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Influence of Stream Habitat and Land Use on Macroinvertebrate Assemblages of The Henry's Fork Watershed

Abstract

We investigated relationships among benthic macroinvertebrate assemblages, stream physical habitat, and land use in the Henry's Fork watershed, Idaho and Wyoming. Macroinvertebrate assemblages were described with five biological metrics: benthic macroinvertebrate density, taxa richness, EPT (Ephemeroptera, Plecoptera, Trichoptera) richness, percent EPT, and percent dominant taxon. Ten physical habitat variables were used to describe the inorganic and organic substrate and channel morphology of the streams sampled. Land use in 10 subwatersheds was assessed using a Geographic Information System (GIS). Pearson product-moment and canonical correlation analyses were used to assess relationships among the macroinvertebrate, habitat, and land-use variables. Macroinvertebrate density, EPT richness, and dominant taxon metrics were highest in spring-fed streams with small, yet likely stable, highly embedded substrates and abundant macrophyte growth. The percent EPT metric was highest in runoff-dominated streams with large, heterogeneous, less embedded substrates. Taxa richness was negatively correlated with percent rangeland, and percent EPT was negatively correlated with percent agricultural land. The EPT richness metric was positively correlated with percent forested land. There were no significant correlations between stream habitat and land use, indicating that land use may have influenced macroinvertebrate assemblages via water quality or physical habitat characteristics not measured in this study.

Key words. aquatic macroinvertebrates, habitat, land use, correlations, watersheds, EPT, spring-fed stream .

Introduction

The Henry's Fork watershed, located in eastern Idaho and western Wyoming, is a diverse landscape containing a variety of stream types. Spring-fed streams draining the Yellowstone Plateau, runoff-dominated streams of the Teton, Centennial, and Henry's Lake mountain ranges, and lowland streams flowing through crop land and cattle pastures all occur in the watershed (see Van Kirk and Benjamin this issue). Because benthic macroinvertebrates are sensitive to surrounding environmental conditions (Rosenburg *et al.* 1986), we would expect variation in land use and stream habitat type across the watershed to result in corresponding variation in macroinvertebrate assemblages.

Land use influences macroinvertebrate assemblages indirectly through effects on physical habitat and water quality. For example, plant cover associated with forested landscapes provides shade to keep water temperatures low, prevents soil

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compaction, reduces runoff, and provides allochthonous material which, along with aquatic macrophytes and algae, is a source of food and cover for invertebrates (Cummins *et al.* 1983, Gregory *et al.* 1987, Rothrock *et al.* 1998). Agricultural and pasture areas can be detrimental to stream health (Richards *et al.* 1993, Richards and Host 1994, Rothrock *et al.* 1998). Cattle can trample stream banks and destroy riparian vegetation (Kauffman *et al.* 1983a). Runoff from agricultural and pasture land can deliver sediment into streams, where it settles and alters substrate particle-size distribution, flow patterns, and channel morphology, all of which affect macroinvertebrate assemblage composition (Rabeni and Minshall 1977, McClelland and Brunsen 1980, Waters 1995). Because of erosion and bank destabilization, streams draining agricultural and pasture lands are often wide and shallow and receive little shade. These conditions promote high rates of primary productivity, which affect macroinvertebrate assemblage composition through changes in trophic structure (Naiman and Sedell 1980, Vannote *et al.* 1980, Bott *et al.* 1985).

The Henry's Fork Foundation has conducted biological and habitat assessments of the conditions of streams in the watershed since 1996. This study investigated relationships among aquatic macroinvertebrate assemblages, stream habitat, and land use in streams of the Henry's Fork watershed. Results of this study will aid natural resource managers in developing strategies to preserve and protect aquatic resources in the watershed.

Materials and Methods

Data Collection

The study area consisted of 10 subwatersheds draining about 3,770 km^2 in the upper two-thirds of the Henry's Fork watershed (Table 1; see Figs. 1 and 3 in Van Kirk and Benjamin this issue for locations of the subwatersheds). Benthic macroinvertebrate and physical habitat data were collected at 96 sites (Table 1) during the summers of 1996, 1997 and 1998 by crews of four to seven interns and research assistants as part of the Henry's Fork Foundation's stream assessment program. Streams were divided into reaches based on channel morphology. Reconnaissance of each stream reach was conducted, and samples were taken from a 200-m section (reach sample) that appeared to be representative of the entire reach.

Macroinvertebrates were collected with a modified Hess sampler (area 0.0726 m^2, mesh size 250 μm) in two riffles within each sample section and with a kick net (50 cm x 50 cm, mesh size 1000 mm) in slower water and along the stream banks. Organisms and any detritus captured in the Hess sampler were immediately preserved in 80 percent methanol and transported to the laboratory. Organisms collected in kick nets were sorted in rough proportion to their abundance and preserved. All organisms were sorted from detritus in shallow pans using magnifying glasses and identified under stereoscopic microscopes using identification criteria in Merritt and Cummins (1996). Mayflies (Ephemeroptera) and stoneflies (Plecoptera) were identified to genus but, because of time constraints, caddisflies (Trichoptera), dipterans, and members of other orders were usually identified only to family.

Macroinvertebrate assemblages were quantified with five metrics. Macroinvertebrate density (individuals/m^2 of stream bottom, calculated from Hess samples) was used as an indicator of nutrient enrichment and to allow assessment of density-related food-chain effects. The other four were standard metrics used in the U.S. Environmental Protection Agency (USEPA) Rapid Bioassessment Protocol (Plafkin *et al* 1989), including two diversity measures,

Table 1. *Benthic macroinvertebrate assemblage metric values for 96 sites in the Henry's Fork watershed.*

