

Fire and fish: a synthesis of observation and experience

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*Abstract.* – Early research concerning the effects of wildfire on aquatic systems focused on effects to soil, erosion, and water yield and quality, with a relatively limited temporal and spatial context. Wildfire generally was perceived as a destructive force threatening aquatic resources (e.g., fish populations) and related values. Subsequent work has integrated physical and ecological processes related to fire, and a broader perception that includes the role of wildfire as a fundamental agent of disturbance that potentially influences heterogeneity, diversity, and productivity in aquatic ecosystems. Integrating earlier summaries with more recent information, it is apparent that wildfire can have dramatic effects on streams and on populations of native fishes, but although mortalities can occur in conjunction with the direct effects of severe fires, such occurrences have been most frequently observed in relatively small streams and over limited extent (1 - 2 km). In contrast, indirect effects linked to the physical and ecological process occurring after a fire can extend over 10s to even 100s of km of stream, and effects may last for decades, and potentially even centuries. Furthermore, wildfire and associated disturbances have been, and likely will continue to be, a proximate cause of extirpation for small, isolated populations of native fishes. In general, however, the effects of wildfire are far less dramatic. In some cases, the effects of wildfires have been difficult to measure, and in others, populations that were initially depressed have rebounded dramatically, even increasing in abundance or extent relative to prefire conditions. Better information is needed to understand where and how the conditions in forests, watersheds, and native fish populations transition from those that may benefit from and are resilient to the effects of wildfire, to those that are vulnerable to those effects. In the interim, basic concepts of resilience developed in this review provide a foundation for the future.

## Introduction

The effects of wildfire on aquatic systems and fishes occurring in them has been linked to the *direct* or immediate influence of the fire on water quality and the *indirect* or subsequent effects on watershed characteristics and processes that influence water quality and quantity, stream channels, and aquatic biota (Gresswell 1999). Early research linking fire and aquatic systems focused on effects to soil, erosion, and water yield and quality, with a relatively limited temporal and spatial context (see Gresswell 1999 for a review). Wildfire generally was perceived as a destructive force threatening aquatic resources (e.g., fish populations) and related values (Rieman and Clayton 1997; Kaufman 2004).

Subsequent efforts have integrated physical and ecological processes related to fire, and these concepts have been temporally categorized as short-term (i.e., < 1 year), mid-term (1-10 yr), and long-term (10s to 100s of years) (e.g., Minshall and Brock 1991; Minshall et al. 1998, 2001; Mihuc and Minshall 2005). Concomitantly, spatial context is critical because heterogeneity in fire severity, stream or watershed characteristics, and ecological communities constrains subsequent events and ecological responses. A broader perception includes the role of wildfire as a fundamental agent of disturbance potentially shaping heterogeneity, diversity, and productivity in aquatic ecosystems (Reeves et al. 1995; Gresswell 1999; Bisson et al. 2003).

The effects of fire and fire related management have been of particular importance to those interested in, or responsible for, management of native fishes. Fish and associated fisheries often hold particular social and economic importance. The sometimes-dramatic short-term effects of fire and postfire disturbance on stream channels, water quality, and mortality of individual organisms can be readily apparent. As a result, attempts to influence fire and its

effects on aquatic systems and fish populations before and, particularly, during and after the fire, have consumed considerable resources, time, and energy, and engendered substantial debate (e.g., Dunham et al. 2003; Rieman et al. 2003; NMFS 2007; Rhodes and Baker 2008; Rieman et al. 2010).

It is our intent to summarize the known effects of fire-related processes in forested biomes of the western USA, briefly review existing knowledge regarding direct and indirect effects to fish, and consider the implications for fish populations. We integrate earlier summaries (e.g., Gresswell 1999; Dunham et al. 2003; Rieman et al. 2003) with more recent information and conclude with a final synthesis, including implications for conserving or restoring the resilience of fish populations to wildfire.

## **Fire Effects**

### *Direct Effects*

Wildfires consume flammable materials, and in the process, shade and cover provided by vegetation and woody debris is altered (Gresswell 1999). If a severe fire burns near or across a stream, water temperature can increase substantially (Hitt et al. 2003). Dissolution of smoke, ash, and volatile compounds can alter pH and concentrations of trace metals, nutrients, and other chemical constituents in streams (Cushing and Olsen 1963; Minshall et al. 1989; Spencer and Hauer 1991; Earl and Blinn 2003; Spencer et al. 2003).

