Limnol. Oceanogr., 41(6), 1996, 1180–1187

The effect of invertebrate consumption on bacterial transport in a mountain stream

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Abstract

Although laboratory studies have shown that filter-feeding invertebrates consume bacteria from stream water, no study has measured bacterial consumption in the field or determined system-level removal rates of sestonic bacteria. To examine bacterial removal rates and consumption by invertebrates, we released fluorescently labeled bacteria (FLB) into a second-order stream at Coweeta Hydrologic Laboratory, North Carolina. We performed two 1-h releases during summer over bedrock habitat that supports many filter-feeders. We calculated uptake length and counted FLB in the guts of seven insect taxa. Uptake length was 78 and 83 m for the two releases, which corresponded to uptake rates of 4.03 and 3.69×10^7 cells m^{-2} min^{-1}. *Simulium*, a filter-feeding blackfly larva, ingested FLB at a rate of 1.4×10^4 cells mg^{-1} min^{-1}, 10 times the rate of other taxa. *Diplectrona* and *Parapsyche*, hydropsychid caddisfly filter-feeders, had ingestion rates between *Simulium* and other taxa. *Epeorus*, a scraping mayfly, and *Tallaperla*, a shredding stonefly, also ingested FLB, presumably from cells that adhered to the substrate. Invertebrate ingestion per square meter of stream bottom was 7% of total stream uptake, with *Simulium* responsible for 91% of the total invertebrate ingestion. Adhesion of FLB to the substrate from the water column seemed to be more important than invertebrate consumption in this stream, and one taxon, *Simulium*, was responsible for most invertebrate consumption of bacteria.

Transport and retention of organic seston are important functions of stream ecosystems because they determine the rate at which particle-associated energy and nutrients are lost from a stream and the degree to which downstream reaches are linked to upstream processes. Recent studies (Jones and Smock 1991; Miller and Georgian 1992; Cushing et al. 1993) have begun to examine uptake length of organic particles in streams by using ground and radiolabeled leaves, corn pollen, and radiolabeled natural seston. All seston released in these studies was >50 μm. No studies have examined the transport of ultrafine (<50 μm) particles in streams; yet much stream seston is <50 μm. In an Appalachian stream, 20–36% of organic seston was between 0.45 and 24 μm (Wallace et al. 1982), and 75–98% of seston was <50 μm in the Salmon River, Idaho (Minshall et al. 1992). In the Ogeechee River, 85% of the seston was <25 μm on seven dates (Wallace et al. 1987). These small particles, because of their slower settling velocities, may have transport properties different from those of large particles used in previous seston transport studies.

Bacteria, which range in size from 0.4 to 2 μm, may represent an important component of this size fraction of the seston. Bacteria represented between 1 and 60% of total sestonic carbon in a blackwater river and from 15 to 100% of the size fraction <12 μm (Edwards 1987). Neither spiralling nor uptake lengths of bacteria are known (Leff et al. 1992). The ability of bacteria to adhere to biofilm may influence their travel distance (Leff et al. 1992), and although the activities of macroinvertebrates seem to have little effect in the entrainment of cells from biofilms (Leff et al. 1994), their impact on bacterial uptake length is potentially greater. Blackfly larvae (Simuliidae) can capture and grow on a diet of bacteria in the lab (Fredeen 1964; Edwards and Meyer 1990) because their cephalic fans can capture submicron-sized particles from the water (Wotton 1976).

Filter-feeding invertebrates retain organic matter transported in streams (Wallace et al. 1977); however, few field studies have quantified their role. Blackflies consumed seston (>0.2 μm) at a rate of 0.01 m^{-1} at a lake outlet in Quebec, which represents a fast uptake of seston (Morin et al. 1988). A radiolabeled phosphorus release demonstrated that particle removal by *Diplectrona*, a net-spinning caddisfly, had little effect on seston transport (Newbold et al. 1983). Georgian and Thorp (1992) indirectly estimated particulate organic matter (POM) removal rates by filter-feeding caddisflies from other studies and determined that caddisfly filter-feeders remove POM much more slowly than they remove animal material. However, none of the studies reviewed by Georgian and Thorp actually compared POM removal by caddisflies with system-level POM removal.