Subwatershed Site	Density (organisms per m²)	Taxa richness	EPT richness	% EPT	% dominant taxon
Island Park Caldera					
Chick Cr.	13140	22	13	65.0	78.1
Buffalo R. upper	7935	19	12	71.0	36.5
Buffalo R. middle 3	7977	18	8	53.0	34.3
Buffalo R. middle 2	5290	20	10	67.0	39.1
Buffalo R. middle 1	5969	16	9	64.0	38.7
Buffalo R. lower	2051	15	11	85.0	46.7
Elk Cr. upper	18529	15	5	45.0	89.7
Elk Cr. lower	6280	13	4	44.0	58.5
Toms Cr. upper	5276	17	6	46.0	51.4
Split Cr.	919	11	4	44.0	54.2
Blue Springs	18416	13	6	55.0	74.9
Antelope Cr. upper	4993	19	9	56.0	27.8
Antelope Cr. lower	16620	18	7	47.0	54.1
E. Thurmon Cr.	19208	23	14	70.0	22.0
Middle Thurmon Cr.	13281	16	8	62.0	60.2
Thurmon Cr.	41188	17	8	62.0	92.5
Warm River					
Warm R. upper	47694	26	14	61.0	35.7
Warm R. middle 2	15672	23	14	70.0	62.8
Warm R. middle 1	3395	19	10	67.0	39.4
Warm R. lower	15361	16	10	71.0	54.7
Partridge Cr. middle	5502	8	2	29.0	83.0
Partridge Cr. lower	8670	11	6	60.0	92.9
Robinson Creek					
Robinson Cr. upper	4017	20	13	72.0	44.4
Robinson Cr. middle	2875	19	12	71.0	44.1
Fish Cr.	4074	19	8	53.0	32.1
Snow Cr. upper	3564	13	4	44.0	55.2
Snow Cr. lower	3310	20	11	61.0	52.0
Little Robinson Cr.	6124	20	13	72.0	31.4
Henry's Lake Outlet					
Targhee Cr. lower	689	14	7	88.0	68.0
Henry's Lake Outlet lower	579	11	6	40.0	28.6
Tygee Cr. upper	1819	13	7	64.0	37.9
Twin Cr. upper	386	15	6	75.0	28.6
Jesse Cr. upper	703	12	4	44.0	54.9
Jones Cr.	96	4	1	20.0	28.6
Stephens Cr.	3637	14	3	38.0	49.6
Meadow Cr. upper	1777	11	6	55.0	30.2
Upper Henry's Fork					
Upper Henry's Fork lower	3663	28	16	66.0	18.0
Moose Cr. upper	468	10	5	50.0	38.2
Lucky Dog Cr.	537	13	2	20.0	43.6
Coffee Pot Cr.	1667	18	9	82.0	41.3
Tyler Cr. upper	1033	9	8	62.0	22.7
Elk Springs	1295	19	5	46.0	32.4
No Name Cr. lower	41	6		50.0	66.7
Sawtell Cr. middle	96	10		17.0	28.6

Table 1. *(cont.)*

Subwatershed Site	Density (organisms per m²)	Taxa richness	EPT richness	% EPT	% dominant taxon
Shotgun Valley					
Yale Cr. middle 1	248	7	3	100.0	88.9
Yale Cr. middle 2	317	11	5	71.0	52.2
E. Fork Hotel Cr.	234	11	5	71.0	35.3
Arange Cr.	868	13	7	88.0	63.0
Icehouse Cr. lower	2163	19	9	53.0	26.1
Meyers Cr. lower	1805	15	6	55.0	36.6
Schneider Cr. upper	1047	15	6	66.0	26.3
Taylor Cr. lower	386	10	3	60.0	57.1
Howard Cr.	441	14	5	71.0	34.4
Sheridan Cr. middle	1392	13	7	58.0	41.6
Sheridan Cr. lower 2	1653	12	4	36.0	49.2
Fall River					
Fall R. upper	2148	24	8	28.8	48.1
Fall R. middle 1	1804	23	10	38.2	30.5
Fall R. middle 3	6773	25	10.5	60.5	36.0
Cascade Cr. upper	482	16	10	80.0	20.0
Cascade Cr. lower	317	15	5	43.5	30.4
Calf Cr. upper	276	13	4	80.0	60.0
Calf Cr. lower	827	15	2	13.3	75.0
Mountain Ash Cr. upper	41	14	0.5	33.3	33.3
Mountain Ash Cr. lower	964	10	8	80.0	55.7
Proposition Cr. upper	386	18	7	78.6	21.4
Proposition Cr. lower	1061	18	10	62.3	23.4
Bechler River					
Bechler R. upper	207	13	6	80.0	20.0
Bechler R. middle 1	1391	20	7	28.2	55.0
Bechler R. lower	799	17	8	36.2	22.4
Little's Fork	110	12	3	100.0	75.0
Ferris Fork	276	9	2	15.0	45.0
Gregg's Fork	317	14	6	56.5	21.7
Phillip's Fork	289	13	3	47.6	52.4
Ouzel Cr.	179	15	5	100.0	61.5
Boundary Cr. upper	207	16	4	80.0	60.0
Boundary Cr. lower	1543	12	5	17.0	47.3
Boone Creek					
N. Boone Cr. upper	41	12	2	66.7	33.3
N. Boone Cr. lower	179	18	4	76.9	53.8
S. Boone Cr. upper	1240	17	10	72.2	23.3
S. Boone Cr. lower	289	11	4	47.6	38.1
S. Fork Middle Boone Cr.	592	16	7	34.9	65.1
Boone Cr. upper	648	20	8	70.2	19.1
Boone Cr. lower	193	18	1	7.1	35.7
Conant Creek					
Conant Cr. middle 1	311	23	5	31.8	36.4
Conant Cr. middle 2	85	18	5	100.0	33.3
Conant Cr. middle 3	113	23	4	62.5	25.0
Conant Cr. lower	57	16	0	0.0	50.0
Hominy Cr.	28	9	0	0.0	100.0
Coyote Cr. lower	14	16		100.0	100.0

Table 1. *(cont.)*

Subwatershed Site	Density (organisms per m^2)	Taxa richness	EPT richness	% EPT	% dominant taxon
Granite Cr. upper	4009	7	2	10.7	79.4
Granite Cr. lower	400	10	2	20.7	34.5
Squirrel Cr. upper	28	15	0	0.0	100.0
Squirrel Cr. middle 1	438	11	0	0.0	100.0
Squirrel Cr. middle 2	396	21	5	75.0	46.4
Squirrel Cr. middle 3	396	14	2	7.1	71.4
Squirrel Cr. lower	344	18	4	20.0	64.0

taxa richness and EPT (Ephemeroptera, Plecoptera, and Trichoptera) richness, and two assemblage composition measures, percent EPT and percent dominant taxon. Taxa richness was defined as number of different taxa found in the combined Hess and kick-net samples, and EPT richness was defined as number of taxa found in the combined Hess and kick-net samples belonging to the orders Ephemeroptera, Plecoptera, and Trichoptera. Percent EPT was the percentage of individuals in the Hess sample that were from the EPT orders, and percent dominant taxon was the percentage of individuals in the Hess sample that were from the most numerous taxon.

We described physical habitat of streams by measuring inorganic and organic substrate characteristics and several stream-channel morphologic variables. Inorganic substrate composition was described using three parameters, two of which were based on a modified Wolman pebble count (Bevenger and King 1995), and the third of which was based on visual assessment. Pebble count data were grouped by particle size according to the 10 size classes defined by Platts *et al.* (1983). The first parameter, substrate size, was calculated by assigning a score to each of the 10 particle-size classes so that the smallest particle-size class received a score of 1, the class of the next smallest particles received a score of 2, and so on up to a score of 10 for the class of the largest particles. Particle counts within the 10 size classes were multiplied by the corresponding weight and summed for each site. A second descriptor of substrate composition, percent fines, was the percentage of substrate particles counted that were <4 mm in diameter. The third inorganic substrate parameter, gravel embeddedness, was determined visually and represented an estimate of the percentage of interstitial space among gravel- and cobble-sized particles that was filled with particles <4 mm in diameter.

