

CHANGES IN NATIVE AND NONNATIVE FISH ASSEMBLAGES AND HABITAT
FOLLOWING WILDFIRE IN THE BITTERROOT RIVER BASIN, MONTANA

by

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ABSTRACT

Wildfire frequency and severity have increased over the past decade but few studies have assessed the effects of large, intense fires on native salmonids in the Intermountain West. I utilized a unique data set with 1-11 years of pre-fire population data in 24 small streams in the Bitterroot River basin in western Montana to determine if habitat changes caused by a large (1,108 km²) wildfire and associated debris flows favored nonnative brook trout *Salvelinus fontinalis* over native westslope cutthroat trout *Oncorhynchus clarkii lewisii* and bull trout *S. confluentus*. I used before-after control-impact (BACI) and extensive post-treatment study designs to determine whether changes in species abundance and habitat increased with increasing burn severity and debris flows. Species abundance was estimated pre- and post-fire with mark-recapture electrofishing and habitat conditions post-fire were assessed by measuring substrate, temperature, large woody debris, and habitat type. Stream temperature and sedimentation generally increased with burn severity whereas habitat complexity decreased with increasing burn severity and presence of debris flows. However, recovery of native trout populations was rapid with populations approaching or surpassing predisturbance levels within three years. In contrast, brook trout recovery was less apparent especially in debris flow reaches as the proportion of brook trout to the total salmonid assemblage decreased each year post-fire. However, one notable exception occurred in a high burn severity reach on Rye Creek, where brook trout increased by 499% and apparently replaced bull trout. Model results indicated that brook trout abundance was negatively related to stream gradient, elevation, and the proportion of a basin that was burned and positively related to watershed area, water temperature, and pool frequency. Spread of nonnative species to reaches where undetected pre-fire (n = 7) occurred irrespective of wildfire disturbance with brown trout *Salmo trutta* being the primary invading species (n = 5) and only one occurrence of brook trout and rainbow trout *Oncorhynchus mykiss* invasion. Although changes in aquatic habitat following wildfire have the potential to favor nonnative fishes, connected cutthroat trout and bull trout populations in the Bitterroot River basin were resilient to disturbance and generally recovered more rapidly than nonnative brook trout.

INTRODUCTION

Across North America, predation, competition, and hybridization with nonnative salmonids, coupled with habitat fragmentation and loss, have become leading threats to the persistence of native salmonid populations (Gresswell 1988; Liknes and Graham 1988; Behnke 1992; McIntyre and Rieman 1995). Although native fish populations in healthy, interconnected habitats are resilient to wildfire disturbance having evolved complex life history strategies for persisting in its wake (Rieman and Clayton 1997), over the last century fire suppression and silvicultural activities in many forested regions have created dense, homogenous stands subject to high-intensity, stand-replacing fires (Agee 1988; Henjum et al. 1994; Rieman et al. 1997; Hessburg and Agee 2003). The effects of these intense wildfires on mixed native and nonnative fish assemblages on a large scale are relatively unknown. Few studies have examined effects of wildfire on native and nonnative fish assemblages with most focused on only a relatively small number of streams (Novak and White 1989; Propst et al. 1992; Rinne 1996; Rieman et al. 1997). However, the potential exists for wildfire to significantly alter stream habitat and to promote invasion of nonnative species on a large scale, thereby exacerbating threats to remaining native fish populations (Dunham et al. 2003). Given the increased frequency of high-intensity wildfire in recent years, it is of increasing interest to determine if wildfire may expedite the decline of native salmonids by reducing habitat quality and thereby further facilitate invasion of nonnatives.

In western North America, invasion by nonnative brook trout *Salvelinus fontinalis* is among the greatest threats to remaining native cutthroat trout *Oncorhynchus clarkii*

populations (Griffith 1988; Fausch 1989; Young 1995). Currently, brook trout are common in stream reaches formerly occupied by cutthroat trout across many parts of its range, with cutthroat trout generally confined to isolated, headwater reaches (Griffith 1988; Dunham et al. 2002). Although this pattern of spatial segregation may be attributed to several factors, habitat degradation resulting from road building, logging, mining, and other anthropogenic activities likely facilitates such assemblage shifts (Moyle and Light 1996). For example, in the Bitterroot River basin, Montana, native bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarkii lewisii* abundance is highest in watersheds or headwater stream reaches with low anthropogenic disturbance, whereas brook trout are more abundant in sites with higher land use disturbance (Clancy 1993; Rich et al. 2003). Similarly, Shepard (2004) observed a positive relationship between brook trout presence and abundance and habitat degradation in stream channels associated with timber harvest.

Though poorly understood, several mechanisms have been hypothesized to allow brook trout to gain a competitive advantage over native salmonids in disturbed habitats. First, the literature suggests brook trout have relatively high survival to emergence under moderate levels of fine sediment in comparison to cutthroat trout. For example, Hausle and Coble (1976) found minimum brook trout survival to emergence of 82% in substrates composed of 25% fine sediment < 2 mm whereas Weaver and Fraley (1993) found that under experimental conditions cutthroat trout survival to emergence was much lower (34%) under similar levels (30%) of fine sediment < 6.35 mm. Second, brook trout appear to be more tolerant of reductions in habitat complexity. Warren and Kraft (2003)

found an overall positive relation between brook trout population response and large woody debris (LWD) removal in 11 pairs of reference and treatment reaches. In contrast, densities of Dolly Varden *Salvelinus malma*, a closely related species to bull trout, declined markedly after removal of LWD in Starrigavan Creek, Alaska (Elliot 1986). In addition, studies have shown occurrence of bull trout to be highly correlated with complex habitats associated with undercut banks, large, deep pools, LWD, and boulders, and negatively associated with the presence of brook trout (Watson and Hillman 1997; Rich et al. 2003). Third, several studies have documented a higher thermal tolerance in brook trout than in either cutthroat trout or bull trout as well as a competitive advantage over these species that increases with increasing water temperature (DeStaso and Rahel 1994; Novinger 2000; Selong et al. 2001; Rodtka and Volpe 2004). For example, results of a laboratory study comparing growth rates and behavioral interactions in bull trout and brook trout over a wide range of water temperatures, demonstrated that the ability of bull trout to compete with brook trout declined significantly with increases in temperature above 14.4°C (T. McMahon, Montana State University, personal communication). Therefore, even small increases in stream temperature could favor brook trout over cutthroat trout or bull trout.

Physical habitat conditions suspected in facilitating invasion of brook trout mirror the habitat changes observed following wildfire (Gresswell 1999). High-intensity wildfire can accelerate erosion and sediment delivery by decreasing water infiltration and increasing surface runoff and peak flows (Swanston 1980; Beschta 1990). In addition, increased flows and sediment delivery may reduce stream habitat complexity and

stability by mobilizing LWD and reducing the number and size of pools (Swanson and Lienkaemper 1978; Harmon et al. 1986; Everest et al. 1987; Trotter 1990; Young and Bozek 1996). Intense wildfires often result in catastrophic debris flows, which are capable of causing extensive channel restructuring, channel scouring, and massive sediment movement and deposition (Swanson and Lienkaemper 1978; Swanson et al. 1987; Lamberti et al. 1991; Rieman et al. 1997). Finally, reduced stream shading following the combustion of canopy cover and streamside vegetation leads to elevated stream temperature (Beschta et al. 1987; Amaranthus et al. 1989). These parallels between habitats degraded from anthropogenic disturbance and from wildfire suggest that wildfire may favor invasion of brook trout or other nonnative fish into native salmonid habitats.

Community assembly theory also supports the hypothesis that wildfire may promote spread and establishment of nonnative fish. Invaders are most likely to become established when native assemblages have been temporarily depleted or disrupted (Moyle and Light 1996). Sharp declines in fish abundance have been documented following high-intensity fire and associated debris flows (McMahon and DeCalesta 1990; Minshall and Brock 1991; Rieman et al. 1997, Jakober 2000); once depleted, biotic resistance to invasion may then be compromised (Moyle and Light 1996).

Brook trout dispersal behavior may also facilitate invasion into fire-disturbed streams. The dispersal stage of invasion can occur through short-distance (diffusion) movements or through long-distance (saltation) movements from source populations (Davis and Thompson 2000; Kraft et al. 2002). Brook trout are highly mobile and may

undergo both diffusion or saltation movements when dispersing from source habitats (Adams 1999). Peterson and Fausch (2003) found that the most frequent movements of brook trout were upstream directed and ≤ 250 m. Therefore, habitats affected by wildfire would most likely be invaded if they are suitable to brook trout and in close proximity to downstream source populations. However, the success of brook trout as invaders is attributed to their ability to undergo long-distance upstream movements facilitating rapid invasion. For example, Peterson and Fausch (2003) documented upstream movements of brook trout up to 2 km. Therefore, even native fish assemblages in headwater stream reaches may be potentially invaded by brook trout following alteration of physical habitat characteristics by wildfire.

The effects of wildfire on remaining native salmonids along with its potential to favor invasion of nonnative fish is of growing concern given the increased frequency, size, and severity of wildfires in recent years. Nationwide, over 49 million ha of forests historically rated as low to moderate wildfire risk are now classified as high risk (Fire Modeling Institute 2001). There are multiple interacting causes for this marked shift in fire regime. High-grade logging, even-aged forestry management, grazing, and fire suppression have interacted to reduce early-seral species and increase the dominance of shade-tolerant and fire-intolerant conifers in multiple, dense understory layers (Hessburg and Agee 2003). This has resulted in wide expanses of homogenous forest landscapes (Hessburg et al. 1999), which has facilitated the spread of forest insects and pathogens reducing tree growth, increasing mortality, and further alteration of forest structure and composition (Hagle and Schmitz 1993). In addition, over the last 15 years the western

U.S. has experienced droughts that have been more severe than any previously recorded in the instrumental meteorological record (National Oceanic and Atmospheric Administration 2002). Thus, it has been hypothesized that drought conditions in concert with substantial increases in ground fuel accumulation and the development of live fuel ladders have left forested landscapes in some vegetation types prone to the large, high-intensity, stand-replacing fires observed in recent years (Hessburg and Agee 2003; Whitlock et al. 2003).

Such an event occurred in the Bitterroot River basin in western Montana in the summer of 2000. Numerous wildfires burned 1,477 km² or 22% of all Bitterroot National Forest land, the largest fire event in the recorded history of the basin (Figure 1). Several of these fires merged, forming the Valley Complex fire, which burned 1182 km² and was the largest fire in the U.S. in that year (National Interagency Fire Center 2005). The following summer, thunderstorms triggered flash floods and debris flows in at least 10 Bitterroot River tributaries (BNFFEIS 2001). Montana Fish, Wildlife and Parks (MFWP) and U.S. Forest Service (USFS) sampling in 2000 and 2001 revealed sharp population declines of bull trout, cutthroat trout, and brook trout in several drainages affected by high-intensity wildfire and debris flows (Jakober 2000; BNFFEIS 2001).

These summer 2000 events provided a unique opportunity to evaluate fish assemblage and habitat changes following wildfire. Bull trout and cutthroat trout are still relatively abundant in the basin whereas brook trout are widely distributed but mostly found in small, lower-elevation streams (Clancy 1993; Rich et al. 2003). The MFWP and the USFS have been periodically monitoring fish populations in over 30 stream reaches

on the Bitterroot National Forest since 1985. The effects of the 2000 Bitterroot wildfires on these stream reaches included varying degrees of burn severity and presence of debris flows. Therefore, the wealth of pre-fire population data provided the ability to employ a before-after control-impact (BACI) study design (Underwood 1992; Smith 2002) to evaluate response of a mixed native and nonnative fish assemblage to fire disturbance on a larger scale and over a greater number of streams than, to my knowledge, has been previously attempted.

My specific objectives were to: 1) compare physical habitat characteristics among streams differing in wildfire severity; 2) compare pre- and post-fire differences in native and nonnative species presence and abundance among streams; and 3) determine how habitat characteristics and distance to a potential source population influence invasion of nonnative fish.

My central hypothesis was that wildfire effects on native fish populations and stream habitat represent a gradient of effects that increases with increasing burn severity and presence of debris flows. My specific predictions were that reaches with low-moderate burn severity, high burn severity, and presence of debris flows would have progressively warmer water temperatures, greater sedimentation, and lower habitat complexity in comparison to unburned reference reaches, which in turn would lead to a post-fire increase in nonnative trout abundance and decrease in native bull trout and cutthroat trout. Additionally, I surmised that the probability of nonnative fish invasion of disturbed reaches was inversely related to distance from a source population.

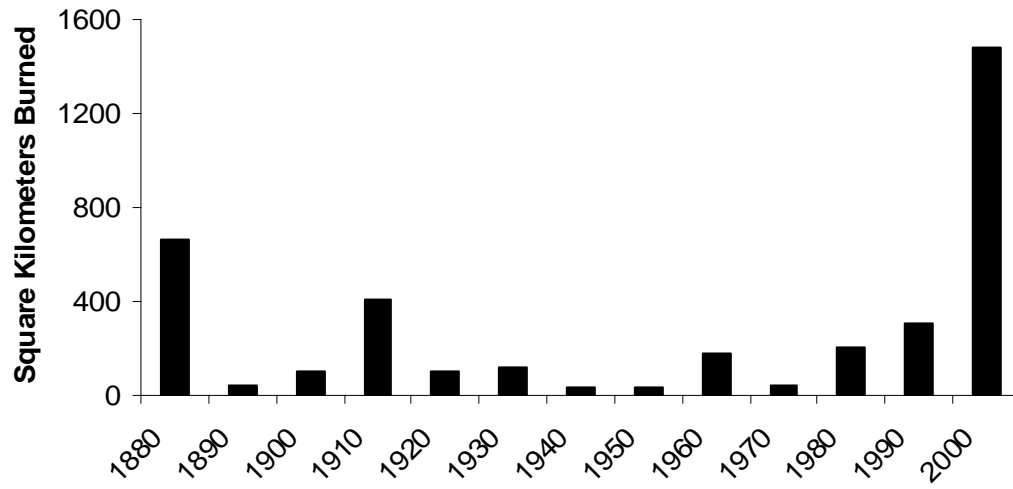


Figure 1. Square kilometers of the Bitterroot National Forest burned by forest fires over the past 120 years (modified from BNFFEIS 2001).

STUDY AREA

The 2804 km² portion of the upper Bitterroot River basin included in this study spans from the Skalkaho Creek drainage in the north to the Montana-Idaho border in the south (Figure 2). In 2000, 1108 km² (39%) of the study area burned, affecting channels of 91 fish-bearing streams (BNFFEIS 2001). This includes 248 km of stream channel burned by moderate- to high-intensity fire, causing near-complete fish kills in Laird and Little Blue Joint creeks and population declines in Chicken, Praine, North Rye, and Rye creeks. In July 2001, a thunderstorm deposited 75 mm of rain in one-half hour over several severely burned drainages with hydrophobic soils, triggering debris flows and blackwater events that caused high sediment deposition, channel scour, and fish kills in Chicken, Laird, North Rye, and Sleeping Child creeks (BNFEIS 2001).

Native fishes of the Bitterroot River basin include westslope cutthroat trout, bull trout, mountain whitefish *Prosopium williamsoni*, longnose sucker *Catostomus catostomus*, slimy sculpin *Cottus cognatus*, and several cyprinid species. Nonnative fish species include brook trout, brown trout *Salmo trutta*, and rainbow trout *Oncorhynchus mykiss*. Basinwide, westslope cutthroat trout are the most abundant salmonid species and are found in most Bitterroot River tributary streams. Bull trout are also common, although they have a more patchy distribution, occurring primarily as isolated headwater resident populations with some remnant populations of fluvial migrants in the East and West Forks of the Bitterroot River (Nelson et al. 2002; Rich et al. 2003). Brook trout are common and occur in 75% of watersheds containing bull trout, although their distributions overlap infrequently (Clancy 1993; Rich et al. 2003). Brown trout and

rainbow trout are common in the mainstem Bitterroot River and the adjacent lower reaches of most tributary streams (Nelson et al. 2002).

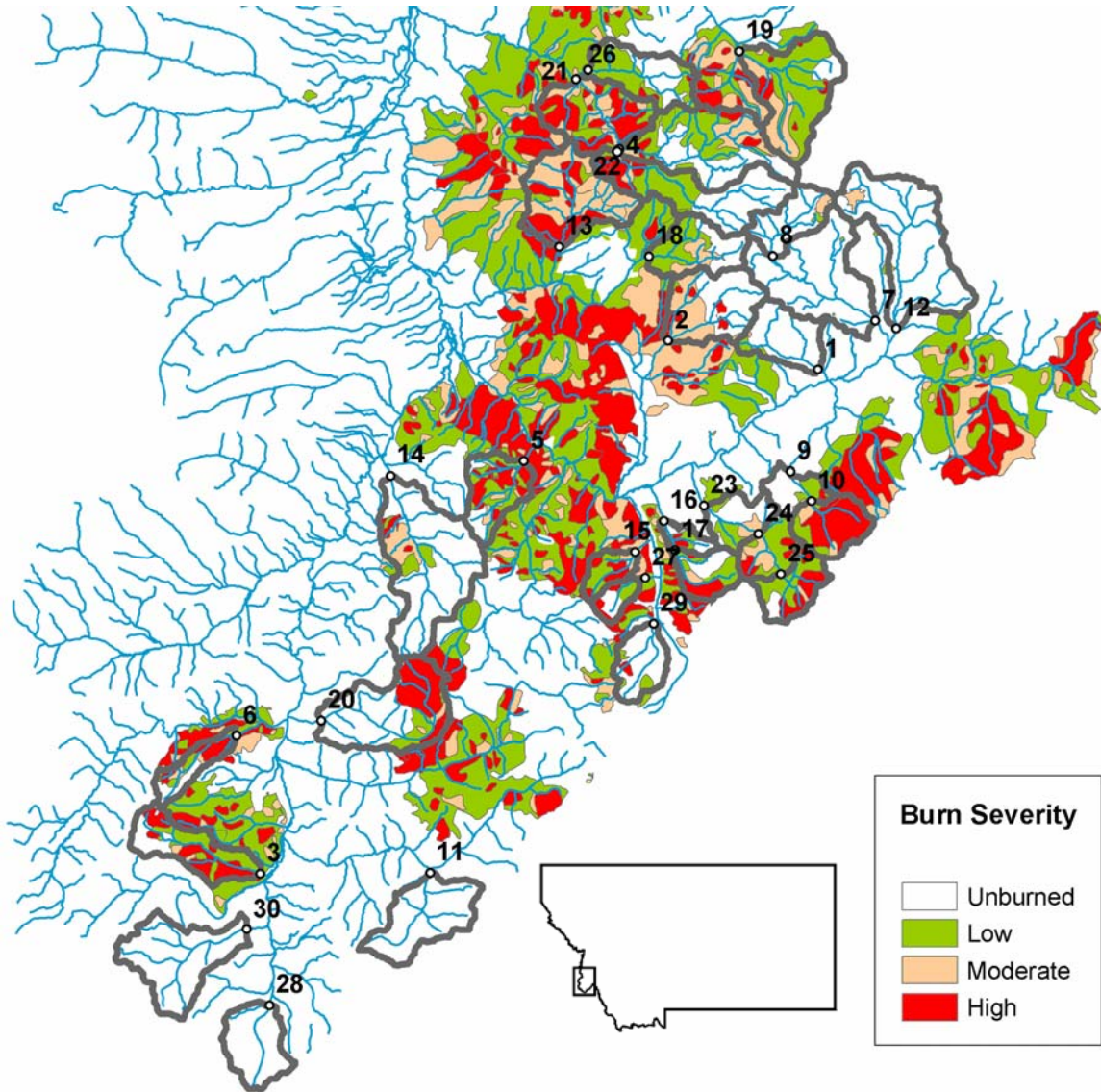


Figure 2. Map of upper Bitterroot River basin study area showing areas of low, moderate, and high burn severity within the watershed area (outlined in gray) upstream of each study reach (numbered 1-30; Table 1).

