

## Deposition, benthic residence, and resuspension of fine organic particles in a mountain stream

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### *Abstract*

We estimated deposition and resuspension rates of natural particulate organic matter (POM) in Bloomington Creek, Idaho, a mountain stream flowing at 225 L s<sup>-1</sup>. POM was collected from the water column, fractionated into two size classes—very fine POM (VFPO, 15–52 μm) and fine POM (FPO, 53–106 μm), and radiolabeled by using <sup>14</sup>C-dimethylsulfate. The labeled particles in each size class and a conservative tracer were released to the stream in metered pulses and then sampled from the water column at six stations extending 1 km downstream for 4 d. Deposition and resuspension rates were estimated by fitting a one-dimensional advection-dispersion model to <sup>14</sup>C-concentrations measured during and after release. Model-estimated deposition velocities were 0.12 (0.09–0.16, 95% confidence interval) and 0.18 (0.10–0.31) mm s<sup>-1</sup> for VFPO and FPO, respectively. There was some (~0.05 mm s<sup>-1</sup>) additional short-term (~20 min) detention of VFPO and FPO that may have been related to transient storage. For VFPO, 34% of deposited particles resuspended after a mean residence time of 13 (6.9–25) h, and the remainder resuspended with a residence time of 7.5 (2.9–19) d. For FPO, these estimates were 17%, 2.4 (1.0–4.9) h, and 2.6 (1.7–4.0) d, respectively. The weighted mean residence times and downstream velocities of particle migration were 5.1 d and 150 m d<sup>-1</sup> for VFPO, and 2.2 d and 230 m d<sup>-1</sup> for FPO. The migration velocities suggest that a significant fraction of particles exported from headwater streams travel long distances and can reach larger riverine or marine environments before mineralization.

Headwater streams export typically more than half of the organic matter that they produce or receive from the landscape, and roughly half of this export is in the form of particulate organic matter (POM) (Golladay 1997; Webster and Meyer 1997). It has long been recognized that the exported organic matter can subsidize downstream ecosystems (Fisher and Likens 1973) and influence the structure of downstream consumer communities and food webs (Vannote et al. 1980; Minshall et al. 1983). Yet the strength of such upstream-to-downstream linkages and the longitudinal scale over which they occur remain unclear. High rates of CO<sub>2</sub> evasion from large rivers suggest that a substantial fraction of transported

organic matter is metabolized before reaching the sea (Cole and Caraco 2001; Richey et al. 2002) and thus point to strong longitudinal linkage within river networks. Conversely, observations that riverine seston is old (Raymond and Bauer 2001) and relatively refractory (Hedges et al. 1994; Webster et al. 1999), together with isotopic evidence that downstream food webs depend primarily on local resources (Finlay et al. 2002; Huryn et al. 2002; Thorp et al. 2002), raise questions as to whether POM contributes to significant upstream–downstream energy linkages.

One factor that may strongly influence such linkages is the residence time of particles within the river. Whether the carbon in a seston particle is consumed or metabolized very near its source, in some downstream reach, or in the marine environment depends not only on its biological availability but also on how rapidly it is transported downstream. The “turnover length” for a form of organic carbon, or the downstream distance it travels until it is mineralized, can be represented as the product of its biological turnover time and downstream velocity (Newbold et al. 1982; Webster et al. 1999). Organic particles move downstream as a series of saltations interspersed by stationary periods in the streambed (Cushing et al. 1993; Webster et al. 1999), so that they migrate downstream at a velocity far slower than that of the

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water. Previous estimates of downstream migration velocity have been calculated as the ratio of the downstream POM flux to the POM standing stock per unit of stream length (see Newbold et al. 1982; Minshall et al. 1992). This approach, however, implicitly assumes that benthic POM in streams and rivers consists of a well-mixed pool that continually and thoroughly exchanges with the overlying suspended POM, and does not address the questions of how frequently exchanges occur and whether the exchange involves the entire stock of benthic POM.

Tracer additions of  $^{14}\text{C}$ -labeled natural seston (Cushing et al. 1993; Minshall et al. 2000) and of surrogates such as spores (Wanner and Pusch 2000), corn pollen (Georgian et al. 2003), bacteria (Hall et al. 1996), and yeast (Paul and Hall 2002) have shown that there is a rapid and continual deposition of fine particles onto the streambed. The delivery of particles to the bed appears to be governed more by turbulence than by gravitational settling (Hall et al. 1996; McNair et al. 1997; Thomas et al. 2001). Retention of particles appears to be strongly influenced by the presence of a biofilm (Battin et al. 2003) and also by mixing into the hyporheic zone (Minshall et al. 2000; Packman and MacKay 2003).

Relatively little is known about the fate of particles once deposited—that is, whether and how rapidly particles are resuspended, whether they tend to accumulate until scoured by rising flows, or whether the deposition of particles is balanced by metabolic degradation. Cushing et al. (1993), after quantifying the deposition of  $^{14}\text{C}$ -labeled seston in an Idaho stream, were able to recover <1% of the originally deposited particles after 24 h and inferred that nearly all of the particles had been resuspended and exported from the reach within this period. Webster et al. (1999) calculated that the fine POM (0.45–1000  $\mu\text{m}$ ) deposition flux in a small Appalachian woodland stream would replace the standing stock of benthic fine POM in  $\sim 19$  h. Neither of these inferences, however, was based on direct observation of particle resuspension.

In the present study, we describe the recovery of resuspended particles during the hours and days after the initial measurement of particle deposition from a metered addition of  $^{14}\text{C}$ -labeled natural organic particles. The estimates of particle transport distance and deposition velocities from the tracer additions described here have been presented elsewhere (Minshall et al. 2000; Thomas et al. 2001; Georgian et al. 2003). We present direct evidence that a large fraction of deposited particles was resuspended within a few days of deposition, and by fitting a transport model to the resuspension dynamics, we estimate benthic residence times prior to resuspension and downstream migration velocities.

## Methods

*Study area*—Bloomington Creek is located in the Bear Lake drainage in the northern Wasatch Mountains of southeastern Idaho. The tracer additions presented here were conducted on a second-order reach (111°33'W, 42°10'N) designated by Minshall et al. (2000) as Middle Bloomington Creek (MBC). The reach has a meandering channel with a

Table 1. Channel and flow characteristics of Middle Bloomington Creek during  $^{14}\text{C}$ -labeled releases of VFPM and FPOM, 6 August 1996.