Three organic substrate parameters were assessed. The large woody debris (LWD) variable was the number of pieces of woody material at least 10 cm in diameter and 1 m in length in contact with the water in the 200-m reach sample. Small woody debris (SWD) was defined as woody material not large enough to be classified as large woody debris. We estimated abundance and assigned a value between 1 (no SWD present) and 5 (abundant SWD), inclusive. Macrophyte coverage was visually estimated as the percentage of stream bottom in the reach sample that was covered by macrophytes.

We measured four variables describing stream-channel morphology. Stream width was the average width at 20 transects in the 200-m reach sample. Width-to-depth ratio was the average width divided by the average depth at the 20 transects. Shading, determined visually, was an estimate of the percentage of stream surface that would be shaded when the sun was at its peak. Stream gradient at various points throughout the reach was measured using a clinometer, and the maximum measurement was used in the analyses.

Land use was quantified using a Geographic Information System (GIS) and USEPA 1:250,000 land-use maps. We calculated the percentage consisting of agricultural, range, and forest land in each of the 10 subwatersheds comprising the study area. All other land uses were combined into a fourth category.

Statistical Analyses

Relationships between individual macroinvertebrate assemblage metrics and stream physical habitat variables were assessed using Pearson product-moment correlations (Zar 1999). The macroinvertebrate metrics were considered as the dependent variables. We used log-transformed density values because macroinvertebrate densities varied widely (Zar 1999). Key relationships were further investigated using scatterplots. Correlation analysis also was performed on a subset of the data that included only runoff-dominated streams. Pearson product-moment correlations were used to investigate relationships between individual macroinvertebrate assemblage and physical habitat variables and land-use variables. For this analysis, data were grouped by subwatershed, and the subwatershed means of the macroinvertebrate and habitat variables were used as dependent variables. Subwatershed land-use percentages were used as the independent variables. All correlations were considered significant when $P \leq 0.05$.

We used canonical correlation analysis (CCA) to investigate relationships between the set of the five macroinvertebrate assemblage metrics and the set of the 10 stream habitat variables. The CCA derived a set of orthogonal linear transformations (five for the macroinvertebrate metrics and 10 for the habitat variables) from the joint covariance matrix of the macroinvertebrate and habitat variables. These transformations were then used to compute the canonical macroinvertebrate and habitat variables as weighted sums of the original data. Each set of weights corresponded to one of the canonical roots in such a way that the transformation corresponding to the first root explained the largest amount of variability in the data, the transformation corresponding to the second root explained the largest amount of variability not already accounted for by the first transformation, and so on (Tatsuoka 1971, Arnold 1981). The correlation between the two sets of canonical variables was first calculated using canonical variables obtained from the full set of transformations, and a Chi-square test (Tatsuoka 1971) was used to determine if the correlation was significant at $\alpha = 0.05$. This procedure was then repeated after eliminating the canonical variables obtained from the pair of transformations accounting for the least amount of variability, repeated again after eliminating the pair accounting for the next least amount of variability, and so on until only one set of canonical macroinvertebrate variables remained. We also investigated the factor structure of the transformations corresponding to the largest three canonical roots. The factor loadings of each variable were derived from the canonical transformations and their corresponding roots and indicated the influence of the given transformation on each of the variables (Tatsuoka 1971). All statistical calculations were performed using Statistica software.

Results

A total of 93 invertebrate taxa (Table 2) was collected from the 96 sample sites

Table 2. *Macroinvertebrate taxa observed at all 96 sites combined.*

Order	Family	Genus
Amphipoda		
Coleoptera	Amphizoidae	
Coleoptera	Dytiscidae	
Coleoptera	Elmidae	
Coleoptera	Haliplidae	
Coleoptera	Hydrophilidae	
Coleoptera	Limnichidae	
Collembola		
Diptera	Athericidae	
Diptera	Blephariceridae	
Diptera	Ceratopogonidae	
Diptera	Chironomidae	
Diptera	Dixidae	
Diptera	Empididae	
Diptera	Simuliidae	
Diptera	Stratiomyidae	
Diptera	Tabanidae	
Diptera	Tipulidae	
Ephemeroptera	Ameletidae	*Ameletus*
Ephemeroptera	Baetidae	*Baetis*
Ephemeroptera	Baetidae	*Barbaetis*
Ephemeroptera	Baetidae	*Callibaetis*
Ephemeroptera	Baetidae	*Paracloeodes*
Ephemeroptera	Ephemerellidae	*Attenella*
Ephemeroptera	Ephemerellidae	*Caudatella*
Ephemeroptera	Ephemerellidae	*Caurinella*
Ephemeroptera	Ephemerellidae	*Drunella*
Ephemeroptera	Ephemerellidae	*Ephemerella*
Ephemeroptera	Ephemerellidae	*Serratella*
Ephemeroptera	Ephemerellidae	*Timpanoga*
Ephemeroptera	Ephemeridae	*Ephemera*
Ephemeroptera	Ephemeridae	*Hexagenia*
Ephemeroptera	Heptageniidae	*Anepeorus*
Ephemeroptera	Heptageniidae	*Cinygma*
Ephemeroptera	Heptageniidae	*Cinygmula*
Ephemeroptera	Heptageniidae	*Epeorus*
Ephemeroptera	Heptageniidae	*Heptagenia*
Ephemeroptera	Heptageniidae	*Rithrogena*
Ephemeroptera	Leptophlebiidae	*Paraleptophlebia*
Ephemeroptera	Siphlonuridae	*Parameletus*
Ephemeroptera	Siphlonuridae	*Siphlonurus*
Ephemeroptera	Tricorythidae	*Tricorythodes*
Hemiptera		
Hirudinea		

Table 2. *(cont.)*

Order	Family	Genus
Hydracarina		
Lepidoptera	Pyralidae	
Megaloptera		
Mollusca		
Odonata		
Oligochaeta		
Pelecypoda		
Plecoptera	Capniidae	*Allocapnia*
Plecoptera	Chloroperlidae	*Alloperla*
Plecoptera	Chloroperlidae	*Kathroperla*
Plecoptera	Chloroperlidae	*Paraperla*
Plecoptera	Chloroperlidae	*Plumiperla*
Plecoptera	Chloroperlidae	*Suwallia*
Plecoptera	Chloroperlidae	*Sweltsa*
Plecoptera	Chloroperlidae	*Utaperla*
Plecoptera	Leuctridae	*Perlomyia*
Plecoptera	Nemouridae	*Amphinemura*
Plecoptera	Nemouridae	*Malenka*
Plecoptera	Nemouridae	*Ostrocerca*
Plecoptera	Nemouridae	*Zapada*
Plecoptera	Perlidae	*Acroneuria*
Plecoptera	Perlidae	*Calineura*
Plecoptera	Perlidae	*Claassenia*
Plecoptera	Perlidae	*Eccoptura*
Plecoptera	Perlidae	*Hesperoperla*
Plecoptera	Perlodidae	*Diura*
Plecoptera	Perlodidae	*Frisonia*
Plecoptera	Perlodidae	*Isoperla*
Plecoptera	Perlodidae	*Salmoperla*
Plecoptera	Perlodidae	*Setvena*
Plecoptera	Pteronarcyidae	*Pteronarcys*
Plecoptera	Taeniopterygidae	*Doddsia*
Trichoptera	Brachycentridae	
Trichoptera	Glossosomatidae	
Trichoptera	Helicopsychidae	
Trichoptera	Hellopsychidae	
Trichoptera	Hydropsychidae	
Trichoptera	Hydroptilidae	
Trichoptera	Lepidostomatidae	
Trichoptera	Limnephilidae	
Trichoptera	Philopotamidae	
Trichoptera	Polycentropodidae	
Trichoptera	Psychomyiidae	
Trichoptera	Rhyacophilidae	
Tricladida	Planarianiidae	

