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Invasion versus Isolation: Trade-Offs in Managing Native Salmonids with Barriers to Upstream Movement

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Abstract: *Conservation biologists often face the trade-off that increasing connectivity in fragmented landscapes to reduce extinction risk of native species can foster invasion by non-native species that enter via the corridors created, which can then increase extinction risk. This dilemma is acute for stream fishes, especially native salmonids, because their populations are frequently relegated to fragments of headwater habitat threatened by invasion from downstream by 3 cosmopolitan non-native salmonids. Managers often block these upstream invasions with movement barriers, but isolation of native salmonids in small headwater streams can increase the threat of local extinction. We propose a conceptual framework to address this worldwide problem that focuses on 4 main questions. First, are populations of conservation value present (considering evolutionary legacies, ecological functions, and socioeconomic benefits as distinct values)? Second, are populations vulnerable to invasion and displacement by non-native salmonids? Third, would these populations be threatened with local extinction if isolated with barriers? And, fourth, how should management be prioritized among multiple populations? We also developed a conceptual model of the joint trade-off of invasion and isolation threats that considers the opportunities for managers to make strategic decisions. We illustrated use of this framework in an analysis of the invasion-isolation trade-off for native cutthroat trout (*Oncorhynchus clarkii*) in 2 contrasting basins in western North America where invasion and isolation are either present and strong or farther away and apparently weak. These cases demonstrate that decisions to install or remove barriers to conserve native salmonids are often complex and depend on conservation values, environmental context (which influences the threat of invasion and isolation), and additional socioeconomic factors. Explicit analysis with tools such as those we propose can help managers make sound decisions in such complex circumstances.*

Keywords: biological invasions, corridors, habitat fragmentation, isolation, salmonids, stream fish

Invasión versus Aislamiento: Pros y Contras del Manejo de Salmónidos con Barreras al Movimiento Río Arriba

Resumen: *Los biólogos de la conservación a menudo enfrentan el hecho de que el incremento de la conectividad en paisajes fragmentados para reducir el riesgo de extinción de especies nativas puede fomentar la invasión de especies no nativas que entran vía los corredores creados, lo cual también incrementa el*

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riesgo de extinción. Este dilema es agudo para peces de arroyo, especialmente salmónidos nativos, porque sus poblaciones frecuentemente son relegadas a fragmentos de hábitat amenazado por invasión desde río debajo de tres salmónidos no nativos cosmopolitas. Los manejadores a menudo bloquean estas invasiones con barreras, pero el aislamiento de salmónidos nativos en arroyos pequeños puede incrementar el riesgo de extinción local. Proponemos un marco conceptual para abordar este problema mundial que enfoca cuatro preguntas principales. Primera, ¿hay presencia de especies de valor para la conservación (considerando legados evolutivos, funciones ecológicas y beneficios socioeconómicos como valores distintos)? Segunda, ¿las poblaciones son vulnerables a la invasión y desplazamiento por salmónidos no nativos? Tercera, ¿estarían amenazadas de extinción local estas poblaciones sí se aíslan con barreras? Y, cuarta, ¿cómo debe priorizarse el manejo entre múltiples poblaciones? También desarrollamos un modelo conceptual de los pros y contras de las amenazas de invasión y aislamiento que considera las oportunidades para que los manejadores tomen decisiones estratégicas. Ilustramos el uso de este marco en un análisis de la compensación invasión-aislamiento del salmón nativo Oncorhynchus clarkii *en dos cuencas contrastantes en el occidente de América del Norte donde la invasión y el aislamiento están presentes y fuertes o lejanos y aparentemente débiles. Estos casos demuestran que las decisiones de instalar o remover barreras para conservar salmónidos nativos a menudo son complejas y dependen de valores de conservación, contexto ambiental (que influye en la amenaza de invasión y de aislamiento) y factores socioeconómicos. El análisis explícito con herramientas como las que proponemos puede ayudar a que los manejadores tomen decisiones sensatas en circunstancias tan complejas.*

Palabras Clave: aislamiento, corredores, fragmentación de hábitat, invasiones biológicas, peces de arroyo, salmónidos

Introduction

It is now well known that habitat destruction and biological invasions are the leading causes of species decline and loss worldwide (Vitousek et al. 1997; Dirzo & Raven 2003). When confronted by both problems, conservation biologists often face the trade-off that managing ecosystems to address one problem precludes solving the other. Human enterprise has fragmented habitats, isolating populations and increasing their risk of extinction (Caughley 1994), so some researchers have proposed connecting habitat fragments with corridors to restore function and ameliorate these effects (Beier & Noss 1998; Dobson et al. 1999). Nevertheless, others argue that enhancing connectivity increases invasions by non-native species and diseases, which also increase extinction risk, and opt for isolating habitats instead (Simberloff et al. 1992; Hess 1994). Although conservation biologists acknowledge this trade-off as an important issue, it has not been widely discussed, and there are few well-documented cases or proposed solutions, even in the burgeoning literature on landscape connectivity (Bennett 1999; Crooks & Sanjayan 2006).

