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Fire and Fish Dynamics in a Changing Climate: Broad- and Local-Scale Effects of Fire-Induced Water Temperature Changes on Native and Nonnative Fish Communities

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Joint Fire Science Program Final Report

Project Title: Fire and Fish Dynamics in a Changing Climate: Broad- and Local-Scale Effects of Fire-Induced Water Temperature Changes on Native and Nonnative Fish Communities

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Abstract: Fire is a key natural disturbance that affects the distribution and abundance of native fishes in the Rocky Mountain West. In the absence of migratory individuals from undisturbed portions of a watershed, persistence of native fish populations depends on the conditions of the post-fire stream environment. Stream temperatures typically warm after fire, and remain elevated until riparian vegetation recovers. An additional threat to native species is that nonnative fishes have invaded many waters, and these species tolerate or prefer warmer water temperatures. Thus, forecasting the long-term effects of fire on native fish populations requires an understanding of fire dynamics (size, distribution, frequency, and severity), the extent and location of changes in riparian forest structure and time to recovery, changes in stream temperatures associated with these forest changes, and how native and nonnative fish respond to changes in water temperature. To perform spatially explicit simulation modeling that examined the relations among fire disturbance, stream temperature, and fish communities, we upgraded and then linked the fire-forest succession model FireBGCv2 to a stream temperature model to project changes in water temperature in the East Fork Bitterroot River basin in Montana under an array of climate and fire management scenarios. Model projections indicated that although climate led to increases in fire severity, frequency, or size, water temperature increases at the basin scale were primarily a consequence of climate-driven atmospheric warming rather than changes in fire regime. Consequently, variation in fire management—fuel treatment or fire suppression—had little effect at this scale, but assumed greater importance at the scale of riparian stands. By revisiting a large number of previously sampled sites in the East Fork Bitterroot River basin in Montana, we evaluated whether bull trout persistence and other native and nonnative fish distributions were related to temperature changes associated with fire and recent climatic trends. Although fires were related to marked increases in summer water temperatures, these changes had a positive effect (westslope cutthroat trout) or a negligible effect (bull trout) on the abundance and distribution of native fish species, whereas the abundance of nonnative brook trout markedly declined in some instances. Fire-related changes in factors other than the thermal regime may have contributed to these patterns. In contrast, at the scale of the entire basin we observed an upward-directed contraction in the distribution of bull trout that was unrelated to fire. We concluded that this may be a response to temperature increases related to climate change.

1. Background and purpose

Fire is a key natural disturbance that affects the distribution and abundance of native fishes in the Rocky Mountain West (Rieman et al. 2003). Although severe fire sometimes may lead to fish population losses, many species have evolved with fire and their populations may be resilient to its effects (Burton 2005; Howell 2006). This resiliency, however, appears predicated on connectivity to robust population segments elsewhere in a basin, and connectivity has been lost in many watersheds because of the extirpation of migratory life histories, installation of migration barriers (such as culverts), or degradation of habitat in many portions of stream networks (Fausch et al. 2006). In the absence of support from nearby populations or individuals, persistence of native fish populations may depend on the extent and duration of changes in the post-fire environment.

Population persistence in native fishes is related to water temperature because it controls fish metabolism and thus influences individual growth and survival. Summer stream temperatures in the Rocky Mountains have been associated with the distribution and persistence of federally threatened bull trout (*Salvelinus confluentus*; Dunham et al. 2003; Rieman et al. 2007) and

federally petitioned subspecies of cutthroat trout (*Oncorhynchus clarkii*; Sloat et al. 2005). Moreover, water temperature can influence invasion success of nonnative fishes that threaten native species. In many parts of the Intermountain West, nonnative brook trout (*Salvelinus fontinalis*) have replaced cutthroat trout (Shepard et al. 2005) and hybridized with bull trout (Kanda et al. 2002). Similarly, brown trout (*Salmo trutta*) have reduced cutthroat trout survival (McHugh and Budy 2006), and rainbow trout (*O. mykiss*) have repeatedly formed hybridized populations with cutthroat trout (Shepard et al. 2005). These nonnative salmonids appear to tolerate or prefer higher water temperatures than do native bull trout and cutthroat trout, and long-term increases in water temperature may favor further inroads by nonnative species.

