Fish Life Histories, Wildfire, and Resilience—A Case Study of Rainbow Trout in the Boise River, Idaho

Amanda E. Rosenberger[1], Jason B. Dunham[2], and Helen Neville[3]

[1]School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK

[2]U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, OR

[3]Trout Unlimited, Boise, ID

Introduction

In this short piece we address the question of how aquatic ecosystems and species can change in response to disturbances, such as those related to the influence of wildfire on stream ecosystems. Our focal species is rainbow trout (*Oncorhynchus mykiss*) in the Boise River, Idaho. Rainbow trout in this system have persisted in the face of widespread and often severe wildfires occurring since the 1990s (Rieman and others 1997; Burton 2005; Dunham and others 2007).

Wildfire can lead to a variety of changes in stream environments (Minshall 2003). In the Boise River, recent wildfires ranged from light to severe burns (Dunham and others 2007), leading to variable changes in riparian and hillslope vegetation, and in some cases initiation of major channel reorganizing events (Benda and others 2003; Miller and others 2003). These events often involved massive erosion of stream channels, sometimes throughout an entire tributary. In the latter case, local populations of rainbow trout were reduced to undetectable levels (Burton 2005). In others, a patchwork of wildfire appeared to eliminate rainbow trout from some reaches of stream, but not others (Rieman and others 1997). Following these wildfires, water temperatures remained elevated for several years, particularly for streams influenced by channel reorganization (Dunham and others 2007; Figure 1). In spite of these dramatic environmental changes, rainbow trout have remained widespread in streams within the Boise River (Dunham and others 2007). What characteristics of this species' biology have conferred resilience in the face of these massive disturbances? What constraints may limit resilience?

One key to species resilience may be the expression of diverse and flexible life histories (Bisson and others 2009; Healey 2009; Waples and others 2009; Greene and others 2010). Our work on rainbow trout suggests the species is flexible in terms of how individuals and populations respond to variable environments, and that responses can be constrained by human influences that alter natural variability. The two major constraints we focus on here are invasions of nonnative trout (Neville and Dunham, in press) and loss of connectivity caused by stream culverts that block fish passage (Neville and others 2009).

Our work in the Boise River focused on smaller streams because both physical (Benda and others 2003; Miller and others 2003; Wondzell and King 2003) and biotic responses to wildfire may be more evident (Dunham and others 2003; Gresswell 1999; Minshall 2003). We recognized three broad classes of streams (Dunham and others 2007): 1) those lacking a recent history of wildfire; 2) streams with a recent history of moderate to high severity wildfire; and 3) streams in watersheds with a recent history of moderate-high severity wildfire that were followed by massive channel reorganization from a debris flow or severe flood. These events

Figure 1. Immediate aftermath of the 2003 Hot Creek Fire in the Boise National Forest. Pictured stream is a fish-bearing tributary to the upper Middle Fork Boise River (photo credit: Joseph Benjamin).

(fires, channel reorganization) occurred from 8-10 years prior to when we sampled fish, allowing for at least 2-3 generations of local reproduction.

We examined patterns of population density among these three classes of streams (for methods see Rosenberger and Dunham 2005; Dunham and others 2007), and found that density of age 1+ fish differed among the three classes of streams (Kruskal-Wallis Analysis of Variance, X^2=5.96, *df*=2, p = 0.02). In streams without a recent history of wildfire densities of age 1+ fish were highest (0.22 fish/m^2), those in burned streams were intermediate (0.17 fish/m^2), and densities in reorganized streams were lowest (0.05 fish/m^2).

