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CHIRONOMIDAE (DIPTERA) SPECIES DISTRIBUTION RELATED TO ENVIRONMENTAL CHARACTERISTICS OF THE METAL-POLLUTED ARKANSAS RIVER, COLORADO

L.P. Ruse¹, S.J. Herrmann², and J.E. Sublette³

ABSTRACT.—Mining in the Upper Arkansas catchment has polluted the river with heavy metals for 140 yr. Pupal and adult chironomid species distribution and sedimentary metal concentrations are provided for 22 stations along 259 km of main river during 1984–85. Complete species identification was achieved only recently. This has produced an unprecedented record of chironomid species distribution for a comparable length of river in the USA. Chemically or physically perturbed sites had poor species richness compared with the next site downstream, suggesting that larvae may drift through unfavorable habitats to benign ones. Using canonical correspondence analysis, we found species composition to be most strongly related to variables expressing the longitudinal axis of the river (distance/altitude, temperature, latitude), while toxicity to zinc was a significant secondary correlate. These river-related environmental variables accounted for a greater proportion of pupal species variation than for adults. This was considered to result from a proportion of adults emerging from habitats beyond the main river. Multivariate analysis identified metal-tolerant and -intolerant species. Generic data revealed the same major trends but indicator taxa were lost. The study provides a disturbed-state reference for monitoring effects of remedial actions begun in 1991, and for comparisons with other Colorado rivers.

Key words: Chironomidae, heavy metals, multivariate analysis, pupal exuviae, adults, spatial distribution, sediments, species richness.

The Arkansas River in Colorado has been polluted by heavy metals since mining began in 1859. Remedial action on the most affected sites started in 1991. There have been many descriptive and experimental studies of pollution effects on benthic macroinvertebrates inhabiting the first 30 km of the river by researchers of the Bureau of Reclamation and Colorado State University (e.g., Roline and Boehmke 1981, Roline 1988, Kiffney and Clements 1993, Clements 1994, Clements and Kiffney 1994). Typically, invertebrates were sampled using mesh sizes of 500 μm or greater and Chironomidae (non-biting midges) were never identified beyond the subfamily level. Armitage and Blackburn (1985) demonstrated that specific identification of Chironomidae distinguished varying degrees of metal pollution as efficiently as using all macroinvertebrate data with chironomids identified only to subfamily. Clements (1994) has accepted that research on metal tolerances of orthoclaidiine species (a subfamily of Chironomidae) is necessary for the Arkansas River. The collection and specific identification of Chironomidae

can be made easier and more efficient by sampling pupal exuviae, compared with larvae (Ferrington et al. 1991). Although exuviae will remain afloat for 2–3 d after adult emergence, they do not drift far before entrapment at river margins or midstream obstacles (McGill 1980, Ruse 1995a). Exuvial collections should therefore be representative of local adult emergence, integrated over a few days before sampling.

In 1983 a major surge of metal sludge in the Upper Arkansas River affected sites 220 km downstream (Kimball et al. 1995). Emerging adult chironomids, and later pupal exuviae, were collected from sites along this length of the Arkansas River during 1984–85 to investigate the effects of metal pollution on species spatial distribution. At that time many individuals could not be identified to species, particularly pupal exuviae. Associations between larvae, pupae, and adults from rivers in Colorado and neighboring states have since enabled specific identification (Sublette et al. 1998). This has led to a retrospective investigation of the relationship between species distribution and available environmental data using statistical

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packages that were not available during the survey period. This study also differed from other research on the Arkansas River by relating invertebrate distribution to sedimentary concentrations of heavy metals rather than water measurements. Kiffney and Clements (1993) found that suspended metal concentrations in the Arkansas River underestimated availability of metals to benthic macroinvertebrates. Bioaccumulated metal concentrations were better related to those measured in sedimentary minerals and periphyton. This survey provides the only reference for measuring the effect of subsequent remedial actions on the chironomid assemblage of the Arkansas River and relating their distribution to sedimentary metal concentrations during a period of severe pollution.

METHODS

Study Sites

Twenty-two sites were chosen along 259 km of the East Fork (EF) and Arkansas River (AR) between Climax and Pueblo, east of the Continental Divide in central Colorado (Fig. 1). We adopted sites EF1 downstream to AR9 from those surveyed by the Bureau of Reclamation and reported by Roline (1988). Other biological surveys of the Upper Arkansas catchment have adopted the same site codes, but since these may refer to different locations, care should be taken when cross-referencing with previous publications.

Metal-rich water enters East Fork between EF1 and EF2 via Leadville Drain, but the greatest source of metals to the catchment comes from California Gulch between AR2 and AR3 (Kimball et al. 1995). This survey occurred between 2 major metal sludge surges into California Gulch on 23 February 1983 and 22 October 1985. Water diverted from the western slopes of the Continental Divide supplements flows from Turquoise Lake and Twin Lakes, entering the Arkansas River above AR4 and AR9, respectively. Iowa Gulch, and diffuse sources of metals between AR4 and AR8, carried discharge from an active mine during the study period. Mining affects other tributaries to the river downstream of AR8, but concentrations of metals are much lower than those found upstream. The Arkansas River was impounded above AR19 by the Pueblo Dam in 1974. Sediment analysis of Pueblo

Reservoir reveals that a substantial metal load is transported there from the Leadville area, particularly due to resuspension of river sediments by snowmelt runoff (Kimball et al. 1995). The U.S. Environmental Protection Agency (EPA) declared the California Gulch catchment and the Arkansas River from above AR2 to below AR3 a Superfund site in 1983. New water treatment plants on the Leadville Drain and California Gulch were in operation by June 1992, and the last major mining operation in Leadville ceased in January 1999.

Biological Data

We collected adult Chironomidae at each site monthly from May 1984 until September 1985 using sweep net, beating sheet, water-skimming, hand-picking and ultraviolet light traps. Adults were dissected in absolute ethanol. Body parts, except for wings and 1 set of legs, were cleared in potassium hydroxide and then all parts slide-mounted in Euparal. Adult Plecoptera and Trichoptera were also collected and are reported in the following paper (Ruse and Herrmann 2000).

We sampled chironomid pupal exuviae using the "Thienemann net technique" (Thienemann 1910): a 200- μ m-mesh net attached to a circular frame on a pole is used to collect floating debris accumulating behind obstacles at river margins. This method supplemented adult collections during a 3-month visiting scholarship by the senior author. Each site was sampled in July, August, and September 1985. The broad emergence period by many temperate, lotic species of Chironomidae should ensure that a large proportion of species present over the whole year are represented by this frequency of sampling (Ruse and Wilson 1984, Ruse 1995b). Samples were refloated, agitated, and randomly subsampled by sieve. All chironomid pupal exuviae were removed from a subsample and sufficient subsamples were sorted to obtain about 200 exuviae, when possible. Exuviae were mounted on glass microscope slides in Euparal or retained in vials of 70% ethanol. Initially identified to generic level, the material remained in excellent condition until 12 yr later when it became possible to determine species. Specific identification was achieved by comparing exuviae with those obtained from adult rearings of larvae and pupae collected subsequently from the Arkansas River and neighboring catchments in

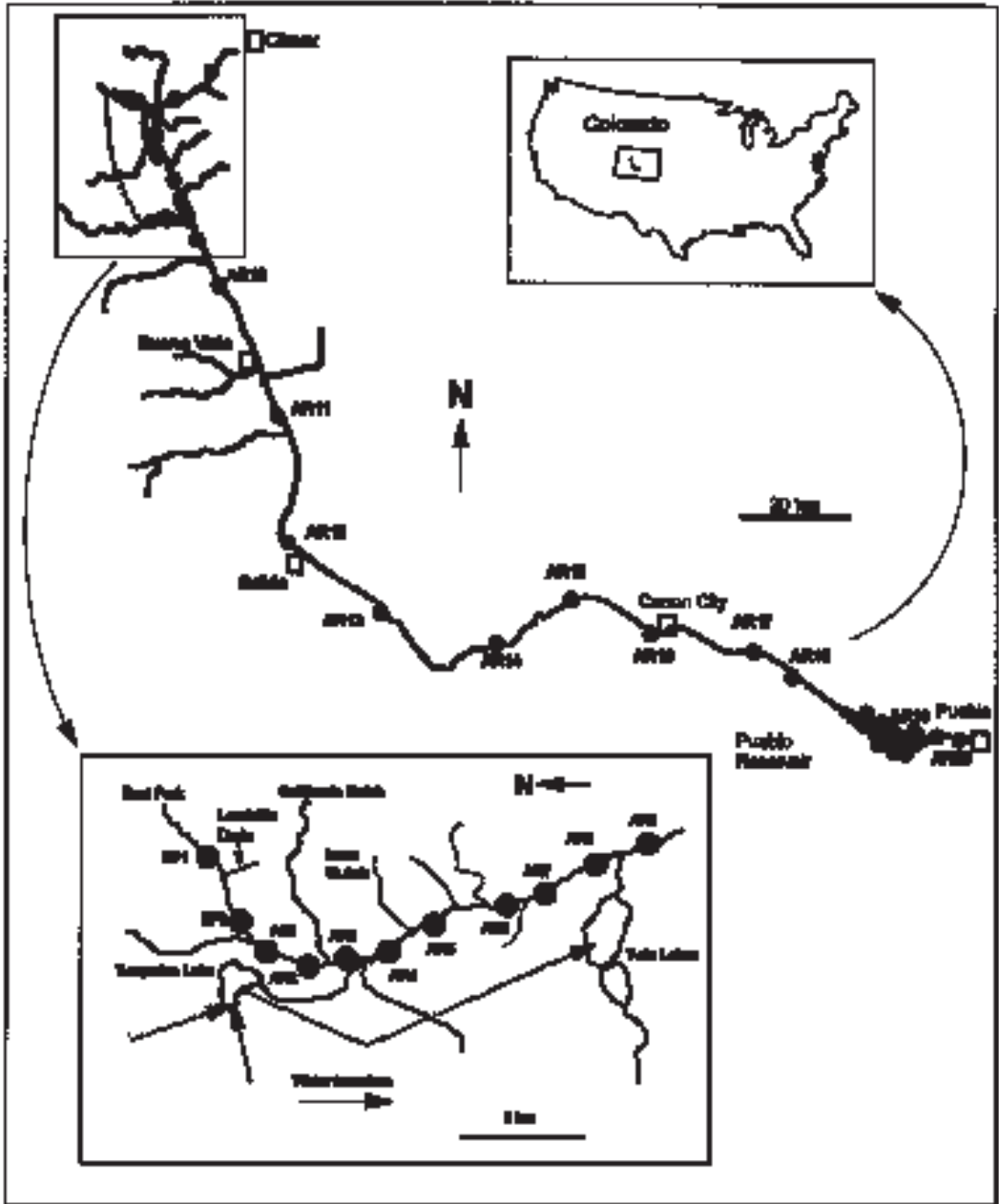


Fig. 1. Upper Arkansas River sampling points.