Direct physical effects can produce mortality of aquatic organisms including fishes, amphibians, invertebrates, and periphyton (Rieman et al. 1997; Gresswell 1999). The causes of mortality have not been definitively identified, but potential mechanisms include rapid increases

in temperature and accumulation of toxic chemicals (e.g., ammonium, trace metals, and cyanide) (Minshall et al. 1989, 1997; Spencer and Hauer 1991; Barber et al. 2003).

The observed spatial pattern of direct effects seems to depend on the extent and severity of fire and size of the watershed (Gresswell 1999). Minshall and Brock (1991), for example, suggested that fire would not directly influence temperature in third order or larger streams. Furthermore, high variability in postfire distribution of fishes in small streams appears to be associated with the heterogeneity of riparian fire severity (Rieman et al. 1997). Mortality or displacement of fishes may be extensive, extending for several kilometers, but effects are often incomplete or patchy within and among stream reaches influenced by fire (Minshall and Brock 1991; Rinne and Neary 1996; Rieman et al. 1997;).

More recently, Howell (2006) found evidence of high to complete mortality or displacement of steelhead (*Oncorhynchus mykiss*), Chinook salmon (*O. tshawytscha*), and brook trout (*Salvelinus fontinalis*) in several moderate to severely burned reaches of three small (<2.6 m width) streams in eastern Oregon. Fish persisted at normal densities in stream reaches immediately downstream of those experiencing more severe fire. Based on observations from streams in northwestern Montana, Jakober (2001) reported that direct effects of several large fires were observable the following year. For example, the majority of fish in a drainage located in northwestern Montana was killed during a fire in 1996, and bull trout appeared to have been extirpated from headwater reaches of two small streams (Jakober and Dentino 2003). In contrast, fish distribution and density were relatively unaffected 1 year after fires that burned in Lolo National Forest during 2000 (Jakober 2002). In the southwestern USA, direct mortalities of fish appear to be less common than those following subsequent hydrologic events (Rinne and Jacoby 2005).

Direct effects may also result from fire suppression activities and the use of fire retardants (Gresswell 1999). Sodium ferrocyanide, a component of a commonly used fire retardant, is known to be toxic to aquatic organisms (Little and Calfee 2002; Pilliod et al. 2003; Angeler and Moreno 2006), but the temporal and spatial extent of these effects have been poorly understood. In fact, Crouch et al. (2006) recently found no evidence that retardant increased the levels of any chemical constituents above those from wildfire alone. The authors suggested that ferrocyanide was elevated through pyrogenic sources (Crouch et al. 2006). Nonetheless, the Forest Service eliminated use of retardants with sodium ferrocyanide in 2007 because of the potential toxicity to aquatic organisms (USDA 2007). The replacement, known commercially as PhosChek, was less toxic in laboratory studies (Little and Calfee 2003). The Forest Service concluded there was little risk for direct mortalities from PhosChek under prescribed operational use (Comas 2007; USDA 2007), but that conclusion remains controversial (NMFS 2007).

### *Indirect Effects*

The indirect effects of wildfire on streams will be influenced and constrained by direct effects, the subsequent supply of materials (e.g., water, sediment, woody debris, nutrients, biological propagules) and energy (insolation), stochastic events (e.g., storms), and the interactions of these factors on physical and biological succession (Gresswell 1999; Dale et al. 2005; Milner et al. 2007). We provide only a brief overview focused on water, sediment, wood, stream temperature, and stream food webs as an example of the dynamic, and often complex, nature of the interactions influencing habitats for fishes.

