

RESEARCH ARTICLE

Trophic interactions among algal blooms, macroinvertebrates, and brown trout: Implications for trout recovery in a restored river

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Abstract

Positive correlation between trout abundance and dissolved metal concentrations along the Upper Clark Fork River (UCFR; Montana, USA) have forced restoration practitioners to seek underlying causes of reduced fish density beyond heavy metal contamination. Throughout the river, nutrient enrichment and summer algal blooms may be hindering full recovery of trout populations. In this study, we evaluated the community structure and metal body burdens of benthic invertebrates and characterized existing trophic linkages between brown trout and dominant invertebrate taxa before and during summer algal blooms in a downstream reach of the UCFR where fish densities are low (20–30 trout/km), and where metal contamination is relevant but minimal compared with upstream. In spring, estimated invertebrate abundance was $1,727 \pm 217$ individuals/m² and dominated by Ephemerellidae and Baetidae families. During summer algal bloom, invertebrate abundance increased 15-fold ($20,580 \pm 3,510$ individuals/m²) mostly due to greater abundance of Chironomidae, Hydropsychidae, and Simuliidae. Copper body burdens (130 ± 42 ppm) were higher than any other heavy metal regardless of season, but detectable concentrations of arsenic, cadmium, and lead were also found. A Bayesian mixing model combining metal burdens and stable isotopes showed that in the spring, trout of average size (355 ± 65 g) relied mostly on epibenthic taxa (Ephemerellidae and Hydropsychidae), contrasting with small (<100 g) and large (>400 g) trout relying heavily on Baetidae, a major component of invertebrate drift. Foraging segregation related to trout size did not occur during summer algal blooms, which may reflect increasing influence of benthic algal proliferation or indicate the indiscriminate use of pool habitats as thermal refugia over summer conditions by trout of different ages.

KEYWORDS

brown trout, heavy metal pollution, river food webs, river restoration, riverine algal blooms, trophic interactions

1 | INTRODUCTION

Over a 100-year period, mining and smelting wastes rich in copper, arsenic, zinc, cadmium, and lead were routinely released into the

headwaters of the Upper Clark Fork River (UCFR), Montana (USA). Following several massive floods, these tailings were deposited throughout the UCFR's channel and floodplain, resulting in stores of contaminated sediments (Moore & Luoma, 1990). Decades of river

and floodplain degradation led to the declaration of the UCFR basin as part of the largest U.S. Environmental Protection Agency (EPA) Superfund Site, and the dedication of millions of dollars “to restore the aquatic resources to baseline conditions” (MDOJ, 2008). Since 2012, restoration endeavours have prioritized the removal of floodplain tailings and extensive revegetation of the river's floodplain (MDOJ, 2008). In 2015, water quality in the UCFR began to show signs of recovery; most river water concentrations had fallen below concentration goals set by restoration practitioners (Atkins, 2012). However, one of the river resources with greatest economic and recreational value—trout populations—have yet to show clear signs of recovery. Existing data indicate a reduced abundance of trout species in the UCFR that is likely tied to decades of unregulated toxic waste disposal, but they also suggest that restoration of trout populations may require additional efforts beyond the removal of metal pollution from the riverine floodplain.

Trout accumulate metals by water borne exposure, through their gills and skin (Spry & Wiener, 1991), and in their diet (Erickson et al., 2010), leading to physiological and ecological implications. Previous studies have assessed the effects of metal body burdens on physiological function (e.g., lipid peroxidation) and ecological processes (e.g., recruitment) for brown trout (*Salmo trutta*) in the UCFR (Farang, Boese, Woodward, & Bergman, 1994; Farang, Stansbury, Hogstrand, Macconnell, & Bergman, 1995); and results clearly illustrate metal bioaccumulation when trout are exposed to concentrations characteristic of upper reaches of the UCFR. Multiple studies have identified historic metal pollution as a significant determinant of the current state of diversity and abundance of trout species in the UCFR (Leon, Saffel, Liermann, Lindstrom, & Selch, 2014; Lindstrom, 2011). Average trout density in the UCFR (approximately 125–210 fish/km) is much lower than in resident populations of the river's metal-free tributaries and nearby river systems of similar size (Al-Chokhachy et al., 2016). However, significant variation in trout abundance is regularly observed among sections of the UCFR. Trout density has been consistently greatest in the upper reaches (average of 478 fish/km) where metal contamination was historically, and is presently, most severe, whereas minimum trout density (<30 fish/km) is found downstream where metal pollution is significantly lower (Moore & Langner, 2012). Throughout the river, trout abundance is much lower than population estimates of 1,250 fish/km on the basis of available habitat (Johnson & Schmidt, 1988), but the much lower trout abundance in river sections with lower metal pollution suggest the existence of additional factors limiting trout abundance and potentially affecting game fish recovery.

Beyond heavy metal pollution, warm temperatures and hypoxia are the factors most likely limiting trout populations in the UCFR. Water temperature is being documented as an increasing risk factor for trout populations in the Pacific northwest United States (Isaak, Wollrab, Horan, & Chandler, 2012). Increased temperatures and nutrient concentrations are necessary causes for the occurrence of riverine algal blooms, which can then lead to nocturnal hypoxia and severe fish mortality in river waters. In a literature review, Naughton (2015) emphasized the need for better understanding of thermal stress, dissolved oxygen (DO) concentrations, and potential dietary constraints to help

guide restoration strategies for the UCFR, indicating that nuisance benthic algae may influence and respond to these environmental factors with implications for trout populations.

The interactions among nutrients, temperature, benthic algae, and fish abundance are certainly relevant in the UCFR. Concerns with nutrient enrichment in the UCFR motivated the establishment of some of the first river water quality standards in the United States, including an algal biomass criterion of 100 mg/m² as chlorophyll-*a* (chl-*a*; Dodds, Smith, & Zander, 1997). High concentrations of dissolved nitrogen (N) and phosphorous (P) in the sunlit UCFR are seen as main drivers of summer algal blooms (Dodds et al., 1997), which are dominated by the filamentous green alga, *Cladophora glomerata*. Nuisance *Cladophora* blooms are ubiquitous throughout the UCFR (Suplee, Watson, Dodds, & Shirley, 2012) and their ecological significance for trophic linkages is not well described. Standing crops that carpet the river bottom seasonally and for a 1–2 month period can reach nuisance levels as great as 600 mg chl-*a*/m² (Watson, 1989) with unknown consequences for the river's food web.