Colorado and New Mexico. The associated material is held by author JES. Unassociated pupal species are designated by the suffix *n-P*.

Environmental Data

At each site water temperature was recorded once during each monthly visit to collect adult insects. The 3 dominant superficial substra-

tum types, among 5 size classes, were assessed visually. Latitude, longitude, altitude, slope, and distance downstream from EF1 were obtained from maps.

We determined metals from 2 samples of submerged fine sand taken at each site during 18–19 October following the 2nd metal sludge surge into California Gulch. These data still

served to characterize the relative contamination of sites by metals emanating from Leadville mines. A 25-mm-diameter PVC pipe was inserted to a depth of 15 cm. Sediments were dried at 70°C for 48 h and ground with a mortar and pestle until they passed through a 250- μ m-mesh sieve. Metals were extracted from triplicate subsamples of approximately 500 \pm 0.1 mg using a sequence of hot digestions and evaporations with nitric and hydrochloric acids (Caravajal et al. 1983). A reagent blank was prepared before and after each set of 6 sediment digestions for a site and taken through the same protocol prior to metals determination. Determination of lead (Pb), iron (Fe), manganese (Mn), zinc (Zn), and copper (Cu) by flame atomic absorption spectrometry followed the methods of Mahan et al. (1987). Cadmium (Cd) was measured by electrothermal atomization atomic absorption spectrometry (Sandoval et al. 1992). The mean concentration of 6 samples from each site was used in subsequent data analysis.

Data Analysis

Species abundances for samples from the same site were combined for both pupal and adult data sets so they could be related to environmental characteristics recorded on only a single occasion. Spatial variation in these data sets was directly compared with environmental variation using canonical correspondence analysis (CCA; Ter Braak and Prentice 1988). CCA selected the linear combination of environmental variables achieving the maximum separation of species by multiple regression along the 1st axis. Subsequent axes were extracted from the residual variation to maximize dispersion of species, provided they were uncorrelated to previous axes. Significance of the regression between biological and environmental data was tested against the possibility of a random association by comparing the *F*-ratio with 99 unrestricted Monte Carlo permutations of these data (Ter Braak 1990). A probability of ≤ 0.05 was considered significant. Forward stepwise regression was used to objectively select variables, one at a time, according to the amount of biological variation each explained. Selection stopped when there was no significant increase in explained variation, tested against Monte Carlo permutations.

Before analysis, we converted chironomid species abundances to percentages of the total

number of individuals identified from a site. Species recorded at 1 site only were omitted from CCA in case of spurious association with a coincidental extreme environmental measurement; their distributions are recorded in the Appendix. An ordinal value representing relative variation in substratum between sites was obtained by assuming a mean particle size for each of 3 categories: boulder/bedrock (215 mm), rubble/gravel (9.5 mm), and sand (0.25 mm). The dominant substratum was assumed to cover 50% of the site, and the next 2 recorded substrata were assumed to cover 30% and 20% of the site, respectively. Mean particle size at each site was calculated from the sum of products of size times proportional coverage. To account for the ameliorating effect of increased hardness on metal toxicity to biota, we calculated EPA hardness-based water quality criterion for Zn (Clements and Kiffney 1995). Water hardness was not measured during this survey, but data were available for sites EF1 to AR9 (Roline and Boehmke 1981, Clements and Kiffney 1995) and for inlet and outlet flows of Pueblo Reservoir (Herrmann and Mahan 1977). The presence of carbonate rocks between AR10 and AR12 and river-exposed deposits of calcium and magnesium near AR16 (Kimball et al. 1995) was also taken into account when estimating water hardness. For each site, we divided the observed sedimentary Zn-loading by the criterion value for assumed water hardness. Resultant ratios were classified into an ordinal scale of toxicity to Zn: $<2.0 = 1$, $2.0-9.9 = 2$, $10.0-19.9 = 3$, $20.0-39.9 = 4$, $>39.9 = 5$. These broad bands reduced the effect of imprecise hardness estimates. Environmental data were not transformed for CCA; measurements of temperature, slope, Zn toxicity, total Mn, and total Fe were normally distributed. Latitude and longitude values were decimalized and only the maximum water temperature recorded at each site was used. Environmental data were standardized to have a mean of zero and unit variance to remove arbitrary variation in units of measurement. CCA species scores were weighted mean sample scores (CANOCO version 3.1 scaling + 2). The analysis was therefore sensitive to relative variation between sites, and it was not necessary to have precise data on particle size or water hardness to relate these characteristics to trends in species distribution.

Direct statistical comparisons of pupal and adult species proportions were made using a χ^2 test of independence (Sokal and Rohlf 1981). The null hypothesis was that proportions of each species collected were independent of sampling method, aquatic netting, or aerial netting. Pupal species unassociated with reared adults were excluded, as were species with expected counts <5 in both data sets.

RESULTS

Environmental Data

The obtuse-angled line of the main river prevented latitude or longitude having the simple linear relationship with distance that altitude had (Table 1). The river gradient was reduced at the last 3 sites, but the trend was variable along most of the watercourse. Mean particle size at the first 11 sites was often smaller than at downstream sites. Site AR10 was characterized by a steep gradient and torrential flow over a substratum dominated by bedrock, boulder, and rubble. Maximum recorded temperatures increased downstream to AR7 but were suppressed below the Twin Lakes confluence until AR13. Hypolimnion flows from Pueblo Reservoir lowered temperature at AR19. Sedimentary total Cu was the only metal to reach a peak at AR3, below California Gulch, while the next most Cu-contaminated sites were AR5 and AR7. Zn toxicity, total Zn, Mn, and Cd peaked at AR5, AR7, or AR8, all reduced-gradient sites compared with AR3, AR4, and AR6. Concentrations of sedimentary Fe below California Gulch remained high throughout the river, except at AR12 and AR19, peaking at AR11.

Pupal Exuviae

A total of 10,120 chironomid pupal exuviae were identified to 127 species from 22 sites. Species abundances are presented in Table 2, with authors' names, for species collected from 2 or more sites. Species and sites in Table 2 are arranged according to the 1st axis of a correspondence analysis (Ter Braak and Prentice 1988) so that downstream turnover in species composition can be assessed. Species richness was lowest at EF2, below Leadville Drain, then increased downstream to the richest site at AR2, above the confluence with California Gulch (Fig. 2). Species richness was poor at AR3, recovered at the 3 sites below Turquoise

Lake confluence, and then declined until AR10. Species numbers were high at AR11–AR12 and depleted below Pueblo Reservoir at AR19. Orthoclaadiinae was the dominant subfamily throughout the survey. There were no obvious downstream trends in total or subfamily species richness except for the absence of Diamesinae below AR12. Classifying pupal exuviae according to presumed feeding modes of their associated larvae (Table 2) revealed a dominance by algal grazers at all sites (Fig. 3). Predators increased from AR13 until Pueblo Reservoir. Detritivores were present in low proportions except at AR10. Filterers appeared from AR16 to AR18.

ORDINATION.—Stepwise regression selected distance downstream, maximum temperature, latitude, and Zn toxicity as significantly correlated with variation in species composition among sites. Altitude was also significant but highly correlated with distance and was excluded to prevent multicollinearity (variation inflation factor = 189; Ter Braak 1990). The 4 selected variables explained 43.4% of biological variation in CCA. The species-environment relationship was significantly different from random for the first 2 CCA axes ($P = 0.01$), accounting for 32.9% of all biological variation and 75.7% of explained variation.

Species turnover among samples was strongly related to change along the longitudinal axis of the river. Dominance of the 1st CCA axis compared with the 2nd resulted in an archlike configuration of sites in Figure 4. Gradient lengths for the first 2 unconstrained (biological data alone) axes were 6.24 and 2.82 s units, respectively. Detrending or reduction of environmental variables did not remove the arching trend, and separation into 2 data sets was impractical for the small number of samples. The 1st CCA axis was most significantly related to downstream distance (canonical coefficient t -value 5.42, intersite correlation 0.97). The 2nd axis was principally related to variations in maximum temperature (t -value 6.05, correlation -0.46) and Zn toxicity (t -value 2.77, correlation -0.29), resulting in lateral spreading of samples upstream of AR9, at AR13, and below Pueblo Reservoir. Sites EF2 and AR3, downstream of the most significant metal inputs of Leadville Drain and California Gulch, respectively, were closely associated. Sites AR5–AR8 had the highest Zn toxicity ratios and similar species composition, although AR5

TABLE 1. Environmental data; mean total metal concentrations are $\mu\text{g g}^{-1}$ dry weight

