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Strategies for Conserving Native Salmonid Populations at Risk From Nonnative Fish Invasions:

Tradeoffs in Using Barriers to Upstream Movement

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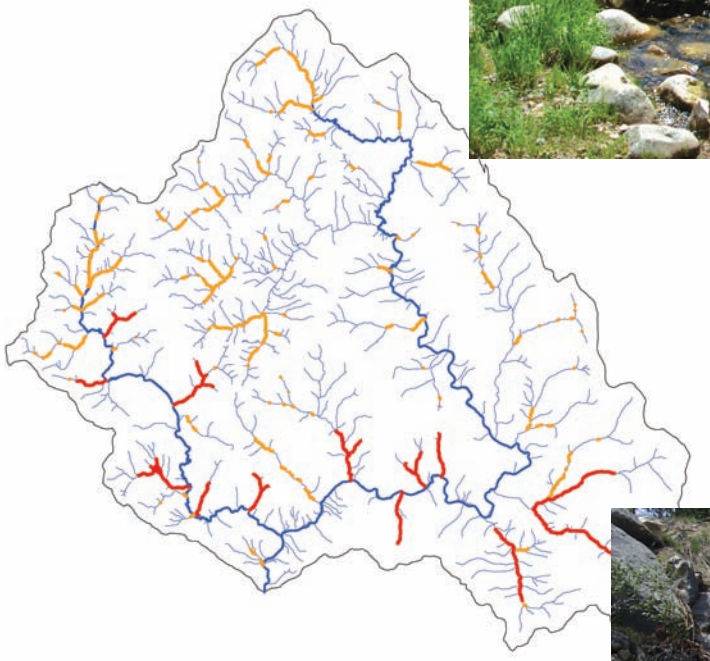

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Abstract

Native salmonid populations in the inland West are often restricted to small isolated habitats at risk from invasion by nonnative salmonids. However, further isolating these populations using barriers to prevent invasions can increase their extinction risk. This monograph reviews the state of knowledge about this tradeoff between invasion and isolation. We present a conceptual framework to guide analysis, focusing on four main questions concerning conservation value, vulnerability to invasion, persistence given isolation, and priorities when conserving multiple populations. Two examples illustrate use of the framework, and a final section discusses opportunities for making strategic decisions when faced with the invasion-isolation tradeoff.

Keywords: barriers to fish movement, biological invasions, conservation biology, isolation management, native salmonids

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***Cover photos and images clockwise from top**: A gabion barrier constructed on North Barrett Creek in the Snowy Range, Wyoming, to prevent upstream movement by nonnative trout (photo by G. T. Allison, U.S.D.A. Forest Service). Nonnative brook trout (top) and native greenback cutthroat trout (bottom) from Hidden Valley Creek, Rocky Mountain National Park, Colorado (photo by K. D. Fausch, Colorado State University). Culvert beneath forest road in Lost Creek, Idaho (photo by J. B. Dunham, U.S. Geological Survey).Map of the North Fork Coeur d'Alene River basin, Idaho, showing stream segments where nonnative brook trout have invaded (red) and potential brook trout habitat (yellow). See Figure 7 in Section VI for details.*

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Executive Summary

Native salmonid populations have declined throughout the world due to a host of human influences, including habitat degradation and loss, invasion of nonnative fishes, and overfishing. In many regions, suitable coldwater habitats for salmonids are found mainly in protected natural areas, so that these fishes are increasingly relegated to smaller and more isolated pieces of their former native ranges. Moreover, populations of native trout and charr in these relatively undisturbed habitats are often at further risk from invasion by nonnative salmonids from downstream. Faced with this dilemma, fisheries managers frequently consider using barriers to upstream movement to prevent invasion and displacement or hybridization. However, in doing so they face a tradeoff because isolating native salmonid populations in small headwater habitats may also increase their risk of extinction. Here we focus on native salmonids in the inland western U.S. (for example, cutthroat trout, *Oncorhynchus clarkii*; bull trout, *Salvelinus confluentus*), but this is an important problem for salmonids and other stream biota worldwide.

This monograph reviews the state of knowledge about the factors that affect this tradeoff between invasion and isolation, and presents a framework for analyzing it and prioritizing conservation actions. Barriers to prevent invasions can pose problems for salmonids because these fish often need to move to complete their life history. Although anadromous salmonids are known for their extensive migrations, freshwater trout, charr, grayling, and whitefish also show remarkable flexibility in life history and diverse movement behaviors. Movements allow fish living in patchy environments to maximize fitness by placing each life history stage in habitats that provide optimum growth and survival. Likewise, in environments that fluctuate seasonally or among years, diverse life histories, and movements allow fish to avoid harsh conditions, or recolonize habitats after catastrophes.

Isolation of fish populations using barriers can extirpate mobile life history types, restrict fish populations to habitats inadequate for long-term persistence, and prevent natural recolonization after catastrophes. Both direct and indirect evidence from field research indicate that isolated populations of cutthroat trout and bull trout are more likely to be extirpated in smaller watersheds, but studies have been conducted in only a few regions. These case studies suggest that these salmonids need approximately 10 km of suitable stream habitat to persist for 25 to 50 years and maintain genetic diversity, although the long-term fate and evolutionary potential of populations in such small watersheds is unknown. Much more research is needed to refine these estimates for all taxa, because the amount of habitat needed for persistence is likely to vary strongly with climate and basin characteristics.

Invasion by three commonly introduced salmonids (brook trout, *Salvelinus fontinalis*; brown trout, *Salmo trutta*; and rainbow trout, *O. mykiss*) can also extirpate inland native stream salmonids, by competition and predation or introgressive hybridization. For example, field research on brook trout in the inland western U.S. showed that they rapidly invade upstream in some regions, and displace or completely eliminate native cutthroat trout by reducing survival during the first two years of life. However, in other regions brook trout invasions appear to have stalled, perhaps limited by environmental factors. Likewise, nonnative rainbow trout often hybridize with native cutthroat trout, and nonnative brook trout with bull trout, but in certain cases environmental factors or isolating mechanisms apparently reduce risks of introgression. More research is needed to understand where each species will invade and displace native species versus where they will coexist or fail to invade.

Because the outcome of invasion and isolation can differ among species of native salmonids, and among regions or habitats, installing barriers is often a complex problem that must be analyzed carefully. Four key questions provide a framework for considering the use of barriers to prevent invasions and conserve native fishes:

1. Is a native salmonid population of important conservation *value* present?
2. Is the population *vulnerable* to invasion and displacement?
3. If the native salmonid population is isolated to prevent invasion, will it *persist*?
4. If there are multiple populations of value, which ones are *priorities* for conservation?

The first step in any conservation plan is to set clear management objectives by considering the values embodied in a native salmonid population. Three conservation values emerge from the literature: evolutionary, ecological, and socio-economic. *Evolutionary value* focuses on distinct species, races, and populations, such as those protected in the U.S. by the Endangered Species Act, many of which are adapted to specific environments. For example, in some regions small remnant populations of native cutthroat trout represent a rare and significant genetic resource. *Ecological value* includes important ecological processes and functions at the population, community, and ecosystem levels. For example, species like salmon and trout have strong effects on trophic webs in aquatic systems, which may also extend into the terrestrial ecosystem. Also of ecological value are species and populations that are self-sustaining, resilient, adaptable, and require minimal inputs of resources to maintain them. *Socio-economic values* include recreational and economic benefits from fishing and tourism. Although values may overlap, often it is not possible to conserve all of them simultaneously in any one location, so effective management will involve clearly defining priorities.

The second question to address for a population of conservation value is whether it is vulnerable to invasion and displacement by, or hybridization with, a nonnative salmonid. This depends on the ability of the invader to be transported to the basin or spread to the target location, establish a reproducing population, and dominate in interactions with the native salmonid. Currently, most transport of nonnative salmonids is by unauthorized introductions by the public. Spread from these initial invasions may be facilitated by long distance movements (that is, “jump dispersal”), or hampered by barriers to upstream movement like cascades and waterfalls. Headwater stocking facilitates downstream dispersal throughout entire drainage basins. Once nonnative salmonids arrive, they tend to establish populations where abiotic regimes of temperature, flow, and natural disturbances allow reproduction and recruitment. Nonnative salmonids may have impacts through competition, predation, hybridization, or spreading parasites or pathogens. Empirical evidence has demonstrated strong individual biotic interactions (competition or predation) with native salmonids, particularly during the first two years of life. Hybridization is also commonplace and spreading in some cases, but rare or localized in others. Recent evidence suggests that movement of nonnative trout may transport nonnative parasites (such

as *Myxobolus cerebralis*, which causes whirling disease) upstream to contact native salmonids.

The third question for valuable populations vulnerable to displacement by a nonnative salmonid is whether the native fish population will persist if isolated using a barrier to prevent upstream invasion. Both direct and indirect field evidence indicate that larger interconnected patches sustain populations longer than do smaller isolated ones. Natural disturbances like fire, flood, drought, and freezing, as well as more subtle climate changes that affect stream flow and temperature, can drive small salmonid populations to extinction. Isolation can eliminate migratory life histories that confer resilience through large fecund adults, the opportunity for gene flow, and recolonization following catastrophic events. Isolation may also interact with habitat degradation and overfishing to reduce population persistence in small isolated stream segments.

The fourth question to address is which native salmonid populations of value are deemed the highest priorities for conservation, given limited management resources. Priorities should be based on the relative conservation values of each population, the risk of losing them, and the feasibility of reducing that risk through management. These values, risks, and opportunities for management may vary strongly across any area of interest, so a strategic, spatially explicit approach is useful. It is important to understand the natural spatial structure of native salmonid populations and their dynamics through time, rather than arbitrarily focusing on individual streams or other geopolitical units. Planning to conserve native salmonids requires maintaining broad representation of the remaining ecological diversity, ensuring there is redundancy (more than one population of each type) to buffer against loss, and considering the resilience and resistance of populations to environmental disturbances. An appropriate goal is to seek a set of populations that represent the diversity of possible conservation values, and that can interact, persist, and evolve to maintain those values through time.

Two examples from the Coeur d'Alene River, Idaho and the Little Snake River, Colorado-Wyoming, illustrate use of the framework in markedly different situations. In the Coeur d'Alene River, brook trout and rainbow trout have invaded some streams, but large amounts of relatively undisturbed habitat remain uninvaded. Here, there are opportunities to use barriers judiciously to protect genetically pure populations of westslope cutthroat trout (*O. c. lewisi*) with evolutionary values from further invasion, and to sustain key ecological and socio-economic values by either retaining or restoring passage for migratory life history forms. In contrast, in the Little Snake River, nonnative trout have invaded almost completely so that many barriers have been installed in headwater streams to protect the evolutionary legacy of remnant Colorado River cutthroat trout (*O. c. pleuriticus*) populations. Unfortunately, there is little possibility for these populations to support the full spectrum of ecological and socio-economic values without large efforts to install barriers and eradicate nonnative trout from downstream segments. Because many of the remnant isolated populations are small, persistence of native cutthroat trout in the basin may depend on maintaining resilient populations through intensive habitat protection or restoration, and on reintroductions by humans if they are extirpated. Priorities could focus on removing nonnative salmonids to allow extending the larger populations downstream and connecting them with other populations.

We developed a decision-space diagram to allow biologists managing a particular basin and set of native salmonid populations of conservation value to consider the available options and make strategic decisions under different circumstances like those in the examples above. These decisions will be influenced primarily by: 1) the degree of isolation of the populations of interest and 2) the degree of invasion threat. If most remaining native populations are in headwater streams and are clearly vulnerable to invasion and displacement, then barriers will be required to protect them from rapid extinction. Given this, strategic decisions available include the number, size, quality, and spatial distribution of habitat patches; the representation and redundancy of populations needed to conserve remaining diversity; and effective protocols for removing nonnative salmonids, and translocating native salmonids to found new populations. The goal should be to develop larger and more connected habitat patches and to move the invasion threat farther away, even though in many cases this is not fully achievable at present. At the other end of the spectrum, if a basin has many large interconnected patches of suitable habitat with native salmonids and the invasion threat is distant or weak, then strategic decisions will involve preventing invasions by controlling the sources and monitoring their spread, preventing fish movement barriers and other types of habitat fragmentation, and maintaining natural ecological processes that provide complex habitats. Other regions of the decision space require different strategies for management, or a mix of strategies, and additional strategic decisions can be made about barrier placement or removal under different scenarios.

Finally, we emphasize that the appropriate use of barriers will depend not only on the current threats of invasion and isolation, but also may change through time as human values shift, as anthropogenic disturbances change, and as climate and natural disturbances are altered. Because we don't fully understand the risks associated with barriers and invasion of non-native salmonids, most management should be considered an experiment and carefully evaluated to improve future efforts. Effective management will require careful monitoring of populations, evaluating the results of such management experiments (for example, the installation or removal of barriers), and investigating the basic processes of invasions and population persistence.

Contents

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Introduction

Native salmonid populations have declined throughout the world due to a host of human effects, including habitat degradation and loss, invasion of nonnative fishes, and overfishing. In many regions, suitable coldwater habitats for salmonids are found mainly in protected natural areas, so that these fishes are increasingly relegated to small pieces of their former native ranges. Moreover, populations of native trout and charr in these relatively undisturbed habitats are often at further risk from invasion by nonnative salmonids, usually from downstream. Faced with this dilemma, fisheries managers frequently consider using barriers to upstream movement to prevent invasion and displacement. However, in doing so they face a tradeoff because isolating native salmonid populations in small headwater habitats may also increase their risk of extinction.

This monograph describes this widespread problem for stream salmonids, reviews the state of knowledge about the factors that affect extinction risks from invasion versus isolation, and presents a framework for analyzing this tradeoff and prioritizing conservation actions. We first briefly review the natural population structure and life history of stream salmonids, focusing on movements that link populations across habitats dispersed throughout the riverscape. We then discuss the effects of isolating salmonid populations above barriers, which restricts these movements and may drive populations extinct, and the effects of invading nonnative salmonids, which may move upstream (or downstream in some cases) and displace native salmonids.

Second, we present a conceptual framework to guide analysis of the tradeoff, focusing on four main questions concerning conservation value, vulnerability to invasion, persistence if isolated, and priorities when conserving multiple populations. We provide two examples to illustrate the use of the framework and show the key elements in the decision process, and end by discussing opportunities for making strategic decisions when faced with this tradeoff.

This paper is limited in scope to native and non-native salmonids and the stream networks they inhabit or could invade, because salmonids dominate vertebrate communities in coldwater streams and are often the main focus of management. However, the tradeoff is also relevant to other aquatic taxa, both vertebrate and invertebrate, so the framework we propose may serve as a foundation for considering similar issues for these groups.

How to Use this Publication

This report is written in seven major sections, to allow readers with different backgrounds to find information quickly. Some points are supplemented with additional material that appears in text boxes, and some important concepts are presented first in the review of knowledge and used again in the framework for analyzing the tradeoff. Sections are arranged as follows:

- ***Section I*** describes why the tradeoff between invasion and isolation is an important problem for salmonids worldwide.
- ***Section II*** summarizes the life history and population structure of stream salmonids, and describes why movement may be critical for their persistence and long-term viability.
- ***Section III*** presents what is known about the effects of isolation by movement barriers on persistence of stream salmonid populations.
- ***Section IV*** discusses the effects of invasion by nonnative salmonids on native salmonids.

- ***Section V*** presents a conceptual framework for analyzing the tradeoff between invasion and isolation.
- ***Section VI*** includes two examples with different constraints to illustrate the use of the framework and show the key elements in the decision process.
- ***Section VII*** discusses opportunities for making strategic decisions when conserving sets of native trout populations in specific watersheds, given different degrees of isolation and invasion threat.

Section I: An Important Problem

Habitat degradation and loss, invasion by nonnative salmonids, and overfishing have reduced the distribution of native salmonids in many regions throughout the world to small enclaves of headwater habitat where they are vulnerable to extinction (Rieman and others 1997b, Harig and others 2000, Kitano 2004). For example, in many watersheds of the eastern U.S., from New England to the southern Appalachian Mountains, native brook trout[1] (*Salvelinus fontinalis*) populations are now restricted to headwater streams that are fragmented by dams, heavily sedimented, and close to dense human populations (Hudy and others 2004). These same watersheds simultaneously have been invaded by nonnative rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) that displace brook trout from downstream habitats (Larson and Moore 1985). Similar combinations of habitat fragmentation and nonnative fish invasions endanger native salmonids and other stream organisms in other regions worldwide (*see Box 1*). These examples illustrate that, although nonnative salmonids do not invade everywhere they are introduced (Fausch and others 2001, Adams and others 2002, Dunham and others 2002a), three widespread invaders (brook, brown, and rainbow trout) have established reproducing populations in many regions outside their native ranges (for example, see Lever 1996, Thurow and others 1997, Fuller and others 1999, Cambray 2003b), and often combine with habitat loss to limit native salmonids or other native fishes to small headwater streams above movement barriers.

Box 1. Examples of habitat fragmentation and invasion for stream fishes worldwide.

