Freshwater Biology (1995) **33,** 439–454

The ordination of benthic invertebrate communities in the South Platte River Basin in relation to environmental factors

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SUMMARY

1. Spatial patterns of benthic-invertebrate communities were examined in the 62 900 km^2 South Platte River Basin in Colorado, Nebraska and Wyoming, U.S.A., to determine major environmental factors associated with invertebrate distribution. Stable substrates were sampled semiquantitatively for invertebrates from 27 July to 7 August 1992, at twenty-one sites. Data on physical and chemical variables were collected concurrently at each site.
2. Four site groups were identified using detrended correspondence analysis (DCA), one in the mountains and three in the plains (braided channels, tributaries near the confluence with the main stem, and sites affected by effluent from wastewater-treatment plants). DCA axis 1 separated sites into the two major ecoregions (Southern Rocky Mountains and Western High Plains), and regression of DCA axis 1 with environmental variables indicated significant relationships primarily with slope, water temperature, specific conductance, and concentrations of organic nitrogen + ammonia and total phosphorus in surface water. Regression of DCA axis 2 with environmental variables indicated significant relationships with channel width and concentrations of nitrate + nitrite in surface water.
3. Invertebrate community composition and structure varied between ecoregions with greater number of taxa and number of insect families in mountain streams than in plains streams. Within an ecoregion, land use affected the invertebrate community.
4. Factors affecting invertebrate community distribution in stream ecosystems are scale dependent.

Introduction

This study was conducted as a part of the U.S. Geological Survey's National Water Quality Assessment (NAWQA) Program which uses an integrated approach (physical, chemical and biological) to assess water quality on a basin-wide scale (Gurtz, 1994). A goal of the South Platte River NAWQA study is to provide a basin-wide assessment of the distribution of stream communities and examine how biological communities can be used to indicate conditions of water quality in the basin.

A first step in understanding how invertebrate communities are related to water quality is to identify the primary chemical and physical variables affecting invertebrate communities within a basin. Stream communities are affected by many factors such as water chemistry (Meyer *et al.*, 1988) and the stream's physical characteristics (Resh & Rosenberg, 1984). Natural variation in invertebrate communities also occurs on many spatial scales (microhabitat to regional; Naiman *et al.*, 1987; Minshall, 1988). Physical factors that affect stream macroinvertebrate communities include substrate (Minshall, 1984; Richards, Host & Arthur, 1993), flow regime (Poff & Ward, 1989), geomorphology (Huryn & Wallace 1987; Statzner, Gore, & Resh, 1988) and temperature (Vannote & Sweeney, 1980; Ward & Stanford, 1982), particularly in streams extending along altitudinal gradients (Ward, 1986). Other factors affecting invertebrate communities are land use (Quinn & Hickey, 1990) and the characteristics of the riparian zone (Gregory *et al.*, 1991).

Altitudinal changes in invertebrate communities along the Saint Vrain River, a tributary of the South Platte River, were described by Ward (1986) and demonstrated natural variability in invertebrate communities primarily in mountain areas, although the study also included a plains site. In contrast, data were collected on a basin-wide scale during the present study to determine how invertebrate communities vary spatially in mountains and plains streams affected by natural and human factors. The objectives of this study were to describe the spatial distribution of invertebrate communities within the South Platte River Basin and to relate this distribution to physical and chemical factors within the basin.

Materials and methods

Description of study area

The South Platte River Basin drains a 62 900-km^2 area including parts of Colorado, Nebraska and Wyoming, U.S.A. (Fig. 1). A detailed description of the basin environmental setting is given in Dennehy *et al.* (1993). There are two major physiographical provinces (Lobeck, 1922), the Southern Rockies (mountain region occupying 25% of basin area) and the Great Plains, which corresponds to the two major ecoregions, Southern Rockies and Western High Plains (Omernik, 1987). Altitude ranges from 850 to 4370 m, which affects climatic, vegetational and physical settings of the streams in the basin (Dennehy *et al.*, 1993). Selected physical characteristics and land-use classifications of sites sampled are presented in Table 1.

Most tributaries originate in the mountains and are characterized as cold-water streams receiving 50–100 cm of annual precipitation. Stream slopes are steep and narrow channels are cut into resistant crystalline bedrock forming riffle/pool habitats with boulder/cobble substrates. Streamflow is perennial and affected by snowmelt runoff in the late spring/summer. From the mountains to the plains, streams cross a transition zone of easily eroded sedimentary bedrock.

Streams in the plains are characterized as warm-water, low-gradient streams that receive less than 50 cm of annual precipitation. The streams flow through easily eroded and transported alluvium, forming mostly run habitats with sand/gravel substrates. Channels are shallow and occasionally braided. Tributaries originating in the plains are intermittent with storm events affecting the streamflow.

Water management in the South Platte River Basin has considerably altered the natural hydrology. The quantity of water has increased due to interbasin transfers from the Colorado, Arkansas and North Platte River Basins. Flow within the basin has been modified in space and time through a complex network of ditches and reservoirs primarily for municipal water supplies and agricultural irrigation (Dennehy *et al.*, 1993). The South Platte River in the eastern part of the basin is now a perennial stream, whereas historically (prior to the 1860s) streamflow was intermittent (Eschner, Hadley & Crowley, 1983).

Land-use/land-cover categories for sampling sites were defined by the Anderson classification system (Anderson *et al.*, 1976). Sites in the mountain and transition zones were dominated by forest, built-up (low-density housing and population), and rangeland classes, with one site affected by mining (Clear Creek at Golden, Table 1). Once streams enter the plains region they flow through urban (high-density housing and population) and agricultural land-use areas, or a mixture of both. The mixed agriculture/urban classification was defined as sites located in agricultural areas that were affected by contaminants from upstream urban areas (not an Anderson classification).

Sampling regime

Twenty-one sites were selected for sampling by stratifying the basin streams by physiographical province/ecoregion, geology, land use/land cover and spatial coverage of the basin (Fig. 1, Table 1). Invertebrate samples were collected from 27 July to 7 August 1992 at sites ranging in altitude from 850 to 3132 m (Table 1). By sampling only once during the summer (low flow), the total number of taxa collected at a site was lower than the total number of taxa reported by Ward (1986) because of the absence of winter species or early emergence. It was assumed that differences in the patterns of invertebrate communities reflect actual differences among sites and not seasonal trends.

