Fish-Movement Ecology in High-Gradient Headwater Streams: Its Relevance to Fish Passage Restoration Through Stream Culvert Barriers

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Executive Summary

Restoration of fish passage through culvert barriers has emerged as a major issue in the Pacific Northwest and nationwide. The problem has many dimensions, including the huge number of potential barriers, uncertainty about which structures are actually barriers, the benefits and risks involved with restoration, and the financial costs and timelines. This report attempts to address what we call "thinking outside of the pipe" in terms of fish passage information needs. This means understanding the value of each potential passage restoration project in the context of other possible projects, and to view individual restoration projects within a larger landscape of habitats and population processes.

In this report we provide a brief review of some essential characteristics of animal movement and examples from a focal group of fishes in Washington State: salmon, trout, and char. While several other fishes and many other species use streams where culvert passage barriers may occur, it is the salmonids that are by far the most widespread and in most cases extending furthest into the headwaters of stream networks in Washington. We begin this report by outlining some basic characteristics of animal movement and then apply that foundation to the case of salmonid fishes. Next we consider the consequences of disrupting fish movement with human-constructed barriers, such as culverts. Finally, this body of evidence is summarized and we propose a short list of what we view as high priority information needs to support more effective restoration of fish passage through culverts.

Movement is an essential mechanism by which mobile animals acquire the resources necessary for the successful completion of their life-cycles. It also plays a crucial role in how animals are distributed across the landscape and the persistence of populations and species. Regardless of how little or how far an animal moves, the purpose (e.g., foraging, reproduction, growth, refuge) and intensity (e.g., short, long, energetic, attenuated) of that animal's movement is intricately related to how its life history requirements change daily and/or seasonally. Animal movement can be differentiated into four general categories: station keeping, ranging, migration, and accidental displacement. Each category and its associated activities can be defined relative to purpose, frequency and pattern, temporal-frame, and spatial-scale.

These movements and activities are expressions of the way animals go about acquiring from the habitats within which they reside the resources they need for survival and the completion of their life-cycles. Station keeping movements and activities (i.e., foraging, commuting, and territorial behavior) typically occur within an animal's home range. Foraging is a regular, reiterative set of movements and activities (e.g., searching, hunting, gathering, collecting, etc.) that facilitate the acquisition of resources. Commuting also is a regular, reiterative movement or activity that not only facilitates resource acquisition but also the avoidance of predators. Territorial behavior includes any number of agonistic movements or behaviors used by an animal to establish or defend territory within its home range. Ranging can be differentiated into movements and activities that facilitate the exploration of or dispersal to new habitat. An exploring individual is one that leaves its home range and travels to a contiguous or disjunct location, and in a short period of time returns to the original home range. Animals that disperse do so by making one-way excursions from their present home range to a new location where they establish a new home range. Migration is generally a regular and predictable long-distance movement undertaken by animals to seasonally move between contiguous and/or disjunct locations. The general expression of migratory movement is for an animal to move relatively quickly through multiple contiguous and/or disjunct habitats from a location that provides resources for growth and maturation to a location that provides resources for reproduction, birth, and the nurturance of offspring. The accidental displacement of animals from their home ranges occurs due to unpredictable environmental stochastic events such as forest and rangeland fires, debris flows, flooding, hurricanes, alteration and fragmentation of habitat by humans, and the introduction of invasive species.

Resident salmonids in headwater streams of the western United States express many of the general types of movements described above. They can be quite mobile and their patterns of movement vary relative to species. Indeed, movement in many salmonid species can extend over long temporal and large spatial scales, is fundamental to the persistence of populations across generations, and is an expression of their diverse life history patterns and their capacity to respond to dynamic environmental conditions and events.

Salmonids are the fish species most often found at the upper limits of headwater streams in the western United States. They are well adapted to life in these streams and have evolved behaviors useful for exploiting the many types of headwater stream habitats. However, to be able to utilize these habitats, individuals must be able to access them. That is why biological corridors and habitat connectivity are so important to the persistence of species, populations, and population-sustaining processes. The presence of salmonid species in headwater streams is further influenced by factors such as stream physical constraints (e.g., channel slope, elevation, stream size, presence of barriers to upstream migration), cycles of naturally occurring environmental and habitat disturbance, and limitation of food resources.

Salmonids have coexisted with the presence of naturally occurring barriers to upstream movement in headwater streams for a very long time. However, when human-placed movement barriers restrict or eliminate the upstream movement of fish and isolate upstream populations, consequences are likely. Impacts include: (1) reduction or elimination of the ability of fish to disperse to or reach upstream habitats; (2) eventual extirpation of mobile life history types from upstream populations; (3) fragmentation and isolation of upstream populations; (4) increased vulnerability to the negative impacts of stochastic environmental and habitat disturbances; (5) restriction of upstream populations to potentially marginal and degraded habitats; (6) prevention of recolonization of disturbed upstream habitats; and (7) population-level genetic impacts such as the disruption of gene flow from downstream populations , increased genetic drift in upstream populations, development of genetic bottlenecks, loss of genetic diversity, and reduced effective population size.

Culverts placed in streams have long been seen as potential impediments to the upstream movement of fish. Four basic levels of culvert-caused restriction to fish passage have been identified: complete; partial; low-flow related; and variable passage due to culvert modification. Numerous studies have identified various factors affecting the ability of fish to pass through culverts including: (1) the behavioral and physiological capacity of different fish species; (2) physical conditions within culverts; and (3) stream channel physical conditions just below the downstream openings of culverts. A few studies have investigated how fish passage may be enhanced by roughening the sides of culverts or retrofitting them with baffles. Ultimately, predicting the impact of any single culvert on fish upstream movement can be problematic without knowledgeable guidance. Several assessment manuals have been developed that can help determine the restrictive capacity and intensity of impact of a culvert on fish passage.

Given what we know of the importance of movement to fishes in headwater streams and the undesirable consequences of disrupting connectivity, the question of fish passage restoration seems to have an obvious answer. That is, fish passage restoration presents a major opportunity to restore connectivity to countless miles of blocked stream habitats in Washington State and throughout the region. However, restoration can be very expensive, resources are almost always limited, and can potentially facilitate invasions by nonnative aquatic species. These considerations lead to questions about tradeoffs and the relative values of individual fish passage restoration projects, within the context of other possible activities, including passage restoration in other locations, or perhaps the value of other management activities to benefit fishes.

The question of priorities for restoration projects may be just as valuable as restoration itself in terms of the balance of planning versus “on the ground” actions that benefit fishes. Managers are well-aware of the need for prioritization. Prioritization schemes are based on assumptions about how biological systems function (e.g., relationships among different factors) and estimates of key parameters (e.g., habitat quality and probability of population persistence). However, information may or may not be available to quantitatively define these relationships, processes, or estimates of basic parameters. Much more could be learned about virtually every aspect of fish movement, habitat requirements, population persistence, characteristics of fish barriers, and so on; and any information addressing these issues would provide relevant contributions. It is clear that a considerable amount of work has been focused on fish movement, local habitat requirements, and characterization of fish barriers. Considerably less work has been done on addressing the actual consequences of fish barriers in terms of their effects on populations, including the following key biological responses of native species: (1) expression of migratory life histories (e.g., species with obligate migration or partial migration); (2) population persistence; and (3) genetic impacts.

Learning about restoration begins with an understanding of existing passage impairment. By understanding the impacts of current barriers on fish populations, we will have a useful template or baseline of information against which the success of restoration can be measured. Two general hypotheses and predictions about restoration are presented on pages 15-16, and a summary of major information needs is presented on page 17. The movement characteristics of selected western US salmonid species and subspecies are summarized in Appendix I, pages 29-32. Answers to WDFW questions concerning headwater stream fish species and populations are presented in Appendix II, pages 33-37.

