Growth and secondary production of aquatic insects along a gradient of Zn contamination in Rocky Mountain streams

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Abstract. Secondary production estimates from several Rocky Mountain streams were used to test hypotheses about the effects of chronic metal contamination on insect populations and ecosystem processes. Quantitative samples of chemistry, habitat, and benthic insects were collected monthly during the ice-free period (May–November) from five 2nd- to 3rd-order streams that varied primarily in Zn contamination. Secondary production was estimated for the 19 dominant taxa using increment-summation, size-frequency, and P/B methods. Uncertainty was estimated by bootstrapping estimates of mean abundance, biomass, and cohort production intervals. Secondary production of metal-sensitive Heptageniidae (*Rhithrogena robusta*, *Cinygmula* spp., and *Epeorus longimanus*) was lower in lightly to moderately contaminated streams than in reference streams. Experiments were done to determine whether herbivore growth was influenced by food quality in contaminated streams. Growth estimates from field and microcosm experiments revealed that low mayfly production in contaminated streams was caused mostly by reduced population abundances. Production of predatory stoneflies was also lower in contaminated streams than reference streams. Estimates of the trophic basis of production revealed that, although the relative contribution to community production from various food sources was similar among streams, total production attributable to algae and animal prey declined in contaminated streams. Much of the reduction in herbivory in contaminated streams was the result of lower production of heptageniids, especially *R. robusta*. Assemblage and taxon-specific estimates of secondary production were sensitive to variation in metal contamination and indicated that relatively low metal concentrations may have ecosystem-wide consequences for energy flow.

Key words: secondary production, stream insects, growth, metals, Rocky Mountains.

Our understanding of how contaminants affect stream ecosystems is based largely on studies of community structure. Various metrics or indices of community structure are popular indicators of ecological responses to anthropogenic stressors (Resh and Jackson 1993). Researchers tend to rely on structural measures of ecological response for at least 2 reasons. First, relative to process or functional measures, estimates of biological structure require less effort. Indeed, many functional measures require measurements taken over long time periods. Second, many researchers perceive that functional indicators are less sensitive to perturbations than structural ones because functional redundancy has been observed in some ecological processes (Schindler 1987, Howarth 1991). Although our understanding of the relationships between ecosystem structure and function is limited (Frost et al. 1995, Covich 1996, Grime 1997), changes in ecosystem structure do not appear to vary concomitantly with ecological

functioning (Lawton 1994, Frost et al. 1995, Grime 1997). Consequently, structural measures alone may provide an incomplete understanding of ecosystem responses to contaminants. Studies that simultaneously examine structure and function (e.g., Schultheis et al. 1997) enhance our understanding of how human activities affect stream ecosystems and also provide insight into the roles of species in ecosystems (Benke and Wallace 1997).

Secondary production is a functional measure of population dynamics that provides insights into individual-, population-, and ecosystem-level processes. Individual bioenergetic processes are manifested as growth rates, which equate to population production when summed across a population (Benke et al. 1988). Secondary production measures the ultimate somatic and reproductive output of a population and is a measure of energy flow through a population. When combined with data on trophic interactions between populations, secondary production represents energy flow through a food web (Benke and Wallace 1997, Hall et al. 2000, Huryn and Wallace 2000). Analyses of secondary production have provided insight into population and

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foodweb dynamics (Benke 1993, Hall et al. 2000), but their application in studies of anthropogenic stress is rare (Benke 1984). Notable examples include the use of secondary production to assess the effects of a pesticide manipulation (Lugthart and Wallace 1992, Whiles and Wallace 1995) and urbanization (Shieh et al. 2002) on stream communities.

Metals from abandoned mines are a dominant environmental stressor in western stream ecosystems (Caruso and Ward 1998, Clements et al. 2000). Most research has examined the influence of metals on community structure and has supported one or more of the following generalizations. First, heptageniid mayflies are often the insect taxon most sensitive to metal exposure (Clements et al. 2000). Second, with the possible exception of some predatory species, stoneflies are generally more tolerant to metals than mayflies (Kiffney and Clements 1994, Clements et al. 2000). Third, insect assemblages at contaminated sites are dominated by a few tolerant species that rapidly colonize disturbed habitats (Leland et al. 1989). Fourth, periphyton communities are sensitive to metals and revert to early successional stages dominated by tolerant species in contaminated environments (Medley and Clements 1998). These patterns are observed consistently in metal-contaminated systems and offer a useful tool for quantifying the severity of biological degradation. The effects of metal contamination on ecological processes are rarely studied, but community metabolism (Hill et al. 1997) and leaf-litter breakdown (Schultheis et al. 1997) are some exceptions.

The purpose of our study was to determine whether secondary production of stream insect populations is influenced by metal contamination. Populations that persist in chronically contaminated environments may suffer from reductions in food quality (Medley and Clements 1998) or sublethal effects of chemical detoxification on metabolism and growth (e.g., cost of tolerance, sensu Wilson 1988, Mulvey and Diamond 1991). Secondary production is the product of population biomass and individual growth rates, so we examined contaminant-induced variation in these processes as probable mechanisms for observed patterns in production. In addition, we used the trophic basis of production to assess potential effects of metal contamination on stream trophic dynamics. We proposed 3 hypotheses about how metal contamination should influence secondary production and energy flow through populations. 1) Population production should change in response to changes in population abundance, but community production should not change except in highly contaminated streams; 2) Metal-induced degradation of periphyton food quality should reduce growth rates of grazing mayflies; and 3) Losses of heptageniid mayflies should reduce the relative importance of autochthonous energy to the food web.

