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ARTICLE

Application of multistate modeling to estimate salmonid survival and movement in relation to spatial and temporal variation in metal exposure in a mining-impacted river

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Abstract: Multistate modeling was used to estimate survival and movement of brown trout (*Salmo trutta*) and westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) in relation to copper concentrations in the mining-impacted Clark Fork River, Montana. Survival probability in the uppermost river segment, where dissolved copper concentrations frequently exceeded acute criteria for aquatic life (range: 31–60 days > 13.4 $\mu g \cdot L^{-1}$), was 2.1 times lower for brown trout and 122 times lower for westslope cutthroat trout compared with survival rates in the lowermost segment that had relatively low dissolved copper (0 days exceedance of acute concentration). Lowest survival for both species occurred in the spring–summer period when dissolved copper concentrations were elevated coincident with higher discharge. Movement among study segments was generally low, and cutthroat trout showed low movement into the uppermost river segment with the most elevated copper levels. Both species showed high rates of movement into tributaries, which coincided with their respective spawning migrations rather than as an apparent avoidance of elevated copper levels. The linkage between survival rate and level of copper exposure for both trout species suggests that additional removal of tailings deposits could improve survival rates.

Résumé : La modélisation multi-états est utilisée pour estimer la survie et les déplacements de truites brunes (*Salmo trutta*) et de truites fardées versant de l'ouest (*Oncorhynchus clarkii lewisi*) au vu des concentrations de cuivre dans la rivière Clark Fork (Montana), une rivière touchée par les impacts de l'activité minière. La probabilité de survie dans le tronçon le plus amont de la rivière, où les concentrations de cuivre dissous dépassent fréquemment les critères d'exposition aigüe pour la vie aquatique (fourchette: 31–60 jours > 13,4 $\mu g \cdot L^{-1}$), était 2,1 fois plus faible pour la truite brune et 122 fois plus faible pour la truite fardée versant de l'ouest que les taux de survie dans le tronçon le plus aval, caractérisé par des concentrations de cuivre dissous relativement faibles (0 jour de dépassement de la concentration associée à une exposition aigüe). Les taux de survie les plus faibles pour les deux espèces ont été observés durant la période printanière et estivale, moment où de fortes concentrations de cuivre dissous coïncidaient avec des débits plus importants. Il y avait généralement peu de déplacements entre les tronçons étudiés, et les truites fardées versant de l'ouest présentaient des déplacements limités dans le tronçon le plus amont de la rivière caractérisé par les plus fortes concentrations de cuivre. Les deux espèces présentaient des fréquences élevées de déplacements vers les affluents, qui coïncidaient avec leurs migrations de frai respectives plutôt que de refléter d'apparents efforts pour éviter de fortes concentrations de cuivre. Le lien entre le taux de survie et le niveau d'exposition au cuivre pour les deux espèces de truite donne à penser que la poursuite du retrait des dépôts de stériles pourrait améliorer les taux de survie. [Traduit par la Rédaction]

Introduction

Water pollution from mining is one of the most detrimental and persistent anthropogenic impacts in fresh waters. Mining can release of large volumes of trace metals and waste material, which, in turn, can adversely affect water quality, physical habitat, fish populations, and aquatic food webs over extensive areas for long time periods (Farag et al. 2003; Luoma et al. 2008; Kiser et al. 2010). The US Environmental Protection Agency (EPA) ranking of hazardous waste sites designates the most contaminated sites as "Superfund" sites, so named for their particularly harmful and far-reaching environmental impacts (Moore and Luoma 1990). One such example is the upper Clark Fork River in southwestern Montana, the largest Superfund site in the United States, where operation of the Butte copper mines from the 1880s to 1960s resulted in deposition of an estimated 99.8 billion kg of mining waste in the floodplain, rendering about 200 km of the river essentially devoid of fish for many decades due to metal toxicity (Phillips and Lipton 1995).

Elevated metal concentrations affect aquatic ecosystems at multiple levels of biological organization (Clements 2000). At the individual level, metal exposure can contaminate prey and bioaccumulate in fish tissues, resulting in a multitude of physiological responses that diminish health and reduce survival, including impaired feeding, food assimilation, and growth (Woodward et al.

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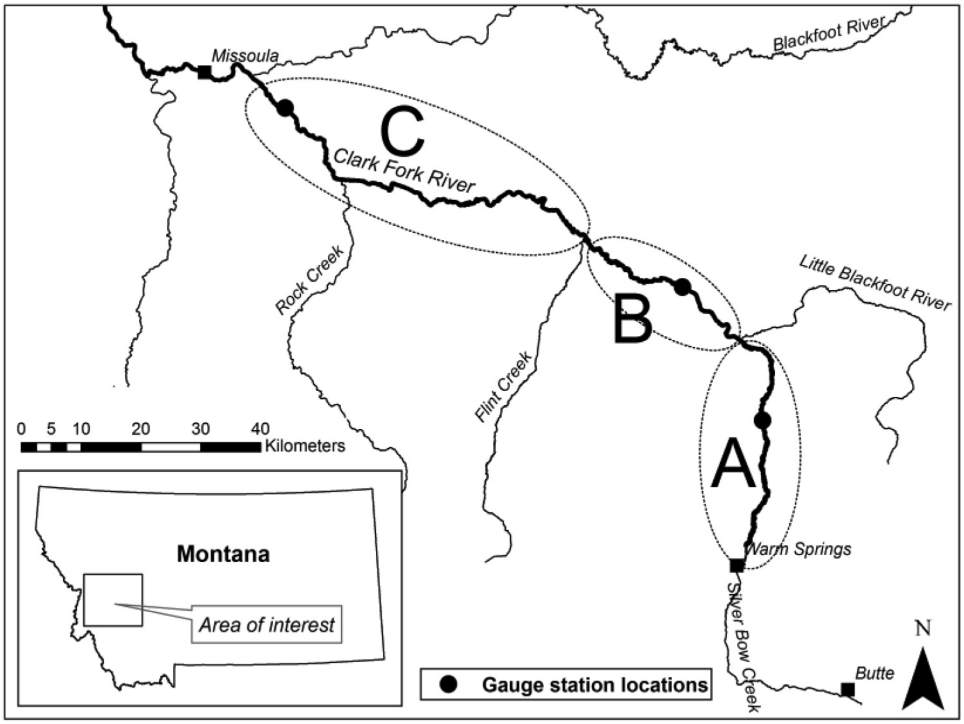
Fig. 1. Three mainstem segments, major tributaries and towns, and discharge, temperature, and metal sampling gauge stations, upper Clark Fork River, Montana, 2009–2011.



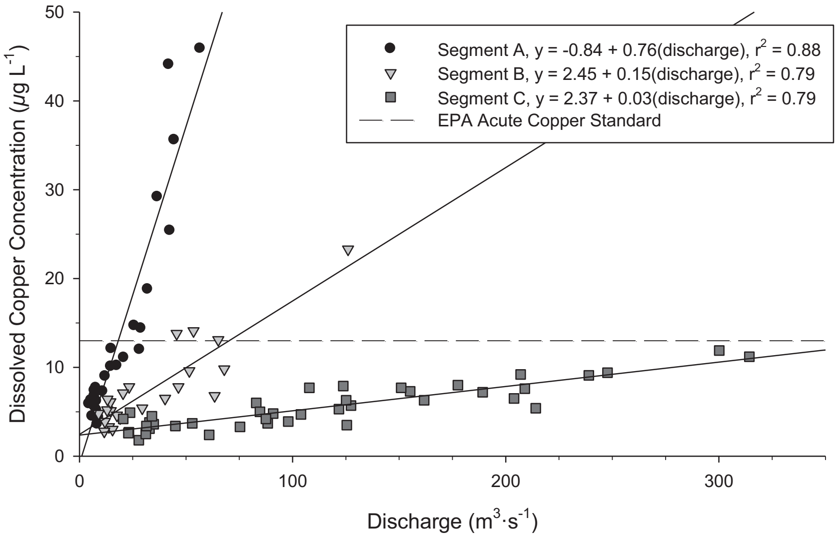
1995*a*; Farag et al. 2000). Direct mortality from metal exposure can occur when metals are mobilized from stream bank and floodplain deposits during high flow events and exceed acute toxicity levels (Marr et al. 1995; Phillips and Lipton 1995; Luoma et al. 2008). Furthermore, behavioral avoidance of waters with elevated concentrations of metals can limit distribution and access to suitable habitat and may occur at concentrations substantially lower than those causing acute effects on survival (Woodward et al. 1995*a*; Goldstein et al. 1999; Svecevicius 2001). At higher levels of organization, changes in fish assemblages occur in response to elevated metal concentrations when species have different physiological sensitivities and behavioral avoidance thresholds to metals. For example, in the western United States, nonnative brown trout (*Salmo trutta*) are less sensitive to metals than cutthroat trout (*Oncorhynchus clarkii*) and rainbow trout (*Oncorhynchus mykiss*), and this variable sensitivity has resulted in a shift toward brown trout dominance in mining-contaminated systems (Hansen et al. 1999*a*).