We performed two releases of fluorescently labeled bacteria (FLB) (Sherr et al. 1987) into a mountain stream to determine the uptake length of bacterial particles in a stream reach and the importance of filter-feeding organisms in the retention of these particles. FLB represent good analogs to natural stream bacteria because they are similar in size and density and because they can be readily determined in both the water column and the guts of organisms by means of epifluorescence microscopy. FLB

Acknowledgments

Thanks to Cesc Peters for ideas, use of materials, and assistance in making fluorescently labeled bacteria. Amy Rosemond, Mike Paul, Chien Wang, and two anonymous reviewers provided comments on earlier drafts of this manuscript.

This research was supported by Research Experience for Undergraduates supplement to NSF grant BSR 90-11661 to J.L.M.

can be cultured in the large amounts necessary to achieve measurable concentrations in invertebrate guts in the field. This study represents the first use of FLB to determine rates at which invertebrates feed on bacteria in a field study.

Methods

Hugh White Creek is a second-order mountain stream draining a forested catchment at Coweeta Hydrologic Laboratory in Macon County, North Carolina. The catchment contains a mixed oak, tulip poplar, and hickory forest that has been the reference site for experiments (*see* Webster et al. 1983). The stream is heterotrophic and heavily shaded by rhododendron. The FLB release site was a 45-m section of high-gradient bedrock outcrop, which we chose for the high densities of filter-feeding invertebrates found there. We performed releases on 7 July and 5 August 1993. Because we were 250 m above a gauged weir, we estimated discharge by multiplying discharge at the weir by the proportion of catchment area upslope of our study site. Discharge for the two releases was 5.7 and 4.4 liters s^{-1}.

To prepare FLB, we inoculated 2 liters of high nutrient broth with *Escherichia coli*; overnight incubation produced $\sim 10^{12}$ cells. The cells were harvested with a centrifuge, resuspended in 100 ml of 0.05 M Na_2HPO_4–0.85% NaCl buffer, and incubated with 20 mg 5-(4,6-dichlorotriazin-2-yl) aminofluorescein (DTAF) for 1 h at 60°C to produce FLB (Sherr et al. 1987). FLB were centrifuged, rinsed, and resuspended in 0.05 M Na_2HPO_4–0.85% NaCl buffer, and sonicated to break up bacterial clumps. The cells were frozen until immediately before release.

We released FLB using a Marriotte bottle and a flowmeter. The methods were similar to those used to determine uptake length of nutrients (Munn and Meyer 1990; D'Angelo et al. 1991). Immediately before the July release of FLB, we released chloride—a conservative tracer—to determine lateral inflow and water velocity. The chloride release showed that there was no lateral inflow along the bedrock outcrop section of this stream; thus, we did not need to correct any of the cell counts for dilution. Nominal transport time was determined by estimating the time for half of the released chloride to pass the downstream end of the reach and subtracting the amount of time for half of the chloride to be released (Triska et al. 1989). Reach length divided by the nominal transport time is stream velocity. The FLB release occurred immediately after the Cl release. We diluted cells to a 5-liter suspension which was released for 1 h. A 1-h release allowed enough time for the insects to ingest a measurable amount of FLB. Flow rate was constantly monitored during the releases and adjusted to a target rate of 80 ml min^{-1}.

FLB in the water was sampled after the bacterial concentrations reached plateau, which took 9 min based on the chloride release. For the July release, we collected one water sample 20 min into the release at 5-m intervals from 5 to 45 m below the FLB dripper and preserved it in 5% Formalin. For the August release, we took two samples at each 5-m interval, one 20 min and one 40 min after the start of the release, to indicate variation in cell concentrations with time. We determined FLB concentrations by passing the cells onto an Irgalan black-stained 0.2-μm polycarbonate filter (Poretics) and counting them under an epifluorescent microscope with an acridine orange filter set at 400× magnification. Concentrations of FLB were 2.1 and 3.1×10^7 cells $liter^{-1}$ at 5 m below the dripper for the July and August releases. Natural bacteria concentrations in the stream were 3.0×10^8 cells $liter^{-1}$, determined by acridine orange direct counts (Hobbie et al. 1977). Total FLB released was 4.3×10^{11} (July) and 4.8×10^{11} (August) cells, determined by multiplying FLB concentrations at the first sampling site by (discharge × time).