Introduction

Restoration of fish passage through culvert barriers has emerged as a major issue in the Pacific Northwest and nationwide. The problem has many dimensions, including the huge number of potential barriers, uncertainty about which structures are actually barriers, the benefits and risks involved with restoration, and the financial costs and timelines. This report attempts to address what we call "thinking outside of the pipe" in terms of fish passage information needs. This means understanding the value of each potential passage restoration project in the context of other possible projects, and to view individual restoration projects within a larger landscape of habitats and population processes, which will be described below. Fortunately, thinking "inside of the pipe" is very well-developed (e.g., FishXing: *http://www.stream.fs.fed.us/fishxing/*). In other words, methods for identification of culverts that are fish passage barriers are well-established, as are design criteria for restoration for individual barriers (Clarkin et al. 2005; see also references posted at *http://www.stream.fs.fed.us/fishxing/*).

At the heart of fish passage restoration is the fundamental goal of restoring viable and productive fisheries and recovery of threatened and endangered species. Fish are not the only organisms affected by passage restoration, and current design criteria attempt to address most aquatic organisms (Clarkin et al. 2005). In practice, priority to passage restoration is often strongly weighted toward fishes. Identification of fish passage barriers may be considered as one of a series of steps in a decision process for an effective restoration program. Understanding which potential passage restoration projects carry the most value to fish or reduce risks most effectively is a critical piece of the decision process which is not well developed. As the investment in fish passage restoration and oversight of those expenditures increases (GAO 2001), the need to resolve issues that extend "outside of the pipe" grows.

In this report we provide a brief review of some essential characteristics of animal movement and examples from a focal group of fishes in Washington State: salmon, trout, and char (for additional detail, see Fausch et al. 2006). While several other fishes and many other species use streams where culvert passage barriers may occur, it is the salmonids that are by far the most widespread and in most cases extending furthest into the headwaters of stream networks in Washington (Fransen et al. 2006). We begin this report by outlining some basic characteristics of animal movement and then apply that foundation to the case of salmonid fishes. Next we consider the consequences of disrupting fish movement with human-constructed barriers, such as culverts. Finally, this body of evidence is summarized and we propose a short list of what we view as high priority information needs to support more effective restoration of fish passage through culverts.

General Characteristics of Fish Movement

Movement is an essential mechanism by which mobile animals acquire the resources necessary for the successful completion of their life-cycles (Greenwood and Swingland 1983; Dingle 1996). It also plays a crucial role in how animals are distributed across the landscape and the persistence of populations and species (Ricklefs 1990; Fausch et al. 2006). An animal's capacity for movement is determined by natural selection and is a function of such things as organism size, habitat, life history traits, and geographic range (Dingle 1996). Movement also has spatial and temporal components. Some movements occur over comparatively short distances within an animal's home range. Home range, as it is used here, is defined as the area traveled by an animal, exclusive of large-scale migrations or uncharacteristic erratic wanderings, for the acquisition of resources needed for survival (Mace et al. 1983; Dingle 1996). These movements are associated with acquiring food, maintenance of territory, refuge seeking, and reproduction (Mace et al. 1983; Pyke 1983; Dingle 1996). Long distance movements undertaken by many animals also are associated with the acquisition of the resources necessary for survival and completion of an individual's life-cycle. However, long distance movements may also occur involuntarily (at least in part) as a response to a naturally occurring displacement event (e.g., forest and rangeland fires, debris flows, flooding, etc.) or as individuals track availability of new and unoccupied suitable habitat (Stenseth 1983; Dingle 1996).

Yet, regardless of how little or how far an animal moves, the purpose (e.g., foraging, reproduction, growth, refuge) and intensity (e.g., short, long, energetic, attenuated) of that animal's movement is intricately related to how its life history requirements change daily and/or seasonally (Rankin 1985, esp., Chapter One: Plankton Migrations and Chapter Two: Movements of Benthic Macroinvertebrates; Dingle 1996). Many aquatic organisms make diel vertical, as well as horizontal excursions to acquire the resources necessary for survival and/or to avoid predation (Kerfoot 1985; Klemer 1985). Many animals, including fishes seasonally travel long distances to habitats suitable for reproduction, resource acquisition and refuge (Sinclair 1983; Dingle 1996). In contrast, there are those species that never travel beyond their home range (e.g., resident salmonids in headwater tributaries), yet travel between and occupy different home range habitats during different seasons (Hilderbrand and Kershner 2000a; Baxter 2002; Hendicks 2003; Colyer et al. 2005).

Animal movement can be differentiated into four general categories: station keeping, ranging, migration, and accidental displacement (Dingle 1996). Each category and its associated activities can be defined relative to purpose, frequency and pattern, temporal-frame, and spatial-scale (Table 1). These movements and activities are expressions of the way animals go about acquiring from the habitats within which they reside the resources they need for survival and the completion of their life-cycles (Southwood 1977).

Station Keeping Movements and Activities

Station keeping movements and activities (i.e., foraging, commuting, and territorial behavior) typically occur within an animal's home range (Hassel and Southwood 1978; Kennedy 1985). Foraging is a regular, reiterative set of movements and activities (e.g., searching, hunting, gathering, collecting, etc.) that facilitate the

CATEGORY	ACTIVITY	PURPOSE	FREQUENCY AND PATTERN	TEMPORAL-FRAME	SPATIAL-SCALE
Station Keeping	Foraging	Acquisition of resources such as food, refuge, oviposition sites, or habitat suitable for reproduction	Regular Reiterative	Short-term Diel	Home range
	Commuting	Acquire resources, Avoid predators	Regular Reiterative	Short-term Diel	Home range
	Territorial Behavior	Establish and/or defend territory	Irregular	Short-term	Home range
Ranging	Exploring	Seeking availability of resources in contiguous or disjunct habitat	Irregular Erratic Round-trip	Variable depending on travel time to habitat being explored	Variable depending on distance to non-home range habitat being explored
	Dispersing	Movement out of natal or present home range due to factors related to resource availability, carrying capacity, etc.	Variable depending on species and age of dispersing individual; One-way	Variable depending on travel time to new habitat	Variable depending on distance to new habitat
Migration	Migrating	Acquisition of resources such as food, refuge, oviposition sites, or habitat suitable for reproduction	Regular Round-trip	Seasonal	Usually relatively long distances, but not always; species and life history dependent
Accidental Displacement		Result of stochastic event	Irregular Erratic	Variable	Variable

Table 1: Characteristics of movement categories and activities (after Kennedy 1985, Lidicker and Stenseth 1992, and Dingle 1996).

acquisition of resources (Stephens and Krebs 1986; Dingle 1996). Once the resource being sought is located and the animal acquires enough of the resource to meet its physiological requirements, foraging will temporarily cease. Commuting also is a regular, reiterative movement or activity that not only facilitates resource acquisition but also the avoidance of predators (Ogden and Quinn 1984; Kennedy 1985; Dingle 1996). Commuting is most often associated with the diel vertical "migrations" of organisms in lakes and marine habitats. However, any animal that moves daily from one home range location to another home range location to acquire resources or avoid predation, and returns to the original location, can be considered to be commuting. Territorial behavior includes any number of agonistic movements or behaviors used by an animal to establish or defend territory within its home range (Dingle 1996). Territorial behavior is usually of short duration and tends to occur irregularly.

Ranging Movements and Activities

Ranging can be differentiated into movements and activities that facilitate the exploration of or dispersal to new habitat (Lidicker and Stenseth 1992; Dingle 1996). An exploring individual is one that leaves its home range and travels to a contiguous or disjunct location, and in a short period of time returns to the original home range. This type of movement tends to be irregular and relatively erratic, yet can provide an exploring animal with information about the availability of resources in new suitable habitat (Lidicker and Stenseth 1992). Animals that disperse do so by making one-way excursions from their present home range to a new location where they establish a new home range. The new home range can be contiguous or disjunct with the original home range. Dispersal is often associated with habitat factors such as resource availability and carrying capacity, the movement of young animals seeking new home ranges, or adults seeking new breeding locations (Dingle 1996).

