North American Journal of Fisheries Management
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujfm20

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Published online: 30 Jan 2014.

To cite this article: Joseph H. Anderson, George R. Pess, Richard W. Carmichael, Michael J. Ford, Thomas D. Cooney, Casey M. Baldwin & Michelle M. McClure (2014) Planning Pacific Salmon and Steelhead Reintroductions Aimed at Long-Term Viability and Recovery, North American Journal of Fisheries Management, 34:1, 72-93

To link to this article: http://dx.doi.org/10.1080/02755947.2013.847875

North American Journal of Fisheries Management 34:72–93, 2014

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1080/02755947.2013.847875

ARTICLE

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Abstract
Local extirpations of Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss*, often due to dams and other stream barriers, are common throughout the western United States. Reestablishing salmonid populations in areas they historically occupied has substantial potential to assist conservation efforts, but best practices for reintroduction are not well established. In this paper, we present a framework for planning reintroductions designed to promote the recovery of salmonids listed under the Endangered Species Act. Before implementing a plan, managers should first describe the benefits, risks, and constraints of a proposed reintroduction. We define benefits as specific biological improvements towards recovery objectives. Risks are the potential negative outcomes of reintroductions that could worsen conservation status rather than improve it. Constraints are biological factors that will determine whether the reintroduction successfully establishes a self-sustaining population. We provide guidance for selecting a recolonization strategy (natural colonization, transplanting, or hatchery releases), a source population, and a method for providing passage that will maximize the probability of conservation benefit while minimizing risks. Monitoring is necessary to determine whether the reintroduction successfully achieved the benefits and to evaluate the impacts on nontarget

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Received September 10, 2012; accepted August 30, 2013

species or populations. Many of the benefits, especially diversity and the evolution of locally adapted population segments, are likely to accrue over decadal time scales. Thus, we view reintroduction as a long-term approach to enhancing viability. Finally, our review of published salmonid reintroduction case studies suggests that large uncertainties remain in the success of reintroduction in establishing self-sustaining populations, particularly for programs employing active methods.

Reintroducing species to areas from which they have been extirpated is a common and sometimes successful approach to conserving biodiversity. Indeed, reintroductions played a prominent role in some of the most spectacular success stories in conservation, including species that have recovered from the brink of extinction such as the Arabian oryx *Oryx leucoryx* (Spalton et al. 1999) and alpine ibex *Capra ibex ibex* (Stüwe and Nievergelt 1991). However, despite considerable cost and effort, reintroduction efforts often fail to establish self-sustaining populations (Wolf et al. 1996; Fischer and Lindenmayer 2000). A recent proliferation of reintroduction literature suggests that scientifically based management principles can improve the efficacy of these efforts (Seddon et al. 2007; Armstrong and Seddon 2008).

Conceptually, reintroductions offer an enormous potential to benefit the conservation of Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss* (anadromous Rainbow Trout). For many anadromous salmonid populations, the primary cause of local extirpation is easily identified: obstructed access to suitable spawning and rearing habitats due to dams or other stream blockages. Large barriers are responsible for extirpation from nearly 45% of the habitat historically occupied by Pacific salmon and steelhead in the western contiguous United States (McClure et al. 2008a). Numerous smaller structures, such as irrigation diversion dams and culverts, also limit access to anadromous salmonid habitat (Gibson et al. 2005). Impassable dams are only one cause of declining salmonid populations and local extirpations (NRC 1996), but they are widespread. The removal or circumvention of dams and other barriers, therefore, provides many opportunities for the reestablishment of natural populations of Pacific salmon.

Despite the potential benefits of reintroduction, regional recovery planners must grapple with a variety of challenges in selecting and implementing such projects. Which populations should be prioritized for reintroduction? What methods should be used to reintroduce anadromous salmonids? How should managers evaluate whether efforts have been successful? Although previous authors have provided general guidelines for fish reintroductions (Williams et al. 1988; Minckley 1995; George et al. 2009; Dunham et al. 2011), the unique biology and management of Pacific salmon and steelhead merit special consideration.

In this paper, we provide recommendations for planning reintroductions of anadromous salmonids, focusing primarily on Pacific salmon and steelhead. Our guidelines are intended to help resource managers design reintroduction programs that contribute to the recovery of Pacific salmon and steelhead listed under the U.S. Endangered Species Act (ESA) by establishing or expanding self-sustaining natural populations. Thus, we present recommendations couched in the terminology, scientific concepts, and broad conservation objectives guiding ongoing salmonid recovery efforts under the ESA (McElhany et al. 2000). The International Union for the Conservation of Nature (IUCN 1998) defined reintroduction as "an attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated." Using this broad definition, we consider a suite of management approaches to reintroduction, including passive strategies, such as barrier removal followed by natural colonization, and active strategies, such as transplanting or hatchery releases.

Reintroductions alter patterns of connectivity among populations. We therefore first develop a metapopulation framework to describe the ecological processes governing population connectivity and their evolutionary consequences. We then broadly overview a set of planning concepts (benefits, risks, and constraints) to help guide scoping efforts and determine if a proposed reintroduction has conservation merit. Next, we describe methods of executing reintroductions that increase the likelihood of achieving benefits while overcoming constraints and reducing risks, including a review of examples in which these methods have been employed. Finally, monitoring is essential to assess whether the effort was successful and, if not, how the program should be modified. Throughout, we focus on biological issues, acknowledging that a socioeconomic cost-benefit analysis will be crucial for policy decisions regarding large-scale restoration projects.

A METAPOPULATION PERSPECTIVE

A regional, landscape perspective is important for effective salmonid recovery (ISAB 2011). We therefore present our recommendations within a metapopulation conceptual framework. A metapopulation is a collection of spatially structured populations inhabiting discrete habitat patches, with dispersal between patches providing some level of connectivity between populations (Hanski and Gilpin 1997). Reintroductions intentionally alter connectivity among populations, so it is important to consider the consequences of such actions on the demography, ecology, and evolution of the metapopulation at large.

The metapopulation concept is readily applied to anadromous salmonids (Schtickzelle and Quinn 2007) and especially the case of population colonization. Pacific salmon have a strong tendency to return to their natal stream but also "stray" and breed in nonnatal streams (Hendry et al. 2004), providing the interpopulation dispersal characteristic of metapopulations. Dispersal, combined with variation in population growth rate, can lead to source–sink dynamics whereby populations with net demographic deficits (i.e., "sinks") are supported by immigration from populations with net demographic excesses (i.e., "sources") (Pulliam 1988). For colonizing Pacific salmon, source population dynamics will, in large part, determine the rate of numerical and spatial expansion (Pess et al. 2012).

Salmonid metapopulations might adopt a variety of different structural configurations depending on the spatial arrangement of habitat, heterogeneity in habitat quality among patches, and connectivity between populations (Schtickzelle and Quinn 2007; Fullerton et al. 2011). Metapopulation structure is useful to conceptualize the potential outcomes of reintroductions (Figure 1). Furthermore, an assessment of metapopulation structure might inform reintroduction methods. For example, a reintroduction that expands an existing population (Figure 1A) or establishes a new well-connected population (Figure 1B) might achieve success through passive natural colonization, whereas active methods might be required for more isolated reintroduction sites (Figure 1C).

Metapopulation structure, and the degree of connectivity among populations, also affects the evolution of locally adapted traits. Spatially structured populations experiencing different selection regimes within a heterogeneous landscape will tend to evolve traits advantageous in each environment, a process that is counterbalanced by connectivity between populations, which tends to homogenize gene pools (Barton and Whitlock 1997). Local adaptation is a fundamental aspect of salmonid population structure (Taylor 1991; Fraser et al. 2011). Furthermore, life history diversity exhibited by locally adapted populations buffers salmonid species against environmental variation, increasing stability and resilience (Greene et al. 2010; Schindler et al. 2010) while reducing extinction risk (Moore et al. 2010).

Increasing population connectivity, an implicit goal of all reintroduction programs, can have both positive and negative consequences on species viability. Some level of connectivity is beneficial because it can lead to the colonization of new habitat (Pess et al. 2012), demographically rescue extant populations experiencing periods of low productivity or abundance (Pulliam 1988), and provide new genetic material essential for fitness in populations suffering from fragmentation (Tallmon et al. 2004). However, excessive connectivity can have negative consequences such as genetic homogenization (Williamson and May 2005) and demographic synchrony (Liebhold et al. 2004), both of which would tend to reduce resilience.

For administering listing and recovery of Pacific salmon under the ESA, the National Marine Fisheries Service (NMFS) uses an explicitly defined population structure. For vertebrates,