We collected seven insect taxa 5–12 m below the release site at the end of each release by scraping the rock face substrate, collecting the debris in a 250-μm-mesh bag, and immediately putting it into Kahle's solution to prevent digestion-regurgitation of FLB. For the second release, we collected blackfly larvae at 0, 5, 10, 15, 20, 30, and 60 min from the time the release started in order to determine the uptake rate of FLB for this taxon. Blackflies were scraped from the substrate, and ~20 individuals were picked from the net and placed into Kahle's solution. All blackflies were collected 10 m below the release site. We collected each blackfly sample slightly upstream of the previous sample so that we did not disturb the organism's feeding behavior. In the laboratory we dissected the guts of 1–3 organisms of the same taxon and size class and carefully removed the contents. Gut contents were sonicated to break up aggregates that can hide FLB, passed onto a 0.2-μm Irgalan black polycarbonate filter, and counted at 400× magnification with an epifluorescent microscope. Because FLB tended to be patchily distributed on the filter, we counted at least 40 randomly selected microscope fields per filter for the 3–9 slides made for each taxon. Standard errors of the 40 fields were 5–10% of the mean for each slide. Differences in FLB ingestion between taxa were determined with a one-way ANOVA on log-transformed data. Comparisons between taxa were made with the Tukey-Kramer method, which is robust to different sample sizes and controls error rate across the experiment (Sokal and Rohlf 1981). FLB data were combined from the two releases to estimate the area-specific uptake rate of the insects.

We estimated standing stock of the seven insect taxa by scraping seven 156-cm^2 patches into a 250-μm-mesh bag along the study reach on 21 July 1993. Other taxa found at this site were not used in this study (e.g. chironomids and predatory stoneflies) because they were too rare for this analysis. The samples were preserved in 90% ethanol and stained with Phloxine B to facilitate sorting. The samples were poured through 1-mm and 250-μm sieves and sorted. When the number of insects in the 250-μm size fraction was high, we subsampled a fourth of the sample. Insects were identified to genus or species with a dissecting microscope and measured with an ocular micrometer. We computed ash-free dry mass (AFDM)

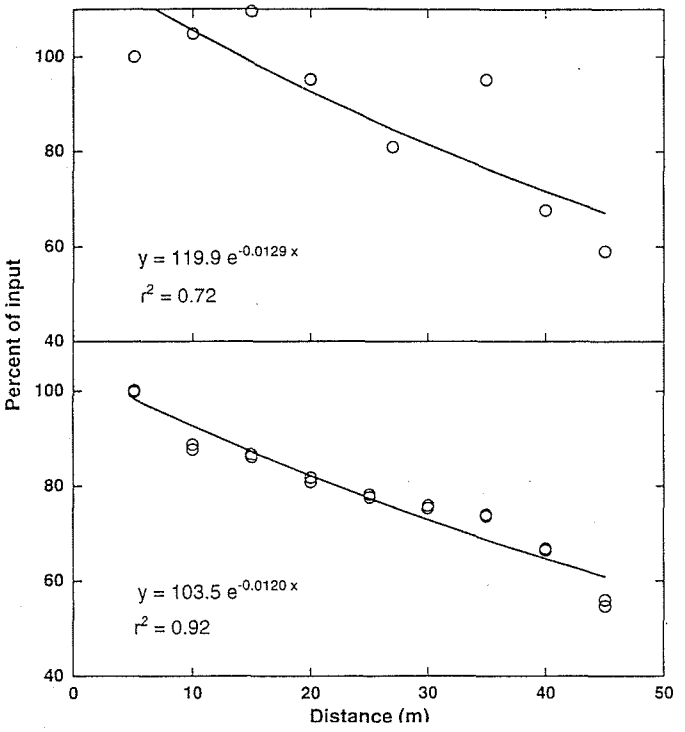

Fig. 1. FLB concentrations in the study reach at plateau concentrations. Top panel—July release; bottom panel—August release. The replicate points during the August release represent samples taken 20 min apart. Percent of input represents percent of the FLB concentration at 5 m. Distance is downstream from the dripper.

for each taxon using length-AFDM regressions for Coweeta invertebrates (Huryn 1986).

Uptake of bacteria was calculated by determining the slope of the linear regression of the natural logarithm of bacteria concentrations with distance downstream (x):

$$\ln N_x = \ln N_0 - kx. \quad (1)$$

N_x is the concentration of FLB in cells liter^{-1} at distance x from the dripper. The inverse of the slope (k) is the uptake length (S), which is the average distance downstream in meters travelled by FLB (Newbold et al. 1981). FLB uptake rate per m^2 (U cells m^{-2} min^{-1}) was determined with the equation (Newbold et al. 1981)

$$U = F/Sw. \quad (2)$$

F is the flux (cells min^{-1}) at any point downstream from the dripper. We averaged cell concentrations at each station below the dripper and multiplied by discharge to estimate an average F for the study reach. w is the wetted width of the stream measured at 5-m intervals through the study reach.

