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Interregional comparisons of sediment microbial respiration in streams

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SUMMARY

1. The rate of microbial respiration on fine-grained stream sediments was measured at 371 first to fourth-order streams in the Central Appalachian region (Maryland, Pennsylvania, Virginia, and West Virginia), Southern Rocky Mountains (Colorado), and California's Central Valley in 1994 and 1995.
2. Study streams were randomly selected from the United States Environmental Protection Agency's (USEPA) River Reach File (RF3) using the sample design developed by USEPA's Environmental Monitoring and Assessment Program (EMAP).
3. Respiration rate ranged from 0 to 0.621 g O_2 g^{-1} AFDM h^{-1} in Central Appalachian streams, 0–0.254 g O_2 g^{-1} AFDM h^{-1} in Rocky Mountain streams, and 0–0.436 g O_2 g^{-1} AFDM h^{-1} in Central Valley streams.
4. Respiration was significantly lower in Southern Rocky Mountain streams and in cold water streams (< 15 °C) of the Central Appalachians.
5. Within a defined index period, respiration was not significantly different between years, and was significantly correlated with stream temperature and chemistry (DOC, total N, total P, K, Cl, and alkalinity).
6. The uniformity of respiration estimates among the three study regions suggests that sediment microbial respiration may be collected at any number of scales above the site-level for reliable prediction of respiration patterns at larger spatial scales.

Keywords: EMAP, microbial respiration, probability-based sampling, regional scale, streams

Introduction

Ecosystem function has been a major focus of stream research over the past 20 years, resulting in greater understanding of system metabolism, nutrient spiralling and the role of the biotic community (e.g. functional feeding groups) in the regulation of these ecosystem processes (Cummins, 1974, 1991). In spite of these advances, regulatory assessment and monitoring of streams continue to focus primarily on the collection of structural information of the stream community (Cairns & Pratt, 1986; Cummins, 1991; Pratt & Cairns, 1996). Structural indicators are relatively easy to quantify and their collection methods are widely accepted by both the scientific and regulatory communities. However, spatial and temporal variability within the stream community may limit their use (Cairns & Pratt, 1986; Cummins, 1991). Functional measures are also variable, but their ability to integrate diverse communities into a few attributes allows easier comparisons among different systems and within one system through time (O'Neill *et al.*, 1986; Cummins, 1988; Pratt & Cairns, 1996).

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Function is an emergent property of an ecosystem and is relatively independent of taxonomic composition. Thus, functional indicators are not restricted to any particular assemblage and are less likely to be constrained by regionally restricted biota. This attribute of functional indicators may allow assessments of stream ecosystems over diverse geographic regions which had previously been limited to comparisons among streams inhabited by similar taxa. Furthermore, functional indicators may provide a direct link to the mechanisms by which stream communities are perturbed and may be useful in diagnosing the causes of environmental degradation (Hill, 1997). Hunsaker *et al*. (1990) have argued that for regional ecological risk assessments to be effective, the system must be defined by both community structure and ecosystem function, with the spatio-temporal boundaries of the system set by functional attributes of the communities inhabiting the system. These authors contend that assessments which are functionally based are likely to have greater applicability across regions.

Community respiration is one of the most commonly measured functional attributes of ecosystems and is a sensitive indicator of ecosystem stress (Matthews *et al*., 1982; Bott *et al*., 1985; Hill & Gardner, 1987). One of the main concerns about the use of functional indicators for monitoring impacts is the perception that natural environmental variability will mask any response to perturbations. However, several researchers have reported lower variability and higher sensitivity for functional measures than for biomass or taxa richness (Crossey & LaPointe, 1988; Boston *et al*., 1993; Niemi *et al*., 1993). Niemi *et al*. (1993) analysed the ability of several measures of chemical and biological structure and function to detect impact and recovery in stream ecosystems. They found that gross primary productivity (GPP) and respiration (R) were more sensitive to perturbations than most structural measures. Similarly, Cairns *et al*. (1992) reported successes in monitoring the impacts of contaminated sediments on microbial community respiration.