Streamflow, $Q$ ( $\text{L s}^{-1}$ )	
Average for reach	225
Release point (0 m)	221
End of reach (1000 m)	278
Current velocity, $v_w$ ( $\text{m s}^{-1}$ )	0.29
Depth, $d$ (m)	0.31
Cross sectional area, $A$ ( $\text{m}^2$ )	0.78
Longitudinal dispersion, $D$ ( $\text{m s}^{-1}$ )	0.7
Transient storage exchange coefficient, $\alpha$ ( $\text{s}^{-1}$ )	$1 \times 10^{-4}$
Hydraulic exchange velocity, $v_h$ ( $\text{mm s}^{-1}$ )	0.031
Return exchange rate from transient storage, $\beta$ ( $\text{s}^{-1}$ )	$9.5 \times 10^{-4}$
Residence time, $1/\beta$ , of water in transient storage (h)	0.29
Cross-sectional area of transient storage, $A_s$ ( $\text{m}^2$ )	0.082
Standardized transient storage area, $A_s/A$	0.105
Water temperature $^{\circ}\text{C}$	5–8

Values are averages for the reach unless otherwise stated. From Minshall et al. (2000).

slope of  $0.018 \text{ m m}^{-1}$  and a substratum of cobble and gravel with some sand. Channel and flow characteristics are presented in Table 1. Annual peak flow occurs in May or June as a result of snowmelt. During the 5 d of the experiment in August, there was no precipitation and flow was stable.

*Physical characterization of the stream*—Stream width ( $w$ ) was calculated as the average of 30–100 measurements. Water velocity ( $v_w$ ) and streamflow ( $Q$ ) were obtained from the dynamics of rhodamine WT released to the stream as a conservative tracer (Minshall et al. 2000), using the one-dimensional advection-dispersion model and parameter estimation procedure of Hart (1995). We calculated wetted channel cross sectional area  $A = Q/v_w$ , and water depth  $d = Q/(v_w w)$ . The model also estimated longitudinal dispersion,  $D$ ; the transient storage zone exchange coefficient,  $\alpha$ ; and the rate of return transfer from transient storage,  $\beta$ . From these parameters we calculated the cross-sectional area of the transient storage zone  $A_s = A\alpha/\beta$ , and the hydraulic exchange velocity  $v_h = d\alpha$ . Values are given in Table 1.

*Suspended and benthic organic matter*—The concentration of transported particulate matter was estimated by passing 108 L of streamwater through nested Nitex® nets of 1000-, 52-, and 15- $\mu\text{m}$  mesh by using a calibrated pump. The material was chilled, minimizing changes in particle size owing to microbial effects and physical disruption by freezing, and transferred to the laboratory. There, particles collected by the 52- $\mu\text{m}$  net were wet-sieved through 106- and 53- $\mu\text{m}$  standard brass sieves, and the fine POM (FPOM, 53–106  $\mu\text{m}$ ) size fraction was retained. Very fine POM (VFPM, 15–52  $\mu\text{m}$ ) consisted of the material collected in the 15- $\mu\text{m}$  net. Material was dried in preweighed crucibles at  $60^{\circ}\text{C}$  ( $\geq 48$  h), weighed, ashed at  $550^{\circ}\text{C}$  for 4 h, and reweighed to determine ash-free dry-mass (AFDM). Replicate samples were collected from each of six stations along the study reach.

Benthic POM was quantified by isolating a  $0.089\text{-m}^2$  section of stream bottom with a stainless-steel cylinder, elutri-

ating the isolated sediments by agitating them, and passing the resulting suspension through nested Nitex® nets (described previously). The elutriation was performed five times before the cylinder was moved. AFDM of each size class was determined as described previously. One sample was collected from each of the six stations.

*Particle tracer experiments*—We conducted particle tracer experiments by (1) collecting natural suspended particulate matter (seston) from the stream, (2) size-fractionating and labeling the seston using  $^{14}\text{C}$ -dimethylsulfate, (3) releasing labeled particles into the stream in conjunction with a hydrologic tracer, (4) observing the temporal and spatial pattern of particle loss from the water column, and (5) collecting particles from the water column at six downstream stations for an extended period of time to estimate resuspension.

Seston from the study site was collected and wet-sieved as described previously into fractions containing VFPO and FPOM. Each fraction was centrifuged, decanted, resuspended in  $\sim 15$  ml of  $0.01$  mol  $\text{L}^{-1}$  NaOH with a vortex mixer, and centrifuged and decanted again. The  $^{14}\text{C}$ -dimethylsulfate was stirred into the pellets for 2 min, and the methylation reaction, which radiolabels the organic matter (Wolfinbarger and Crosby 1983), was allowed to proceed at room temperature for 40 min. The reaction was stopped by adding 5–10 ml of water, and the slurry was washed, re-centrifuged, and decanted five times to remove all unreacted dimethylsulfate. Subsamples of the final suspension were counted by liquid scintillation to measure labeling efficiency, which ranged from 0.3–5%. Cushing et al. (1993) found that this procedure did not affect the size or shape of the particles or their appearance under scanning electron microscopy.

For each release, labeled particles were resieved into a continuously mixed suspension, then metered into the study reach through a 10-mm-diameter tube suspended a few centimeters from the water surface. The particles entered just upstream from a riffle, which produced thorough vertical and lateral mixing within a few meters of downstream transport. Two releases were conducted on 6 August 1996. The first, consisting of 11  $\mu\text{Ci}$  of  $^{14}\text{C}$ -labeled VFPO and 20 ml of rhodamine WT, was metered into the stream at 1240 ml  $\text{min}^{-1}$  for 10 min beginning at 0950 h. The second release consisted of 7.4  $\mu\text{Ci}$  of  $^{14}\text{C}$ -labeled FPOM and 39 ml of rhodamine WT and was metered into the stream at 1500 ml  $\text{min}^{-1}$  for 8 min beginning at 1530 h. During the passage of each release pulse, grab samples were collected in wide-mouth (7-cm-diameter) 910-ml glass jars from mid-depth in the thalweg at points 50, 100, 250, 500, 750, and 1000 m downstream from the point of release. Beginning 1–2 h after the passage of the respective pulse, periodic samples were taken from the water column to estimate resuspension. These “net-concentrated” samples were collected 250, 500, and 1000 m downstream from the point of release by pumping 565 L of water at  $\sim 2$   $\text{L s}^{-1}$  through nested Nitex® mesh nets (1000, 52, and 15  $\mu\text{m}$ ). In the laboratory the contents from the 52- $\mu\text{m}$  nets were further sieved through a 106- $\mu\text{m}$  sieve. The nets allowed detection of particles at concentrations in the range of 0.01–1.0 disintegrations per minute (dpm)  $\text{L}^{-1}$ , well below the limit of detection for the grab samples ( $\sim 2$  dpm  $\text{L}^{-1}$ ).