Methods

Study sites

Our study was conducted in 5 streams in central Colorado (Fig. 1). These streams drain high gradient watersheds that are U-shaped glacial valleys with sparse soil development and vegetative cover. About 25% of the land cover is bare rock, which is confined to the highest elevations (up to 4300 m asl). The dominant terrestrial habitat type is a mixture of subalpine tundra and alpine willow (*Salix* spp.). Scattered evergreens occur in valley bottoms at lower (<3300 m asl) elevations. Loamy, skeletal soils thinly cover bedrock, which is composed mostly of metamorphic gneisses or felsic composites. Streams are covered by ice and snow for 6 to 7 mo each year, followed by a characteristic snow-melt-driven hydrograph throughout the rest of the year. The streams are predominately riffle habitats with small to large cobble.

Preliminary sampling was used to select streams that varied in metal contamination but were otherwise similar in habitat and physicochemical characteristics. Five-hundred m study reaches that were similar in elevation and valley form were selected on each stream. Watershed area and slope, stream gradient, mean pH, channel width, annual degree days, and elevation varied $<1.5\times$ among study streams (Table 1). Median discharge and conductivity varied $\sim2\times$. In contrast, mean annual alkalinity varied $28\times$ and Zn concentrations varied $12\times$ among streams. Mean daily temperature ranged from 0°C (November–April) to 11°C (August) (DMC, unpublished data). Average temperatures of contaminated streams were within the range observed in reference streams. Zinc concentrations in reference streams were generally below
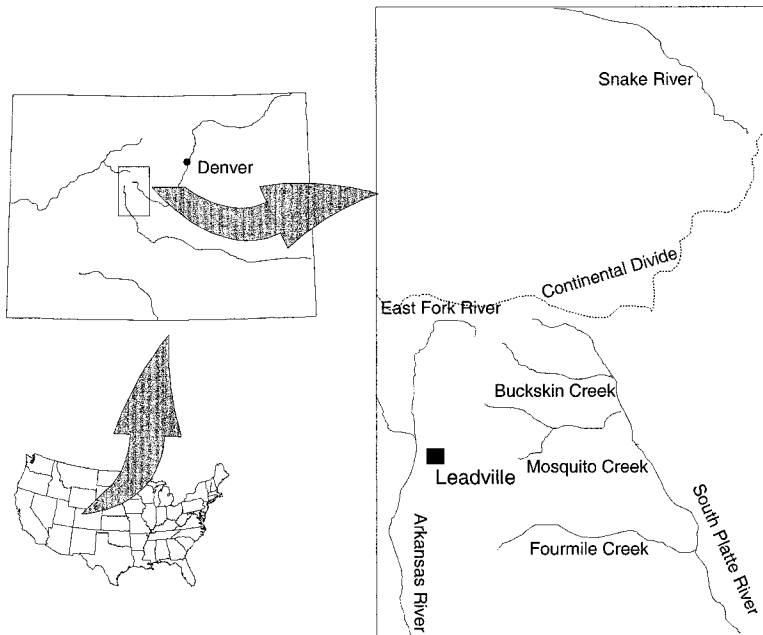
FIG. 1. Location of study streams in central Colorado.

TABLE 1. Environmental conditions of 5 study streams in central Colorado, May 1998 to May 1999. Zn ratio = the ratio of measured dissolved Zn concentrations to the US Environmental Protection Agency hardness-adjusted chronic criterion value. Annual ranges are given for chemical measures.

Stream	East Fork	Fourmile	Buckskin	Mosquito	Snake
Metal category	Reference 1	Reference 2	Low	Intermediate	High
Mean annual dissolved Zn (µg/L)	36	56	105	210	293
	14–105	20–102	54–228	68–442	122–447
Mean annual Zn ratio	0.8	0.6	1.7	2.6	7.1
	0.3–3.3	0.3–1.5	0.6–3.2	1.4–4.9	3.8–8.8
Mean annual alkalinity (mg/L)	34	114	55	70	4
	19–55	64–180	28–119	37–112	0–10
Mean annual hardness (mg/L)	57	125	84	104	45
	24–108	80–226	40–154	46–162	17–62
Mean annual conductivity (µS/m)	119	237	169	200	117
	39–225	146–280	70–253	65–290	48–153
Mean annual pH	7.4	8.0	7.8	7.9	6.7
	6.7–8.5	7.5–8.9	7.1–9.0	7.4–9.0	5.7–8.2
Mean annual temperature[a] (°C)	3.5	2.7	2.8	3.3	3.0
Annual degree days	1201	918	939	1089	1007
Elevation (m asl)	3202	3283	3217	3249	3144
Watershed area (km²)	31.2	23.3	22.1	32.2	29.0
Mean stream gradient (°)	25	22	30	26	26
Median discharge (m³/s)	0.168	0.241	0.270	0.428	0.198
Mean channel width (m)	3.57	3.86	4.16	3.96	4.81

[a] Mean annual water temperature based on continuous (2 h) measurements

the US Environmental Protection Agency (USEPA) criterion for chronic toxicity, whereas concentrations in the low Zn stream were ~2× the chronic criterion. Zinc levels were 2 to 4× the chronic criterion in the intermediate Zn stream and up to 9× the chronic criterion value in the high Zn stream (Table 1). Although Zn is the dominant metal contaminant in these streams, it most often occurs in a mixture with Cd and Cu (Clements et al. 2000). Many metal-contaminated streams in mining regions also are affected by metal precipitates on the substrate (McKnight and Feder 1984), but this type of degradation was not present in our study streams.

Water chemistry

Water chemistry was measured bimonthly from May to October and monthly during the remainder of the year. On each sampling occasion, pH and conductivity were measured with hand-held probes (Quickchek® models 106, 116, Orion Research, Inc., Beverly, Massachusetts). A 15 mL grab sample was filtered (0.45 μm) for dissolved metal analysis and immediately acidified to pH <2.0 with concentrated nitric acid. A 1 L grab sample was taken from a riffle area, stored on ice, and returned to the laboratory for analysis of alkalinity and total hardness using standard methods (APHA 1992). Analyses for Cd, Cu, and Zn were performed on an atomic absorption spectrophotometer (minimum detection limit 1 μg/L). Metals data are reported only for Zn because concentrations of Cd and Cu were at or below analytical detection limits. Zinc concentrations were standardized using the hardness-adjusted chronic criterion value set by USEPA (CDPHE 1999) because metal toxicity varies with water hardness. The ratio of the measured metal concentration to the chronic criterion value was calculated for each sample date. The chronic criterion value represents a threshold below which aquatic life should be unaffected, so ratios >1 indicate potential toxic effects.