METHODS

Study Design

Thirty representative study reaches varying from 122 to 305 m on 24, 2nd- to 4th-order Bitterroot River tributary streams were selected based on existence of pre-fire population data and a range of burn effects (treatments; Table 1). Of these, 28 study reaches had 1 to 11 years of pre-fire electrofishing data collected from 1985 to 1999 by MFWP and the USFS, and all 30 study sites had 2 to 3 years of post-fire fish population data. All but one reach located on Waugh Creek maintained at least a seasonal high water connection to source populations facilitating examination of changes in species composition with ensuing recolonization of native and nonnative fish.

Thirteen of the 30 reaches were unburned and were classified as reference reaches for comparison to 17 treatment reaches. The treatment reaches were then classified into three treatments based on degree of burn severity (low-moderate and high) and presence of debris flows. Burn severity describes the effect of a wildfire in terms of the amount of surface and soil organic matter consumed and is generally determined by examining soil characteristics altered by soil heating during the disturbance (DeBano et al. 1998). However, by the onset of this study in 2002, the soil surrounding most study reaches had revegetated making on-site soil-based severity classification problematic. As a result, I classified burn severity by visually examining vegetation characteristics correlated with soil-based burn severity (USDA 1995, BNFFEIS 2001). Areas where conifer canopies and riparian vegetation were mostly consumed were classified as high-severity ($n = 6$), reaches with at least 20% of conifer trees with scorched but not completely consumed

needles and riparian vegetation were classified as moderate-severity ($n = 4$), and low-severity reaches were classified as having a mostly intact, live canopy with a few scattered burned individual trees ($n = 3$). Because there were few study reaches in the low- and moderate-severity categories, these reaches were grouped together into a low-moderate-severity category for statistical analysis. Four burned reaches that had experienced debris flows in 2001 were classified as debris flow.

Pre- to post-fire changes in fish abundance between treatment and unburned reference reaches were assessed with a Before-After-Control-Impact (BACI) study design (Underwood 1992; Wiens and Parker 1995; Murphy et al. 1997; Smith 2002). To meet the requirements of this design, some of the study reaches were excluded from the data set for the BACI analysis. On streams with multiple sampling reaches ($n = 5$) only one study reach per stream was selected for inclusion in analyses to avoid possible pseudoreplication. Selected reaches were those that had the greatest number of years of pre-fire data and a treatment that would maximize the number of sites in each treatment category. In addition, five reaches (three high-severity and two reference) with less than two years of pre-fire data were excluded from the analysis because a single year of abundance data may not be representative of average trends. This yielded 10 treatment and 8 reference reaches for the BACI analysis. Population trend data from sampled sites not included in the BACI analysis are shown in Appendix B.

Because pre-fire habitat data were not available for many study reaches, I employed an extensive post-treatment study design (Hicks et al. 1991) to assess effects of fire on physical habitat variables among 9 reference and 14 treatment reaches. Habitat

data were collected post-fire for 27 reaches. However, to avoid pseudoreplication, only one study reach per stream was selected for inclusion, resulting in the omission of four sites from the complete dataset.

Fish Population Assessment

Mark-recapture electrofishing was used to compare pre- to post-fire change in presence, abundance, and size structure of salmonid populations among treatments. Sampling protocols were identical to those employed prior to the 2000 fires to ensure sampling consistency (Clancy 2001). Fish were captured with a battery-powered Smith-Root backpack electrofisher emitting a smooth DC wave-form to minimize injury (Dalbey et al. 1996). Sampling consisted of one marking run and one recapture run per study reach. On marking runs, fish were identified to species, measured (total length mm), weighed to the nearest 0.1 gram with an Ohaus electronic balance, and marked with a left pelvic fin clip. Recapture sampling was conducted four to seven days after marking runs, thus giving fish adequate time to redistribute throughout the reach and achieve equal capture probability between sampling runs. On recapture runs, length and weight of unmarked fish and length of recaptured fish was recorded.

Estimated fish abundance was generated using the modified Peterson estimator,

$$\hat{N} = \frac{(M + 1)(C + 1)}{R + 1} - 1, \text{ which minimizes bias associated with small sample sizes}$$

(Chapman 1951). In this equation, \hat{N} equals the estimated fish abundance, M equals the total number of fish captured and marked on the marking run, C equals the total number of fish captured on the recapture run, and R equals the total number of marked fish that

Table 1. Attributes of the 30 representative stream reaches included in this study. Reach number corresponds to reach locations in Figure 2. The number following each stream name indicates the distance (km) of the lower bound of the study reach from the stream mouth. Treatment refers to the disturbance classification of each reach. Asterisks indicate reaches affected by debris flows in 2001. Also included are the number of years pre- and post-fire population abundance data and species presence/absence based on surveys prior to the 2000 fires (Adapted from MFWP presence/absence data base; P = present and A = absent).

Reach #	Name	Treatment	Stream Order	No. Years Data		Native Fish Abundance		Nonnative Fish Abundance		
				Pre-fire	Post-fire	Westslope Cutthroat	Bull	Brook	Brown	Rainbow
1	Bertie Lord Cr. 0.3	Reference	3	3	3	P	P	P	A	A
7	Martin Cr. 12.1	Reference	3	4	2	P	P	A	A	A
8	Martin Cr. 2.1	Reference	4	6	3	P	P	A	A	A
10	Meadow Cr. 9.0	Reference	3	6	4	P	P	A	A	A
11	Mine Cr. 0.3	Reference	4	2	3	P	A	P	A	A
12	Moose Cr. 2.3	Reference	4	4	3	P	P	A	A	A
14	Piquet Cr. 2.1	Reference	3	2	3	P	P	P	P	P
20	Slate Cr. 2.6	Reference	3	4	3	P	P	P	A	A
23	Tolan Cr. 3.4	Reference	3	2	3	P	P	P	A	A
27	Waugh Cr. 1.1	Reference	2	2	3	P	A	P	A	A
28	West Fk Bitterroot R. 64.4	Reference	3	1	3	P	P	P	A	A
29	West Fk Camp Cr. 0.5	Reference	3	1	3	P	A	P	A	A
30	Woods Cr. 1.4	Reference	3	1	3	P	P	P	A	A
17	Reimel Cr. 6.1	Low	3	3	4	P	P	P	A	A
19	Skalkaho Cr. 33.2	Low	3	3	2	P	P	A	A	A
24	Tolan Cr. 8.2	Low	3	5	3	P	P	A	A	A
2	Cameron Cr. 16.3	Moderate	3	1	2	P	A	P	A	A

Table 1. Continued.

Reach #	Name	Treatment	Stream Order	No. Years Data		Native Fish Abundance		Nonnative Fish Abundance		
				Pre-fire	Post-fire	Westslope Cutthroat	Bull	Brook	Brown	Rainbow
4	Divide Cr. 0.2	Moderate	3	4	3	P	P	A	A	A
21	Sleeping Child Cr. 16.4	Moderate*	4	11	4	P	P	P	A	A
22	Sleeping Child Cr. 23.3	Moderate	3	3	3	P	P	A	A	A
26	Two Bear Cr. 1.3	Moderate	3	1	3	P	P	A	A	A
3	Chicken Cr. 1.6	High*	3	0	4	P	P	P	A	A
5	Laird Cr. 2.3	High*	3	2	4	P	P	P	A	P
6	Little Blue Joint Cr. 2.3	High	3	0	3	P	P	P	A	A
9	Meadow Cr. 11.7	High	2	3	3	P	P	A	A	A
13	North Rye Cr. 3.1	High*	3	5	4	P	A	P	A	A
15	Prairie Cr. 1.6	High	2	1	4	P	A	P	A	A
16	Reimel Cr. 4.2	High	3	3	4	P	A	P	A	A
18	Rye Cr. 20.0	High	3	5	4	P	P	P	A	A
25	Tolan Cr. 11.7	High	3	1	3	P	P	A	A	A

were recaptured. Estimates included only fish ≥ 75 mm due to low capture efficiency of smaller fish with electrofishing. Because lengths of study reaches varied from 122 to 305 m, population estimates were standardized to number of fish per 100 m and are hereafter referred to as abundances. Although the sampled populations were not truly closed, it was assumed that abundances provided a reasonable population index for comparisons.

Analysis of abundance data required exclusion or manipulation of 45 (13%) of the 352 total species-specific estimates conducted. Six estimates were excluded because of high variance (standard error > 50) and low numbers of recaptures ($< 10\%$; Seber 1982). To prevent overestimation of abundance for 39 estimates with few marked fish and no recaptures (19 bull trout and 20 brook trout estimates), the number of recaptures was estimated by multiplying the number of unmarked fish (captured on the recapture run) by the mean capture probability for the respective species. To normalize abundance values of all estimates, estimates of cutthroat, bull, and brook trout 75 mm and longer were log transformed ($\log_{10}(X \text{ (estimated number per 100 m)} + 1)$) (Green 1979). Fish population changes among treatments were compared by individual species and by the total salmonid abundance. Total salmonid abundance was calculated as the sum of individual estimated species abundances. Proportion of brook trout in relation to total salmonid abundance was also used as an additional measure of fish assemblage change to determine if brook trout proportion increased in wildfire-affected reaches. Young:adult ratio (YAR) was used to examine temporal differences in population size structure among reference and treatment reaches post-fire. Young:adult ratio was determined by first plotting length-frequency distributions to identify length values that separated large and

small fish (Tonn et al. 2003). Lengths of young fish corresponded to the first node of the length-frequency distribution and adult fish comprised the longer remaining nodes (St-Onge and Magnan 2000). The young fish node corresponded to 75-110 mm for westslope cutthroat trout, 75-100 mm for bull trout, and 75-120 mm for brook trout.

Distance to a known source population was used to determine if reaches closer to source populations were more likely to be invaded by nonnative species. The Bitterroot Fisheries Presence/Absence database (MFWP 2003) was used to determine where species boundaries occurred to the nearest 0.1 km from a stream mouth. Species boundaries were defined as the closest known connected tributary or previously sampled reach where a potentially invading species was present prior to the 2000 wildfires (Table 2). The distance from each study reach to the nearest source population was then calculated for each potentially invading species. I defined invasion by the spread of a nonnative species to a reach where previously undetected or by a significant ($P \leq 0.05$) increase in abundance from the pre-fire mean.

Habitat

Habitat data included measurements of large woody debris (LWD), substrate, habitat type, water quality, and water temperature. Total length, length within bankfull boundaries, and diameters of LWD ≥ 2 m in length and ≥ 10 cm in diameter (within the bankfull channel) were measured for 21 study reaches in 2002 and 22 reaches in 2003. Diameter was measured at both ends of each piece with a measuring stick in 2002 and calipers in 2003. Total length and length within the bankfull channel were measured with a reel tape. If the larger end was attached to a root mass, diameter and length were

Table 2. Distance from each reach to a known source population of each potentially invading species.

Study Reach	Species	Distance to Source (km)
Bertie Lord 0.3	Rainbow Trout	0.3
	Brown Trout	0.3
Cameron Cr. 16.3	Rainbow Trout	16.3
	Brown Trout	16.3
Divide Cr. 0.2	Brook Trout	6.9
	Rainbow Trout	23.3
	Brown Trout	6.9
Laird Cr. 2.3	Brown Trout	2.3
Martin Cr. 2.1	Rainbow Trout	2.1
	Brown Trout	2.1
Martin Cr. 12.1	Brook Trout	12.1
	Rainbow Trout	12.1
	Brown Trout	12.1
Meadow Cr. 9.0	Brook Trout	9.0
	Rainbow Trout	9.0
	Brown Trout	9.0
Meadow Cr. 11.7	Brook Trout	11.7
	Rainbow Trout	11.7
	Brown Trout	11.7
Moose Cr. 2.3	Brook Trout	2.3
	Brown Trout	2.3
North Rye Cr. 3.1	Rainbow Trout	8.7
	Brown Trout	8.7
Prairie Cr. 1.6	Rainbow Trout	6.0
	Brown Trout	6.0
Reimel Cr. 4.2	Brown Trout	4.2
	Rainbow Trout	4.2
Reimel Cr. 6.1	Rainbow Trout	6.1
	Brown Trout	6.1
Rye Cr. 20.0	Rainbow Trout	20.0
	Brown Trout	20.0
Skalkaho Cr. 33.2	Brook Trout	6.1
	Rainbow Trout	12.1
	Brown Trout	12.1
Sleeping Child Cr. 16.4	Rainbow Trout	13.4

Table 2. Continued.

Study Reach	Species	Distance to Source (km)
Sleeping Child Cr. 23.3	Brook Trout	6.9
	Rainbow Trout	20.3
	Brown Trout	6.9
Tolan Cr. 3.4	Rainbow Trout	3.4
	Brown Trout	3.4
Tolan Cr. 8.2	Brook Trout	4.8
	Rainbow Trout	4.8
	Brown Trout	4.8
Tolan Cr. 11.7	Brook Trout	8.4
	Rainbow Trout	8.4
	Brown Trout	8.4
	Rainbow Trout	12.2
	Brown Trout	1.3
Waugh Cr. 1.1	Rainbow Trout	8.0
	Brown Trout	8.0
West Fork Bitterroot R. 64.4	Brook Trout	6.1
West Fork Camp Cr. 0.5	Rainbow Trout	11.1
	Brown Trout	11.1

measured from the widest part of the trunk adjacent to the root mass. In 2003, instead of physically measuring total length and diameter of large wood outside of the bankfull channel, dimensions were estimated for all pieces that met the minimum size criteria for sampling. To quantify estimation error, every fourth piece was both measured and estimated. In addition, the total volume and volume within the bankfull channel of each LWD piece was then calculated using the equation for volume of a truncated cone $[(1/3)(\pi)h(r_1^2 + r_2^2 + r_1r_2)]$, where h = the length and r_1 and r_2 = the radii at each end of a LWD piece.

Substrate size composition was characterized by pebble counts and percent surface fines estimates. Pebble counts were conducted using a zig-zag procedure

(Bevenger and King 1995) along the entire reach. Counts were made by walking heel-to-toe upstream across the channel alternating from the bankfull mark on one streambank to the bankfull mark on the opposite bank. At every seventh step, the first pebble touched with the index finger at the tip of the boot was measured along the intermediate axis to the nearest mm. Traverses were made across the channel until 100 pebbles were measured. Pebble sizes were categorized as fine (< 2 mm), gravel (2-64 mm), cobble (64-256 mm) and boulder (> 256 mm). Substrate diversity (scale of 0 to 1) was determined 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 < 2 mm in diameter (Overton et al. 1997). The grid was randomly tossed into each pool tail-out five times. Pool tail-outs were sampled by progressing upstream from the start to the end of each reach or until a minimum of 10 tail-outs had been sampled. Mean percent surface fines for the entire reach was determined by averaging percent fines measurements.

Habitat units within each reach were delineated at base flow in late August to allow comparisons of percent pool and riffle habitat among treatments. Length of each habitat type to the nearest 0.1 m was measured with a hip chain. Habitats were classified using modified R1/R4 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 with a maximum depth of at least 1.5 times crest depth were categorized as obstruction pools, trench pools, plunge pools, or dammed pools. The formative feature for each pool was classified as LWD, standing tree or root wad, boulder, meander,

traverse bar, bedrock, beaver dam, bank, or human structure. Pool width was measured to the nearest 0.1 m at a representative pool cross section; maximum depth and crest depth were recorded in cm using a meter stick. Residual pool volume was computed by multiplying residual pool depth by pool surface area (Overton et al. 1997). Habitat measurements in each study reach were combined to calculate an index of habitat complexity (Kershner et al. 1997), based on percent surface fines, substrate diversity, volume of LWD within the bankfull channel, residual pool depth, and percent pools.

Bankfull and wetted widths were measured to the nearest 0.1 m with a metric reel tape at 50-m intervals to classify stream size. Stream gradient was measured over the lowermost 50 m of each study reach using a hand level, steadying staff, and stadia rod (McMahon et al. 1996).

To quantify burn severity at the watershed scale, total watershed area upslope of each study reach and area of low, moderate, and high burn severity upslope of each reach were generated from BNF aerial map data (BNF 2001; Figure 2) using ARCVIEW by the Montana State University Geographic Information Analysis Center. Elevation for the downstream end of each study reach was also estimated from ARCVIEW maps. In addition, to account for differences in anthropogenic disturbance among sites, road density upslope of each study reach within 100 m of the stream was also calculated.

Differences in water quality among study reaches were compared by measuring conductivity, nitrate ($\text{NO}_3\text{-N}$), ammonium ($\text{NH}_4\text{-N}$), and inorganic phosphorus ($\text{PO}_4\text{-P}$) concentrations. Conductivity was measured with a HANNA digital conductivity meter. Water samples were collected in 125 ml bottles from the thalweg in each study reach

during receding spring flows (June 2002). Each sample was immediately filtered in the field through a 0.70 μm membrane filter using a field filtration hand pump. Samples were stored on dry ice and analyzed within 48 hours of collection by the Montana State University Soil Analytical Laboratory for nitrate, ammonium, and inorganic phosphorus.

