

**Anadromous Salmonid Reintroductions:
General Planning Principles for Long-term Viability and Recovery**

Final Review Draft

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Section I. General principles for Salmonid Reintroductions

Introduction

Reintroducing animals to areas which they have been extirpated has emerged as a common and 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 very brink of extinction (e.g., Arabian oryx: Spalton et al. 1999, alpine ibex: Stüwe and Nievergelt 1991). However, despite considerable cost and effort, reintroduction efforts often fail to establish self-sustaining populations (Fischer and Lindenmayer 2000, Wolf et al. 1996) so there is no guarantee of success. A recent explosion of reintroduction literature suggests that scientifically based management principles can substantially improve the efficacy of these efforts (Armstrong and Seddon 2008, Seddon et al. 2007).

Reestablishment of self-sustaining natural production offers an enormous potential to benefit the conservation of Pacific salmon (*Oncorhynchus* spp.). For many populations of salmon, the primary cause of local extirpation is easily identified: obstructed access to suitable spawning and rearing habitats by dams or other stream blockages. In total, Pacific salmon (*Oncorhynchus* spp.) have been extirpated from 44% of the habitat they historically occupied by large barriers alone in western contiguous United States (McClure et al. 2008a). In addition to these substantial barriers, there are countless smaller structures such as water diversion dams, culverts (Gibson et al. 2005), and 'push-up' dams that also limit access to anadromous salmonid habitat. Although dams are clearly not the only cause of declining salmon populations or local extirpations (National Research Council 1996), they are one of the most widespread and their removal or circumvention provide countless opportunities for reintroduction throughout the native ranges of Pacific salmon.

Any salmonid reintroduction effort will have to grapple with a variety of challenges throughout the process. First, which of the many populations that have suffered complete or partial extirpation should be prioritized for reintroduction? In order to maximize effectiveness, conservation planners must consider the conservation benefit of a particular project so that it can be weighed against the risks, costs and compared to other management options (including other reintroduction sites). Second, what methods should be used to reintroduce salmon and steelhead? Captive breeding and artificial propagation has been crucial to reintroduction success

in many species, but also carries genetic (Frankham 2008, Fraser 2008) and ecological risks (Kostow 2009) that could compromise the probability of population establishment or reduce the viability of non-target populations. Third, how should management evaluate whether or not efforts have been successful? This judgment will determine if reintroduction methods should be adapted based on initial results, and additionally inform the best practices in future programs elsewhere.

Depending on the location and execution methodology, there are also a number of potentially insidious biological risks associated with salmonid reintroductions. Well intended efforts could have undesirable consequences such as facilitating invasion by nonnative species (Fausch et al. 2009) or promoting the spread of disease (Walker et al. 2008). The source population may suffer if it cannot sustain removal of individuals for translocation or broodstock, and if nonlocal fish are propagated and released at the reintroduction site, excessive straying could erode the genetic structure of nearby extant populations. Thus, “do no harm” should serve as a guiding principle for reintroduction efforts (George et al. 2009), and careful planning, execution and monitoring of reintroduction programs are essential components of ensuring their long-term success.

There are also a number of constraints that will affect whether or not reintroduced fish effectively establish a population. The number, size, and spatial arrangement of barriers will largely determine reintroduction pathways, and may require prioritization among multiple alternative options. Habitat quality within the new habitat, including likely future changes due to climate or land use patterns, will ultimately govern the reproductive success of colonists and early life survival of their offspring. In addition, out of basin survival during migration through downstream dams and in the ocean will have a large influence on the success of reintroductions. Finally, there are a number of evolutionary considerations that will affect the selection of a source population, management during colonization, and the time frame needed to achieve recovery objectives

In this paper, we provide recommendations for planning reintroductions of anadromous salmonids. These guidelines are intended to help design reintroduction programs that establish or expand self-sustaining natural populations that contribute to the recovery of salmon and steelhead listed under the U.S. Endangered Species Act (ESA). The initial focus is on the Interior Columbia River basin because this area has suffered dramatic declines in population

status. Our approach includes first, evaluating the biological net benefits by identifying the goals and potential benefits of reintroduction and characterizing the biological risks and constraints of a reintroduction. Then, revisiting the risks and constraints in order to explore costs and benefits of alternative execution approaches, and finishing with monitoring population status following reintroduction. A major element of our framework is the identification of reintroduction benefits to recovery objectives, because these will inform the precise actions taken during reintroduction. Importantly, we constructed our framework in the context of achieving broad, species (or ESU)-wide conservation objectives. We focus on biological issues, anticipating that for those reintroduction efforts that are likely to have high conservation potential, a socioeconomic cost-benefit analysis will follow.

Interior Columbia River Basin

The Columbia River basin encompasses more than 640,000 km² with a diverse array of aquatic and terrestrial habitats in the Pacific Northwest. This region historically produced about 8 to 16 million salmon and steelhead annually (Chapman 1986, Northwest Power Planning Council 1986), one of the largest runs of anadromous salmon in the world. However, salmon populations in the Columbia basin have undergone substantial decline following settlement of the region by euro-Americans (Lichatowich 1999). Currently, there are 13 Evolutionary Significant Units (ESUs, which meet the definition of “Distinct Population Segment”), listed as threatened or endangered under the U.S. Endangered Species Act (ESA) in the Columbia River basin alone. Interior regions east of the Cascade mountains have suffered higher proportional population loss than coastal areas (Gustafson et al. 2007), suggesting that human impacts have been more severe and/or the salmon inhabiting the interior are more vulnerable to human activities, which range from overfishing, hydroelectric development, habitat degradation, and hatchery supplementation (National Research Council 1996).

Under the ESA, ESUs are the unit, for salmonids, that can be listed as threatened or endangered. Once ESUs were listed, Technical Recovery Teams (TRTs) were convened to describe population structure (i.e. identify units that were demographically independent on a 100-year time frame (ICTRT 2003, McElhany et al. 2000)), and to establish biological viability criteria for populations and ESUs. Nearly all TRTs, including the Interior Columbia TRT (ICTRT) also recognizes major population groups (MPGs) consisting of multiple populations

that share genetic, geographic and habitat characteristics within the ESU. Within each population, the ICTRT also identified spawning areas, both major and minor depending on the quantity of habitat, in order to describe viability criteria based on finer scale spatial structure.

The interior Columbia offers substantial opportunities for salmon reintroduction. Approximately 55 % of the area in the Columbia River basin historically occupied by salmon (Figure 1) and steelhead (Figure 2) is blocked by dams or other barriers (National Research Council 1996). There are also a number of areas, such as Panther Creek in the Salmon River drainage, that have been extirpated due to mining impacts or other large-scale habitat alterations, even without the presence of a barrier to passage (Platts 1972). If carefully planned and executed, reintroduction offers the potential to contribute to the improved status, long-term viability and recovery of listed interior Columbia ESUs, and may, under unique conditions, reduce short-term extinction risk or provide additional benefits such as harvest.

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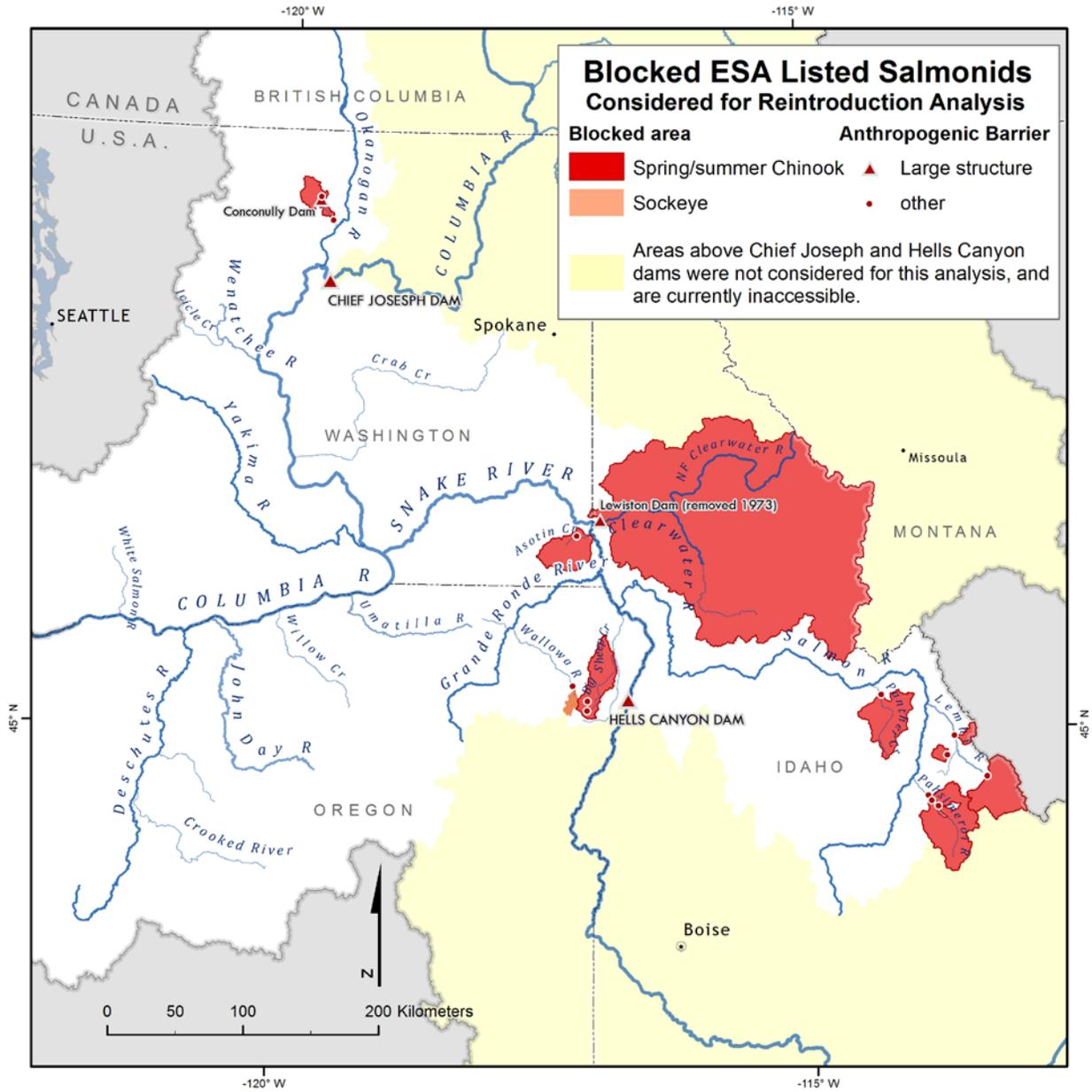


Figure 1. Areas historically occupied by spring/summer Chinook salmon and sockeye salmon that no longer support viable populations within the interior Columbia River basin below Hells Canyon (Snake River) and Chief Joseph (Columbia River).

