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Emergence Flux Declines Disproportionately to Larval Density along a Stream Metals Gradient

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ABSTRACT: Effects of contaminants on adult aquatic insect emergence are less well understood than effects on insect larvae. We compared responses of larval density and adult emergence along a metal contamination gradient. Nonlinear threshold responses were generally observed for larvae and emergers. Larval densities decreased significantly at low metal concentrations but precipitously at concentrations of metal mixtures above aquatic life criteria (cumulative criterion accumulation ratio (CCAR) $\geq$ 1). In contrast, adult emergence declined precipitously at low metal concentrations (CCAR $\leq$ 1), followed by a modest decline above this threshold. Adult emergence was a more sensitive indicator of the effect of low metals concentrations on aquatic insect communities compared to larvae, presumably because emergence is limited by a combination of larval survival and other factors limiting successful emergence. Thus effects of exposure to larvae are not manifest until later in life (during metamorphosis and emergence). This loss in emergence reduces prey subsidies to riparian communities at concentrations considered safe for aquatic life. Our results also challenge the widely held assumption that adult emergence is a constant proportion of larval densities in all streams.
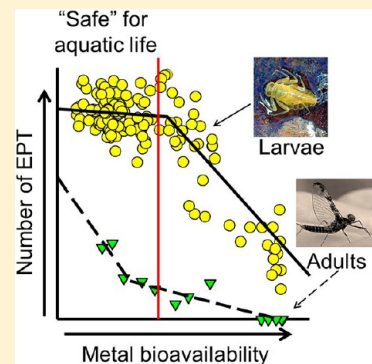
INTRODUCTION

Research investigating the effects of contaminants on aquatic insects has primarily focused on larvae and has largely ignored the adult life stage.[1−3] Of the aquatic insects that emerge from streams as flying adults, most never return to the aquatic environment.[4] The few that do return can replenish the stream with eggs to sustain future populations;[5−7] while the vast majority are either important prey subsidies for riparian consumers or enter the detrital food web in the terrestrial environment.[5,8−10] This aquatic-terrestrial linkage provides critical support for terrestrial food webs,[8,11−13] as well as the transport of contaminants between aquatic and terrestrial ecosystems.[14−17] However, very little is known about how larval exposure to contaminants affects emergence and the important ecological processes (e.g., reproduction, feeding riparian consumers) that adult insects provide.[16−18]

Relationships between larval exposure to contaminants and adult emergence rates are poorly understood for stream insect communities. Single-species laboratory studies have linked larval exposure to effects on adult life stages and subsequent generations;[19−27] however, observations on aquatic insect communities from the field are lacking. Larvae of the model organism *Chironomus dilutus* exposed to metal-contaminated sediment experienced decreased growth rate, longer time to emergence, and lower emergence rates.[22,25,28] In some cases, stress from metal exposure decreases somatic and gonadal growth below a threshold necessary for successful emergence.[19,20,22,25,28] Slower growth rates presumably result from energetic costs associated with the immediate need to regulate

or detoxify internalized metals.[29] This regulation may not translate to larval mortality, but it could disrupt the physiologically demanding process of metamorphosis, thereby reducing adult emergence. If so, then effects of metal exposure on larvae and adults may be decoupled, resulting in different responses, depending on the life-stage considered. Specifically, adult emergence could be limited at lower concentrations of metal in water than larval density if larval compensatory responses to metals reduce larval mortality but consume resources necessary for emergence. Because the effect of metal exposure on emergence is unknown, it is unclear if aquatic life criteria protect the community of emergent aquatic insects that sustain healthy aquatic and terrestrial ecosystem function.