Both positive and negative responses by game fish species have been documented under conditions of nutrient enrichment and nuisance algal growth (Askey et al., 2007). Specifically, increases in N and P concentrations are known to cause increases (subsidy response) and decreases (stress response) in brown trout density (Esselman, Stevenson, Lupi, Riseng, & Wiley, 2015) and production (Jonsson, Jonsson, & Ugedal, 2011). How algal blooms influence trout foraging and dietary preferences in the UCFR remains relatively unknown. In addition, the role that filamentous algae may play as a pathway for the incorporation of heavy metals into the food web remains a concern, especially for the UCFR (Farang, Woodward, Goldstein, Brumbaugh, & Meyer, 1998). In this study, we assessed trophic interactions among filamentous algae, macroinvertebrates, and brown trout to evaluate potential dietary constraints and metal burdens associated with excessive algal growth that may contribute to suppressed trout abundance in lower sections of the UCFR where metal contamination is less severe. Our specific goals were to (a) compare community structure and abundance of benthic invertebrates before and during summer algal blooms, (b) quantify metal body burdens of aquatic invertebrates and brown trout during these two contrasting periods of algal abundance, and (c) examine trophic linkages between brown trout and dominant benthic invertebrate taxa before and during summer algal blooms. To do this, we used a combined approach incorporating metal burdens and stable isotope composition of carbon (C) and N in consumers and their resources to construct representative food webs. Contemporary data collected in this study were also compared with existing records of macroinvertebrate and trout abundance to place results influenced by ongoing restoration into a historic context.

2 | METHODS

2.1 | Study site and sampling design

Sampling of benthic invertebrates and brown trout was conducted before (April 12–15, 2016) and during (July 19–21, 2016) the summer

algal bloom in the UCFR along an approximately 10-km-long river reach—herein after referred to as study reach (Figure S1). Historic data on trout densities verify that both fish density (approximately 25 fish/km; Cook, Elam, Liermann, Lindstrom, & Saffel, 2016) and Cu concentrations (approximately 600 ppm, J. Moore, University of Montana, unpublished data) within the study reach were substantially lower than observed further upstream. In our study reach, diel changes in dissolved oxygen (DO) concentrations were monitored over 26 days during maximum algal standing stocks using a miniDOT logger (PME; California, USA). Water temperature was monitored every hour over 2 years at the bottom of our study reach using a HOBO Pendant data-logger. Temperature data were compared with patterns derived from 8 years of daily temperature monitored at two USGS gauging stations located 160 and 40 km upstream of the study reach (Figure S1). During each sampling event, dominant aquatic habitats within the study reach were sampled using a river canoe and standard field methods for macroinvertebrates (Hauer & Resh, 2017). Brown trout were captured along the study reach by a Montana Fish Wildlife and Parks (Montana-FWP) personnel, in coordination with our invertebrate sampling. Further details on the study site in relation to existing monitoring by the State of Montana can be found in Figure S1.

2.2 | Algae, invertebrate, and fish sampling

To address the extent to which abundance of benthic algae, invertebrate, and trout observed in our study was typical for downstream sections of the UCFR, we compared data collected in this study with monitoring data from previous years collected by different state agencies. We quantified benthic abundance of chl-*a* in 2015 and 2016 using similar methods and locations (top and bottom of the study reach) to those used by the Tri-State Water Quality Commission and the Montana Department of Environmental Quality (Montana-DEQ) since 1998. At the top and bottom of our study reach, we removed all benthic algae from 3 to 5 randomly located plots (0.6 m²/plot), and froze all sample material within 4–6 hr after collection for later assessment of chl-*a*. In 2015, benthic chl-*a* was sampled five times (July–September), whereas during the 2016 algal bloom, algal abundance was sampled eight times (mid-June to late September). Summer chl-*a* abundance serves a surrogate of the magnitude of the algal bloom observed in this study and in previous years.

For macroinvertebrate assessment, a total of 10 habitats (five riffles and five runs) randomly distributed along the study reach were sampled before and during benthic algal bloom by collecting two samples using a 500- μ m mesh Surber sampler (sample area = 0.25 m²). Samples were preserved in 70% ethanol until laboratory sorting and identification. Invertebrate abundance was compared with historical conditions using monitoring data (Montana-DEQ data for 2010–2016, Atkins, 2012). Those data provide a historical reference for invertebrate abundance in our study site but caution must be taken on the comparison because benthic invertebrate sampling by Montana-DEQ is routinely conducted in September and thus mostly representative of post-bloom conditions. Following quantitative invertebrate collection, we

conducted 10–15 kicknet samplings within each habitat and pooled samples together in one or more sorting trays in which the most abundant families identifiable in the field—as well as small fish (Cottidae) when present—were collected and stored in dry ice for metal burden and stable isotopes analysis (SIA). Specimens selected for analysis of metal content were collected using plastic forceps and kept in glass vials to avoid contamination. Varying numbers of individuals per taxa (1–30) were collected to provide required minimum biomass for SIA and metal analysis. Finally, we collected a total of five random samples along the study reach during each sampling event including periphyton (i.e., epilithic aufwuchs), Fine Benthic Organic Matter (FBOM), filamentous algae (*C. glomerata*), and cyanobacteria *Nostoc* spp. when found.