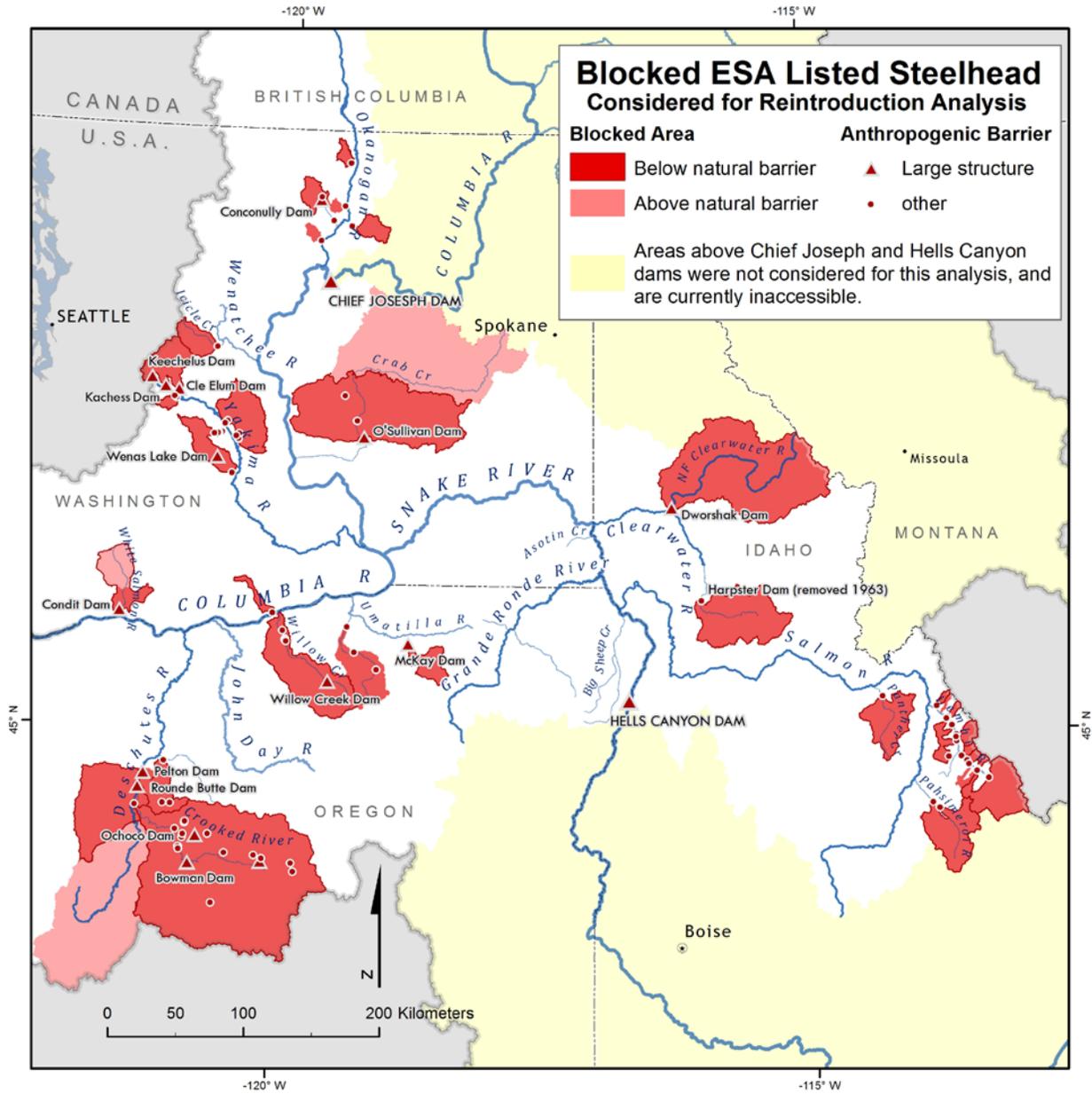


Figure 2. Areas historically occupied by steelhead that no longer support viable populations within the interior Columbia River basin below Hells Canyon (Snake River) and Chief Joseph (Columbia River).

Establishing goals, objectives and identifying potential benefits

Goals, objectives and benefits are closely tied to each other. Establishing goals is a key first step for any project. For conservation projects, goals typically include re-establishment or maintenance of a self-sustaining population, or the long-term persistence of an ecosystem and its functions, but can also include other societal benefits such as recreational opportunities, harvest of particular species or ecosystem services (Tear et al. 2005). Although our focus is on reintroductions for conservation and recovery purposes, the steps we outline are appropriate for any reintroduction effort. From goals, should flow specific and measurable objectives, which provide the benchmarks to determine when and if a project has achieved success. Finally, identifying potential benefits of a project allows one to determine whether the proposed project is consistent with the goals and objectives and thus provides an initial check for whether a project is appropriate to pursue.

Establishing goals

The goals of a reintroduction effort can inform the approaches and strategies for re-establishing a population as well as the metrics used to judge when success has been achieved. Thus, establishing those goals clearly is a key element of any reintroduction effort, since reintroductions can have goals other than enhancing population and ESU viability. From a general perspective, these could include restoration of ecosystem functions (Byers et al. 2006), raising awareness of conservation issues (Vettorazzo et al. 2009), stimulation of local economies (Lindsey et al. 2005), or providing social and cultural benefits. For salmon and steelhead, the most obvious additional goal is providing harvest opportunities for recreational, commercial or tribal fisheries.

In this paper, we assume that a primary goal of these reintroduction efforts is reducing extinction risk and contributing to long-term recovery for ESA-listed anadromous salmonids. A first step in establishing goals for a reintroduction effort is to determine the desired status of population(s) targeted for recovery. The ICTRT developed a set of scenarios of desired population status for populations within each MPG in the Interior Columbia that are consistent with biological viability goals (ICTRT 2007), and we use these as our basis. In other regions, similar planning efforts should consider the biological attributes of a viable population, ESU, or

species. In situations where goals are not dictated by legal requirements (such as the ESA and its various processes), goals are best developed with robust stakeholder input and collaboration as well as consideration of trade-offs between alternative, and potentially conflicting, goals (Tear et al. 2005).

Establishing objectives

A second component of developing expectations for any project, including reintroductions, is developing explicit objectives, or a picture of the desired ‘end-state.’ As with any well defined objectives, reintroduction objectives (Tear et al. 2005) are:

- measurable
- time-limited (i.e. the time in which the objectives are to be achieved is specified and realistic)
- specific
- scientifically-based

McElhany et al. (2000) advanced a framework for evaluating the viability of salmon populations and ESUs listed under the ESA based on four parameters: abundance, productivity, spatial structure, and diversity. The ICTRT applied these general recovery concepts in the development of detailed biological criteria and metrics specific to the populations, MPGs and ESUs within the Interior Columbia (ICTRT 2007). The ICTRT criteria have been incorporated into recovery plans developed by local stakeholder groups within each watershed contained ESA-listed populations. We use these criteria, which are based on McElhany et al.’s (2000) viability parameters, in this effort.

There exists a fundamental distinction in the contribution to recovery objectives between reintroductions that expand an extant population and those that establish new populations. Reintroduction can enhance the viability of an existing population by targeting a region continuous with the current spawning distribution. In this case, long term demographic coupling between the reintroduction area and the initial source of colonists is consistent with recovery objectives. On the other hand, reintroductions can target extirpated populations that historically functioned as autonomous units and are currently isolated from occupied habitats. In order to contribute to recovery objectives, these areas must, at some point, become demographically independent, self-sustaining, and genetically divergent from the source population. Simply occupying habitat is not sufficient to demonstrate establishment of a new population, the area

must have its own evolutionary and demographic trajectory or else it will simply be a spatial extension of an existing population.

Determining likely benefits of a reintroduction

Estimating the magnitude and nature of the potential benefits afforded by reintroduction is a primary element of planning, and is the first step in determining whether a potential reintroduction will support ultimate goals sufficiently to pursue further planning and implementation. Benefits will provide the basis of evaluating overall project effectiveness, and must be weighed against the risks and constraints in prioritizing amongst multiple reintroduction sites (Figure 3). Expected progress towards recovery criteria must also be compared to the social and economic costs of reintroduction actions (e.g., barrier removal) in determining whether or not to proceed with a project. Many of the concepts fundamental to the four viability parameters are couched in metapopulation ecology (Hanski 1999), which is readily applied to anadromous salmonids (Schtickzelle and Quinn 2007). We consider ESUs and MPGs analogous to metapopulations, with MPGs perhaps more restrictive in application to metapopulation models because of their smaller spatial scale. Re-occupation of an area can have effects at the population, the Major Population Group (MPG) and the ESU levels, and all of these should factor into a cost-benefit analysis. Benefits are also dependent upon the current status of the population, MPG or ESU, because the most effective reintroductions will address a viability characteristic that is currently impaired. In this section, we explain the importance of each viability parameter and how reintroduction could improve their status.

Abundance. Abundance is the total number of fish in a population, MPG, or ESU, and is important to viability for a variety of reasons. First, high abundance serves to shield a population from extinction due to stochastic variability (Lande 1993). Second, genetic processes that can reduce fitness such as loss of diversity, inbreeding and accumulation of deleterious mutations are more severe at low population sizes (Allendorf and Luikart 2007). Third, abundance will affect population dynamics through density-dependent processes. Compensation, or increasing productivity at low abundances due to greater per capita resource availability, is often observed in salmon (Ricker 1954) and would suggest that populations are resilient to low abundances. However, depensatory processes (also known as the Allee effect) may decrease per capita growth

rate at low densities (Courchamp et al. 1999, Liermann and Hilborn 2001), and this would tend to increase the risk of extinction for low abundance populations. Finally, low abundances may

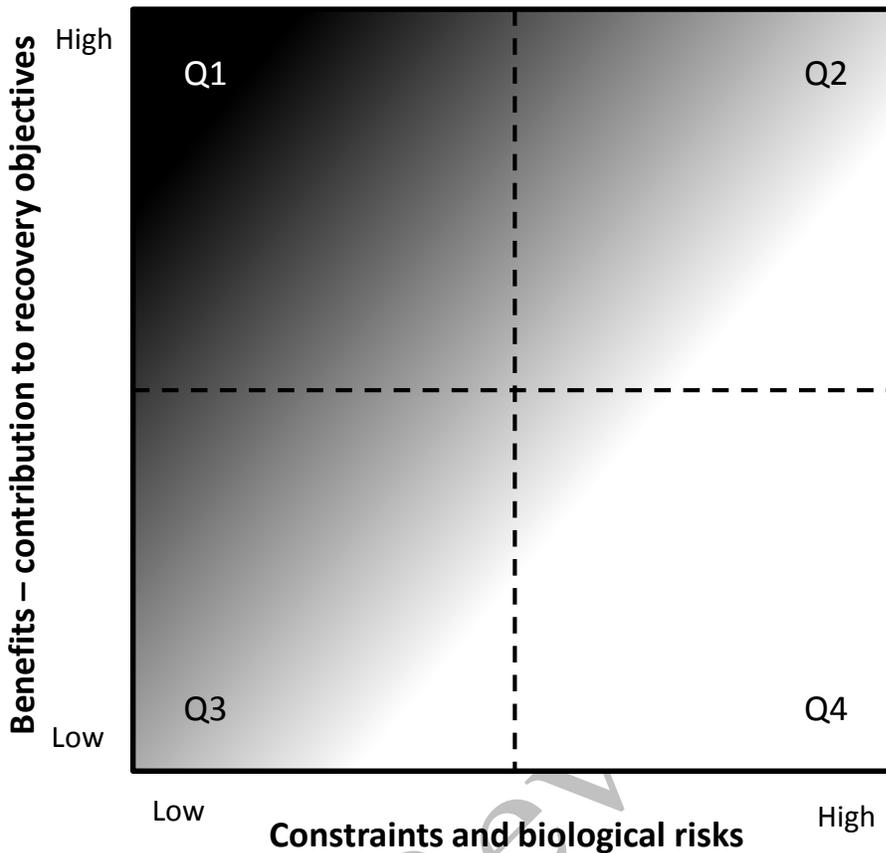


Figure 3. Framework for gauging net benefit of reintroduction options. In each case, the contribution to recovery objectives (positive outcomes) are weighed against the constraints to implementation and the biological risks (unintended negative consequences) of the project. In quadrant 1 (Q1), the benefits are high and the overall constraints and risks are low, providing the best opportunity for reintroduction to effectively contribute to recovery objectives. Quadrant 2 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 and 4 relatively low benefits; some in quadrant 2 may be selected owing to low risk and ease of execution, whereas those in quadrant 4 will generally be avoided.

decouple ecological feedbacks important for healthy, productive salmon populations such as deposition of marine derived nutrients (Gende et al. 2002) and increasing the quality of spawning gravels through bioturbation (Moore et al. 2004).

Reintroductions can improve the abundance of both populations and larger units such as MPGs and ESUs. At the population scale, reintroduction can boost the capacity of an existing

population if the target area expands, and is relatively continuous with, the current spawning distribution. Ideally, the potential for numerical growth within extant populations are roughly determined by the proportional increase in occupied habitat and should be evaluated relative to pre-determined management thresholds (e.g. the ICTRT's minimum abundance criteria). Thus, reintroductions in populations that are restricted to a small proportion of their historical habitat with current abundances well below target levels will be most valuable. In addition, reintroduction can establish a new, discrete, demographically independent population rather than expand an existing one, and this would have significance to the number of populations (hence abundance) within an MPG or ESU. Adding populations reduces extinction risk of the entire ESU most rapidly for ESUs with few populations (Ruckelhaus et al. 2003), so the benefits of reintroduction will be greatest in these depauperate regions. This is related to the concept of spatial structure, and discussed more thoroughly in that section.

Productivity. Productivity is one of the most fundamental drivers of long-term persistence of a population or metapopulation, and is generally defined as the ratio of number of animals in general t to the number of animals that produced them in generation $t - 1$. Considered in isolation from one another, populations whose productivity exceeds replacement are self-sustaining, whereas those with continual negative growth rates, even with current high abundance, cannot persist in the long-term. Whether or not a population is a source (net demographic excess) or a sink (net demographic deficit) will largely depend on habitat quality, and migration between populations allows for coupled population dynamics (Dias 1996). Given sufficient connectivity, highly productive populations can support the persistence of sinks (Pulliam 1988) and foster colonization of currently unoccupied areas.

Reintroductions can have either positive or negative impacts on productivity of a given population, MPG or ESU, depending on the quality of the new habitat and survival through migration and ocean rearing. At all levels of population structure, a reintroduction effort that results in a 'sink' is of far less value for long-term viability than one that is at least self-sustaining. Indeed, reintroduction to a sink would result in a net loss if the animals would have been more productive in their natal habitat. The risk of a sink primarily applies to reintroductions that use a natural (rather than hatchery) populations as the source, so it is

dependent on execution methodology. In general, therefore, higher quality habitats and systems with fewer migration corridor impairments are likely to provide the greatest benefit.

