

Aquatic species invasions in the context of fire and climate change

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INTRODUCTION

This paper focuses on the nexus among native and nonnative fishes with respect to fire and climate change in the western U.S. Although many taxa are involved, I emphasize native and nonnative salmonids because these are obligate coldwater species that might be expected to respond strongly to fire and because most research has been conducted on these fishes. Also, forested lands in federal ownership in the western U.S. represent the stronghold for many native coldwater taxa and are the subject of fire, fuels, and water management. I caution, however, that climate change, coupled with a growing human population and increasing demands for certain ecosystem services (e.g., water for domestic, agricultural, and industrial use) may alter the species of concern, their interaction, and the geographic focus of this issue.

OVERVIEW: NONNATIVE AQUATIC SPECIES

In waters of the western U.S., invasions of nonnative aquatic species are both exceptionally frequent and frequently detrimental to native aquatic species. For example, in Oregon, Washington, and Idaho, 120 nonnative forms of fish, crustaceans, mollusks, and amphibians have become established, and nonnative species constitute about half of the taxonomic diversity of fishes in these three states (ISAB 2008; Sanderson et al. 2009). Declines in native species have coincided with the establishment of these nonnative taxa. All inland forms of trout and charr in the western U.S.—the subspecies of cutthroat trout (*Oncorhynchus clarkii*), Gila trout (*O. gilae gilae*), Apache trout (*O. g. apache*), and bull trout (*Salvelinus confluentus*)—have been proposed for federal listing under the Endangered Species Act or are currently listed, and nonnative species invasions have been identified as a cause of decline in all petitions and recovery plans. Moreover, introductions of nonnative species are expected to continue because of the growing globalization in trade that intentionally or inadvertently includes many new species (Cox 2004). Vehicle-based aquatic recreation also facilitates their spread; nonnative mussels, aquatic plants, and pathogens are being distributed throughout the country amid debris on boats, boat trailers, and perhaps even on wading boots (Gates 2007; Idaho Invasive Species Council 2007; Benson and Raikow 2009). In the late 19th and 20th centuries, state and federal agencies introduced many nonnative fishes to promote fishing, but more recently illegal angler-assisted transport of sportfish or baitfish is the leading cause of the spread of nonnative fishes (Rahel 2004). Many of these species form the basis of economically valuable and socially prized fisheries, even in remote wilderness settings (Dunham et al. 2004). Consequently, the enhancement, monitoring, or control of nonnative aquatic species is often a management priority.

What facilitates invasions?

Although invasions of nonnative species are common, they are not necessarily inevitable (e.g., Fausch et al. 2001). Invasion success is in part attributable to propagule pressure, because the number of introductions and number of individuals introduced is positively correlated with establishment (Lockwood et al. 2005). A second characteristic leading to establishment is habitat matching, in which the receiving environment is suitable for an introduced species throughout its life history. For example, many high mountain lakes provide excellent conditions for the growth

and maturation of introduced salmonids stocked for angling, but because they lack inlets or outlets with fluvial spawning habitat, these populations decline relatively rapidly unless they are refounded by stocking. Alternatively, where such spawning habitats are present, nonnative trout readily establish in many instances and these locations serve as springboards for invasions elsewhere in a watershed (Adams et al. 2001). This points out another aspect of successful invasions: spread. Watershed connectivity permits nonnative fishes to move throughout a basin, sometimes with surprising speed. Brook trout (*Salvelinus fontinalis*) that were passed over a migration barrier in a small Wyoming stream were found up to 4 km upstream within a month (M. K. Young, unpublished data), and summer movements of 2-3 km by this species are common (Gowan and Fausch 1996). Iowa darters (*Etheostoma exile*), native to the Mississippi River basin, were first detected in the Yampa River in the Colorado River basin in 2003; by 2007, they were observed 229 km downstream in the Green River in Utah (Walford and Bestgen 2008).