Prior to mining, native bull trout (*Salvelinus confluentus*) and westslope cutthroat trout (*O. clarkii lewisi*) were widespread throughout the upper Clark Fork River drainage (Luoma et al. 2008). However, surveys in the late 1800s to the 1950s found very few or no fish in the river from Silver Bow Creek, near Butte, Montana, downstream to Rock Creek, near Missoula, Montana (Phillips and Lipton 1995). Water, sediments, and aquatic invertebrates contained high levels of copper, zinc, lead, cadmium, and arsenic (Axtmann and Luoma 1991). A series of remediation efforts began in the 1960s to alleviate the primary source of trace metals, Silver Bow Creek, a headwater tributary of the upper Clark Fork River (Fig. 1; Phillips and Lipton 1995). These activities included installation of liming ponds and a wastewater treatment plant and, more recently, removal of stream channel and floodplain sediments containing high metal concentrations. Following remediation in Silver Bow Creek, metal concentrations downstream in the upper Clark Fork River declined substantially (Luoma et al. 2008; Hornberger et al. 2009), and trout began to recolonize in the 1970s after an ostensibly century-long absence (Phillips and Lipton 1995). Nonnative brown trout are now the dominant trout species, but nonnative rainbow trout and native westslope cutthroat trout and bull trout, which are low to moderately abundant in nearby, uncontaminated rivers, are rare (Luoma et al. 2008). Currently, metal concentrations in sediments in the upper Clark Fork River decline exponentially downstream (Axtmann and Luoma 1991; Luoma et al. 2008; Hornberger et al. 2009), as do metal concentrations in fish and macroinvertebrate tissues (Farag et al. 1995). However, dissolved metal concentrations, especially copper, continue to periodically exceed acute criteria for aquatic life (13.4 $\mu g \cdot L^{-1}$; USEPA 2007) during pulses of high discharge during spring runoff and summer thunderstorms (Nimick and Moore 1991; Luoma et al. 2008).

Trout population estimates conducted in the 1990s (summarized in Luoma et al. 2008) suggested mean trout densities in the upper Clark Fork River were about 10% of expected trout density compared with noncontaminated reference reaches in nearby rivers. More recent surveys, using similar sampling methodology in the same initial sampling reaches, suggested similar trout densities (Lindstrom 2011; Cook et al. 2015). Thus, although there has been widespread rebound of trout populations in the upper Clark Fork River after remediation, continued periodic pulses of elevated copper concentrations exceeding the acute criteria level and incomplete recovery of trout population density to premining levels suggest that continued mortality might still be inhibiting trout population recovery, particularly for more metal-sensitive species like cutthroat trout. Additional limiting habitat factors present in the river basin (e.g., elevated temperature and movement barriers) might also contribute to reduced trout abundance (Clark Fork Coalition 2011; Cook et al. 2015).

We examined factors limiting trout abundance in the upper Clark Fork River by estimating survival and movement rates of brown trout and westslope cutthroat trout using telemetry data in a multistate model. Multistate modeling facilitates estimation of survival and movement relative to different "states" (Buchanan and Skalski 2010; Perry et al. 2010); in our study, we examined how trout survival and movement rates varied in relation to spatial and temporal differences in copper exposure. We assessed whether trout

Fig. 2. Relationships between dissolved copper concentration and discharge (*Q*) for the three mainstem segments on the upper Clark Fork River, Montana (2009–2011 combined). The dashed line is the acute toxicity standard for copper by the EPA (13.4 μg·L⁻¹ at water hardness of 100 mg·L⁻¹; USEPA 2007). Caution should be used in extrapolating dissolved copper concentrations to discharges beyond minimum and maximum observations.



in the upper Clark Fork River exhibit lower survival and higher avoidance rates (*i*) in areas with higher copper concentrations, specifically the upper 63 km of the river where mining tailing deposits are still widespread compared with downstream sections with lower exposure and (*ii*) during time periods of increased copper exposure that likely occur during spring and summer when snowmelt or rainfall events increase stream discharge and mobilize copper into the water column from sediments (Luoma et al. 2008). Additionally, we assessed whether survival and movement responses to copper exposure are more pronounced in cutthroat trout due to their heightened metal sensitivity (Woodward et al. 1995*b*).

Methods

Study area

The study area included the upper Clark Fork River, from the confluence of Silver Bow and Warm Springs creeks, near Warm Springs, Montana, downstream to the confluence with the Blackfoot River, near Missoula, Montana (189 river kilometres), and associated tributaries (Fig. 1). As noted, extensive metal contamination from upstream copper mining that occurred from the 1880s to the 1960s had major negative effects on the upper Clark Fork River, but tributaries exhibited little or no metal contamination (Luoma et al. 2008). We divided the mainstem river study section into three segments (Fig. 1) based on segment boundaries used in previous studies that assessed spatial patterns in sediment metal concentrations (Axtmann and Luoma 1991; Hornberger et al. 2009): Segment A was a 63 km-long section from near the headwaters of the Clark Fork River at Warm Springs downstream to the Little Blackfoot River confluence; Segment B (42 km) was bounded downstream by the Flint Creek confluence; and Segment C (84 km) extended downstream to the Blackfoot River confluence. Downstream segment boundaries were junctions of major tributaries that dilute copper concentrations in the main stem (Axtmann et al. 1997; Luoma et al. 2008).

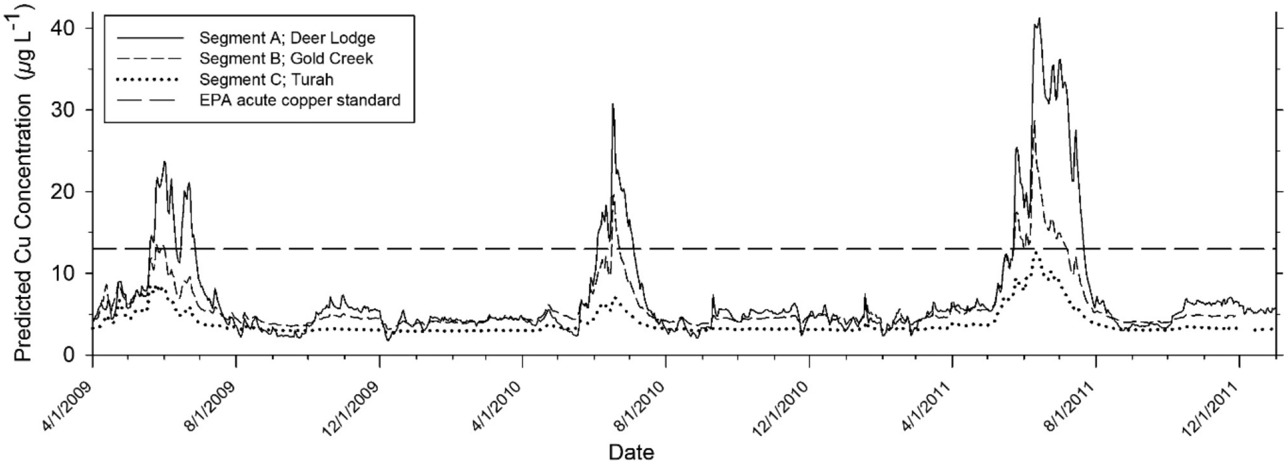
Physical habitat and water quality

Among the three study segments, we compared physical habitat, temperature, and copper exposure. For physical habitat, we measured floodplain width and area every kilometre based on the 50-year flood boundary using ArcMap Version 9.3.1 (Esri 2009). The area of streamside tailing deposits for each segment (Brooks and Moore 1989) was summed from existing GIS data (Montana State Library, GIS Layers for Clark Fork Superfund Site; https://mslservices.mt.gov/Geographic_Information/Data/DataList/datalist_Details.aspx?did={33b14155-3366-42a0-b50c-1e21d5224fe0}) and divided by total floodplain area to obtain percentage of floodplain contamination per segment. Dissolved copper concentration was determined from metal data in water samples collected eight times per year at US Geological Survey (USGS) discharge gauge stations located within each study segment (Fig. 1). The relation between copper concentration and discharge was calculated for each gauge station across all 3 sampling years (*n* = 23–39) separately using simple linear regression (see Hornberger et al. 2009). The resulting regressions (Fig. 2) were then used to predict daily copper concentrations in each segment based on daily discharge (Fig. 3). Annual acute copper exposure in each segment was calculated as the number of days exceeding the EPA acute dissolved copper concentration to protect aquatic life (13.4 μg·L⁻¹; USEPA 2007), based on the observed water hardness of 100 mg·L⁻¹ in the upper Clark Fork River. Mean daily copper exposures were also calculated by season (exact dates listed below) and compared among segments. In tributaries, dissolved copper concentration was derived from USGS water samples collected intermittently from 2000 to 2011 from three relatively uncontaminated reference tributaries: Little Blackfoot River, Flint Creek, and Rock Creek. Maximum daily temperature for each segment was determined from thermograph data collected at each of the USGS gauge stations.