Spatial structure. Spatial structure refers to the arrangement of populations across the landscape, the distribution of spawners within a population, and the processes that produce these patterns. Homing to discrete natal spawning sites allows salmonids to evolve adaptations to the local environmental conditions (Taylor 1991), whereas immigration from one population to another (i.e., 'straying') promotes genetic and demographic connectivity between populations. Some level of connectivity is beneficial because it can provide new genetic material essential for fitness in demes suffering from fragmentation (Tallmon et al. 2004) and demographically rescue populations experiencing periods of low productivity or abundance (Pulliam 1988). However, excessive connectivity can have negative consequences such as genetic homogenization (Barbanera et al. 2010) and demographic synchrony (Liebhold et al. 2004), both of which would tend to reduce resilience (see next section on Diversity). Finally, spatial structure affects extinction probability because with dispersed subunits, a single impact or catastrophe is less likely to affect the entire population than a single aggregation of individuals (Good et al. 2008).

Reintroductions offer an opportunity to restore historical patterns of spatial structure and connectivity. The risk of extinction due to single catastrophic event would be decreased the most in MPGs or ESUs with relatively few extant populations (Ruckelhaus et al. 2003). In terms of connectivity, reintroductions that reduce the isolation of extant populations will be the most valuable. In practice, this can be estimated as the extent to which a newly established population would reduce gaps (potentially measured in stream kilometers) between spawning areas or populations that were not historically separated. Given the spatial arrangement, models of dispersal, and estimates of historic abundances, reintroduction could also target areas that historically had a significant role in metapopulation connectivity and served as sources supporting less productive populations (Fullerton et al. in press). Within populations, the topology of spawning areas should also be considered, as a reintroduction that creates a dendritic structure from a linear one is more beneficial than a reintroduction that extends a simple linear arrangement.

Diversity. Phenotypic, genetic and life-history diversity provide stability and resilience to unpredictable natural and anthropogenic environmental change. Analogous to the performance of financial portfolios spread amongst many assets, life history diversity increases population productivity (Greene et al. 2010) and enhances ecosystem services (Schindler et al. 2010). Discrete populations spanning a heterogeneous landscape tend to exhibit asynchronous population dynamics in response to climatic change and local environmental conditions (Crozier and Zabel 2006, Rogers and Schindler 2008). Asynchrony is thought to result from within species life history diversity, complex population structure and local adaptations (Hilborn et al. 2003, Schindler et al. 2010), and reduces extinction risk (Moore et al. 2010). Two primary factors, both of which can be ameliorated to some extent by reintroductions, have tended to reduce the diversity of Pacific salmon. In many cases, dams have truncated diversity by non-randomly blocking access such that certain landscape features, habitat types or hydrologic regimes are under-represented in extant populations relative to the historical distribution of salmon populations (Beechie et al. 2006, McClure et al. 2008a). Dams have also homogenized accessible aquatic habitats through river regulation (Poff et al. 2007), and in the Columbia River basin, may have reduced life history diversity by narrowing the temporal windows for both adult and juvenile survival. Secondly, large-scale hatchery releases have genetically homogenized salmon populations and narrowed the range of important life history traits (McClure et al. 2008b).

Efforts to establish self-sustaining salmon populations can enhance the diversity of a population, MPG, or ESU in a variety of ways. In some cases, contributions to diversity can be assessed directly. For example, barrier removal may provide seaward access for genetically distinct population segments of facultatively migratory species (e.g., *O. mykiss*) that historically had anadromous components but do not currently. Indirect measures can also highlight the potential for reintroduction opportunities to enrich diversity. Reintroductions into rare or unusual habitat types may provide the evolutionary template for unique local adaptations and life history traits. For example, by relaxing an anthropogenic selective pressure, removal of a barrier that restricted passage to a narrow seasonal window time would allow a greater diversity of run-timings. Managing reintroduction areas for natural production also offers a means of reducing the homogenizing influence of artificial propagation in regions where stray hatchery fish have eroded population structure. Several considerations (i.e., origin of broodstock, number of

generations domesticated, etc.) will affect the magnitude of this effect on case by case basis, and hatchery-related issues are discussed more thoroughly in the *Execution* section. Both direct and indirect measures can be used at the MPG/ESU and the population levels. However, more substantive differences in habitat type or other measures are needed to support a large effect at the MPG or ESU level diversity.

Time frame to achieve benefits

Consideration of the time frame required to achieve reintroduction benefits will help frame expectations and establish temporal benchmarks. Some very few reintroductions – for instance, those that provide access to high quality habitat in a population currently occupying a severely degraded stream – may provide immediate benefits within a generation or two, but most will require a decadal perspective. An explicit timeline from the outset of reintroduction will help manage expectations. If an implemented project suffers initial setbacks and lacks a scientifically based timeline of expectations, managers could unnecessarily abandon reintroduction or alter the execution methodology in a way that is not consistent with the ultimate goals. Anticipating the time over which results are likely to occur will also aid in the design of an appropriate monitoring program. Temporal expectations will depend on attributes of the reintroduction area and the viability parameters that the project is intended to enhance. In general, reintroduction has the potential to improve abundance and productivity much faster than diversity because the evolution of traits and new life history strategies takes many generations.

Reintroduction has the most immediate potential to increase population abundance and productivity. Pacific salmon have demonstrated an ability to rapidly colonize habitat made available by provision of fish passage or restored stream flow, barrier removal, as significant increases in abundance have been observed within 10 years (Bryant et al. 1999, Kiffney et al. 2009, Pess et al. in review). The time to achieve the full potential increase in abundance will depend on the quantity of previously unoccupied habitat, as larger areas will generally take longer to reach capacity than smaller ones. The rate of any increase in productivity will be greatest for populations or MPGs that are currently limited to poor quality habitats but reintroduced to high quality habitats. The specific reintroduction techniques will also have a strong influence on the time required to boost abundance and productivity (detailed discussed in *Execution* section). Increasing abundance via reintroduction may take longer in interior

populations relative to coastal areas due to the influence of out of basin constraints such as migration survival through multiple hydropower systems.

The full benefits to diversity will take longer to accrue because some level of adaptive evolution is required. Salmonids exhibit substantial phenotypic plasticity (Hutchings 2011), so reintroduction to novel habitat types may permit immediate non-genetic diversification of behavioral or morphological phenotypes. For example, providing access to tributaries in a population previously restricted to the mainstem river will allow juveniles to adopt new rearing strategies. However, adaptive evolution to new environments and development of genetic substructure, both key components of reintroduction diversity benefits, will take multiple generations to accumulate. Salmonids have evolved population structure within 20 years of introduction to new environments (Ayllon et al. 2006), but studies providing evidence that such divergence is adaptive have occurred over 50 (Hendry et al. 2000) to 100 year (Koskinen et al. 2002, Quinn et al. 2001) time frames.

Generally, reintroductions with a high potential for evolutionary diversification will take longer to achieve the full benefit. Reintroduction to large watersheds with a complex arrangement of numerous sub-basins, disparate ecoregions and distinct spawning reaches provide the greatest opportunity to enhance diversity, but will require multiple rounds of colonization, establishment and development of reproductive isolation. The time to observe adaptive evolution would be further increased if the area in question had no evolutionary legacy and was sourced with a distantly related population. On the other hand, expansion of an extant population into a new habitat similar to previously occupied areas offers less opportunity for diversification, but historic patterns of substructure could be realized sooner.

Finally, it is often worth considering trade-offs between shorter and longer-term perspectives. In some cases, there may be greater benefits to viability that can be accrued with a longer-term (and often more difficult) effort that contrast with smaller benefits in a shorter time frame. Thus, the amount of benefit, the time and effort in which the benefit can be achieved and the uncertainty in achieving those benefits all factor into developing appropriate objectives and strategies for reintroductions.

Evaluating Biological Risks and Constraints

The other half of evaluating a potential reintroduction's overall biological impacts is assessing biological risks and constraints to establishing a self-sustaining population or expansion of an existing population. We define risks as unintended negative consequences to non-target species or other populations, spawning areas, or life history types of the reintroduced species. Reintroduction planners must evaluate the potential for the reintroduction effort itself to worsen conditions for existing populations either demographically, ecologically, or genetically. Constraints are biological factors that will determine whether or not the reintroduction effort will effectively contribute to viability objectives. Our definition of constraints does not include political, social or economic feasibility. Initial colonists are likely to be affected by the factors currently limiting viability in existing populations near the reintroduction site, and delineating constraints is intended to ensure that newly available habitat does not become a sink area. Identifying both risks and constraints is a crucial component of reintroduction planning (Figure 4).

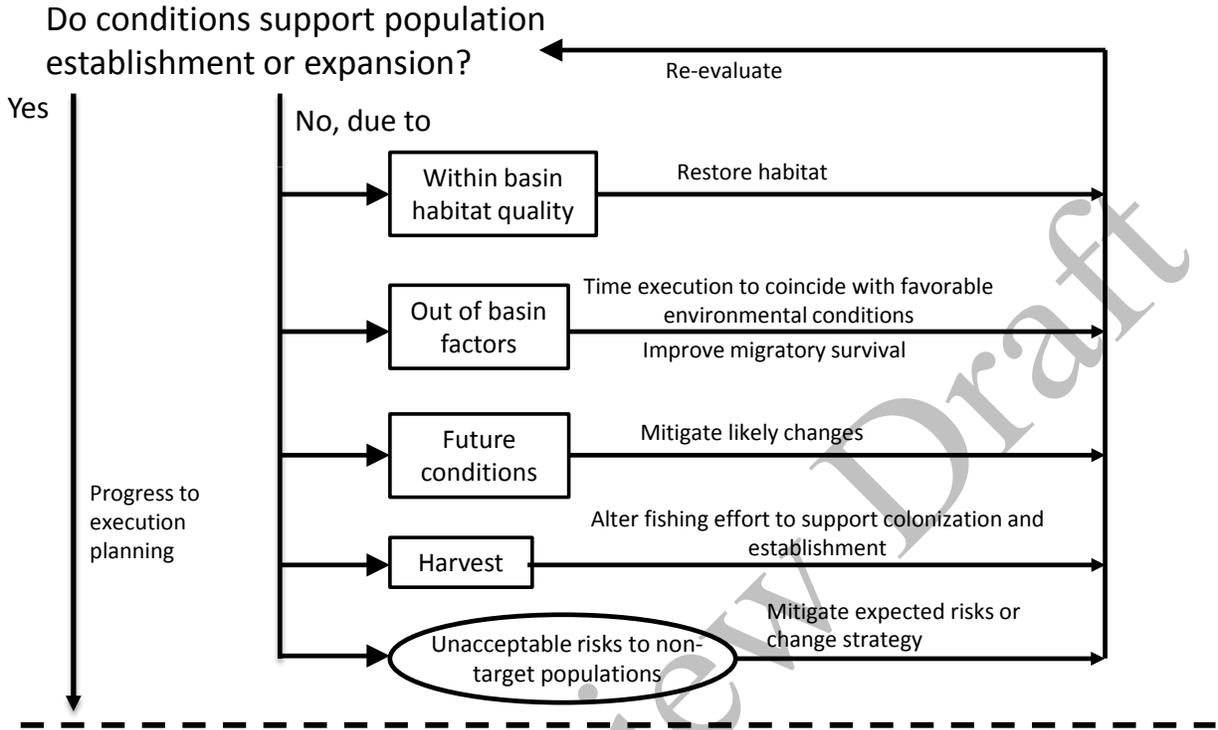
Biological Risks

Biological risks from reintroductions include those effects that have the potential to worsen any population's performance relative to the overall objectives for the population or the species/ESU. These would typically be inadvertent, side-effects of the reintroduction actions, including:

- Transmission of disease from translocated or out-planted fish
- 'Mining' a source population
- Invasion by non-native species
- Excessive straying

Disease transmission. Reintroductions might also introduce risk of spreading 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 reared, have been implicated as vectors of diseases such as bacterial kidney disease (BKD) to wild populations (reviewed in Naish et al. 2008). Reintroduced animals might also be vulnerable to