- **Native charr in northern Japan -** Habitats of native Dolly Varden (*Salvelinus malma*) and white-spotted charr (*Salvelinus leucomaenis*) in Hokkaido Island, northern Japan, have been highly fragmented by channelization and erosion control dams constructed mainly during the last 35 years (Morita and Yamamoto 2002), and downstream populations are now being displaced by nonnative rainbow trout and brown trout (Takami and Aoyama 1999, Kitano 2004).
- **Native brown trout in Switzerland -** Habitat for native brown trout in tributaries to the Rhine River has been fragmented by human activities over a long period. These populations now face invasion by rainbow trout, which are apparently better adapted to the altered flow regime (Peter and others 1998).
- **Native stream fishes in the Southern Hemisphere -** Native stream fishes in New Zealand, Australia, Venezuela, Chile, Sri Lanka, and South Africa are being decimated by habitat alteration and introduced brown trout and rainbow trout, and persist primarily in small headwater enclaves above waterfalls that the nonnatives cannot ascend (Townsend and Crowl 1991, Crowl and others 1992, Pethiyagoda 1994, Ruiz and Berra 1994, Pefaur and Sierra 1998, Pascaul and others 2002, Cambray 2003a, Gajardo and Laikre 2003).
- **Other native stream biota -** Native stream fishes are blocked from Great Lakes tributaries by barriers built to exclude nonnative sea lamprey (*Petromyzon marinus*; Smith and Jones 2005), and certain life stages of native amphibians and invertebrates that use stream corridors in the Rocky Mountains are also blocked by barriers (Clarkin and others 2003, Adams and others 2005).

[1] Fishes of the genus *Salvelinus* are charr, but here we use the accepted common names for brook trout and bull trout (*S. confluentus*). Throughout, we use the common names of fishes published by the American Fisheries Society (Nelson and others 2004).

Dams, diversions, and culverts that create barriers to upstream movement are among the most common agents that fragment habitat. In the conterminous U.S., there are estimated to be about 77,000 dams at least 2 m high (6 feet) that store at least 62 X 10^3 m^3 (50 acre-feet) of water (U.S. Army Corps of Engineers 2006). This total does not include the huge number of smaller dams and diversions for domestic water supply or micro-hydropower developments, nor the hundreds of thousands of road culverts that create impassable barriers for fish (GAO 2001). In addition, after early settlers degraded downstream habitats and overexploited fish populations (Wohl 2001), they often translocated fish above natural barriers like waterfalls to establish new populations in headwater habitats. Regardless of whether barriers to upstream movement are anthropogenic or natural, they fragment stream habitat in watersheds, simultaneously protecting native salmonid populations from impending invasions but potentially hastening their extinction from environmental catastrophes or small population effects (Caughley 1994). They also disrupt movements of other fishes, amphibians, and invertebrates (Warren and Pardew 1998, Vaughan 2002, Clarkin and others 2003, Adams and others 2005), and may have similar effects on these taxa.

In this monograph, we focus on the tradeoff in extinction risks for native salmonids of the inland western U.S. Native cutthroat trout (*O. clarkii*) were restricted to headwater streams by early mining, logging, grazing, overfishing, and water diversions (Gresswell 1988, Young 1995), and many of these remnant habitats were subsequently invaded by nonnative brook, brown, and rainbow trout that exclude or hybridize with cutthroat trout (Figure 1; Behnke 1992, Dunham and others

Figure 1—Populations of native cutthroat trout (top; S. Emmons image) in the inland western U.S. have often been invaded by nonnative brook trout (bottom; K. Morita image) originally introduced in either downstream or upstream habitats.

2002a). Likewise, bull trout and native rainbow trout in the Pacific Northwest and Canada face similar problems (Rieman and others 1997b, Thurow and others 1997). Although this tradeoff is just coming to light in many regions of the world, it has become a controversial topic in the inland western U.S. There, fish biologists that seek to conserve native cutthroat trout and bull trout disagree over the merits of building new barriers to limit upstream invasions and preserve remaining native salmonid populations versus removing barriers to allow movement of native fish and thereby enhance the chances for population persistence (Dunham and others 2002a, Peterson and others 2004, Shepard and others 2005).

This issue is also important because conservation biologists in general face the same tradeoff – that managing ecosystems to address habitat fragmentation precludes isolating them to prevent invasions. Some conservation biologists have proposed connecting fragments of habitat with corridors to reduce extinction risks (Beier and Noss 1998, Dobson and others 1999), whereas others have argued that increasing connectivity opens the door to nonnative species and diseases (Simberloff and Cox 1987, Simberloff and others 1992, Hess 1994). However, there are few well-documented cases of the problem or potential solutions, even in the extensive literature on landscape connectivity (Bennett 1999, Soulé and Terborgh 1999, Crooks and Suarez in press).

Section II: Movement and Salmonid Life Histories

Barriers and invasions potentially pose problems for salmonids because these fishes often move to fulfill their life history. Within a fish's lifetime, local environments often become marginal or inadequate for its needs, prompting movement to increase or maintain fitness (Thorpe 1994, Brannon and others 2004; *see Box 2*). A general model of life history developed for fishes (Harden Jones 1968), and refined for stream fishes (Schlosser and Angermeier 1995) and salmonids (Northcote 1997), holds that 1) movements link together habitats required for spawning, growth, and refuge from harsh conditions, and 2) these habitats are often dispersed throughout the riverscape (Schlosser 1991, Fausch and others 2002).

Although anadromous salmonids are well known for their spectacular migrations to and from the ocean, freshwater salmonids also show a great diversity of movement behaviors (for example, Meka and others 2003; *see Box 2*). Salmonids show remarkable flexibility in expression of life-history types, including co-occurring (sympatric) populations of the same species with different life histories, alternative life histories within a common gene pool, and phenotypic plasticity of a single genotype under different environmental conditions (Hendry and others 2004a, Hutchings 2004). Distinct forms that co-occur in the same watershed, or even the same stream, allow a single species to exploit diverse

Box 2. Fish movement and migration.

Theory: Movement of organisms, both within and between generations, is a response to an environment that is patchy in space or through time (Wiens 1976). The theory of animal migration is based on the premise that organisms move to place each life-history stage in suitable habitat to maximize fitness (Northcote 1978, 1992, Dingle 1996, Hendry and others 2004a, 2004b).

Migratory Life History Types: Fishes that migrate within freshwater are termed **potamodromous** (Gresswell 1997), but four additional terms are more commonly used to describe the diversity of movement behavior in freshwater fish (see below). Nevertheless, salmonids display great plasticity and variation in movement behavior, which often defies this simple typology.

Lacustrine salmonids complete their life cycle entirely within lakes.

Adfluvial fish migrate from lakes into rivers to spawn, and juveniles later descend to lakes to grow. For example, "coaster" brook trout in tributaries of Lake Superior (Huckins and others in press), and Lahontan cutthroat trout in Pyramid Lake, Nevada (Snyder 1917, Behnke 1992), display adfluvial life histories, spawning in tributaries but moving downstream to large lakes to grow to large adult sizes.

Fluvial fish complete their life cycle within riverine environments, but may use tributaries for spawning and juvenile rearing. For example, bull trout in the northern Rocky Mountains and Dolly Varden in rivers in northern Japan display fluvial life histories, spawning and rearing in tributary streams but moving downstream into larger rivers to grow to adulthood (Rieman and McIntyre 1993, Rieman and Dunham 2000, Koizumi and Maekawa 2004).

Resident salmonids complete their life cycle entirely within tributary streams, but may range widely seeking suitable habitats for spawning, feeding, or refuges (Gowan and others 1994, Fausch and Young 1995).

environments (Carl and Healey 1984, Bagliniere and others 1989, Brannon and others 2004) or persist in the face of variable or uncertain ones (Rieman and Clayton 1997). Populations may include both resident and migratory individuals (Rieman and others 1994, Zimmerman and Reeves 2000), and the migratory forms may display substantial variation in the extent and timing of movements (Brannon and others 2004). The expression of different life-history types is apparently partly under genetic control, yet plastic in response to environmental conditions (Gislason and others 1999, Hendry and others 2004a), which can produce strong variation in life histories both within and among distinct environments (Taylor 1990, Jonsson and Jonsson 1993, Yamamoto and others 1999). Recent evidence also suggests that when a species is exposed to a novel or changing environment, new life histories (for example, resident vs. migratory forms, seasonal timing of migration) may emerge relatively quickly, in several decades or less (Näslund and others 1993, Quinn and others 2001, Hendry and others 2004b, Riva Rossi and others 2004).

Movement is important not only in spatially patchy environments, but also in those that fluctuate through time so that fish are periodically reduced or extirpated in some habitat patches. Dispersal that contributes to gene flow, provides demographic support (that is, immigration that offsets mortality or increases population growth rate; see Stacey and Taper 1992, Hilderbrand 2003), or allows recolonization can be critical to persistence of these populations across generations. Subdivided populations that interact strongly through movements among them are termed metapopulations (Hanski 1999), although salmonid populations are unlikely to fit simple theoretical models (see Harrison and Taylor 1997, Dunham and Rieman 1999). Such metapopulation dynamics may be particularly important in watersheds where major disturbances like drought, flood, fire, and debris flows create and destroy habitat, leaving a mosaic of habitats in different successional stages (Reeves and others 1995, Neville and others in press). Salmonid populations that have evolved in these dynamic environments may also have evolved diverse life histories, especially movement behaviors, that ensure long-term persistence at larger scales (Thorpe 1994, Heino and Hanski 2001). For example, migratory fish may be critical to long-term persistence because returning adults that fail to home to their natal watershed disperse and recolonize or support other habitats (Quinn 1993, Tallman and Healey 1994, Hendry and others 2004b). In other cases diversity in migratory timing and the occurrence of multiple age classes "at large" in downstream rivers, lakes, or oceans during major disturbances can allow fish to quickly recolonize the disrupted habitats (Rieman and others 1997a) or move to newly created ones (Leider 1989).

Small-stream salmonids may not exhibit the dramatic migrations of forms with access to larger habitats, but movement is still a critical behavioral component. These fishes may move tens to thousands of meters daily, seasonally, or during their lifetime to seek suitable habitats. For example, foraging cutthroat trout in small streams have been observed to move over 150 m during the diel cycle (Young and others 1997), and spawning runs of such fish have exceeded 2 km (Young 1996). Movements in fall and winter, associated with declining water temperatures and ice formation, have been of similar magnitude (Brown and Mackay 1995, Jakober and others 1998). Moreover, mobility is common among cutthroat trout of all ages in small streams, and is not simply attributable to a few wandering individuals (Peterson and Fausch 2003a, Schmetterling and Adams 2004).

Thus, movement plays important roles in stream salmonid populations, and yet remains poorly described (Gowan and others 1994, Rieman and Dunham 2000). The advent of advanced technologies such as radiotelemetry, PIT tags, and otolith microchemistry has enabled recognition of some aspects of trout movements (Rieman and others 1994, Fausch and Young 1995, Meka and others 2003, Wells and others 2003), but a full understanding awaits sampling that is continuous over scales of space and time broad enough to track individuals of all life histories throughout their life cycles (Baxter 2002, Fausch and others 2002). Such understanding remains a central issue for research because movement may be the key to population persistence in variable and changing environments (Rieman and Dunham 2000).

Section III: Effects of Isolation

Given the potential for extensive movements by salmonids both within and among generations, it is clear that barriers like dams or culverts could extirpate mobile life history types, restrict populations to habitats inadequate for long-term persistence, and prevent recolonization in the event of population extinction. Barriers might also disrupt movement of other aquatic organisms, and potentially change the structure of whole communities. However, even for salmonids, which are relatively well studied, evidence for negative effects of isolation in headwater streams is still emerging. There is some direct evidence from studies of barriers in Japan and translocation of cutthroat trout in the inland western

U.S., and indirect evidence from patch occupancy in both countries. There is also indirect evidence from molecular genetics and population models, which we summarize briefly.

Direct Evidence

Direct evidence for negative effects of isolation on headwater stream salmonid populations comes from two studies where barriers were built, or fish were translocated above barriers, and the results measured. In both cases, investigators fit relationships between watershed area and species occurrence, allowing empirical estimates of the watershed areas required for a specified probability of population persistence (for example, 0.50 or 0.90). We caution that these estimates may not be easily generalized to other regions, because watersheds that support habitat of sufficient size, length, or complexity to sustain native salmonid populations can differ markedly in area, depending on climate, geology, and other factors. In addition, different species, and even subspecies, of salmonids may have different life history characteristics that allow persistence despite isolation. Despite this complexity, these studies do show that watershed area is strongly associated with population persistence, and they provide first approximations of relevant size thresholds.

Morita and Yamamoto (2002) measured occurrence of whitespotted charr in 52 headwater fragments above erosion control dams (all >2 m high) in mountain streams of southern Hokkaido Island, Japan, and found that both watershed area and time since isolation had important effects on population persistence (Figure 2). The authors inferred that all sites had charr populations before the dams were built, because habitat was no different than at 32 control sites that supported charr. Seventeen of the 52 populations had been extirpated in the 30 years since most barriers had been built, and 12 of the 35 remaining populations were predicted to go extinct in the next 50 years. Overall, they predicted that a minimum watershed area of 2.3 km^2 is needed to have a 50 percent chance of sustaining a population for 50 years, and their figure shows that about 9 km^2 is needed to have a 90 percent chance. Southern Hokkaido receives much more precipitation than the inland western U.S. so much smaller watersheds sustain perennial streams. However, this study shows that useful relationships can be developed from historical records and relatively simple field measurements.

Further work on extant populations of these charr revealed additional ecological effects of the barriers. Morita and others (2000) reported that growth rates of whitespotted charr juveniles in three rivers were higher above dams than below, likely due to the lower spawning and fry density upstream. This resulted in more fish remaining resident than smolting, a common response to increased juvenile growth rates (Thorpe and Metcalfe 1998, Hendry and others 2004a). Moreover, growth rates of fish transplanted from below to above the dam in one of the streams also increased and smoltification decreased, indicating that the changes were due to phenotypic plasticity rather than rapid evolution.

In the second study, Harig and Fausch (2002) measured persistence of allopatric greenback cutthroat trout (*O. c. stomias*) and Rio Grande cutthroat trout (*O. c. virginalis*) in segments of 28 streams (1.0 to 20.5 km long) in Colorado and New Mexico where they had been translocated above barriers during the previous 3 to 31 years. The models they fit predicted that translocations in watersheds >14.7 km^2 had a >50 percent chance of establishing a reproducing population, whereas in smaller watersheds populations were more likely to die out or remain at low abundance. Watersheds of >33 km^2 were predicted to have a >90 percent chance of establishing a reproducing population, a goal more in line with many conservation assessments. The empirical data used to develop the model showed that the 13 stream segments where cutthroat trout reproduced consistently were, on average, 7.3 km long (range: 1.8 to 20.5) and drained watersheds that averaged 23 km^2, although 6 of the shortest also included lakes.

Virtually all of the *historical* stream populations of these two subspecies of cutthroat trout were isolated from nonnative salmonid invasions above natural barriers. In most cases, they were probably translocated there by early settlers. This suggests that at least some populations of these subspecies can adapt to such habitats and persist for decades. Indeed, Harig and Fausch (2002) found that 32 of the 70 historical populations persisted in stream fragments with watersheds smaller than 14.7 km^2. However, these may be at greater risk of eventual extinction due to insufficient habitat, an effect Tilman and others (1994) referred to as an "extinction debt" that is yet to be paid (see Hanski 1997 for review). Finally, we note that other studies have also reported loss of stream fish populations above barriers, and reductions in fish species richness upstream versus downstream of barriers, in other temperate and tropical rivers (Winston and others 1991, Fausch and Bestgen 1997, Peter 1998, Schmutz and Jungwirth 1999, Pringle and others 2000). These observations lend further direct evidence for the negative effects of isolation.

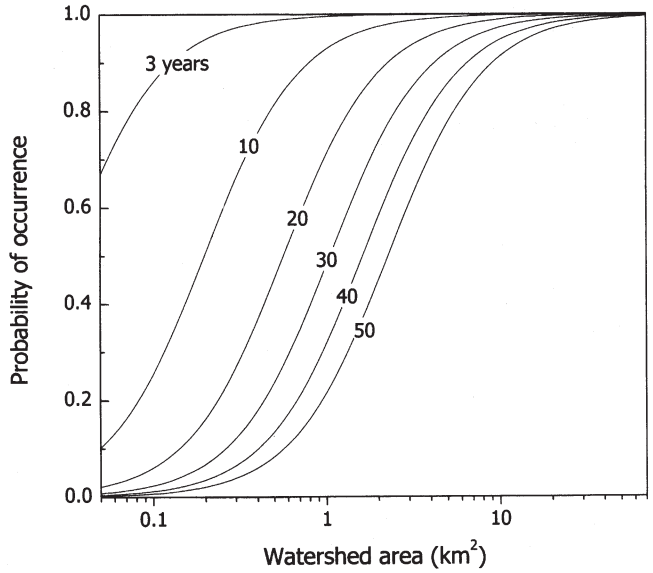

Figure 2—Probability of whitespotted charr (top; K. Morita image) persistence above erosion control (sabo) dams (bottom; K. Fausch image) in southern Hokkaido Island, Japan, as a function of watershed area (from Morita and Yamamoto 2002; used with permission). Curves (center) were predicted from a logistic regression model of presence/absence as a function of watershed area, time since damming, and stream gradient for 52 sites above dams. The family of curves in the figure predicts the probability of population persistence in headwater streams that have been isolated for different time periods (given average gradient). Watersheds >10 km^2 have a high probability of sustaining these charr populations for 50 years, according to the model, but different salmonid species in different environments may have markedly different relationships.