A 15-ml subsample was removed from each 910-ml water sample in the field to determine rhodamine WT concentration, and the remaining water was filtered through a 5- $\mu\text{m}$  cellulose nitrate filter. Filters were covered with liquid scintillation cocktail in the laboratory and radioassayed by using a Wallace model 1415 liquid scintillation analyzer. The amount of seston on the filters had no quenching effect on the radioassay. The resuspension samples were dried, combusted on a Packard Oxidizer, and assayed for  $^{14}\text{C}$ . Rhodamine WT was measured by using a Hitachi F-2000 Fluorescence Spectrometer.

*Modeling*—We estimated resuspension rates of deposited particles by fitting a transport model to the  $^{14}\text{C}$ -tracer data. The model represents the concentration dynamics of labeled particles suspended in the water column, including downstream advection, longitudinal dispersion, dilution, and first-order transfers to (deposition) and from (resuspension) streambed sediments. Deposition is partitioned into three benthic compartments distinguished by differing resuspension rates. We selected three, rather than more or fewer compartments, during the process of parameter estimation as described below. The model is similar to those used for solute and tracer dynamics in streams (see Bencala and Walters 1983; Runkel 1998), and is a modification of that of Cushing et al. (1993). The model numerically solves the equations:

$$\frac{\partial C}{\partial t} = -\frac{1}{A} \frac{\partial v_w A C}{\partial x} + \frac{1}{A} \frac{\partial}{\partial x} \left( A D \frac{\partial C}{\partial x} \right) - v_{\text{fot}} \frac{C}{d} + k_{r1} \frac{B_1}{d} + k_{r2} \frac{B_2}{d} + k_{r3} \frac{B_3}{d} \quad (1)$$

$$\frac{\partial B_i}{\partial t} = v_{fi} C - k_{ri} B_i \quad i = 1, 3 \quad (2)$$

$C$  is the concentration of  $^{14}\text{C}$ -labeled particles (dpm  $\text{m}^{-3}$ ) in the streamwater as a function of time ( $t$ ) and downstream distance ( $x$ );  $v_{\text{fot}}$  is the total mass transfer coefficient for particle removal from the water column ( $\text{m s}^{-1}$ ) equal to the sum of  $v_{f1}$ ,  $v_{f2}$ , and  $v_{f3}$ , the transfer coefficients into benthic compartments 1, 2, and 3, respectively;  $B_1$ ,  $B_2$ , and  $B_3$  are the densities of labeled particles (dpm  $\text{m}^{-2}$ ) in each of the respective benthic compartments as functions of  $t$  and  $x$ ; and  $k_{r1}$ ,  $k_{r2}$ , and  $k_{r3}$  are rates at which particles are returned from the respective benthic compartments to the water column.

The hydrologic parameters,  $v_w$ ,  $A$ ,  $D$ , and  $d$ , vary as a function of distance, and their values (Table 1) were obtained both from direct measurements and from the conservative tracer dynamics as previously described. The unknown parameters ( $v_{f1}$ – $v_{f3}$ , and  $k_{r1}$ – $k_{r3}$ ), were assumed uniform throughout the reach and were estimated by inverse modeling of the  $^{14}\text{C}$ -labeled particle dynamics. To do this, we coupled the transport model (Eqs. 1 and 2) to UCODE (Poeter and Hill 1998), an automated least-squares estimation procedure. Scott et al. (2003) demonstrated the efficacy of UCODE for inverse modeling of stream solute dynamics. In the UCODE implementation, we assigned higher weightings to the net-concentrated resuspension samples than to the grab samples taken during passage of the release pulse. Before weighting, the resuspension data contributed only