Radiotelemetry

Survival and movements of brown trout and westslope cutthroat trout were assessed using radio transmitters that were implanted into trout systematically over the study area at a distribution of ~1 tag per 0.8 river kilometres. A total of 183 adult brown trout and 70 westslope cutthroat trout (282–570 mm total length) were radiotagged. Cutthroat trout were identified as pure westslope cutthroat trout or slightly hybridized with rainbow trout based on visual characteristics (Weigel et al. 2002). Fish were captured by a boat-mounted electrofisher in April, prior to spring runoff, in 2009 (brown trout, *n* = 70; cutthroat trout, *n* = 21), 2010 (brown trout, *n* = 59; cutthroat trout, *n* = 33), and 2011 (brown trout, *n* = 9; cutthroat trout, *n* = 11). An additional 45 brown trout and five cutthroat trout were radiotagged in September 2010 in the main stem and in the lower reaches of Flint Creek and the Little Black-

Fig. 3. Predicted dissolved copper concentrations ($\mu g \cdot L^{-1}$) in relation to discharge in the upper Clark Fork River, Montana, for study Segments A (Deer Lodge sampling station), B (Gold Creek), and C (Turah), using linear regression equations from Fig. 2. The dashed line is the acute toxicity standard for dissolved copper by the EPA (13.4 $\mu g \cdot L^{-1}$) at water hardness of 100 $mg \cdot L^{-1}$ (USEPA 2007).



foot River to assess survival and movement in tributaries and potential seasonal differences in post-tagging survival.

Trout were anesthetized with tricaine methanesulfonate, measured to the nearest millimetre, weighed to nearest 0.1 g, and implanted with 8 or 10 g internal transmitters (dependent on body weight) with external antennas (Lotek Wireless, Newmarket, Ontario, 148.500 to 148.560 MHz). Tags were inserted in small incisions made dorsally to the pelvic girdle. The trailing external antenna was extruded through a small hole made dorsally to the vent via a shielded hollow needle (Ross and Kleiner 1982). Incisions were closed with sutures and instruments sterilized between procedures to minimize risk of infection. The mean relative weight (Anderson and Neumann 1996) of tagged fish was 93 (range: 66–121) for brown trout and 101 for cutthroat trout (range: 45–138). Tag weight was less than the recommended 4% of total body weight (Zale et al. 2005). Radiotags were programmed to a 12 h on : 12 h off schedule to prolong battery life (685 to 877 days). Following surgery, fish were placed in a live cage until they regained equilibrium (~10 min) and were released near the point of capture.

Radiotag relocations were obtained weekly over the entire study area from April 2009 to December 2011 (138 weeks), except during winter months (January and February) when surveys were conducted every 2 weeks. Relocations were made primarily from roads using a combination of a vehicle-mounted omnidirectional antenna and a directional three-element Yagi antenna. Areas with limited road access were surveyed by boat. Trout position was triangulated using a Lotek SRX 400 receiver and coordinates recorded with a global positioning unit. Relocation accuracy was estimated to be 100 m based on trials using dummy tags. Relocation error was considered minimal given that our focus was on movement among long study segments (42 to 84 km long). Fish location was converted to distance upstream from the lower boundary of the study area (Blackfoot River confluence) using ArcMap.

Sixty-seven percent (171 of 256) of radiotags were equipped with motion (mortality) sensors; mortality was assumed to occur when unique radio signals emitted by motion sensors (indicating no movement) were detected. For trout without mortality-sensor radiotags, we assumed that mortality had occurred if a given tag was relocated in the same location for several weeks and no movement of the tag was detected when investigators prodded and waded through the tag relocation site.

Survival and movement analysis

We first plotted Kaplan–Meier survival curves (Kaplan and Meier 1958) for each species and each of the 3 study years over the entire study area. This analysis was used to examine overall seasonal patterns of survival associated with discharge and to assess evidence of mortality that might have occurred shortly after tagging and thereby biased our evaluation of the relationship between survival and metal contamination levels.

Survival and movement were then examined in more detail using multistate mark–recapture analysis of telemetry data (Arnason 1972, 1973; Hestbeck et al. 1991; Brownie et al. 1993) following the approach of Buchanan and Skalski (2010) and Perry et al. (2010). During each (typically weekly) tag–relocation period, a relocated trout was categorized as being in one of five "states": the first four states were assigned to live fish and indicated whether they were occupying one of the three mainstem study segments (A, B, or C) or were in a tributary (T). The fifth state was assigned to fish that died during the relocation period anywhere in the study area ("dead state"; D). A separate tributary state was designated because tributaries had distinctly different habitat characteristics than mainstem habitat segments (much lower copper concentrations and the presence of irrigation structures that could restrict movement or affect survival). Angling pressure and angling-related mortality are low in the study area and thus were unlikely to influence survival rates (P. Saffel, J. Lindstrom, and B. Liermann, unpublished data).

Weekly encounter histories were created for each individual based on the state determined for the week. Fish that were last encountered alive and that went undetected in a given week were assigned a 0 for that week. For the small number of cases where we had evidence that transmitter batteries had likely failed prior to the end of the study, we truncated the encounter histories after the failure occurred. The multistate model provided estimates of the weekly probabilities of transitioning from one state to any other state. The weekly transition probabilities, which combined information on survival and movement (Buchanan and Skalski 2010), indicated whether a fish (*i*) remained alive in its current location (river segment or tributary); (*ii*) remained alive and moved to another location; or (*iii*) died. The model allowed the transition probabilities to vary by the location occupied at the start of the week, by species, and over different time periods. The weekly probability of remaining alive was the complement of transitioning to the dead state. For example, for an individual starting the week in Segment A, the weekly probability of mortality was the probability of transitioning from states A to D; the weekly probability of staying alive somewhere in the study area was the sum of transition probabilities A to A, A to B, A to C, and A to T. We then used weekly survival estimates to compare seasonal and annual survival rates for brown trout and westslope cutthroat trout occupying each study segment (A, B, C, or T). Seasonal survival estimates were calculated as the product of the weekly survival estimate for the season in question. Annual survival estimates were calculated as the product of the seasonal survival estimates. The standard errors (SEs) for seasonal and annual survival estimates were estimated using the delta method (Powell 2007) in Program R (R Development Core Team 2010) and the "msm" package (Jackson 2011).

A set of competing multistate models that constrained transition probabilities through time and space were developed to further assess evidence for differences in survival and movement rates among the four different spatial states (three mainstem segments and all tributaries) and among four different time states (seasons). Seasonal differences in survival and movement were determined by grouping weekly transition rates into four biologically meaningful time periods: spring (20 March to 15 June), characterized by high discharge and elevated dissolved copper concentrations (>10 μg·L^{-1}); summer (16 June to 15 September), characterized by low discharge, low copper concentrations (3–6 μg·L^{-1}), and higher temperatures interspersed with occasional pulses of high copper concentrations during elevated discharges from summer thunderstorms (Luoma et al. 2008); fall (16 September to 20 December), characterized by low discharge, declining temperature, and low copper concentrations; and winter (21 December to 20 March), characterized by low discharge, temperature, and copper and presence of ice cover. Additionally, we also tested a single-season "spring only" model, which allowed spring transition rates to vary while other seasons were held constant, and a "combined season" model that combined spring and summer transition rates and fall and winter transition rates. The spring only model was developed to examine if the higher copper concentrations during spring runoff (>10 μg·L^{-1}) were the most influential on survival and movement patterns. The combined season model was developed to examine if the presumed elevated copper levels in spring and summer and low levels in fall and winter better explained observed survival and movement than a full four-season model. In all, ten different combinations of survival and movement rate models were evaluated, with independent estimates computed for brown trout and cutthroat trout separately (Appendix A, Table A1). For all models, we combined data from all 3 years of the study because temporal trends were similar among years.

Models were run in Program MARK (White and Burnham 1999). Prior to model selection, we evaluated goodness of fit for our most complex model using the median $\hat{c}$ procedure in Program MARK (White and Burnham 1999). Because there was no evidence for overdispersion among any of the models tested (median $\hat{c}$ = 0.99, 95% CI: 0.97–1.01), we based model selection on AIC$_c$ (adjusted for sample size) rather than QAIC$_c$ values (Burnham and Anderson 2002). We considered the model with the lowest value to be the best and evaluated the plausibility of other models based on the difference between the AIC$_c$ value for the top model and that of every other model (ΔAIC$_c$). For a model with ΔAIC$_c$ values of <2, 4–7, and >10, there is substantial, some, and no evidence, respectively, that differences were statistically significant (Burnham and Anderson 2002).

We subsequently used the best approximating model (combined season) to test whether degree of copper exposure could potentially influence movement and survival. To do this, we input estimates of weekly survival and movement into a matrix population projection model (Caswell 2001) to calculate (*i*) the number of weeks that a fish would remain alive from the start of the year conditional on its starting location (A, B, C, or T) and (*ii*) how many weeks it would spend in each segment while it remained alive. As in our multistate model, the possible transitions that could be made each week consisted of a fish (1) remaining alive in its current location (river segment or tributary); (2) remaining alive and moving to another location; or (3) dying. The probabilities of the weekly transitions were determined state of an individual at the start of the week. If an individual moved to a new location, the transition probabilities estimated by the multistate model for that location were used to project that individual in the next week.

The weekly transition probabilities were also allowed to vary by week in accordance with the temporal structure of weekly survival rates from the combined season model. For example, different transition rates were used in projection model for the 26-week-long spring–summer and fall–winter periods.

Finally, to incorporate the uncertainty that was associated with estimating the transition probabilities, we used Monte Carlo simulations of the projection model, where each simulation consisted of projecting the location and live or dead status of one trout forward for 10 years. We simulated projections for 400 000 trout, with 100 000 starting out in each river segment. The actual transition probabilities used in each step of each projection for a given week and location were randomly drawn based on the estimated mean and variance from the combined season model; the log-odds values were then back-transformed to the 0–1 probability scale for use in the simulation. All calculations were completed using the "popbio" package in Program R (Stubben and Milligan 2007).