Here we address uncertainty in contaminant effects across insect life stages by comparing larval density (individuals/m^2) and adult emergence flux (individuals/m^2/d) from two studies of a gradient of stream metal contaminations in the central Colorado Rocky Mountains.[16,30] Specifically, we hypothesized that adult emergence would be reduced at aqueous metal concentrations below that which causes declines in larval densities, due to natural and enhanced mortality during metamorphosis from the larval to adult life stage. From the shape of the responses we can infer differences in how the two life stages respond to similar levels of metals in order to develop
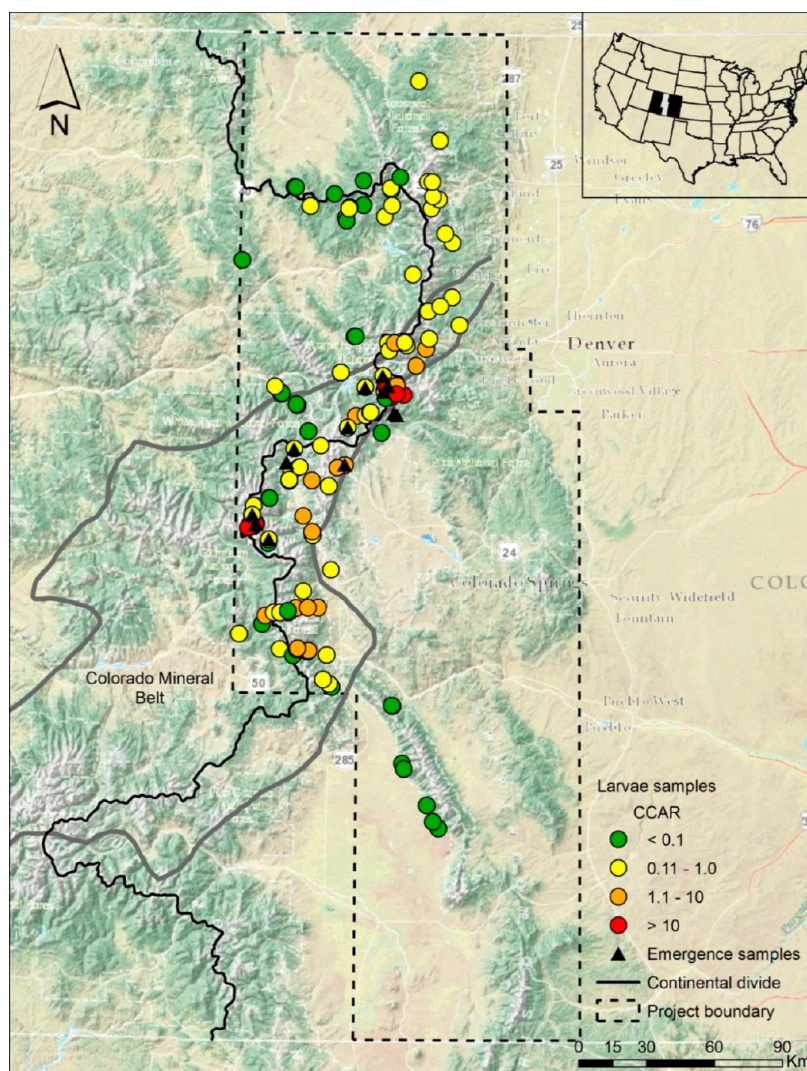
Figure 1. Map of the study area depicting the location of larvae samples and emergence samples collected from throughout the central Colorado Rocky Mountains. Larvae samples are color coded to show the spatial distribution of metal concentration in water. CCAR - Chronic criterion accumulation ratio. CCAR ≤ 1 is presumed safe for aquatic life.

a more complete understanding of how metals affect both life stages and interact to alter aquatic and riparian ecosystem linkages.

■ EXPERIMENTAL SECTION

Study Area. The study area is central Colorado from Wyoming to the New Mexico border including most of the Rocky Mountains in Colorado (Figure 1). This area includes the Colorado Mineral Belt that has been mined for the past 150 years. The climate is temperate continental, and generally receives 50 cm of precipitation annually, mostly as snow in winter or as rain between June and August. The land use is predominately alpine and subalpine forests with little other development except for the presence of abandoned mines.[30−32] Sample locations targeted were underlain by a single predominate lithology so that water chemistry and aquatic insect responses could be related to lithology for the purpose of developing biological and geochemical baselines for the sampled region.[31] Sample locations ranging from extremely high metal concentrations to reference conditions were distributed throughout the region (Figure 1). Catchment (e.g., basin area, land use) and sample location (e.g., discharge,

elevation) descriptors commonly used as habitat variables were not strongly correlated with the metals gradient and did not generally describe mean responses by aquatic insect larvae.[31,33] The emergence data were collected from a subset of locations sampled for larvae to capture the range of metal concentrations observed in the previous study. The emergence study specifically employed a spatial block design (high, medium, low metal streams sampled in spatial groups) to control for random spatial variation in emergence.[16] This spatial block was only important for explaining variation in the biomass ($mg/m^2/d$) of emergent dipterans (mean response across the gradient was unchanged) and was not employed in the models here to facilitate model comparisons between larval density and emergence flux data.[16]

Sample Locations. We collected water and benthic macroinvertebrate larvae during summer base flow conditions (July to September) from 2003 through 2007 at 125 sites. Most sites were sampled once, though 12 sites were sampled multiple times to capture interannual variability resulting in a total of 149 samples in total.[30,33,34] Insect emergence was measured in August of 2011 during summer base flow (2011 was an unusually high flow year) and peak emergence at 14 of these

