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## Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t927035360>

### Influence of Fire on Native and Nonnative Salmonid Populations and Habitat in a Western Montana Basin

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First published on: 25 February 2011

**To cite this Article** Sestrich, Clint M. , McMahon, Thomas E. and Young, Michael K.(2011) 'Influence of Fire on Native and Nonnative Salmonid Populations and Habitat in a Western Montana Basin', Transactions of the American Fisheries Society, 140: 1, 136 — 146, First published on: 25 February 2011 (iFirst)

**To link to this Article:** DOI: 10.1080/00028487.2011.557019

**URL:** <http://dx.doi.org/10.1080/00028487.2011.557019>

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ARTICLE

## Influence of Fire on Native and Nonnative Salmonid Populations and Habitat in a Western Montana Basin

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### Abstract

Anticipated increases in the frequency and severity of wildfire may threaten the persistence of native salmonid populations in headwater streams in western North America. This study used extensive pre- and postfire data to assess whether wildfire leads to hypothesized declines in native westslope cutthroat trout *Oncorhynchus clarkii lewisi* and bull trout *Salvelinus confluentus* populations along with increases in the prevalence and abundance of nonnative brook trout *S. fontinalis*. Postfire cutthroat trout density was negatively correlated with the proportion of basin area that burned at moderate to high severity, but the declines in density after fires were less pronounced for bull trout and brook trout. Recovery of cutthroat trout was generally rapid in severely affected reaches. Contrary to expectation, there was no evidence of a marked increase in abundance or invasion by brook trout after wildfire. Brook trout exhibited the most severe declines in debris flow-affected reaches among all species and exhibited less recovery in severely burned reaches than did cutthroat trout. Increased stream temperature was the most significant habitat change that followed wildfire, the mean maximum water temperature during summer months increasing by 2–6°C in severely burned reaches. In contrast, burned area percentage was unrelated to large woody debris density, the percentage of surface fines, substrate diversity, or the percentage of pool habitat. The characteristically high variability in fish and habitat responses to wildfire will continue to pose a challenge for the understanding and management of fire in aquatic ecosystems.

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Wildfires pose considerable risk to the persistence of native salmonid populations in western North America (Rieman et al. 2003). High-severity, stand-replacing fires have increased in frequency in recent decades (Westerling et al. 2006). Populations of native, nonanadromous salmonids confined to short segments of headwater streams may be vulnerable to short-term stressors during such fires, including temporary changes in water temperature or chemistry (Hitt 2003; Spencer et al. 2003), as well as debris flows and blackwater events associated with high-intensity rainfall within the first few postfire years (Bozek and Young 1994; Brown et al. 2001; Howell 2006). Fires can also

lead to longer-term changes in stream characteristics that may be detrimental to native fish populations. Fire-caused mortality of overstory vegetation is associated with higher summer water temperatures (Dunham et al. 2007), and streams in severely burned basins often have reduced channel stability and complexity but higher sediment loads, especially those influenced by debris flows (Benda et al. 2003; Wondzell and King 2003). Bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarkii lewisi* in the northwestern United States appear sensitive to increases in water temperature and fine sediment (Shepard 2004; Ripley et al. 2005; Rieman et al. 2007).

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Received July 30, 2010; accepted October 28, 2010

Moreover, fall-spawned bull trout embryos in unstable channels may suffer increased mortality from substrate scouring associated with increased recruitment of transient bed sediment and loss of in-channel large woody debris (LWD; Shellberg et al. 2010).

In addition, it has been hypothesized that wildfires can promote invasions by nonnative species if native fish populations are reduced or habitats are altered in ways that favor nonnative species (Dunham et al. 2003). Of particular concern in the Rocky Mountains are nonnative brook trout *S. fontinalis*, which often displace native cutthroat trout and bull trout in small streams (Dunham et al. 2002; Rieman et al. 2006). Several studies have shown that brook trout invasion and abundance are associated with habitat changes that mirror those associated with wildfire (Rich et al. 2003; Warren and Kraft 2003; Shepard 2004).

Yet the responses of native and nonnative fishes to fire are inconsistent. Populations of native species often rebound rapidly after fires or show few effects (Rieman and Clayton 1997; Dunham et al. 2007), whereas in other cases local extirpation has been observed (Brown et al. 2001). Nonnative fishes have also shown variable responses, from rapid recovery to extirpation (Novak and White 1989; Rinne 1996; Howell 2006). The effects of fire on fish are further complicated by within-burn patchiness in fire severity, the likelihood and extent of debris flows, recovery times among habitat features, and species distribution and abundance across land- and riverscapes (Gresswell 1999; Miller et al. 2003; Rieman et al. 2003). In addition, because wildfires are episodic and unpredictable, studies of fire effects on fishes have generally relied on case studies of one or a few streams; few have prefire data or data from unburned watersheds, thus making it difficult to isolate fire effects from natural variation or anthropogenic actions (McMahon and DeCalesta 1990; Gresswell 1999). In this study, we used extensive pre- and postfire data from burned and unburned watersheds in western Montana to evaluate salmonid population and physical habitat responses after several large wildfires. We tested the hypotheses that wildfire was related to declines in native westslope cutthroat trout and bull trout populations and to increases in the prevalence and abundance of nonnative brook trout.

## STUDY AREA

The study area constituted 2,804 km<sup>2</sup> of the upper Bitterroot River basin in west-central Montana, which includes the Bitterroot National Forest (BNF). Stream flows are snowmelt driven and typically peak from mid-May to early June. The landscape is dominated by stands of Douglas-fir *Pseudotsuga menziesii*, Engelmann spruce *Picea engelmannii*, and lodgepole pine *Pinus contorta*. Large wildfires in 2000 burned 1184 km<sup>2</sup> in a complex mosaic that varied in severity. Intense thunderstorms in late July 2001 triggered flash floods and debris flows in several burned drainages, resulting in substantial channel scouring, high sediment inputs, and fish kills (BNF 2001).

