these pupae are unusual in that their gill filaments are reduced to two per side, and are much more robust than the gills of most other species. The base of the gill is inserted at the dorsum of the prothorax of the pupa, and the first filament extends ventrally down the pupal head. The second filament extends anteriorly a short distance then bends ventrad, parallel to the first filament. This arrangement leaves a long, narrow gap laterally, between the first and second filaments and a diamond- or oval- shaped gap dorsally between the two gills. These gaps open into a chamber located between the four filaments. For cocoons of this species Re=1,200, k/d=1.0. Water flows around the cocoon and forms two pairs of vortices. One pair (cv) is found inside the chamber formed by the four gill filaments; the other (av) is just downstream of the gills. The vortices inside the chamber receive water from the side through the gap between the filaments. Water leaves through the gap at the top of the gills. These pupae were collected from a microhabitat with an attached boundary layer.

Despite the differences in the pattern of flow past differently shaped cocoons, there are at least three important similarities in the flow pattern around the cocoons of all five species; 1) the presence of a so[illegible]x around the cocoon, 2) upward flow at the anterior (downstream) end of [illegible], and 3) vortices that either touch or envelop the gill filaments.

A solenoidal vortex forms when an object projects out of the substratum into the boundary layer (Sedney 1973, Lugt 1983). It is to be expected, therefore, that a black fly cocoon would have a solenoidal vortex. The structure of the solenoidal vortex may affect the structure of the vortex pairs downstream of the cocoon.

The upward flow of pairs of vortices just downstream of pupae probably results from a pressure difference across the upper and lower part of this region. This pressure difference is caused by the faster flow over the top of this region relative to flow closer to the substratum. Faster flow results in lower pressure (Vogel 1981) which, in effect, sucks water up along the region just anterior of the cocoon (Vogel 1981: 54, Fig. 4.8b). The faster flow at the top is a result of: 1) the velocity gradient of the boundary layer in which the pupa is submerged. In a boundary layer, velocity of flow is zero at the substratum and increases with distance from the substratum (Schlichting 1979, Vogel 1981). 2) The physical displacement of water by the cocoon which, because of the principle of continuity (Vogel 1981), results in acceleration of the water as it flows over the cocoon.

The water sucked up by the pressure difference has an angular momentum imposed upon it by the velocity gradient of the boundary layer (Lugt 1983). When the water flows around the anterior end of the cocoon and is sucked upward by the pressure difference, this angular momentum results in the formation of one or two pairs of spiral-shaped vortices.

The upward flowing, spiral-shaped vortices downstream of the pupae are similar to flow patterns past the larvae of black flies reported by Chance & Craig (1986). Sedney (1973) reported flow patterns characterized by solenoidal vortices, and by upward spiraling, downstream vortices for a variety of shapes including squat cylinders, spheres, hemispheres and irregular globs of plasticine. The work he reviewed was carried out in boundary layer flow in air at $Re \approx 10^5$ and k/s ranging from 0.45 to 1.9. Davis (1986) reported similar flow patterns around a sphere immersed in water where $Re=75$. However, the downstream vortices were not well defined probably because of the low Re. Such results show that the solenoidal vortex and downstream vortex pair are produced by bluff-bodies in a wide variety of conditions. Therefore it cannot be concluded that the shapes of the pupae and cocoons has evolved to produce these vortices. However, the proximity of the gills to the vortices is probably an evolutionary adaptation, because it is apparent in five species with structurally different pupae and cocoons. While other factors may determine cocoon and gill filament structure, cocoons are is always configured so as to maintain proximity between gills and vortices.

The observation that these vortices form around or next to the gill filaments in each of these structurally different pupae and cocoons suggest that they serve an important function, probably related to gaseous exchange. They may directly facilitate gaseous exchange at the plastron surface of the gill filaments by ensuring that a steady supply of water is carried past it. Alternatively, they may indirectly help gaseous exchange by preventing colonization of the plastron by periphyton, or the settling of fine particles upon the gills. Resolution of the function of the vortices remains the subject of future investigations.

Glendhill et al. (1982) reported that pupae of S. ornatum are more heavily parasitized by mites than pupae of S. equinum. They hypothesized that the boot-shaped cocoon and the inflated gill filaments of S. equinum reduce the likelihood that a mite will colonize a pupa. It is possible that the boot-shape cocoons of S. virgatum, S. arcticum, and S. malyschevi and the enlarged gill filaments of S. canadense are also mechanisms for reducing parasitization by mites.