Habitat variables

Discharge was estimated bimonthly from May to October and monthly during the remaining ice-free period. Water velocities (cm/s) were measured with a flow meter (Marsh–McBirney model 200, Fredrick, Maryland) at 20 cm intervals across the stream in a section of the channel with a minimum of turbulent flow and eddies. Depth to the nearest cm also was measured at each point, and discharge (m^3/s) was calculated using the continuity equation (Gore 1996). Ice and snow prevented discharge measurements from November to April, so average winter discharge was equated to the mean of the November and April estimates.

Temperature was monitored continuously (every 2 h) with data loggers (Optic Stow-Away®, Onset Computer Corp., Pocasset, Massachusetts). Stream channel width was measured during low flow as the width of the wetted channel at 10 equally spaced (10 m) transects throughout the study reach. Basin size, stream slope, and elevation of each basin were estimated with digital elevation models and topographic maps (1:24,000 scale) published by the US Geological Survey.

Benthic invertebrates

Sampling and processing.—Quantitative benthic macroinvertebrate samples were collected monthly from May to November. Five 0.1 m^2 samples were collected in riffle areas with a Hess sampler (150 μm Nitex® net) and preserved in 5% formalin. In the laboratory, each sample was placed in a white enamel pan and large (>1–3 mm) and rare animals were removed and counted. Large pieces of organic debris were removed and discarded, and the remainder of each sample was spread evenly across a small plastic tray. Subsamples were taken with randomly placed cores (2 cm diameter) that each removed 8% of the total volume. Initially, 3 subsamples were taken, and animals were removed and counted under 40× magnification. Additional subsamples were taken until ~300 individual insects had been removed (Elliott 1971). Animals were identified to species (subfamily for midges) and body lengths of ≥50 (when available) randomly selected individuals were measured to the nearest 0.1 mm using an ocular micrometer. Family and generic length–mass relationships of Benke et al. (1999) were used to convert body length measurements to dry mass.

Production calculations.—Secondary production was estimated using 3 methods, with some modifications because of our inability to sample

during winter. The increment summation method (Benke 1996) was used for taxa that exhibited distinct cohorts based on length–frequency analyses. The size–frequency method (Benke 1996) was used for all other insects, with the exception of chironomids. Estimates of the cohort production interval (CPI) for these taxa were obtained from our own length–frequency analyses or from the literature (DeWalt et al. 1994, DeWalt and Stewart 1995). Because the study streams were frozen and inaccessible from November to May, the average of the last (usually November) sample in the fall and the first (usually May) sample in the spring was used to estimate biomass (increment summation method) or length frequencies (size–frequency method) for winter months. Most taxa exhibited little or no growth during this period.

Chironomid larvae generally did not exhibit distinct cohorts over our sampling invervals. However, chironomid cohorts could be identified in one stream, so data from that stream were used to calculate production in a variety of ways to determine which method would be most appropriate for all streams. Production estimates obtained with the increment summation method, production/biomass (P/B) ratios, and empirical models (Benke 1993) differed by <50%. In contrast, production estimates using instantaneous growth (Huryn and Wallace 1986) were 5 to 6× higher than the other methods. Literature estimates of temperature-specific growth rates for Chironomidae (e.g., Huryn 1990, Huryn and Wallace 1986, Hauer and Benke 1991) established in the eastern US probably overestimate production in Colorado alpine streams because of differences in temperature, taxonomic composition, and overall system productivity. Therefore, annual P/B ratios from the literature (Tokeshi 1995) were used to calculate chironomid production in all streams. Estimates of P/B ratios of Orthocladiinae common at high latitudes were 1.4 to 2.3 (Tokeshi 1995). Orthoclads were common in our study sites, so this range of P/B ratios was used to estimate production and uncertainty for Orthocladiinae. Frequency distributions of reported P/B ratios for Chironominae had a mode from 1 to 3 (Tokeshi 1995), particularly for taxa known to be merovoltine, so this range of P/B values was used to calculate production and uncertainty for Chironominae.

Uncertainty associated with production estimates was quantified with a bootstrapping procedure (e.g., Brey 1990, Huryn 1996). Bootstrapping is a nonparametric resampling procedure used to estimate sampling variance of variables with complex or unknown frequency distributions and in situations where adequate replication is logistically difficult (Efron 1982). All data used to estimate production were randomly resampled 1000 times with replacement (Wilkinson and Engelman 1996). These data were then used to calculate 1000 estimates of biomass and production. For the size–frequency method, CPI also was resampled from a distribution of estimates obtained from the literature (Huryn 1996). Random values of P/B within the ranges reported from the literature were used for chironomids. Vectors of 1000 estimates were then used to calculate approximate 95% confidence intervals for production using the bias-corrected percentile method (Meyer et al. 1986).