Pre- and post-fire changes in water temperature were assessed for nine reference reaches and nine treatment reaches. Pre-fire temperature data were collected by MFWP and BNF. Pre- and post-fire water temperatures were recorded using Onset Hobo and Optic StowawayTM thermographs. Prior to deployment, thermographs used in temperature measurements were tested for accuracy by the method of Chandler et al. (2002) and were then programmed to take measurements every 2.5-hours. In each study reach, a single thermograph was deployed in a well-mixed pool or run shielded from solar radiation. Because pre-fire thermographs were always deployed from July 19 to September 30 at all sites, I based calculations of temperature metrics on this standard 74-day time period. Temperature metrics included the averages of daily mean temperature, daily maximum temperature, daily minimum temperature, and diel temperature fluctuation. Degree-days were calculated as the sum of mean daily temperatures over the standard time period whereas maximum weekly maximum temperature (MWMT) was determined by calculating the maximum seven-day average of daily maximum water temperature (Sloat 2001). Maximum weekly maximum temperature was used to identify conditions of potential high stress to salmonids because it allows identification of periods of sustained high water temperature.

Statistical Analysis

Before-After Population Comparison

A before-after analysis was employed to ascertain the significance of pre- and post-fire changes in species abundance and brook trout proportion for each treatment using paired *t*-tests. Because sample sizes within each treatment were low (≤ 8), normality could not be assumed. An Anderson Darling test for normality was significant for violation of the normality assumption ($P < 0.05$). Therefore, a Wilcoxon matched-pairs nonparametric test was used.

Because there was a relatively high amount of variation in pre- and post-fire changes among study reaches within each treatment, two-sample *t*-tests were also used to determine if species abundances were different pre- and post-fire for each of the 23 individual study reaches with at least two years of pre-fire and post-fire data. Analyses were conducted with PROC TTEST in SAS using the folded form of the *F* statistic to test for equality of the two variances (Steel and Torrie 1980). When variances were not equal, *P*-values were generated with Satterthwaite's approximation.

BACI Population Comparison

A BACI pre/post pairs analysis comparing pre- to post-fire changes in species abundance and brook trout proportion among reference, low-moderate-severity, high-severity, and debris flow reaches was used to determine whether abundance change was a result of wildfire disturbance. For each species, I calculated the amount of change in $\log_{10}(x + 1)$ abundance that occurred in each reach for the average of all post-fire years relative to the pre-fire average (Murphy et al. 1997). The mean post – pre \log_{10}

abundance change (Δ) for a given species was then calculated for each treatment and converted to percent change (percent change = $[(10^{\Delta} - 1) \times 100]$ following the approach outlined by Murphy et al. (1997) for analysis of BACI data. The changes in mean species abundance and brook trout proportion were compared among reference, low-moderate-severity, high-severity, and debris flow reaches using one-way analysis of variance (ANOVA). The Tukey-Kramer multiple-comparison procedure was then used to test for pair-wise differences. A population impact was attributed to wildfire or debris flow effects if the mean change in species abundance between the pre-fire and post-fire periods was significantly different among reference, low-moderate-severity, high-severity, or debris flow treatments.

To examine temporal changes in species abundance among treatments, the difference in abundance between each post-fire year (2001, 2002, 2003) and the pre-fire mean value was calculated for each study reach and compared among treatments using ANOVA.

Habitat Characteristics

Post-fire differences in LWD, substrate, percent pool habitat, water quality, and habitat complexity metrics were compared among reference, low-moderate-severity, high-severity, and debris flow reaches using ANOVA as described previously. Percent metrics were arcsine square-root transformed prior to analysis.

Potential changes in water temperature following wildfire were assessed by comparing pre- and post-fire differences in temperature metrics among treatments with ANOVA. Simple linear regression was used to determine the association between 2002

MWMT and proportion of a drainage upslope of each study reach with moderate-to high-severity burn (sample size was largest in 2002).

Modeling Brook Trout Abundance

To provide further insight into the influence of habitat conditions and level of disturbance on brook trout abundance at the reach- and basin-scales, I used an information-theoretic model comparison (Burnham and Anderson 1998; Anderson et al. 2000; Stephens et al. 2005). Because of the relatively small sample size ($n = 23$ observations), a restricted set of possible explanatory variables was used in each model to prevent over-fitting. Candidate sets of ecologically meaningful reach-scale and basin-scale multiple regression models included variables related to disturbance (proportion of a basin burned, linear kilometers of roads within 100 m of stream channels, degree-days, and percent surface fines; Clancy 1993; Minshall and Robinson 1995; Minshall et al. 1997; Isaak and Hubert 2001) and variables identified by other studies as potentially influencing brook trout abundance at the local, reach scale (LWD, channel gradient, and pool frequency; Fausch 1989; Kozel and Hubert 1989; Rich et al. 2003; Shepard 2004) and at the larger drainage-basin scale (watershed area, as a surrogate for stream size, and elevation; Paul and Post 2001; Dunham et al. 2002; Rich et al. 2003). Degree-days was included as a reach-scale variable because stream temperatures may vary along stream gradients (Danehy et al. 2004) and temperature data were collected only within discrete study reaches rather than continuously at multiple sites along stream gradients. From these sets of explanatory variables, I generated a subset of models that contained various

combinations of variables. The response variable used in the models was $\log_{10}(x+1)$ -transformed brook trout abundance.

Only 2003 data were used in modeling for two reasons: first, sample sizes were largest in that year; second, it was assumed that the most recently collected data would best represent the cumulative conditions of recovering aquatic habitat and fish populations post-fire. To meet the assumptions of linear regression, all percent data were arcsine square-root transformed and watershed area and linear kilometers of roads were square-root transformed prior to analyses.

Spearman rank correlation was used as a variable selection tool to test for collinearity among variables (Table 3). When two variables had a correlation of ≥ 0.70 or were functionally related (degree-days and MWMT for example), the variable with the strongest correlation with brook trout abundance (Table 4) and the highest functional significance was selected (Watson and Hillman 1997; Rich et al. 2003).

Model selection was conducted using “all subsets regression” within the PROC REG procedure in SAS (SAS for Windows version 8.02). Akaike’s Information Criterion, adjusted for small sample sizes (AIC_c) was used to rank candidate models (Akaike 1973; Burnham and Anderson 1998). However, because AIC_c is a relative ranking statistic, candidate models were ranked by ordering the relative differences among AIC_c values from low to high by subtracting the lowest value from all other values (ΔAIC ; Burnham and Anderson 1998). The relative plausibility of each model was interpreted by calculating its Akaike weight w_i (Burnham and Anderson 1998). A model was not treated as the single “best” model unless its Akaike weight was at least

eight times the value of the next highest weight as recommended by Royall (1997). However, if there was no single best model, then models for which $\Delta\text{AIC} \leq 2$ were considered competing models (Burnham and Anderson 1998). For each variable in a model, the coefficient of partial determination (r^2) was calculated, using the `pcorr2` option in SAS, as a descriptive measure of the contribution of each explanatory variable when all other variables were included (Neter et al. 1996).

Table 3. Spearman rank correlations (bold indicates correlations ≥ 0.70) between pairs of A) reach and B) basin-scale habitat variables used to eliminate correlated variables from regression analyses. A minus sign indicates a negative association between variables.

A	Degree-days	Volume LWD / 100 m	Gradient	% Surface Fines	# Pools /100 m	% Pools					
Degree-days											
Vol. LWD / 100 m	-0.10										
Gradient	-0.06	-0.01									
% Surface Fines	0.18	0.04	-0.43								
# Pools/100 m	0.56	-0.02	-0.30	0.32							
% Pools	0.29	-0.09	-0.49	0.37	0.80						

B	Drainage Area	Area Burned	Burn Density	Mod-High Density	Area Low	Area Mod	Area High	Km roads	Road Density	Elevation
Drainage Area										
Area Burned	0.54									
Burn Density	-0.16	0.67								
Mod-High Density	-0.15	0.60	0.86							
Area Low	0.30	0.72	0.52	0.24						
Area Mod	0.42	0.75	0.56	0.59	0.43					
Area High	0.21	0.77	0.70	0.80	0.44	0.47				
Km roads	0.33	-0.05	-0.32	-0.17	-0.25	0.27	-0.20			
Road Density	0.09	-0.17	-0.27	-0.13	-0.35	0.19	-0.28	0.95		
Elevation	-0.20	-0.44	-0.44	-0.45	-0.34	-0.37	-0.44	-0.19	-0.21	

Table 4. Spearman rank correlations and significance (* = $P < 0.10$; ** = $P < 0.05$) between brook trout abundance and habitat variables. A minus sign indicates a negative association between variables. The number of reaches in each correlation is given by n.

Scale	Variables	n	Correlation	P
Landscape	Total Surface Area km ²	23	0.17	0.43
	Area Burned km ²	23	-0.15	0.50
	Burn Density-% Area Burned	23	-0.20	0.35
	% Area burned by Mod-High-severity	23	-0.10	0.64
	Area Burned Low-severity km ²	23	-0.12	0.58
	Area Burned Moderate-severity km ²	23	-0.06	0.78
	Area Burned High-severity km ²	23	-0.05	0.81
	Roads km	23	0.23	0.28
	Road Density (km/km ²)	23	0.17	0.44
	Elevation	23	-0.14	0.52
Reach	Treatment	23	-0.08	0.72
	Bankfull Width m	23	-0.12	0.59
	Wetted Width m	23	-0.19	0.39
	Wetted/Bankfull Width m	23	-0.10	0.65
	% Gradient	18	-0.69	<0.01**
	Elevation	23	-0.14	0.52
	% Surface Fines	22	0.22	0.32
	% Fine 0-2 mm	23	0.20	0.35
	% Gravel 2-64 mm	23	0.42	0.05**
	% Cobble 64-256	23	-0.26	0.23
	% Boulder 256-1000 mm	23	-0.53	0.01**
	Substrate Diversity	23	-0.26	0.23
	# LWD/100 m	19	-0.01	0.96
	Total Volume LWD/100 m	19	0.05	0.83
	Total Bankfull Volume LWD/100 m	19	0.13	0.59
	LWD With Rootwad	19	-0.09	0.73
	LWD Local	19	0.13	0.60
	Conductivity (umhos)	17	-0.01	0.96
	Degree-days	17	0.43	0.08*
	MWMT	17	0.40	0.11
	# Pools/100 m	22	0.47	0.03**
	Total Resid Pool Volume/100 m	23	0.22	0.31
	% Pool Habitat	23	0.40	0.06*
	% Boulder-formed Pools	23	-0.44	0.04**
	% Bank Formed Pools	23	0.37	0.08*
	% LWD Formed Pools	23	0.11	0.62
	% MDR Formed Pools	23	0.29	0.18
	% Standing Tree or Rootwad Formed Pools	23	-0.09	0.68
	% Transverse Bar Formed Pools	23	0.34	0.12
	% Pools Beaver Dam Formed	23	0.36	0.09*
Habitat Complexity	19	0.07	0.76	

RESULTS

Fish Assemblage Changes

Mean capture probability for all salmonid species combined was 0.39 and varied little among species with the exception of rainbow trout which had a higher value but were only captured in a few sites (Table 5). Capture probability was not significantly different pre- and post-fire for any species.

Table 5. Comparison of pre- and post-fire capture probability (± 1 SE) among species using the Z-test for difference of two proportions. n = number of estimates.

Species	Mean Capture Probability		n	P
	Pre	Post		
Cutthroat Trout	0.40 (0.01)	0.39 (0.02)	193	0.92
Bull Trout	0.33 (0.02)	0.35 (0.03)	103	0.83
Brook Trout	0.44 (0.03)	0.42 (0.04)	65	0.86
Rainbow Trout	0.63 (0.38)	0.47 (0.07)	5	0.22

Before-After Comparisons

The magnitude of pre- to post-fire change in species abundance was relatively low in reference, low-moderate-severity, and high-severity treatments compared to the debris flow treatment (Table 6). Changes in reference reaches were not significant with total species abundance decreasing an average of 12% ($P = 0.70$), cutthroat trout increasing slightly by 7% ($P = 0.77$), bull trout increasing by 23% ($P = 0.75$), and brook trout decreasing by 24% ($P = 0.78$; Table 6). Similarly, there were no significant pre- to post-fire species abundance changes in low-moderate or high-severity reaches, though sample sizes were low ($n \leq 4$). In contrast, total salmonid abundance and cutthroat trout abundance in debris flow reaches declined significantly from the pre-fire average by 84% ($P < 0.01$) and 81% ($P = 0.02$), respectively. Brook trout also declined post-fire in abundance (87%) in debris flow reaches but not significantly (Table 6).

High variability in abundance change among individual study reaches within their perspective treatments contributed to the overall lack of significant pre- to post-fire differences. Among reference reaches, three of 11 (27%) reference reaches had significant ($P < 0.05$) increases in post-fire cutthroat trout abundance, whereas two reaches had significant ($P < 0.05$) decreases in brook trout (Bertie Lord Creek) and bull trout (Woods Creek) abundance (Appendix A: Table 1). Among treatment reaches, significant decreases and increases in abundances for all three salmonid species were observed. The most dramatic of these included a 52% decrease in bull trout abundance ($P = 0.03$) and a 499% increase in brook trout abundance ($P = 0.03$) that resulted in the apparent replacement of bull trout by brook trout in the high-severity Rye Creek 20.0 study reach (Appendix B: Figure 2). This was the only treatment reach with a significant increase in brook trout abundance post-fire. Finally, high variation in brook trout abundance change among reaches contributed to the lack of significance in the debris flow treatment. This is attributed to a small decline (20%) in abundance in the Sleeping Child Creek 16.4 reach (Appendix A, Table 1) relative to declines in other debris flow reaches (97% Laird Creek 2.3 and 92% North Rye Creek 3.1).

In addition to pre- to post-fire changes, temporal trends in species abundance were apparent within reference, low-moderate-severity, high-severity, and debris flow treatments during the post-fire period. Mean species abundance in reference reaches declined during the post-fire period with cutthroat trout, bull trout, and total species abundance exceeding the pre-fire average in 2001, but decreasing to below pre-fire levels

by 2003. Brook trout were the exception in reference reaches, increasing from 49% below the pre-fire mean in 2001 to within 22% of the pre-fire mean by 2003.

Species abundance in low-moderate and high-severity reaches increased rapidly during the post-fire period with populations approaching or surpassing pre-fire levels by 2002. For example, cutthroat and bull trout in low-moderate-severity reaches increased from 15% and 10% above the pre-fire mean in 2001 to 26% and 45%, respectively, above the pre-fire mean in 2002 (Table 6). Similarly, brook trout abundance in the single low-moderate-severity reach exceeded pre-fire levels by 74% in 2002. In high-severity reaches, though 41% and 8% below the pre-fire mean in 2001, cutthroat trout and bull trout populations increased rapidly to within 2% and 26% above the pre-fire mean by 2003.

Total and single species abundance generally showed marked (-80%) declines in debris flow reaches in the post-fire period with a notable degree of recovery three years after disturbance in all but brook trout (Table 6). In 2002, one year after the debris flows, cutthroat trout populations in debris flow reaches were 86% less than the pre-fire mean ($P < 0.05$; Table 6). However, by 2003, cutthroat abundance increased markedly to 35% below the pre-fire mean. Bull trout, though present at only two debris flow-affected sites and at low densities, surpassed pre-fire abundance by 2002. In contrast, brook trout showed little evidence of recovery in debris flow reaches from 2001 (88% below pre-fire mean) to 2003 (87% below pre-fire mean).

Overall, disturbed reaches with mixed native and nonnative fish assemblages shifted toward native species during the post-fire period. Brook trout as a proportion of

total salmonid abundance decreased over the post-fire period in treatment reaches, but increased in reference reaches (Table 7). For example, brook trout proportion in high-severity reaches decreased from 13% above the pre-fire mean in 2001 to 4% above the pre-fire mean in 2003. As cutthroat and bull trout populations in debris flow reaches recovered from the fire relative to brook trout, the proportion of brook trout in debris flow reaches decreased each consecutive year following the fires from 16% below the pre-fire mean in 2001 to 21% below the pre-fire mean in 2003.

Table 6. Results of before-after analysis comparing percent change in species abundances in each treatment for the post-fire average and each post-fire year relative to the pre-fire average (number of reaches in parentheses) with *t*-tests. A negative percent change indicates that species abundance decreased in the post-fire period. Asterisks indicate significance: * = $P < 0.10$; ** = $P < 0.05$; *** = $P < 0.001$.

Species	Treatment	Percent Change			
		Post-Pre	2001-Pre	2002-Pre	2003-Pre
Total All					
	Reference	-12.23 (8)	23.18 (8)	12.00 (8)	-50.99 (8)
	Low-Mod	85.29 (4)	134.87 (3)	187.40 (3)	60.85 (4)
	High	-8.93 (3)	-2.50 (3)	14.02 (3)	-32.05 (3)
	Debris	-83.94 (3) **	-94.59 (3) **	-84.29 (3) **	-51.31(3) *
Cutthroat					
	Reference	7.15 (8)	41.25 (8)	0.00 (7)	-12.90 (7)
	Low-Mod	9.65 (4)	14.82 (2)	25.89 (3)*	7.15 (4)
	High	-25.87 (3)	-41.12 (3)	-2.28 (3)	-30.82 (2)
	Debris	-80.95 (3)**	-92.41 (3)**	-85.87 (3)**	-35.43(3)
Bull					
	Reference	23.03 (7)	47.91 (7)	38.04 (6)	-8.80 (7)
	Low-Mod	23.03 (3)	9.65 (3)	44.54 (2)***	23.03 (3)*
	High	17.49 (2)	-8.80 (2)	25.89 (2)	44.54 (2)
	Debris	-14.89 (2)	-49.88 (2)	23.03 (2)	0.00 (2)
Brook					
	Reference	-24.14 (7)	-48.71 (6)	7.15 (7)	-22.38 (7)
	Low-Mod	-64.52 (1)	na	73.78 (1)	-92.76 (1)
	High	41.25 (2)	73.78 (2)	47.91 (2)	7.15 (2)
	Debris	-87.12 (3)	-87.70 (3)	-87.12 (3)	-86.51 (3)

BACI Comparisons

Significant pre- to post-fire population changes among treatments identified in pre/post pairs analyses occurred only for total species and cutthroat trout abundance. During the post-fire period, total species abundance decreased significantly in debris flow versus low-moderate-severity reaches ($P < 0.05$; Table 7) indicating debris flow effects. This was in part due to an 85% post-fire increase in total species abundance that occurred in low-moderate-severity reaches. Cutthroat trout in debris flow reaches also responded negatively relative to cutthroat trout in reference and low-moderate-severity reaches ($P < 0.01$; Table 7) indicating significant debris flow effects.