One of the most ubiquitous and long-term changes to stream habitat associated with fire is the warming of stream temperatures. Fire can remove riparian vegetation, and increased direct solar radiation to the stream surface from the loss of riparian shade is a primary cause of fire-related warming of summer water temperatures (Amaranthus et al. 1989). Nevertheless, effects of fire on water temperatures and fish populations are not uniform, but depend on burn severity, size, location, and proximity to fish populations, because downstream reaches may cool rapidly if riparian shade is present (Johnson 2004). Alternatively, fire-caused warming of large portions of a stream network could shrink the amount of suitable habitat resulting in native salmonid extirpation, particularly if nonnative species are present. Thus, forecasting the long-term effects of fire on water temperatures and native fish populations requires an understanding of fire dynamics—the size, distribution, frequency, and severity of fires across a landscape—as well as the extent and location of changes in riparian forest structure and the time necessary for riparian stands to recover. It will also depend on the distributions of native and nonnative fishes and their responses to changes in water temperature.

Given this background, our objectives were to address two questions from the RFA09-0001, task B statement: 1) At what spatial and temporal scales can patterns of change and recovery from fire and post-fire disturbance be predicted? 2) How are patterns and scaling of fire and postfire disturbances changing because of climate change, changes in disturbance regimes, or other factors, and how might these changes influence the persistence of populations? We investigated these issues using two approaches. First, we upgraded and linked the fire-forest succession model FireBGCv2 to a stream temperature model to predict changes in water temperatures under an array of climate models and fire and fuels management scenarios at scales from the stand to the watershed. Given that climate change is affecting fire patterns (Westerling et al. 2006) and air temperature (a good predictor of water temperature), tools that assist managers in predicting changes in the distribution of fire and the influence of fire management on stream temperatures (and potentially the distribution and abundance of native fishes) are a critical need. Second, to validate expectations about fire-related responses of fishes, we conducted immediate and longterm post-fire sampling to examine fire-related changes in the abundance and distribution of native and nonnative trout species and their habitats. Moreover, we evaluated whether changes in the distribution of bull trout were attributable to the effects of fire, climate, or other factors. The information below is summarized from Mahlum et al. (2011), Sestrich et al. (2011), Holsinger et al. (in review), and Eby et al. (in review).

2. Study description and location

We focused our investigations in the East Fork Bitterroot River (EFBR) basin, a snowmelt-dominated, 105,487-ha watershed (elevations, 1,225–2,887 m) in west-central Montana, USA (Figure 1). This area has experienced recent fire (55,000 ha burned in 2000 and 4,000 ha in

2007) and has extensive weather (1956–present), stream temperature (1993–present), and fish community (1985–present) datasets. Annual precipitation averages 41 cm (range, 26–57 cm) with most falling as snow from November to March. Flows peak in May and June as warming temperatures melt the snowpack. The area has primarily a mixed-severity historical fire regime (Arno et al. 2000) often with short intervals between low-to-medium intensity fires (mean frequencies of 11–30 years) except in steep terrain, lower-subalpine, and north-facing slopes where stand-replacing fires are more typical (Arno 1976). Beyond the native and nonnative trout noted earlier, a variety of native fish inhabit the basin including slimy sculpin (*Cottus cognatus*), mountain whitefish (*Prosopium williamsoni*), and longnose suckers (*Catostomus catostomus*). The watershed is a core conservation area for bull trout (MBTSG 1995).

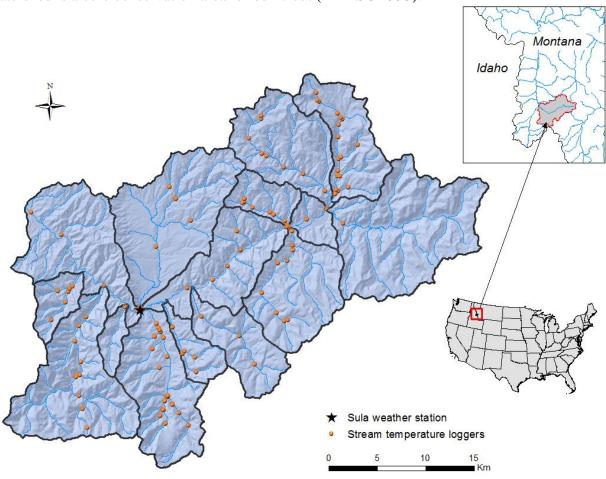


Figure 1. Location of East Fork Bitterroot watershed study area with subwatersheds and major stream networks.