One group for which this invasion-isolation trade-off is acute is stream biota, because both native organisms and non-native invaders can access habitat only through the stream corridor, not through the terrestrial matrix. This feature makes habitat in dendritic stream systems highly prone to fragmentation (Fagan 2002). For example, movements or migrations of native fishes and other native aquatic biota to use complementary habitats or recolonize segments where populations have been lost can be stopped by a single dam, diversion, or impassible culvert (Fausch et al. 2002). Nevertheless, managers may also consider retaining or constructing such barriers to prevent invasion from downstream by non-natives. Hence, biologists face a clear trade-off because the barriers designed to protect native populations from invasions may also hasten their extinction by creating small populations isolated in habitat fragments (Novinger & Rahel 2003; Fausch et al. 2006). This dilemma will become more prevalent globally as barriers are constructed to limit the spread of non-native fishes, amphibians, and associated parasites and diseases.

Although the literature contains examples of the consequences of invasions and isolation for other fishes (Smith & Jones 2005), the problem has been studied most for salmonids (e.g., trout and charr). Native salmonids have declined throughout the world due to habitat loss, invasions, and overfishing (Behnke 2002), and are increasingly relegated to small pieces of their native ranges in protected headwater streams (e.g., Shepard et al. 2005). Ironically, 3 salmonid species—rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*), and brown trout (*Salmo trutta*)—are among the most widely introduced fishes worldwide (Fausch et al. 2001; Cambray 2003; Kitano 2004). These now cosmopolitan species often invade upstream and displace native salmonids and other biota from these protected habitats, resulting in calls for "isolation management" to conserve native species (Dunham et al. 2004; Fausch et al. 2006).

We reviewed this problem for native stream salmonids and propose a framework for decisions about installing or removing barriers to conserve these fishes. We first define the problem, and then outline 4 questions to guide analysis of the trade-off. We also develop a simple conceptual model of opportunities for strategic decisions given the joint trade-off of invasion and isolation threats.

We then illustrate use of the framework by applying it to contrasting examples for native cutthroat trout (*O. clarkii*) in the western United States.

A Widespread Problem

Managers of salmonids and their habitats throughout the world are often faced with the invasion-isolation trade-off. For example, native brook trout from New England to the southern Appalachian Mountains (U.S.A.) are restricted to headwater streams that are fragmented by dams and degraded by human development (Hudy et al. 2004). These same watersheds have been invaded by non-native rainbow and brown trout that displace brook trout from downstream habitats (Larson & Moore 1985; Fausch 2008). In Japan many populations of native charr (*Salvelinus* spp.) are isolated in headwater streams highly fragmented by erosion-control dams (Morita & Yamamoto 2002), whereas downstream populations are being displaced by non-native rainbow and brown trout (Morita et al. 2004). Similar circumstances confront native brown trout in Switzerland (Peter et al. 1998) and native stream fishes throughout the Southern Hemisphere (e.g., Cambray 2003; McDowall 2006).

This invasion-isolation dilemma is especially acute for native salmonids in inland western North America, including cutthroat trout, bull trout (*Salvelinus confluentus*), and some subspecies of rainbow trout. Extensive water development, mining, logging, grazing, and overfishing have fragmented many populations and restricted them to headwater streams (Young 1995). For example, there are an estimated 77,000 "large" dams (those $\geq$2 m high that store $\geq$62,000 m^3 of water; U.S. Army Corps of Engineers 2006) in the conterminous United States, and countless impassable smaller dams, diversions, and road culverts in the region. Many of the remnant native salmonid populations have been invaded by non-native trout that exclude, or hybridize with, the natives (Behnke 1992; Dunham et al. 2002). This has led managers to consider either more barriers to block invasions or converting temporary barriers, such as impassable culverts, into permanent structures.

A Framework for Analyzing Trade-Offs

Biologists charged with conserving native salmonids often disagree over the relative merits of building new barriers to limit upstream invasions versus removing barriers to allow recolonization, demographic support, or movement to complementary habitats to enhance population persistence (Shepard et al. 2005; Peterson et al. 2008). This is primarily because the outcomes of invasion and isolation differ among locations and among populations of non-native and native salmonids, probably because of differences in evolutionary history, habitat and other abiotic factors, and time since isolation. For example, fisheries biologists charged with conserving westslope cutthroat trout (*O. c. lewisi*) east of the Continental Divide in Montana (U.S.A.) argue strongly for isolating these populations with barriers because of concerns about invasion by brook and rainbow trout, whereas biologists west of the Continental Divide argue as strongly for removing barriers to restore connectivity because of concerns about the importance of movement for population persistence. Biologists in different regions or different agencies have tended to focus on only one strategy, leaving new biologists and administrators who lack direct experience confused about how to proceed. Therefore, we developed a conceptual framework to analyze the trade-off, based on 4 key questions: (1) Is a native salmonid population of important conservation value present? (2) Is the population threatened by invasion and displacement by non-native salmonids? (3) Would this population be threatened with local extinction if isolated? (4) How does one prioritize among several populations of conservation value?

