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Stream insects as passive suspension feeders: effects of velocity and food concentration on feeding performance

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Abstract Benthic suspension feeders are important components of aquatic ecosystems, often dominating the use of space and influencing patterns of material cycling between the water column and benthos. Biomechanical theory predicts that feeding by these consumers is governed by the flux (i.e., product of food concentration and velocity) of particulate material to their feeding appendages. We performed a laboratory flume experiment to test how feeding by larval black flies (*Simulium vittatum* Zett.) responds to independent manipulations of flow and food concentration. We quantified larval body posture, flick rate of the labral fans, and ingestion rate as a function of two concentrations of a baker's yeast/chalk suspension (0.96 and 4.44 mg l^{-1}) and five water velocities (20, 30, 45, 60, and 90 cm s^{-1}). Using analysis of covariance, we found that both flick rate and ingestion rate increased in a decelerating manner with increasing velocity, while fan height decreased linearly with increasing velocity. In contrast, food concentration had no effect on any aspect of feeding behavior. Thus, although both velocity and food concentration contribute to particle flux, our results indicate that the two were not substitutable under the range of conditions tested here.

Keywords Suspension feeding · Benthic-pelagic coupling · Streams · Black fly · Hydrodynamics

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Introduction

Benthic suspension feeders remove particulate organic matter from the water column and transform it into products that are available to the benthic community (e.g., body mass, fecal pellets, mucus, silk). This direct conduit of benthic-pelagic coupling has been shown to be important in both freshwater (e.g., Wallace and Merritt 1980; Wallace and Webster 1996) and marine habitats (e.g., Wildish and Kristmanson 1997), and may be amplified where suspension feeders form dense populations (e.g., mussel beds, oyster reefs, aggregations of insect larvae). In fact, under favorable conditions benthic suspension feeders can remove 50% or more of particulate material from near-bed waters (Glynn 1973; Frechette et al. 1989; Butman et al. 1994), although seston removal rates integrated over the whole water column are probably much lower, even in shallow streams (e.g., 1 to 2%, Wallace and Merritt 1980; Wallace and Webster 1996). Nevertheless, seston removal by suspension feeders can influence such important processes as nutrient spiraling (Newbold et al. 1982; Wotton et al. 1996), food availability and growth of benthic organisms (Peterson and Black 1987; Frechette et al. 1989; Butman et al. 1994) and benthic energy flow and secondary production (Dame et al. 1984; Frechette and Bourget 1985; Wotton 1988; Malmqvist et al. 2001).

To understand the temporal and spatial patterns of material cycling and benthic-pelagic coupling, we need to determine the factors that contribute to ingestion rates of benthic suspension feeders. For example, foraging theory based on aerosol filtration principles predicts that the maximum ingestion rates of passive suspension feeders should occur at intermediate velocities (Rubenstein and Koehl 1977; Shimeta and Jumars 1991). At slower velocities, ingestion rates should be reduced due to a low flux of particles as well as lowered filtering efficiency caused by thick boundary layers surrounding filter elements. In contrast, when velocities are very high, ingestion rates should be reduced by filter clogging (due to increased particle flux) or by lowered filter performance

due to high drag. This example highlights the importance of both flow and food concentration (i.e., flux) in determining suspension feeding rates and, hence, the strength of benthic-pelagic coupling.

Larval black flies (Diptera: Simuliidae) inhabit a wide range of stream and river environments, and have proven to be a particularly useful group for understanding suspension feeder ecology. For example, larvae often demonstrate strong preferences for a restricted range of ambient velocities (Lacoursière 1992; Fonseca and Hart 1996) and exhibit spatial patterns within aggregations (Hart 1986; Ciborowski and Craig 1989) that may allow them to achieve higher ingestion rates. Moreover, experimental studies have demonstrated that the morphology of feeding structures (=labral fans) can be a phenotypically plastic response to variations in ambient flow conditions (Zhang and Malmqvist 1996, 1997; Palmer and Craig 2000) or seston loads (Lucas and Hunter 1999; Palmer and Craig 2000). Collectively, these results support the view that natural selection has molded the behavior and morphology of black flies to increase larval ingestion rates, and imply that flow will be a critical factor affecting feeding and associated processes (e.g., benthic-pelagic coupling, habitat selection, and growth).

Larval ingestion rates are likely to be controlled by a suite of interacting factors, including particle concentrations, flow patterns, larval posture, and particle handling behavior. Larvae reside either partially or fully within the momentum boundary layer, in which water velocity tends to increase with height above the bed (e.g., Vogel 1994; Hart et al. 1996). Therefore, changes in larval posture that alter the height at which the labral fans are positioned above the bed can in turn affect the flux of particles to larvae. Several studies have suggested that larval posture represents a response to drag forces that usually deflect the larval body towards the bed, as well as to larval behaviors that can position the fans farther above the bed than might otherwise occur (e.g., Chance and Craig 1986; Hart et al. 1991; Lacoursière and Craig 1993). As suspended particles are intercepted by the labral fans, they are transferred to the mouth via periodic "flicking" motions (Craig and Chance 1982). Experimental studies have demonstrated that the rate of fan flicking is strongly affected by both velocity and particle concentration (Schröder 1980, 1987a; Craig and Chance 1982; Hart and Latta 1986).

Although a number of independent studies have examined how particular components of larval feeding behavior are affected by either water velocity or particle concentration, we presently lack an understanding of the way that feeding behavior responds as an integrated system to the effects of both velocity and seston concentration. Accordingly, we conducted a factorial experiment in a laboratory flume to examine the effects of velocity and particle concentration on the posture, flick rate, and ingestion rate of *Simulium vittatum* larvae. We initiated this study with the following predictions: (1) larval head height above the bed will decrease with increasing velocity, and will also be higher under low food concentrations; (2) flick rate will asymptotically increase with velocity and be higher under high food concentrations; (3) ingestion rate will increase asymptotically with velocity and increase with food concentration.

