

Genetic Variation Reveals Influence of Landscape Connectivity on Population Dynamics and Resiliency of Western Trout in Disturbance-Prone Habitats

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Introduction

Salmonid fishes have evolved and persisted in dynamic ecosystems (Waples and others 2008) where disturbance events vary in frequency, magnitude, timing, and duration (Gresswell 1999; Dale and others 2001), as well as the specific nature of associated effects (e.g., changes in thermal or flow regimes, geomorphology, or water chemistry; Reeves and others 1995; Benda and others 2004; Bisson and others 2005). In the western United States, one of the major drivers of disturbance in stream ecosystems is fire (Reeves and others 1995; Rieman and Clayton 1997; Gresswell 1999). Although there is a growing consensus that fish populations can ultimately benefit from the productive and heterogeneous habitats created by fire (Reeves and others 1995; Benda and others 2003; Minshall 2003; Rieman and others 2003), to persist they obviously have to withstand the immediate and shorter-term effects of fire, which can reduce or even extirpate local populations (Rieman and Clayton 1997; Brown and others 2001; Burton 2005; Sestrich 2005). Movement among interconnected stream habitats is thought to be an important strategy enabling persistence during and following fire, and there is mounting concern that the extensive isolation of salmonid populations in fragmented habitats is reducing their resiliency to fire (Gresswell 1999; Dunham and others 2003; Rieman and others 2003).

In spite of this concern, there are few direct observations of salmonid responses to fire. In fact, guidance is based largely on a broader understanding of the influences of landscape structure and disturbance in general on salmonid fishes (Dunham and others 2003; Rieman and others 2003), and there is considerable uncertainty about how best to manage for salmonid resilience to wildfire. Studies are limited by the difficult logistics of following fish responses in the face of unpredictable events such as wildfires. Therefore, BACI (Before-After-Control-Impact) study designs are nearly impossible, and replication is similarly challenging because fires are often low-frequency events. Furthermore, conventional ecological study approaches (e.g., studies of fish distribution, abundance, life histories, and movement) are logistically difficult to implement (but see Dunham and others 2007). Overall, a major challenge to understanding resilience of salmonid populations in fire-prone environments is related to moving beyond localized case studies to those with broader applicability in wildfire management (Dunham and others 2003).

Genetic data can be useful for overcoming many of the limitations inherent in ecological studies (Neville and others 2006a; Schwartz and others 2006). Here

we review several case studies of western trout where population genetic data have provided insight about fish responses to fragmentation and disturbance more generally, and specifically in relation to fire. Results of these studies confirm the importance of movement and landscape connectivity for ensuring fish persistence in fire-prone landscapes, and highlight the usefulness of genetic approaches for broad-scale evaluation and monitoring of population responses to fire and related management actions.

General Effects of Fragmentation on Trout Populations

We begin with a brief review of several mechanisms by which habitat fragmentation may reduce the likelihood of persistence for salmonid populations. General consequences of isolation include increased risk of extinction from random demographic and genetic processes due to small population size (McElhany and others 2000), reduced potential for re-colonization or repopulation following disturbance (“metapopulation dynamics”; Gilpin and Hanski 1991), and decreased habitat diversity and “internal dynamics,” which can affect population persistence (Pickett and Thompson 1978). Isolated populations are typically smaller, and so are likely to have greater temporal fluctuations or other stochastic effects that increase variation in individual reproductive success and lead to smaller effective population sizes (Waples 1990, 2002) and frequent population bottlenecks (Neville and others 2006a). The consequent loss of genetic diversity from stronger genetic drift and increased frequency of inbreeding in these small isolated populations lowers adaptive capacity (Bijlsma and Loeschcke 2011) and can increase the risk of extinction (Frankham 2005). Additionally, in smaller, simplified habitat patches fish cannot move to use a full complement of alternate local habitats that might bolster recruitment, provide refugia, or facilitate metapopulation dynamics (Dunning and others 1992; Schlosser 1995; Ebersole and others 2001; Ebersole and others 2003). Small populations are thus more vulnerable to physical disturbance because of the increased likelihood that a single event will affect the entire population. Finally, isolation of western trout populations has greatly reduced the occurrence of a migratory life history (Young 1995; Fausch and others 2009). Where present, migratory individuals using alternate habitats can boost reproductive capacity (Jonsson and others 2001; Morita and others 2009) and potentially buffer populations from environmental variability and disturbances, such as fire (Dunham and others 1997; Rieman and others 1997b; Dunham and others 2003; Neville and others 2006a).