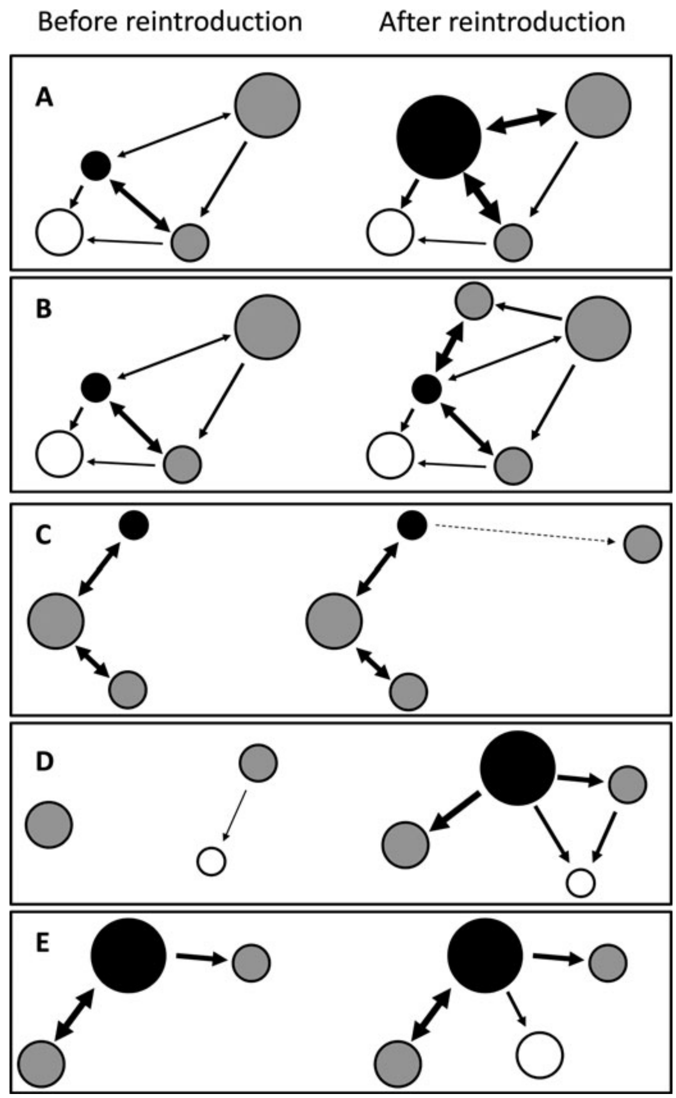

FIGURE 1. Possible effects of reintroduction on metapopulation structure are as follows: **(A)** increase the abundance of the existing population, **(B)** establish a new, independent population well connected to the metapopulation, **(C)** establish a new, independent population isolated from the other populations, **(D)** establish a new, independent mainland population in a historic mainland–island metapopulation, and **(E)** establish a new, independent sink population in a historic mainland–island metapopulation. In these diagrams, the size of the circle represents habitat capacity, the shade represents population density (darker shades are more dense), the thickness of the arrows represents the magnitude of connectivity, and the dashed lines indicate intermittent connectivity. These scenarios are not intended to represent all possible outcomes.

the ESA allows listing of Distinct Population Segments (DPSs), subspecies, or entire species. For Pacific salmon, the NMFS has defined a DPS to be an Evolutionary Significant Unit (ESU), which is a population or group of populations that is both substantially reproductively isolated from other populations and represents an important component of the evolutionary legacy of the species (Waples 1991). For steelhead, the NMFS uses the joint NMFS–U.S. Fish and Wildlife Service DPS definition

(NMFS 2006). We refer to both Pacific salmon ESUs and steelhead DPSs as ESUs in this paper for consistency and brevity. Similar to metapopulations, most Pacific salmon ESUs contain multiple independent populations that interact through dispersal (e.g., Myers et al. 2006; Ruckelshaus et al. 2006). Furthermore, metapopulation concepts are explicitly considered in the criteria used to evaluate the viability of Pacific salmon and steelhead ESUs and the populations within them (McElhany et al. 2000).

PLANNING CONCEPTS: BENEFITS, RISKS, AND CONSTRAINTS

Before implementing a reintroduction, it is essential to comprehensively consider the potential outcomes. Poorly planned reintroduction efforts might waste resources that would be better invested in other conservation approaches or, worse, impair the viability of an extant population. In evaluating a potential reintroduction, there are three primary concepts to consider: the benefits if the reintroduction is successful, the risks of causing biological harm to extant populations, and the constraints that might prevent population establishment. Weighing the potential benefits against the risks and constraints will help determine whether or not to implement a proposed reintroduction (Figure 2).

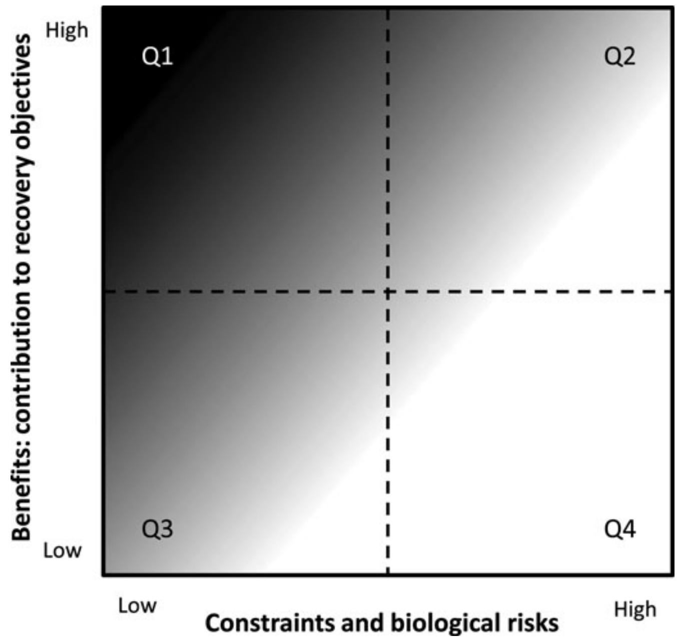

FIGURE 2. Framework for gauging the net benefit of reintroduction options, with darker colors representing a higher likelihood of contributing to conservation and recovery goals. In each case, the benefits are weighed against the constraints and risks of the project. In quadrant 1 (Q1), the benefits are high and the overall constraints and risks are low, providing the best opportunity for reintroduction to effectively contribute to the recovery objectives. Quadrant 2 (Q2) also has a high potential benefit, but either the difficulty in implementation or the risk of a negative outcome makes projects in this region less attractive. Both quadrants 3 (Q3) and 4 (Q4) have relatively low benefits; some in quadrant 3 may be selected owing to the low risk and ease of execution, whereas those in quadrant 4 will generally be avoided.

Benefits

Due to our focus on ESA-listed salmonids, we assess benefits with the same criteria used to evaluate recovery under the ESA. The biological viability of salmonid ESUs and the populations within them is dependent upon four characteristics: abundance, productivity, spatial structure, and diversity (McElhany et al. 2000). We use these same attributes for evaluating the potential benefits of a reintroduction that successfully establishes a self-sustaining population (Table 1). Abundance, productivity, and spatial structure (i.e., connectivity) are variables in metapoulation models useful for guiding salmonid management (Cooper and Mangel 1999; Fullerton et al. 2011; Pess et al. 2012), and diversity promotes resilience at a broad, regional (hence metapopulation) scale (Moore et al. 2010; Schindler et al. 2010).

Numerical increases in abundance and productivity are perhaps the most obvious benefits afforded by reintroductions.

TABLE 1. Potential benefits of a successful reintroduction.

Type	Definition	Potential benefit afforded by reintroduction
Abundance	Total number of naturally spawned fish in a population or ESU	Increase the carrying capacity of an existing population or establish a new, discrete, demographically independent population
Productivity	Numerical ratio of recruits in generation t to the spawners that produced them in generation $t-1$	Increase average vital rates (e.g., reproductive success, survival) of an extant population or ESU by reestablishing occupancy of high quality habitat
Spatial structure	Geographic arrangement of fish across the landscape and connectivity of populations linked by dispersal	Reduce isolation of extant populations, thereby restoring natural patterns of dispersal and connectivity within the metapopulation
Diversity	Variation in morphological, behavioral, and genetic traits within a population or ESU	Reestablish occupancy of habitats that are rare or underrepresented within the extant distribution, thereby promoting ecological and evolutionary processes responsible for local adaptation and diverse life histories

Increased abundance has several beneficial consequences, including shielding a population from extinction due to stochastic variability (Lande 1993), minimizing genetic processes that can reduce fitness in small populations (Allendorf and Luikart 2007), exceeding thresholds for depensatory density-dependent processes (Liermann and Hilborn 2001), and providing marine-derived nutrient subsidies to aquatic and riparian ecosystems (Gende et al. 2002). Status evaluations of ESA-listed Pacific salmon and steelhead populations focus on numerical productivity (Ford 2011), or population growth rate as it is known in the ecological literature, so recruits per spawner is also an important variable to consider. Reintroductions can have either positive or negative impacts on the productivity of a given population or ESU, depending on the quality of the new habitat and survival through migration and ocean rearing. In general, a reintroduction resulting in a "sink" has far less value for long-term viability than a reintroduction yielding a self-sustaining population. Indeed, reintroduction to a sink would result in a net loss if the animals would have been more productive in their natal habitat. However, in highly connected metapopulations, sinks may increase the stability of the entire system by promoting higher abundance in source populations (Foppen et al. 2000).

Reintroductions that reduce the isolation of formerly connected extant populations will benefit spatial structure (Figure 1). In practice, this can be estimated as the extent to which a newly established population would reduce gaps between spawning areas or populations that were not historically separated. Given the spatial arrangement, models of dispersal, and estimates of habitat capacity, reintroduction could target areas that might have a significant role in metapopulation connectivity and serve as sources supporting less productive populations (Figure 1D; Fullerton et al. 2011; Pess et al. 2012). In addition, at the ESU scale, dispersion of populations across the landscape helps reduce vulnerability to catastrophic events (Good et al. 2008), so increasing spatial complexity via successful reintroduction will reduce ESU extinction risk.

Reintroductions can enhance salmonid diversity through a variety of mechanisms. Dams often selectively block access to certain habitat types, particularly snowmelt-dominated headwater streams (Beechie et al. 2006; McClure et al. 2008a). Therefore, reintroductions into habitats that are rare or underrepresented within the extant species distribution may promote unique local adaptations and life history traits. Barrier removal may provide seaward access for populations of facultatively migratory species (e.g., *O. mykiss*) that historically had anadromous components (Brenkman et al. 2008b). Reintroductions to large watersheds with multiple tributaries and subbasins also offer opportunities to enhance diversity through the evolution of population substructure and local adaptation to distinct spawning areas. In general, a reintroduction that establishes a new locally adapted population will provide a greater benefit to diversity than one that expands an existing population (Figure 1A, 1B).

