

# Role of silk threads in the dispersal of larvae through stream pools

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## Keywords

black fly; stream pool; silk; hydrodynamics; drift.

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Editor: Nigel Bennett

Received 23 March 2009; revised 5 May 2009; accepted 11 May 2009

doi:10.1111/j.1469-7998.2009.00598.x

## Abstract

The slow flow found in stream pools should lead to increased larval deposition in habitat unsuitable to many benthic invertebrates such as the larvae of the black fly *Simulium tribulatum*. To increase their chances of successfully transiting a pool, these larvae may use silk threads previously thought to facilitate settlement in fast-flowing habitat. In this study, we tested two ways in which these threads can affect a larva's transport in slow flow. First, a significant decrease in the fall velocity, which should lead to increased drift distance, was found between live (with silk) and dead (without silk) larvae falling in a laboratory chamber. The reduction due to the presence of silk varied over the natural range of larval sizes from a maximum of a 36% reduction for neonates to only 14% for the largest late-instar larvae. A second possible role of silk, that of increasing the chance of resuspension in slow flow due to increased drag forces, was tested using dynamically scaled models of neonate and late-instar larvae. The coefficient of drag ( $C_d$ ) was determined for both model types, with and without scaled silk threads, under conditions recreating a range of naturally occurring Reynolds numbers ( $Re$ ). A significant increase in  $C_d$  was found due to the presence of silk for both life stages across relevant ranges in  $Re$ . The results of this study show that the presence of silk threads should significantly increase the distance larvae travel and their chances of being resuspended should they be deposited on the bed of a pool. Further, the same threads may act to both limit transport in regions of preferred fast flow, while maximizing transport through regions of unsuitably slow flow.

## Introduction

In freshwater streams, the heterogeneous nature of the hydrodynamic environment (Davis & Barmuta, 1989; Hart, Clark & Jasentuliyana, 1996; Bond, Perry & Downes, 2000) may have serious fitness consequences for species that rely on ambient flow to facilitate larval dispersal (Butman, 1986; Abelson & Denny, 1997). Flow conditions can dictate local food availability (Lesser, Witman & Sebens, 1994; Finelli, Hart & Merz, 2002) and predation pressures (Malmqvist & Sackmann, 1996; Hart & Merz, 1998) leading to differential fecundity and survival. Predicting where, and to what conditions dispersing larvae will be delivered is therefore critical to understanding the spatial distribution and demographics of their populations.

An example of an organism for which there is a growing understanding of their interaction with the flow environment is the black fly *Simulium tribulatum*. These flies have benthic, aquatic larvae and flying, terrestrial adults. Best known as pests for humans and prey for fish, they are also an excellent model species for investigating how organisms interact with their hydrodynamic environment. As filter

feeders, *S. tribulatum* seek out regions of fast flow which provide a suitable flux of suspended organic matter for feeding, and a refuge from predators such as flatworms (Hansen, Hart & Merz, 1991; Fonseca & Hart, 2001). Competition for the best flow conditions often leads to overcrowding, conspecific aggression and subsequently diminished feeding opportunities. Under these conditions, these non-swimming larvae actively detach from the bed to drift downstream in search of better conditions (Fonseca & Hart, 1996). Settlement within the same riffle may be difficult, however, due to drag and other hydrodynamic forces impacting the larvae under fast-flow conditions (Fonseca & Hart, 2001; Fingerut, Hart & McNair, 2006). Because the streams these larvae live in consist of alternating fast-flowing riffles and slow-flowing pools, being swept out of a riffle means that they will invariably enter, and possibly be deposited in, a pool. Deposition in a pool exposes larvae to an increased risk of predation, and decreased feeding opportunities due to a decreased flux of food (Hart & Merz, 1998; Fonseca & Hart, 2001). It is therefore critical that larvae be able to limit their deposition in, and increase their ability to leave, these regions.