Native fishes present in the study area were westslope cutthroat trout, bull trout, mountain whitefish *Prosopium williamsoni*, longnose sucker *Catostomus catostomus*, slimy sculpin *Cottus cognatus*, and longnose dace *Rhinichthys cataractae*. Nonnative fish species include brook trout, brown trout *Salmo trutta*, and rainbow trout *O. mykiss*. Westslope cutthroat trout were abundant in most Bitterroot River tributaries. Bull trout were patchily distributed, primarily as isolated headwater populations (Nelson et al. 2002; Rich et al. 2003). Brook trout were present in most of the Bitterroot River tributaries that also contained bull trout (Clancy 1993; Rich et al. 2003). Brown trout and rainbow trout were largely confined to the main-stem Bitterroot River and the lower reaches of large tributaries (Nelson et al. 2002).

## METHODS

**Study design.**—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 second- to fourth-order Bitterroot River tributaries in basins that had burned to various extents in 2000 (Table 1). Reaches had 1–11 years of prefire fish abundance estimates collected from 1985 to 1999; all had 2–3 years of postfire abundance estimates (2001–2003). Burn severity (low, moderate, or high) was determined using the visual classification system developed by the U.S. Forest Service (USFS 1995) and applied by BNF personnel in their postfire assessment (BNF 2001). Burn area for each drainage was determined from burn severity maps with use of ArcView (ESRI 1995).

**Field sampling.**—Summertime (July–September) mark-recapture electrofishing was used to determine salmonid abundance, size structure, and species composition. Fish were captured with a battery-powered backpack electrofisher emitting a smooth DC waveform to minimize potential injury of the fish. Most prefire and all postfire sampling consisted of one marking run and one recapture run per study reach. During the marking run, fish were identified to species, measured (total length, mm), and given a fin clip. Recapture sampling was conducted 4–7 d after the marking run to enable fish to redistribute throughout the reach and to minimize differences in capture probability between sampling runs. Several estimates (~25%) failed to meet minimum sample sizes of captures or recaptures for unbiased Petersen estimates (Robson and Regier 1964; Ricker 1975). Because correlations between modified Petersen estimates with at least 10 recaptures and counts of unmarked fish at least 75 mm in length captured in each reach (all fish captured during the marking run plus all unmarked fish captured during the recapture run) were large and significant for individual species ( $r = 0.83\text{--}0.91$ ,  $P < 0.001$ ), we opted to use counts for analyses of density (which also generated results comparable to analyses of modified Petersen estimates but with greater power because of larger sample sizes; results not shown). Given that fish movement was unrestricted between mark and recapture runs, we regarded counts as positively biased. Six prefire counts were

TABLE 1. Characteristics of study reaches in the southern Bitterroot River basin, Montana. Percentage burned refers to moderate to high-severity burns. Density (number/100 m) refers to the range in counts of all unmarked salmonids captured in electrofishing runs before (1985–1999) and after (2001–2003) the 2000 fires; the numbers in parentheses are the numbers of years sampled in each period. Location coordinates based on North American Datum 1983 (NAD83).

| Stream                            | Basin area<br>(km <sup>2</sup> ) | % burned | Density    |            | Elevation<br>(m) | Latitude<br>(N) | Longitude<br>(W) |
|-----------------------------------|----------------------------------|----------|------------|------------|------------------|-----------------|------------------|
|                                   |                                  |          | Pre fire   | Post fire  |                  |                 |                  |
| Bertie Lord                       | 22.1                             | 1.1      | 33–48 (3)  | 18–39 (3)  | 1,530            | 45.911          | 113.787          |
| Cameron                           | 33.1                             | 47.1     | 64–66 (2)  | 16–93 (3)  | 1,495            | 45.938          | 113.929          |
| Chicken                           | 27.0                             | 42.9     |            | 6–50 (3)   | 1,554            | 45.599          | 114.327          |
| Divide                            | 48.3                             | 24.9     | 37–50 (4)  | 48–63 (3)  | 1,621            | 46.064          | 113.968          |
| Laird <sup>a</sup>                | 22.6                             | 43.2     | 33–42 (2)  | 0–35 (3)   | 1,355            | 45.862          | 114.068          |
| Little Blue Joint                 | 12.5                             | 50.6     |            | 23–124 (3) | 1,530            | 45.689          | 114.344          |
| Martin lower                      | 50.4                             | 2.8      | 32–59 (6)  | 24–53 (3)  | 1,641            | 45.945          | 113.735          |
| Martin upper                      | 18.3                             | 7.3      | 46–75 (6)  | 39–49 (2)  | 1,924            | 45.990          | 113.828          |
| Meadow lower                      | 30.8                             | 56.5     | 50–73 (6)  | 97–106 (3) | 1,809            | 45.849          | 113.820          |
| Meadow upper                      | 19.9                             | 82.5     | 14–21 (3)  | 19–70 (3)  | 1,902            | 45.829          | 113.802          |
| Mine                              | 33.0                             | 0.0      | 60–80 (2)  | 46–79 (3)  | 1,708            | 45.596          | 114.170          |
| Moose                             | 59.9                             | 2.4      | 31–59 (5)  | 27–61 (3)  | 1,634            | 45.940          | 113.715          |
| North Rye <sup>a</sup>            | 40.7                             | 94.7     | 48–90 (5)  | 6–26 (3)   | 1,373            | 46.001          | 114.029          |
| Piquett                           | 66.0                             | 11.7     | 77–96 (2)  | 18–63 (3)  | 1,315            | 45.856          | 114.193          |
| Prairie                           | 9.7                              | 53.9     | 46 (1)     | 13–95 (3)  | 1,490            | 45.801          | 113.967          |
| Reimel lower                      | 21.1                             | 37.7     | 58–84 (3)  | 5–68 (3)   | 1,454            | 45.820          | 113.940          |
| Reimel upper                      | 15.0                             | 40.5     | 54–111 (3) | 42–49 (3)  | 1,542            | 45.801          | 113.930          |
| Rye                               | 23.0                             | 20.1     | 27–104 (5) | 32–80 (3)  | 1,626            | 45.993          | 113.943          |
| Skalkaho                          | 43.1                             | 29.1     | 31–74 (4)  | 48–76 (2)  | 1,608            | 46.124          | 113.851          |
| Slate                             | 49.5                             | 33.6     | 57–88 (2)  | 36–77 (3)  | 1,495            | 45.698          | 114.265          |
| Sleeping Child lower <sup>a</sup> | 124.8                            | 37.5     | 20–52 (13) | 8–17 (3)   | 1,391            | 46.110          | 114.005          |
| Sleeping Child upper              | 41.7                             | 17.8     | 39–58 (4)  | 23–37 (3)  | 1,626            | 46.064          | 113.968          |
| Tolan lower                       | 48.8                             | 33.0     | 26–46 (4)  | 51–80 (3)  | 1,486            | 45.829          | 113.902          |
| Tolan middle                      | 32.8                             | 41.8     | 30–54 (5)  | 46–76 (3)  | 1,744            | 45.809          | 113.851          |
| Tolan upper                       | 17.2                             | 39.3     | 17 (1)     | 29–67 (3)  | 1,846            | 45.782          | 113.833          |
| Two Bear                          | 26.2                             | 6.5      | 21 (1)     | 21–36 (3)  | 1,463            | 46.117          | 113.994          |
| West Fork Bitterroot              | 23.2                             | 0.0      | 11 (1)     | 38–40 (3)  | 1,756            | 45.513          | 114.322          |
| West Fork Camp                    | 17.5                             | 6.2      | 17 (1)     | 20–64 (3)  | 1,553            | 45.753          | 113.952          |
| Waugh                             | 6.9                              | 31.9     | 24–31 (2)  | 19–66 (3)  | 1,528            | 45.783          | 113.958          |
| Woods                             | 40.2                             | 0.0      | 26–37 (2)  | 38–55 (3)  | 1,636            | 45.563          | 114.341          |

