

## Research Article

# Organic carbon spiraling in an Idaho river

Steven A. Thomas<sup>1,\*</sup>, Todd V. Royer<sup>2</sup>, Eric B. Snyder<sup>3</sup> and Jeffrey C. Davis<sup>4</sup>

<sup>1</sup> Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA

<sup>2</sup> Department of Biological Sciences, Kent State University, Kent, OH 44242, USA

<sup>3</sup> Biology Department, Grand Valley State University, Allendale, MI 49401, USA

<sup>4</sup> Aquatic Restoration and Research Institute, P.O. Box 923, Talkeetna, AK 99676, USA

Received: 2 December 2004; revised manuscript accepted: 25 July 2005

**Abstract.** In running water ecosystems, the use of community attributes to infer biological integrity is widespread. In contrast, functional variables like energy flow and elemental cycling have received considerably less attention. In this study, we quantify organic carbon spiraling in four reaches of the Middle Snake River (MSR). We calculated organic carbon (OC) turnover rates ( $K_{OC}$ ), mean velocities ( $V_{OC}$ ), and turnover lengths ( $S_{OC}$ ) by quantifying suspended and benthic pools of organic carbon and measuring metabolic rates using both open-system and chamber approaches. Ultra-fine particulate organic car-

bon (UPOC) dominated both transported and benthic OC in all study reaches.  $K_{OC}$  was lowest where benthic standing stocks were greatest and  $K_{OC}$  was elevated in summer relative to spring and fall.  $V_{OC}$  was negatively correlated with benthic OC standing stock and greatest in spring and early summer when river discharge was highest. Turnover lengths ( $S_{OC}$ ) ranged from 11–108 km and were strongly related to temporal patterns in  $V_{OC}$ . Comparison of the Snake River with other river systems suggests that MSR is more retentive and homogeneous than rivers of similar size in North America.

**Key words.** Organic carbon; ecosystem metabolism; spiraling; Snake River; carbon turnover.

## Introduction

Human activities impact river ecosystems in many ways, including the alteration of hydrology and geomorphology (Ward and Stanford, 1983; Dynesius and Nilsson, 1994) and changes in sediment and element loading (Maybeck, 1982; Waters, 1995). Bioassessment of rivers is based primarily on attributes of the invertebrate and fish communities (e.g., Karr, 1999; Hawkins et al., 2000), although the need to incorporate functional measures in bioassessment has been recognized (Gessner and Chauvet, 2002). Material cycling and energy flow represent core concepts in ecosystem ecology and

their application to lotic ecosystems is well developed (Odum, 1956; Minshall, 1978; Newbold et al., 1981). Recent studies have documented biome-scale variability in ecosystem metabolism and nutrient retention in small streams (Peterson et al., 2001; Mulholland et al., 2001; Webster et al., 2003) and have suggested that functional measures will help assess how human activities impact streams and rivers. The River Continuum Concept (Vannote et al., 1980; Minshall et al., 1985) provides a theoretical framework for understanding ecosystem function, but surprisingly few empirical studies have compared the functional properties of large rivers (but see Young and Huryn, 1997; 1999).

Organic carbon is supplied to lotic ecosystems from autochthonous and allochthonous origins. The combined processes of biological utilization and downstream transport determine the ecological fate of these resources (Elwood et al., 1983). The relationship between these

\* Corresponding author phone: +1-607-255-1067;  
e-mail: sat43@cornell.edu  
Published Online First: November 30, 2005

processes has been used to evaluate the ecological efficiency of rivers (Fisher, 1977; Newbold et al., 1982). The coincident processes of downstream transport and biological activity result in the deformation of elemental cycles into spirals with the direction of flow serving as a central axis (Webster and Patten, 1979). Three facets of the spiraling approach make it useful in the analysis of stream and river ecosystems. First, spiraling provides a means of measuring, reporting, and conceptualizing nutrient cycling in lotic environments. Second, the spiraling concept explicitly addresses the interactions between hydrodynamic characteristics and the ecological processes that control nutrient cycling rates. Finally, spiraling emphasizes the tight coupling between spatial and temporal dimensions in streams.

Though most frequently used to describe the cycling of dissolved nutrients, spiraling also is effective in describing the processing of organic carbon in streams (Newbold et al., 1982). Organic carbon turnover length ( $S_{OC}$ ) is defined as the distance traveled within a river by a carbon atom in an organic form (Newbold et al., 1982). As such, values of  $S_{OC}$  are a function of the mean velocity at which organic carbon moves downstream ( $V_{OC}$ ) and the rate at which organic carbon is oxidized by biotic activity ( $K_{OC}$ ). Together, these variables provide a means of quantifying the transport and fate of organic carbon and provide metrics for comparing the functional attributes of stream ecosystems.

In this paper, we examine organic carbon spiraling in four reaches of the Middle Snake River (MSR) in Southern Idaho, USA. Our goal is to document temporal and spatial variability in OC spiraling in this ecosystem and to assess whether OC spiraling in the Middle Snake River differs from that of other rivers in this region subject to less human alteration. We hypothesized that organic carbon turnover length ( $S_{OC}$ ) would be reduced in the MSR relative to other locations because: a) high organic matter accumulation reduces the net longitudinal velocity of the organic matter pool ( $V_{OC}$ ), and b) nutrient enrichment increases organic matter processing rates, decreasing OC turnover times ( $K_{OC}$ ).

## Materials and methods

### Study site

The Snake River headwaters begin in northwestern Wyoming and eastern Idaho, after which the river flows west through southern Idaho across the Snake River plain, a predominately agricultural area with numerous water withdrawals for irrigation. The present study was conducted in the Middle Reach of the Snake River, a 152 km segment between Milner and King Hill, Idaho. In this segment, the river flows through a deep canyon (ca. 80–100 m) with an average channel gradient of 0.33%. Land use

in the surrounding watershed is dominated by irrigated agriculture and livestock grazing, and several municipalities are located along the MSR. The MSR receives nutrient and sediment inputs from point and non-point sources, including groundwater, irrigation returns, municipal sewage discharges, and aquaculture facilities. During the study, the MSR was nutrient rich (Royer et al., 1995), with an average  $NO_3 + NO_2$  concentration of 1.28 and 1.54 mg N/L in 1993 and 1994, respectively. Total phosphorus concentrations were similarly high, with an average of 172 and 151  $\mu\text{g/L}$ , respectively, in 1993 and 1994.