Genetic Characterization and Monitoring of Populations

Because fragmentation and disturbances such as fire are expected to affect the genetic characteristics of populations, genetic data can be used as an indirect measurement of these processes. In fact, for many questions (e.g., measurements of abundance or dispersal rates), genetic assessments requires less time and less expense than traditional methods such as mark-recapture and radio telemetry (Schwartz and others 2006). Additionally, genetic approaches can provide information about temporal dynamics or cryptic influences that may not be captured by traditional methods. In such cases, evaluations of population characteristics are often more accurate than traditional methods (Neville and others 2006a). For instance, population fluctuations or founder events following fires may not be reflected in a

current census if a population has recovered demographically (Dunham and others 2007), but these events may have had significant long-term effects on effective population size and can be captured using genetic approaches (e.g., they might be expected to show evidence of population bottlenecks, particularly if they are isolated). As another example, there is growing concern that invasion of nonnative trout and hybridization with native species may become more prevalent following fire-related disturbances (Dunham and others 2003). Detecting hybridization in the field can be difficult, but hybridization can be assessed with confidence using genetic techniques (Boecklen and Howard 1997). Genetic approaches should be particularly valuable for capturing impacts from fire or other disturbances on natural populations, then, because samples can be collected across large landscapes (Manel and others 2003), and a sample collected at one point in time can provide a retrospective view of influences that may have affected a population over decades (a “snapshot,” but one that provides information about past influences). After an initial assessment, genetic data can then be collected periodically to monitor changes in population characteristics through time (Schwartz and others 2006).

Applications of Genetic Data for Evaluating Effects of Fragmentation and Disturbance

Using genetic diversity as an indicator, several recent studies of trout populations demonstrate how movement and life history variability are related to population resilience in fragmented and disturbance-prone landscapes. Neville and others (2006b) evaluated genetic characteristics of Lahontan cutthroat trout *Oncorhynchus clarkii henshawi* residing in high-desert stream habitats vulnerable to different types of disturbances including fire. The study area encompassed one of the last interconnected and relatively pristine stream networks in the current range of this fish. Because some streams in the network were degraded and isolated by barriers, this system provided a rare example of diverse movement and life history variation in a complex habitat that could be contrasted with population characteristics in isolated habitats within the same catchment. The mainstem river, a hypothesized migratory corridor connecting several tributaries, was found to maintain high genetic diversity and contain a mixture of genotypes representing fish from different streams that likely moved into mainstem river habitats when not spawning in the tributaries. In contrast, samples from physically connected but high-elevation tributaries where fish were thought to express a ‘resident’ life history showed moderate levels of differentiation from other samples and lower genetic variability within samples, confirming a certain degree of demographic and geographic segregation from migratory forms (Northcote and Hartman 1988; Varley and Gresswell 1988; Northcote 1992). Fish from habitats isolated by culverts or natural barriers had the lowest effective population sizes and levels of genetic diversity, often exhibited severe genetic bottlenecks, and were highly differentiated from other populations (patterns observed in other trout and charr populations isolated above barriers, Taylor and others 2003; Yamamoto and others 2004; Wofford and others 2005; Morita and others 2009). In one case, a population above a small natural waterfall that was thought to have been extirpated by drought (Dunham 1996) was later recolonized. Therefore, fish from interconnected larger habitats in this study seemed to maintain spatially segregated life history forms and functioning metapopulation dynamics, both of which are likely to contribute to the overall viability of this network of populations in a harsh desert environment (see

Rieman and Dunham 2000). Populations in isolated habitats exhibited negative genetic effects of isolation, likely resulting from the small and demographically unstable nature of these populations. It is not surprising that many isolated populations across the historic range of the subspecies have disappeared in recent decades (Elliott and others 1997).

Other studies have also highlighted the importance of habitat connectivity and complexity in disturbance-prone environments. Disturbances such as landslides and debris flows are common throughout the range of coastal cutthroat trout *Oncorhynchus clarkii clarkii*. In western Oregon, however, these fish exist in several ecoregions differing significantly in landscape attributes such as stream gradients, topology (arrangement of tributary branching), and connectivity, all of which might influence the effect of disturbances on local populations (Guy and others 2008). For example, the interior Cascades ecoregion is characterized by steep streams with little branching structure, but the Coast Range ecoregion is lower gradient and has highly dendritic stream systems with few instream barriers to movement. Accordingly, Guy and others (2008) found patterns of genetic diversity to reflect these landscape characteristics in each ecoregion. The authors had hypothesized that Coast Range populations would show genetic resilience to disturbance, given that a disturbance in any single stream would affect only a portion of a dendritic system, where the capacity for dispersal from other parts of the network was high. As expected, they found the Coast Range populations exhibited greater genetic diversity than populations from the Cascades ecoregion, where landslides and debris flows in steep single-channel streams likely affected whole populations directly with little possibility for subsequent gene flow. Other patterns related to the physical distances separating habitats suggested that genetic structure in the Coast Range ecoregion were driven by within-watershed dispersal, whereas in the Cascades ecoregion genetic drift and disturbance-associated population bottlenecks seemed to be the dominant factor influencing genetic patterns. The study design could not differentiate between influences of disturbance regimes *versus* historical influences related to colonization of the two ecoregions; however, Guy and others (2008) suggest that the effect of disturbances may be greater in habitats with reduced connectivity and complexity where fish have little ability to respond to these events by movement (see also Gresswell 1999). These results should inspire further investigation into these connections.