Presence of significant disturbance effects varied temporally during the post-fire years 2001-2003 for total species abundance, cutthroat trout, and brook trout proportion. During 2002, one year after the debris flows, total species and cutthroat trout abundance relative to the pre-fire mean in debris flow reaches were significantly lower than reference, low-moderate-severity, and high-severity reaches ($P < 0.01$; Table 7). However, by 2003 total species and cutthroat abundance change in debris flow reaches was not significantly different from other treatments suggesting population recovery ($P = 0.89$; Table 7). In contrast, there were no significant differences in pre- to post-fire brook trout proportion change among treatments until 2003. In that year, the proportion of brook trout in the low-moderate-severity and debris flow treatments relative to the pre-fire mean proportion was significantly lower than that of high-severity and reference reaches underscoring lack of brook trout recovery relative to other species ($P = 0.03$; Table 7).

Table 7. Results of pre/post pairs analysis comparing the amount of change (untransformed mean abundance shown \pm 1 SE, with number of reaches in parentheses) in $\log_{10}(x+1)$ species abundance and brook trout mean proportion post-fire and for each post-fire year relative to the pre-fire mean among reference, low-moderate-severity, high-severity, and debris flow reaches (ANOVA). Across a row, values not sharing a common lowercase letter are significantly different ($P < 0.05$; Tukey-Kramer multiple-comparison test).

Species	Metric	<i>P</i>	Reference	Low-Moderate	High	Debris Flow
Total All Species	Post-Pre	0.046	0.65 \pm 20.86 (8) ab	18.50 \pm 16.39 (4) ac	-5.65 \pm 34.37 (3) ab	-77.08 \pm 14.48 (3) bd
	2001-Pre	0.002	11.50 \pm 24.53 (8) a	23.15 \pm 23.85 (3) a	-12.9 \pm 12.06 (3) a	-92.48 \pm 18.32 (3) b
	2002-Pre	0.002	2.30 \pm 8.06 (8) a	46.29 \pm 9.82 (3) a	-3.16 \pm 38.54 (3) a	-85.19 \pm 18.06 (3) b
	2003-Pre	0.706	-11.84 \pm 33.62 (8)	7.23 \pm 25.80 (4)	-0.87 \pm 57.44 (3)	-53.58 \pm 7.20 (3)
Cutthroat	Post-Pre	0.007	3.37 \pm 5.52 (8) a	5.35 \pm 8.70 (4) a	-3.86 \pm 18.47 (3) ab	-50.27 \pm 5.17 (3) b
	2001-Pre	0.000	17.58 \pm 8.79 (8) a	6.14 \pm 6.64 (3) a	-19.07 \pm 11.12 (3) a	-62.69 \pm 8.15 (3) b
	2002-Pre	0.002	-0.41 \pm 4.06 (8) a	12.97 \pm 10.10 (3) a	1.71 \pm 20.61 (3) a	-58.98 \pm 7.02 (3) b
	2003-Pre	0.892	-5.68 \pm 9.91 (7)	4.94 \pm 13.26 (4)	5.78 \pm 24.58 (3)	-29.14 \pm 4.61 (3)
Bull	Post-Pre	0.941	0.61 \pm 2.69 (7)	6.95 \pm 2.76 (3)	10.10 \pm 11.74 (2)	-2.21 \pm 2.85 (2)
	2001-Pre	0.461	1.60 \pm 3.57 (7)	3.74 \pm 8.32 (3)	2.71 \pm 4.35 (2)	-3.69 \pm 3.69 (2)
	2002-Pre	0.998	2.90 \pm 3.19 (7)	13.20 \pm 1.70 (2)	10.79 \pm 12.43 (2)	-0.90 \pm 1.85 (2)
	2003-Pre	0.861	-2.68 \pm 2.56 (7)	6.40 \pm 2.94 (3)	16.81 \pm 18.45 (2)	-2.04 \pm 3.00 (2)
Brook	Post-Pre	0.225	-0.32 \pm 16.48 (7)	-8.02 \pm 0 (1)	-13.35 \pm 21.83 (2)	-24.44 \pm 13.16 (3)
	2001-Pre	0.166	-8.49 \pm 18.41 (7)	NA	6.26 \pm 4.70 (2)	-24.46 \pm 13.31 (3)
	2002-Pre	0.079	0.29 \pm 5.79 (7)	33.79 \pm 0 (1)	-19.09 \pm 22.69 (2)	-24.41 \pm 13.08 (3)
	2003-Pre	0.382	7.23 \pm 26.68 (7)	-49.82 \pm 0 (1)	-27.22 \pm (2)	-24.44 \pm 13.09 (3)
Brook Proportion	Post-Pre	0.275	-5.26 \pm 4.40 (9)	-12.98 \pm -- (1)	8.08 \pm 0.94 (2)	-18.47 \pm 12.01 (3)
	2001-Pre	0.253	-9.84 \pm 6.01 (9)	NA	13.17 \pm 11.08 (2)	-16.24 \pm 13.77 (3)
	2002-Pre	0.118	-1.13 \pm 3.84 (9)	14.45 \pm -- (1)	7.00 \pm 3.42 (2)	-17.69 \pm 10.63 (3)
	2003-Pre	0.031	-1.47 \pm 3.76 (8) a	-40.41 \pm -- (1) b	4.07 \pm 11.67 (2) a	-21.49 \pm 12.09 (3) ab

Lack of statistical significance in the pre/post pairs analysis was often associated with small sample size, high variation among reaches, or outliers. Total species abundance in debris flow reaches decreased relative to reference reaches but not significantly because of an outlier (90% decrease in Piquet Creek). Although brook trout abundance declined by 87% in debris flow reaches and increased by 49% in high-severity reaches, these changes were not significantly different from each other or other treatments ($P = 0.3$; Table 7) due to small sample size and high variability among reaches. For example, in the high severity treatment ($n = 2$) brook trout abundance increased substantially (499%) in the Rye Creek 20.0 reach and declined (67%) in the Reimel Creek 4.2 reach (Appendix A, Table 1). Bull trout changed little across all treatments, but they occurred in relatively few sites and typically at low densities.

Wildfire also appeared to strongly influence length-frequency distributions. In reference and low-moderate-severity reaches, length frequencies were skewed to the left for all species post-fire with young:adult ratios typically from 1 to 4 indicating a high proportion of juvenile fish (Figures 3-5). In high-severity reaches, cutthroat trout and bull trout showed some abundance decline and evidence for reduced recruitment in the year after the fire (2001), but had marked increases in YAR in 2002 and 2003. In 2002, cutthroat trout YAR in high-severity reaches surpassed YAR in reference reaches by 116%. Similarly, brook trout, having the greatest apparent decrease in recruitment of all species in high-severity reaches, increased dramatically from 2002 (YAR = 0.7) to 2003 (YAR = 4.8) surpassing YAR in reference reaches (YAR = 1.9). In contrast, many fewer fish were present in debris flow reaches among all species categories with much reduced

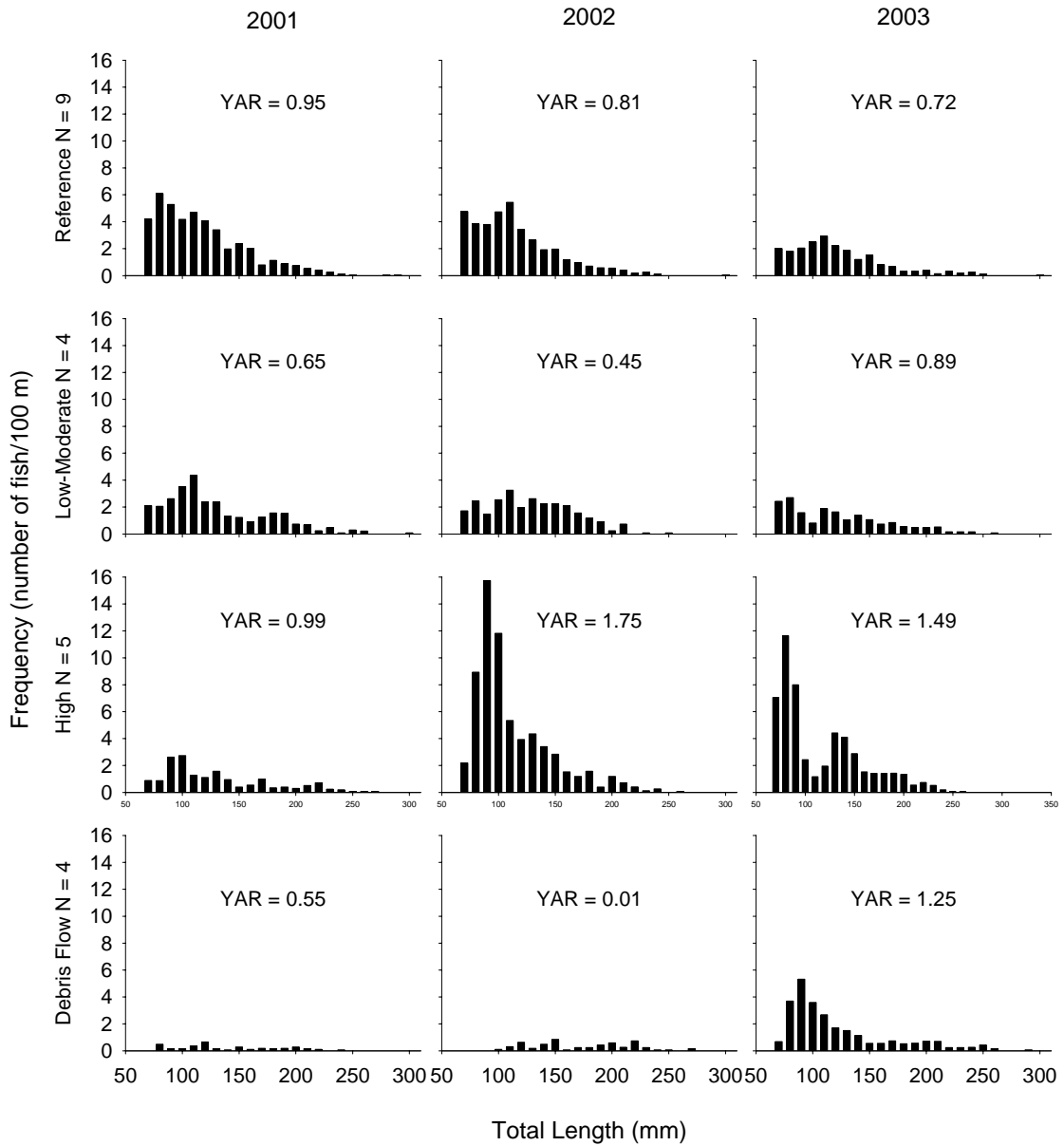


Figure 3. Combined length-frequency distribution and young:adult ratio (YAR) of cutthroat trout populations in 2001, 2002, and 2003 among reference, low-moderate-severity, high-severity, and debris flow reaches.

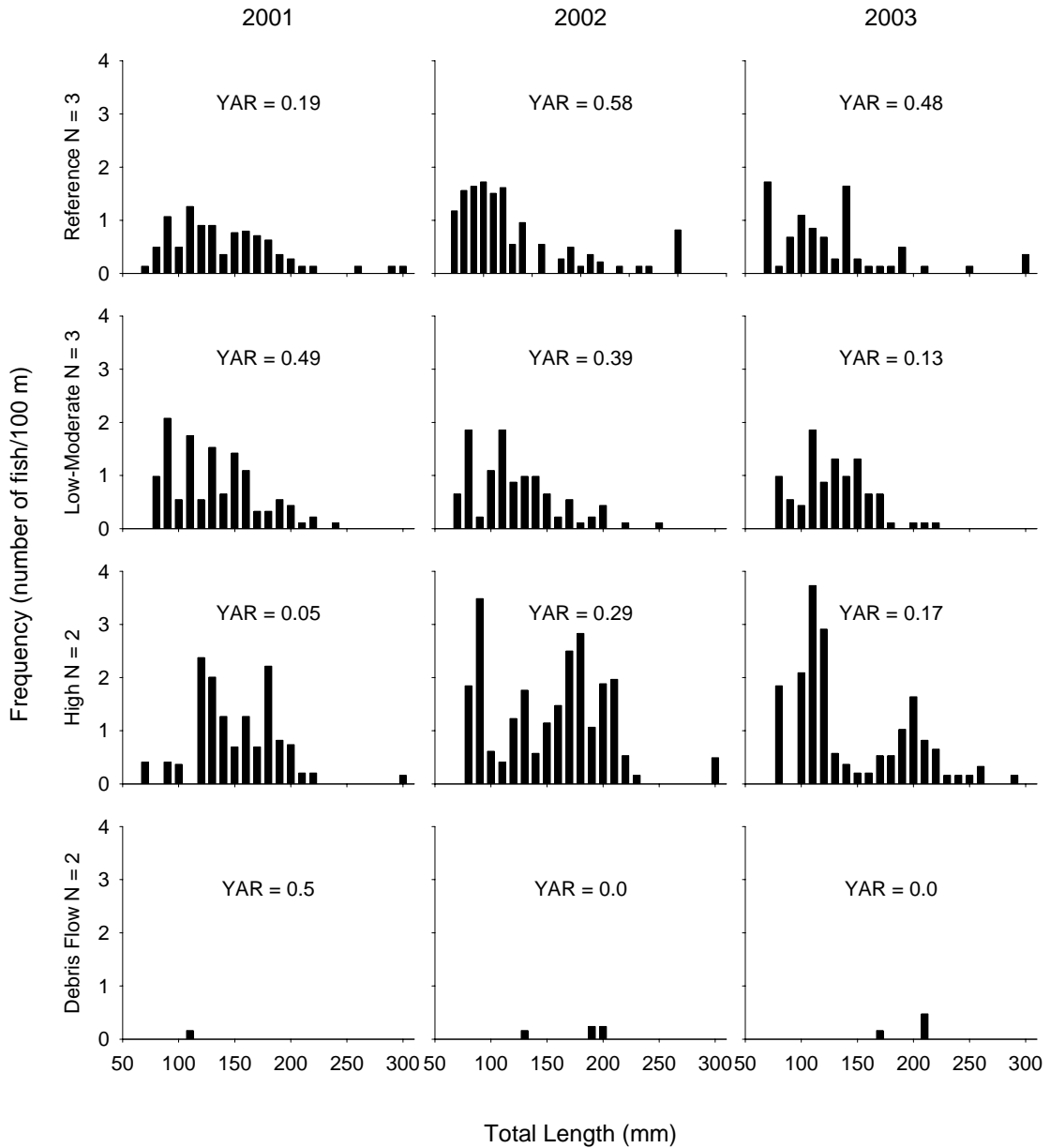


Figure 4. Combined length-frequency distribution and young:adult ratio (YAR) of bull trout populations in 2001, 2002, and 2003 among reference, low-moderate-severity, high-severity, and debris flow reaches.

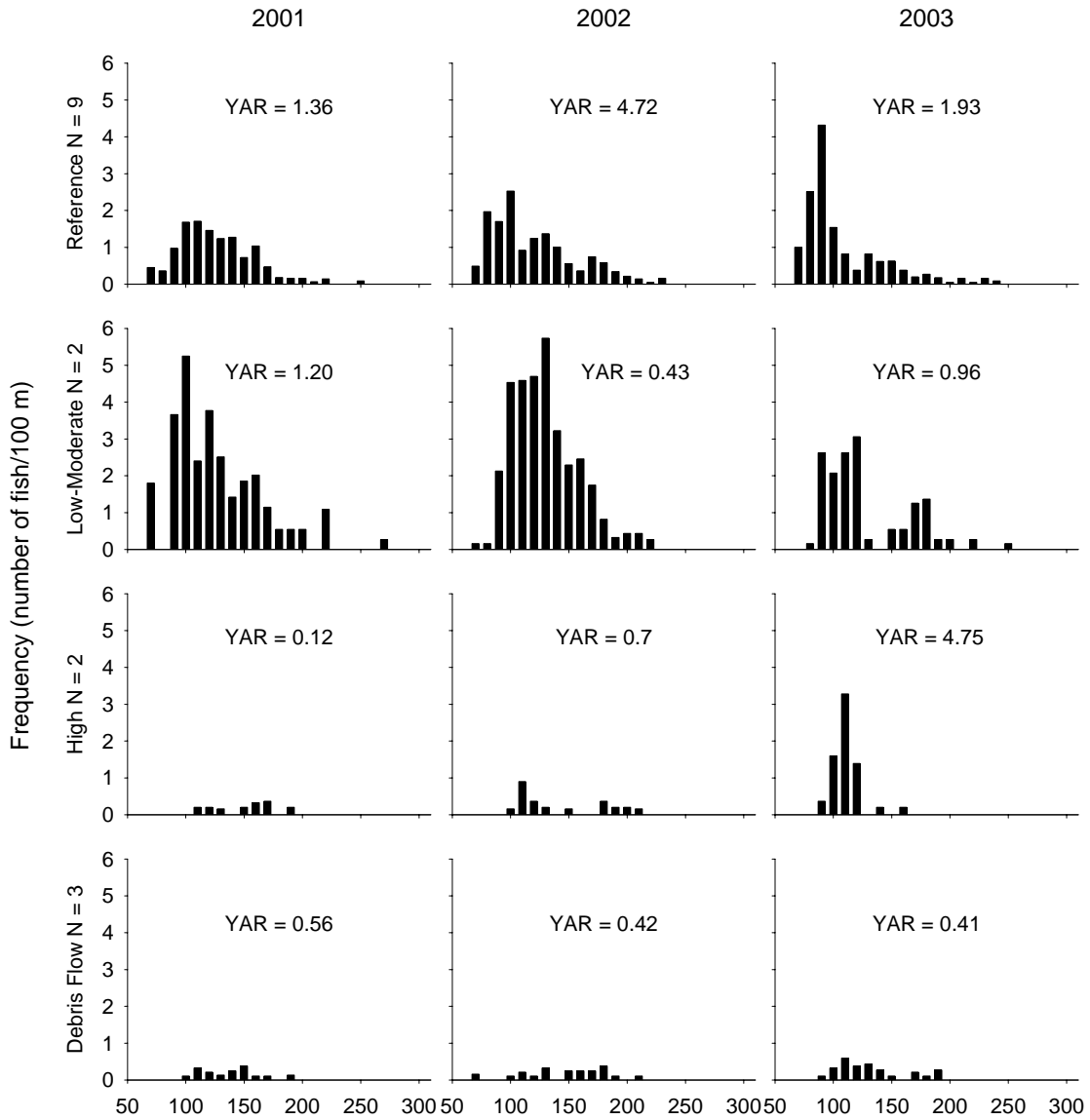


Figure 5. Combined length-frequency distribution and young:adult ratio (YAR) of brook trout populations in 2001, 2002, and 2003 among reference, low-moderate-severity, high-severity, and debris flow reaches.

recruitment. Cutthroat trout showed some evidence of juvenile recruitment by 2003 in debris flow reaches, but brook trout abundance and recruitment remained quite depressed compared to reference and other fire-affected reaches.