Materials and methods

Larval collection and maintenance

We collected *S. vittatum* larvae from Taylor Run (a third-order stream near Route 322 in West Chester, Chester County, Pennsylvania) during mid summer, and rapidly transported them to the laboratory in small plastic containers filled with stream water. Prior to their placement in the experimental flume, larvae were held in a 20-l artificial stream (Hart and Latta 1986) that was filled with untreated well water from the Swarthmore College campus. We maintained a mean velocity over the cross section of the artificial stream of ≈14 cm s^{-1} and a temperature range of 24–25°C (similar to conditions in Taylor Run). We provided a diet of baker's yeast at a concentration of ~1 mg l^{-1}, and changed the water in the artificial stream daily. Larvae were acclimated in this artificial stream for at least 12 h before experimentation, but they were never held in this stream for >2 days prior to their use in the experiment. For one entire treatment combination (i.e., 60 cm s^{-1} low food), however, larvae were inadvertently acclimated for <12 h; data from this trial were subsequently discarded.

The flume and velocity profiles

We conducted our experiments in a recirculating, gravity-driven acrylic flume filled with untreated well water. Water entered the main flume channel (17.6 cm wide×112 cm long×10 cm high) from a head tank and exited the channel into a sump tank, from which the water was pumped back to the head tank. Water velocity (nominal range 20–90 cm s^{-1}) and depth (range 1.5–3 cm) were controlled via changes in the bed slope, discharge from the head tank, and plastic weirs at the flume exit. An 8×20-cm central working section was demarcated 70 cm downstream from the channel entrance, and the flume bottom was left bare. We maintained the water temperature at 24.1±0.4°C (±SD) over the course of our experiments.

We examined the effect of flow on larval feeding behavior by creating five nominal water velocities (i.e., 20, 30, 45, 60, and 90 cm s^{-1}). Flow conditions were chosen to mimic velocities experienced by black flies in Taylor Run (e.g., Hart et al. 1996). Vertical velocity profiles were measured at five locations in the working section (i.e., its four corners, as well as its center) to quantify stream-wise and cross-stream variation in flow conditions. Velocities were measured at four heights above the bed (i.e., 0.03 cm, 0.13 cm, 0.23 cm, 0.53 cm) at a sampling frequency of 20 Hz for 204.8 s (4,096 pts) using a computer-based analog to digital system (National Instruments LPM16) and a Dantec 55 M hot-film anemometer (6% overheat) and 70-µm diameter probe (type R14) (see also Hart et al. 1996). The hot-film probe was calibrated using stroboscopic flow visualization (e.g., Fonseca and Hart 1996).

The experiment

At the beginning of each day, we filled the experimental flume with 250 l of untreated well water and allowed it to run continuously thereafter. Once the flow was adjusted and velocity profiles were measured, pre-dissolved baker's yeast (particle size range= 2–10 µm) was added to the flume water yielding a final concentration of either 1.2 mg l^{-1} (low food) or 6 mg l^{-1} (high food). We then quickly transferred (<60 s exposure to air) 20–40 larvae from the small artificial stream to the working section of the experimental flume. We allowed larvae to acclimate for 5–10 min before beginning the experiment.

At the beginning of each feeding trial, colored chalk particles (size range 5–70 µm) were added to the flume water, providing a visible gut marker for quantifying ingestion rates. The resulting chalk concentrations (2.5 mg l^{-1} and 12.5 mg l^{-1} for the low and high food treatments, respectively) preserved the five-fold difference in yeast concentration between the two treatments and ensured that food quality (≈33% nutritive yeast particles) as determined by the ≈1:2 yeast to chalk ratio was the same for both treatments. The combination of yeast and chalk produced a total seston concentration of 3.7 mg l^{-1} and 18.5 mg l^{-1} for the low and high food treatments, respectively. These seston characteristics are similar to those commonly encountered by black fly larvae in the field. For example, although we did not sample at the time of these experiments, recent measurements show average seston concentrations in Taylor Run of 10–14 mg l^{-1} and particle sizes from 6 to 84 µm. Similar organic loads (Morin et al. 1988c), particle size ranges (Kurtak 1978; Wotton 1992), and seston concentrations (Morin et al. 1988a, 1988b, 1988c) have been reported for other natural streams. Potential changes in particle concentration during a trial (e.g., due to ingestion or sedimentation) were assessed by comparing the dry mass of seston at the beginning and end of each trial. A single water sample (1–4 l) was collected at the start and end of each trial and filtered onto pre-combusted, pre-weighed glass fiber filters (0.47 µm). Dry mass estimates were obtained after these filters were dried at 60°C for a minimum of 24 h.

Feeding behavior data for a given trial were gathered for all larvae except those that moved out of the working section or those likely to experience disrupted velocity fields due to their close proximity to other larvae (e.g., Ciborowski and Craig 1989; Clark and Hart 1995). We used a horizontally oriented camera to assess the posture of an individual larva relative to the flume bed, and deployed a vertically oriented camera (positioned beneath the flume bed) to record its flick rate. The posture and flick rate of a given larva were recorded simultaneously by the two cameras for ~90 s, after which the cameras were repositioned to videotape the next larva.

The total feeding time for larvae during a particular trial ranged between 33 and 76 min, depending on the experimental treatment. For example, the duration of a feeding trial was greater when expected gut passage times were longer (e.g., at low velocities and low particle concentrations). At the end of each trial, each focal larva was gently removed from the flume and placed in an individually labeled vial containing 95% ethanol. The total feeding time for a particular larva was defined as the elapsed time between the addition of colored chalk and the time when that larva was removed from the flume.

Following each trial, we replaced the ethanol solution in each vial with a 10% KOH solution, and allowed the larva's body wall to clear for 24 h. We then measured the body length of each larva using a dissecting scope fitted with an ocular micrometer. We also used a camera lucida to trace the outline of each larva and the portion of its gut filled with colored chalk. The outline of the gut was cut out and weighed; the resulting mass of the paper was used as a surrogate for gut volumes to calculate ingestion rates. This procedure was necessary because irregularities in gut geometry precluded the use of a simple metric of gut filling such as the length of gut that contained colored chalk (e.g., Hart and Latta 1986). The ingestion rate for an individual was calculated by dividing the paper mass (∝gut volume filled with colored chalk) by the elapsed time between the beginning and end of its feeding trial.