Site	Latitude (Deg.)	Longitude (Deg.)	Max. temp. ($^{\circ}\text{C}$)	Altitude (m)	Slope (%)	Dist. (km)	Zinc tox.	Total Cu	Total Zn	Total Pb	Total Mn	Total Fe	Total Cd	Mean particle size (mm)
EF1	39.28	106.22	13.0	3042	1.1	0.00	1	13.9	132	19.0	374	8981	0.40	2.9
EF2	39.27	106.33	13.6	2969	1.1	6.35	2	10.5	935	88.9	824	8014	0.84	4.6
AR1	39.25	106.32	14.5	2944	1.6	7.87	2	6.0	548	69.8	824	6376	0.90	4.6
AR2	39.23	106.35	14.2	2905	1.4	11.11	2	4.8	320	41.0	602	5773	0.57	4.6
AR3	39.22	106.35	14.4	2899	1.4	11.18	3	157.0	2374	779.0	825	30400	2.97	4.6
AR4	39.20	106.35	16.1	2865	1.0	14.48	3	39.7	917	267.0	730	12570	1.37	4.6
AR5	39.17	106.33	17.4	2835	0.5	20.49	5	80.0	2836	865.0	780	31000	3.50	4.6
AR6	39.13	106.32	18.1	2795	1.7	22.86	4	46.6	1679	451.0	1149	15760	2.70	4.6
AR7	39.12	106.30	18.6	2771	0.8	25.91	5	72.6	3038	763.0	1017	30100	4.23	4.6
AR8	39.08	106.28	17.8	2748	0.7	29.08	4	47.6	2392	582.0	1474	18570	1.65	24.0
AR9	39.07	106.28	16.0	2743	0.4	30.35	2	16.5	508	176.0	368	12360	0.83	4.6
AR10	38.97	106.20	15.5	2573	1.1	45.85	2	14.0	420	161.4	590	11350	0.73	115.0
AR11	38.78	106.08	16.5	2338	0.9	71.75	2	21.7	401	112.7	473	32170	0.58	21.9
AR12	38.53	106.02	17.5	2143	0.6	104.77	2	6.8	135	39.0	123	6910	0.52	21.9
AR13	38.43	105.82	19.4	2033	0.5	129.28	2	15.5	263	59.6	256	20740	0.82	21.9
AR14	38.40	105.58	19.2	1879	0.6	156.59	2	17.6	269	36.3	448	27370	0.50	21.9
AR15	38.47	105.40	19.9	1746	0.6	177.80	2	19.0	309	59.1	438	30070	0.73	21.9
AR16	38.43	105.25	21.5	1618	0.7	195.45	2	18.0	332	39.5	399	23720	0.35	21.9
AR17	38.31	105.00	21.5	1535	0.4	217.80	1	9.8	129	12.9	229	18690	0.38	3.2
AR18	38.26	104.92	21.7	1497	0.3	228.98	1	11.0	198	7.8	290	12410	0.78	3.2
AR19	38.19	104.70	19.6	1444	0.2	253.74	1	4.8	28	1.0	84	6810	0.25	45.3
AR20	38.19	104.67	21.0	1431	0.3	258.56	1	6.3	68	10.2	143	18820	0.08	4.6

TABLE 2. Proportions of pupal exuviae species at each site: 1 = 0.1–4.9%; 2 = 5.0–9.9%; 3 = 10.0–19.9%; 4 = 20.0–39.9%; 5 = 40.0+%. G = Grazer, D = Detritivore, P = Predator, F = Filterer.

Code	Species name	Trophic group	Site																					
			E	E	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A					
			1	2	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
PROC_SUB	<i>Procladius subletti</i> Roback	P	1	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
THIE_FUS	<i>Thienemannimyia fusciceps</i> (Edwards)	P	1	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DIAM_HET	<i>Diamasa heteropus</i> (Coquillett)	G	-	-	-	1	1	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
POTT_MON	<i>Pothastia montium</i> (Edwards)	D	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PAGA_PAR	<i>Pagastia partica</i> (Roback)	D	2	1	1	1	-	1	1	-	1	-	1	-	1	1	-	-	-	-	-	-	-	-
HYDR_FUS	<i>Hydrobaenus fuscistylus</i> (Goetghebuer)	G	4	5	-	1	2	1	1	1	1	1	1	-	1	1	-	-	-	-	-	-	-	-
HYDR_PIL	<i>Hydrobaenus pilipes</i> (Malloch)	G	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DIPL_CUL	<i>Diplocladius cultriger</i> Kieffer	D	-	-	-	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EUKI_ILK	<i>Eukiefferiella ilkleyensis</i> (Edwards)	G	-	1	1	2	1	1	1	1	-	1	-	1	1	1	-	1	-	-	-	-	-	-
EUKI_2-P	<i>Eukiefferiella</i> sp. 2-P	G	-	1	1	1	2	1	1	1	-	-	-	1	-	1	-	-	-	-	-	-	-	-
EUKI_n9	<i>Eukiefferiella</i> n. sp. 9	G	1	1	-	3	2	1	1	-	-	-	-	1	-	-	1	-	1	-	1	-	-	-
ORTH_DUB	<i>Orthocladius dubitatus</i> Johannsen	C	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ORTH_LUT	<i>Orthocladius luteipes</i> Goetghebuer	G	-	-	1	1	1	1	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
ORTH_APP	<i>Orthocladius appersoni</i> Soponis	G	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ORTH_5-P	<i>Orthocladius</i> sp. 5-P	G	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ORTH_NIG	<i>Orthocladius nigrinus</i> Malloch	G	-	3	-	1	1	1	1	-	1	1	-	1	1	-	-	-	-	-	-	-	-	-
ORTH_OBU	<i>Orthocladius obumbratus</i> Johannsen	G	-	-	-	1	1	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
PARA_n3	<i>Paratrichocladius</i> n. sp. 3	G	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
PSEC_SPI	<i>Psectrocladius spinifer</i> (Johannsen)	G	-	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RHEO_EMI	<i>Rheocricotopus emimelobus</i> Sæther	G	-	3	1	1	3	1	1	1	1	1	-	1	1	-	-	1	-	-	-	-	-	-
TVET_PAU	<i>Tvetenia paucunca</i> (Sæther)	G	-	-	4	4	4	1	1	1	1	1	1	-	1	1	-	-	1	1	-	-	-	-
CORY_LOB	<i>Corynoneura lobata</i> Edwards	G	-	-	1	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CORY_5-P	<i>Corynoneura</i> sp. 5-P	G	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
KREN_CAM	<i>Krenosmittia camptophleps</i> (Edwards)	G	-	1	1	1	1	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
THIE_5-P	<i>Thienemanniella</i> sp. 5-P	G	1	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
POLY_n1	<i>Polypedilum</i> n. sp. 1	D	1	-	1	1	1	1	1	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-
TANY_8-P	<i>Tanytarsus</i> sp. 8-P	D	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TANY_n5	<i>Tanytarsus</i> n. sp. 5	D	-	-	1	1	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-
BRUN_EUM	<i>Brundiniella eumorpha</i> (Sublette)	P	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CRIC_BIF	<i>Cricotopus bifurcatus</i> Cranston & Oliver	G	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CRIC_n18	<i>Cricotopus</i> n. sp. 18	G	-	-	1	1	-	1	1	2	2	1	1	-	2	1	1	-	-	1	-	-	-	-
CRIC_19P	<i>Cricotopus</i> sp. 19-P	G	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HETE_MAE	<i>Heterotrissocladius maeeri</i> Brundin	D	-	-	-	-	-	1	1	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-
ORTH_FRI	<i>Orthocladius frigidus</i> (Zetterstedt)	G	4	3	1	1	1	5	4	4	4	5	4	1	1	-	-	1	-	-	-	-	-	-
KREN_HAL	<i>Krenosmittia halvorseni</i> (Cranston & Oliver)	G	-	-	-	-	-	-	1	1	2	1	1	1	-	-	-	-	-	-	-	-	-	-
SERG_ALB	<i>Sergentia albescens</i> (Townes)	P	1	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CRIC_TRE	<i>Cricotopus tremulus</i> (Linnaeus)	G	-	-	1	1	1	1	1	1	1	1	-	1	2	1	1	1	1	1	1	1	-	1
CRIC_SLO	<i>Cricotopus slossonae</i> Malloch	G	-	-	2	1	1	-	1	1	1	1	2	1	2	1	2	1	1	1	1	1	-	1
ORTH_RVA	<i>Orthocladius rivicola</i> Kieffer	G	1	1	4	2	2	4	4	3	3	2	3	4	1	4	3	4	4	4	4	4	2	-
ORTH_MAL	<i>Orthocladius mallochi</i> Kieffer	G	1	-	-	1	1	1	3	3	3	2	2	1	1	2	2	3	1	1	1	1	-	1
ORTH_10P	<i>Orthocladius</i> sp. 10-P	G	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
THIE_1-P	<i>Thienemanniella</i> sp. 1-P	G	-	-	2	1	2	1	-	1	-	-	-	-	1	-	-	-	-	1	1	1	-	-
POLY_ALB	<i>Polypedilum albicorne</i> (Meigen)	D	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-
MICR_n6	<i>Micropsectra</i> n. sp. 6	D	-	-	-	1	1	1	-	-	-	1	1	-	-	1	-	1	-	-	-	-	-	1

was closer to sites downstream of outflows from Turquoise Lake and Twin Lakes (AR4, AR9, and AR10).