Extensive stands of macrophytes were common in the Middle Snake and were dominated by *Ceratophyllum demersum*, *Potamogeton pectinatus*, and *P. crispus*. Blooms of planktonic and epiphytic algae were frequent during the spring and summer months, and the filamentous alga, *Cladophora*, formed large mats among the stands of macrophytes. Plant biomass in the MSR can exceed 2,000  $\text{g/m}^2$  in dry mass, with *Cladophora* accounting for 50% of the total biomass during the summer period (M. Falter, personnel communication).

Our research was conducted at four sites within the MSR. Each site consisted of a river reach ranging in length from 0.5–1.0 km with minimal lateral inputs. Sites were chosen based on spatial relationships with suspected sources of nutrient and sediment delivery, proximity to an upstream mixing region, and logistical constraints, such as boat access. Site 1 was upstream of most point and non-point pollution sources and had a sediment composition of cobble, gravel and sand. Site 2 was ~10 km downstream of Site 1 and below the discharge of a major wastewater treatment facility, several agricultural return channels, and effluent from an aquaculture facility. Site 3 was 2 km downstream of Site 2 and was exposed to the effluent from an additional aquaculture facility and discharge from a tributary draining an agricultural watershed. Site 4 was 6 km downstream of Site 3 and was not exposed to additional sediment and nutrient loading of substantial magnitude.

### Transported organic matter

Transported coarse, fine, and ultra-fine particulate organic carbon fractions (CPOC, FPOC, and UPOC, respectively) were collected each season over the same period of time community metabolism was measured (see below). Samples were collected every 8 h for 24 h from the left quarter, middle and right quarter of the up- and downstream boundary of each research site. CPOC and FPOC samples were collected using suspended nested Nitex™ nets (CPOC net = 1000  $\mu\text{m}$  mesh; FPOC net = 52  $\mu\text{m}$  mesh). The volume of water passing through each set of nets was determined by measuring the water velocity at the mouth of the nets using a water velocity meter. After collection, all samples were frozen and returned to the laboratory

where they were thawed and dried at 80°C for at least 24 h and weighed. Next, samples were combusted for 3 h in a muffle furnace at 550°C, re-weighed, and the ash-free dry mass (AFDM) determined as the difference between the initial dry mass and ending ash weight corrected to 100% of each sample. AFDM measurements were converted to carbon using a 48.4% conversion (Royer et al., 1995). Transported particulate carbon concentrations were calculated by dividing a sample's carbon content by the product of the water velocity, collection time and the area of the collar used to suspend the nets

Transported UPOC (0.45–52 µm) was estimated by combining water collected using a Van Dorn sampler from the first, second, and third quartile of transects defining the up- and downstream boundary of each site. UPOC was isolated by sieving the sample through a 52 µm mesh net to remove all large particles and then collecting the remaining particulate material on a 0.45 µm Whatman GFF filter. All filters were frozen and returned to the laboratory where each sample was dried at 80°C for at least 24 h, cooled to ambient temperatures in a desiccator, weighed, combusted for 3 h in a muffle furnace at 550°C, cooled, and re-weighed. Ash-free dry mass and carbon content were determined as described above.

Dissolved organic carbon (DOC) was collected in the field coincident with the sampling of particulate fractions. Water samples were filtered through a pre-combusted 0.45 µm Whatman glass fiber filter and frozen. Samples were thawed in the laboratory, preserved with sulfuric acid, and shipped to the USEPA Region 10 Organic Laboratory for analysis (Seattle, Washington, USA).

### **Benthic organic matter**

Benthic organic matter was collected from each site in September of 1993, and July and September in 1994. Thirty samples of benthic material from each site were obtained using a petite ponar dredge. Samples within a site were collected using a random stratified design in which equal numbers of samples ( $n = 10$ ) were collected from the right, middle, and left thirds of each study reach. In the laboratory, samples were fractionated into UPOC, FPOC, and CPOC using an appropriate sieve series (CPOC and FPOC) and filtering a sub-sample of the remaining suspension through a 0.45 µm Whatman glass fiber filter for UPOC. Each size fraction was dried at 80°C for at least 24 h and AFDM and carbon content determined as described above.

### **Organic matter turnover**

Metabolic turnover rates of the organic carbon pool were determined using a combination of open system techniques (*sensu* Odum, 1956; Bott, 1996) and component specific chamber measurements (*sensu* Dodds

and Brock, 1998). Multiple methods were necessary to establish spiraling behavior of specific carbon fractions (e.g. FPOM vs. UPOM) and to quantify autotrophic respiration (see below).

*Biotic processing of the total organic pool.* Total organic matter turnover was derived from segment-averaged respiration rates, estimates of gross photosynthetic productivity ( $P_G$ ) and photosynthesis:respiration ratios ( $P_G:R$ ) for specific members of the autotrophic community. Segment-scale metabolic activity was quantified using the upstream-downstream, oxygen mass balance approach (Odum, 1956; Bott, 1996). Briefly, this technique quantifies the change in oxygen concentration as water travels between an upstream and a downstream sampling site and corrects these changes for the reaeration flux between the atmosphere and the water column to estimate daily respiration and photosynthetic activity occurring between the 2 sampling sites.

As a major component of the atmosphere, oxygen is readily diffused across the air-water interface. The rate and direction that oxygen crosses this surface is a function of several variables, including the dissolved oxygen deficit, mean water depth, and average water velocity (Bott, 1996). In this study, changes in dissolved oxygen due to reaeration were corrected using equations presented by Bennett and Rathbun (1972) and Janzer et al. (1977). Community respiration ( $R$ ) was determined by summing the reaeration-corrected rate of change in dissolved oxygen at night, as outlined by Bott (1996). Daily respiration rates were obtained assuming a linear increase in respiration from the pre-sunrise rate to the post-sunset peak.  $P_G$  was determined by subtracting the respiration rate calculated above from the diffusion corrected rate of change in oxygen and summing over the daylight period. Respiration and production rates in oxygen were converted to carbon using a respiratory and photosynthetic quotient of 1.

*Chamber measurements of respiration and photosynthesis.* Re-circulating plexiglass metabolism chambers were used to measure respiration and photosynthetic activity of specific ecological compartments of the Middle Snake River ecosystem. Measures were conducted to estimate the heterotrophic contribution to overall respiration ( $R_{net}$  in equation 3; below) and to determine the specific turnover rates of FPOC and UPOC+DOC.

The chambers used in this study were Aliquot™ Red Deer metabolism chambers, which are similar to those used by Dodds and Brock (1998). Each chamber consisted of a 60 × 24 × 10 cm chamber containing three hydraulic baffles. Water was re-circulated through each chamber using an in-line submersible pump. Water was withdrawn from and returned to the chamber using a hydraulically-efficient manifold system. Internal dis-

solved oxygen concentration was monitored using Royce 900<sup>tm</sup> dissolved oxygen probes and meters. All chamber incubations occurred below Site 2 and were variable in duration, depending on metabolic activity and ambient light conditions. Incubation water was sieved using a 52  $\mu\text{m}$  Nitex<sup>TM</sup> net and water renewal occurred when oxygen fell below 50% saturation or increased above 120% saturation.