(Table 1). Macroinvertebrate density ranged from 14 to over 40,000 individuals/m^2, taxa richness ranged from 4 to 28, EPT richness ranged from 0 to 16, percent EPT ranged from 0 to 100, and percent dominant taxon ranged from 19 to 100 (Table 1). Subwatershed mean macroinvertebrate density was highest in the Warm River subwatershed and lowest in the Boone

Table 3. *Benthic macroinvertebrate assemblage metric means and standard deviations by subwatershed.*

	Density (organisms per m²)		Taxa richness		EPT richness		% EPT		% dominant taxon	
Subwatershed	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Island Park Caldera	11692.0	9910.8	17.0	3.2	8	3.1	58.5	11.8	53.7	21.2
Warm River	16049.0	16296.2	17.2	6.9	9	4.7	59.7	15.7	61.4	23.0
Robinson Creek	3994.0	1135.7	18.5	2.7	10	3.5	62.2	11.7	43.2	9.9
Henry's Lake Outlet	1210.8	1160.6	11.8	3.5	5	2.1	53.0	22.0	40.8	15.0
Upper Henry's Fork	1100.0	1181.9	14.1	7.2	6	5.1	49.1	22.1	36.4	15.1
Shotgun Valley	959.5	699.3	12.7	3.1	5	1.8	66.3	17.3	46.4	18.5
Fall River	1370.8	1907.0	17.4	4.8	7	3.5	54.4	24.1	39.4	17.9
Bechler River	531.8	528.9	14.1	3.1	5	1.9	56.1	32.4	46.0	18.9
Boone Creek	454.7	411.4	16.0	3.3	5	3.3	53.7	25.4	38.4	16.2
Conant Creek	509.2	1064.9	15.5	5.2	2	2.1	32.9	38.1	64.6	29.0

Creek subwatershed (Table 3). Mean taxa richness values ranged from 11.8 in the Henry's Lake Outlet subwatershed to 18.5 in the Robinson Creek subwatershed (Table 3). Mean values for EPT richness ranged from 2 in the Conant Creek subwatershed to 10 in Robinson Creek. Mean percent EPT values were highest in Shotgun Valley (66.3%) and lowest in the Conant Creek drainage (32.9%; Table 3). Percent dominant taxon ranged from 38 percent in the Boone Creek drainage to 65 percent in the Conant Creek drainage (Table 3).

Island Park Caldera streams, which were primarily spring fed, had the smallest substrate, highest percentage of fines, highest gravel embeddedness, highest width-to-depth ratio, and the highest percent macrophyte coverage (Table 4). The largest mean substrate was found in the runoff-dominated streams of the Bechler River drainage, which were often underlain by large sections of bedrock (Table 4). Gradients were highest in the Fall and Bechler river drainages in southwestern Yellowstone National Park.

Land-use types in the study area consisted mainly of agricultural land, rangeland, and forest (Table 5). The Fall River and Conant Creek subwatersheds were highest in agricultural use, and Shotgun Valley and Henry's Lake Flats were highest in percent rangeland (Table 5). Forest was the dominant land type in all subwatersheds and exceeded 80 percent of the land area in the Warm River, Robinson Creek, Island Park Caldera, Upper Henry's Fork, Bechler River, and Boone Creek subwatersheds (Table 5).

Pearson product-moment correlations indicated that benthic macroinvertebrate assemblage characteristics were most dependent on stream inorganic substrate characteristics (substrate size, percent fines, and gravel embeddedness), maximum stream gradient, and macrophyte coverage (Table 6). Macroinvertebrate density was positively correlated with gravel embeddedness, width-to-depth ratio, macrophyte coverage, stream width, and percent fines, and negatively correlated with substrate size, maximum stream gradient, and small woody debris (Table 6). Taxa richness and EPT richness were both positively correlated with gravel embeddedness, macrophyte coverage, and stream width. The percent EPT metric was negatively correlated with percent fines, whereas percent dominant taxon showed a positive correlation with percent fines. When all spring-fed

Table 4. *Physical habitat variable means and standard deviations by subwatershed.*

	Substrate size (rating)		% fines		Gravel embeddedness (%)		Large woody debris (pieces per 200 m)		Small woody debris (rating)		Macrophyte cover (%)		Stream width (m)		Shading (%)		Maximum gradient (%)		Width/Depth ratio	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Island Park Caldera	180.8	72.2	58.9	23.2	44.1	18.7	58.4	66.3	2.1	1.1	30.3	25.1	22.7	31.9	9.8	8.5	0.1	0.0	86.1	156.3
Warm River	369.8	103.1	18.3	12.6	39.0	10.8	50.3	48.8	3.5	1.6	4.5	4.6	15.4	11.0	10.2	10.3	0.6	1.2	27.1	16.9
Robinson Creek	365.3	74.7	16.0	12.4	30.0	6.2	58.5	34.6	4.3	0.8	7.0	7.9	5.6	3.8	20.0	12.6	0.3	0.3	16.5	11.0
Henry's Lake Outlet	334.5	170.3	27.6	34.8	25.6	28.2	42.3	45.9	3.4	1.6	1.3	3.5	6.0	4.7	41.3	34.4	2.7	2.3	15.6	5.7
Upper Henry's Fork	327.0	123.6	24.9	21.5	2.8	4.5	74.4	59.3	3.6	1.3	8.1	23.0	6.8	11.9	29.0	38.9	1.9	1.9	15.3	12.9
Shotgun Valley	373.2	61.8	15.5	9.0	9.5	11.7	31.5	34.7	2.8	1.5	0.0	0.0	4.0	2.4	51.1	34.3	3.2	2.2	21.7	15.4
Fall River	424.5	97.1	11.3	11.9	17.4	16.7	71.4	59.8	3.2	1.1	3.7	5.7	14.7	19.5	9.4	16.9	14.8	14.6	32.2	35.0
Bechler River	524.7	194.9	27.9	39.2	10.5	7.4	21.0	26.3	2.1	0.7	3.3	6.1	14.1	15.6	3.6	1.4	19.6	13.7	35.1	37.2
Boone Creek	423.6	182.0	21.7	22.4	13.8	7.0	19.0	14.9	3.9	1.1	5.3	13.1	7.5	2.9	13.6	16.3	5.2	4.7	23.6	7.3
Conant Creek	378.6	72.2	31.2	35.3	11.9	7.6	21.6	26.5	4.2	1.3	3.1	6.6	6.2	3.0	35.1	25.6	6.3	6.6	18.0	20.5