Species toward the top left of Figure 4 were most abundant at, or restricted to, upstream sites. *Diplocladius cultriger* was present below California Gulch but absent from the most contaminated sites. Several *Orthocladius* species

were associated with high sedimentary metal-loadings. *Krenosmittia camptophleps*, which lives among coarse gravel, was found above and below California Gulch but was absent at sites with the highest sedimentary Zn-loadings. Other species with an upstream distribution and which may be sensitive to high sedimentary Zn concentrations were *Eukiefferiella*

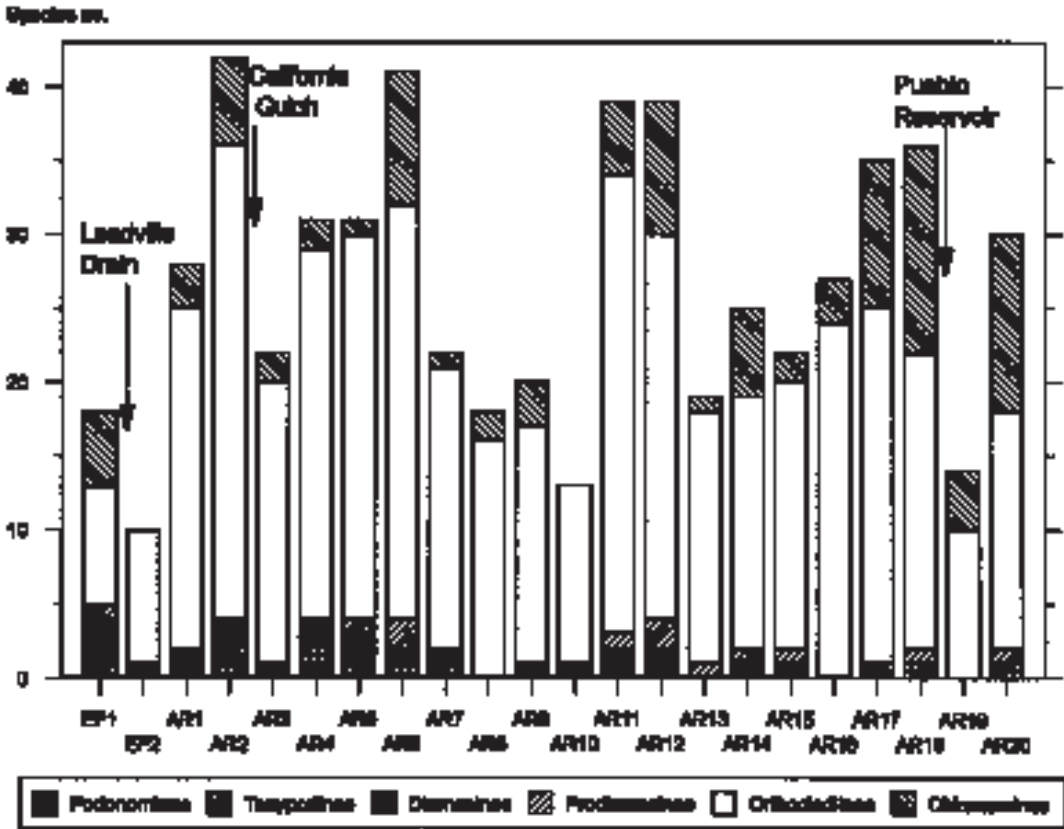


Fig. 2. Pupal subfamily species richness at each site.

main river, apparently unaffected by high Zn toxicity. In the bottom right quarter, *Cardiocladius platypus* was also present at most sites but particularly abundant below AR12 until Pueblo Reservoir. Some species found at downstream sites were also present upstream of AR5 and largely absent at the most toxic sites. These included *Eukiefferiella coerulea*, *E. sp. 5-P*, *Nanocladius spinipennis*, and *Phaenopsectra profusa*. In the lower half of Figure 4, the diamesine *Pagastia orthogonia*, the orthoclad *Brillia flavifrons*, *Cricotopus globistylus*, *Thienemanniella xena*, and *Orthocladus sp. 8-P*, and the chironomine *Demicyptochironomus (irmaki) n. sp. 1* were restricted to 2 or 3 sites at intermediate elevations from AR11 to AR13. These sites, in the driest part of the catchment, receive high inputs of dissolved major ions from soft sedimentary and carbonate rocks. *Parametrioctenus lundbeckii* was more widely distributed than these species but was most abundant at AR11 and AR12.

Species toward the far right of Figure 4 were more abundant downstream of AR11. The orthoclad *Cricotopus trifascia*, *C. blinni*, *Lopescladius hyporheicus*, and *Thienemanniella sp. 3-P* and several Chironominae were restricted to these downstream sites. Species located in the top right cluster were most associated with the 2 sites downstream of Pueblo Reservoir.

Adults

Seventeen surveys provided 3896 adult Chironomidae comprising 198 species. In addition, adult *Dianesa leona* Roback and *D. caena* Roback were collected nonrandomly from shelf ice and boulders during winter (Herrmann et al. 1987) and excluded from this analysis. Species abundances are presented in Table 3, with naming authors, for those species found at 2 or more sites, and rearranged by correspondence analysis. There was no obvious downstream trend in species richness (Fig. 5). Fluctuations resembled those exhibited by

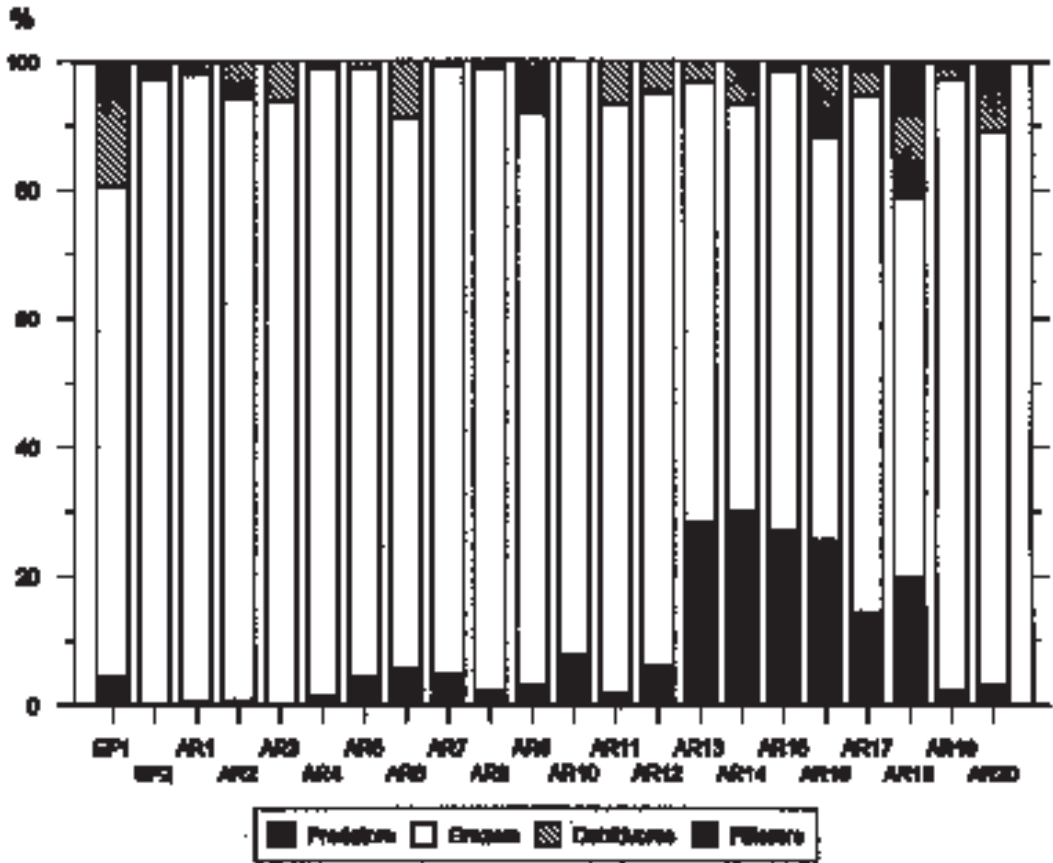


Fig. 3. Proportions of pupae classified by trophic group at each site.

pupal data except at sites AR5, AR7, and AR20. Species richness fell downstream of Iowa Gulch at AR5 and increased at the next 2 sites. Both Leadville Drain and California Gulch preceded falls in species richness while the poorest site was AR10. Species richness declined after Pueblo Reservoir, contrasting the recovery exhibited by pupae from AR20. Adult data confirmed the dominance by Orthocladiinae among pupal exuviae although species of Chironominae were relatively more abundant. Adult Diamesinae were found at all sites except AR18 (if *D. leona* is included), while Tanypodinae and Podoninae were also more widely collected compared with pupal data.

The relative abundance of Chironominae is reflected in the increased importance of detritivores in Figure 6 compared with pupal data. Grazers were dominant at all sites except AR5,

which was dominated by Chironominae, and at AR18 where they were the rarest trophic group. Grazers and detritivores were co-dominant at AR12. Filterers were an important component of the chironomid assemblage at AR18 but, as with pupal data, were absent below Pueblo Reservoir.

ORDINATION.—Latitude, Zn toxicity, and particle size were the only significant variables selected, explaining 22.3% of biological variability. Total Fe was interchangeable with Zn toxicity, but the latter was used to maintain comparability with pupal data. Only the 1st CCA axis was significant ($P = 0.01$), explaining 9.8% of all biological variation and 43.8% of the species-environment relationship. Length-wise variation, best explained by latitude, was again the dominant influence along the primary axis (t -value 19.2, correlation -0.94). Zn toxicity (t -value 2.3, correlation -0.44) and



Fig. 4. CCA ordination of pupal data. Arrows indicate importance and direction of maximum change in species composition among samples as the variable increases. Open circles used for sites, points for species. Species codes from Table 2.

particle size (t -value 6.3, correlation 0.11) were also significantly related to biological variation along the first axis.