<sup>a</sup>Reach influenced by a debris flow.

based on catches from two removal passes, but these data were used only for assessment of invasions and extirpations (see below).

An issue in long-term studies is whether similar sampling methods have been used to ensure that data are comparable over time and that any changes in abundance are not the result of methodological differences (Wiens and Parker 1995). Although similar electrofishing methods had been used over the 18-year span of the study, the assumption that sampling methods were consistent was tested by comparing capture probability (based on modified Petersen estimates for instances where at least 10 marked fish were captured in the recapture run) between prefire and postfire abundance estimates with a Z-test for difference of two proportions (Zar 1984). Prefire and postfire capture proba-

bilities were not significantly different for cutthroat trout (pre, 0.43; post, 0.44;  $P = 0.76$ ), bull trout (0.40, 0.37;  $P = 0.57$ ), or brook trout (0.49, 0.44;  $P = 0.53$ ).

Water temperatures were recorded every 2.5 h using electronic thermographs. In each study reach, a single thermograph was positioned in the shade within a well-mixed pool or run. Because thermographs were deployed from at least 19 July to 30 September at all sites, two temperature metrics—mean minimum daily temperature and mean maximum daily temperature—were calculated over this 74-d interval.

Measurements of LWD, substrate, and channel unit characteristics were used to assess the effects of fire on stream habitats. We defined LWD as pieces within the bank-full channel greater

than 10 cm in diameter and 2 m long. Total counts were standardized to number of pieces per 100 m of stream. We used pebble counts and estimates of surface fines to assess substrate composition. Pebble counts were conducted using the zig-zag procedure described by Bevenger and King (1995), in which substrate particle size was measured at every seventh step across the bank-full channel. Substrate size was measured along the intermediate axis to the nearest millimeter; this continued until 100 pebbles were measured. Substrate size categories were fines (<2 mm), gravel (2–64 mm), cobble (64–256 mm), and boulder (>256 mm). Substrate diversity was determined by using the Shannon–Weaver index (Shannon and Weaver 1949). Percent surface fines measurements were collected at pool tail-outs with a 49-point grid by counting the number of grid intersections with substrate less than 2 mm in diameter (Overton et al. 1997). The grid was randomly tossed into each pool tail-out five times. We sampled up to 10 pool tail-outs, beginning from the bottom of the reach, and estimated the mean percent surface fines for the entire reach.

Habitat types in each reach were delineated and measured at base flow in late August to allow comparisons of pool habitat among treatments. Habitats were classified using the R1/R4 stream habitat methodology (Overton et al. 1997). Each fast-water habitat unit was classified as a riffle or run. Slow-water habitats that were at least as long as they were wide and had a maximum depth of at least 1.5 times crest depth were categorized as pools.