Coordination with Montana-FWP personnel ensured that benthic invertebrates and trout samples were collected within a week of each other. A comparison of trout population estimates (fish/km) in the year this study was conducted with previous years was possible because Montana-FWP has monitored trout abundance in this same study reach since 2008. Brown trout were captured along the study reach using a 14-foot long aluminium drift boat equipped with an electrofishing unit with fixed booms, owned and managed by Montana-FWP. Individual trout were measured for length and wet weight upon collection and then preserved at –20°C until further processing. Detailed explanations of the laboratory procedures employed to analyse benthic chl-*a*, invertebrate abundance, SIA, and metal body burdens are available in the Supplementary Information.

2.3 | Data analysis

All statistical analyses were performed using R software version 3.5.0 (R Development Core Team, 2008). Differences in daily water temperature between the two USGS gauging stations of interest were tested using a paired *t* test on the original data. Macroinvertebrates community composition in the UCFR was assessed using non-metric multidimensional scaling (NMDS) on the basis of the Bray–Curtis dissimilarity distances among taxa abundance calculated by the “metaMDS” function from the *vegan* package (Oksanen et al., 2018). Prior to the NMDS analysis, all taxa representing less than 5% of the total abundance were removed. Statistical differences in macroinvertebrates community similarity before and during algal bloom were tested using the “anosim” function from *vegan*. Statistical differences in metal body burdens of invertebrate taxa between pre-bloom and summer events were tested using Student's *t* test after data for metal burdens were log-transformed.

To identify potential food sources for brown trout before and during algal blooms, we employed a combination of metal burdens and SIA following methods described by Soto, Benito, Gacia, Garcia-Berthou, and Catalan (2016). In this analysis, isotope mixing models are performed in a Bayesian framework allowing for the use of spatial and temporal differences in invertebrate metal body burdens as prior information to contrast with isotopic inference. Concentrations in dominant prey are used to estimate the relative contribution of dominant taxa to the trout's diet and then used as prior information to

solve mixing models for stable isotopic data within a Bayesian framework. Detailed steps of the mixing model analysis using metal and SIA data are available as Supplementary Information. Mixing models were performed using the *siar* package in R (Parnell & Jackson, 2013). For all models, we employed the C and N content for each source (Phillips & Koch, 2002) and trophic discrimination factors with usual uncertainty ($\delta^{15}\text{N} = 3.4 \pm 0.7\text{‰}$ and $\delta^{13}\text{C} = 1.6 \pm 0.6\text{‰}$; Post, 2002).

3 | RESULTS

3.1 | Physicochemical data on potential limiting factors

During summer 2016, average benthic algal abundance at upstream and downstream stations was $81.05 \text{ mg chl-}a/\text{m}^2$, only 53.4% of the long-term average for this site ($151.7 \text{ mg}/\text{m}^2$), and this was especially true at the downstream end of the study reach where chl-*a* standing crops were only $32.1 \text{ mg}/\text{m}^2$ (Table S1).

A comparison of daily mean temperatures in the upper river section and nearby our study site did not show significant differences ($t = -0.957$; $df = 2,349$, p value = .338) for over approximately 8 years of record (Figure S2a). At the downstream end of the study reach, water temperature reached maximum values of 26.1°C over a 2-year period (Figure S2b). Moreover, potential thermal stress (water temperature exceeding 19.5°C ; Elliott, Hurley, & Fryer, 1995) occurred for 2–14 hr a day during the summers of 2015 and 2016, and again during multiple full days in summer 2017 (Figure S2c). However, even during the particularly warm summer of 2017, evidence of water column hypoxia ($\text{DO} < 4 \text{ mg/L}$) in our study reach was not observed over a 3-week period (Figure S3).

3.2 | Composition and metal burdens of benthic invertebrates

Comparisons of benthic invertebrate communities before and during algal bloom showed significant differences in both total abundance and species composition (Table S2 & S3). In spring, prior to the algal bloom, abundance of aquatic insects in our study reach averaged $1,727 \pm 217$ individuals/ m^2 (mean \pm standard error), whereas summer invertebrate density increased 15-fold to $20,580 \pm 3,510$ individuals/ m^2 . On average, macroinvertebrate abundance in our study reach ($11,153 \pm 2,014$ individuals/ m^2) was similar to mean density observed in nearby monitoring during previous years ($8,848 \pm 2,802$ individuals/ m^2 ; Figure S1, Montana-DEQ). The spring macroinvertebrate community included 21 insect families (species richness (S) = 18/sample, $H' = 1.65$), with dominant taxa composed of mayflies (Ephemeroptera and Baetidae, Figure 1). Families found only during spring included Lepidostomatidae and Chloroperlidae, representing together less than 1% of all individuals. During the summer algal bloom, taxonomic richness decreased to 15 species/sample ($H' = 1.76$) and abundance was dominated both by increased densities of Chironomidae and Hydropsychidae, and by taxa almost exclusively

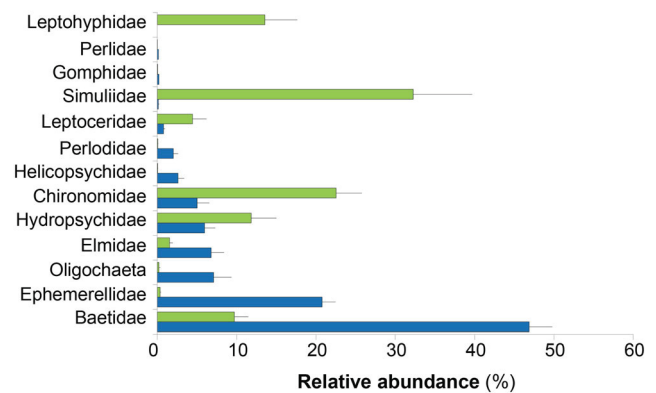


FIGURE 1 Relative abundance of principal invertebrate families found in the spring (blue) and summer (green) samplings. Values are means (\pm standard error) of percent contribution to total macroinvertebrate abundance for each taxa of interest [Colour figure can be viewed at wileyonlinelibrary.com]

found during summer conditions (e.g., Simuliidae, Leptohyphidae, Figure 1). Across both samplings, invertebrate predators (e.g., Gomphidae, Perlidae) persisted as part of the benthic community, but were scarce ($<1\%$ of total abundance; Table S2 & S3). These differences in community composition between spring pre-bloom and summer communities during the algal bloom were evident and illustrated by a significant separation along the first NMDS axis of the benthic samples corresponding to each sampling event (Figure 2, ANOSIM $R = .998$, $p = .001$).