Outlining the time frame required to achieve reintroduction benefits will help set expectations and establish benchmarks for monitoring. Some reintroductions may provide immediate benefits within a generation or two, but those requiring adaptation to new habitat will likely take decades. If an implemented project suffers initial setbacks and lacks a scientifically based timeline of expectations, it might be unnecessarily abandoned or altered before it has a chance to succeed. In general, reintroduction can provide benefits to viability characteristics that change on ecological time scales (abundance, productivity, and spatial structure) faster than benefits to diversity, which will accumulate over generations as a reintroduced population becomes demographically independent and evolves in response to local selective pressures. Salmonids have developed population structure within 20 years of introduction to new environments (Ayllon et al. 2006); evidence that such divergence is adaptive has been found after 50–100 years (Hendry et al. 2000; Quinn et al. 2001; Koskinen et al. 2002).

Moreover, in some cases adaptive evolution might be necessary to observe significant increases in abundance. Indeed, there is often a time lag from the initial introduction of an invading species to population growth that might be explained by evolutionary processes required to increase population fitness (Sakai et al. 2001). Dams have altered the evolution of traits such as adult spawn timing, embryonic development rate, and juvenile migration strategies (Angilletta et al. 2008; Williams et al. 2008), so some level of adaptive evolution may be necessary to overcome this "Darwinian debt" if reintroduction includes restoration of the natural flow regime (Waples et al. 2007b).

Risks

We define risks as unintended or undesirable negative consequences for nontarget species or nontarget populations of the reintroduced species (Table 2). Minimizing those risks is important if a reintroduction is to have a positive overall conservation effect (George et al. 2009). Here we outline the concepts underlying four categories of risk: evolutionary, demographic, ecological, and disease. More details on minimizing them are provided below in the Executing a Reintroduction section.

In terms of evolutionary risks, reintroduction could result in genetic homogenization, reduced fitness, or both. Transfers of fish between basins and large-scale hatchery releases, historically common practice throughout the Pacific Northwest, have eroded population structure that is essential for the local adaptation and hence fitness of salmonid populations (Williamson and May 2005; Eldridge and Naish 2007; McClure et al. 2008b). Hatchery fish often have lower fitness than wild fish when both groups breed sympatrically (Araki et al. 2008). Thus, although hatchery releases may provide short-term demographic benefits, they may compromise fitness in the long term, thereby limiting the probability of recovery (Bowlby and Gibson 2011). In many cases, populations or spawning areas near the reintroduction site are of conservation concern. Fish

TABLE 2. Summary of the major reintroduction risks, defined as unintended or undesirable negative consequences for nontarget species, nontarget populations, spawning areas, or life history types of the reintroduced species.

Type	Description	Methods of minimizing risk
Evolutionary	Homogenized population structure and reduced fitness within reintroduction site and adjacent areas	Avoid geographically and genetically distant source populations; opt for natural colonization rather than hatchery releases or transplanting; design passage facilities to minimize straying to adjacent areas
Demographic	Depletion of source population via removal of adults or gametes for reintroduction	Ensure that source population can sustain removal for multiple successive years or opt for natural colonization rather than hatchery releases or transplanting
Ecological	Invasion by nonnative species and suppression of preexisting native species within reintroduction site	Design passage facilities with selective access; avoid hatchery releases that alter density-dependent ecological interactions
Disease	Spread of pathogens	Establish baseline disease levels prior to reintroduction; screen individuals for pathogens prior to release

released into the reintroduction site, and their offspring, may not return there as adults, so fitness reductions and the erosion of population structure of the wild populations in adjacent spawning areas are potential consequences of excessive straying.

Reintroductions also pose demographic risks because the removal of individuals from the source population may harm its viability. If reintroduced fish experience poor reproductive success, the new habitat may become a sink that depletes an extant population but fails to provide the benefit of a newly established self-sustaining population. Transplanting or collecting broodstock from wild populations will exacerbate this risk, but it applies in concept to natural colonization as well. Ensuring that the population donating colonists has a net demographic excess (i.e., it is a true "source" in metapopulation source–sink dynamics) will help reduce demographic risks.

Nonnative fishes present a serious conservation threat to salmonids in the Pacific Northwest (Sanderson et al. 2009) and may invade the reintroduction site following barrier removal (Fausch et al. 2009). Invasion might not only reduce the likelihood of reintroduction success but also threaten preexisting native species. A careful examination of the likelihood of nonnative dispersal into the new habitat entails identifying any proximate populations of nonnative fishes and evaluating habitat suitability above the barrier. It is also important to consider whether reintroduction might suppress preexisting native species (which might be threatened or endangered themselves) through competition or predation. The few empirical assessments of reintroduction impacts have found little effect on preexisting native species (Pearsons and Temple 2007; Buehrens 2011).

Finally, reintroductions have potential to spread disease (Viggers et al. 1993). Colonists may serve as vectors of disease spread within the species they are intended to benefit, thereby hindering conservation efforts (Walker et al. 2008), or transmit pathogens to other species or resident life history types currently occupying the target site. Hatchery fish in particular, due to the crowded conditions in which they are typically reared, may act as vectors of disease transfer to wild populations (reviewed in Naish et al. 2008). Reintroduced animals might also be vulnerable to endemic pathogen strains within new habitat, and this could decrease the likelihood of successful population establishment if the effect is severe. Establishing a baseline of pathogen densities within the area prior to reintroduction will permit monitoring of disease during reintroduction (Brenkman et al. 2008a), and screening captively reared or transplanted animals prior to release will minimize the risk of spreading disease. Both are important components of reintroduction.

Constraints

We define a constraint as a factor limiting the ability of colonists to establish a self-sustaining population (Table 3). In some cases, an extirpated area may have a high potential to benefit long-term recovery, but current conditions do not support a reintroduction. Evaluating whether the original causes of the extirpation have been adequately ameliorated is an important step in determining whether a site is "reintroduction ready" (IUCN 1998). Importantly, more than one factor may have led to the original extirpation, and in many cases determining a logical sequence of restoring functioning conditions will be an important component of the reintroduction effort. Here, we describe the primary constraints affecting the ability of colonists to reach the reintroduction site, their reproductive success, and the survival of their offspring.

In many cases, migration barriers are the most obvious constraint to the reestablishment of a natural population. Evaluating the best methods for providing passage at barriers is heavily dependent on engineering and social considerations such as the geological setting, human benefits derived from the barrier, and expense. Furthermore, many river systems with reintroduction opportunities have more than one blockage to anadromous

TABLE 3. Summary of constraints to reintroductions, defined as factors that might limit the ability of colonists to establish a self-sustaining population.

Type	Description	Required action
Barriers	Engineering issues; prioritization among multiple blockages in a watershed or region	Removal or circumvention
Habitat quality	Poor habitat quality will limit reproductive success of colonists and survival of their offspring	Restoration prior to reintroduction
Migratory and ocean survival	Poor survival along migration corridor and during ocean residence	Improve survival through downstream dams; estuary restoration; wait for favorable ocean conditions or scale expectations to match poor ocean conditions
Harvest	Reduces number of potential colonists and survival of their offspring	Reduce fishing pressure on potential source population(s) during colonization
Interactions with other species and populations	Competition and predation from native and nonnative species	Suppress predator population or transport fish during migration to avoid predators
Changing conditions	Climate and land-use change will alter geographic patterns of habitat suitability	Prioritize reintroductions that enhance diversity, are likely to serve as refuges in a warming climate, or are located in river networks whose high connectivity will allow species distributions to shift in response to climate change

passage, requiring prioritization among multiple removal or circumvention options.

The quality of habitat in the reintroduction site will have a large effect on colonist productivity. In gauging habitat quality within an area targeted for reintroduction, planners should consider the requirements of all life phases. Spatially explicit models incorporating known fish–habitat relationships (e.g., Scheuerell et al. 2006; Burnett et al. 2007; Pess et al. 2008) can help identify potentially productive streams; determining the anthropogenic degradation of habitats can draw on the many efforts (largely expert opinion) to identify degraded habitat (e.g., subbasin or recovery plans). Where habitat quality is low due to anthropogenic disturbance, habitat restoration may be necessary for successful reintroduction and premature efforts to put fish into degraded habitat may simply be a waste of resources. For example, liming of rivers affected by acidification (Hesthagen and Larsen 2003) and reducing pollution (Perrier et al. 2010; Kesler et al. 2011) were necessary components of reestablishing Atlantic Salmon *Salmo salar* runs in Europe. When restoration is necessary, process-based restoration will maximize the long-term sustainability of habitat improvements (Beechie et al. 2010).

Interactions with existing species in the target area could influence the likelihood of a successful reintroduction. Dams that block salmonid habitat often create the warm, lentic reservoirs preferred by nonnative fishes (e.g., Channel Catfish *Ictalurus punctatus*, Smallmouth Bass *Micropterus dolomieu*, Yellow Perch *Perca flavescens*, and Walleye *Sander vitreus)* and "native invaders" (e.g., Northern Pikeminnow *Ptychocheilus oregonensis*), species that consume a considerable quantity of salmonids (Sanderson et al. 2009; Carey et al. 2012). Competition and predation from preexisting species might not be confined to reservoirs or degraded habitats. Nonnative Brook Trout *Salvelinus fontinalis*, for example, have invaded relatively pristine, free-flowing streams throughout the Pacific Northwest (Sanderson et al. 2009) and may have suppressed populations of ESA-listed Chinook Salmon *O. tshawytscha* (Levin et al. 2002). Slimy Sculpin *Cottus cognatus*, a native generalist predator, reduced the recruitment success of reintroduced Atlantic Salmon (Ward et al. 2008).

Due to climate forcing (Mantua et al. 2010) and alterations in land use (Bilby and Mollot 2008), salmonid habitat quality is likely to change over the time required for a reintroduction to result in a self-sustaining population. Thus, the likely future condition of the reintroduction site is an important consideration in reintroduction planning efforts. Climate and land-use models can inform restoration opportunities (Battin et al. 2007; Lohse et al. 2008) but have been applied to relatively few watersheds. In the absence of large-scale predictive models, two qualitative guidelines for reintroductions warrant consideration. First, dams selectively block access to certain habitat types (Beechie et al. 2006; McClure et al. 2008b), suggesting that reintroduction to mountain headwater reaches with higher elevations and cooler temperatures may provide refuges in a warming climate. Second, maintaining a diversity of habitat types will buffer against uncertainty in the response of salmonid populations to climate change (Schindler et al. 2008), suggesting that reintroduction should target habitats that are unique, rare, or underrepresented in the current species distribution.