This study set out to answer several questions: What is the range of estimates of sediment microbial respiration in synoptic surveys of streams from different regions of the United States? Are these estimates consistent with those reported by other investigators? What is the association between respiration and stream chemistry? Within a defined index period, does stream sediment microbial respiration within the region vary from year to year? Do stream sediment microbial respiration rates, and their relationships with potential controlling variables, differ among regions?

Methods

Study areas and survey design

Three areas were included in this study, the Central Appalachian region of the eastern United States, the Southern Rocky Mountains of Colorado, and the Central Valley of California. These three areas were selected to address watershed land use, acid precipitation, coal and base metal mining and agricultural impacts on stream ecosystems. The Central Appalachian region extends north-east from northern North Carolina to the Catskill Mountains of New York and from the eastern seaboard west to the Western Allegheny Plateau of eastern Ohio (Fig. 1a). The Central Appalachian region is an area of uplifted sedimentary and metamorphic rock characterized by limestone and shale valleys, gneiss and sandstone ridges, and shale and limestone plateaus. The study area is subdivided into the Blue Ridge, Central Appalachian Plateau, Central Appalachian Ridge and Valley, Northern Appalachian Plateau and Uplands, Western Allegheny Plateau, and combined Piedmont/Coastal Plain ecoregions (Omernik, 1987). The Southern Rocky Mountains ecoregion (Omernik, 1987) extends from the New Mexico-Colorado border north to Rocky Mountain National Park, and west to the Gunnison River drainage. This region is underlain by metamorphic rock and is characterized by steep, rocky slopes. The local mineralogy is dominated by crystalline formations rich with veins of base metal sulfides. The Central Valley ecoregion extends from south of Bakersfield north to Redding, and west from the Sierra foothills to the eastern boundary of the Coastal Range (Omernik, 1987) (Fig. 1c), and is characterized by sedimentary bedrock in the valleys and volcanic outcrops in the foothills.

In this paper, we present data collected by the United States Environmental Protection Agency's Environmental Monitoring and Assessment Program surveys conducted in 1994 and 1995. Each year,