The collars of boot-shaped cocoons may protect the gill filaments from abrasion by suspended particles, while the vortex pair inside the collar ensures that they are ventilated. The gills of pupae with slipper-shaped cocoons may be protected from abrasion by their location downstream of the pupa. As the water curves around the front of these pupae, large, dense particles such as sand grains may continue travelling in a straight line because of their inertia. This prevents them from curving around the anterior part of the pupa and entering the vortex. Pupae with boot-shaped, and those with slipper-shaped cocoons appear to have different mechanisms for protecting their gills from abrasion. Although the data are still limited, it appears that pupae with boot-shaped cocoons are more common in situations with attached boundary layers while those with slipper-shaped cocoons are more common under separated boundary layers. It is possible that different mechanisms for protecting gills from abrasion work better under different flow conditions.

The structure of the cocoon and the gill filaments, appears to have evolved so that the gill filaments maintain their proximity to vortices while allowing adaptations to selective pressures not directly related to gaseous exchange.

In contrast to pupae, the filter-feeding larvae of black flies exhibit little variability in structure. Most taxonomic characters of larvae are microscopic features of the head capsule which do not affect the shape of the head capsule (Currie 1986). Small changes in shape may have a profound effect on flow patterns around black fly larvae, which may affect their filter-feeding efficiency (Chance and Craig 1986). Although larvae are structurally similar, they adapt to selective pressures by exhibiting a wide range of behaviours (Eymann & Friend 1988), to avoid predators (Wotton 1986), to move across the substratum (Barr 1984), and to adapt to different flow conditions (Lacoursière 1989, chapter 4, 5). Therefore, it may be concluded that larvae are structurally similar because; 1) only a limited number of shapes will lend themselves to efficient filter feeding, and 2) changes in behaviour can adapt the organism to other selection pressures.

The behaviours of pupae appear to be restricted to microhabitat colonization and cocoon spinning by pharate pupae, and to rotation of the abdomen by pupae. Consequently, evolutionary adaptations of pupae are more likely to involve structural change. Most of these are restricted to gills and cocoons because the shape of the pupae is probably determined by the shape of the adult. Efficiency of gaseous exchange at the gill filaments of pupae is not as dependent on shape as is filter-feeding efficiency by larvae. This allows selective pressures such as parasitization by mites, and possibly, abrasion by suspended particles, to affect the evolution of the shape of pupae and cocoons.

References

Barr, W. B., 1984. Prolegs and attachment of Simulium vittatum (sibling IS-7) (Diptera: Simuliidae) larvae. Can. J. Zool. 62: 1355-1362.

Chance, M. M. & D. A. Craig, 1986. Hydrodynamics and behaviour of Simuliidae larvae (Diptera). Can. J. Zool. 64: 1295-1309.

Currie, D. C., 1986. An annotated list of and keys to the immature black flies of Alberta (Diptera: Simuliidae). Mem. ent. Soc. Can. No. 134.

Davis, J. A., 1986. Boundary layers, flow microenvironments and stream benthos. In P. De Deckker, and W. D. Williams. (eds.) Limnology in Australia. CSIRO, Melbourne. 293-312.

Eymann, M. & W. G. Friend, 1988. Behaviors of larvae of the black flies Simulium vittatum and S. decorum (Diptera: Simuliidae) associated with establishing and maintaining dispersion patterns on natural and artificial substrates. J. insect Behavior. 1: 169-186.

Glendhill, T., J. Cowley & R. J. M. Gunn. 1982. Some aspects of the host:parasite relationships between adult blackflies (Diptera; Simuliidae) and larvae of the water-mite Sperchon setiger (Acari; Hydrachnellae) in a small chalk stream in southern England. Freshwat. Biol. 12: 345-357.

Kim, K. C., & R. W. Merritt, 1987. Black Flies; Ecology, Population Management, and Annotated World List. The Pennsylvania State University. University Park. 528 pp.

Lacoursière, J. O., 1989. Suspension-feeding behaviour of black fly larvae (Diptera: Simuliidae) : Hydrological perspectives. University of Alberta. Ph. D. Thesis.

Lacoursière, J. O., 1990. A small flume for study of the influence of hydrodynamical factors in benthic invertebrate behaviour. J. n. am. benthol. Soc. 9: in press.

Lugt, H. J., 1983. Vortex Flow in Nature and Technology. John Wiley and Sons. Toronto. 817 pp.

Maitland, P. S. & M. M. Penney, 1967. The ecology of the Simuliidae in a Scottish river. J. anim. Ecol. 36:179-206.