Trophic analysis.—The trophic basis of production was estimated by assigning production of populations to various food sources based on diet analyses. Diet analyses were performed differently for non-predators and predators. Non-predator foreguts were removed with surgical scissors, and the homogenized contents were mounted onto microscope slides (CMC-10® mounting medium, Master Chemical, Elk Grove, Illinois). The guts of larger insects (>5 mm) were mounted individually, but guts of ≤20 individuals of smaller taxa often were combined and homogenized. The gut contents of ≥30 individuals from each taxon were represented for each sampling date (usually 3/season). Chironomids were mounted whole using CMC-10®, which increases the transparency of soft tissues and allows observation of gut contents. Each slide was systematically scanned at 200× magnification using a compound microscope with an ocular grid. One thousand grid cells/slide were categorized based on the particle type with the greatest areal coverage within the cell. Food categories included: diatoms, other algae, animal matter, fine detritus, and coarse detritus. The mean frequency of each food category was used to estimate the proportion of that item in the diet. For predators, guts of individual animals were removed as previously described, and the contents were examined using a dissecting scope at 40× magnification. Intact heads and whole organisms were then identified to genus or subfamily, and body

length was measured or estimated (in cases where only head capsules or parts of bodies remained). Body length was converted to dry mass using the equations of Benke et al. (1999) to calculate the relative biomass of each prey species.

The methods of Benke and Wallace (1980) were used to estimate the trophic basis of production. Net production efficiency and assimilation efficiencies were not measured directly. Therefore, average values from the literature (Benke and Wallace 1980, Huryn 1996) were used, and net production efficiency was assumed to be 0.54 for all populations. The same literature was used for values of food-specific assimilation efficiencies, which were: 10% for coarse and fine detritus, 42% for diatoms, 27% for other algae, and 79% for animal prey. Gross production efficiency for each food type was calculated as the product of net production efficiency and assimilation efficiency. The relative contribution of each food type to population production was calculated as the product of gross production efficiency and the % of that food type eaten. The relative contributions were then converted to percentages and multiplied by population production to obtain the amount of production attributed to that food type.

Growth comparisons.—The hypothesis that metals altered growth was tested by comparing growth rates of mayflies among study streams. We limited growth rate comparisons to mayflies because these taxa are metal-sensitive and have distinct cohorts. Cohort growth rates were estimated by fitting exponential growth models to relationships between mean mass and time (Hawkins 1986). Specific growth (Waters 1977) was calculated using regression analysis with the equation: $W_t = W_o e^{kt}$, where W_o = mean mass at time 0, W_t = mean mass at time t, and k = instantaneous coefficient of growth. Calculation of growth by regression allowed error estimation and, consequently, rigorous statistical comparisons among streams. Tests for differences in growth rely on the assumption that growth curves are exponential. Data were plotted to examine this assumption. Among stream growth rates were compared for each species using analysis of covariance (SYSTAT version 10, SPSS Inc., Chicago, Illinois). Field-estimated growth rates are notoriously variable, so the threshold of statistical significance was relaxed

to $p < 0.10$ in an attempt to avoid type II statistical errors.

Growth experiment.—An experiment was done to test the hypothesis that periphyton in metal-contaminated streams had reduced food quality. The growth of *Baetis tricaudatus* was measured after feeding on periphyton from contaminated and reference sites for 8 d. Unglazed ceramic tiles were placed in shallow (<0.5 m) riffles of one reference stream (East Fork), the intermediate Zn stream (Mosquito), and the high Zn stream (Snake) in June 1998. After a 30 d colonization period, tiles were removed, placed in aerated insulated coolers, and returned to the Stream Research Laboratory at Colorado State University. Four tiles were placed in each of 5 chambers constructed of 350 μm mesh, which were placed in flow-through microcosms (see full description of microcosms in Kiffney and Clements 1994). Five *B. tricaudatus* from the Cache la Poudre River, a nearby unpolluted stream, were placed in each growth chamber. The experiment used 5 chambers as replicates from each stream. Initial and final body lengths of mayflies were measured after anesthetizing them with CO_2. Specific growth (G) was calculated using the mean initial and final masses across individuals within each replicate chamber. Growth among treatments was compared with ANOVA.

Periphyton food quantity and quality from each site were determined by measuring chlorophyll a and ash free dry mass (AFDM) on ungrazed control tiles at the end of the feeding experiment. Periphyton was scraped from all control tiles with a hard bristle brush. A random aliquot was removed from the slurry, and chlorophyll a was measured (APHA 1992). The remaining sample was dried to constant mass at 60°C and combusted at 500°C for 1 h. Samples were reweighed after cooling in a desiccator for 1 h, and AFDM was calculated as the difference between dry mass and ashed mass. Mean AFDM and chlorophyll a among streams were compared with ANOVA.

Results

Macroinvertebrate assemblage composition

Thirty-nine insect taxa were collected during our study. Of these, 14 were too rare to calculate production, and 6 species of *Rhyacophila* were

lumped because of uncertainty associated with identification of early instars. Early instars of *Taenionema pallidum* and *Doddsia occidentalis* (subfamily Brachypterinae:Taeniopterygidae), were indistinguishable, so these species were lumped because they had similar life histories and growth patterns. Production was calculated for the remaining 18 taxa, which represented 85 to 95% of the total abundance and biomass at all sites.

The composition of insect assemblages varied among streams (Appendix). Chironomidae (mostly Tantarsini and Orthocladiini) were abundant in all streams. Heptageniids and baetids were abundant in reference and low Zn streams, while *Prosimulium* spp., *Zapada* spp., and *Suwallia* spp. were abundant in intermediate and high Zn streams. The biomass of Chironominae (mostly Tanytarsini) was high in all but the intermediate Zn streams, where the biomass of *Baetis tricaudatus* was high. The biomass of heptageniids was high in reference and low Zn streams, while the biomasses of other mayflies and stoneflies were were high in intermediate and high Zn streams.

Annual production of major taxa

Heptageniid annual production was negatively related to Zn contamination, but production of other mayfly species was not (Table 2). All mayfly taxa were too rare for production estimates in the high Zn stream. Production of *E. longimanus* and *Cinygmula* spp. varied ~2× between reference streams, but was significantly higher than in all contaminated streams. Production of *R. robusta* varied ~4× between reference streams and was higher than in all contaminated streams. Baetid production varied ~1 to 4× between reference streams, but was not significantly different than low or intermediate Zn streams. Production of *D. doddsi* was similar among reference streams and the intermediate Zn stream.