Table 1. Results of AIC$_c$ Analysis and Summary of Regression Models between Larval Density (Number of Individuals/m^2) or Adult Emergence (Number of Individuals/m^2/4 days) and Stream Metal Concentrations[a]

		larvae[b]					model slope[c]	emergence[b]					model slope[c]
		AIC$_c$	Δ$_i$	ω$_i$	threshold	95% C.I.		AIC$_c$	Δ$_i$	ω$_i$	threshold	95% C.I.	
total	Piecewise	129.54	0.00	<u>1.00</u>	1.49	1.11−9.30	0.01	33.52	8.17	0.02	0.24	0.17−10.47	−0.02
	linear	170.85	41.31	0.00			−0.43	25.36	0.00	<u>0.98</u>			−0.35
Chironomidae	Piecewise	202.72	0.00	<u>1.00</u>	1.11	0.18−57.35	0.09	37.09	8.16	0.02	0.22	0.34−257.05	−0.05
	linear	214.41	11.69	0.00			−0.28	28.94	0.00	<u>0.98</u>			−0.37
EPT	Piecewise	91.54	0.00	<u>1.00</u>	1.49	1.16−5.53	−0.06	0.25	0.00	<u>0.59</u>	0.27	0.16−10.47	−1.15
	linear	148.16	56.62	0.00			−0.51	1.01	0.75	0.41			−0.28
Ephemeroptera	Piecewise	157.39	0.00	<u>1.00</u>	1.20	0.75−2.60	−0.10	−8.51	0.00	<u>0.97</u>	0.55	0.23−10.47	−0.80
	linear	185.18	27.78	0.00			−0.53	−1.23	7.29	0.03			−0.24
Heptageniidae	Piecewise	84.39	0.00	<u>0.95</u>	1.16	0.76−2.17	−0.11	−10.85	0.00	<u>0.98</u>	1.25	0.20−13.49	−0.53
	linear	90.24	5.85	0.05			−0.32	−3.03	7.82	0.02			−0.16
Baetidae	Piecewise	181.35	0.00	<u>0.85</u>	1.36	0.19−4.63	−0.15	0.92	0.00	<u>0.61</u>	0.47	0.22−10.47	−0.69
	linear	184.76	3.40	0.15			−0.39	1.84	0.91	0.39			−0.16

[a]Δ$_i$, AIC$_c$ standardized by subtracting the minimum AIC$_c$ score from each of the candidate models. ω$_i$, Akaike weight is the probability the model is the best model among the candidate set with the most probable model underlined. [b]Larvae and adult data were log $x + 1$ transformed. [c]Slopes reported are either the initial piecewise regression slope or the slope for the linear model.

sites selected to capture the full metals gradient observed in the previous study.[16] Sample locations for both studies were approximately 50- to 100 m reaches located at high elevation (mean = 2975 ± 287 m a.s.l.), first−third order streams (mean basin area (36 ± 58 km^2), with mean discharge (11 ± 15 cfs) and were dominated by medium sized cobble substrate (mean D_{50} = 38 ± 14 mm).[30,31]

Larval Density and Emergence Flux. Detailed method descriptions were previously published.[16,30] Briefly, five replicate benthic samples were collected using a 0.1 m Hess sampler (350 μm mesh net) in shallow (<0.5 m) riffle areas to maximize richness.[35] Samples were preserved in 80% ethanol, subsampled to a 300 count, and identified to the lowest practical taxonomic level (genus or species for most taxa).[35,36] Means of the five samples were used to calculate density (number of insect larvae/m^2). Emergence was measured using four replicate traps placed on pools and slack water from 14 different streams, 12 of which were the same as those sampled for larvae. Pools and slack water were targeted because emergence is greater from these habitats than in riffles and contains both pool and riffle dwelling organisms.[16,37,38] Emergence traps were 1 m^2 plastic structures that float at the water's surface and were covered with 500 μm mesh with a collection bottle at the top.[37] Traps were deployed for 4 days, a sufficient time to characterize emergence.[16,37,38] Samples were collected, frozen in the field, and maintained that way until counted and identified to family in the lab.[39] We calculated either density (number/m^2 for larvae) or emergence flux (number/m^2/4 days for adults) for a variety of invertebrate community metrics that have demonstrated a sensitivity to metal contamination.[2,31,40] These metrics included total (all organisms), Chironomidae, Ephemeroptera + Plecoptera + Trichoptera (EPT), and Ephemeroptera, Baetidae, and Heptageniidae. Larval density metrics in general are thought to be sensitive to metals and were the most comparable metric to emergence.[2]