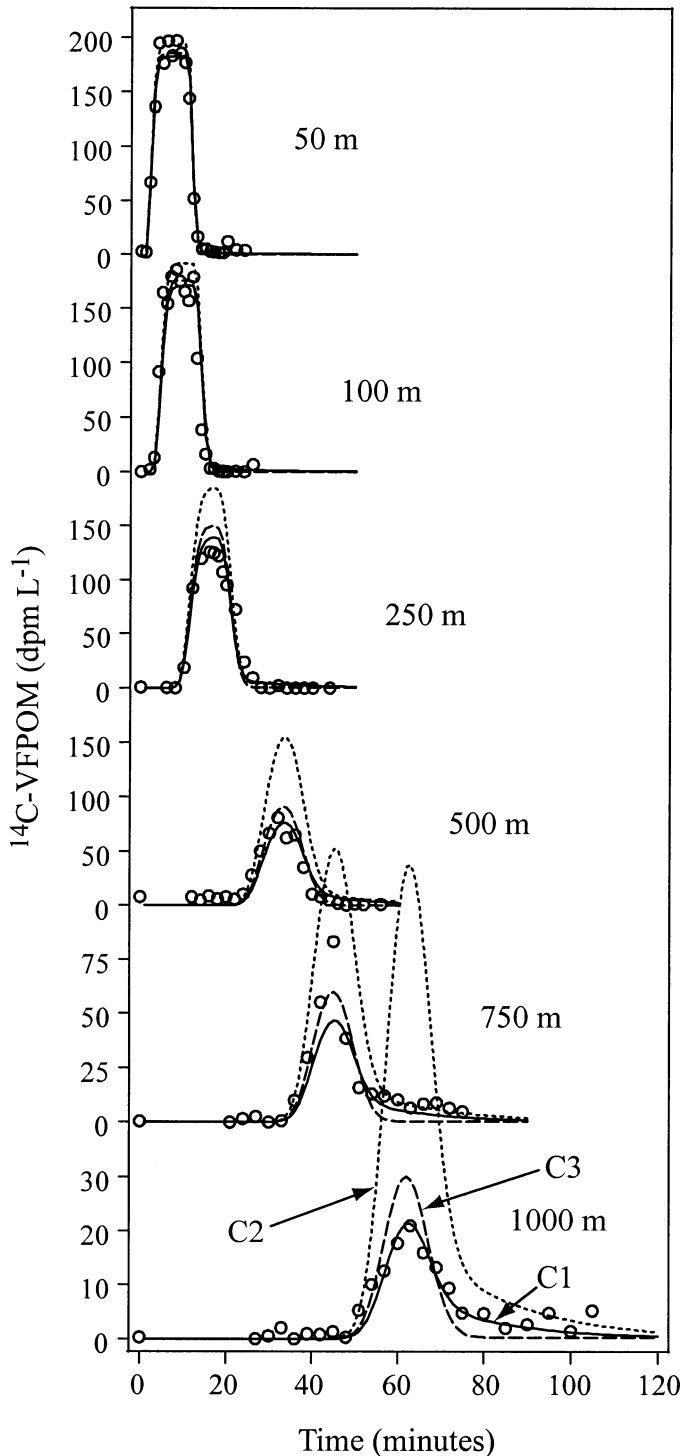


Fig. 1.  $^{14}\text{C}$ -labeled VFPOM concentration in Bloomington Creek, 6 August 1996, at six sampling stations 50 m to 1000 m downstream from a 10-min metered release. The points represent observed concentrations. Curve C1 (solid line) is the final model simulation of the VFPOM data. Curve C2 (dotted) simulates the hypothetical conservative behavior—no particle deposition. Curve C3 (dashed) simulates deposition only, without temporary detention in compartment 1. Note expansion of vertical scale at downstream stations. Curves that extend into a higher panel retain the scale of origin.

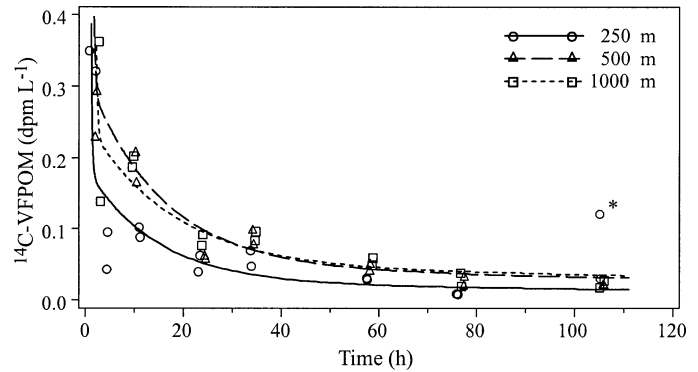


Fig. 2. Postrelease measured concentrations of resuspended  $^{14}\text{C}$ -labeled VFPOM (symbols) together with model simulated concentrations (curves), for three stations (250 m, 500 m, and 1000 m, respectively) downstream from the point of release. The point denoted by an asterisk was not included in the parameter estimation.

$\sim 0.001\%$  of the total residual sums of squares and had no influence on the parameter estimates. We selected weighting factors so that both groups of samples contributed equally to the total squared error.

Grab samples for FPOM taken during the passage of the pulse at 1000 m were not sufficiently above detection to include in the modeling. However, the labeled-FPOM dynamics were simulated for the entire reach, so that the subsequent resuspension collections taken at 1000 m could be included in the analysis.

## Results

*Benthic standing stocks and water column concentrations*—The mean standing stocks of benthic POM during the period of the release were (mean  $\pm$  1 standard deviation)  $4.1 \pm 3.4 \text{ g AFDM m}^{-2}$  of VFPOM and  $11 \pm 15 \text{ g m}^{-2}$  of FPOM; the average concentrations of suspended particles were  $0.53 \pm 0.33 \text{ g m}^{-3}$  of VFPOM and  $0.31 \pm 0.16 \text{ g m}^{-3}$  of FPOM (data not shown).

*Deposition and resuspension of VFPOM*—Inverse modeling of the passage of the release pulse of  $^{14}\text{C}$ -labeled VFPOM through the study reach (Fig. 1) and of the resuspension dynamics over the subsequent 4.5 d (Fig. 2) yielded the estimates for deposition and resuspension rates in Table 2. The final model included three benthic compartments with three distinct (no overlap in confidence interval) resuspension rates ( $k_{r1}$ – $k_{r3}$ ). The residual sums of squares for the three-compartment model were 14% lower than that for the best two-compartment model (data not shown), and 38% lower when considering the resuspension data alone. For these reasons, and because, in our subjective visual evaluation, the two-compartment model did not adequately reproduce the resuspension dynamics, we selected the three-compartment model. For this model, the weighted correlation coefficient between observed and simulated values was 0.97.

Figure 1 shows the model simulation of the labeled VFPOM dynamics (as a solid line, curve C1) and, for comparison, two other simulations. The second curve (C2) reproduces the conservative tracer dynamics (Minshall et al.



Table 2. Model-estimated deposition and resuspension rates.

Transfers to benthic compartments	VFPOM			FPOM		
	$v_f$ (mm s <sup>-1</sup> )	% total transfer	% total deposition	$v_f$ (mm s <sup>-1</sup> )	% total transfer	% total deposition
Compartment 1, $v_{f1}$	0.047 (0.030–0.073)	28		0.052 (0.018–0.15)	23	
Compartment 2, $v_{f2}$	0.041 (0.024–0.069)	25	34	0.030 (0.018–0.050)	13	17
Compartment 3, $v_{f3}$	0.078 (0.055–0.11)	47	66	0.15 (0.12–0.17)	64	83
Total transfer, $v_{f\text{tot}} = v_{f1} + v_{f2} + v_{f3}$	0.17	100		0.23	100	
Total deposition, $v_{\text{dep}} = v_{f2} + v_{f3}$	0.12		100	0.18		100
Transport distance, $S_p$ (m)	750			510		

Transfers from benthic compartments	VFPOM		FPOM	
	Resuspension rate, $k_r$ (s <sup>-1</sup> )	Residence time, $T_b = 1/k_r$ (h or d)	Resuspension rate, $k_r$ (s <sup>-1</sup> )	Residence time, $T_b = 1/k_r$ (h or d)
Compartment 1, $k_{r1}$	$1.3 \times 10^{-3}$ ( $8.2 \times 10^{-4}$ – $1.9 \times 10^{-3}$ )	0.22 h	$1.7 \times 10^{-3}$ ( $6.3 \times 10^{-4}$ – $4.4 \times 10^{-3}$ )	0.17 h
Compartment 2, $k_{r2}$	$2.1 \times 10^{-5}$ ( $1.1 \times 10^{-5}$ – $4.0 \times 10^{-5}$ )	13.4 h	$1.2 \times 10^{-4}$ ( $5.6 \times 10^{-5}$ – $2.7 \times 10^{-4}$ )	2.4 h
Compartment 3, $k_{r3}$	$1.6 \times 10^{-6}$ ( $6.0 \times 10^{-7}$ – $4.0 \times 10^{-6}$ )	7.5 d	$4.5 \times 10^{-6}$ ( $2.9 \times 10^{-6}$ – $6.8 \times 10^{-6}$ )	2.6 d
Weighted mean residence time, $T_{\text{bav}}$ (compartments 2 and 3)		5.1 d		2.2 d

95% confidence intervals given in parentheses.