Indirect Evidence

Several lines of indirect evidence also indicate that small watershed size and isolation reduce persistence of headwater salmonid populations. This evidence comes primarily from studies of patch occupancy (patches are defined as continuous networks of suitable stream habitat; Dunham and others 2002b), but other indirect evidence also comes from colonization after barrier removal, and genetics and population models (*see Box 3*). In the first study of patch occupancy for salmonids, Rieman and McIntyre (1995) reported that bull trout in the Boise River basin in Idaho had approximately a 50 percent chance of occurrence in patches >25 km^2 (which support about 5 km of stream habitat), and more than an 80 percent chance in patches >80 km^2 (about 9 km of stream habitat). This suggested that populations in smaller patches were more vulnerable to local extinction than those in larger patches. In a second study, Dunham and others (1997) reported that Lahontan cutthroat trout (*O. c. henshawi*)

Box 3. Additional indirect evidence on isolation.

Genetics: Isolation of small populations can cause loss of genetic diversity and random genetic drift (Rieman and Allendorf 2001). In turn, this can lead to a loss of phenotypic variation and evolutionary potential (Allendorf and Ryman 2002), and potentially to reduced effective population size (Waples 2004) and inbreeding depression, both of which could hasten extinction of salmonid populations isolated above barriers (for example, Soulé and Mills 1998, Frankham 2005). However, these mechanisms have not been demonstrated in headwater stream salmonids, and there has been only limited work to discriminate effects of habitat size and isolation. Examples include:

- Yamamoto and others (2004) found lower genetic diversity and increased genetic drift in whitespotted charr above barriers versus below in three watersheds in Hokkaido.
- Wofford and others (2005) reported that genetic diversity decreased and genetic drift increased for coastal cutthroat trout (*O. c. clarki*) isolated above more versus fewer barriers in a small headwater stream in Oregon.
- Neville and others (in press) reviewed evidence for salmonids, and found that barriers were consistently associated with lower genetic diversity within populations.

Population models: Population models have been used to 1) estimate total population sizes and compare them to theoretical guidelines, and 2) simulate the effects of isolation, population size, survival, and environmental variation on persistence and genetic variation.

- Rieman and Allendorf (2001) used individual-based models to estimate population sizes needed to sustain genetic variation in bull trout. They argued that few local populations would maintain genetic variation indefinitely without gene flow from surrounding populations.
- Morita and Yokota (2002) used an individual-based model to predict persistence of whitespotted charr populations. Persistence increased with larger populations and higher adult survival, but decreased substantially for small populations after 30 to 100 years in the model, suggesting that smaller populations are at a higher risk of eventual extinction.
- Hilderbrand (2003) modeled inland cutthroat trout populations and found that persistence increased with increases in population size, immigration from adjacent source populations, and juvenile survival, and with decreases in environmental variation.

in the Great Basin were more likely to occur in patches that were connected to other occupied patches along stream networks. This suggested that populations were more likely to persist in less isolated patches. Further research in the Boise River basin showed that both larger patch size and smaller distance to occupied patches were important predictors of bull trout presence (Dunham and Rieman 1999). In both locations, disturbances like floods, droughts, fires, and debris flows can extirpate these two salmonids from whole stream segments (Rieman and Clayton 1997, Dunham and others 2002b), so movement is required to recolonize habitat fragments and maintain local populations.

Three recent studies have also shown the importance of larger connected patches in supporting headwater salmonid populations. Rich and others (2003) found that bull trout were more likely to be present in tributaries of Montana watersheds where there was a strong source population in the mainstem river downstream. Koizumi and Maekawa (2004) reported that Dolly Varden were more likely to occur in larger spring-fed tributaries of a Hokkaido river that were closer to other occupied tributaries than in smaller and more distant ones. Young and others (2005) used data from extensive electrofishing surveys to calculate that streams of 3.4 to 12.9 km in length were needed to sustain 500 to 5000 age-1 and older greenback or Colorado cutthroat trout (*O. c. pleuriticus*). These population size thresholds have been proposed as sufficient to maintain genetic diversity (n=500) and long-term evolutionary potential (n=5000; Allendorf and others 1997, Hilderbrand and Kershner 2000, Young and Harig 2001), rather than simply to ensure relatively short-term persistence (that is, 50 to 100 years). It is typical that half or fewer of the extant populations of native cutthroat trout in various regions are found in streams long enough to support populations of these sizes (see Kruse and others 2001, Young and others 2002, Young and Guenther-Gloss 2004, Young and others 2005). Nevertheless, indirect evidence from field studies like these is particularly relevant because they encompassed the large spatial scales at which land managers must set priorities and make decisions about resource management (Fausch and others 2002).

Once habitats are made available by removing barriers, recolonization of unoccupied habitat appears likely. The many examples of barrier removal followed by rapid and extensive upstream colonization in fishes (Hart and others 2002 and citations therein) serve as circumstantial evidence that renewed access to headwater habitats above dams, particularly spawning areas, may increase the persistence of downstream populations (Smith and others 2000). Similarly, streams that have lost fish populations because of drought, severe floods, fire-related disturbances, or pollution are often quickly repopulated (Larimore and others 1959, Sigler and others 1983, Fausch and Bramblett 1991, Rieman and Clayton 1997, Roghair and others 2002), and habitats available for the first time (for example, following glacial retreat; Milner and Bailey 1989) typically develop fish populations in a predictable sequence. In some circumstances, fishes require extended periods to colonize newly available habitats downstream (Hepworth and others 1997), or may be more likely to colonize other habitats following displacement by floods (Leider 1989) or in response to high densities (Gowan and others 1994, Isaak and Thurow 2006).

Section IV: Effects of Invasions by Nonnative Salmonids

The other main factor in the tradeoff addressed here is upstream invasion by nonnative trout that may reduce or eliminate native salmonids in headwater streams. As we described above, rainbow, brown, and brook trout have been transported and released in most countries and regions that have suitable coldwater habitat for salmonids (Lever 1996, Rahel 2000). In the western U.S., many of these introductions began in the 1870s with the arrival of large numbers of Euroamerican settlers, who further spread these fishes by railroad, horseback, and on foot (Wiltzius 1985, Alvord 1991, Wiley 2003). State and federal agencies assumed responsibility for most stocking thereafter (Wiltzius 1985), which still continues in some parts of this region (Epifanio 2000). For example, brook trout were first released in the 11 western states between 1872 and 1912 (MacCrimmon and Campbell 1969) and are still stocked in 7 of them (Dunham and others 2002a).

Displacement of Native Salmonids

Where barriers to upstream movement are lacking, nonnative salmonids like brook trout can move rapidly upstream and colonize habitat occupied by native salmonids (Gowan and Fausch 1996, Peterson and Fausch 2003a). There have been multiple observations of rapid declines in native salmonid populations after these nonnative trout invasions, such as declines of cutthroat trout after nonnative brook trout and rainbow trout invasion in western U.S. streams (Gresswell 1988, Behnke 1992, Young 1995). These effects have been studied in detail using both experimental and correlative approaches.

At the scale of 1- to 10-km stream segments, several field removal experiments in which all age classes of the native and invaded populations were measured provide strong evidence of invader impacts. Peterson and others (2004) found that abundance of native Colorado River cutthroat trout fry and juveniles increased after four years of brook trout removal in a Colorado stream, compared to a control stream, because survival of age-0 cutthroat trout increased 13 fold and that of age-1 fish doubled after brook trout removal. In contrast, no such increase occurred in another pair of streams at higher elevation, because cutthroat trout recruitment often failed, apparently due to cold temperatures (Coleman and Fausch 2006). Surprisingly, survival of adult cutthroat trout was unaffected by brook trout removal in either set of streams.

Several other nonnative trout removal experiments conducted at the stream segment scale have also been followed by increased native trout abundance. Moore and others (1983, 1986) removed nonnative rainbow trout from entire lengths of four streams above barriers in Great Smoky Mountains National Park for 6 years. They reported increases in abundance of native brook trout compared to three control streams where abundance changed little. Shepard and others (2002) found that a westslope cutthroat trout (*O. c. lewisi*) population increased seven fold after removing brook trout from above a barrier in a Montana stream for 8 years. The decade-long removal of brook trout with piscicides and electrofishing from a stream in Crater Lake National Park, Oregon resulted in an almost three fold increase in abundance of native bull trout (Buktenica and others 2001, Renner 2005). However, encouraging anglers to remove brook trout from an Alberta stream inhabited by native bull trout and westslope cutthroat trout was ineffective and failed to reduce brook trout numbers (Stelfox and others 2001).

Strong declines in native trout after nonnative trout invasion have led investigators to propose competition and predation as likely mechanisms. These mechanisms have been studied extensively in controlled laboratory and field experiments at small scales (see reviews in Fausch 1988, 1998, Dunham and others 2002a, Peterson and Fausch 2003b), but results are often difficult to generalize to larger spatial and longer time scales (Rieman and others 2006). An exception is experiments designed to explicitly consider environmental factors like temperature across a range of natural conditions, either in the field (McHugh and Budy 2005) or by simulating conditions in the laboratory (Taniguchi and Nakano 2000).

Finally, field sampling at various scales provides correlative evidence of the effects of nonnative trout invasions. For example, brook trout appear to have displaced cutthroat trout in a Nevada watershed (Dunham and others 1999), and bull trout in an Idaho watershed (Rieman and others 2006), where the native and nonnative species co-occurred. However, the effects were highly variable among streams. Rich and others (2003) showed that bull trout occurrence in small low-gradient streams below barriers in a Montana watershed was strongly associated with complex habitat structure and strong neighboring populations that could provide demographic support, but was negatively associated with presence of brook trout (Figure 3). Townsend and Crowl (1991) and McIntosh (2000) reported strong negative correlations between brown trout and native galaxiid abundance in stream segments below barriers throughout two New Zealand watersheds, and provided experimental evidence that predation by large brown trout was the cause. At the scale of channel units, Morita and others (2004) used an extensive field survey to provide evidence that brown trout excluded native whitespotted charr from individual pool-riffle sequences in a Hokkaido stream, whereas rainbow trout apparently excluded the charr from pools to adjacent riffles. These data at relatively small spatial scales support conclusions about the effects of these nonnative trout invasions in Hokkaido derived from broad field surveys (Takami and Aoyama 1999, Kitano 2004).

In contrast to examples where nonnative salmonids clearly displaced native trout, other cases show that nonnative salmonids apparently failed to invade all habitat, or had little effect on native trout when they did invade. Fausch (1989) reported that brook trout failed to invade certain high-gradient streams with cutthroat trout in several Rocky Mountain regions (see also Rieman and others 1999, Paul and Post 2001). He suggested various hypotheses including limited upwelling groundwater required for egg incubation and winter floods that scour eggs or fry. Likewise, Adams and others (2002) found that brook trout invasion had apparently stalled in more than half the tributaries studied in a pristine Idaho watershed, based on comparison with historical data (see Section V for more details). Novinger and Rahel (2003) found no increase in native cutthroat trout in four small Wyoming streams isolated by barriers after 5 to 8 years of removing brook trout by electrofishing, suggesting that the brook trout had little effect. They attributed this primarily to lack of critical resources or abiotic conditions needed for cutthroat trout recruitment and survival (see Harig and Fausch 2002, Sloat and others 2005, Coleman and

Figure 3—Bull trout presence in Montana and Idaho watersheds is often positively associated with complex physical habitat and strong populations in neighboring watersheds. However, bull trout (fish at bottom) presence has also been found to be negatively associated with brook trout (top) in certain watersheds, suggesting that this nonnative salmonid either uses different habitats than bull trout or displaces them (K. Morita image).

Fausch 2006), or to lack of demographic support from adult spawners. Fausch and others (2001) found that rainbow trout invasion in various regions worldwide was most successful where flow regimes were similar to those in their native range, and reported that this widely introduced species was apparently unable to invade in at least one region where flooding was frequent during fry emergence. Although there has been no comprehensive analysis to date of locations where nonnative salmonids have *failed* to invade, and the environmental correlates, such research is clearly needed to explain differences in invasion success and provide tools for managing the invasion-isolation tradeoff.

Hybridization, Pathogens, and Parasites

Hybridization is an additional process by which nonnative salmonids can adversely affect native salmonids (Allendorf and others 2001, 2004). Hybridization has obvious genetic influences, but ecological effects are also possible. Hybrids of many salmonid crosses are fertile (Suzuki and Fukuda 1971), which leads to backcrossing of hybrids with parental types and gene flow between genetically distinct populations, subspecies, or species, a condition called introgression (Rhymer and Simberloff 1996). If backcrossing is extensive and hybrid individuals also mate among themselves, the resulting population is termed a hybrid swarm. For example, introgressive hybridization of native cutthroat trout with rainbow trout is widespread throughout the western U.S. (Leary and others 1998, Peacock and Kirchoff 2004). Weigel and others (2003) reported that hybridization of westslope cutthroat trout with rainbow trout was more prevalent in the downstream segments of an Idaho watershed, despite an apparent absence of migration barriers. They inferred that harsh abiotic factors upstream limited rainbow trout more than cutthroat trout. In contrast, Hitt and others (2003) reported that hybrids between the two species were spreading upstream throughout a large Montana watershed, and inferred that introgression would expand because it appeared that hybridization was limited more by demographic factors like movement than abiotic factors that could limit spread.

Other cases suggest that hybridization can be restricted. For example, when brook trout invade and mate with bull trout, hybrids and subsequent backcrosses appear to have reduced fertility or survival (Kanda 1998, Kanda and others 2002). Although such hybridization may not result in hybrid swarms (Kanda and others 2002), it does represent wasted reproductive effort by the native fish. Because invading brook trout can mature at an earlier age and have higher reproductive potential (Power 1980, Kennedy and others 2003), hybridization could still lead to displacement of bull trout (Leary and others 1993, Rieman and others 2006). Recent evidence indicates that maintenance of large migratory bull trout may limit hybridization with smaller resident Dolly Varden

through size-assortative mating (Redenbach and Taylor 2003). Assortative mating and differential habitat use (B. Rieman and J. Dunham, personal observation) might similarly limit hybridization between large migratory bull trout and smaller resident brook trout, further highlighting the potential importance of migratory life histories and stream interconnections in maintaining the integrity of native salmonid populations.

Last, invading nonnative trout infected with pathogens or parasites may transmit them to native salmonid populations. For example, the myxozoan parasite *Myxobolus cerebralis* that causes whirling disease has a resistant spore stage that can remain latent for decades (El-Matbouli and others 1992), and is transmitted to trout fry through oligochaete (*Tubifex*) intermediate hosts. Nehring and Thompson (2003) and Nehring (2004) reported invasion of the parasite 25 km upstream in one Colorado watershed, and 4 km upstream in two smaller streams, apparently via rainbow trout and brown trout movement. In the first case, this movement brought the parasite to within about 3 km of a population of native Colorado River cutthroat trout. In contrast, Peterson and others (2004) found no evidence that brook trout invading native cutthroat trout habitat in four other Colorado streams were infected with the parasite, but the distance to an infected source population was unknown.

Section V: A Framework for Analyzing Tradeoffs

The information presented above makes clear that fisheries managers often face a dilemma: nonnative trout invasions can reduce or extirpate native salmonid populations, yet barriers to prevent these invasions can lead to extinction of native salmonids because of isolation. However, the outcomes of invasions and isolation differ among species and stocks of native and nonnative salmonids due to their evolutionary history, and among locations due to habitat characteristics, environmental variation, and time since isolation. This means that installation or removal of barriers to promote persistence of native salmonid populations is often a complex problem that must be analyzed in the context of these ecological and evolutionary constraints. Such efforts will also be influenced by conservation goals and the available opportunities and management resources. Here, we propose a conceptual framework that explicitly considers these factors. We outline a process that incorporates the preceding synthesis of existing knowledge as well as the experience of field biologists. We illustrate the concept with examples from two basins in the Rocky Mountains that have markedly different settings and constraints, and end by considering an overall strategy for making decisions.

Four key questions provide a framework for considering the use or removal of barriers to conserve native fishes in any stream or network of streams.

1. Is a native salmonid population of important conservation *value* present?
2. Is the population *vulnerable* to invasion and displacement by nonnative salmonids?
3. If the native salmonid population is isolated, will it *persist*?
4. If there are multiple populations of value, which ones are *priorities* for conservation?

Although these questions are relatively simple, each leads to more questions or dimensions that must be considered in any decision (Table 1; see Dunham and others 2002a), so we address each in turn.

Conservation Values

A first step in developing any native salmonid management plan is to consider the conservation values associated with the populations of interest (Table 1). Without a clear concept of the relative values of different populations that could be managed, it is impossible to set specific management objectives. What constitutes value varies markedly among government and tribal agencies, those who study or manage native fish species, and the interested public. For natural resource management agencies, conservation of biodiversity is a widely held goal, and the conservation literature presents a diverse set of guidelines toward that end (*see Box 4*).