On a single day, we were able to complete three replicate feeding trials for a particular combination of the experimental treatments (e.g., low food, 30 cm s^{-1}). Between each trial, we removed suspended particles from the water by passing it through four 0.1-µm cartridge filters (Keystone Filter) for at least 20 min at a rate of 250 l min^{-1}. The total experiment required 10 days, and spanned a period of 2 weeks. We ran all five velocity treatments for the high food concentration during the first week, followed by the same set of velocity treatments for the low food concentration during the second week. For both the low and high food treatments, the order of velocity treatments among days was randomized.

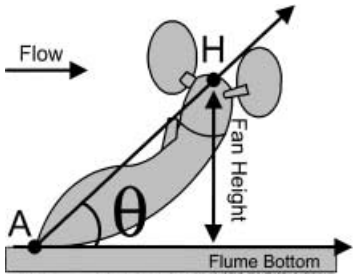

Fig. 1 Schematic showing the orientation of a typical black fly larva in flow and the posture measurements made from the videotape. Fan height was estimated from the sine of the angle (θ) formed by the intersection of the flume bottom with a line segment joining the larva's head (*H*) and its attachment point with the flume bottom (*A*). Because fan height and the body angle (θ) are closely related, our analyses used fan height as the metric of posture

Our experimental design represents a compromise between the ideal of complete randomization and logistical practicality. For example, the difficulty of establishing and quantifying specific near-bed flow conditions prevented us from replacing water or changing flow treatments between trials. Instead, we filtered flume water between trials to remove yeast and chalk, and ran all three trials of a particular velocity treatment on a single day. As a consequence, our design is not randomized with respect to potential among-trial effects of solutes that may have remained in the water after filtering, nor to possible among-day variations in the chemistry of well water. The potential for pseudoreplication appears to be small, however, because our results did not vary systematically with trial order, and because well water quality usually exhibits little day-to-day variation. Similarly, we completed all the velocity treatments for the low food treatment during the first week of the experiment and repeated those velocities for the high food treatment in the second week, rather than interspersing the low and high food levels during the 2-week period. Thus, our ability to assess the food treatment effect could be confounded by changes in larval size between these 2 weeks. We compensated for this potential artifact by standardizing our results to mean larval body length (see Statistical Analyses below).

Video analysis

The flick rate of a focal larva was quantified by counting the total number of times that either labral fan was fully abducted and adducted during a 50-s segment of videotape (e.g., Hart and Latta 1986). We made replicate measurements of larval posture from three still video frames. For each larva, the position of the head and abdomen were located and digitized in each video frame, ogether with a standardized length scale. From these digitized points, we calculated the angle of inclination and fan height (Fig. 1). Because these two measures are highly correlated (e.g., Hart et al. 1991), we chose fan height as a metric of larval posture.

Statistical analyses

We used linear regression to describe the relationship between velocity and (ln-transformed) height above the bed for each velocity profile, and compared slopes and intercepts of the five profiles for each treatment using analysis of covariance (ANCOVA) (Zar 1984; SAS Institute 1990). Because spatial variation in these velocity profiles was small, we calculated an overall mean profile for each of the nine velocity×food treatments. In addition, we used the mean velocity at 0.23 cm height (a height at which labral fans were commonly positioned) for each mean profile to represent a typical velocity experienced by the larvae in that treatment.

Table 1 Full models used in analysis of covariance testing flow effects on larval feeding. *Y* is larval fan height, flicking rate, or ingestion rate depending on the analysis. In all cases *food* is treated as a class variable, while *velocity*, $velocity^{0.5}$, and $velocity^2$ are covariates. Non-significant variables were iteratively eliminated from analyses, and the model with highest r^2 chosen as best fit

Y=velocity+food+velocity×food
Y=$\log_{10}$(velocity)+food+$\log_{10}$(velocity)×food
$\text{Log}_{10}(Y)$=velocity+food+velocity×food
$\text{Log}_{10}(Y)$=$\log_{10}$(velocity)+food+$\log_{10}$(velocity)×food
Y=$(\text{velocity})^{0.5}$+food+$(\text{velocity})^{0.5}$×food
$(Y)^{0.5}$=velocity+food+velocity×food
$(Y)^{0.5}$=$(\text{velocity})^2$+food+$(\text{velocity})^2$×food
Y=velocity+$(\text{velocity})^2$+food+velocity×food

We tested for differences in seston concentration between food treatments, velocity treatments, and at the beginning and end of a trial using a three-way repeated measures ANOVA (SAS Institute 1990). This test adjusts for the potential lack of independence between seston concentrations at the beginning and end of a single trial.

We introduced 20–40 larvae into the flume at the start of each trial, and were able to obtain usable data from an average of 60% (±16 SD) of these individuals. No fewer than eight larvae were usable in any given trial. Despite our efforts to minimize larval size variation during the course of the experiments, some differences in body size inevitably occurred, and this was manifested both as differences in body length among trials within a treatment, as well as among treatments (statistical analyses not presented for brevity). To compensate for these differences, we performed a series of linear regressions of the $\log_{10}$ of ingestion rate, fan height, and flick rate on the $\log_{10}$ body length for each trial (e.g., Charpentier and Morin 1994; Morin et al. 1988b). We then used the regression coefficients from these analyses to predict a corrected ingestion rate, flick rate, and fan height for a larva of average length (grand mean length=0.51 cm) in each treatment combination. This mean body length was within the range of body lengths used in each trial, thus ensuring that predictions were not extrapolations. By standardizing the results for body size, we have compensated for any artifact introduced by differences in larval size between trials or treatments. The resulting predictions were used in all subsequent analyses.