We calculated uptake rate of FLB by invertebrates by multiplying the uptake of FLB per milligram AFDM (measured from the gut analyses) by the standing stock of insects in the study reach of Hugh White Creek.

We estimated settling velocity of FLB using a modification of Stokes' law from Dietrich (1982), which is the velocity at which the cells settle in still water. The density of bacterial cells is 1.09 g cm^{-3} (Bratbak and Dundas 1984). The cells were rod-shaped, with an average length of 1.95 μm. We assumed a nominal diameter of 1.08 μm and corrected for shape (*see* Dietrich 1982). We also calculated depositional velocity, which is the apparent velocity of cell movement from the water column given uptake rate, stream velocity, and depth. The depositional velocity of FLB during the July release was estimated as $v_{dep} = dv_{wat}k$ (Cushing et al. 1993), where v_{wat} is the water velocity calculated from the chloride transport (0.2 ms^{-1}), and d is the average depth of the stream (0.04 m) as measured directly. The Froude number for the entire reach (Fr = $v_{wat}/(gd)^{1/2}$, where g is acceleration due to gravity) was 0.32.

Results

The uptake rates (k) for FLB were 0.0129 m^{-1} for the July release and 0.0120 m^{-1} for the August release, which correspond to uptake lengths (S) of 77 and 83 m for the two releases. These distances were quite similar, even though variability of the FLB concentrations was higher in the July release (Fig. 1). For the August release, there was little difference in the concentration of FLB in the water column 10 and 40 min into the release. The slope of FLB concentrations in the August release (Fig. 1) had portions steeper than the regression slope which corresponded to higher uptake rates. The areas of increased uptake were probably due to different flow velocities along the 45-m section of bedrock outcrop. Uptake rates per m^2 of stream bottom of FLB from the water column were also similar for each of the releases: 4.03×10^7 cells m^{-2} min^{-1} for the July release and 3.69×10^7 cells m^{-2} min^{-1} for the August release.

The depositional velocity of FLB was 9.3×10^{-5} ms^{-1} compared to the calculated settling velocity of 5.5×10^{-8} ms^{-1}. Settling of FLB from the water column by gravity probably played little role in the removal of FLB from the water column because depositional velocity was 1,690 times higher than settling velocity.

We estimated the FLB ingestion rate of seven insect taxa found at the study site: *Simulium,* a filter-feeding blackfly, which had high biomass (Table 1), had the highest mass-specific ingestion after 1 h compared to all other invertebrates in the study reach except *Diplectrona* (Fig. 2). However, when we considered the ingestion rate from the time-course (*see below*), *Simulium* ingestion rate was significantly higher than all other taxa (Fig. 2). There was high variability in FLB ingestion by all taxa. One small *Rhyacophila* had an ingestion rate comparable to *Simulium* (Fig. 2), whereas another *Rhyacophila* had extremely low ingestion. Early instar *Rhyacophila* tend to be detritivorous, even though it is considered to be a predator (R. Hall pers. obs). Note that nonfilter-feeding taxa, such as *Epeorus* and *Tallaperla,* ingested FLB at rates that overlapped those of the two net-building caddisflies. *Blepharicera* had low ingestion compared to other taxa.

The amount of FLB ingested during the 1-h trial underestimated feeding rates of blackflies. During the time-

Table 1. Insect taxa used in this study and the estimated area-specific uptake of FLB (cells m^{-2} min^{-1}) for each. Functional feeding groups are based on Lugthart and Wallace (1992).

Group	Taxon	Order	Biomass (mg m^{-2})	Abundance (ind. m^{-2})	FLB uptake
Filterer	*Simulium* spp.	Diptera	173	4,800	2.4×10^6
	Parapsyche cardis	Trichoptera	145	2,060	4.4×10^4
	Diplectrona modesta	Trichoptera	96	4,950	1.4×10^5
Scraper	*Epeorus* sp.	Ephemeroptera	177	122	1.8×10^4
	Blepharicera williamsae	Diptera	13	230	1.2×10^2
Shredder	*Tallaperla maria*	Plecoptera	6	6	2.8×10^2
Predator	*Rhyacophila* spp.	Trichoptera	15	187	3.6×10^4

