Effects of fire on fish populations: landscape perspectives on persistence of native fishes and nonnative fish invasions

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Abstract

Our limited understanding of the short and long-term effects of fire on fish contributes to considerable uncertainty in assessments of the risks and benefits of fire management alternatives. A primary concern among the many potential effects of fire is the effects of fire and fire management on persistence of native fish populations. Limited evidence suggests vulnerability of fish to fire is contingent upon the quality of affected habitats, the amount and distribution of habitat (habitat fragmentation), and habitat specificity of the species in question. Species with narrow habitat requirements in highly degraded and fragmented systems are likely to be most vulnerable to fire and fire-related disturbance. In addition to effects of fire on native fish, there are growing concerns about the effects of fire on nonnative fish invasions. The role of fire in facilitating invasions by nonnative fishes is unknown, but experience with other species suggests some forms of disturbance associated with fire may facilitate invasion. Management efforts to promote persistence of fishes in fire-prone landscapes can take the form of four basic alternatives: 1) pre-fire management, 2) post-fire management, 3) managing fire itself (e.g., fire fighting), and 4) monitoring and adaptive management. Among these alternatives, pre-fire management is likely to be most effective. Effective pre-fire management activities will address factors that may render fish populations more vulnerable to the effects of fire (e.g., habitat degradation, fragmentation, and nonnative species). Post-fire management is also potentially important, but suffers from being a reactive approach that may not address threats in time to avert them. Managing fire itself can be important in some contexts, but negative consequences for fish populations are possible (e.g., toxicity of fire fighting chemicals to fish). Monitoring and adaptive management can provide important new

information for evaluating alternatives, but proper implementation is often hampered by inadequate study designs and inconsistent financial and institutional support. The challenge for providing better management guidelines will be to add solid empirical data and models to assess the relevance of emerging concepts and theories, and provide a sense of where and when fires pose significant risks and/or benefits to fishes.

1. Introduction

Our limited understanding of the short and long-term effects of fire on fish contributes to considerable uncertainty in assessments of the risks and benefits of fire management alternatives (Rieman and Clayton 1997, Bisson et al., this issue). Part of the controversy in fire management is related to the diverse and complex effects that fire can have on aquatic ecosystems (Bisson et al., this issue). The effects of fires are contingent on a variety of factors, including their timing, location, area, extent, and intensity, the characteristics of the terrestrial and aquatic ecosystems that are affected, characteristics of the species therein, and a host of indirect physical and ecological linkages (McMahon and deCalesta 1990; Gresswell 1999). The challenge to researchers attempting to understand the effects of fire on fish is to define the critical subset of fire-related influences and modifying factors that drive important biological responses at a variety of scales. For management, the challenge is to apply this understanding to identify and prioritize specific management activities to benefit fish populations in fire-prone landscapes (Rieman and Clayton 1997; Burton et al. 1999; Rieman et al., this issue; Bisson et al., this issue).

Fires can have many specific influences on aquatic ecosystems, including decreased stream channel stability, greater and more variable discharge, altered coarse woody debris delivery and storage, increased nutrient availability, higher sediment delivery and transport, and increased solar radiation and altered water temperature regimes (McMahon and deCalesta 1990; Young 1994; Reeves et al., 1995; Minshall et al., 1997, 2001; Benda et al., 1998; Gresswell 1999; papers in this issue). These influences can be generated

independently of fire, or through interactions between fire and a variety of other influences, including climate, topography, geology, and land use. An understanding of these specific influences is needed, but we believe they must be considered within the larger context of dynamic landscape and watershed processes (Reeves et al., 1995; Benda et al., 1998) and the biological mechanisms through which native fishes have evolved to persist in these systems (Schlosser 1994; Rieman et al., 1997; Rieman and Dunham 2000).

Our focus in this paper is on fire as an agent of disturbance, and how fish respond to disturbance in general and fire in particular. The effects of fire and related disturbances can be considered on a continuum of spatial and temporal perspectives (Gresswell 1999). Our focus is on larger spatial (>10^2m) and longer temporal (>1 yr) scales – a domain typically associated with landscapes and populations (Frissell et al., 1986; Urban et al., 1987; Allen 1998). The growing list of threatened, endangered, and sensitive fishes in western North America (Rieman et al., this issue), has intensified the focus on population persistence and the need to develop management priorities on larger scales (e.g., Rieman et al., 2000, 2001). We begin by reviewing ecological concepts of disturbance, natural variability, and new (and a few old) ideas about persistence of species in dynamic landscapes. To put these concepts into perspective, we review selected studies documenting responses of fish populations to disturbance, including that caused by fire. The geographic scope of our review is weighted toward fishes (primarily salmonids) inhabiting fluvial systems in western North America, but the general concepts should be applicable to a wide variety of taxa and environments. In addition to fire effects on native fishes, we provide perspectives on potential relationships between fire and

invasions of nonnative fishes. Nonnative fishes have been widely established throughout the region (Fuller et al., 1999) and are an increasingly important management concern. Like fire effects on native fish, nonnative fish invasions are poorly understood (e.g., Fausch 1988; Moyle and Light 1996). Though our understanding of the effects of fire on fish is admittedly incomplete, we conclude with a discussion of the general alternatives for managing fires, and our thoughts about their potential benefits for fish population persistence.