Table 5. *Land use (percent) by subwatershed.*

Subwatershed	Agriculture	Rangeland	Forest	Other
Island Park Caldera	0	7	90	3
Warm River	1	5	93	1
Robinson Creek	3	3	92	2
Henry's Lake Outlet	8	27	46	19
Upper Henry's Fork	8	5	83	4
Shotgun Valley	9	30	56	5
Fall River	34	8	55	3
Bechler River	0	12	83	5
Boone Creek	0	8	84	8
Conant Creek	42	7	49	2

streams were removed from the analysis, correlations between macroinvertebrate assemblages and habitat changed. Macroinvertebrate density was no longer correlated with percent fines, whereas the diversity metrics (taxa richness and EPT richness) became positively correlated with percent fines (Table 7). The spring-fed streams supported higher densities of macroinvertebrates than runoff-dominated streams, and their substrates were more embedded than those of runoff-dominated streams, which contributed substantially to the positive correlation between macroinvertebrate density and embeddedness (Fig. 1).

Canonical correlation analysis of the five macroinvertebrate assemblage metrics and the 10 physical habitat variables identified three significantly correlated ($P \leq 0.05$) sets of canonical variables that explained 53, 33, and 22 percent of the variation in the data (Table 8). Removal of the canonical macroinvertebrate variables corresponding to the third and second roots resulted in sets that showed no significant correlation. Density, EPT richness, and taxa richness were the main macroinvertebrate factors corresponding to the first canonical root, and gravel embeddedness, substrate size, maximum gradient, and

Table 6. *Pearson product-moment coefficients of correlation (r_{ij}) between macroinvertebrate assemblage metrics and physical habitat parameters (all sites included, n = 96). An asterisk indicates that the correlation is significant at $\alpha = 0.05$.*

	Substrate size	% fines	Gravel embeddedness	Large woody debris	Small woody debris	Macrophyte cover	Width	Shading	Maximum gradient	Width/ depth ratio
Density	-0.37*	0.38*	0.60*	0.11	-0.24*	0.40*	0.27*	-0.16	-0.45*	0.20*
Taxa richness	0.06	-0.08	0.30*	0.01	-0.08	0.20*	0.32*	-0.30*	-0.12	0.17
EPT richness	-0.05	-0.05	0.36*	0.21*	-0.14	0.20*	0.35*	-0.20	-0.27*	0.22*
% EPT	0.20*	-0.21*	0.10	0.16	0.07	-0.02	0.07	0.05	0.04	0.09
% dominant taxon	-0.14	0.27*	0.20*	-0.05	0.12	0.09	-0.15	0.16	-0.03	-0.08

Table 7. *Pearson product-moment coefficients of correlation (r_{ij}) between macroinvertebrate assemblage metrics and physical habitat parameters for runoff-dominated streams (n = 73). An asterisk indicates that the correlation is significant at $\alpha = 0.05$.*

	Substrate size	% fines	Gravel embeddedness	Large woody debris	Small woody debris	Macrophyte cover	Width	Shading	Maximum gradient	Width/ depth ratio
Density	-0.07	0.00	0.28*	0.09	-0.11	0.15	0.29*	0.01	-0.33*	0.27*
Taxa richness	0.17	-0.27*	0.19	0.00	0.02	0.09	0.42*	-0.27*	-0.07	0.19
EPT richness	0.12	-0.31*	0.12	0.24*	-0.04	0.00	0.37*	-0.10	-0.18	0.26*
% EPT	0.31*	-0.37*	0.01	0.20	0.15	-0.15	-0.05	0.10	0.09	0.00
% dominant taxon	0.00	0.16	0.12	-0.11	0.13	0.06	-0.20	0.21	0.05	-0.13

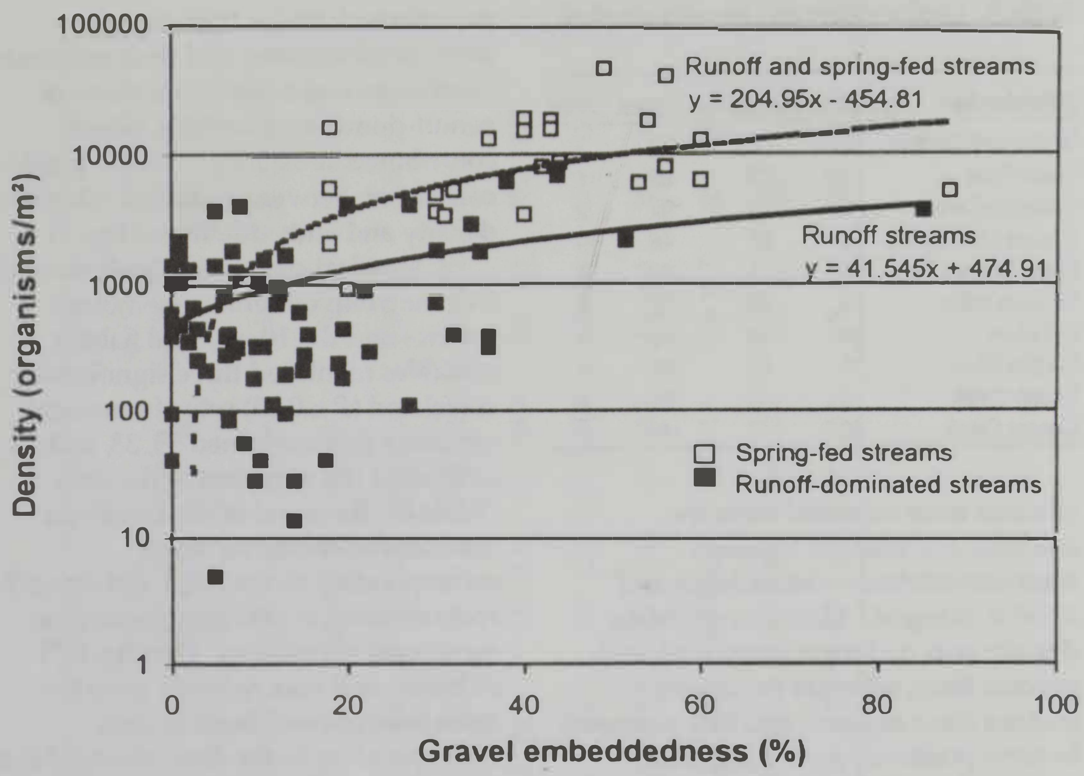

Figure 1. *Benthic macroinvertebrate density versus gravel embeddedness in spring-fed and runoff-dominated streams in the Henry's Fork watershed.*