Conservation Value

Considering the trade-offs of managing trout invasions with barriers involves a form of risk assessment (Francis & Shotton 1997). Risk includes both the probability of an undesirable event associated with a threat (e.g., local extinction caused by invasion) and the conservation "value" that would be lost. If there is little value, there is little risk. Therefore, the first step is to consider whether the stream of interest supports a native salmonid population of important conservation value. The elements of conservation value can be complex (Noss 1990; Young 2000; Groves 2003), but we suggest that 3 general types emerge (e.g., Angermeier et al. 1993): evolutionary, ecological, and socioeconomic. Evolutionary values encompass the traditional goals of conservation biology and focus on the elements of biological diversity including native species, phenotypes, and genes (Young 2000). For example, the U.S. Endangered Species Act (ESA) protects "evolutionarily significant units" and "distinct population segments" of listed species that represent adaptation to unique and varied environments (Waples 1995; McElhaney et al. 2000). The value of these populations increases as they become rare and decreases as diversity is lost through restricted expression of life histories, genetic bottlenecks, or hybridization and introgression (e.g., Allendorf et al. 1997).

Ecological values focus on ecological patterns, processes, and functions at the population, community, or ecosystem levels and have become an important focus of restoration ecology (Young 2000; Noss et al. 2006). These values can be distinct from evolutionary values (Callicott 1995), and many have been recognized only recently. Examples of important ecological processes include dispersal of salmonids in metapopulations, which allows persistence despite disturbance or changing environments (Rieman & Clayton 1997), and translocation of nutrients and energy upstream and into adjacent terrestrial ecosystems by migratory fishes and their predators (Willson & Halupka 1995; Koel et al. 2005). Populations that provide these important ecosystem services, and are resilient and self-sustaining with minimal management, embody more ecological values than those that are vulnerable to extinction or that threaten the persistence of other important communities or ecosystems (Fausch et al. 2006).

Socioeconomic values include other ecosystem services, such as commercial and sport fishing or tourism from wildlife viewing. These values are the most obvious to the public and often influence budgets and priorities of management agencies. Nevertheless, Tear et al. (2005) argue that to avoid subverting conservation to political expediency, conservation objectives should not be dictated strictly by socioeconomic values. Indeed, native salmonid populations also have intrinsic values (Callicott 2006), which are partly embedded in the 3 values described above. Moreover, biologists should recognize that decisions to use barriers to manage fishes vulnerable to invasion may be influenced by a broad range of societal interests beyond conservation and restoration (Wilhere 2008).

Conservation of all 3 values simultaneously may be possible in some large wilderness river networks, such as those in Idaho, Montana, and Alaska (U.S.A.), because most trout populations may support all 3 values (Fig. 1). In systems disrupted by habitat degradation and non-native species invasions, however, only a few populations of native trout in remnant wilderness can retain all three values. Genetically pure trout populations isolated in small headwater fragments conserve primarily evolutionary values, but may have limited ecological functions. Conversely, hybrid trout and wild non-native trout may retain significant ecological and socioeconomic values, but have limited or no evolutionary value. Put-and-take hatchery trout provide only socioeconomic values. Other values are possible (e.g., isolated pure trout may also have socioeconomic values), but disrupted systems have much less potential to support all values simultaneously than natural systems.

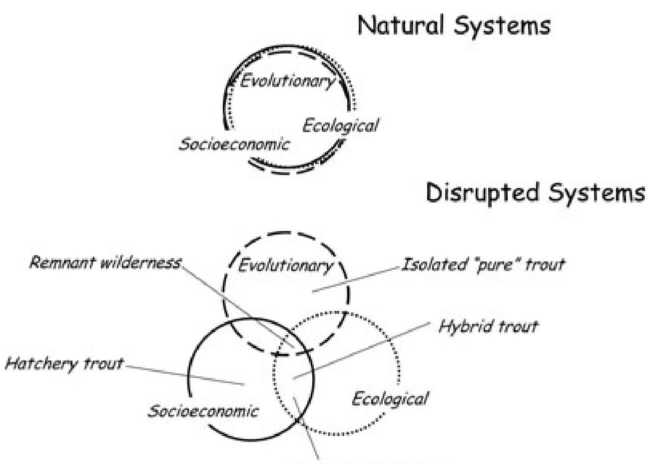

Figure 1. A Venn diagram showing relationships among fish populations that embody different conservation values in natural versus disrupted ecosystems (after Fausch et al. 2006). Circles represent all populations with significant evolutionary, ecological, or socioeconomic values.

As a specific example, main-stem river populations of cutthroat trout may have hybridized with non-native rainbow trout and be introgressed, reducing their evolutionary value (Allendorf et al. 2001). Nevertheless, these populations may still include large migratory fish that fulfill ecological functions, such as translocating nutrients and feeding eagles and bears (Koel et al. 2005), and provide substantial socioeconomic value because they are highly prized by anglers. In contrast, small populations of small native cutthroat trout isolated above barriers in headwater streams may have important evolutionary values but currently express little of the other 2 values. Therefore, conservation biologists often will need to define what sets of values to conserve in which locations and select those of highest value for analysis of the invasion-isolation trade-off.

Threat of Invasion and Displacement

For each native salmonid population of conservation value selected for analysis, the next question is whether it is vulnerable to invasion and displacement by non-native salmonids. The invasion process can be divided into 4 main steps: transport, establishment, spread, and impacts (Kolar & Lodge 2001). We consider transport and spread together because they have the same effect of bringing non-natives in contact with natives.