Metal body burdens in the most abundant invertebrates families and trout tissues showed contrasting results across trophic level, tissues, and heavy metals (Table 1). Body burdens of Cu were measurable during both sampling events, whereas Cd, As, and Pb were only detected in the spring (Table 1). Average body burdens for Cu, As, Cd, and Pb in primary consumers found in both spring and summer seasons (Baetidae and

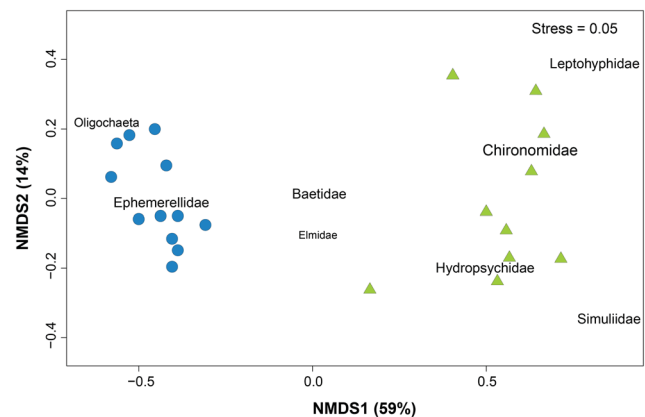


FIGURE 2 Results of nonmetric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity distance measures on abundance data at the family level. Taxa accounting for less than 5% of total abundance in one season or another were removed prior to the analysis. Site scores are labelled by season as before (blue dots) and during (green triangles) summer algal bloom. Taxa scores are labelled by corresponding insect family with font size proportional to the average relative abundance across seasons [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Mean (\pm Standard error) for heavy metal body burdens of most dominant macroinvertebrate taxa (same for which SIA data was collected) and brown trout (liver and dorsal fin muscle) before and during summer algal bloom

Time period	Cu (ppm)	As (ppm)	Cd (ppm)	Pb (ppm)
Pre-bloom				
Baetidae	108 \pm 19 [*]	6.3 \pm 2.5 [*]	10.0 \pm 0.7 [*]	bd
Ephemeroellidae	186 \pm 21	10.1 \pm 2.3	9.8 \pm 0.9	bd
Hydropsychidae	232 \pm 151	11.2 \pm 1.8 [*]	1.3 \pm 0.4 [*]	20.1 \pm 4.2 [*]
Perlodidae	76 \pm 5	4.1 \pm 0.0	1.5 \pm 0.4	bd
Perlidae	87 \pm 16	5.0 \pm 2.0 [*]	1.5 \pm 0.6 [*]	bd
Gomphidae	92 \pm 45	4.6 \pm 2.1 [*]	1.4 \pm 0.4 [*]	bd
<i>Salmo trutta</i> (fin)	2 \pm 1	bd	bd	bd
<i>Salmo trutta</i> (liver)	191 \pm 88 [*]	bd	bd	bd
Bloom				
Baetidae	34 \pm 3 [*]	bd [*]	bd [*]	bd
Leptohyphidae	128 \pm 36	bd	bd	bd
Hydropsychidae	113 \pm 50	bd	bd	bd
Simuliidae	94 \pm 68	bd	bd	bd
Chironomidae	68 \pm 23	bd	bd	bd
Perlidae	104 \pm 32	bd [*]	bd [*]	bd
Gomphidae	64 \pm 5	bd [*]	bd [*]	bd
<i>Salmo trutta</i> (fin)	1 \pm 1	bd	bd	bd
<i>Salmo trutta</i> (liver)	21 \pm 17 [*]	bd	bd	bd

Note. Asterisks (*) indicate significant differences in heavy metal body burdens between pre-bloom and bloom conditions calculated by Student's *t* tests for each heavy metal and taxa of interest (*p* value < .5). Minimum detection limit was used for *t* test comparisons when metal body burdens were below analytical detection.

Abbreviation: bd = below detection

Hydropsychidae) were greater in pre-bloom conditions (Table 1). Hydropsychidae was the only taxa with Pb concentrations above our detection limit for any of the two seasons (Table 1). Invertebrate predators, such as Perlidae and Gomphidae, had similar Cu body burdens between seasons but lower concentrations of As and Cd during summer algal blooms (Table 1). Metal concentration in trout fin tissue did not differ significantly between samplings for any heavy metal in contrast to liver tissues that showed greater concentrations of Cu in the spring (Table 1). Overall, biomagnification (i.e., greater heavy metal concentrations in organisms at the top of the food chain) was not observed for any heavy metal. Conversely, average values of most heavy metals seem to be lower at higher trophic levels, but large variation across taxa and tissues suggest cautionary interpretations of these results.

3.3 | Trophic interactions before and during algal blooms

Carbon isotopic signatures of basal resources were substantially enriched in comparison with macroinvertebrates and trout ^{13}C signatures (Figure 3), and this was especially true for periphyton and FBOM