Procunier, W. S. & J. A. Shemanchuk, 1983. Identification of sibling species of black flies in Alberta using polytene chromasome analysis. In L. J. L. Sears, & T. G. Atkinson. (eds.) Research Highlights - 1982. Agriculture Canada Research Station, Lethbridge, Alberta.

Schlichting, H., 1979. Boundary Layer Theory. McGraw-Hill Book Company. Toronto. 817 pp.

Sedney, R., 1973. A survey of the effects of small protuberances on boundary-layer flows. American Institute of Aeronautics and Astronautics Journal. 11:782-792.

Vogel, S., 1981. Life in Moving Fluids: The Physical Biology of Flow. Princeton University Press. Princeton. 352 pp.

Wotton, R. S., 1986. The use of silk life-lines by larvae of Simulium noelleri (Diptera). Aquatic Insects. 8: 255-261.

Figure 1. Flow pattern around the cocoon and pupa of S. vittatum. A) Plan view; a stream tube approaches the cocoon and splits, flowing around either side of the solenoidal vortex (sv). Some of this water flows under the gill filaments (gf) where it forms a pair of vortices which rises up through the gill filaments, growing in width as it rises. B) Side view. The stream tubes of the vortex come closer together as the vortex rises above the gill filaments, indicating that the water is accelerating under the influence of faster flowing water farther from the substratum. Scale bar represents 1 mm. Re=1,500, k/d=1.0.

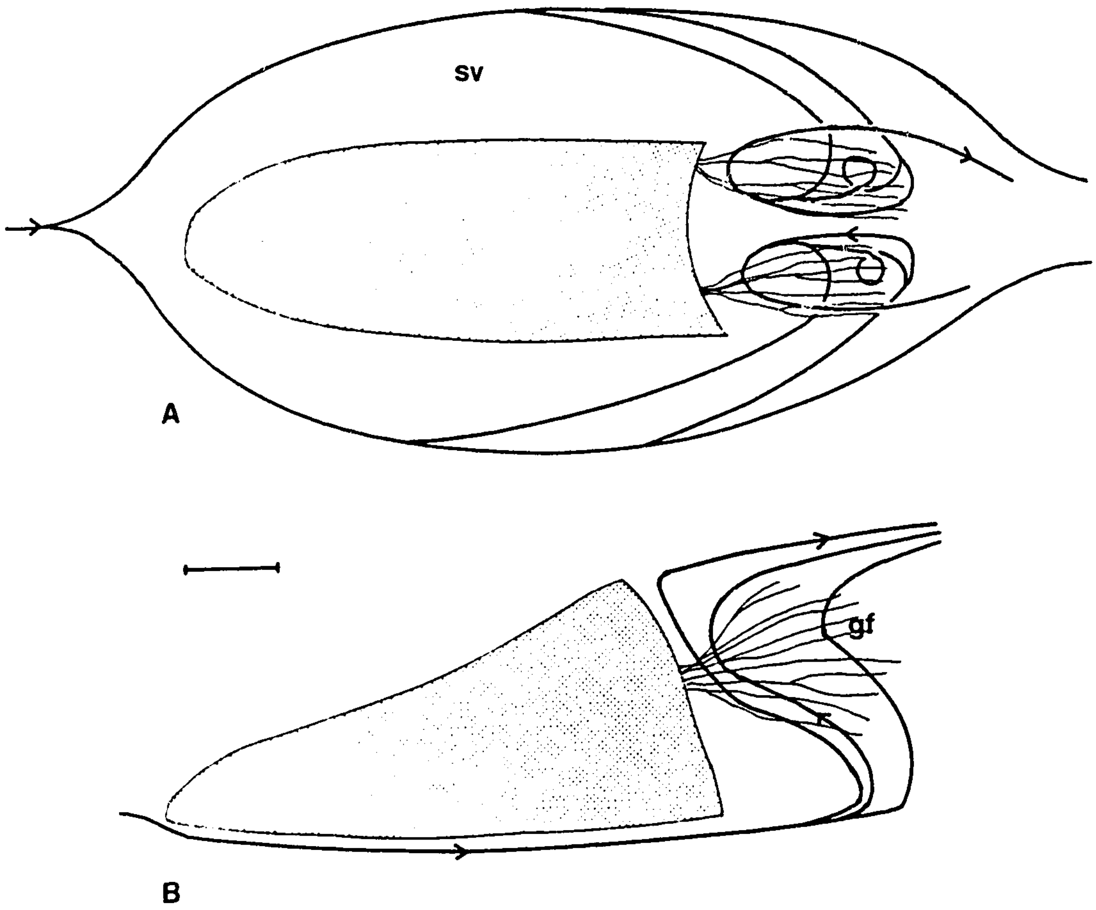

sv
A
gf
B

Figure 2. Flow pattern around the cocoon and pupa of S. arcticum. A) Plan view, showing two connected pairs of vortices, one anterior to the cocoon (av) and one inside its collar (cv). B) Side view. The vortex pair inside the collar receives water from the vortex pair anterior to the cocoon through the anterior fenestrae (af), and from water flowing along the side of the cocoon and in through the lateral fenestrae (lf). Scale bar represents 1 mm. Re=1,450, k/d=1.4.