Climate and fire simulation

Spatially explicit ecosystem landscape models can address questions about climate-induced changes in landscape pattern (Turner et al. 1995) and land management measures (Cushman et al. 2011) through integrating climatic influences on biogeochemical cycles, vegetation dynamics, disturbance regimes, and hydrologic processes (Littell et al. 2011). We used the landscape ecosystem process model FireBGCv2 which assimilates a mechanistic, individual tree succession model with a spatially explicit fire model to stochastically simulate fire ignition, spread, and its

effects on ecosystem components (Keane et al. 2011). We assembled a 9-year stream temperature database (2001–2009) from 116 sites distributed widely throughout the EFBR based on monitoring conducted by the U.S. Forest Service (USFS), University of Montana, and the State of Montana (Figure 1). We used data collected during the summer (June–September), the warmest and most thermally stressful period for most aquatic species, and summarized thermograph readings (typically taken at 0.5- to 2.0-hour intervals) into daily maxima—a metric highly sensitive to radiation gains associated with loss of riparian shading (Dunham et al. 2007; Isaak et al. 2010). We used a 3x3 factorial design to evaluate the effects of two factors, climate and fire management, on stream temperature where each combination of factorial levels was considered a scenario. Three climate levels were simulated: historical (H), and A2 (hot, dry) and B2 (warm, wet) to represent potential conditions under future greenhouse gas emissions. For fire management, we modeled three types of policy approaches: no suppression, fuel treatment with no suppression, and contemporary suppression. We evaluated climate and fire management effects on fire regimes using a generalized linear mixed model (GLMM) approach and two-way ANOVAs. We tested for significant differences in three variables describing fire effects: fire size, biomass consumed by fire as a proxy for severity, and frequency. We assessed stream temperature response to climate and fire management at three spatial scales – subwatershed, inside fire perimeters, and within riparian burns. We first summarized each year's average weekly maximum temperature (AveWMT) from seven-day running averages of daily temperatures, and then calculated weighted means of AveWMT at each spatial scale across the appropriate 30-m stream pixels for each simulation year.

Fish response to fire

We used data from 30 reaches (mean length 263 m, range 122-305 m; mean wetted width 3.7 m, range 1.3–7.9 m) on 24, 2nd- to 4th-order Bitterroot River tributaries in basins that burned to varying extents in 2000. Most reaches had 1–11 years of pre-fire fish abundance estimates collected from 1985 to 1999 and all had 2–3 years of post-fire abundance estimates (2001–2003). Burn severity (low, moderate, or high) was determined using the visual classification system developed by the U.S. Forest Service and applied by Bitterroot National Forest personnel in their post-fire assessment. Burn area for each drainage was determined from burn severity maps using ArcView. Summertime (July–September) mark-recapture electrofishing was used to determine salmonid abundance, size structure, and species composition.

We used linear regression to relate biotic and physical variables to the total area upslope of each study reach classified as having moderate to high burn severity (burns expected to lead to substantial overstory tree mortality). Pre-fire to post-fire changes in fish abundance among reaches were assessed with a BACI study design (Smith 2002) using 1991 as the pre-fire year and 2001 as the post-fire year because this pairing had the largest sample sizes for each species (n = 13-21). We analyzed abundance of the three most common salmonid species: westslope cutthroat trout, bull trout, and brook trout. To assess possible recovery after wildfire, a similar analysis compared density changes by species among reaches (n = 18-30) between one and three years post-fire (2001 and 2003). Invasions by new species were defined as the detection of a species in a new site during post-fire years. Extirpations were defined as the failure to detect a species at a site where it had been detected in pre-fire years.

Water temperature response to fire

Onset Hobo temperature loggers were calibrated and placed in pools or runs shielded from direct solar radiation. Stream temperature was recorded every 2 h from 19 July to 30 September between 1993 and 2007, but not all sites were measured every year. To gauge the effects of these fires on water temperatures, we divided sites into a reference group, in which 0–6% of the watershed burned but only in upland areas, and two fire-affected groups: sites within a riparian area burn (within-burn) and sites downstream of a riparian area burn (below-burn). At within-burn sites, fires of differing severity affected 34 to 100% of the watershed upstream of the site. Below-burn sites were 1.7–6.9 km downstream of the fire perimeter and 20–95% of the watershed above these sites burned. We employed a BACI design to evaluate immediate post-fire effects on maximum water temperature. To evaluate the immediate effect of fires, we used one-way ANOVA and Tukey's pairwise HSD tests to compare maximum temperature differences between September 1999 and September 2000 (the first post-fire month) and between all 3 months in 1999 and 2001 for reference, below-burn, and within-burn sites. We also noted whether maximum temperatures reached or exceeded 20°C at any site before or after the 2000 fires.

Bull trout occupancy, fire, and climate

Between 2009 and 2011, we revisited 77 sites on streams previously sampled between 1993 and 1995 (Rich et al. 2003) within the connected portions of the East Fork Bitterroot River basin to examine whether bull trout occupancy had changed. We relocated the sites and replicated the sampling methods of the earlier study. Presence in a section was defined by the capture of ≥ 2 bull trout, at least one of which was less than 250 mm. We used field measures and GIS spatial data layers to assess covariates potentially related to bull trout occupancy. Because we did not have a single year with temperature data at every site and annual variation in temperature is large, we used a stream temperature model (Holsinger et al. in review) that allowed standardized representation of relative temperatures among sites. To account for variation in probability of detection we used program PRESENCE 4.1 to estimate detection probability, occupancy, and extirpation or colonization rates.