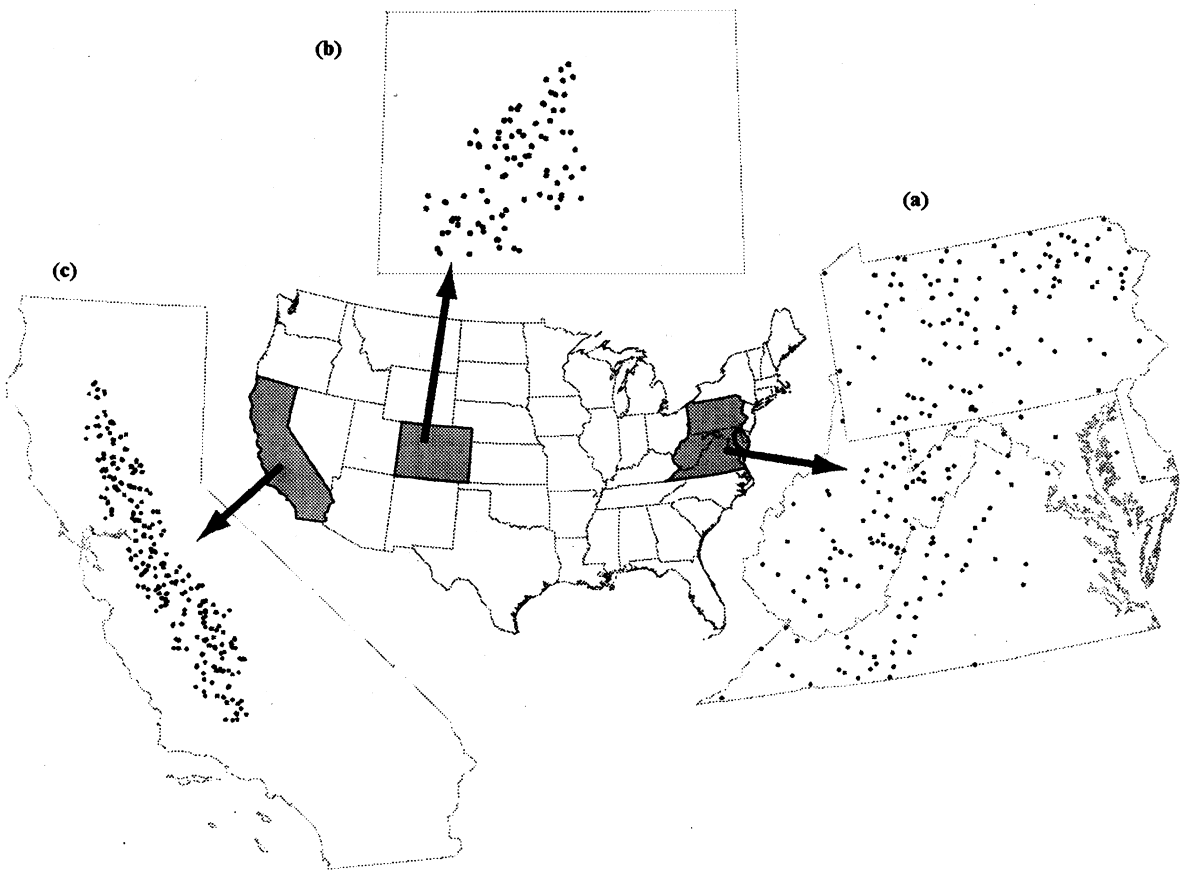

Fig. 1 Study streams of the Central Appalachian (a), Southern Rocky Mountain (b), and California Central Valley (c) regions.

sampling sites for each study area were selected using a randomization method with a spatial systematic component. The stream network on the digitized version of the 1 : 100 000 scale United States Geological Survey topographic maps was used as the sample frame. The survey was restricted to streams classified as first, second, and third-order (2nd–4th order in Colorado) (Strahler, 1957) on the 1 : 100 000 scale map. Sample probabilities were set so that roughly equal numbers of streams from each stream order category would appear in the sample. Each site had a sample weight (expansion factor) calculated as the inverse of the probability of selecting that site. Summing the sample weight of each site in the data set yields the total stream length in the study population. Thus, by using the sample weights in data analysis, inference can be made to the entire population of streams in the study area. Streams were sampled during an annual low flow index period (late April–early July in the Central Appalachians; August–September in Southern Rocky Mountains and Central Valley), in each year. In the field, a stream reach ranging from 150 to 500 m (based on 40 times the mean wetted width) was delineated around each randomly chosen sampling point. In total, data were collected from 371 different streams representative of 164 800 km of streams in the Central Appalachian region, 28 800 km of streams in the Southern Rocky Mountains, and 43 064 km of streams in the Central Valley.

Chemistry

Stream chemistry in all three regions consisted of collection of a 4-L cubitainer and four 60 mL syringes of stream water in a flowing portion near the middle of the stream at each sampling site. The syringes were sealed with a Luer-lock valve to prevent gas exchange. All samples were placed on ice and sent by overnight courier to the analytical laboratory. The syringe samples were analysed for pH, dissolved inorganic carbon (DIC), and monomeric aluminium,

and the cubitainer sample was split into aliquots and preserved within 48–72 h of collection. Detailed information on the analytical procedures used for each of the aliquots can be found in USEPA (1987). In brief, base cations, iron (Fe), and manganese (Mn) were determined by atomic absorption, anions (sulphate, nitrate, chloride) by ion chromatography, dissolved organic carbon (DOC) and DIC by a carbon analyser, and total N and P by persulphate oxidation and colorimetry. For metal analyses of the Southern Rocky Mountain and Central Valley samples, two 500 mL samples of stream water were collected. One sample was acidified (2 mL HNO_3) immediately for analyses of total metals concentrations. The other was filtered (glass fibre, 1.0 μm average pore size) then acidified for dissolved metals analyses. Both aliquots were analysed in the laboratory using an ICP spectrophotometer (USEPA, 1987).