Results

Habitat and water quality

Study segments differed substantially in extent of mining tailings deposits and dissolved copper concentration. Segment A had a wide floodplain (mean ± SE: 704 ± 43 m) with extensive mining tailing deposits (63.3 ha; mean 1 ha tailings·river km^{-1}; 2.3% of total floodplain area) and dissolved copper concentrations that regularly exceeded EPA acute standards for dissolved copper (13.4 μg·L^{-1}; USEPA 2007), especially during high discharge, with peak copper levels of 24–46 μg·L^{-1} during the 3 study years (Fig. 3). Segment B also had a wide floodplain (686 ± 115 m) but contained much less extensive floodplain tailings (15.6 ha; mean 0.4 ha·km^{-1}; 0.1% of floodplain) and peak dissolved copper concentrations during the 3 study years (14–29 μg·L^{-1}) that exceeded acute levels only during peak discharge events. Segment C had a relatively narrow floodplain (410 ± 31 m), floodplain mining tailing deposits were absent, and dissolved copper concentrations were well below acute criteria even during periods of high discharge (Fig. 3).

Relationships between dissolved copper and discharge developed for each segment separately (Fig. 2) showed that copper exposure differed widely among the study segments. Predictions of daily copper concentration derived from copper-discharge regressions revealed that the mean number of days annually when dissolved copper concentration exceeded the acute level (13.4 μg·L^{-1}) over the 3-year study averaged 42 days for Segment A (range 31–60 days), 12 days in Segment B (range 5–44 days), and 0 days in Segment C (Fig. 3). Copper exposure also varied seasonally among segments, with mean concentrations highest in spring and summer and lowest in fall and winter (Fig. 3), and declined with distance downstream. During spring, mean daily copper concentration in Segment A was 9.6 μg·L^{-1} (range 6.2–12.2 μg·L^{-1}), 7.9 μg·L^{-1} in Segment B (range 6.4–12.2 μg·L^{-1}), and 5.1 μg·L^{-1} in Segment C (range 3.8–5.8 μg·L^{-1}). Copper exposure declined during summer months but remained elevated; the mean value was 9.5 μg·L^{-1} in Segment A (range 6.2–14.6 μg·L^{-1}), 6.4 μg·L^{-1} in Segment B (range 5.1–8.1 μg·L^{-1}), and 4.2 μg·L^{-1} in Segment C (range 3.6–5.1 μg·L^{-1}). During fall and winter, dissolved copper concentrations were low and generally similar across all segments and did not exceed the chronic criteria of 8.9 μg·L^{-1} in any segment (USEPA 2007); the mean was 4.7 μg·L^{-1} in Segment A (range 4.1–5.5 μg·L^{-1}), 4.3 μg·L^{-1} in Segment B (range 4.1–4.6 μg·L^{-1}), and 3.1 μg·L^{-1} in Segment C (range 2.9–3.2 μg·L^{-1}). In contrast with the main stem, dissolved copper concentrations in the three tributaries tested ranged from 0.0 to 1.7 μg·L^{-1}.

Table 1. Number (percent) of survivors and mean survival time (weeks) of brown trout and cutthroat trout by radiotagging implantation events in the upper Clark Fork River, Montana, 2009–2011.

	Year	No. tagged	No. survived (%)	Mean survival time in weeks (range)
Brown trout	2009 (S)	70	19 (27.1)	60 (2–138)
	2010 (S)	59	12 (20.3)	34 (3–87)
	2010 (F)	45	13 (28.9)	37 (4–65)
	2011 (S)	9	5 (23.8)	21 (5–34)
	Total	183	49 (26.8)	$\bar{x} = 38$
Cutthroat trout	2009 (S)	21	1 (4.8)	31 (4–136)
	2010 (S)	33	2 (6.1)	18 (1–86)
	2010 (F)	5	2 (40.0)	41 (9–65)
	2011 (S)	11	0 (0.0)	11 (3–24)
	Total	70	5 (7.1)	$\bar{x} = 25$

Note: "S" refers to spring (April) tagging and "F" (September) to fall tagging.

Water temperature varied little among segments. Mean maximum water temperatures during the summer (15 June – 15 September) were about 1 °C warmer in Segment C than in Segments A and B; weekly means were 16.1 to 18.4 °C in Segment A, 16.4 to 18.6 °C in Segment B, and 18.1 to 18.6 °C in Segment C. Maximum water temperatures across years were similar among all segments (22.2 to 22.9 °C, below the upper lethal temperature for brown trout of 24.7 °C; Elliott 1981), as were the mean number of days exceeding 20 °C (A = 16 days, B = 13 days, C = 21 days). However, these maximum water temperatures exceeded the upper lethal temperature of westslope cutthroat trout (19.6 °C; Bear et al. 2011).

Survival and movement

A total of 6389 relocations were used to estimate survival and movement for the 183 radiotagged brown trout and 70 westslope cutthroat trout during the 138-week-long study period. The mean number of relocations was 35 times per individual during weekly surveys. Mortality was confirmed for 134 brown trout and 65 cutthroat trout during the study (Table 1). Survival time of both species ranged widely, from 1 to 138 weeks, with mean survival times per tagging event varying from 21 to 60 weeks for brown trout and from 11 to 41 weeks for westslope cutthroat trout (Table 1). Fifty brown trout (26.8%) and five westslope cutthroat trout (7.1%) were alive at the end of the study, surviving from 37 to 138 weeks post-tagging.

Seasonal survival patterns calculated from Kaplan–Meier survivorship curves were similar for both species across years, showing highest mortality in the spring during elevated discharge (April–June), moderate mortality in summer (July–September), and little to no mortality in fall and winter (Fig. 4). Annual survival of westslope cutthroat trout from Kaplan–Meier analysis was low (0.09 to 0.29), about half that of brown trout (0.38 to 0.61). Among-year survival patterns were similar for both species (i.e., survival was relatively low in 2010, intermediate in 2009, and high in 2011).

The combined season spring and summer model yielded the best-fitting model from the multistate model analysis, and ΔAIC_c values of other models were >26.4, suggesting virtually no support for other models (Table A1). Detection probability, an important consideration in multistate mark–recapture analyses (Perry et al. 2010), was high for both species with a weekly detection probability of 0.56 (0.01 SE) and a 0.96 (<0.01 SE) probability of being detected at least once over 4 weeks. Additionally, the probability that fish remained in the study area and were relocated after tagging was also very high (0.99, <0.01 SE).

Estimated survival rates calculated from the combined season model varied substantially by species, location, and season. Weekly mean survival rates across all locations were 0.981 for brown trout (range 0.970 to 0.992) and 0.927 for westslope cutthroat trout (range 0.758 to 0.996; Table 2). For both species, seasonal survival rates were lowest during the spring–summer period (mean 0.550 for brown trout, range 0.467 to 0.653; mean 0.199 for westslope cutthroat trout, range, 0.085 to 0.378) when dissolved copper concentrations were elevated (>10 μg·L^{-1}; Fig. 3). Survival rates were considerably higher in the fall–winter period when copper concentrations were low (3–6 μg·L^{-1}), especially for westslope cutthroat trout (brown trout: mean survival 0.673, range 0.554 to 0.814; westslope cutthroat trout: mean survival 0.438, range 0.001 to 0.905).

Annual survival rates across all locations were low for both species but especially so for westslope cutthroat trout (Table 2). Mean annual survival was 0.38 for brown trout (range 0.273 to 0.531) and 0.12 for westslope cutthroat trout (range 0.001 to 0.342), about one-third that of brown trout. Annual survival rates from the multistate modeling and Kaplan–Meier estimations were similar. Lowest seasonal and annual survival for both species occurred in mainstem Segment A, which had the highest amount and percentage of floodplain mine tailings and frequent exceedance of acute copper criteria during high discharges. In this segment, mean annual survival was 0.273 for brown trout and 0.001 for westslope cutthroat trout. In contrast, survival rates for both species were considerably higher in Segment C, which had no floodplain mining deposits and low dissolved copper concentrations. The probability of survival in Segment C was 2.1 times higher than that in Segment A for brown trout (0.530 versus 0.273) and 122 times higher for cutthroat trout (0.122 versus 0.001). Brown trout survival in Segment B, with intermediate levels of copper contamination, was also intermediate to the rate in other mainstem segments, averaging 0.354. Highest westslope cutthroat trout survival was observed in Segment B (0.342). Survival rates for westslope cutthroat trout in tributaries, where there was little or no dissolved copper, were nearly as low as in the most contaminated segment (A), especially during the spring–summer period (0.085). In contrast, brown trout survival in tributaries was much higher, comparable to survival rates for Segment B (0.343). Mortality was confirmed for 29.6% of brown trout (8 of 27) and 57.1% of cutthroat trout (16 of 28) that exhibited a distinct movement from the main stem into tributaries during respective spawning migrations.

Estimates from the population models suggested that brown trout survived longer than westslope cutthroat trout in almost all segments and seasonal periods (brown trout range 18.7 to 23.5 weeks; cutthroat trout range 2.9 to 26.0 weeks; Table 3). Brown trout occupying Segment A at the start of each season had the lowest life expectancy (mean 18.7 weeks in the spring–summer period and 20.6 weeks in the fall–winter period), about 2 weeks less than that in other segments. Westslope cutthroat trout life expectancy was lowest in Segment A and in tributaries (mean 9.1 weeks, range 2.9 to 15.5 weeks), less than half that of other segments (mean 19.5 weeks, range 15.0 to 26.0 weeks).