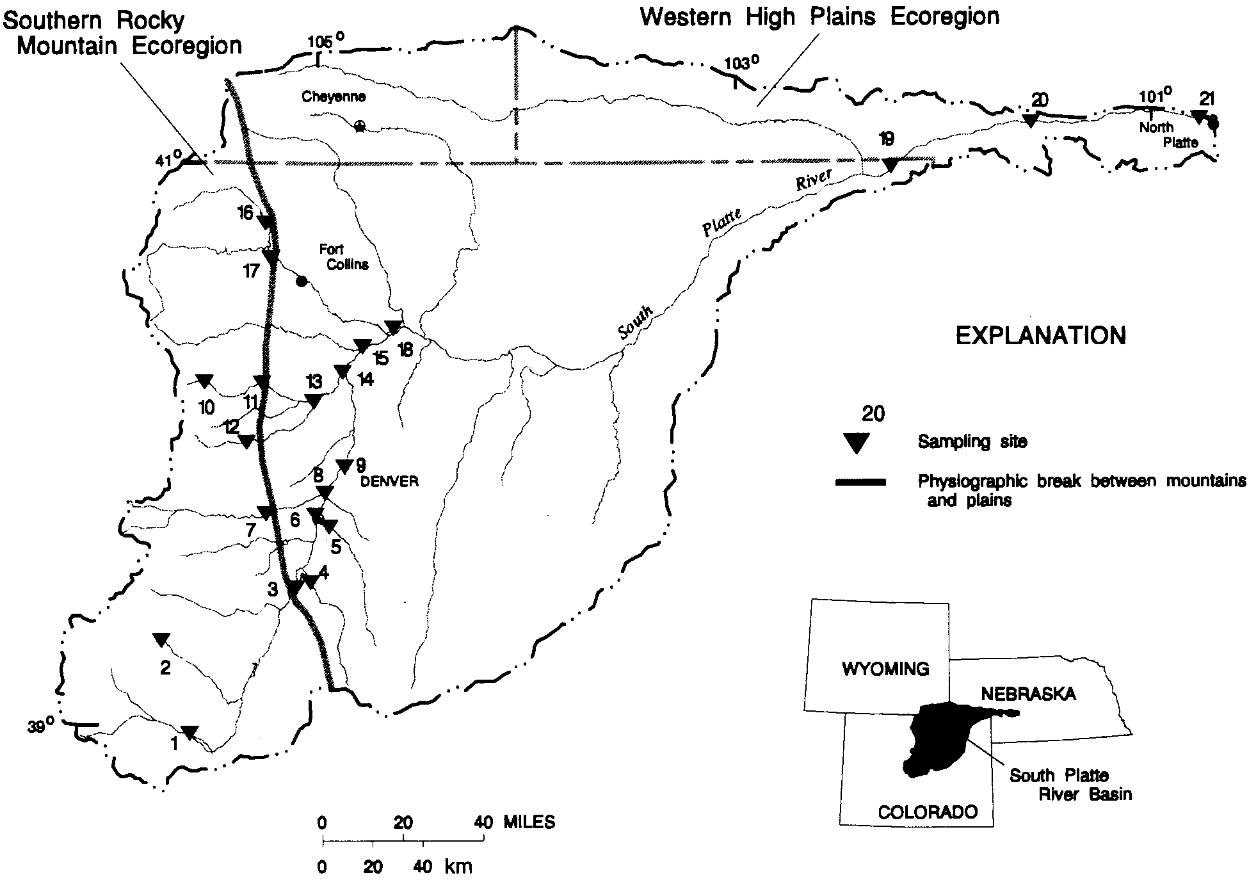

Fig. 1 Map of the South Platte River Basin showing the location of sampling sites. Site numbers and names are listed in Table 1.

Invertebrate sampling

Quantitative samples of invertebrates were collected from the habitat (i.e. sites of stable substrates such as rocks, gravel, gravel with attached macrophytes, or wood) within a stream reach assumed to have the most diverse fauna for that reach. Stable substrates in sandy channel streams typically are sites of most biological productivity (Benke *et al.*, 1984), and as such, these sites are suggested to be the best habitat to sample for among-site comparisons (Richards *et al.*, 1993). Two sampling methods were used to collect invertebrates. A composite of three Surber samples (total area = 0.2787 m^{-2}, 210-μm mesh) were taken in riffle areas. At two sites where run habitats dominated (SPRO and SPNP, Table 1), snags (submerged woody debris) were cut and placed into a 210-μm-mesh net and invertebrates were removed. Samples were preserved in 70% ethanol, identified to lowest possible taxon, and counted. Surface area of snags was estimated by wrapping a snag with aluminium foil and measuring the area of the foil.

Environmental variables

Discharge (Buchanan & Somers, 1969), stream velocity and channel width and depth were measured, the dominant and subdominant bed substrate types (Meador *et al.*, 1993) were recorded, and a qualitative assessment of algal abundance (abundant, common, rare, absent) was made at one or two transects near the invertebrate collection site. Samples of surface and hyporheic (8–64 cm below the stream channel) water were collected and analysed for ammonia-N, nitrate + nitrite-N, nitrite-N, organic nitrogen + ammonia, and total phosphorus (McMahon *et al.*, 1994). Hyporheic water samples were collected to

Table 1 Selected physical characteristics, land-use classification, site groupings defined by detrended correspondence analyses (DCA), macrophyte and algal abundance and invertebrate density and number of taxa at sites sampled in the South Platte River Basin

Site no. (Fig. 1)	Site name	Site abbr.	Land use*	DCA category†	Drainage area (km^2)	Altitude (m)	Algal abundance	Invertebrate density (no. m^{-2})	No. of invertebrate taxa
1	South Platte River above eleven-mile Canyon Reservoir near Hartsel, CO	SP11	R	P/bc	2279	2625	rare	3690	30
2	Tarryall Creek below Rock Creek near Jefferson, CO	TARR	R	M	596	2749	rare	6640	25
3	South Platte River at Waterton Canyon, CO	SPWA	F	M	6788	1672	common	10 600	25
4	Plum Creek near Sedalia, CO	PLUM	B	P/bc	816	1682	common	14 400	26
5	Cherry Creek at Glendale, CO	CHGL	U	P/t	1046	1622	rare	5160	11
6	Cherry Creek at Denver, CO	CHDE	U	P/t	1059	1577	common	802	14
7	Clear Creek at Golden, CO	CLGO	B/M	M	1036	1736	rare	1980	10
8	Clear Creek at mouth near Derby, CO	CLMO	U	P/t	1062	1585	common	2450	15
9	South Platte River at Henderson, CO	SPHE	A/U	P/bps	12 207	1525	abundant	3290	12
10	North Saint Vrain Creek near Allens Park, CO	NSVR	F	M	84	3132	common	16 600	36
11	Saint Vrain Creek at Lyons, CO	SVLY	B	M	549	1613	absent	18 100	32
12	Boulder Creek near Orodell, CO	BOOR	F	M	264	1776	common	4430	27
13	Boulder Creek at mouth near Longmont, CO	BOMO	A/U	P/bps	1137	1481	abundant	4950	14
14	Saint Vrain Creek at the mouth near Platteville, CO	SVMO	A/U	P/t	2528	1445	rare	3300	13
15	Big Thompson River at mouth near LaSalle, CO	BTMO	A/U	P/t	2145	1426	absent	100	12
16	North Fork Cache la Poudre River at Livermore, CO	NFCA	R	M	1396	1742	common	16 500	28
17	Cache la Poudre River at mouth of canyon near Fort Collins, CO	CAMC	F	M	2735	1591	rare	3300	19
18	Cache la Poudre River near Greeley, CO	CAGR	A/U	P/bps	4861	1405	abundant	2650	6
19	South Platte River at Julesburg, CO	SPJU	A	P/bc	60 070	1051	common	3700	14
20	South Platte River at Roscoe, NB	SPRO	A	P/bc	61 901	960	rare	20 300	13
21	South Platte River at North Platte, NB	SPNP	A	P/bc	62 937	850	rare	15 200	17

* R, rangeland; F, forest; B, built-up; U, urban; B/M, built-up with mining influence; A/U, agriculture and urban; A, agriculture. Land-use categories from Anderson *et al.*, 1976.