Invasion by nonnative species occurred at about the same rate in both treatment (4 of 17) and reference study reaches post-fire (3 of 13) (Figure 6). Though generally only rarely sampled in study reaches, brown trout accounted for 5 of 7 of all apparent nonnative fish invasions (≤ 2 fish per site), including 2 reference reaches and 3 treatment reaches. No incidences of brook trout invasion post-fire were observed in the four reference reaches and only one incidence of invasion among treatment reaches (1 of 7) (one 216-mm fish in the moderate-severity Sleeping Child Creek 23.3 reach in 2003). Rainbow trout were not detected in any treatment reaches where absent pre-fire, but did invade 1 of 11 reference reaches (14 fish in Tolan Creek 3.4 reach from 2001 to 2003). In addition, a bull trout was captured in an unburned reference reach post-fire (Mine Creek 0.3). Cutthroat trout were present in all reaches pre- and post-fire.

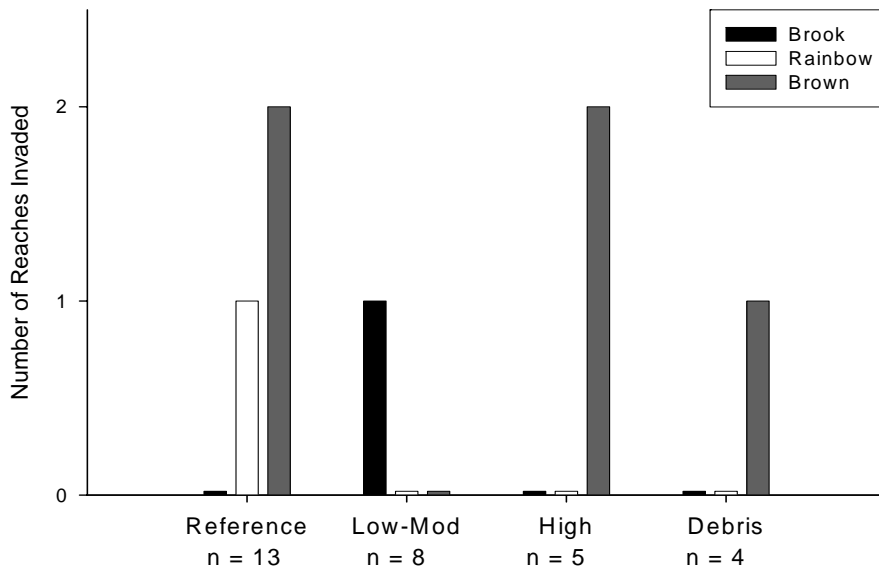


Figure 6. Summary of invasion occurrences by species among reference and burned study reaches. n = the total number of reaches examined in each category.

Distance to source populations did not appear to influence invasion. Distances to source populations of potential invading trout species were similar for uninvaded and invaded reaches (6.4 ± 0.89 vs. 5.0 ± 1.3 km, $P = 0.79$) and for treatment and reference stream reaches (6.7 ± 0.9 vs. 5.5 ± 1.1 km, $P = 0.43$). However, among invaded reaches affected by wildfire, the distance to source populations was about twice that of invaded reference reaches, although the difference was not statistically significant (6.3 ± 2.1 vs. 3.8 ± 1.6 km, $P = 0.19$).

Habitat

Abundance of LWD was not significantly different among study reaches ($P = 0.08$; Table 8). However, the average amount of LWD in debris flow reaches was less than half of that in reference and low-moderate-severity reaches. High-severity reaches had the highest densities of LWD of all treatments and were on average about 25% higher than reference and low-moderate-severity reaches and 214% higher than debris flow reaches.

Substrate composition and diversity were statistically similar ($P > 0.05$) among all treatments, however there were some notable differences in particle size distribution among them. High-severity reaches had both the greatest percentage of surface fines collected at pool tail-outs (36%) and proportion of fines < 2 mm measured from pebble counts (34%). In contrast, debris flow reaches had relatively small amounts of fine sediment with the lowest percent surface fines (29%). Debris flow reaches also had the greatest percentage of cobble-sized particles of all treatments (37%) and the highest

substrate diversity (67%). In contrast, reference reaches had the lowest substrate diversity of all treatments (58%).

Percent pool habitat and pool-forming features were generally similar among treatments ($P > 0.05$; Table 8). Percent pool habitat varied slightly from 15% in debris flow reaches to 22% in reference reaches with the primary pool-forming feature in all treatments being LWD. However, debris flow reaches tended to have a higher proportion of boulder-formed pools with the percentage of pools formed by large wood (32%) being lower than that of reference (57%), low-moderate-severity (55%), and high-severity (68%) reaches ($P = 0.22$). Although not significantly different, reference reaches tended to have a higher percentage (10%) of bank-formed pools than did low-moderate-severity (2%), high-severity (0%), and debris flow reaches (5%) ($P = 0.30$).

Habitat complexity was similar among reference and treatment reaches ranging from a value of 34 in debris flow reaches to 39 in reference reaches ($P = 0.11$; Table 8). Although debris flow reaches had the fewest pools and least LWD of all treatments, substrate diversity was relatively high (67%) and percent surface fines low (29%), which contributed to the overall similarity in habitat complexity among treatments.

Concentrations of ammonium, orthophosphate, and nitrate determined from water samples collected in June 2002, two years after the fire, were low overall. Ammonium and orthophosphate concentrations were below the lower detectable range of the analytical equipment (0.05 mg /L) except for one high-severity study reach with 0.15 mg /L ammonium. Although nitrate levels in treatment reaches (0.06 mg /L) were 3 times higher than in reference reaches (0.02 mg /L), there were no significant differences

Table 8. Results of analyses comparing habitat metrics measured post-fire (mean \pm SE, with number of reaches in parentheses) among reference, low-moderate-severity, high-severity, and debris flow reaches (ANOVA). Percent values are arcsine square-root transformed.

Habitat Metric	<i>P</i>	Reference	Low-Moderate	High	Debris Flow
Number LWD/100 m	0.082	50.9 \pm 7.8 (8)	51.1 \pm 11.4 (4)	63.9 \pm 9.4 (4)	20.3 \pm 6.6 (3)
% Surface Fines	0.810	29.4 \pm 4.2 (9)	30.9 \pm 6.4 (5)	36.0 \pm 6.5 (5)	28.8 \pm 2.3 (3)
% Fines	0.114	24.6 \pm 3.2 (9)	21.1 \pm 4.0 (5)	33.5 \pm 2.6 (5)	23.3 \pm 2.3 (4)
% Gravel	0.533	45.6 \pm 2.8 (9)	40.2 \pm 5.4 (5)	45.7 \pm 3.1 (5)	39.9 \pm 3.2 (4)
% Cobble	0.259	30.9 \pm 3.3 (9)	32.0 \pm 6.7 (5)	23.1 \pm 2.1 (5)	36.6 \pm 2.9 (4)
%Boulder	0.063	6.1 \pm 2.4 (9)	18.5 \pm 5.0 (5)	7.1 \pm 2.4 (5)	13.3 \pm 4.5 (4)
Substrate Diversity	0.294	58.0 \pm 2.2 (9)	64.1 \pm 5.6 (5)	60.3 \pm 2.8 (5)	66.9 \pm 3.4 (4)
% Pool Habitat	0.755	26.2 \pm 4.4 (9)	26.5 \pm 3.5 (5)	24.8 \pm 3.5 (5)	19.0 \pm 7.9 (4)
Sum Resid. Pool Vol.	0.472	36.3 \pm 14.6 (9)	19.5 \pm 2.3 (5)	13.6 \pm 3.2 (5)	16.2 \pm 7.3 (4)
Number Pools/100 m	0.842	2.8 \pm 0.5 (9)	3.7 \pm 1.1 (5)	3.4 \pm 0.8 (5)	3.1 \pm 1.1 (3)
% Pools Boulder-formed	0.893	13.9 \pm 7.4 (9)	22.2 \pm 14.6 (5)	22.4 \pm 6.8 (5)	20.9 \pm 12.3 (4)
% Pools Bank Formed	0.301	12.1 \pm 5.0 (9)	3.5 \pm 3.5 (5)	0 \pm 0 (5)	6.9 \pm 6.9 (4)
% Pools LWD Formed	0.219	50.6 \pm 6.6 (9)	47.3 \pm 7.8 (5)	59.7 \pm 9.8 (5)	29.8 \pm 12.4 (4)
% Pools MDR Formed	0.779	5.0 \pm 4.7 (9)	12.3 \pm 6.2 (5)	4.4 \pm 6.2 (5)	5.6 \pm 7.0 (4)
% Pools STR Formed	0.913	9.0 \pm 4.8 (9)	6.0 \pm 6.5 (5)	10.6 \pm 6.5 (5)	12.7 \pm 7.3 (4)
% Pools TRANS Formed	0.999	3.9 \pm 3.2 (9)	3.5 \pm 4.4 (5)	3.7 \pm 4.4 (5)	3.9 \pm 4.9 (4)
% Pools BVRDM Formed	0.699	2.7 \pm 1.7 (9)	0 \pm 2.3 (5)	0 \pm 2.3 (5)	0 \pm 2.6 (4)
Habitat Complexity	0.106	38.8 \pm 1.2 (8)	36.2 \pm 1.1 (4)	35.3 \pm 1.0 (4)	34.2 \pm 2.1 (3)
Nitrate (mg/L)	0.468	0.02 \pm 0.003 (7)	0.07 \pm 0.05 (4)	0.05 \pm 0.02 (4)	0.05 \pm 0.03 (3)
Conductivity (umhos)	0.820	0.04 \pm 0.005 (6)	0.06 \pm 0.02 (3)	0.04 \pm 0.03 (3)	0.04 \pm 0.02 (4)

among reference, low-moderate-severity, high-severity, and debris flow reaches ($P = 0.47$; Table 8). Conductivity was similar for all treatments ($P = 0.82$; Table 8).

Although stream temperature increased in both reference and treatment reaches during the post-fire period, temperature increases in treatment reaches were substantially higher than increases in reference reaches. Daily minimum temperature increased significantly in high-severity reaches by 2.2 °C from pre- to post-fire in comparison to reference reaches, which increased by only 0.6 °C (Table 9; Figure 7). In addition, daily maximum temperature in all burned reaches increased from 10.5 °C pre-fire to 13.6 °C post-fire (3.1 °C increase) in comparison to reference reaches, which increased from 11.1 °C to 11.6 °C (0.5 °C increase) ($P < 0.001$). Post-fire daily maximum temperature reached 23 °C in a debris flow-affected reach of North Rye Creek on July 24, 2002. Similarly, the pre- to post-fire increase in MWMT was significantly greater for high-severity (6.6 °C) and debris flow (4.4 °C) reaches than for reference reaches (1.0 °C) ($P < 0.001$). Furthermore, daily mean temperature in low-moderate-severity and high-severity reaches increased significantly ($P < 0.001$) post-fire by 1.8 °C and 3.5 °C respectively, relative to reference reaches which increased by only 0.6 °C. The pre- to post-fire change in degree-days followed a similar pattern, increasing by 262 degree-days in high-severity reaches compared to 47 degree-days in reference reaches ($P < 0.001$).

Stream temperature also increased with increasing burn severity. Average daily minimum temperature increased from 7.2 °C to 8.6 °C in low-moderate-severity reaches and from 7.5 °C to 9.7 °C in high-severity reaches. The pre- to post-fire increases in average maximum temperature, mean temperature, MWMT, and degree-days were also

significantly greater for high-severity reaches than for low-moderate-severity reaches ($P < 0.001 - 0.01$; Table 9; Figure 7). For example, MWMT in high-severity reaches increased from 12 °C pre-fire to 18.5 °C post-fire whereas MWMT in low-moderate-severity reaches increased from 12.5 °C to 15.1 °C. Maximum weekly maximum temperature was positively correlated to the proportion of burned area within a watershed ($r^2 = 0.25$; $P = 0.01$).

The diel temperature range increased substantially in the post-fire period in reaches affected by wildfire relative to reference reaches. The mean diel temperature range increased significantly ($P < 0.02$) in treatment reaches during the post-fire period relative to reference reaches, which decreased by 0.1 °C on average (Table 9; Figure 7). Pre- to post-fire diel temperature range also increased with increasing burn severity with daily temperature fluctuation in high-severity reaches 2.2 °C greater than in low-moderate-severity reaches ($P < 0.02$). Post-fire increase in diel temperature range in debris flow reaches (2.3 °C) also exceeded increases in reference and low-moderate-severity reaches. These differences in diel temperature fluctuation were largely due to substantial increases in daily maximum water temperature relative to increases of lower magnitude in daily minimum temperature (Figure 7).

Table 9. Comparison of water temperature metrics (mean \pm SE) among reference, low-moderate-severity, high-severity, and debris flow reaches (ANOVA). Within a column, post minus pre temperature values without a letter in common are significantly different ($P < 0.05$; Tukey-Kramer multiple-comparison test).

		Degree-days	MWMT	Avg. Min	Avg. Max	Avg. Mean	Avg. Max-Min
Reference ($n = 9$)	Pre	685.7 \pm 25.4	13.6 \pm 0.6	7.4 \pm 0.3	11.1 \pm 0.4	9.2 \pm 0.4	3.7 \pm 0.3
	Post	732.3 \pm 21.2	14.6 \pm 0.5	8.0 \pm 0.3	11.6 \pm 0.3	9.8 \pm 0.2	3.6 \pm 0.4
	Post-Pre	46.6 \pm 9.6 a	1.0 \pm 0.3 a	0.6 \pm 0.1 a	0.5 \pm 0.2 a	0.6 \pm 0.2 a	-0.1 \pm 0.2 a
Low-Moderate ($n = 5$)	Pre	632.5 \pm 48.9	12.5 \pm 1.0	7.2 \pm 0.6	10.1 \pm 0.8	8.6 \pm 0.6	2.8 \pm 0.2
	Post	760.9 \pm 43.1	15.1 \pm 0.8	8.6 \pm 0.5	12.3 \pm 0.7	10.3 \pm 0.6	3.6 \pm 0.3
	Post-Pre	128.4 \pm 33.3 ab	2.6 \pm 0.6 ab	1.4 \pm 0.4 ab	2.2 \pm 0.5 b	1.8 \pm 0.4 b	0.8 \pm 0.2 ab
High ($n = 2$)	Pre	643.5 \pm 27.5	12.0 \pm 1.3	7.5 \pm 0.5	9.9 \pm 1.0	8.7 \pm 0.4	2.4 \pm 0.6
	Post	905.5 \pm 32.2	18.5 \pm 0.1	9.7 \pm 0.5	15.2 \pm 0.3	12.2 \pm 0.4	5.4 \pm 0.2
	Post-Pre	262.0 \pm 59.7 c	6.6 \pm 1.2 c	2.2 \pm 0.6 b	5.3 \pm 1.0 c	3.5 \pm 0.8 c	3.0 \pm 0.4 c
Debris Flow ($n = 2$)	Pre	781.8 \pm 0.8	14.8 \pm 0.3	9.2 \pm 0.2	12 \pm 0.4	10.6 \pm 1.1	2.9 \pm 0.6
	Post	909.2 \pm 13.8	19.2 \pm 2.5	10 \pm 0.8	15.1 \pm 1.8	12.3 \pm 0.2	5.1 \pm 2.5
	Post-Pre	127.4 \pm 13.1 abc	4.4 \pm 2.2 bc	0.8 \pm 0.6 ab	3.1 \pm 1.4 bc	1.7 \pm 0.2 abc	2.3 \pm 1.9 bc
Post-Pre P -value		< 0.00	< 0.00	0.01	< 0.00	< 0.00	< 0.00

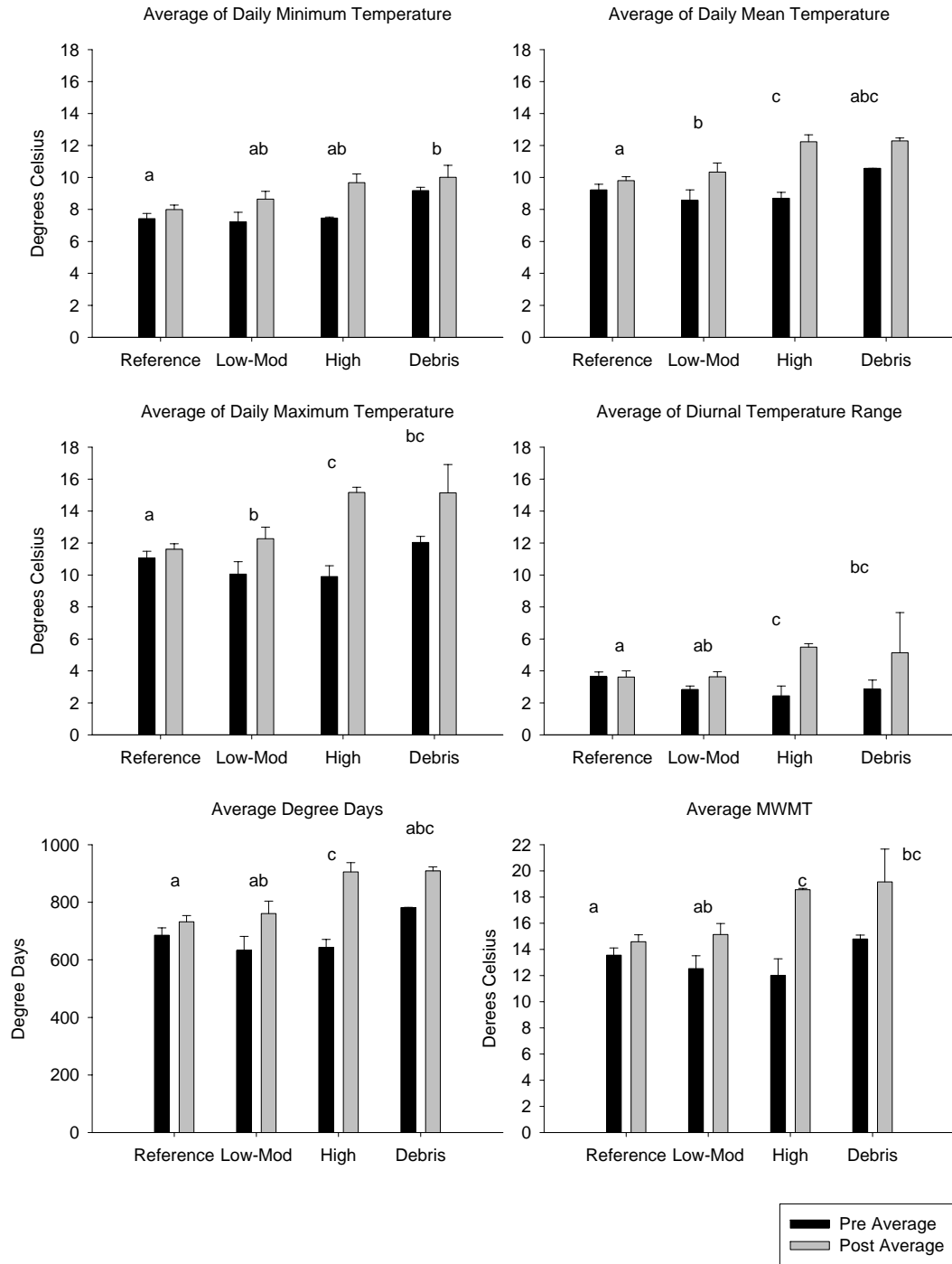


Figure 7. Average pre- and post-fire daily minimum, mean, maximum, diel temperature range, degree-days, and MWMT (+ 1 SE) among reference, low-moderate-severity, high-severity, and debris flows reaches. Dissimilar letters indicate significant differences in pre- to post-fire change among treatments (P < 0.05; Tukey-Kramer multiple-comparison procedure).