There was no arch effect in Figure 7 because the first 2 axes were of similar importance (4.41 and 3.56 s units). A north-to-south distribution of sites occurred along the 1st axis, with lateral spreading of closely situated upstream sites. Sites with the highest Zn toxicity were positioned together in the top left of Figure 7, while the least toxic sites were placed diagonally opposite. Sites AR12–AR16 and AR19 had relatively large mean substratum

particle sizes and site EF1 had the smallest. Site AR10 had the largest particle size, but its position reflects the greater importance of latitude and Zn toxicity. The association between *Krenosmittia halvorseni* and the most Zn-toxic sites revealed by pupal data was supported by adult collections. Also in the top left of Figure 7, two cold-water adapted species, *Paracladius alpicola* and *Cladopelma viridula*, as well as *Orthocladius subletti* and *Polypedilum trigonum* were all present at AR7 (high Zn toxicity) and AR11. Adult *Micropsectra nigripila* were collected from East Fork downstream

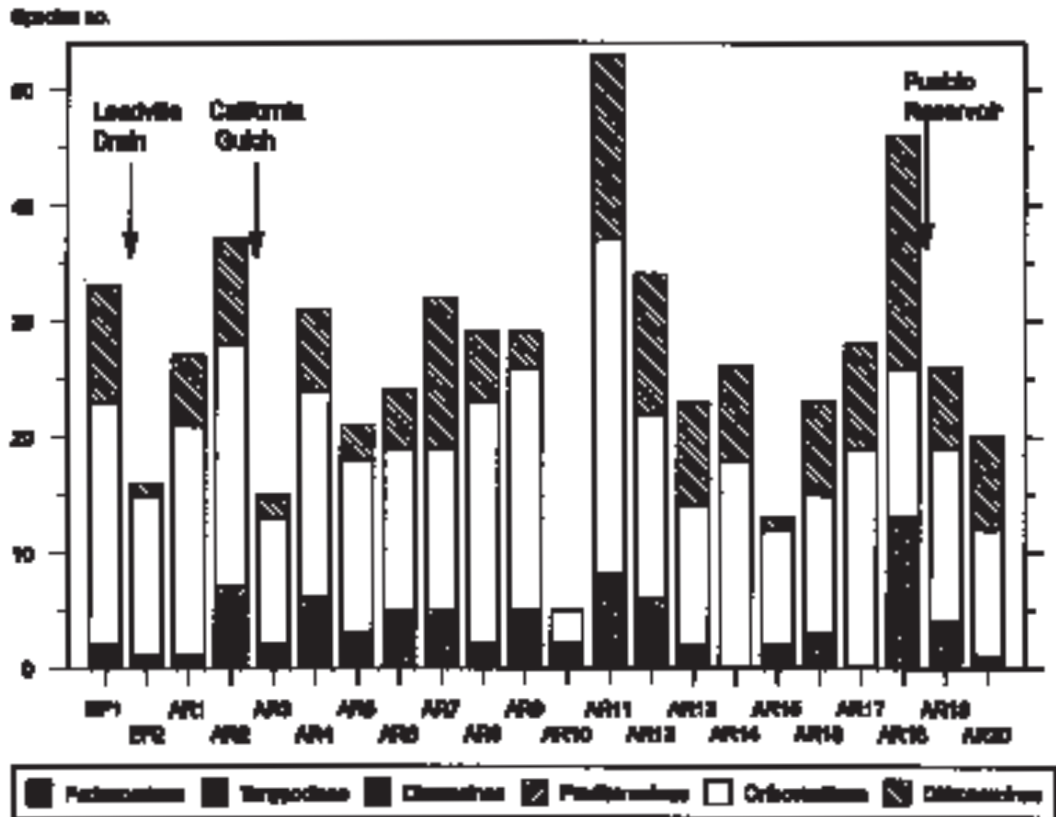


Fig. 5. Adult subfamily species richness at each site.

to AR16, dominating collections from AR5, whereas pupal exuviae were found only at AR11. *Gymnometriocnemus brumalis* is probably terrestrial; it was absent from pupal collections but adults were collected from AR4, AR5, and AR12, between 2000 and 3000 m. Adults of *Cricotopus coronatus* were found at sites with high Zn toxicity or at intermediate altitude. Both adult and pupal collections of *Orthocladus frigidus* and *O. nigrinus* indicated that these were montane species tolerant of Zn concentrations downstream of California Gulch.

Among downstream-distributed species located toward the lower right of Figure 7 were a few species that also occurred upstream of AR4. *Procladius subletti* and *Limnophyes* n. sp. 3 were collected at EF1 and AR2, respectively, were absent at the most Zn-toxic sites, and were present in the vicinity of Pueblo Reservoir. Pupal exuviae of *P. subletti*, however, were collected at AR6. Adult *Cricotopus*

bicinctus and *Parametriocnemus lundbeckii* were both widely distributed except at Zn-toxic sites; however, their pupal exuviae were found at toxic sites. Adult and pupal *C. infuscatus* had a downstream distribution but tolerated metals at AR8. *Smittia* n. sp. 3, *Polypedium digitifer*, and *Micropsectra logani* (pupae at AR6) were collected from the first 4 sites above California Gulch and then disappeared until AR17, or further downstream.

Independence of Sampling Method

In a test for association between pupal and adult data, $\chi^2 = 5908.5$, significantly ($P < 0.001$) exceeding the critical $\chi^2_{.05[65]}$ of 106.0 for associated data. Species most affected by the method of sampling were *Micropsectra nigripila* (pupae fewer than expected, adults greater), *Rheotanytarsus* n. sp. 1 (pupae greater, adults fewer), *Orthocladus rivicola* (adults fewer), *O. obumbratus* (adults greater), *Diamesa heteropus*

TABLE 3. Proportions of adult species collected at each site (see Table 2 for explanation).

Code	Species name	Trophic group	Site																						
			A 1	A 2	A 7	A 8	A 3	A 4	A 5	A 6	A 5	A 6	A 7	A 8	A 9	A 1	A 2	E 1	E 2	A 1	A 2	A 3	A 4	A 1	
LARS_PLA	<i>Larsia planensis</i> (Johannsen)	P	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
PARO_KIE	<i>Parochlus kiefferi</i> (Garrett)	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-
DIAM_DAV	<i>Diamesa davisi</i> Edwards	G	-	-	-	-	-	-	-	-	-	1	-	-	2	-	-	-	-	-	-	-	-	3	4
DIAM_SPI	<i>Diamesa spinacies</i> Sæther	G	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	2	3	
PAGA_ORT	<i>Pagastia orthogonia</i> Oliver	D	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-
PAGA_PAR	<i>Pagastia partica</i> (Roback)	D	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	1	-	
ODON_FER	<i>Odontomesa ferringtoni</i> Sæther	D	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	1	-	
HYDR_FUS	<i>Hydrobaenus fuscistylus</i> (Goetghebuer)	G	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	1	-	
ACRI_NIT	<i>Acricotopus nitidellus</i> (Malloch)	D	-	-	-	-	-	-	-	-	-	2	-	-	1	2	-	-	-	-	-	-	-	-	
BRIL_FLA	<i>Brillia flavifrons</i> Johannsen	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	3	1	-	1	-	
CRIC_BIF	<i>Cricotopus bifurcatus</i> Cranston & Oliv.	G	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	2	-	1	-	-
CRIC_TIB	<i>Cricotopus tibialis</i> (Meigen)	G	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	
CRIC_GLO	<i>Cricotopus globistylus</i> Roback	G	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	
EUKI_n4	<i>Eukiefferiella</i> n. sp. 4	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	
ORTH_FRI	<i>Orthocladus frigidus</i> (Zetterstedt)	G	-	-	-	-	-	1	-	1	2	1	4	2	1	-	3	4	1	-	-	-	3	-	
ORTH_SUB	<i>Orthocladus subletti</i> Soponis	G	-	-	-	-	-	-	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-		
ORTH_WIE	<i>Orthocladus wiensii</i> Sæther	G	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	2	-	-		
PARA_ALP	<i>Paracladius alpicola</i> (Zetterstedt)	G	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	
PARA_n3	<i>Paracladius</i> n. sp. 3	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	
PSEC_SPI	<i>Psectrocladius spinifer</i> (Johannsen)	G	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	1	-	
RHEOCRn1	<i>Rheocricotopus</i> n. sp. 1 (nr. chalybeatus)	G	-	-	-	-	-	-	-	-	1	-	1	1	1	-	1	-	1	-	-	-	-	-	
RHEO_EMI	<i>Rheocricotopus eminelobus</i> Sæther	G	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	1	2	1	1	-		
TOKU_ROW	<i>Tokunagaia rouensis</i> (Sæther)	D	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	3	-	-		
TVET_PAU	<i>Tvetenia paucunca</i> (Sæther)	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	1	1	-	-		
LIMN_ELT	<i>Limnophyes eltoni</i> (Edwards)	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	2	-	-		
LIMN_NAT	<i>Limnophyes natalensis</i> (Kieffer)	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1		
GYMN_BRU	<i>Gymnometriocnemus brumalis</i> (Edwards)	G	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	-	-	1	-	
KREN_n1	<i>Krenosmittia</i> n. sp. 1	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-		
KREN_HAL	<i>Krenosmittia halvorseni</i> (Cranston & Oliver)	G	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	
LIMN_n1	<i>Limnophyes</i> n. sp. 1	G	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	4	1	3	1		
LIMN_n2	<i>Limnophyes</i> n. sp. 2	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	-	1		
METR_BRU	<i>Metriocnemus brusti</i> Sæther	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	1		
LIMN_n4	<i>Limnophyes</i> n. sp. 4	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-		
PARAPSEU	<i>Paraphaenocladus pseudirritus</i> nearticus Sæther & Wang	D	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	3		
PARAPNAS	<i>Paraphaenocladus nasthecus</i> Sæther	D	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1		
SMIT_ATE	<i>Smittia aterrima</i> (Meigen)	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-		
SMIT_n1	<i>Smittia</i> n. sp. 1	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	2		
THIE_ELA	<i>Thienemaniella</i> spp.	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-		
CHIR_RIP	<i>Chironomus riparius</i> Meigen	D	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1	2		
CLAD_VIA	<i>Cladopelma viridula</i> (Linnaeus)	D	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-		
DICR_NER	<i>Dicrotendipes nervosus</i> (Staeger)	D	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1		
PARA_NIX	<i>Paracladopelma nixe</i> (Townes)	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-		
POLY_ALB	<i>Polypedilum albicorne</i> (Meigen)	D	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-	2	1	1	1		
POLY_TRI	<i>Polypedilum trigonus</i> Townes	D	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-		
TANY_Tn2	<i>Tanytarsus</i> n. sp. 2	D	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	-	1		
CRIC_COR	<i>Cricotopus coronatus</i> Hirvenoja	G	-	1	-	1	-	-	-	-	1	3	3	2	2	1	-	-	-	-	-	-	-	-	
CRIC_SLO	<i>Cricotopus slossonae</i> Malloch	G	-	-	1	-	-	-	-	-	1	-	1	1	1	-	1	1	1	-	1	1	1		
CRIC_SYL	<i>Cricotopus sylvestris</i> (Fabricius)	G	-	-	-	1	-	-	-	-	-	1	-	1	1	1	-	-	-	-	-	-	-		
EUKI_n9	<i>Eukiefferiella</i> n. sp. 9	G	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-		
ORTH_NIG	<i>Orthocladus nigrilus</i> Malloch	G	-	-	-	-	1	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	2		
LIMN_ASQ	<i>Limnophyes asquamatus</i> Andersen	G	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	1	-	-	1	-	1		
PSEU_FOR	<i>Pseudosmittia forcipata</i> (Goetghebuer)	G	-	-	-	-	1	-	-	-	-	-	-	-	1	-	2	-	-	-	-	-	1		