3. Key findings, context, and management implications

Climate and fire simulation

Fire regimes were significantly different across all climates and most fire management strategies. As climates warmed, fires became larger and more frequent. Suppression decreased fire frequency but increased severity compared to no-management and fuel treatment approaches. The effect of fuel treatment was similar to the no-management strategy indicating that higher treatment levels were needed to alter fire regimes. Solar radiation incident on streams varied among climates, and suppression decreased solar radiation.

Climate had a large effect on stream temperature across all three spatial scales; fire severity only became important at local scales. At the subwatershed scale, the top model included climate and fire management, both fire covariates, and all two-way interactions, with climate having the greatest influence on stream temperatures. Stream temperatures were 5.0°C higher in the A2 climate and 1.7°C higher in the B2 compared to the historical climate. Both fire covariates significantly influenced stream temperature, but their effect size was small. Similarly, sensitivity analyses indicated that air temperature was the main driver of stream temperature change but solar radiation became more important at a finer scale.

Our results suggest that future climate conditions will cause major changes to fire regimes in the EFBR but the rise in air temperatures from climate warming will have larger systemic effects on stream temperatures than vegetative changes related to wildfire activity or management measures. Fires increased in size and frequency in our climate change simulations. Fire suppression also clearly altered fire regimes (doubling severity and decreasing frequencies by about 90%), including concomitant increases to stream-side solar radiation. Yet regardless of scale, these significant changes to wildfire induced only nominal effects to stream temperature compared to the overarching influence of air temperature.

Because fire disturbance only minimally affected stream temperature response across all spatial scales, it is not surprising that fire management measures also had little effect on instream thermal conditions. Fire suppression in our simulations strongly reduced the extent of landscape burned and increased fire severities across all climates, but at broad spatial and temporal scales, the effects on stream temperature were small compared to the influence from climate change. Our fuel reduction treatments (targeting 7% of the landscape per year) did not alter fire regime characteristics or stream temperature indicating that more intensive treatments, perhaps on the order 20% or more (Collins et al. 2010), were needed to affect fire regimes. However given that fire only marginally affected stream temperatures and that imposing fire suppression did significantly modify fire regimes without noticeable effect on stream temperatures, we suspect that more intensive fuel treatments would at best only minimally affect stream temperatures. We emphasize that our modeling approach implemented both suppression and fuel treatments to effect change at a landscape scale and over long temporal periods. We did not evaluate the benefits from site-specific strategic measures that over short periods could facilitate resilient forest and stream habitats and maintain local thermal refuges. Rieman et al. (2010) discuss examples such as focusing treatments at locations sufficiently distant from critical spawning and rearing habitats of cold-water fish species. This type of integrated and careful planning will be especially important for conserving sensitive fish populations as they face particular stressors with climate change (Luce et al. 2012) while working to minimize the potential for extensive, high-severity fires in landscapes with mixed-severity fire regimes and a recent history of fire exclusion (Collins et al. 2010).

Although our modeling approach contained uncertainty in estimating the influence of fire on stream temperature, the relative magnitude of influence between air temperature and fire disturbance on stream temperatures is reasonable and highlights the potential limitations of fire management tools to affect or mitigate the impacts from climate change on stream temperature when considered over long time spans and an extensive expression of fire effects across a landscape. Managers of aquatic systems may need to find other solutions to tackle climate change impacts on stream temperatures perhaps by focusing on simply adapting to increases or formulating broader strategies for restoration and improvement of riparian vegetation. Nonetheless, we stress that when fire management efforts are implemented to reduce fuel continuity and loading, especially for near-term benefits, the spatial context should be carefully considered to ensure conservation of high-quality riparian habitat in areas critical to sensitive native fish populations.

Fish response to fire

Negative effects of the 2000 fires on fish densities were modest. Although the proportion of basin area that burned at moderate to high severity was negatively related to the difference between 2001 and 1991 densities of all species, this effect was significant only for westslope

cutthroat trout, not for brook trout or bull trout. Following fire, however, increases in density tended to be proportionately larger in basins that had greater fire effects. The proportion of basin area that burned at moderate to high severity was positively related to the difference between 2003 and 2001 densities of bull trout and westslope cutthroat trout but not of brook trout. There was little evidence that fires were related to the arrival or loss of fish species in the sampled reaches. There were few instances of invasions and extirpations post-fire, and these shifts appeared largely unrelated to fire severity. In all cases, detections of new species in the post-fire years never exceeded 1-2 fish in any reach. Brown trout had the greatest number of invasions (n = 5).