*Water and Sediment.*—Changes in supplies of water and sediment are commonly observed after wildfire (Legleiter et al 2002). Short- or mid-term changes reflect alteration of vegetation

and soils associated with severity and extent of the fire, geology and geomorphology, and the duration, intensity, and timing of postfire precipitation (Swanson 1981; Rinne and Neary 1996; Wondzell and King 2003). Peak flows and erosion can increase substantially, but the magnitude of response is related to factors pertaining to the watershed and weather (Robichaud et al. 2005). For example, hydrophobic (water repellent) soils have been linked to floods and increased erosion in some cases, but effects are influenced by fire severity, soil texture, and vegetation type. Mass failures, debris flows, and flood catalyzed by fire have been important in the history of many watersheds and may be primary drivers in the long-term sediment supply for those systems (Reeves et al. 1995; Benda et al. 2003; May and Gresswell 2003; Meyer and Pierce 2003; Moody and Martin 2009). Dramatic increases in erosion that follow some fires tend to decline within 10 years as vegetation is reestablished (McNabb et al. 1989; Burton 2005; Luce 2005; Robichaud et al. 2009); however, the process may extend as root strength fails in fire-killed trees. The fire-hydrologic interaction has been characterized as an episodic pattern of disturbance and recovery that contributes to important variation of stream conditions in space and time (e.g., Reeves et al. 1995; May and Gresswell 2003; Miller et al. 2003).

*Temperature.* –Water temperatures commonly increase following fire, sometimes by several degrees, but increases are not universal (Gresswell 1999; Dunham et al. 2007). Postfire increases in water temperature have been associated primarily with loss of forest and riparian shading (Gresswell 1999; Isaak et al. 2010), but channel simplification, topographic shading, hyporheic flow, and the hydrologic changes accompanying fire can both accentuate and ameliorate these changes (Amaranthus et al. 1989; Dunham et al. 2007). Subsequent declines in stream temperature have been predicted with recovery of riparian canopy (Rieman and Clayton 1997), but recent work in the Boise River basin suggests that elevated temperatures can persist

for one to two decades in some cases (Dunham et al. 2007). Changes might even become permanent if fires initiate a transition to new vegetation communities associated with climate change (Isaak et al. 2010).

*Woody debris.* –Wildfire can play a key role in the recruitment of woody debris to streams (Reeves et al. 1995; May and Gresswell 2003; Miller et al. 2003). Wood is important because it controls channel morphology, sediment and water routing, and the heterogeneity of structure that may be important habitat for fishes and other organisms (Keller and Swanson 1979). In contrast to the fire-related hydrological changes that can attenuate within 10 years, changes in the recruitment of woody debris can extend for decades (Reeves et al. 1995; Gresswell 1999; Scheidt 2006). Postfire accumulation of wood is related to the prefire forest, severity of the fire, and processes associated with wood routing and storage in the channel (May and Gresswell 2003; Scheidt 2006). Woody debris may even decline following fire if a large proportion of the vegetation (including instream debris jams) is burned completely, or if remaining wood is transported out of the system during periods of elevated discharge (Swanson and Lienkaemper 1978). Mid-term accumulation may occur with toppling of fire-killed trees, undermining of riparian trees with increased flow and bank erosion, or the transport of wood from upslope via debris flows or avalanches (Swanson and Lienkaemper 1978; Scheidt 2006). Longer-term recruitment may depend on the rate that mature trees develop. The interaction of processes controlling the supply, accumulation, transport and storage of woody debris can lead to substantial variability within and among individual streams, or across time (e.g., May and Gresswell 1993; Young et al. 2006). The capacity of a stream system to store and continually rework stored materials, however, may also lead to relatively stable or uniform conditions in some systems (Scheidt 2006).

*Food Webs.* –A handful of studies before 1989 provided a limited perspective on wildfire and responses in biological communities and food webs in streams (Gresswell 1999). In general, it is clear that fire and subsequent effects can disrupt invertebrate communities in segments of small streams, and that at longer time scales, effects depend on the severity and extent of the fire, subsequent hydrologic disturbance, and the characteristics and recovery of riparian vegetation. There is a substantial body of literature that initially defined the anticipated responses of stream communities and food webs to the extended effects of wildfire (e.g., Minshall et al. 1989, 1997, 1998, 2001, 2004; Robinson and Minshall 1996; Minshall 2003; Earl and Blinn 2003; Mihuc and Minshall 2005). The generalized prediction emerging from this work can be summarized as an ecological succession in a temporal frame (Minshall et al. 1989; Gresswell 1999; Dunham et al. 2003; Minshall et al. 2004).

The short- term effects of postfire disturbances are related to the biophysical template following the fire, and responses can be dramatic, varying from virtually undetectable to the complete loss of invertebrates and algae. Where disruption is great, invertebrate and algal communities are often recolonized quickly, but abundance and diversity may continue to vary (Earl and Blinn 2003; Minshall et al. 2004).