We suggest that three general classes of conservation value emerge from the literature (for example, Angermeier and others 1993): *evolutionary*, *ecological*, and *socio-economic* (Figure 4). *Evolutionary* conservation values are considered explicitly by the U.S. Endangered Species Act (ESA), which calls for designating evolutionarily significant units and distinct population segments (Waples 1995). Here the focus is on distinct species, stocks, and populations that have evolved in, and adapted to, unique and varied environments. Genetic and ecological divergence are important criteria (Allendorf and others 1997) and the full representation of diversity at regional scales (10^4 to 10^5 km^2) has been a focus of ESA-related management efforts to conserve evolutionary legacies (Waples 1995, U.S. Fish and Wildlife Service 1998b). Some species such as westslope cutthroat trout and bull trout can show substantial genetic and phenotypic divergence among tributaries within a

Table 1—Four questions to consider when evaluating the tradeoff of managing native salmonid populations using barriers to isolate them from invasions (after Dunham and others 2002a, S. Dunham unpublished). The answer to each question depends on further dimensions or considerations (right column) for a more complete analysis of the tradeoff.

Main questions	Further dimensions or considerations
1. Is a native salmonid population of important conservation *value* present?	• Evolutionary values • Ecological values • Socio-economic values

2. Is the population *vulnerable* to invasion and displacement by nonnative salmonids?	• Transport and spread
	• Establishment
	• Effects
	  ○ Displacement
	  ○ Coexistence
	  ○ Hybridization
	  ○ Transmit parasites or pathogens

3. If the native salmonid population is isolated, will it *persist*?	• "Small population" phenomena
	  ○ Loss of genetic variability
	  ○ Demographic stochasticity
	  ○ Environmental stochasticity
	  ○ Catastrophes
	• Loss of migratory life histories
	• Synergistic factors

4. If there are multiple populations of value, which ones are *priorities* for conservation?	• Identify conservation units
	• Prioritize populations
	  ○ Representation
	  ○ Redundancy
	  ○ Persistence
	  ○ Feasibility
	• Consider viability
	• Confront uncertainty

single river basin (10^2 to 10^3 km^2), arguing for conserving distinct populations at this scale as well (Allendorf and Leary 1988, Leary and others 1998, Quinn and others 2001, Hendry and others 2004b). From this perspective, evolutionary conservation values are highest for distinct populations that represent a substantial or unique portion of extant genetic diversity, occupy unique or remnant habitats, or exhibit diverse or unusual life histories (Allendorf and others 1997, Halupka and others 2003, Shepard and others 2005).

Ecological conservation values include important ecological processes and functions at the population, community, or ecosystem levels of organization. For example, species like salmon and trout can have strong effects on trophic networks in aquatic systems (Simon and Townsend 2003), which can even cross the ecosystem boundary into adjacent terrestrial ecosystems (Spencer and others 1991, Willson and Halupka 1995, Baxter and others 2004, Koyama and others 2005). As already discussed, some populations may be the key to persistence of others through dispersal, gene flow, demographic support, and metapopulation-like processes (Schlosser and Angermeier 1995, Rieman and Dunham 2000). Thus, dispersal from stronghold or source populations may allow the entire network to persist in the face of disturbance or changing environments. Similarly, the full expression of life-history diversity within populations may confer resilience to environmental disturbance (Rieman and Clayton 1997, Brannon and others 2004) and in some cases resistance to invasion. Ecological value can be far more varied than these simple examples, but a key point is that the structure and function — that is, the composition and roles of individuals or populations — are ecologically important. We may value essential

Box 4. Components of value for biodiversity.

Different authors have proposed different systems for considering the requirements for, and values of, sustaining biodiversity:

- Noss (1990) and Groves (2003) proposed that sustaining biodiversity requires conserving three attributes of ecosystems: composition, structure, and function. Composition includes the unique elements such as species or genes. Structure represents the distribution, interconnections, and interactions of those elements. Function represents the key processes or ecological products or influences that result (for example, secondary production).
- Noss and Cooperider (1994) described four explicit values of biodiversity: direct utilitarian (for example, harvestable protein), indirect utilitarian (for example, clean water), recreational/aesthetic (for example, fishing), and intrinsic spiritual/ethical aspects.
- Allendorf and others (1997) focused on biological values defined by the potential evolutionary and ecological consequences of extinction. Thus, extinction may result in loss of evolutionarily distinct, rare, and genetically diverse populations, as well as loss of members of unique communities or environments, or of "conservation umbrella" species.
- Callicot and Mumford (1997) outlined a classic debate in natural resource and biodiversity management: whether ecosystem sustainability might be met through either of two potentially distinct objectives - conserving ecosystem *integrity* or conserving ecosystem *health*. Integrity refers to the native species complex, interactions, and diversity, whereas health describes a system that still retains its function and organization but not necessarily the native elements. The differences between the two have proven controversial. Although we can conserve ecological processes without the native community, functional ecosystems might still be substantially impoverished (Callicott 1995, Groves 2003). Nevertheless, conservation of ecological process remains an important challenge that should not be overlooked, even when there is little hope of conserving native diversity or integrity represented by "ghost" or "relict" species (Meyer 2004).

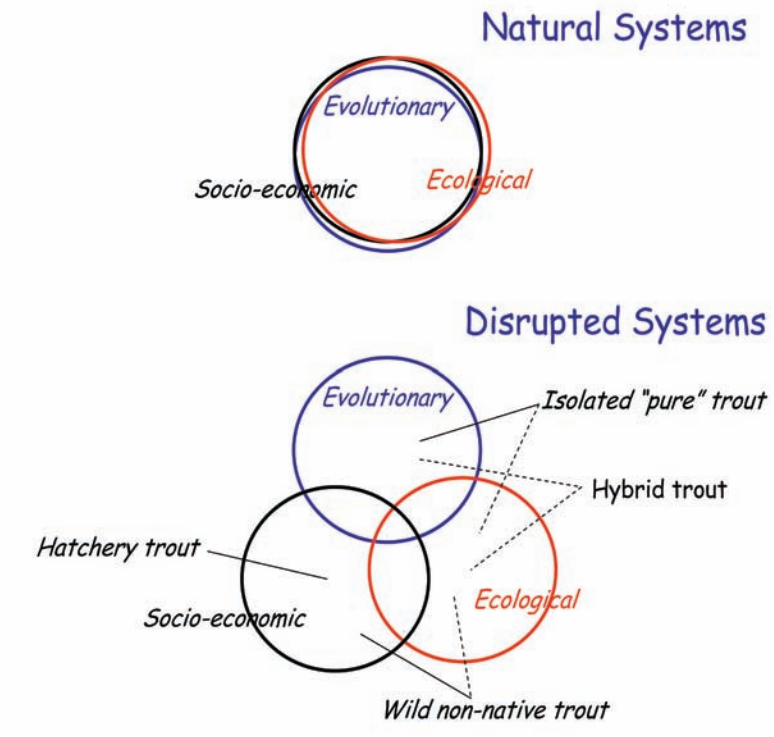

Figure 4—Distribution of three conservation values in salmonid populations in natural and disrupted stream systems. In natural systems (top) all values may be represented in the same species distributions. In systems disrupted by human development and the introduction and invasion of non-native salmonids (bottom), all of these conservation values often cannot be supported in the same streams or fish communities. For example, isolation of genetically pure native trout populations may conserve primarily evolutionary values (solid line), but limited ecological functions and values (dashed line). There is currently much debate about whether hybrid trout retain significant ecological functions and values, but most are considered to have limited or no evolutionary value. Hatchery trout in a put-and-take fishery could have significant socio-economic value but no evolutionary or ecological values. This simple classification is not mutually exclusive (for example, isolated pure trout may also have socio-economic conservation values) and different values may overlap depending on the system and the species and forms involved. However, in disrupted systems the potential to represent all conservation values simultaneously is likely to be far more limited than in natural systems.

ecological services that are provided, or the ability of an ecosystem and its elements to organize, reorganize, and respond to changes by rebounding, adapting, and evolving. From a management perspective, we value species, populations, and communities that are self-sustaining, resilient, and adaptable because they don't require continual input of resources and energy to maintain them. However, a key issue is that although evolutionary and ecological values sometimes overlap, they are not the same thing (Callicott 1995, Callicott and Mumford 1997). For example, a genetically introgressed cutthroat trout population could retain significant ecological value, but have little evolutionary value (Figure 4; Allendorf and others 2004). From this perspective, ecological conservation values are higher for populations that are large, productive, and interconnected, and fill roles similar to those in the original ecosystem. Likewise, they are less for populations that are vulnerable to extinction without extraordinary conservation effort, or those that threaten the persistence of ecosystem structure and function that we hope to maintain (for example, fish populations that are vectors of disease).

Socio-economic conservation values are perhaps the most evident to fisheries managers who are anxious to conserve the recreational and economic benefits from fishing, tourism, and associated activities. These values may be more obvious because they can be quantified in economic terms, capture the public interest, and often dictate the budgets and activities of management agencies. They are also important because they can leverage conservation resources for other species and populations that may hold significant evolutionary and ecological values. For example, conserving salmon may also protect lamprey (Petromyzontidae; Lee and others 1997, Thurow and others 1997). Like the first two values, socio-economic values can also vary among local populations of conservation interest.

Recognizing distinct evolutionary, ecological, and socio-economic conservation values for a particular population or set of populations is important because they may afford very different opportunities for conservation and the implementation or removal of barriers. In some large wilderness rivers such as the Middle Fork Salmon River in Idaho or the South Fork Flathead River in Montana, undeveloped watersheds and native species complexes clearly support substantial values in all three categories (Figure 5). But habitat and populations in most river systems throughout the region have been substantially altered, so that convergence of all three conservation values in any single population is rare (Figure 4). For example, main-stem populations of cutthroat trout may be large and composed of individuals with mobile life

Figure 5—In relatively pristine wilderness river basins like the Middle Fork Salmon River, Idaho, shown here (Sulphur Creek, Frank Church River of No Return Wilderness; R. Thurow image), native salmonid assemblages can support substantial evolutionary, ecological, and socio-economic values simultaneously. However, most river systems have been substantially altered, so convergence of all three conservation values in any single location is rare.

histories, but tend to be introgressed and co-occur with nonnative salmonids, whereas headwater populations are generally small and isolated yet offer the best prospects for being genetically pure. As suggested above, the mainstem populations may hold significant ecological value, but little evolutionary value, whereas the opposite may be true of the headwater populations. In these cases, the prioritization of conservation efforts is challenging because the tradeoffs are difficult or uncertain. Should we favor populations that represent remnant elements of evolutionary history or those that have the potential to evolve and adapt in the future (Meyer 2004)? Should we favor locally hybridized populations that may retain some elements of local adaptation (Dowling and Childs 1992, Peacock and Kirchoff 2004), or should we replace them with a genetically pure stock that represents many pooled populations (Leary and others 1998)? Should we maintain access for large migratory fish that support a key fishery even though local populations will be vulnerable to invasion and hybridization, or should we isolate the local populations to conserve genetic purity (Allendorf and others 2004)?

It is clear that all three conservation values are important depending on the context, and often fisheries managers will be faced with a mix of objectives and possibilities. Opportunities to conserve evolutionary values, for example, may be very restricted and viewed as immediate priorities in a few distinct areas if they are to be conserved at all (see Shepard and others 2005). Therefore, conservation of native, wild locally-adapted populations with diverse life history forms will often be a primary goal. Yet as Meyer (2004) suggested, even in cases where we cannot conserve an intact evolutionary legacy, we may still be able to conserve some ecological processes and evolutionary potential. Toward this end, sustaining wild slightly-hybridized native trout populations that retain much evolutionary potential to fill important ecological roles will often be a second priority, followed by wild populations of non-native trout that support important ecological and socio-economic values. Finally, in habitats that cannot sustain wild trout populations, usually due to lack of reproduction or recruitment, stocking hatchery fingerlings or adults may be desired to support valuable fisheries, so long as these do not threaten ecological or evolutionary values of other populations (for example, by introgressive hybridization, or transmitting parasites or pathogens). This hierarchical approach embodies the principle that certain values are irreplaceable and should not be forfeited, but that inability to conserve one set of values does not eliminate the possibility of realizing others.

Vulnerability to Invasion

If a native salmonid population of important conservation value is present, the second question to address is whether it is vulnerable to invasion and displacement by nonnative salmonids (Table 1). The invasion process has been divided into three or four basic steps (Vermeij 1996, Kolar and Lodge 2001, Dunham and others 2002a), which can be summarized as transport, establishment, spread, and impacts. For simplicity, we discuss transport and spread together, since they have the same effect of bringing nonnative salmonids in contact with native ones. Given this, assessing vulnerability to invasion requires asking three main questions about the stages of invasion, shown in Table 2.

Transport and spread—Whether nonnative salmonids are transported to specific locations by humans will depend on interest in them for recreation or food, and distances to sources of fish for introduction. Although most agencies now evaluate fish stocking more carefully than in the past (Rahel 1997, 2000), unauthorized introductions by the public are burgeoning. For example, Rahel (2004) calculated that unauthorized introductions of nonnative fishes in five regions throughout the U.S. accounted for 90 percent of the new introductions during 1981 to 1999, compared to only 15 to 43 percent during all previous periods. Disgruntled anglers may translocate nonnative fishes back to their favorite fishing sites above barriers after they have been removed using chemicals or electrofishing (U.S. Fish and Wildlife Service 1998a, Rahel 2004). Established populations of nonnative salmonids close to native fish populations (for example, just downstream from accessible barriers, or a short distance by road) provide a source for such unauthorized introductions (Thompson and Rahel 1998, Dunham and others 2004, Rahel 2004, Munro and others 2005).

The spread of nonnative species without the aid of humans will depend on distance from a source population and the time available for colonization, and on their tendency for long-distance movement, their rate of population growth, and the resistance of the corridor to fish dispersal (With 2002, Hastings and others 2005). If invasions spread as an advancing front, they will arrive sooner when source populations are close. However, nonnative salmonids like brook trout and brown trout can also move long distances (Young 1994, Gowan and Fausch 1996, Peterson and Fausch 2003a) and can have high intrinsic population growth rates (McFadden 1961, Power 1980, Kennedy and others 2003), both of which increase invasion rates (Kot and others 1996, Lewis 1997,

Table 2—A hierarchy of three main questions to assess whether nonnative salmonids will invade and have negative effects on populations of native salmonids (after Vermeij 1996, Dunham and others 2002a). The three main stages of invasion considered are influenced by additional factors shown on the right.

Main questions about the invasion process	Factors influencing invasion process
1. Are invaders likely to be transported or spread to the location that native salmonids inhabit?	• Proximity of sources for unauthorized introductions • Distance to source population and time for invasion • Tendency for frequent or long distance dispersal • Population growth rate • Resistance of the stream corridor to invasion

2. Can the invaders establish a reproducing population?	• Environmental resistance - habitat suitability
	  ○ Temperature regime
	  ○ Flow regime
	  ○ Stream size
	  ○ Gradient
	  ○ Productivity
	• Propagule pressure
	• Biotic resistance from native biota

3. Will the invaders displace native salmonids by competition, predation, introgression, or transmission of parasites or pathogens, or will they coexist?	• Biotic interactions and demographic rates may change with abiotic factors (for example, temperature and flow) • Habitat modification may favor invaders • Introgressive hybridization may be irreversible • Parasites and pathogens may be dispersed by invaders

Hastings and others 2005). Therefore, trout invasions appear to advance through a combination of frequent short distance movements at the upstream margin (Rodríguez 2002), combined with less frequent long-distance movements, termed "jump dispersal" (Peterson and Fausch 2003a). For example, direct measurements of brook trout movement by tagging and recapture in Colorado streams revealed that they ranged up to 2 to 3 km within 100-day summer sampling periods, with a bias toward upstream movement (Riley and others 1992, Gowan and Fausch 1996). Brown trout movements of similar distances, and three that reached 23 to 96 km, were detected by telemetry in Wyoming streams (Young 1994).

Stream segments with high-gradient reaches or waterfalls may provide resistance to invasion from downstream, but source populations in headwater lakes or stream reaches can spread downstream throughout watersheds. Several syntheses of data from the Rocky Mountains suggested that brook trout are less successful at establishing populations in streams with gradients steeper than 4 to 7 percent (Fausch 1989, Rieman and others 1999). However, a mark-recapture study in Idaho showed that brook trout ascended slopes of 13 to 22 percent, although immigrants in steeper channels were larger fish and moved more slowly (Adams and others 2000). In experimental flumes, adult brook trout ≥15 cm could jump over waterfalls up to about 75 cm high from plunge pools ≥40 cm deep (Kondratieff and Myrick 2006), but field results suggest that they may also be able to ascend higher barriers either by penetrating interstices at low flow (Thompson and Rahel 1998) or finding alternate routes at higher flow (Adams and others 2000). In contrast, Adams and others (2001) found that brook trout dispersed downstream from headwater lakes where they were stocked, through high-gradient channels up to 80 percent slope and over an 18-m high waterfall, potentially invading many reaches inaccessible from downstream. Likewise, Paul and Post (2001) reported that brook trout introduced in an Alberta watershed spread downstream disproportionately from stocking locations to colonize reaches at lower elevations. There is also some evidence from northern Montana suggesting that hybrids of rainbow X cutthroat trout may disperse more widely than native cutthroat trout (Hitt and others 2003), thereby increasing spatial spread. Rahel (2004) emphasized that fisheries managers should assume that any nonnative species that is introduced and becomes established in a basin will eventually colonize other suitable and accessible habitats.