*Submerged macrophytes.* Plant material incubated within each metabolism chamber was collected from Site 3 and all chambers were filled with ambient river water collected from the chamber location (between Sites 2 and 3). Collection of aquatic macrophytes was conducted by hand to insure intact specimens for each experimental run. Macrophytes incubated in 1993 included *Potamogeton pectinatus*, *Ceratophyllum demersum*, and *Cladophora glomerata* (a dominant member of an extensive epiphyte community). Plants were attached to the upstream baffle of each chamber using monofilament line. The stems of each incubated plant were severed under water to inhibit air bubble formation in the vascular tissue that may have developed during handling.

*Epilithon.* Rocks and associated epilithon were collected from a depth of 0.5–1.0 m from Site 1 and Site 3. Collection was conducted by hand to insure intact communities and to observe the existing orientation of the rock with respect to flow. Prior to incubation, chambers were filled with river water that had passed through a 52  $\mu\text{m}$  Nitex<sup>TM</sup> mesh net (FPOC-free) from the location where rocks were collected.

*FPOC.* Fine particulate organic carbon (FPOC) was collected using nested Nitex<sup>TM</sup> nets. Nets selectively retained particles 53–1000  $\mu\text{m}$  in diameter. Each metabolism chamber was filled with river water as described above (FPOC-free). Upon initiating incubation, a known volume of concentrated FPOC was added into each chamber. An equal volume of this slurry was collected, frozen, and returned to the laboratory for analyses of ash free dry mass (AFDM).

*Ultra-Fine and dissolved organic matter.* In each of the incubations described above, a UPOC+DOC “blank” was run to account for metabolic activity associated with these smaller organic carbon fractions and microbial growth on chamber surfaces. The metabolic activity of UPOC+DOC metabolism was distinguished from that associated with chamber biological fouling using distilled water blanks. Water samples for analysis of UPOC and DOC were collected prior to incubations and processed as described above.

Linear regression was used to determine component-specific respiration rates during night incubations.

Respiration were calculated as the difference in the rate of change in dissolved oxygen ( $R = dO_2/dt$ ) between treatment and control chambers. Daily gross photosynthetic rates were determined using an enzyme saturation model (Platt et al., 1980) and measurements of photosynthetically active radiation (PAR). The model was of the form:

$$P_i = P_{max} (1 - e^{-aI}) \quad (1)$$

where  $P_i$  = gross photosynthetic rate ( $P = dO_2/dt$ ) at PAR intensity  $I$ ,  $P_{max}$  = maximum gross photosynthetic rate, and  $a$  = a constant that describes the initial rate of increase in photosynthesis and ranged from 0.003 to 0.009. Photosynthetically active radiation was measured every 5 min throughout the day using a LiCor<sup>TM</sup> submersible sensor positioned at the top of the metabolic chamber. Photosynthesis-irradiance relationships were used to scale chamber incubations to daily rates so that a 24-h P:R ratio could be calculated for each compartment.

*Carbon spiraling indices.* Indices of carbon spiraling were calculated using equations developed by Newbold et al. (1982) and applied by Minshall et al. (1992):

$$V_{oc} = \frac{TOC \times Q}{BOC \times w} \quad (2)$$

$$K_{oc} = \frac{R_{het}}{BOC + (TOC \times z)} \quad (3)$$

$$S_{oc} = \frac{V_{oc}}{K_{oc}} \quad (4)$$

$$IR = \frac{v_{wat}}{V_{oc}} \quad (5)$$

where:  $V_{oc}$  = the net longitudinal velocity of organic carbon (m/day), TOC = total transported organic carbon concentration ( $\text{g}/\text{m}^3$ ),  $Q$  = discharge ( $\text{m}^3/\text{day}$ ), BOC = total organic carbon benthic standing stock ( $\text{g}/\text{m}^2$ ),  $w$  = mean river width (m),  $K_{oc}$  = the biotic turnover rate ( $\text{day}^{-1}$ ),  $R_{het}$  = heterotrophic respiration rate,  $z$  = mean water depth,  $S_{oc}$  = organic carbon turnover length (m), IR = the index of retention, and  $v_{wat}$  = mean water velocity.

Overall respiration as measured by open system methods includes the contribution of autotrophic respiration. Organic carbon turnover, from the spiraling perspective, is strictly a function of heterotrophic respiration ( $R_{het}$ ; Young and Huryn, 1999). The relationship between heterotrophic and total respiration can be quantified using:

$$R_{het} = R_{total} - \rho P_G \quad (6)$$

where  $\rho$  equals the fraction of  $P_G$  oxidized by autotrophic respiration. In calculating respiratory activity attributed to heterotrophic organisms ( $R_{het}$ ), McIntyre et al. (1964) estimated values of  $\rho$  equaling 0.14 and 0.42 in grazed and ungrazed streams, respectively. Other researchers

have assumed values of  $\rho$  equal to 0.50 (Webster and Meyer, 1997) and 0.20 (Young and Huryn, 1999). In this study,  $\rho$  was calculated as the inverse of the mean daily  $P_G$ :R ratio of the various autotrophic components (e.g. periphyton, macrophytes) measured in re-circulating metabolism chambers, average weighted for relative abundance. Using this approach,  $\rho$  equaled 0.39.