We did not use two-way ANOVA to evaluate the experimental results because the exact velocities produced for a particular nominal velocity treatment (e.g., 30 cm s^{-1}) sometimes differed between the high and low food treatments. Instead, we used a series of ANCOVAs to tease apart any treatment effects as well as describe the form of the relationship between larval feeding and velocity (Table 1). These eight models were chosen to explore both linear and curvilinear forms of the velocity-feeding relationship (Rubenstein and Koehl 1977; Shimeta and Jumars 1991) and to determine the best method of reducing heteroscedasticity in the data (Zar 1984). Following the procedures for a stepwise regression analysis, we started with the full model and iteratively removed non-significant variables (e.g., $P>0.05$). Once all non-significant variables were removed from the models, the model with the highest r^2 was chosen as the best fit (Zar 1984; SAS Institute 1990). In addition, the chosen model had to satisfy the assumption of homoscedasticity, which was tested by correlation analyses between trial means and variances or SDs.

Results

Velocity profiles

Velocity profiles were measured at five designated positions in the flume's working section for a given velocity×food treatment. Velocity was also monitored periodically with a small propeller flowmeter at a downstream location during the three trials of several treatments, which demonstrated that flow conditions exhibited little among-trial variation (D. D. Hart, unpublished data). The profiles displayed features consistent with expected flume boundary-layer conditions such as the log-linear relationship between velocity and height above the bed (e.g., Vogel 1994) (Fig. 2). For example, when velocity was regressed on ln height, 44 of the 45 regression slopes were significantly >0 ($P<0.05$, one-tailed *t*-test of H_o: slope=0), and the remaining slope was marginally significant ($P<0.1$). Moreover, the average r^2 for these regressions was 0.95 (SD=0.06, $n=45$).

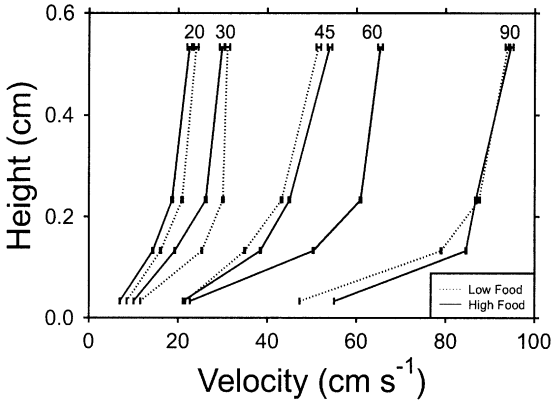

Fig. 2 Mean velocity profiles measured for each treatment combination (velocity×food). Presented are the mean and SD of velocities measured at the four corners and center of the flume's working section

We used ANCOVA to test for differences in slopes and intercepts among the five velocity profiles that were measured for each velocity×food treatment. For six of the nine analyses, there were no significant slope or intercept differences among profiles from the five different locations ($P>0.05$). Of the remaining three analyses, one each was characterized by a difference among slopes, a difference among intercepts, or a difference among both slopes and intercepts. Although we acknowledge that significant horizontal spatial variation in flow conditions was present in about one third of the treatment combinations, such within-treatment flow variation was small compared to between-treatment variation in flow conditions (e.g., compare the size of within-group SDs in Fig. 2 with the size of between-group differences), and should have a relatively small effect on our results.

A more focused assessment of experimental flow conditions can be gained by examining velocities at heights that are particularly relevant to the process of larval feeding. Accordingly, we examined velocity patterns at 0.23 cm height, which represents a typical height above the bed at which the labral fans were positioned. The average coefficient of variation for the five velocities measured at 0.23 cm height for each treatment was 7%, indicating that horizontal flow variation at fan height was quite low. Given the relatively small within-treatment variation among the velocity profiles, as well as the

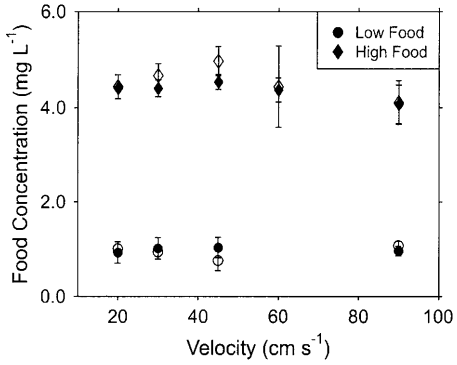

Fig. 3 Mean and SD of food concentrations for the three trials in each treatment combination (velocity×food). *Open symbols* represent the concentration of material at the beginning of a trial, while *filled symbols* represent that at the end of a trial

low coefficient of variation for these "fan height velocities," we combined the five profiles to generate a single, average velocity profile for each velocity×food treatment (Fig. 2). Moreover, all subsequent analyses of relationships between larval feeding behavior and flow are based on mean velocities measured at 0.23 cm height (i.e., in the vicinity of the labral fans).

Food concentration

There was an obvious difference in seston concentration between the two food treatments (Fig. 3, ANOVA, $F_{1,20}$= 1003.59, P=0.0001). In contrast, there was no difference in average seston concentration among velocity treatments (ANOVA, $F_{4,20}$=0.9, P=0.481), nor between the beginning and end of a trial (ANOVA, $F_{1,20}$=0.01, P=0.919). Therefore, within each food treatment and throughout each trial, larvae experienced similar food concentrations.

Measured seston concentrations were 0.96 mg l^{-1} (±0.10 SD) and 4.44 mg l^{-1} (±0.26 SD) for the low and high food treatments, respectively; about one-third of the nominal values introduced into the flume. This discrepancy may have arisen from several factors. For example, moisture retained in the dried yeast or chalk will lower the effective concentration of either solute once they are dissolved. In addition, both the yeast and chalk may have contained fractions that were not retained on our 0.47-µm filter or sedimented out in the flume sump, and were therefore not measured. Because yeast and chalk were taken from the same supplies for each trial, because food concentrations were equal among trials, and because the five-fold difference between treatments was maintained, the effects of this reduction in food supply are expected to be equivalent in all trials.