High mortality during migration and ocean rearing due to impaired migratory corridor, poor ocean conditions, or harvest pressure may limit reintroduction success. Passage through

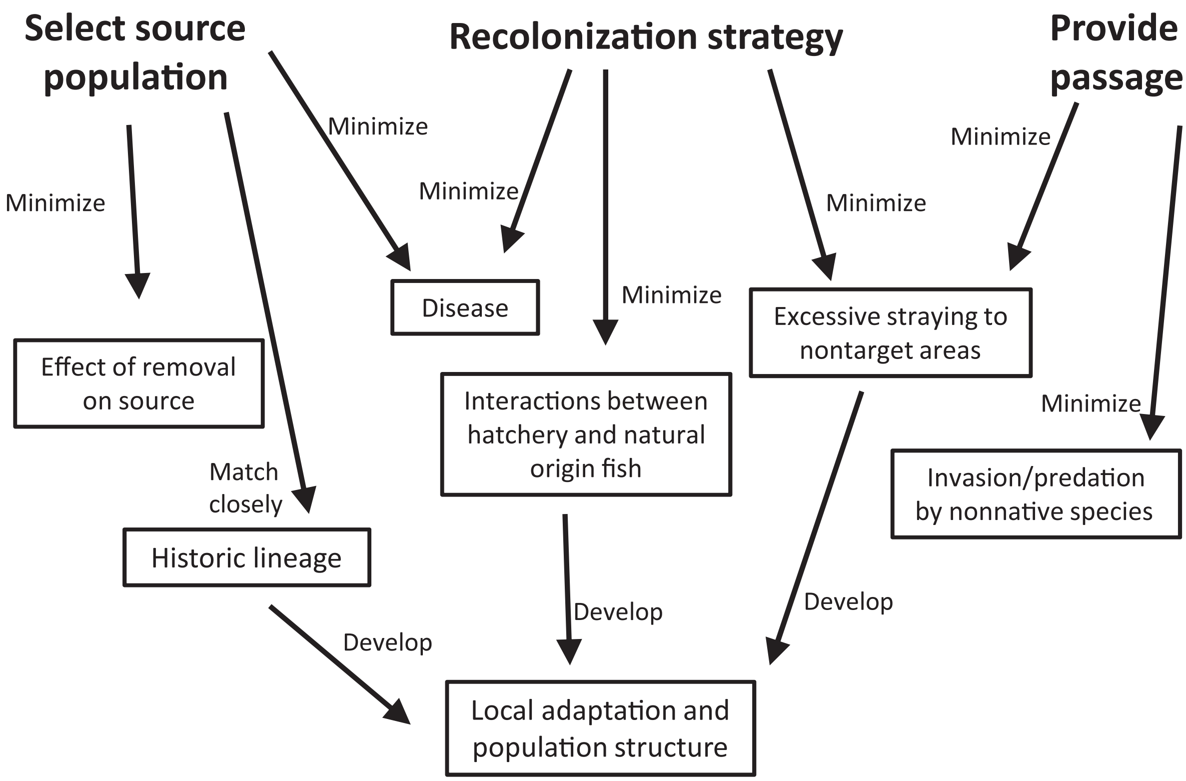

FIGURE 3. Minimizing biological risks in reintroduction planning. Biological risks are unintended negative consequences that may harm nontarget species, other populations, spawning areas, or life history types of the reintroduced species.

downstream dams, for example, may reduce the migratory survival of juveniles, either directly or through delayed effects that manifest in subsequent life stages (Budy et al. 2002; Schaller and Petrosky 2007). Dams may also cause the delay and eventual failure of upstream-migrating adults (Caudill et al. 2007). It is possible to improve survival through dams, even large ones (Ferguson et al. 2007), and this may be an essential action prior to reintroduction. Marine survival patterns are also a major determinant of salmonid population productivity. Ocean survival responds to long-term climatic processes such as the Pacific Decadal Oscillation (Mantua et al. 1997), as well as short-term processes such as interannual variation in sea surface temperature, marine upwelling, and river conditions experienced during migration (Mueter et al. 2005; Scheuerell and Williams 2005; Scheuerell et al. 2009; Petrosky and Schaller 2010). As our ability to identify favorable ocean and river conditions improves (e.g., Burke et al. 2013), there may be opportunities to time reintroduction efforts to favorable conditions. Harvest rates vary among ESUs and in some cases may limit recolonization potential. Fishing quotas set on aggregate stocks may constrain the ability to selectively reduce harvest rates on individual colonizing populations and their sources.

EXECUTING A REINTRODUCTION: COLONIZATION, SOURCE POPULATION, AND PASSAGE

In this section, we discuss the strategies for recolonization, the choice of a source population, and, in the case of reintroductions involving barriers, the techniques used to provide passage. Decisions related to these three execution elements will largely determine reintroduction risks (Figure 3). We define the colonization strategy as the mechanism of fish movement into the reintroduction site; it can be either passive (natural colonization) or active (transplanting or hatchery releases). We suggest that it is important to consider the colonization strategy and source population as two separate planning decisions. For example, even in cases where a hatchery stock is the source, it may be possible to reduce evolutionary risks by allowing hatchery adults to colonize naturally rather than planting hatchery-produced juveniles.

Colonization Strategy

The three basic types of colonization strategies are natural, transplant, and hatchery release. Importantly, these approaches differ in the effects on the viability parameters that will ultimately be used to judge the success or failure of a reintroduction. In general, natural colonization is the lowest-risk approach because it minimizes the interruption of natural biological processes. Transplanting and hatchery releases can immediately place fish in the reintroduction site, but tend to increase the risks associated with reintroduction relative to natural colonization. Fortunately, active reintroduction strategies will be most necessary for isolated reintroduction sites (e.g., Figure 1C), the very situations where evolutionary risks of straying to neighboring extant populations are the lowest. In general, a precautionary

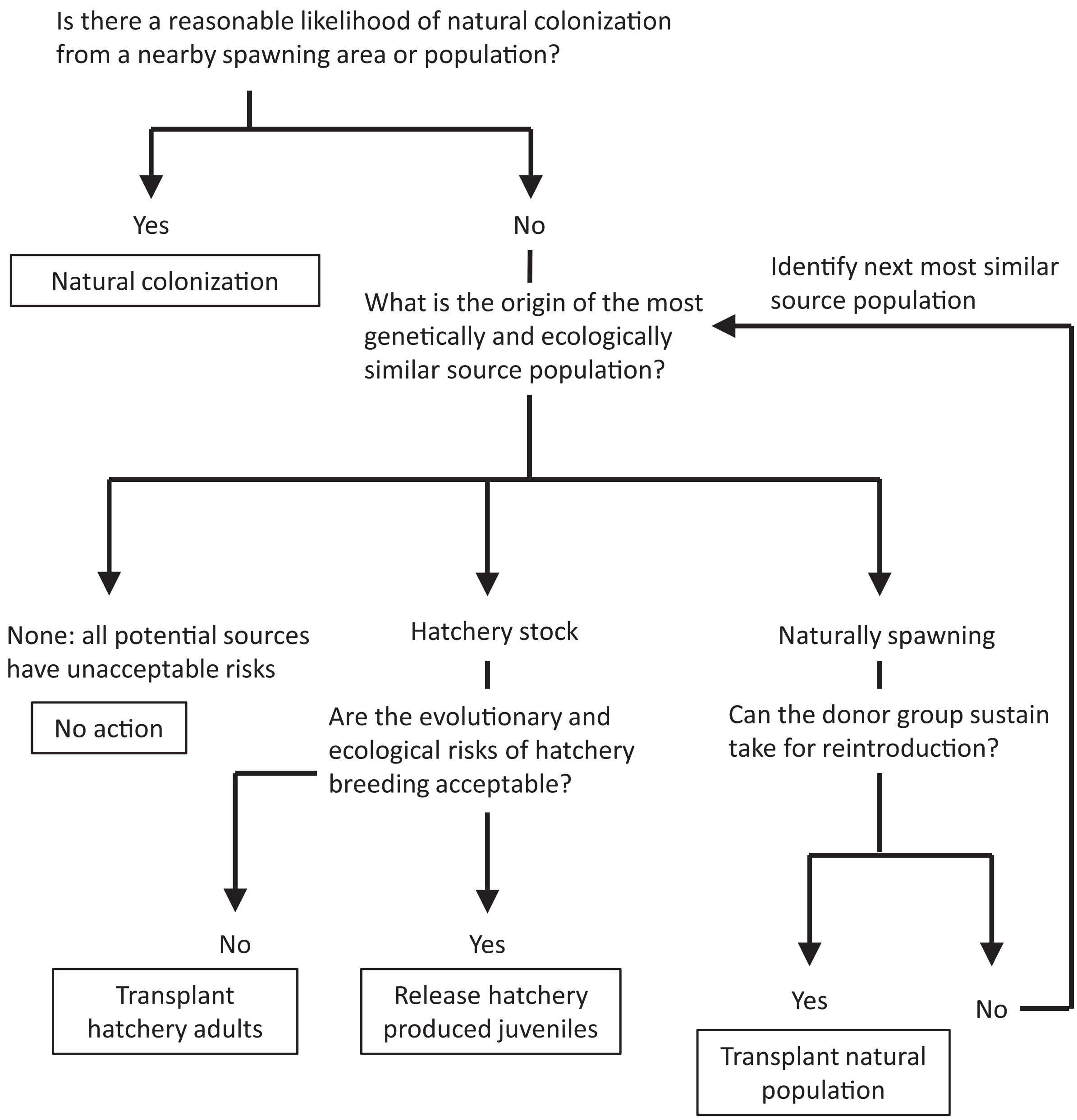

FIGURE 4. Decision framework for selecting a low-risk colonization strategy and source population. This diagram does not encompass every possibility but is intended to highlight the key decisions affecting reintroduction risks. Boxes indicate decision endpoints.

approach, outlined in Figure 4, adopts the lowest risk colonization strategy that has a reasonable chance of promoting long-term improvement in population and ESU viability.