Migration

Migration is generally a regular and predictable long-distance movement undertaken by animals to seasonally move between contiguous and/or disjunct locations (Dingle 1996; Northcote 1998; Meka et al. 2003). The general expression of migratory movement is for an animal to move relatively quickly through multiple contiguous and/or disjunct habitats from a location that provides resources for growth and maturation to a location that provides resources for reproduction, birth, and the nurturance of offspring. Location, as it is used here, can be particular habitats within an animal's home range or disjunct home ranges that are separated by relatively long distance. However, the migratory movement of anadromous salmonids from their natal stream to the ocean and back appears to occur along a continuum rather than between particular separate locations, especially the continuous movement of adults during the marine-phase of their life-cycle. Nonetheless, migration is usually a seasonally-associated round-trip movement, and the distance traveled and number of times an individual completes this journey varies by individual condition and species.

Accidental Displacement

There are times when animals are unpredictably and involuntarily forced to move from their home range by environmental stochastic events (Caughley 1994, Dingle 1996).

These accidental displacements are typically rare relative to any given animal population yet occur often, worldwide (Pechmann et al. 1991; Alford and Richards 1999). Examples of displacement events include forest and rangeland fires, debris flows, flooding, hurricanes, alteration and fragmentation of habitat by humans, and the introduction of invasive species.

Other Definitions of Migration and Dispersal

As with many terms in ecology and evolutionary biology, the definitions of migration and dispersal are not standardized (Dingle 1996), and different usages can be quite confusing. Some useful examples are described by Neville et al. (2006a): "…it is necessary to clarify how we define two key terms related to connectivity: migration and dispersal. In population genetics, migration is often used to describe gene flow – the transfer of genetic material among populations. In the salmonid literature, and with most other ecological fields, migration is defined as the movement of individuals from natal habitats across landscapes or regions to utilize complementary habitats (Dunning et al. 1992) in completing their life cycle. We use this definition of migration whenever possible. The term "dispersal" is also used confusingly across disciplines. In most of the ecological literature, the movement of individuals into non-natal habitats for breeding is often referred to as dispersal. In the salmonid literature this is referred to as "straying", but to avoid confusion we use the term dispersal (Rieman and Dunham 2000). Generally, some dispersing individuals will breed successfully, whereas others may not." In this report we follow the conventions outlined in Neville et al. (2006a).

Characteristics of Salmonid Movement in Headwater Streams

Almost 50 years ago Gerking (1959) proposed the "restricted movement paradigm" hypothesizing that resident stream fish moved very little. At the same time, long-distance movements by salmonids in streams have been documented for decades (e.g., Bjornn and Mallet 1964). More recently, this "restricted movement paradigm" has been challenged and concepts regarding fish movements have been greatly expanded (Grant and Noakes 1987; Gowan et al. 1994; Schlosser 1995; Fausch and Young 1995; Rodriguez 2002) indicating that resident salmonids in headwater streams can be quite mobile, and that their patterns of movement are diverse and vary relative to species (see Appendix I). Indeed, movement is fundamental to the persistence of salmonid populations across generations. It is an expression of their diverse life history patterns and their capacity to respond to dynamic environmental conditions and events (Fausch et al. 2006). Some resident salmonids in headwater tributaries can be relatively static and sedentary, moving at the channel unit level (e.g., pool, riffle, cascade, step, etc.) up to <1.5 km (e.g., Heggenes et al. 1991; Hilderbrand and Kershner 2000a; Hendricks 2003; Schrank and Rahel 2004); whereas other individuals move often and over long distances of from 2-194 km (Bjornn and Mallet 1964; Gowan and Fausch 1996; Baxter 2002; Schrank and Rahel 2004; Zurstadt and Stephan 2004). The movement patterns of resident salmonids also vary daily (Thurow 1997; Young et al. 1997; Baxter 2002) as well as seasonally (Gowan and Fausch 1996; Hilderbrand and Kershner 2000a; Baxter 2002; Hendricks 2003; Schrank and Rahel 2004; Zurstadt and Stephan 2004; Colyer et al. 2005; Mellina et al. 2005; Muhlfeld and Marotz 2005). This spatial and temporal variability in movement is, in part, related to local environmental conditions (Brenkman et al. 2001) such as high spring flow and runoff (Gowan and Fausch 1996; Mellina et al.

2005; Muhlfeld and Marotz 2005), discharge (Brenkman et al. 2001; Hendricks 2003; Hostettler 2005), stream channel size and slope (Adams et al. 2000), and water temperature (Swanberg 1997; Brenkman et al. 2001; Muhlfeld and Marotz 2005). Other factors affecting salmonid movement include the size of individuals (Adams et al. 2000), characteristics of and requirements for spawning (Gowan and Fausch 1996; Hilderbrand and Kershner 2000a; Schrank and Rahel 2004), the acquisition of resources (e.g., food and suitable habitat; Fausch and Young 1995), and the presence of artificial barriers (e.g., dams and culverts; Zurstadt and Stephan 2004).

The complex life-cycles of resident salmonids in headwater streams of the western United States can extend over long temporal and large spatial scales, and require multiple habitats for completion (Schlosser 1995; Swanberg 1997; Hilderbrand and Kershner 2000a; Harig and Fausch 2002). The quality and landscape geometry of these habitats also are critical to the long-term persistence of populations (Schlosser 1995; Hanski 1999; Rieman and Dunham 2000; Neville et al. 2006b). In this landscape-level context, movement imparts to resident fish the ability to access essential habitats that meet their physiological needs and their requirements for spawning, rearing, and refuge provided that the connectivity of these multiple habitat types remains intact (Schlosser 1995; Hanski 1999; Rosenfeld et al. 2002; Neville et al. 2006a). Many anadromous salmonids also utilize headwater streams for spawning and rearing, and stream network continuity and connectivity are important landscape-level attributes associated with the successful completion of their life-cycles (Isaak et al. In Press). For example, recent studies have documented that intermittent headwater streams contribute to survival of anadromous salmonids (e.g., Wigington et al., In Press; Ebersole et al., In Review); and without access to these specialized habitats survival of individuals could be compromised, with possible population consequences.

Salmonids in headwater streams of the western United States express many of the general types of animal movement (Table 1). Station keeping movements and activities are well represented by coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) because the movement patterns of this species in headwater streams are relatively restricted (Heggenes et al. 1991; Hendricks 2003). Hendricks (2003) found that a high proportion of radio-tagged individuals did not change channel units on a daily basis, but did move from these units to other channel units as they foraged for food. He also found that some individuals, while foraging, actually commuted from an initial channel unit to new areas of the stream for feeding and refuge and then returned to the original channel unit. Several studies have identified territorial behavior associated with feeding locations in various salmonid species (e.g., brown trout, Salmo trutta; brook trout, Salvelinus fontinalis; coho salmon, *Oncorhynchus kisutch*; cutthroat trout), although not all individuals within a population equally express this behavior (Grant and Noakes 1987; Martel 1996; Sabo and Pauley 1997). The ability of salmonids to disperse is crucial to the continued persistence of populations in headwater streams. Larson et al. (2002) labeled as dispersers, rainbow trout (*Oncorhynchus mykiss*) that emigrated from a larger stream in which they had been present for decades, into a smaller tributary stream, eventually establishing a resident population in the smaller stream. Lamberti et al. (1991) also documented the dispersal of cutthroat trout that had been displaced downstream by a catastrophic debris flow back to the impacted upstream reaches one year after the event. Migratory movements by salmonids in headwater streams can be expressed in several ways. Some species such as resident bull trout (*Salvelinus confluentus*) and westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) make within-basin migrations of variable distance (e.g., 2-194 km) for spawning (Swanberg 1997; Zurstadt and Stephan 2004); whereas anadromous salmonids such as coho (*Oncorhynchus kitsuc*h) and chinook salmon (*Oncorhynchus tshawytscha*) are well known for their long distance migrations from natal streams to the Pacific Ocean, eventually returning to their natal streams to spawn and complete their life-cycle. There are also salmonid species such as mountain whitefish (*Prosopium williamsoni; Coregoninae*) and westslope cutthroat trout that make within-basin migrations of variable distance to winter refuge habitats (Baxter 2002; Zurstadt and Stephan 2004).