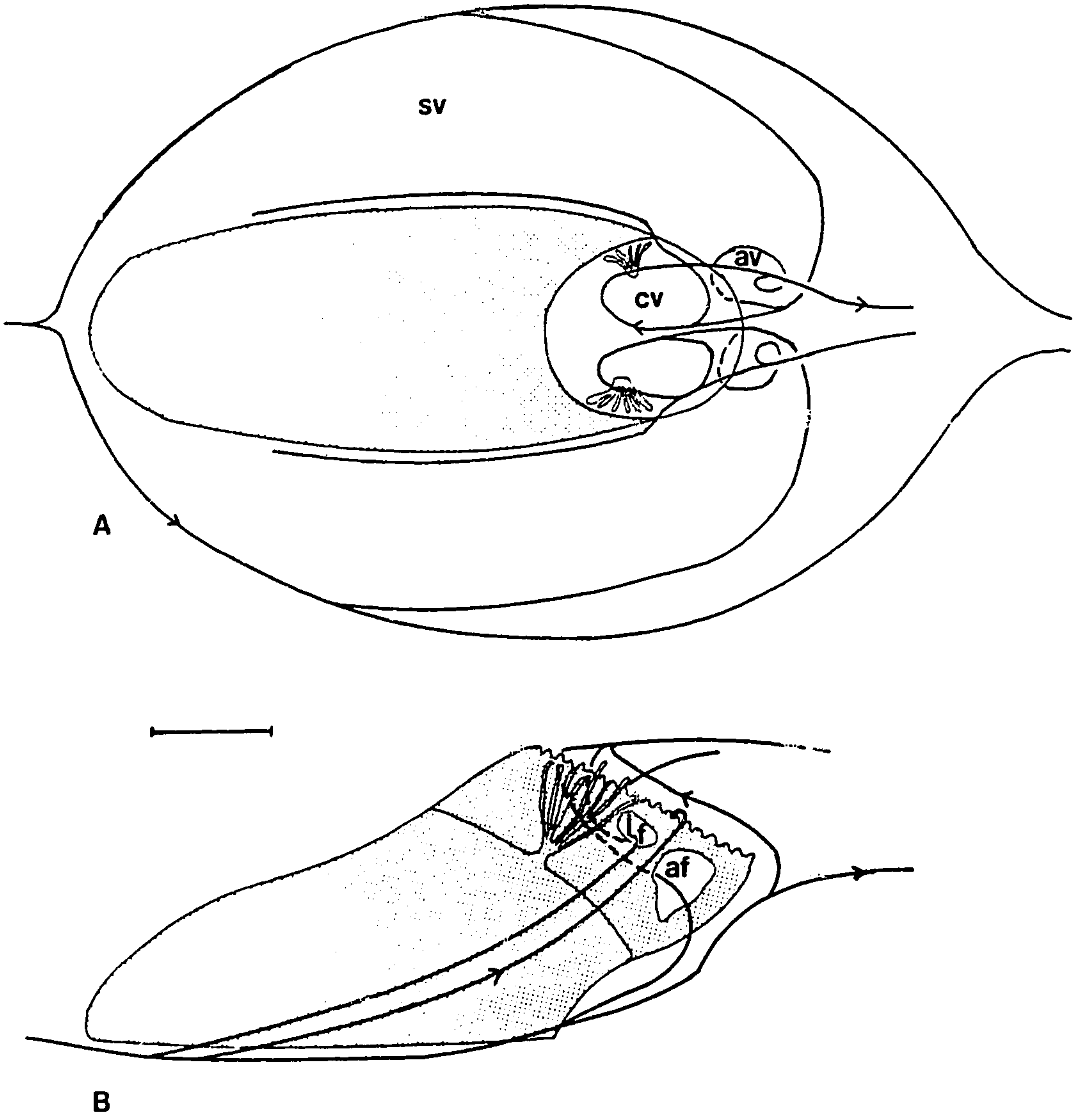

sv
av
cv
A
af
B

Figure 3. Flow pattern around the cocoon and pupa of *S. virgatum*. A) Plan view, showing two unconnected pairs of vortices, one anterior to the cocoon (av) and one inside its collar (cv). Water flows over the dorsum of the cocoon, in through the posterior fenestrae (pf) of the collar, and through the band of gill filaments, after which it forms a pair of vortices (cv). B) Side view. Water of the vortex pair inside the collar exits through the lateral fenestrae (lf) or out the top of the collar. There appears to be no exchange of water between the two pairs of vortices. Scale bar represents 1 mm. Re=1,260, k/d=1.2.