2. Disturbance and natural variability

Disturbance is an important theme in ecology, but the definition of what constitutes a disturbance, even with respect to fire, remains imprecise. An oft-used definition is "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (Pickett and White 1985). Implicit in this definition is a spatial and temporal scale. Furthermore, the point at which these events can be considered disturbances depends on how severely they disrupt a given entity. For example, if an event results in the loss of only a few individuals within a short time period, it may not be considered a "disturbance" to the entire population. There are a variety of natural phenomena that can cause disturbance, including physical processes such as climate and associated fires, floods, droughts, and landslides, and biotic factors, such as disease outbreaks, herbivory, and nonnative species invasions (Rogers 1996; Dale et al., 2001).

Because organisms are believed to be adapted to the range of variability in conditions they normally encounter in the absence of human disturbance, variation outside of these bounds may be more disruptive. Disturbance must therefore be considered in the context of the evolutionary history of a species. For example, most freshwater environments have experienced dramatic changes in the past 10,000 years, and extinctions of many species have occurred as a result (e.g., Hocutt and Wiley 1986; Lichatowich 1999). However, many other species have persisted and even diversified because of these changes (e.g., Smith and Skulason 1996; Willson 1997; Schluter 1999). Disturbance does not necessarily imply increased environmental variability. Some disturbances (e.g., dams and river flow regulation; Poff et al., 1997) lead to decreases in environmental variability that may be detrimental to some freshwater fishes. Because disturbance is a fundamental characteristic of aquatic ecosystems, many species have adapted life histories that are shaped by, and may depend on such events (Resh et al., 1988). Nonetheless, there are conditions where fire and fire-related disturbance can pose short-term risks to fish populations. Over longer time scales, habitats generated by such events may be more productive than those where natural disturbance has been suppressed or altered by human influences (Reeves et al., 1995; Matthews 1998).

The evolutionary connection to environmental variability provides a rationale to manage habitats that express the full distribution of natural variability (Resh et al., 1988; Dunning et al., 1992; Poff et al., 1997; Landres et al., 1999). The concept of natural variability includes elements of disturbance that may cause substantial disruption on a local scale. In aquatic ecosystems in the western United States, localized disturbances initiated by fires, floods, and wind can have a profound influence on physical

environments, with attendant effects on fish populations (Benda et al., 1998). The traditional approach to managing disturbance focused on static ecosystem and landscape conditions, and "command and control" management to minimize their influences (Callicott and Mumford 1997). More recent emphasis has been placed on restoration and preservation of natural processes and variability in aquatic ecosystems (Anonymous 1995; Reeves et al., 1995; Frissell and Bayles 1996; Ebersole et al., 1996; Beechie and Bolton 1999).

3. Stability and persistence in dynamic landscapes

In the context of this paper, stability can be defined in terms of conditions that support persistence of local populations, or related groups of local populations (Rieman et al., 1993; McElhany et al., 2000). Stability, as commonly defined in ecology, consists of resistance, the ability of a system (where the term "system" refers to a wide variety of biological conditions; e.g., population, community, or ecosystem properties) to remain unchanged in the face of external influences, and resilience, the ability to recover from a disturbance (see Gunderson 2000). Stability can be expressed in terms of a single state (e.g., a pre-defined set of conditions), but typically there is a range of conditions that a system may return to following a disturbance (Ebersole et al., 1996). In practical terms, the problem we are concerned with here is to identify characteristics of a system that will provide a measure of stability (e.g., persistence) for native fishes in a dynamic (fire-prone) landscape.

Pickett and Thompson (1978) considered the problem of species persistence in the context of designing nature reserves. They reasoned that persistence of many species is increasingly dependent on the internal dynamics of nature reserves. This is due to continuing external (outside of reserves) habitat loss and fragmentation, and resulting loss of connectivity among reserves (Groom and Schumacher 1993). Decreasing connectivity reduces persistence because the reserve is isolated from sources of demographic support, including recolonization. Thus, dynamics <u>within</u> reserves are increasingly important for population persistence. From this, Pickett and Thompson (1978) recommended that reserves maintain a "minimum dynamic area" defined as "the smallest area with a natural disturbance regime, which maintains internal recolonisation sources, and hence minimizes extinction."

Key relations within a minimum dynamic area include 1) the size of local disturbances relative to the size of the total habitable area; 2) effects of local disturbances on the total population size within an area; 3) the probability that an area will effectively recover or return to a state resembling pre-disturbance conditions; 4) the length of time required for a locality to recover following a disturbance; 5) the temporal and spatial synchrony of disturbances within an area (related to recovery time); and 6) mobility or dispersal ability of the affected species (Pickett and Thompson 1978). Because species respond to disturbance in many different ways, the internal dynamics of a given area must be sufficient to support a wide range of disturbance-driven conditions.

The concept of minimum dynamic area is an integration of ideas from disturbance ecology and patch dynamics. Reserves are viewed as mosaics of patches (i.e., smaller areas within a reserve), created by the interplay of disturbance and succession. The

dynamics of aquatic landscapes can be viewed in terms of the development of both geomorphic and biotic characteristics (Drury and Nisbet 1971; Benda et al., 1998). Initial changes in the local stream environment caused by fire will persist for varying lengths of time, giving way to post-fire changes in physical and biological characteristics (e.g., Reeves et al., 1995; Minshall et al., 1997). Thus, patterns of habitat availability and occupancy by various species may be highly variable in time, and patchy on a variety of scales (Kotliar and Weins 1990; Pringle et al., 1988; Dunham et al., 2002).