Slow flow and subsequently reduced turbulence leads to the deposition of particles with small fall velocities such as larvae. This increased deposition should lead to pools acting as sinks, with more larvae entering at the upstream boundary then leaving at its downstream edge. However, of the few studies that have looked for this effect (e.g. Waters, 1962; Martin & Knight, 1989) some have found a sink effect and some have not. This may be partially explained by differences in study species and variations in pool hydrology, which in at least one case (Kovalak, 1978) included regions of fast flow along the pool margin that were suitable for oviposition.

To increase their chances of successfully transiting a pool, *S. tribulatum* larvae may attempt to affect their transport via silk threads. These threads, produced before entering the water column, scale with larval size, (~6 times their 0.6–7 mm body lengths) (Fingerut *et al.*, 2006). Their presence may affect the distance that the larvae travel in two ways. First, the increased drag afforded by the silk should diminish their fall velocities, making them more likely to drift through the pool before being deposited. Similar mechanisms involving secretory threads have been shown to lower fall velocities of larval clams (Prezant & Chalermwat, 1984), mussels (Sigurdsson, Titman & Davies, 1976) and tube worms (Olivier & Retiere, 2006). Second, silk threads may increase the chance of resuspension from the bed. Such a use of silk has been shown to allow spiderlings to ride otherwise insufficiently strong updrafts (Humphrey, 1987; Suter, 1991).

In this study, we test the effect that silk threads may have on the ability of larvae to successfully transit stream pools by both decreasing the rate at which they are delivered to the bed and increasing their chances of being resuspended if deposition occurs. We directly measure the changes in fall velocity due to the presence of silk threads on live (silk is present) and dead (silk is not present) larvae across the range of larval sizes, and using dynamically scaled models investigate differences in the coefficient of drag for both neonate and late-instar larvae over the range of Reynolds number (*Re*) flow regimes that each would experience in the field.

## Methods

### Field collections and culturing

We collected eggs from *S. tribulatum* populations in a riffle ~50 m downstream of the Lake Galena Dam on the North Branch of Neshaminy Creek in Bucks County, PA (latitude 40°17'17", longitude 75°12'15"). Egg masses laid on floating cedar dowels placed in the stream were gently scraped off the wood surface *in situ* and transported back to the laboratory in stream water. Eggs were hatched in incubators containing high oxygen concentrations and suitable velocities (Hart, 1986). Neonate larvae (~600 µm long) were collected on a daily basis to maximize the chance that individuals were still first-instar larvae. Older instars were collected directly off of the dowels or on nearby rocks and

vegetation, kept in similar aerated incubators and used within 48 h of collection.

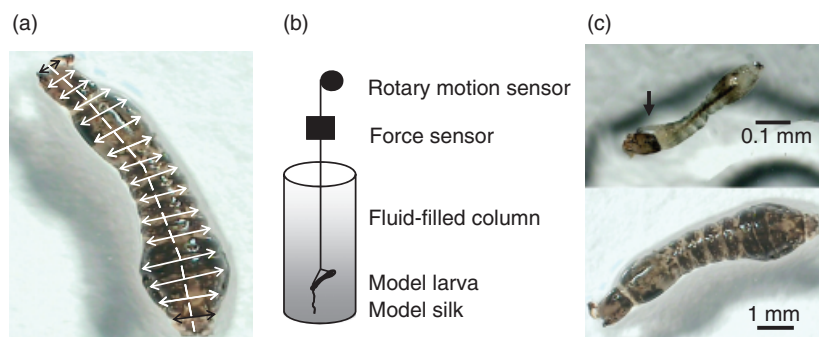
To characterize the flow conditions in the field and determine the range of *Re* regimes that would need to be matched in the laboratory, velocity measurements were taken 2 cm off the bed using a Sontek Acoustic Doppler Velocimeter (Sontek/YSI, San Diego, CA, USA) every 5 m along a 100 m streamwise transect in a pool downstream of the riffle where the eggs and larvae were collected.