Table 8. *Canonical correlations between macroinvertebrate assemblage metrics and physical habitat variables. Factor structure of the roots is given in Table 9.*

Number of canonical variable pairs removed	Canonical r^2	Chi-square statistic	Degrees of freedom	*P*
0	0.53	139.29	50	0.00
1	0.33	72.29	36	0.00
2	0.22	36.48	24	0.05
3	0.13	14.84	14	0.39
4	0.03	2.24	6	0.90

macrophyte coverage were the main habitat loading factors corresponding to this root (Table 9). The ordination along root 1 shows that invertebrate density, as well as the two diversity metrics (taxa richness and EPT richness), were negatively correlated with substrate size and maximum gradient and positively correlated with gravel embeddedness,

Table 9. *Factor loadings of transformations corresponding to the first three (largest three) canonical roots.*

Variable	Root 1	Root 2	Root 3
Macroinvertebrate assemblage metrics			
Density	0.97	0.11	0.20
Taxa richness	0.45	0.62	-0.62
EPT richness	0.59	0.75	0.05
% EPT	0.05	0.29	-0.13
% dominant taxon	0.19	-0.70	-0.23
Physical habitat variables			
Substrate size	-0.52	0.33	-0.44
% fines	0.58	-0.61	0.24
Gravel embeddedness	0.87	-0.09	-0.18
Large woody debris	0.07	0.28	0.29
Small woody debris	-0.30	-0.10	-0.28
Macrophyte cover	0.59	-0.08	-0.09
Width	0.36	0.47	-0.10
Shading	-0.25	-0.34	0.25
Maximum gradient	-0.59	-0.04	-0.33
Width/depth ratio	0.26	0.24	0.02

percent fines, and macrophyte coverage (Fig. 2). This pattern indicated that high densities and diversities of macroinvertebrates often occurred in

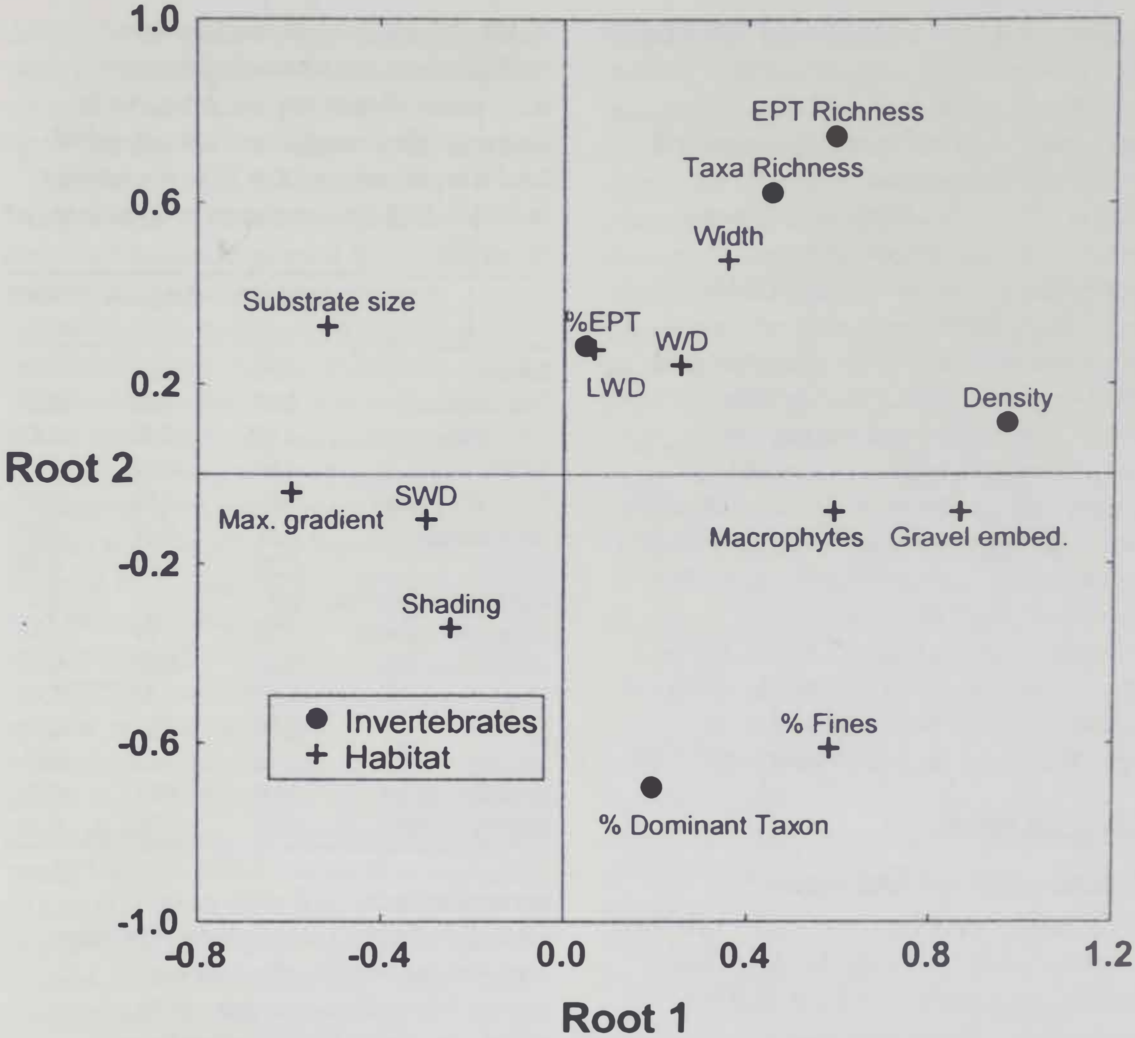

Figure 2. *Ordination of first and second canonical roots. Positive relationships are indicated by points that are near one another at the end of an axis. Negative relationships are indicated by points that are at opposite ends of an axis.*

low gradient streams that had abundant macrophyte growth and small, highly embedded substrates. Percent dominant taxon, EPT richness, and taxa richness were the main loading macroinvertebrate factors corresponding to the second canonical root, and percent fines and stream width were the main habitat loading factors corresponding to this second root (Table 9). The ordination along root 2 shows that the diversity metrics were negatively correlated with percent fines and positively correlated with stream width (Fig. 2). Additionally, percent dominant taxon was negatively correlated with the two diversity metrics and stream width, and positively correlated with percent fines along this root. The pattern along the second root indicated that streams with high diversity but with low percent dominant taxon were often wide with a low percentage of fine material in the substrate. Taxa richness was the main macroinvertebrate loading factor corresponding to the third canonical root. Habitat loadings were more evenly distributed in the third root than in the two previous roots; however, substrate size showed slightly higher loading in the third root than in the second (Table 9).