2000, parameters from Table 1) but is scaled to the VFPOM release so that it represents the <sup>14</sup>C concentrations expected in the absence of deposition. The third curve (C3) simulates particle removal from the water column ( $v_{\text{fot}} > 0$ ) in the absence of any return ( $k_{r1}, k_{r2}, k_{r3} = 0$ ). For C3,  $v_{\text{fot}}$  was set equal to 0.11 mm s<sup>-1</sup>, the deposition velocity,  $v_{\text{dep}}$ , previously obtained for this experiment from a nonlinear regression of integrated transport versus distance (Thomas et al. 2001). Thus, the areas under the C3 curves approximate the areas under the data points for the respective stations. Comparison of actual <sup>14</sup>C concentrations (and their simulated dynamics, curve C1) with curve C3 at the downstream-most stations (750 and 1000 m) shows some shift of particles from the pulse and into the tail, in a pattern resembling the transient storage dynamics of the conservative tracer (curve C2). In fact, transfer velocity of VFPOM into model compartment 1 ( $v_{f1} = 0.047$  mm s<sup>-1</sup>) (Table 2) was similar to the hydraulic exchange velocity ( $v_h = 0.031$  mm s<sup>-1</sup>) (Table 1), and the residence time of particles in compartment 1 ( $T_{b1} = 1/k_{r1} = 0.22$  h) was comparable to the residence time of water in transient storage ( $1/\beta = 0.29$  h). Despite these similarities, we hesitate to conclude that compartment 1 represents particles transported into and returned from transient storage because we would expect transient storage zones to effectively filter or otherwise retain particles. Compartment 1 might instead represent a brief detention of particles on streambed surfaces at rates only coincidentally similar to those of transient storage. The relative merits of these possibilities are discussed below, but regardless of interpretation we do not, in the present study, consider particles that entered compartment 1 as having been truly “deposited.” Thus, the estimated total rate of particle removal ( $v_{\text{fot}}$ ) of 0.17 mm s<sup>-1</sup> (Table 2) includes transfer into all three compartments, whereas the estimated particle deposition velocity ( $v_{\text{dep}}$ ) of 0.12 mm s<sup>-1</sup> includes deposition only into com-

partments 2 and 3. Based on this deposition velocity, the estimated transport distance for particles,  $S_p = v_w d / v_{\text{dep}}$ , was 750 m.

Although >90% of the particles initially transferred to compartment 1 were returned to the water column during passage of the pulse and at concentrations detectable in the grab samples (Fig. 1), the return of <sup>14</sup>C-labeled VFPOM to the water column from compartment 1 was also evident in the first net-concentrated samples, 1–3 h after release (Fig. 2). Compartment 1 influenced the steeply declining portion of the simulation curves in Fig. 2. These steeply declining curves are actually extensions of the tails shown in Fig. 1 but appear to be much steeper by virtue of axis scaling. Beyond 3 h, the simulated influence of compartment 1 was negligible.

The second model compartment reproduced the resuspension dynamics observed between 4 and 40 h after the release (Fig. 2). Deposition into this compartment ( $v_{f2} = 0.041$  mm s<sup>-1</sup>) (Table 2) accounted for 25% of the total simulated particle removal, and the residence time ( $T_{b2}$ ) was 13.4 h. The third compartment generated nearly all of the resuspension after 40 h. Deposition into compartment 3 ( $v_{f3} = 0.078$  mm s<sup>-1</sup>) accounted for the remaining 47% of the total particle removal, and the residence time ( $T_{b3}$ ) was 7.5 d.

Of the total “deposited” particles (those transferred into compartments 2 and 3 but not compartment 1), 34% went into compartment 2 and 66% into compartment 3 (Table 2). The weighted mean residence, or time to resuspension, for compartments 2 and 3 combined,  $T_{\text{bav}} = (v_{f2}T_{b2} + v_{f3}T_{b3})/v_{\text{dep}}$ , was 5.1 d.

The simulated cumulative export of VFPOM from the reach (1000 m) at 110 h was 6.3 μCi or 60% of the 10.6 μCi that were released to the stream. An estimated 7.9 μCi were initially deposited into compartments 2 and 3, whereas 2.7 μCi passed directly through. The simulated export of