Chemical Analysis. Detailed methods and quality assurance/control procedures were previously published.[16,30] Briefly, water samples from all sites were collected and preserved in the field using standard U.S. Geological Survey (USGS) methods and to comply with data requirements for the Biotic Ligand model (BLM).[41,42] Most samples were analyzed using inductively coupled plasma mass spectrometry (Perkin-Elmer SciexElan 6000 ICP-MS) whereas samples from 21 sites collected in 2003 were analyzed by furnace atomic absorption (Perkin-Elmer model 372). Detection limits for metals in water for the larvae study varied between sampling periods as follows: Cadmium (Cd; 0.01 μg/L in 2003, 0.02 μg/L in 2004−2007), Copper (Cu; 0.01 μg/L in 2003, 0.5 μg/L in 2004−2007), and Zinc (Zn; 5 μg/L in 2003, 0.5 μg/L in 2004−2007). Detection limits (Perkin-Elmer SciexElan 6000 ICP-MS) for the emergence study were 0.02, 0.5, and 3.0 μg/L for Cd, Cu, and Zn, respectively.

Determination of Metal Mixture Toxicity. Most metal-contaminated streams in Colorado are affected by mixtures of Cd, Cu, and Zn, so we used a cumulative measure (assuming additive metal toxicity) of aqueous metal toxicity. The chronic criterion accumulation ratio (CCAR) is a metric that modifies BLM outputs for use as a toxic-unit model or hazard quotient model and assumes additive toxicity of trace-metal mixtures on the basis of BLM-predicted outputs.[30,42] The CCAR is defined as the ratio of the BLM-calculated accumulated free metal ion on the biotic ligand to that accumulated on the biotic ligand in water at the U.S. EPA criterion value, summed for trace metals of interest at a location. The CCAR method uses the BLM to account for site-specific influences of water quality on metal toxicity to aquatic organisms. CCAR is defined as

$$\sum \text{CCAR} = \sum_i \frac{\text{BLM calculated site specific [gill metal]}}{\text{BLM calculated [gill metal] at CCC}}$$

where BLM calculated site specific [gill metal] and BLM calculated [gill metal] at continuous chronic concentration
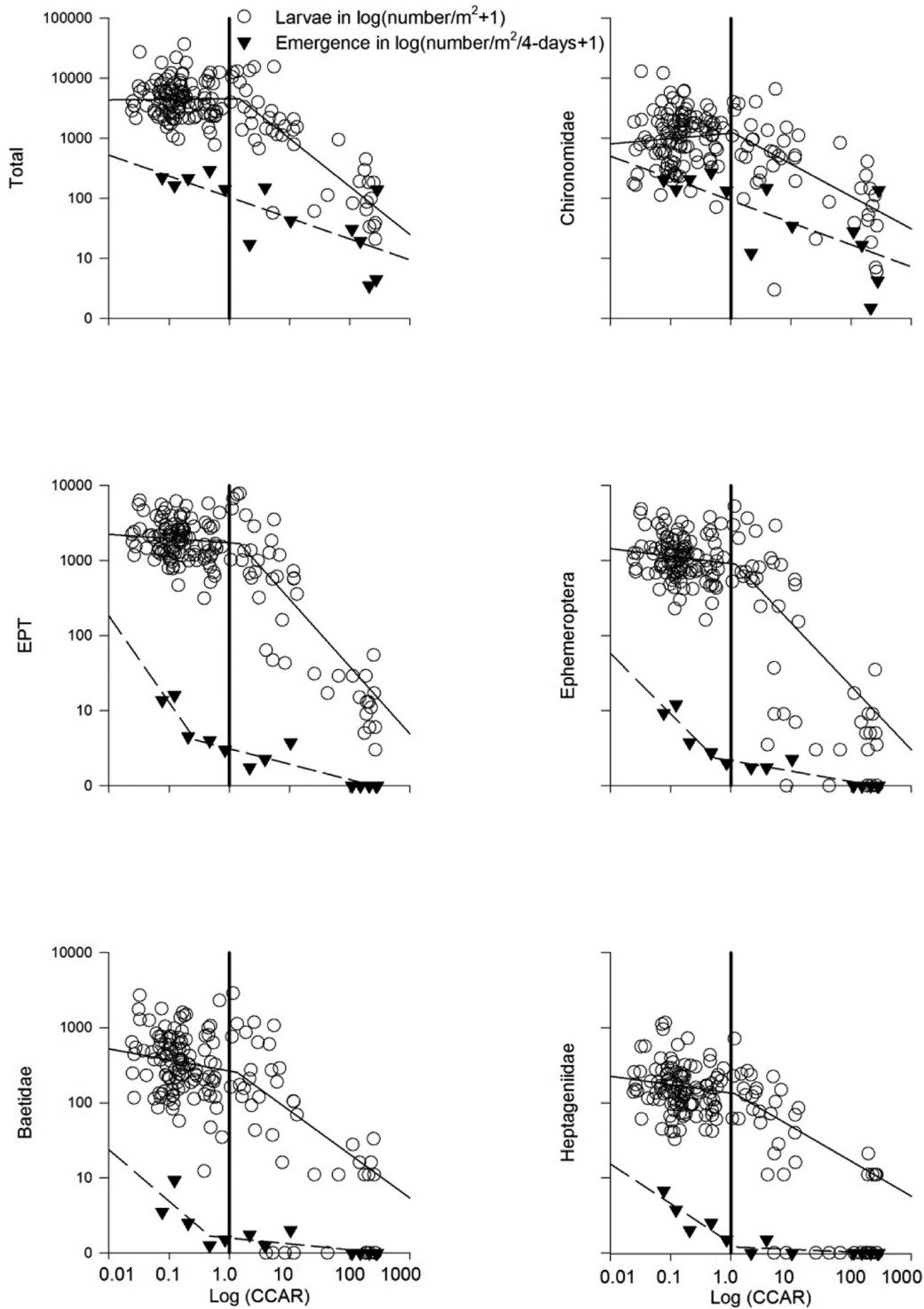
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Figure 2. Response of aquatic insect larvae (open circles, solid line) and emergence (filled triangles, dashed line) along a gradient of metal bioavailability (CCAR). Piecewise regressions depict thresholds where rates of change are sufficiently different to require a different slope to describe mean response. CCAR, chronic criterion accumulation ratio. CCAR (vertical black bar) ≤ 1 is presumed safe for aquatic life.