In the mid-term (1-10 yr), diversity in aquatic communities tends to increase and productivity can be high with increased sunlight, stream temperatures, and nutrient flux. Where the riparian canopy is substantially reduced, foodwebs are expected to shift from largely allochthonous to autochthonous sources of carbon, with a concomitant response in trophic guilds of macroinvertebrates (or shifts feeding strategies by individual species; Mihuc 2004) and detrital respiration. Recent research has provided additional evidence that severe wildfire can stimulate primary production and a shift to primary consumers that support a greater biomass of

predatory insects, potentially fish, and even consumers in linked riparian communities (Malison 2008; Malison and Baxter 2010).

In the longer term (10-300 yr), watershed processes are anticipated to interact with succession in terrestrial and riparian vegetation. Influx of wood generally leads to organic litter accumulation. Trophic pathways are anticipated to shift from autochthonous toward allochthonous carbon sources as riparian vegetation increases and the canopy closes (Minshall et al. 1989). Recent research has generally supported these predictions and extended the perspective (Minshall et al. 2004; Robinson et al. 2005), but changing climate may constrain future riparian communities leading to unanticipated outcomes.

The long-term effects of wildfire on macroinvertebrate communities and food webs remain speculative, largely because direct evidence from empirical studies of that temporal extent simply does not exist. The results clearly depend, however, on the myriad interactions between disturbance, terrestrial succession, and watershed process that directly and indirectly influence the legacy of materials and linkages within, and between terrestrial and aquatic systems (Dale et al. 2005; Milner et al. 2007, 2008; Pettit and Naiman 2007).

### *Fish Population Responses*

Stream environments can change quickly during or following a fire (e.g., a single flood event) and may be catastrophic in ecological terms (including local extirpation of organisms in individual stream reaches). Concomitantly, indirect effects of wildfire often initiate or constrain processes, and responses can extend for decades and even centuries. Wildfire clearly plays an important role in supply of food and materials and the heterogeneity of channel conditions that contribute to the mosaic and productivity of habitats (Reeves et al. 1995; May and Gresswell

2003; May and Lee 2004). Although direct and indirect effects of wildfire can induce fish mortality, the long-term consequences for fish populations and assemblages will ultimately depend on the legacies of material, biota, and the associated physical and ecological processes that shape them. Understanding these changes ultimately requires a population-level perspective.

The response of fish populations to the direct and indirect effects of wildfire has been a focus of considerable interest in the last two decades. Because fires are hard to predict, most of the early research was opportunistic. In some cases, wildfires burned in watersheds where pre-existing population data facilitated before-after comparisons (e.g., Novak and White 1990; Rinne and Neary 1996; Rieman et al. 1997), but inference was also gained from comparisons among burned and unburned streams, or the temporal trajectory of populations associated with the immediate effects of fire (Minshall and Brock 1991; Rieman et al. 1997). Initial research focused principally on description of changes in distribution and abundance of extant populations or segments of populations (Rieman et al. 1997; Gresswell 1999), but subsequent syntheses considered a broader context of population and ecological processes (Rieman and Clayton 1997; Dunham et al. 2003; Heck 2007).

Although historic information suggested that direct effects of fire could produce substantial fish mortality (Minshall and Brock 1991; Rinne and Neary 1996; Rieman et al. 2007), we know of no examples of population extirpation associated with immediate effects of wildfires. In general, population level implications of wildfire appear to depend on longer-term processes.

Reductions in abundance, contraction in distribution, and even local extirpation have been reported with the indirect effects of large fires (Bozek and Young 1994; Rinne and Neary 1996;

Gresswell 1999; Rieman et al. 1997; Rinne and Carter 2008). Extreme effects, including local extirpations, have most often been observed in the southwestern USA (Rinne and Neary 1996). Negative consequences are related to diminished water quality associated with postfire ash flows, loss of habitat connectivity during periods of drought and intermittent flows, violent postfire flooding, and loss of food base and habitat (Rinne 2003, 2004; Rinne and Carter 2008). Fish populations in the Southwest may be especially vulnerable because the spring and early summer fire season is followed by monsoon in late summer (Rinne 2004). When heavy rains follow severe fire, and heavy ash or “slurry flows” have been reported (Rinne and Neary 1996).