The 2000 wildfires appeared to temporarily depress populations of the most abundant salmonid in this basin. Consistent with the observation of fish kills in reaches exposed to moderate- to high-severity fire, post-fire abundances of westslope cutthroat trout relative to a pre-fire year were lower in basins exposed to a higher proportion of stand-replacing fire. Immediate declines in abundance following fire have been repeatedly observed among native salmonids in the western U.S. (Brown et al. 2001; Burton 2005), among non-salmonid fishes in this region (Rinne and Carter 2008), and among non-salmonids elsewhere (Lyon and O'Connor 2008), and are typically attributed to spikes in water temperature or changes in water chemistry during fires, or to post-fire debris flows or blackwater events resulting from high-intensity rainfall on burned slopes (Gresswell 1999).

Because post-fire changes in density were based on larger numbers of reaches, fish responses were easier to detect. The density of both native species increased as the proportion of burned area increased. To some extent this may reflect rapid recovery from post-fire declines via increased local recruitment or recolonization from adjacent unaffected reaches. Alternatively, this could also demonstrate a positive response to burned conditions. Post-fire stream environments are characterized by higher light levels, warmer water temperatures, and nutrient pulses (Gresswell 1999; Spencer et al. 2003; Isaak et al. 2010) that persist until regrowth of riparian vegetation alters nutrient pathways and shades the stream. Total abundance of macroinvertebrates often declines immediately after fire and functional feeding groups generally shift (Minshall 2003), but post-fire increases in drifting organisms (Mellon et al. 2008) may increase prey availability to salmonids. Moreover, warmer water temperatures are hypothesized to increase the probability of population establishment and persistence for cutthroat trout in particularly cold streams (Cooney et al. 2005). Although the notion that fires may improve conditions for salmonid populations is largely unstudied, our results in combination with these related findings suggests that it warrants further examination.

There were also changes in nonnative species following fire, but not as we hypothesized. Surprisingly, brook trout failed to exhibit either positive or negative responses to fire despite changes in westslope cutthroat trout abundance. Notably, brook trout showed the most severe declines in debris flow-affected reaches, and exhibited much less recovery in severely burned reaches than did cutthroat trout. We had anticipated that warmer post-fire conditions coupled with the short generation times of brook trout (Kennedy et al. 2003) would lead to their expansion within and among sites. Their failure to show a positive response may reflect that this species is poorly adapted to some aspects of the post-fire stream environment, such as lower channel stability or greater sediment transport (Benda et al. 2003). We also suspect that part of our inability to detect responses is attributable to their relatively low abundance in the Bitterroot River basin. Given that this species can rapidly invade waters occupied by westslope cutthroat trout, that their populations often rebound quickly following fires or other disturbances (Howell

2006), and that fluvial connections among streams in most of this basin are intact, other factors may be limiting the success of this species in the basin. In contrast, brown trout first arrived in several reaches immediately following the fires, but were present in very low numbers. This species favors warmer water temperatures than do either of the native salmonids or brook trout (Elliott 1994), which may have contributed to this spread. In addition, numbers of brown trout have been increasing in the main-stem rivers in recent decades (C. Clancy, Montana Fish, Wildlife and Parks, unpublished data). Whether their recent appearance reflects a nascent invasion in now-suitable habitat or exploration by itinerant individuals from nearby source populations is not yet known.

Natural disturbances, such as wildfire, have played a critical role in the evolutionary history of native fishes in the western U.S. and are important in maintaining aquatic ecosystem health and complexity. Our results support the contention that connected native fish populations appear resilient to seemingly catastrophic high-severity wildfire disturbance and debris flows (Bisson et al. 2009) and are capable of rapid recovery even when in sympatry with nonnative fishes. With the increasing frequency and severity of wildfire on the landscape expected to continue (Hessburg and Agee 2003), maintaining connectivity within stream networks and metapopulations to allow repopulation of native fishes in reaches defaunated by wildfire may be critical. Although the potential may exist for wildfire to favor invasion of nonnative fishes, the chronic nature of many anthropogenic disturbances likely plays a greater role in facilitating nonnative fish invasions than does wildfire (Moyle and Light 1996; Ross et al. 2001).