The sizes of fish at different ages were also different among streams. For the youngest three age classes (0+, 1+, 2+), fish were smallest in unburned streams and largest in reorganized streams (A. Rosenberger and J. Dunham, unpublished). This paralleled the pattern of water temperature in these streams, with unburned streams being coldest and reorganized streams being warmer (Dunham and others 2007). Warmer water temperatures could lead to faster metabolism and growth, if sufficient food is available (Hughes and Grand 2000). Additionally, fish in warmer streams may experience a longer growing season, and thus more opportunity to gain a larger size. Even though summer temperatures in the warmest streams exceeded levels that can be stressful to individuals, availability of suitable temperatures in spring and fall can still lead to faster growth (e.g., Tattam 2007). Faster growth may also be attributed to lower population densities and less intraspecific competition (Grant and others 1998; Ward and others 2006), especially in reorganized streams.

In parallel with growth, age at maturity was youngest in the warmer reorganized streams (A. Rosenberger and J. Dunham, unpublished data). A few individuals in reorganized streams began maturing as early as their first summer (age 0+), with the frequency of mature individuals increasing in the 1+ and 2+ age classes. By age 1+, we observed that 27% of the total number of fish sampled were mature, with males predominating among mature individuals (83% of total mature individuals). For the age 1+ cohort, larger males and females were much more likely to be mature. By age 2+ the length differences were no longer significant, perhaps reflecting the influences of size-selective mortality or emigration. In other words, fish that grew faster and matured at age 1+ may have reproduced and died, thus leaving behind only slower growing fish in the 2+ age class, or older fish may have emigrated. The pattern of growth and maturity we observed has been observed repeatedly in other salmonids grown in captivity (Wysujack and others 2008) and in the field (Olsson and others 2006; McMillan and others, in press).

We also compared genetic responses of rainbow trout to changes in habitat associated with wildfire in the Boise and adjacent Payette River basins (Neville and others 2009). We hypothesized that disturbances associated with wildfire and channel reorganization should lead to losses of genetic variation within local populations. Given that populations can potentially be extirpated by disturbances associated with wildfires (Burton 2005), or reduced in distribution (Rieman and others 1997) or abundance (see above), it is reasonable to expect that genetic drift may lead to losses of genetic diversity.

We surveyed genetic variability in samples of rainbow trout collected from 55 small streams representing gradients of disturbance that paralleled our fish population surveys (Dunham and others 2007). We found that variability was similar among streams representing unburned, burned, and reorganized classes, as described above. In contrast, in streams that were isolated by human-caused fish passage barriers (impassable road culverts), we found losses of genetic variability were more likely, as has been found consistently in many similar studies (Neville and others 2006). In some locations, we found unexpectedly high levels of hybridization with nonnative cutthroat trout (*O. clarkii*) and hatchery rainbow trout introduced historically for sport fisheries, although hybridization was not related to fire history (Neville and others 2009; see also Neville and Dunham, in press). Overall, genetic variability within populations was most strongly associated with habitat size, with greater diversity observed in larger habitats. These results highlighted the importance of habitat size and connectivity, both critical factors influencing the resilience of fish in dynamic environments (Rieman and Dunham 2000; Dunham and others 2003; Bisson and others 2009).

In summary, we observed responses of individuals and populations in association with influences of wildfire (e.g., increased water temperatures), and in association with human influences, such as fragmentation of habitat and introductions of nonnative trout. Fish in streams most dramatically impacted by wildfires grew faster, but matured earlier in life with some evidence for shorter overall lifespan resulting from early reproduction. In non-scientific terms, these fish appeared to adopt a "live fast – die young" strategy, but the genetic basis of these responses is unknown. More recent changes, such as loss of genetic variability and changes in allele frequencies due to hybridization were linked to human influences.

Implications for Species Resilience In the Face of Disturbance

In the case of responses of rainbow trout to wildfire and other human influences in the Boise River, we find that wildfire changes both ecosystems and species. We also found that human influences have fragmented habitats (e.g., movement barriers at road crossings) and constrained opportunities for rainbow trout to express its full range of life histories (e.g., because of hybridization with nonnative trout). These constraints appear to operate in ecological time, but ultimately may also constrain the evolutionary potential of rainbow trout. For example, if isolated populations lose substantial amounts of genetic variability or if genomes become compromised by hybridization with nonnative cutthroat trout these fish may have less capacity for evolutionary responses to their environment. Maintaining opportunities for natural expression of diverse phenotypes may be critical to long-term productivity, persistence, and continued evolutionary resilience of rainbow trout (Bisson and others 2009; Healey 2009; Waples and others 2009; Greene and others 2010).