† M, mountain; P/bc, plains/braided channel; P/t , plains/tributary; P/dps, plains/downstream from point source.

determine whether groundwater was a source of nutrients to surface water (McMahon *et al.*, 1994). Analyses of nutrient concentrations followed methods described in Fishman (1993) and Patton & Truitt (1992). Dissolved oxygen and temperature, pH, and specific conductance were measured *in situ* in surface and hyporheic waters.

Values of altitude, sinuosity, slope and stream order were derived from 1:24 000 scale topographical maps (Meador *et al.*, 1993).

Data analyses

Ordination of sites by taxa was performed using detrended correspondence analyses (DCA) on natural log-transformed abundance data using the FORTRAN program DECORANA (Hill, 1979). Analyses included the sixty-six taxa that were collected at more than one site and composed greater than 0.5% of the total abundance of organisms (taxa with asterisks in Table 2). These criteria for the inclusion of taxa in the analyses were used to decrease the effect of rare species. Ordination by DCA arranges sites with similar taxonomic composition to cluster more closely together and produces site scores that can be related to environmental variables. From the DCA ordination plot, four site groups were identified: mountains, plains/braided channel, plains/tributary, and plains/downstream from point source. Invertebrate taxa, functional feeding groups, and environmental variables were further defined based on these four site groups.

Univariate analyses of environmental variables, comparison of linear regression analyses of DCA axis 1 and 2 to individual environmental variables, and analyses of variance (ANOVA) among site groups were made using SAS statistical programs (SAS, 1990). Natural log or square-root transformations were performed on environmental variables to achieve approximate normal distribution of the data.

A Shannon diversity index was calculated using the dominant taxa (excluding rare taxa) for each site (Shannon & Weaver, 1963). Phi values were calculated for the dominant and subdominant substrate sizes and the mean substrate size (Folk, 1980). All invertebrate taxa including rare taxa were assigned to functional feeding groups using Merritt & Cummins (1984) for insects and Pennak (1978) for non-insects.

Results

A total of 104 invertebrate taxa were collected from all twenty-one sites in the stream survey (Table 2). Invertebrate density and number of taxa at a site ranged from 100 to 20 300 organisms m^{-2} and six to thirty-six taxa/site (Table 1). Invertebrate density in streams of the Southern Rockies ecoregion (mountains) ranged from 1980 to 18 100 m^{-2} and streams of the Western High Plains ecoregion (plains) ranged from 100 to 20 300 m^{-2}. The mean number of taxa at a site was greater in the mountains (mean = 25; range = 10–36, $n = 9$) compared with the plains (mean = 14; range = 6–26, $n = 12$)(ANOVA, $P < 0.005$, Table 1).

The relative magnitude of eigenvalues for each DCA axis is an expression of the relative importance of the axis. DCA axis 1 (eigenvalue = 0.44) and axis 2 (eigenvalue = 0.28) accounted for about 72% of the variance in the data set, whereas, DCA axis 3 (eigenvalue = 0.16) and DCA axis 4 (eigenvalue = 0.10) together accounted for < 30% of the variance and were not strongly correlated to any measured environmental variables. In contrast, regression of DCA axis 1 and 2 scores with environmental variables indicates significant relationship with seven physical and seven surface- and hyporheic- water chemistry variables for DCA axis 1 and two physical and four surface-water chemistry variables for DCA axis 2 (Table 3). Thus, DCA axis 1 separated sites in the mountains (Southern Rocky Mountain ecoregion) from sites in the plains (Western High Plains ecoregion) based primarily on stream slope, water temperature, specific conductance, and surface water organic nitrogen + ammonia and total phosphorus concentrations; each variable accounted for 48% or more of the variance in DCA axis 1 scores ($P < 0.05$, $r^2 \geqslant 0.48$; Table 3). DCA axis 2 separated sites in the plains based on surface water nitrate + nitrite concentrations and channel width, which accounted for 36 and 32%, respectively, of the variance in DCA axis 2 scores ($P < 0.05$, $r^2 > 0.30$, Table 3). Four site groups were then identified from plotting DCA axis 1 and 2 scores: mountains, plains tributaries near their confluence with the South Platte River (plains/tributary), plains streams with braided channels (plains/braided channel), and plains sites affected by wastewater-treatment-plant effluent (plains/downstream from point source) (Fig. 2).

The South Platte River above eleven-mile Canyon

Table 2 Presence (+) and absence (−) of all species by site groupings as defined by detrended correspondence analyses (DCA). The high altitude site SP11 was not included in the braided plains grouping. *Taxa used in DCA analyses. Taxa without asterisks are considered to be rare

			Plains		
Taxonomic group		Mountain	Braided channel	Tributary	Down-stream from point source
Platyhelminthes					
*Turbellaria		−	−	−	+
Annelida					
*Oligochaeta		−	+	+	+
Hirundinea	*Eropbdella punctata punctata* (Leidy)	−	+	−	+
	Helobdella stagnalis (Linnaes)	−	−	−	+
	Moorebdella fervida (Verrill)	−	−	−	+
Mollusca					
Gastropoda					
Physidae	**Physella* sp.	−	+	−	+
Arthrodpoda					
Arachnida					
Acari	*Hydracarina	+	−	+	−
Euphausiacea					
Isopoda	*Licereus* sp.	−	+	−	−
Amphipoda	*Gammarus* sp.	−	+	−	−
	**Hyallela azteca* (Saussure)	−	+	−	−
Insecta					
Ephemeroptera					
Baetidae	**Baetis bicaudatus* (Dodds)	+	+	+	−
	**Baetis tricaudatus* (Dodds)	+	+	+	+
	**Acentrella insignificans* (McDunnough)	+	+	−	−
Heptageniidae	*Cinygmula* sp.	+	+	−	−
	Epeorus albertae (McDunnough)	+	−	−	−
	Epeorus deceptivus (McDunnough)	+	−	−	−
	Epeorus longimanus (Eaton)	+	−	−	−
	**Heptagenia* sp.	−	+	−	−
	**Rhithrogena hageni*	+	−	−	−
Leptophlebiidae	**Choroterpes* sp.	+	−	−	−
	Paraleptophlebia sp.	+	−	−	−
Ephemerellidae	*Drunella coloradensis* (Dodds)	+	−	−	−
	Drunella doddsi (Needham)	+	−	−	−
	**Ephemerella inermis* (Eaton)	+	−	−	−
Tricorythidae	**Tricorythodes minutus* (Traver)	+	+	+	+
Caenidae	**Caenis* sp.	−	+	−	−
Odonata					
Calopterygidae	*Hataerina* sp.	−	+	−	−
Protoneuridae	*Argia* sp	−	−	−	+
	Enallagma sp.	−	−	−	+
Coenagrionidae		−	−	−	+
Gomphidae		−	+	−	+
Plecoptera					
Pteronarcyidae	**Pteronarcella badia* (Hagen)	+	−	−	−
	Pterinarcys californica (Newport)	+	−	−	−
Nemouridae	*Amphinemura banski* (Baumann and Gaufin)	+	−	−	−
	Zapada cinctipes (Banks)	+	−	−	−
Capniidae	*Eucapnopsis* sp	+	−	−	−
Perlidae	**Hesperoperla pacifica* (Banks)	+	−	−	−
Perlodidae	*Cultus* sp.	+	−	−	−
	Isogenoides sp.	+	−	−	−
	Skwala sp.	+	−	−	−