Distribution of Salmonids in Headwater Streams

Salmonids are the fish species most often found at the upper limits of headwater streams in the western United States (Wydoski and Whitney 1979; Kruse et al. 1997; Latterell et al. 2003; Cole et al. 2006; Fransen et al. 2006). They are well adapted to life in these streams and have evolved behaviors useful for exploiting the many types of headwater stream habitats (Northcote 1992; Fausch et al. 2002; Neville et al. 2006b). However, to be able to utilize these habitats, individuals must be able to access them. That is why biological corridors and habitat connectivity are so important to the persistence of species, populations, and population-sustaining processes (Fausch and Young 1995; Rosenberg et al. 1997; Dunham and Rieman 1999; Bryant et al. 2004; Muhlfeld and Marotz 2005; Neville et al. 2006a). Stream network connectivity supports and maintains the mobile and migratory life history patterns of stream fish that reside in or utilize headwater streams for the completion of their life cycles (Schlosser 1995; Neville et al. 2006a). The connectivity of stream habitats also facilitates upstream and downstream dispersal, allowing individuals to access suitable habitats for reproduction, rearing, growth, and refuge (Kruse et al. 2001; Jackson 2003; Schrank and Rahel 2004; Neville et al. 2006a), as well as the ability to recolonize habitats after disturbance (Dunham et al. 1997; Rieman et al. 1997; Roghair et al. 2002; Dunham et al. 2003). The ability of fish to move relatively unrestricted within and among habitats also contributes to the maintenance of total and effective population size (Hilderbrand and Kershner 2000b; Kruse et al. 2001; Neville et al. 2006a, b, c), gene flow and genetic heterozygosity (Morita and Yokota 2002; Yamamoto et al. 2004; Neville et al. 2006a), and the diversity of species and fish assemblages (Peter 1998; Schlosser and Kallemeyn 2000).

The presence of salmonid species in headwater streams is further influenced by factors such as stream physical constraints (Kruse et al. 1997; Dunham et al. 1999), cycles of environmental disturbance (Reeves et al. 1995; Dunham et al. 2003), and limitation of food resources (Hughes 1998). Kruse et al. (1997) found that the upstream distribution of Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) in northwestern Wyoming streams was constrained by channel slope (i.e. ≥10%), elevation (i.e., >3182 m), stream size (i.e., wetted width), and the presence of barriers to upstream movement. Three studies of the distribution of fish in western and eastern Washington streams also determined that the upstream occurrence of trout (*Oncorhynchus spp.*) was constrained by the physical characteristics of stream channels (esp., diminishing channel size and increasing gradient), the diminishing availability of water, and the presence of natural and human-constructed barriers (Latterell et al. 2003; Cole et al.; 2006; Fransen et al. 2006). Unpredictable environmental disturbances to headwater streams can severely reduce local fish population size as well as lead to extirpation of populations from upstream habitats (Kruse et al. 2001; Dunham et al. 2003). According to Reeves et al.

(1995), local fish populations come and go in these dynamic headwater stream environments and it is the ability to escape disturbed habitats and then eventually recolonize them that contributes to the persistence of fish populations in these habitats (Breitburg 1992; Breitburg and Loher 1994; Dunham et al. 1997; Rieman et al. 1997). The impact of food limitation on fish distribution appears to be indirect and related to density- and size-dependent effects (Chapman 1966; Grant and Kramer 1990; Dunham and Vinyard 1997; Hughes 1998). For instance, as the size of individuals within a population increases the carrying capacity of a food- or space-limited habitat decreases. This could lead to small, isolated and fragmented populations in upstream locations that can be quite vulnerable to the negative impacts of environmental stochastic disturbances (Lamberti et al. 1991; Ensign et al. 1997; Morita and Yokota 2002; Roghair et al. 2002).

Impacts of Human-Placed Barriers on Fish Populations

Salmonids have coexisted with the presence of naturally occurring barriers to upstream movement in headwater streams for a very long time. However, when human-placed movement barriers restrict or eliminate the upstream movement of fish and isolate upstream populations, consequences are likely. The most obvious effect of human-placed barriers is that they reduce or eliminate the ability of fish to disperse to or reach upstream habitats. Thus, the ability of downstream populations to support declining upstream populations is reduced or potentially eliminated (Jackson 2003); the ability of anadromous salmonids to reach important headwater spawning and rearing sites is also decreased or eliminated (Wigington In Press; Ebersole In Review); and upstream species richness is attenuated (Winston et al. 1991). These barriers, by reducing or eliminating the upstream migratory phase of a species' life cycle can eventually extirpate mobile life history types from upstream populations (Nelson et al. 2002; Jackson 2003; Colyer et al. 2005; Fausch et al. 2006; Neville et al. 2006a). As barriers decrease or eliminate upstream movement, remnant populations above the barriers become fragmented and isolated (Kruse et al. 2001; Jackson 2003), and potentially more vulnerable to the negative impacts of unpredictable environmental events that impact headwater streams (Kruse et al. 2001; Dunham et al. 2003). Human-placed barriers to upstream movement also diminish the capacity for long-term persistence of upstream populations by restricting them to potentially marginal and degraded habitats (Peter 1998; Hilderbrand and Kershner 2000b; Pringle et al. 2000; Jackson 2003; Fausch et al. 2006) and preventing the recolonization of disturbed upstream habitats (Fausch et al. 2006). Population-level genetic impacts due to isolation include the disruption of gene flow from downstream populations (Jackson 2003), increased genetic drift in upstream populations (Griswold 1996; Castric et al. 2001; Guy 2005; Wofford et al. 2005), development of genetic bottlenecks and the loss of genetic diversity (Yamamoto et al. 2004; Guy 2005; Wofford et al. 2005; Neville et al. 2006a, b), and reduced effective population size (Neville et al. 2006a, b, c).

Several case-studies help illustrate the potential impacts of human-placed barriers on headwater stream fish populations:

1. Morita and Yamamoto (2002) examined the impact of the placement of erosion control dams across streams in southwestern Hokkaido, Japan, on the persistence of white-spotted char (*Salvelinus leucomaenis*) populations above the dams. They found that of 52 study sites above dams, white-spotted char were absent from 17 of the sites, whereas char occupied all undammed upstream reaches surveyed. Morita and

Yamamoto (2002) attributed the absence of char at the 17 sites to time since isolation of the population, and decreasing watershed size and stream channel gradient. They speculated that 12 more above-dam populations would disappear in the next 50 years.

2. Hilderbrand and Kershner (2000b), examining abundance data for isolated populations of three cutthroat trout subspecies (O. c. lewisi, O. c. pleuriticus, and O. c. utah) in headwater streams of Idaho, Montana, and Utah found that stream length could be related to the diminished persistence of upstream fish populations. They concluded that if barriers were placed in headwater streams for the purpose of isolating native trout from introduced nonnative trout, there would typically be insufficient space (i.e., stream length) above the barriers to maintain the necessary effective population size to support viable native cutthroat trout populations in the face of isolation.
3. Kruse et al. (2001) also studied the potential for using barriers to isolate native trout from introduced nonnative species. They studied 23 northwestern Wyoming stream populations of Yellowstone cutthroat trout (*O. c. bouvieri*) and determined that 21 of the populations would be large enough to minimize demographic risks of extinction. However, only seven populations would be large enough to maintain genetic viability (i.e. minimize potential for inbreeding and maintain within-population variability). They also speculated that even these populations, because of their sizes, would potentially be susceptible to extinction due to some unpredicted and catastrophic environmental disturbance.
4. Wofford et al. (2005) assessed the effects of barriers on genetic variation in coastal cutthroat trout (*O. c. clarkii*) in an isolated headwater stream in western Oregon. They found that the barriers strongly influenced genetic structure and that the above barrier population had reduced gene flow and diversity, as well as increased genetic differentiation and drift. They concluded that these genetic consequences of habitat fragmentation and isolation could potentially compromise the long-term persistence of the population.
5. Morita and Yokota (2002), using a simple individual-based model that assimilated population regulation mechanisms for white-spotted char, assessed the viability of populations fragmented and isolated above erosion control dams (also see Morita and Yamamoto 2002, above). They determined that the persistence of populations decreased substantially beginning around 30+ years since isolation. This was especially relevant for populations with small carrying capacity and low adult survival. The general conclusion was that small fragmented and isolated populations were not viable.
6. Neville et al. (2006c) studied 55 populations of rainbow trout in headwater streams in central Idaho to compare within-population patterns of genetic diversity in relation to isolation by culvert barriers, habitat size, and history of wildfire-related disturbance. Diversity was greater in larger habitats that were not isolated by culvert barriers, and wildfire-related disturbance had no detectable influence. This was in spite of the fact that some populations studied were known to be completely or nearly extirpated by wildfire-related debris flows ten years before. The strong influence of culverts underscored the importance of connectivity to rainbow trout populations.