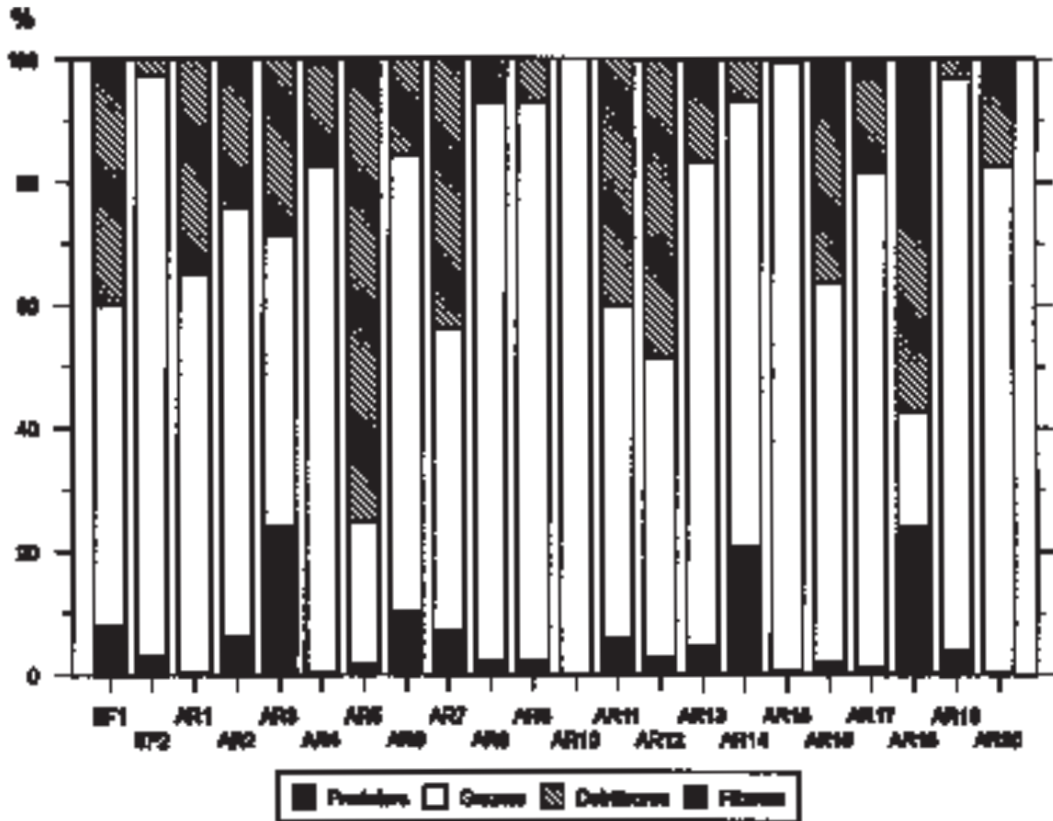


Fig. 6. Proportions of adults classified by trophic group at each site.

(adults greater), and *Polypedilum scalaenum* (adults greater). Species sampled equally well as pupae and adults (combined $\chi^2 < 1.6$) were *Pagastia partica*, *Cricotopus herrmanni*, *Tvetenia vitracea*, *Cricotopus blinni*, and *Phaenopsectra profusa*.

Effect of Classification Level

Generic adult data were ordinated to investigate the influence of taxonomic level because of the large number of species in this data set. Stepwise regression selected maximum water temperature, total Cu, and mean particle size, explaining 25.1% of generic adult chironomid variability. The first 2 axes were significant (both $P = 0.04$), together explaining 18.3% of biological variation. The primary axis was significantly explained by temperature (t -value 6.93), while all 3 variables significantly explained the 2nd axis, particle size being the least important. Despite the overlap of temperature and particle size vectors in Figure 8,

the 2 variables were independent (Pearson correlation -0.18 , $r_{.05[20]} = 0.42$) and all variance inflation factors were below 1.1. Sites were approximately ordered from warmest to coolest along the diagonal of the temperature vector in Figure 8. Almost at right angles was a gradient of metal contamination; AR3 had almost twice the Cu concentration of the next most contaminated samples from AR5 (Table 1). Except for AR3, sites were closer to the origin of Figure 8 than they were in a species CCA. No genera were solely associated with AR3; the closest genera were *Paraphaenocladius* (2 species used for adult CCA), *Metriocnemus* (1 sp.), and *Krenosmittia* (2 sp.). These genera were found at several upstream sites but particularly the most metal-contaminated (AR3–AR8). In the lower half of Figure 8, *Parametriocnemus* (1 sp.) exhibited metal intolerance revealed by species CCA, as did *Tvetenia* (2 sp.). Responses of other adult species,



Fig. 7. CCA ordination of specific adult data. Explanation as for Figure 4, species codes from Table 3.

previously highlighted as metal-intolerant, have been lost among the conflicting trends of their congeners within species-rich genera such as *Procladius* (4 sp.), *Cricotopus* (13 sp.), and *Polypedilum* (7 sp.). *Orthocladius* (8 sp.), *Chironomus* (4 sp.), *Eukiefferiella* (4 sp.), and *Diamesa* (4 sp.) were also central to the ordination because of counterbalancing species distributions. *Limnophyes* (7 sp.) was associated with low-temperature sites, as only 2 species appeared downstream of AR9, and in small proportions. *Micropsectra* was associated with metal-impacted sites due to the distribution of *M. nigripila* and *M. polita* and despite occurrences of *M. logani*.

DISCUSSION

Comparisons of Pupal and Adult Data

An unprecedented description of chironomid species distribution has been provided for 259 km of a major U.S. river. Proportional species abundances across the 22 Arkansas River sites were not equally represented by samples of pupal exuviae and adults. Greater proportions of adult detritivores indicated that sources of associated larvae may have included lentic, semi-terrestrial, and terrestrial habitats beyond the Arkansas River. The absence of small-bodied *Corynoneura* and

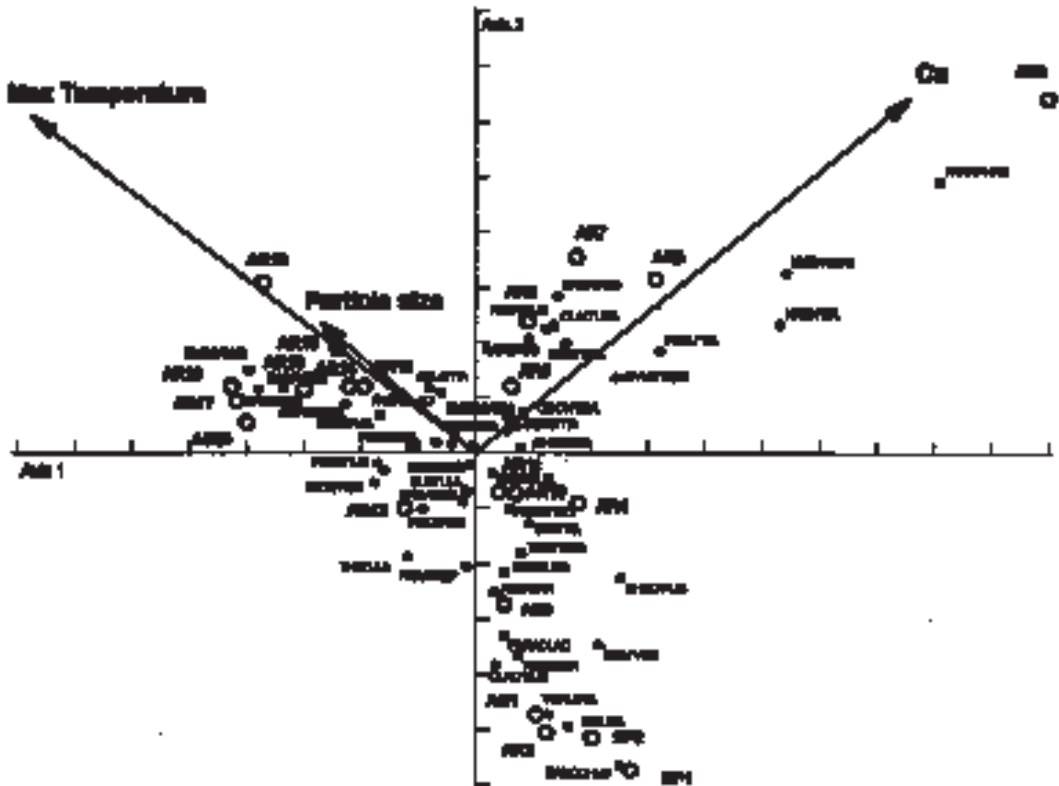


Fig. 8. CCA ordination of generic adult data. Explanation as for Figure 4.