**Statistical analyses.**—We used linear regression to relate biotic and physical variables to the arcsine-square-root-transformed proportion of total area upslope of each study reach classified as having moderate to high burn severity (burns expected to lead to substantial overstory tree mortality). All analyses were conducted in R (version 2.11.0; R Development Core Team 2010). The number of reaches included in each analysis varied because not all variables were measured in all reaches in all years, and not all species were present in all reaches. Because the number of streams that were electrofished annually varied widely in the prefire interval, prefire to postfire changes in fish abundance among reaches were assessed with a BACI study design (Underwood 1992; Smith 2002); we used 1991 as the prefire year and 2001 as the postfire year because this pairing had the largest sample sizes for each species ( $n = 13$ –21). This approach was also appropriate because regional synchrony in stream fish abundance is relatively high (Myers et al. 1997; Lobón-Cerviá 2004), and our two most distant sites were less than 75 km apart. We analyzed abundance of the three most common salmonid species: westslope cutthroat trout, bull trout, and brook trout. Densities were standardized as counts of fish per 100 m,  $\log_{10}(x + 1)$  transformed, and compared among reaches before and after wildfire by calculating  $\Delta$  ( $= \log$ -transformed postfire density— $\log$ -transformed prefire density) for each reach (Wiens and Parker 1995; Murphy et al. 1997). To assess possible recovery after wildfire, we used a similar analysis comparing density changes by species among reaches

( $n = 18$ –30) between 1 and 3 years postfire (2001 and 2003). Postfire size structure and recruitment were assessed by calculating the percentage of young fish (primarily ages 0–1) by species (Tonn et al. 2003) among reaches in 2002 and 2003. Lengths of young fish corresponded to the first node of the length-frequency distribution (St-Onge and Magnan 2000). The young fish node was 75–110 mm for westslope cutthroat trout, 75–100 mm for bull trout, and 75–120 mm for brook trout. Percentages were arcsine-square-root-transformed, and regression analyses were conducted only for samples that contained at least five fish of a given species. Finally, invasions by new species were defined as the detection of a species in a new site during postfire years. Extirpations were defined as the failure to detect a species at a site where it had been detected in prefire years. Larger thresholds, that is, the presence of more individuals, could have been adopted, but the presence (or absence) of one individual constitutes the beginning of an invasion (or onset of extirpation). Also, the multiple years of sampling in the pre- and postfire periods imply that detection rates should be relatively high. We also compared the number of invasions and extirpations between low- and high-severity fire reaches; low severity was defined as study streams with less than the median percentage of basin area burned by moderate- to high-severity fire (median, 30.5%), and high severity was defined as the percentage of basin area burned was greater than the median percentage.

Pre- and postfire water temperature data were available for 18 reaches. More consistent measurement among prefire years permitted us to average data for water temperature metrics for the prefire and postfire periods in each reach before calculating pre-/post- differences. Because other prefire physical habitat data were unavailable, we used an extensive posttreatment study design (Hicks et al. 1991) to assess effects of fire on physical habitat for 22–27 reaches measured in 2003.

## RESULTS

Crews captured 24,303 trout longer than 75 mm in the 30 study reaches during the 15-year prefire and 3-year postfire study periods. Cutthroat trout constituted 71% of all salmonids captured and were found in all reaches. Bull trout represented 15% of the total and were present in 25 reaches, whereas brook trout represented 14% of the catch and occupied 20 reaches. Rainbow trout constituted 0.3% of the catch and occurred in four reaches. Only 13 brown trout were captured, occurring in seven reaches. Prefire trout densities were generally similar within study streams (Table 1).

### Fish Abundance and Distribution

The 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 (Figure 1), this effect was significant only for westslope cutthroat trout ( $n = 21$ ,  $P = 0.03$ ,  $r = -0.46$ ) and not for brook trout ( $n = 13$ ,

$P = 0.41$ ,  $r = -0.25$ ) or bull trout ( $n = 18$ ,  $P = 0.19$ ,  $r = -0.32$ ). After fires, 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 ( $n = 24$ ,  $P = 0.03$ ,  $r = 0.44$ ) and westslope

cutthroat trout ( $n = 30$ ,  $P = 0.002$ ,  $r = 0.53$ ) but not brook trout ( $n = 18$ ,  $P = 0.39$ ,  $r = -0.22$ ; Figure 2).

Wildfire had a minor effect on fish length-frequency distributions. Although the proportion of young fish in a reach declined as the proportion of the basin upstream that burned at moderate to high severity increased for all species-year combinations, this relation was significant only for brook trout in 2002 ( $n = 12$ ,  $P = 0.02$ ,  $r = -0.65$ ; Figure 3).

There was little evidence that fires were related to the arrival or loss of fish species in the sampled reaches. The few instances of invasions and extirpations postfire appeared to be largely unrelated to fire severity (Figure 4). In all cases, detections of new species in the postfire years never exceeded 1–2 fish in any reach. Brown trout had the greatest number of invasions ( $n = 5$ ).

### Habitat

Greater fire effects were associated with increases in postfire maximum water temperatures but not with other habitat characteristics. Though there was an increase in mean minimum daily temperature with an increase in the proportion of basin area burned in most streams, the correlation was not significant ( $P = 0.15$ ;  $r = 0.35$ ; Figure 5). For mean maximum daily temperature, however, the differences were significantly correlated ( $P = 0.003$ ;  $r = 0.65$ ; Figure 5), the basins with greater than the median area burned (30.5%) showing maximum water temperature increases of about 2–6°C. In contrast, burned area prevalence was unrelated to LWD density ( $n = 22$ ;  $P = 0.40$ ;  $r = -0.19$ ), the percentage of surface fines ( $n = 26$ ;  $P = 0.63$ ;  $r = 0.10$ ), substrate diversity ( $n = 27$ ;  $P = 0.70$ ;  $r = 0.08$ ), or the percentage of pool habitat ( $n = 27$ ;  $P = 0.33$ ;  $r = -0.20$ ; Figure 6).