1. Sequence planning



2. Execution planning

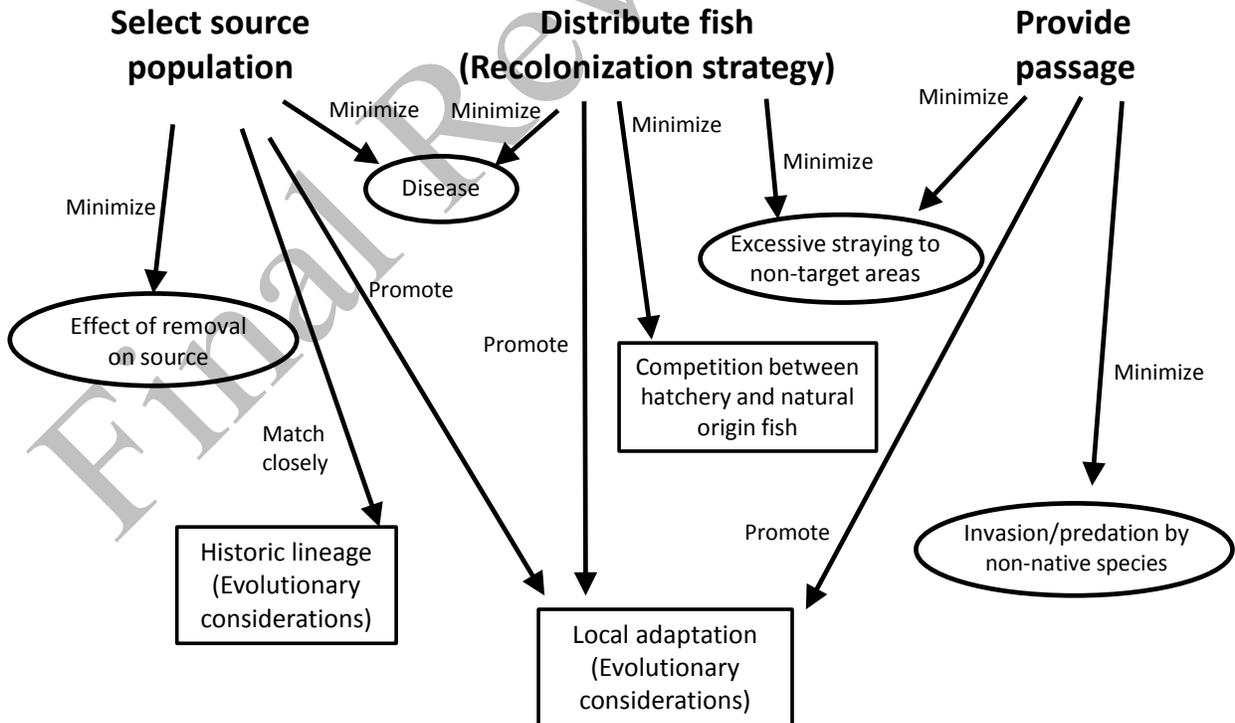


Figure 4 (previous page). Role of constraints (boxes) and biological risks (ovals) in reintroduction planning. Constraints are factors that will affect whether or not the reintroduction will effectively contribute to viability objectives, and are not to be confused with political, social or economic feasibility. Biological risks are unintended negative consequences that may harm non-target species or other populations, spawning areas, or life history types of the reintroduced species. We distinguish between sequence planning, which determines if a particular site is ready for reintroduction, from execution planning, which considers the benefits and conceivable negative consequences of specific actions (highlighted in bold) that actively or passively reintroduce fish to new habitat. There will certainly be overlap in these planning phases (i.e., continue to monitor effects of harvest and restore habitat during reintroduction), but we think this distinction is important to ensure that every effort has a good chance of success prior to barrier removal or active movement of fish.

endemic pathogen strains within new habitat, and this could decrease the likelihood of successful population establishment if the effect is severe. Thus, establishing a baseline of pathogen densities within the area prior to reintroduction will permit monitoring of disease during reintroduction (Brenkman et al. 2008), and screening captive-reared or translocated animals prior to release will minimize the risk of spreading disease. Both are important components of reintroduction.

Mining source populations. If a source population for a reintroduction effort is at very low abundance or density, removing fish for the reintroduction effort (whether naturally or anthropogenically) can harm that population (referred to as ‘mining’ the source population). Even in situations where abundance is relatively high, it will be important to consider whether the removal of fish for reintroduction elsewhere will lower population status below critical thresholds, such as those identified by the ICTRT (i.e., ‘viable,’ ‘maintained,’ ‘low risk’ and ‘high risk’). This concern primarily applies to natural origin source populations because in the context of long-term recovery, maintenance of the hatchery population is of lower concern than developing self-sustaining, viable ESUs. More details are outlined in the *Execution* section.

Invasion by non-native species. Even if non-natives are not currently present at the reintroduction site, they may invade if reintroduction involves barrier removal (Fausch et al. 2009). This might not only reduce the likelihood of reintroduction success, but also threaten pre-

existing native species, and so a careful examination of the likelihood of non-native dispersal into the new habitat is required. Similar to the process for reintroduction, this would entail identifying any proximate populations of non-native fishes, and evaluating habitat suitability above the barrier. Although there may be some ‘biotic resistance’ of a pre-existing fish community to non-native invaders, in general this effect will be less important than habitat factors (Benjamin et al. 2007, Moyle and Light 1996). In cases where there is a reasonable likelihood of invasion by aggressive non-native species, a selective access strategy should be employed.

Excessive straying. Reintroduction efforts that result in increases in straying, even if unintentional, have the potential to negatively affect other extant populations or spawning areas of the target population. This is particularly true when the reintroduction is heavily reliant on hatchery-origin fish. The proportion of spawners that are of hatchery origin is a viability metric (ICTRT 2007), due to the risk of introgression from domesticated stocks. Excessive straying from a reintroduction has the potential to worsen the fitness and the measured status of other populations. More details provided in *Execution* section.

Biological Constraints

In some cases, an extirpated area may have a high potential to benefit long-term recovery, but immediate circumstances do not support a reintroduction. To have the best chance of success, conditions encountered by colonists, both within the new habitat and during their migration to and from it, should be able to support a productive population. Planners must therefore consider whether or not a stream is “reintroduction ready,” including whether the original causes of the extirpation have been adequately ameliorated. Factors (overview in Table 1) to consider include (but are not limited to):

- Presence of barriers
- Habitat quality
- Out-of-basin factors (or out of immediate area factors, if not salmonids), including harvest
- Interactions with pre-existing species and populations
- Likely habitat changes due to climate and land use
- Natural selection and evolutionary considerations

Each of these elements will affect the risk associated with different reintroduction strategies. Of particular note are the factors that led to the original extirpation, since their persistence is likely to cause a reintroduction to fail (IUCN 1998).

Table 1. Variables that affect salmonid colonization, adapted from Pess et al. (2008) and Pess (2009).

Variables which affect salmonid recolonization	Likely to disperse & colonize	Not likely to disperse & colonize
Barriers to movement	Few, small	Many, large
Distance from source population	Near	Far
Habitat area	Large	Small
Source population size	Large	Small
Source population stray rate	High	Low
Life history adaptation to local habitat characteristics	High	Low
Habitat type and condition	Similar habitat types to source population, Good condition	Different habitat types to source population, Poor condition
Interaction with existing fish population	Positive	Negative

Overall, one must understand the key factors that determine survival and productivity across the entire life cycle in order to establish reasonable expectations for success and maximize the benefit of reintroduction efforts. Once these factors have been identified, planners must

implement actions in a logical sequence that will vary from location to location. Some sites may require habitat restoration and some may require amelioration of high mortality along the migration corridor, but in general these actions should occur prior to any movement of fish into a reintroduction site. At the outset of developing a reintroduction plan, there are many inter-related considerations that confound decision making, so it is difficult to know where to begin. Our goal in this section is to outline the key planning elements that agencies must consider in developing an appropriately sequenced reintroduction strategy with a strong opportunity for success.

Barriers. Barriers to passage provide two types of constraints: engineering constraints related to passage (discussed fully in the ‘Execution’ section) and the presence of multiple blockages in a system, either in sequence or in an arrangement that “prunes” multiple tributaries from access. In each case, issues associated with each barrier should be assessed separately to determine the biologically optimal approach to removal.

In a sequential arrangement, the order in which barriers are best removed will be affected by the order in which they occur (downstream to upstream), engineering constraints associated with each barrier, sedimentation or other factors related to any reservoir and the quantity and quality of habitat behind each barrier. In “pruned” watersheds, the quality and quantity of habitat available behind each will be a primary driver determining the biologically most important barriers for removal. It is also important to note that there may be partial barriers that restrict passage by some species but not others, or permit passage at high but not low flow periods. Logistically important for sequencing barrier removals are the permitting and engineering processes that are typically required for these efforts.

Habitat quality. Habitat quality above and below any existing or former barrier is a key element of the likely success of a reintroduction effort. Quite simply, reintroducing fish to poor or degraded habitat is much less likely to be successful than a reintroduction in a pristine or restored habitat (Griffiths et al. 2011). It is important to distinguish areas that historically provided only marginal habitat from those whose productive potential is currently curtailed by anthropogenic disturbance. Streams that only supported ephemeral populations or components of populations prior to human impacts will likely contribute little to ESU viability via

reintroduction. Conversely, unoccupied streams with strong potential for habitat improvement through restoration could provide long term and lasting conservation benefits. Spatially explicit models, such as the intrinsic potential metric developed by the ICTRT (ICTRT 2007, Appendix C), can help identify historically productive streams; determining anthropogenic degradation of habitats can draw on the many, largely expert-opinion efforts to identify degraded habitat (e.g. sub-basin planning, recovery plans, watershed plans, etc.). More quantitative empirical or modeling approaches may be available in the near future as recently implemented monitoring programs come to fruition (e.g. Intensively Monitored Watershed Programs, ISEMP, etc.)

In gauging habitat quality within an area targeted for reintroduction, planners should consider the requirements of all life phases. Adults will require spawning gravels with oxygen rich upwelling, and their offspring will flourish in stream reaches with abundant prey resources and complex channels that provide cover from predators. As monitoring and experimental programs continue, it may be possible to ultimately provide quantitative guidelines of physical parameters such as sinuosity or woody debris loadings, although these are not possible now. In the interim, qualitative and expert assessments are useful. Adjacent occupied habitats that are qualitatively similar to an area considered for reintroduction may provide a helpful benchmark for gauging habitat quality. If the productivity of the extant population is consistently below replacement, then reintroduction has a low probability of developing sustained natural production. In these situations, efforts must either first focus on habitat restoration in the area targeted for reintroduction, select reintroductions sites where the habitat quality is markedly better than the extant portions of the population, or both.

Stream flow is an important attribute that deserves special focus. For watersheds with multiple dams, adequate releases from upstream dams may be necessary to secure high quality habitat within the previously inaccessible area. Insufficient stream flows cause immediate problems such as reducing the area of accessible habitat and creating barriers at natural features that are passable at higher discharge. Flow reductions also raise streams temperatures, and this can create thermal migration barriers, increase vulnerability to disease, and reduce growth by raising energetic demands for metabolic maintenance. In the long term, flow reduction also interrupts natural hydrologic processes that are crucial for the creation and maintenance of anadromous fish habitat, and can lead to channel simplification, sedimentation, and reduced connectivity to off-channel habitat in the floodplain (Poff et al. 1997). Within degraded habitats

that historically supported productive populations, allowing expression of the natural flow regime is a primary method of process-based restoration that will maximize the long term sustainability of habitat improvements (Beechie et al. 2010).

Out of basin factors. Factors limiting survival and population productivity outside the area considered for reintroduction are also important. The low abundances characteristic of colonization will increase an incipient population's vulnerability to episodes of high mortality. If the effect is severe, low survival during the migration to and from the reintroduction site as well as in the ocean phase could induce or exacerbate an Allee effect that further reduces productivity and prevents population establishment (Deredec and Courchamp 2007). Migration through the large hydroelectric projects within the Columbia-Snake system has been identified as a primary factor limiting salmon recovery. Large mainstem dams may increase mortality of juveniles, either directly or through delayed effects that manifest in subsequent life stages (Budy et al. 2002, Schaller and Petrosky 2007), or 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. Some reintroduced populations may also experience low survival through passable dams in tributaries of the Columbia and Snake (e.g., Roza Dam on the Yakima River). Finally, downstream barging of salmon through impoundments, a common management approach intended to reduce in-river mortality of Snake River smolts, can reduce homing fidelity when they return as adults (Keefer et al. 2008). This would tend to reduce the effectiveness of reintroduction efforts that depend on precise homing by a relatively small number of initial population founders produced (or released) in the new habitat.

Low survival during the ocean phase, due to natural fluctuations or perhaps the lingering effects of migration through dams (Kareiva et al. 2000, Welch et al. 2008), could also limit reintroduction success. Ocean survival is difficult, if not impossible, to ameliorate; ocean conditions (both negative and positive) should be considered when evaluating whether objectives have been achieved. Regional factors such as ocean conditions can also provide benefits. As our ability to identify ocean (Mueter et al. 2005) and river conditions (Petrosky and Schaller 2010) associated with high returns improves, there may be opportunities to time our reintroduction efforts in ways that are likely to maximize success.