Pearson product-moment correlations between subwatershed mean macroinvertebrate assemblage metrics and land use showed that taxa richness and EPT richness were negatively correlated with the percentage of surrounding rangeland and agricultural land, respectively (Table 10). Mean percent EPT was positively correlated with the percentage of forested land (Table 10). Seemingly little correlation occurred between stream habitat variables and land use. The significant positive correlation between shading and percent rangeland was caused by autocorrelation; the two subwatersheds with the highest mean shading, Henry's Lake Outlet and Shotgun Valley, also contained the highest percent rangeland, even though many of the stream sample sites within these two subwatersheds were located in the forested portion of the subwatersheds.

Discussion

Relationships Between Macroinvertebrates and Habitat

Macroinvertebrate densities were highest in streams with small (high percentage of particles <0.4 cm in diameter), embedded substrates. In contrast, Rabeni and Minshall (1977) found that macroinvertebrate density was greatest at sites where substrate particles ranged from 2.5 to 3.5 cm in diameter. Erman and Erman (1984), in an experiment to test macroinvertebrate selection of substrate, also found that medium-sized substrate was selected over small substrates. Other studies, however, reported results similar to ours. In a study of sediment influence on macroinvertebrate assemblages, Lenat *et al.* (1981) found that densities increased in stable-sand areas and concluded that during low-flow conditions, small substrate can serve as adequate habitat. However, during high flow the small substrate becomes disturbed and less suitable for habitation.

Taxa richness and EPT richness

Table 10. *Pearson product-moment coefficients of correlation (r_{ij}) between macroinvertebrate and habitat variables (subwatershed means) and subwatershed land-use percentage (n = 10). An asterisk indicates that the correlation is significant at* $\alpha = 0.05$.

	Agriculture	Rangeland	Forest
Density	–0.49	–0.24	0.58
Taxa richness	0.05	–0.82*	0.55
EPT richness	–0.68*	0.28	0.41
% EPT	–0.50	–0.38	0.69*
% dominant taxon	0.26	–0.19	0.01
Substrate size	0.06	–0.01	–0.02
% fines	–0.23	–0.06	0.19
Gravel embeddedness	–0.34	–0.18	0.37
Large woody debris	0.01	–0.29	0.18
Small woody debris	0.32	–0.30	–0.10
Macrophyte cover	–0.29	–0.38	0.49
Width	–0.16	–0.37	0.40
Shading	0.26	0.65*	–0.61
Maximum gradient	0.29	0.01	–0.23
Width/depth ratio	–0.24	–0.20	0.36

generally increased with gravel embeddedness, macrophyte coverage, and stream width. Studies on macroinvertebrate responses to substrate composition often have indicated that diversity is correlated with substrate size and the amount of fine material (sand and silt). Richards and Host (1994), in a study of streams on the north shore of Lake Superior, found that taxa richness had a negative relationship with embeddedness and the amount of fine substrate. Other studies also have reported a decrease in diversity as substrate size decreased (Pennak and Van Gerpen 1947, Allan 1975, McClelland and Brunsen 1980). In contrast to these studies, our results indicated an increase in diversity (taxa and EPT richness) as embeddedness increased. This relationship was probably caused by the influence of spring-fed streams, which had embedded substrates but also had high taxa richness and EPT richness metric values. When spring-fed streams were removed from the correlation analysis, diversity metrics were not correlated with embeddedness but were negatively correlated with percent fines, in agreement with the studies cited above.

Richards *et al.* (1993), in a comparison of streams from several different basins, reported that the lowest percent EPT and highest percent dominant-taxon sites were found in the basin with the smallest substrate. Most studies have reported that dominant taxon was positively correlated with embeddedness and fines and negatively correlated with substrate size. Our results were similar to these in that percent EPT decreased as fines increased and percent dominant taxon increased with percent fines.

The patterns discussed above appear related, at least in part, to the hydrologic characteristics of the streams. Lenat *et al.* (1981) reported that in areas of small substrate, invertebrate densities could be high if the substrate was stable. In our study, subwatersheds with the highest macroinvertebrate densities (Island Park Caldera and Warm River) contain streams that are spring-fed and have relatively constant flows, which may allow for stability in the small substrates. Macroinvertebrate density increased as substrate size decreased and as percent fines and gravel embeddedness increased, indicating that these metrics were highest in substrates composed of small particles, i.e., those characteristic of the spring-fed streams. In fact, spring-fed streams did have both higher macroinvertebrate densities and a greater degree of embeddedness than runoff-dominated streams (Fig. 1). In our study, taxa richness and EPT richness, which were positively correlated with gravel embeddedness, also were highest in spring-fed streams, which are primarily found in the Island Park Caldera, Warm River, and part of the Robinson Creek subwatersheds (Table 3). The relationships between macro-invertebrate density and diversity and macrophyte coverage also are probably related to stream hydrology; macrophytes were common in spring-fed streams but rare in runoff-dominated streams. Macrophytes generally are unable to establish in streams with high variability in discharge, but in the more constant-flow regime of the spring-fed streams, they provide habitat for macroinvertebrates (Van Kirk and Martin this issue). Macrophytes thereby contributed to dense and diverse assemblages found in most of the spring-fed streams in this study.

Although macroinvertebrate diversity metrics increased with embeddedness and percent fines, the composition metric, percent EPT, was negatively correlated with percent fines and, unlike EPT richness, was not higher in spring-fed streams than in runoff-dominated streams. This may be related to the higher density of organisms found in spring-fed streams than in runoff-dominated streams. More organisms were collected from spring-fed streams than from runoff-dominated streams, increasing the chances of collecting rare organisms and arriving at higher EPT richness metric values in the spring-fed streams. Although more EPT taxa were found in spring-fed streams, abundance of these organisms in relation to abundance of other organisms was not higher therein.

Removal of the spring-fed streams from the analysis rendered relationships that apparently were dependent on spring creeks less prominent (Table 7). These relationships included correlations between the various macroinvertebrate density and diversity metrics and gravel embeddedness (Fig. 1) and macrophyte coverage. However, macroinvertebrate density remained correlated (although more weakly) with maximum gradient, width, and gravel embeddedness, indicating that macroinvertebrate density probably increases as runoff-dominated streams become larger, lower in current velocity, and more fertile. EPT richness and percent EPT increased both as percent fines decreased and as stream width increased when spring-fed streams were removed from the analysis, indicating that wider runoff-dominated treams, with larger and likely more stable substrate, had the most diverse and abundant EPT assemblages. This pattern also was evident in the second canonical correlation in which streams with high EPT richness and high taxa richness but low dominant taxon metrics often were wide with low percentages of fines in the substrate. Fines may be less stable in the runoff-dominated streams than in pring-fed streams and less able to support sensitive EPT taxa.