Water temperature response to fire

We did not detect short-term spikes in water temperature at fire-affected sites in August 2000 during the wildfires. Temperature effects were, however, apparent immediately after the fires. Mean maximum temperatures increased more from September 1999 to September 2000 at within-burn sites than at sites not directly influenced by fire, and these increases were also evident when comparing monthly values between 1999 and 2001. There were no significant differences in maximum temperature changes between reference and below-burn sites in any comparison. We observed differences among groups in the number of sites exceeding 20°C before and after the 2000 fires. The highest recorded temperature in any stream from 1993 to 1999 was 18.4°C. The highest recorded temperature at reference sites from 2001 to 2007 was 18.6°C, whereas 60% of within-burn sites exceeded 20°C in either July or August (with a maximum temperature of 22.0°C in July and 21.7°C in August), as did 14% of below-burn sites. There was substantial variation both among streams and years, but post-fire recovery of water temperatures at within-burn sites was not evident. Regression analysis failed to detect a significant decline in the mean maximum difference between unburned and within-burn sites from 2001 to 2007 in July, August, or September. Maximum water temperature differences between unburned and within-burn sites were significantly greater in July (2.0°C) and August (1.7°C) than in September (1.3°C) .

We did not detect short-term spikes in stream temperature in August 2000 during the fires, despite that several of the sites exposed to fire burned at high severity. It is possible that the interval between temperature measurements in this study precluded detection of thermal peaks during the fires, but it seems unlikely that the entire warming event would be missed because conduction from the recently burned stream banks to the water column would have sustained high temperatures for several hours (Feller 1981; Hitt 2003). A more plausible explanation is that watershed size moderated temperature increases because not all portions of a basin were

simultaneously burning and because the mostly third- and fourth-order streams in our sample exhibited greater resistance to direct radiative heat transfer (Webb et al. 2008) than the mostly smaller streams previously studied (Cushing and Olson 1963; Feller 1981). In addition, smoke during the August 2000 fires may have diffused direct solar radiation and prevented immediate post-fire temperature increases at within-burn sites despite their loss of riparian vegetation.

Nevertheless, by September 2000 and in subsequent years, increases in maximum temperatures were ~1–3°C greater at within-burn sites than at below-burn and reference sites. These temperature increases were comparable to those in other streams affected by fire (Amaranthus et al. 1989; Hitt 2003; Dunham et al. 2007) or riparian timber harvest (Moore et al. 2005). The significantly greater differences in July and August relative to those in September probably reflect the waning influence of direct solar radiation on air, soil, and water temperatures caused by the seasonal decline in sun angle (Flint and Flint 2008).

We observed no differences in post-fire maximum temperature increases between reference and below-burn sites, implying that warming associated with burned areas was fairly localized. All of our below-burn sites were over 1.5 km from riparian burns, and temperature declines of 0.5−2.0°C • 100 m⁻¹ are common as streams flow from unshaded to shaded reaches (Rayne et al. 2008). If water temperatures near burn perimeters were on average warmed by 1.5−2.0°C (typical of the within-burn sites), cooling attributable to evaporation, hyporheic exchange, and conduction to the substrate (Moore et al. 2005) in the unburned downstream reaches could have returned temperatures to pre-fire norms over relatively short distances.

There was no indication that maximum water temperatures at within-burn sites were decreasing 7 years after the fires. This pattern has been observed in the first few years following fire or riparian timber harvest in other watersheds (Feller 1981; Macdonald et al. 2003), typically over longer intervals (11 years, Dunham et al. 2007; 15 years, Johnson and Jones 2000). In some cases, maximum temperature differences between reference and disturbed sites in these studies lessened or disappeared as deciduous vegetation was re-established. The larger fire-affected streams in the present study may be slower to respond because pre-fire riparian stands consisted largely of conifers, and even where forbs, grasses, and shrubs were present, their initial regrowth was probably less effective in reducing solar radiation than in smaller streams (Quinn and Wright-Stow 2008). In addition, because these are relatively high-elevation, snowmelt-dominated systems, recovery of all forms of riparian vegetation will be slower than in lower-elevation, rain-dominated systems (Moore et al. 2005). Although additional shade may be provided at within-burn sites when fire-killed trees accumulate as downed wood in and over the channels, it may be several decades before maximum temperature differences between burned and unburned sites return to pre-fire levels.

Bull trout occupancy, fire, and climate

We detected bull trout at 26 of the 41 sites where they were previously observed (15 potential extirpations). Of the 36 sites without bull trout in the original survey, we detected bull trout at 5 sites. Thirty-one of the 77 sites had adjacent riparian burns during the period between surveys, 12 of which were from medium- to high-severity fires. The top model for estimating probability of detection included only large woody debris and width as covariates. Once these were accounted for, we used the field data to examine occupancy trends. Most covariates in models for estimating colonization or extirpation rates were uninformative because of small effect sizes or large standard errors. No covariates were retained in the top model for estimating colonization. For estimating extirpation, the three top models included either no covariate or the

single covariates of elevation or temperature. Estimated extirpation rates increased approximately 3-fold from cooler to warmer sites and high- to low-elevation sites.