course measurement, the number of FLB in *Simulium* guts stopped increasing after 30 min (Fig. 3). Thirty minutes probably corresponds to the gut passage time for *Simulium* (i.e. the rate of FLB egested after 30 min equals the rate ingested). Uptake between 0 and 10 min seemed to be slower than uptake between 10 and 30 min (Fig. 3). The FLB took ~1 min to travel 10 m to the blackflies; otherwise the FLB concentration in the water was constant during the entire trial. Thus there was no effect due to FLB availability. Instead, bacteria captured within the first 10 min were probably not entering the region of the gut that we dissected to count ingested FLB. We therefore calculated the ingestion rate of the bacteria based on the slope of the regression of bacteria in the gut between 10 and 30 min of the uptake trial (Fig. 3). The mass-specific ingestion rate for *Simulium* was 1.4×10^4 cells mg^{-1} min^{-1}. Because the amount of FLB in blackfly guts levels off at 3.0×10^5 cells mg^{-1} (avg of the 30- and 60-min numbers), not determining the ingestion of FLB with time underestimated blackfly ingestion rate by a factor of three.

The area-specific uptake of FLB attributable to the seven macroinvertebrates in this study was 2.7×10^6 cells m^{-2} min^{-1}, which was a slight overestimation of invertebrate uptake because we sampled between 5 and 12 m below the dripper. Because uptake is concentration-dependent, there should have been lower ingestion rates downstream, where FLB concentrations were lower. Of this total, FLB uptake by *Simulium*, 2.4×10^6 cells m^{-2} min^{-1}, represented 91% of invertebrate consumption and was due to *Simulium*'s high biomass and high mass-specific ingestion rate of FLB (Table 1). The taxon with the highest rate other than *Simulium* was *Diplectrona*, which also filter feeds. However, when we compared removal of FLB due to invertebrate consumption to total removal from the water column (Fig. 1), we found that invertebrate

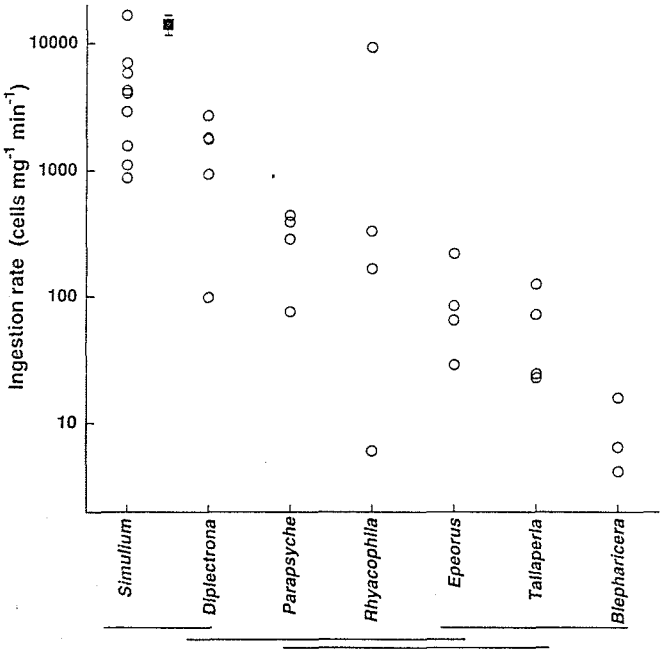

Fig. 2. FLB ingestion by insects. Taxa are ranked from high to low mean ingestion; note log scale. Individual insects—O; ingestion rate calculated for *Simulium* during the time-course trial—■. Error bars are the 95% C.I. Lines below taxa names represent results from one-way ANOVA: taxa that share the same line are not significantly different ($P > 0.05$).

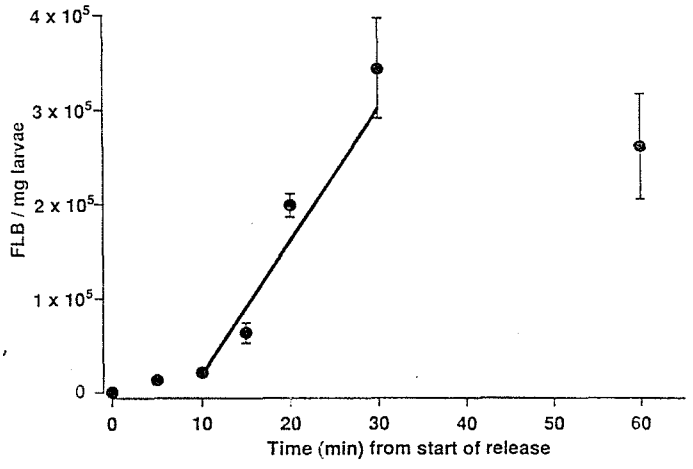

Fig. 3. FLB ingestion by *Simulium*. Error bars are 1 SE; error bars are too small to see from 0 to 10 min ($n = 3$). The line is a least-squares regression of time and FLB ingestion to determine the feeding rate between 10 and 30 min ($y = 1.41\times10^4 x - 1.22\times10^5$, $r^2 = 0.94$).