Influence of Habitat on Brook Trout Abundance

The best approximating model for predicting abundance of brook trout was a combined reach-scale and basin-scale model that included gradient and elevation ($R^2 = 0.67$). However, ten other models, three containing reach-scale habitat variables (gradient, degree-days, and pool frequency), three containing only basin-scale variables (proportion of basin burned, elevation, and watershed area), and four containing reach- and basin-scale variables (gradient, elevation, kilometers of roads, watershed area, and pool frequency) had ΔAIC_c scores ≤ 2 and could not be discounted (Table 10). The most parsimonious reach-scale model included only stream gradient while the best approximating basin-scale model included only proportion of a basin burned upstream of a study reach.

Three variables accounted for most of the variation in the best approximating reach-scale, basin-scale, and combined reach- and basin-scale models. Stream gradient, which was negatively associated with brook trout abundance, was the most important reach-scale predictor explaining 47% of the variation in brook trout abundance ($P < 0.00$; Table 11). In the best two approximating basin-scale models, proportion of a basin burned, negatively associated with brook trout abundance, explained 10.8 – 16.5% of the variation in brook trout abundance. In the best approximating combined reach- and basin-scale model, gradient and elevation, both negatively associated with brook trout abundance explained 52% and 11% of the variation in brook trout abundance, respectively. Of lesser importance, linear kilometers of roads, positively correlated with

brook trout abundance, explained 1% of the variation in brook trout abundance in the second best approximating reach- and basin-scale combined model.

The post-fire brook trout invasion that occurred in the Rye Creek 20.0 reach may be explained by habitat characteristics. First, degree-days, pool frequency, and linear km of roads within 100 m of the stream channel were higher in Rye Creek than the majority of study reaches. For example, degree-days in Rye Creek were higher than 74% of all study reaches, pool frequency exceeded that of 77% of all other study reaches, and linear kilometers of roads within 100 m of the stream channel were higher than 63% of all study reaches. Stream gradient was also relatively low in Rye Creek, being lower than 57% of all reaches.

Delayed brook trout recovery in debris flow reaches may also be explained by post-disturbance habitat characteristics. Although debris flow reaches were located at elevations lower than all but one study reach, percent stream gradient was relatively high (3.4 – 4.6%). Furthermore, debris flow reaches also had the lowest percent pool habitat (19%) of all treatments; a variable positively associated with brook trout abundance and that accounted for 12.6% of the variation in the third highest ranking reach and reach- and basin-scale models.

Table 10. Results of multiple linear regression models to predict $\log_{10}(x + 1)$ brook trout abundance/100 m in Bitterroot tributary streams at the reach-scale, basin-scale, and both scales combined; K = number of model parameters, R^2 = coefficient of multiple determination, AIC_c = Akaike's Information Criterion corrected for small sample size, ΔAIC_c = Akaike's Information Criterion differences, and w = Akaike weights.

Model	K	R^2	AIC_c	ΔAIC_c	w
A) Reach-scale habitat ($n = 23$ observations)					
Gradient	2	0.58	-26.74	0.00	0.24
Gradient, degree-days	3	0.62	-26.13	0.61	0.18
Gradient, pool frequency	3	0.60	-25.30	1.44	0.12
Gradient, LWD, degree-days	4	0.65	-24.45	2.29	0.08
Gradient, LWD	3	0.58	-24.30	2.44	0.07
Gradient, surface fines	3	0.58	-24.26	2.48	0.07
Gradient, surface fines, degree-days	4	0.63	-23.76	2.98	0.05
Gradient, degree-days, pool frequency	4	0.63	-23.44	3.30	0.05
Gradient, surface fines, pool frequency	4	0.62	-22.93	3.81	0.04
B) Basin-scale habitat ($n = 23$ observations)					
Proportion basin burned	2	0.11	-19.37	0.00	0.24
Elevation, proportion basin burned	3	0.18	-18.67	0.70	0.17
Watershed area	2	0.04	-17.59	1.78	0.10
Km roads	2	0.02	-17.30	2.07	0.08
Elevation	3	0.13	-17.20	2.17	0.08
Watershed area, proportion basin burned	2	0.02	-17.18	2.19	0.08
Proportion basin burned, km roads	3	0.11	-16.84	2.53	0.07
Elevation, watershed area, proportion basin burned	4	0.18	-15.78	3.59	0.04
Elevation, proportion basin burned, km roads	4	0.18	-15.74	3.63	0.04
C) Reach- and basin-scale habitat ($n = 23$ observations)					
Gradient, elevation	3	0.67	-28.35	0.00	0.09
Gradient, elevation, km roads	4	0.71	-28.00	0.35	0.07
Gradient	2	0.58	-26.74	1.61	0.04
Gradient, elevation, watershed area	4	0.69	-26.55	1.80	0.04
Gradient, elevation, pool frequency	4	0.68	-26.35	2.00	0.03
Gradient, degree-days	3	0.62	-26.13	2.22	0.03
Gradient, elevation, km roads, LWD	5	0.73	-25.77	2.58	0.02
Gradient, elevation, degree-days	4	0.67	-25.76	2.59	0.02
Gradient, elevation, km roads, pool frequency	5	0.73	-25.67	2.68	0.02
Gradient, elevation, LWD	4	0.67	-25.65	2.70	0.02
Gradient, elevation, proportion basin burned	4	0.67	-25.55	2.80	0.02
Gradient, elevation, proportion basin burned, km roads	5	0.72	-25.53	2.82	0.02
Gradient, elevation, surface fines	4	0.67	-25.46	2.89	0.02
Gradient, pool frequency	3	0.60	-25.30	3.05	0.02
Gradient, elevation, km roads, degree-days	5	0.71	-24.96	3.39	0.02
Gradient, km roads	3	0.59	-24.90	3.45	0.02
Gradient, elevation, watershed area, km roads	5	0.71	-24.86	3.49	0.02

Table 11. Results of multiple linear regression that assessed the relationship between brook trout abundance and reach- and basin-scale habitat variables showing parameter estimates, standard error = SE, coefficients of partial determination = r^2 , and significance of variables = P .

Scale	Model	Variable	Parameter Estimate	SE	r^2	P	
Reach	1	Intercept	2.903	0.570		0.000	
		Gradient	-0.243	0.059	0.469	0.006	
	2	Intercept	1.863	0.967		0.071	
		Gradient	-0.262	0.054	0.584	0.001	
		Degree-days	0.001	0.001	0.119	0.149	
	3	Intercept	2.564	0.675		0.001	
		Gradient	-0.248	0.063	0.477	0.001	
		Pool Frequency	0.103	0.067	0.122	0.143	
	Basin	1	Intercept	0.919	0.261		0.002
Proportion basin burned			-0.008	0.005	0.108	0.126	
2		Intercept	2.944	1.539		0.070	
		Elevation	-0.001	0.000	0.082	0.197	
		Proportion basin burned	-0.010	0.005	0.165	0.060	
3		Intercept	0.097	0.537		0.859	
		Watershed area	0.087	0.098	0.036	0.386	
Reach/Basin		1	Intercept	4.879	1.452		0.004
			Gradient	-0.267	0.060	0.525	0.000
	Elevation		-0.001	0.001	0.107	0.158	
	2	Intercept	5.152	1.592		0.005	
		Gradient	-0.272	0.062	0.529	0.000	
		Elevation	-0.001	0.000	0.118	0.150	
		Km roads	-0.028	0.059	0.013	0.642	
	3	Intercept	2.903	0.570		0.000	
		Gradient	-0.243	0.059	0.469	0.006	

DISCUSSION

Stochastic events such as wildfire or flooding and pervasive threats from competition and hybridization with nonnatives are among the greatest extinction risks to isolated or impaired native salmonid populations in the western U.S. (Brown et al. 2001; Dunham et al. 2003; Rieman et al. 2003). Because evidence suggests that these processes may not operate independently, the continuing trend of frequent, high-severity wildfire on the landscape may leave remaining native salmonid populations at an increased extinction risk from nonnative fish invasions (Dunham et al. 2003). To test this hypothesis, I utilized a unique data set composed of both pre- and post-disturbance and control and impact population data across a large drainage basin to determine if wildfire facilitates invasion of nonnative fish and increases risk of local extirpation.

Fish Assemblage Changes

My results indicate that wildfire disturbance does have the potential to facilitate changes in mixed native and nonnative fish assemblages. However, the direction of these changes was, for the most part, opposite of that predicted. In 2003, three years post-fire, the proportion of brook trout to cutthroat and bull trout remained below the pre-fire mean in five of seven fire-affected reaches. Cutthroat and bull trout populations recovered rapidly with mean abundance exceeding the pre-fire mean in 5 of 10 and 5 of 7 affected reaches. In contrast, brook trout exhibited delayed recovery with mean abundance in five of six fire-affected reaches remaining below the pre-fire mean in 2003.

The exception to this pattern was the large increase in brook trout that occurred in the high burn severity reach in Rye Creek. By 2003, three years post-fire, brook trout

abundance increased by 499%, from less than 1% of a mixed cutthroat, bull, and brook trout assemblage to 16% of a cutthroat/brook trout assemblage, with bull trout now absent. In contrast, brook trout abundance declined by 67% from the pre-fire mean in the other high-severity reach (Reimel Creek 4.2). Given the high variation in brook trout population response in these two streams, there was no strong evidence to support my hypothesis of high-severity wildfire promoting increased brook trout abundance at least in the first few years following wildfire disturbance.

Changes in fish assemblages were most prominent in reaches influenced by fire-induced debris flows. The proportion of brook trout to cutthroat and bull trout in debris flow reaches declined relative to reference reaches and burned reaches without debris flows in 2002. This was likely because of the difference in the ability of cutthroat and brook trout populations to undergo short-term recovery. By 2003, two years after the initial fire-induced debris flows, cutthroat trout abundance had increased markedly from 92% below to 35% below the mean pre-fire abundance and bull trout abundance equaled the pre-fire mean. In contrast, brook trout showed no sign of recovery, decreasing in proportion to native fish each subsequent year following the debris flow event and remaining 87% below the pre-fire mean in 2003.

Length-frequency data suggest that the limited recovery of brook trout and decreased proportion in debris flow reaches was a result of poor recruitment relative to that of cutthroat trout. Brook trout YAR in debris flow reaches was lower than in reference reaches and burned reaches without debris flows, and declined each year after the debris flow event. In comparison, abundant age-0 (25-35 mm TL) cutthroat trout

were observed in Laird Creek just one year after the debris flow with overall cutthroat trout YAR in debris flow reaches peaking in 2003, and exceeding YAR in reference reaches and burned reaches without debris flows.

These results are novel because previous studies following debris flows examined recovery of cutthroat or brook trout in allopatry rather than as mixed assemblages. Lamberti et al. (1991) found that cutthroat trout populations in Quartz Creek, Oregon, though decimated by a debris flow in 1986, recovered to predisturbance densities by 1987 and exceeded densities in an upstream reference reach. Similar to my findings, rapid recovery of cutthroat trout in Quartz Creek was attributed to elevated recruitment as fry densities (200/100 m) were four times higher than in an upstream reference reach. Similarly, a brook trout population that was eliminated from the lower 1.9 km of the Staunton River, Virginia, by a massive debris flow recovered to predisturbance levels in three years (Roghair et al. 2002). Again, this rapid recovery was associated with increased post-debris flow recruitment as demonstrated by age-0 brook trout density exceeding pre-debris flow levels in one year. Rapid recovery of a brook trout population following a wildfire-induced debris flow was also observed in Bonita Creek, Arizona (Rinne 1996). In contrast to Roghair et al. (2002) and Rinne (1996), I found large declines in all brook trout populations in streams experiencing debris flows and little recovery for the first three years post-disturbance.

Population recovery in debris flow reaches, though relatively fast for native species, was slower than in burned reaches unaffected by debris flows. By 2002, two years post-fire, mean cutthroat, bull, and brook trout abundance approached or surpassed

mean pre-fire levels in burned reaches without debris flows, whereas cutthroat trout and brook trout populations in debris flow reaches were substantially below pre-fire means (35% and 87%, respectively) two years post-debris flow (2003). With the exception of Laird Creek, channel instability in debris flow reaches continued through 2002 with additional mudslides in North Rye Creek filling pools with fine sediment, inundating spawning and rearing habitat, and likely suppressing recruitment and delaying population recovery.

The overall rapid recovery of fish populations was not unexpected given the results of other wildfire studies (Novak 1989; Rieman et al. 1997) showing rapid recovery in stream reaches that had connection to nearby unaffected source populations. In my study, all 17 fire-affected study reaches maintained at least a seasonal high water connection to nearby source populations. However, because of this connectivity I also expected more incidences of brook trout invasion in reaches that they did not occupy prior to the disturbance. I found brook trout invaded only one of seven fire-affected reaches where the species was not detected in pre-fire sampling. This invasion occurrence consisted of one 216-mm brook trout captured in the moderate-severity Sleeping Child Creek 23.3 reach approximately 6.9 km upstream from the closest known source population. The distance of this movement was consistent with brook trout observations in previous studies commonly exhibiting “jump dispersal” over similar distances (Shetter 1968; Gowan and Fausch 1996; Adams et al. 2001; Peterson and Fausch 2002).

Surprisingly, brown trout were the primary invading species comprising 5 of 7 of all apparent invasion occurrences (2 in reference reaches and 3 in affected reaches). However, the number of invaders was low, with no more than two fish captured per reach in a given year. Of these, one instance of invasion consisted of an adult brown trout captured in the high-severity Meadow Creek reach located 11.8 km upstream from the confluence with the East Fork Bitterroot River. Because a single juvenile brown trout was captured in each of two reference reaches and two fire-affected reaches relatively close to the East Fork source population (1.1 – 4.2 km), juvenile brown trout may undergo movements into suitable rearing habitat in the lower reaches of tributary streams regardless of fire effects. An alternative hypothesis is that if brown trout spawning in tributary streams does occur, a majority of offspring out migrate to the East Fork at age-0, leaving few individuals rearing in tributaries.

Because invaded reaches were not significantly closer to source populations (5.0 km \pm 1.3 km) than uninvaded reaches (6.4 km \pm 0.89) it did not appear that the distance to a source population influenced the likelihood of invasion. However, because the mean distance to source populations of invaded burned reaches was nearly twice that of invaded reference reaches, post-fire conditions in burned streams may have facilitated upstream movements over longer distances than in reference streams. This could occur if water temperature was limiting distribution of nonnatives and temperature increases in burned streams increased the linear distance of suitable habitat beyond that of reference reaches. Because species boundaries used to calculate distance to source populations were determined from discrete locations (previously sampled reach or closest known

tributary) rather from continuous presence/absence sampling, it is also possible that observed patterns in distance to source data were overestimated.

Although I did not sample source populations in this study, supplemental data provided by MFWP suggests that changes in fish assemblages and rate of population recovery may be directly related to relative abundance of the nearest source population. For example, Laird Creek, a debris flow-affected tributary to the East Fork Bitterroot River, experienced marked recruitment and recovery of cutthroat trout relative to brook trout. This may be a result of the cutthroat trout source population being larger than the brook trout source population in the East Fork. For example, MFWP population data for monitoring reaches upstream and downstream from the mouth of Laird Creek indicated that brook trout were uncommon in the East Fork and on average comprised only 0.3% of the fish assemblage relative to cutthroat trout (9%)(Table 12). Similarly, in another debris flow reach (Chicken Creek, a site excluded from BACI analyses for lack of pre-fire data), brook trout increased only slightly from 4 fish/100 m in 2001 to 8 fish/100 m in 2003 relative to cutthroat trout which increased from 4 fish/100 m in 2001 to 102 fish/100 m in 2003 (Appendix B, Table 2). This disparity in recovery mirrored the fish assemblage structure of the nearest source population, the West Fork Bitterroot River, where brook and cutthroat trout composed 18% and 78% of the fish assemblage, respectively. This pattern was also observed in the Rye Creek study reach, which experienced a substantial post-fire increase in brook trout abundance. Fish population data collected in Rye Creek, 9.4 km downstream from the invaded reach during 2001 (Table 12), indicate the presence of a relatively strong downstream brook trout source

population (23/100 m). In addition, the abundance of brown trout in the East Fork (50% of the salmonid assemblage in the lower reaches of the East Fork and 18% in the middle reaches) may be related to the five apparent brown trout invasions in East Fork tributary streams.

Table 12. Salmonid relative abundance data (MFWP, Hamilton, MT, data files) and percent composition (in parentheses) for source populations in the East and West Forks of the Bitterroot River and Rye Creek. “River km” indicates the distance in kilometers of each sampling location from the stream mouth.

Stream	River (km)	Year	Cutthroat	Bull	Brook	Brown	Rainbow
East Fork Bitterroot River							
	A (4.0)	2003	31 (13%)	2 (1%)	0 (0%)	100 (43%)	97 (42%)
		2004	24 (10%)	1 (0%)	0 (0%)	135 (56%)	83 (34%)
		Mean	28 (12%)	2 (1%)	0 (0%)	118 (50%)	90 (38%)
	B (19.3)	2003	13(5%)	1(0%)	2(0.8%)	49(18%)	200 (75%)
		2004	25(9%)	2(1%)	1(0.4%)	50(18%)	203 (72%)
		Mean	19 (7%)	2 (1%)	2 (0.6%)	50 (18%)	202 (74%)
West Fork Bitterroot River							
	A (54.7)	1998	97 (78%)	7 (6%)	21(17%)	0 (0%)	0 (0%)
		1999	88 (79%)	2 (2%)	21(19%)	0 (0%)	0 (0%)
		Mean	93 (78%)	5 (4%)	21 (18%)	0 (0%)	0 (0%)
Rye Creek							
	A (10.6)	2001	187 (72%)	0 (0%)	71(28%)	0 (0%)	0 (0%)
		2003	66 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
		2004	131 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
		Mean	128 (84%)	0 (0%)	24 (16%)	0 (0%)	0 (0%)

Habitat

With the exception of water temperature, no significant differences ($\alpha = 0.05$) in habitat metrics were detected among treatments. This was in part due to low sample size ($n < 23$) and inter-site variability. However, trends among treatments were apparent with sediment levels, stream temperatures, and habitat complexity generally varying with degree of burn severity as hypothesized. Reference reaches tended to have a lower percentage of surface fines, lower water temperatures, and slightly higher habitat

complexity than treatment reaches. Also, percent surface fines and water temperature increased with increasing burn severity whereas mean habitat complexity decreased slightly with increasing burn severity.