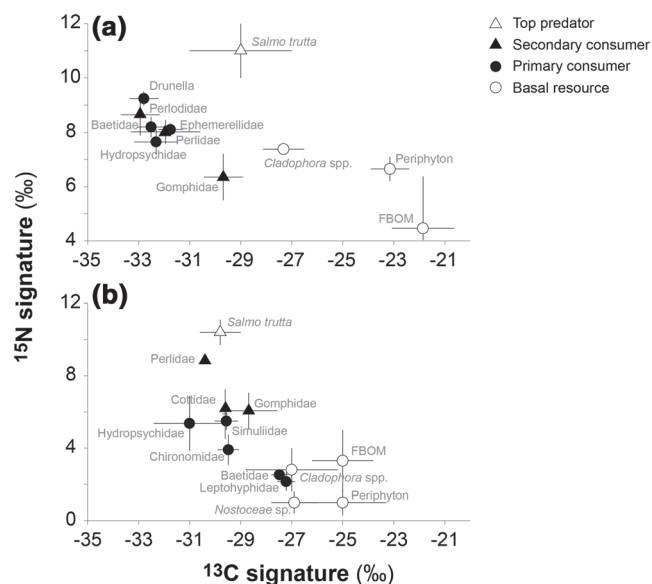


FIGURE 3 Biplot of ^{13}C and ^{15}N signatures for principal basal resources, consumers, and brown trout before (a) and during (b) the summer algal bloom. Putative trophic positions are shape- and colour-coded as indicated in the legend. FBOM corresponds to Fine Benthic Organic Matter. Data are means \pm standard error for each isotopic signature. Note the different scales for vertical axes in spring and summer plots

during pre-bloom conditions (Figure 3a). Nitrogen isotope signatures for benthic algae (i.e., *C. glomerata*, periphyton, mean values 7.4 and 6.7‰) were enriched compared with FBOM (4.5 \pm 2.1‰) during spring when all basal resources were heavier than corresponding summer values. Lighter ^{15}N signatures were recorded during the algal blooms for Nostocaceae (1.0 \pm 0.6‰) and periphyton (1.1 \pm 0.7‰), which were in turn depleted in comparison with *C. glomerata* and FBOM samples (2.8 \pm 1.2‰ and 3.3 \pm 1.7‰, respectively; Figure 3 b). In general, most ^{15}N signatures for basal resources and consumers decreased from spring to summer (Figure 3). Starting with basal resources, trophic discrimination of ^{15}N (3.4 \pm 0.7‰; Post, 2002) suggested the existence of a total of three and four trophic levels in the spring and summer, respectively (Figure 3). In the spring, no clear isotopic distinction between herbivorous taxa and secondary consumers was observed, resulting in a three-level food chain including basal resources, invertebrates, and trout (Figure 3a). In addition, some unexpected patterns in ^{15}N signatures of specific invertebrate taxa were observed during spring, including depleted ^{15}N values for some predatory taxa (Gomphidae) and relatively enriched ^{15}N values of *C. glomerata* (Figure 3a). During the algal bloom, range of ^{15}N was widened (1.1–11.2‰) and clear separation of primary and secondary consumers was found (Figure 3b). Despite a general shift to more depleted ^{15}N signatures during the bloom, trout isotopic signatures remained relatively similar between the two sampling events (Figure 3). No significant correlations were found between trout size (weight or length) and ^{13}C or ^{15}N signatures.

Results of Bayesian mixing models generated distinct food webs during spring and summer (Figure 4) and notably identified the

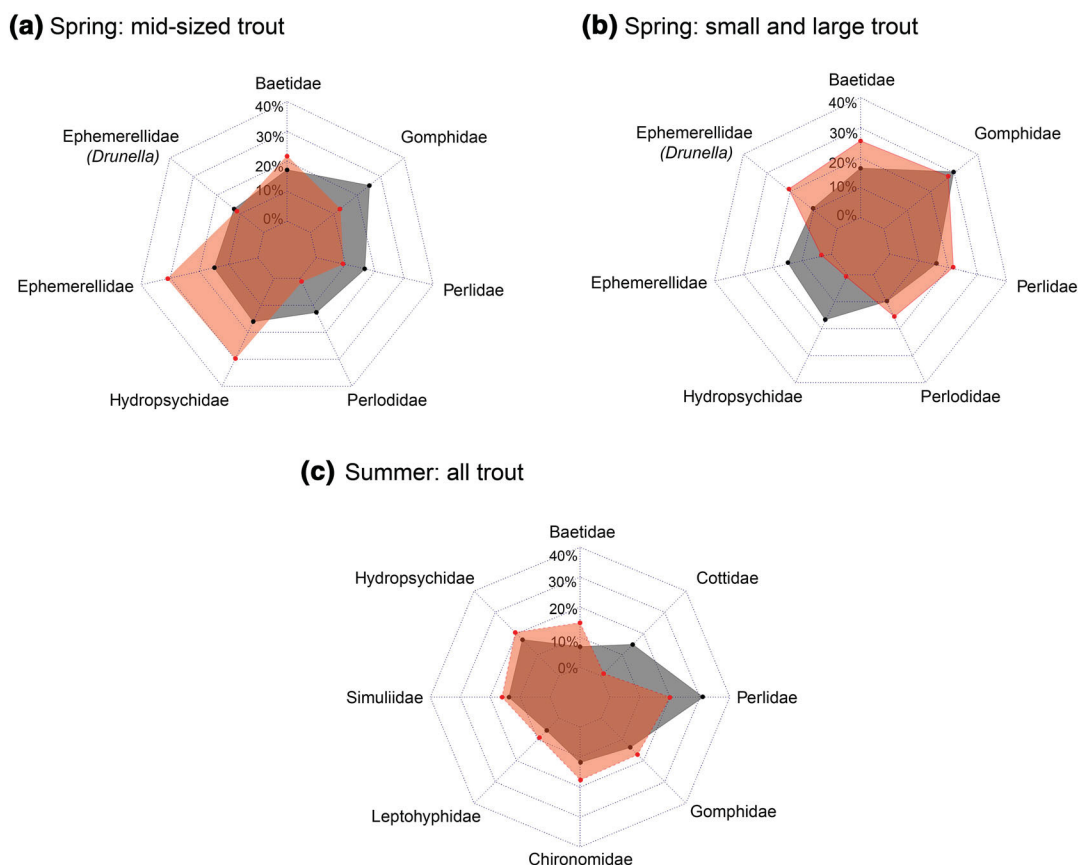


FIGURE 4 Radius plots showing estimated contribution of each food source to brown trout diet from SIAR models relying exclusively on ^{13}C and ^{15}N signatures (grey polygons) and models using metal data as prior information and SIA as likelihood estimations (red polygons). Panels represent mixing models results for mid-sized trout in the spring (a), small (<100 g) and large (>400 g) trout in the spring (b), and all trout during the summer algal bloom (c). Dots are average estimations of dietary contributions calculated from the posterior distribution generated by each SIAR model. Uncertainty associated with average estimations can be found in Table S4 [Colour figure can be viewed at wileyonlinelibrary.com]