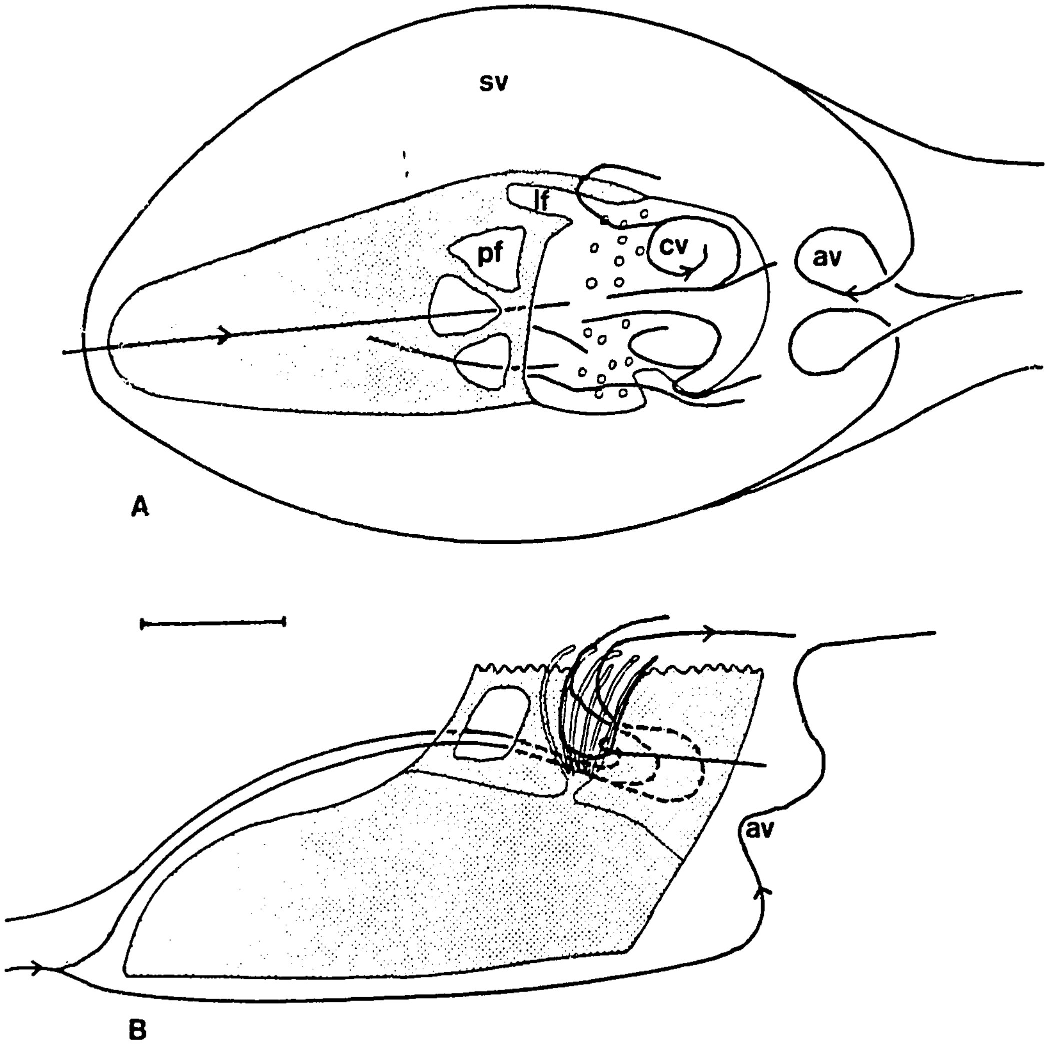

sv
lf
pf
cv
av
A
av
B

Figure 4. Flow pattern around the cocoon and pupa of S. malyschevi. A) Plan view, water from outside the solenoidal vortex (sv) and water flowing along the sides of the cocoon form the vortex pair anterior to the cocoon (av). As this vortex pair rises it widens and flows over top of the collar but does not appear to contribute to flow of water inside it (cv). B) Side view. Most of the water of the vortex pair inside the collar appears to come from water flowing along the sides of the cocoon and in through the fenestrae (f). Scale bar represents 1 mm. Re=840, k/d=0.90