Transport of non-native species depends on human interest in them for angling or food and the distances from source populations (Fausch et al. 2006). Management agencies now evaluate stocking more carefully (Rahel 1997), but unauthorized introductions by the public are burgeoning. Rahel (2004) calculated that unauthorized introductions in 7 U.S. regions accounted for 90% of new introductions during 1981–1999, but only 15–43% during all previous periods. Populations of non-natives just downstream from barriers, or easily accessed by roads, provide source populations, and disgruntled anglers may translocate non-natives back to their favorite fishing sites after removals (Dunham et al. 2004). Once established, non-native salmonids often quickly spread upstream throughout watersheds because they can have high population growth rates and move long distances, which fosters invasions via jump dispersal (Peterson & Fausch 2003). Waterfalls and high-gradient reaches can hamper upstream invasions, but stocking non-natives in headwater lakes allows them to spread downstream throughout large watersheds (Adams et al. 2001).

Establishment of non-native salmonids can be influenced by environmental resistance, biotic resistance, and repeated introductions (Moyle & Light 1996). Invasions are often limited mainly by abiotic factors that provide environmental resistance, such as temperature, flow regime, stream size, and habitat factors correlated with stream gradient (Fausch et al. 2006). For example, Fausch et al. (2001) report that rainbow trout establishment in several Holarctic regions is most successful where flooding regimes match those in their native range. In some cases, non-natives may establish because they are better adapted, by chance, to abiotic conditions such as flooding regimes than the natives because of their respective evolutionary histories (Fausch 2008). Nevertheless, biotic resistance from native pathogens can also hamper establishment by non-native salmonids (Fausch 2007). A main predictor of establishment for various organisms is propagule pressure, which is the number and frequency of non-natives released. Propagule pressure for the widely introduced rainbow trout may be among the highest for any vertebrate (Fausch 2007).

Impacts from displacement of native salmonids by non-natives are common (Dunham et al. 2002; Peterson et al. 2004), probably because the species are similar and biotic interactions like competition and predation can be intense in these simple assemblages. In other cases, however, the invasion may stall or the species may coexist (Shepard 2004; Rieman et al. 2006), most likely because of abiotic factors that hamper demographic rates, such as low temperatures that reduce growth and fecundity (Adams 1999; Benjamin et al. 2007). Finally, non-natives may also hybridize with natives or transmit diseases or parasites throughout watersheds, both of which are usually irreversible. Nevertheless, both effects can be modified by local abiotic factors and so remain difficult to predict (Hitt et al. 2003; Weigel et al. 2003). In summary, whether non-native salmonids successfully invade and displace native salmonids depends strongly on environmental context, so specific information about abiotic environments and the evolutionary history of native salmonids often will be needed to make accurate predictions.

Threat of Extinction if Isolated

If the population of interest is at risk of invasion and displacement, then managers may consider the intentional use of barriers to isolate it. Barriers can pose problems for salmonids because individuals often move among complementary habitats required for breeding, rearing, feeding, and refuge from harsh conditions (Schlosser & Angermeier 1995). Isolation by barriers also disrupts gene flow among populations (Neville et al. 2006). Barriers may select against migratory behavior (Morita et al. 2000), which can include partial migration in which only a portion of the population migrates (Hendry et al. 2004). Nevertheless, there is also evidence that migratory life histories can be re-expressed given the opportunity (Pascual et al. 2001).

The consequences of isolation may include increased risk of extinction due to genetic effects or the stochastic demography of small populations, reduced resilience due to loss of migratory life histories, and the loss of recolonization, demographic support, or dispersal among populations (Rieman & Dunham 2000; Rieman & Allendorf 2001; Letcher et al. 2007). Studies of local populations upstream of movement barriers in Japan and the western United States provide empirical evidence of the negative effects of isolation on persistence and genetic diversity (e.g., Harig & Fausch 2002; Morita & Yamamoto 2002; Neville et al. 2006). Watershed areas predicted to ensure high probability of persistence for 50 years vary widely, however, probably due to climate, geology, and species characteristics. In addition, population models (e.g., Morita & Yokota 2002; Letcher et al. 2007), have extended a general theoretical understanding of the effects of fragmentation to salmonids.

One of the most important theoretical and empirical predictors of persistence following isolation has been the length of the resulting stream network, rather than simply watershed area. For example, Young et al. (2005) used extensive surveys of cutthroat trout density in long segments of Colorado and Wyoming (U.S.A.) streams to calculate that about 10 km of stream are needed to sustain an effective population size of 500 fish. This threshold is thought sufficient to maintain long-term evolutionary potential (Allendorf et al. 1997) rather than simply short-term persistence. These larger networks may include not only greater population size, but also more internal complexity and diversity of habitats, which reduces vulnerability to catastrophic events (Fausch et al. 2006).

Priorities among Multiple Populations

So far, we have addressed the invasion-isolation trade-off for individual streams and local populations, but biologists must often consider multiple populations distributed throughout watersheds that represent different opportunities and competing objectives. Different stakeholders may hold different values, so managers need to define which values they hope to conserve and where. These priorities are important because constructing or removing barriers is expensive and logistically difficult. Reconciliation can be challenging, but spatially extensive analyses may allow managers to satisfy different objectives simultaneously (Noss et al. 2006). Native salmonids often occur as local populations in patches of suitable habitat nested within larger patch networks, subwatersheds, and regions (Rieman & Dunham 2000). Thus, the final step in our framework is for managers to consider all populations of sufficient conservation value collectively, how they interact via movements and migration, and the factors that threaten them. Our process follows from the general concepts of conservation planning.