existence of unique trophic interactions linked either to small and large individuals (Figure 4a) or to mid-sized (Figure 4b) trout during spring, but a single food web for all trout during summer (Figure 4c). During spring pre-bloom conditions, models derived exclusively from SIA suggested comparable contributions to trout diet for dominant taxa, regardless of trout size (Figure 4a-b, grey polygons). However, the same pre-bloom models augmented by metal burdens as informative priors revealed different dietary preferences for two distinct groups of trout on the basis of their size. Trout individuals of average size (355 ± 65 g) relied mostly on Ephemerellidae and Hydropsychidae, whereas both small (<100 g) and large (>400 g) trout displayed a broad diet on the basis of multiple taxa, representing primary and secondary consumers (Figure 4a-b). For mid-sized trout, metal concentrations of invertebrates increased with their proportional contribution to trout diet ($b = 0.0012$; $r^2 = 0.79$; p value < .01), whereas prey taxa with lower Cu body burdens contributed the most to small and large trout diet ($b = -0.0016$; $r^2 = 0.91$; p value < .01). After detrending the effect of body size, Cu burdens of mid-sized trout were significantly greater than those found for individuals belonging to the small/large size class (Student's t test; p value < .001). Together, these data highlight the role of dietary preferences on trophic transfer and resultant trout metal burdens. Because models derived exclusively from SIA did not

partition trout dietary preferences by size (Figure 4a,b, grey polygons), prior information on the basis of metal body burdens appears to have been central to the recognition of distinct food webs for the two putative groups of trout (Figure 4a,b).

In the summer, mixing models based exclusively on SIA and models combining metal and isotope data were in good agreement for all taxa with the exception of sculpins (Cottidae) as well as Perlidae whose decreased contribution following prior inclusion translated to small increases in contribution by concomitant taxa (Figure 4c). During the summer algal bloom, trout populations in the lower UCFR relied heavily (47% of their diet) on those taxa whose relative abundance increased the most compared with their spring numbers, including filter feeders (Hydropsychidae and Simuliidae), and Chironomids (Figures 2 & 4c). Results of the same mixing models using Perlidae family as the top consumer showed a $31 \pm 6.7\%$ contribution of Hydropsychidae, which in turn appear to rely heavily ($48 \pm 5.3\%$) on *C. glomerata* as a food resource; no prior information was available for this last estimation as metal concentrations of basal resources were not determined. Overall, results suggested a strong trophic link between *C. glomerata*, Hydropsychidae, Perlidae, and brown trout during summer conditions.

4 | DISCUSSION

4.1 | Food web linkages influencing trout metal burdens

Field studies in the UCFR focusing on the transport of heavy metals through the food chain have highlighted the importance of progressive movement from water through sediment, periphyton, invertebrates, and finally fish, in which signs of bioaccumulation were frequently observed (Farag et al., 1998). Distinct functional feeding groups of benthic invertebrates (e.g., collectors and filter feeders) rely heavily on suspended particles and periphyton, enabling the propagation of heavy metals from sediment sources through filter feeders and grazer taxa (Bundschuh & McKie, 2016) to predatory fish. This same pathway is likely to be influential for our study reach wherein filter feeders (e.g., *Hydrophsyche* spp.) were a relevant food resource for brown trout in both seasons, whereas representing one of the taxa with greatest metal concentrations, as documented by others for the UCFR (Hornberger, Luoma, Johnson, & Holyoak, 2009).

Prior to the summer algal bloom, body burdens of As, Cu, Cd, and Pb in aquatic invertebrates observed in our study were of similar magnitude to those previously found in the UCFR (e.g., Farag et al., 1994). During the algal bloom, however, metal body burdens were lower on average for most of the invertebrate taxa and trout tissues. A number of abiotic and biotic factors may influence seasonal changes in body burdens. Greater discharge during spring compared with summer is usually associated with increased dissolved and particulate metal concentrations in the UCFR (Atkins, 2012). Greater fish mortality is typically found during high spring run-off (Marr et al., 1995; Schreck, Saffel, Liermann, Lindstrom, & Selch, 2012). Therefore, reduced metal concentrations of prey taxa during summer algal blooms may simply reflect decreased river loads of heavy metals at base flow.

Opposing perspectives exist concerning the influences of enhanced algal growth on the propagation of metal toxins in aquatic systems. Some have argued that enhanced primary production in streams may promote propagation of toxicants to consumers through greater uptake by periphyton (Stewart, Hill, & Boston, 1993). *Cladophora glomerata* is in fact known to have an affinity for heavy metal cations (e.g., Cu and Cd, Akin & Unlu, 2013). Others have argued that enhanced productivity in aquatic systems should reduce accumulation in consumers through bloom or growth dilution phenomena (Ward, Nislow, Chen, & Folt, 2010). Bloom dilution occurs when enhanced cell division in growing algae leads to decreased metal content per gram of algal biomass, whereas growth dilution occurs among consumers with enhanced somatic growth resulting from bottom-up stimulation by greater primary production (Walters et al., 2015). Our results did not unequivocally support either perspective. For instance, significantly higher concentrations of cations such as Cu and Cd were found in some aquatic invertebrates during times of lowest algal biomass but not in many other taxa. A robust assessment of metal content in primary producers is

lacking, and specific consumer resource relationships may be required to elucidate metal transfer associated with increased algal abundance.