Harvest. Successful colonization, particularly under a strategy of natural colonization (see “Execution”), is intimately linked to source population abundance, so harvest management can be another important factor to consider. Abundance of spawners on the spawning ground can be a driver of stray rates, as breeding opportunities in an area become harder or easier to find. As a result, altering the fishing rate on the source population could change the colonization rate, and thus affect the success of a reintroduction effort.

While both harvest intensity and management measures vary from ESU to ESU in the Interior Columbia, current harvest restrictions for fisheries that impact Interior Columbia stocks are relatively (and in some cases very) constrained to address concerns for demographic risks and to provide for increased spawning levels in response to improvements in, for example, habitat or hydropower impacts (Ford et al. 2010). In these situations, recolonization planning should include explicit consideration of the effects of the current harvest regime on both the reintroduction area and on source populations. Since harvest rates (at least in the mainstem) are set on aggregate stocks, they might differentially affect natural return rates from spawners in the newly colonized, low-density areas. In addition, where natural recolonization would be the preferred strategy (see “Execution”) the potential benefits of modifying harvest schedules to maintain reduced harvest rates on natural source populations to increase straying rates may be beneficial. Evaluating these options would also need to consider the potential for increased straying from reduced harvest from less desirable sources, such as hatchery stocks. Thus, there may be a need to evaluate hatchery and harvest measures jointly.

Depending upon the location of the reintroduction opportunity, assessments could include evaluating adjustments to localized fisheries and/or aggregate mainstem fisheries. In general, because of the relatively fragile status of threatened and endangered populations, and the societal desire to increase harvest as populations increase, ensuring that trade-offs between increased harvest and reduced abundance are consistent with reintroduction strategies (and vice versa) will be an important component of achieving goals and objectives.

Interactions with pre-existing species and populations. Interactions with species or populations that inhabit the target area prior to reintroduction could have important consequences. In some cases these interactions may be negative (e.g., competition or predation)

and reduce the likelihood of reintroduction success, and in others, they could be positive. In this section, we consider the ecological effects of native species, non-native species, and members of the same species on reintroduction.

In general, interspecific interactions with pre-existing native fauna in the reintroduction areas are unlikely to suppress establishment of a population. Species that naturally occur in sympatry are more likely to have evolved niche separation in resource use (Fausch 1988), and this would tend to minimize ecological interactions such as competition and predation. Complex habitats may further reduce interspecific competition between historically sympatric species by providing a broader array of resource niches (Young 2001) and ultimately permit a more diverse stream fish assemblage (Reeves et al. 1993). Two factors could increase the ecological interaction between reintroduced species and native prior inhabitants. The first is large-scale habitat alterations that have altered the balance of available resources. For example, native pikeminnow have thrived in reservoirs created by dams in the Columbia River. This has boosted their abundance, and consequently increased the rate of predation on juvenile salmonids (Beamesderfer and Rieman 1991, Rieman et al. 1991). Secondly, competition amongst sympatric natives will also tend to increase at greater densities (Harvey and Nakamoto 1996), and this might influence the choice of reintroduction strategy because hatchery supplementation will create a more rapid density increase. Finally, there is also the possibility of reproductive interaction. Depending on the species and location, hybridization with native and introduced species could occur (Ostberg et al. 2004), and such a result could undermine the conservation benefit of reintroduction even if a self-sustaining population is established.

Non-native species pose a significant threat to the viability of salmon populations, both through predation and competition (Sanderson et al. 2009). It is conceivable, and in some cases even likely, that non-native predation could reduce the likelihood of population establishment. Depensatory processes could magnify predation impacts at the low densities typical of recolonization by (Liermann and Hilborn 2001). Similar to native species, the impacts of non-native species will be strongest in highly modified habitats. Non-native fishes such as channel catfish (*Ictalurus punctatus*), smallmouth bass (*Micropterus dolomieu*), yellow perch (*Perca flavescens*), and walleye (*Sander vitreus*) have thrived in the warm, clear, lentic reservoirs that are created by dams (Sanderson et al. 2009). Many of these dams block salmon migration and are therefore the target of reintroduction programs, so this is a sequencing issue that planners are

likely to face. A trap and haul reintroduction program may help mitigate high expected mortality of juveniles that must migrate through reservoirs containing abundant non-native populations (further discussion in “providing passage section”).

Facultatively migratory species such as *O. mykiss* or bull trout are a special case in which reintroduced fish may reproduce with resident members of their own species. For example, McMillan et al. (2007) found that resident rainbow trout and anadromous steelhead trout spawned together throughout an entire watershed on Washington state’s Olympic Peninsula. Purely resident life forms of *O. mykiss* can also colonize downstream areas, spawn, and contribute to the anadromous population by producing a small percentage of the emigrating smolts (Ruzycki et al. 2009). Such interactions could positively benefit colonization by providing additional reproductive potential to increase the rate of spatial and numerical expansion. Furthermore, pristine populations of *O. mykiss* unrestricted by barriers are likely to exhibit partial anadromy in which a single, panmictic, interbreeding group contains both resident and migratory forms (McPhee et al. 2007). Therefore, reintroduction of anadromous into areas with isolated resident populations is likely to increase the range of life history strategies, and this would be a significant benefit to diversity. The degree of anadromy will likely be determined by patterns of growth and survival. Anthropogenically modified systems that have reduced migratory survival may favor residence over anadromy (Satterthwaite et al. 2010, Waples et al. 2007), so providing ocean access to resident populations previously isolated by barriers does not necessarily ensure expression of anadromous life histories.

In sum, a reintroduction evaluation should consider the possibility that non-native species and native species might interact as a result of the effort. Approaches to ameliorate negative effects (and thus improve the likelihood of success of the effort) can then be developed and appropriately sequenced in the reintroduction plan.

Changing conditions – climate and land use. Climate change effects are already being felt in the range of salmonids, and affect both freshwater and marine environments. In the Columbia basin, hotter summer temperatures are will likely reach levels that induce thermal stress in salmonids (Mantua et al. 2010). In general, current predictions suggest that there will be increased winter precipitation, drier summers and an overall reduction in snowpack, changes that changes are likely to lead to shifts in the timing and quantity of peak, average and low flows

(CIG 2009). Effects will differ from location to location, with the most dramatic changes likely to be in areas with “transitional” hydrographs. Transitional areas currently include peaks in the hydrograph driven by both snowmelt and rain, and are likely to lose or have a reduced peak from snowmelt as climate change progresses (Beechie et al. 2006). In the marine environment, warmer temperatures are expected to significantly reduce the quantity of thermal habitats currently occupied by Pacific salmon (Abdul-Aziz et al. 2011).

These changes will almost certainly alter the distribution of high and low quality habitats for salmonids, and may, in fact, alter their range altogether. For instance, Crozier et al. (2008b) predicted reductions in abundance and increased extinction risk of Chinook salmon in the Salmon River basin due to changes in stream flow and temperature associated with climate change. Areas that are currently at the edge of salmonids’ ranges may be rendered less or completely unsuitable for them. Conversely, some areas not currently suitable or of low quality may become higher quality.

In a reintroduction effort, then, the likely future conditions of the area to be occupied must also be considered in order not to waste time, resources and opportunities to improve population status. However, currently extirpated areas are in general at higher elevations than areas that are still occupied (McClure et al. 2008b), suggesting that many of these areas are likely to be suitable, and may, in fact, serve as refuges for future populations. Currently, while down-scaled climate models are available for the Pacific Northwest (CIG 2009), there have only been a few, local applications of these models to assess impacts on existing salmonid populations (Battin et al. 2007, Crozier et al. 2008b, Honea et al. in prep, Walters et al. in prep). Even more rare are efforts to jointly consider changes in land use and resulting changes in flow and temperature (but see Bartz et al. 2006). Until larger-scale, standardized assessments of habitat suitability (including currently unoccupied areas) under climate change have been conducted, qualitative rather than quantitative assessments of likely changes in climate, land use and resulting habitat conditions can still be included. Uncertainty in these areas is likely to be reduced as our ability to quantitatively model and understand climate change impacts improves over time.

Even in the absence of detailed models, a number of general observations suggest reintroduction approaches that incorporate climate change considerations. First, maintaining a diversity of habitat types will buffer against uncertainty in the response of salmon populations to

climate change (Schindler et al. 2008). This would suggest targeting unique but currently inaccessible habitats for reintroduction is an effective conservation strategy. Second, salmon will have some capacity to adapt to changing environmental conditions (Crozier et al. 2008a), so there is a potential to promote evolution of traits that are likely to confer fitness advantages in the future by using reintroduction to enhance the viability of populations currently inhabiting watershed with warm temperatures. Finally, due to the anticipated changes in flow patterns, water regulation at existing dams may be an important component of maintaining suitable migration corridor conditions, and should be considered in the planning and execution of reintroduction efforts.

Climate change is not the only process that will alter future habitat suitability. As human population grows and alters its distribution, land use and land cover are also likely to change over time. Many of these changes will be impossible to predict precisely, but general human demographic changes and consequent likely land use changes should also be factored into considerations for reintroductions. For example, are future land uses in an area considered for reintroduction likely to degrade salmonid habitat? Alternatively, might changes make a particular area more attractive for salmonids, and thus increase its potential value to the ESU?

Evolutionary considerations. Changes in morphology, behavior and life history in response to natural selection, as well as other evolutionary processes will also influence the reintroduction dynamics and likelihood of population establishment. Current patterns of intra-specific diversity are largely shaped by recolonization of newly ice free habitats at the end of the last glacial advance ~16,000 years ago (Waples et al. 2008). In their natural state, freshwater environments are quite dynamic due to natural processes such forest fires, landslides, volcanism, and floods, but are nonetheless sufficiently stable for salmon populations to evolve adaptations to local conditions (Taylor 1991). Humans have disrupted this natural balance between environmental change and adaptation in numerous ways (Waples et al. 2009), and the substantial changes to the fluvial environment that follow construction of dams and other barriers have evolutionary consequences for salmon (McClure et al. 2008a, Waples et al. 2007). For example, dams likely introduced strong selection on adult spawn timing and embryonic development rate (Angilletta et al. 2008) and juvenile migration strategies (Williams et al. 2008).

Salmon populations occupying these altered environments will, over time, evolve to maximize their fitness. Therefore contemporary salmon populations spawning below long-standing artificial barriers probably will not have the same distribution of traits that existed in the historical population above the barrier, resulting in erosion of adaptation to habitats targeted for reintroduction. Consequently, these populations are unlikely to immediately display high fitness in areas upstream of the barrier even if they are the direct descendants of the populations that originally occupied those areas. Various studies suggest that salmonid populations can adapt relatively rapidly (several generations) to new conditions (e.g., Quinn et al. 2001), but the need to adapt is an important factor to include in planning efforts.

Extirpated area will vary substantially in the extent to which their evolutionary legacy is retained, affecting a variety of reintroduction processes. In some locations, a lineage has been entirely extirpated so reintroduction must originate from a distantly related source, whereas other efforts seek to expand an existing population from a mostly intact lineage. As previously mentioned, reintroductions will take longer to effectively contribute to recovery under the former scenario compared to the latter because some level of adaptive evolution and divergence from the source is required. In some areas, an anadromous lineage is restricted to a resident fish isolated above a dam (Clemento et al. 2009), so flooding the area with hatchery fish, even those originating from nearby or related populations, could compromise the integrity of the only remaining ancestral population. In other areas, a unique life history pattern endemic to an area is confined to a hatchery population, so these hatchery fish may be most appropriate reintroduction source. The Dworshak hatchery, which harbors B-run summer steelhead extirpated by Dworshak Dam on the North Fork Clearwater River, provides a good example.

Sequencing planning summary. It is important to evaluate each reintroduction situation holistically, considering the entire life cycle, all life stages, all limiting factors and threats, as well as the specific reintroduction approach. Sequencing the management actions that target improving the key environmental limiting factors along with the specific timeline and approach for reintroduction is required to maximize the likelihood of success. This may include significant habitat improvements downstream or upstream of the blocked area as well as consideration or alteration of hatchery, harvest and other human impacts on these species.

Execution

Reintroduction planning will require some iterative work – determining the sequencing of actions to support reintroductions, for example, is not entirely independent of developing execution strategies for effecting the reintroduction (i.e., getting the right fish into the right place at the right times). In addition, many of the risks and constraints that are relevant in determining the overall benefit of a project also must be considered in the execution strategy (Figure 4). In this section, we discuss the strategy for colonization of the new area, the choice of a source population, and, in the case of reintroductions involving barriers, the techniques used to provide passage. We define the colonization strategy as the intended mechanism of fish movement into the reintroduction site, and it can be either passive (volitional or natural colonization) or active (transplanting or hatchery releases). Selection of the source population and the colonization strategy are intertwined such that some colonization strategies imply a particular type of source population. Regardless of the colonization strategy and source, reintroductions above barriers must also provide passage through or around the blockage and any associated impoundment. We summarize factors important for executing reintroductions in Table 1.