Thienemanniella adults indicated that aerial nets were ineffective at catching these midges. The large proportion of predators among pupal data from sites AR13–AR18 was due to rheophilic *Cardiocladius platypus*, which may have been underrepresented in adult collections. Assuming adult data included individuals from external sources, this would explain why river-related environmental variables accounted for less biological variation than that achieved with pupal data. Despite discrepancies in expected numbers of species, there were similarities in species distribution between the 2 life stages. Examples cited were *Krenosmittia halvorseni*, *Orthocladus nigrinus*, *O. frigidus*, and *Cricotopus infuscatus*. Both pupal and adult collections revealed the presence of filterers upstream of Pueblo Reservoir and their absence downstream. Herrmann and Mahan (1977) found that turbidity at the outlet was typically lower than in the reservoir, or at the inlet, during the first 2 yr of its existence.

Site AR18 was observed to have faster current than sites below the reservoir. Species sampled equally well as adults and pupae may have had broad emergence patterns, being multivoltine or asynchronous. Cool-adapted *Diamesa heteropus*, as well as *Orthocladus obumbratus*, were underrepresented as pupae because their main emergence period had passed before pupal exuviae were collected. Adults of *O. obumbratus* were collected from AR16–AR20 while pupal exuviae were obtained from cooler stations at AR2–AR7. *Micropsectra nigripila*, the most abundant adult species, and *Polypedilum scalaenum* were also better represented in adult collections. Both species prefer lentic habitats and may have originated from extraneous sources. Rheophilic *Rheotanytarsus* n. sp. 1 and *Orthocladus rivicola* were the most abundant pupal species and were underrepresented in adult collections, probably because they were “diluted” by species from other sources.

Species Richness

Collections of pupal exuviae typically reveal greater species richness than direct sampling of stream habitats for larvae (Ferrington et al. 1991, Ruse 1995a). The present study obtained greater species richness from adult collections. This could be explained partly by adults originating from extrinsic habitats. Additionally, 17 months of adult sampling would increase the number of species obtained compared with 3 months of pupal sampling. The pupal total of 127 species compares favorably with species totals for other montane or subalpine streams presented in a review by Lindegaard and Brodersen (1995), which gave an average montane species total of 71 (range 26–144). The total of 200 adult species was not comparable with surveys of larvae or pupal exuviae because of their uncertain origin. Both pupal and adult data exhibited a decline in species richness at the 1st site below Leadville Drain and again below California Gulch, the major sources of metal pollution. Sites with the highest sedimentary concentrations of Zn, Pb, Mn, and Cd (AR5, AR7, AR8) had about average species richness. Other research on the effects of metal-polluted mine drainage on chironomids has demonstrated a reduction in species richness (Winner et al. 1980, Armitage and Blackburn 1985, Yasuno et al. 1985, Wilson 1988). Conversely, Cranston et al. (1997) demonstrated an increase in chironomid species richness below a mine adit, which they attributed to a greater pool of tolerant species in Australia compared with northern, temperate regions. Neither pupal nor adult data conformed to the downstream trend of increasing species richness found by Ward (1986) in a neighboring catchment. Pupal and adult data sets revealed a low number of species from site AR10, which had the coarsest substratum and a strong current. Clements and Kiffney (1994) reported a reduced macroinvertebrate species richness at a site approximately 10 km downstream of our site AR10. The next site downstream, AR11, had the highest number of adult species and the 3rd highest number of pupal species. Larvae of species avoiding sites with metal inputs (EF2, AR3) or with high physical stress (AR10) may have drifted through to the next site, increasing its species richness. The effect is less dramatic below California Gulch because of high sedimentary metal concentrations further downstream. Williams (1989), who pump-

sampled with 50- μ m-mesh nets, has suggested that Chironomidae actively redistribute themselves and colonize preferred habitats through drifting, particularly as 1st or 2nd instars. This behavior would explain the contrast in species richness between sites EF2 and AR1, AR3 and AR4/6, and AR10 and AR11.

Species Distribution and the Effect of Metals

Environmental measurements most correlated with a successive downstream turnover in species composition (distance/altitude, latitude, and temperature) were aligned with the primary CCA axis of both data sets. Pupal data best reflected a smooth downstream gradient in species turnover. In a neighboring river, Ward (1986) classified 4 zones of species assemblage related to altitudes between 3414 m and 1544 m, although chironomid taxa showed much greater overlap than did Plecoptera and Trichoptera. A longitudinal zonation among Chironomidae was suggested by Ward and Williams (1986) when Chironomini replaced Orthocladinae in a 36-km-long Canadian river. In the Arkansas River pupal Chironominae increased from AR17 downstream, except below the reservoir outlet, but there was no evidence for altitudinal zonation rather than succession. The most abrupt changes were anthropogenic: mining, regulation, and impoundment. In the pupal CCA, localized effects of metal pollution within a 20-km reach were overwhelmed by effects of downstream succession along 259 km of the river. The importance of altitude and latitude to macroinvertebrate species structure, mediated through their effect on temperature, has been demonstrated locally by Ward (1986) and globally by Jacobsen et al. (1997). Latitude was strongly related to distance but, because it changed most between sites EF1 and AR12, it also had a correlation with chironomid species variability among metal-polluted sites. Longitude varied most between sites AR13 and AR20, where there was relatively less species variability; consequently, it was never selected by forward regression after latitude had been chosen. In a study of 6 Colorado streams, including the Arkansas River, Clements and Kiffney (1995) found that altitudinal variation confounded the effects of metal on benthic macroinvertebrates. Using CCA, we noted that metal pollution still had a significant explanatory value in

our study, even when generic-level adult data were considered. Herrmann and Mahan (1977) found that metal-enriched water was reaching Pueblo Reservoir, and subsequent research by Kimball et al. (1995) confirmed that metal inputs, and their transportation, extend throughout 250 km of river. Sites AR3 and AR5–AR8 were extreme examples of metal pollution, whereas concentrations of sedimentary Zn at remaining sites were still high downstream to Pueblo Reservoir. The work of Kiffney and Clements (1993) revealed that macroinvertebrates bioaccumulated more Zn and Cd at site AR5 than at AR3 while the reverse was usually true for Cu. These results are in accord with distributions of chironomid species reported here.

Metal-tolerant assemblages of chironomid species below California Gulch are evident from Tables 2 and 3. Individual species were highlighted for their tolerance or intolerance, some of which have been connected previously with metal impacts by other researchers. In the English Pennines, Wilson (1988) found a high proportion of *Krenosmittia camptopleps* below a Zn-polluted mine adit although the species was absent from a neighboring river of the same catchment which was also Zn polluted. Wilson suspected that metal pollution alone was not determining species distribution. In the Arkansas River this species was replaced by its congener *K. halvorseni* at sites with the highest sedimentary Zn-loadings. In the same catchment studied by Wilson, *Orthocladius frigidus* was found by Armitage and Blackburn (1985) in moderately Zn-polluted sites (0.77–1.68 mg L⁻¹) but was absent at higher concentrations (2.08–7.6 mg L⁻¹). *O. frigidus* reached its highest proportions at sites AR4 and AR8; these sites have recorded suspended Zn concentrations within the moderate range (Roline and Boehmke 1981, Kimball et al. 1995) but could be exposed to higher concentrations in spring (Clements 1994). The study of Elam's Run in Ohio by Winner et al. (1980) provided evidence of metal tolerance for several Arkansas River species that inhabited sites AR3–AR8: *Orthocladius dubitatus*, *O. obumbratus*, *Cricotopus bicinctus*, *C. infuscatus*, *Diplocladius cultriger*, and *Larsia planensis* (adult). Waterhouse and Farrell (1985) drew attention to *C. bicinctus* being succeeded by *C. infuscatus* along a gradient of declining metal pollution in Elam's Run. *C. bicinctus*

was a minor component of the Arkansas River chironomid assemblage, even at the most metal-polluted sites. *C. bicinctus* did appear below Leadville Drain at EF2 (adults) and below California Gulch at AR5 and AR7 (pupae), while *C. infuscatus* did not appear until AR8 with a predominantly downstream distribution (pupae and adults). *C. slossonae* was absent from the 2 most metal-polluted sites on Elam's run, but was present at all the most polluted Arkansas River sites. *Eukiefferiella claripennis* was not found in Elam's Run, but its presence at Zn-polluted sites was recorded by the 2 English studies mentioned (Armitage and Blackburn 1985, Wilson 1988) and was tolerant of severely Cu-contaminated (>50 µg L⁻¹) streams in southwest England (Gower et al. 1994). *E. claripennis*, distributed extensively along the Arkansas River, was subdominant to *Orthocladius* species within pupal collections at the most metal-polluted sites.

Species indicated as intolerant of severe heavy-metal pollution included some new species: *Eukiefferiella* n. sp. 9, *E. sp. 5-P*, *Limnophyes* n. sp. 3, and *Tanytarsus* n. sp. 5. *E. coerulea* avoided the most toxic sites and was also reported by Wilson (1988) to be absent at Zn-polluted sites. Specific comparison of metal tolerance, especially across widely separated river systems, has its limitations. Postma et al. (1995) have demonstrated that chironomid populations from metal-polluted rivers can exhibit less sensitivity to some metals compared with conspecifics derived from unpolluted sites. They suggest this has a genetic basis.

Future Study

This study of the Arkansas River during 1984–85 provides a reference for assessing changes that have occurred since remediation work began in 1991. Now that Leadville mines have ceased operating, subsequent monitoring of chironomid species distribution would record how the Arkansas River responds. Biomonitoring using generic-level data would save time, provided there was no significant loss of information. Generic data reduced the amount of unexplained species variation that probably arose from the uncertain origin of the rarer adult species. There was more homogeneity of generic assemblages between sites, although sensitivity to Cu pollution, or perhaps suspended metals, was greater than with specific

data. Generic data revealed the same 2 major gradients, of longitudinal variation and metal contamination, identified by specific adult and pupal data. Multivariate analysis of 10 benthic macroinvertebrate data sets by Bowman and Bailey (1997) led them to suggest that if trade-offs were necessary to investigate community variation, it would be better to sacrifice taxonomic resolution than quantitative data. An analysis of specific- and generic-level chironomid data along a metal-pollution gradient by Waterhouse and Farrell (1985) revealed good agreement when using nonspecific diversity indices, but important information was lost if indicators within species-rich genera were relied upon. The importance of specific identification of chironomid indicators of metal pollution was stressed by Gower et al. (1994) using CCA, although this was addressed to researchers relying on subfamily chironomid data. The metal-related distribution of several species belonging to the genera *Cricotopus*, *Orthocladius*, and *Eukiefferiella* would have been lost if identification of Arkansas River pupae and adults had been generic only. Even among 2 species of *Krenosmittia*, pupal data revealed a distinct difference in metal-related distribution. Generic data would be adequate for a large-scale description of environmental influences but would have diminished value when monitoring recovery of individual sites.