Although high-severity reaches were less complex than low-moderate-severity reaches, they had the highest density of LWD of all treatments. This is in part due to a mean increase of 27 pieces (61%) of LWD/100 m from 2001 to 2003 that likely resulted from increased recruitment of burned trees to stream channels due to blowdown (Lyon 1984).

In general habitat parameters in debris flow reaches, though not significantly different from other treatments, varied as hypothesized. Debris flow reaches were the least complex of all treatments because the debris flow events removed a majority of LWD and filled pools with sand, gravel, and cobble. Increased movement of LWD resulting from wildfire and debris flows is well documented (Swanson and Lienkaemper 1978; Young and Bozek 1996; Swanson et al. 1998). As a result, debris flow reaches had less LWD than burned reaches without debris flows, the lowest percent pool habitat of all treatments, and the lowest proportion of pools formed by LWD. Although debris flow reaches had the highest diversity of substrate particle sizes, illustrating the importance of disturbance in maintaining substrate diversity, they also had the lowest surface fines and lowest gravel composition of all treatments, likely a result of low LWD and hence a reduced capacity to retain small substrates (Harmon et al. 1986; Trotter 1990; Faustini and Jones 2003).

Following wildfire, nutrient concentrations in streams may increase temporarily from diffusion of smoke gases and leaching of ash into stream waters followed by a rapid return to background levels within several weeks of the disturbance (Spencer and Hauer 1991). However, nutrient concentrations may periodically increase with spring runoff, remaining elevated for at least five years post-disturbance (Hauer and Spencer 1989). Though I found no significant differences among treatments, average nitrate levels from samples collected during spring runoff 2002 (two years post-fire) in treatment reaches (0.06 mg/L) were about three times higher than in reference reaches (0.02 mg /L). However, with the exception of three burned reaches with nitrate levels ranging from 0.10 mg/L to 0.2 mg/L, values were within the range (< 0.07 mg/L) of those reported for control sites by Hauer and Spencer (1998). Given the limited detectable range for ammonium and orthophosphate concentrations by the analytical equipment, I was unable to detect levels < 0.05 mg/L, which were within the range of increases reported by Hauer and Spencer (1998). In addition, because water sample collection was not replicated temporally, ammonium and orthophosphate concentrations in Bitterroot study streams may have been elevated before or after the time of sampling.

Increased stream temperature was the most significant habitat change following wildfire. Stream temperature increased from pre-fire levels in all treatments, but post-fire increases varied markedly among them. In reference reaches, maximum daily temperature increased by 0.5 °C on average, due to climatic variation, compared to a 2.2 °C increase in low-moderate-severity reaches and 5.3 °C increase in high-severity reaches. Average post-fire MWMT in high-severity reaches was 19.2 °C and was as high

as 20.8 °C in the Reimel Creek 4.2 reach, approaching lethal levels for bull trout and westslope cutthroat trout (Selong et al. 2001; Bear 2005). A study of post-fire temperature change in 20 Yellowstone National Park, U.S.A. streams over five years following the wildfires of 1988, also found that stream water temperatures in burned catchments often exceeded 20 °C (Minshall et al. 1997).

As maximum daily water temperature increased with burn severity following wildfire, so did diel temperature range. On average, diel temperatures in high-severity and debris flow reaches fluctuated by 5.4 °C and 5.1 °C compared to just 3.6 °C in reference and low-moderate-severity reaches. Similarly, Johnson and Jones (2000) found that stream temperatures in a watershed that was clear-cut and burned had similar diel fluctuations (6-8 °C) to a patch-cut watershed with debris flows (5-6 °C) and both watersheds had larger fluctuations than an unharvested reference watershed (1-2 °C).

Observed differences in daily minimum, maximum, and mean temperature and diel temperature fluctuation among reference, low-moderate, high-severity, and debris flow reaches were likely driven by the amount and condition of riparian vegetation and conifer canopy cover regulating the amount of solar radiation reaching stream channels (Albin 1979; Amaranthus 1989; Johnson and Jones 2000). Evidence for the relationship between water temperature and canopy cover is given by the observed positive association ($R^2 = 0.25$) between water temperature (MWMT) and the proportion of a drainage with moderate-to-high-severity burn effects. Although I did not quantify the amount of canopy cover and stream shading at the study sites, all reference reaches had intact riparian vegetation and overstory and likely more stream shading than other

reaches. Low-moderate-severity reaches tended to have riparian vegetation and overstory that were only partially consumed by fire thus having moderate temperature increases while high-severity reaches generally had riparian vegetation and conifer canopies that were mostly consumed and had relatively large temperature increases. Therefore, riparian vegetation and canopy characteristics probably explain some of the variation in stream temperatures among treatments.

In addition to solar inputs, conduction from near-stream alluvial substrates in riparian areas with consumption of riparian vegetation and canopy cover by fire may contribute to stream temperature increases (Johnson and Jones 2000). This is because direct solar radiation may increase the temperature of alluvial substrates that can conduct heat to streams (Hondzo and Stefan 1994; Evans et al. 1995). Johnson and Jones (2000) hypothesized that this phenomenon may be responsible for the increases in minimum stream temperature and would explain the increases in minimum stream temperature that I observed in burned Bitterroot study reaches.

It is uncertain how long stream temperatures in wildfire-affected Bitterroot streams will take to return to background levels. Given that many riparian plant species are well adapted to wildfire disturbance, are capable of rapid reestablishment, and contribute to recovery of streamside habitats (Dwire and Kauffman 2003), it is likely that water temperatures in some affected streams will return to background levels within a few years. However, stream temperatures may remain elevated for decades. Johnson and Jones found that, after 30 years, diel fluctuations in two disturbed watersheds had decreased by 4-6 °C and were identical to a reference watershed. Similarly, Albin (1979)

found no difference in diel temperature fluctuation between a stream in an unburned watershed and a stream in a watershed with burns 36 and 45 years old. However, daily average temperature of the stream in the burned watershed remained 1.3 to 2.2 °C warmer than the unburned watershed.

Pre- and post-fire temperature data from burned treatment and unburned reference reaches provided the unique ability to distinguish stream temperature increases caused by climatic variation from those caused by wildfire disturbance. In a before-after study design lacking controls, trends may often be a result of changes unrelated to the impact itself (Smith 2002). Thus, without reference reaches, I would have mistakenly attributed the entire increase in stream temperature to the disturbance rather than a proportion of increase to climatic variation. Furthermore, a post-fire comparison of stream temperature between reference and treatment reaches would have eliminated the ability to identify the pre- to post-fire increase in water temperature that occurred in both reference and treatment reaches, also preventing the distinction between treatment effects and climatic change. Therefore, when possible, studies of environmental impacts should employ both pre-disturbance data and controls.

Influence of Habitat on Brook Trout Abundance

My modeling results indicated that post-fire brook trout abundance over all reaches was associated with lower stream gradient, lower elevation, warmer stream temperature, greater linear kilometers of road within 100 m of stream channels upstream of each study reach, higher pool frequency, and with basins having a lower percentage of area burned. Other studies have also found channel gradient, elevation, water

temperature, and roads to be similarly related to brook trout abundance in a similar fashion (Chislolm and Hubert 1986; Fauch 1989; Clancy 1993; Adams 1999; Paul and Post 2001).

Although multiple regression models included only post-fire population and habitat data, the observed pre- to post-fire changes in brook trout abundance and proportion in burned reaches can be attributed to probable fire-induced changes in habitat characteristics that were important predictors of brook trout abundance. For example, the negative association between area of basin moderately-to-severely burned and brook trout abundance provides evidence that brook trout may be relatively intolerant of wildfire effects.

Stream gradient, the most important predictor of brook trout abundance in my models, may potentially limit brook trout performance if higher than 3% (Fausch 1989; Kozel and Hubert 1989). This was likely in debris flow reaches where stream gradient ranged from 3.4% to 4.6% and the proportion of brook trout to cutthroat trout and bull trout declined each year post-fire. It is uncertain whether debris flows were capable of causing an increase in stream gradient over the entire lengths of study reaches. However, debris flows did remove LWD and other pool-forming features which create a stepped profile within higher-gradient stream segments, forming pools and trapping smaller substrates. As a result, debris flow reaches were dominated by larger substrates with relatively low amounts of small gravel. The literature suggests that a lack of small spawning gravel could contribute to the observed assemblage shift in debris flow reaches. A comparison of mean substrate size at spawning sites among 11 salmonid species

(Keeley and Slaney 1996) using data compiled from the literature (Witzel and MacCrimmon 1983; Young et al. 1989; Kondolf and Wolman 1993; Thurow and King 1994) indicated that brook trout use smaller substrates than do cutthroat trout and most other salmonid species. This would help explain the lack of brook trout recruitment relative to cutthroat trout recruitment observed in debris flow reaches.

Pool habitat, another important predictor of brook trout abundance, was also lower in debris flow reaches than other treatments and may have contributed to the decline in brook trout relative to cutthroat and bull trout. Because brook trout are expected to have hierarchical dominance in slow-water habitats (Cunjak and Green 1984; Griffith 1988), they would not have a competitive advantage over cutthroat trout and bull trout in debris flow reaches.

A combination of relatively high percent pool habitat, increased water temperature, and fine sediment in an overall low gradient (2.5%) channel may have contributed to the post-fire invasion of brook trout in the Rye Creek reach. In contrast to debris flow reaches, this reach had abundant pools. Given that brook trout may be dominant in slow-water habitats (Cunjak and Green 1984; Griffith 1988), cutthroat and bull trout were likely at a competitive disadvantage. Also, because of higher temperature tolerances, the elevated mean post-fire MWMT in Rye Creek ($18.6\text{ }^{\circ}\text{C} \pm 1.2\text{ }^{\circ}\text{C}$) may have had a differential effect on cutthroat, bull, and brook trout. The predicted ultimate upper incipient lethal temperature (UUILT) and optimal growth temperature of westslope cutthroat trout ($21.8\text{ }^{\circ}\text{C}$ and $13.6\text{ }^{\circ}\text{C}$; Bear 2005) and bull trout (20.9 and 13.2 ; Selong et al. 2001) are lower than those reported for brook trout (25.3 ; Brown 1974 and $14.0\text{ }^{\circ}\text{C}$;

McMahon in preparation). Studies have shown that even small differences in optimal thermal range such as these may govern the outcome of species competitive interactions (De Staso and Rahel 1994; Taniguchi and Nakano 2000; Rodtka and Volpe 2004). For example, Novinger (2000) found that age-0 brook trout gained a competitive advantage over age-0 cutthroat trout that increased at warmer water temperatures. In addition, brook trout have a significant competitive advantage over bull trout at temperatures above 14.4° C (T. McMahon, Montana State University, personal communication). Finally, relatively high sediment levels (70%, the highest recorded for any reach in 2003) may also have influenced brook trout invasion in Rye Creek. Brook trout tend to have higher survival to emergence than do cutthroat and bull trout in high sediment habitats (Hausle and Coble 1976, Irving and Bjornn 1984; Weaver and Fraley 1991; MBTSG 1996). For example, Clancy (1993) found that bull trout densities tended to be low in Bitterroot tributary streams with high amounts of fine sediment. Thus, elevated levels of fine sediment likely contributed to the fish assemblage change in Rye Creek. Similar to these observations in Rye Creek, Shepard (2004) surmised that increases in water temperature, changes in amount of pool habitat, and increased levels of fine sediment influenced brook trout invasion in Libby Creek in southwestern Montana.

Stream discharge may also have influenced fish assemblages. Although I did not record velocity or discharge data in any study reaches, peak flow during 2003 in the Bitterroot River near Darby was 67% above average (USGS 2005; Figure 8). The proportion of brook trout to other salmonids decreased by 3% in reference and 21% in

treatment reaches from 2002 to 2003 suggesting that brook trout were less tolerant of high flow events than native fish.

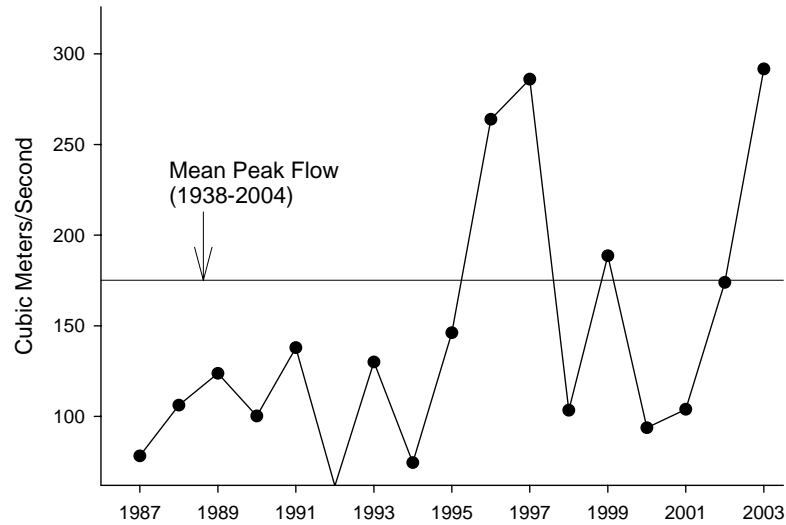


Figure 8. Peak discharge cfs in the Bitterroot River near Darby, MT from 1987 through 2003. Mean peak flow from 1938 to 2004 is indicated by a horizontal line. Modified from (USGS 2005).

Conclusions and Recommendations

The relatively large number of fire-affected streams and reference streams with predisturbance population data over a large spatial scale in the upper Bitterroot River basin provided a unique opportunity to study fish population recovery from wildfire disturbance. My results indicate that although native fish populations recovered rapidly from wildfire disturbance, differential effects on nonnative fish can and do occur in the first three post-fire years. Brook trout were less tolerant of post debris flow conditions than cutthroat trout while habitat conditions in one high burn-severity study reach facilitated invasion. These shifts are likely related to stream gradient, amount of available pool habitat, the degree to which water temperatures remain elevated post-fire,

substrate composition, high discharge events, and the strength of source populations of native and nonnative species.

As we strive to conserve and restore native salmonid populations we must consider the unintended consequences of our management actions. Constructing barriers to protect species from competition and hybridization with nonnatives may leave native species susceptible to extinction risk from genetic bottlenecks or stochastic events such as wildfire (Rieman et al. 1993; Dunham et al. 1997; Kruse et al. 2001; Novinger and Rahel 2003). Conversely, maintaining connected populations and metapopulations hedges bets against extinction risk from genetic bottlenecks and stochastic events, but may leave native populations susceptible to competition or hybridization with nonnatives (Rieman and McIntyre 1993).

Although results of my study and others suggest that connected native fish populations are resilient to high-severity wildfire disturbance and appear to recover rapidly, further laboratory and field research is needed to develop a better understanding of physical and biological conditions that favor nonnative fish invasions. Case studies examining pre- to post-fire change in fish assemblages and habitat continuously over longitudinal stream gradients would lend valuable insight into invasion mechanisms including determination of invasion rate and how abundance and proximity of nonnative source populations influence invasion. Additional experiments comparing competitive interactions among cutthroat, bull, and brook trout in a variety of habitats and over a range of temperatures and flow regimes would also lend valuable insight into invasion mechanisms. Because of the limited duration of this study (3 years), future studies

should also be initiated to examine long-term effects of wildfire disturbance on mixed native and nonnative fish assemblages. For example, continued monitoring by Montana Fish, Wildlife and Parks and the Bitterroot National Forest would determine if brook trout will displace cutthroat trout in Rye Creek. Such studies would provide valuable insight into whether invasion risk increases or decreases over time as habitat conditions stabilize in fire-affected streams.

With the increasing frequency and severity of wildfire on the landscape expected to continue (Hessberg and Agee 2003; Hann et al. 1998; USDA 2000), managers should work to maintain connectivity of stream networks and metapopulations to allow repopulation of native fishes in reaches defaunated by wildfire (Dunham and Rieman 1999; Rieman and Dunham 2000). However, given our limited knowledge of the mechanisms that facilitate nonindigenous fish invasions, it is important to monitor the distribution and abundance of nonnatives as well as determine watersheds at risk of high-severity wildfire. Watersheds or stream reaches at risk of both high-severity wildfire and in close proximity to robust nonnative source populations may be at increased risk during the post-fire period. In these cases, it may be necessary to manage vegetation in riparian areas and uplands to simultaneously reduce the risk of high-severity wildfire and invasion. This could include prescribed burns or a disturbance-based approach to timber harvest to approximate natural disturbance patterns (Brown et al. 2001; Bonar 2004). However, extensive fuels management projects that repeat past timber harvest activities may exacerbate problems (Rieman et al. 2003). Therefore, vegetation manipulation should maintain the interaction of large woody debris with stream channels, minimize

transport and delivery of fine sediment, and maintain canopy cover to the extent necessary to prevent stream temperature increases that could facilitate fish community shifts. Finally, severely burned watersheds at high risk of invasion should be given priority when considering post-fire rehabilitation efforts.

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 and therefore should be preserved. Connected native fish populations are resilient to seemingly “catastrophic” high-severity wildfire disturbance and debris flows and are capable of rapid recovery even when in sympatry with nonnatives. Although the potential may exist for wildfire to favor invasion of nonnative fishes, my findings suggest that the chronic nature of many anthropogenic disturbances likely plays a greater role in facilitating nonnative fish invasions than does wildfire (Griffith 1988; Leary et al. 1993; Moyle and Light 1996; Ross et al. 2000).

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APPENDICES

APPENDIX A

TABLE OF STATISTICAL RESULTS FOR INDIVIDUAL STUDY REACHES
IN THE BITTERROOT RIVER BASIN

Table 1. Results of two-sample *t*-tests comparing pre- and post-fire log ($x + 1$) estimated abundance (number of fish/100 m) for each study reach with at least two years pre- and post-fire data. Asterisks indicate significance: (* = $P < 0.05$). Also shown are mean pre- and post-fire actual estimated abundances and percent change calculated from log₁₀ differences.