The effect of velocity and food concentration

Neither food concentration nor the food×velocity interaction term were significant components in any of the ANCOVA models tested (P>>0.05 in all cases), indicating that the slopes and elevations of the regression lines were not different. Because food concentration had no significant effect on any of the three components of larval feeding behavior, data from both food treatments were pooled to test the final regression models.

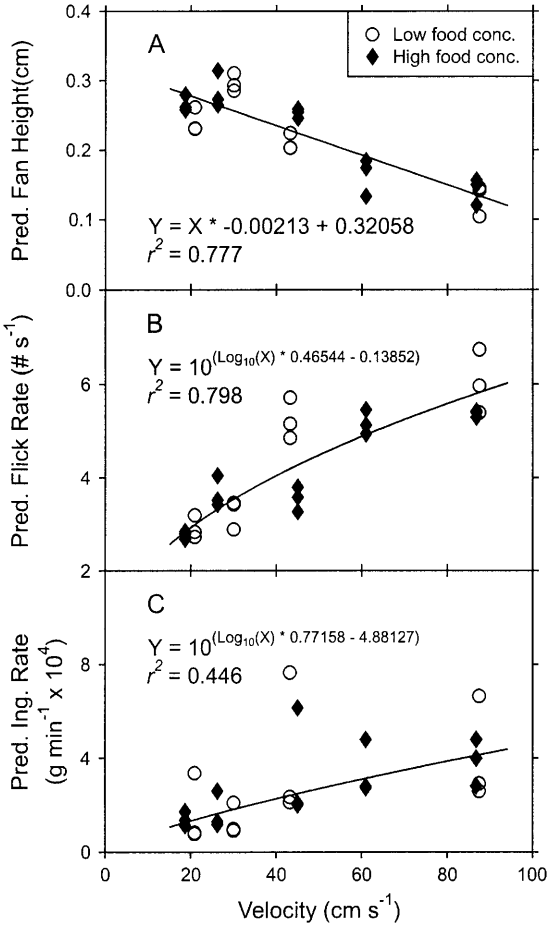

Fig. 4 The relationship between predicted (*Pred.*) **A** fan height, **B** flick rate, and **C** ingestion (*Ing.*) rate and velocity (measured at 0.23 cm height) for each food treatment. Represented are body size-corrected values predicted from log-log regressions of each feeding component on larval body length along with the best-fit regression line

Fan height declined linearly with increasing velocity (Fig. 4). The best-fit model was a simple linear regression between fan height and velocity (r^2=0.777, P<0.001). In contrast, both flick rate and ingestion rate showed a slight curvilinear response to increasing velocity (Fig. 4). For both of these feeding components a log-log relationship was the best-fit model (flick rate, r^2=0.798, P<0.001; ingestion rate, r^2=0.446, P<0.001). In all three cases, neither variances nor SDs were correlated with the means (Pearson's product correlation, $|r|$<0.391, P>0.300), thus satisfying the assumption of homoscedasticity (e.g., Zar 1984).

We chose velocity at a height of 0.23 cm to be a standard metric for the near-bed flow conditions experienced by larval black flies in this study. As Fig. 4 shows, how-

ever, the predicted fan height actually ranged between 0.1 and 0.3 cm over the range of velocities tested. Therefore, we used the mean velocity profiles described above to predict the velocity at mean fan height for each trial, and then used this fan-height velocity as the independent variable in our ANCOVA models. In each case, the best-fit ANCOVA model was the same as that found when using velocity at 0.23 cm. This indicates that our results are robust to modest variation in velocity (up to 20%).

Discussion

The goal of our experimental study was to provide a more complete understanding of the ways in which water velocity and food concentration affect a suite of linked feeding responses in larval black flies, an important group of passive suspension feeders inhabiting streams and rivers (e.g., Wotton et al. 1995, 1996). Our treatments spanned a nearly five-fold range of near-bed velocities and seston concentrations, which is representative of the range of variation that larvae experience in nature for these two components of particle flux (e.g., Hart et al. 1996; Morin et al. 1988a, 1988b). In general, our results indicated that variations in near-bed velocity had a strong effect on feeding behavior, whereas differences in food concentration had no detectable effect on the components of feeding that we studied. We explore these results in turn, and conclude by identifying several types of mechanistic studies that are needed to extend our understanding of feeding performance in these consumers.

Posture

Several studies have demonstrated that larval posture is strongly affected by flow (Chance and Craig 1986; Schröder 1987b; Hart et al. 1991; Lacoursière and Craig 1993), and our results support this view. Specifically, the height at which labral fans were positioned above the bed was greater at lower velocities, so that fan heights at velocities of about 20 cm s^{-1} were 50–100% greater than those at 90 cm s^{-1}.

Some workers have concluded that these flow-dependent changes in larval posture are primarily a passive "bending" response to increasing drag (Chance and Craig 1986; Schröder 1987b). In contrast, others have suggested that posture also reflects behavioral adjustments designed to balance the benefits of greater particle flux derived from higher fan heights with the corresponding increase in drag costs that larvae incur at such heights (Hart et al. 1991; Lacoursière and Craig 1993). For example, Hart et al. (1991) observed that larval black flies reduced their fan height in response to an experimental increase in food concentration. They suggested that a higher food concentration allowed larvae to position their fans closer to the bed where drag forces were lower, yet where particle flux was similar to that previously available only much higher above the bed. In the present study, there was no significant difference in larval posture between the two food concentration treatments.

We suspect that procedural differences between our study and earlier studies may have contributed to these different fan height-food concentration relationships. For example, differences in feeding history between the two experiments may have produced different internal states (sensu Mangel and Clark 1988) in the larvae, thereby affecting the net benefits of a change in feeding posture. Specifically, larvae were housed for 2 days in natural stream water with no supplemental food prior to the experiment by Hart et al. (1991), whereas larvae in the present study were fed supplemental high quality particles (i.e., baker's yeast) for 1–2 days prior to the experiment. We cannot yet provide a mechanistic explanation for how the relationship between posture and food level should vary with feeding history. Nonetheless, these differing results suggest that feeding behavior may be quite sensitive to the prior feeding experience of larvae.