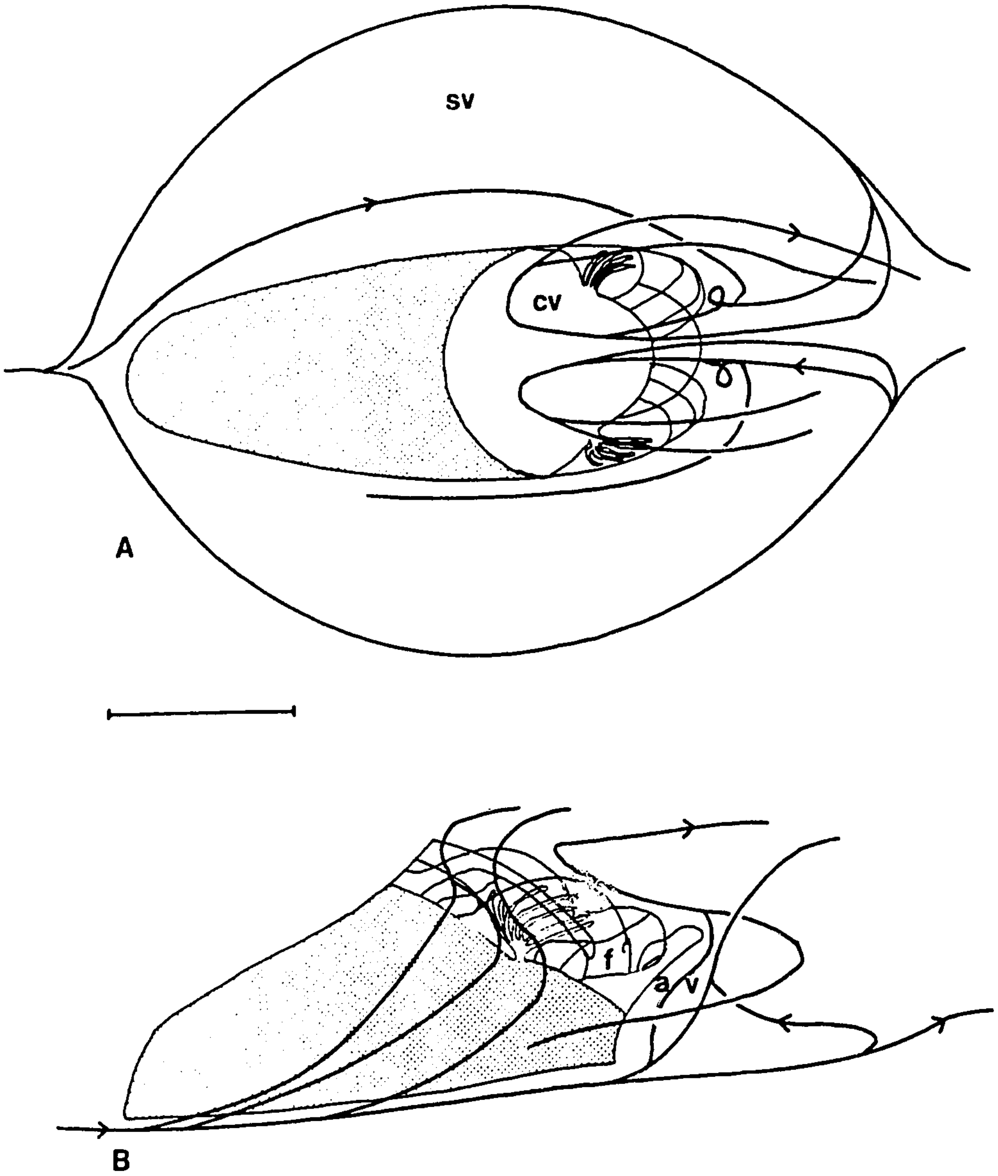
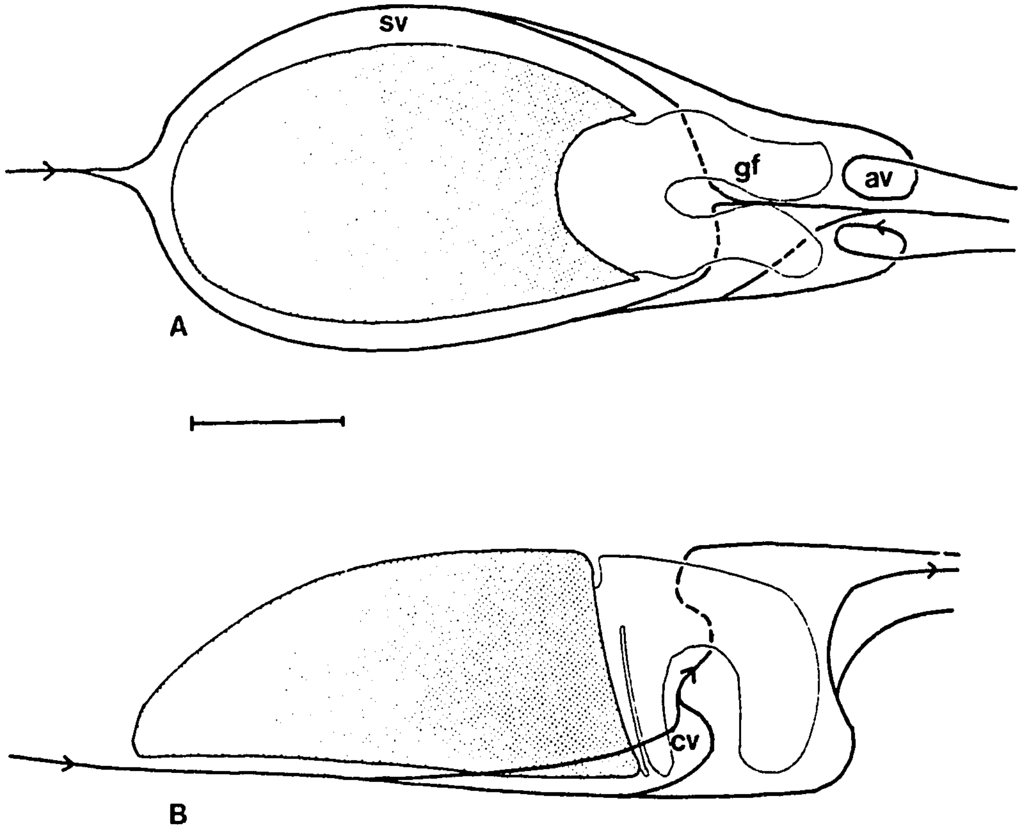