Sediment microbial respiration

Microbial respiration on fine-grained, surface sediments (top 2 cm) was estimated as the change in dissolved oxygen (DO) concentration within sealed incubation chambers. Sediments were collected from depositional areas along the length of each stream reach. These sediments were combined, stirred for ≈ 1 min with a plastic scoop, and subsampled taking care to include only fine-grained sediments. Approximately 10 mL of sediment were placed in each of five labelled, 50 mL screw-top centrifuge tubes. A sixth tube for each site was filled with stream water only to correct for changes in DO not attributable to the sediment. Each tube was filled to the top (no head space) with stream water of known DO concentration and temperature, sealed, and incubated on-site for 2 h in the dark at ambient temperatures (closed ice chest half filled with stream water). Dissolved oxygen and temperature were measured using a YSI, Inc. Model 58 meter with either Model 5730 or Model 5905 stirring probe (YSI, Inc., Yellow Springs, OH). Accuracy of this meter and its probes is conservatively estimated by the manufacturer to be ± 0.03 mg O_2 L^{-1}. Following incubation, DO in each tube was re-measured, the overlying water in each tube was decanted, and the remaining sediment saved for analysis of ash free dry mass. Sediment samples were stored frozen until analysis (Hill, 1993; Hill *et al.*, 1997).

Sediments were partially thawed and transferred from centrifuge tubes to aluminium drying pans. Sediments were oven-dried (60 °C, 5 days), weighed, and combusted (525 °C, 30 min). Following combustion, samples were re-wetted (to re-hydrate clays), and dried again (60 °C, 3 days) before re-weighing to determine ash free dry mass (AFDM).

Dissolved oxygen changes in the tubes were corrected for sample volume and divided by sample AFDM to yield specific respiration (mg O_2 g^{-1} AFDM h^{-1}). For comparison with respiration data reported by other stream ecologists, we have converted specific respiration to daily respiration (g O_2 m^{-2} d^{-1}) by extrapolating surface area of sediments in our tubes (7 $cm^{2)}$ and assuming a constant rate of respiration throughout the day.

Statistical analyses

The Shapiro–Wilk test for normality revealed that the respiration data were not normally distributed for any of the study regions (Appalachians $W = 0.776$, $P < 0.0001$; Central Valley $W = 0.764$, $P < 0.0001$; Rockies $W = 0.586$, $P < 0.0001$). One-way analyses of variance on ranked respiration data, with Sheffe's multiple comparison procedure, were used to test differences among regions and temperature classes and between years (Quade, 1966; SAS, 1998). The relationships between respiration rate and stream chemistry were evaluated using the Spearman rank correlation procedure. All statistical analyses were performed using SAS for Windows 7.0 (SAS, 1998).

Results

Sediment microbial respiration in streams in the three study regions ranged from 0 to 0.621 mg O_2 g^{-1} AFDM h^{-1}, with regional means (± SE) of 0.101 ± 0.008 mg O_2 g^{-1} AFDM h^{-1}, 0.034 ± 0.004 mg O_2 g^{-1} AFDM h^{-1}, and 0.089 ± 0.009 mg O_2 g^{-1} AFDM h^{-1} for streams of the Central Appalachians, Southern Rockies, and Central Valley, respectively (Table 1). Respiration in streams of the Appalachians and Central Valley was similar, but respiration in Southern Rockies streams was significantly lower (Table 1). Respiration was not significantly different among years, with the exception of the Southern Rockies streams which exhibited lower respiration in 1995 (Table 1).

Table 1 Comparison of means, standard error of the means (± SE), and ranges of sediment microbial respiration from streams in the Central Appalachians (APP), Colorado's Southern Rockies (SR), and California's Central Valley (CCV) regions. Means which are not significantly different are indicated by the same letter (Sheffe groups)