Ultimately, the magnitude of any change in feeding benefits or drag costs in response to a shift in posture depends on the shape of the momentum boundary layer. For example, Hart et al. (1991) argued that a unit decrease in fan height will produce a much greater reduction in velocity in the steep gradients that are generally associated with fast flows than in the gradual gradients more typical of slow flows. In contrast, the velocity profiles measured here [and in the field by Hart et al. (1996)] suggest that this generalization may sometimes be unwarranted. For example, the difference in water velocity between 0.1 cm and 0.3 cm above the flume bed (i.e., the range of fan heights observed here) steadily increased from 6 cm s^{-1} in the 20 cm s^{-1} treatment to 17 cm s^{-1} in the 65 cm s^{-1} treatment, conforming to the prediction by Hart et al. (1991). In the 90 cm s^{-1} treatment, however, this velocity difference was actually less than or equal to that in the 65 cm s^{-1} treatment, because the steepest part of the gradient was found below 0.1 cm (Fig. 2). Thus, in highly sheared flows where the steepest portion of the velocity gradient is contained below fan height, there may be little or no benefit or cost associated with changes in fan height. Moreover, velocity profiles in the field are often much more complicated than the well behaved gradients measured in flume flows (Hart et al. 1996). For this reason, further research is needed to determine how larvae adjust their posture in the more complicated velocity gradients that are common on natural stream beds.

Flick rate

The flick rate of *S. vittatum* larvae increased about two-fold in response to a five-fold increase in velocity. The decelerating shape of this relationship agrees with the results of earlier studies (e.g., Schröder 1980, 1987a), although the velocity at which *S. vittatum*'s flick rate

might be expected to level off is higher than the maximum velocities used in our experiment. Ultimately, the maximum attainable flick rate must be set by the fixed time needed to complete a single fan abduction and adduction sequence. Craig and Chance (1982) measured this time to be ≈0.0466–0.090 s for *S. vittatum*, resulting in an upper bound of 11–21 flicks s^{-1}. Given that these theoretical maximum flick rates are 2–4 times greater than the highest flick rates we observed, other factors must have been acting to produce the decelerating relationship between flick rate and velocity that we observed. For example, the labral fans become increasingly deformed by the greater drag forces associated with high velocities (Schröder 1987b; Lacoursière and Craig 1993). Thus, although the average particle flux through a fixed projected area should rise linearly with velocity, such fan bending reduces the projected area of the fan exposed to flow. These alterations in fan configuration with increasing velocity can potentially set an upper limit on the rate at which particles are intercepted, which may help to explain the observed nonlinear flick rate-velocity relationship.

We had assumed that if individuals tend to flick after a given number of particles have accumulated (i.e., via the "fixed number rule" of Hart and Latta 1986), then larvae exposed to a high food concentration should flick faster than those in low food treatments. In contrast to our expectation, and to the results of Hart and Latta (1986) who observed a significant increase in flick rate with food concentration when velocity was held constant, food concentration had no effect on flick rate. Hart and Latta, however, studied a different black fly genus and examined a much wider range of food concentrations (i.e., ~0–200 mg l^{-1}). In fact, a re-examination of the regression equation presented in Hart and Latta (1986) indicates that an increase in food concentration from 0.96 to 4.44 mg l^{-1} would have caused a flick rate increase of only 0.03 flicks s^{-1}. In both their study and ours, such a small treatment effect would be obscured by the large within-group variation that is typical of flick rate data.

Ingestion rate

Ingestion rate was positively related to velocity, although the strength of this relationship (i.e., in terms of the r^2 value) was lower than either the flick rate-velocity or posture-velocity relationships. This lower r^2 value probably results from ingestion rate being the product of multiple interacting variables (e.g., flow, food concentration, posture, flick rate, feeding history), and thus subject to greater sources of variation. Although the relationship between ingestion rate and velocity was significantly curvilinear, it did not level off over the velocity range that we studied. Similar results were reported by Charpentier and Morin (1994) who observed steadily increasing ingestion rates for *S. venustum* and *Prosimulium mixtum/fuscum* over a velocity range of 24–133 cm s^{-1} (measured 2 cm above the bed using a Gurley Pygmy meter). In contrast, studies with several other species have observed more pronounced declines in ingestion rate at higher velocities. For example, ingestion rates of *S. tuberosum* reached a maximum at 100 cm s^{-1} before declining at 133 cm s^{-1} (Charpentier and Morin 1994). Similarly, the maximum ingestion rate of *S. ornatum* larvae occurred at a velocity between 19 and 36 cm s^{-1} (measured within 0.5 cm of the bed using a deflection-type meter connected to a strain gauge), and declined when the velocity was increased to 53 cm s^{-1} (Malmqvist and Sackman 1996). These different patterns point to important interspecific variation in feeding response to flow, which is presumably a fundamental cause of differences in the velocity preferences of different species (Crosskey 1990). For example, the ingestion rate of *S. vittatum* increased with velocity up to at least 90 cm s^{-1}, which is consistent with the observed preference of this species for velocities as high as 100 cm s^{-1} (D. D. Hart and D. M. Fonseca, unpublished manuscript). Unfortunately, we cannot yet make broad inferences about links between larval velocity preferences and the form of the ingestion rate-velocity relationship due to the paucity of quantitative interspecific data describing both feeding behavior and near-bed velocity preferences.

Food concentration did not affect either the slope or intercept of the ingestion rate-velocity relationship. As discussed for the flick rate results, the absence of a significant difference in ingestion rate between food treatments may simply reflect the combination of large within-group variation and the narrow range of food concentrations. Nonetheless, this absence of a food treatment effect appears to be consistent with the work of Morin et al. (1988b), who showed that at a velocity of 40–50 cm s^{-1}, the ingestion rate of *S. venustum/verecundum* larvae did not increase with food concentration above a threshold concentration of ≈4 mg l^{-1}. We found that *S. vittatum*'s ingestion rate was insensitive to a five-fold change in food concentration (0.96–4.44 mg l^{-1}), although it continued to increase with increases in velocity. As discussed below, our results indicate that these two components of particle flux (velocity and particle concentration) can have qualitatively different effects on larval feeding behavior.