## Results

### Transported organic carbon

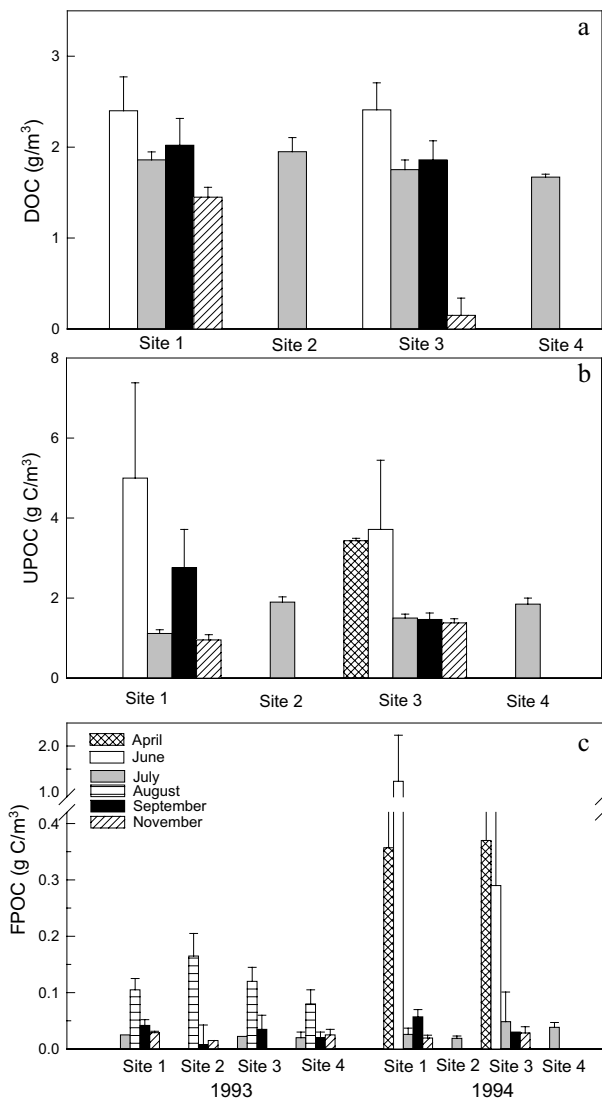
Transported OC was quantified as FPOC, UPOC, and DOC because little or no CPOC was collected in the nets. Dissolved organic carbon (DOC) was the second most abundant category of organic carbon in transport, accounting for 25% of the total longitudinal flux. DOC transport, although variable, generally decreased through the growing season. Spatially, DOC was similar among sites and remained so through time, except in November when DOC at Site 3 was 74% lower than at Site 1 (Fig. 1a).

Sestonic UPOC (0.45–52  $\mu\text{m}$ ) comprised the largest portion of organic carbon in transport in the MSR (overall mean UPOC = 68% of total transported OC, Fig. 1b). Transported UPOC varied in time and space with the highest concentrations found in spring, which were ~2–5 times greater than those in summer and fall. High discharge accompanied higher concentrations of sestonic UPOC in April. However, discharge in June of 1994 was no greater than later dates that year. Rather, high UPOC in transport at this time corresponded to elevated sestonic algae (Royer, 1995). Spatially, no discernable pattern was present in UPOC transport (Fig. 1b).

Transported FPOC ranged from 0.009 to 5.34 g AFDM/m<sup>3</sup> (Site 2 in September 1993 and Site 1 in June 1994, respectively) (Fig. 1c). Average FPOC concentrations were similar between 1993 and 1994. In 1993, FPOC concentrations in August were greater than those observed in all other months. In 1994, temporal variability in transported FPOC was similar to, but more exaggerated than observed for UPOC. In 1994, FPOC concentrations were 1–2 orders of magnitude greater

**Table 1.** Total, fine and ultra-fine particulate organic carbon spiraling parameters calculated for the Middle Reach of the Snake River.

Site	Date	Discharge	Water Velocity	BOC	Transported OC	$R_{\text{het}}$	$V_{\text{OC}}$	$K_{\text{OC}}$	$S_{\text{OC}}$	$T_t$	IR
		m <sup>3</sup> /d	m/d	g C/m <sup>2</sup>	g C/m <sup>3</sup>	g C/m <sup>2</sup> /d	m/d	d <sup>-1</sup>	m	d	
<b>Total OC</b>											
1	April	4,685,714	12,892	436	4.99	1.00	410	0.0022	184,161	449	32
1	June	4,746,885	13,059	436	7.44	2.00	619	0.0044	141,187	228	21
1	July	5,175,084	13,120	435	2.75	1.70	250	0.0038	65,120	261	53
1	September	1,450,981	4,544	1,164	3.83	2.50	36	0.0021	17,105	469	125
2	July	7,340,544	14,806	1,388	2.90	4.70	134	0.0034	40,022	298	110
3	April	7,707,571	15,652	1,499	5.15	2.30	164	0.0015	107,645	659	96
3	June	7,095,859	14,407	1,499	5.21	4.10	152	0.0027	56,248	369	95
3	July	7,976,725	16,147	1,499	2.43	3.30	80	0.0022	36,362	456	203
3	September	4,893,696	11,423	1,672	2.32	6.10	42	0.0036	11,531	275	273
3	November	3,914,957	9,137	1,672	2.16	2.20	31	0.0013	23,753	763	293
4	July	8,710,779	20,281	693	2.73	5.00	389	0.0071	54,982	141	52
<b>FPOC</b>											
3	April	7,707,571	15,652	520	0.37	3.20	34	0.0061	5,515	163	462
3	June	7,095,859	14,407	520	0.29	0.66	24	0.0013	19,240	787	590
3	June	7,095,859	14,407	520	0.29	0.19	24	0.0004	67,875	2,778	590
3	July	7,976,725	16,147	520	0.05	3.14	5	0.0060	768	166	3,479
3	November	3,914,957	9,137	973	0.03	2.25	1	0.0023	312	433	12,678
<b>VFPOC + DOC</b>											
3	April	7,707,571	15,652	952	4.44	0.24	222	0.0003	886,629	4,000	71
3	June	7,095,859	14,407	952	6.13	0.06	282	0.0001	4,697,109	16,667	51
3	June	7,095,859	14,407	952	6.13	1.42	282	0.0015	193,032	685	51
3	July	7,976,725	16,147	952	3.25	2.66	168	0.0028	60,688	361	96
3	July	7,976,725	16,147	952	3.25	3.83	168	0.0040	42,237	251	96

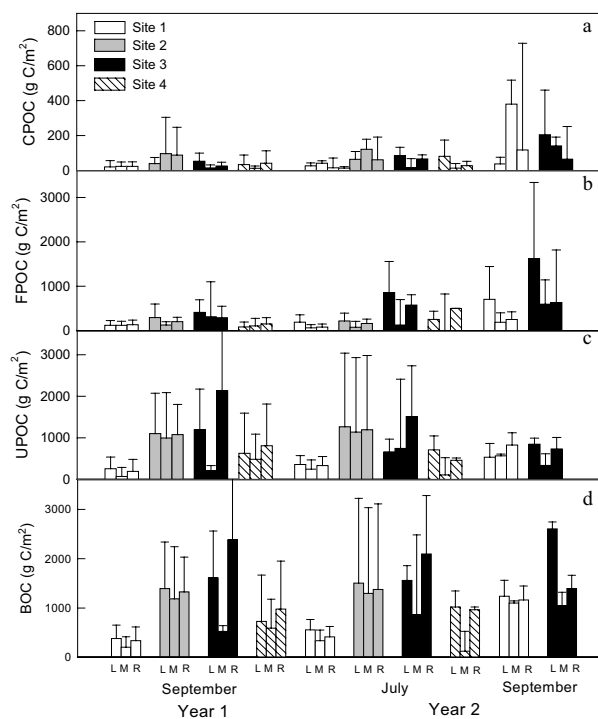


**Figure 1.** Transported dissolved, ultra-fine, and fine particulate carbon (DOC, UPOC, and FPOC, respectively) in the Middle Snake River. DOC and UPOC data are from 1994 only. Error bars represent +1 standard deviation.

during spring than in summer and fall. No consistent spatial pattern was observed in transported FPOC in the Middle Snake River.