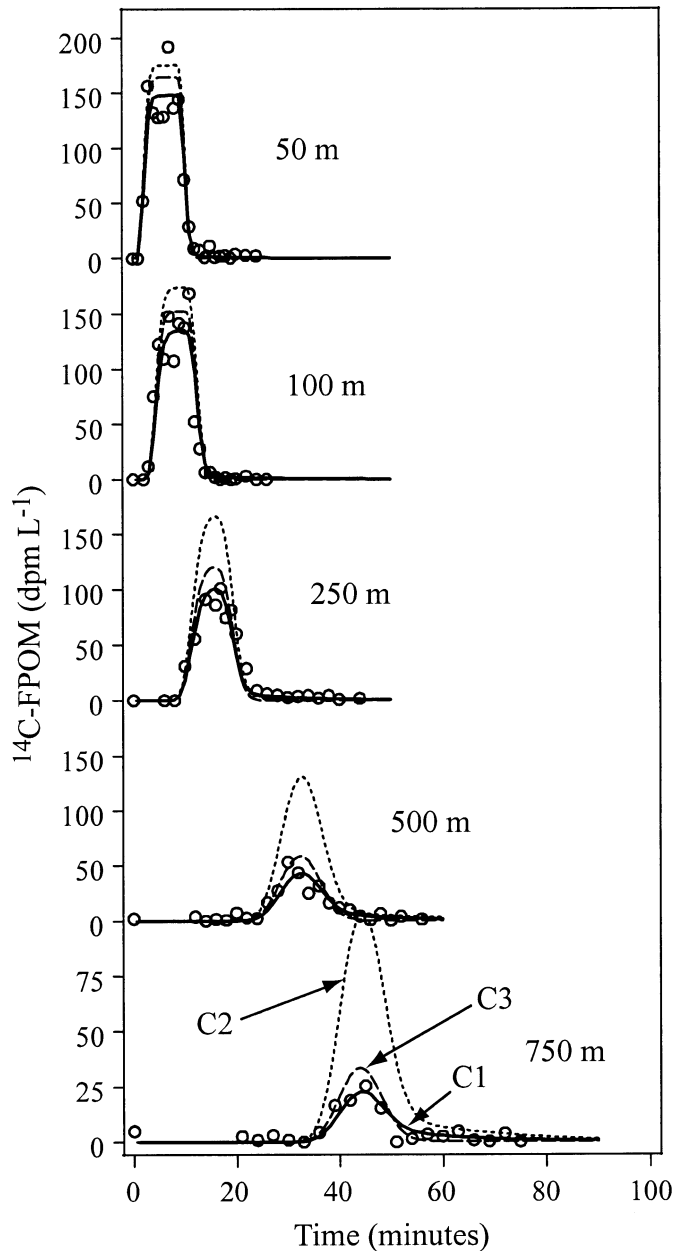


Fig. 3.  $^{14}\text{C}$ -labeled FPOM concentration in Bloomington Creek, 6 August 1996, at five sampling stations 50 m to 750 m downstream from an 8-min metered release. The points and lines are as described for Fig. 1. Note expansion of scale at downstream stations.

VFPOM during the resuspension phase was  $3.5 \mu\text{Ci}$  (the total export of  $6.3 \mu\text{Ci}$  less the  $2.7 \mu\text{Ci}$  of initial pass-through), representing 44% of the initial deposition. Because the simulation reasonably approximated the measured data up to 110 h, these figures represent a rough mass-balance accounting of the whole experiment. That is, as of 110 h, 60% of the released  $^{14}\text{C}$  had been recovered in the export and 40% was inferred to have remained in the reach (of which 98% was in compartment 3). This remaining 40% was being exported at  $\sim 9\%$  per day (consistent with the model-estimated 7.5-d residence time for compartment 3), so that it is reasonable to assume that we would have recovered

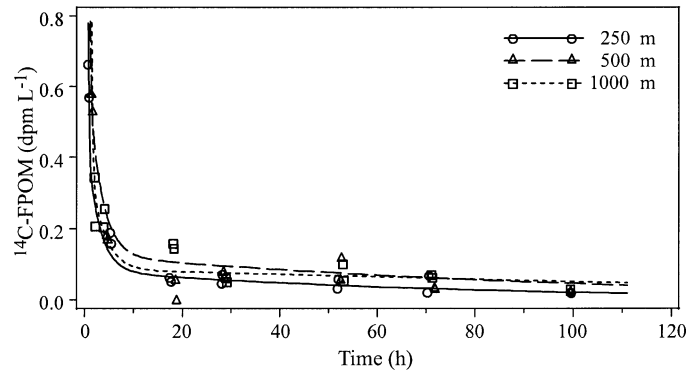


Fig. 4. Postrelease measured concentrations of resuspended  $^{14}\text{C}$ -labeled FPOM (symbols) together with model simulated concentrations (curves) for three stations (250 m, 500 m, and 1000 m, respectively) downstream from the point of release.

most of the remaining particles by sampling suspension for an additional week or two.

*Deposition and resuspension of FPOM*—The dynamics of the released FPOM during passage through the reach (Fig. 3) and during the period of resuspension sampling (Fig. 4) were qualitatively similar to those of VFPOM. The comparison of the three-compartment model with the two-compartment model was nearly the same as observed in the VFPOM modeling, both quantitatively and subjectively, so the final model included three compartments. The transfer of particles into compartment 1 was somewhat larger, and the residence time in compartment 1 was slightly shorter, than for VFPOM (Table 2). As a result, these rates bore less resemblance to the transient storage parameters (Table 1) than did those for VFPOM ( $v_{r1}$  was 67% higher than  $v_h$ , and  $k_{r1}$  was 75% higher than  $\beta$ ). The total FPOM deposition velocity,  $v_{dep}$ , of  $0.18 \text{ mm s}^{-1}$  was 49% greater than for VFPOM, and the FPOM transport distance (510 m) was correspondingly shorter than for VFPOM (750 m). This shorter transport distance accounts for the lack of measurable  $^{14}\text{C}$  in the FPOM release pulse as it passed the 1000-m station. Deposition of FPOM into compartment 2 was similar to that for VFPOM, but deposition into compartment 3 ( $v_{\beta} = 0.15 \text{ mm s}^{-1}$ ) was nearly twice that estimated for VFPOM (Table 2) and accounted for 64% of the total particle removal from the water column. The estimated residence times for FPOM (Table 2) in compartments 2 (2.4 h) and 3 (2.6 d) were considerably shorter than were the corresponding residence times of VFPOM (13.4 h and 7.5 d, respectively), although the 95% confidence intervals of the FPOM resuspension rates overlap with those of VFPOM for each the three compartments. The weighted-average residence time for FPOM in compartments 2 and 3 combined was 2.17 d, less than half of that observed for VFPOM.

The mass balance for the FPOM experiment was similar to that of VFPOM. As of the last sampling event (100 h after the release), 60% of the  $7.4 \mu\text{Ci}$  that were released had been exported from the 1000-m reach. During the passage of the release pulse, 85% of the released  $^{14}\text{C}$  was deposited into compartments 2 and 3, and the subsequent export of

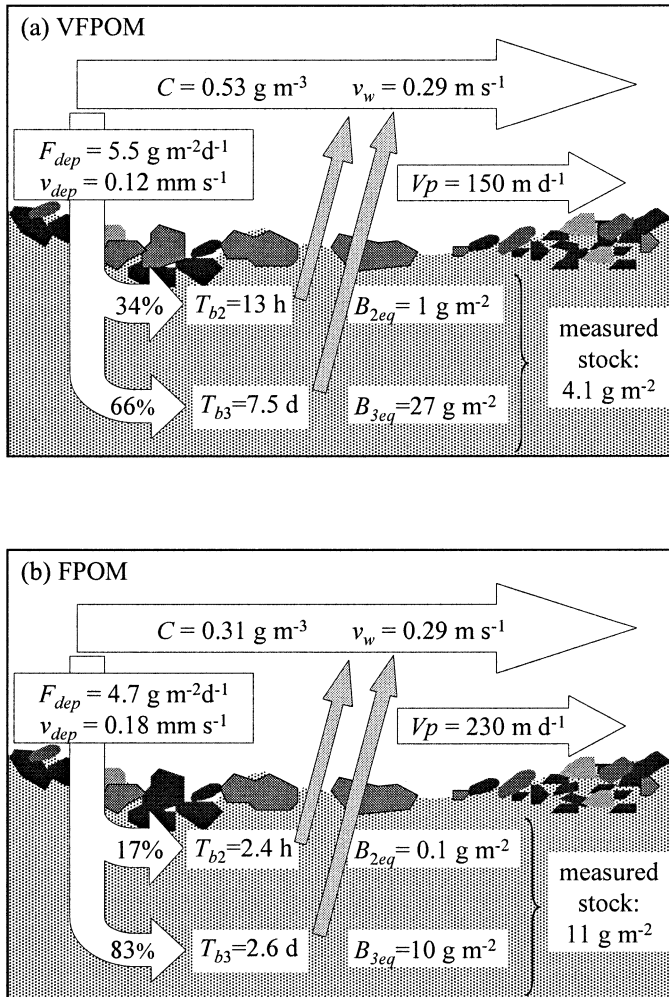


Fig. 5. Standing stocks and fluxes of VFPOM (a) and FPOM (b) in Bloomington Creek from direct measurements and model-estimated deposition and resuspension rates.