### Fall velocity experiments

Fall velocity trials took place in 25 × 40 × 72 cm fall chamber filled with dechlorinated tap water. Larvae were measured before each trial and placed into eight size classes (0.6, 1, 2, 3, 4, 5, 6 and 7 mm). Two treatments were run for each size class (live and dead). Larvae were only counted as live if they displayed movement during their fall. Dead larvae were heat-killed with ~90 °C water and cooled to room temperature. Larvae were transferred, and killed for the non-silk treatment, in small plastic weighboats. No evidence of silk production was seen in these dishes for either treatment. Therefore, as any threads must have been produced once in, or as they entered, the fall chamber, only live larvae would have fallen with attached silk. For each trial, larvae were gently placed into the water column and left to fall. Trials were recorded to a digital video recorder [Everfocus ESDR100 with attached Horita digital in-video stopwatch (Horita Co., Mission Viejo, CA, USA)] with a Sony AVC-D7 camera (Sony Corp of America, New York, NY, USA) whose field of view was set at the vertical mid-point of the water column, which allowed enough time for larvae to reach terminal velocity. Each larva was recorded for at least five times its body length and observed during its descent to ensure that it was not attached to the surface via its silk thread. For each size class 20 fall velocities were measured by determining the position of larvae over multiple frames using SigmaScan Pro software. The effect of larval size on fall velocity was determined with linear regression while the effect of the presence of silk on fall velocity was compared between treatments (with and without silk) using ANCOVA to account for the covariate of larval size (Zar, 1974).

### Drag measurement experiments

Scale models of both neonate (0.6 mm) and late-instar (6 mm) larvae were produced in lead based on measurements from field-collected larvae. Models were used instead of actual larvae because there is no way to eliminate the larvae's silk production without killing them. The use of dead larvae would have introduced a number of other factors that could have had a significant influence on the resuspension rate of these particles, including particle orientation and the differential attachment strength to the bed. To produce measurable forces, it was necessary to increase the scale of the models to 100:1 for the neonates and 10:1 for the late-instar.



**Figure 1** (a) Measurement points for width and length used in determining the form of neonate and late-instar larval models. (b) Schematic of the drag trial setup showing the positions of the motion sensor, force sensor and orientation of the larval model in the fluid-filled column. (c) Photos of neonate (top) and late-instar (bottom) larvae. The thoracic proleg, which is particularly prominent in the neonates is noted by the arrow.

To determine the shape of the larvae, digital still images of multiple neonate and late-instar larvae were captured using a Hitachi KP-D20A CCD camera (Hitachi Kokusai Electric America, Ltd, Woodbury, NY, USA), and Flashbus Spectrim (Integral Technologies, Indianapolis, IN, USA) framegrabber. Measurements of the larval shape were then determined using SigmaScan (Fig. 1a). The models were first sculpted out of clay (Sculpy Mark III), and then cast in silicone (RTV325) to produce a negative mold from which the final lead model was produced. The delicate morphology of the labral fans, used for feeding, could not be reproduced in the models. However, as observations of larvae under pool-like conditions showed that the fans were not extended when not feeding, their absence from the models is not problematic. The silk for these trials was mimicked with a thin (0.5 mm) flexible silver chain that was dense enough to settle into the proper position below the model, and was scaled to the length of the models (6 times body lengths). For those trials in which the chain was used, it was attached with super glue to the ventral face of the head, reproducing the natural point of silk production and attachment.

To determine whether or not the presence of silk threads would increase the chance of larval resuspension we towed models at varying speeds, both with and without silk, through a fluid-filled column while measuring the tension with a force transducer. Because of the increased size of the models it was necessary to increase the viscosity of the fluid to mimic field flow conditions. These flow conditions can be characterized using the non-dimensional  $Re$ . Three different fluids were used to reproduce the ranges in  $Re$  that were relevant for each lifestage (see 'Results'). The medium (100 cP,  $1.3 \text{ kg L}^{-1}$ ) and low (25 cP,  $1.2 \text{ kg L}^{-1}$ ) viscosity fluids were sucrose solutions prepared by dissolving table sugar in deionized water. To produce a sufficiently viscous solution to replicate the lowest part of the  $Re$  range we used castor oil (540 cP,  $0.98 \text{ kg L}^{-1}$ ). Viscosity and density were determined for all three fluids using a kinematic viscometer tube (Fisher Scientific, Pittsburgh, PA, USA) and a pycnometer bottle.