We found human influences within local habitats to be important, but human impacts may stem from influences or constraints operating much further downstream. For example, major dams in place in the Boise River and downstream in the Snake River have prevented migration of rainbow trout to the sea to express a "steelhead" life history. Steelhead trout were common in the Boise River and other nearby streams prior to their extirpation by these large dams (Busby and others 1996). In locations where migratory fish are available to recolonize empty habitats, populations can be highly resilient to disturbance. Examples include migrants within freshwater systems (e.g., Rieman and others 1997; Dunham and others 1997), but also migrants from marine ecosystems, such as salmon and steelhead (Bisson and others 2005; Howell and others 2006; Bisson and others 2009).

Even without a steelhead life history present, freshwater resident rainbow trout appear resilient in the face of wildfire, except in the smallest and most isolated habitats, as would be expected in theory and from the few empirical data available for salmonid fishes (Dunham and others 2003). Resilience is shown in the ability of rainbow trout to rapidly recolonize habitats following disturbance, variable responses to changing environments (e.g., growth, age at maturity), and maintenance of large enough numbers of adults to avoid genetic drift in the face of disturbance. Lower resilience is evident when other constraints imposed by humans (e.g., movement barriers, nonnative trout) limit the species' ability to respond to disturbance (Bisson and others 2009; Healey 2009; Waples and others 2009; Greene and others 2010).

Finally, results of this work point to the importance of evaluating multiple responses of a species to wildfire. If, for example, we had relied only on ecological responses, we would have missed critical threats posed by intra and inter-specific hybridization. Furthermore, evaluating only distribution or abundance of a species provides only limited insights into possible mechanisms contributing to resilience. This has important implications for evaluating potential effects of wildfire or fire management alternatives on aquatic species. Whereas it is obvious that we need to understand more about processes that contribute to species responses to wildfire, studies of species responses typically address only the net results of such processes: presence or abundance. Because both of these responses can be influenced by multiple underlying processes, presence or abundance can offer only limited insight into the complex interplay of the underlying genetic, environmental, and demographic drivers. In conclusion, to better understand species responses in the face of changes in aquatic ecosystems caused by wildfire (or any other disturbance) we need to better understand the processes that constrain or contribute to resilience.

Acknowledgements

Thanks to Bruce Rieman and David Pilliod for constructive comments on an earlier version of this manuscript.

References

Armstrong J. D., P. S. Kempa, G. J. A. Kennedy, M. Ladle, N. J. Milner. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fisheries Research 62: 143-170.

Benda, L. E., D. J. Miller, T. Dunne, G. H. Reeves, and J. K. Agee. 1998. Dynamic landscape systems. Pages 261-288 in R. J. Naiman and R. E. Bilby, editors. River ecology and management. Springer, New York, N.Y., USA.

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, M. Pollock, and G. Pess. 2004. The network dynamics hypothesis: how river networks structure riverine habitats. BioScience 54: 413-427.

Bisson, P. A., J. B. Dunham, and G. H. Reeves. 2009. Freshwater ecosystems and resilience of Pacific salmon: habitat management based on natural variability. Ecology and Society 14: 45. [online] URL: http://www.ecologyandsociety.org/vol14/iss1/art45/.

Burton, T. A. 2005. Fish and stream habitat risks from uncharacteristic wildfire: observations from 17 years of fire-related disturbances on the Boise National Forest, Idaho. Forest Ecology and Management 211: 140-149.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of West Coast steelhead from Washington, Idaho, Oregon, and CaliforniaNOAA Tech. Memo. NMFS-NWFSC-27. United States Department of Commerce. 275 pp.