Movement among segments was relatively rare and varied by species. For both species, fish had a high probability of remaining in the stream segment in which they were initially located at the beginning of each season (Table 3). For brown trout, the probability of remaining in the same segment was similar across all segments and seasons, ranging from 0.936 to 0.980·week^{-1} (Table A2). Westslope cutthroat trout moved more frequently, and the weekly probability of residency in the same segment ranged from 0.653 to 0.985. Movement to other segments was highest during spawning, and westslope cutthroat trout moved from the main stem to tributaries during the spring–summer period (mean residence time 4.0–4.6 weeks) and brown trout moved into tributaries during the fall–winter period (mean residence time 1.6 to 4.6 weeks).

Although both species usually remained in the original tagging segment, model analysis suggested that both species typically spent some time in all other segments (Table 3). Brown trout from each segment were also found in three other locations (mean

Fig. 4. Kaplan–Meier monthly survivorship curves with 95% confidence intervals for radiotagged brown trout and westslope cutthroat trout in the upper Clark Fork River, Montana, 2009–2011.

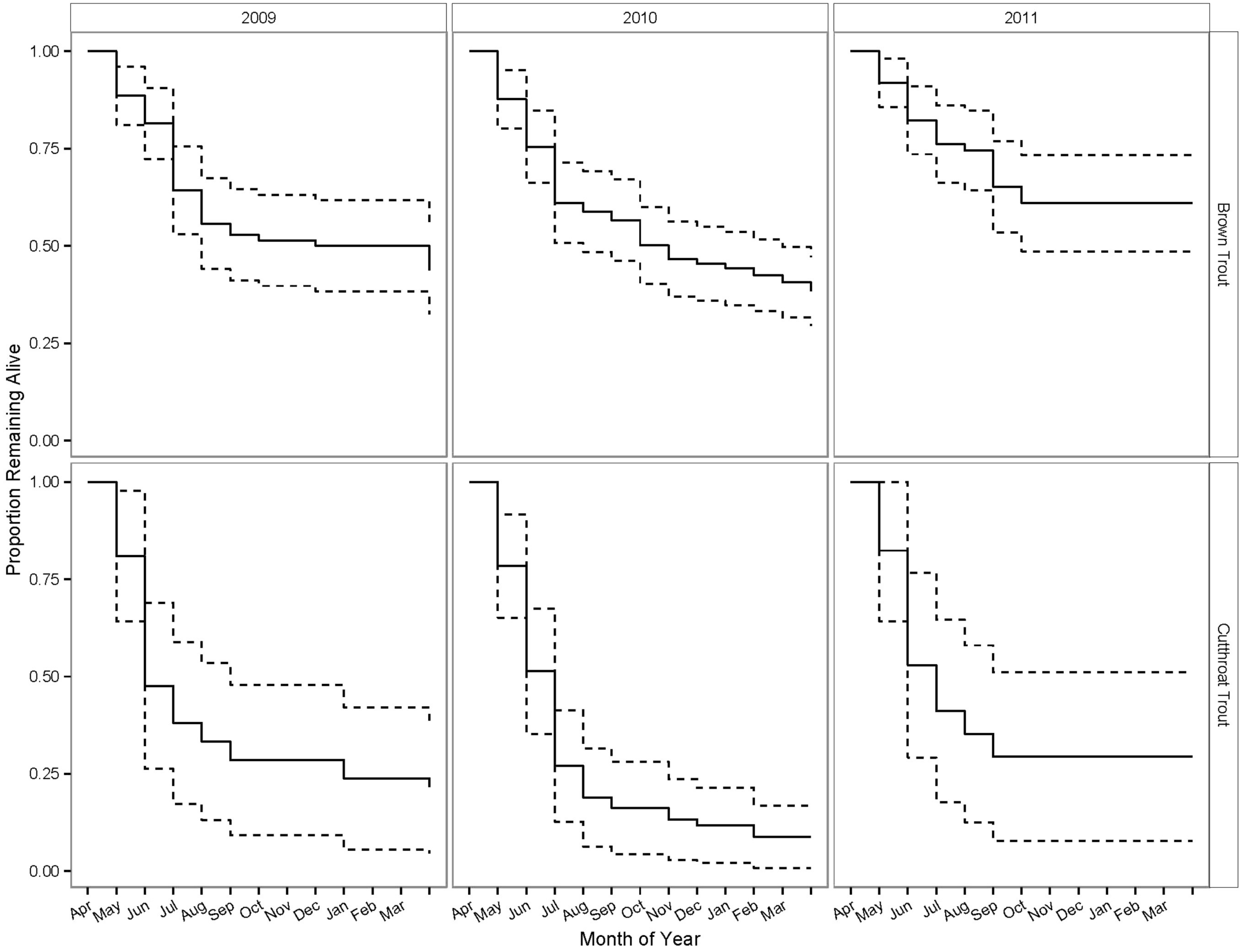


Table 2. Weekly, seasonal, and annual estimates of survival (standard error (SE) in parentheses) of brown trout and westslope cutthroat trout in the three mainstem segments (A, B, C) and in tributaries (T) of the upper Clark Fork River, Montana, during two combined seasonal periods of spring and summer (SS) and fall and winter (FW).

	Segment	Season	Weekly	Seasonal	Annual
Brown trout	A	SS	0.971 (0.004)	0.467 (0.051)	
		FW	0.980 (0.005)	0.584 (0.079)	0.273 (0.047)
	B	SS	0.975 (0.005)	0.519 (0.068)	
		FW	0.985 (0.006)	0.681 (0.100)	0.354 (0.004)
	C	SS	0.984 (0.003)	0.653 (0.060)	
		FW	0.992 (0.003)	0.814 (0.067)	0.531 (0.010)
	T	SS	0.978 (0.008)	0.560 (0.118)	
		FW	0.981 (0.005)	0.613 (0.087)	0.343 (0.087)
Cutthroat trout	A	SS	0.912 (0.035)	0.090 (0.092)	
		FW	0.758 (0.175)	0.001 (0.004)	<0.001 (<0.001)
	B	SS	0.963 (0.015)	0.378 (0.151)	
		FW	0.996 (0.002)	0.905 (0.040)	0.342 (0.139)
	C	SS	0.947 (0.011)	0.244 (0.074)	
		FW	0.974 (0.012)	0.499 (0.164)	0.122 (0.055)
	T	SS	0.909 (0.019)	0.085 (0.047)	
		FW	0.960 (0.038)	0.347 (0.355)	0.029 (0.034)

Table 3. Estimated mean number of weeks (SE in parentheses) brown trout and westslope cutthroat trout would occur in each of three mainstem segments (A, B, C) and in tributaries (T) of the upper Clark Fork River, Montana, during two 26-week periods of spring and summer (SS) and fall and winter (FW).

			Mean weeks per segment				
	Segment at start	Season	A	B	C	T	Total
Brown trout	A	SS	**17.4** (0.8)	0.6 (0.1)	<0.1 (<0.1)	0.7 (0.3)	18.7
		FW	**16.2** (0.9)	0.6 (0.1)	0.9 (<0.1)	2.9 (0.3)	20.6
	B	SS	0.6 (0.4)	**17.5** (1.2)	0.9 (0.5)	0.7 (0.5)	19.7
		FW	1.7 (0.2)	**14.9** (0.2)	0.6 (<0.1)	4.6 (0.3)	21.8
	C	SS	0.4 (0.5)	0.9 (0.4)	**19.2** (1.1)	1.0 (0.5)	21.5
		FW	0.8 (0.1)	0.4 (0.1)	**20.7** (0.8)	1.6 (0.1)	23.5
	T	SS	1.1 (0.2)	2.1 (1.3)	0.1 (0.1)	**18.7** (3.2)	22.0
		FW	2.8 (0.8)	2.2 (0.7)	2.5 (0.2)	**13.8** (1.1)	21.3
Cutthroat trout	A	SS	**5.3** (1.4)	0.4 (0.3)	2.3 (0.9)	4.6 (1.7)	12.6
		FW	**5.4** (3.8)	0.0	0.0	0.0	5.4
	B	SS	0.7 (0.6)	**8.8** (1.6)	2.1 (0.8)	4.6 (1.4)	16.2
		FW	0.0	**26.0** (0.0)	0.0	0.0	26.0
	C	SS	0.3 (0.6)	0.6 (0.4)	**10.1** (1.2)	4.0 (1.2)	15.0
		FW	0.0	0.0	**19.4** (2.8)	0.0	19.4
	T	SS	0.2 (0.2)	0.9 (0.6)	5.0 (1.6)	**9.4** (2.6)	15.5
		FW	0.2 (0.3)	0.7 (0.8)	0.0	**2.0** (0.1)	2.9

Note: Bold values represent the time spent (weeks) in the same segment from the start to end of each 26-week time period. Total represents the sum of weeks fish would likely survive across all segments.

1.3 weeks, range 0.7 to 2.5 weeks). There was no evidence for avoidance of Segment A by brown trout or of a greater tendency to move during the spring–summer season when discharge and copper concentrations were elevated. However, westslope cutthroat trout from Segments B, C, and T rarely moved into Segment A (mean residence in Segment A: 0.4 weeks per season; range 0 to 0.7 weeks).