Another recent genetic study of 55 stream populations of rainbow trout (*Oncorhynchus mykiss*) in the Boise and Payette river basins of Idaho suggested similar influences of isolation on population resilience in the face of disturbance (Neville and others 2009). This study was designed specifically to compare the effects of wildfire and related disturbance *and* habitat fragmentation, and incorporated the natural variability in fire history across these watersheds over the last several decades. The authors compared genetic diversity in samples without a history of recent wildfire to those with a history of stand-replacing wildfire, as well as those that had experienced both wildfire and a severe channel-reorganizing disturbance that may have extirpated or greatly reduced fish populations. Stream habitats also varied in size (catchment basin area) and isolation caused by human-constructed road culverts. Surprisingly, there was no evidence that fish from streams with different fire histories had different levels of genetic diversity; overall, fish in watersheds that had experienced wildfires and associated channel reorganizing events maintained similar levels of genetic variability as fish in streams with no known disturbance. Genetic diversity did increase, however, with increasing habitat size, and was lower in populations found above culvert barriers. Recent demographic assessment of a subset of these trout populations sheds detailed light

on the rapid recolonization (Rieman and others 1997a; Burton 2005; Dunham and others 2007) and flexible life history strategies that enable populations to recover quickly after fire in interconnected stream networks (Dunham and others, this volume). Furthermore, results of genetic analyses suggest that human influences such as barriers to dispersal may pose greater threats to populations of native trout than wildfire (Neville and others (2009).

In total, these recent studies yield substantial empirical evidence of a linkage between landscape structure and resilience as indicated by genetic diversity in salmonid fishes. Because genetic diversity can be used to characterize connectivity and population dynamics (Neville and others 2006a), these relationships underscore the importance of connectivity for both the persistence and long-term viability of salmonids (see McElhany and others 2000; Dunham and others, this volume). The genetic examples presented here support the growing consensus that salmonid fishes are able to withstand disturbances, including fire (Waples and others 2008), if given a habitat template for expression of various movement and life history strategies (Schlosser and Angermeier 1995; Hendry and Stearns 2004; Dunham and others this volume).

Management Implications

Given the link between stream network connectivity and population resilience, an obvious management strategy would be to reconnect trout habitats wherever physically possible to allow dispersal processes to occur naturally. But management decisions today are complicated by wide-spread invasions and hybridization with nonnative fishes which, it has been hypothesized, may be facilitated following fires (Dunham and others 2003). Although examples in this paper suggest that strategies promoting the isolation of populations above artificial barriers may not be successful, short-term isolation may be the only alternative for preserving the integrity of native populations in cases where invasion is certain (Fausch and others 2009).

This issue emphasizes the usefulness of genetic data for monitoring native trout populations in the context of fire management. Where isolation is deemed necessary, genetic techniques have potential for evaluating the probability of persistence of isolated populations over time (see Yamamoto and others 2004, for an example with white-spotted charr *Salvelinus leucomaenis*) by assessing the effective population size prior to and following isolation, and evaluating the effects of any observed perturbations, such as fire. Genetic data are a powerful tool for monitoring threats from hybridization where native populations are at risk of invasion by congenators (e.g., Neville and Dunham, in press), and can be helpful in prioritizing management resources by evaluating the genetic integrity (i.e., whether or not they have already been hybridized) of above-barrier populations before barrier removals are planned and executed.

Wherever possible, therefore, information concerning the genetic characteristics of a population should be integral to assessments of trade-offs associated with isolation or connectivity (Kruse and others 2001; Peterson and others 2008; Fausch and others 2009). Undoubtedly, consideration of these trade-offs will become even more complex as suitable habitat becomes further fragmented and degraded in association with climate change, and the need for improving resiliency through restoring and reconnecting habitats increases (Rahel and others 1996; Rieman and others 2007; Williams and others 2009). Long-term monitoring of the genetic 'health' and purity of populations (Dunham and others 1999) will be

highly valuable in fire-prone habitats, especially when paired with insight from other ecological methods evaluating movement (e.g., telemetry or stable isotope analysis, see examples in Balkenhol and Waits 2009; Sepulveda and others 2009). This type of research will continue to improve our understanding of the complex mechanisms by which salmonids have adapted to the effects of fire (e.g., Dunham and others, this volume). Furthermore, genetic research on habitat connectivity and complexity underscores the need to develop a broad-based forest management strategy that focuses on protecting remaining fish populations and habitat from invasion and further anthropogenic degradation, while restoring degraded habitat and connectivity among habitats.

Acknowledgements

We thank Bruce Rieman, Doug Bateman, Phaedra Budy and an anonymous reviewer for helpful comments on earlier drafts of this manuscript.

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