The potential for a severe disturbance is coupled with the fact that many of remaining native fish populations in the Southwest are limited to small streams isolated from any source of immigration (Brown et al. 2001). In fact, many fishes in the region have been formally listed as threatened or endangered under ESA, and therefore, there is substantial concern that wildfires could negatively influence persistence. In some cases, rescue efforts have been initiated to capture surviving fish during, or immediately following, a fire and move them to a secure environment (e.g., hatchery) until habitat conditions in the burned watershed stabilized (Brooks 2006; A. Unthank, USDA Forest Service Regional Office, Albuquerque, NM personal communication).

Despite the potentially deleterious consequences, population collapses have not been ubiquitous in the aftermath of even very large fires. In some cases, fire had little apparent effect (Gresswell 1999; Riggers 2001; Jakober 2002). In others, abundance was seriously depressed, and reach-level extirpation occurred; however, populations rebounded relatively quickly (e.g., 1-6 years; Novak and White 1990; Rieman et al. 1997; Jakober and Dentino 2003). The emerging context of disturbance ecology and metapopulation dynamics and documented population

resurgence resulted in a hypothesis of recovery strongly mediated by the expression of migratory life histories and by dispersal from refugia not influenced by the fire and subsequent events (Rieman and Clayton 1997; Rieman and Dunham 2000; Dunham et al. 2003).

Recent research has sustained this view. In an extensive study of 32 watersheds that burned in large fires on the Boise National Forest between 1986 and 1994, Burton (2005) found that even where reach or broader-scale extirpation of fishes had occurred, recolonization through dispersal was complete. Howell (2006) reported rapid (within 4 years) recovery of rainbow and steelhead populations through immigration from habitats not influenced by postfire disturbances. Debris flows actually provided new habitat for Chinook salmon by destroying a culvert and promoting access to new areas above the former barrier (Howell 2006). Similarly, fire-flood generated debris fans in the Middle Fork Salmon River created new habitat used by spawning Chinook salmon within months of the events (R. Thurow USDA Forest Service, Rocky Mountain Research Station, Boise Idaho, personal communication of unpublished data). Examples of rapid responses now extend beyond the North American continent, and recovery of native fishes within 24-36 months of extirpation following extensive postfire sediment flows has been documented in Australia (Lyon and O'Conner 2008).

In fact, evidence that fishes exhibit resilience to fire is unmatched by recovery from anthropogenic disturbance (Neville et al 2009). Dunham et al. (2007) contrasted two levels of postfire disturbance (burn-and-debris-flow and burn-only) with unburned streams in the Boise River basin, but severity of disturbance did not have substantial influence on the distribution of either rainbow trout (*O. mykiss*) and tailed frogs (*Ascaphus truei*) within 10 years following fire. It appeared that even if effects from wildfire (e.g., elevated summer water temperature) continued for a decade or more, human activities that reduce the capacity of organisms to

respond to disturbance may be a greater threat to persistence than wildfire (Dunham et al 2007). Similarly, Neville et al. (2009) found no evidence of genetic bottlenecks associated with fire related disturbance in 55 streams affected by the Boise fires, but genetic diversity decreased in relation to human caused migration barriers (i.e. impassable road culverts).

The potential spread of nonnative species facilitated by fire-related disturbance is another important issue for some dwindling native fish populations (Dunham et al. 2003). Because stream temperature can affect the relative distribution and interaction of native and nonnative species (e.g., McHugh and Budy 2005; Rieman et al. 2006; Benjamin et al. 2007; McMahon et al. 2007), it has been suggested that warming of streams affected by wildfire may lead to expansion of nonnative species (e.g., brook trout or brown trout *Salmo trutta*) and concomitant contraction of native species, like bull trout *S. confluentus* and cutthroat trout (Dunham et al. 2007; Isaak et al. 2010). Results of a recent study in the Bitterroot River watershed where bull trout and westslope cutthroat trout co-occur with nonnative brown trout, brook trout, and rainbow trout suggested that native salmonids were resilient to fire (Sestrich et al. 2011). Although nonnative trout invaded 4 of 17 stream sections within the burned area, the invasion rate was similar in sections that did not burn. Habitat conditions declined, but native trout populations actually exceeded pre-disturbance levels 3 years following the fire (Sestrich et al. 2011).