Evidence for patch dynamics in fish populations comes from recent studies of metapopulation structure in fishes (e.g., Schlosser and Angermeier 1995; Rieman and Dunham 2000; Angermeier et al., 2002; Dunham et al., 2002). A metapopulation consists of a network of habitat patches potentially interconnected by dispersal. At any point in time some or all patches in a network may be occupied by local breeding populations. Patterns of patch occupancy in a metapopulation fundamentally depend on patch-specific rates of local extinction and recolonization. Available evidence suggests fish populations are more likely to occur, and thus persist, in larger, less isolated habitats (Dunham et al., 1997; Rieman and McIntyre 1995; Dunham and Rieman 1999; Dunham et al., 2002).

The mechanisms to explain persistence in metapopulations (Rieman and Dunham 2000) are related to those described by Pickett and White (1978) for minimum dynamic area. Persistence of local populations in larger patches may be due to larger population size, or to complex internal dynamics, which likely represent a broader diversity of habitat conditions present in larger patches. Persistence in smaller patches may be explained by demographic support (dispersal) from nearby populations. Because the

dynamics of extinction and recolonization for fishes likely occur on long (>10 yr) time scales, direct evidence for metapopulation dynamics is difficult to obtain (Dunham and Rieman 1999). Accordingly, it is not clear if current patterns of patch occupancy in putative metapopulations represent an equilibrium between local extinctions and recolonization, or a systematic decline in patch occupancy, with populations in the smallest patches being the first ones to go extinct (Rieman and Dunham 2000).

In addition to metapopulation dynamics, there are several related spatial processes that may be important for population persistence in dynamic landscapes. Dunning et al., (1992) recognized four types of spatial relationships that could affect populations in landscapes: landscape complementation, landscape supplementation, source-sink dynamics, and neighborhood effects (see also Schlosser 1995). Landscape complementation occurs when a species requires two or more habitat types during its life cycle (e.g., Northcote 1992; Baxter 2002). Loss of any required habitat type could result in a local extinction, as has been the case with some species of Pacific salmon upstream of migration barriers. Landscape supplementation refers to availability of multiple habitats with similar functions. The ability to choose among alternatives allows some insurance against loss of a single key area (e.g., a single spawning habitat). An example of supplementation on a large scale occurred when steelhead trout (Oncorhynchus mykiss) from streams altered by a volcanic eruption (Mount Saint Helens) dispersed from their natal habitats to use alternative spawning areas (Leider 1989). Source-sink dynamics refer to the movements of individuals from areas with high reproductive rates to areas with negative reproductive rates (Dias 1996). Without support from source populations, sink populations would perish. Schlosser (1995) provided an example of

possible source-sink dynamics for midwestern fish communities in streams influenced by beaver ponds that served as sources, and Adams (1999) provided a potential example for brook trout persisting in stream habitats below headwater lakes. Neighborhood effects occur when movement of individuals among adjacent patches affects species' abundance independent of habitat productivity within a patch. An example for fish would be occurrence of species characteristic of mainstem streams in the lower reaches of tributary streams (Gorman 1986).

4. Responses of fish to disturbance and fire

As is evident from the preceding discussion, emerging conceptual and theoretical developments highlight a variety of important considerations in understanding and managing the effects of disturbance and fire on fish populations. The complexity of these developments stands in contrast to the relatively limited number of empirical examples for fishes, particularly in reference to fire. Detenbeck et al., (1992) reviewed general responses of temperate stream fishes to disturbance, classifying disturbances as "pulse" or "press" based on the duration of an event relative to the life span of the longest-lived affected individuals. Detenbeck et al., (1992) found that population recovery time was substantially longer (5 - >52 yr) for press disturbances, in comparison to pulse disturbances (~30d-6 yr). Evidence from a subsample of case studies indicated recovery from disturbance was faster in sites closer to sources of recolonization and free of movement barriers. For pulse-type disturbances recovery times were longer for species with large size at reproduction (>20 cm), specialized spawning habitats (e.g., rock-

substrate), and movements characterized by anadromy or limited home ranges (e.g., due to natal homing or philopatry). Among taxonomic groups, percids, cyprinids, and centrarchids were found to recover relatively quickly from pulse disturbances, whereas catostomids were intermediate in response, and salmonid fishes were the slowest to recover.

The effects of fire on aquatic systems may be direct and immediate or indirect and occurring over an extended period (Gresswell 1999). Direct effects relate to short-term biological and physical changes that result directly from burning. Indirect effects of fire occur over a longer temporal scale as a result of fire-induced changes to the biota and physical environment. Beyond the immediate fire period, Minshall et al., (1990) suggested effects of fire on aquatic ecosystems can be considered in terms of mid-term and long-term consequences. Mid-term effects could be expected to peak in the first decade following the fire when changes are most dramatic (Figure 1). Long-term effects coincide with revegetation of watersheds and stream channel reorganization in the aftermath of fire.