Conservation planning involves decisions on the number, distribution, and characteristics of populations to conserve, along with the actions required to mitigate threats (e.g., installing or removing barriers). Common guidelines for prioritization include representation, redundancy, resilience (i.e., the "3 Rs"; McElhany et al. 2000; Groves 2003; Tear et al. 2005), and feasibility. Representation traditionally refers to selecting populations that include the full range of ecological and evolutionary diversity within a region, including unique alleles, life-history types, and species assemblages (Allendorf et al. 1997). Here it also includes representation of values deemed important by managers and the public. A reserve-design algorithm may help optimize this selection on the basis of multiple criteria (Ruckelshaus et al. 2003). Managers often lack detailed information for such analyses, so they may seek instead to conserve diverse habitats that support the expression of distinct life histories (Beechie et al. 2006; McGrath et al. 2009), evolutionary legacies (Allendorf et al. 1997), or key production areas for important fisheries.

Redundancy is important because no local population is immune to extinction. Accordingly, it is prudent to conserve multiple populations to minimize the chance that all will be lost simultaneously and to provide a source for recolonization if some are lost. One strategy is to select widely distributed populations to minimize vulnerability to the same disturbance (Good et al. 2008).

Resilience refers to populations that persist despite natural or human-caused disturbance or environmental change (Gunderson 2000). Small populations or those in habitats that are degraded or prone to catastrophic disturbance are less likely to persist than large populations or those in productive, complex habitats with adequate refugia. Migratory individuals can also contribute to resilience through increased fecundity and high population growth rates.

Feasibility means conservation actions should be cost effective, sustainable, and socially and environmentally acceptable. Constructing barriers, or removing them by replacing impassible road culverts, is costly. Therefore, projects that provide the greatest benefits for the least cost will be favored, if all else is equal. Similarly, eradication or control of non-native salmonids is expensive and not always successful (Meyer et al. 2006*a*), so each project should be carefully evaluated (Peterson et al. 2009). Moreover, barriers to non-natives also block other aquatic organisms that may need to move to persist and maintain productive aquatic and riparian communities (Willson & Halupka 1995), so these ecological services also must be considered.

Conceptual Model of the Trade-off

Based on the framework above, the logical conclusion in some cases may be to isolate native salmonid populations because the invasion threat is imminent and the effects strong. In others, the decision may be to reconnect populations because the invasion is far away or the effects are weak. Here we combine considerations about the degree of invasion threat with those for the degree of isolation to propose a conceptual model that allows biologists to consider the joint trade-off for their particular basin and set of salmonid populations of conservation value (Fausch et al. 2006). This model can help biologists understand where their populations lie in the trade-off space, and why other biologists in other regions with populations that lie elsewhere in the space may have different management priorities. Most importantly, it is intended to help managers consider their available options, make strategic decisions, and justify these to stakeholders.

The trade-off space is defined by two axes, the degree of invasion threat and the degree of isolation (Fig. 2). If most native salmonid populations in a given basin are remnants in headwater habitats and invaders are advancing upstream rapidly and displacing them (Fig. 2, upper left), the main focus of management will be to intentionally isolate populations above barriers to protect them and to translocate these populations in other patches to replicate them. For managers in this situation, strategic decisions for conserving the remaining evolutionary legacy involve optimizing the number, size, and spatial distribution of patches to buffer against local extinctions and correlated catastrophic disturbances (Rieman & McIntyre 1993). Other strategic decisions include removing or controlling invaders, and restoring habitat quality to enhance population resilience.

At the opposite end of the spectrum, if native trout occupy a large stream network of interconnected habitats and the invasion threat is distant or invader effects are weak (Fig. 2, lower right), then options include preventing invasions at their source, preventing fish movement barriers and management activities that fragment habitat, monitoring the spread of non-natives and habitat degradation, and maximizing the opportunity for natural ecological processes to create and maintain habitat. For example, managers could minimize sources of non-native fishes (e.g., streamside ponds) for unauthorized or accidental introductions and vectors such as roads that foster introductions (Trombulak & Frissell 2000).