Given the low density of riparian vegetation along the UCFR, senescing tissue of *C. glomerata* is thought to be the dominant source of fine particulate matter on the stream bottom, which represents as much as 30% of all benthic organic matter during summer blooms (Banish, 2017). The putative algal origin of these particles is in close agreement with the similarity in ^{13}C and ^{15}N signatures observed in summer for FBOM and *C. glomerata*. Hornberger (2006) showed that more than 90% of the Cu body burden gained by *Hydrophsyche* spp. is diet-borne. Hence, elevated Cu concentration for this taxa during the time of high algal abundance may be associated with metal-laden *C. glomerata*, its transformation to FBOM, and a subsequent trophic link to *Hydrophsyche* spp. and brown trout apex predators. Hence, our results suggest that algal blooms of *C. glomerata* may potentially reduce metal bioavailability for the invertebrate community as a whole through bloom dilution, whereas concomitantly explaining the greater Cu concentrations in filter feeders *Hydrophsyche* spp. compared with Cu burdens observed by Hornberger et al. (2009) at a similar location but critically later in the algae growing season (August).

4.2 | Seasonal variation in trophic structure: implications of changing basal resources

Four trophic levels were identified during summer with separation of brown trout, predatory insects (e.g., Perlidae), herbivorous taxa, and basal resources evident from ^{15}N signatures. Separation of macroinvertebrate taxa into distinct trophic levels before the algal bloom was difficult due to much lower variation in $\delta^{15}\text{N}$ signatures during spring. This is likely derived from increased temporal variation in ^{15}N signatures at lower trophic levels (Post, 2002), especially for basal resources (Peipoch, Marti, & Gacia, 2012). Both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values may integrate relatively recent but past isotopic conditions in food sources that no longer exist at the time of consumer sampling. Large differences in ^{13}C signatures (8–10‰) between consumers and basal resources (e.g., FBOM and *C. glomerata*) were observed during both sampling events, differences well beyond those expected from trophic discrimination (Post, 2002). Variation could reflect the influence of changing water velocity on ^{13}C signatures (Finlay, Power, & Cabana, 1999) or changes in composition of inorganic carbon sources (Rosenfeld & Roff, 1992). Similar differences (i.e., 10‰) in ^{13}C signatures of algae have been found within the Colorado River (Shannon, Blinn, Haden, Benenati, & Wilson, 2001), and others have attributed ^{13}C differences of this kind to temporal variation in basal resources (Cucherousset, Aymes, Santoul, & Cereghino, 2007). Overall, large isotope variation in basal resources and primary consumers contrasted with small differences in trout isotopic signatures between seasons, reflecting the effects of slower biomass turnover on isotope signatures of larger organisms (del Rio & Carleton, 2012).

4.3 | Algal abundance and fish body size: Influences on brown trout dietary preferences in the UCFR

In his review of competition and habitat segregation among stream-swelling salmonids, Hearn (1987) emphasized that competition for space serves as a surrogate for resource access, in that, preferred habitats are those with minimal energy demand but near swift flows that are typically areas of greatest drift. The importance of drifting prey for trout and charr is well-documented (Baxter, Fausch, & Saunders, 2005; Wyatt F. Cross et al., 2011; Forrester, Chace, & McCarthy, 1994). At the same time, many studies have shown how trout can rely heavily on benthic insects foraged from the stream bottom (Baxter, Fausch, Murakami, & Chapman, 2004; Jansen, Slettovold, Finstad, & Langeland, 2002), particularly when drifting invertebrates are scarce or unavailable (Baxter et al., 2004; Stephens & Krebs, 1986; Zhang & Richardson, 2007). Feeding preferences can change in response to prey availability, interspecific interactions with other fish species, or intraspecific dynamics. Brown trout are aggressive fish with dominance determined by body size with larger individuals occupying deeper and faster habitats (Greenberg, Bergman, & Eklov, 1997), where encountering drifting prey is likely more frequent (Hearn, 1987). This intercohort competition (Ayllon, Nicola, Parra, Elvira, & Almodovar, 2013) represents an intraspecific segregation that shifts foraging modes spatially so that larger dominant individuals forage preferentially on abundant prey, whereas smaller subordinate fish are displaced to utilize other (i.e., epibenthic) species. Others have shown temporal segregation in access to preferred habitats with larger brown trout occupying optimal drift-feeding habitat at dusk when prey are most abundant (Alanara, Burns, & Metcalfe, 2001). The extent and intensity of territoriality and niche overlap among cohorts, however, changes with fish density and prey availability. Ayllon et al. (2013) noted that habitat selection among young-of-the-year, juvenile, and adult brown trout varied with density such that younger individuals were dominated by older (i.e., larger) fish, but that smaller fish can expand their range of selected habitat when density of intercohort competitors is low. Moreover, older trout often did not respond to densities of much younger fish despite their potential to negatively influence final performance (Ayllon et al., 2013; Kaspersson, Hojesjo, & Bohlin, 2012). The degree of territoriality in feeding among cohorts of brown trout also varies with prey availability. Alanara et al. (2001) showed that a greater distinction in foraging allocation occurred associated with brown trout body size when resources were in greater demand.

In the UCFR, distinct feeding behaviour by brown trout of different size classes likely explains why our mixing models recognized unique trophic linkages and associated dietary preferences on the basis of fish size during the spring. Average-size trout relied heavily on non-predatory scrapers (Ephemeroptera) or filter-feeders (e.g., Hydropsychidae), taxa associated with epibenthic habitats that are not commonly found in the drift (Bruno, Bottazzi, & Rossetti, 2012). In contrast, small and large fish relied heavily on Baetidae during spring, the single most abundant taxon and a family commonly found in the drift (Forrester et al., 1994). During a single sampling event conducted at dusk a few days after our pre-bloom sampling, Baetidae

represented 63–80% of the total invertebrates found in the drift (data not shown). These results suggest that under low densities of prey and predator, the different dietary preferences of brown trout prescribed to fish size may reflect forage mode distinction between cohorts. Specifically, niche overlap between small and large individuals observed in the UCFR seems plausible given the very low densities of trout that prompted our investigation and the research showing the expansion of foraging habitats by small fishes given low densities of larger fish (Ayllon et al., 2013; Kaspersson et al., 2012). Under these conditions, large trout individuals may not have perceived small individuals as significant competitors. The fact that apparent foraging segregation among individuals of large and intermediate size classes occurred in the spring, but not in the summer (with a 15-fold increase in invertebrate density), may reflect how increased prey availability can lead to reduced intercohort niche partitioning (Alanara et al., 2001). Moreover, the thermal stress we observed during summer months may force brown trout to periodically cease foraging segregation. Elliott (2000) reported indiscriminate use of pool habitats as thermal refugia during summer conditions by trout of different ages.