To this point, the emphasis has been on dispersal and migration as key mechanisms behind population-level responses of fishes to fire, but research examining sublethal effects of habitat changes provides some evidence that phenotypic plasticity and adaptation to the effects of fire are mechanisms that may contribute to population resilience as well. In one recent study, habitat characteristics and growth of coastal cutthroat trout (*O. clarkii clarkii*) were evaluated in

severely and moderately burned watersheds and an unburned control (Heck 2007). Stream temperature increased following the removal of riparian vegetation during the fire, and growth of fish in burned watersheds was greater than in the unburned control. Increased water temperatures and a longer growing season may have triggered a bottom-up response resulting in an increased growth of cutthroat trout, but longevity decreased (Heck 2007). Apparently, survival in these headwater streams was limited by the maximum size of the individual trout, and faster growing individuals reached the critical point at an earlier age. In a study of nine tributaries of the Boise River (i.e., three each of reference, burned, and burned with channel reorganization), there was a direct relationship between growth and maturation rate, and level of disturbance 10 years following fire (A. Rosenberger, University of Alaska, personal communication of unpublished data). Such adaptation could be critical to persistence of some isolated populations (Letcher et al. 2007).

### **Summary, Implications, and Conclusions**

Wildfire can have dramatic effects on streams and on populations of native fishes. Mortalities have been associated with the direct effects of severe fires, but these consequences have been most frequently observed in relatively small streams and over limited extent (1 - 2 km). Indirect effects linked to the physical and ecological process occurring after a fire can extend over 10s to even 100s of km of stream, however, and effects may last for decades, and potentially even centuries. Wildfire and associated disturbances have been, and likely will continue to be, a proximate cause of extirpation for small populations of native fishes. In general, however, the effects of wildfire are far less dramatic. In some cases, the effects of

wildfires have been difficult to measure, and in others, populations that were initially depressed have rebounded dramatically, even increasing in abundance or extent relative to prefire conditions.

Gresswell (1999) suggested that over much longer time scales (decades to millennia), fish were well adapted to disturbances occurring at the frequency of wildfire. Recent evidence suggests that effects of disturbance in individual habitat patches are greatest on individuals and local populations that are least mobile, and early speculation to that effect (Warren and Liss 1980; Rieman and Clayton 1997; Gresswell 1999) has been supported by recent findings. Because habitat fragmentation is directly linked to the ability of fish to move among disparate portions of a stream network, this factor alone may be much more critical to the persistence of western salmonids than disturbance related to wildfire. There is a growing body of evidence that watershed characteristics including size, complexity (number and arrangement of tributaries), connectivity, and management history play a major role in the population structure and resilience at multiple levels of biological organization across disturbance-prone landscapes (Wofford et al. 2005; Neville et al. 2006; Guy et al. 2008).

Clearly, context shapes the effects of wildfire on populations and communities of native fishes. Fish are most vulnerable to both direct and indirect effects of fire where populations are restricted to relatively small areas of habitat, and risk is greatest in isolated stream segments or small networks in steep, confined drainages where severe fires are likely to burn a large proportion of the headwaters and riparian corridor. Where populations are relatively large, have access to diverse, well-connected habitats and/or the capacity to adapt to changing environments, vulnerability is lessened; in many cases, the capacity and even the productivity of habitat can even be improved following wildfire (e.g. Malison and Baxter 2010).

The differences in context are evident among individual populations and watersheds across the landscape. Some populations within a basin may be highly vulnerable to any form of disturbance, but others are much less so (e.g., Guy et al. 2008; Peterson et al. 2008; Neville et al. 2009). Populations of Chinook salmon, bull trout, and other species that migrate over large expanses of habitat in the Pacific Northwest and northern Rocky Mountains have fared well in response to the major fires of recent decades. Managers in these systems may tend to worry less about wildfire than the more chronic effects of watershed development. They may even see wildfire as beneficial for creating or expanding new habitats (e.g., Howell 2006). In contrast, managers concerned with remnant populations of native fishes isolated by invasive species and dewatered stream channels in the central Rocky Mountains and the Southwest may view the next wildfire as the catalyst for local extirpation, or even species level extinction (e.g., Brown et al. 2001; Rinne 2004; Brooks 2006).