sv
cv
A
f
a
v
B

Figure 5. Flow pattern around the cocoon and pupa of S. canadense. A) Plan view, showing two pairs of vortices, an anterior vortex (av) downstream of the swollen gill filaments (gf) and one inside a chamber created by the gill filaments (cv). Note the relatively thin solenoidal vortex (sv). The vortex in the chamber gets water via a gap in the sides and loses water through a diamond- or oval-shaped hole at the top. B) Side view. The vortex pair (cv) inside the chamber receives water through the gap in the side and loses water through the hole at the top. Scale bar represents 1 mm. Re=1,200, k/d=1.0.


sv
gf
av
A
cv
B

8. CONCLUSIONS

Flow of water is generally considered to be the dominant physical force in the environment of subimaginal black flies. All life stages from egg to pupa are exposed to flowing water for at least part of their duration. Pupae (Burton 1966) and filter-feeding larvae require flowing water to complete development.

Larvae of black flies remain stationary as water flows past them, resulting in drag on the larvae. To remain attached to the substratum, the attachment must be stronger than the drag force acting on the larvae. This was shown to be true for at least one species of black fly (S. vittatum) (chapter 2). Larvae of black flies feed primarily by filter feeding, and an effective filtering apparatus is expected to generate considerable drag (Soluk and Craig 1988). It is shown in chapter two that approximately one half the total drag on a larva is exerted on the fans, although these fans are only a small part of the larva. Extrapolation from the data indicates that drag will never exceed the strength of attachment at velocities commonly encountered in rivers or streams. This suggests that behaviours of larvae, such as establishment of clumped dispersion patterns, are not mechanisms for preventing detachment.

Larvae of black flies have two behavioural mechanisms that can alter the nature of flow past them; 1) the occupation of microhabitats with certain flow characteristics (chapter 3), and 2) the establishment of dispersion patterns that alter flow conditions near a group of larvae (chapter 6). Chapter three shows that larvae were never found under a separated boundary layer, and that they appear to be more common in accelerating flow. Flow over substrata with an attached boundary layer is less turbulent than that over substrata with a separated boundary layer, and areas of accelerating flow are less turbulent than areas of non-accelerating flow. This suggests that larvae avoid areas of highly turbulent flow. Perhaps this is because turbulence affects their filter-feeding efficiency, as suggested in Shimeta and Jumars (in press). Clearly this area requires further attention.