Relationships Between Macro-invertebrates and Land Use

Taxa richness and EPT richness were negatively correlated with the percentages of rangeland and agricultural land in the ubwatersheds, and percent EPT was positively correlated with the amount of forest land (Table 10). Cattle grazing is common in the Henry's Fork watershed, especially in the Shotgun Valley and Henry's Lake Outlet subwatersheds. Cattle grazing can cause streambank erosion, which results in increased rates of sediment delivery and deposition (Kauffman *et al.* 1983a). Cattle also can damage riparian vegetation, which can in turn affect stream communities (Kaufman *et al.* 1983b). Riparian zones add organic matter and woody debris to the stream, reduce runoff, and protect streambanks. Elimination of riparian vegetation can change water quality and overall stream dynamics (Gregory 1980). Cropland, such as the seed-potato fields found in the Henry's Fork watershed, can contribute sediment, nutrients, and pesticides to streams via overland flow. These agricultural inputs affect physical habitat and water quality, both of which, in turn, affect benthic macroinvertebrate assemblages (Wang *et al.* 1997). These patterns indicated that, in the Henry's Fork watershed, as agriculture and grazing increase in a subwatershed, macroinvertebrate diversity, as measured by the taxa richness and EPT richness metrics, decreases.

Relationships Between Stream Habitat and Land Use

Although macroinvertebrate assemblage metrics and land use appear to be related, stream habitat variables were unrelated to land use (Table 10). The influence of land use on the macroinvertebrate assemblages probably occurred through changes in water quality instead of physical habitat alteration or through some aspect of stream habitat that we did not measure. The Shotgun Valley and Henry's Lake Outlet subwatersheds, which had high percentages of rangeland and low taxa richness values, receive inputs of phosphorus from sedimentary rocks located in the Centennial and Henry's Lake mountains (Montgomery Watson 1996, Anderson 1996, Roessler 1996). This nutrient enrichment, in conjunction with the high percentage of rangeland in the e subwatersheds, may reduce diversity and the abundance of sensitive EPT taxa. Pesticides or other chemicals used in agriculture also may affect macroinvertebrate assemblages.

Many of the streams in the Henry's Fork watershed, especially those located in the Island Park Caldera, Warm River, and Robinson Creek subwatersheds are fed by groundwater springs (see Benjamin this issue). Because of their low gradients and low variability in discharge, spring-fed streams are less able to transport bedload compared to runoff-dominated streams (but see Simon this issue). Furthermore, spring-fed streams in our study area have small surface drainage networks relative to their discharge, thus limiting the opportunity for delivery of coarse inorganic material from the watershed into the stream channel. Although most of the spring-fed streams flow through forested land, substrates in these streams tend to be small and embedded, as is typical of streams flowing through agricultural or other nonforested land where surface runoff events can deliver large inputs of fine sediment. In contrast to the forested spring-fed streams in our study, forested streams are usually higher in gradient and therefore have larger, less embedded substrates than streams flowing across nonforested landscapes (Vannote *et al.* 1980). Because sediment inputs can be associated with particular types of land use, correlations between stream habitat and land use often are observed. In our case, however, the small, embedded substrates of the Island Park Caldera and Warm River subwatershed streams most likely were associated with inherent geologic and hydrologic characteristics rather than with land use. The abundance of these types of streams in our study may have prevented detection of relationships between land use and physical habitat across the study area.

Our inability to explain variability in physical habitat characteristics with variability in land use may also be a result of the coarse-scale GIS analysis that was used to compute the percentages of land use in the subwatersheds. A finer-scale land-use coverage, e.g., 1:24,000, may be necessary for an analysis that provides a more accurate and detailed description of land use than the 1:250,000 scale land-use coverage used in this study. Relationships between land use and physical habitat also may have been difficult to discern because of the small data set that was used for this part of the study. Ten data points, i.e., land-use estimates for the 10 subwatersheds, were used to assess relationships with averaged habitat and biological data for the sites within these subwatersheds. Calculation of land use for the drainage area of each individual sample site, rather than average land use around all sites in a subwatershed, would better estimate the influence of land use on habitat at a particular point along the stream. The influence of land use on stream habitat at a subwatershed scale also could be assessed more accurately if the stream sampling procedure was stratified by land-use type, with allocation of sample sites within a particular land-use type proportional to the percentage of that type within the subwatershed.

Potential Sources of Error

Collection methods, taxonomic procedures, subsampling criteria, and selection of metrics used to describe macroinvertebrate assemblages are potential sources of error that may have limited the reliability of the biological data used here. The use of Hess samplers in only one type of habitat (riffles) may have resulted in samples that were not necessarily representative of the streams from which they were taken. Benthic macroinvertebrates colonize other habitats in addition to riffles such as undercut banks, root mats, woody debris, and aquatic vegetation. Failure to sample these habitats (especially in streams where the optimal habitat did not occur in riffles) may result in calculation of metrics that are not representative of the macroinvertebrate assemblage. Kick-net samples from banks and snags may have compensated for some of these limitations; however, percent EPT and percent dominant taxon were computed only from individuals collected in the Hess samples. Metrics also may have been affected by different levels of taxonomy we used for different orders of macroinvertebrates. Identifying mayflies and stoneflies to genus while identifying caddisflies and other taxa only to family may have skewed the diversity metrics.

Visual assessments by intern of habitat parameters, including gravel embeddedness, macrophyte coverage, and shading, are potential sources of error in this study. Other habitat and morphological characteristics not investigated here, such as bankfull depth, riparian area quality, stream bank stability, pool variability, and channel sinuosity can influence macroinvertebrate assemblages, and can be influenced, in turn, by land use. These characteristics might have contributed to our understanding of the relationships we investigated had we assessed them.

Conclusions

The composition and structure of benthic macroinvertebrate assemblages in the Henry's Fork watershed appear closely associated with stream habitat characteristics. In particular, several macroinvertebrate assemblage metrics were correlated with gravel embeddedness, percent fines, macrophyte coverage, and stream width. Macroinvertebrate density and diversity (EPT richness and taxa richness) metrics were highest in areas with fine, yet apparently stable, highly embedded ubstrates that were often associated with spring-fed streams. Percent EPT was negatively correlated with percent fines and po itively correlated with substrate size and was not higher in spring-fed streams than in runoff-dominated streams. When the spring-fed streams were removed from the analysis, EPT richness, taxa richness, and EPT were negatively correlated with percent fines, indicating that fine substrate may have been suitable for benthic colonization in spring-fed streams but not in runoff streams, possibly because of differences in substrate stability associated with flow variability. Taxa richness and EPT richness were negatively correlated with rangeland and agriculture, respectively, and percent EPT was positively correlated with forested land. However, none of the physical habitat variables were correlated with land use, indicating that land use did not influence macroinvertebrate assemblage composition through effects on the physical habitat characteristics we measured. Instead, effects of land use on macroinvertebrates may have occurred through effects of water quality, in the form of nutrient enrichment or chemical inputs from agricultural or pasture land or through physical habitat characteristics not measured in this study.

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