Other circumstances will require different strategies. Some basins are under little threat from invasion or the effects are weak because the native salmonids resist invasion, but the habitat is fragmented by many barriers

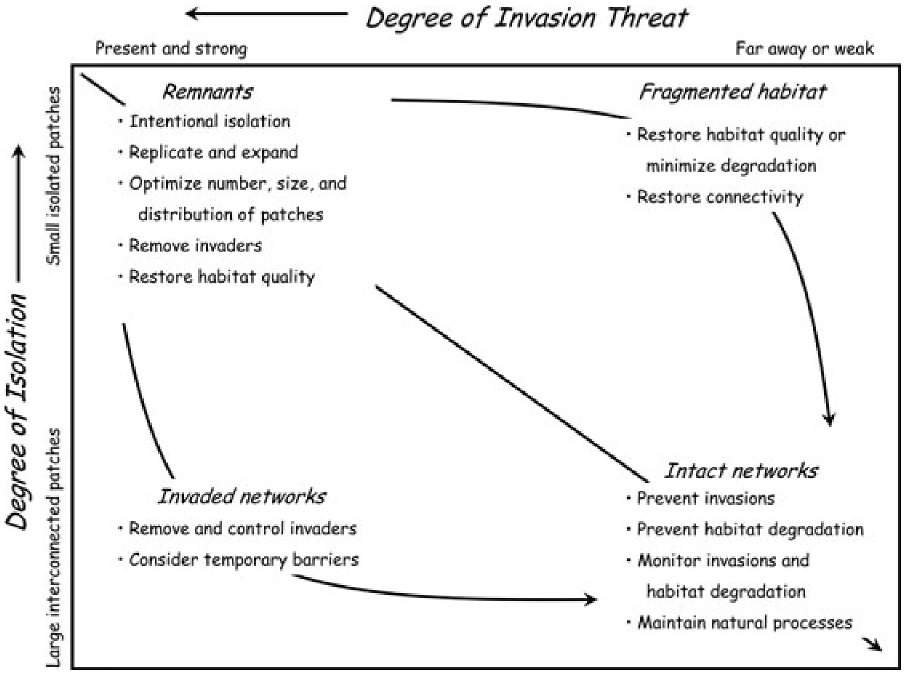

Figure 2. A conceptual model of the opportunities for strategic decisions when managing the joint invasion-isolation trade-off for native salmonid populations of conservation value (after Fausch et al. 2006). Examples of strategic decisions to maximize conservation of remaining populations under different degrees of invasion and isolation threat are shown. Arrows pointing toward the lower right show the overall goal of management, which is to conserve interconnected populations in stream networks free of invaders.

that restrict movement (Fig. 2; upper right). Here, strategic decisions include restoring habitat quality in the small patches to minimize local extinctions, and removing barriers or providing fish passage to restore connectivity and ecological function, perhaps by allowing large spawning fish to migrate into tributaries. In contrast, other basins may have large networks of relatively intact habitat, but non-native trout have invaded and are widespread (Fig. 2, lower left). Strategic decisions here involve prioritizing subbasins for the difficult task of removing non-native trout, which may require constructing temporary barriers and working successively downstream. Therefore, within this trade-off space the overall goal should be to move toward the lower-right corner, where interconnected populations can function and evolve in intact stream networks free of invaders, and to keep from being pushed into the upper-left corner, where only a few small populations remain in habitat fragments at risk of invasion and options for managing them are limited.

Unauthorized introductions above barriers require other strategic decisions not considered in this trade-off space. If native populations are restricted to many small patches above barriers (Fig. 2, upper left), managers could construct several barriers spaced near the downstream end of the most accessible ones and monitor these buffer zones to guard against invasions, but the original stream fragments are usually too short to justify other measures. In contrast, in large remote basins with intact habitat (Fig. 2, lower right), it would be strategic to place barriers in inaccessible locations some distance upstream from access points to minimize unauthorized introductions.

Although each combination of threats from isolation and invasion favors particular actions, managers may select a mixed strategy to hedge against uncertainty. For example, many cutthroat trout subspecies consist of multiple small populations isolated above barriers to prevent invasion, each at relatively high risk of extinction from stochastic environmental factors (e.g., Hirsch et al. 2006; Meyer et al. 2006*b*). The current management strategy is to find and conserve these many small populations, translocate fish to found new populations or restore those lost to local extinctions, and simultaneously work to develop networks of interconnected metapopulations in larger basins that are remote or protected. In the worst case, if downstream barriers that protect these metapopulations from invasions are breached and invasions proceed quickly, fish from the smaller replicate populations can be used to refound them.

Two Examples

We used examples from 2 different subspecies of cutthroat trout in 2 different geographic regions to illustrate analyses based on our framework and opportunities for strategic decisions for contrasting cases in different portions of the trade-off space. Each example included constraints that make addressing the invasion-isolation dilemma challenging.

Colorado River Cutthroat Trout in the Little Snake River

Colorado River cutthroat trout (*O. c. pleuriticus*) occupy only about 13% of their historical range, occurring primarily in small isolated populations above barriers that prevent invasions of non-native brook and rainbow trout (Hirsch et al. 2006). One basin with substantial high-quality habitat is the Little Snake River in southern Wyoming and northwestern Colorado (Fig. 3). Here, the goal of management has been to retain evolutionary values because Colorado River cutthroat trout are the focus of a long-term multistate conservation effort to prevent listing under the ESA. In this basin Colorado River cutthroat trout have been reduced to 15–20 remnant populations occupying 160–190 km of up to 38 streams (Young et al. 1996; Hirsch et al. 2006). In many cases occupied stream segments are fragmented by natural or artificial barriers or the true distribution of cutthroat trout is incompletely known. Several populations are introgressed with rainbow trout or Yellowstone cutthroat trout (*O. c. bouvieri*), but others remain pure. Loss of migratory fish that probably once inhabited the main-stem rivers has eliminated important ecological values. Socioeconomic values are also low because angling for cutthroat is incidental given the scattered populations, difficult access, small size of adult fish, and regulations prohibiting or limiting harvest.