Dunham, J. B., M. K. Young, R. E. Gresswell, and B. E. Rieman. 2003. Effects of fire on fish populations: landscape perspectives on persistence of native fishes and nonnative fish invasions. Forest Ecology and Management 178:183-196.

Dunham, J. B., Vinyard, G. L. & Rieman, B.E. 1997. Habitat fragmentation and extinction risk of Lahontan cutthroat trout. North American Journal of Fisheries Management 17: 910-917.

Dunham, J. B., A. E. Rosenberger, C. H. Luce, and B. E. Rieman. 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. Ecosystems 10: 335-346.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169-175.

Fausch, K. D., B. E. Rieman, J. B. Dunham, M. K. Young, and D. P. Peterson. 2009. Invasion versus isolation: trade-offs in managing native salmonids with barriers to upstream movement. Conservation Biology 23: 859-870.

Grant, J. W. A., S. Ó. Steingrímsson, E. R. Keeley, and R. A. Cunjak. 1998. Implications of territory size for the measurement and prediction of salmonid abundance in streams. Canadian Journal of Fisheries and Aquatic Sciences 55(Suppl. 1): 181-190.

Greene, C. M., J. E. Hall, R. K. R. Guilbault and T. P. Quinn. 2010. Improved viability of populations with diverse life history portfolios. Biology Letters. 6: 382-386.

Gresswell, R. E. 1999. Fire and aquatic ecosystems in forested biomes of North America. Transactions of the American Fisheries Society 128: 193-221.

Healey, M. C. 2009. Resilient salmon, resilient fisheries for British Columbia, Canada. Ecology and Society 14(1): 2. [online] URL: http://www.ecologyandsociety.org/vol14/iss1/art2/.

Heck, M. P. 2007. Effects of wildfire on growth and demographics of coastal cutthroat trout in headwater streams. M.S. Thesis, Oregon State University, Corvallis, OR. 77 pp.

Hendry, A. P. and S. C. Stearns, editors. 2004. Evolution illuminated: salmon and their relatives. Oxford University Press, Oxford, U.K.

Howell, P. J. 2006. Effects of wildfire and subsequent hydrologic events on fish distribution and abundance in tributaries of North Fork John Day River. North American Journal of Fisheries Management. 26: 983-994.

Hulse, D. and S. V. Gregory. 2004. Integrating resilience into floodplain restoration. Urban Ecosystems 7: 295-314.

Hughes, N., and Grand, T. 2000. Physiological ecology meets the ideal-free distribution: Predicting the distribution of size-structured fish populations across temperature gradients. Environmental Biology of Fishes 59: 285-289.

Isaak, D. J., Thurow R. F., Rieman B. E. and Dunham J. B. 2003. Temporal variation in synchrony among chinook salmon (*Oncorhynchus tshawytscha*) redd counts from a wilderness area in central Idaho. Canadian Journal of Fisheries & Aquatic Sciences 60: 840–848.

Isaak, D. J., C. H. Luce, B. E. Rieman, D. E. Nagel, E. E. Peterson, D. L. Horan, S. Parkes, and G. L. Chandler. 2010. Effects of climate change and recent wildfires on stream temperature and thermal habitat for two salmonids in a mountain river network. Ecological Applications 20: 1353-1371.

Jonsson, B. & Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3: 348-365.

Leu, M., Hanser, S. E., Knick, S. T. 2008. The human footprint in the West: a large-scale analysis of anthropogenic impacts: Ecological Applications 18: 1119-1139.

McMillan, J. R., J. B. Dunham, G. H. Reeves, J. S. Mills, and C. E. Jordan. In press. Individual condition and stream temperature influence early maturation of rainbow and steelhead trout, *Oncorhynchus mykiss*. Environmental Biology of Fishes.