Why do velocity and food concentration have different effects on feeding behavior?

Much of the research on suspension feeders emphasizes the critical role that particle flux plays in determining particle capture (e.g., Shimeta and Jumars 1991; Wildish and Kristmanson 1997). Given that the flux of particles is a function of both particle concentration and flow characteristics in the vicinity of the feeding appendages, we might expect the effect of a unit change in particle concentration to be similar to a unit change in velocity (i.e., if the two are substitutable resources sensu Alstad 1987; Tilman 1982). Evidence in support of this flux-

based model is mixed, however. Bertness et al. (1991) and Sanford et al. (1994) favored seston flux as the primary determinant of barnacle growth rate when they reported elevated growth when barnacles were exposed to high food concentrations and/or high flow velocities. In contrast, we found that velocity, but not food concentration or flux, had a strong positive effect on feeding behavior.

Results with active suspension feeders are equally mixed with studies of several bivalves showing positive, negative, and no relationship between flow (or flux) and growth rate (Wildish et al. 1987; Cahalan et al. 1989; Grizzle et al. 1992; Judge et al. 1992; Lenihan et al. 1996). Differences in feeding response among these studies should be expected given the range of feeding mechanisms and morphologies represented, and caution should be exercised in comparing results of growth studies (a cumulative effect of feeding and other variables) and direct measurements of ingestion rate. Nonetheless, our inability to generalize about the effects of flow and food concentration on suspension feeding is a clear indication that more research is needed to tease apart these complex relationships.

Our results suggest that velocity and food concentration are somehow decoupled in the feeding process of black flies. One mechanism that may contribute to this decoupling is the transfer of particles from the labral fan to the mouth. For example, it is possible that the seston concentration was high enough to saturate the particle capture rate at all velocities tested. Therefore, the fans always had the same number of particles to transfer to the mouth per flick, regardless of food treatment. Under these conditions, ingestion rate would be determined primarily by flick rate, which was influenced only by velocity. While this hypothesis is plausible for the results we obtained, it cannot explain the results of Hart and Latta (1986) who found that both flick rate and ingestion rate responded positively to increases in food concentration.

Several types of studies are needed to reconcile our results with previous studies and to understand more completely the role of larval black flies and other suspension feeders in benthic-pelagic coupling. First, further experiments can help to identify the factors controlling flick rate and its relationship to ingestion rate. Second, a comprehensive analysis of the effects of feeding history and internal state on suspension feeding rates is needed to reconcile several studies cited here and to determine the effects of natural variations in food supply on feeding in the field. Third, controlled feeding experiments under field boundary layer conditions are required to determine how the shape of the momentum boundary layer affects posture and feeding in these and other passive suspension feeders. Finally, a more complete understanding of particle flux through the labral fans and analogous structures (e.g., barnacle cirri) is needed to account for the separate roles played by flow and particle concentration in determining ingestion rate. Taken together, such studies can detail the links between food concentration, velocity, and ingestion rate, thereby increasing our understanding of the roles that benthic suspension feeders play in controlling carbon flow through aquatic ecosystems.

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References

Alstad DN (1987) A capture-rate model of net-spinning caddisfly communities. Oecologia 71:532–536

Bertness MD, Gaines SD, Bermudez D, Sanford E (1991) Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. Mar Ecol Prog Ser 75:91–100

Butman CA, Frechette M, Geyer WR, Starczak VR (1994) Flume experiments on food supply to the blue mussel *Mytilus edulis* L. as a function of boundary-layer flow. Limnol Oceanogr 39:1755–1768

Cahalan JA, Siddall SE, Luckenbach MW (1989) Effects of flow velocity, food concentration and particle flux on growth rates of juvenile bay scallops *Argopecten irradians*. J Exp Mar Biol Ecol 129:45–60

Chance MM, Craig DA (1986) Hydrodynamics and behaviour of Simuliidae larvae (Diptera). Can J Zool 64:1295–1309

Charpentier B, Morin A (1994) Effect of current velocity on ingestion rates of black fly larvae. Can J Fish Aquat Sci 51:1615–1619

Ciborowski JJH, Craig DA (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

Clark BD, Hart DD (1995) Disturbances to flow introduced by feeding black fly larvae. Am Zool 35:113A

Craig DA, Chance MM (1982) Filter feeding in larvae of Simuliidae (Diptera: Culicomorpha): aspects of functional morphology and hydrodynamics. Can J Zool 60:712–724

Crosskey RW (1990) The natural history of blackflies. Wiley, New York

Dame RF, Zingmark RG, Haskin E (1984) Oyster reefs as processors of estuarine materials. J Exp Mar Biol Ecol 83:239–247

Fonseca DM, Hart DD (1996) Density-dependent dispersal of black fly neonates is mediated by flow. Oikos 75:49–56

Frechette M, Bourget E (1985) Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. Can J Fish Aquat Sci 42:1158–1165

Frechette M, Butman CA, Geyer WR (1989) The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. Limnol Oceanogr 34:19–36

Glynn PW (1973) Ecology of a Caribbean coral reef. The *Porites* reef flat biotope. Part 2. Plankton community with evidence for depletion. Mar Biol 22:1–21

Grizzle RE, Langan R, Howell WH (1992) Growth responses of suspension-feeding bivalve molluscs to changes in water flow: differences between siphonate and nonsiphonate taxa. J Exp Mar Biol Ecol 162:213–228

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

Hart DD, Latta SC (1986) Determinants of ingestion rates in filter-feeding larval blackflies (Diptera: Simuliidae). Freshwater Biol 16:1–14

Hart DD, Merz RA, Genovese SJ, Clark BD (1991) Feeding postures of suspension-feeding larval black flies: the conflicting demands of drag and food acquisition. Oecologia 85:457–463