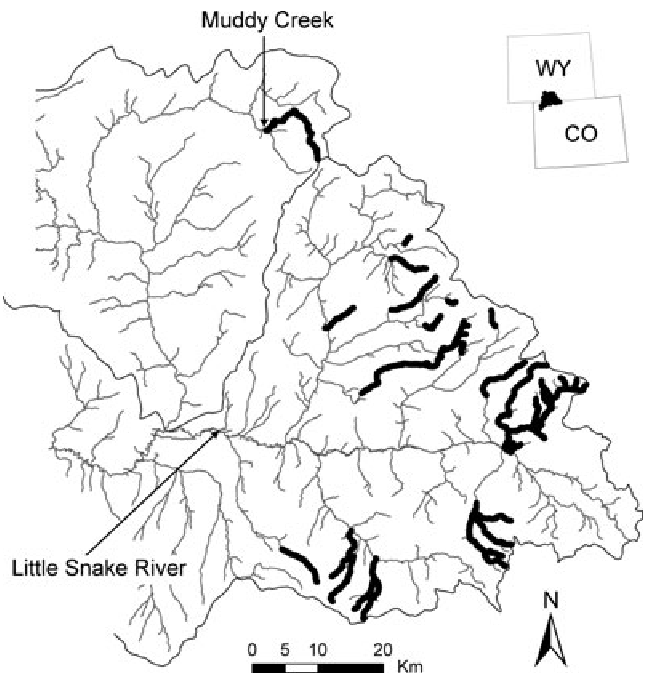

Figure 3. Headwaters of the Little Snake River and Muddy Creek in Colorado and Wyoming showing current estimated distribution of Colorado River cutthroat trout populations (thick black line; after Hirsch et al. 2006; Fausch et al. 2006). Arrows from stream names point to estimated original downstream limits of native trout before invasions by non-native trout.

Cutthroat trout populations in the basin are subject to a high degree of threat from both invasion and isolation. Many headwater tributaries in Wyoming are disrupted by transbasin water diversions, several of which fragment once-contiguous populations of cutthroat trout. Nevertheless, these and other artificial or natural barriers also block invasions of non-native salmonids that were first introduced in the 1930s and now occupy most of the basin. Only 4 cutthroat trout populations occupy >10 km of connected habitat and probably contain enough individuals to afford security against long-term loss of genetic variation (Young et al. 2005). Most others inhabit isolated stream segments <3 km long and consist of a few hundred fish, placing them at risk of extirpation from environmental disturbances.

Given these constraints, this example falls primarily within the upper left corner of the trade-off space (Fig. 2), where strategic decisions involve selecting the best patches available for conserving isolated populations. Genetic structure is unknown, so the priority has been to conserve as many remnant populations as possible to maximize redundancy and representation of any remaining biodiversity. Maintaining a broad distribution of populations throughout the basin would also minimize the threat of simultaneous extinction. Persistence of existing populations is being enhanced by extending their distribution downstream, which involves building or modifying barriers and using chemical treatments or repeated intensive electrofishing to remove non-native species. Additional priorities include restoring connectivity by providing fish passage around water diversions, and extending cutthroat trout distribution downstream to connect adjacent fragments and reduce local extinction risk. Although our framework would not likely alter most current management priorities, the trade-off space does allow managers to justify isolation management, maintenance of a broad distribution of remnant populations, and future expansion of the network downstream.

Westslope Cutthroat Trout in the Upper Coeur d'Alene River

In contrast to the restricted distribution of Colorado River cutthroat trout, westslope cutthroat trout persist in about 59% of their native range, including large interconnected wilderness basins in the northern Rocky Mountains (Shepard et al. 2005). Nevertheless, in many basins non-native invasions and habitat fragmentation pose important threats. One such basin is the North Fork Coeur d'Alene River in northern Idaho (Fig. 4), where mining, stream dredging, clearcut logging and log drives, extensive road building, and overfishing have degraded habitats and depressed fish populations.

Ecological and socioeconomic conservation values are the primary focus of cutthroat trout management in the basin. Local populations and natal habitat for cutthroat trout are found in small to moderate sized tributary