It is clear that barriers to upstream movement restrict and often eliminate access to potentially critical upstream habitats. Limiting or eliminating dispersal and effectively fragmenting and isolating populations are key factors that increase the extinction risk for populations (Soulé 1983). Duncan and Lockwood (2001), examining the extinction risk among the world's freshwater fish families, found no indication that a unifying set of intrinsic biological or ecological traits could predict taxonomic patterns of extinction. Rather, they hypothesized that extrinsic factors such as the damming of rivers and other human caused alterations of freshwater aquatic environments, even in headwater streams, were important drivers of the worldwide decline in freshwater fish species. Although many factors contribute to the persistence or extinction of headwater stream fish populations, the potential capacity for the continued long-term persistence of small populations fragmented and isolated above human-placed barriers remains problematic (Fausch et al. 2006).

Culverts and Fish Passage

Culverts placed in streams have long been seen as potential impediments to the upstream movement of fish. Laird (1988) identified four basic levels of culvert-caused restriction to fish passage: complete; partial; low-flow related; and variable passage due to culvert modification. Numerous studies have identified various factors affecting the ability of fish to pass through culverts. Some studies have examined the behavioral and physiological capacity of different fish species to move upstream through culverts; other studies have identified several types of physical conditions within culverts that impact fish passage; and still others have examined the impact of stream channel physical conditions just below the downstream openings of culverts on fish movement upstream (Table 2). A few studies have investigated how retrofitting culverts may enhance fish passage. For example, Bates and Powers (1998) found that a culvert with moderately roughened walls enhanced juvenile coho salmon passage through the culvert because the roughness created a less turbulent boundary layer which the fish could use, especially when water velocity was high; and McEnroe (2005) determined that a culvert retrofitted with baffles allowed juvenile steelhead trout to maintain their position within the culvert, and to move upstream in higher numbers than through a non-retrofitted culvert. Ultimately, predicting the impact of any single culvert on fish upstream movement can be problematic without knowledgeable guidance. Several assessment manuals have been developed that can help determine the restrictive capacity and intensity of impact of a culvert on fish passage. A well-known and rich source of information on fish passage through culverts is FishXing (*http://www.stream.fs.fed.us/fishxing/*). Pess et al. (2005) provide a detailed evaluation of fish responses to the reconnection of isolated habitats through the removal of culverts and other barriers to migration.

Information needs for fish passage restoration through culverts

Given what we know of the importance of movement to fishes in headwater streams and the undesirable consequences of disrupting connectivity, the question of fish passage restoration seems to have an obvious answer. That is, fish passage restoration presents a major opportunity to restore connectivity to countless miles of blocked stream habitats (Roni et al. 2002; Pess et al. 2005) in Washington State and throughout the region. The problem is that restoration can be very expensive (e.g., >$100,000 USD per

Table 2: General factors affecting the upstream movement of fish through culverts.

FACTOR	REFERENCE
Behavioral limitation willingness of individual to move through or over barrier (even if barrier is submerged or only partially restrictive) seasonal timing of upstream movement relative to depth and velocity of water in culvert	 Binder and Stevens 2004 Laird 1988
Physiological swimming capacity of species	Binder and Stevens 2004
Barrier type and culvert length	Belford and Gould 1989 Warren and Pardew 1998
Water velocity through culvert relative to culvert length	Belford and Gould 1989 Baker and Votapka 1990 Fitch 1995
Turbulence level of water inside culvert	Fitch 1995
Water depth inside culvert	Baker and Votapka 1990 Fitch 1995
Stream channel characteristics below downstream opening of culvert Height of culvert lip above water surface Size of plunge pool	 Bateman, unpubl. Data Fitch 1995 Binder and Stevens 2004 Kondratieff and Myrick 2005

project) and resources are almost always extremely limited (GAO 2001). Less obvious is the potential for passage restoration to facilitate invasions by nonnative aquatic species (e.g., Fausch et al. 2006). These considerations lead to questions about tradeoffs and the relative values of individual fish passage restoration projects, within the context of other possible activities, including passage restoration in other locations, or perhaps the value of other management activities to benefit fishes. In other words, the question of priorities for restoration projects may be just as valuable as restoration itself in terms of the balance of planning versus "on the ground" actions that benefit fishes.

Managers are well-aware of the need for prioritization. Various schemes for prioritization of fish passage restoration projects are available or in development, such as the national Fish Passage Decision Support System currently implemented by the U.S. Fish and Wildlife Service (*http://fpdss.fws.gov/index.jsp*), and within the Pacific Northwest, the U.S. Forest Service, Region 6 (David Heller, personal communication), Washington Department of Fish and Wildlife (David Price, personal communication), and Rocky Mountain Region (Fausch et al. 2006).

Prioritization schemes are based on assumptions about how biological systems function (e.g., relationships among different factors) and estimates of key parameters (e.g., habitat quality and probability of population persistence) (Roni et al. 2002). Information may or may not be available to quantitatively define these relationships, processes, or estimates of basic parameters. This is true of most management applications, which represent an integration of quantitative inference and expert opinion. Here we summarize what we view to be high priority information needs, based on our review of the issues and evidence surrounding fish passage restoration through culverts in Washington State and throughout the Pacific Northwest.

Identifying Key Biological Responses of Native Populations to Barriers

Much more could be learned about virtually every aspect of fish movement, habitat requirements, population persistence, characteristics of fish barriers, and so on. Any information addressing these issues would provide relevant contributions. However, we see areas where certain information needs are higher priority, relative to decisions about priorities for fish passage restoration. From our review, it is clear that a considerable amount of work has been focused on fish movement, local habitat requirements, and characterization of fish barriers (e.g., FishXing). Considerably less work has been done on addressing the actual consequences of fish barriers in terms of their effects on populations, including the following key biological responses of native species:

- Expression of migratory life histories (e.g., species with obligate migration or partial migration)
- Population persistence (e.g., Morita and Yamamoto 2002), and
- Genetic impacts (e.g., Neville et al. 2006a, b, c).

These three categories of biological responses represent important population characteristics related to the long-term persistence and viability of fish populations.

Threats of Invasion by Nonnative Fishes

The tradeoffs involved with fish passage restoration to benefit native fishes versus facilitating invasions by nonnative fishes have been thoroughly reviewed in a separate report (see Fausch et al. 2006). Our recommendation for information needs related to this issue is similar to those for native species. Models to understand the influence of existing barriers on the success of invasions (e.g., as indicated by probability of occurrence) and monitoring and evaluation of responses of invasive species to passage restoration would provide very useful information. In the following section we provide more detailed examples of how this might be accomplished.

Relevance for Fish Passage Restoration

We see the issues highlighted above as high priorities because they address validation of key assumptions in existing prioritization schemes and the need to monitor the effectiveness of passage restoration (GAO 2001). Management actions will proceed with or without new information, but as the level of investment in fish passage restoration grows, so will the questions about priorities and effectiveness. Both could be continually evaluated and modified based on what is learned from new information suggesting more effective management alternatives.