Class		*N*	Respiration ± SE (mg O_2 g^{-1} AFDM h^{-1})	Sheffe group	*P*-value
Region	APP	174	0.101 ± 0.008	A	0.0001
	SR	102	0.034 ± 0.004	B	
	CCV	95	0.089 ± 0.009	A	
Year	1994	158	0.078 ± 0.008	A	0.7572
	1995	213	0.081 ± 0.006	A	
Region by year	APP 1994	112	0.104 ± 0.007	A	0.5479
	APP 1995	62	0.094 ± 0.009	A	
	SR 1994	51	0.040 ± 0.005	A B	0.1522
	SR 1995	51	0.028 ± 0.004	B	
	CCV 1994	45	0.098 ± 0.009	A	0.3363
	CCV 1995	50	0.081 ± 0.009	A	
Temperature class	Cold	171	0.050 ± 0.005	A	0.0001
	Warm	200	0.104 ± 0.008	B	
Region by temp. class	APP cold	91	0.069 ± 0.008	A	0.0001
	APP warm	83	0.136 ± 0.014	B	
	SR cold	79	0.028 ± 0.004	A	0.0005
	SR warm	23	0.055 ± 0.012	B	
	CCV cold	1	0.084		
	CCV warm	94	0.089 ± 0.009	A	0.7154

Table 2 Mean (± SE) concentrations for chemistry variables and temperature measured for streams in the Central Appalachians, Colorado's Southern Rockies, and California's Central Valley regions

Variable	Central Appalachians	Southern Rockies	Central Valley
Alkalinity (mg L^{-1})	509 ± 53	1458 ± 155	117 ± 12
Ca (μeq L^{-1})	687 ± 61	1079 ± 77	1780 ± 260
Cl (μeq L^{-1})	159 ± 17	147 ± 58	165 ± 38
DOC (mg L^{-1})	2.00 ± 0.12	4.11 ± 0.45	7.58 ± 0.90
K (μeq L^{-1})	34.2 ± 1.7	27.7 ± 4.2	86.2 ± 11.1
Mg (μeq L^{-1})	394 ± 51	410 ± 41	1610 ± 229
Mn (μg L^{-1})	0.23 ± 0.11	0.87 ± 0.26	7.93 ± 2.17
Na (μeq L^{-1})	197 ± 19	551 ± 164	3362 ± 749
NH_3 (μeq L^{-1})	0.97 ± 0.20	0.60 ± 0.57	0.98 ± 0.20
Total N (μg L^{-1})	854 ± 120	393 ± 85	843 ± 300
pH	6.97 ± 0.06	ns	ns
Total P (μg L^{-1})	26.7 ± 2.9	51.9 ± 5.8	455 ± 116
TSS (mg L^{-1})	9.9 ± 1.5	19.3 ± 3.9	64.8 ± 14.4
Ag (μg L^{-1})	ns	ns	126 ± 6
Al (μg L^{-1})	87.7 ± 43.8	313 ± 174	252 ± 18
Cd (μg L^{-1})	ns	1.81 ± 0.22	1.58 ± 0.08
Cr (μg L^{-1})	ns	ns	1.80 ± 0.07
Cu (μg L^{-1})	ns	29.9 ± 19.8	30.8 ± 5.5
Fe (μg L^{-1})	98 ± 34	172 ± 68	124 ± 22
Hg (μg L^{-1})	ns	ns	0.12 ± 0.01
Pb (μg L^{-1})	ns	ns	4.94 ± 1.78
Se (μg L^{-1})	ns	ns	1.11 ± 0.11
Zn (μg L^{-1})	ns	177 ± 44	86 ± 19
Temperature (°C)	14.9 ± 0.3	12.0 ± 0.4	21.0 ± 0.3

Table 3 Five strongest Spearman correlations (*Rs*) and associated statistics between sediment microbial respiration (mg O_2 g^{-1} AFDM h^{-1}) and chemistry co-variables in Central Appalachian, Southern Rockies, and Central Valley streams in 1994 and 1995. Only those variables with significant correlations ($P < 0.10$) are included