What is the minimum number of fish necessary to establish a self-sustaining population? This is a crucial question applicable to all three colonization strategies whenever the goal is to establish a new population (e.g., Figures 1B–1E). On one hand, depensatory processes (Allee effects) may depress productivity at low densities through a variety of mechanisms (Courchamp et al. 1999; Liermann and Hilborn 2001) and, if the effect is severe, prevent population establishment following reintroduction (Deredec and Courchamp 2007). On the other hand, reintroduced species, particularly those with an extensive stream-rearing juvenile phase, may be released from density-dependent processes during colonization and enjoy high survival due to the lack of competition (Pess et al. 2011). Although the ultimate result will depend heavily on the constraints (Table 3), the choice of colonization strategy will have a strong influence on the number of fish that reach the reintroduction site. Here, we outline the benefits and risks of each colonization strategy, providing empirical examples if they are available.

Natural colonization.—Pacific salmon can rapidly exploit newly accessible habitat through natural colonization, which we define as volitional dispersal into a reintroduction site without human-assisted transport. Following construction of a fishway circumventing an anthropogenic blockage, Pink Salmon *O. gorbuscha* naturally dispersed upstream and established self-sustaining populations in multiple subbasins of the Fraser River, British Columbia, within a decade (Pess et al. 2012). Chinook Salmon and Coho Salmon *O. kisutch* immediately colonized habitat made accessible by modification of a dam on the Cedar River, Washington (Kiffney et al. 2009; Burton et al. 2013), and both species produced a significant number of returning adult offspring that bypassed the dam in the next generation (Anderson et al. 2010; Anderson et al. 2013a). In this system, extensive dispersal by juvenile Coho Salmon, including immigration into a tributary where survival was relatively high, contributed to colonization success (Pess et al. 2011; Anderson et al. 2013b). Steelhead and fluvial Rainbow Trout accessed Beaver Creek, Washington, in the very first season after barrier removal (Weigel et al. 2013). Atlantic Salmon naturally colonized rivers in Estonia, Norway, England, and France following improvements in water quality (Hesthagen and Larsen 2003; Perrier et al. 2010; Griffiths et al. 2011; Kesler et al. 2011), and some of these examples resulted from long-distance dispersal. Dam removal promoted natural colonization of the Upper Salmon River, New Brunswick, by Atlantic Salmon, though this population later crashed to near zero abundance for unknown reasons (Fraser et al. 2007).

In some cases, increasing water releases from dams has promoted natural colonization. In the Bridge River, British Columbia, Coho Salmon, Chinook Salmon, and steelhead were observed immediately following restoration of flow to a 4-km reach that had been dewatered for decades (Decker et al. 2008). Experimental water releases from dams on the Alouette and Coquitlam rivers, British Columbia, led to the reappearance of Sockeye Salmon *O. nerka* after 90 years of extirpation, and genetic and otolith analysis confirmed that the anadromous adults were the offspring of resident kokanee (lacustrine Sockeye Salmon) (Godbout et al. 2011).

Natural disturbances and circumvention of natural barriers provide additional examples of natural colonization. Steelhead recolonized the Toutle River, Washington, to relatively high densities 7 years after a catastrophic destruction following the eruption of Mount Saint Helens (Bisson et al. 2005). Natural colonization tends to proceed more slowly (e.g., decades) in initially barren glacial emergent streams, as evidenced by rates of Coho Salmon and Pink Salmon colonization in Glacier Bay, Alaska (Milner and Bailey 1989; Milner et al. 2008). Several salmonid species rapidly colonized Margaret Creek, Alaska, following construction of a fish ladder at a falls, although the Coho Salmon and Sockeye Salmon populations were supplemented by hatchery releases (Bryant et al. 1999).

Establishing a self-sustaining population via natural colonization is contingent on a reasonable likelihood of natural dispersal into the new habitat. The probability of colonization, in turn, is determined by metapopulation attributes such as the location of the potential source population, abundance of the source population, and stray rate (i.e., connectivity) as a function of distance (Pess et al. 2012). Despite these observations, it is difficult to predict precise colonization rates following barrier removal. Most examples of natural colonization by Pacific salmon in Table 4 had nearby, relatively robust source populations, but colonization rates of isolated reintroduction sites are likely to be much lower. Furthermore, one might predict colonization rate to vary by species, but there are few multispecies comparisons to guide expectations (Table 4). In this situation, habitat preferences and life history patterns offer a means to make species-specific predictions (Pess et al. 2008).

Natural colonization minimizes anthropogenic disturbance to biological processes during population establishment and expansion. Natural colonization provides the greatest opportunity for the evolution of locally adapted traits through natural selection on individuals that disperse into the new habitat, sexual selection during reproduction of the initial colonists, and natural selection on their offspring. In many cases, evolution resulting from the novel selection pressures during colonization may increase population fitness and the likelihood of establishment (Kinnison and Hairston 2007). In the Cedar River, Washington, strong selection on the breeding date and body size of Chinook Salmon and Coho Salmon colonists emphasized the importance of natural and sexual selection in promoting local adaptation during reintroduction (Anderson et al. 2010, 2013a).

Transplanting adults.—In areas that are isolated or distant from extant populations, long-distance dispersal from extant populations may be unlikely. In these cases, transplanting can ensure that an adequate number of adult fish reach the reintroduction site. Under this strategy, adult fish are trapped at one location then transported to the reintroduction site, where they are released to breed naturally. Here, we describe the process and consequences of transplanting from both hatchery and wild sources.

Although stock transfers have been common for Pacific salmon, there are relatively few examples in which only adults were released (Withler 1982). In programs that combined transplanted adults with hatchery releases (e.g., Burger et al. 2000; Spies et al. 2007), it is difficult to isolate the effects of each strategy. In a reintroduction or supplementation context, transplants often involve surplus hatchery adults. For example, hatchery-origin spring Chinook Salmon were transplanted to Shitike Creek, Oregon because the habitat was considered underseeded 15 years after dam removal and produced a significant fraction of the juveniles captured the following spring (Baumsteiger et al. 2008). Atlantic Salmon that had spent their entire lives in captivity successfully spawned following release into Wilmot Creek, Ontario (Scott et al. 2005b). Transplanting adults is frequently used to circumvent large dams and reservoirs in a “trap and haul” strategy (Table 5), and we discuss this approach further in the Providing Passage section below.

TABLE 4. Examples of anadromous salmonid reintroductions from the published literature.

Location	Date initiated	Species	Colonization strategy	Passage provision	References
Fraser River, British Columbia	1947	Pink Salmon	Natural colonization	Fishway	Pess et al. 2012
Clearwater River, Idaho	1960	Chinook Salmon	Hatchery juveniles	Dam removal	Narum et al. 2007
Upper Salmon River, New Brunswick	Mid-1960s	Atlantic Salmon	Natural recolonization	Dam removal	Fraser et al. 2007
Connecticut River, Connecticut, Massachusetts, Vermont, and New Hampshire	1967	Atlantic Salmon	Hatchery juveniles	Fishways	Gephard and McMenemy 2004; Ward et al. 2008
River Thames, England	1975	Atlantic Salmon	Natural colonization and hatchery juveniles	None	Griffiths et al. 2011
Rivers Rhine, Ems, Weser, and Elbe, Germany	1978	Atlantic Salmon	Hatchery juveniles	Primarily fishways	Monnerjahn 2011; Schneider 2011
Point Wolfe River, New Brunswick	1982	Atlantic Salmon	Hatchery juveniles	Dam removal	Fraser et al. 2007
Sawtooth Valley lakes, Idaho	1993	Sockeye Salmon	Hatchery juveniles	None	Griswold et al. 2011; Kalinowski et al. 2012
Middle Fork Willamette River, Oregon	1993	Chinook Salmon	Transplanted adults	Trap and haul	Keefer et al. 2010, 2011
Various Norwegian rivers	Mid-1990s	Atlantic Salmon	Natural colonization and hatchery juveniles[a]	None	Hesthagen and Larsen 2003
Seine River, France	Mid-1990s	Atlantic Salmon	Natural colonization	None	Perrier et al. 2010
River Selja, Estonia	Mid-1990s	Atlantic Salmon	Natural colonization and hatchery juveniles[b]	None	Väsemagi et al. 2001
Bridge River, British Columbia	2000	Chinook Salmon, Coho Salmon, steelhead	Natural colonization	Increased water releases from dam	Decker et al. 2008
Wilmot Creek, Ontario	2000	Atlantic Salmon	Transplanted adults	None	Scott et al. 2005a, 2005b
Salmon River, New York	2000	Atlantic Salmon	Hatchery juveniles	None	Coghlan and Ringer 2004
Shitike Creek, Oregon	2002	Chinook Salmon	Transplanted adults	Dam removal	Baumsteiger et al. 2008
Cedar River, Washington	2003	Chinook Salmon, Coho Salmon	Natural colonization	Fishway	Kiffney et al. 2009; Anderson et al. 2010, 2013a, 2013b; Pess et al. 2011; Burton et al. 2013
Various Lake Ontario tributaries, New York	2003	Atlantic Salmon	Hatchery juveniles	None	Coghlan et al. 2007

TABLE 4. Continued.