Annual production of several plecopteran taxa was negatively related to Zn contamination (Table 2). Production of *Megarcys signata* was similar between reference streams and ~50% lower in the low and intermediate Zn streams. *Suwallia* spp. was probably represented by several species (B. Kondratieff, Colorado State University, personal communication) with varying life history patterns. Production of *Suwallia* spp.

was similar between reference streams and significantly lower in all contaminated streams. Production of *Taenionema pallidum/Doddsia occidentalis* was not statistically different among reference and low Zn streams, but these species were absent from the intermediate and high Zn streams. *Zapada* spp. was 1 of only 3 taxa consistently collected in the high Zn stream, and it also occurred in all other streams. Production of *Zapada* spp. varied <2× among all but the high Zn stream, where it was ~75% lower than in the remaining streams. Production of several plecopteran and trichopteran taxa did not vary significantly among streams, or they were not consistently collected. These taxa included *Sweltsa* spp., *Paraleuctra* spp., *Kogotus modestus*, *Arctopsyche grandis*, and *Rhyacophila* spp.

Annual production of some Diptera taxa varied significantly with Zn contamination (Table 2). Production of Chironominae (mostly Tanytarsini) was highest in reference streams and significantly lower in the intermediate and high Zn streams. In contrast, Orthocladiinae production was similar among all but the high Zn stream. Production of *Prosimulium* spp. was highest in the intermediate Zn stream and lowest in the high Zn and a reference stream, but statistically similar among all other streams.

Total assemblage production varied >120× along the Zn gradient (Table 2, Fig. 2). Total assemblage production was similar between reference streams and significantly higher (~50%) than in the low and intermediate Zn streams, where production was similar. Total assemblage production was significantly lower in the high Zn stream than all other streams.

Trophic basis of production

The contribution of various food sources to community production was markedly different along the Zn gradient (Table 3). Primary producers (algae and diatoms) were the largest energy source to insect populations with two exceptions. Insect populations in Reference 2 and the high Zn stream derived most of their energy from animal prey and fine detritus, respectively. Animal prey was also an important energy source, except in the high Zn stream where negligible energy was attributable to this source. Fine detritus was generally the 2nd or 3rd most important energy source, except in the high metals stream where it was the most important

TABLE 2. Summary of production (mg dry mass m^{-2} y^{-1}) for 19 taxa collected in 5 streams in central Colorado, 1998 to 1999. P = production, CI_{upper}, CI_{lower} = upper and lower 95% confidence intervals, respectively. Zero value indicates taxon was either absent or too rare for calculation of production.

Taxon	Reference 1		Reference 2		Low Zn		Intermediate Zn		High Zn	
	P	CI_{lower} CI_{upper}	P	CI_{lower} CI_{upper}	P	CI_{lower} CI_{upper}	P	CI_{lower} CI_{upper}	P	CI_{lower} CI_{upper}
Epeorus longimanus	284	199 368	545	421 663	104	71 152	87	30 152	0	– –
Cinygmula spp.	651	370 963	239	171 337	86	57 115	125	82 159	0	– –
Rhithrogena robusta	356	264 468	1366	1044 1734	721	583 871	103	77 137	0	– –
Baetis bicaudatus	129	71 178	527	371 752	202	125 307	192	148 244	0	– –
B. tricaudatus	269	198 344	180	134 230	99	64 133	484	266 691	0	– –
Drunella doddsi	171	136 213	145	84 212	81	60 100	136	82 196	0	– –
Megarcys signata	408	221 750	377	376 378	106	33 181	183	71 318	0	– –
Kogotus modestus	297	156 499	0	– –	0	– –	0	– –	0	– –
Suwallia spp.	177	119 265	215	167 294	59	27 110	30	13 52	5	0 14
Sweltsa spp.	0	– –	126	75 220	96	8 197	0	– –	0	– –
Zapada spp.	24	14 37	27	21 34	46	37 54	25	18 32	6	3 10
Paraleuctra spp.	63	52 77	0	– –	11	7 18	0	– –	0	– –
Taenionema pallidum / Doddsia occidentalis	133	32 240	117	56 178	65	46 86	0	– –	0	– –
Arctopsyche grandis	183	120 238	0	– –	0	– –	131	61 241	0	– –
Rhyacophila spp.	781	361 1338	482	0 1451	294	214 422	102	43 178	0	– –
Prosimulium spp.	9	0 36	44	21 70	27	10 46	70	28 119	5	0 9
Chironominae	469	204 849	767	354 1274	257	105 400	2	1 3	14	3 27
Orthocladiinae	61	22 107	39	26 59	30	26 59	46	17 90	9	6 13
Total	4465		5196		2284		1716		39	

source. Coarse detritus was a major energy source only in the high Zn stream. In addition to these qualitative differences in the relative importance of energy sources, the secondary production attributable to primary producers appeared to decline as Zn contamination increased.