Responses of fish populations to fire and fire-related disturbance have been documented in a limited number of studies, mostly for salmonid fishes. The influence of fire on persistence of native salmonid populations is highly variable. In some cases, local extinctions have been observed in response to fire, particularly in areas where populations of fishes have been isolated in small headwater streams. For example, fire-related population losses halted proposals to downlist the endangered Gila trout (Oncorhynchus gilae) in New Mexico (Propst et al., 1992). Gila trout may be more vulnerable to fire and other sources of disturbance because populations persist only as

small, isolated enclaves in habitats that currently experience high-intensity fires (Propst et al., 1992). Analyses of factors affecting persistence of Gila trout have emphasized the importance of restoring a natural fire regime (see Hessburg and Agee this issue; Whitlock et al., this issue), and increasing habitat size (Brown et al., 2001).

In larger interconnected systems, fish populations appear to be more resilient to the effects of fire. The importance of connectivity was evident in studies of salmonid responses to fires that burned through two tributary streams in the Boise River basin in the early 1990s (Rieman et al. 1997). In one stream, a local population of bull trout (Salvelinus confluentus) was probably extirpated, at least temporarily, following a severe burn and associated channel disturbances. The population was reestablished within a year through spawning returns of migratory individuals that were presumably outside of the system during the fire and related disturbances. If this system did not support bull trout with migratory life history, which depends strongly on connectivity, the rapid recovery of this population following disturbance may not have been realized. Burned reaches in both streams in this study also experienced temporary declines in abundance of rainbow trout, particularly of smaller (<75 mm) size classes (Rieman et al., 1997; unpublished data). Populations in the burned reaches recovered quickly (within 1 yr) following fires. In this case, repopulation of burned reaches likely occurred through dispersal from adjacent unburned reaches. Thus, in this example, local or internal refuges on a smaller spatial scale were important for rainbow trout, whereas life history variability and movement on a larger spatial scale was important for bull trout.

A second case study suggests the timing and location of life history events may also be important for fish population responses to fire. Novak and White (1989) attributed rapid

increases in rainbow trout density and biomass to movement of spring-spawning migratory rainbow trout in the year following a post-fire flood. In contrast, beaver dams and low discharge apparently limited access by fall-spawning migratory brown trout (Salmo trutta), and this species did not show rapid post-fire recovery (Novak and White 1989). The timing of life history events (e.g., spawning and juvenile rearing) in relation to disturbance has been found to be important for recovery of salmonids in several studies (e.g., Strange et al., 1992).

The evidence from salmonids and fishes in general (Detenbeck et al., 1992; Rieman and Dunham 2000), provides support for the general ecological mechanisms hypothesized to promote stability of populations in dynamic landscapes. The apparent relationships between habitat size, isolation, life history diversity, and response to fire may be related to the spatial and temporal dynamics of fire itself. Within individual watersheds, variability in response to fire generally occurs at spatial scales of 10^2-10^3 m, and major effects on aquatic habitats (e.g., debris flows or catastrophic flooding) are generally observed over time periods of 10^0-10^2 years (Miller et al., this issue). Even fires that cover large areas are internally patchy (Lertzman et al. 1998), leaving areas of undisturbed habitat in watersheds where fish populations may persist and recolonize disturbed areas (Rieman et al., 1997). Thus, in larger habitats, it is less likely that a fire or fire-generated disturbance will affect all occupied habitats simultaneously.

Existing evidence suggests fires and disturbance in general can pose greater threats to fishes when habitats become fragmented and otherwise altered by human activities (Figure 2). In part the continuum of hypothesized responses should also depend on habitat specificity (Figure 2; Rey-Benayas et al. 1999). For example, bull trout have

more specific habitat requirements than some other species of salmonids, and may therefore exist in more fragmented habitats, and be more sensitive to human disturbance (Lee et al. 1997). It is important to recall that habitat fragmentation involves a decline in average habitat size and connectivity among remaining habitats (e.g., by habitat loss or movement barriers). Accordingly, degradation of habitat quality should pose much greater risks to population persistence in a fragmented system (Gilpin and Soulé 1986). Characteristics of individual species may render them more vulnerable to the influences of habitat fragmentation and degradation. For example species with narrow habitat requirements (e.g., bull trout) should be more sensitive than species with more "generalist" habitat requirements (e.g., rainbow trout). Species or populations with complex life histories requiring multiple habitats (Rey Benayas et al., 1999; Rieman and Dunham 2000) may also be more vulnerable. For example, populations of rainbow trout with a dominant migratory component (e.g., anadromous "steelhead") may be more vulnerable to habitat fragmentation than populations with largely resident life histories. Though existing evidence is consistent with many aspects of ecological theory, specific guidance for identifying where and when fires pose threats to native fishes is still lacking. Thus, managers are left to rely on general conceptual guidance from theory and a handful of case studies. Attempts to focus inferences on broader (i.e., beyond case studies within individual streams) spatial and temporal patterns of responses to fire and fire-related disturbance would be useful for providing further guidance for fire management alternatives to benefit native fishes.

5. Nonnative fish invasions and fire

Although we may regard native fish populations in large, interconnected, and less degraded habitats as relatively resilient to environmental changes wrought by fire (Figure 2), one change in many systems signifies a different threat: invasions by nonnative fishes. In many instances, invasions by nonnative species may be relatively benign (Rosenzweig 2001), but there are abundant examples of the relatively rapid loss of native fishes apparently caused by nonnative species (Minckley and Deacon 1991; Young 1995; Moyle and Light 1996; Claudi and Leach 1999). How fire might influence the interaction between native and nonnative fish species is unknown but is of substantial concern.