Establishment—All three main salmonid invaders have established reproducing populations in most U.S. states where they are not native (Rahel 2000), although they have not invaded all waters to which they have access (Fausch and others 2001, Adams and others 2002, Dunham and others 2002a). Establishment of a nonnative salmonid population will depend on both environmental resistance (habitat suitability) and "biotic resistance" by native species, as well as chance events (Moyle and Light 1996). Habitat suitability for native and nonnative salmonids in streams is often governed by temperature regime (Meisner 1990, Rahel and Nibbelink 1999, Harig and Fausch 2002, Dunham and others 2003a), flow regime (Jowett 1990, Jager and others 1999, Strange and Foin 1999, Fausch and others 2001), stream size (Rahel and Nibbelink 1999, Rieman and others 1999), habitat factors correlated with gradient (Fausch 1989, Adams 1999), and stream productivity (Kwak and Waters 1997). Because many of these factors influence fish at thresholds, measurements across a wide range of each variable often show that establishment is relatively predictable from simple physiological tolerances (*see Box 5*). In other cases, simultaneous consideration of a host of variables may be required (Moyle and Light 1996, Marchetti and others 2004).

A main predictor of success of deliberate introductions or translocations of nonnative species is "propagule pressure" (Kolar and Lodge 2001, Hilderbrand 2002, Marchetti and others 2004), which refers to the number of releases and the number of individuals per release. These data indicate that repeated stocking of nonnatives can eventually increase likelihood of establishment. In part, this may be due to rare events, such as years with unusual weather, which favor nonnative species and allow them to establish "beach head" populations and subsequently invade (Moller 1996, Moyle and Light 1996).

Intact assemblages of native fishes may also provide biotic resistance that prevents nonnative salmonids from invading, especially when the assemblages include more species. Current theory in invasion biology holds that assemblages with more species provide fewer "niche opportunities" for invaders (Shea and Chesson 2002, Chase and Liebold 2003), defined as opportunities for invading species to increase from low densities due to abundant unused resources or a lack of natural enemies. This theory may explain why brook trout in western North America are least successful at invading Pacific Northwest coastal watersheds that support intact runs of salmon and anadromous trout (*Oncorhynchus* spp.) with many diverse life history types that use a wide variety of food and space resources.

Box 5. Examples of environmental resistance that limits invading salmonids.

Several examples indicate that abiotic factors like low temperature and flooding regimes can limit establishment of nonnative salmonids, but each may interact with other factors.

Low temperature: Low temperature limits salmonid recruitment by delaying egg development and hatching which causes higher egg mortality (Stonecypher and others 1994), and by reducing fry growth and lipid storage which causes higher overwinter mortality due to starvation (Biro and others 2004, Coleman and Fausch 2006). Low temperature also limits growth of adults, which reduces fecundity and recruitment.

- Rahel and Nibbelink (1999) found that upstream limits of brown trout in a Wyoming watershed could be explained by a combination of cold temperature and small stream size.
- Adams (1999) reported that reduced fecundity at low temperatures could account for the upstream limit of brook trout in a Montana stream.
- Clark and others (2001) inferred that lower fecundity due to lower temperatures limited invading rainbow trout in the northern Appalachian Mountains.

Flooding regime: Flooding during incubation or emergence of fry from gravel redds may limit establishment of nonnative salmonids.

- Nehring and Anderson (1993) and Latterell and others (1998) found that recruitment of nonnative brook, brown, and rainbow trout in sets of Colorado rivers was lowest in years when snowmelt runoff flows were highest, probably because fry emerge just before or during these flow peaks and are displaced.
- Fausch and others (2001) reported that nonnative rainbow trout were least likely to establish reproducing populations in several regions worldwide where flooding occurred during fry emergence in early summer, and most likely to establish in regions where flow regimes most closely matched those in their native range along the Pacific coast of North America.

Displacement, coexistence, and other effects—In many cases, after nonnative salmonids are transported or spread to a stream and establish a reproducing population, they reduce or displace native salmonids (Waters 1983, Behnke 1992, Peterson and others 2004), but in other cases the invasion may stall or the two may coexist (Shepard 2004, Rieman and others 2006). Adams and others (2002) reported that upstream limits of brook trout distribution and recruitment advanced over a 25-year period in fewer than half the streams resampled in an undisturbed Idaho watershed. Whether displacement or coexistence occurs may depend on abiotic factors like temperature that affect biotic interactions among individuals at the local scale, or on temperature and flow regimes that affect demographic responses at larger scales. For example, at the local scale, DeStaso and Rahel (1994) reported that brook trout were behaviorally dominant over Colorado River cutthroat trout at warmer temperatures in an artificial stream, whereas neither was dominant at colder temperatures (but see Novinger 2000). However, it is more likely that the effects of temperature and other abiotic factors will play out at riverscape scales by changing demographic rates. For example, low temperature may reduce growth or fecundity of nonnative salmonids and thereby limit their latitudinal distribution (Clark and others 2001) or upstream invasion (Adams 1999, Weigel and others 2003, Benjamin 2006). Alternatively, changes in environmental conditions that favor productivity of non-native species might allow them to invade new habitats and displace native species. Moller and Van Kirk (2003) reported that nonnative rainbow trout have been more successful at invading and displacing native Yellowstone cutthroat trout (*O. c. bouvieri*) where flow regimes were modified to favor rainbow trout over cutthroat trout. Shepard (2004) suggested that brook trout were more likely to displace westslope cutthroat trout where habitat had been degraded by land management activities. Likewise, Olsen and Belk (2005) suggested that native fishes were less likely to coexist with non-native predators such as brown trout if habitat had been degraded so that off-channel refugia were lost. These examples also suggest that judicious management of flow and temperature regimes, and physical habitat structure, to achieve more natural states might favor native species (Poff and others 1997, Fausch and others 2001), and allow some level of coexistence with nonnative species. This idea would benefit from careful study using an adaptive management approach at watershed scales (see Walters 1986).

Two other possible effects of invaders are hybridization and introduction of parasites or pathogens. Although invasions of nonnative salmonids can sometimes be eradicated (Moore and others 1983, Knapp and Matthews 1998), especially if caught in the early stages (Simberloff 2003), neither hybridization nor introduction of parasites or pathogens to a native salmonid population is usually reversible. Only in cases where hybrids have substantially lower survival or fertility, as perhaps for brook trout hybridizing with bull trout (see above), could hybridization be reversed. Introductions of parasites like *Myxobolus cerebralis* are also apparently irreversible once established, and may be transmitted farther by movements of invading salmonids upstream or downstream from infected source populations (see above; Nehring and Thompson 2003, Nehring 2004). However, whether conditions are favorable to persistence and expansion of pathogens may depend on local environmental conditions, and even past watershed management (Anlauf 2005).

Isolation and Population Persistence

If a native salmonid population is vulnerable to a nonnative salmonid invading from downstream, one management alternative is to construct a barrier to fish movement to prevent the invasion. However, then the influence of isolation caused by the barrier on persistence of the native salmonid population becomes an important question (Table 1). Isolation or fragmentation of habitat has several important effects on native salmonids (Table 3; Rieman and Dunham 2000, Dunham and others 2003b), including declines in population and habitat size. Small populations can be more vulnerable to extinction because of a loss of genetic variability, random changes in demographic processes and rates (demographic stochasticity), and environmental fluctuations (environmental stochasticity), collectively known as "small population" phenomena (Caughley 1994). Large-scale perturbations or "catastrophes" that severely reduce populations and habitats can be important for both small and large populations, particularly if they are confined to a set of spatially restricted habitats that could be affected by the same disturbance, such as hurricanes, earthquakes, fires, floods, droughts, and temperature extremes (Propst and others 1992, Brown and others 2001). Moreover, disturbances that pose little threat to larger, interconnected populations may become a threat when populations are highly fragmented (Dunham and others 2003b).

Isolation also eliminates migratory life histories, which confer resilience to local populations. Populations with migratory individuals are spread across many different habitats and may therefore be less vulnerable to

Table 3—Basic threats to the persistence of single, isolated salmonid populations, and guidelines for addressing each threat (see Rieman and McIntyre 1993, Allendorf and others 1997, McElhany and others 2000 for more detailed criteria). Criteria for multiple populations are given elsewhere *(see Box 6*).

Threat	Guidelines
Loss of genetic variability	Maintain enough adults to minimize loss of genetic variability through drift and inbreeding.
Loss of resilience	Maintain or restore the condition of local habitats or reduce sources of mortality to compensate for lost fecundity and potential productivity due to loss of migratory adults.
Demographic stochasticity	Maintain enough adults and year classes to minimize the probability that chance demographic events drive local populations extinct.
Environmental stochasticity	Maintain a large enough population size and wide distribution within the isolated habitat to persist in the face of common environmental fluctuations.
	Ensure that human influences do not result in habitat degradation or substantial changes to environmental regimes that reduce survival.
Catastrophes	Maintain a large enough habitat and population size, and wide distribution, to ensure resilience in the face of rare, high-magnitude environmental changes.
	Ensure that human influences do not alter the frequency and magnitude of natural catastrophes in a way that threatens remnant populations, or create new catastrophes (for example, toxic chemical spills, introductions of invasive species) that pose threats.

disturbances influencing a single habitat. For example, short-term local extirpations of cutthroat trout by drought (Dunham and others 1997) and bull trout by wildfire (Rieman and others 1997a) were likely reversed by returns of migratory fish that were in habitats outside of the systems during the disturbance. Isolation or other influences that lead to loss of migratory life histories restrict a population spatially and thus increase the vulnerability to local disturbances. Isolation also reduces the opportunity for exchanges of individuals among local habitats, which may reduce the demographic stability of some populations (Hilderbrand 2003). Finally, migratory fish are typically larger and more fecund, which may provide important demographic support to existing populations, and possibly resistance to invading salmonids (Dunham and others 2002a).

Threats posed by isolation cannot be considered alone. Synergistic feedbacks among threats can lead to the demise of local populations (for example, an "extinction vortex," Gilpin and Soulé 1986). Many factors can modify population responses of salmonid fishes to isolation and strongly influence local persistence, including angling, habitat degradation, and habitat and life history characteristics. The negative effects of angling on native trout populations can be substantial, even if regulations restrict harvest (Post and others 2003), particularly for large migratory fish that are highly desirable to anglers. Habitat degradation often leads directly to habitat fragmentation in stream networks, and also reduces survival and population size making populations less resilient and more vulnerable to other threats. Habitat degradation can influence salmonids at a variety of spatial scales. Local factors that are strongly altered by land management, such as temperature, sediment, stream discharge, and instream cover, are commonly cited as degrading habitat (Bjornn and Reiser 1991). At broader scales, the status of

salmonid populations has been consistently associated with the distribution of land management activities, including road density and management intensity (Thurow and others 1997, Baxter and others 1999). Habitat and life history characteristics can also influence the probability of salmonid population persistence in the face of isolation. For example, Koizumi and Maekawa (2004) observed that Dolly Varden charr were more likely to persist in smaller isolated habitats if they were strongly influenced by groundwater, which provided more stable and favorable conditions over time. Rieman and Dunham (2000) argued that cutthroat trout were more resistant to local extinction in small habitat patches than were bull trout. These examples illustrate that other environmental conditions and species characteristics may mitigate or exacerbate the effects of isolation.

Considering Priorities among Multiple Populations

To this point, our framework has addressed the tradeoff of invasion and isolation for single populations. Fisheries managers and conservation biologists have no lack of problems to consider at this scale, but often move from one project (that is, the implementation or removal of a barrier) to the next as the need or opportunity arises. Typically, this is done while struggling with limited financial, capital, and human resources. However, to be most effective it is important to avoid incremental or "ad hoc" solutions and carefully prioritize use of limited resources (Pressey 1994, Allendorf and others 1997, Groves 2003). This can be facilitated through a systematic assessment of risks (Francis and Shotton 1997). Characterizing risk implies understanding: 1) the probability of an event (for example, a nonnative salmonid invasion), 2) the effects of the event if it actually occurs (for example, probability of ecological displacement or genetic introgression following invasion), and 3) the value that could be lost. Thus, a "threat" is a factor that *could* negatively impact a population, and a "risk" is the probability that a given factor *will* have an impact on something we value.

A simple example can illustrate these three components of risk for native cutthroat trout. First, the probability of invasion may be higher for cutthroat trout populations closer to sources of invasion by brook trout, increasing the first component of risk. Second, the effects of invasion may be greater for some cutthroat trout populations because they are less resistant to invasion, either due to their weaker population status or because they live in habitats that favor brook trout, increasing the second component of risk. Third, the conservation value of some cutthroat trout populations may be higher than others because they represent relatively rare pure genomes or life history types, increasing the third component of risk. In contrast, populations farther from invasion sources, more resistant to invasion, or of lower conservation value would be at lower risk. Therefore, these would be lower priorities as candidates for constructing barriers to prevent invasions. These are simple examples, and tradeoffs can become more complicated as multiple factors and populations, spatial structure, and the general principles of conservation planning are considered.

The first step in planning is to identify the fundamental units of conservation and determine how they are arranged across spatial scales. Native salmonids often occur as collections of local populations distributed across habitats that are nested within larger subbasins (Rieman and Dunham 2000). This creates a hierarchy of spatial structure at scales ranging from local "patches" of suitable habitats (Dunham and others 2002b) to patch networks, and even larger aggregations or regional networks (Table 4). Moreover, some habitats may be potentially occupied but currently vacant. We emphasize that "scale" as used here should be based on how fish populations are organized across the landscape, and not on a fixed spatial scale or stream network structure. In many cases, the natural structure of local populations has been modified by human activities, such as barriers that fragment habitats. In other cases for rare taxa, only one local habitat exists, such as for the Paiute cutthroat trout (*O. c. seleniris*). Whatever the case, it is important to carefully consider the biology of the target species and how it interacts with the larger landscape, to define local populations, habitat patches, patch networks, or other units for use in conservation planning (Dunham and others 2002b, Fausch and others 2002, Wiens 2002).

The second step is to establish priorities for management of the potential conservation units. Ultimately, managers will need to decide on the number, distribution, and characteristics of populations they will attempt to conserve and the actions required (that is, installing or removing barriers). The conservation literature is replete with proposals outlining goals for such efforts, but the most common include *representation, redundancy, persistence,* and *feasibility* (Scott and Csuti 1997, Groves 2003). Moreover, a formal decision process must also acknowledge that setting priorities is inherently *uncertain* (Ludwig and others 1993, McElhany and others 2000). In practice, these goals do not always translate neatly into specific guidelines (*see Box 6*), but we discuss each separately here to emphasize their individual importance.

Table 4—Potential relationships between conceptual scales at which natural populations of salmonid fishes are structured (Dunham and others 2002b) and units of conservation as defined in practice (following the Draft Bull Trout Recovery Plan; U.S. Fish and Wildlife Service 2002).

Conceptual Scale	Draft Bull Trout Recovery Plan	Description
Patch	Local Population	A patch may be occupied or not at present, whereas local populations are based on occupancy. Occupied patches and local populations are characterized by frequent (daily to seasonal) interactions among individuals.
Patch network or metapopulation	Core Area	Local aggregation of patches or local populations characterized by less frequent (annual to decadal) interactions.
Subbasin	Recovery Unit	Naturally discrete aggregations of patch networks or core areas within larger drainage basins that potentially interact over long time scales (100s to 1000s of years).
Region	Distinct Population Segment	Major biogeographic units that characterize distinct evolutionary lineages.

Representation refers to how well local populations and habitats reflect the full suite of ecological and evolutionary conditions that are expressed within a given area (Lawler and others 2003, Ruckelshaus and others 2003). In conservation planning, it is nearly always the case that only some of the "pieces" can be protected or restored. Accordingly, it is important to identify and protect those that provide the most complete representation of the original population characteristics (for example, allele frequencies, life history types, species occupancy or composition) and habitat conditions (for example, spatial distribution, successional stage), as well as the conservation values defined above.

Redundancy is a key component of conservation planning because no local population or habitat is immune to extinction or catastrophic events (Moyle and Sato 1991). Therefore, it is prudent to "not put all your eggs in one basket," and instead to conserve multiple examples of all the representative pieces. Although many have struggled to identify the minimum number and distribution of local populations necessary to insure persistence of a metapopulation (see Rieman and McIntyre 1993) that number will always depend on the local environments and events that are difficult to predict. In general, more populations will be necessary as individual populations become more vulnerable (for example, smaller), the potential for catastrophic disturbances increases, or the potential for simultaneous disturbance across sets of local populations increases (Hanski and Gilpin 1997). Replicate populations are especially important when all are isolated above barriers, to allow reintroduction if local extinctions occur but habitats remain suitable (Lubow 1996).

Persistence is a function of the resilience of individual populations, as well as the larger network of populations (Table 4). Factors contributing to the persistence of individual populations in the face of isolation and invasion were considered above, and have been addressed in detail for salmonids (Rieman and McIntyre 1993, Allendorf and others 1997, McElhany and others 2000). Populations that appear unlikely to persist may be low priorities for conservation actions. Persistence of multiple populations must usually be considered at several scales. For example, the dynamics of local habitats and populations may create a metapopulation, which may be nested within a larger collection of core areas that characterize a recovery unit, and ultimately a distinct population segment (DPS) or evolutionarily significant unit (ESU; Table 4). Whereas the spatial structure and temporal dynamics may be difficult to quantify precisely (Rieman and Dunham 2000, Fausch and others 2002), it is important to consider these factors because persistence of any single population may depend strongly on influences from adjacent populations or habitats. We strongly encourage readers to consult key references (Rieman and McIntyre 1993, Allendorf

Box 6. Guidelines for viability of multiple salmonid populations (partially excerpted and modified from McElhany and others 2000; see also Rieman and others 1993, Allendorf and others 1997).