Mayfly growth rates

Growth rates varied significantly among streams for some heptageniids (*Cinygmula* spp. and *Rhithrogena robusta*), but growth rates of all other mayflies were similar among streams (Table 4). *Cinygmula* spp. growth was 8× higher in
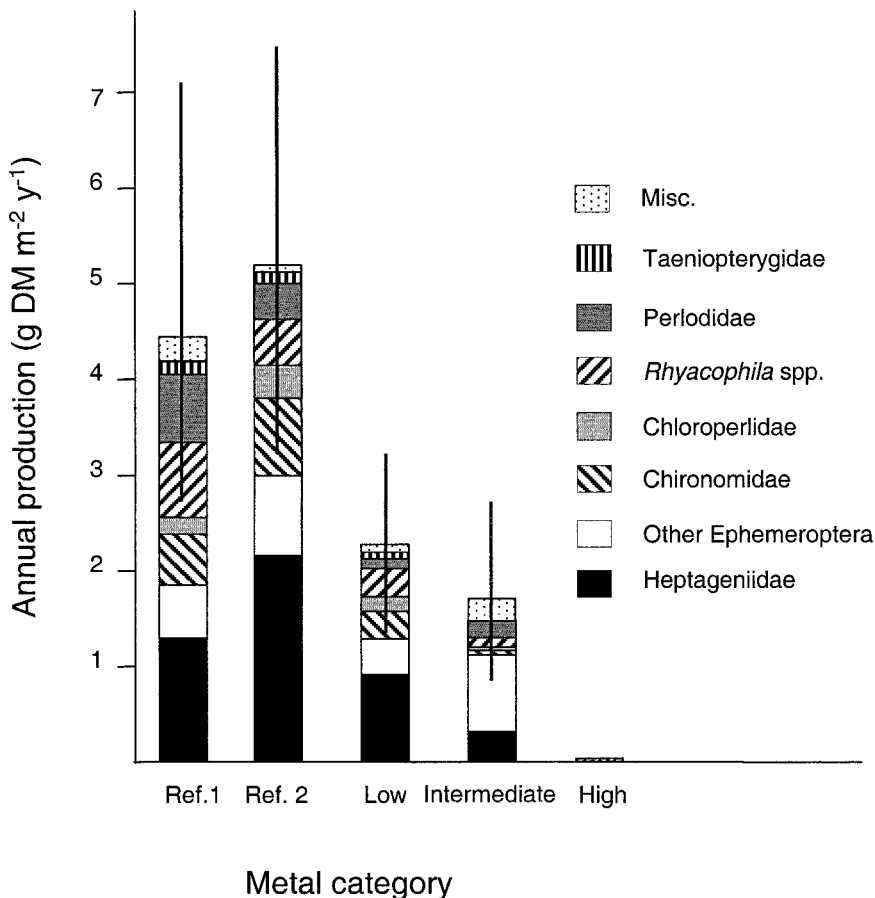
FIG. 2. Annual production of insect assemblages in 5 Colorado streams varying in metal contamination. Error bars represent 95% confidence intervals for total community production estimates. Misc. category includes: *Zapada* spp., *Paraleuctra* spp., *Arctopsyche grandis*, and *Prosimulium* spp. DM = dry mass, Ref. = reference.

the intermediate Zn stream than all other streams, where growth was similar. Growth of *R. robusta* was lower in the low and intermediate Zn streams than in the reference streams.

Growth experiment

Periphyton quantity and quality varied significantly along the Zn gradient. Periphyton

TABLE 3. Secondary production attributable to major food sources in 5 Colorado streams with varying levels of Zn contamination, 1998.

	Total production attributable to food sources $(mg\ dry\ mass\ m^{-2}\ y^{-1})$				
Food type	Reference 1	Reference 2	Low Zn	Intermediate Zn	High Zn
Algae	357	416	320	120	3
Diatoms	1429	1455	639	618	4
Fine detritus	1741	520	708	429	22
Coarse detritus	45	156	91	17	9
Animal prey	893	2650	525	532	<1

from the reference stream contained 2× more chlorophyll *a* than periphyton from the intermediate Zn stream, and >50× more chlorophyll *a* than periphyton from the high Zn stream (Fig. 3A). Periphyton from the reference stream contained 2× more organic matter than periphyton from intermediate and high Zn streams (Fig. 3B). Specific growth of *B. tricaudatus* that fed on periphyton from the reference stream was ~30 to 50% higher than for individuals that fed on periphyton from contaminated streams (Fig. 3C).

Discussion

Secondary production

Secondary production is an underused yet powerful endpoint for assessing ecosystem degradation. Secondary production consistently has shown responses to anthropogenic stressors (Raddum and Fjellheim 1993, Whiles and Wallace 1995, Stone and Wallace 1998). Moreover, secondary production analyses integrate population- and community-level processes (Lugthart and Wallace 1992), and if coupled with measures of anthropogenic stress, increases the ecological relevance of observed stressor responses. Secondary production is the product of individual growth and population density (Huryn and Wallace 2000), so it may be influenced by any anthropogenic stressor that affects these processes. As shown by the effects of metal pollution, both individual growth and population abundance may often be directly or indirectly affected.

Contaminant effects on population abundance.— Chronic contaminant exposure may affect secondary production directly by reducing population abundance through toxicity. Our observations of reduced mean annual population density and biomass of heptageniid mayflies and some stoneflies in contaminated streams are in agreement with numerous studies. Clements et al. (2000) reported negative correlations of heptageniid and predatory stonefly population densities with metal contamination across 95 sites throughout Colorado. Similar findings were reported among 6 streams (Clements and Kiffney 1995), above and below metal inputs on a single stream (Clements 1994), before and after metal remediation (Clements et al. 2002), and in experimental microcosms (Kiff-

ney and Clements 1996a). This collective evidence, in addition to our observations, suggests that reductions of heptageniid and predatory stonefly secondary production in Zn-contaminated streams is largely caused by reduced population abundance. However, Clements (1999) reported that chronic contaminant exposure influenced the vulnerability of mayflies to stonefly predation and suggested that reduced mayfly abundance in contaminated streams may also be the result of higher vulnerability to predators. Last, size-dependent sensitivity to acute and chronic contaminant exposure has been documented for some invertebrates (Green et al. 1986, Kiffney and Clements 1996b) and may alter population size distribution, biomass, and ultimately production. This effect was probably not significant in our study because we did not observe a relationship between mean individual body size (mass) and Zn contamination.