resuspended FPOM was equivalent to 47% of this initial deposition.

**Particle fluxes and equilibrium standing stocks**—Based on the  $v_{dep}$  of  $0.12 \text{ mm s}^{-1}$  and the concentration,  $C$ , of suspended VFPOM of  $0.53 \text{ g AFDM m}^{-3}$ , the deposition flux ( $F_{dep} = v_{dep}C$ ) of VFPOM onto the streambed was  $5.5 \text{ g m}^{-2} \text{ d}^{-1}$  (Fig. 5a) and the deposition flux of FPOM was  $4.7 \text{ g m}^{-2} \text{ d}^{-1}$  (Fig. 5b). The total (VFPOM + FPOM) deposition flux was therefore  $\sim 10 \text{ g m}^{-2} \text{ d}^{-1}$ .

The deposition flux into compartment  $i$  divided by the respective resuspension rate yields the predicted equilibrium benthic standing stock:  $B_{ieq} = v_{fi}C/k_{ri}$ . The total predicted equilibrium stock ( $B_{eq} = B_{2eq} + B_{3eq}$ ) of VFPOM was  $28 \text{ g m}^{-2}$ , consisting of  $1.0 \text{ g m}^{-2}$  in compartment 2 and  $27 \text{ g m}^{-2}$  in compartment 3 (Fig. 5a). Similarly, the total predicted equilibrium stock of FPOM was  $10 \text{ g m}^{-2}$ , consisting of only  $0.1 \text{ g m}^{-2}$  from compartment 2 and the balance from compartment 3 (Fig. 5b).

**Downstream migration velocity**—The average velocity at which a particle moves downstream, or its migration veloc-

ity,  $V_p$ , was calculated as the downstream water velocity times the fraction of time that a particle is in suspension, i.e.,  $V_p = v_w T_w / (T_w + T_{bav})$  (Webster et al. 1999), in which  $T_w = d/v_{dep}$  and  $T_{bav}$  (Table 2) are the residence times of a particle in the water column and the streambed, respectively. The migration velocity for VFPOM was  $150 \text{ m d}^{-1}$  (Fig. 5a) and for FPOM was  $230 \text{ m d}^{-1}$  (Fig. 5b).

## Discussion

**Transient storage and short-term detention**—It is an open question whether transient storage in streams strongly influences particle deposition. The removal of suspended particles by hyporheic exchange has been demonstrated in laboratory flumes (Packman and MacKay 2003). Minshall et al. (2000) reported a significant correlation between the standardized size of the transient storage zone ( $A_s/A$ ) and deposition velocity, although this relationship might have been confounded by stream size. Paul and Hall (2002), on the other hand, found no influence of transient storage on deposition. In the present study, we found that both VFPOM and FPOM were briefly detained within the reach at rates that could not be statistically distinguished from the detention of water in transient storage. It is therefore tempting to suggest that this brief retention, described by model compartment 1, represented a simple advective transport to and from the transient storage zones. This interpretation implies, however, that particles passed through transient storage without ever being deposited, and thus provides no evidence that transient storage zones enhanced deposition. Somewhat paradoxically, particles that actually were deposited (for longer than a few minutes) in transient storage zones would have appeared, in the model, in compartment 2 or 3 (depending on residence) rather than in compartment 1. This leaves open the possibility, therefore, that transient storage did play a significant role in particle deposition but one that the present study could not distinctly identify. We suggest two competing explanations for the dynamics of our model compartment 1. The first is that they are not related to transient storage but instead represent a very brief deposition of particles on streambed surfaces at rates that, by chance, are similar to those of transient storage of water. The second is that they actually do reflect transient storage, which in turn implies that the bulk of the transient storage is unlikely to be in hyporheic zones, where deposition would rapidly occur (Packman and MacKay 2003), but instead in lateral areas that are either deep enough or maintain sufficient turbulence to keep the particles in suspension.

Our distinction of total particle removal ( $v_{floss}$ , transfer to all three compartments) from particle deposition ( $v_{dep}$ , transfer only into compartments 2 and 3) was based, in part, on maintaining consistency with previous studies of particle deposition that typically estimate particle loss by integrating the area under the concentration-versus-time curve of the release pulse. More than 90% of the particles that entered compartment 1 returned to the water column during passage of the pulse and so contributed to the integrated areas as though they had never been deposited or otherwise detained. Thus, the previously published estimates of  $v_{dep}$  for this ex-



periment ( $0.11 \text{ mm s}^{-1}$  for VFPOM [Thomas et al. 2001] and  $0.17 \text{ mm s}^{-1}$  for FPOM [Minshall et al. 2000]), which were based on the integrated areas, are nearly the same as those of the present study ( $0.12 \text{ mm s}^{-1}$  and  $0.18 \text{ mm s}^{-1}$ ), which were based on dynamic simulation.

*Particle resuspension*—Of the particles considered as truly deposited, the resuspension dynamics of both VFPOM and FPOM were better described by two compartments (two distinct residence times) than by one. It seems likely that the two compartments represent a statistical partitioning of a spectrum of retention times rather than two distinct classes of particle fate or behavior.

The average residence times of particles on the stream bed, which ranged from hours to days, would appear to be longer than can be explained by turbulent fluctuations alone. During the 4.5 d of postrelease sampling, there were no precipitation events or discernible flow fluctuations. We suggest that biological processes, such as invertebrate activity (Wallace et al. 1991) and biofilm dynamics (Lock 1981; Battin et al. 2003), influence particle resuspension.