Groups of larvae of black flies exhibit one of three dispersion patterns; spaced, banded and clumped. In chapter 4, it is shown that the dispersion pattern exhibited by a group of larvae is determined by the species composition of the group, and by the velocity of the water flowing over it.

In chapter 5, a group of larvae consisting of two species that would exhibit different dispersion patterns in a group consisting of a single species is examined. It is shown that the dispersion pattern of groups is determined by the most common species in the group and by the velocity of water flowing over the group.

Spaced and banded dispersion patterns were shown to modify the characteristics of flow past groups of larvae (chapter six). The spaced dispersion pattern, which has been shown to increase filter-feeding efficiency at low food availabilities (Ciborowski and Craig 1989), results in only subtle alterations of the system of vortices described by Chance and Craig (1986) around isolated larvae. However, this pattern results in a significant reduction in the buffeting experienced by larvae. Since buffeting is believed to indicate levels of turbulence, spaced dispersion patterns may be a mechanism for reducing the turbulence of water flowing through a group of larvae.

A larva within a banded dispersion pattern did not have the same system of vortices around it as that observed around an isolated larva. A band acted as a single obstacle to flow, and consequently, had its own flow pattern. The most important feature of this flow pattern appears to be the acceleration of water flowing through the fans of larvae. Banded dispersion patterns were exhibited by larvae of C. dacotensis at lower water velocities (chapter 4), and it has been shown that they can filter feed more efficiently at higher water velocities than those at which it exhibits a banded dispersion pattern (Kurtak 1978). For *C. dacotensis* formation of a banded dispersion pattern may be a mechanism for increasing water velocity to a level at which filter feeding is more efficient.

A passive filter-feeding organism, such as a larval black fly, does not create its own current. This has important consequences for the ecology of these organisms, because creating a current requires expenditure of energy. As a result, the concentration of suspended food particles required to make the benefits of filter feeding outweigh its costs may be higher for active filter feeders than for passive ones. There is probably a threshold concentration of particles below which filter feeding is no longer cost-effective. It can be hypothesized that this threshold is lower for passive filter feeders living in rivers or streams, than for active filter feeders living in impoundments. For this reason, an impoundment outlet is often occupied by large populations of filter feeders.

Larvae and pupae of black flies have similar patterns of flow around them. Both have a solenoidal vortex, a pattern common to all objects in a boundary layer (Lugt 1983). Pupae appear to differ from larvae in that they are less streamlined. This is apparent because a well defined pair of vortices, common to bluff bodies in a boundary layer (Sedney 1973), can be seen downstream of the pupae (chapter 7).

Both larvae and pupae appear to be morphologically adapted to harness the energy of vortices. Larvae appear to use the downstream arms of the solenoidal vortex in filter feeding (Chance and Craig 1986), while pupae may use the downstream vortices in respiration. In both, the organisms have become adapted to harness the energy of vortices that are an inevitable consequence of the shape and microhabitat of the organisms. This indicates that flow of water has been an important factor in shaping the behaviour and ecology of subimaginal black flies.

Literature cited

Burton, J. 1966. Observations on cocoon formation, pupal stage, and emergence of the adult of Simulium damnosum Theobald in Ghana. Ann. Trop. Med. Parasit. 60: 48-56.

Chance, M. M., and D. A. Craig. 1986. Hydrodynamics and behaviour of Simuliidae larvae (Diptera). Can. J. Zool. 64: 1295-1309.

Ciborowski, J. J. H., and D. A. Craig. 1989. Factors influencing dispersion of larval black flies (Diptera: Simuliidae): effects of current velocity and food concentration. Can. J. Fish. Aquat. Sci. 46: 1329-1341.

Kurtak, D. C. 1978. Efficiency of filter-feeding of black fly larvae (Diptera: Simuliidae). Can. J. Zool. 56: 1608-1623.

Lugt, H. J. 1983. Vortex Flow in Nature and Technology. John Wiley and Sons. Toronto.

Sedney, R., 1973. A survey of the effects of small protuberances on boundary-layer flows. American Institute of Aeronautics and Astronautics Journal. 11:782-792.

Shimeta, J., and P. A. Jumars. 1991. Physical mechanisms and rates of particle capture by suspension feeders. Ocean. Mar. Biol. Ann. Rev. In press.

Soluk, D. A., and D. A. Craig. 1988. Vortex feeding from pits in the sand: A unique method of suspension feeding used by a stream invertebrate. Limnol. Oceanogr. 33: 638-645.