As mentioned above, relatively few studies have documented the responses of fishes to fire. Nevertheless, there appears to be little difference in the response of native and nonnative salmonids in western U.S. streams to fire-related effects. For example, migratory nonnative rainbow trout originating from a Missouri River reservoir rapidly recolonized a tributary that had undergone floods and elevated suspended sediment concentrations following fire (Novak and White 1989), as did migratory native bull trout that refounded a population in a burned Idaho watershed (Rieman et al., 1997). Similarly, post-fire floods containing high levels of suspended sediment eliminated two isolated populations of nonnative brook trout (Salvelinus fontinalis) and rainbow trout in Arizona (Rinne 1996), and isolated populations of native Gila trout in New Mexico (Propst et al. 1992).

Moyle and Light (1996) argued that habitat degradation resulting from activities such as road building, logging, grazing, mining, water diversion, or other development tends to favor nonnative fish species. The pattern of strong populations of native salmonids in wilderness areas compared to populations elsewhere on federal lands supports this notion (Rieman and Apperson 1989; Knapp 1996; Kershner et al. 1997). Yet many of the changes in stream environments that might result in the first decade after intense wildland fire—increased sedimentation, greater channel instability, or higher nutrient concentrations—are similar to those that result from many land management practices. Thus it is plausible that severe fires may lead to conditions favoring invasions by nonnative fishes. Moreover, the effects of fires on stream habitats, particularly at lower elevations, are compounded by the legacy of human activities. Anthropogenic effects tend to be chronic and may stall or alter pathways of forest and stream recovery typical of more pristine sites (Rieman and Clayton 1997).

Moyle and Light (1996) suggested that successful invasions of nonnative fish were inevitable if the abiotic environment was suitable for their reproduction and growth. Brook trout, brown trout (Salmo trutta), and rainbow trout are widely distributed throughout the western U.S. (Young 1995; Lee et al., 1997; Fuller et al., 1999), suggesting an abundance of suitable environments. Nevertheless, there are periodic examples of the failure of these nonnative species to invade, implying biotic resistance by native fish communities or environmental resistance in the form of habitats unsuitable for invasion. Fausch et al., (2001) concluded that on a global scale, rainbow trout became successfully established in habitats outside their native range only when those habitats had hydrologic regimes resembling that of the North American Pacific Coast, and that

biotic resistance, in the form of pathogens and other fishes, also impeded their establishment in European watersheds. Perhaps the case of brook trout in the upper Snake River basin in northwestern Wyoming is analogous. Despite years of widespread stocking, brook trout have failed to establish fluvial populations in this region, which is characterized by very cold temperatures, late snowmelt runoff, high sediment loads, and marked habitat instability (Kiefling 1978), yet native cutthroat trout (Oncorhychus clarki) continue to thrive (Behnke 1992). Elsewhere, biotic and environmental resistance to invasions may be more tenuous, relying on healthy native fish populations in undisturbed habitats (Moyle and Light 1996). An example may be in central Idaho, where the upstream progression of populations of brook trout in several Idaho basins has changed little over 20 years despite the absence of physical barriers to their movement (Adams et al. 2002). Under these circumstances, short-term reductions in native fish communities and habitat disruption associated with fire may reduce the collective resistance of such watersheds to invasions, particularly if nonnative fishes dominate in waters downstream or in adjacent basins.

We have focused on the possibility that fire may increase the probability of successful invasion by nonnative fishes, but also acknowledge the alternative: fires may favor native fishes. Their evolutionary history in western U.S. streams includes exposure to a variety of climates, geologies, landscapes, and disturbances, to which the life history traits of many species may be sensitive (cf. Montgomery et al., 1999). If native fishes do tend to dominate following fire, then exclusion of fire may explain some success of nonnative species in parts of the western U.S. Moreover, short-term establishment of nonnative species following fire does not necessarily equate with permanent

displacement or replacement of native species, although we know of no examples of successful reinvasions by native species.

6. Management implications

Both ecological theory and limited empirical evidence on the responses of fish to fire and related disturbances suggests that management will be most effective when broad-scale habitat requirements are explicitly addressed. The general importance of broad-scale or watershed approaches to management of aquatic ecosystems has long been recognized (e.g., Doppelt et al. 1993; Beechie and Bolton 1999), and guidelines for watershed analyses are available for regulatory applications (e.g., Anonymous 1995). Less obvious are the specific processes that affect persistence of native fishes and invasions by nonnative species in dynamic landscapes, although habitat size, quality, and connectivity are clearly important (Figure 2). Defining the specific relevance of these landscape characteristics to fish populations is the subject of continuing study and debate (Schlosser and Angermeier 1995; Schlosser 1995; Rieman and Dunham 2000; Angermeier et al., 2002; Dunham et al., 2002), and will require close collaboration among diverse disciplines in research and management.

Given the inherent complexities of the responses we wish to understand, and our limited ability to quantify them, it is impossible to expect simple or precise management guidance. Uncertainty in particular is a key consideration because the likelihood of fire and specific responses cannot be specified with a single number. Rather, the likelihood of any event is more realistically described as a distribution of probabilities. However,

decision support systems for dealing with this type of uncertainty have been applied to many forest management problems (e.g., Marcot et al., 2001; Rieman et al., 2001).