• **Some populations should exceed minimal guidelines for long-term viability**. Larger and more productive ("resilient") populations may be able to recover from a catastrophic event that would cause the extinction of smaller populations. Furthermore, such populations may serve as important sources of dispersing fish to less productive habitats. A collection of local populations that contains some populations with high abundance and productivity is less likely to go extinct in response to a single catastrophic event that affects all populations. It should be recognized that populations or habitats serving as sources and sinks may exchange roles over time.

• **Populations that display diverse life-histories and phenotypes should be maintained**. When local populations each have a fair degree of life history diversity (or other phenotypic diversity), a collection of local populations is less likely to go extinct as a result of correlated environmental catastrophes or changes in environmental conditions that occur too rapidly for an evolutionary response. In addition—assuming phenotypic diversity is caused at least in part by genetic diversity—maintaining diversity allows natural evolutionary processes to operate. Note that to protect genetic diversity, it may be necessary to maintain several populations with the same phenotype.

• **Habitat patches should not be destroyed faster than they are naturally created.** Salmonid habitat is dynamic; suitable habitat is continually being created and destroyed by natural processes. Human activities should not decrease either the total area of habitat OR the number of habitat patches.

• **Maintain some habitat patches that appear to be suitable or marginally suitable, but currently contain no fish.** In the dynamics of natural populations, there may be time lags between the appearance of empty but suitable habitat (by whatever process) and the colonization of that habitat. If human activity is allowed to render habitat unsuitable when no fish are present, the population as a whole may not be sustainable over the long term.

• **Natural rates of straying among subpopulations should not be substantially increased or decreased by human actions.** This guideline means that habitat patches should be close enough together to allow dispersal and expansion of the population into under-used patches during times when productivity is high. Also, dispersal should not be much greater than natural levels because increased dispersal may reduce a population's viability if fish wander into unsuitable habitat or interbreed with genetically unrelated fish.

• **Some populations should be geographically widespread.** Spatially correlated environmental catastrophes are less likely to drive a widespread collection of local populations to global extinction.

• **Some populations should be geographically close to each other**. On long temporal scales, having populations geographically close to one another facilitates connectivity among existing populations. Thus, a viable collection of local populations requires both widespread AND spatially close populations.

• **Populations should not all share common catastrophic risks**. A collection of local populations that do not share common catastrophic risks is less likely to be driven to extinction by correlated environmental catastrophes. Maintaining geographically widespread populations is one way to reduce risk associated with correlated catastrophes, but factors unrelated to spatial proximity may be important. For example, geographically distant populations with similar vulnerability to broad-scale climate influences may share common catastrophic risks.

• **Evaluations of status should take into account uncertainty about among-population processes.** Our understanding of spatial and temporal process and interactions among local populations is very limited. Because most collections of local populations of salmonid fishes are believed to have been historically self-sustaining, the historical number and distribution of populations serves as a useful "default" goal, unless better evidence is available.

and others 1997, McElhany and others 2000) to develop individual applications. Although throughout this monograph we address persistence of populations, we realize that the broader goal of viability may more often be the conservation target of interest (*see Box 7*).

Feasibility means that conservation actions should be cost effective, sustainable, and socially and environmentally acceptable. If all else is equal, projects leading to the most efficient implementation or removal of barriers should be those that will produce the greatest benefit (for example, reduction in risk) for the least cost. Cost must be considered not only for the immediate project, but also for long-term maintenance. Constructing barriers or replacing impassible road culverts with ones that allow fish passage is costly, so only a few can be implemented each year. Efforts to control or eradicate nonnative salmonids have proven expensive and are not always successful (Dunham and others 2002a), so thoughtful evaluation of the cost-effectiveness of these efforts will be important. Constructing or removing barriers can have other environmental effects as well. Barriers to non-native fish are also barriers to other aquatic organisms that may need to move to persist and maintain productive aquatic and riparian communities. Barriers also disrupt flows of water and materials (for example, sediment) that shape upstream and downstream habitats or affect floodplains and human infrastructure.

Finally, it is clear that conservation planning decisions are inherently *uncertain*. For example, our understanding is very limited about where brook trout will invade, how long isolated populations of native fishes will persist, and how these differ among different environments and species or subspecies. This creates genuine disagreement among biologists who have experience in different regions. Although these limitations can be frustrating, we will never have all the answers and decisions must be made, so confronting uncertainty must become part of the management process (Ludwig and others 1993, Francis and Shotton 1997, McElhany and others 2000). Ludwig and others (1993) suggested that managers should favor decisions that are robust to uncertainty (that is, the outcome is likely to be favorable regardless of our knowledge). When this is impossible, it is important to hedge, probe the system to learn, and favor reversible actions. For example, hedging could include maintaining redundant populations and constructing barriers in some systems but not others to learn more about what happens, through careful monitoring. Some barriers may also be viewed as short-term, reversible actions to prevent impending invasions, while learning more about the threats of isolation. We are uncertain when the effects of barriers become irreversible because, for example, migratory forms are lost. Recent work suggests that the evolution or re-expression of migratory life histories and colonization of newly accessible habitats can occur quickly (Hendry and Stearns 2004, Quinn 2005). However, until research or management experiments clearly demonstrate that the effects of isolation can be reversed, any intentional isolation must be viewed as a calculated risk, balanced against the threat of invasion.

Box 7. Persistence vs. viability.

Often the terms "persistence" and "viability" are used interchangeably, but here we recognize viability as a larger conservation objective. The basic impetus for conservation planning is not simply to guarantee persistence of a species, but to ensure that natural ecological and evolutionary processes are allowed to continue and perhaps change through time. For a single species, this broader view of maintaining process, not just persistence, is referred to here as "viability" (see McElhany and others 2000). In the prioritization process, this may equate to conservation of both evolutionary and ecological values simultaneously. For example, evolutionary values can be associated with genetically pure but isolated populations that may persist for some time, but if those populations cannot evolve and adapt with changing environments they may not be viable in the long term. Populations that are likely to persist *and* remain viable represent a higher overall value and logically a higher priority in any assessment of risk. In short, persistence is generally viewed as a necessary but not sufficient objective for attaining full conservation of a species.

Section VI: Two Examples of Invasion and Isolation Tradeoffs

We use the Coeur d'Alene River basin in northern Idaho and the Little Snake River basin in southern Wyoming and northern Colorado (Table 5) as examples of relatively complex and simple systems, respectively, to show how our conceptual framework can be used to

Table 5—Aspects of the physical characteristics, trout populations, and management issues in the Coeur d'Alene River basin, Idaho, and Little Snake River basin, Colorado-Wyoming.

Characteristic	Coeur d'Alene River	Little Snake River
Basin area (ha)	232,112	288,344
Elevation range (m)	600 to 2,100	1,900 to 3,300
Period of peak precipitation (form)	November to January (snow and rain)	March to April (snow)
Primary land management activities	mining, logging	grazing, water development
Cutthroat trout subspecies	westslope cutthroat trout	Colorado River cutthroat trout
Life histories present	resident, fluvial, adfluvial	resident
Cutthroat trout distribution (km)	1,063	160 to 190
Other sympatric native salmonids	bull trout[1] mountain whitefish	mountain whitefish[1]
Sympatric nonnative salmonids	brook trout, rainbow trout	none[2]
Brook trout distribution (km)	92	unknown but widespread and much greater than cutthroat trout
Ranking of cutthroat trout population values	socio-economic > ecological > evolutionary	evolutionary > ecological > socio-economic
Management emphases	maintain fishery for fluvial and adfluvial fish	create and enlarge remnant cutthroat trout populations
Management tactics	restrict harvest, improve habitat, remove barriers, install barriers, stock sterile rainbow trout	remove brook trout, install barriers, translocate cutthroat trout

[1]Neither cutthroat trout subspecies currently coexists with these salmonids.
[2]Colorado River cutthroat trout largely persist only above barriers preventing invasions of nonnative trout, but individuals occasionally drift downstream over barriers to form sympatric assemblages.

consider the tradeoffs in managing invasions and isolation. There are many factors that affect conservation of native salmonids, including the history and extent of land management, location of natural and anthropogenic barriers to fish movement, introduction and invasion of nonnative salmonids, and goals of fisheries managers. These issues vary markedly across the western U.S., and it is beyond our scope to explore them in great detail here. Our goal is to use the framework outlined above to consider the opportunities and priorities that emerge in each case. However, we caution that these are not intended to be specific proposals for management.

Coeur D'Alene River

Background—The upper Coeur d'Alene River basin in northern Idaho (Figure 6) has two major branches, the North Fork and Little North Fork Coeur d'Alene rivers, each with numerous 2nd- to 4th-order tributaries. The basin has relatively low topographic relief (approximately 600 m), but is influenced by a mixture of climatic processes. The hydrograph is predominantly driven by melting snow, but the Pacific maritime influence and the relatively low elevation of much of the basin result in some winter rain. Rain-on-snow floods during winter

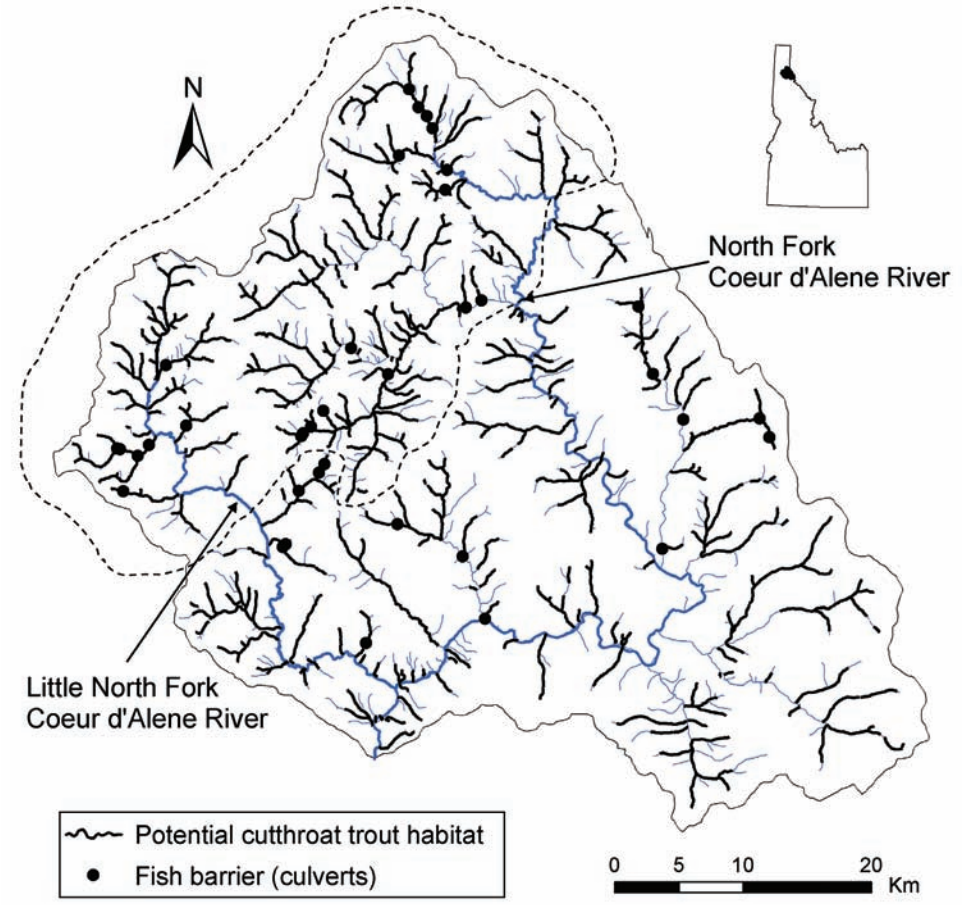

Figure 6—Predicted distribution of spawning and rearing habitat for westslope cutthroat trout (bold stream segments), and road culverts believed to be complete barriers to all fish passage (dots). Spawning and rearing habitat was predicted from associations between young-of-the-year cutthroat trout and stream size (Dunnigan 1997, Abbott 2000), gradient, and confinement (Moore and Gregory 1988, Lentz 1998), and from direct field observations of spawning adults (J. Dupont, Idaho Fish and Game, personal communication). Barriers were identified by the Panhandle National Forests stream crossing inventory. The dotted line encompasses the area believed to support cutthroat trout populations that have not been hybridized by rainbow trout. Some segments above barriers outside this area may also retain pure cutthroat trout. One headwater tributary in the northeast portion of the basin has hybridized trout and so was excluded from this area.

storms are more common than in much of the range of westslope cutthroat trout. There are no headwater lakes in the basin that serve as sources for downstream invasion or modify the hydrologic and thermal regimes of downstream habitats.

Disruptive management and development have been extensive. Hard rock mining, dredging, log drives down streams, clearcut logging, extensive road building, and overfishing have degraded habitats and depressed trout populations, especially in the lower half of the basin. In addition, road crossings have created barriers to fish movements in many tributaries. Native salmonids included westslope cutthroat trout, mountain whitefish (*Prosopium williamsoni*), and bull trout, although bull trout are now presumed to be extirpated. Because of its unusual geomorphic and climatic characteristics (for example, heterogeneous geology and frequent winter flooding), the Coeur d'Alene River basin could represent a unique evolutionary template for westslope cutthroat trout (for example, Allendorf and others 1997). Resident and migratory trout occur throughout the basin, including fluvial and adfluvial fish that reach 350 to 450 mm (14 to 18 inches). Brook trout and rainbow trout were introduced between 1900 and 1950, and both have become established in parts of the system. Hybrid swarms of cutthroat trout X rainbow trout are common in the lower tributaries, but hybrids declined or were absent entirely in samples upstream.

Restrictive angling regulations (that is, size limits, gear restrictions, and catch-and-release) were first imposed on portions of the basin in the 1970s. Hatchery rainbow trout have been stocked in the main-stem rivers for decades, but less so in recent years. Now, only sterile fish are planted to reduce the risk of further hybridization. Habitat management has focused on road obliteration, channel reconstruction, and barrier removal. The trout populations have responded and the upper river has recently become a renowned fly fishing destination for wild trout.

Conservation values—Evolutionary, ecological, and socio-economic conservation values are all considered important in the Coeur d'Alene River basin, but the last two are dominant management objectives. A productive, diverse, and resilient population of trout with a large migratory component is an emphasis of natural resource managers. The sport fishery for large cutthroat trout in the main-stem rivers plays a significant role in the economy of local communities, particularly as traditional extractive industries (for example, timber harvest and mining) are replaced by tourism.

Conservation of evolutionary value (which might be compromised by hybridization) has been a secondary concern, primarily because hybridized trout that may be morphologically indistinct from genetically pure cutthroat trout are widespread and have been considered part of the formally recognized taxonomic group (U.S. Fish and Wildlife Service 2003, Campton and Kaeding 2005). There is still controversy on this issue (Allendorf and others 2004, 2005). Little work has explored the different ecological roles of cutthroat trout, rainbow trout, or their hybrids, but abundant populations of the latter two can become established in habitats once occupied by cutthroat trout. A general assumption seems to be that rainbow trout or their hybrids may persist, evolve ecological roles, and support fisheries that are surrogates for native cutthroat trout, with little loss of the associated ecological functions and values (see Quist and Hubert 2004). However, although native and non-native trout are likely to have similar roles at some levels of ecological organization (McGrath 2004), in other cases non-native trout have very different effects (Baxter and others 2004). Little research has been done to clarify the ultimate ecological implications of introgression or displacement of cutthroat trout by other salmonids, so some undefined risk remains.

To illustrate the fundamental units of conservation and the distribution of local populations needed to maintain all conservation values, we mapped the potential distribution of spawning and rearing habitat for cutthroat trout. We assumed that natal habitats define local populations (Table 4), and represent the critical habitats vulnerable to invasion and isolation. We used simple models based on landscape and channel characteristics associated with the distribution of juvenile fish (Dunnigan 1997, Abbott 2000) and observations of spawning areas by local fisheries biologists. We concluded that stream segments potentially important to conservation of ecological and socio-economic values occur in tributary systems throughout the basin (Figure 6).

Segments potentially important for maintaining evolutionary value are more restricted. Extensive hybridization is common in the lower tributaries, but pure populations are found in the upper portions of both the Little North Fork and North Fork subbasins (B. Rieman, unpublished data). Therefore, it seems likely that genetically pure populations of westslope cutthroat trout important for conserving evolutionary values also support socio-economic and ecological values in the upper part of the basin. Road crossings have also created barriers to movements of trout in many tributaries (Figure 6), and these may have temporarily prevented the invasion of rainbow trout and the extent of hybridization. Genetically pure populations of cutthroat trout may persist above some barriers, but surveys are needed to confirm this.

Vulnerability to invasion—Brook trout are well established in some tributaries of the Little North Fork and the lower North Fork Coeur d'Alene rivers. To consider habitats most vulnerable to future invasion and displacement of westslope cutthroat trout, we used an approach similar to that described above to map potential habitat for brook trout (Figure 7). Our predictions suggest that brook trout could ultimately occupy and potentially displace cutthroat trout from portions of many tributaries throughout the basin. If the invasion proceeded to the ultimate limits it could leave habitat for cutthroat trout highly fragmented. A complete invasion would threaten all three conservation values associated with the existing trout populations, although brook trout might still fill some of the ecological roles played by salmonids in these streams (see McGrath 2004). The most vulnerable habitats are tributaries adjacent to, or habitats upstream of, current populations of brook trout where propagule pressure should be highest. However, brook trout remain patchily distributed, even though they have been established in some tributaries for at least 60 years (Maclay 1940). Brook trout and cutthroat trout also appear to coexist in some streams. Whether the brook trout invasion is stalled or advancing very slowly is unknown, so it also is not clear that invasion and displacement is imminent even in sites close to potential source populations.