### DISCUSSION

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 (BNF 2001), postfire abundances of westslope cutthroat trout relative to a prefire year were lower in basins exposed to a higher proportion of stand-replacing fire. Immediate declines in abundance after fire have been repeatedly observed among native salmonids in the western United States (Brown et al. 2001; Burton 2005), among nonsalmonid fishes in this region (Rinne and Carter 2008), and among nonsalmonids elsewhere (Lyon and O'Connor 2008). These declines are typically attributed to spikes in water temperature or changes in water chemistry during fires, or to postfire debris flows or blackwater events resulting from high-intensity rainfall on burned slopes (Gresswell 1999). Bull trout have declined shortly after fire in nearby basins (Rieman et al. 1997), but such declines were not apparent in the Bitterroot River basin. Although the lack of a significant decline in bull trout may indicate less vulnerability to fire effects, it may also be an artifact of low statistical power as a result of relatively small sample sizes.

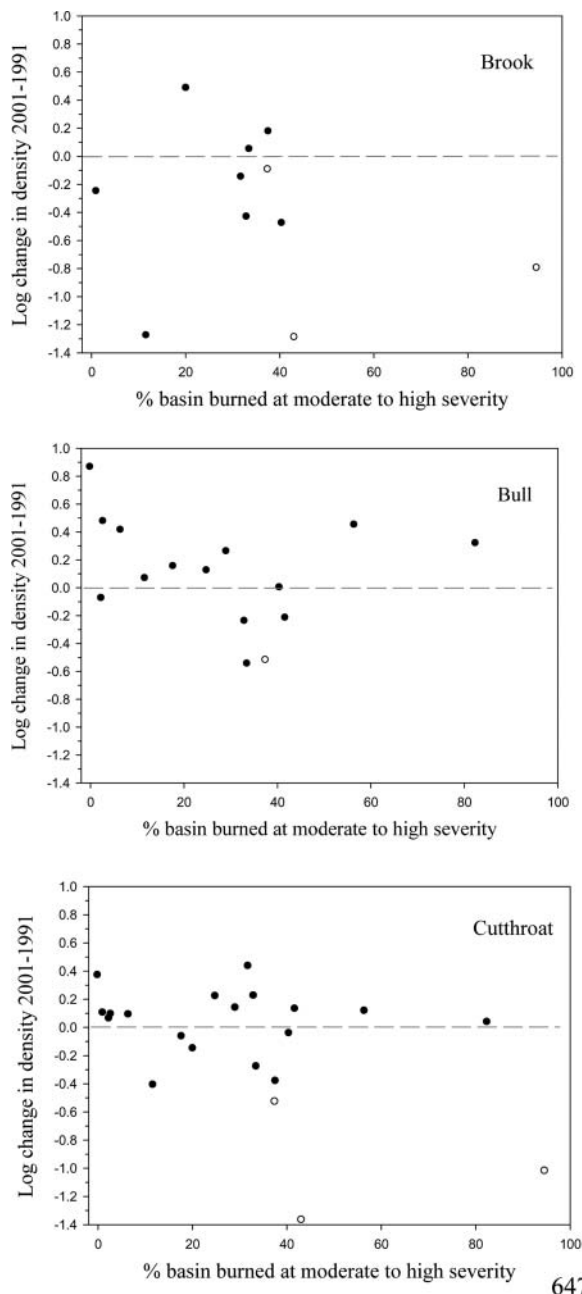


FIGURE 1. Change in fish densities ( $\log_{10}[\{\text{number}/100 \text{ m}\} + 1]$ ) between 2001 (postfire) and 1991 (prefire) for brook, bull, and westslope cutthroat trout in streams with (open circles) and without (filled circles) debris flows in the Bitterroot River basin in relation to the proportion of the basin burned at moderate to high severity. The horizontal reference line indicates zero change in density.