Table 2. Parameters from seston uptake studies.

Seston characteristics		Fall velocity (mm s^{-1})				
Type	Size (μm)	Depositional	Settling	Depos./ settling	Uptake length (m)	Reference
Natural	53–102	0.07–0.16	1.0–1.3	0.07–0.12	580–800	Cushing et al. 1993
Pollen	87–88	0.21–0.25	0.26–0.31	0.81–0.82	122–190	Miller and Georgian 1992
FLB	2	0.093	0.000055	1,690	80.3	This study

consumption represented only 7% of total FLB uptake. Thus, most FLB were removed from the water column by processes other than invertebrate ingestion. The uptake length of FLB that was solely a result of *Simulium* filtering was found by substituting the area-specific uptake rate for FLB due to *Simulium* ($U_{Simulium}$) into Eq. 2 and solving for S. The uptake length of FLB due only to *Simulium* was 1,420 m ($k = 7.1 \times 10^{-4}$ m^{-1}). Thus, if FLB were removed from the stream only by *Simulium* filtering and not by physical processes, and if *Simulium* density were as uniformly high as it is in the bedrock outcrop, the average travel distance for FLB would be 1.4 km.

Discussion

Uptake length of FLB—The 80-m uptake length of FLB along the bedrock outcrop cascade is either shorter than or similar to the few studies that examined uptake of larger particles in a stream. Corn pollen uptake lengths were 122–190 m in a second-order New York stream (Miller and Georgian 1992). Natural seston uptake lengths were 580–800 m in second- and third-order Idaho streams (Cushing et al. 1993). A Virginia coastal plain stream had uptake lengths of ground leaves ranging 2–84 m (Jones and Smock 1991). Because of differences in geomorphology between Hugh White Creek and these other streams, comparing the seston depositional velocity between the three studies is more informative than comparing uptake length. A comparison of depositional velocity permits consideration of the role of water depth and velocity in determining particle uptake. Both velocity and channel depth were important determinants of uptake of lycopodium spores from the water column in a laboratory study (Reynolds et al. 1990).

Depositional velocity was relatively similar between the three sites (Table 2), whereas settling velocity varied 24,000-fold between the studies. Although Miller and Georgian (1992) found that settling velocity approximately equaled depositional velocity, Cushing et al. (1993) found settling velocity to be 10 times higher than depositional velocity; they postulated that shear stress along the stream bottom was too great to allow deposition. In contrast, settling velocity was 1,690 times less than depositional velocity in our study, which suggests that settling velocity is not a useful correlate of uptake length of particles over a range of sizes. Both Cushing et al. (1993) and Miller and Georgian (1992) used particles larger than FLB used in our study (Table 2). FLB do not settle from the water column but are more likely to chemically adhere to the substrate. Bacteria often adhere to substrate by using exopolymers found on their cell walls (Kjelleberg 1984); however, we do not know how the use of heat-killed *E. coli* affects these surface polymers and thus their ability to adhere to the substrate.

Increasing depth may also decrease FLB uptake length (Reynolds et al. 1990) but via a mechanism other than settling. Shallow depths and turbulent flow in this reach increase the probability that an individual cell will contact and adhere to the substrate and not simply shorten the distance through which it needs to settle. Another factor that contributes to short uptake length of FLB is moss, which covers much of the bedrock outcrop and serves to trap particles (Smith-Cuffney 1987). Substrate strongly affects seston transport. Webster et al. (1987) found that seston uptake lengths in channels were 4 m over gravel or artificial turf substrate and 212 m over smooth fiberglass. Even though the mechanism of uptake of FLB is most likely different than that for a large particle with a settling velocity about equal to its depositional velocity, depositional velocity may be a better, albeit empirical, predictor of uptake length of different size particles in streams than is settling velocity.