In spite of the unavoidable complexities and uncertainties, we believe it is useful to provide a general discussion of management alternatives for dealing with fish population persistence in fire-prone landscapes. To do so, we follow the framework provided by Dale et al., (2001; Table 1), which leads to four basic fire management alternatives: 1) pre-fire management, 2) post-fire management, 3) managing fire itself (e.g., fire fighting), and 4) monitoring and adaptive management. The relative merits of these alternatives can be considered in the context of more specific fire management questions (Table 2), some of which have been addressed above (see also Bisson et al., this issue; Rieman et al., this issue), and in developing applications (e.g., Burton et al. 1999; Harkins et al. 1999; Miller et al. 1999).

The option of managing before the disturbance (pre-fire management) has some clear advantages. A proactive approach to preparing an ecosystem to be resilient in the face of fire is analogous to fire safety advice commonly dispensed to people living in the wildland-urban interface. Pre-fire management is focused on the risks posed by fire in different areas, such as the probability of ignition and fire severity (Table 2). Other considerations include subsequent effects of fires, such as increases in the likelihood of debris flows and catastrophic flooding (Cannon 1999), which in turn may depend on a variety of climatic, geological, and geomorphic conditions (Benda et al., this issue; Meyer and Pierce, this issue; Miller et al., this issue; Wondzell and King, this issue; Table 2). In pre-fire management, it is insufficient to consider the effects of fire alone, if managers are to address the full spectrum of risks. As we have discussed in this paper,

many other sources of disturbance on landscapes can interact with fire to affect native fishes. These include a variety of human influences, including habitat loss, degradation, and fragmentation, and nonnative species invasions. In places where these factors pose threats, persistence of populations is already compromised, and the effects of fire could be more severe. An improved strategy would be to implement pre-fire management actions that alleviate these human influences in places where they pose the greatest threat. Because time and resources are extremely limited, prioritization of pre-fire management activities is most likely to provide the greatest benefit to fish populations. Common examples include restoration of fish passage (WDFW 1998; GAO 2001), and management of roads (Gucinski et al., 2001; Luce et al., 2001; Roni et al., 2002).

Even in habitats with minimal human influence (e.g., wilderness and unroaded areas), the effects of fire on fish could be a concern to managers. In some cases such habitats provide important refuges for remnant populations of threatened and endangered species or endemic species that occur nowhere else. If conditions supporting these species in these habitats are likely to change in response to fire, it may be justified to exert a measured human influence to maximize their probabilities of persistence. Pre-fire management alternatives may be more challenging and controversial to identify and implement in such situations, and a comprehensive analysis of alternatives may be of particular significance (Rieman and Clayton 1997; Rieman et al., 2001).

The option of directly managing the disturbance (fire) itself may involve no action (allow fires to burn), selective suppression of some burns, or complete suppression of all fires. Fire suppression is a popular management alternative for a variety of reasons that go beyond specific concerns about fish and aquatic ecosystems. Decisions to control or

suppress fires can have both beneficial and detrimental effects on aquatic ecosystems (Rieman and Clayton 1997). Furthermore, fire suppression activities can have important direct influences on fishes and aquatic ecosystems. For example, many fire retardants are toxic to fishes, and could have detrimental influences on fish populations if applied inappropriately (Norris et al. 1991; Gaikowski et al., 1996). Physical disruption resulting from construction of roads, fire breaks, and other activities associated with fire suppression may be important as well as disruption to existing planned projects in an area subject to wildfire.

Once an area has burned, it is important to consider the range of post-fire rehabilitation options. Following fires, a variety of treatments are often rapidly applied to minimize undesirable effects (e.g., Burned Area Emergency Rehabilitation on National Forest lands), but the consequences of these treatments are poorly documented, particularly at the watershed scale (Robichaud et al., 2000). Other post-fire rehabilitation options include those mentioned for pre-fire management. But because many of the more dramatic responses of aquatic ecosystems to fire (e.g., debris flows and catastrophic flooding) tend to happen in the first few years following a fire (e.g., Figure 1), it may not be possible to complete post-fire management activities or realize a biological response from them until the major risks posed by fire have passed. For these reasons, we believe that proactive alternatives (pre-fire management) are most likely to have beneficial effects for fish, especially where habitat fragmentation and degradation have been identified as problems.

A major limitation to evaluating the relative merits of pre-and post-fire management, or managing fire itself, is lack of information. These alternatives may be complemented

by new information gained through monitoring and adaptive management. Monitoring and adaptive management are two different, but potentially complementary activities that can potentially help to better understand the effects of fire and associated management alternatives (Bisson et al., this issue). Unfortunately, managers often lack the resources to follow design and implement successful monitoring programs, and a variety of regulatory and institutional barriers can hinder adaptive management (Walters 1997; Moir and Block 2001). Even if these barriers are overcome, there are significant problems with the precision, accuracy, and utility of existing monitoring approaches, and careful attention to monitoring protocols is essential (Thompson et al., 1998). Nonetheless, continued improvements in applications of existing methods and new technologies, such as geographic information systems and remote sensing (Johnston 1999; papers in Gollberg et al. 2001), promise to increase the ability of managers to provide cost-effective information in a timely fashion.