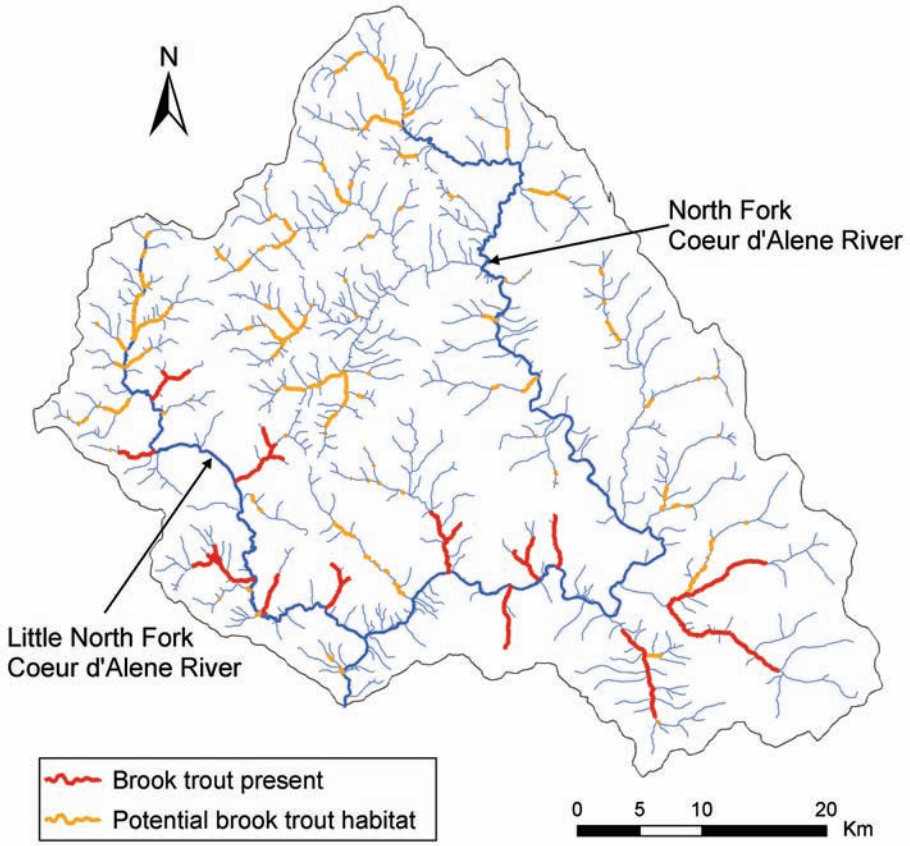

Figure 7—Known (red stream segments) and potential (yellow segments) distribution of brook trout in the upper Coeur d'Alene River basin. Potential brook trout habitat was predicted based on associations between brook trout distributions and stream size and channel gradient (Fausch 1989, Rieman and others 1999, Rich and others 2003, Petty and others 2005). However, brook trout could invade farther than indicated here because the models are simple approximations and some fish may disperse beyond their primary habitats. The brook trout distribution in the Coeur d'Alene River basin does not appear to have advanced in recent decades, so other factors like temperature or winter flooding may limit the distribution to less than predicted here.

The threat of invasion by rainbow trout and their hybrids appears more immediate than invasion by brook trout. Rainbow trout or their hybrids could ultimately invade throughout the system even without further stocking of fertile rainbow trout because hybridization may facilitate dispersal (Hitt and others 2003, Allendorf and others 2004). Thus, conservation of evolutionary values associated with pure populations of cutthroat trout in the headwaters or any accessible tributaries throughout the basin is threatened. The distribution of rainbow trout genes may be constrained by elevation or thermal gradients (Weigel and others 2003) so the risks of hybridization are probably greater for populations closer to the advancing front. In contrast, conservation of ecological and socio-economic values is of less concern because hybridized trout may retain many of these values.

Persistence with isolation—Westslope cutthroat trout have persisted in isolated stream segments throughout the region, but little information is available to directly estimate the probability of persistence as a function of isolation time, habitat condition, or network size. Without data for this taxon we can only assume westslope cutthroat trout face threats similar to those outlined in the preceding discussions for other salmonids. Consequently, we anticipate that stream networks with less than about 10 km of connected suitable habitat will be at increased risk of local extinction from stochastic, demographic, and genetic processes. The risks will increase as network size declines, habitat is degraded, or the potential for catastrophic disturbance increases. Populations that are isolated will also lose any demographic resilience associated with migratory life histories unless the isolated network is large enough to support more productive

main-stem habitats that serve as foraging areas supporting faster growing individuals. Moreover, the basin is vulnerable to winter rain-on-snow floods associated with slow-moving, moist winter storms, which can create catastrophic disturbances especially in the aftermath of large fires. These events could drive small populations extinct, so any strategy depending on intentional isolation should consider spatial replication across broad scales to reduce the potential for simultaneous extinctions.

Potential priorities and actions—Priorities for management in this basin might include both removing and constructing barriers as well as improving habitats to enhance the resilience of local populations. Because there is still opportunity to provide some representation and diversity of all primary conservation values, a mix of strategies could be important. In general, constructing barriers could be used to conserve evolutionary values in remaining genetically pure populations, whereas removing barriers could be used to conserve and expand the potential distribution of large migratory trout that represent important ecological and socio-economic values.

There may be an unusual (albeit costly) opportunity to conserve all three conservation values simultaneously. The fishery and resilience of the remaining cutthroat trout populations depend strongly on migratory life histories and the connection of tributary and main-stem habitats. However, these connections could allow both brook trout and rainbow trout to expand throughout the system. The brook trout invasion appears most imminent in the Little North Fork subbasin, whereas the risks are probably lower in the North Fork where the distance from potential sources is much greater. In contrast, the rainbow trout invasion may extend throughout the system. Large barriers might be used to conserve evolutionary as well as ecological and socio-economic values if they could isolate tributary-river networks where pure populations *and* migratory life histories still persist (Figure 8). The best opportunity for this appears to be in the headwaters of both river subbasins where pure populations and multiple tributary networks are linked to the main-stem rivers. Intentional barriers could be installed first in the headwaters of the Little North Fork Coeur d'Alene River because brook trout and rainbow X cutthroat trout hybrids are present immediately downstream (Figures 6, 7, and 9). If this proved successful and invasions continued to advance in the North Fork, large barriers could be installed with the benefit of the experience gained in the first project. Although large barriers like low-head main-stem dams and diversions are possible, they may not be feasible. Large barriers would be expensive, would disrupt important ranging movements of large fish and potentially other species in the upper rivers (J. Dupont, Idaho Fish

Figure 8—Pure populations of large fluvial westslope cutthroat trout (P. Valcarce, Limnophoto, image) might be conserved in the upper North Fork Coeur d'Alene River basin by using barriers to prevent upstream invasion and hybridization by nonnative rainbow trout. If this were successful, the native cutthroat trout would support all three types of conservation values.

and Game Department, Coeur d'Alene, unpublished data), and could have negative effects on hydrologic and geomorphic processes. Barrier management of this scale would require significant commitment of resources and environmental compromises.

More modest alternatives might include strategic use of barriers to conserve representative genetic diversity and evolutionary values in smaller stream networks throughout the basin. Existing impassable culverts have isolated several relatively large (5 to 10 km) habitat networks across the system (Figure 9). If remnant populations above these barriers have not been hybridized or invaded by brook trout, culverts could be replaced by intentional barriers to protect these populations indefinitely. Good barrier sites must be geomorphically stable and economically feasible, and the isolated stream network should support a productive population and be large enough to ensure long-term persistence. Larger networks and more intact habitats would be higher priorities.

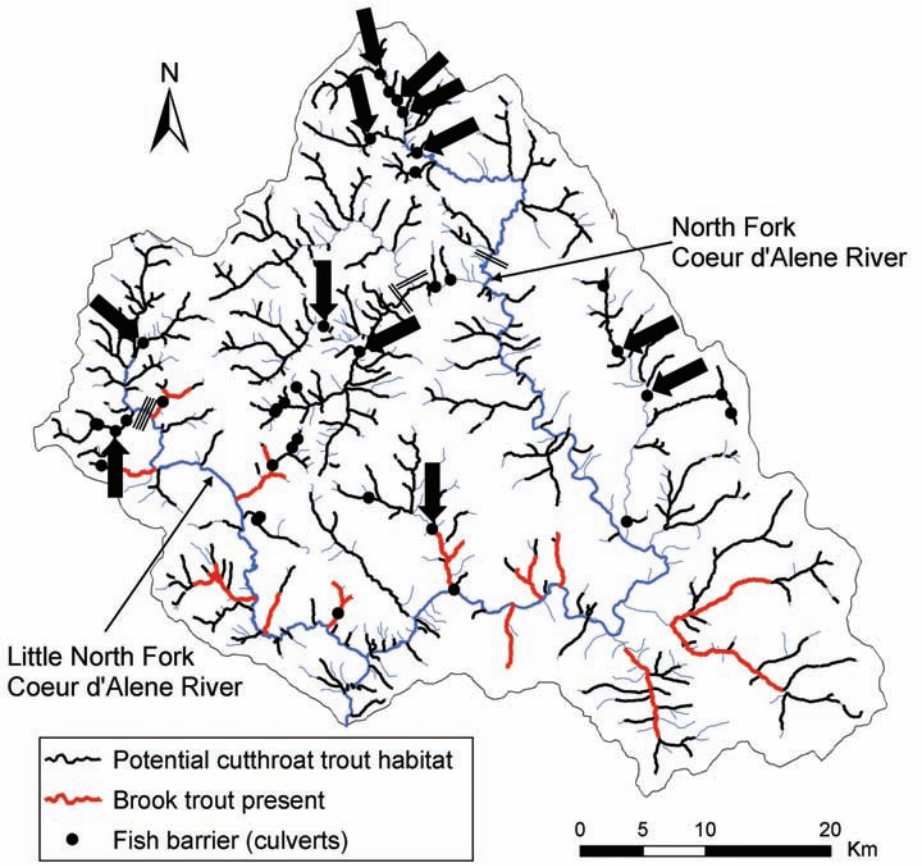

Figure 9—Opportunities and potential priorities for installing and removing barriers that isolate native cutthroat trout in stream networks. The double parallel lines represent sites where large barriers might be used to isolate relatively large stream networks that could protect socio-economic, evolutionary, and some ecological values simultaneously (but see cautions about feasibility in the text). The four parallel lines represent a similar site that might be a high priority because brook trout and rainbow X cutthroat trout hybrids occur in nearby tributaries downstream. The black arrows point to existing culvert barriers that are candidates either for conversion to intentional barriers to conserve remnant genetic diversity, or for removal to expand connectivity and restore ecological and socio-economic values. All other barriers above intentional barriers could be removed to expand the isolated network. The benefits of intentional isolation would depend on the genetic integrity of the population above the existing barrier, the condition of the habitat, and the ability to create a spatially diverse collection of isolated networks throughout the basin. It would also depend on the feasibility of creating the barrier. Other existing barriers that are high in the headwaters of tributaries are lower priorities for either permanent barriers or removal because there is limited potential habitat above the site. Such small areas would either be vulnerable to local extinction if isolated or contribute relatively little to the broader network if removed.

Because we are considering only evolutionary values at this stage, representation, redundancy, and spreading of risk also become important criteria for selecting sites for barriers. However, there has been no detailed genetic inventory to guide management. Genetic similarity tends to decline with distance among salmonid populations (Quinn 2005), and environmental conditions influencing local adaptation probably do also. If the goal is to represent as much of the genetic diversity and evolutionary legacy for westslope cutthroat trout as possible, the logical objective would be to conserve populations widely distributed throughout the system. Broad representation would also minimize the threat of simultaneous extinctions from large catastrophic disturbances.

Barriers other than those selected above could be removed to extend connectivity and conserve or restore ecological and evolutionary values in other areas of the basin. Barriers that currently isolate small fragments of potential cutthroat trout habitat might be lower priorities for removal than those that could expand the network, regardless of the values in question (Figure 9).

Little Snake River

Background—Much different circumstances characterize the Little Snake River basin in southern Wyoming and northern Colorado (Table 5, Figure 10). The climate is typical of the central Rocky Mountains. The first snowfall is in September or October, annual

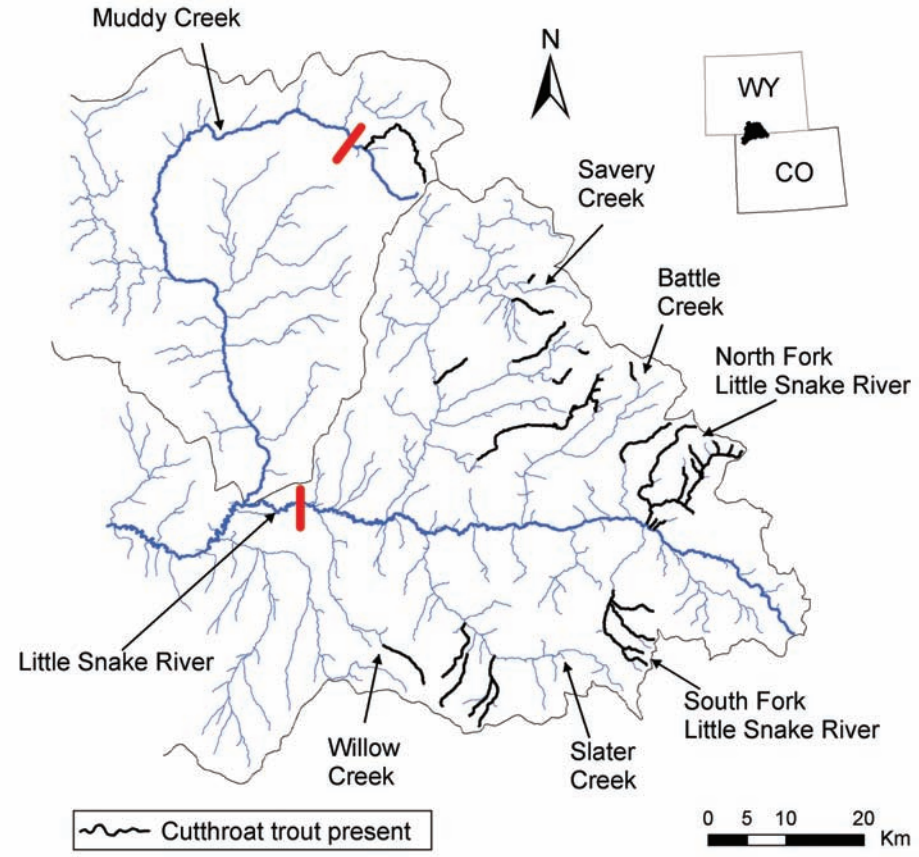

Figure 10—Headwaters of the Little Snake River, showing the current estimated distribution of populations of Colorado River cutthroat trout as bold stream segments (after Hirsch and others 2006). In many cases stream segments shown as occupied are fragmented by natural or artificial barriers, or the true distribution of native cutthroat trout is incompletely known. Estimates of the lowermost extent of trout habitat in the Little Snake River main stem in 1955 (Eiserman 1958) and in the Muddy Creek headwaters are denoted by solid red bars.

precipitation peaks in March and April in the form of snow, and there may be heavy rains associated with monsoonal storms in July and August (Knight 1994). Peak discharge is caused by snowmelt runoff in June, with occasional localized stormflows in late summer. Elevations range from 1900 m at the mouth of Muddy Creek near Baggs, Wyoming, to over 3300 m in the headwaters. Streams pass through three major vegetation types: sagebrush grasslands with riparian gallery forests at the lowest elevations, extensive aspen stands at mid-elevation sites, and coniferous forests higher in the basin.

Land ownership and use are typical of many watersheds in the western U.S. Lower-elevation valleys are privately owned and higher-elevation lands are in the public domain. Historically this region served as a hub of grazing activity. For example, in the early 1900s over 10 million sheep annually were pastured on summer range or herded on stock driveways on the Wyoming side alone (Thybony and others 1985). Livestock grazing continues at much lower intensity, although sedimentation, riparian alteration, and irrigation diversions associated with agriculture have altered fish habitat quality and tributary access for decades (Eiserman 1958). Resource extraction on public lands, such as hard rock mining and timber harvest, is less than it was historically, but recreational use of public lands has increased with population growth in much of the mountain West, and publicly-built and user-created roads and trails are extensive. An exception is a large portion of the uppermost North Fork basin (Figure 10), which lies within the Huston Park Wilderness Area. Finally, the entire North Fork basin has undergone water development. Flows of all perennial tributaries pass through water collection structures that block upstream migrations of fish and fragment some populations of cutthroat trout. In addition, portions of the high spring flows (and probably juvenile fish) are diverted into a pipeline transferring water east underneath the Continental Divide. Water development is also projected or underway in adjacent Wyoming basins, several of which harbor populations of cutthroat trout.