Colonization strategy

There are three basic types of colonization strategies, in increasing order of artificial human influence on the colonization process: natural, translocation, and hatchery releases. 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 most conservative approach with respect to the area being colonized because it minimizes interruption of fundamental biological processes and therefore introduces the least risk to viability parameters. Conversely, hatchery releases are the most aggressive approach because they immediately place large numbers of fish in the reintroduction site, but at a cost of increased risk to diversity viability metrics, and potentially to productivity metrics as well, due to the generally lower fitness of hatchery fish (Araki et al. 2008). A precautionary approach adopts the lowest risk colonization strategy that has a reasonable chance of promoting long term improvement in population and ESU viability. Figure 5 outlines a decision framework for strategy selection.

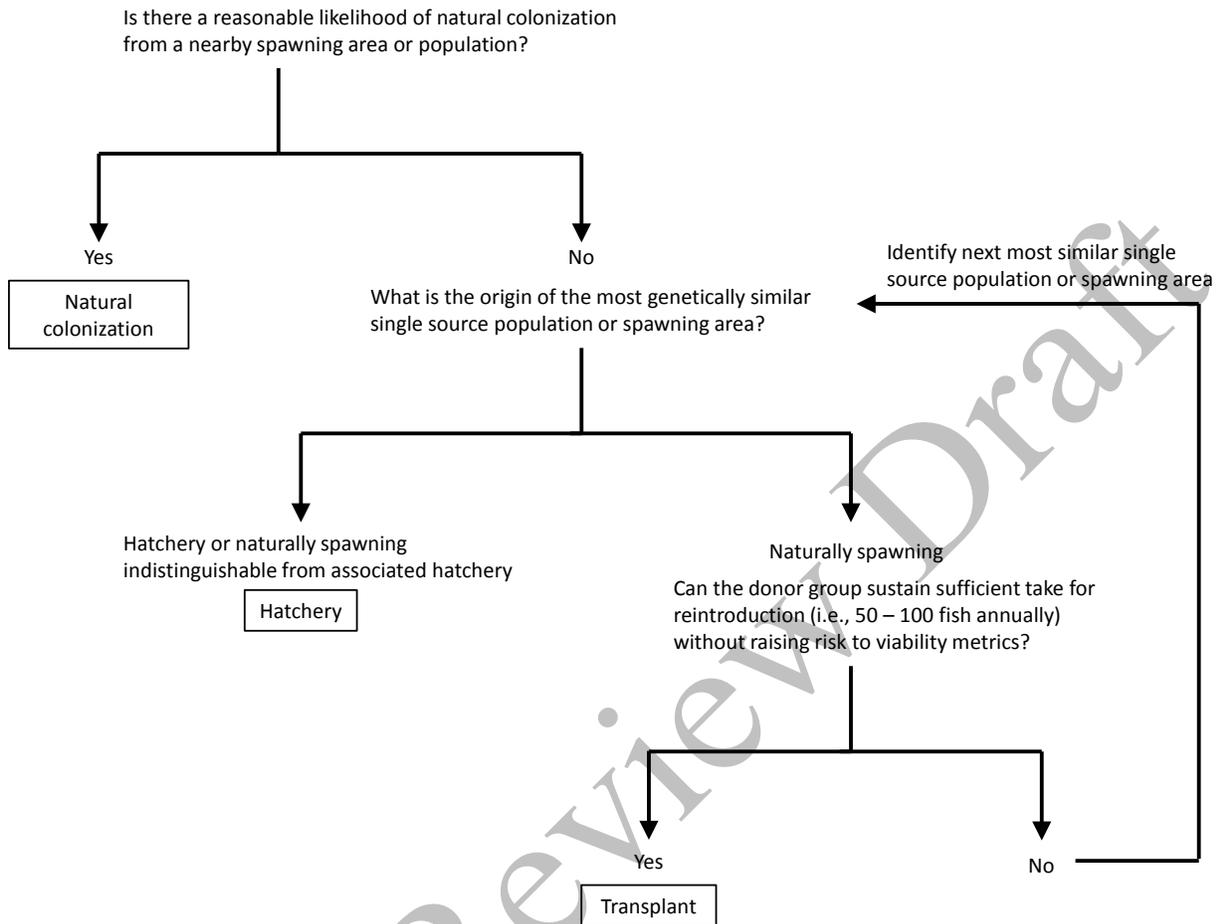


Figure 5. Decision tree for determining colonization strategy.

Natural colonization. Natural colonization minimizes anthropogenic disturbance to the biological processes during population establishment and expansion. This includes selection of the individuals that disperse into the new habitat, sexual selection during reproduction of the initial colonists, and natural selection on their offspring. It provides opportunity for the evolution of locally adapted traits. 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). This might be particular true for salmon reintroductions because of the artificial selection regime induced by migration barriers (McClure et al. 2008a), and the likelihood that contemporary colonizers will not match the phenotypes of the fish that historically occupied the reintroduction site. Any increases in population fitness would likely

translate to greater abundance and productivity, so over time, allowing for natural patterns of evolution could benefit these viability parameters.

Establishing a self-sustaining population via natural colonization is contingent on a reasonable likelihood of natural dispersal into the new habitat. It also implies that the source population will be nearby occupied reaches within the population or in an adjacent population. Although salmon are famous for their homing instinct by which they return to spawn in their natal stream, some proportion “stray” and breed elsewhere (Hendry et al. 2004). In a salmon reintroduction context, the number of strays dispersing into newly accessible habitat will likely be determined by the abundance and distance of the source population (Pess 2009); straying increases with increased abundance and with smaller distances.

Natural salmonid recolonization into newly re-opened habitats can occur relatively quickly. Rivers that were unoccupied due to the eruption of Mt. St. Helens, for example, were re-occupied at relatively high density within 7 years of the eruption (Bisson et al. 2005, Leider 1989, Lucas and Pointer 1987). Many other studies of newly opened habitat document recolonization within five to thirty years, with most taking between one to two decades (Bryant et al. 1999, Burger et al. 2000, Glen 2002, Kiffney et al. 2009, Milner et al. 2007, Pess 2009, Pess et al. 2003, Withler 1982). These studies provide some reasonable expectations for the amount of time that is required in a natural recolonization effort, and are useful for establishing objectives.

Transplanting. For areas that are isolated and distant from extant populations, natural colonization may be unrealistic within time scales desired by management. In cases where the reintroduction site is so isolated that long-distance dispersal from extant populations is unlikely, transplanting can ensure that an adequate number of adult salmon 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. Here, we describe the process and consequences of transplanting but discuss the selection of the source population separately.

Transplanting allows for natural patterns of natural and sexual selection within the new habitat, and thus has many of the same benefits discussed above for natural colonization. One difference is that transplanting introduces artificial selection of the individuals that reach the reintroduction site. In some cases, natural selection during migration could be important for

evolution of traits (i.e., body morphology or energy reserves) advantageous for a particular migration route (i.e., long or steep) (Quinn et al. 2001). The degree to which artificial selection of transplants differs from natural selection during migration is dependent on the choice of which individuals are transplanted.

Aspects of salmon behavior and ecology may affect the success of transplanting. Adult salmon will be naïve in the waters to which they are transplanted, and will not recognize the odors they encounter. As demonstrated by experimental translocations, these individuals may eventually depart the reintroduction site in search of their natal stream without spawning (Blair and Quinn 1991). On the other hand, the offspring of any adults that do spawn will spend the entire freshwater phase, from embryonic incubation to the smolt migration, within the reintroduction site. Compared to hatchery releases, this will increase their exposure to natal odors, and perhaps enhance the precision of homing during their return migration as adults.

In general, reintroductions with many individuals are more likely to be successful (Fischer and Lindenmayer 2000, Wolf et al. 1996), so reintroduction should maximize the total number transplanted. Although there are no firm guidelines for the total number to reintroduce, Williams et al. (1988) observe that 50 individuals (25 males and 25 females) 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. The transplant group should accurately represent the age distribution of the source population and a one to one sex ratio will maximize effective population size.

However, the effect of translocation must be considered not only on the new population, but also on the population from which fish are taken. Removing large numbers of fish from an already depressed population (as many or most in threatened and endangered ESUs are) means that the risk to that source population is increased. ‘Mining’ populations in this way can thus have strong negative effects, and these effects must be included in a cost-benefit analysis of alternative approaches. In these situations, ensuring that there are sufficient numbers in the source population may be an important precursor to the reintroduction effort.

Hatchery releases. The third colonization strategy is a hatchery introduction that would stock artificially propagated fish within the reintroduction site. Hatchery oriented reintroductions will be most appropriate when the ultimate goal is an immediate increase in

population abundance. The specifics vary by program, but hatchery production generally reduces early life mortality that occurs in the egg incubation or rearing phase relative to natural spawning. 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 natural origin fish from a low abundance source population. However, even if managed properly, hatchery releases may jeopardize goals of self-sustaining natural production.

Several issues related to hatchery propagation and releases will likely limit their contribution to long-term viability. First, hatchery releases could induce density dependent processes that would limit the growth, survival and other vital rates of naturally produced fish (Kostow and Zhou 2006). Even if hatchery releases are the primary colonization strategy, there will likely be some natural straying; interaction between hatchery and naturally produced fish will also likely occur in downstream portions of the currently occupied population. As the viability status focuses on natural production (McElhany et al. 2000), reduced performance of natural origin fish may actually reduce the likelihood or lengthen the time frame to achieving reintroduction viability objectives. Negative ecological consequences due to high density hatchery releases may also ensue for other important species that are being reintroduced simultaneously or inhabited the site prior to reintroduction.

In addition, large proportion of hatchery fish on the spawning grounds in the reintroduction site may reduce the productivity of the incipient population (Chilcote et al. 2011). Increasing population or ESU productivity will often be one of the ultimate goals of reintroduction, and thus hatchery releases could undermine big picture recovery objectives. Low productivity would decrease the likelihood of achieving the establishing a self-sustaining population. Hatchery releases would likely reduce two other viability parameters, diversity and spatial structure, because they tend to homogenize populations and erode differentiation between spatially segregated spawning areas or populations (McClure et al. 2008b). Hatchery fish may not home precisely to the release site even if they are acclimatized there (Dittman et al. 2010), indicating that a hatchery oriented reintroduction may also increase risk to diversity and spatial structure of nearby proximate populations. The specific breeding protocols and rearing practices

will influence the severity of the effect, but some level of long term risk to these viability metrics is unavoidable.

A crucial consideration for hatchery reintroductions is the length of time over which supplementation is planned. Sustained hatchery releases at high levels are rated as contributing high risk to ICTRT viability metrics (ICTRT 2007); productivity metrics can also be lowered. A precautionary model for hatchery-based reintroductions would aim for a brief, pulsed release of one to two generations, followed by cessation of releases. 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 after releases have ceased. Specifying the timeline for phasing out releases in a detailed plan prior to reintroduction will help prevent institutionalization of the hatchery efforts. Abundance targets for natural origin fish, produced both by natural strays and by hatchery-origin adults spawning naturally in the reintroduction site, would indicate when the incipient population has sufficient reproductive potential to no longer need supplementation. The period after releases would allow managers to determine if natural abundance truly increased, or it was simply masked by artificial production (McClure et al. 2008b). Some pulsed reintroductions may well fail to establish populations, and this result would indicate that the donor stock was not appropriately adapted for the reintroduction site or there exists some other factor, either within the reintroduction site or elsewhere in the migratory route, that limits survival.

Choice of source population

Ultimately, the most successful reintroductions will be founded by fish with life history and morphological characteristics that are compatible with the environmental characteristics of the area that is newly opened (Pess 2009). Thus, the choice of source population is linked to the method of introduction – whether that method is natural recolonization or hatchery outplanting – and is a critical component of implementing a reintroduction effort. Source populations that are most likely to contribute to the long-term success of not only the reintroduction, but also the long-term viability of the population, MPG or ESU will be:

- Genetically and ecologically appropriate to the area to be reintroduced,

- Abundant enough (strong enough status) to absorb the removal of individuals without harm to the source population.

Anadromous salmonids are noted for their high degree of local adaptation (Quinn 2005, Taylor 1991); many of the morphological and life history traits that are integral to that adaptation have relatively high heritability (Carlson and Seamons 2008). Thus, choosing fish that are genetically and ecologically similar to the original (historical) population in re-opened habitats will improve chances of a successful reintroduction.