Larvae were suspended with monofilament line, head down, at a  $43^\circ$  angle within the cylinder (Fig. 1b). This angle corresponded to the average measured from still images of settled larvae in a recirculating flume under pool-like condi-

tions. For each trial both the force transducer (Vernier wireless dynamics sensor system, Vernier Software & Technology, Beaverton, OR, USA) and the rotary motion sensor (PASCO, PASCO Scientific, Roseville, CA, USA) measuring the model's velocity were zeroed. The model was then lowered into the 15 cm diameter, 1.3 m high PVC column to sit for 3 min to allow turbulence in the fluid to dissipate, and the silk (if present) to settle below the model (Fig. 1b). A value from the force transducer was then taken for use in calibrating the tension during the trials.

Once settled, the model was pulled upwards by winding the monofilament onto a spool powered by an electric motor. The force measured by the transducer, and the velocity measured by the rotary motion sensor, was collected using a Vernier datalogger (Vernier Software & Technology, Beaverton, OR, USA) at 100 Hz. At least four different speeds (replicated three times each) were used for each model type (neonate and late-instar) under each of the two conditions (silk and no silk) in each fluid. In each trial, a region of constant velocity lasting at least 1 s was used to determine the mean tension force. The range of velocities in each fluid was bounded at the low end by the force transducer's detection limit and at the high end by the need to capture at least a second of recording time once the model reached a steady speed.

The recorded tension force was used to calculate a non-dimensional parameter, the coefficient of drag ( $C_d$ ) (Faber, 1995), allowing us to make inferences about the effect of silk on real larvae.  $Re$  and  $C_d$  data were linearized with log transformation to account for the power relationship between the two variables (Faber, 1995). The effect of silk on the drag coefficients for each model type, over the relevant  $Re$  range, was then analyzed via ANCOVA to account for variations in  $Re$  between treatments. In addition, the difference in  $C_d$  at a given  $Re$  between the model types was calculated across the entire range of  $Re$  via ANCOVA, allowing us to investigate the effect of body morphology.

## Results

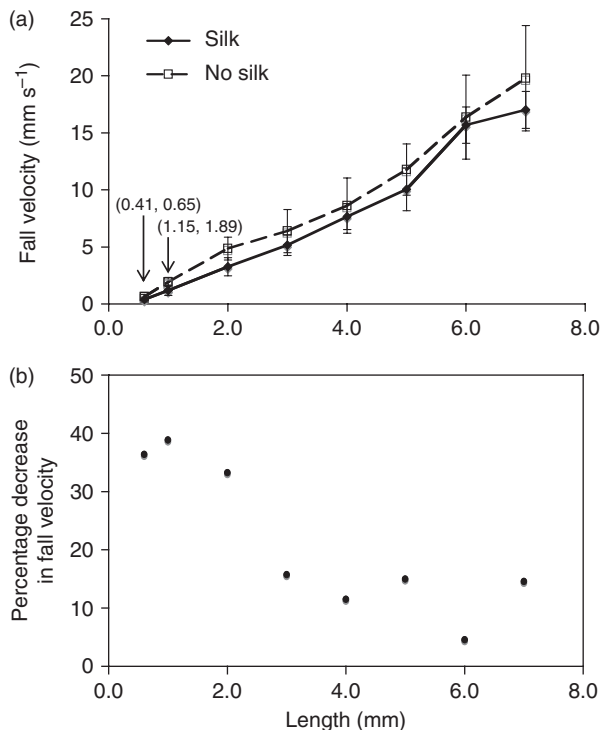
### Field flow conditions

Near-bed velocities ranged from  $5.5$  and  $22.1 \text{ cm s}^{-1}$  (10th and 90th percentiles). This variation, combined with a