It is apparent that managers face a growing list of problems in dealing with the impacts of fire on fish. We have emphasized the effects of fire on fish population persistence, because of the increasing influence of threatened and endangered species on land management. Other important concerns include effects of fire on productivity of key species, life history, and ecosystem effects of fish (e.g., Power 1992). The long list of issues and uncertainties may seem overwhelming, but an important part of solving any problem is to identify the elements of the problem itself. In this sense, there has been significant progress. The traditional focus on site-specific fish "populations," habitat features, and management prescriptions has been enriched by concepts and theory from new disciplines, such as landscape ecology, conservation biology, invasion biology, and

new technologies for data collection, analysis, and organization. Management policy and regulations are increasingly shaped by these influences, but specific guidance for implementation is often lacking or uncertain (Bisson et al., this issue). The challenge for providing better guidance will be to add solid empirical data and models to assess the relevance of emerging concepts and theories.

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Table 1. Four alternatives for managing disturbance (modified from Dale et al., 2001), with examples of potential management activities.

Alternative	**Examples**
Managing the system before the disturbance (pre-fire management)	• Altering habitat structure (e.g., harvest schedules and prescribed fire for riparian and upland forests, physical improvements to stream channels, mitigation of road effects) • Modifying landscape structure (e.g., enhancing connectivity among habitats, preservation or restoration of multiple, large, high quality habitats)
Managing the disturbance (managing fire itself)	• Restoration of natural processes to mimic natural variability (e.g., natural fire regimes) • Rapid responses to reduce the impacts of disturbance (e.g., active suppression of wildfires)
Managing recovery (post-fire management)	• Manage to speed recovery following a disturbance event (e.g., postfire rehabilitation)
Monitoring for adaptive management	• Measure conditions before and after disturbance to update our understanding of the influences of fire • Understand how fire interacts with other sources of disturbance • Implement studies to understand the effects of different management actions

Table 2. General considerations and specific questions to ask about the effects of fire on fishes. Examples of specific management actions that may be associated with these considerations are described above (Table 1).

General considerations	Examples of specific questions
Is fire an issue?	• What is the probability that a fire will occur in a given area? • If a fire occurs, how severe or widespread will the fire likely be? • How different are present fire regimes from "natural" fire regimes?
Physical response to fire	• What kinds of physical responses to fire are most likely (e.g., Benda, this issue; Miller et al., this issue; Meyer and Pierce, this issue; Wondzell and King, this issue)? • What is the likely spatial and temporal pattern (location, distribution, and scale) of physical responses?"
Fish population and habitat responses	• How important are likely physical responses to fish habitat and populations? • What other kinds of constraints (e.g., land use, nonnative invasions) are acting to compromise fish populations and habitats? • What are the short-term and long-term risks <u>and</u> benefits of fire and related disturbances to fish populations and habitats?
Conflicting and complementary interests	• Will fire management for aquatic resources conflict with protection of other forest values? • Where are the opportunities to benefit multiple resources (Rieman et al., 2000)?