Nevertheless, invasions of nonnative species sometimes stall or remain relatively contained even when abiotic conditions appear favorable for their advance. Adams et al. (2002) noted that the upstream extent of brook trout in several Idaho watersheds had remained unchanged over two decades despite the absence of migration barriers. In some cases this has been ascribed to introduced populations requiring extended periods of time to overcome small initial populations, as well as a delayed increase in fitness as natural selection operates on the genome of the founding individuals or new arrivals contribute genomic diversity (Carroll et al. 2007; Roman and Darling 2007). It has been posited that strong populations of native fishes may prevent or delay nonnative invasions, but presently there appears to be little empirical support for this hypothesis (Moyle and Light 1996).

Some examples of invasive species and their effects

The responses of native aquatic species to nonnative invasions are mixed. In some locations, native fishes have persisted in sympatry with nonnative fishes for extended periods, and in others nonnatives rapidly replaced the indigenous fauna. These responses have sometimes involved the same native-nonnative species pairs. Because the effects of introductions are specific to the native and the introduced taxa, I focus this discussion on the effects of three nonnative trout—brook trout, brown trout (*Salmo trutta*), and rainbow trout (*O. mykiss*)—on cutthroat trout native to the inland western U.S.

Brook trout and brown trout

Brook trout have been linked to the loss of headwater populations of cutthroat trout in many portions of the inland West (Behnke 1992; Young 1995; Dunham et al. 1999). Often, the mortality of young cutthroat trout exposed to brook trout is high enough to produce recruitment failure (Dunham et al. 2002; Shepard et al. 2002; McGrath and Lewis 2007). Peterson et al. (2004) demonstrated that age-0 cutthroat trout survival was near zero in the presence of brook trout, and that the suppression of brook trout led to large increases in survival of age-0 and age-1 fish. Yet how brook trout replace cutthroat trout remains unknown. Both competition and predation have been suggested as mechanisms that may work in concert with the tendency for brook trout to mature at younger ages and have greater size-specific fecundity than do cutthroat trout (Kennedy et al. 2003).

Brook trout, however, are not universally successful at displacing cutthroat trout from small streams. Whereas cutthroat trout populations east of the Continental Divide in Montana appear particularly vulnerable to displacement, similar populations to the west have persisted in sympatry for decades. This difference may be attributable to differences in winter climate (Shepard 2004; Fausch et al. 2006). This geographic difference also coincides with the prevalence of large cutthroat trout with fluvial life histories that may provide a demographic buffer to the presence of brook trout. And at smaller scales, the distribution of habitats serving as demographic sources—such as warmer water or reaches in unconfined river valleys (Benjamin et al. 2007)—and sinks could be controlling brook trout establishment and spread (Adams 1999; Castric et al. 2001; Petty et al. 2005).

The effects of brown trout on inland cutthroat trout are less studied, but appear to be similar to those of brook trout. Brown trout have been shown to be competitively superior to cutthroat trout in laboratory trials (Wang and White 1994) and field enclosures (McHugh and Budy 2005). In addition, de la Hoz Franco and Budy (2005) felt that the presence of brown trout truncated the downstream distribution of Bonneville cutthroat trout (*O. c. utah*) in the Logan River, and McHugh and Budy (2006) observed an array of subtle but significant changes in the growth and behavior of cutthroat trout in the presence of brown trout. The influence of brown trout on cutthroat trout appears to have a geographic signature; the most pronounced effects are on Rio Grande cutthroat trout (*O. c. virginalis*) in New Mexico (Paroz 2005) whereas there are many examples of long-term sympatry between more northerly subspecies of cutthroat trout and brown trout. An important element that may be facilitating coexistence at higher latitudes is that brown trout tend to be found in larger streams at lower elevations and do not occupy many tributaries used by cutthroat trout for spawning, reducing interactions between brown trout and juvenile cutthroat trout. This downstream-upstream partitioning of stream habitats by brown trout and other salmonids (Weigel and Sorensen 2001) and their absence from small, high-elevation streams in the central Rocky Mountains (Bozek and Hubert 1992; Rahel and Nibbelink 1999) is thought to be related to their poor recruitment at low water temperatures (Jensen and Johnsen 1999; McHugh and Budy 2005). Because brown trout eggs and fry are also vulnerable to high flows during the latter part of incubation through the early stages of emergence (Lobón-Cervía and Mortensen 2005), the timing of peak discharge in these environments may also present an obstacle to more-upstream invasions.