Our results differ from those of Cushing et al. (1993), who inferred that >99% of the deposition entered a compartment with a residence time of 1.5–3 h before resuspension, whereas the remaining 0.4% entered a compartment with a residence time of 17 d. Cushing et al. (1993) worked in Smiley Creek, Idaho, a tributary to the Salmon River, and therefore the differences may represent stream-to-stream variation. However, modeled resuspension dynamics for Smiley Creek were based on dynamics of  $^{14}\text{C}$  recovered from the streambed rather than on direct collection of resuspended material. The relatively high apparent rate of initial export might have been, in part, an artifact of low benthic sampling efficiency.

*Particle fluxes and equilibrium standing stocks*—The combined VFPOM + FPOM deposition flux of  $\sim 10 \text{ g AFDM m}^{-2} \text{ d}^{-1}$  is probably far larger than the metabolic consumption of organic matter in the stream. Ecosystem respiration was not measured in Bloomington Creek, but Minshall et al. (1992) reported daily respiration of  $0.3 \text{ g C m}^{-2} \text{ d}^{-1}$  ( $\sim 0.6 \text{ g m}^{-2} \text{ d}^{-1}$  as AFDM) in a comparable fourth-order reach of the Salmon River, Idaho. Similarly, the mean heterotrophic respiration among 22 intensively studied streams, distributed among seven biomes, was  $265 \text{ g C m}^{-2} \text{ yr}^{-1}$  or  $\sim 1.6 \text{ g AFDM m}^{-2} \text{ d}^{-1}$ , ranging to a maximum of  $7.3 \text{ g AFDM m}^{-2} \text{ d}^{-1}$  (Sinsabaugh 1997). Thus, if the deposited particles were not resuspended relatively quickly, there would be a rapid accumulation of particles in the stream bed. The absence of such accumulations qualitatively confirms our observation of rapid resuspension. The predicted equilibrium benthic standing stock of  $28 \text{ g m}^{-2}$  for VFPOM was roughly sevenfold greater than the measured stock of  $4.1 \text{ g m}^{-2}$  obtained from benthic sampling, whereas the predicted and measured stocks of FPOM were in close agreement ( $10 \text{ g m}^{-2}$  and  $11 \text{ g m}^{-2}$ , respectively). We do not have a satisfactory explanation for the discrepancy between predicted and measured VFPOM stocks. We had expected that measured stocks might be higher than predicted stocks, reflecting the presence of an isolated, nonexchanging pool of benthic POM. We obtained the opposite result, which suggests that

the VFPOM stock was underestimated. Some losses were known to occur because the benthic sampler could not be fully sealed at high velocities, and these losses may have preferentially affected VFPOM.

*Downstream migration velocity and turnover length*—We estimated downstream migration velocities of  $150 \text{ m d}^{-1}$  and  $230 \text{ m d}^{-1}$  for VFPOM and FPOM, respectively. These tracer-based estimates of migration velocity are consistent with previous mass-based estimates, which have been calculated as the ratio of the width-specific downstream flux of POM to the standing stock. Minshall et al. (1992) reported values of  $V_p$  for six sites in the Salmon River, Idaho, that ranged from  $12 \text{ m d}^{-1}$  at a second-order site ( $Q = 40 \text{ L s}^{-1}$ ) and increased with stream size to  $17,000 \text{ m d}^{-1}$  at an eighth-order site ( $Q = 167,000 \text{ L s}^{-1}$ ). Their estimates apply to total, rather than size-fractionated, POM, but the POM was dominated by VFPOM and FPOM. At the fourth-order site (Salmon River at Smiley Creek), which was most comparable to Bloomington Creek, but with a fivefold greater flow, they estimated a  $V_p$  of  $365 \text{ m d}^{-1}$ , or roughly twice the average of the Bloomington Creek estimates. Webster et al. (1999) estimated a  $V_p$  of  $44 \text{ m d}^{-1}$  for an Appalachian stream with a flow of  $20 \text{ L s}^{-1}$  or  $\sim 10\%$  that of Bloomington Creek.

The mass-based estimates of  $V_p$  implicitly assume that the entire benthic stock exchanges with the transported particles and is thus transported downstream at the migration velocity. The rough agreement between the mass-based and our tracer-based estimates lends support to this assumption. However, streams vary widely in their storage of benthic POM (Jones 1997), and the resuspension dynamics of streams with much greater POM stocks than that in Bloomington Creek remain unknown. One possibility is that deposited particles mix actively into the larger benthic pool, which would increase the time-to-resuspension and slow the downstream migration velocity. Alternatively, deposited particles may mix with a small fraction of the benthic POM and resuspend quickly, much as in Bloomington Creek. This would leave most of the POM isolated from the water column, either to be slowly metabolized in situ, or to be suspended and transported downstream under periods of high flow.

The downstream migration velocities that we report are also consistent with studies of sediment transport that used quite different approaches. Udelhoven et al. (1997) correlated the longitudinal patterns in the color of suspended particles with those of the sediments and concluded that most suspended particles originated from a “a highly mobile thin surficial sediment layer enriched in organic carbon.” Bonniwell et al. (1999), using the decay of cosmogenic radioisotopes in an Idaho stream, estimated that sediments at baseflow were suspended every 6.2 d and passed through a 25-km reach in 124 d (implying a  $V_p$  of  $200 \text{ m d}^{-1}$ ). Thus, both the time to resuspension and the migration velocity agree well with our estimates.

Our migration velocities, multiplied by biological turnover times of 0.7 yr (derived from respiration measurements of VFPOM and FPOM from the Salmon River, Idaho) (Minshall et al. 1992), yield turnover lengths of 38 km for VFPOM and 59 km for FPOM. These are comparable to the estimate by Webster et al. (1999) of 42 km for fine POM



(~1–1000  $\mu\text{m}$ ) in a second-order Appalachian stream. Our estimated turnover lengths are sufficiently long to transport many particles to larger streams. Yet, for two reasons, they must be considered as minimal estimates of the true average distance that POM would travel until mineralization within a river system. First, the turnover lengths were calculated for a second-order stream, but as particles move downstream into larger reaches, their turnover length increases (Minshall et al. 1992; Webster et al. 1999). Second, they refer to base-flow conditions, whereas higher flows would produce more transport (Wallace et al. 1991), longer transport distances (Verhoff et al. 1979; Bonniwell et al. 1999), and therefore longer turnover lengths. Thus, our results represent only a first step toward quantifying the fate of organic particles through a river network, but they are nonetheless consistent with the hypothesis that organic carbon originating in head-water streams contributes significantly to the metabolism of mid-to-large size rivers.

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