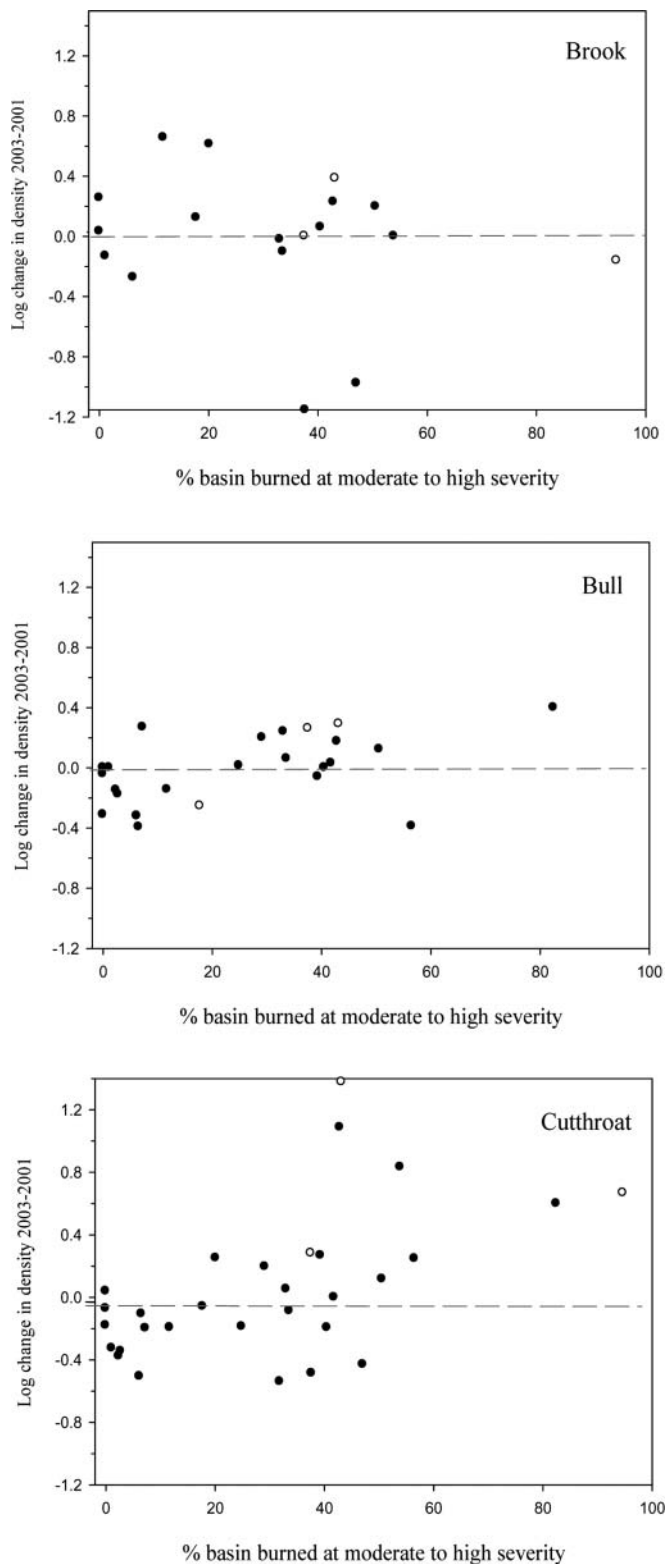


FIGURE 2. Postfire change in fish densities ( $\log_{10}[\{\text{number}/100 \text{ m}\} + 1]$ ) between 2001 and 2003 for brook, bull, and westslope cutthroat trout in streams with (open circles) and without (filled circles) debris flows in the Bitterroot River basin in relation to the proportion of the basin burned at moderate to high severity. The horizontal reference line indicates zero change in density.

Because the postfire 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 postfire declines via increased local recruitment (Lamberti et al. 1991) or recolonization from adjacent unaffected reaches (Rieman and Clayton 1997). Alternatively, this could also demonstrate a positive response to burned conditions. Postfire 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 postfire 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 suggest that further examination may be warranted.

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 postfire 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 indicate that this species is poorly adapted to some aspects of the postfire 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 (Shepard 2004), that their populations often rebound quickly after fires or other disturbances (Roghair et al. 2002; 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 after the fires but were present in very low numbers. This species favors warmer water temperatures than do either of the native salmonids or the brook trout (Elliott 1994; Rahel and Nibbelink 1999), a factor that 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

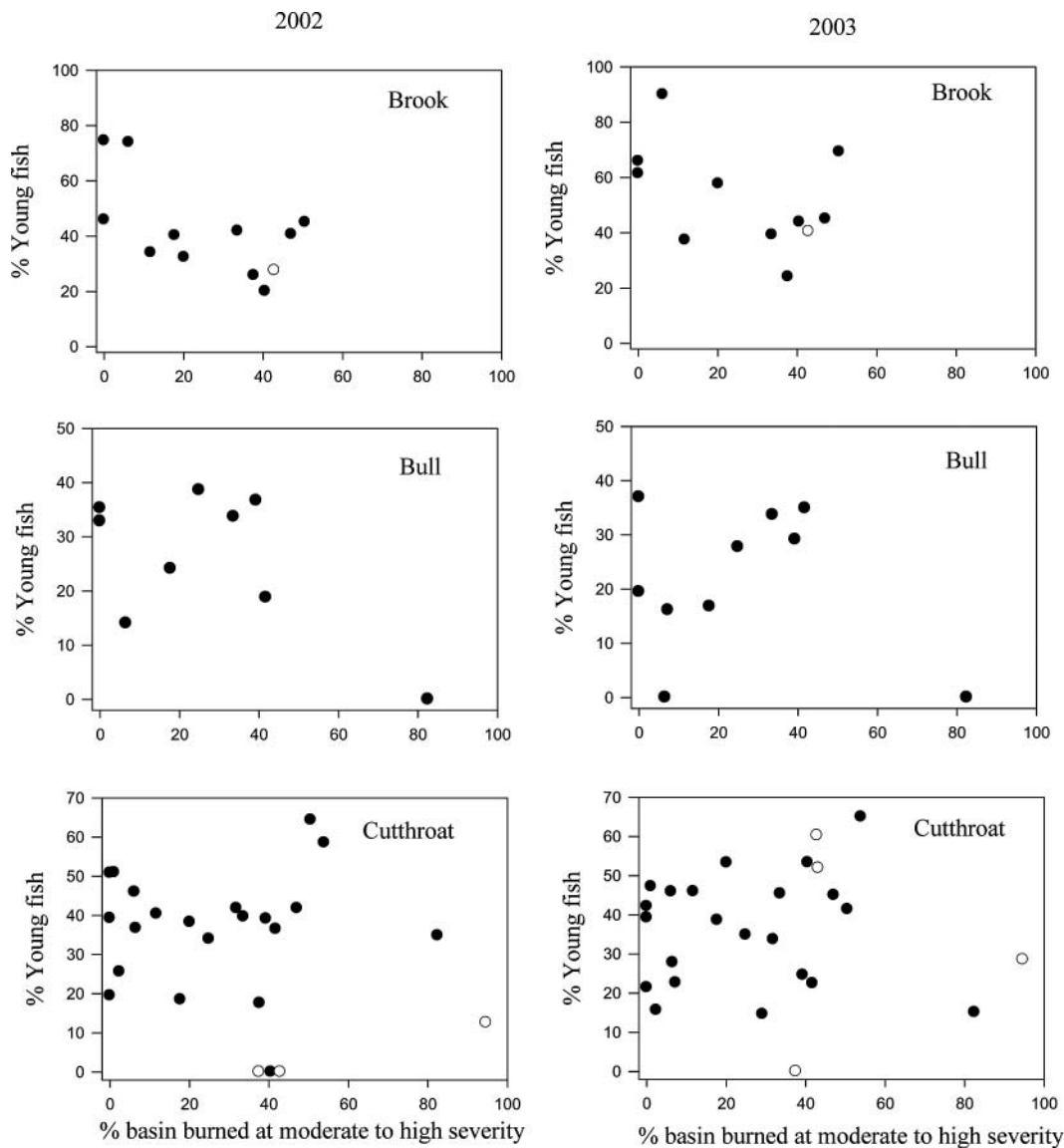


FIGURE 3. Changes in the percentage of young fish, by species, in study streams in relation to the percentage of the basin burned at moderate to high severity 2–3 years after the major wildfire in the Bitterroot River basin in 2000. Sites with debris flows are indicated by open circles, those without debris flows by filled circles.

itinerant individuals from nearby source populations is not yet known.