Rainbow trout

Rainbow trout from coastal streams in the western U.S. have been widely introduced into inland waters originally containing cutthroat trout (Behnke 1992). Despite that these species tend to spawn at different times—cutthroat trout usually spawn after peak flows and rainbow trout before them—and in different places—cutthroat trout more often use small tributaries (De Rito 2004; Muhlfeld 2008)—hybrids frequently appear where the species co-occur (Shepard et al. 2005). These hybrids are fertile and are capable of backcrossing with genetically pure fish of either source and with other hybrids, leading to introgression of nonnative genes into the cutthroat trout population. The spread of nonnative genes appears to rely primarily on straying by hybrid cutthroat trout rather than pure nonnative trout (Hitt et al. 2003; Rubidge and Taylor 2004), although feral populations of rainbow trout in river main stems or a reservoir have also been implicated (Weigel et al. 2003; Rubidge and Taylor 2005). First-generation hybrids do not appear to be at a selective disadvantage relative to parental stocks, but the fitness of later-

generation hybrids is greatly reduced (Muhlfeld 2008). Despite this, introgression appears to progress via occasional reproductive bonanzas from hybrids and from rainbow trout parental stock (Muhlfeld 2008), and eventually rainbow trout genes may pervade virtually all remaining individuals to produce a hybrid swarm within a particular area (Allendorf et al. 2001).

Although the probability of hybridization tends to rise with the number of introductions (Colautti 2005), spatial patterns in the distribution of nonnative genes are complex. Weigel et al. (2003) reported that proximity to a source of stocked fish was only weakly related to hybridization between cutthroat trout and rainbow trout. Instead, larger streams at lower elevations were more likely to contain hybridized populations regardless of stocking location. They argued that isolating mechanisms, such as different spawning and emergence times or habitat preferences between adults of each species, were preventing hybridization from developing in headwater populations of cutthroat trout (Henderson et al. 2000; Ostberg and Rodriguez 2006). In contrast, Hitt et al. (2003), Rubidge and Taylor (2005), and Muhlfeld (2008) detected the upstream progression of hybrids between rainbow trout and cutthroat trout over time, and concluded that hybrid swarms would eventually occupy most of these waters except those with migration barriers.

DO FIRES FAVOR NONNATIVE FISHES?

The immediate and long-term effects of wildfire on aquatic ecosystems and fish populations are the subject of this volume (Rieman et al., this volume) and of previous syntheses (Gresswell 1999; Young et al. 2003), thus are reviewed only briefly here. The thermal or water chemistry changes associated with severe wildfire have led to direct mortality of trout populations (Rinne 1996; Howell 2006), although many populations have endured such fires with few or no ill effects or showed only temporary declines (Rieman and Clayton 1997; Burton 2005; Sestrich 2005). More problematic may be post-fire floods, blackwater events, and debris torrents triggered by summer thunderstorms that have reduced or eliminated salmonid populations (Bozek and Young 1994; Brown et al. 2001). Nevertheless, the majority of events are in small (<2.6 km²), steep (>20%) basins (Parrett et al. 2003), and these would usually not threaten entire populations (Rieman and Clayton 1997; but see Brown et al. 2001). The probability of such events often declines rapidly in subsequent years (Cannon 1999).