Location	Date initiated	Species	Colonization strategy	Passage provision	References
Alouette and Coquitlam rivers, British Columbia	2005	Sockeye Salmon	Natural colonization	Increased water releases from dams	Godbout et al. 2011
River Purtse, Estonia	2005	Atlantic Salmon	Natural colonization and hatchery juveniles[c]	None	Kesler et al. 2011
Beaver Creek, Washington	2005	Steelhead	Natural colonization	Fishways	Weigel et al. 2013

[a]Colonization strategy varied by river.
[b]Genetic analysis indicates that natural dispersal, not hatchery releases, were primarily responsible for colonization.
[c]Hatchery releases commenced after natural colonization was observed.

Conceptually, transplanting allows for natural patterns of natural and sexual selection within the new habitat and thus has many of the benefits of natural colonization. The offspring of any adults that successfully spawn will spend the entire freshwater phase, from embryonic incubation to the smolt migration, within the reintroduction site. Compared with hatchery releases, this will increase their exposure to natal odors and local geomorphic, hydrologic, and biotic conditions, all of which are likely to promote local adaptation. However, transplanting introduces artificial selection of the individuals that reach the reintroduction site. In some cases, natural selection during migration could be important for the evolution of traits (i.e., body morphology or energy reserves) that are advantageous for a particular migration route (i.e., long or steep) (Quinn et al. 2001). Thus, considering the run timing, size, and other phenotypic traits of individuals selected for transplantation is an important component of minimizing the negative, unintended consequences of transplanting.

The number and frequency of transplants is an important consideration. Reintroductions with many individuals are more likely to be successful (Wolf et al. 1996; Fischer and Lindenmayer 2000), but with few salmonid examples, it is difficult to provide precise guidance on the number to transplant. Metapopulation structure might provide guidance, as reintroduction sites isolated from the regional metapopulation are unlikely to receive large numbers of natural colonists and, therefore, will require a greater number of transplanted fish than those connected to potential source populations. Williams et al. (1988) observed that 50 individuals (25 males and 25 females, annually) is the absolute minimum for establishing a hatchery population in a controlled setting, so transplanting to a dynamic river environment will certainly require a greater number of fish. Some fraction of transplanted adults may die prior to spawning (Keefer et al. 2010) or depart the release site because they fail to detect natal odors (Blair and Quinn 1991). Continuing transplants for a full generation and into a second generation provides additional reproductive potential and new genetic material that may reduce the impact of a genetic bottleneck (e.g., Hedrick and Fredrickson 2010). In addition, selecting the highest quality habitat within the reintroduction site for the release site may increase the reproductive success of the colonists.

We suggest that reintroduction should maximize the total number of fish transplanted while minimizing the risks (Table 2), which are likely to increase as the number of fish transplanted increases. Given the same total number of transplanted fish, risks might be reduced by releasing a small number of fish each year for many years rather than many fish for a short period. The release strategy will affect density-dependent processes, which in turn will affect both the performance of the reintroduced species and the ecological risks of reintroduction. For example, it may be possible to reduce density-dependent processes by dispersing colonists among several release sites (Einum et al. 2008). With few empirical examples, the outcomes of these risks are difficult to precisely predict a priori, highlighting the importance of a well-designed monitoring program.

Hatchery releases.—The third colonization strategy is a hatchery reintroduction that stocks artificially propagated juvenile fish or eggs within the reintroduction site. There are a number of examples of reintroductions releasing hatchery-produced juveniles (Table 4). In the Clearwater River, Idaho, out-of-basin stocks were used to reintroduce ocean- and stream-type Chinook Salmon; these hatchery populations are now sustained by returns to the Clearwater River, and the naturally produced juveniles of the two run types are genetically distinct (Narum et al. 2007). Hatchery releases of Atlantic Salmon reintroduced to the Connecticut River (flowing through Connecticut, Massachusetts, Vermont, and New Hampshire) are also sustained by local returns (Gephard and McMenemy 2004). However, abundances in the Connecticut River and in other reintroduced New England populations have continued to decline despite heavy stocking, and there is very little natural spawning because most returning adults are bred in captivity (Wagner and Sweka 2011). A captive broodstock hatchery program has played an essential role in the persistence of Snake River Sockeye Salmon, which reached critically low abundances in the mid-1990s (Griswold

TABLE 5. Examples of proposed, ongoing, or relatively recent reintroduction programs for Pacific salmon, steelhead, and Bull Trout *Salvelinus confluentus*.

River basin	Species	Comments on execution
Elwha River, Washington	Chinook Salmon, steelhead, Coho Salmon, Pink Salmon, Chum Salmon *O. keta*, Sockeye Salmon, Bull Trout	Removal of Elwha and Glines Canyon dams; for some species, adults trapped within lower Elwha River relocated above former dam site
Umbrella Creek and Big River, Ozette Lake, Washington	Sockeye Salmon	Hatchery releases for both locations; some natural colonization of Big River prior to hatchery releases
Cowlitz River, Washington	Chinook Salmon, Coho Salmon, steelhead	Hatchery releases, trap and haul above Mayfield, Mossyrock, and Cowlitz Falls dams
Clackamas River, Oregon	Bull Trout	Transplanted juvenile and adult fish from Metolius River
North Santiam River, Oregon	Chinook Salmon, steelhead	Trap and haul adults above Big Cliff and Detroit dams
South Santiam River, Oregon	Chinook Salmon, steelhead	Trap and haul adults above Foster and Green Peter dams
Calapooia River, Oregon	Chinook Salmon, steelhead	Removal of Brownsville, Sodom, and Shearer dams
McKenzie River, Oregon	Chinook Salmon	Trap and haul adults above Cougar and Trail Bridge dams
White Salmon River, Washington	Chinook Salmon, steelhead, Coho Salmon	Removal of Condit Dam
Hood River, Oregon	Chinook Salmon	Removal of Powerdale Dam; hatchery releases derived from neighboring Deschutes River
Deschutes River, Oregon	Chinook Salmon, steelhead, Sockeye Salmon	Hatchery releases for Chinook Salmon and steelhead; passage for adults and juveniles around Reregulation, Pelton, and Round Butte dams
Umatilla River, Oregon	Chinook Salmon, Coho Salmon	Hatchery releases
Yakima River, Washington	Sockeye Salmon, Coho Salmon	Sockeye Salmon: adults captured at Priest Rapids Dam transplanted above Cle Elum Dam; Coho Salmon: hatchery releases
Wenatchee River, Washington	Coho Salmon	Hatchery releases
Methow River, Washington	Coho Salmon	Hatchery releases
Okanogan River, Washington	Chinook Salmon, Sockeye Salmon	Hatchery releases for both species; passage above McIntyre Dam for Sockeye Salmon
Walla Walla River, Washington	Chinook Salmon	Hatchery releases
Lookingglass Creek, Oregon	Chinook Salmon	Hatchery releases derived from nearby Catherine Creek
Big Sheep Creek, Oregon	Chinook Salmon	Transplant surplus hatchery adults captured in adjacent Imnaha River
Pine Creek, Oregon	Chinook Salmon, steelhead	Transplant surplus hatchery adults captured at Hells Canyon Dam
Klamath River, California and Oregon	Chinook Salmon, Coho Salmon, steelhead	Proposed removal of Iron Gate, Copco 1, Copco 2, and J.C. Boyle dams
San Joaquin River, California	Chinook Salmon	Proposed under San Joaquin River Restoration Settlement Act

et al. 2011). Although this population is demographically dependent on the hatchery, abundance has grown substantially in recent years and progress has been made towards the reestablishment of natural reproduction. The hatchery has retained approximately 95% of the genetic diversity present in the founders of the captive broodstock program (Kalinowski et al. 2012).

There are also examples of hatchery reintroductions, mainly of Atlantic Salmon, that have failed, or that have had insufficient time, to generate persistent returns of hatchery fish. Despite decades of stocking nonlocal Atlantic Salmon on the Thames River, most adult Atlantic Salmon observed recently have dispersed naturally from nearby river systems (Griffiths et al. 2011). Although some Atlantic Salmon returned to Point Wolfe Creek, New Brunswick, following 4 years of hatchery releases, the population subsequently crashed, similar to neighboring populations in the inner Bay of Fundy (Fraser et al. 2007). Atlantic Salmon have been reintroduced to several rivers in Germany, but these populations are still demographically reliant on importing nonlocal eggs and fry despite some observations of natural spawning (Monnerjahn 2011). Finally, the initial phase of

Atlantic Salmon reintroduction to tributaries of Lake Ontario in New York State has focused on experimental testing of various release strategies and sites in an effort to maximize survival (Coghlan and Ringler 2004; Coghlan et al. 2007).

Overall, despite initial successes in establishing hatchery populations in some systems, we found no clear-cut examples in which a reintroduction employing hatchery releases yielded a self-sustaining naturalized population. Importantly, even the most successful programs to date continue to release hatchery fish, so it is largely uncertain whether any natural spawning would persist without supplementation. It is worth noting, however, that hatchery releases have been used to introduce self-sustaining salmonid populations to new locations not previously inhabited by the species in question. Out-of-basin hatchery releases established multiple self-sustaining populations of Sockeye Salmon in Lake Washington, Washington, but it is uncertain whether these areas historically supported anadromous fish (Gustafson et al. 1997; Spies et al. 2007). Other examples include Sockeye Salmon in Frazer Lake, Alaska (Burger et al. 2000), Pink Salmon in the Great Lakes (Kwain 1987), and Chinook Salmon in New Zealand (Quinn et al. 2001). Collectively, these results suggest that it is possible to establish runs of anadromous fish through hatchery releases, and perhaps failed reintroduction efforts did not adequately solve the problems that caused extirpation in the first place (i.e., constraints).

Employed in a conservation setting, hatcheries generally aim to reduce the early life mortality that occurs in the egg incubation and juvenile-rearing phase relative to that of natural spawning (Waples et al. 2007a). Thus hatchery releases have the potential to approach juvenile-rearing carrying capacities faster than the other two approaches, and this may ultimately lead to a greater number of adults returning to the reintroduction site within a generation or two of reintroduction. In addition, hatchery releases may provide opportunities to test the effectiveness of new passage facilities without risking wild fish from a low-abundance source population.