heterogeneous bed-topography (mud, gravel and bedrock), should lead to wide variations in the types of flow conditions larvae would experience depending on where they were deposited. Further, due to the large size of the late-instar larvae compared with the neonates, and the increase in flow speed with height off the bed due to boundary layer flow, we would expect  $Re$ 's for late-instar larvae to be at least an order of magnitude greater than those for neonates at any given position in the pool.  $Re$ 's experienced by neonate larvae would be between 0 and  $\sim 130$  (equivalent to an average flow speed of 0 and  $22 \text{ cm s}^{-1}$ , respectively) due to their small size and the slow-flow conditions expected so near to the bed ( $< 1 \text{ mm}$ ). By comparison, the  $Re$ 's experienced by late-instar larvae could range up to  $\sim 1000$  but would not be expected to drop below 30 (equivalent to an average flow speed of  $0.5 \text{ cm s}^{-1}$  over the length of their body) due to their size.

### Fall velocity trials

Observations of falling larvae showed a clear difference in their orientation depending on whether they were alive or dead. Dead larvae fell with their bodies oriented horizontally, while live larvae fell with their bodies oriented along the axis of their fall. Average fall velocity increased by a factor of 45 over the range of larval sizes (0.6–7.0 mm) for



**Figure 2** (a) Fall velocities recorded for larvae with (live) and without (dead) silk by larval length in a laboratory fall chamber. Parenthetical values represent data points (live, dead) for the two smallest larval sizes whose values may be difficult to discern from the graph. (b) The percentage decrease in fall velocity due to the presence of silk, by size class.

larvae with silk ( $F$  test:  $F = 664.4$ , d.f. = 1,158,  $P < 0.001$ :  $r^2 = 0.81$ ), and a factor of 30 without ( $F$  test:  $F = 2396.9$ , d.f. = 1,158,  $P < 0.001$ :  $r^2 = 0.94$ ), disproportionate to the factor of 12 increase in body length. Across the entire size range the presence of silk caused a significant decrease in the fall velocity (ANCOVA  $F = 24.55$ , d.f. = 1,317,  $P < 0.001$ ; Test for homogeneity of regressions  $F = 6.66$ , d.f. = 1,317,  $P = 0.25$ ) (Fig. 2a). This difference did not increase at the same rate as the fall velocity of larvae without silk, leading to a decrease in the relative effectiveness of silk to slow the larval fall velocity from 36% for neonates (0.6 mm in length) to just 14% for the largest late-instar larvae (Fig. 2b).

### Drag trials

Measurements of morphology indicated that neonates generally have a more 'hour-glass' shape to their body with their head averaging  $\sim 90\%$  of the width of the posterior region and a more protruding thoracic proleg (Fig. 1c). Late-instar larvae, by comparison, only reached 71% of the maximum width measured in the posterior region.

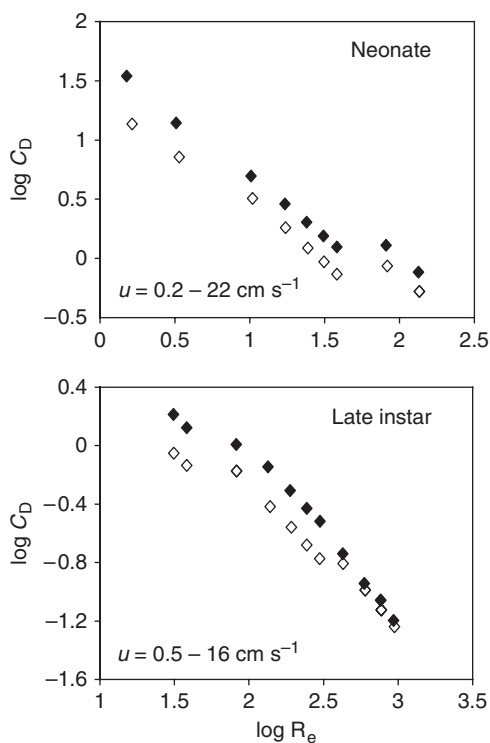
Log transformation of both  $Re$  and  $C_d$  produced linear relationships between the two variables for both life stages in the presence and absence of silk ( $r^2$  for all treatments  $> 0.96$ ) over the relevant ranges in  $Re$ . Analysis of the transformed data with ANCOVA indicated that there was a significant increase in  $C_d$  due to the presence of silk for both model types. The effect of silk on  $C_d$  over the range of  $Re$  tested was not, however, the same for both larval types. No difference was seen between the slopes of the silk and no-silk treatments for neonates; the presence of silk on the late-instar model caused a greater increase in  $C_d$  at lower  $Re$  than at higher  $Re$  (Table 1, Fig. 3).