Secondary effects of fire may depress or boost populations. Channel stability often declines following fire because of the loss of riparian vegetation, increases in stream flow produced by reductions in evapotranspiration, and increases in sediment, but regrowth and resprouting of vegetation eventually attenuate off-channel contributions of sediment and water. Infall of fire-killed snags will spike in the first few decades following fire (Lyon 1984; Bragg 2000), which may lead to extremely complex channels with an array of complementary habitats. Growth rates of salmonids in burned streams have been observed to increase (Dunham and Rosenberger, this volume). Although this may in part be attributable to temporary changes in water chemistry, it is more likely that decreased shading increases primary productivity that leads to greater macroinvertebrate abundance and food availability (Wilzbach et al. 2005). Because water temperatures are directly related to the amount of solar radiation reaching the water surface (Johnson 2004), post-fire temperatures tend to increase, sometimes by several degrees (Dunham et al. 2007; Mahlum et al. 2011). Warming may harm or bolster population growth rates depending on the pre-fire temperature regime (Dunham et al. 1999; Harig and Fausch 2002;

Schrank et al. 2003). Streams previously too cold for consistent reproduction or rapid growth may support larger, more stable populations, whereas those that are already relatively warm may become seasonally uninhabitable. Both conditions will gradually revert to their original state as canopy cover and stream shading increase (Luce et al., this volume), given that climatic patterns remain relatively constant.

It is sometimes thought that habitat degradation and disturbance in fluvial systems favors nonnative species either by creating conditions more suitable for them or by depressing the abundance of native species (ISAB 2008). Consequently, it has been hypothesized that post-fire habitats with increased water temperature, light, sediment transport and deposition, and channel instability may favor nonnative salmonids (Dunham et al. 2003). At present, there is little evidence to refute or support this hypothesis. Similar to native salmonids, nonnative brook, brown, and rainbow trout have occasionally been eliminated from headwater streams during or after severe fires (Rinne 1996; Burton 2005). Furthermore, connectivity with unaffected portions of a watershed has facilitated the rapid recolonization of post-fire habitats (Novak and White 1990; Howell 2006), as has been observed for native species (Rieman and Clayton 1997).

Evaluations of the post-fire responses of sympatric populations of native and nonnative salmonids are more informative, but few such studies have been done (but see Howell 2006). One example involved monitoring the response of several native and nonnative species of salmonids in small watersheds throughout the Bitterroot River basin following fires in 2000 (Sestrich 2005; Sestrich et al. 2011). Declines in or the extirpation of all salmonid species were observed in some but not all of the watersheds that experienced high-severity fire. Where such declines were observed, westslope cutthroat trout (*O. c. lewisi*) and bull trout tended to recover rapidly and sometimes exceeded pre-fire abundances within 3 years. In contrast, brook trout were slower to respond and in some cases their abundance remains depressed (M. Jakober, Bitterroot National Forest, unpublished data). Brown trout, however, appeared in several monitoring reaches for the first time after the fires. Whether this was attributable to suitable post-fire environments or their ongoing population growth in river main stems (C. Clancy, Montana Fish, Wildlife and Parks, unpublished data) is uncertain.

In summary, there is little evidence that nonnative fishes show greater resistance to short-term habitat changes wrought by severe fire than do native species. Moreover, some native species may exhibit greater resilience to fire-related disturbance, in part because this represents a portion of the disturbance regime with which they evolved (Lytle and Poff 2004; Waples et al. 2008). Nonetheless, I caution against generalizing the results of the limited research on this issue because the severity of habitat alteration, the environmental context of affected streams (e.g., their position in the watershed and arrangement of habitats), and the aquatic community (e.g., the abundance, diversity, and life histories of native and nonnative species) will influence the outcome. Because post-fire habitat changes—particularly warmer water temperatures—may persist for decades or centuries, long-term shifts to nonnative species remain possible.