Learning about restoration begins with an understanding of existing passage impairment. By understanding the impacts of current barriers on fish populations, we will have a useful template or baseline of information against which the success of restoration can be measured. For instance, a few specific hypotheses and predictions about restoration could include the following:

- Hypothesis: Passage barriers (A) reduce the size and dispersal connectivity of fish populations upstream, thus (B) decreasing the number of breeders or genetically effective size of local populations, (C) decreasing connectivity to migratory habitats, and (D) increasing the chance that a population may be locally extirpated.

- Some predictions about existing barriers:
  - Fish populations should be less likely to occur upstream of fish passage barriers relative to similar habitats without barriers.
  - Genetic variability of populations upstream of barriers should be reduced relative to populations sampled from similar habitats without barriers.
  - Species or individuals with migratory life histories should be less likely to be present upstream of barriers relative to similar habitats without barriers.
- Some predictions about restoration:
  - Restoration of fish passage should result in colonization of suitable habitats upstream of former barriers.
  - Within-population genetic variability should increase in populations upstream of former barriers.
    - Species or individuals with migratory life histories should be more likely to occur in habitats upstream of former barriers.

- Hypothesis: Fish passage restoration will increase the probability of invasion by nonnative species, which will have negative impacts on desirable native fishes.
  - Predictions
    - Nonnative species will be more likely to occur in streams without barriers or in those where passage has been restored
    - Native species will be less likely to occur in habitats where nonnative species are present

The preceding examples are very simplistic hypotheses and predictions and do not constitute a full study design to address all of the necessary measurable influence or "covariates" that could affect the outcome of restoration. For example, the success of invasion by nonnative species is likely conditioned on several different factors, including habitat suitability, dispersal ability, and biotic resistance in the receiving community (Dunham et al. 2002; Fausch et al. 2006). Other responses may also be relevant in the case of nonnatives (e.g., hybridization of closely related natives and nonnatives). The tools of landscape ecology, geographic information systems, molecular genetic markers, sampling methods, etc., are all now in place and available to address the impacts of barriers and develop testable hypotheses about restoration for design of effectiveness monitoring programs. The cost of research, monitoring, and evaluation would be very small in proportion to the huge costs associated with actual restoration and the overwhelming size of the problem. For example, in Bureau of Land Management and Forest Service lands alone in Oregon and Washington, the cost of fish passage restoration is estimated at over $375 million dollars (GAO 2001). Given these costs and uncertainties about restoration, some investment in research, monitoring, and evaluation seems very cost effective.

Relevance of Barriers in Intermittent Streams

Another growing issue is the importance of intermittent streams to fishes. Use of such habitats by fish has long been known, but more recent work reviewed here has shown that intermittent streams can be very important to salmon and trout, as well as other fishes. Better broad-scale models to predict and map the locations of such habitats by focal fish species might prove very useful, especially for anadromous species and perhaps native char in headwater streams. In the case of anadromous species, most of the obvious passage barriers in perennial streams have been restored, or are on a list of top priorities for local managers. It may be the case that many additional opportunities remain for fish passage restoration in intermittent streams. Research of this nature would be most effective with a team-based approach that integrates domain experts in biology, hydrology, and related disciplines. Since the focus of this literature review and requested assistance concerns higher-gradient streams, it is not clear how important this issue is if lower-gradient streams are omitted. We suspect that lower-gradient intermittent streams are much more likely to be important to fish, but this assumption is not tested. In some areas, char in particular can use smaller and higher gradient streams (e.g., Dolly Varden char S. malma in southeast Alaska; M. Bryant, Pacific Northwest Research Station, personal communication, 2005; see also Koizumi and Maekawa 2004).

Conclusions

In summary, the major information needs identified here include:

- Identifying key biological responses of native populations to barriers
    - life history
    - population persistence/occurrence
    - genetic indicators of population size;
- Threats of invasion by nonnative fishes and other species with potential impacts to native fishes; and
- Identification of intermittent streams with high value to native fish populations.

Desired outcomes from this new work would include the following:

- Improved procedures for prioritization of fish passage restoration projects at broad scales (from validation with new information)
- Improved response designs for effectiveness monitoring of restoration success: e.g., what to measure?
- Improved efficiency and learning about effective fish passage restoration and increased viability and productivity of important fisheries and threatened and endangered species.
- More efficient allocation of limited resources to fish passage restoration that maximizes benefits to native species.

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Appendix I: Movement Characteristics of Species and Subspecies

1. Bonneville Cutthroat Trout (*Oncorhynchus clarkii utah*)
   - Movement Patterns
     1. Relatively mobile, although seasonal (post-spawning continuum of 0.5-86.0 km)
     2. Greatest movement activity and distance: Spring (spawning, post-spawning)
     3. Variable-sporadic movement and limited distance: Summer-Winter (≤0.5 km)
     4. Individuals above barriers moved more frequently and had larger home ranges than individuals below barriers
     5. Important to maintain drainage connectivity and seasonal migration corridors
   - Dominant Movement Types
     1. Station keeping (Summer-Winter)
     2. Migratory (spawning; Spring)
   - Study locations: southeast Idaho, western Wyoming, and northern Utah
   - References: Hilderbrand and Kershner 2000a; Schrank and Rahel 2004; Colyer et al. 2005
2. Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*)
   - Movement Patterns
     1. Relatively short within-basin distances, primarily at the channel unit-scale with smaller proportion of population making reach- and segment-scale movements
     2. Seasonal component: greatest movement in April associated with peak spawning; least movement in October associated with low discharge
     3. Unit-scale movements common throughout year
     4. Reach- and segment-scale movements typically occur in winter and spring
     5. Habitats occupied by individuals change relative to discharge, water temperature, as well as spawning, refuge requirements, and feeding
   - Dominant Movement Types
     1. Station keeping
     2. Categories
        - No movement (0 channel units)
        - Local movement (1-5 channel units)
        - Longer distance movements (>5 channel units)
        - Pulsed movement (variable 1-3 above)
   - Study locations: western British Columbia; southwest Oregon
   - References: Heggenes et al. 1991; Hendricks 2003
3. Westslope Cutthroat Trout (*Oncorhynchus clarkii lewisi*)
   - Movement Patterns
     1. Seasonal with long distances and widespread distribution

        - Fall: downstream migration up to 194 km
        - Winter: sedentary downstream
        - Spring: upstream migration up to 475 km (related to spawning, water temperature, and discharge)
        - Summer: sedentary upstream
    2. Many individuals demonstrate homing behavior, returning to the same upstream channel habitat previously occupied
    3. Important to maintain habitat heterogeneity and drainage connectivity and account for diverse migratory behavior
  - Dominant Movement Types
    1. Station keeping (Summer and Winter)
    2. Migratory (Fall downstream; Spring upstream)
  - Study locations: central Idaho; central Oregon
  - References: Zurstadt and Stephan 2004; Starcevich 2006
4. Rainbow Trout (*Oncorhynchus mykiss*)
  - Movement Patterns (non-anadromous)
    1. Unique seasonal movements suggest potential for discrete within-basin population structure (see Meka et al. 2003)
        - Summer-Winter: sedentary
        - Spring: increased upstream movement (can be long range up to >372-607 km) related, in part, to discharge
    2. Age-0 fish movement habitat-related (see Mitro and Zale 2002): in sections with simple bank habitat in autumn; then move to and over-winter in sections with complex bank habitat, high gradient, and large substrate
  - Dominant Movement Types
    1. Station keeping: Summer-Winter
    2. Migratory: Spring
  - Study locations: north-central British Columbia; southwest Alaska; southeast Idaho
  - References: Mitro and Zale 2002; Meka et al. 2003; Mellina et al. 2005
5. Bull Trout (*Salvelinus confluentus*)
  - Movement Patterns
    1. Seasonal upstream and downstream migrations vary by:
        - Population
        - Time of year (Spring, Fall)
        - Distance (reported mean distances of 33 and 63 km; range 9-129 km)
    2. Migrations usually occur at night and are relatively rapid
    3. Individuals typically return to or near sites from which they migrated