Without hatchery influences, the most closely related fish will be, in order from most to least similar, fish from the same population, the same MPG and the same ESU. Because ESUs were designated as comprising lineages with distinct evolutionary legacy (Busby et al. 1996, Myers et al. 1998, Waples 1991), using fish outside the ESU for a reintroduction effort is a high risk strategy, as it may compromise the genetic characteristics and local adaptation within the ESU, as well as have a lower chance of success. When genetic analysis is not possible (or logical inferences from feasible genetic analysis is not relevant), analysis of landscape characteristics can provide a surrogate for ecological similarity. This approach infers that similar habitats promote evolution of similar traits, and could use a combination of several metrics including elevation, precipitation, hydrologic (i.e., discharge) patterns or composite metrics such as EPA ecoregions.

Potential sources that have hatchery influences are more complicated to evaluate, and will often involve some degree of compromise. As with wild fish, hatchery individuals that are most closely related to the likely historical population will pose the lowest risk and the greatest chance of success. There are several additional genetic and phenotypic concerns with hatchery fish, but a primary issue is domestication selection – salmon bred in captivity will adapt to the hatchery environment and this can reduce the fitness of fish released into the wild (Ford 2002). This process accumulates over time, making populations that have been artificially propagated for many generations less like their wild counterparts than those that have been in captivity for few generations (Frankham 2008), meaning that their adaptation to the hatchery environment has increased. However, the absolute degree of domestication will obviously depend on how integrated or segregated the hatchery program is from a wild population (Mobrand et al. 2005). Thus, an evaluation of hatchery stocks includes considering:

- what the original source of the hatchery stock was (local being least risky, composite stocks derived from several ESUs being the most risky, as they are the most genetically different)
- the period of time and number of generations the stock has been artificially propagated (with fewer generations being less risky)
- whether the hatchery has been operated as an integrated or segregated program (with fully integrated least risky, and fully segregated most risky, since genes selected for by domestication will accumulate the most in these cases)

Each case will be unique, and in some cases benefits of local origin may be outweighed by the costs of long-term hatchery propagation, or vice versa. Local environmental conditions, population structure, and characteristics of stocks with which introduced fish may mingle are also relevant.

In any reintroduction involving the active transplantation or removal of fish from the source population, it is essential that a wild donor population be sufficiently abundant and stable to support the removal of individuals. Transplanting cannot introduce risk by depleting the source population to benefit a reintroduction with an uncertain outcome, and violates the “do no harm” guiding principle (George et al. 2009). Abundance relative to biological viability thresholds set by the ICTRT (2007) and other TRTs provide a useful benchmark for judging the capacity of potential source population to support removal of fish from one population for a reintroduction effort in another. In some cases, managers must either wait for the most appropriate stock to recover to levels that could sustain removal for reintroduction or select a less desirable stock that can immediately provide sufficient donors without risk to the source. This is a difficult trade-off, especially because recovery of depleted potential source populations is uncertain and could take several generations under optimistic scenarios. Combining salmon from multiple populations within a single MPG may benefit genetic diversity of the colonist group or introduce outbreeding depression, which would lower fitness (Huff et al. 2010). Monitoring should track the source population abundance during reintroduction to ensure that the source population remains healthy.

In sum, there are a variety of factors that must be considered simultaneously when choosing the “best” source population, and the “best” method for moving them into the new habitat, and trade-offs between risk factors are highly likely. For example, a newly opened area

that is intended to contribute to the long-term viability of an ESU might be better repopulated actively (with translocation) of locally-derived hatchery fish that have been bred artificially for only a short time, than allowed to be recolonized naturally by strays from a nearby population that has been heavily supplemented with out-of-ESU hatchery fish. When the goal of a reintroduction is something other than long-term viability, factors other than biological similarity may have greater weight.

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 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 fish ladders for adults and screened bypass facilities for juveniles. In some cases, especially for partial barriers, simply increasing stream flows via releases from upstream dams or irrigations diversions is all that will be needed to provide volitional passage. In comparison to trap and haul operations, volitional fish passage facilities are generally preferred 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. However, depending on the design, water velocity and gradient may restrict passage to certain species or size classes. If poorly designed, passage facilities could increase the risk of straying into non-target populations or spawning areas.

Barrier or dam removal is a special case of volitional passage that it essentially restores a channel to its natural condition, and will thus provide substantial benefits beyond salmon recovery. Dam removal repairs riverine ecosystem processes such as the 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). Rehabilitation of these processes will certainly provide long term benefits for the salmon and steelhead population 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 reducing short term extinction risk, and these ‘side-effects’ as well as plans for any re-vegetation of reservoir areas are important to include in the sequencing process.

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 would be handled before passed upstream, and would be most appropriate for adult fish ladders that circumvent barriers. Although such structures would increase operation and maintenance costs, they would allow managers to exclude fish that could undermine reintroduction objectives. For example, in a reintroduction designed to enhance diversity through the evolution of distinct, locally adapted population subunits, excluding the homogenizing influence of hatchery fish would be beneficial. Furthermore, without selective access, undesirable non-native fishes may invade (Fausch et al. 2009), and this may not only decrease reintroduction success, but also negatively impact pre-existing resident species. The benefit of incorporating selective access will be directly proportional to the likelihood of colonization by hatchery or non-native fish and the consequences of their presence. Such structures would also provide a large benefit to research and monitoring because they would permit precise counts and measurements of fish. These benefits should be weighed against the cost in making a final decision.

A trap and haul operation will be appropriate for situations where volitional passage is not logistically, technically, or biologically possible, and fish must be actively moved upstream and/or downstream around barriers. Large dams, especially when several occur in sequence, are more likely to require trap and haul than small structures. Space or engineering constraints may prevent the design of safe and effective fish passage facilities. Particularly for juveniles, impoundments may present challenges that cannot be overcome with volitional passage if swirling currents confuse fish navigation or if an abundance of predators would reduce survival below a level consistent with self-sustaining production. Selection or exclusion of particular groups of fish will be fundamentally simple, and trap and haul allows reintroduction to target specific sites for release. For example, spawning adults could be released into the highest quality habitat or dispersed amongst several upstream reaches in order to reduce density dependent effects on their offspring (Einum et al. 2008). The distinction between a natural colonization strategy employing trap and haul versus a transplanting strategy may be fuzzy, but will largely depend on the selection of the source population.

In determining whether to adopt a volitional or trap and haul passage plan, special consideration must be given to the life stage of the juvenile migrants in the targeted population. In general, younger migrants (i.e., fry or subyearling rather than yearling) will be more vulnerable in reservoirs, where predation is often size selective (Poe et al. 1991). Smaller, younger fish may also suffer greater injury or mortality than larger fish when navigating through dam passage facilities (Ferguson et al. 2007) due to swimming speed limitations. Combined, these observations suggest that populations with fry or subyearling migrants are more likely to require a trap and haul approach through large hydroelectric and water storage projects. In addition, some species may fare better than others owing to differences in the timing of downstream migration through reservoirs (Durkin et al. 1970, Sims 1970). If neither trap and haul nor fish passage facilities are possible, dam removal may be the only option for a viable population.

Monitoring

Monitoring is an essential component of any reintroduction program (George et al. 2009, IUCN 1998, Williams et al. 1988). Monitoring of ecological systems refers to sampling something in an effort to detect change in physical, chemical or biological parameters or processes (Roni 2005). It is only by monitoring that it is possible to determine whether reintroduction was successful or unsuccessful and whether there are negative or positive effects on neighboring populations. In the event that reintroduction does not proceed as expected, monitoring is critical to understand how the program can be modified to achieve the desired results.

As with most conservation efforts, project goals should inform the selection and measurement of specific metrics following implementation (Tear et al. 2005). These objectives should be stated as unambiguously as possible and sufficiently focused so that evaluating them is both possible and informative. In this case, the ultimate goal for a reintroduction is to benefit one or more of the viability parameters (abundance, productivity, spatial structure, and diversity), so these should be the target of monitoring efforts. Thus documenting any change in these parameters, both within the reintroduction site and in the parent population and ESU, should be the overall objective of monitoring efforts.

The specific monitoring methods will vary by viability metric. Techniques used to enumerate fish within the reintroduction site (e.g., spawning surveys or weir counts) will be most effective to assess any changes in abundance and productivity. A time series of abundance estimates within the reintroduction site will also help determine whether or not the population is self-sustaining, although genetic analysis or tagging may be needed to separate recruits produced within the reintroduction site from strays produced elsewhere. Reintroduction will change the stock-recruit relationship for a stock, so an abundance time series will also help redefine management benchmarks for the stock within the Fishery Management Plan. Surveys designed to assess habitat occupancy would be the best approach to monitoring changes in spatial structure, as the expansion of population range and elimination or reduction of gaps between spawning areas would indicate a positive change.

Diversity will probably be the most difficult viability metric to evaluate because evolutionary changes will take time to accumulate. However, the criteria used to gauge the potential reintroduction benefit to diversity should be used to guide the monitoring program. For example, if reintroduction offered a chance to restore steelhead in one of the few populations that had both a winter and summer run in an ESU (e.g., White Salmon River), then monitoring should focus on migratory timing and other traits characteristic of these life histories. In some reintroductions, it will be necessary to evaluate genetic divergence, either from the source population or among distinct sub-basins within the reintroduction site, in order to demonstrate enhanced diversity. Screening markers with adaptive significance (e.g., Martinez et al. 2011, Matala et al. 2011) will allow monitoring to identify divergence on shorter time scales than neutral loci because selection enacts genetic change faster than drift or mutation. If direct methods (e.g., genetic analysis) for assessing diversity are not possible, monitoring may rely on indirect methods such as occupancy of different ecoregions or spawner composition (hatchery vs. natural origin).

A second objective for monitoring should be to assess the factors that affected whether or not reintroduction established a self-sustaining population. Although a “build it and they will come” philosophy is appropriate for barrier removals directly above existing productive population and below high quality habitat, in other cases, the reasons the populations was extirpated in the first place are both numerous and complex. Consequently, although some limiting factors may have been addressed prior to reintroduction, others may still exist that will

limit project success. In these situations, monitoring is essential to understand the factors that limit reintroduction success, and if possible, suggest alternate reintroduction strategies that might lessen the impact of existing bottlenecks. For projects involving barrier removal, this requires an evaluation of passability at the former barrier at a minimum. More detailed measurement of biological parameters such as survival rates during rearing and migration, growth, habitat use, interactions between species, or other ecological parameters will increase the likelihood that monitoring will elucidate why a reintroduction succeeded or failed. Considering physical processes such as rates of change in water, sediment, wood, and nutrients, rather than just amount, also provides information into how habitats are functioning. This is especially important if habitat modifications were made as part of the reintroduction effort.

The timeline over which responses are expected and alternative reintroduction strategies are considered is crucial consideration. Lessons from invasion biology indicate that there is often a time lag from initial introduction to population growth and spatial expansion that might be explained by evolutionary processes required to increase population fitness (Sakai et al. 2001). Even proximate source populations may not possess the adaptations or genetic composition of fish that historically occupied a reintroduction site. If evolutionary processes are a necessary component of successful population establishment and expansion, it may take many generations (i.e., decades not years) to observe a significant abundance increase sought by management. Therefore, it is important not to declare failure and employ more aggressive reintroduction methods (e.g., large scale hatchery releases) if a reintroduced population maintains low abundances but does not immediately display exponential growth. Unrealistic expectations for quick results or impatience could lead to policies that jeopardize long term goals.

Another important consideration for management are impacts on extant populations, and these fall into two broad categories. First, monitoring impacts on other species within the reintroduction site will highlight any changes in community structure. Reintroduction could have either positive (e.g., nutrient enrichment through carcass deposition) or negative (e.g., competition) effects on pre-existing fauna that may be of conservation concern or support important fisheries. Barrier removal without selective access may also expose streams to invasion by non-native species, and surveys should aim to determine if invasion occurs so that harmful consequences can be mitigated and avoided in future reintroductions. Secondly,

reintroductions may impact extant portions of the same species. A primary concern should be hatchery reintroductions that may increase rates of straying to nearby natural spawning areas. Monitoring of stray rates following reintroduction will be crucial to evaluating whether the benefits of reintroduction outweigh any increased risk to spatial structure and diversity viability metrics.

In some cases, monitoring of contemporary populations offers a unique opportunity to learn about reintroduction ecology and the role that hatchery stocking should play. There are several areas in the interior Columbia where salmon and steelhead were extirpated by historic barriers that have since been removed. In some of these areas, (e.g., Chinook salmon in the Clearwater River, made accessible by removal of Lewiston Dam in 1973), reintroduction efforts used heavy hatchery stocking. If stocking hatchery fish has effectively established a naturalized population, then natural spawning should persist if hatchery releases are terminated in some or all of the basin. Coupled with a focused monitoring in the natural production areas, such actions could provide crucial information for ongoing and future reintroductions elsewhere.

Gauging a Reintroduction's Contributions to Recovery and ESU status: When Does it Count Biologically?