Class	*n*	Co-variables	R_s	*P*-value
Overall study	371	Temperature	0.36655	0.0001
		Dissolved organic carbon	0.29658	0.0001
		K	0.25342	0.0001
		Cl	0.24944	0.0001
		NH_3	0.24585	0.0001
Central Appalachians	174	Dissolved organic carbon	0.50493	0.0001
		Total P	0.37121	0.0001
		Temperature	0.33087	0.0001
		Total N	0.25300	0.0008
		Cl	0.22523	0.0028
Southern Rockies	102	Total suspended solids	0.47711	0.0119
		Temperature	0.26202	0.0077
		Cl	0.26202	0.0085
		Alkalinity	0.23464	0.0182
		K	0.22694	0.0218
Central Valley	95	Dissolved organic carbon	– 0.24544	0.0858
		Alkalinity	– 0.24120	0.0915
		Total N	0.20924	0.0419
Cold streams	171	Dissolved organic carbon	0.26059	0.0073
		Total N	0.21435	0.0155
		K	0.20940	0.0060
		NH_3	0.18659	0.0145
		Cl	0.14950	0.0517
Warm streams	200	Total N	0.29634	0.0001
		Mg	– 0.13537	0.0560
		Temperature	0.12508	0.0784

Microbial communities in aquatic sediments are known to fall into two categories based on optimal temperatures. Psychrotolerant communities exhibit metabolic optima at temperatures below 15 °C, and mesophilic communities reach metabolic optima above 15 °C (Thamdrup & Fleischer, 1998). We used this criterion to classify our study streams, based on temperature at the time of collection, as cold (≤ 15 °C) or warm water systems. Estimates of respiration in cold water streams in the Appalachians and the Southern Rockies were significantly lower than those for warm water streams in the same region (Table 1). This relationship did not hold for Central Valley streams, but only one stream in this region was classified as a cold water stream.

Stream chemistry varied significantly among the three regions (Table 2). For example, the Central Appalachians and the Central Valley had significantly higher nutrient concentrations than the Southern Rockies, but lower alkalinity and metal concentrations. Correlations of sediment microbial respiration with chemical variables were evaluated by region and temperature class (Table 3).

Discussion

Sediment microbial respiration rates for streams in the Central Appalachian study region were similar to rates reported for low-order streams of the eastern United States (Webster *et al*., 1995; Sinsabaugh, 1997; Hill *et al*., 1998). Reported respiration rates ranged from 0.3 g O_2 m^{-2} d^{-1} for a third order forested stream in Michigan (Brown & King, 1987) to 16.6 g O_2 m^{-2} d^{-1} for first order grassland streams in Illinois (Wiley *et al*., 1990). Our mean respiration rate for Central Appalachian streams is similar to the overall average of 4 g O_2 m^{-2} d^{-1} reported by Webster *et al*. (1995) for first to third order streams in the eastern United States.

Few estimates of sediment microbial respiration are reported for Rocky Mountain streams, but several researchers have reported community respiration

estimates based on open channel or chamber changes in dissolved oxygen. Our measures of sediment microbial respiration in Southern Rocky Mountain streams are higher than most estimates for community respiration in Rocky Mountain streams (McConnell & Sigler, 1959; Pennak & Lavelle, 1979; Crossey & LaPointe, 1988; Hill *et al*., 1997), though our mean respiration rate is similar to those reported for streams from Idaho and Montana (Wright & Mills, 1967; Bott *et al*., 1985).

Comparisons of Central Valley stream respiration estimates are hampered by a lack of studies reporting respiration from streams in that region. Our estimates of sediment microbial respiration are in the range of values reported for agricultural and prairie streams in the Midwest (Gelroth & Marzolf, 1978; Bott *et al*., 1985; Hill & Gardner, 1987; Wiley *et al*., 1990), and for desert streams (Minshall, 1978; Lewis & Gerking, 1979; Busch & Fisher, 1981; Grimm & Fisher, 1984).