Caution is necessary when comparing FLB uptake to uptake of natural bacteria. Although the 2-μm cells are smaller than other seston particles experimentally released into streams, they are >0.5-μm native bacteria. Native bacteria may also have more extracellular polysaccharide, which could affect their affinity for substrate. FLB may be more easily captured by filter-feeders than native bacteria are, although blackflies should be adept at capturing particles <0.5 μm (Wotton 1976). We used large *E. coli* because culturing small bacteria in the quantities necessary for our releases (1×10^{12} cells) would have been difficult due to the large volume of dilute culture media needed to grow many small cells. Dilute culture media cause cells to be smaller and overall cell yield (no: $liter^{-1}$) to be lower.

FLB uptake lengths are similar to nutrient uptake lengths in bedrock-outcrop habitats in the same stream (Munn and Meyer 1990). Uptake lengths were 69 m for DOC, 86 m for Ca^{2+}, 136 m for NO_3^-, and 40 m for PO_4^{3-} during a summer release at a discharge of 3.1 liters s^{-1} over bedrock outcrop sites. The similarity of nutrient and

FLB uptake lengths suggests that physical processes, such as contact with the stream bottom, determine uptake of both dissolved and particulate matter—albeit by vastly different mechanisms.

Invertebrate FLB ingestion—FLB ingestion by *Simulium* was much higher than all other taxa. Laboratory studies have shown that *Simulium* can capture and grow on a diet of bacteria (Fredeen 1964; Edwards and Meyer 1987). Its cephalic fans enable it to capture submicron and even colloidal particles (Wotton 1976) by intercepting them with mucus-covered microtrichia (Ross and Craig 1980). Bacteria may be important for blackfly diets in streams, especially where bacterial concentrations are high (Edwards 1987). By examining a time-course of FLB ingestion, we found FLB ingestion rates 3 times higher than those we found by measuring gut FLB after 1 h. *Simulium* gut passage time has been found to be <1 h (Mulla and Lacey 1976; Wotton 1978). We did not measure time-courses for other taxa; however, most of these taxa had ingested much less FLB at the end of the hour release than *Simulium,* had and they are larger organisms that likely have longer gut passage times. The other filter-feeders, *Diplectrona* and *Parapsyche,* ingested less FLB than *Simulium* did. Each is a net-building filterer, but their meshes range from 42 to 191 μm for 1st- through 5th-instar *Diplectrona,* and 49–302 μm for 1st- through 5th-instar *Parapsyche* (Georgian and Wallace 1981). These nets are too coarse to efficiently capture 2-μm FLB. However, both caddisfly taxa consumed FLB, suggesting that some FLB stick to particles or the net and are consumed by caddisflies. Given that *Parapsyche* are more predaceous than *Diplectrona* (Benke and Wallace 1980; R. Hall pers. obs.), which is detritivorous, higher consumption of FLB by *Diplectrona* is to be expected.

We found FLB in guts of deposit-feeding organisms, which is not surprising given that most FLB removal was presumably by adhesion to the substrate. Scrapers, which consume biofilm or ingest particles, apparently consumed FLB that adhered to the substrate. Much of *Stenonema* (a collector-gatherer mayfly) production in a blackwater river was derived from bacterial carbon in wood biofilm, which forms from adhesion of sestonic bacteria and detritus to wood (Edwards and Meyer 1990; Benke et al. 1992; Couch and Meyer 1992). Thus, recently deposited seston and bacteria may represent a food source for deposit-feeders. Nonetheless, deposit-feeders are not able to consume FLB at the same rate as filter-feeding *Simulium* does. *Blepharicera,* a scraper, had low FLB ingestion. It lives in habitat similar to *Simulium*: sheer rock faces with no moss, where there may have been little FLB adhesion to the substrate. The high variability within taxa prevented us from discerning FLB ingestion rate differences between most taxa. However, this variability is most likely due to differences in FLB ingestion caused by the microhabitat of each individual and not to counting error. During the time-course experiment, the variability of ingestion rates was small relative to *Simulium* samples collected after 1 h. Samples of *Simulium* in the time-course trial were collected from spots in close proximity, as opposed to randomly along the 7-m reach where the rest of the invertebrates were sampled.