Discussion

Mining effects on water and habitat quality have the potential to affect fish survival and distribution over large areas, but population-level effects from contamination exposure are notoriously difficult to quantify (Luoma and Rainbow 2008; Hamilton et al. 2016). Demographic responses to contaminants in the past have been estimated indirectly by relating in situ water contamination levels to laboratory-derived toxicity experiments, in situ cage survival studies, tissue burdens from wild fish, and behavioral avoidance thresholds (Farag et al. 2003; Luoma et al. 2008). To our knowledge, our study is the first to relate degree of contaminant exposure to direct estimates of fish survival and movement at a population level over a large spatial scale.

Our results demonstrated that annual and seasonal survival for both adult brown trout and cutthroat trout were strongly associated with the distinct spatial and temporal differences in level of copper exposure among study segments. Annual survival rates among mainstem study segments of brown trout (0.27–0.53), and especially those of westslope cutthroat trout (0.001–0.34), were generally well below expected. For example, Vincent (1987) reported an annual survival of 0.67 for adult brown trout in the unimpaired Madison River in southwestern Montana. In a review of trout survival rates in Rocky Mountain (USA) rivers, Carlson and Rahel (2007) reported a mean annual survival rate of 0.43 (95% CI: 0.38–0.48) for cutthroat trout and 0.44 (95% CI: 0.36–0.52) for brown trout (see also Cook et al. 2015). Survival rates across study years were notably the lowest in the upstream segment (A) where dissolved copper concentration and percentage of floodplain mine tailing deposits were greatest. In this 63 km-long upstream segment, there were over 63 ha of floodplain tailings, and dissolved copper concentrations frequently exceeded the EPA acute criteria threshold.

In contrast, annual survival rates were substantially higher for brown trout and especially greater for cutthroat trout in downstream river segments with little or no floodplain copper deposits and substantially reduced acute and chronic exposure to dissolved copper. Catch-curve analysis of brown trout survival in the upper Clark Fork River in 2013–2015 documented a similar pattern of survival, and survival rates were lowest in Segment A (0.35) and increased with distance downstream (0.54, Segment B; 0.68, Segment C) (Cook et al. 2015).

The strong spatial gradient in dissolved copper is similar to results from previous studies in the upper Clark Fork River showing an exponential downstream decline in copper accumulations in sediment and in macroinvertebrate and fish tissues in relation to upstream floodplain source deposits (Axtmann and Luoma 1991; Farag et al. 1995; Hornberger et al. 2009). Study results were also consistent with prior evidence for mobilization of dissolved copper from floodplain deposits in this system during high discharges in spring and summer (Brooks and Moore 1989; Hornberger et al. 2009). Particularly noteworthy was evidence for exceedance of the acute criteria threshold for dissolved copper, ranging from 31–60 to 5–44 days in the upper and middle river segments, respectively, despite remediation efforts upstream.

Temporal differences in survival provided further support of a linkage between survival rates and copper exposure level. In all 3 study years, Kaplan–Meier survival estimates for both species were lowest when peak pulses of copper exceeded acute levels during elevated spring discharge, and survival remained low during summer months when copper levels were chronically elevated. In contrast, survival was high in all segments during fall and winter when copper levels were much lower ($<5\ \mu g \cdot L^{-1}$), even in Segment A, the most contaminated upstream segment with the lowest spring–summer survival rates. Multistate model seasonal survival estimates exhibited a similar pattern, and mean fall–winter survival across all segments was 22% higher than spring–summer survival for brown trout and 54% higher for westslope cutthroat trout. Seasonal survival estimates generally increased downstream coincident with decreasing copper exposure, regardless of estimator.

The observed seasonal survival patterns of upper Clark Fork River trout were unusual, as periods of high mortality in riverine adult trout populations generally occur during winter (Needham et al. 1945; Carlson and Letcher 2003), immediately postspawning (DeRito et al. 2010), or during summer low flow (Elliott et al. 1997). In our study, fall–winter survival for both species was higher than spring–summer survival, and we did not observe a pronounced postspawning mortality in brown trout in the fall during spawning. Similarly, though some postspawning mortality of cutthroat trout was observed in late June after peak spawning (see below), the majority of spring–summer mortalities occurred in the spring (April–mid-June) prior to spawning.

High mortality in trout was not limited to periods of exposure to acute levels of dissolved copper, and it appears chronic exposure to elevated copper may have also contributed to low survival in the upper Clark Fork River. For example, chronic exposure to trace metals, especially copper, can lead to reduced growth, reduced feeding rates, and reduced swimming performance (Atchison et al. 1987; Marr et al. 1995; Woodward et al. 1995*a*; Farag et al. 2000). Other physiological impairments caused by copper toxicity that can decrease trout survival include reduction in chemoreceptor function (Hansen et al. 1999*b*; McIntyre et al. 2008) and inhibition of lateral line development (Linbo et al. 2006). The latter response has been documented at dissolved copper concentrations as low as $2.0\ \mu g \cdot L^{-1}$ (Sandahl et al. 2007), a concentration below that observed in all mainstem study segments. Survival rates and life expectancy estimates were substantially lower for westslope cutthroat trout than for brown trout in all segments, a finding observed in previous studies that suggests *Oncorhynchus* species are more sensitive to trace metal contamination than brown trout are (Hansen et al. 1999*a*).

The lack of strong behavioral avoidance of river sections by either species during elevated copper levels was unexpected. Matrix analysis showed that tagged brown and cutthroat trout spent the majority of time in the segment of initial tagging, even when tagged in segments with high copper exposure levels. Previous laboratory studies using salmonids without an exposure history to copper demonstrated avoidance of waters with dissolved copper concentrations as low as $12.0\ \mu g \cdot L^{-1}$ (Woodward et al. 1995*b*; Goldstein et al. 1999; Hansen et al. 1999*a*; Svecevicius 2001), well below peak copper levels in Segments A and B. However, we did not observe large-scale movements into uncontaminated tributaries or to downriver segments during periods of peak copper levels. We did observe movement into tributaries, but movement coincided with spawning timing rather than as an apparent avoidance to elevated copper levels. Chronic exposure to elevated copper has been shown to induce olfactory impairment and reduce avoidance to copper and, in some cases, may also result in preference for elevated copper levels equivalent to rearing exposure levels (Svecevicius 2001; Hansen et al. 1999*a*; McIntyre et al. 2008). These factors may explain the unexpected lack of avoidance of high copper levels in our study.

The apparent linkage between survival rate and the degree of copper exposure that we observed for both brown trout and westslope cutthroat trout in the upper Clark Fork River suggests that further reduction of dissolved copper levels could improve survival rates. Removal of tailings deposits in the uppermost 7 km of Segment A in the early 1990s reduced accumulation of copper in water, sediments, and macroinvertebrate tissues (Hornberger et al. 2009). Our findings suggest that more extensive removal of tailings deposits in this segment would result in further decreases in copper concentration both in this segment and farther downstream (Luoma et al. 2008; Hornberger et al. 2009) and improve trout survival rates accordingly.

The unexpectedly low survival rates of adult brown trout and westslope cutthroat trout in uncontaminated tributaries, especially during their respective spawning seasons, indicated other mortality sources beyond metal exposure are important in the system. Tributaries in the upper Clark Fork River have multiple anthropogenic factors that are likely affecting mortality, including unscreened irrigation canals, dewatering, and presence of migration barriers at irrigation diversion dams (Saffel et al. 2011). We found that cutthroat trout have particularly high tributary mortality and are susceptible to entrainment in unscreened irrigation canals in the late spring – early summer when returning to the main stem after spawning (Mayfield 2013). Improved fish passage and flows during spawning and rearing, therefore, could potentially increase survival and trout recruitment in the main stem, although the scope for recovery is unknown because we did not quantify these factors in our study.

There are several possible confounding factors that could have influenced our results. First, we focused on the effects of copper as the main factor affecting survival as it occurs in the most lethal concentrations, but Clark Fork water and sediments contain a complex mix of other trace metals (Marr et al. 1995; Hornberger et al. 2009), and the interacting effects of multiple metals and other synergistic factors in the system (water temperature, pH) are not well understood (Cusimano et al. 1986; Cook et al. 2015). However, in situ survival studies of caged brown trout generally mirrored our findings, showing acute exposure to copper during peak flows and delayed mortality occurring during the declining limb of the hydrograph in late June coincident with a rise in water temperatures (Cook et al. 2015). Second, tagging could also have affected survival of fish already stressed from metal exposure.

However, we did not observe unusually high mortality in the month following tagging, and mean survival times post-tagging were 23 and 44 months for westslope cutthroat trout and brown trout, respectively. Moreover, the similarity in the spatial pattern of survival rates derived independently from catch-curve analysis further suggests that tagging did not significantly bias survival estimates.

In sum, our results support the hypothesis that continued exposure to acute and chronically elevated dissolved copper concentrations is a primary factor for the incomplete recovery of trout populations in the upper Clark Fork River. Moreover, our findings suggest that survival could be substantially improved for brown trout and westslope cutthroat trout by additional removal of remaining floodplain tailings. Future research on quantifying mortality factors in tributaries during spawning migrations and on identifying sources of brown trout and westslope cutthroat trout recruitment would aid remediation efforts for alleviating limiting factors in the system.