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APPENDIX. Species found at only 1 site, either as pupal exuviae or adults. Listed in alphabetical order within tribes.

Species name	Pupa/Adult	Site
<i>Derotanyptus alaskensis</i> (Malloch)	A	AR3
<i>Psectrotanyptus dyari</i> (Coquillet)	A	AR7
<i>Radotanyptus submarginella</i> (Sublette)	A	AR11
<i>Ablabesmyia basalis</i> (Walley)	A	AR7
<i>Ablabesmyia monilis</i> (Linnaeus)	A	AR11
<i>Ablabesmyia</i> sp.	A	AR2
<i>Conchapelopia pallens</i> (Coquillet)	P	AR18
<i>Pentaneura inconspicua</i> (Malloch)	A	AR18
<i>Telopelopia okoboji</i> (Walley)	A	AR18
<i>Thienemannimyia barberi</i> (Coquillet)	A	AR18
<i>Thienemannimyia senata</i> (Walley)	A	AR18
<i>Zavrelinyia</i> sp. 1-P	P	AR4
<i>Procladius prolongatus</i> Roback	A	AR11
<i>Procladius ruris</i> Roback	A	AR7
<i>Tanyptus neopunctipennis</i> Sublette	A	AR18
<i>Tanyptus nubifer</i> Coquillet	A	AR18
<i>Tanyptus stellatus</i> Coquillet	A	AR18
<i>Diamesa garretti</i> Sublette & Sublette	A	AR12
<i>Prodiamesa olivacea</i> (Meigen)	A	AR2
<i>Cardiocladius</i> n. sp. 2	A	AR14
<i>Cricotopus intersectus</i> (Staeger)	A	AR19
<i>Cricotopus lestralis</i> (Edwards)	A	AR6
<i>Cricotopus sylvestris</i> (Fabricius)	P	AR12
<i>Cricotopus tricinctus</i> (Meigen)	A	AR5
<i>Cricotopus trifasciatus</i> (Panzer)	A	AR5
<i>Cricotopus vierriensis</i> Goetzghebuer	P	AR12
<i>Cricotopus</i> n. sp. 18	A	AR8
<i>Cricotopus</i> sp. 14-P	P	AR4
<i>Cricotopus</i> sp. 15-P	P	AR2
<i>Cricotopus</i> sp. 18-P	P	AR12
<i>Cricotopus</i> sp. 20-P	P	AR11
<i>Cricotopus</i> sp. 21-P	P	AR20
<i>Eukiefferiella brevineris</i> (Malloch)	A	AR4
<i>Eukiefferiella</i> n. sp. 4	P	AR11
<i>Eukiefferiella</i> n. sp. 8	A	AR9
<i>Eukiefferiella</i> sp. 10-P	P	AR17
<i>Heterotrissocladius</i> sp.	A	AR7
<i>Nanocladius anderseni</i> Saether	A	AR17
<i>Nanocladius distinctus</i> (Malloch)	A	AR17
<i>Nanocladius rectinervis</i> (Kieffer)	A	AR15
<i>Orthocladius anteilis</i> (Roback)	A	AR15
<i>Orthocladius appersoni</i> Soponis	A	AR15
<i>Orthocladius carlatus</i> (Roback)	A	AR11
<i>Orthocladius dorenius</i> (Roback)	A	AR1
<i>Orthocladius holsatus</i> Goet	A	AR2
<i>Orthocladius nanseni</i> Kieffer	P	AR11
<i>Orthocladius trigonolabis</i> Edwards	P	AR5
<i>Orthocladius</i> sp. 13-P	P	AR19
<i>Paracladius conversus</i> (Walker)	P	EF1
<i>Paratrichocladius skirwithensis</i> (Edwards)	A	EF1
<i>Psectrocladius vernalis</i> (Malloch)	A	AR16
<i>Rheocricotopus chapmani</i> (Edwards)	A	AR11
<i>Metriocnemus</i> n. sp. 2	A	AR6
<i>Metriocnemus</i> n. sp. 5	A	AR11
<i>Limnophyes hastulatus</i> Saether	A	AR2
<i>Corynoneura</i> sp. 2-P	P	AR1
<i>Lopescladius hyporheicus</i> Coffman & Roback	A	AR16
<i>Parakiefferiella subaterrima</i> (Malloch)	P/A	EF1/AR20
<i>Paraphaenocladius exagitans</i> (Johannsen)	A	AR11
<i>Paraphaenocladius tonsuratus</i> Saether & Wang	A	AR5
<i>Smittia polaris</i> (Kieffer)	A	AR8
<i>Smittia</i> n. sp. 2	A	EF1
<i>Rheosmittia</i> sp. 1-P	P	AR1

<i>Thienemanniella similis</i> (Malloch)	P	AR1
<i>Thienemanniella xena</i> (Roback)	A	AR18
<i>Thienemanniella</i> n. sp. 2	P/A	AR16/AR17
<i>Thienemanniella</i> sp. 6-P	P	AR11
<i>Chironomus stigmaterus</i> Say	A	AR20
<i>Chironomus</i> n. sp. 5	A	AR20
<i>Chironomus</i> n. sp. 8	A	AR12
<i>Cladopelma</i> sp. 4-P	P	AR6
<i>Cryptochironomus fulvus</i> (Johannsen)	A	AR18
<i>Cryptochironomus</i> sp.	P	AR17
<i>Cryptotendipes casuarina</i> (Townes)	A	AR11
<i>Cryptotendipes</i> sp. 2-P	P	EF1
<i>Cyphomella gibbera</i> Saether	A	AR18
<i>Demicryptochironomus (irmaki)</i> n. sp. 1	A	AR18
<i>Dicrotendipes crypticus</i> Epler	A	AR18
<i>Dicrotendipes lobiger</i> (Kieffer)	A	AR2
<i>Dicrotendipes modestus</i> (Say)	A	AR18
<i>Glyptotendipes</i> sp.	A	AR19
<i>Microtendipes caelum</i> Townes	A	AR11
<i>Nilothauma babiji</i> (Rempel)	A	AR14
<i>Parachironomus abortivus</i> (Malloch)	A	AR18
<i>Parachironomus arcuatus</i> (Goetghebuer)	A	AR18
<i>Parachironomus directus</i> (Dendy & Sublette)	A	AR19
<i>Parachironomus tenuicaudatus</i> (Malloch)	A	AR19
<i>Paracladopelma undine</i> (Townes)	A	AR11
<i>Paracladopelma</i> n. sp. 2	P	AR17
<i>Paracladopelma</i> sp. 4-P	P	AR6
<i>Paratendipes fuscitibia</i> Sublette	A	AR7
<i>Paratendipes subequalis</i> (Malloch)	A	AR6
<i>Paratendipes thermophilus</i> Townes	P	AR17
<i>Polypedilum artifer</i> (Curran)	A	EF1
<i>Polypedilum fuscipenne</i> (Meigen)	A	AR12
<i>Polypedilum illinoense</i> (Malloch)	P/A	AR18/AR18
<i>Polypedilum pedatum</i> Townes	A	AR12
<i>Polypedilum scalaenum</i> (Schrank)	P	AR16
<i>Polypedilum</i> sp. 2-P	P	AR18
<i>Polypedilum</i> sp. 8-P	P	AR18
<i>Polypedilum</i> sp. 9-P	P	AR17
<i>Stictochironomus varius</i> (Townes)	A	AR19
<i>Pseudochironomus rex</i> Hauber	A	AR12
<i>Robackia claviger</i> (Townes)	P/A	AR17/AR18
<i>Stictochironomus annulicrus</i> (Townes)	A	AR2
<i>Stictochironomus</i> n. sp. 1	P/A	AR18/AR18
<i>Pseudochironomus pseudoviridis</i> (Malloch)	A	AR18
<i>Cladotanytarsus</i> n. sp. 2	A	AR6
<i>Cladotanytarsus</i> n. sp. 3	A	AR2
<i>Cladotanytarsus</i> sp. 3-P	P	AR2
<i>Micropsectra logani</i> (Johannsen)	P	AR6
<i>Micropsectra nigripila</i> (Johannsen)	P	AR11
<i>Micropsectra</i> n. sp. 3	A	AR4
<i>Micropsectra</i> n. sp. 5	A	AR2
<i>Micropsectra</i> n. sp. 6	A	EF1
<i>Paratanytarsus dubius</i> (Malloch)	A	AR12
<i>Paratanytarsus similatus</i> (Malloch)	A	AR11
<i>Paratanytarsus tenuis</i> (Meigen)	A	AR11
<i>Paratanytarsus</i> n. sp. 1	A	AR7
<i>Stempellinella</i> sp. 1-P	P	AR12
<i>Sublettea coffmani</i> (Roback)	A	AR1
<i>Tanytarsus bathophilus</i> Kieffer	A	AR11
<i>Tanytarsus fimbriatus</i> Reiss & Fittkau	A	AR11
<i>Tanytarsus pallidicornis</i> (Walker)	A	AR12
<i>Tanytarsus</i> n. sp. 1	A	AR20
<i>Tanytarsus</i> n. sp. 6	P	AR12
<i>Tanytarsus</i> n. sp. 13	A	AR7
<i>Tanytarsus</i> sp. 2-P	P	AR6