(CCC) are measurements developed from BLM end points. BLM calculated site specific [gill metal] is the BLM-predicted accumulation of the ith trace metal on the biotic ligand (gill surface), calculated by running the BLM in speciation mode using site-specific water-quality parameters. BLM calculated [gill metal] at CCC is the BLM-predicted accumulation of the ith trace metal on the gill surface, calculated using the "normalization chemistry" water-quality parameters from

Table 1a,[43] and the ith metal CCC concentration (Cd, 0.25 μg/L; Cu, 9.0 μg/L; Zn, 120 μg/L at hardness =100 mg/L $CaCO_3$). The CCC is developed by averaging toxicity test data across species and genera to determine a concentration of trace metal that will be protective of 95% of the species at a specific site. We are using CCAR to predict toxicity to aquatic insect communities, individual species of which have differential sensitivity to trace metals. By using the CCC rather than a

species-specific response point such as the lethal accumulation (i.e., LA_{50}) for a daphnids or fathead minnows, we can predict toxicity more generally to the community and account for the modifying effects of several water-quality parameters known to determine trace-metal uptake and bioavailability (e.g., pH, DOC, alkalinity, and major cations). At CCAR ≤ 1, metal concentrations are theoretically below CCC and are presumed to be protective of 95% of aquatic organisms; however, negative effects on benthic insect communities have been documented below this threshold.[30,33,44]

Data Analysis. We fit linear and piecewise linear regressions to the larval and adult emergence data to compare differences in response using R software (version 2.7.2).[45] Larval and emergence data were log $(x + 1)$ transformed and CCAR was log transformed to improve homogeneity of variance and normality. Other covariates were not considered in this modeling as previous analysis demonstrated the metals gradient was sufficient to describe mean invertebrate responses and few other factors were strongly correlated with the metals gradient.[30,31,33] Log transforming count data with zero counts can result in some bias.[46,47] Zero counts were rare for larvae but somewhat more common for emergence, so we performed the following analyses with both raw counts and transformed emergence data and found no meaningful differences between results.