Effects of blackflies on FLB uptake—Many researchers have examined ingestion rates by filter-feeders and discussed their role in the retention of organic matter in streams (e.g. Wallace et al. 1977; Benke and Wallace 1980; Morin et al. 1988). Most studies, however, do not compare invertebrate ingestion with concomitant measures of seston uptake. Our study demonstrates a means to observe invertebrate FLB ingestion and compare it to whole-stream uptake of FLB. If whole-stream seston uptake is short relative to uptake due to insects, than we can conclude that insects exert little control over FLB uptake. In Hugh White Creek, blackflies had a relatively small, but measurable, influence on seston uptake (i.e. uptake length of FLB due to blackflies was 1.4 km compared with the measured FLB uptake length of 80 m). Because the study site was bedrock outcrop with more filter-feeders than there were in other areas of the stream, ingestion rates of FLB were likely higher there than in other reaches. Newbold et al. (1983) determined that seston uptake length due to the dominant filter-feeder, *Diplectrona,* was 37 km, 26 times greater than the bacterial uptake length attributable to blackflies in our study. Georgian and Thorp (1992) compared seston removal among filtering caddisflies based on literature values of secondary production or ingestion rates and extrapolated to an uptake rate (k). FLB removal due to *Simulium* (7.1×10^{-4} m^{-1}) in our study was higher than the uptake rate of total particulate organic matter by all caddisflies in their study. McCullough et al. (1979*a,b*) measured ingestion for both a net-spinning caddisfly and a blackfly and concluded that seston removal due to invertebrate consumption was 1×10^{-4} m^{-1}, 7 times lower than removal by blackflies in our study.

Morin et al. (1988) used a combination artificial stream and a whole-stream larval removal experiment to determine the influence of blackfly feeding on seston transport at a lake outlet. Blackfly seston uptake at the small lake outlet was ~0.01 m^{-1}, 14 times greater than blackfly uptake in Hugh White Creek. Larval removal increased seston concentrations, which demonstrated that larvae were primarily responsible for seston removal in this lake outlet. Hence the impact of filter-feeders on seston removal was greater in this lake outlet habitat than it was on bedrock in a mountain stream.

Under what conditions might blackflies shorten seston uptake length in a stream? First, stream hydraulics must be such that depth is low and velocity is high (i.e. maximize v_{wat}/d). Decreasing depth exposes a larger fraction of the water column to filtering. Particles in a deep stream will be less readily filtered or removed abiotically (*see* Reynolds et al. 1990). Increasing velocity will increase the delivery rate of particles to the filterer (higher consumption) and may increase the uptake length of the particle. Thus, low depth and high velocity streams (i.e. with a high Froude number) should have the highest potential for filterer effects. Indeed, Wetmore et al. (1990) found that blackflies selected attachment sites with high Froude

numbers (0.7). Filterer abundance must also be high. Blackfly abundance in Hugh White Creek was <2% of that in the lake outlet (Morin et al. 1988) and on the low end of densities provided by Wotton (1987), who reported densities up 1.2×10^6 m^{-2}. Morin et al. (1988) suggest that discharge/width must be minimized, which essentially means that minimizing depth maximizes filterer control. Seston removal in their lake outlet was 14 times higher than in Hugh White Creek, yet lake outlet blackfly biomass was 134 times higher and had a clearance rate that was 3 times higher. Hugh White Creek discharge/stream width was 3.1 liters s^{-1} m^{-1}, which was lower than the lake outlet value of 44 liters s^{-1} m^{-1} (Morin et al. 1988). Thus, the lower discharge/stream width ratio gives blackflies a proportionally higher effect on seston transport in Hugh White Creek than at the lake outlet.

Our study provided a means of quantifying the effect that a single taxon (e.g. *Simulium*) can have on the ecosystem process of bacterial transport in a stream. Because of *Simulium*'s ability to capture ultrafine particles, it is potentially able to influence downstream transport of bacteria and has a larger effect on bacterial transport than other taxa have. However, *Simulium* in the study reach had little effect on bacterial uptake length relative to physical processes, which readily removed bacteria from the water column. Blackfly abundance was relatively low in our study, so the potential for blackflies to regulate bacterial transport will be greater in streams with higher blackfly abundance. If blackfly densities in Hugh White Creek reached 48,000 m^{-2} (10× measured abundance) and all variables remained the same, blackflies would be capable of removing 60% of the FLB in transport, shortening uptake length from 1.4 km to 142 m. This blackfly density is well within the range of observed abundances in other systems (Wotton 1987). In aquatic environments where blackfly density and v_{wat}/d are high, blackflies have the potential to regulate bacterial transport.

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Submitted: 22 September 1995
Accepted: 5 December 1995
Amended: 22 February 1996