Table 2 *Continued*

			Plains		
Taxonomic group		Mountain	Braided channel	Tributary	Down-stream from point source
*Chloroperlidae		+	+	+	−
Trichoptera					
Philopotamidae	*Chimarra utahinsis* (Ross)	+	−	−	−
Psychomyiidae	*Psychomyia flavida* (Hagen)	+	−	−	−
Hydropsychidae	**Arctopsyche grandis* (Banks)	+	−	−	−
	**Hydropsyche* sp.	+	+	+	−
	**Cheumatopsyche* sp.	−	+	−	−
Rhyacophilidae	*Rhyacophila brunnea* (Banks)	+	−	−	−
	Rhyacophila vaccua (Milne)	+	−	−	−
Glossosomatidae	**Anagapetus* sp.	+	−	−	−
	**Glossosoma* sp.	+	−	−	−
Hydroptilidae	**Agraylea* sp.	−	−	+	−
	**Hydroptila* sp.	+	+	+	−
Brachycentridae	**Brachycentrus americanus* (Banks)	+	−	−	−
	**Brachycentrus occidentalis* (Banks)	+	−	−	−
Lepidostomatidae	**Lepidostoma* sp.	+	−	−	−
Helicopsychidae	*Helicopsyche borealis* (Hagen)	+	−	−	−
Leptoceridae	*Nectopsyche* sp.	+	−	−	−
	**Oecetis* sp.	+	+	−	−
Lepidoptera		+	−	−	−
Coleoptera					
Elmidae	**Heterlimnius* sp.	+	+	−	−
	**Optioservus* sp.	+	−	−	−
	**Zaitzevia parvula* (Horn)	+	−	−	−
Chrysomelidae	*Donacia* sp.	−	−	−	+
Diptera					
Deuterophlebiidae	*Deuterophlebia coloradensis* (Pennak)	+	−	−	−
Tipulidae	**Antocha* sp.	+	−	−	−
	Dicranota sp.	+	−	−	−
	Hexatoma sp.	+	−	−	−
	Tipula sp.	+	−	−	−
Psychodidae	**Psychoda* sp.	−	−	+	−
Culicidae	**Aedes* sp.	−	−	+	−
Simuliidae	**Simulium* sp.	+	+	+	+
Ceratopogonidae	**Bezzia* sp.	+	+	−	−
Chironomidae					
Tanypodinae					
Pentaneruini	**Arctopelopia* sp.	+	+	+	−
	**Thienemannimyia* sp.	+	−	−	−
	**Zavrelimyia* sp.	+	−	−	−
Diamesinae					
Diamesini	**Diamesa* sp.	+	−	−	−
	**Pagastia* sp.	+	−	−	−
Prodiamesinae	**Odontomesa* sp.	+	−	+	−
Orthocladiinae					
Corynoneurini	**Corynoneura* sp.	+	−	−	−
	**Thienemanniealla* sp.	+	+	+	−
Orthocladiini	**Cricotopus* (Isoclasius) sp.	−	−	−	−
	**Cricotopus sylvestris* (Fabricuis)	+	−	+	+
	**Cricotopus trifascia* (Edwards)	+	+	+	+
	**Eukefferiella* sp.	+	+	+	−
	**Nanocladius* sp.	−	+	+	+
	**Orthocladius*	+	+	+	+
	**Rheocricotpus* sp.	+	−	+	−
	**Synorthocladius* sp.	+	−	−	−

Table 2 *Continued*

			Plains		
Taxonomic group		Mountain	Braided channel	Tributary	Down-stream from point source
Chironominae					
Chironomini	**Chironomus* sp	–	–	–	+
	**Cryptochironomus* sp.	+	–	+	–
	**Dicrotendipes* sp.	–	–	+	+
	**Microtendipes* sp.	+	–	–	–
	**Parachironomus* sp.	–	–	+	–
	**Polypedilum* sp.	+	+	+	+
Tanytarsini	**Cladotanytarsus* sp	+	+	+	–
	**Micropsectra* sp.	–	–	+	–
	**Paratanytarsus* sp.	–	+	–	–
	**Sublettea* sp.	+	–	–	–
	**Tanytarsus* sp.	+	+	–	+
Athericidae	*Atherix pachypus* (Bigot)	+	–	–	–
Empididae	**Chelifera* sp.	+	–	–	–
	**Hemerodromia* sp.	+	+	–	–
Ephydridae		–	+	–	–
*Muscidae		–	–	+	–
Total number of taxa =		74	35	28	22

Reservoir near Hartsel (SP11, Fig. 2) was the only high-altitude (> 1590 m) site that grouped with the plains/braided channel sites. This site had a lower stream slope (2.1 m km^{-1}) and wider channel (channel width = 33.2 m) compared with other mountain sites (Table 4). Also, *Physella* sp. and *Gammarus* sp., which are characteristic of plains streams, were collected at this site (Table 2). This site was not included in the physical, nutrient, and invertebrate community-data analyses (except Shannon diversity) described below because it was not located in the Western High Plains ecoregion.

Stream slope and substrate size decrease, whereas water temperature, specific conductance (Table 4), surface-water-nutrient concentrations (nitrate + nitrite, organic + ammonia, nitrite, ammonia and total phosphorus; Fig. 3) and hyporheic water nitrate concentrations increase as streams flow from the mountains to the plains. Within the plains, the plains/braided channel sites had wide braided channels (Table 4) and lower concentrations of surface water nitrate + nitrite and total phosphorus (Fig. 3) compared with plains/tributary and plains/downstream from point-source sites. Specific conductance and surface-water-nutrient concentrations (Table 4, Fig. 3) were similar for plains/tributary and plains/downstream from point-source sites. Plains/downstream from point-source sites had the highest mean nitrate + nitrite concentrations in hyporheic water compared with all sites (Fig. 3), and algae also were abundant at these sites (Table 1).

Comparison of Shannon diversity indices at sites plotted across the DCA ordination diagram show the general pattern of greatest diversity in the mountains (Fig. 4). Diversity values averaged 2.86 (range = 2.15–3.04) for mountains, 2.67 (range = 2.51–2.95) for plains/braided channel, 2.36 (range = 1.78–2.67) for plains/tributary and 1.92 (range = 1.76–2.22) for plains/downstream from point-source sites. Diversity was significantly different among groups (ANOVA, $P = 0.0005$). Mountain sites had greater diversity than plains/tributary and plains/downstream from point-source sites but was not different from plains/braided channel; diversity in plains/braided channel and plain/tributary sites was not different but both had greater diversity than plains/downstream from point-source sites (Duncan's multiple range test, $P < 0.05$).