Scatter plots suggested nonlinear and possible threshold responses for aquatic insect larval density and emergence. Piecewise linear regressions fit two linked line segments connected at a threshold where an abrupt change in response required a different slope to fit the regression.[48,49] We chose piecewise linear regression over broken stick or bent cable regression because we wanted to estimate a discrete break in the data while maintaining a continuous response function. This approach allowed us to evaluate a discrete threshold in the biological response relative to metal concentrations. SiZer R package was used to estimate the piecewise regression because it accounts for different bandwidth optima and has a lower false detection rate with small sample sizes.[50] The threshold and 95% confidence intervals were estimated using a bootstrap method to resample the raw data 1000 times.[49] Linear models were also fit, and Akaike information criteria (AIC_c corrected for small sample size) were used to determine if a threshold model or a nonthreshold model (linear) was the better model for each invertebrate metric considered.[51] AIC_c was standardized by subtracting the minimum AIC_c score from the model AIC_c values to derive Δ_i and to facilitate model ranking. Akaike weights (ω_i) were calculated to determine the probability of a model being the better model in the candidate set. The top models for both data sets were used to compare the responses of larvae and emergence to metals.

RESULTS

Effects of Metals on Aquatic Insects. The average density for larvae was 4914 ± 4732 individuals/m^2 (mean ± 1 SD). The dominant taxa were Ephemeroptera, Plecoptera, Trichoptera, Diptera, and Coleoptera (Elmidae), accounting for 86% of individuals.[31] Larval densities declined for some groups at CCAR ≤ 1, but all metrics sharply declined at CCAR ≥ 1 (Figure 2). The piecewise regression model best described larval responses to metals in all cases (Table 1). The threshold was lowest for Chironomidae (CCAR = 1.11) followed in rank order by Heptageniidae (1.16), Ephemeroptera (1.20), Baetidae (1.36), EPT (1.49), and total density (1.49). The

slopes for the first line segment of models describing EPT, Ephemeroptera, Baetidae, and Heptageniidae larval responses were negative; while they were slightly positive for Chironomidae and total density.

Mean emergence flux across streams was 108 ± 94 individuals/m^2/4 days. These consisted almost entirely of Chironomidae (92% of individuals, 27% of biomass) followed by EPT (3.2% of individuals, 55% of biomass).[16] In contrast to larval densities, emergence declined sharply for all metrics at CCAR ≤ 1 with slopes approaching zero at CCAR ≥ 1 (Figure 2). Linear models were better for total and Chironomidae emergence whereas piecewise models were the top models for EPT, Ephemeroptera, Baetidae, and Heptageniidae emergence (Table 1). Initial slopes for all piecewise models of emergence were negative, and the thresholds were all below CCAR = 1 except for Heptageniidae (CCAR = 1.25, Table 1). Models for emergence flux resulted in larger confidence intervals for the threshold estimate than those for larval density likely due to the small sample size.

Comparison of Larval Density and Adult Emergence Flux. Comparisons of larval density and emergence flux metrics supported the idea that larval exposure to metals can cause effects on emergence, especially for EPT, Ephemeroptera, Baetidae, and Heptageniidae (Figure 2). Emergence declined more than an order of magnitude at relatively low concentrations of metals (CCAR ≤ 1), whereas larval density declined at a relatively slower rate. Emergence approached zero at CCAR between 1 and 10 even though larvae occurred in moderate densities (10–1000 individuals/m^2) for most metrics. Larvae persisted in low densities (10–100 individual/m^2) at CCAR between 10 and 100, but emergence was virtually eliminated except Chironomidae persisted. Chironomidae emergence at these metal concentrations comprised virtually all of total emergence. Metrics for larvae and emergence were not measured in the same units (number of individuals/m^2 versus number of individuals/m^2/4-days, respectively), so direct comparison of absolute numbers is not appropriate. However, a comparison of the shape of the responses, as we have done here, is appropriate for gaining insights into the relative sensitivity of larvae and adult emergence to stream metal contamination.