    4. Juvenile emigration from natal habitat can occur in two pulses (Spring and Fall) – juveniles can stay in natal tributaries for up to 3 years
    5. Some populations can be non-migratory residents in headwater tributaries
    6. Timing and extent of movement related to water temperature and discharge
    7. Important to maintain drainage connectivity and diversity of complex habitats over large spatial-scale
  - Dominant Movement Types:
    1. Station keeping
    2. Migratory: variable distances for spawning and return to non-spawning habitat
  - Study locations: northwest Washington; northwest Idaho; northwest Montana
  - References: Swanberg 1997; Brenkman et al. 2001; Baxter 2002; Muhlfeld and Marotz 2005; Downs et al. 2006

6. Brook Trout (*Salvelinus fontinalis*)
  - Movement Patterns
    1. Upstream dispersal typically occurs in Summer
    2. Highest movement rates occur relative to runoff and before spawning, although overall summer movement relatively high
    3. Movement of up to 3.4 km relatively common
    4. Upstream dispersal restricted, in part, by channel gradient (although capable off moving into upstream habitat with steep gradient), size of individual, and barriers such as nearly vertical falls
  - Dominant Movement Type
    1. Station keeping with upstream dispersal
  - Study locations: central Idaho; northern Colorado
  - References: Gowan and Fausch 1996; Adams et al. 2000

7. Mountain Whitefish (*Prosopium williamsoni*)
  - Movement Patterns
    1. Variable types of seasonal movement
       - Single summer reach-no fall migration
       - Single summer reach-fall migration of varying length (3-95 km) to over-wintering habitat-return to summer habitat
       - Multiple summer reaches-fall migration to over-wintering habitat-return to summer habitat
       - Summer reach-fall migration to over-wintering habitat-no return to summer habitat
  - Dominant Movement Types
    1. Station keeping
    2. Migration (roundtrip to over-wintering habitat)

- Study locations: northeast Oregon; southeast Washington
- References: Baxter 2002

8. Largescale Suckers (*Catostomus macrocheilus*)
   - Movement Patterns
     1. Seasonal movement from upstream habitats (Spring-early Summer) to downstream over-wintering habitats (beginning mid-summer through early Fall)
     2. Long distance movements: 17.2-300 km; mean = 111 km
     3. Minimal movement during winter
     4. Return to upstream habitats in Spring
   - Dominant Movement Types
     1. Station keeping
     2. Migration (roundtrip to over-wintering habitat)
   - Study locations: northeast Oregon; southeast Washington
   - References: Baxter 2002
9. Anadromous salmonids (*coho, Oncorhynchus kisutch; chinook, Oncorhynchus tshawytscha*)
   - These species utilize headwater tributaries for reproduction and as rearing habitats for offspring
   - Recent research has documented the importance of permanent as well as intermittent headwater streams for the continued survival and persistence of anadromous salmonid populations
   - Important environmental factors include maintenance of drainage connectivity, habitat size and quality, and availability of residual pool habitats in intermittent streams
   - Study locations: central Idaho; southwest Oregon
   - References: Ebersole et al. In Review; Isaak et al. In Press; Wigington et al. In Press

Appendix II: Questions from Washington DFW (answers in italic)

1. At what life stages is it important that headwater fish move upstream through road crossings?

   According to current guidelines, the standard is to allow passage of all species and life stages (Clarkin et al. 2005). For salmonid fish in particular, movement of smaller fish and therefore earlier life stages will be the obvious limiting factor in considering fish passage barriers, because movement of individuals during these life stages is most likely to be impeded. Work on movement of very small fish (<60 mm) is lacking, although it is generally believed fish of such small size do not move substantial distances. However movement of larger fish (>60 mm) is known to play an important role in allowing access to seasonally productive habitat and to refugia.

2. Are there physical cues where upstream movement by headwater fishes might be expected with respect to flow, seasons, and channel characteristics (e.g., gradient, roughness, pools, etc), disturbance, others?

   In general, temperature and discharge are believed to be the dominant "proximate" cues that influence upstream migration of fishes in headwaters. In other words, changes in these physical factors influence movement of fish during seasons in which upstream migration is most common. Within a given season, these factors can vary dramatically across years, and lead to substantial within-season variability in the timing and duration of upstream migration.

   The seasonal window of migration (e.g., fall versus spring) is believed to be attuned to selection for spawn timing and location, and represents an "ultimate" influence (i.e., presumably shaped by natural selection to maximize individual fitness) on upstream migration. Channel characteristics are more likely an "ultimate" factor influencing migration by fish in headwater streams, representing natural selection for use of refugia or spawning areas suitable for maximizing pre-spawning survival of adults, egg incubation, and juvenile rearing. Use of such habitats may also be conditioned on population density and spatial geometry (size and isolation) of habitats, and the roles of spatial geometry versus local habitat quality are likely scale-dependent. At larger spatial extents, the importance of geometric factors is likely to be more obvious than local factors traditionally associated with habitat quality (e.g., cover, sediment, temperature).

3. How would you characterize the movement behaviors of headwater fishes?

   Movement behaviors of fish vary according to the spatial and temporal scale of movement under consideration. Migration and dispersal over longer times and distances are the most relevant considerations for fish passage restoration. Migration in salmonid fishes is typically defined in terms of the origin and destination of the migratory circuit. For example, a "fluvial" life history refers to individuals that migrate from natal spawning areas to larger riverine habitats and back. Various terms relating to different destinations have been proposed. As the evidence mounts for salmonid fishes in terms of direct (e.g., telemetry, mark and resight) and indirect (e.g., molecular markers) study of movements, it is becoming increasingly clear such classifications can lead to an overly simplistic view of the complex life histories of salmonid fishes. To develop a more realistic view of migration in salmonid fishes, new classifications would benefit by considering the following:

   - *The "journey" between endpoints of migration, and more specifically patterns of use in what are believed to be migratory corridors.*

- *The possibility of multiple endpoints in migration, including a clear definition of what defines an "endpoint." For example, it is common for salmonids to move through multiple habitats during migration, and "stopovers" or exploratory excursions into different habitats may occur as is the case with other migratory species (Dingle 1996).*
- *Differences among life stages in migratory behavior. Most research has focused on migration of large adult fish, but smaller individuals and earlier life stages can have considerably different patterns of migration and habitat use. For example, so-called "subadult" bull trout (generally referring to migratory fish <300 mm) show much more extensive use of stream habitats than do larger "adult" bull trout, including frequent use of small tributaries and intermittent streams (J. Dunham, personal observations).*
- *The motivation for migration. It is critical to identify why fish migrate (e.g., for refuge, feeding, reproduction) in any classification of migratory behavior (e.g., Table 1).*

We are not aware of significant attempts to include these considerations into a more rigorous definition of migratory behavior by salmonid fishes, and such an effort would indeed be challenging. However, it is likely that we are not able to detect important patterns of migratory habitat use and selection with current classifications and methods of study. This may be more important for understanding habitat use in the higher order portions of stream networks and less so for headwater streams. In some cases, however, more study of the use of headwater streams by fish may be warranted (e.g., "subadult" trout and char).

Dispersal is less understood than migration. It is an important process in terms of maintaining gene flow and spatial processes that contribute to persistence of fishes – especially those in dynamic headwater habitats (Rieman and Dunham 2000). Of the methods available to understand patterns of dispersal, molecular markers have perhaps proven the most effective for understanding interactions between fish in headwater streams and higher order stream habitats, as well as patterns of interaction among headwater streams (Neville et al. 2006a).