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References

Anderson, R.O., and Neumann, R.M. 1996. Length, weight, and associated structural indices. *In* Fisheries techniques, second edition. *Edited* by B.R. Murphy and D.W. Willis. American Fisheries Society, Bethesda, Maryland. pp. 447–482.

Arnason, A.N. 1972. Parameter estimates from mark–recapture experiments on two populations subject to migration and death. Res. Pop. Ecol. **13**: 97–113. doi:10.1007/BF02521971.

Arnason, A.N. 1973. The estimation of population size, migration rates, and survival in a stratified population. Res. Pop. Ecol. **15**: 1–8. doi:10.1007/BF02510705.

Atchison, G.J., Henry, M.G., and Sandheinrich, M.B. 1987. Effects of metals on fish behavior: a review. Env. Biol. Fish. **18**: 11–25. doi:10.1007/BF00002324.

Axtmann, E.V., and Luoma, S.N. 1991. Large-scale distribution of metal contamination in the fine-grained sediments of the Clark Fork River, Montana, U.S.A. Appl. Geochem. **6**(1): 75–88. doi:10.1016/0883-2927(91)90064-V.

Axtmann, E.V., Cain, D.J., and Luoma, S.N. 1997. Effect of tributary inflows on the distribution of trace metals in fine-grained bed sediments and benthic insects of the Clark Fork River, Montana. Env. Sci. Tech. **31**: 750–758. doi:10.1021/es960417y.

Bear, E.A., McMahon, T.E., and Zale, A.V. 2011. Comparative thermal requirements of westslope cutthroat trout and rainbow trout: implications for species interactions and development of thermal protection standards. Trans. Am. Fish. Soc. **136**(4): 1113–1121. doi:10.1577/T06-072.1.

Brooks, R., and Moore, J.N. 1989. Sediment-water interactions in the metal-contaminated floodplain of the Clark Fork River, Montana, U.S.A. GeoJournal, **19**: 27–36.

Brownie, C., Hines, J.E., Nichols, J.D., Pollock, K.H., and Hestbeck, J.B. 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. Biometrics, **49**(4): 1173–1187. doi:10.2307/2532259.

Buchanan, R.A, and Skalski, J.R. 2010. Using multistate mark–recapture methods to model adult salmonid migration in an industrialized river. Ecol. Model. **221**: 582–589. doi:10.1016/j.ecolmodel.2009.11.014.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Carlson, A.J., and Rahel, F.J. 2007. A basinwide perspective on entrainment of fish in irrigation canals. Trans. Am. Fish. Soc. **136**(5): 1335–1343. doi:10.1577/T06-111.1.

Carlson, S.M., and Letcher, B.H. 2003. Variation in brook and brown trout survival within and among seasons, species, and age classes. J. Fish Biol. **63**(3): 780–794. doi:10.1046/j.1095-8649.2003.00191.x.

Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. 2nd edition. Sinauer Associates, Sunderland, Massachusetts.

Clark Fork Coalition. 2011. Aquatic restoration strategy for the upper Clark Fork Basin: elements of an integrated approach [online]. Available from https://clarkfork.org/wp-content/uploads/2014/07/CFC-UCF_AquaticRestStrat_2011.pdf.

Clements, W.H. 2000. Integrating effects of contaminants across levels of biological organization: an overview. J. Aquat. Ecosys. Stress Recov. **7**(2): 113–116. doi:10.1023/A:1009927612391.

Cook, N., Saffel, P., Liermann, B., Lindstrom, J., and Selch, T. 2015. Upper Clark Fork River fisheries monitoring study: 2014 annual report. Montana Fish, Wildlife and Parks report, Missoula, Montana.

Cusimano, R.F., Brakke, D.F., and Chapman, G.A. 1986. Effects of pH on the toxicities of cadmium, copper, and zinc to steelhead trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. **43**(8): 1497–1503. doi:10.1139/f86-187.

DeRito, J.N., Zale, A.V., and Shepard, B.B. 2010. Temporal reproductive separation of fluvial Yellowstone Cutthroat Trout from Rainbow Trout and hybrids in the Yellowstone River. N. Am. J. Fish. Manage. **30**(4): 866–886. doi:10.1577/M09-006.1.

Elliott, J.M. 1981. Some aspects of thermal stress on freshwater teleosts. *In* Stress and fish. *Edited by* A.D. Pickering. Academic Press, New York. pp. 209–245.

Elliott, J.M., Hurley, M.A., and Elliott, J.A. 1997. Variable effects of droughts on the density of sea-trout *Salmo trutta* populations over 30 years. J. Appl. Ecol. **34**(5): 1229–1238. doi:10.2307/2405234.

Esri. 2009. ArcMap 9.3.1. Environmental Systems Resource Institute, Redlands, California.

Farag, A.M., Stansbury, M.A., Hogstrand, C., MacConnell, E., and Bergman, H.L. 1995. The physiological impairment of free-ranging brown trout exposed to metals in the Clark Fork River, Montana. Can. J. Fish. Aquat. Sci. **52**: 2023–2050.

Farag, A.M., Suedkamp, M.J., Meyer, J.S., Barrows, R., and Woodward, D.F. 2000. Distribution of metals during digestion by cutthroat trout fed benthic invertebrates contaminated in the Clark Fork River, Montana and the Coeur d'Alene River, Idaho, U.S.A., and fed artificially contaminated *Artemia*. J. Fish Biol. **56**: 173–190. doi:10.1111/j.1095-8649.2000.tb02093.x.

Farag, A.M., Skaar, D., Nimick, D.A., MacConnell, E., and Hogstrand, C. 2003. Characterizing aquatic health using salmonid mortality, physiology, and biomass estimates in streams with elevated concentrations of arsenic, cadmium, copper, lead, and zinc in the Boulder River watershed, Montana. Trans. Am. Fish. Soc. **132**: 450–467. doi:10.1577/1548-8659(2003)132<0450:CAHUSM>2.0.CO;2.

Goldstein, J.N., Woodward, D.F., and Farag, A.M. 1999. Movements of adult Chinook salmon during spawning migration in a metals-contaminated system, Coeur d'Alene River, Idaho. Trans. Am. Fish. Soc. **128**(1): 121–129. doi:10.1577/1548-8659(1999)128<0121:MOACSD>2.0.CO;2.

Hamilton, P.B., Cowx, I.G., Oleksiak, M.F., Griffiths, A.M., Grahn, M., Stevens, J.R. et al. 2016. Population-level consequences for wild fish exposed to sublethal concentrations of chemicals — a critical review. Fish Fisher. **17**(3): 545–566. doi:10.1111/faf.12125.

Hansen, J.A., Woodward, D.F., Little, E.E., DeLonay, A.J., and Bergman, H.L. 1999*a*. Behavioral avoidance: possible mechanisms for explaining abundance and distribution of trout species in a metal-impacted river. Env. Toxic. Chem. **18**(2): 313–317. doi:10.1002/etc.5620180231.

Hansen, J.A., Rose, J.D., Jenkins, R.A., Gerow, K.G., and Bergman, H.L. 1999*b*. Chinook salmon (*Oncorhynchus tshawytscha*) and rainbow trout (*Oncorhynchus mykiss*) exposed to copper: neurophysiological and histological effects on the olfactory system. Env. Toxic. Chem. **18**(9): 1979–1991. doi:10.1002/etc.5620180917.

Hestbeck, J.B., Nichols, J.D., and Malecki, R.A. 1991. Estimates of movement and site fidelity using mark–resight data of wintering Canada geese. Ecology **72**: 523–533.

Hornberger, M.I., Luoma, S.N., Johnson, M.L., and Holyoak, M. 2009. Influence of remediation in a mine-impacted river: metal trends over large spatial and temporal scales. Ecol. Applic. **19**(6): 1522–1535. doi:10.1890/08-1529.1.

Jackson, C.H. 2011. Multi-state models for panel data: The msm package for R. J. Stat. Soft. **38**(8): 1–29. doi:10.18637/jss.v038.i08.

Kaplan, E.L., and Meier, P. 1958. Nonparametric estimation from incomplete observations. J. Am. Stat. Assoc. **53**: 457–481. doi:10.1080/01621459.1958.10501452.

Kiser, T., Hansen, J., and Kennedy, B. 2010. Impacts and pathways of mine contaminants to bull trout (*Salvelinus confluentus*) in an Idaho watershed. Arch. Env. Contam. Toxic. **59**: 301–311. doi:10.1007/s00244-009-9457-x.

Linbo, T.L., Stehr, C.M., Incardona, J.P., and Scholz, N.L. 2006. Dissolved copper triggers cell death in the peripheral mechanosensory system of larval fish. Environ. Toxicol. Chem. **25**(2): 597–603. doi:10.1897/05-241R.1. PMID:16519324.

Lindstrom, J. 2011. Upper Clark Fork River fish sampling: 2008–2010. Montana Fish, Wildlife and Parks, Helena, Montana.

Luoma, S.N., and Rainbow, P.S. 2008. Metal contamination in aquatic environments: science and lateral management. Cambridge University Press, New York.

