

NOAA Technical Memorandum NMFS-NWFSC-141



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

<https://doi.org/10.7289/V5/TM-NWFSC-141>

April 2018

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northwest Fisheries Science Center



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

<https://doi.org/10.7289/V5/TM-NWFSC-141>

Michelle McClure,^{1a} Joseph Anderson,^{1a} George Pess,^{1b} Tom Cooney,^{1c}
Rich Carmichael,² Casey Baldwin,³ Jay Hesse,⁴ Laurie Weitkamp,^{1c}
Damon Holzer,^{1c} Mindi Sheer,^{1c} and Steve Lindley⁵

¹Northwest Fisheries Science Center
2725 Montlake Boulevard East
Seattle, Washington 98112
^a Fishery Resource Analysis and Monitoring Division
^b Fish Ecology Division
^c Conservation Biology Division

²Columbia Basin Fish and Wildlife Authority
851 Sixth Avenue #300
Portland, Oregon 97204

³Washington Department of Fish and Wildlife Research Field Office
3515 State Highway 97A
Wenatchee, Washington 98801

⁴Nez Perce Tribe
P.O. Box 365
Lapwai, Idaho 83540

⁵Fisheries Ecology Division
Southwest Fisheries Science Center
110 McAllister Way
Santa Cruz, California 95060

April 2018

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northwest Fisheries Science Center
<https://www.nwfsc.noaa.gov/index.cfm>

NOAA Technical Memorandum NMFS-NWFSC Series

The Northwest Fisheries Science Center of NOAA's National Marine Fisheries Service uses the NOAA Technical Memorandum NMFS-NWFSC series to issue scientific and technical publications. Manuscripts have been peer-reviewed and edited. Publications in this series can be cited in the scientific and technical literature. Technical editing services at NWFSC are provided by Al Brown.

The Northwest Fisheries Science Center's NOAA Technical Memorandum NMFS-NWFSC series continues the NMFS-F/NWC series established in 1970 by the Northwest and Alaska Fisheries Science Center, which subsequently was divided into the Northwest Fisheries Science Center and the Alaska Fisheries Science Center. The latter uses the NOAA Technical Memorandum NMFS-AFSC series.

NOAA Technical Memorandums NMFS-NWFSC are available at the Northwest Fisheries Science Center website, <https://www.nwfsc.noaa.gov/index.cfm>.

Reference this document as follows:

McClure, M., J. Anderson, G. Pess, T. Cooney, R. Carmichael, C. Baldwin, J. Hesse, L. Weitkamp, D. Holzer, M. Sheer, and S. Lindley. 2018. Anadromous Salmonid Reintroductions: General Planning Principles for Long-Term Viability and Recovery. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-141. <https://doi.org/10.7289/V5/TM-NWFSC-141>

Contents

Figures.....	v
Tables.....	vi
Abstract.....	vii
Introduction.....	1
Interior Columbia River Basin.....	2
Establishing Goals and Objectives and Identifying Potential Benefits.....	5
Establishing Goals.....	5
Establishing Objectives.....	6
Determining the Likely Benefits of a Reintroduction.....	6
Abundance.....	7
Productivity.....	8
Spatial structure.....	9
Diversity.....	9
Time Frame to Achieve Benefits.....	10
Evaluating Biological Risks and Constraints.....	12
Biological Risks.....	13
Disease transmission.....	13
Source population mining.....	13
Invasion by non-native species.....	13
Excessive straying.....	14
Biological Constraints.....	14
Barriers.....	15
Habitat quality.....	15
Out-of-basin factors.....	16
Harvest.....	17
Interactions with pre-existing species and populations.....	18
Changing conditions: Climate and land use.....	19
Evolutionary considerations.....	20
Summary.....	21

Execution.....	22
Colonization Strategy.....	22
Natural colonization.....	22
Translocation.....	24
Hatchery releases.....	25
Choice of Source Population.....	26
Providing Passage.....	28
Monitoring.....	30
Conclusion.....	33
References.....	34

Figures

Figure 1. Areas historically occupied by spring/summer Chinook salmon and sockeye salmon that no longer support viable populations	3
Figure 2. Areas historically occupied by steelhead that no longer support viable populations	4
Figure 3. A framework for gauging the net benefit of reintroduction options.....	7
Figure 4. The role of constraints and biological risks in reintroduction planning	12
Figure 5. Decision tree for determining colonization strategy.....	23