Large disturbances will likely continue in all of these regions. The watersheds of the Rocky Mountains and interior west have been shaped by disturbances linked to wildfire, large storms, and the flux, routing, and storage of water (in groundwater, snow and ice), sediment, and wood. On evolutionary time scales, large fires, mass erosion events, floods, and even local extinctions have likely been common (e.g., Bennett 1990; Reeves et al. 1995; Meyer and Pierce 2003), and yet many species and populations of fishes have persisted and adapted (Gresswell 1999). Management might alter the frequency and magnitude of particular disturbance processes, but it likely cannot eliminate large and intense watershed events (e.g., Kirchner et al. 2001; Istanbuloglu et al. 2002). In fact, frequency and/or magnitude of some disturbances may even increase with changing climate (e.g., McKenzie et al. 2004; Westerling et al. 2006). Furthermore, the extent of thermal habitats for coldwater salmonids and the connectivity among

refugia are expected to decline, further increasing the vulnerability of some populations (Rieman et al. 2007; Williams et al. 2009; Haak et al. 2010; Isaak et al., 2010)

So how can managers respond to the challenges posed by changing fire regimes and the conservation of native fishes and diverse aquatic ecosystems? In general, options can be categorized as management before, during, and after fire (Dale et al. 2001; Dunham et al. 2003), but a framework for monitoring and adaptation is critical in all cases (Dunham et al. 2003). Management before fire includes maintaining or restoring the resistance or resilience to disturbance before the next disturbance occurs. Conditions contributing to resistance and resilience in populations emerge repeatedly in the discussion above and elsewhere (e.g., Gresswell 1999; Dunham et al. 2003; Bisson et al. 2003; Rieman and Isaak 2010). Conservation or restoration of relatively large networks of habitat and the physical and ecological processes that maintain them, the broad expression and adaptation of life histories, and the potential for connections within, and among populations are all critical. In essence, resilience will depend on a spatial and temporal structure and diversity in populations and habitats that can absorb or benefit from the effects of fire.

In some cases only remnant habitats exist and reconnection or expansion to support resilience and adaptive potential is not possible or desirable (e.g., the potential invasion of nonnative species). The only alternative may lie in attempts to change the character of disturbance. For example, by reducing the extent or grain of severe fire, even small populations may have some chance of persisting. Considerable discussion has focused on the management of fuels through prescribed fire or thinning as a tool for altering the severity of fire, if not its extent (Reinhardt et al. 2008; Rieman et al. 2010). Continued debate about the potential utility of such efforts is related to the tradeoffs between the potentially damaging effects of

management relative to the effects of the fires (Rhodes and Baker 2008; Rieman et al. 2010) that may occur with, or without that management (Littell et al. 2009).

If the conditions supporting the resilience and adaptation of populations cannot be created before a large fire occurs, managers are left with limited options. They might attempt to suppress or mitigate effects during or after the fire. Although extraordinary measures could make the difference between extinction and persistence (e.g., Brown et al. 2001), there is some question whether postfire watershed remediation can even influence the kinds of events that might actually threaten populations (Backer et al. 2004). Regardless of their efficacy, these actions can be extraordinarily expensive and necessarily will be limited in the extent or number of populations, streams, or watersheds that might be considered. Concomitantly, there are other activities (e.g., salvage logging) that can be detrimental to particularly vulnerable populations in the postfire environment (Beschta et al 2004; Karr et al. 2004; Reeves et al. 2006).

Clearly, better information is needed to understand where and how the conditions in forests, watersheds, and native fish populations transition from those that may benefit from and are resilient to the effects of wildfire, to those that are vulnerable to those effects. At what point is a population too small or too isolated to persist? Can we actually influence the character of fire to alter that balance? How do we weigh the threats and benefits of aggressive management? Peterson et al. (2008), Dare et al. (2009), and Rieman et al. (2010) offer some tools that may help refine this discussion and offer some approaches that can begin to answer these questions. Further collaboration between researchers and managers could extend this process. In the interim, the basic concepts of resilience outlined repeatedly throughout this review provide a critical foundation for the future.

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