CLIMATE CHANGE, FIRE, AND NONNATIVE FISHES

Climate change is expected to alter global patterns in the distribution of flora and fauna (Wilson et al. 2005). Based on recent modeling (IPCC 2007), climate in the western U.S. is projected to warm substantially before the end of this century. In montane environments, this warming is

expected to cause more winter precipitation to fall as rain rather than snow (Knowles et al. 2006), leading to smaller winter snowpacks (Mote et al. 2005). In many streams in this region, earlier runoff and a longer low flow period are already evident (Stewart et al. 2005), and greater flow intermittency in summer is anticipated (Boughton et al. 2009). Besides discharge, the primary change in physical habitat is expected to be an increase in water temperature. As a consequence, populations of obligate coldwater species such as salmonids are predicted to retreat upstream to smaller waters to track suitable thermal environments (Rieman et al. 2007; Wenger et al. 2011a,b) and more temperature tolerant species will likely spread upstream as well (Rahel and Olden 2008). Initially, these may include nonnative coldwater species that prefer slightly warmer temperatures e.g., brown trout (McHugh and Budy 2005) and rainbow trout (Sloat et al. 2002; Bear et al. 2007), but additional warming may favor coolwater species such as smallmouth bass (*Micropterus dolomieu*; Sharma and Jackson 2008), which are already widely distributed and expanding in rivers in the inland West (LaVigne et al. 2008; Walford and Bestgen 2008). Mobile life history forms of native species that migrate downstream will encounter a gauntlet of potentially hostile nonnative species as well increasing areas of thermally unsuitable habitat and larger numbers of barriers to movement; selection against such forms may strongly favor resident life history strategies. Thus, the collective consequences of these changes will be to reduce overall occupied habitat and exacerbate the current patterns of population isolation for native coldwater fishes (Neville et al., this volume).

Climate change is also expected to increase the frequency, severity, and extent of fires (Westerling et al. 2006). Combined effects of climate change and fire would place fish populations at even greater risk of extirpation during or shortly after severe wildfire because of low or no connectivity, fewer refuges, and smaller occupied habitats (Isaak et al., this volume). Thereafter, the loss of shading from stand-replacing fire in riparian zones and from associated debris torrents may further increase water temperatures to the extent that some sites may become uninhabitable for coldwater species. Moreover, climate warming coupled with severe fire may cross an ecological threshold that results in state changes in some forested basins in the western U.S. This might include a shift from forest types adapted to infrequent severe fire to those tolerant of more frequent fire (Keane et al. 2008) or from forested areas to grasslands (Schoennagel et al. 2008). Such wholesale changes in the terrestrial vegetation and disturbance dynamics would alter stream conditions, probably leading to additional upstream incursions of nonnative species and the further diminution of habitats occupied by native coldwater fauna.

Climate change, fire, and nonnative species invasions are likely to redirect future management efforts. Whereas the present emphasis is on in situ habitat and population protection and restoration, in the future population salvage (Brooks 2006), assisted migration (cf. Millar et al. 2007), anthropogenic refounding, thermal mitigation (e.g., by increasing and retaining shading), and refuge designation (e.g., finding those areas most likely to provide suitable habitats for native species despite climate change) may assume importance as management tools in pre- and post-fire environments. The changing management of other resources may also provide some unforeseen opportunities for aquatic species management. The predicted decline in surface water available for human use under many climate change scenarios has led to proposals to build additional high-elevation reservoirs to store water for late summer release (Bates et al. 2008). Such waters could become de facto refuges of native species that tolerate or require lentic habitats, and reservoir releases could increase (and sometimes cool) streamflow adequately to

maintain coldwater species downstream. This should not be regarded as a panacea for native fish; reservoirs are often the target for nonnative species introductions that then spread elsewhere (Havel et al. 2005).

There is substantial uncertainty associated with the rate of change and locations most likely to experience the greatest effects from climate change, in part because of the low predictability of whether, when, and how much major drivers of global climate, such as the North Atlantic circulation and El Niño-Southern Oscillation, will contribute (Kriegler et al. 2009). Nevertheless, all trends and forecasts suggest a substantially altered and warmer climate in the western U.S. in this century. Retaining ecosystem services and providing habitats suitable for the persistence and evolution of the native aquatic fauna (Dunham and Rosenberger, this volume) under the constraints imposed by a changing climate, altered disturbance regime, and array of exotic newcomers represents a critical challenge in the not-so-distant future.

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