Tables

Table 1. Variables affecting salmonid recolonization 15

Abstract

Local extirpations of Pacific salmon, often due to dams and other stream barriers, are common throughout the western United States. Reestablishing salmonid populations in areas they historically occupied has substantial potential to assist conservation efforts, but best practices for reintroduction are not well established. In this report, we present a framework for planning reintroductions designed to promote recovery of salmonids listed under the Endangered Species Act. Prior to implementation, managers should first describe the benefits, risks, and constraints of a proposed reintroduction. We define benefits as specific biological improvements toward recovery objectives. Risks are potential negative outcomes of reintroductions that could worsen conservation status rather than improve it. Constraints are biological factors that will determine whether the reintroduction successfully establishes a self-sustaining population. We provide guidance for selecting a recolonization strategy (natural colonization, transplanting, or hatchery releases), a source population, and methods for providing passage that will maximize the probability of conservation benefit while minimizing risks. Monitoring is necessary to determine whether the reintroduction successfully achieves the benefits, and to evaluate impacts on nontarget species or populations. Many of the benefits, especially diversity and the evolution of locally adapted population segments, are likely to accrue over decadal time scales. Thus, we view reintroduction as a long-term approach to enhancing viability.

Introduction

Reintroducing animals to areas from 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 [*Oryx leucoryx*; Spalton et al. 1999] and alpine ibex [*Capra 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 (Seddon et al. 2007, Armstrong and Seddon 2008).

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 have been extirpated by large barriers alone from 44% of the habitat they historically occupied in the 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 (NRC 1996), they are one of the most widespread, and their removal or circumvention provides 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 a) weighed against the risks and costs and b) 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 have been crucial to reintroduction success in many species, but also carry genetic (Frankham 2008, Fraser 2008) and ecological risks (Kostow 2009) that could compromise the probability of population establishment or reduce the viability of nontarget 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 the 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 the 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, its management during colonization, and the timeframe 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 and 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: 1) evaluating the biological net benefits, by identifying the goals and potential benefits of reintroduction and characterizing the biological risks and constraints of a reintroduction; 2) revisiting the risks and constraints in order to explore the costs and benefits of alternative execution approaches; and 3) monitoring the 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 conservation objectives at the level of a species (or an evolutionarily significant unit, ESU). 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, NPPC 1986), one of the largest runs of anadromous salmon in the world. However, salmon populations in the Columbia River basin have undergone substantial decline following settlement of the region by euro-Americans (Lichatowich 1999). Currently, there are 13 ESUs (which meet the definition of Distinct Population Segments¹) listed as threatened or endangered under the ESA in the Columbia River basin alone (NMFS 1997, 1999, 2005a). 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 include overfishing, hydroelectric development, habitat degradation, and hatchery supplementation (NRC 1996).

¹ A distinct population segment is a vertebrate population or group of populations that is discrete from other populations of the species and significant in relation to the entire species. NOAA Fisheries and the U.S. Fish and Wildlife Service released a joint policy defining the criteria for identifying a population as a DPS (USOFR 1996). The ESA provides for listing species, subspecies, or distinct population segments of vertebrate species.

Under the ESA, ESUs are the unit, for salmonids, that can be listed as threatened or endangered (Waples, 1995). Once ESUs were listed, Technical Recovery Teams (TRTs) were convened to describe population structure (i.e., to 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 recognize major population groups (MPGs) consisting of multiple populations that share genetic, geographic, and habitat characteristics within an 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.