**Benthic organic matter**

Ultra-fine particles (UPOC) dominated the benthic organic carbon pool (Fig. 2). Significant differences occurred among size fractions of OC ( $p < 0.01$ ) and post-hoc testing indicated that UPOC was significantly greater than FPOC or CPOC ( $p < 0.01$ ), but that FPOC and CPOC abundance were not significantly different ( $p = 0.552$ ). UPOC comprised 65% of all material collected, FPOC equaled 28%, and CPOC 7%. Significant



**Figure 2.** Benthic Organic Carbon standing stocks in the Middle Snake River: (a) coarse particulate organic carbon (>1000µm), (b) fine particulate organic carbon (52–1000µm), (c) ultra-fine particulate organic carbon (0.45–52µm) and (d) total organic carbon. L, M and R refer to the left, middle, and right thirds of the channel.

differences were also detected for sampling location within a site (left, right, and middle thirds;  $p < 0.01$ ), but not among sites ( $p = 0.427$ ). Total benthic OC was greater on either bank than in the middle of the channel (Fig. 2d). Significant differences in total BOC were not observed between years ( $p = 0.867$ ) or sampling dates within a year ( $p = 0.578$ ).

**Carbon spiraling**

*Respiration rates.* Total ecosystem respiration ( $R_{tot}$ ) ranged from 1.25–10.61 g C/m<sup>2</sup>/d. Variability in  $P_G$  spanned a similar range, 0.88–10.37 g C/m<sup>2</sup>/d. Applying equation 6 produced estimates of  $R_{het}$  that ranged from 0.86–6.05 g C/m<sup>2</sup>/d. Total OC turnover rates ( $K_{OC}$ ; eq. 3) ranged from 0.0013 to 0.0071 d<sup>-1</sup>. In July,  $K_{OC}$  was greatest at Site 4 and lowest at Site 3 (Table 1). Variability in  $K_{OC}$  was influenced by variations in BOC and  $R_{het}$  ( $r^2 = 0.20$  and 0.25, respectively) but insensitive to changes in transport concentration (C;  $r^2 < 0.01$ ). Temporally, OC turnover rates tended to be higher in summer than in April or November. At Site 1,  $K_{OC}$  declined substantially in September, resembling  $K_{OC}$  values in April. In contrast,  $K_{OC}$  remained high through September at Site 3.

The inverse of  $K_{OC}$  represents the mean turnover time ( $T_t$ ) of the OC pool (Table 1).  $T_t$  ranged from 141 d at Site 4 in July to 658 d at Site 3 in April.

FPOC and UPOC+DOC respiration was determined directly from biomass-specific respiration rates determined in the metabolism chambers. Respiration rates associated with FPOC ranged from 0.0004–0.0061  $d^{-1}$  (Table 1). Similarly, UPOC+DOC respiration rates ranged from 0.0001–0.0040  $d^{-1}$ . Multiplying respiration rates by standing stock measurements from Site 3 predicted areal respiration rates of 0.19–3.20 and 0.06–3.83  $g\ C/m^2/d$  for FPOC and UPOC+DOC, respectively (Table 1). These estimates fall within the same range as those determined by open system analysis but poorly reflect the temporal variability observed in the latter data set and, at times, exceeded open system values (e.g. April and July, data not shown).

*Longitudinal velocity.* The net downstream velocity of the total OC pool in the MSR ranged from 31–619 m/d (Table 1). Variation in  $V_{OC}$  was primarily a function of the relative abundance of transported versus benthic organic carbon (TOC:BOC;  $r^2 = 0.91$ ,  $p < 0.01$ ) rather than changes in discharge ( $r^2 = 0.02$ ,  $p = 0.65$ ).  $V_{OC}$  was higher in the spring months than in summer and fall, similar to trends observed in transported UPOC and FPOC. However, while trends in  $V_{OC}$  and transported UPOC were similar, the magnitude of temporal variation in these parameters was not due to the influence of benthic UPOC and transported DOC (Table 1).  $V_{OC}$  was higher at Site 1 than Site 3. In July,  $V_{OC}$  declined progressively from Site 1 to Site 3, but increased dramatically at Site 4.

The longitudinal velocity of FPOC at Site 3 was considerably lower than that of the total organic pool, ranging from 1–34 m/d. A consistent decline in the  $V_{OC}$  of FPOC was observed through the growing season, reflecting the diminishing pool of transported FPOC during that time (Fig. 1c). UPOC+DOC velocity was higher than total OC at Site 3 and peaked in June.

*OC turnover length.* Turnover length ( $S_{OC}$ ) ranged from 11–184 km (September at Site 3 and June at Site 1, respectively) (Table 1) and was more strongly associated with  $v_{wat}$  and  $V_{OC}$  ( $r^2 = 0.62$  and  $0.55$ , respectively) than BOC ( $r^2 = 0.44$ ). Turnover length was consistently greater at Site 1 than Site 3. However,  $S_{OC}$  varied little among sites in July when data were available from all locations (Table 1).  $S_{OC}$  declined from April to September at Sites 1 and 3, but increased again in November at Site 3. FPOC-specific  $S_{OC}$  ( $S_{FPOC}$ ) was shorter and  $S_{UPOC+DOC}$  was much longer than  $S_{OC}$  calculated for the entire OC pool (Table 1).

*Index of retention.* The index of retention (IR) varied by an order of magnitude, ranging from ~30–300 (Table 1).

Variation in IR was most strongly associated with BOC ( $r^2 = 0.66$ ,  $p = 0.02$ ) rather than transported OC or water velocity ( $r = 0.41$  and  $0.12$ ,  $p = 0.11$  and  $0.52$ , respectively). Variation in IR through the growing season was opposite that observed in  $V_{OC}$  (Table 1). IR suggested that retention increased from Site 1 to Site 3, but decreased between Site 3 and 4. FPOC was more effectively retained (relative to water) than the overall OC pool and became increasingly so through the year, differing by a factor of 4 in April but by more than 40 by November. UPOC+DOC retention was low and without a distinct temporal trend (Table 1).