Most studies of dispersal using molecular markers have focused on single stream networks. Comparisons among different networks to contrast the influence of historical (e.g., post-glacial dispersal) and local landscape characteristics (e.g., spatial structure, habitat quality, disturbance, barriers) on dispersal would help considerably in terms of understanding the nature of dispersal by fishes in headwater streams (e.g., Costello et al. 2003). In other words, broader-scale comparative studies of dispersal in headwater fishes would help to disentangle the influences of long-term historical processes versus landscape influences at intermediate spatio-temporal scales, and small-scale influences, such as barriers and localized disturbance (Neville et al. 2006a).

4. How far do headwater fish move?

   There is no characteristic distance that headwater fish move, but maximum distances can range into hundreds of kilometers for non-anadromous species. Anadromous fish migrate thousands of kilometers, primarily within marine environments, in addition to their well-known long distance upstream migrations into river networks.

5. How would you characterize the demographic effects of populations by artificially limiting movement of those fish that might be expected to move?

   Experience with headwater fishes shows that catastrophic factors are most likely to cause local extinctions (Dunham et al. 2003), and that demographic factors, while important, may be less likely to cause extinction unless population sizes are extremely low. Because headwater stream systems are naturally dynamic, the fishes that live in them are invariably those species with life histories tuned to rapid reproduction and the ability to move extensively within stream *networks when necessary. Thus, they are demographically resilient and plastic in the face of highly variable environments susceptible to unpredictable catastrophic environmental events. See Bisson et al. (2005) for an excellent case study whose results demonstrate, in part, the resiliency and plasticity of headwater stream salmonids.*

6. Considering demographic and genetic characteristics of headwater fish populations, how would you define a population within the stream network?

   Defining "populations" is one of the most difficult issues in ecology and may best be viewed in terms of different criteria and purposes for which operational units are defined. For example, new methods of genetic analysis (Neville et al. 2006a) can be used to cluster individuals into "populations" (based on theoretical expectations of linkage and Hardy-Weinberg equilibrium) or groups of individuals more likely to interbreed with each other than with individuals in other groups. Discontinuities in habitats can also be used to define what may be considered as "populations" for analyses of species occurrence or persistence (e.g., Dunham et al. 2002). In practice, both views may be useful for identifying "populations" and for understanding processes influencing fish population dynamics. For example, in the case of Lahontan cutthroat trout (O. c. henshawi), Dunham et al. (2002) defined "patches" of potentially suitable habitats based on environmental gradients and modeled the probability occurrence of cutthroat trout "populations" in patches. A finer-scale look at genetic structuring within one of the larger patches revealed significant spatial variability, however (Neville et al. 2006b). Thus, we view definitions of "populations" as dependent upon the objective of the study or management application, and the criteria and spatial scales of interest.

7. Considering demographic and genetic risks to headwater fish populations, at what scale(s) would you consider the consequences of not providing passage?

   The consequences of not providing passage include increased probability of extinction, loss of genetic variability that could lead to inbreeding or more likely loss of evolutionary potential, as reviewed on pages 14-19. It should be noted that the persistence of isolated and fragmented populations above impassable barriers is primarily affected by external forcing factors (e.g., catastrophic disturbance), whereas the long-term viability of these populations is influenced more by intrinsic factors affecting populations (e.g., genetic, demographic). See Fausch et al. (2006) for a discussion of "persistence" versus "viability" as management goals.

8. If we were to not provide headwater fish passage in forested landscapes under some circumstances, how might we identify/quantify or otherwise address the cumulative effects to fish populations in individual and neighboring streams?

   The issue of cumulative effects relative to fish passage is best considered in a spatial context. Within a particular watershed or stream network, the total amount of potentially suitable and known or probable occupied habitat could be considered relative to different scenarios involving removal of fish passage barriers. This would provide a simple, network-scale view of habitat gain or loss for different scenarios. A more spatially explicit view of cumulative effects would involve analyses of connectivity and size of habitats, which have been repeatedly demonstrated to be key factors driving fish populations in headwater streams (Fausch et al. 2006). A variety of metrics describing connectivity are available for describing fragmentation of stream networks (e.g., Isaak et al., in press) and could be used to estimate potential spatial cumulative effects of retaining or removing individual barriers or types of barriers across a stream network. This would be a relatively straightforward and inexpensive process that could utilize a geographic information system with basic spatial data and information on barrier locations and extent of fish distributions (e.g., Fransen et al. 2006).

Time may also factor into cumulative effects assessments since some risks are time-dependent (see next answer).

9. How much habitat can be omitted from access without incurring genetic or demographic risks to headwater fish populations?

   This question can only be addressed by studying these influences relative to existing barriers or by monitoring the impacts of passage restoration in a carefully designed study. Predictive models of the genetic or demographic effects of barriers could be developed to provide basic guidelines for "how much is enough" or alternatively "how much is not enough" in terms of identifying opportunities for fish passage restoration. An effort like this is currently underway in central Idaho, where genetic variability in rainbow trout from 55 different streams is being studied in relation to influences of habitat size, culvert barriers, and wildfire-related disturbance (Neville et al. 2006c). The goal is to develop a predictive model of the effects of these different factors to gain an understanding of which factors are most influential and where restoration could provide the greatest benefit to fish populations. Sometimes these models can lead to unexpected implications. For example, conventional wisdom would dictate we restore fish passage for larger habitats first. However, populations in small habitats are more vulnerable to extinction over short time frames (e.g., Morita and Yamamoto 2002) and may merit greater priority in time, even if small populations are less valuable overall than large populations. Prescriptions will clearly vary on a case-specific basis.

10. How many fish and over what intervals is needed to alleviate genetic consequences of isolation (genetic drift, inbreeding, etc)?

    This is a difficult question to answer in practice. Based on theory, the rule of "one migrant per generation" or OMPG is commonly prescribed to minimize the chances of inbreeding and loss of evolutionary potential via genetic drift while allowing local populations to maintain their genetic distinctness (see Wang 2004 for a recent analysis). In other words, this is a balance between the forces of drift and "migration." Here "migration" as used in the OMPG rule corresponds to what we define as "dispersal." OMPG is based on the effective rate of gene flow – in other words, dispersing individuals that actually breed with the new population they move into. OMPG does not hold if dispersing individuals do not have the same reproductive success as fish in the receiving population. The key to finding an appropriate rule of thumb is an understanding of the relative genetic contributions of dispersing individuals to the receiving population – they are likely not random. In the face of this uncertainty it is commonly recommended that 1-10 individuals per generation may be needed to provide sufficient gene flow among artificially isolated populations.

    In the broader context, there is the question of "what is natural" in terms of gene flow? Fish populations are often naturally isolated, even in the absence of obvious physical barriers to movement in headwaters. There has not been enough comparative work (see answer to #3 above) of gene flow among basins for headwater fishes to provide some general prescriptions for expected patterns of gene flow or dispersal relative to the spatial structure of stream networks and other factors that influence fish movement (e.g., Neville et al. 2006a). We view the question of "what is natural" as more important than basic prescriptions derived from OMPG.

11. Are there science-based reasons for developing headwater fish passage criteria that differ among major land uses (i.e., forested, agricultural, or urban)?

    There could be a variety of possibilities depending on the criteria in question. It is well-known that lands with different uses and the streams draining them exhibit different physical dynamics and patterns of fish occurrence. In the context of a cumulative effects analysis, this *could lead to very different views of restoration priorities as described above. However, there is nothing inherently unique about different land uses per-se other than their impacts on the key considerations for identifying the impacts of different alternatives for passage restoration.*

12. Are there other questions related to this topic that you recommend be addressed?

    These are described in the literature synthesis. Two very important issues not addressed in this list are the need for a rigorous monitoring and evaluation program for fish passage restoration and consideration of the value of intermittent streams for fish populations, especially anadromous species of high value. There are many other issues that could be addressed, but relative to the objectives that appear most urgent for fish passage restoration, these two issues would seem to merit higher priority.

13. Given the above questions, how would you summarize the movement/connectivity needs of resident fish in headwater streams over the short-term (day-to-day) and long-term (years) considering the dynamic nature of stream channels, disturbance, and recolonization?

    To answer this question would be to repeat what we have provided in the literature synthesis, so we refer to that for the answer.