DISCUSSION

Emerging adult aquatic insects were drastically reduced at metal concentrations that had only modest effects on larval density, indicating that adult emergence flux may be a more sensitive measure of metals contamination than larval density. These observations support our hypothesis and the idea that the total effect of metals exposure during early life stages is not manifested until later life stages. Furthermore, this is the first evidence that the relative sensitivity of these life stages to contaminants changes over a gradient of exposure suggesting that the proportion of emergers/larvae is not constant across all streams. Emergence was substantially impaired at low metal concentrations (CCAR ≤ 1), suggesting that stream metals at low concentrations could have strong effects on riparian systems via diminished prey subsidies.[16,17] At higher concentrations, metals also cause losses in stream structure and function (e.g., reduced biodiversity and organic matter processing associated with benthic insect communities).[40,52] The mechanisms driving these patterns can be both physiological[29] (e.g., dynamic regulation of metals) and ecological[18] (e.g., intermediate disturbance hypothesis). Our
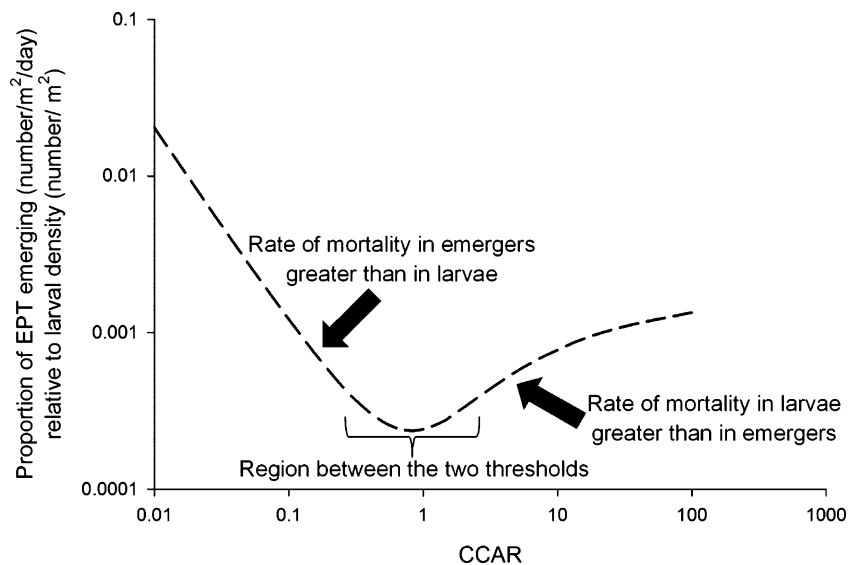
Figure 3. Change in the proportion of adult:larvae EPT density across a metals gradient. The proportion of emerging aquatic adults is assumed to be a constant fraction of benthic invertebrate standing stock in uncontaminated aquatic ecosystems.[18] Metals cause this proportion to be nonlinear owing to the high rate of mortality in emergent adults at lower metal concentrations and the increasing likelihood to emerge as an adult as larvae survive increasing metal concentrations. Dotted line, calculated by taking the proportion of mean EPT emergence relative to mean EPT larval density as estimated by the regression lines in Figure 2. CCAR, chronic criterion accumulation ratio. CCAR $\leq$ 1 is presumed safe for aquatic life.

findings suggest that considering adult life stages when developing aquatic life criteria could protect the ecological role these insects serve in both aquatic and terrestrial environments.

Emergence was a more sensitive indicator of metals contamination than larval density. Decreases in mean adult aquatic insect emergence were greater than decreases in larvae at low to intermediate metal concentrations. This is not to say that the effects of metals on larvae were not ecologically significant (previous research has demonstrated otherwise[30,33,34]), but that emergence is even more limited by metals than is larval density. In general, our perceptions of metric sensitivity derived from past studies of insect larvae[2,30] hold true for adult emergence. Metrics thought to be sensitive to metals such as EPT, Ephemeroptera, and Heptageniidae declined in response to increasing metal concentrations at rates greater than those for total density, Chironomidae and Baetidae density. These taxa-specific sensitivities in part drive differences observed in the composition of larvae vs emerged aquatic insect assemblages.

Two different but related mechanisms, found in the literature, could explain why emergence declines more readily than larvae densities. First, larvae can use physiological mechanisms to minimize toxicity (i.e., sequestration and elimination) to maximize survival at low to intermediate levels of metals (CCAR 0.1−1.0).[29] However, at higher metal concentrations (CCAR $\geq$ 1.0) these compensating mechanisms are no longer effective, and significant mortality is observed (threshold response in larval density declines observed in Figure 2). Thus larval mortality, particularly at intermediate to high metal concentrations, limits adult emergence. Drift is unlikely to contribute to this response because (1) these streams are open systems with source habitats upstream from the sample location and (2) invertebrates with a history of metal exposure, such as those in this study, do not show increased rates of drift when exposed to a metals gradient in the laboratory, whereas naive organisms do.[53,54] Second, and perhaps more importantly, larvae face a trade-off between

allocating resources toward physiological compensatory mechanisms to survive metals exposure or toward somatic or gonadal growth. Energy expended on detoxifying metals at lower metal concentrations could not be used for growth, slowing development, delaying metamorphosis, and limiting emergence.[19,20,22,25,28,55−59] Our data suggest emergence is grossly limited at metal concentrations where larval survival is only slightly diminished (CCAR $\leq$ 1). Thus, low metal concentrations substantially limit emergence (even if larvae are plentiful) while intermediate to high metal concentrations significantly limit larval survival (Figure 2). Future laboratory and field studies should be designed to further evaluate the mechanisms that drive our field observations.