Increased stream temperature was the most significant habitat change following wildfire. Mean maximum water temperatures were as much as 6°C warmer after the fires. This change is consistent with similar observations on small streams throughout the western United States (Minshall et al. 1997; Burton 2005; Dunham et al. 2007) and is probably driven by the post-fire increase in solar radiation that reaches the channel after the burning of riparian vegetation (Albin 1979; Amaranthus et al. 1989; Johnson and Jones 2000). It is uncertain how long the summer water temperatures in wildfire-affected streams in the Bitterroot River basin will be elevated. Given that many ripar-

ian plant species are well adapted to wildfire disturbance, are capable of rapid reestablishment, and contribute to recovery of streamside habitats (Dwire and Kauffman 2003; Pettit and Naiman 2007), water temperatures in some affected streams will probably return to prefire norms (disregarding patterns attributable to climate change) within a few decades. Johnson and Jones (2000) found that, after 30 years, diel fluctuations in two disturbed watersheds in central Oregon had decreased by 4–6°C and were identical to a reference (unaffected) watershed.

Whether these warmer temperatures will lead to further invasions of nonnative fish remains uncertain. The predicted ultimate upper incipient lethal temperature and optimal growth temperature of westslope cutthroat trout (Bear et al. 2007) and bull trout

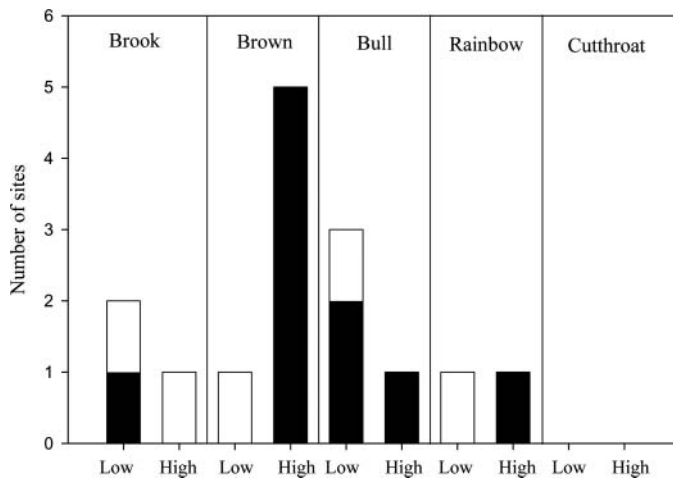


FIGURE 4. Number of invasions (black bars) and extirpations (white bars) in study streams with low and high percentages of the drainage burned by moderate- to high-severity fire (low percentage = less than median fire severity across all drainages [30.5%]; high = greater than median fire severity across all drainages).

(Selong et al. 2001) are lower than those reported for brook trout (Brown 1974; McMahon et al. 2007) and brown trout (Elliott 1994). In addition, even small differences in optimal thermal range may govern the outcome of interspecific competition (DeStaso and Rahel 1994; Taniguchi and Nakano 2000; Rodtka and Volpe 2004). For example, Novinger (2000) found that age-0 brook trout held a competitive advantage over age-0 cutthroat trout, which increased at warmer water temperatures. Similarly, brook trout have a significant competitive advantage over bull trout at temperatures above 14.4°C (McMahon et al. 2007). Increases in water temperatures in the western United States associated with climate change are predicted to greatly decrease suitable habitat for bull trout (Rieman et al. 2007), and fire may exacerbate this trend.

Somewhat unexpectedly, we did not observe any relation between burned area prevalence and measures of channel characteristics. The absence of prefire data prevented use of pre-/post-fire comparisons and weakened our ability to observe fire effects. Furthermore, the study reaches reflected an array of channel types and management histories that would tend to obscure any fire-related differences. Finally, the effects of the fires themselves made some changes difficult to detect; channel position and substrate changed annually in some of the more fire-affected streams because of greater sediment transport (C.M.S., unpublished data).

It was also clear that temperature and fish responses to fire were somewhat idiosyncratic. For example, the paucity of sites with debris flows did not permit separate analyses of their effects, but we expected such locations to display the greatest extremes in water temperature and fish response (confer Dunham et al. 2007); however, this was not always the case. Despite the fact that nearly the entire North Rye Creek basin burned at moderate to high severity and a debris flow altered the study reach in 2001, changes in mean minimum water temperature from pre- to postfire were almost nil. High variance also characterized some of the differences in fish abundance before and after the fire at sites with less severe fire effects. Spatial and temporal variability appear to epitomize the short-term post-fire environment for fishes (Gresswell 1999; Bisson et al. 2003) and will continue to pose a challenge for the understanding and management of fire in relation to aquatic ecosystems.