4.4 | Nutrient enrichment and trophic interactions in the UCFR: implications for Cladophora abundance and influence

From a theoretical perspective, secondary productivity for all trophic levels should be enhanced under nutrient-rich conditions that promote increased rates of primary production (Dodds, 2006; Thorp & Delong, 1994). It is reasonable to argue that increased algal production may have enhanced macroinvertebrate productivity, size, and apparent density given the propensity for taxa in the UCFR to be multivoltine (*pers. comm.*, Sean Sullivan, Rithron Associates, Inc.). Density responses to resource availability, however, are complicated by species life histories (Benke, 1984), dispersal and colonization (Robinson, Minshall, & Rushforth, 1990), and resultant distribution (Power, Matthews, & Stewart, 1985). Ultimately, trophic support for consumers depends on prey production (Cross et al., 2011; Cross et al., 2013). In any case, we documented a significant increase in the overall abundance of aquatic invertebrates during the summer algal bloom at the UCFR. This was especially true for those taxa that together accounted for 47% of the summer diet for brown trout on the basis of combined inference from metal burdens and stable isotopes. From this particular perspective, seasonal blooms of filamentous algae may represent a bottom-up enhancement of energy flow through basal resources, macroinvertebrate consumers, and fish. It is important to note, however, that the mixing models employed here provide only relative proportions of diets for consumers, generated independently of prey abundance, and lacking information on the magnitude of energy flow from resource to consumer.

Several examples of top-down effects on primary producer standing crops and rates of production exist in the literature (Huryn, 1998; Lamberti & Resh, 1983). In her seminal paper on river food webs, Power (1990) concluded that within a system with similar conditions

to the UCFR in terms of nutrient availability, light, and seasonal blooms of *Cladophora*, classic theory of trophic control (Fretwell, 1977; Hairston, Smith, & Slobodkin, 1960) was applicable to riverine food webs, and therefore algal production should be limited by herbivores in food webs with even numbers of trophic levels. Our results provide compelling evidence of a 4-level food chain in the UCFR during summer elucidated through (a) the broad range in $\delta^{15}\text{N}$ (~10‰) existing between basal resources and brown trout, and (b) results of our mixing models indicating trout consumption of predatory insects that prey upon filter feeders (Hydropsychidae and Simuliidae) relying on fine suspended particles of algal biomass in a river system with reduced allochthonous input of organic matter. However, a study of the distinct phenological stages of *Cladophora* in the UCFR did not observe evidence of abundant grazers or herbivory on algal mats (Banish, 2017). Although brown trout have provided top-down control in other river systems (Huryn, 1998; Power, Parker, & Dietrich, 2008), the extent to which the existing trophic system in the UCFR functions as a classic 4-level food web remains unclear. Although a lack of research directly addressing the potential for intensive herbivory to limit algal abundance in the UCFR clearly does not preclude its existence, it is possible that low trout abundance due to other factors (temperature, habitat quality, metal pollution) limits the intensity of consumer control predicted by a trophic cascade despite the existence of a food web with an even number of trophic levels that includes brown trout as apex predators.

4.5 | Trophic relationships, restoration, and trout recovery efforts in the Upper Clark Fork River

Nutrient enrichment and high water temperature increase algal productivity in aquatic ecosystems and evidence exists to suggest that greater autochthonous production in river systems enhances fish biomass and production (e.g., Thorp & Delong, 1994). On the other hand, excessive levels of N and P may disturb trophic dynamics in ways detrimental to trout by favouring abundance of invertebrate taxa that trout do not usually feed upon, impairing visual or physical access to prey, or providing competitive advantage to other fish groups (e.g., minnows and suckers). Many studies have reported increased macroinvertebrate abundance in nutrient polluted rivers (Friberg, Skriver, Larsen, Pedersen, & Buffagni, 2010; Gulis, Ferreira, & Graca, 2006) and some of them have also shown trout species benefiting from the increased resources or decreased competition with other fish species (Askey et al., 2007; Frey, Bell, Hambrook Berkman, & Lorenz, 2011). However, other studies have indicated that nutrient enrichment had a negative effect on trout biomass (Jonsson et al., 2011; Wang, Robertson, & Garrison, 2007). Our analysis of the existing trophic interactions between brown trout and the invertebrate community in the UCFR documented existing dietary relationships before and during the development of nuisance levels of *C. glomerata*. Nutrient enrichment and its influences on the river's food web is one of multiple ecological stressors potentially affecting trout density and production. Others include metal contamination (Frag et al., 1995), isolation from

reproductive habitat in adjacent tributaries (Cook et al., 2016), and thermal stress (Isaak et al., 2012). The removal of floodplain tailings is already reducing metal contamination and improving water quality (Atkins, 2012). Moreover, increased river–floodplain connectivity due to the removal of contaminated alluvium may enhance fish access to adjacent tributaries. Much less clear is how restoration will help reduce thermal stress on trout populations of the UCFR. Our study showed signs of thermal stress on brown trout for several hours a day over multiple summers, which suggest the critical and relatively unknown role that high temperatures may play on the recovery of trout populations. Thermal stress seems to be a widespread phenomenon in the UCFR and yet it is unlikely that ongoing restoration efforts will help decrease water temperatures at the short-term. Restoration efforts currently underway are being pursued with the concomitant and persistent influences of nutrient enrichment and thermal stress. Therefore, it remains critical to quantify production of prey populations and establish the trophic basis for fish production (e.g., Cross et al., 2011, 2013) to discern how efficiently prey production is transferred to trout populations throughout the development of riverine algal blooms.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, M. P., upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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