Bioclimatic models accounting for climate change predict an array of phenological changes and range shifts in freshwater aquatic species (Ficke et al. 2007; Beer and Anderson 2013). Alteration in the timing of life history events has been relatively widely observed (Wedekind and Küng 2010; Crozier et al. 2011; Warren et al. 2012). In contrast, confirmation of predictions that stenothermic cold-water fishes should be undergoing distributional shifts to cooler, highelevation refuges has been elusive (but see Hari et al. 2006; Comte and Grenouillet 2013), particularly in North America (Isaak and Rieman 2013). By revisiting historically sampled sites within a river network that encompasses a broad temperature and elevation gradient, we demonstrated that extirpation rates of bull trout were highest at warmer, low-elevation sites over the last two decades. This coincided with increases in summer stream temperatures in the East Fork Bitterroot River basin by as much as 0.30°C (July temperatures; Mahlum et al. 2011). Moreover, neither colonization nor extirpation rates were related to variables reflecting habitat, biotic interactions, or recent disturbance. Collectively, we interpret these findings as evidence of changes in habitat occupancy of bull trout related to climate change, and believe they constitute the first empirical evidence substantiating the many predictions of this pattern (Rieman et al. 2007; Ruesch et al. 2012).

Only those covariates most closely related to the decreased thermal suitability of bull trout habitat—water temperature and elevation—appeared in the top models for estimating extirpation rates. This may seem surprising, given that occupancy models for bull trout have included an array of habitat and biotic variables (e.g., Wenger et al. 2011). A critical distinction is that we did not model where bull trout are currently found; rather, we examined what influenced changes in that distribution over the last two decades. Consequently, it might be expected that elevation (represented in a linear function across a broad range) would not explain the distribution of bull trout in the Bitterroot River basin (Rich et al. 2003) but was our best predictor of locations from which bull trout would be extirpated. We attribute most of the explanatory power of elevation in our model to its relation to water temperature, but acknowledge that it can, in part, represent effects of other variables, such as the presence of nonnative species or the effects of fire. In this study, however, neither were informative contributors to models of changes in bull trout occupancy. At the sites we examined in the East Fork Bitterroot River, brook trout occupancy slightly declined between the earlier (12 sites on 6 streams) and later (8 sites on 5 streams) surveys. And because our modeling approach directly accounted for the increases in water temperature associated with moderate and severe fire, any changes associated with this variable would have reflected its other influences on habitat, such as increased autochthonous productivity, macroinvertebrate community shifts, or channel alteration (Gresswell 1999).

4. Future work

Modeling necessitates simplification of real-world processes, and several aspects of our modeling design limited fully capturing biophysical processes that affect stream temperature. For example, for the sake of modeling efficiency, we did not incorporate the downstream accumulation of heat but instead estimated water temperatures independently at each stream cell based on its predictors (i.e., air temperature, stream flow, solar radiation, elevation, channel slope, and contributing area). Including the influence of upstream conditions required characterizing the hydraulic retention time of water through each reach and contact time during which energy exchanges occur (Johnson 2003; Poole and Berman 2001)—a challenging task

demanding vastly more simulation time and computer memory. As well, solar radiation estimates used to build the stream temperature regression model contained uncertainty because data were unevenly distributed across their potential range. Future studies could improve solar radiation estimates through the use of high-resolution (e.g., 1×1 m) mapping (Cristea and Burges 2010) or by intensive field measurements at stream temperature monitoring sites.

We found that in a core, connected conservation area for bull trout, patterns in local extirpation were consistent with the predicted effects of stream temperature warming, which is also underway in this basin. We acknowledge that these findings reflect patterns from only one river basin. Nevertheless, their consistency with predictions from bioclimatic models highlights the need to examine basins throughout the range of bull trout (and other aquatic species) to improve our understanding of how cold-water species may be altering their distributions through time. To that end, revisiting historically sampled sites across a range of elevations within a stream network to examine changes in occupancy constitutes a powerful approach for exploring the effects of climate change (Isaak and Rieman 2013).

Stand-replacing fire in riparian zones leads to chronic increases in summer stream temperatures (Dunham et al. 2007; Mahlum et al. 2011), and has the potential to contribute to site-specific changes in habitat occupancy by stream fishes. The anticipated increases in fire extent or frequency attributable to climate change (Westerling et al. 2006) may lead to more profound shifts, or outright extirpations, of populations. Yet that no studies have demonstrated persistent losses of bull trout populations (or other non-isolated populations of stream salmonids; Rieman and Clayton 1997; Howell 2006; Dunham et al. 2007; Sestrich et al. 2011) implies that concerns about the consequences of wildland fire for stream salmonids may, in many cases, be overstated (Burton 2005). Consequently, we urge the follow-up of earlier work that examined the short-term (<1–3 year) effects of fire on fish populations. Rather than examine one or a few streams from a limited area, such sampling should be undertaken broadly across many locations for which there are available data to permit a comprehensive assessment of the longer-term responses of fishes to fires. Such work has the potential to alter the priorities and strategies employed by land and fire managers planning for and dealing with wildland fire.