Contaminant effects on individual growth.—Individual growth rates can be affected by chronic contaminant exposure if contaminants reduce the quality or quantity of consumable resources. Previous observational and experimental work showed reduced cell densities and periphyton biomass in metal-contaminated Colorado streams (Medley and Clements 1998). These observations are supported by the results of the feeding experiment, but only partially by estimated growth rates from field data, even though estimates of periphyton biomass and chlorophyll *a* suggested that less food was available for grazing consumers in contaminated streams than in reference streams. There are at least 2 explanations for this observation. First, genetic alteration or physiological acclimation may allow insects in chronically contaminated sites to detoxify metals at little energetic cost. Mayflies persisted and grew in contaminated streams despite elevated metal levels in their tissues (DMC, unpublished data). A 2nd possibility is that individuals from contaminated streams were able to compensate for either greater energetic costs or low food quality by increasing their food consumption. If food resources are limiting, then low population abundances in contaminated streams may allow greater per capita consumption, thereby offsetting the effects of lower food quality and quantity. Hawkins (1986) demonstrated a similar pattern in several Oregon streams that differed in food quality and quantity. Increased consumption has been observed

TABLE 4. Growth-rate statistics for mayfly taxa in 4 Colorado streams, 1998 to 1999 (mayfly taxa were absent from the high Zn stream). $W_t = W_0 e^{kt}$, where W_t = mean mass at time t, W_0 = mean mass at time 0, and k = instantaneous coefficient of growth. n = number of sampling dates and r^2 = coefficient of determination for fit of exponential growth model. Metal categories are as in Table 1.

Metal category	Baetis bicaudatus			Baetis tricaudatus			Cinygmula spp.			Epeorus longimanus		
	k	n	r^2	k	n	r^2	k	n	r^2	k	n	r^2
Ref. 1	0.015	5	0.96	0.072	4	0.96	0.013	6	0.86	0.046	5	0.92
Ref. 2	0.014	7	0.86	0.072	4	0.99	0.013	7	0.86	0.046	5	0.94
Low	0.012	5	0.98	0.061	4	0.96	0.013	6	0.79	0.030	5	0.98
Intermed.	0.013	6	0.95	0.066	4	0.90	0.083	4	0.90	0.050	5	0.93
ANOVA[a]	$F = 0.489$			$F = 0.364$			$F = 12.118$			$F = 2.516$		
	$p = 0.69$			$p = 0.78$			$p < 0.01$			$p = 0.11$		

[a] F-statistic and p values reported are for tests of equal ks among streams in an ANCOVA model

in a variety of animals feeding on low quality food (Chen and Folt 1993, Wheeler et al. 1998).

A second way that individual growth may be affected by chronic contaminant exposure is through alterations of net production efficiency. Aside from reductions in the assimilation efficiency of food resulting from lower food quality, contaminants may alter physiological processes that control other aspects of an organism's energy budget (Adams et al. 1992, Beyers et al. 1999), including feeding efficiency (Brown et al. 1987, Gorham and Vodopich 1992). For example, metal exposure increased respiration rates in mayflies (Herrmann and Anderson 1986), and acidic pH increased respiration of damselfly nymphs (Gorham and Vodopich 1992). We did not directly measure all portions of the energy budget, but it was probably unaffected by Zn for most mayfly taxa because growth rates appeared to be similar among reference and contaminated streams. There were, however, 2 exceptions. Growth of *Cinygmula* spp. in the intermediate Zn stream was anomalous, largely because of a unique life history. *Cinygmula* spp. early instars appeared in the fall in all other streams, but they first appeared in spring in the intermediate Zn stream, suggesting a unique species or subspecies. In contrast, reduced growth rates of *R. robusta* in contaminated streams were likely caused by alterations of the energy budget.

Collectively, our data suggest that metal-induced reductions in population density and biomass appear to be the primary factors regulating variation in population production among contaminated streams. Apparent metal-induced reductions in food quality and individual energetics may be offset by increased consumption for some herbivorous species. In contrast, the dominant (in terms of biomass) herbivore, *R. robusta*, exhibited reduced individual growth rates, population density, and biomass in contaminated streams relative to reference streams. These results suggest that some sensitive species suffer individual- and population-level energy losses in contaminated streams.

Trophic basis of production

We were able to link variation in population abundances associated with Zn to population and ecosystem energetics by estimating the trophic basis of secondary production along a contamination gradient. Our results illustrate the importance of herbivory in headwater Rocky Mountain streams and the likelihood that low to moderate Zn contamination has far-reaching effects on energy flow in these ecosystems. The reduction in production attributable to primary producers was largely caused by a single insect species, *R. robusta*. Several heptageniid species were common herbivores at our study sites, but *R. robusta* was the dominant algal consumer in reference streams, was highly sensitive to metals, and displayed reduced growth rates in contaminated streams. Low individual growth rates, population abundance, and biomass of heptageniids clearly resulted in large energetic deficits in contaminated streams relative to reference streams. Furthermore, reduced energy flow through predators in the high Zn stream suggests that energetic losses at the primary

TABLE 4. Extended.

Rhithrogena robusta			Drunella doddsi		
k	n	r^2	k	n	r^2
0.012	6	0.64	0.012	9	0.87
0.011	12	0.86	0.013	8	0.85
0.006	9	0.81	0.014	7	0.88
0.009	6	0.75	0.013	6	0.74
$F = 3.633$			$F = 0.116$		
$p = 0.03$			$p = 0.95$		

consumer level also may influence higher trophic levels. Declines in energy flow to predators were also observed in a Colorado stream influenced by stressors (not quantified) associated with urbanization and agriculture (Shieh et al. 2002).

Comparisons with other secondary production studies

Our estimates of secondary production compare reasonably well with those from streams in other regions. Heptageniid mayfly production in our reference streams was within the ranges reported for western US and Appalachian streams (Robinson and Minshall 1998, Stone and Wallace 1998). Our estimates of *Baetis* spp. production were somewhat lower than other reports (Peterson et al. 1993, Benke and Jacobi 1994, Robinson and Minshall 1998). Our estimates of community production in reference streams are similar to streams with comparable discharge and temperature (Benke 1993). In contrast, our community production estimates from contaminated streams are among the lowest reported (see review by Huryn and Wallace 2000).