The total number of invertebrate taxa was greatest in the mountains, and the plains/downstream from point-source sites had the least number of taxa (Table 2). Invertebrate density was significantly different among DCA site groups (ANOVA, $P = 0.0254$). Mean invertebrate density was 9700 m^{-2} (range = 1980–18 100) for mountains, 13 400 m^{-2} (range = 3700–20 300) for plains/braided channel, 2380 m^{-2} (range = 100–5160) for plains/tributary and 3630 m^{-2} (range = 2650–4950) for plains/downstream from point-source

Table 3 Environmental variables having a significant regression with detrended correspondence analyses (DCA) axis 1 and 2 scores

Environmental variable	r^2	P
DCA axis 1		
Physical characteristics		
Drainage area*	0.29	0.0073
Altitude*	0.28	0.0082
Sinuosity	0.20	0.0237
Slope*	0.59	0.0001
Stream order	0.28	0.0132
Mean substrate size*	0.16	0.0426
Water temperature	0.50	0.0002
Surface-water chemistry		
Specific conductance	0.68	0.0001
Nitrate + nitrite concentrations†	0.30	0.0054
Nitrite concentrations†	0.25	0.0122
Organic N + ammonia concentrations†	0.48	0.0003
Ammonia concentrations†	0.18	0.0333
Total phosphorus concentrations†	0.52	0.0001
Hyporheic-water chemistry		
Nitrate + nitrite concentrations†	0.27	0.0094
DCA axis 2		
Physical characterstics		
Channel width	0.32	0.0047
Mean phi	0.15	0.0458
Surface-water chemistry		
Nitrate + nitrite concentrations†	0.36	0.0022
Nitrite concentrations†	0.27	0.0086
Ammonia concentrations†	0.25	0.0123
Total phosphorus concentrations†	0.23	0.0163

* Natural log transformation used for analysis.
† Square-root transformation used for analysis.

sites. Invertebrate density was not different among mountain, plains/tributary, and plains/downstream from point-source sites or between mountain and plains/braided channel sites; however, invertebrate density at plains/braided channel sites was greater than plains/tributary and plains/downstream from point-source sites (Duncan's multiple range test, $P < 0.05$).

Mean number of taxa/site was twenty-five (range = 10–36) for mountains, eighteen (range = 13–26) for plains/braided channel, thirteen (range = 11–15) for plains/tributary and eleven (range = 6–14) for plains/downstream from point-source sites. The mean number of invertebrate taxa also was significantly different among site groups (ANOVA, $P = 0.0049$). There was no significant difference among plains sites or between mountain sites and plains/braided channel sites; mountain sites, however, had a greater number of taxa than plains/tributary and plains/downstream from point-source sites (Duncan's multiple range test, $P < 0.05$).

The taxonomic composition of invertebrates differed among site groups (Table 2). Only six taxa occurred in all four site groups, which included two mayflies (*Baetis tricaudatus* and *Tricorythodes minutus*), one blackfly (*Simulium* sp.), and three chironomid taxa (*Cricotopus trifascia*, *Orthocladius* sp. and *Polypedilum* sp.) (Table 2). Two families of mayflies (Leptophlebiidae and Ephemerellidae), five families of Plecoptera (Pteronarcyidae, Nemouridae, Capniidae, Perlidae, and Perlodidae), seven families of Trichoptera (Philopotamidae, Psychomyiidae, Rhyacophilidae, Glossosomatidae, Brachycentridae, Lepidostomatidae and Helicopsychidae), two families of Diptera (Deuterophlebiidae and Tipulidae), one subfamily of Chironomidae (Diamesinae), and Lepidoptera were collected only in the mountains. Planaria (Turbellaria), Oligochaeta, leeches (Hirudinea), snails (*Physella* sp.), Isopoda, Amphipoda, Caenidae (Ephemeroptera), and Psychodidae (Diptera) were collected only in the plains region (Table 2). In the order Trichoptera, *Arctopsyche grandis* was collected only in mountain sites, and *Cheumatopsyche* sp. was collected only in the plains region.

Relative abundance of invertebrate orders and non-insects varied among site groups (Fig. 5). Diptera and Ephemeroptera composed 69% or more of relative abundance at all site groups (Fig. 5) and Trichoptera was the third most abundant group at all site groups except for the plains/downstream from point-source sites. Plecoptera and Coleoptera composed 2% of the relative abundance in mountain sites but were rare (< 0.2%) or absent in plains sites (Fig. 5, Table 2). In contrast, non-insects composed 2% or more (2% for plains/tributary, 3% for plains/braided channel, 30% for plains/downstream from point-source) of the relative abundance in plains sites but were rare (< 0.2%) in mountain sites. Relative abundance of Ephemeroptera increased in plains/braided channel and plains/tributary sites. Plecoptera and Trichoptera were not collected at the plains/downstream from point-source sites.

Composition of functional feeding groups also varied among site groups (Fig. 6). Collector−gatherers were the dominant functional feeding-group in all site groups (Fig. 6). Functional feeding group composition for mountain and plains/braided channel sites were similar; collector−gatherers, collector−filterers, and shredders composed 93.5–94.6% of the total, and

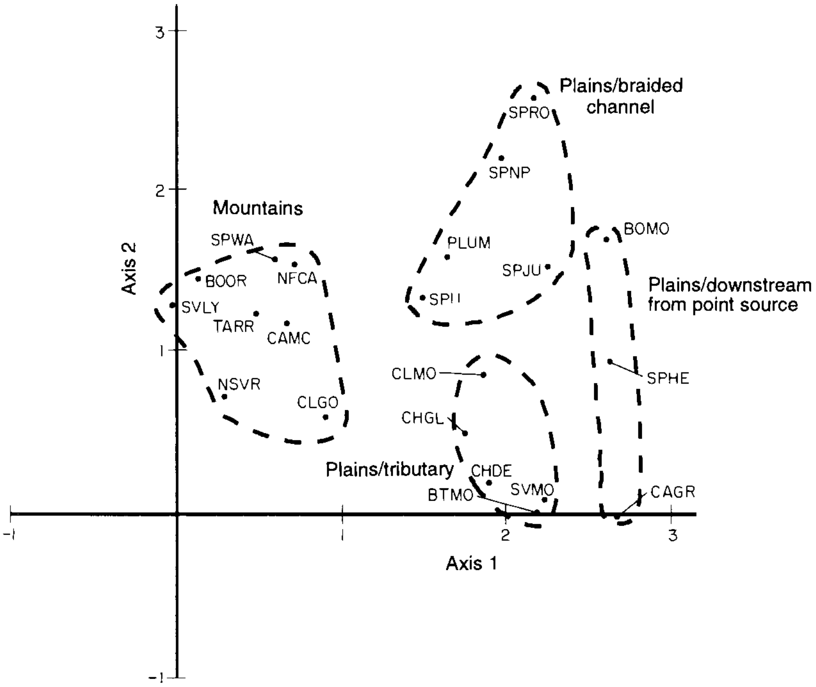

Fig. 2 Detrended correspondence analyses (DCA) ordination plot of site scores on the first two DCA axes and identification of site groups. Site abbreviations are listed in Table 1.