## Discussion

Understanding organic matter dynamics in river ecosystems requires integrating knowledge of biological activity with hydrological transport. Carbon turnover length is one means of effectively coupling these processes. The longitudinal movement of OC in streams is envisioned as a saltation process in which individual particles remain spatially stable when in the benthos but move downstream at the mean water velocity when suspended (Elwood et al., 1983; Newbold et al., 1982; Minshall et al., 1992; Cushing et al., 1993). A number of recent studies have used labeled particles to quantify deposition distances (e.g. Minshall et al., 2000; Thomas et al., 2001). However, the number of deposition-resuspension events that occur over the lifetime of a particle remains unclear, although estimates of saltation frequency have recently been estimated (Newbold et al., 2005).

### OC velocity ( $V_{OC}$ )

Fluvial geomorphologists have long identified a positive relationship between stream discharge and suspended load (Leopold and Maddock, 1953). Less is known about the relationship between discharge and transported organic matter, although a positive relationship is often presumed because of the association between inorganic particles and organic biofilms (Webster et al., 1988). We expected that discharge would be positively associated with estimates of  $V_{OC}$  via associated increases in transported OC and consequent reductions in benthic OC. In this study, these associations were not observed for either total transported OC or transported FPOC. Insufficient data were available to statistically assess the association between discharge and transported UPOC+DOC, but an inverse relationship is indicated in Table 1. One explanation for the poor relationship between suspended OC and stream flow may be the influence of sestonic primary production during specific time periods. Low sestonic chlorophyll a concentrations observed in July relative to other months supports this conclusion (Royer et al., 1995).

Additionally, changes in external loading (e. g. organic sediment discharged from aquaculture facilities) may have influenced the observed pattern, although data are not available to either support or refute this hypothesis. The poor relationship between transported OC and discharge translated to an equally poor association between  $V_{OC}$  and discharge ( $r^2 = 0.02$ ,  $p = 0.71$ ). Spatial variability in  $V_{OC}$  reflected differences in the magnitude of the BOC pool ( $r^2 = 0.71$ ,  $p < 0.01$ ).  $V_{OC}$  in the MSR was less variable among sites than measures of  $V_{OC}$  in similar-sized reaches of the Salmon River (336–17,547 m/d; Minshall et al., 1992) and the Kootenai River (36–7,858 m/d; Snyder and Minshall, 1994).

Minshall et al. (1992) introduced the index of retention (IR) for assessing the retentive capacity of stream reaches with respect to OC transport. As IR approaches 1, streams act as conduits delivering materials downstream at rates approaching  $v_{wat}$ . In the Salmon River, Minshall et al. (1992) demonstrated that IR declined as streams coalesced into rivers. In 2 river segments bracketing the discharge observed in this study, they calculated IR values of 28 and 1.2, whereas values of IR in the MSR ranged from 30–162, indicating that the Middle Snake River is considerably more retentive of OC than similar size reaches of the Salmon River. FPOC and UPOC+DOC retention differed considerably from one another and bracketed estimates for the total organic matter pool (Table 1), indicating that much of the export of organic matter from the MSR is ultra-fine particles or part of the dissolved load.

### OC turnover ( $K_{OC}$ )

Another measure used to calculate turnover length is the OC turnover rate ( $K_{OC}$ ). In the MSR,  $K_{OC}$  was most strongly influenced by  $R_{het}$  and to a lesser extent BOC. Within a site, variability in  $K_{OC}$  closely followed changes in  $R_{het}$ . Lower turnover in April relative to June and July probably reflected temporal patterns in temperature and OC quality rather than nutrient limitation since nutrient diffusing substrates failed to illicit a strong biofilm response (S.A. Thomas, unpublished data). Changes in benthic OC between July and September strongly influenced turnover rates at Site 1 (0.018 and 0.009, respectively). Conversely, moderate changes in benthic OC between July and September at Site 3 were compensated by higher  $R_{het}$ , increasing OC turnover in September relative to July (Table 2). Therefore, it appears that the temporal variability of OC turnover observed in this study was probably a function of variable microbial activity (as reflected in  $R_{het}$ ) rather than temporal changes in BOC. However, spatial variance in  $K_{OC}$  was controlled by the interaction between areal respiration and benthic OC concentration.

Turnover rates of FPOC and UPOC+DOC correlated poorly with total OC turnover. In April 1994, mean turno-

ver times of FPOC and UPOC+DOC straddled estimates of total OC (163, 4000, and 658 d, respectively). Alternatively, cycling rates of FPOC and UPOC+DOC were much slower than those estimated for the total OC pool in June and faster in July (Table 1). Back calculating areal respiration rates from chamber measurements frequently resulted in rates greater than those estimated using open system techniques. These inconsistencies may have resulted from inadequate representation of ambient conditions in the chamber, poor representation of FPOC and UPOC+DOC in the incubated material, or errors associated with our estimates of benthic standing stocks. For example, FPOC and UPOC activity (benthic and transported) was assessed while the material was suspended in the re-circulating chamber, and may have increased oxygen availability and aerobic respiration relative to benthic environments. Alternatively, metabolically active UPOC and FPOC benthic standing stocks may have been poorly sampled. The petite ponar dredge used in this study is capable of sampling 20 cm of surface sediments. However, benthic standing stocks greater than our estimates would have led to an under estimation of respiration by chamber versus open system methods. Rather, our methods may have collected material that was less metabolically active than the incubated material.

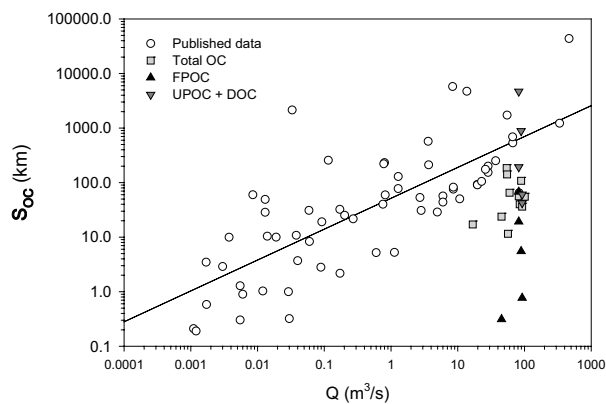
### OC turnover length ( $S_{OC}$ )

Comparing turnover lengths among systems for assessing the efficiency of specific river reaches to use OC resources is compromised by the influence of discharge (Young and Huryn, 1999). The index of retention (IR) allows comparison of retention among streams of varying size. However, IR conveys no information regarding the biological use of OC during the saltation sequence. To address this issue, Young and Huryn (1999) accumulated data from previous studies and regressed discharge against turnover length. They then compared individual sites to the common regression line to assess the relative retentive capacity of specific streams. We have conducted a similar analysis to place the Middle Snake River data set into a broader geographic context (Fig. 3). The  $S_{OC}$  data for the total OC pool from the MSR are consistently below the common regression line, indicating that these sites turnover OC resources over shorter distances than would be predicted given their discharge. Temporal variation in  $S_{OC}$  was equally influenced by variation in  $K_{OC}$  and  $V_{OC}$ . Increased summer turnover rates complemented declining longitudinal transport to produce declining turnover distances through the 1994 growing season (April to September).