Cumulatively, the effects of mixtures of Cd, Cu, and Zn alter the relationship between emergence and larval densities. In uncontaminated streams, only a fraction of the larval production of a stream is converted to emergent production, and it has been previously assumed that this fraction is relatively unaffected by other factors.[18,60] Our results suggest that this fraction can be altered as a result of metals contamination. To test this idea we used the empirical models in Figure 2 for EPT to calculate the proportion of adult emergence relative to larval densities (Figure 3). The proportion of emergers/larvae declined sharply at low metal concentrations, likely due to a combination of failed metamorphosis and reduced larval survival. At intermediate metal concentrations, this proportion continued to decline mostly because larvae survival was limited by metals. At high metal concentrations, the proportion of emergers increased, possibly because some individual larvae are more tolerant of metals and able to emerge, or a mathematical artifact caused by the fact that larval density is decreasing at a rate faster than emergence. These results suggest that the relationship between larval density and emergence is not static and that estimating effects of larval conditions on cross-ecosystem linkages requires explicit modeling of the effect of aquatic contaminants on emergence over a gradient of exposure.

Metals in streams can simultaneously alter the flow of energy resources in stream and riparian ecosystems.[16,17] In stream ecosystems, metals limit the density[33] of aquatic invertebrates and thus food for aquatic predators like fish[61] whereas shifts in community composition[2] reduce organic matter processing[40] and secondary production of larvae.[52] Riparian food webs are dependent on emergent aquatic insects as subsidies,[8,9,62] and here we found these subsidies to be reduced at concentrations considered safe for aquatic life. These effects are likely particularly severe in the American West where streams are affected by abandoned hard rock mines and natural acid rock drainage.[31] Many streams in this region drain arid landscapes that are relatively unproductive compared to streams.[4] Furthermore, insect communities from western streams are more highly adapted for synchronized emergence and for abilities to disperse from the stream than in other ecoregions of the contiguous US.[63] These qualities of western streams make emergent aquatic insects a plentiful and predictable source of the nutrients and water that riparian consumers need in an environment where both are scarce.[64]

The effects of contaminants (organic or inorganic) on aquatic insect emergence might have large consequences on future populations and communities that inhabit the same or adjacent habitats. Adult survival and reproduction are the ultimate measure of fitness. Decreased emergence or delayed/desynchronized emergence could reduce swarm size and thus reduce opportunities for successful sexual reproduction.[20,65] Not only would there be fewer females available to return to the stream (only 2−20% of all emerged insects do), but the likelihood that eggs will get fertilized will also be reduced.[10,20] Very few adults are thought to return to the stream, even in uncontaminated systems,[4] and genetic analysis suggests stream reaches are repopulated primarily by a few females from the same or nearby stream reaches.[66] Even so, a single female can lay hundreds or thousands of viable eggs ensuring at least the persistence of that population; however, maternal transfer of some organics and metals may decrease egg viability.[23,24,67] Finally, colonization patterns can be altered by pesticides such that aquatic insects will oviposit more frequently in contaminated habitats than in uncontaminated habitats.[68] Thus, streams where contaminants limit emergence could become ecological sinks, habitats where adult females deposit eggs that will not survive or where larvae cannot successfully emerge. All these mechanisms would culminate in fewer viable eggs in the stream and thus smaller future populations.

Our findings on the effects of metals on aquatic insect emergence have implications for the development of aquatic life criteria and benchmarks. Aquatic life criteria are intended to protect 95% of aquatic species and are traditionally derived from laboratory toxicity data.[44] Recent progress and methods development now make field data useful for the development or validation of new aquatic life standards.[69,70] However, adult life stages have yet to be considered in criteria or benchmark development. Aquatic insect emergence could be a useful measure for development of standards to protect aquatic life and as an end point to understand the effects of human disturbance on aquatic and riparian ecosystems.

Adult emergence proved to be more sensitive to metals than larval density in our study. This sensitivity potentially could affect the state of future larval populations and communities, which provide critical resources to riparian ecosystems. In our study, collection of emergence samples took less effort than larvae samples because there was less detritus to sift through

and identification was easier. Although this may not be the case for all studies or streams, emergence sampling was a cost-effective technique that produced data that were a more sensitive indicator of the effects of contaminants on aquatic and riparian ecosystems than larvae. Aquatic life standards inclusive of adult emergence data would protect both larval and adult life stages and ecosystem services to both aquatic and terrestrial ecosystems. Standards that did consider emergence data would guard against these newly realized risks to terrestrial ecosystems, a concept not currently considered in most aquatic life standards.

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Notes
The authors declare no competing financial interest.

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