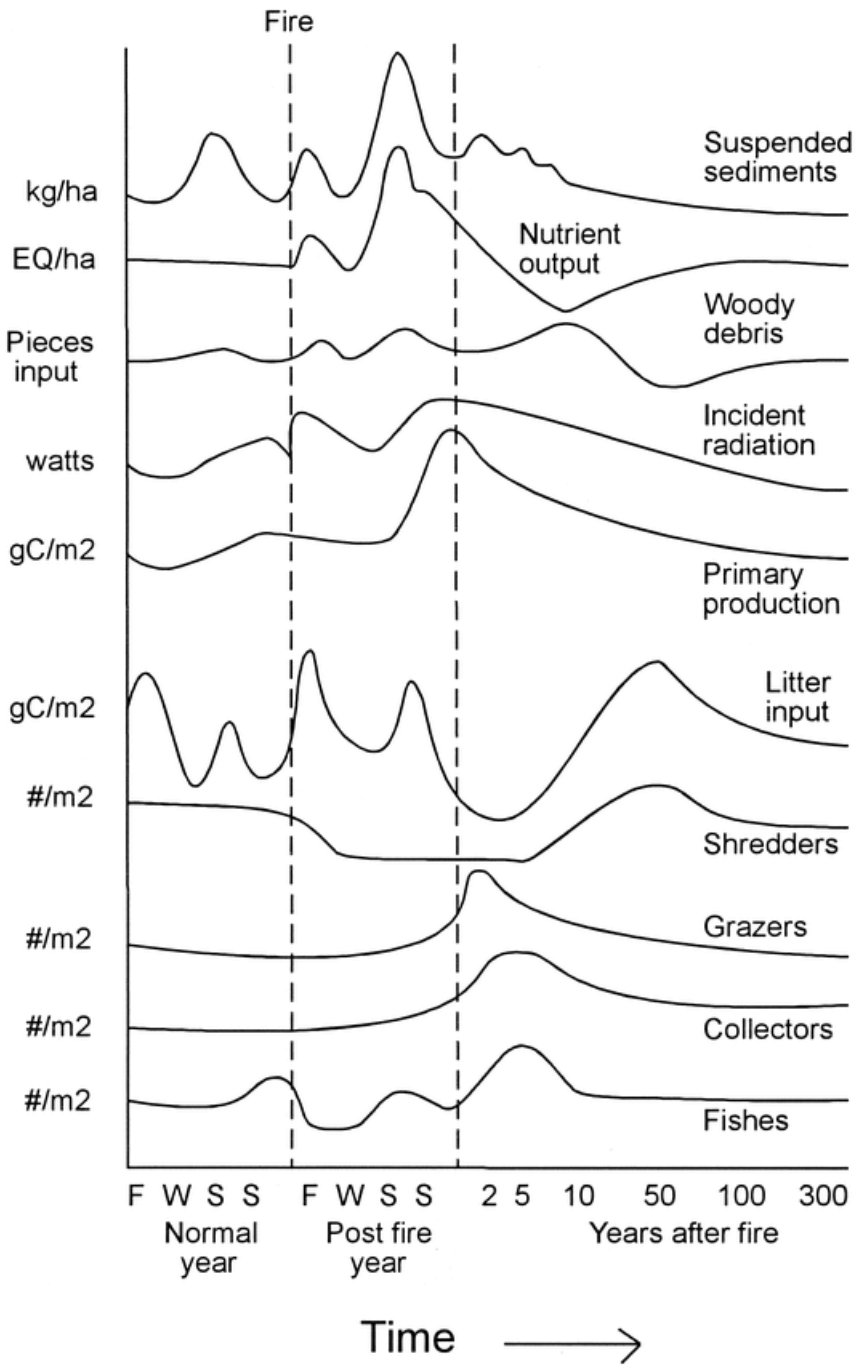

Figure 1. A generalized temporal sequence of selected events in response of aquatic ecosystems to fire (from Gresswell 1999, used by permission). Note the "pulsed" inputs of sediment and nutrients that may occur in the first few years of a fire. Other major "pulsed" fire-related disturbances, such as catastrophic debris flows or flooding in streams typically occur in the first few years following a fire.

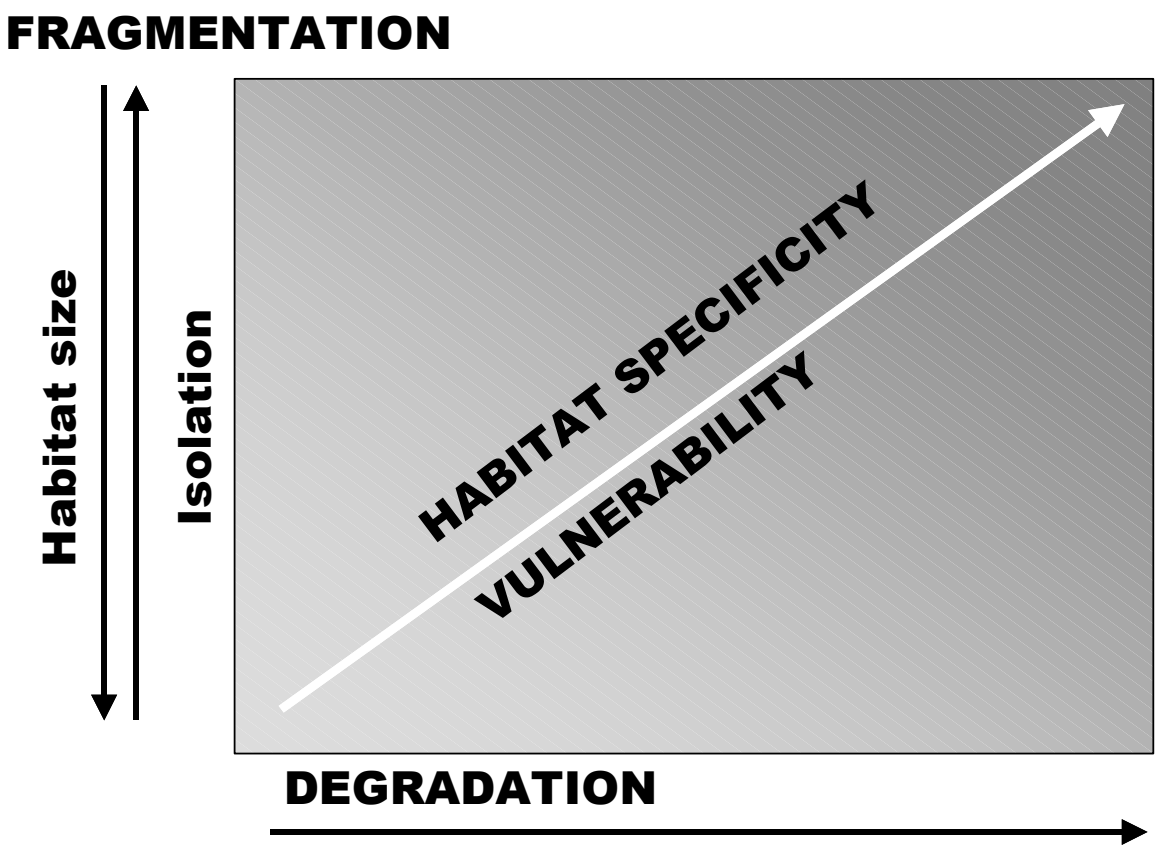

Figure 2. Illustration of hypothesized relationships between vulnerability of a species to fire, and the effects of habitat fragmentation, habitat specificity, and environmental degradation. Species with specialized habitat requirements that occur in degraded and fragmented habitats should be most vulnerable to fire and related disturbance.