However, even if managed properly, hatchery releases pose significant evolutionary and ecological risks. Domestication selection, or adaptation to a captive-breeding environment, can reduce the fitness of animals released into the wild (Frankham 2008) as well as the fitness of the wild component of a supplemented population (Ford 2002). Indeed, hatchery fish often have lower reproductive success than naturally spawned fish when both groups breed sympatrically in the wild (Araki et al. 2008), and domestication selection, which can occur in a single generation, seems a likely mechanism (Christie et al. 2012; Ford et al. 2012). Large-scale hatchery programs tend to erode population structure more than small ones (Eldridge and Naish 2007), so the risk of genetic homogenization is likely to be proportional to the number of fish released. In terms of ecological risks, hatchery releases could induce density-dependent processes that would limit the growth, survival, and other vital rates of naturally produced fish (Buhle et al. 2009; Kostow 2009).

These risks apply not only to the incipient population within the reintroduction site but also to any nearby extant populations. Hatchery reintroduction programs should therefore aim to minimize straying to proximate extant populations. Acclimating juvenile hatchery fish in the target area prior to release may improve the precision of homing (Dittman et al. 2010). Hatchery fish released into a reintroduction site may also interact ecologically with juvenile wild fish originating from proximate spawning areas in downstream rearing habitats, potentially competing for limited resources. The specific breeding protocols and rearing practices will influence the severity of these ecological and evolutionary effects, but some level of risk is unavoidable.

An important consideration for hatchery reintroductions is the length of time over which supplementation is planned. Evolutionary and ecological risks will tend to increase with the duration and magnitude of hatchery releases. A precautionary model would aim for a brief release of one to two generations, followed by cessation for at least a similar time frame, accompanied by a monitoring program to track performance. Such a pulsed release would provide the initial demographic boost to establish a population in an area unlikely to be colonized naturally and subsequently permit natural and sexual selection to shape local adaptation and the expression of natural diversity patterns. In the event that more than a generation or two of supplementation is needed to rebuild the run, specifying a timeline for phasing out releases in a detailed plan prior to reintroduction will help prevent hatchery efforts from becoming institutionalized. Abundance targets for naturally spawned fish would indicate when the incipient population has sufficient reproductive potential without supplementation. Contingencies for short-term environmental trends would permit flexibility in the timeline should poor migratory or ocean survival delay population establishment.

Choice of Source Population

Source populations with life history, morphological, and behavioral traits compatible with the target area will increase the probability of successful reintroduction. Anadromous salmonids are frequently adapted to local environmental conditions (Taylor 1991; Fraser et al. 2011), and so some source populations may be more successful than others during colonization. For example, following circumvention of a natural barrier, multiple populations of Sockeye Salmon were introduced to Fraser Lake, Alaska, and each preferentially colonized the habitats most similar to the source (Burger et al. 2000). Reintroductions employing transplants or hatchery releases must explicitly choose a source population; evaluating potential sources of natural colonization will help predict patterns of population expansion (Pess et al. 2008) and interpret reintroduction results (Burton et al. 2013). We suggest that reintroduction planners consider the genetic and ecological characteristics of potential source populations.

In general, selecting a source genetically similar to the historic population that inhabited the reintroduction site would maximize the benefits and reduce the risks of a reintroduction. Matching the genetic lineage of the extirpated population or spawning area as closely as possible helps ensure that following a successful reintroduction, regional population structure would accurately represent natural patterns of evolutionary diversity and thus contribute to long-term ESU viability. The evolutionary risks of straying to adjacent populations during reintroduction will be reduced if the source is genetically similar to these populations. In practice, genetic analysis may not be possible, so one might assume an isolation-by-distance model (e.g., Matala et al. 2011) and use the distance along the river corridor between the reintroduction site and source as a coarse guide for comparing options. Regardless of the specific criteria, ESUs were designated to comprise lineages with a distinct evolutionary legacy (Waples 1991), so reintroductions using sources with out-of-ESU ancestry would rarely, if ever, be expected to provide clear conservation benefits to an ESU.

Ecological considerations should focus on the morphological and behavioral traits of the source population and whether they are well suited for the reintroduction site. One approach is to assume that similar habitats promote the evolution of similar traits and evaluate metrics such as elevation, precipitation, and hydrologic patterns or composite indices such as the U.S. Environmental Protection Agency's ecoregions. However, sometimes genetic and ecological patterns will be in conflict. Some coastal rivers, for example, contain both fall- and spring-run Chinook Salmon populations, which are more genetically similar to each other than to other populations of the same run type in different major rivers (Waples et al. 2004). In these cases, selecting a source population will involve some degree of compromise.

Potential source populations affected by hatchery production require special consideration. Three main factors will determine the ecological and genetic suitability of a hatchery stock. The first is its origin. Stocks that were founded with individuals collected near the reintroduction site, preferably within the same basin, present less evolutionary risk than more distantly related stocks. Many of the most widespread hatchery stocks are mixed-lineage, composite-origin stocks with significant contributions from several populations, sometimes from separate ESUs (Busby et al. 1996; Myers et al. 1998). Although these stocks are probably the most available, and hence logistically practicable for reintroductions, they also pose much greater evolutionary risks than locally derived stocks. A second consideration is the current breeding protocol. Programs that operate under an integrated model by consistently incorporating wild or naturally spawned broodstock (without posing demographic risks to that population) will reduce (but not eliminate) domestication selection compared with segregated programs (Mobrand et al. 2005). A final consideration is the number of generations that the stock has been artificially propagated. Domestication selection accumulates over time, making populations that have been artificially propagated for many generations less similar to their wild counterparts than stocks that have been in captivity for few generations (Araki et al. 2008; Frankham 2008). In some cases, a hatchery stock directly derived from native fish that inhabited the reintroduction site may retain the only genetic legacy of the extirpated population and may be desirable for that reason.

What are the options if there is an unacceptable demographic risk of depleting the most attractive source population? In some cases, managers must either wait for the most appropriate stock to recover to levels that could sustain removal or select a less desirable stock that can immediately provide sufficient donors. This is a difficult trade-off, especially if recovery of depleted potential source populations is uncertain or is expected to take several generations even under optimistic scenarios. When removal does occur, monitoring should track the source population abundance during reintroduction to ensure that it remains healthy. If a single population cannot sustain removal for reintroduction, it may be possible to combine individuals from several sources. From a genetic perspective, this could have either positive or negative consequences. On one hand, mixing sources could benefit the genetic diversity of the colonist group, but on the other, it could lower fitness via outbreeding depression (Huff et al. 2010).

Finally, for facultatively migratory species, the presence of resident conspecifics may provide additional reproductive potential and serve as a source population. For example, resident Rainbow Trout frequently spawn with anadromous steelhead (McMillan et al. 2007; Pearsons et al. 2007). In fact, *O. mykiss* often exhibit partial anadromy in which a single, panmictic, interbreeding population contains both resident and migratory individuals (McPhee et al. 2007; Heath et al. 2008). Resident populations isolated by dams may retain significant anadromous ancestry and the physiological traits of smoltification (Clemento et al. 2009; Godbout et al. 2011; Holecek et al. 2012). However, if selection against anadromy has occurred in the resident population, it is also possible that secondary contact with reintroduced anadromous fish might decrease the rate of anadromy in the combined population. Life history models (Satterthwaite et al. 2009, 2010) offer one method of predicting the complicated interactions between resident fish and reintroduced anadromous populations. Regardless, we suggest that promoting the persistence and reproductive contribution of resident fish directly descended from formerly anadromous populations inhabiting the reintroduction site will ultimately contribute to local adaptation, diversity, and long-term viability.

Providing Passage

Providing passage is relevant to all reintroductions involving barriers regardless of the colonization strategy or the choice of source population. This must include passage for adults migrating upstream to spawning grounds as well as juveniles migrating downstream towards the ocean. Plans for passage can be categorized as either volitional or active transport (i.e., trap and haul).

Under volitional passage, a barrier is modified or removed such that fish arrive at the site under their own power, swimming through or around and eventually past the former blockage. Primary examples include culvert replacements, dam removals, engineered step-pools, fish ladders, increased releases from upstream dams, and screened bypass facilities for juveniles. Volitional fish passage facilities have advantages over more managed methods because they operate constantly, require little if any handling, are less stressful to the fish, are mechanically less likely to break, and are less costly to maintain and operate. A primary biological consideration is the degree to which passage structures reduce juvenile and adult migrant survival relative to a free-flowing river. Unnaturally high mortality imposed by passage at barriers will have to be compensated for elsewhere in the lifecycle to maintain a self-sustaining population. Furthermore, depending on the design, water velocity and gradient may restrict passage to certain species or size-classes, reducing the diversity of the incipient population. If poorly designed, passage facilities could increase the risk of straying into nontarget populations or spawning areas.

Barrier or dam removal is a special case of volitional passage that will provide substantial ecological benefits beyond salmonid recovery. Dam removal can repair riverine ecosystem processes, such as natural flow regime, sediment and wood transport, and nutrient cycling, that create and maintain habitat for many plants and animals (Poff and Hart 2002; Roni et al. 2008). The rehabilitation of these processes, especially where they have been substantially altered, will certainly provide long-term benefits for the Pacific salmon and steelhead populations targeted for reintroduction. However, in the short term, dam removal is a disturbance that may increase turbidity and deposit fine sediment downstream or mobilize toxic-laden materials (Stanley and Doyle 2003). Therefore, it is an approach most appropriate for enhancing long-term viability rather than rapid increases in abundance, and these "side effects" are important considerations for the planning process. Several recent dam removals (Table 5) provide important opportunities to study the salmonid response to dam removal.

In some cases, it may be possible to incorporate selective access into a volitional passage strategy. This would involve a weir, gate, or trap such that fish are handled prior to upstream passage. Such structures increase operation and maintenance costs and may adversely affect adults due to increased handling. However, they also allow managers to exclude fish that could undermine reintroduction objectives. For example, excluding the homogenizing influence of hatchery colonists may benefit diversity and excluding nonnative fish would reduce the ecological risks of reintroduction. Such structures would also assist research and monitoring because they would permit precise counts and measurements of fish.