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Deliverables		
Type	Description	Delivery Dates
Refereed publications	(1) examining the persistence of bull trout & cutthroat associated with habitat changes from fires, highlighting areas of most risk. (2) testing whether we see predictable shifts in fish communities occurring as a function of changing habitat quality (potential growth) associated with both climate & wildfire. (3) describing which fire & landscape characteristics best predict the magnitude, spatial scale, & duration of water temperature response to fire for stream reaches & tributaries. (4) describing simulated responses of fish communities to stream temperature changes examining landscape & fire characteristics that put populations at highest risk & whether these risks can be reduced by fuel management.	 As of September 2013: Holsinger & Keane (2011) Fire and fish dynamics in a changing climate. Fire Management Today 71, 19–23. Mahlum et al. (2011) Effects of wildfire on stream temperatures in the Bitterroot River basin, Montana. International Journal of Wildland Fire, 20, 240–247. Sestrich et al. (2011) Influence of fire on native and nonnative salmonid populations and habitat in a western Montana basin. Transactions of the American Fisheries Society, 140, 136–146. Holsinger et al. In review. Relative effects of climate change and wildfires on stream temperatures: a simulation modeling approach in a Rocky Mountain watershed. Climatic Change. Eby et al. In review. Evidence of climate-induced range contractions for bull trout (Salvelinus confluentus) to cooler, higher elevation sites in a Rocky Mountain watershed, U.S.A. Nature Climate Change. Eby et al. In preparation. Decadal effects of wildfire on fish communities in a western Montana watershed. Ecology of Freshwater Fishes.
Ph.D. dissertation	A dissertation focused around the synergistic effects of wildfire & climate change on the distribution of nonnative fish & consequences of these shifts for native fish.	June 2013 • The student withdrew from the program.
Non-refereed publication	A General Technical Report that demonstrates how our modeling & methods could be applied to other watersheds, with recommendations.	 April 2012 Keane et al. 2011. The FireBGCv2 landscape fire and succession model: a research simulation platform for exploring fire and vegetation dynamics. U.S. Forest Service General Technical Report RMRS-GTR-255.
Computer model	Updated FireBGCv2 simulation model, expanding domain to riparian habitat.	December 2009 Complete

Spatial dataset	All temperature, habitat, & fish data collected will be provided to MFWP & USFS for their statewide (regional) data bases. ArcTool Object developed to create stream temperature graphs in ArcGIS at monitoring locations in the East	September 2011 Fish data (via MFISH) Temperature data (via NoRRTN) August 2013 Complete
Web-based data archive	Fork Bitterroot watershed Comprehensive dataset for the East Fork Bitterroot Basin, including time series of stream temperatures under various climate & fire management scenarios, fisheries data, maps, & publications.	December 2011 Fish data (via MFISH) Temperature data (via NoRRTN)
Workshops	Local: Through a series of workshops, we plan to work with local fire & fisheries managers on development of scenarios specific to their concerns & present results. Regional: We will present information about the methods, results, & simulations to the Region 1 Fisheries Biologist meeting (annually in December). In year 2, we will present methods, demonstrate the models, & get feedback on useful potential simulations to explore for the region. We will report on final results in year 3.	2009-2013 • March 2011; October 2011; April 2012; March 2013; November 2013
Conference/ Symposia	We will participate in & present results at national aquatic ecology & regional fuel conferences.	 Young MK. Fishes, water, and fire in a changing climate: causes and consequences of future water temperature regimes. Bitterroot Water Forum, Hamilton, MT, 6 January 2010. Holsinger et al. Fire and fish dynamics in a changing climate. RMRS Climate Change webinar series, 13 October 2011. Eby et al. The effects of climate change and wildfire on stream temperature and native fishes in Montana, U.S.A. College of Natural Resources, Royal University of Bhutan. Lobesa, Bhutan. 15 June 2011. Eby et al. Evidence of impacts of warming streams temperatures and wildfire on trout distribution. Western Division of the American Fisheries Society, 25 March 2012. Holsinger et al. Stream temperatures increase under future climates, regardless of fire management strategies. RMRS Fire Sciences seminar series, 19 April 2012. Holsinger et al. 5th International Fire Congress, Portland, OR, 3 December 2012. Young M, Eby L, Holsinger L, Helmy O, Jakober M, Clancy C.