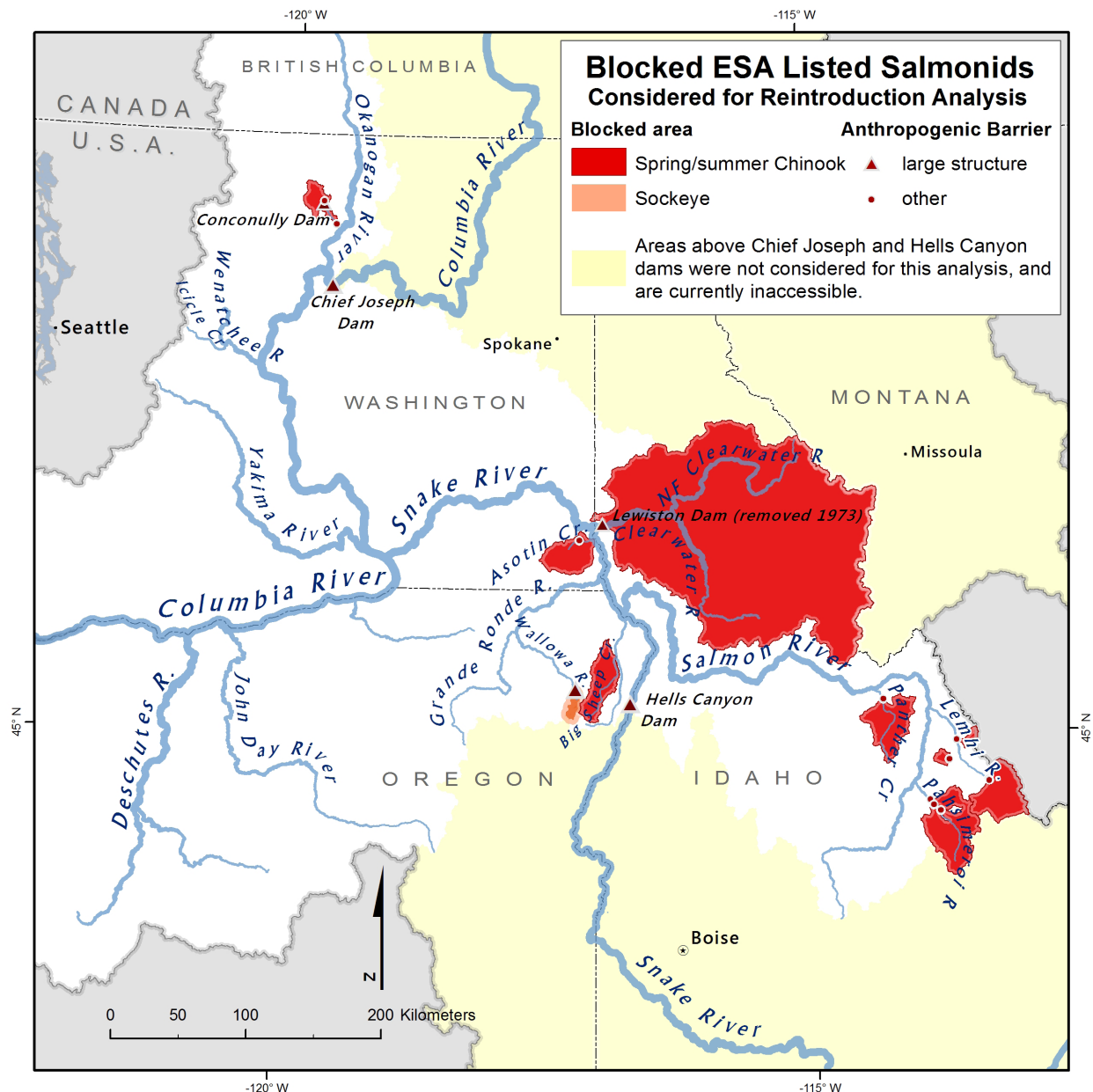


Figure 1. Areas historically occupied by spring/summer Chinook salmon and sockeye salmon that no longer support viable populations within the interior Columbia River basin below Hells Canyon (Snake River) and Chief Joseph (Columbia River).

The interior Columbia River basin offers substantial opportunities for salmon reintroduction. Approximately 55% of the area historically occupied by Chinook (*Oncorhynchus tshawytscha*) and sockeye (*O. nerka*) salmon (Figure 1) and steelhead (*O. mykiss*; Figure 2) is blocked by dams or other barriers (NRC 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 River ESUs, and may, under unique conditions, reduce short-term extinction risk or provide additional benefits such as harvest.