Table 4 Physical and chemical characteristics (mean ± standard deviation) by site groupings as defined by detrended correspondence analyses (DCA) in the South Platte River Basin. * = Environmental variable having a significant regression with DCA axis 1 or 2 (see Table 3)

		Plains		
Attribute/constituent	Mountains	Braided channel	Tributary	Downstream from point source
Physical characteristics				
*Drainage area (km^2)	1681 ± 2227	46 431 ± 30 433	1568 ± 714	6068 ± 5633
*Slope (m km^{-1})	14.0 ± 15.6	2.5 ± 2.4	3.7 ± 2.2	1.8 ± 1.0
*Altitude (m)	2001 ± 592	1136 ± 373	1531 ± 89	1470 ± 61
*Sinuosity	1.40 ± 0.35	1.10 ± 0.05	1.10 ± 0.08	1.10 ± 0.05
*Stream order	5 ± 1	6 ± 1	5 ± 1	6 ± 0
*Width (m)	10.0 ± 5.2	33.6 ± 21.2	7.6 ± 2.8	15.2 ± 2.7
Average channel depth (m)	.28 ± 0.15	0.12 ± 0.11	0.25 ± 0.16	0.38 ± 0.24
Bank height (m)	5.7 ± 7.4	1.3 ± 0.6	2.4 ± 2.1	8.7 ± 12.2
Dominant substrate size (phi)	−5.6 ± 2.7	0 ± 1.3	−2.5 ± 4.3	−6.0 ± 1.7
Subdominant substrate size (phi)	−4.3 ± 4.4	−2.5 ± 1.8	−6.9 ± 8.3	−1.8 ± 2.0
Mean phi	−4.1 ± 2.2	−4.0 ± 2.4	−4.0 ± 3.1	−2.1 ± 1.3
*Mean substrate size (mm)	199 ± 565	25 ± 77	36 ± 237	63 ± 14
Discharge (m^3 s^{-1})	3.50 ± 3.99	2.89 ± 3.12	2.68 ± 3.26	1.79 ± 1.91
Average channel velocity (m s^{-1})	0.49 ± 0.19	0.52 ± 0.13	0.53 ± 0.16	0.29 ± 0.17
*Water temperature (°C)	16 ± 3	25 ± 5	21 ± 3	22 ± 2
Surface-water chemistry				
pH	7.56 ± 0.73	8.35 ± 0.13	7.98 ± 0.33	7.93 ± 0.85
Dissolved oxygen (mg l^{-1})	10.4 ± 1.9	10.0 ± 1.2	7.7 ± 1.1	11.3 ± 6.3
*Specific conductance	15 ± 87	1268 ± 746	1135 ± 483	1137 ± 272
Hyporheic-water chemistry				
Nitrite (mg l^{-1})	0.012 ± 0.005	0.010 ± 0	0.012 ± 0.004	0.160 ± 0.260
Organic N + ammonia (mg l^{-1})	0.76 ± 0.98	0.52 ± 0.72	0.64 ± 0.53	1.83 ± 2.32
Ammonia (mg l^{-1})	0.45 ± 0.64	0.27 ± 0.49	0.32 ± 0.47	1.09 ± 1.66
Total phosphorus (mg l^{-1})	0.13 ± 0.22	0.18 ± 0.27	0.26 ± 0.38	0.83 ± 1.19

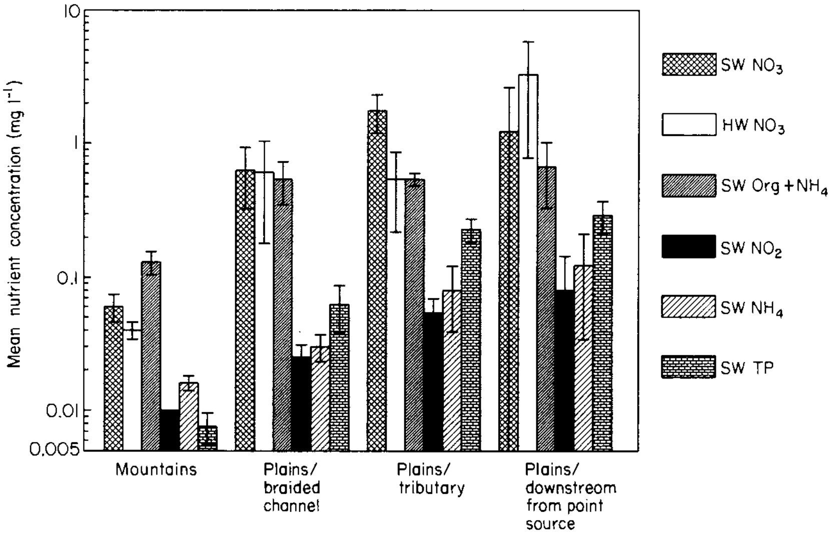

Fig. 3 Mean chemical characteristics of site groupings as defined by detrended correspondence analyses. Error bars = standard error; SW, surface water; HW, hyporheic water; NO_3, nitrate + nitrite-N; Org, organic nitrogen + ammonia-N; NO_2, nitrite-N; NH_4, ammonia-N; TP, total phosphorus.

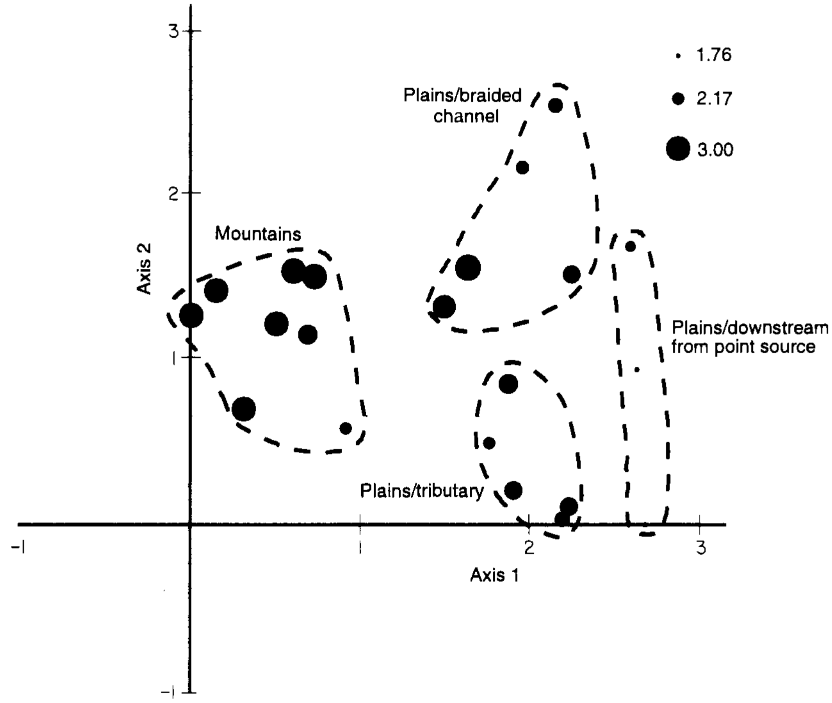

Fig. 4 Shannon diversity index for each site displayed across detrended correspondence analyses (DCA) ordination axes. The larger the circle, the greater the diversity. See Fig. 2 for site abbreviations associated with each circle.

scrapers and predators composed less than 7% of the total. Plains/tributary and plains/downstream from point-source had similar functional feeding-group composition; collector–gatherers, collector–filterers, and predators composed 93.1–93.5% of the total, and shredders and scrapers composed less than 7% of the total.