Use of secondary production to assess contaminant effects

Our results demonstrate that estimates of secondary production and its trophic basis were sensitive and informative measures of contaminant effects on streams. A rich literature exists on the use of benthic macroinvertebrate community structure to assess the ecological effects of human perturbations. Structural measures
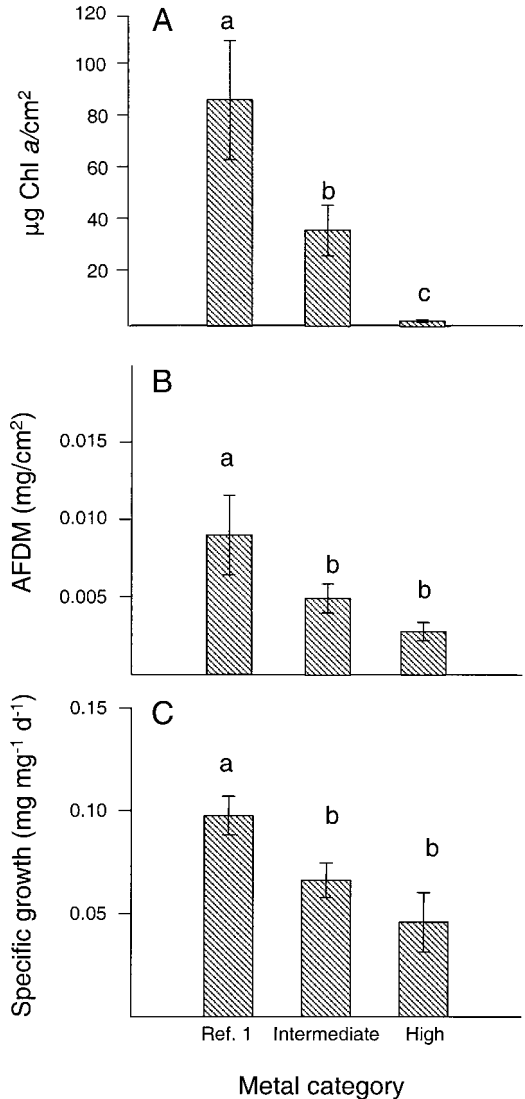

FIG. 3. Biomass (mean ±1 SE) of chlorophyll *a* (A) and organic matter (B) as ash free dry mass (AFDM) on tiles colonized in 3 streams of varying metal contamination in central Colorado, 1998. Growth rates (C) of *Baetis tricaudatus* during 8 d grazing trial on tiles colonized with periphyton from streams of varying metal contamination. Means with different superscripts were significantly different ($p < 0.05$) using Bonferroni post-hoc test.

such as taxa richness and diversity are ecologically relevant and provide insight into the ecosystem consequences of human alterations. Nevertheless, functional measures of populations and communities are needed to completely character-

ize anthropogenic disturbances. A plethora of research documents the effects of metals on the community structure of Rocky Mountain stream ecosystems. These studies collectively indicate that mayfly assemblages are disproportionately affected by metal contamination. However, the importance of *R. robusta* and other heptaganiids to the energetics of Rocky Mountain streams has not been quantified previously. Consequently, we could say little about how metal-induced variation in community structure might influence stream ecosystem functions. We feel that the present study has improved our understanding of this relationship.

Studies of ecosystem functions in headwater Rocky Mountain streams are rare despite the ecological and recreational importance of these systems. Our study was the first to estimate overall insect assemblage production in Rocky Mountain streams and to relate this functional measure to an important environmental stressor. Macroinvertebrate production in these streams is comparable to that of other similar-sized systems, but our results suggest that some ecosystem functions may be compromised in streams with Zn concentrations close to the chronic criterion value. Given that >30% of streams in the southern Rocky Mountain ecoregion contain metals ≥2× the USEPA chronic criterion (Clements et al. 2000), the effects of metal contamination on stream ecosystems may be more severe and widespread than previously thought.

Acknowledgements

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APPENDIX. Mean annual abundance and biomass of 19 dominant taxa in 5 Colorado streams, 1998. DM = dry mass. Missing values indicate the taxon was not collected. Ref. = Reference, Intermed. = Intermediate.

Metal category	Abundance (no./m²)					Biomass (mg DM/m²)				
	Ref. 1	Ref. 2	Low	Intermed.	High	Ref. 1	Ref. 2	Low	Intermed.	High
Taxon										
Epeorus longimanus	565	571	285	130	3	28	68	19	8	2
Cinygmula spp.	1624	243	95	272	2	83	58	20	24	<1
Rhithrogena robusta	210	602	771	31	1	126	160	100	22	2
Baetis bicaudatus	881	1547	553	673	1	23	105	31	34	<1
B. tricaudatus	1009	316	260	663	1	22	29	13	126	<1
Drunella doddsi	356	145	190	371	2	26	25	11	25	<1
Megarcys signata	78	41	9	10	1	87	73	27	58	2
Kogotus modestus	66	–	–	–	–	43	–	–	–	–
Suwallia spp.	500	350	150	90	12	60	46	18	12	4
Sweltsa spp.	–	310	160	–	–	–	34	67	–	–
Zapada spp.	310	130	290	130	220	10	9	15	5	1
Paraleuctra spp.	130	10	50	–	–	24	2	20	–	–
Taenionema pallidum/										
* Doddsia occidentalis*	575	457	194	–	–	17	18	10	–	–
Arctopsyche grandis	28	<1	<1	41	<1	57	<1	<1	35	<1
Rhyacophila spp.	230	30	20	30	1	168	49	7	23	<1
Prosimulium spp.	250	220	30	1200	17	2	6	29	8	1
Chironominae	12,560	6650	330	2060	40	207	361	116	1	6
Orthocladiinae	3880	3810	1400	3270	560	30	21	16	24	5
Total	23,252	15,433	7758	8974	862	1013	1065	520	405	29