Native fishes are relatively few. Colorado River cutthroat trout once ranged throughout the basin, sympatric with mottled sculpin (*Cottus bairdi*) and mountain whitefish in the colder upper reaches, and perhaps with some members of the now-rare Colorado River fauna, such as Colorado pikeminnow (*Ptychocheilus lucius*), in the warmer downstream reaches of the main stem. Eiserman (1958) considered the Little Snake River near the mouth of Willow Creek and the town of Dixon as the downstream extent of trout (Figure 10). Below this point the river was regarded as too warm and silty to provide trout habitat in summer, as were many of the lower portions of Muddy Creek. Brook, brown, and rainbow trout were first introduced in the 1930s (Eiserman 1958) and currently dominate fish communities in coldwater portions of the basin, whereas cutthroat trout are relegated almost solely to short stream segments protected from upstream invasions by barriers. A waterfall near its mouth protected the North Fork Little Snake River population, one of the largest of this subspecies, from early invasions. Later ones were thwarted by some of the first barriers built (in the mid-1970s) specifically to prevent upstream invasions of nonnative fishes. The main stem has a mix of species, including nonnative channel catfish (*Ictalurus punctatus*), but does not appear to retain any native salmonids.

Presently, from 160 to 190 km of up to 38 streams are believed to contain 15 to 20 distinct populations of Colorado River cutthroat trout (Figure 10; Young and others 1996, Hirsch and others 2006). These populations display different degrees of hybridization with rainbow trout or Yellowstone cutthroat trout, but a few populations appear to have retained their genetic integrity. Some populations in Colorado may have resulted from early stocking of Colorado River cutthroat trout originating from Trappers Lake, an adfluvial population in the headwaters of the White River basin in northwestern Colorado. No lakes in the Little Snake River basin were known to contain this subspecies.

Conservation values—Colorado River cutthroat trout have been the subject of intensive management in this basin (Speas and others 1994), primarily for their evolutionary values. Their populations are rare enough that each receives individual attention, and the focus of management is to maintain all existing populations. We infer from the extensive tributary network (for example, Battle, Savery, and Slater creeks) that fluvial cutthroat trout once existed. If so, their loss has reduced or eliminated ecological values such as demographic support of resident cutthroat trout populations, transfer of nutrients upstream, and providing food for terrestrial predators like bears (Koel and others 2005). Socio-economic values contribute little to the current management of Colorado River cutthroat trout. Angling for cutthroat trout is an incidental activity, primarily because their populations are scattered, most streams are small and difficult to access by automobile, and adult fish do not reach large sizes because of the short growing season at high elevations. Moreover, regulations prohibiting or limiting harvest have been in place for decades.

Vulnerability to invasion—Following decades of stocking (Eiserman 1958, Wiltzius 1985), brook trout and rainbow trout have become widely distributed in most available habitats, and there is little evidence of environmental or biotic resistance to their continued spread should additional waters become accessible. For example, within four years of an illegal introduction just above the artificial barrier in the main-stem North Fork Little Snake River, brook trout had spread to three tributaries and ascended 8 km up the main stem despite the robust population of Colorado River cutthroat trout already present (M. Young, personal observation). In addition, perennial streams lacking fish are exceptionally rare, and presumably contain geological or artificial barriers, or habitat unsuitable for trout.

Persistence with isolation—Nearly all remaining populations of Colorado River cutthroat trout persist only above barriers (Figure 11), yet individuals in some of these populations migrate hundreds or thousands of meters to spawn (Young 1996) and move extensively for foraging (Young and others 1997). Nevertheless only four populations occupy more than 10 km of connected habitat and probably contain enough individuals to afford security from the long-term loss of genetic variation (Allendorf and others 1997, Young and others 2005). Most populations inhabit stream segments less than 3 km (often due to natural or artificial barriers that fragment habitat), likely consist of a few hundred fish at most (Young and others 2005), and are at a heightened risk of extirpation from an array of natural disturbances, such as drought or post-wildfire debris torrents. Similar populations of this subspecies, and salmonids elsewhere in the inland West, have suffered this fate (M. Fowden, Wyoming Game and Fish Department, personal communication; Brown and others 2001, Dunham and others 2003b).

Potential priorities and actions—Currently, most populations of Colorado River cutthroat trout in this basin inhabit short headwater stream segments and are probably at an elevated risk of extirpation. The genetic structure of these populations has not been studied, so the most conservative approach would be to attempt to

Figure 11—In the Little Snake River watershed, Colorado River cutthroat trout persist only in headwater streams, above barriers to upstream invasion by nonnative brook, brown, and rainbow trout (M. Young image).

conserve all populations to maximize redundancy and representation of whatever genetic diversity remains. From this perspective, the smallest populations are at the greatest risk. The probability of persistence of all populations regardless of size could be enhanced by extending their distribution downstream to suitable habitats currently occupied by nonnative species once the latter have been removed. This approach could be particularly valuable if it connects populations to additional streams that decrease the risk of population loss from localized catastrophic events. In addition, there may be opportunities to restore connectivity by providing fish passage around water diversions, and to achieve redundancy by introducing genetically pure populations into additional, nearby waters that were previously occupied by cutthroat trout. Such efforts are underway (B. Wengert, Wyoming Game and Fish Department, and D. Brauch, Colorado Division of Wildlife, personal communication), as are attempts to identify waters where such actions could be undertaken (Hirsch and others 2006). Nevertheless, attempts to establish populations in locations with access to additional streams or to refugia that permit natural recolonization has been, and will be, challenging. Overcoming water management issues, resolving private land-public land conflicts, and locating sites suitable for barrier installation render this a long-term, site-specific solution unless other methods for controlling nonnative fishes become available. The feasibility of any of these actions will likely guide the ultimate selection of sites for further work.

Where suitable habitat exists but cutthroat trout populations are absent, the primary conservation actions involve repeated chemical treatment or intensive electrofishing to remove nonnative species and installing artificial barriers to prevent reinvasions. This work has been challenging. Occasionally, treatments have not killed all nonnative fish present, forcing biologists to repeat treatment of some streams or abandon reclamation in others. Some barriers were passable to upstream migrating brook trout, or became so after damage by high flows. In other cases brook trout were introduced above these structures by anglers, apparently to retaliate for restricted harvest of cutthroat trout or the loss of individually prized fisheries for nonnative trout. In these latter cases, preservation of populations may rely more on road closures, persistent public outreach, and a regular law enforcement presence than on fish population management.

Finally, the relatively few indigenous populations of Colorado River cutthroat trout remaining have served as a source for fish stocked elsewhere in the basin, either by direct transfers or indirectly as broodstock used in hatcheries or off-site ponds. Although the use of lakes as broodstock refugia has been successful elsewhere (K. Rogers, Colorado Division of Wildlife, personal communication), it has been repeatedly attempted with limited success in this area. Use of hatchery or semi-wild broodstocks argues for adopting genetic management plans to ensure such stocks do not deviate from wild populations (Mobrand and others 2005).

Section VII: Making Strategic Decisions

The framework we presented in Section V outlines important questions to consider when managing the invasion-isolation tradeoff. For biologists faced with a particular basin and set of native salmonid populations that represent important conservation values, the next step is to consider the available options and make strategic decisions, before setting priorities for action. A lesson from the two examples presented above is that the best solutions for conserving native salmonids are not the same in all regions. For example, in the Coeur d'Alene River basin the main issues are whether nonnative salmonids will invade and displace or hybridize with native cutthroat trout, and how much habitat will be required to sustain important migratory life history types if they are isolated. In contrast, in the Little Snake River basin the primary issues are locating any remaining pure populations, replicating them in headwater streams above barriers after removing nonnative salmonids, and improving the probability of persistence of these many isolated populations.

Despite these fundamental differences among regions, the two examples illustrate that fisheries managers do have opportunities to make strategic decisions under these different circumstances. For any given basin and particular set of salmonid populations of conservation value, these decisions will be influenced primarily by two conditions: 1) the degree of isolation of the populations of interest, and 2) the degree of invasion threat (Figure 12). For example, if most native salmonid populations in the basin are in small isolated patches, the invasion of nonnative salmonids is either imminent or relatively complete, and the invaders have strong negative effects (as in the Little Snake River basin; upper left corner of Figure 12), then barriers will be required to protect most populations from rapid extinction. Given this, the strategic decisions available include: 1) the size, habitat quality, and number of patches needed to ensure persistence of a minimum number of the isolated

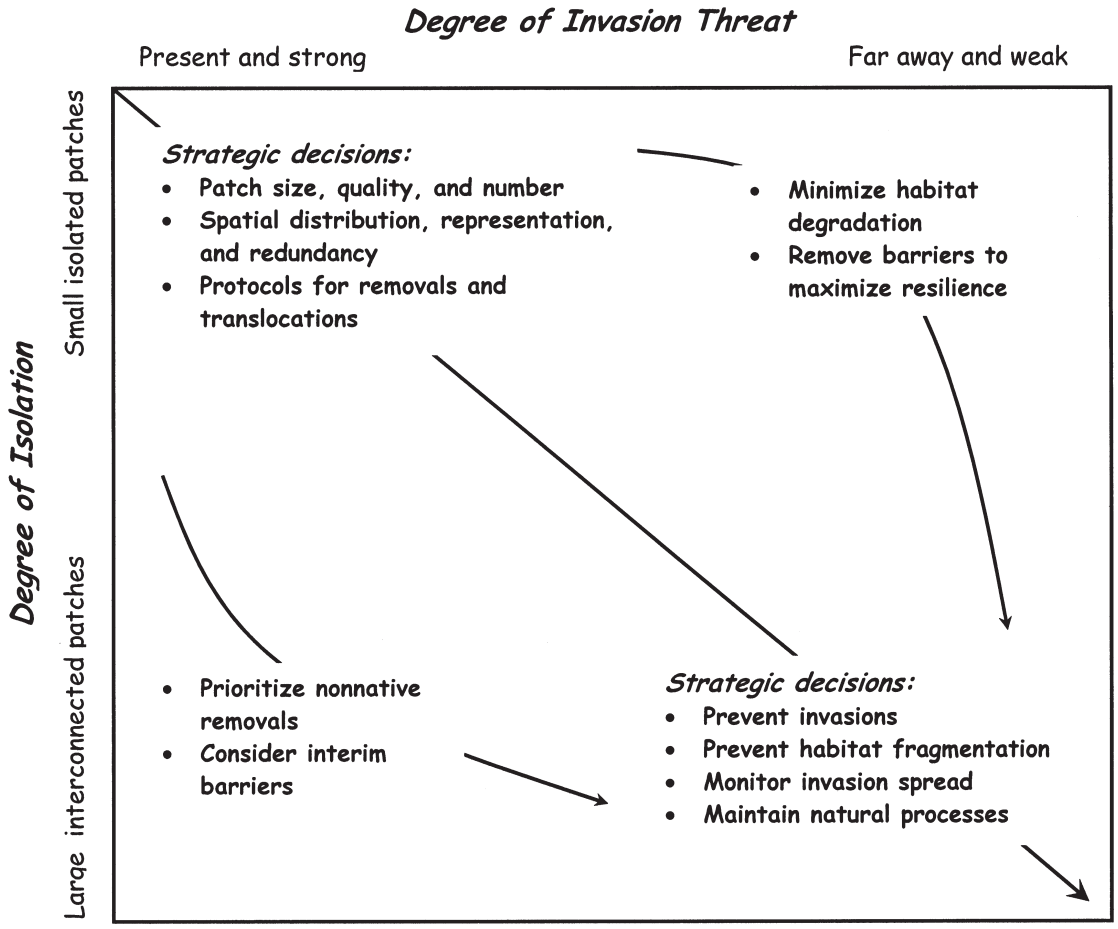

Figure 12—A conceptual diagram of the opportunities for strategic decisions when managing the invasion – isolation tradeoff for native salmonid populations of conservation value. Examples of strategic decisions to maximize conservation of remaining populations in several regions of the decision space are shown.

populations through time; 2) the representation of as much genetic, morphological, behavioral, and habitat diversity as possible; 3) the spatial distribution and redundancy of populations to avoid extinction of evolutionary lineages by correlated catastrophic disturbances; and 4) working out protocols for effective removal or control of nonnative trout, and subsequent translocations of native trout. Despite these strong constraints on management options, the goal of these decisions is to move the set of native salmonid populations toward the lower right corner of this decision space where the invasion threat is farther away and patches are larger and more connected, even though in many cases this goal is not fully achievable at present.

At the opposite end of the spectrum, if a manager is fortunate to have many large interconnected patches with native salmonids, and the invasion threat is far away or the effects of the invader are weak, then strategic decisions will involve: 1) preventing invasions, 2) preventing fish movement barriers or land uses that fragment habitat, 3) monitoring the spread of any nonnative salmonids in the basin, and 4) ensuring that natural processes continue to provide the habitat heterogeneity that sustains the native populations (Figure 12; lower right corner). For example, a key strategy might be to minimize sources of nonnative fishes that could foster unauthorized introductions (Rahel 2004) and educate the public about their dangers to native biota (Cambray 2003a, 2003b). Likewise, under this scenario managers have more opportunity to ensure representation and redundancy of populations, and to experiment and monitor to learn and thereby reduce future uncertainty.

Some managers will find themselves in other regions of this decision space, where different strategies are required. For example, a basin may have little invasion threat but many culverts or diversions that fragment headwater stream habitats (Figure 12; upper right corner). In this situation, a strategic decision would be to minimize habitat degradation (and improve habitat) in these small patches to prevent further extinctions, and increase connectivity by removing barriers where feasible to maximize resilience of these populations. In contrast, other managers may find that their basin has large patches of habitat isolated by natural barriers, but that nonnative trout were stocked above them and the invasion is nearly complete (lower left corner). In this case they may prioritize some of these basins for the difficult task of removing nonnative trout, which may require building temporary barriers to prevent upstream invasion while successive treatments are used to extend habitat downstream for native salmonids. This will require strong public relations and a long-term commitment of agency funding and time. Overall, an understanding of where their native salmonid populations lie in this decision space will help managers develop strategic decisions for other possible scenarios.

When barriers are used to prevent invasions, human translocation of nonnative salmonids above them may also be a problem, requiring further strategic decisions. If native salmonids are restricted to many small patches above barriers (Figure 12, upper left), managers could construct several barriers at intervals (for example, 1 km) near the downstream end and monitor the buffer zone as insurance against reintroductions, but the stream fragments are usually too short to justify other measures. In contrast, in a large basin of intact and relatively remote habitat where strong invaders are removed in stages (lower left), a strategic decision would be to place the downstream barrier in an inaccessible location to minimize human translocations. If temporary barriers were constructed for the project, the materials could be left on site to allow replacing barriers quickly if translocations occur at a downstream barrier.

Finally, where constraints are strongest (Figure 12; upper left corner), it is likely that managers will select a mixed strategy and hedge their bets against uncertainty. This may include conserving many small populations that persist above barriers, translocating among replicates when they go extinct (Lubow 1996, Hilderbrand 2002), and working to protect or develop larger populations in remote or protected basins (see Shepard and others 2005 for an example). In the worst case, if barriers on the large populations are breached by human or natural agents and invasions proceed quickly, fish from the smaller replicate populations can be used to refound them.

Epilogue: What do We Need to Know?

Conserving native salmonids at risk from invasions in the western U.S. is a widespread, long-term, and expensive problem, so investment in better information to improve decisions is likely to pay off. In developing this synthesis we found important uncertainties about the key processes that drive the tradeoff between invasion and isolation. These often emerged as differences in opinion among the authors and among reviewers, based on their data and experience in different regions and with different species and subspecies of salmonids. From these discussions, we found three main questions in need of research to inform better management:

- *What are rules of thumb for stream length or watershed area needed to sustain different salmonid species and subspecies in isolated populations above barriers?* — It is clear that the size of the stream network can strongly affect the resilience, persistence, and viability of isolated salmonid populations. However, these effects also vary strongly with environmental conditions and the evolutionary history of species or populations. Basic field data on species occurrence and an inventory of natural and anthropogenic barriers can be used to develop models to estimate risk of extinction with time (see Section III). Rapid progress could be made by using existing data and collaborating with biologists already engaged in inventory and monitoring programs throughout the region.
- *What environmental, ecological, and evolutionary factors control where the main nonnative salmonids will invade?* — The extent and effects of nonnative invasions appear to vary substantially across the interior West. In many regions, it is not clear whether invasions are continuing or stalled, and whether the process depends on changing climate and even evolution of the species involved. Management of invasions, and the effective use of barriers and limited management resources, would benefit from a better understanding of where and how invasion and displacement is likely to progress.
- *Does life history diversity of native salmonids buffer invasion and allow coexistence? If so, how?* — Conventional wisdom and life history theory suggest that migratory forms could be more resilient and resistant to invasion than resident life history types, due to differences in demographic processes and habitat use.

However, little is known about this topic so more specific hypotheses and observations need to be developed, followed by empirical analysis and simulation.

Although some initial research has been conducted on each of these questions for specific species or environments (Dunham and Rieman 1999, Adams and others 2002, Harig and Fausch 2002), more is needed to allow accurate predictions on which to base sound management. Likewise, many other questions need to be answered for a more complete understanding of the tradeoff (see Dunham and others 2002a, Peterson and Fausch 2003b, Dunham and others 2004) and the feasibility of different management options. In addition, a careful monitoring program followed by widespread reporting of the results would rapidly advance our understanding of the need for, and effects of, barriers used to manage populations of native trout throughout the western U.S

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