Discussion

Characteristics of invertebrate communities

Macroinvertebrate species richness and functional-feeding groups of major taxonomic groups are predicted to change along a gradient from small to large streams in the Rocky Mountains (Bruns *et al.*, 1982;

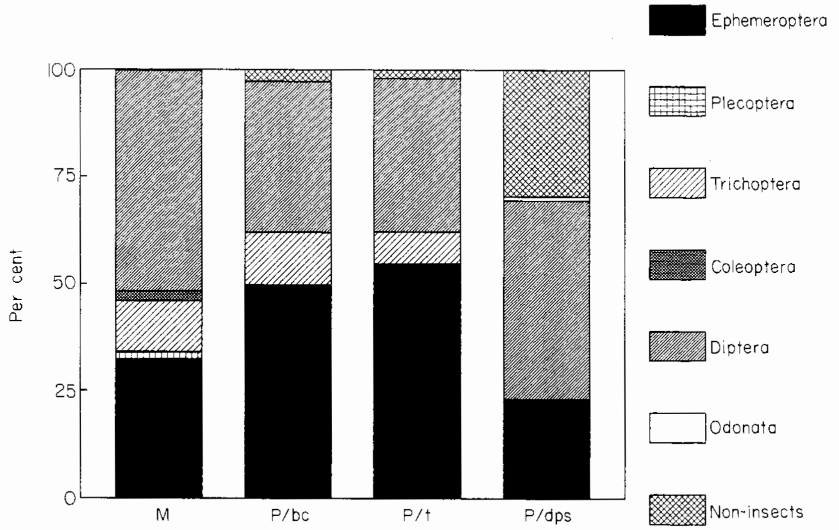

Fig. 5 Relative abundance of invertebrates (insect orders or non-insect taxa) for site groupings as defined by detrended correspondence analyses. M, mountains; P/bc, plains/braided channel; P/t, plains/tributary; P/dps, plains/downstream from point-source.

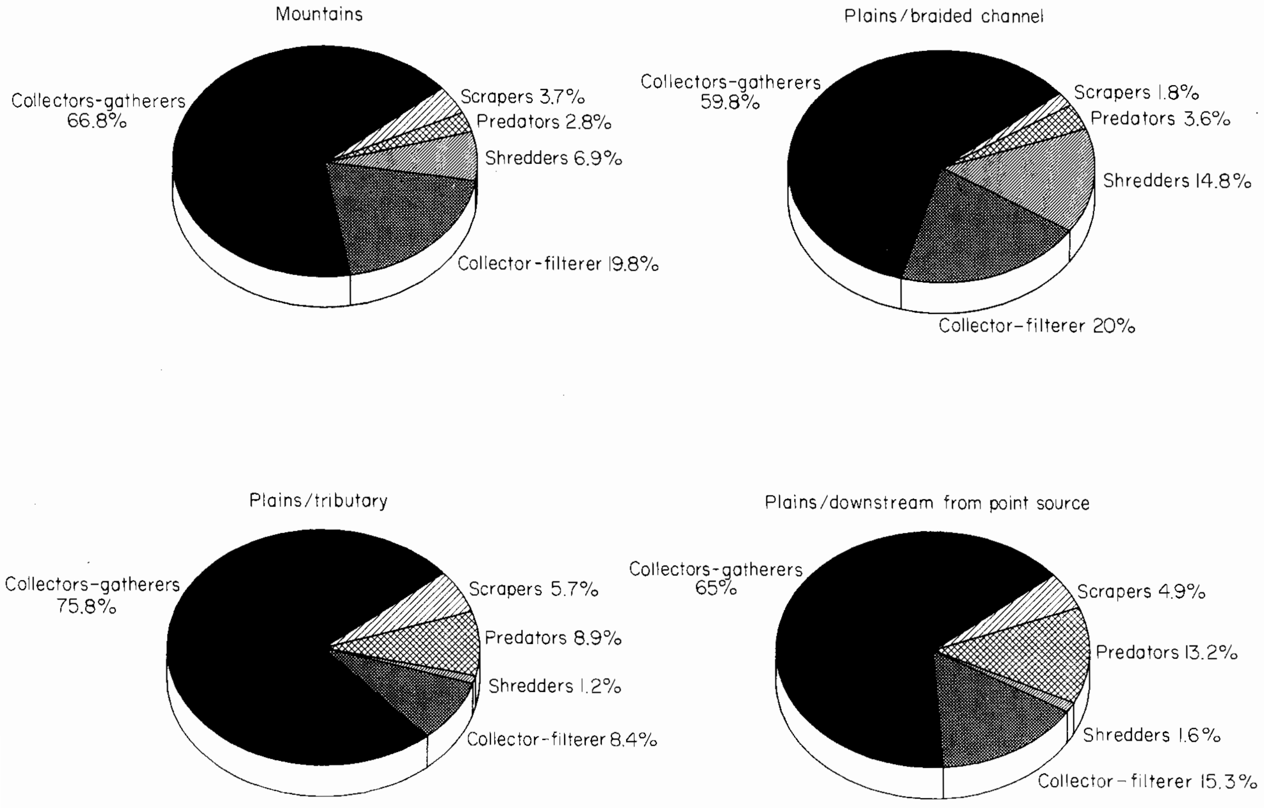

Fig. 6 Relative abundance of functional feeding groups for site groupings as defined by detrended correspondence analyses.

Bruns & Minshall, 1985; Bruns, Hale & Minshall, 1987). In general, the number of filterers and overall taxa increase with increasing stream size (Richards & Minshall, 1992). Ward (1986) reported an increase in macroinvertebrate density, biomass and total number of taxa from the mountains to the plains in the Saint Vrain River, Colorado. In our study, comparison of invertebrate density and number of taxa from high to low altitude in mountain sites did not show this general pattern. Sites sampled in the mountains in this study were comparable with the middle and lower altitude sites described by Ward (1986). Patterns of invertebrate community distributions observed in our study may have been different if seasonal data had been collected. Ward (1986) noted that total species richness would be less at middle and lower altitudes at mountain sites if only summer data were used because of the absence of stoneflies. In addition, species of other taxonomic groups, such as Chironomidae, Trichoptera and Coleoptera that occur during winter would be missed if only summer samples were collected (Ward, 1986). Furthermore, samples in this study were collected basin-wide rather than longitudinally along a single tributary. Thus, variability among streams within the mountains may mask longitudinal patterns.

In contrast to Ward (1986), the results of this study indicated greater number of taxa per site in the mountains compared with the plains. The plains site used by Ward (1986) was located at an altitude of 1544 m, had hard substrates, and would be considered the transition zone between mountains and plains for this study; taxa at this site probably represent cold- and warm-water species. Plains sites in this study typically were located below this transition zone and had finer-grained, less stable substrates and higher nutrient concentrations than the plains site described by Ward (1986). These physical and chemical differences probably resulted in lower number of taxa at plains sites in this study.

Although invertebrate density and number of taxa differed between this study and that of Ward (1986), invertebrate community composition in the mountains and plains regions were similar. Ward (1986) reported that the orders Plecoptera, Trichoptera, Ephemeroptera and Diptera dominated mountain sites, and three orders of insect (Collembola, Odonata, Lepidoptera), Amphipoda, Hirudinea and Gastropoda were collected only in the plains sites. The data for this study indicate a similar pattern, with the exceptions that Collembola were not collected at any sites and Lepidoptera were collected only in mountain sites. The distribution of invertebrate families within insect orders also were similar to families reported by Ward (1986).