Active transport, sometimes called trap and haul, is most appropriate for situations in which volitional passage is not logistically, technically, or biologically possible. Large dams, especially several occurring in sequence, are more likely to require trap and haul than small structures due to engineering and socioeconomic constraints. Particularly for juveniles, impoundments may present challenges that cannot be overcome with volitional passage, such as low water velocity that disrupts fish migration, predators that reduce survival below acceptable levels, or downstream passage routes that cannot be engineered to be safe and effective. Selection or exclusion of particular groups of fish will be fundamentally simple. Passage via trap and haul is similar in concept to a transplanting colonization strategy and thus has many of the same benefits, risks, and consequences.

Trap and haul, often combined with hatchery releases, is employed in several ongoing large-scale reintroduction efforts (Table 5). These examples will provide crucial case studies to evaluate the success and refine the methods of reintroducing Pacific salmon and steelhead above large, high-head dams. Research on the Middle Fork Willamette River, Oregon, has found significant prespawn mortality related to poor condition of spring Chinook Salmon adults prior to release and warm temperatures encountered in the migration corridor (Keefer et al. 2010). In addition, juvenile mortality at dams was high and deep-water passage routes severely restricted passage in the spring, when Chinook Salmon would ordinarily migrate downstream but reservoirs were filling rapidly (Keefer et al. 2011).

Despite few published examples, we suspect that at high-head dams, transporting adults upstream is much easier (and less expensive) than providing safe, efficient downstream passage for their offspring. Juvenile fish will be vulnerable to size-selective predation in reservoirs (Poe et al. 1991; Fritts and Pearsons 2006) and dam passage mortality unless they are collected and routed around these hazards. Survival rates will vary by species, life stage, and timing of migration but are likely to depend on the efficiency of juvenile collection methods and the design of engineered bypasses at dams. In some cases, successful reintroduction will require a mechanistic understanding of dam passage mortality, but this is difficult to predict generally and varies substantially by dam. For example, some studies have found greater mortality in small fish (Ferguson et al. 2007) while others found greater mortality in large fish (Keefer et al. 2011). Consequently, detailed studies of route-specific juvenile mortality rates are likely to be an essential component of reintroductions involving active transport (Keefer et al. 2011).

Execution Overview

One thing is clear—each case will be unique, and reintroduction planners will face trade-offs between the benefits and risks in selecting a colonization strategy, choosing a source population, and providing passage. These options need not be mutually exclusive, as a carefully planned reintroduction program may decide to use multiple colonization strategies. A precautionary model would initially adopt a low-risk approach and monitor its success, thereby permitting a scientific evaluation of whether higher-risk strategies are necessary. For active reintroduction strategies, planners could view an initially small release as a pilot study to assess reintroduction benefits and risks prior to full implementation.

Our review of the salmonid reintroduction literature (e.g., Table 4) suggests that there are large uncertainties in the success of reintroduction in establishing self-sustaining populations, particularly for programs employing active colonization strategies. Despite the increased risks of methods such as transplanting adults and hatchery releases, we found no direct evidence that these approaches have established a demographically independent, self-sustaining natural population. It is possible that situations in which active methods have been employed are inherently more difficult, but a lack of rigorous scientific evaluation precludes us from describing the benefits, risks, and constraints more explicitly or quantitatively. We strongly encourage managers of reintroduction efforts to disseminate results so that we may build on lessons learned in planning future programs.

MONITORING

Monitoring is an essential component of any reintroduction program (Williams et al. 1988; IUCN 1998; George et al. 2009), permitting an assessment of whether or not the reintroduction was successful. Monitoring before, during, and after the reintroduction provides information on both the target and neighboring populations that is needed to evaluate modifications to the program execution in an adaptive management feedback loop. In addition, monitoring provides the data that is essential for the effective planning of future programs.

We suggest that the monitoring program focus on the benefits, risks, and constraints likely to have a large impact on the success of the project. First, in order to quantify the benefits and determine if the goals have been achieved, unambiguously stating project objectives at the outset will help identify specific monitoring metrics (Tear et al. 2005). Second, for reintroductions in which the initial planning efforts identified some risks (Table 2), there must be monitoring in order to determine whether the benefits outweighed the risks. Third, monitoring constraints will promote a mechanistic understanding of why a reintroduction succeeded or failed. Even where barriers block migration, other factors may have contributed to extirpation. Consequently, although some biological constraints (Table 3) may have been addressed prior to reintroduction, others may persist that will limit project success. Identifying factors that limit survival and reproductive success will provide insight towards alternative reintroduction strategies that might lessen a negative impact. The specific monitoring methods will vary depending on the benefits, risks, and constraints of the reintroduction effort; Roni (2005), Johnson et al. (2007), and Schwartz (2007) provide guidance on establishing a robust monitoring program.

It is difficult to provide general criteria on whether a reintroduction effort has succeeded or failed because every situation is likely to be different. However, writing a detailed reintroduction plan, including specific viability targets or benchmarks, is a crucial component of project implementation. This will simplify interpretation of monitoring data, clarify any need for adaptive management during the program, and prevent the institutionalization of actions (e.g., hatchery releases) that impose risk to nontarget populations or spawning areas. In deriving targets and benchmarks, the reintroduction plan should explicitly consider patterns in annual abundance, productivity, and survival of comparable populations. We strongly urge all entities conducting or planning reintroductions to write a publicly available implementation plan that includes robust monitoring because it is essential to a scientifically rigorous reintroduction effort and will improve our ability to effectively conserve species in the future.

CONCLUSIONS

We have based our approach to planning, executing, and monitoring reintroductions upon the broad conservation goals and scientific principles guiding the recovery of ESA-listed Pacific salmon and steelhead populations. We acknowledge that there are other possible goals for reintroductions, including providing harvest opportunities, which might lead to different approaches than those described here. Although our recommendations are specifically designed for ESA recovery, more generally they are intended to promote the natural demographic, ecological, and evolutionary processes essential to the conservation benefit of all reintroductions, regardless of formal listing status. Even in cases where ESA recovery is not the primary goal, the concepts discussed here will help evaluate the overall conservation value of a reintroduction (Figure 5).

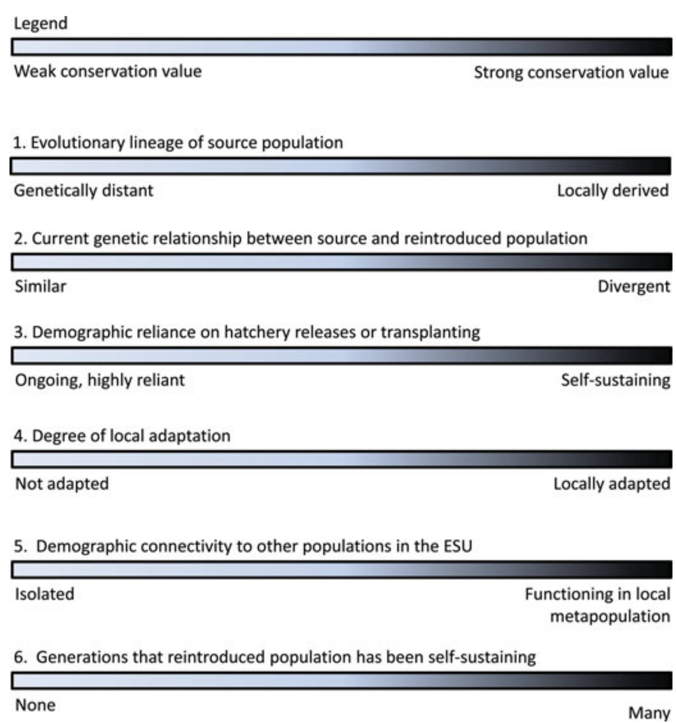

FIGURE 5. Factors to consider in evaluating the conservation value of reintroductions. Each bar is intended to represent a gradient of outcomes in between the extremes described at either end. The extent to which natural demographic, ecological, and evolutionary processes operate uninterrupted will strongly influence the overall conservation value of a reintroduction.

Despite the number of salmonid reintroductions (e.g., Tables 4 and 5), the science of reestablishing previously extirpated salmonid populations is still in its infancy. We found few direct assessments of reintroduction benefits, risks, and constraints, forcing us to provide general, qualitative rather than specific, quantitative recommendations. If reintroduction is to become a successful recovery tool, it is essential that monitoring and dissemination of results become standard practice in nearly every program. Rigorous scientific evaluation is particularly important for projects at large dams or those using active colonization strategies because they face the highest constraints and greatest risks.

The number and scale of Pacific salmon and steelhead extirpations suggest that reintroduction offers great potential to advance salmon recovery. However, complicated trade-offs, challenging obstacles, and uncertainty over the ultimate result confront reintroduction planners. Combined with the multiple generations probably required to achieve potential benefits, this suggests that reintroduction will rarely be a quick fix for improving the status of an ESU or population at immediate risk of extinction. It is also important to remember that reintroduction is only one management option. In some cases, reintroduction may be essential for the conservation of a particular life history type or evolutionary lineage. In other cases, management strategies designed to improve the reproductive success, survival, and productivity of extant populations might offer a better return on the investment dollar than reintroduction. We suggest that evaluating the potential benefits, risks, and constraints is necessary to weigh reintroduction against other management options and ensure that reintroductions contribute to long-term population and ESU viability.

ACKNOWLEDGMENTS

Funding support for J.H.A. was provided by the U.S. National Research Council's Research Associateship Program. Discussions with the Recovery Implementation Science Team contributed to the concepts presented in this paper. We thank Lynne Krasnow, Ritchie Graves, Rick Gustafson, and four anonymous reviewers for helpful comments on earlier drafts of the manuscript.

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