Stream	Treatment	Cutthroat Trout			Bull Trout			Brook Trout		
		Pre	Post	% Change	Pre	Post	% Change	Pre	Post	% Change
Bertie Lord Cr. 0.3	Reference	56.2	51.7	-14.0	0.4	0.2	-13.5	4.3	0.7	-67.2*
Martin Cr. 2.1	Reference	60.3	55.3	-9.6	4.7	5.9	26.8	0.1	0.0	-4.6
Martin Cr. 12.1	Reference	104.1	80.8	-20.3	18.5	19.8	59.2			
Meadow Cr. 9.0	Reference	59.0	103.4	73.5*	35.9	31.1	164.2			
Mine Cr. 0.3	Reference	27.5	36.8	14.9	0.0	0.6	54.6	72.3	144.3	87.9
Moose Cr. 2.3	Reference	61.7	61.5	-1.4	11.1	9.5	-13.8			
Piquet Cr. 2.1	Reference	72.6	37.2	-28.6	0.7	0.4	-14.9	110.6	32.1	-85.9
Slate Cr. 2.6	Reference	97.5	95.3	-2.2	24.0	14.1	-40.2	2.9	4.9	46.6
Tolan Cr. 3.4	Reference	34.7	79.4	135.4*	1.3	0.8	-18.8	22.3	12.8	-31.1
Waugh Cr. 1.1	Reference	29.7	40.3	15.5				0.5	0.0	-32.6
Woods Cr. 1.4	Reference	24.7	60.2	138.8*	1.6	15.9	454.2*	5.3	11.6	76.4
Reimel Cr. 6.1	Low-Mod	40.7	36.0	-15.2	0.4	0.2	-13.5	77.6	33.2	-55.1*
Skalkaho Cr. 33.2	Low-Mod	50.5	47.6	-1.1	33.0	38.7	22.7			
Tolan Cr. 8.2	Low-Mod	52.2	82.1	61.7*	33.3	36.2	9.0			
Cameron Cr. 16.3	Low-Mod	58.2	48.2	-16.2				52.4	44.4	-64.8
Divide Cr. 0.2	Low-Mod	50.0	54.4	7.8	15.2	42.7	38.0			
Sleeping Child Cr. 23.3	Low-Mod	57.1	35.2	-36.3*	13.1	7.7	-36.5	0.0	0.1	9.9
Meadow Cr. 11.7	High	15.7	46.8	164.2*	9.7	31.5	190.6*			
Reimel Cr. 4.2	High	37.4	5.8	-83.4*				78.0	42.8	-67.2
Rye Cr. 20.0	High	104.8	93.6	-9.6	1.6	0.0	-51.8*	0.1	8.6	499.1*
Laird Cr. 2.3	Debris	62.1	14.7	-88.4	0.0	0.6	56.2	46.0	0.5	-96.9*
North Rye Cr. 3.1	Debris	85.6	25.3	-75.9*				28.6	1.4	-91.5*
Sleeping Child Cr. 16.4	Debris	57.1	14.0	-75.0*	8.5	3.5	-53.0*	0.6	0.2	-19.5

APPENDIX B

POPULATION TREND DATA FOR INDIVIDUAL STUDY REACHES IN THE
BITTERROOT RIVER BASIN

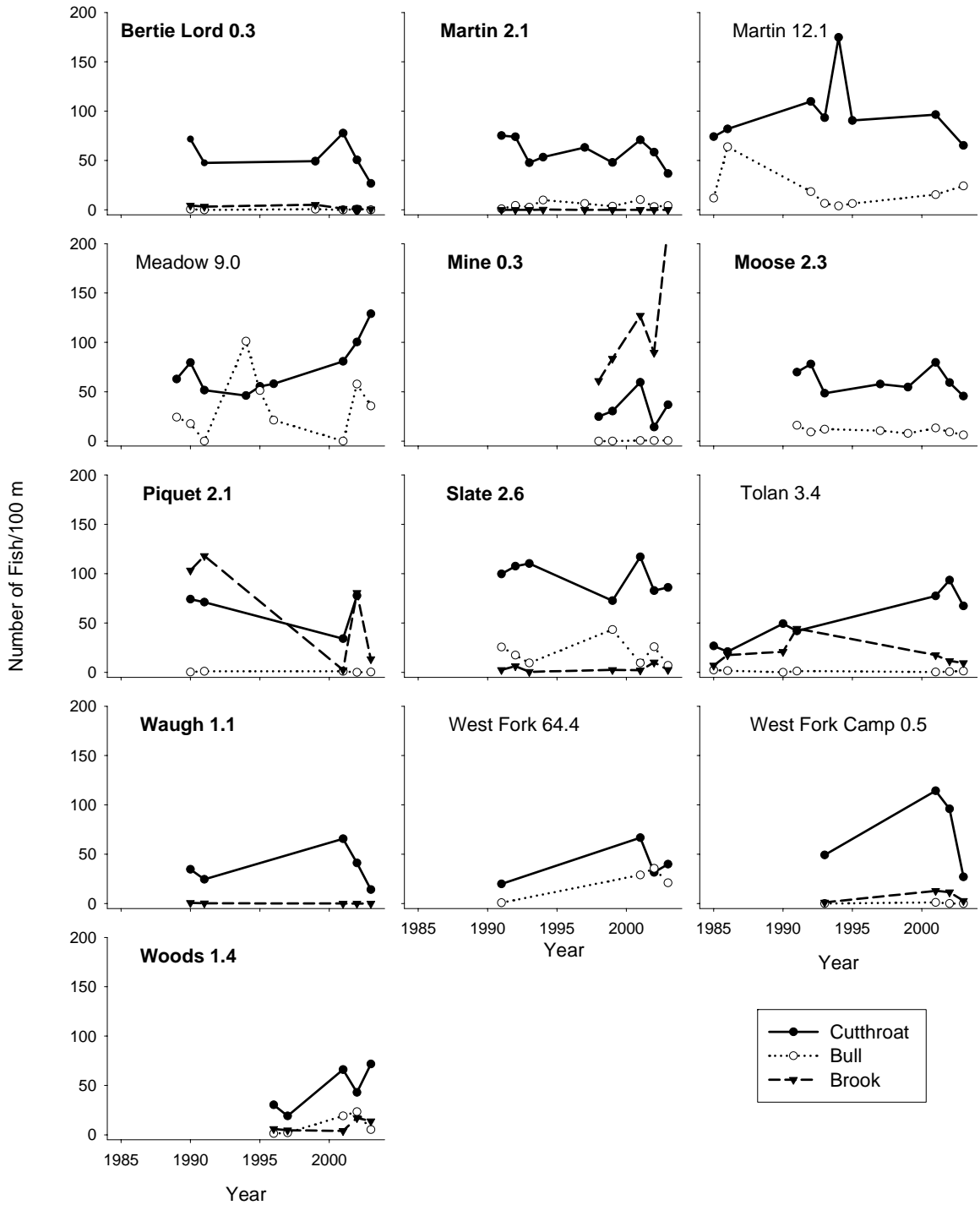


Figure 1. Temporal trends in estimated number of fish/100 m in reference reaches. Bold names indicate reaches used in BACI analyses. Numbers associated with each stream name refer to distance (km) from stream mouth.

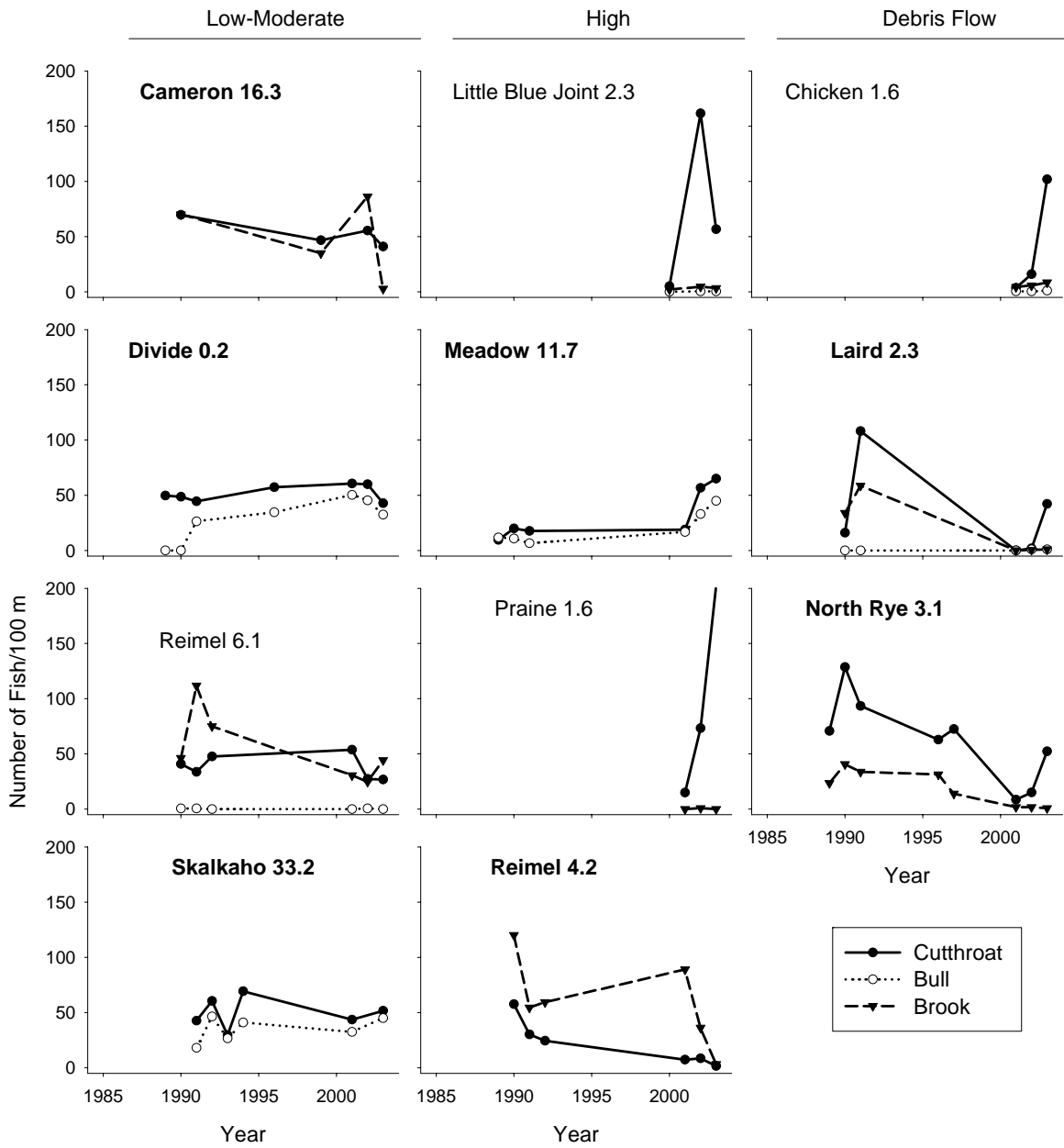


Figure 2. Temporal trends in estimated number of fish/100 m in treatment study reaches. Bold names indicate reaches used in BACI analyses. Numbers associated with each stream name refer to distance (km) from stream mouth.

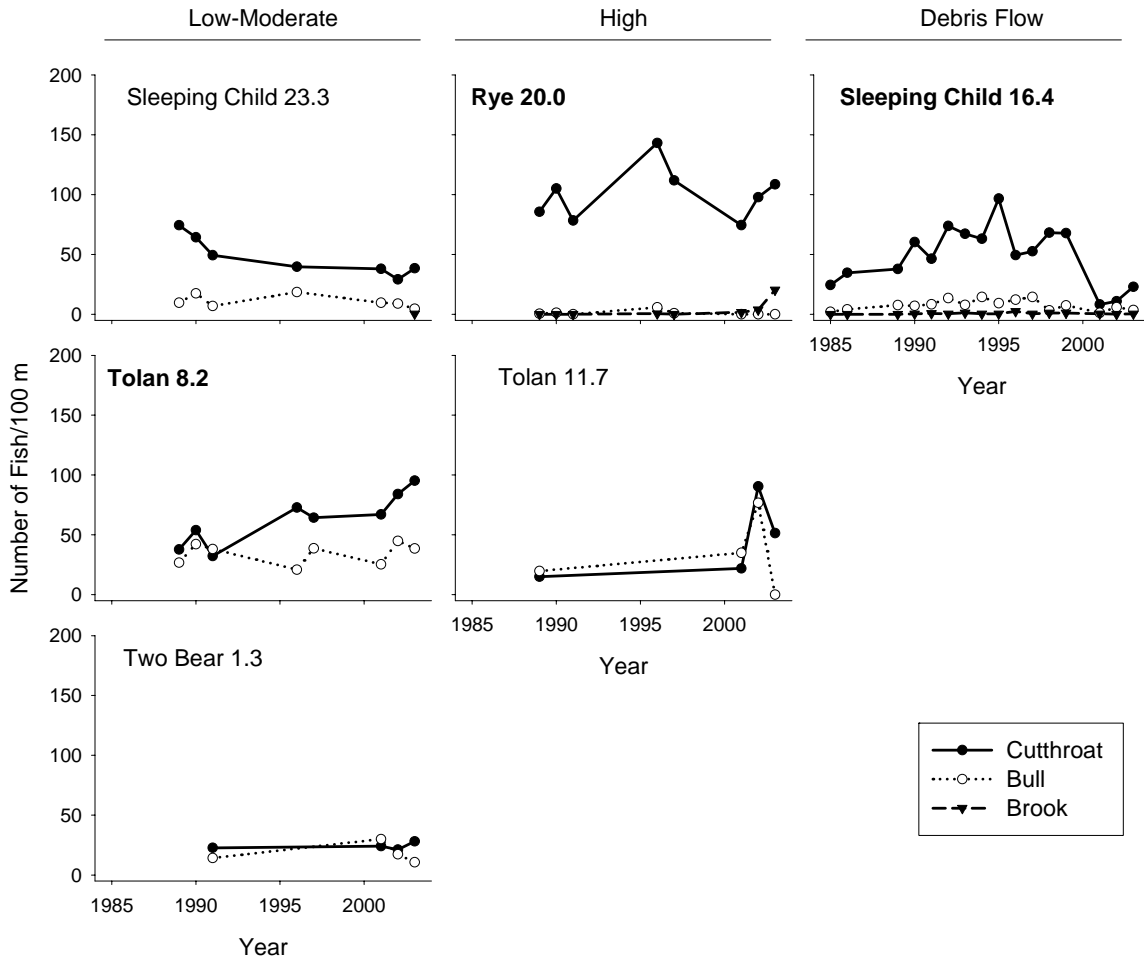


Figure 2. Continued.

APPENDIX C

LOCATION DATA FOR STUDY REACHES IN THE BITTERROOT RIVER BASIN

Table 1. Location [latitude, longitude (degrees.degrees), and legal description] and length (m) of 30 representative stream reaches included in this study. “Stream km” indicates the distance in kilometers of each reach from the stream mouth.

Stream	Stream (km)	Length (m)	Legal Description	Reach Start		Reach End	
				Latitude	Longitude	Latitude	Longitude
Bertie Lord Creek	0.3	183	T2N, R18W, Sec 24bda	45.91649	113.787	45.90875	113.784
Cameron Creek	16.4	305	T2N, R19W, Sec 11acc	45.93822	113.929	45.93900	113.926
Chicken Creek	1.6	305	T3S, R22W, Sec 4cc	45.59878	114.327	45.59954	114.329
Divide Creek	0.2	305	T4N, R19W, Sec 28ca	46.06400	113.968	46.06390	113.977
Laird Creek	2.3	210	T1N, R20W, Sec 3cd	45.86230	114.068	45.86087	114.070
Little Blue Joint Creek	2.3	305	T2S, R22W, Sec 5cad	45.69068	114.344	45.68986	114.347
Martin Creek	2.1	305	T2N, R17W, Sec 8aa	45.94540	113.735	45.94688	113.738
Martin Creek	12.1	305	T3N, R18W, Sec 22cc	45.98996	113.828	45.99202	113.830
Meadow Creek	9.0	305	T1N, R18W, Sec 10db	45.84888	113.820	45.84600	113.819
Meadow Creek	11.7	305	T1N, R18W, Sec 23ab	45.82924	113.802	45.82682	113.801
Mine Creek Creek	0.3	183	T3S, R21W, Sec 10nw	45.59550	114.170	45.59454	114.169
Moose Creek Creek	2.3	305	T2N, R17W, Sec 9ac	45.94016	113.715	45.94213	113.714
North Rye Creek	3.1	244	T3N, R20W, Sec 24b	46.00128	114.029	46.00317	114.028
Piquett Creek	2.1	305	T1N, R21W, Sec 10ac	45.85600	114.193	45.85547	114.194
Prairie Creek	1.6	122	T1N, R19W, Sec 28dc	45.80039	113.967	45.80118	113.967
Reimel Creek	4.2	183	T1N, R19W, Sec 22dac	45.81960	113.940	45.81843	113.939
Reimel Creek	6.1	183	T1N, R19W, Sec 35bab	45.80070	113.930	45.79815	113.930
Rye Creek	20.0	244	T3N, R19W, Sec 22d	45.99280	113.943	45.99208	113.941
Skalkaho Creek	33.2	305	T4N, R18W, Sec 4cb	46.12422	113.851	46.12191	113.849
Slate Creek	2.6	244	T2S, R22W, Sec 1ba	45.69797	114.265	45.69879	114.263
Sleeping Child Creek	16.4	305	T4N, R19W, Sec 7d	46.11004	114.005	46.10770	114.002
Sleeping Child Creek	23.3	305	T4N, R19W, Sec 28ca	46.06400	113.968	46.06178	113.970
Tolan Creek	3.4	305	T1N, R19W, Sec 24ab	45.82862	113.902	45.82712	113.900
Tolan Creek	8.2	305	T1N, R18W, Sec 28bc	45.80927	113.851	45.80764	113.850
Tolan Creek	11.7	244	T1S, R18W, Sec 4bd	45.78192	113.833	45.78023	113.831
Two Bear Creek	1.3	305	T4N, R19W, Sec 8ba	46.11655	113.994	46.11514	113.990
Waugh Creek	1.1	213	T1N, R19W, Sec 4bbc	45.78252	113.958	45.78225	113.961

Table 1. Continued.

Stream	Stream (km)	Length (m)	Legal Description	Reach Start		Reach End	
				Latitude	Longitude	Latitude	Longitude
West Fork Bitterroot River	64.4	244	T4S, R22W, Sec 4cdd	45.51264	114.320	45.50612	114.324
West Fork Camp Creek	0.5	183	T1S, R19W, Sec 16ba	45.75262	113.952	45.75113	113.953
Woods Creek	1.4	152	T3S, R23W, Sec 20	45.56278	114.341	45.56280	114.342