Despite differences in the taxonomic composition among site groups, a notable feature is the similarity in the functional-feeding group composition between mountain and plains/braided channel sites. Although different in physical attributes, both site groups were less enriched (i.e. lower surface-water nutrient concentrations) compared with plains/tributary and plains/downstream from point-source sites. Collector–gatherers, collector–filterers and shredders were the dominant groups. In contrast, the nutrient-enriched (plains/tributary and plains/downstream from point-source) sites were dominated by collector–gatherers and collector–filterers and had a greater proportion of predators and scrapers compared with the mountain and plains/braided channel sites. Ward (1986) reported collector–gatherers and scrapers to be the dominant functional feeding groups at most mid- to lower-altitude mountain sites and the plains sites in the St Vrain River. The low proportion of scrapers at the non-enriched sites in the present study was interesting considering that periphytic algae were visible at most sites.

Ecoregions and land use

Results from the DCA analyses separated invertebrate communities based on the two dominant ecoregions, Southern Rockies and Western High Plains. Similarly, Whittier *et al.* (1988) reported that the clearest differences between biotic assemblages and physiochemical attributes measured were between montane and non-montane regions in Oregon. Corkum (1989) also reported distinct differences in benthic invertebrates between streams in mountain and plains regions of north-west North America. In contrast Quinn & Hickey (1990) could not readily group invertebrate communities into ecoregions for New Zealand streams, and their results indicate that land use (i.e. catchment development) is more important than regional factors in determining the characteristics of river invertebrate communities.

Within an ecoregion, land use can be an important large-scale factor affecting composition and structure of invertebrate communities. In the Southern Rocky

Mountain ecoregion, Clear Creek at Golden had the lowest Shannon diversity index value, number of taxa and invertebrate density compared with other mountain sites and was the only site affected by mining. Differences in invertebrate communities among forest, range, and built-up land use in the mountain sites were not as distinct as compared with different invertebrate communities found in plains sites. In the Western High Plains ecoregion, geomorphology and land use affected invertebrate distribution as defined by DCA analyses. Land use was an important factor affecting nutrient concentrations and invertebrate communities. Sites in the plains/tributary group were located in urban or a mixture of agriculture/urban land use. These sites had higher nitrite, ammonia, and total phosphorus concentrations than sites in the plains/braided channel; higher nutrient concentrations probably represent urban affects on stream-water chemistry. The plains/braided channels were wider and shallower than other plains sites and land use primarily was agriculture or built-up, and nutrient concentrations were lower than other plains sites. Invertebrate density and total number of taxa were greater and functional-feeding group composition was different in the plains/braided channel sites compared with other plains sites. The land use at the plains/downstream from point-source sites was mixed agriculture/urban; however, these sites were below the major municipal discharges into the South Platte River Basin (Dennehy *et al.*, 1993) and nutrient concentrations were high. Organic pollution from point sources, such as waste-water effluent, generally decreases the number of insect species (Hynes, 1960) as was shown in this study. In addition, community composition was altered at these sites (i.e. absence of Trichoptera, greater proportion of non-insect taxa) compared with plains/tributary and plains/braided channel sites. The plains/downstream from point-source sites were located in a rich algal zone (Table 1) where Oligochaeta dominated and oxygen concentrations were high. This region is characterized by having increased numbers of snails and an abundance of Chironomidae (Wiederholm, 1984). The presence of Oligochaeta, *Physella* sp., *Simulium* sp., and dominance of Chironomidae genera and the absence of Trichoptera are characteristic of a stream reach effected by organic pollution (Wiederholm, 1984). Similarly, Quinn & Hickey (1990) reported that gross organic pollution and runoff were important affects on community composition at some sites in New Zealand streams. Although spatial assemblages of invertebrate communities appear to be related to land-use patterns, specific cause and effect relations cannot be addressed in the present study.

Environmental factors affecting invertebrates

As noted in other large basin-scale studies, a combination of environmental factors affected the invertebrate distribution and abundance within the South Platte River Basin. Differences in invertebrate communities occurred between mountains and plains and were most highly correlated with differences in stream slope, specific conductance, water temperature (Table 3) and surface water organic nitrogen + ammonia and total phosphorus concentrations and to a lesser extent to factors such as drainage area, altitude, sinuosity, stream order, mean substrate size, and ammonia, nitrite, and nitrate + nitrate concentrations. As previously discussed, differences in invertebrate communities among sites within the plains region varied according to geomorphology and land-use affects on nutrient concentrations. With the exception of nitrate + nitrite concentrations, nutrient concentrations in the hyporheic waters were not related to the invertebrate community. McMahon *et al.* (1994) reported that groundwater effects on surface-water nutrient concentrations were related to a combination of factors such as redox conditions of groundwater, land use and proximity of site to sources of nutrients in the South Platte River Basin. In British streams, different environmental factors were useful in describing invertebrate communities depending on the spatial scale examined (Furse *et al.*, 1984; Wright *et al.*, 1984). For instance, substratum characteristics, alkalinity, total oxidized nitrogen (i.e. nitrate + nitrite) were useful in distinguishing invertebrate communities among rivers in Great Britain, whereas discharge, distance from source, width, and depth were useful in distinguishing within river sites and slope and altitude were useful in distinguishing within and between sites in rivers. Quinn & Hickey (1990) reported that silty and sandy substrates and recent severe flooding caused low biomass and taxonomic richness; whereas catchment development and related environmental factors (i.e. increased periphyton, increased water temperature) had the most widespread important effect on community composition. Corkum (1989) determined that biogeographical features (latitude, altitude, slope, distance from Pacific Ocean) and hydrological variables (current velocity, mean depth) were most useful in delineating site groupings in a survey of streams in north-western North America. Within basins, Ormerod & Edwards (1987) determined that water chemistry (pH or total hardness) and associated geology were the dominant correlates with macroinvertebrate assemblages, along with slope or distance from source in the River Wye. Richards *et al.* (1993) reported that substrate variables were the most important factors explaining variation in macroinvertebrate communities in a Michigan agricultural watershed. As demonstrated by all these studies, the type of environmental factors affecting invertebrate community distribution in stream ecosystems differs based on the spatial scale (regional, basin, within stream) examined and the large-scale environmental gradients (e.g. altitude) present within the study area. For the South Platte River Basin, ecoregions and physical (geomorphology) and chemical factors (as affected by land use) within ecoregions are dominant factors affecting invertebrate distribution.

Acknowledgments

This study was supported by the U.S. Geological Survey's National Water Quality Assessment Program: South Platte River Study. We thank K.F. Dennehy, J.R. Ortiz, R.C. Averett, V. Averett, R.C. Petersen, L.R. DeWeese, P.B. McMahon, D.W. Litke, J.E. Paschal, R.B. Swanson, G.D. McElhany, and K.L. Findell for field assistance. We thank H.V. Leland for assistance in data analyses. We thank H.V. Leland, K.F. Dennehy, R.G. Striegl, T.M. Short and an anonymous referee for their critical review of the manuscript. This paper is dedicated to the memory of Robert C. Averett (deceased June 25, 1993) whose leadership in aquatic ecology and inspiration to aquatic ecologists will be missed.

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(*Manuscript accepted 2 December 1994*)