Hart DD, Clark BD, Jasentuliyana A (1996) Fine-scale field measurement of benthic flow environments inhabited by stream invertebrates. Limnol Oceanogr 41:297–308

Judge ML, Coen LD, Heck KL (1992) The effect of long-term alteration of in situ currents on the growth of *Mercenaria mercenaria* in the northern Gulf of Mexico. Limnol Oceanogr 37:1550–1559

Kurtak DC (1978) Efficiency of filter feeding of black fly larvae (Diptera: Simuliidae). Can J Fish Aquat Sci 56:1608–1623

Lacoursière JO (1992) A laboratory study of fluid flow and microhabitat selection by larvae of the black fly *Simulium vittatum* (Diptera: Simuliidae). Can J Zool 70:582–596

Lacoursière JO, Craig DA (1993) Fluid transmission and filtration efficiency of the labral fans of black fly larvae (Diptera: Simuliidae): hydrodynamic, morphological, and behavioural aspects. Can J Zool 71:148–162

Lenihan HS, Peterson CH, Allen JM (1996) Does flow speed also have a direct effect on growth of active suspension-feeders: an experimental test on oysters. Limnol Oceanogr 41:1359–1366

Lucas P, Hunter FF (1999) Phenotypic plasticity in the labral fan of simuliid larvae (Diptera): effect of seston load on primary-ray number. Can J Zool 77:1843–1849

Malmqvist B, Sackman G (1996) Changing risk of predation for a filter-feeding insect along a current velocity gradient. Oecologia 108:450–458

Malmqvist B, Wotton RS, Zhang Y (2001) Suspension feeders transform massive amounts of seston in large northern rivers. Oikos 92:35–43

Mangel M, Clark CW (1988) Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, N.J.

Morin A, Back C, Chalifour A, Boisvert J, Peters RH (1988a) Effect of blackfly ingestion and assimilation on seston transport in a Quebec lake outlet. Can J Fish Aquat Sci 45:705–714

Morin A, Back C, Chalifour A, Boisvert J, Peters RH (1988b) Empirical models predicting ingestion rates of black fly larvae. Can J Fish Aquat Sci 45:1711–1719

Morin A, Constantin M, Peters RH (1988c) Allometric models of simuliid growth rates and their use for estimation of production. Can J Fish Aquat Sci 45:315–324

Newbold JD, O'Neill RV, Elwood JW, Van Winkle W (1982) Nutrient spiraling in streams: implications for nutrient limitation and invertebrate activity. Am Nat 120:628–652

Palmer RW, Craig DA (2000) An ecological classification of primary labral fans of filter-feeding black fly (Diptera: Simuliidae) larvae. Can J Zool 78:199–218

Peterson CH, Black R (1987) Resource depletion by active suspension feeders on tidal flats: Influence of local density and tidal elevation. Limnol Oceanogr 32:143–166

Rubenstein DI, Koehl MAR (1977) The mechanisms of filter feeding: some theoretical considerations. Am Nat 111:981–994

Sanford E, Bermudez D, Bertness MD, Gaines SD (1994) Flow, food supply and acorn barnacle population dynamics. Mar Ecol Prog Ser 104:49–62

SAS Institute (1990) SAS/STAT user's guide. Version 6, fourth edn. SAS Institute, Cary, N.C.

Schröder P (1980) Zur Ernährungsbiologie der Larven von *Odagmia ornata* Meigen (Diptera: Simuliidae). 1. Die Filtriertätigkeit unter dem Einfluss von Fliessgeschwindigkeit, Wassertemperatur und Futterdonzenration. Arch Hydrobiol [Suppl] 59:43–52

Schröder P (1987a) Filter feeding activity of blackfly larvae (Diptera: Simuliidae) in relation to stream velocity and food supply. Arch Hydrobiol [Suppl] 77:161–182

Schröder P (1987b) Deflection of filter-feeding blackfly (Diptera: Simuliidae) larvae by stream velocity. Arch Hydrobiol [Suppl] 77:39–49

Shimeta J, Jumars PA (1991) Physical mechanisms and rates of particle capture by suspension-feeders. Oceanogr Mar Biol Annu Rev 29:191–257

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton, N.J.

Vogel S (1994) Life in moving fluids, second edn. Princeton University Press, Princeton, N.J.

Wallace JB, Merritt RW (1980) Filter-feeding ecology of aquatic insects. Annu Rev Entomol 25:103–132

Wallace JB, Webster JR (1996) The role of macroinvertebrates in stream ecosystem function. Annu Rev Entomol 41:115–39

Wildish DJ, Kristmanson DD (1997) Benthic suspension feeders and flow. Cambridge University Press, Cambridge

Wildish DJ, Kristmanson DD, Hoar RL, DeCoste AM, McCormick SD, White AW (1987) Giant scallop feeding and growth responses to flow. J Exp Mar Biol Ecol 113:207–220

Wotton RS (1988) Very high secondary production at a lake outlet. Freshwater Biol 20:341–346

Wotton RS (1992) Feeding by blackfly larvae (Diptera: Simuliidae) forming dense aggregations at lake outlets. Freshwater Biol 27:139–149

Wotton RS, Malmqvist B, Ashelford K (1995) The retention of particles intercepted by a dense aggregation of lake-outlet suspension feeders. Hydrobiologia 306:125–129

Wotton RS, Constantine PJ, Malmqvist B (1996) Spiraling of particles by suspension feeders in a small lake-outlet stream. Can J Zool 74:758–761

Zar JH (1984) Biostatistical Analysis, second edn. Prentice-Hall, Englewood Cliffs, N.J.

Zhang Y, Malmqvist B (1996) Relationships between labral fan morphology, body size, and habitat in North Swedish blackfly larvae (Diptera: Simuliidae). Biol J Linn Soc 59:261–280

Zhang Y, Malmqvist B (1997) Phenotypic plasticity in a suspension-feeding insect, *Simulium lundstromi* (Diptera: Simuliidae), in response to current velocity. Oikos 78:503–510