Comparison of larval morphologies showed a significantly greater  $C_d$  measured for the neonatal form compared with the late-instar at the same  $Re$ . (ANCOVA  $F = 21.74$ , d.f. = 1,94,  $P < 0.01$ ). This difference in  $C_d$  was not constant increasing as  $Re$  increased as evidenced by a significant difference in the regressions (test for homogeneity of regressions  $F = 5.84$ , d.f. = 1,93,  $P = 0.02$ ) between the two models over the  $Re$  (1.5–1000) tested.

**Table 1** Summary of ANCOVA results for comparisons of coefficients of drag for model larvae with and without silk attached over relevant ranges of  $Re$

Model	d.f.	$F$	$P$
Neonate ( $Re = 1.5\text{--}134$ )			
ANCOVA	1,52	53.83	$< 0.01$
Homogeneity of regressions	1,51	3.32	0.07
Late-instar ( $Re = 31\text{--}940$ )			
ANCOVA	1,64	56.54	$< 0.01$
Homogeneity of regressions	1,53	11.99	$< 0.01$

$P$  values represent the effect of the presence of silk.  $Re$ , Reynolds number.



**Figure 3** Coefficient of drag calculated for model larvae with (closed symbols) and without (open symbols) silk as they were towed vertically through fluid-filled columns recreating a range of Reynolds number conditions. Error bars denoting standard deviation are within the size of the data points. Corresponding real-world velocities for the range of  $Re$  for each larval type are provided.

## Discussion

This study shows that due to the increased drag imparted by silk threads, larvae can lower their fall velocity and possibly increase their chances of being resuspended after deposition. Both of these effects should lead to a greater chance of successfully traveling through areas of unsuitably slow flow.

### Effect of silk on fall velocities

In this study, larvae with silk threads were shown to have significantly smaller fall velocities than larvae without silk (Fig. 2). This decrease can be attributed to the presence of threads based on the orientation of the larvae during their descent. Larvae in the no-silk treatment (which fell sideways) would be predicted, due to the larger cross-sectional area exposed in the direction of the fall, to fall slower than the silk treatment (which fell vertically) (Gerhart & Gross, 1985). The results, however, show the opposite pattern with two possible causes for live larvae falling more slowly: extension of labral fans or presence of silk. Though the labral fans have been shown to be hydrodynamically significant in previous studies (Eymann, 1988; Thomson *et al.*, 2004), examination of the video showed no fan extension while falling. It is not known why larvae do not use their

fans in this manner but it is possible that their deployment leads to tangling of the threads or other disruption of its effectiveness. This left us with the presence of silk as the only other difference between the live and dead treatments. While silk could not be observed on the video due to its size ( $\sim 3 \mu\text{m}$ ), it was possible to ‘catch’ falling live larvae by passing a thin wire above the them, indicating that they were indeed trailing silk threads.

A decrease in fall velocity should result in all sizes of larvae traveling farther before deposition (Elliott, 1971; McNair, Newbold & Hart, 1997). The difference in distance traveled due to the presence of silk, however, would vary greatly with larval size. The distance larvae travel before hitting the bed can be predicted by the formula  $x = uh/w_s$ , where  $u$  is the average horizontal fluid velocity,  $h$  is the height of the water column and  $w_s$  is the larva’s fall velocity. The pools downstream of the riffle in which these larvae were collected average  $\sim 100$  m in length, 25 cm in depth and an average mid-column water velocity of  $\sim 15 \text{ cm s}^{-1}$  (Schamel, 2008). Using the measured fall velocities for both neonate and the largest late-instar larvae we can calculate that without silk the smallest larvae would travel 58 m compared with only 1.9 m for the largest. When the silk effect is included the differences are even greater: the added travel distance due to silk for the largest larvae starting at the water’s surface would only be 0.3 m, whereas the neonates could extend their distance an additional 33 m. This effect, combined with their already small fall velocity, should allow at least some of the smallest larvae to drift through the entire  $\sim 100$  m pool before contacting the bed.