There currently is no consensus on how best to identify ESUs (reviewed by Fraser and Bernatchez 2001), with both strictly genetic criteria suggested by some (e.g., Moritz 1994) and more comprehensive factors, including life history and distribution suggested and applied by others (Ryder 1986, Waples 1991). More recently, Hey et al. (2005) suggested that ecological function should be an important component of defining conservation units. Pacific salmonid ESUs in the U.S. were originally defined by shared genetic and life history attributes as well as ecological and geographic cohesion (Waples 1991, Waples 1995). Since the original ESU delineations (Busby et al. 1996, Gustafson et al. 1997, Hard et al. 1996, Johnson et al. 1997, Myers et al. 1998, Weitkamp et al. 1995), ESUs have been further defined to exclude stocks that have been subject to, and relatively isolated in, artificial propagation programs for many generations (NMFS 2005a, NMFS 2005b). At the time that ESUs were originally defined, the Biological Review Teams (BRTs – scientific groups charged with identifying ESU boundaries and assessing their status) worked to identify the historic extent of ESUs. At the time of listing,

policy decisions were made to define some ESU boundaries by areas occupied at the time of those decisions, and in most cases excluded large extirpated areas (e.g., NMFS 1997, NMFS 1999). These joint geographic, genetic and historical criteria can complicate determining whether and how a reintroduction contributes to ESU viability.

In fact, there are a variety of situations, including reintroductions, in which it may be important to determine whether descendants of fish that did not belong to the target ESU should “count” toward the status of that target ESU, or if it should be considered as separate from that ESU. These include: 1) situations in which fish have been introduced to a previously inaccessible area or into an area previously occupied by a now-extinct ESU; 2) evaluations of populations at transition zones; 3) situations where in the past, out-of-ESU fish were introduced within historical boundaries of extant ESUs; and 4) range changes (contractions and expansions) due to environmental or anthropogenic change. We provide general considerations about the range of biological factors that would be important in deciding whether fish that are part of a reintroduction or introduction (natural or anthropogenic) should “count” toward that ESU’s status in these situations, although any particular situation will need to be evaluated on its own merits. Importantly, this type of consideration is only important in the situation of multiple ESUs belonging to the same species – while each ESU has been assumed to have an independent evolutionary trajectory, over evolutionary time, there is exchange between ESUs. In addition, there are a range of legal questions that are affected by ESU designations and range. Here, we treat only biological considerations.

Two overarching concepts drive our discussion. First, we recognize that ESU boundaries were unlikely to have been static, even historically. In fact, defining boundaries for some ESUs was extremely challenging (e.g., mid-Columbia and lower Columbia steelhead ESU, Busby et al. 1996), and there is, in these cases, a high degree of uncertainty associated with the placement of boundary populations into a particular ESU. Moreover, with climate change and similar large-scale disturbances, we anticipate that evolutionarily linked groups of fish (ESUs) are likely to fluctuate not only in abundance, but also in their distribution across the landscape. Changing environmental conditions are also likely to lead to adaptive phenotypic change as well. Thus, we do not anticipate that the currently defined geographic or phenotypic and genetic boundaries of ESUs are etched in stone, as it were – we suggest that those boundaries could change as conditions change, depending on the balance of changes in survival, migration (due to changes in

habitat quality) and adaptation to those environmental changes. Second, to meet recovery goals, as articulated above, the choice of source population and other execution methodology (i.e. actions to effect the reintroduction) should be designed to minimize these concerns; in other words, out-of-ESU stocks should be a last choice for reintroductions in order to minimize risk and maximize utility to the receiving or target ESU for recovery purposes.

Factors that affect the role that a group of fish plays in an ESU include the following, in rough order of priority (priority is likely to vary with the specific context of a reintroduction, including whether it is a whole population reintroduction or a within-population reintroduction) (Figure 4):

- The genetic lineage of the fish in the reintroduction or introduction
- Degree of genetic differentiation from the target ESU (or population in the case of within-population reintroductions)
- Whether the population or area is self-sustaining, or dependent on continuing hatchery inputs
- Local adaptation and divergence from the source (less important for within-population reintroductions with local source)
- Metapopulation or population dynamics
- Time period over which the reintroduction has been self-sustaining

Genetic lineage of reintroduced fish. The original lineage of fish involved in a reintroduction will have a very large impact on the degree of benefit that the reintroduction can confer on the target population/ESU. In general, fish that are derived from a long-term artificial propagation program, or that are more distantly related will pose higher risk to the population/ESU than introductions from more local sources (see “Execution” and Figure 6).

Differentiation from/similarity to target ESU. This factor is particularly relevant in situations where a less directly related stock has been used as a source for the reintroduction, and in situations where a population is on a boundary between ESUs, or the original ESU designation was uncertain. The degree of genetic similarity between fish in the recolonization area and fish in the ESU or population that the reintroduction is intended to enhance can provide substantial information about the appropriateness of considering the benefits of the recolonized area for the target ESU.

Together, these two factors (genetic lineage of introduced fish and differentiation from the target ESU) are very important for assessing the role that the reintroduction can play in ESU/population status. If the value of both these factors for a reintroduction is far to the right in Figure 6, for example, the status of the reintroduced population would be relevant to consider when assessing ESU status, even if other factors were far to the left; in situations where the values for these factors are shifted left, in order to consider the reintroduction's benefit to the ESU, the other factors would need to be shifted to the right. Again, the specific context and circumstances of each case will vary and should be considered.

Self-sustaining. A reintroduction effort that results in a self-sustaining population (or component of a population) is demonstrating not only that conditions are favorable, but also that the specific fish are well-matched ecologically and evolutionarily to the environment.

Importantly, assessing whether a population is self-sustaining should also include evaluations across multiple environmental conditions (e.g., ocean or climatic regimes) and across the entire life cycle. In addition, in populations that are supplemented, when considering where to place a population on a scale such as that in Figure 6, both the duration of the supplementation and the intensity (e.g., proportion of fish in the population of hatchery origin) should be considered.

Locally adapted or divergent from source. This factor is closely tied to "self-sustaining," as a population that is not locally adapted is unlikely to sustain itself naturally. A population that is adapted to local environmental and ecological conditions will have greater success in the long-run. A variation of local adaptation is demonstrated divergence from the source population, when that source population was not locally derived or was derived from a long-term artificial propagation program. Either of these conditions suggests that population is adapting to conditions in the area of reintroduction.

Metapopulation/population dynamics. The role that the reintroduction plays in overall demographic processes at larger levels is also an indicator of its contribution to ESU status. A reintroduced population that is receiving strays from within the ESU or MPG and sending strays to other populations at normative rates is functioning within the metapopulation. (Similar concept can be applied to within population reintroductions). In some cases (with robust monitoring), this type of demographic exchange may be detectable before genetic signals, particularly from neutral loci, can be detected.

Time period. Reintroduction efforts that result in populations that are self-sustaining or have relatively high status over longer periods of time are of greater benefit to the ESU than for those with a shorter track record. Longer periods of time imply that the population is adaptable to the full range of environmental conditions experienced in that area and across the life-cycle.

Overall, because of the several factors that contribute to a population “belonging” to an ESU, as well as the nearly limitless permutations of individual circumstances, it will be important to conduct an evaluation of these factors within the context of the ultimate (and clearly articulated) goals and objectives of the project (in the case of a reintroduction) or of a conservation strategy (in the event of introductions or range expansions.) This will provide the best guidance about which of the factors are most important in such determinations.

Final Review Draft

Legend

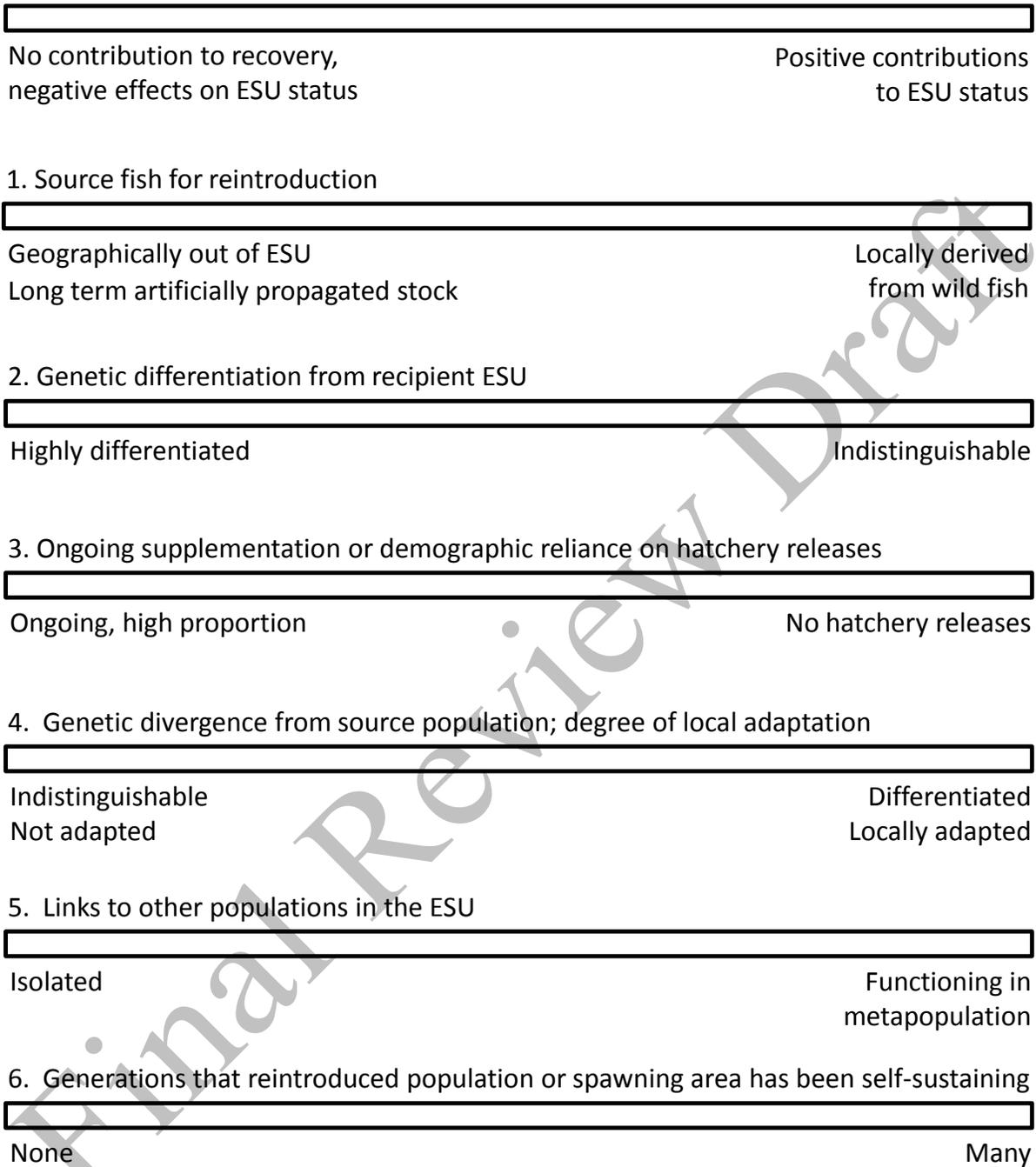


Figure 6. Factors to consider when gauging whether a population-level reintroduction contributes to ESU status. The same factors would be used for a within-population reintroduction, but the factors would be judged at a smaller scale (e.g. out-of-ESU in factor 1 would be judged as out-of-population). All factors move from negligible contributions to ESU status on the left to the most biologically eligible to contribute to ESU status on the right.

Conclusion

Reintroductions have the potential to contribute substantially to long-term viability, recovery and conservation goals by improving the spatial structure, diversity, abundance, and in some cases, productivity of populations and ESUs. However, reintroduction is not typically a tool that is appropriate as a short-term contingency action meant to bolster numbers when abundance suddenly and dramatically plummets.

There are several key planning elements of determining whether to engage in a reintroduction effort. Program managers must evaluate the potential benefits of a successful effort to overall recovery goals and objectives and assess the biological risks that the reintroduction might pose to existing populations or other species. They must also determine a sequence of actions that reduces or eliminates other factors limiting nearby extant populations that are likely to serve as the source population, and assess the risks and benefits of alternative execution strategies (i.e., methods for distributing fish). Reintroduction efforts should not be initiated until this full suite of planning and evaluation has been conducted. In some cases, risks may outweigh benefits, and in others, current conditions may not support population establishment and expansion. In this planning, it will be important to consider adding a precautionary buffer – in other words, to do more than the minimum anticipated to mitigate risks or constraints -- in the event of unforeseen impacts, or impacts that are greater than originally anticipated.

Finally, robust monitoring tied to project goals and objectives will ensure that the project achieves its ultimate goals. First, it will provide information about whether or not objectives have been met. Second, it will allow managers to identify unforeseen consequences, and support appropriate responses to such events. Finally, it will provide the information needed to assess whether a reintroduction contributes to overall ESU status.

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