Natural disturbances, such as wildfire, have played a critical role in the evolutionary history of native fishes in the western United States and are important in maintaining aquatic ecosystem health and complexity (Reeves et al. 1995). 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 increasing frequency and severity of wildfire on

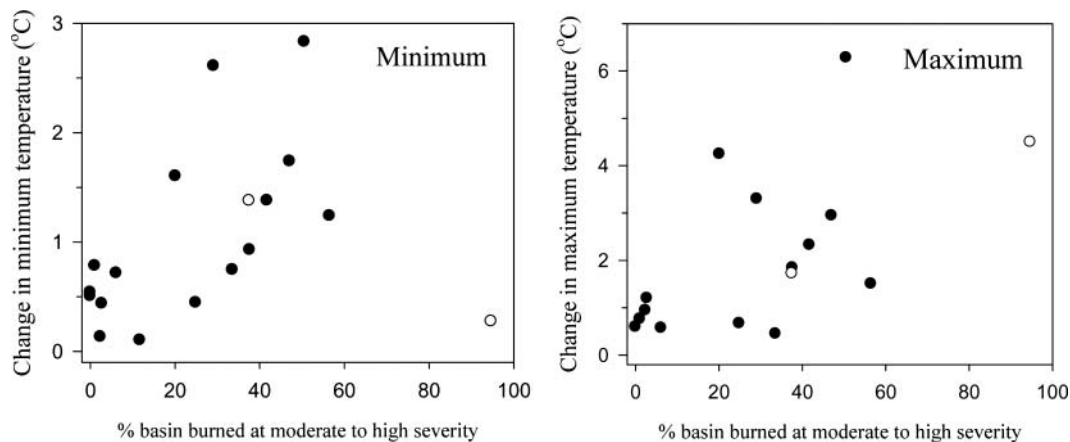


FIGURE 5. Changes in daily minimum and maximum water temperatures in relation to the percentage of the basin burned at moderate to high severity after the major wildfire in the Bitterroot River basin in 2000. Sites with debris flows are indicated by open circles, those without debris flows by filled circles.

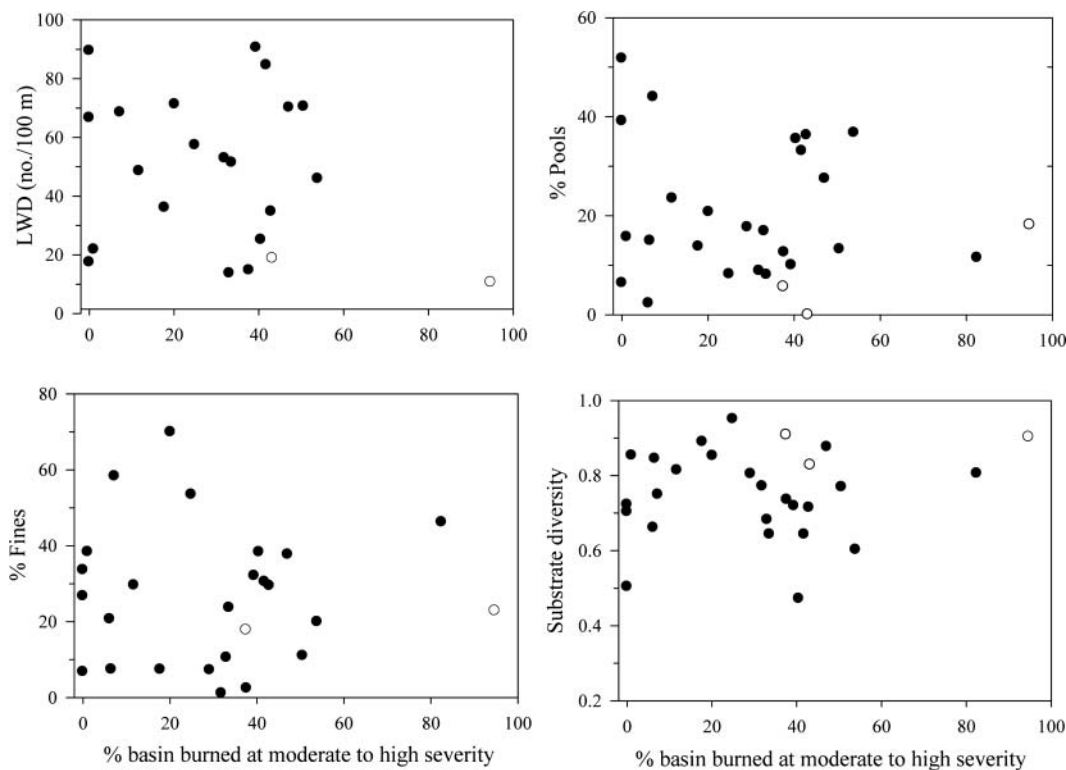


FIGURE 6. Relationships between habitat features measured in 2003 (large woody debris [LWD], percent pools, percent fines, and substrate diversity) and the percentage of the basin burned at moderate to high severity in the Bitterroot River basin in the 2000 wildfire. Sites with debris flows are indicated by open circles, those without debris flows by filled circles.

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 (Dunham and Rieman 1999; Rieman and Dunham 2000). Although the potential may exist for wildfire to favor invasion of nonnative fishes, the chronic nature of many anthropogenic disturbances probably plays a greater role in facilitating nonnative fish invasions than does wildfire (Griffith 1988; Moyle and Light 1996; Ross et al. 2001).

## ACKNOWLEDGMENTS

We thank Chris Clancy, Leslie Nyce (Montana Fish, Wildlife and Parks), and Mike Jakober (Bitterroot National Forest) for their assistance with study site selection and access to prefire data. Bill Bailor, Chris Anderson, Troy Jaecks, Holly McKinney, Marc Sestrich, Darin Watschke, Chuck Dentino, Jennifer Sestrich, Nathan Olson, and Jon McCubbins assisted with field data collection. Andrew Munro provided technical assistance throughout the study. We thank Chris Guy and Brad Shepard for their review of an earlier draft of the manuscript. Funding was provided by the Bitterroot Ecosystem Management Research Project, Bitterroot National Forest, and the U.S. Forest Service, Rocky Mountain Research Station. The study is based on a master's thesis by C. Sestrich at Montana State University.

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