Luoma, S.N., Moore, J.N., Farag, A.M., Hillman, T.H., Cain, D.J., and Hornberger, M. 2008. Mining impacts on fish in the Clark Fork River, Montana: a field ecotoxicology case study. *In* The toxicology of fishes. *Edited by* R.T. DiGuilio and D.E. Hinton. CRC Press, Boca Raton, Florida. pp. 779–804.

Marr, J.C.A., Bergman, H.L., Parker, M., Lipton, J., Cacela, D., Erickson, W., and Phillips, G.R. 1995. Relative sensitivity of brown and rainbow trout to pulsed exposures of an acutely lethal mixture of metals typical of the Clark Fork River, Montana. Can. J. Fish. Aquat. Sci. **52**(9): 2005–2015. doi:10.1139/f95-792.

Mayfield, M.P. 2013. Limiting factors for trout populations in the upper Clark Fork River Superfund site, Montana. M.Sc. thesis, Montana State University, Bozeman, Montana.

McIntyre, J.K., Baldwin, D.H., Meador, J.P., and Scholz, N.L. 2008. Chemosensory deprivation in juvenile coho salmon exposed to dissolved copper under varying water chemistry conditions. Env. Sci. Tech. **42**: 1352–1358. doi:10.1021/es071603e.

Moore, J.N., and Luoma, S.N. 1990. Hazardous wastes from large-scale metal extraction. Environ. Sci. Technol. **24**: 1279–1285.

Needham, P.R., Moffett, J.W., and Slater, D.W. 1945. Fluctuations in wild brown trust populations in Convict Creek, California. J. Wild. Manage. **9**(1): 9–25. doi:10.2307/3795940.

Nimick, D.A., and Moore, J.N. 1991. Prediction of water-soluble metal concentrations in fluvially deposited tailings sediments, Upper Clark Fork Valley, Montana, U.S.A. Appl. Geochem. **6**: 635–646. doi:10.1016/0883-2927(91)90074-Y.

Perry, R.W, Skalski, J.R., Brandes, P.L., Sandstrom, P.T., Klimley, A.P., Ammann, A., and MacFarlane, B. 2010. Estimating survival and migration route probabilities of juvenile Chinook salmon in the Sacramento–San Joaquin River Delta. N. Am. J. Fish. Manage. **30**: 142–156. doi:10.1577/M08-200.1.

Phillips, G., and Lipton, J. 1995. Injury to aquatic resources caused by metals in Montana's Clark Fork River basin: historic perspective and overview. Can. J. Fish. Aquat. Sci. **52**: 1990–1993. doi:10.1139/f95-190.

Powell, L.A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. Condor, **109**(4): 949–954. doi:10.1650/0010-5422(2007)109[949:AVODPU]2.0.CO;2.

R Development Core Team. 2010. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org.

Ross, M.J., and Kleiner, C.F. 1982. Shielded-needle technique for surgically implanting radio-frequency transmitters in fish. Prog. Fish-Cult. **44**: 41–43. doi:10.1577/1548-8659(1982)44[41:STFSIR]2.0.CO;2.

Saffel, P., Liermann, B., Lindstrom, J., Knotek, L., Mostad, T., and Fox, C. 2011. Prioritization of areas in the Upper Clark Fork River basin for fishery enhancement [online]. Montana Fish, Wildlife, and Parks report. Missoula, Montana. Available from https://dojmt.gov/lands/upper-clark-fork-river-basin/.

Sandahl, J.F., Baldwin, D.H., Jenkins, J.J., and Scholz, N.L. 2007. A sensory system at the interface between urban stormwater runoff and salmon survival. Env. Sci. Tech. **41**(8): 2998–3004. doi:10.1021/es062287r.

Stubben, C.J., and Milligan, B.G. 2007. Estimating and analyzing demographic models using the *popbio* package in R. J. Stat. Soft. **22**: 1–23. doi:10.18637/jss.v022.i11.

Svecevicius, G. 2001. Avoidance response of rainbow trout *Oncorhynchus mykiss* to heavy metal mixtures: a comparison with acute toxicity tests. Bull. Env. Contam. Toxic. **67**: 680–687. doi:10.1007/s001280177.

USEPA. 2007. Aquatic life ambient freshwater quality criteria — copper. US Environmental Protection Agency Report 822-R-07-001.

Vincent, E.R. 1987. Effects of stocking catchable-size hatchery rainbow trout on two wild trout species in the Madison River and O'Dell Creek, Montana. N. Am. J. Fish. Manage. **7**: 91–105. doi:10.1577/1548-8659(1987)7<91:EOSCHR>2.0.CO;2.

Weigel, D.E., Peterson, J.T., and Spruell, P. 2002. A model using phenotypic characteristics to detect introgressive hybridization in wild westslope cutthroat trout and rainbow trout. Trans. Am. Fish. Soc. **131**: 389–403. doi:10.1577/1548-8659(2002)131<0389:AMUPCT>2.0.CO;2.

White, G.C., and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study, **46**(Suppl.): 120–138. doi:10.1080/00063659909477239.

Woodward, D.F., Farag, A.M., Bergman, H.L., DeLonay, A.J., Little, E.E., Smiths, C.E., and Barrows, F.T. 1995*a*. Metals-contaminated benthic invertebrates in the Clark Fork River Montana: effects on age-0 brown trout and rainbow trout. Can. J. Fish. Aquat. Sci. **52**(9): 1994–2004. doi:10.1139/f95-791.

Woodward, D.F., Hansen, J.A., Bergman, H.L., DeLonay, A.J., and Little, E.E. 1995*b*. Brown trout avoidance of metals in water characteristic of the Clark Fork River, Montana. Can. J. Fish. Aquat. Sci. **52**: 2031–2037. doi:10.1139/f95-794.

Zale, A.V., Brooke, C., and Fraser, W.C. 2005. Effects of surgically implanted transmitter weights on growth and swimming stamina of small adult westslope cutthroat trout. Trans. Am. Fish. Soc. **134**: 653–660. doi:10.1577/T04-050.1.

Appendix A

Table A1. Model selection results for the 10 multistate models tested using various combinations of survival and movement rates.

	Movement rates		Survival rates				
Model	Spatial	Temporal	Spatial	Temporal	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight
1	Variable	Spring–summer constant; fall–winter constant	Variable	Spring–summer constant; fall–winter constant	14 489.41	0.00	1.00
2	Variable	Spring separate; other seasons constant	Variable	Spring separate; other seasons constant	14 515.80	26.39	0.00
3	Variable	Constant	Variable	Constant	14 556.89	67.48	0.00
4	Constant	Constant	Variable	Constant	14 566.89	77.49	0.00
5	Variable	Variable seasons	Variable	Variable seasons	14 575.41	86.00	0.00
6	Variable	Constant	Variable	Variable seasons	14 579.13	89.72	0.00
7	Constant	Constant	Variable	Constant	14 634.61	145.21	0.00
8	Constant	Constant	Constant	Constant	14 639.66	150.26	0.00
9	Constant	Variable seasons	Constant	Variable seasons	Did not converge		
10	Variable	Variable seasons	Constant	Variable seasons	Did not converge		

Note: "Constant" indicates that the model held transition rate estimates equal for all locations segments (spatial) or seasonal time periods (temporal). "Variable" indicates models that allowed transition rate estimates to vary. "Did not converge" refers to models where maximum likelihood estimates could not be calculated, even using the alternative optimization method in Program MARK (White and Burnham 1999). For all models, survival and movement rates were estimated independently for each species.

Table A2. Estimated probability of weekly residency (SE in parentheses) of brown trout and cutthroat trout in the three mainstem segments (A, B, C) and in tributaries (T) of the upper Clark Fork River, Montana, during two combined seasonal periods of spring and summer (SS) and fall and winter (FW).

			Segment at end			
	Segment at start	Season	A	B	C	T
Brown trout	A	SS	**0.965** (0.004)	0.003 (0.001)	0.0	0.003 (0.001)
		FW	**0.956** (0.008)	0.002 (0.002)	0.003 (0.005)	0.019 (0.005)
	B	SS	0.002 (0.002)	**0.967** (0.006)	0.004 (0.006)	0.003 (0.002)
		FW	0.007 (0.004)	**0.946** (0.011)	0.0	0.032 (0.009)
	C	SS	0.001 (0.001)	0.004 (0.002)	**0.975** (0.004)	0.004 (0.002)
		FW	0.003 (0.002)	0.001 (0.001)	**0.980** (0.005)	0.008 (0.004)
	T	SS	0.005 (0.005)	0.009 (0.006)	0.0	**0.964** (0.010)
		FW	0.017 (0.005)	0.015 (0.005)	0.014 (0.005)	**0.936** (0.010)
Cutthroat trout	A	SS	**0.912** (0.051)	0.0	0.0	0.105 (0.042)
		FW	**0.653** (0.175)	0.0	0.0	0.0
	B	SS	0.011 (0.010)	**0.901** (0.023)	0.0	0.062 (0.020)
		FW	0.0	**0.985** (0.002)	0.0	0.0
	C	SS	0.003 (0.003)	0.003 (0.003)	**0.884** (0.004)	0.004 (0.002)
		FW	0.0	0.0	**0.974** (0.012)	0.0
	T	SS	0.0	0.009 (0.006)	0.073 (0.018)	**0.828** (0.026)
		FW	0.031 (0.031)	0.019 (0.019)	0.0	**0.897** (0.041)

Note: Bold values are the probabilities of a fish remaining in the same segment at the start and end of the time period.