Miller, D., C. Luce, and L. Benda. 2003 Time, space, and episodicity of physical disturbance in streams. Forest Ecology and Management 178: 121-140.

Minshall G.W. 2003. Responses of stream benthic macroinvertebrates to fire. Forest Ecology and Management 178: 155-162.

Neville, H., Dunham, J. B., Peacock, M. 2006. Assessing connectivity in salmonid fishes with DNA microsatellite markers. Pages 318-342 in Crooks, K. R., Sanjayan, M., editors. Connectivity conservation, Conservation Biology Series No. 14. Cambridge University Press, Cambridge, UK.

Neville, H., J. Dunham, A. Rosenberger, J. Umek, and B. Nelson. 2009. Influences of wildfire, habitat size, and connectivity on trout in headwater streams revealed by patterns of genetic diversity. Transactions of the American Fisheries Society 138: 1314-1327.

Neville, H., and J. Dunham. In press. Patterns of hybridization of non-native cutthroat trout and hatchery rainbow trout with native redband trout in the Boise River, Idaho. North American Journal of Fisheries Management.

Olsson, I. C., L. A. Greenberg, E. Bergman, and K. Wysujack. 2006. Environmentally induced migration: the importance of food. Ecology Letters 9: 645-651.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, Washington, USA.

Railsback, S. F., H. B. Stauffer and B. C. Harvey. 2003. What can habitat preference models tell us? Tests using a virtual trout population. Ecological Applications 13: 1580-1594.

Reeves, G. H., Benda, L. E., Burnett, K. M., Bisson, P. A. & Sedell, J. R. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. In: Nielsen, J. L., ed. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society Symposium 17. Bethesda, Maryland. pp. 334-349.

Rieman, B.E., Lee, D.C., Chandler, G., Myers, D. 1997. Does wildfire threaten extinction for salmonids: responses of redband trout and bull trout following recent large fires on the Boise National Forest. Greenlee, J., editor. Proceedings of the Conference on Wildfire and Threatened and Endangered Species and Habitats, November 13-15, 1995, Coeur d'Alene Idaho. Washington: International Association of Wildland Fire, Fairfield. p 47-57.

Rieman, B. E, and J. B. Dunham. 2000. Metapopulations and salmonid fishes: a systhesis of life history patterns and empirical observations. Ecology of Freshwater Fish 9:51-64.

Rosenberger, A.E., Dunham, J.B. 2005. Validation of abundance estimates from mark–recapture and removal techniques for rainbow trout captured by electrofishing in small streams. North American Journal of Fisheries Management 25: 1395-1410.

Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. Bioscience 41: 704-712.

Sestrich, C. M. 2005. Changes in native and nonnative fish assemblages and habitat following wildfire in the Bitterroot basin, Montana. M.S. Thesis, Montana State University, Bozeman, MT. 93 pp.

Tattam, I. A. 2006. Seasonal life history of *Oncorhynchus mykiss* in the South Fork John Day River, Oregon State University: Corvallis, OR. 145 pp.

Waples, R. S. 2004. Salmonid insights into effective population size. Pages 295-314 in A. P. Hendry and S. C. Stearns, editors. Evolution illuminated: salmon and their relatives. Oxford University Press, Oxford, U.K.

Waples, R. S., G. R. Pess, and T. Beechie. 2008. Evolutionary history of Pacific salmon in dynamic environments. Evolutionary Applications 1: 189-206.

Ward, A. J. W., M. M. Webster, P. J. Hart, J. B. Paul. 2006. Intraspecific food competition in fishes, Fish and Fisheries 7: 231-261.

Wondzell, S. M., King, J. G. 2003. Postfire erosional processes in the Pacific Northwest and Rocky Mountain regions. Forest Ecology and Management 178: 75-88.

Wysujack, K., Greenberg, L. A., Bergman, E. and Olsson, I. C. 2008. The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. Ecology of Freshwater Fish 18: 52-59.