### $V_{OC} - K_{OC}$ diagrams

Organic Carbon turnover lengths provide one means of comparing and contrasting streams with respect to their



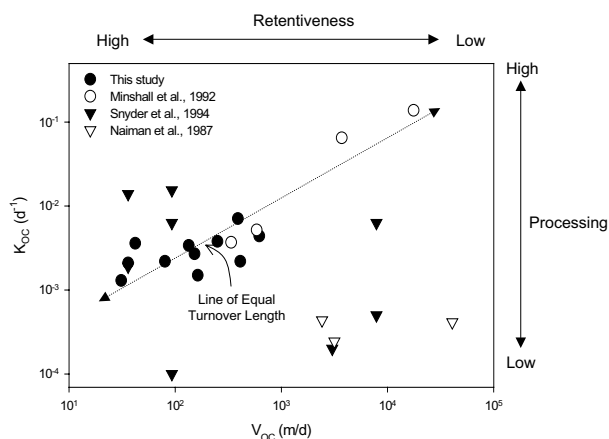


**Figure 3.** The relationship between discharge and organic carbon turnover length. Previously reported data are from Young and Huryn (1997, 1999), Minshall et al. (1983, 1992), and Webster and Meyer (1997).

efficiency of OC use. Shorter  $S_{OC}$  values indicate that organic substrates are metabolized closer to their origin within the stream, although dissimilar stream reaches can produce the same turnover length. For example, the Salmon River at Shoup (Minshall et al., 1992) and our Site 1 had similar summer OC turnover lengths (65 and 66 km, respectively) despite differing substantially with respect to OC transport (3702 vs. 1238 m, respectively), OC turnover (0.057 and 0.012/d, respectively), benthic OC (15 and 436 g/m<sup>2</sup>, respectively) and transported OC (0.9 and 14.9 g/m<sup>3</sup>, respectively).

Plotting  $V_{OC}$  versus  $K_{OC}$  creates an ecological space defined by rates of biological processing and hydrological transport. Webster et al. (1999) first used this format to assess the cycling and transport dynamics of various types of detritus (e.g. wood, twigs, leaves, etc). Using this format to compare the Middle Snake River to other large rivers for which these indices can be calculated (Fig. 4) indicates that the MSR is considerably more homogeneous than other large rivers, especially with respect to OC turnover rates ( $K_{OC}$ ). This graphical approach also discriminates between the Salmon River (Minshall et al., 1992) and the MSR, despite the similar  $S_{OC}$  values discussed above.

Our results indicate that conditions in the Snake River have retarded OC transport and promoted turnover rates relative to comparable river systems in Idaho (Minshall et al., 1992, Snyder and Minshall, 1994) and elsewhere (Naiman et al., 1987; Young and Huryn, 1999). The Middle Snake River is influenced by a host of human activities, including flow regulation, nutrient enrichment and sediment loading. Proportional changes in transport and turnover can potentially maintain a consistent turnover length. In the Snake River, the accumulation of organic rich sediments and the reduction of discharge events ca-



**Figure 4.** The mean velocity of organic carbon ( $V_{OC}$ ) versus the cycling rate of organic carbon ( $K_{OC}$ ) in the Middle Snake River (this study), the Salmon River (Minshall et al., 1992), the Kootenai River (Snyder et al., 1995), and the Matamek and Moisie Rivers (Naiman et al., 1987). The dashed line represents a single turnover length ( $V_{OC} / K_{OC} = \text{constant}$ ).

table of moving these sediments have outpaced increase in turnover rates to reduce turnover lengths relative to those expected for rivers of comparable size.

Organic carbon spiraling is an ecosystem parameter that combines structural (BOC, TOC, Q, etc) and functional attributes of a river. By combining transport properties with ecological processes, spiraling addresses two dominant but competing characteristics of stream ecosystems. In this study, we quantify organic carbon spiraling in a river subject to a variety of human activities and discuss how this system compares to rivers of similar size in North America for which data are available. Spiraling metrics provide a set of ecosystem scale variables for comparing river ecosystems. Our research suggests that these variables may be sensitive to human activity and, as such, provide an ecosystem scale metric for assessing river health.

## References

- Bennett, J. T. and R. E. Rathburn, 1972. Rearation in Open Channel Flow. U. S. Geologic Survey Professional Paper 737, 75 pp.
- Bott, T. L., 1996. Primary production and community respiration. In: F. R. Hauer and G. A. Lamberti (eds.), *Methods in Stream Ecology*, Academic Press, New York, pp. 533–556.
- Cushing, C. E., G. W. Minshall and J. D. Newbold, 1993. Transport dynamics of fine particulate organic matter in two Idaho streams. *Limnology and Oceanography* **38**: 1101–1115.
- Dodds, W. K. and J. T. Brock, 1998. A portable flow chamber for in situ determination of benthic metabolism. *Freshwater Biology* **39**: 49–59.
- Dynesius, M. and C. Nilsson, 1994. Fragmentation and Flow Regulation of River Systems in the Northern Third of the World. *Science* **266**: 753–762.