### Effect of silk on resuspension

For those larvae that are not able to transit regions of slow flow in one trip, resuspension may be facilitated by the presence of silk threads. Comparison of dynamically scaled model larvae, with and without silk, showed that the presence of threads led to a significant increase in the coefficient of drag across the range of flow conditions each lifestage would be exposed to in stream pools. This increase in the coefficient indicates that larvae would experience a larger drag force as well.

Predicting the exact conditions under which a particle will be resuspended by turbulent flow, and therefore what the actual effect of silk will be for either life stage, is difficult. Though engineering models are available to predict the transport of passive particles such as sediment, predictions for biotic, non-spherical particles, particularly ones that can vary their adhesion and orientation relative to the bed, are highly sensitive to particle shape, orientation and surrounding bed-grain size (Fischenich, 2001) and beyond the scope of this study. Qualitatively, however, the increased drag forces on a larva should decrease the velocity or turbulence level near the bed necessary for resuspension (Dey, 2003; Olivier & Retiere, 2006).

The differences in  $C_d$  that were observed between the two models at similar  $Re$  may reflect competing needs of the larvae at different times of their life. Scaled to the same size

there was a significant increase in the  $C_d$  for the neonate morphology compared with that of the late-instar, increasing from just 5% in the lowest  $Re$  regime to 29% in the highest. For larger larvae, which are usually able to out-compete smaller larvae for the fastest microhabitats with the largest fluxes of suspended food, their streamlined shape may reduce the drag they experience, making it easier to remain attached to the bed and feed where velocities can be  $> 1 \text{ m s}^{-1}$ . For neonates, who make up the majority of the drifting population (Crosskey, 1990; Fonseca & Hart, 1996), the need to facilitate dispersal may be paramount and even a small increase in drag may be advantageous.

### Role of silk

Though silk plays an integral role in the black fly's life cycle, including attachment to the bed for feeding and construction of its pupal cases, relatively little is known about its use in thread form (Adler, Currie & Wood, 2004). Larvae have been shown to produce threads before dispersing and those threads have been shown to greatly increase the chances of larvae making and maintaining contact with the bed after drifting, particularly in regions of fast flow where hydrodynamics forces (e.g. drag, acceleration reaction) would otherwise impede settlement (Fonseca & Hart, 2001; Fingerut *et al.*, 2006).

This study provides evidence that larvae may be able to use the same silk threads that increase the chance of remaining in a riffle to increase their chances of transiting an adjacent pool. At first glance, these goals appear to be contradictory: increasing stopping ability while also increasing the ability to disperse farther. The different hydrodynamic regimes found in pools and riffles, however, may enhance the appropriate effect of the silk in each situation. For larvae already on the bed in slow flow, the production of silk from glands at the anterior end of the larvae would place it as far away as possible from the bed where flow would be fastest due to boundary conditions, and the chance of contact with the bed is minimized. Further, when drifting in the slow-flow conditions the larval body would, as seen in the fall velocity trials, most often ride below the silk. Therefore the silk would not increase the chances of making contact with the bed and would not limit downstream movement. In fast flow, however, where making contact is paramount, the turbulent nature of the riffles should spin and randomize the orientation of the silk-larva complex such that the silk would ride below the larvae at least part of the time (Fingerut *et al.*, 2006). This would increase the effective size of the larvae and its chances of making and maintaining contact with the bed. Therefore, both uses for the silk can exist simultaneously without one interfering with the effectiveness of the other.

### Acknowledgments

This research was supported by the Saint Joseph's University Summer Scholars and Faculty Development Funds.

Funding for graduate student was provided by the National Science Foundation grant GK-12 0440506. The authors thank Douglas Jerolmack, Scott McRoberts and two anonymous reviewers for their thoughtful comments on earlier drafts. This is publication #17 of the Institute for Potamological Biofluidynamics.

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