While there appears to be little experimental evidence linking benthic community respiration with stream temperature, there are abundant data showing significantly higher respiration in the summer compared to winter (Webster *et al*., 1995). Using temperature as the independent variable in linear regression models of respiration has produced mixed results. Bott *et al*. (1985) reported that temperature accounted for 35–38% of the variance associated with respiration measurements in first to fourth order streams in Michigan, Oregon, and Pennsylvania, but no significant relationship between respiration and temperature in Idaho streams. Hedin (1990) also reported that temperature was not a significant contributor ($r^2 = 0.21$, $P > 0.05$) to a respiration model for a New Hampshire stream. Similarly, temperature only accounted for 14% of the variance in community respiration in streams draining Texas prairies (Hill & Gardner, 1987). We found that temperature was a significant correlate of respiration in Central Appalachian and Southern Rockies streams, but not in Central Valley streams (Table 3). Fuss & Smock (1996) reported that temperature explained about 70% of the variance in respiration rates on leaves and wood in a blackwater stream, but only 4% of the variance in respiration rates on surface sediments. Comparison among these studies, however, is complicated by differences in sampling frequency and methodology. Mindful of these differences, evidence from this study and others suggests that temperature might, for reasons which are still unclear, influence benthic community respiration to different degrees in different streams.

Few studies have looked at chemical variables in relation to community respiration. Bott *et al*. (1985) considered alkalinity, nitrogen and phosphorus, in addition to temperature. Alkalinity, nitrogen and phosphorus were significant variables in the multiple regression models of respiration in streams in Idaho, Michigan, Oregon & Pennsylvania. Hedin (1990) also related respiration to concentrations dissolved organic carbon (DOC). Fuss & Smock (1996) found that nitrogen concentrations were strongly related to respiration in surficial and hyporheic sediments in a first-order, coastal Virginia stream. Concentrations of total N and DOC were significantly related to respiration in the present study. Similarly, stream ecologists have believed that stream metabolism should be related to DOC concentration. However, Hedin (1990) reported no significant correlation ($R = -0.02$, $P > 0.05$) between respiration and DOC in New Hampshire streams.

While nutrients are known to stimulate leaf litter breakdown (Elwood *et al*., 1981; Newbold *et al*., 1983), Peters *et al*. (1987) reported no stimulation of microbial activity related to nitrogen and phosphorus additions. We found that sediment microbial respiration in both Central Appalachian and Central Valley streams was significantly related to water-column concentrations of total P, total N and Cl. Except in coastal environments, Cl concentrations in streams is low and its presence in the stream at concentrations above 100 μeq L^{-1} is indicative of anthropogenic disturbances (residual chlorine from water and waste water treatment, road salts, and agricultural applications of fertilizers) (Herlihy *et al*., 1998). The correlation of respiration with N, P and Cl suggests that respiration may be linked to stream enrichment from human activities.

Functional measures have not been extensively used in environmental monitoring, but several researchers have demonstrated the utility of functional assessments of perturbations. Stressors such as metals, chlorine, pesticides, oil and channel desiccation have been shown to depress GPP, net primary productivity (NPP) and/or R (Matthews *et al*., 1982; Hill & Gardner, 1987; Crossey & LaPointe, 1988; Hill *et al*., 1997).

Ecosystem functions are intricately related to environmental variables but, because of the complex-

ities of ecosystems, are not often strongly correlated with them in studies involving large spatial scales. Understanding the relationship between ecosystem metabolism and environmental factors requires an approach to data interpretation that is sensitive to scale-dependent constraints (O'Neill *et al*., 1986).

We set out to answer several questions. First, the ranges of respiration values measured by this study of Central Appalachian, Southern Rockies, and California Central streams are within that reported by other investigators who have worked in this region or in similar environments. Of the studies of stream community respiration cited, ours is one of a few to employ a probability sampling design using consistent methods over a large regions. The fact that our results are consistent with those collected from site-specific studies suggests that the probability approach, with its inherent statistical powers, is valid for regional-scale studies of stream communities.

Second, sediment microbial respiration is significantly related to temperature and a number of chemical variables. However, the strength of these correlations ($R < 0.50$) indicates that the relationship is not one of simple causality, and predictions based on these correlations would require more complex models and further research.

Third, the lack of significant differences in sediment microbial respiration between years suggests that regional estimates may be based on one-time sampling if sampling occurs within the same sampling index period (season, flow conditions, etc.) from year to year.

Finally, sediment microbial respiration is fairly uniform, and similarly correlated to stream chemistry, among the diverse regions studied. The implication for regional-scale studies is that estimates of sediment microbial respiration may be collected at any number of scales above the site-level for reliable prediction of respiration patterns at larger spatial scales.

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