- Elwood, J. W., J. D. Newbold, R. V. O'Neill and W. Van Winkle, 1983. Resource spiraling: an operational paradigm for analyzing lotic ecosystems. In: T. D. Fontaine III and S. M. Bartell (eds.), *Dynamics of Lotic Ecosystems*, Ann Arbor Science Publishers, Ann Arbor, pp. 3–28.
- Fisher, S. G., 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U.S.A. *Internationale Revue ges. Hydrobiologie* **62**: 701–727.
- Gessner, M.O. and E. Chauvet, 2002. A case for using litter breakdown to assess functional stream integrity. *Ecological Applications* **12**: 498–510.
- Hawkins, C. P., R. H. Norris, J. N. Hogue and J. W. Feminella, 2000. Development and evaluation of predictive models for measuring the biological integrity of streams. *Ecological Applications* **10**: 1456–1477.
- Janzer, V. J., J. R. Knapton, L. J. Schroder II, K. V. Slack and D. W. Stephens, 1977. Diel oxygen curve method for estimating primary productivity and community metabolism in streams. In: P. E. Greeson (ed.), *Techniques of Water-Resource Investigations of the United States Geological Survey*, United States Government Printing Office, pp. 270–279.
- Karr, J. R., 1999. Defining and measuring river health. *Freshwater Biology* **41**: 221–234.
- Leopold, L. B. and T. Maddock, Jr., 1953. The hydraulic geometry of stream channels and some physiographic implications. U.S. Geological Survey Professional Paper 252, 57 pp.
- McIntyre, C. D. and H. K. Phinney, 1964. Laboratory studies of periphyton production and community metabolism in lotic ecosystems. Technical Paper No. 1798, Oregon Agricultural Experimental Station.
- Meybeck, M., 1982. Carbon, nitrogen, and phosphorus transport by world rivers. *American Journal of Science* **282**: 401–450.
- Minshall, G. W., 1978. Autotrophy in stream ecosystems. *Bio-Science* **28**: 767–771.
- Minshall, G. W., K. W. Cummins, R. C. Peterson, C. E. Cushing, D. A. Bruns, J. R. Sedell and R. L. Vannote, 1985. Developments in Stream Ecosystem Theory. *Canadian Journal of Fisheries and Aquatic Sciences* **42**: 1045–1055.
- Minshall, G. W., R. C. Petersen, T. L. Bott, C. E. Cushing, K. W. Cummins, R. L. Vannote and J. R. Sedell, 1992. Stream ecosystem dynamics of the Salmon River, Idaho: an 8<sup>th</sup>-order system. *Journal of the North American Benthological Society* **11**: 111–137.
- Minshall, G. W., S. A. Thomas, J. D. Newbold, M. T. Monaghan and C. E. Cushing, 2000. Physical factors influencing fine organic particle transport and deposition in streams. *Journal of the North American Benthological Society* **19**: 1–16.
- Mulholland, P. J., J. L. Tank, J. R. Webster, W. B. Bowden, W. K. Dodds, S. V. Gregory, N. B. Grimm, S. K. Hamilton, S. L. Johnson, E. Marti, W. H. McDowell, J. L. Merriam, J. L. Meyer, B. J. Peterson, H. M. Valett and W. M. Wollheim, 2001. Can uptake length in streams be determined by nutrient addition experiments? Results from an interbiome comparison study. *Journal of the North American Benthological Society* **21**: 544–560.
- Naiman, R. J., J. M. Melillo, M. A. Lock, T. E. Ford and S. R. Riece, 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. *Ecology* **68**: 1139–1156.
- Newbold, J. D., J. W. Elwood, R. V. O'Neill, W. Van Winkle, 1981. Nutrient spiraling in streams: The concept and its field measurement. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 860–863.
- Newbold, J. D., P. J. Mulholland, J. W. Elwood and R. V. O'Neill, 1982. Organic Carbon Spiraling in stream ecosystems. *Oikos* **38**: 266–272.
- Newbold, J. D., S. A. Thomas, G. W. Minshall, T. Georgian and C. E. Cushing, 2005. Deposition, benthic residence, and resuspension of fine organic particles in stream ecosystems. *Limnology and Oceanography* **50**: (in press).
- Odum, H. T., 1956. Primary production in flowing waters. *Limnology and Oceanography* **1**: 102–117.
- Peterson, B. J., W. M. Wollheim, P. J. Mulholland, J. R. Webster, J. L. Meyer, J. L. Tank, E. Marti, W. B. Bowden, H. M. Valett, A. E. Hershey, W. H. McDowell, W. K. Dodds, S. K. Hamilton, S. Gregory and D. D. Morrall, 2001. Control of nitrogen export from watersheds by headwater streams. *Science* **292**: 86–90.
- Platt, T., C. L. Gallegos and W. G. Harrison, 1980. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *Journal of Marine Research* **38**: 687–701.
- Royer, T. V., 1995. The Decomposition of Plant Material in the Middle Reach of the Snake River, Idaho. MS thesis, Idaho State University, Pocatello, Idaho.
- Royer, T. V., C. T. Robinson and G. W. Minshall, 1995. Ecological Structure and Function of the Middle Reach of the Snake River. Volume I: Water Quality and Benthic Biomonitoring. Idaho Department of health and Welfare, Division of Environmental Quality.
- Snyder, E. B. and G. W. Minshall, 1994. Ecosystem metabolism and nutrient dynamics in the Kootenai River in relation to impoundment and flow enhancement for fisheries management. Idaho Fish and Game Department.
- Thomas, S. A., J. D. Newbold, G. W. Minshall, T. Georgian, M. T. Monaghan and C. E. Cushing, 2001. The influence of particle size on seston deposition in streams. *Limnology and Oceanography* **46**: 1415–1424.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell and C. E. Cushing, 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130–137.
- Ward, J. V. and J. A. Stanford, 1983. The serial discontinuity concept of lotic ecosystems. In: T. D. Fontaine and S. M. Bartell (eds.), *Dynamics of Lotic Ecosystems*, Ann Arbor Science, Ann Arbor, pp. 29–42.
- Waters, T. F., 1995. *Sediment in Streams: Sources, Biological Effects, and Control*. American Fisheries Society Monograph 7, Bethesda, Maryland, USA.
- Webster, J. R., E. F. Benfield, S. W. Golladay, R. F. Kazmierczak, W. B. Perry and G. T. Peters. 1988. Effects of watershed disturbance on stream seston characteristics. In: W. T. Swank and D. A. Crosley (eds.), *Forest hydrology and ecology at Coweeta*, Springer-Verlag, New York, pp. 279–294.
- Webster, J. R. and B. C. Patten, 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. *Ecological Monographs* **49**: 51–72.
- Webster, J. R. and J. L. Meyer (eds.), 1997. Stream organic matter budgets. *Journal of the North American Benthological Society* **16**: 3–161.
- Webster, J. R., E. F. Benfield, T. P. Ehrman, M. A. Schaeffer, J. L. Tank, J. J. Hutchens and D. J. D'Angelo, 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. *Freshwater Biology* **41**: 687–705.
- Webster, J. R. et al., 2003. Factors affecting ammonium uptake in streams: an inter-biome perspective. *Freshwater Biology* **48**: 1329–1352.
- Young, R. G. and A. D. Huryn, 1997. Longitudinal patterns in organic matter transport and turnover along a New Zealand grassland river. *Freshwater Biology* **38**: 93–107.
- Young, R. G. and A. D. Huryn, 1999. Effects of land use on stream metabolism and organic matter turnover. *Ecological Applications* **9**: 1359–1376.