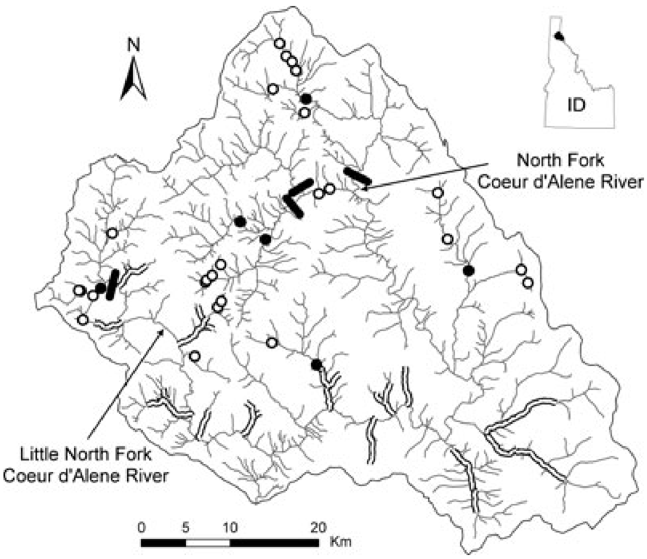

Figure 4. Headwaters of the North Fork Coeur d'Alene River, Idaho, showing opportunities to install or remove barriers to conserve native westslope cutthroat trout (after Fausch et al. 2006). Outlined segments show where non-native brook trout have become established. Thick black bars show where large barriers might be used to prevent upstream invasion by brook trout and rainbow x cutthroat trout hybrids (which occur in the lower main-stem rivers). Filled circles show culverts that could be converted to permanent barriers to conserve a broadly distributed representation of genetically pure native cutthroat trout in headwater segments, although 4 would not be needed if large barriers were installed. Open circles show culverts that could be removed to expand isolated networks or to restore connectivity for ecological and socioeconomic values linked to migratory fish.

streams, but generally not in the main-stem rivers. Large migratory fish that spawn in tributaries support an important sport fishery in the main-stem rivers, but most populations are heavily introgressed with rainbow trout that became established 30–60 years ago. Evolutionary values are less important to residents and managers, but will be conserved if they do not compromise important fisheries.

Cutthroat trout in this basin are subject to moderate but uncertain degrees of threat from both invasion and isolation. Nonnative brook trout are well established in some lower tributaries, but remain patchily distributed, despite having been established >60 years (Fig. 4). The basin is vulnerable to winter rain-on-snow floods from maritime storms, which may hamper brook trout invasions because their eggs incubate in streambed gravel through winter (Dunham et al. 2002; Fausch 2008), unlike spring-spawning cutthroat and rainbow trout. Genetically pure cutthroat trout still persist in the upper basin and in small resident populations above impassable road culverts in some lower tributaries.

Different cutthroat trout populations in this example fall in several regions of the trade-off space, so a mix of strategies will be required to conserve a range of values and hedge against uncertainty regarding future invasions. Large barriers could conserve substantial portions all 3 values simultaneously if they isolated relatively large upstream networks of river main stem and tributaries where pure populations and migratory life histories still persist (Fig. 4). It is uncertain, however, whether the large, low-head dams needed would be feasible, given their expense and their potential to disrupt fish movements important to a trophy fishery, as well as movements of other aquatic biota. Other alternatives include the strategic placement of barriers to conserve representative pure populations in smaller networks of headwater tributaries and removal of culverts that create barriers to provide access to migratory (though likely hybridized) populations that support a productive fishery and important ecological functions. Culverts far upstream would be lower priorities for removal because limited habitat would be gained above them. Because genetic inventories are lacking, populations selected for conservation should be widely distributed to represent both a range of environments and as much genetic, phenotypic, and ecological diversity as possible. Initially, biologists from 2 agencies that manage these habitats and fisheries tended to disagree about the use of barriers. Our framework helped focus discussion that clarified values each hoped to conserve, and provided an objective process to prioritize management of native fish populations and invasions across the basin rather than focusing on individual streams.

Conclusion

In our experience isolation management of native salmonids with barriers has been largely subjective. Often the trade-offs are relatively clear to biologists with experience in a particular region, and they focus on one action, but in a different region biologists consider different trade-offs and select an alternative action. Other biologists with limited experience may base decisions on personal philosophy or simply what has worked elsewhere. When these different decisions cannot be clearly articulated and supported, the process appears inconsistent to the public or administrators controlling funding, and becomes contentious. Our goal is to provide a framework and conceptual model that can improve communication and generate more objective decisions. With appropriate information, the process can be quantified further. In Peterson et al. (2008) we developed a Bayesian belief network (BBN) that formalizes the framework and provides an objective evaluation of the alternatives for 2 well-studied species, native westslope cutthroat trout and invading brook trout. That work could easily be extended to other well-studied salmonid species and ecosystems.

Our approach is also likely to be applicable elsewhere. Biologists face invasion-isolation trade-offs in many ecosystems, terrestrial and aquatic, due to increases in both non-native invasions and habitat fragmentation. For example, in terrestrial ecosystems along the southern California coast, patches of native coastal scrub embedded in the suburban matrix provide important habitat for communities of mammals, birds, reptiles, and invertebrates that interact in closely connected food webs (Crooks & Soule 1999). Analysis of extinction risk, based on patch size and isolation, has been the focus of several studies aimed at reserve design (e.g., Bolger et al. 1997; Crooks et al. 2001). Creating corridors and narrow gaps across the suburban matrix that promote movements by native species may prevent local extinctions, but also allows non-native red fox (*Vulpes vulpes*) to invade (Lewis et al. 1993). The fox can have strong predation effects on rare species, creating an invasion-isolation trade-off similar to the one we describe for stream salmonids. Moreover, the corridors also allowed October 2007 wildfires to spread more quickly among houses, raising controversy over their ecological importance (K. Crooks, personal communication). As habitats become increasingly fragmented and species become dependent on movement through narrow corridors for population persistence, these trade-offs will become more critical. Thus, explicit analyses with frameworks and tools such as those we applied to stream salmonids will become increasingly important as human pressures conflict with conservation values.

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