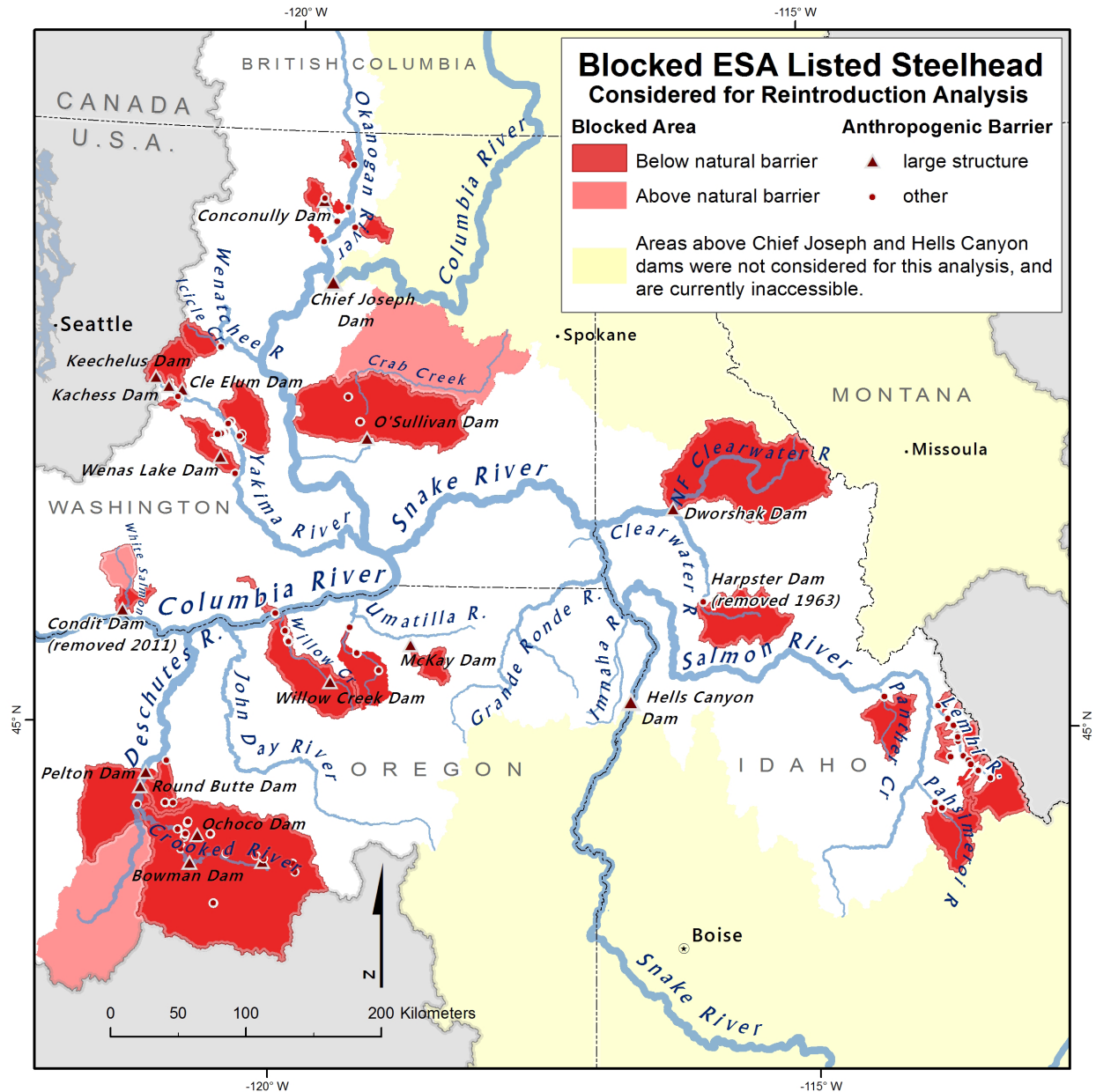


Figure 2. Areas historically occupied by steelhead that no longer support viable populations within the interior Columbia River basin below Hells Canyon (Snake River) and Chief Joseph (Columbia River).

Establishing Goals and 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 the 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 such goals should flow specific and measurable objectives, which provide the benchmarks to determine when and if a project has achieved success. Finally, identifying the potential benefits of a project allows one to determine whether the proposed project is consistent with its 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 is clearly 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 the risk of extinction and contributing to the long-term recovery of ESA-listed anadromous salmonids. A first step in establishing goals for such 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 River basin 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 all 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 River basin (ICTRT 2007). The ICTRT criteria have been incorporated into recovery plans developed by local stakeholder groups within each watershed containing 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 the Likely Benefits of a Reintroduction

Estimating the magnitude and nature of the potential benefits afforded by a reintroduction is a primary element of planning, and is the first step in determining whether a potential reintroduction will support its ultimate goals sufficiently to pursue further planning and implementation. Benefits will provide the basis of evaluating the overall effectiveness of the project, and must be weighed against the risks and constraints in prioritizing among multiple reintroduction sites (Figure 3). Expected progress toward the 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. Reoccupation of an area can have effects at the population, MPG, and ESU levels, and

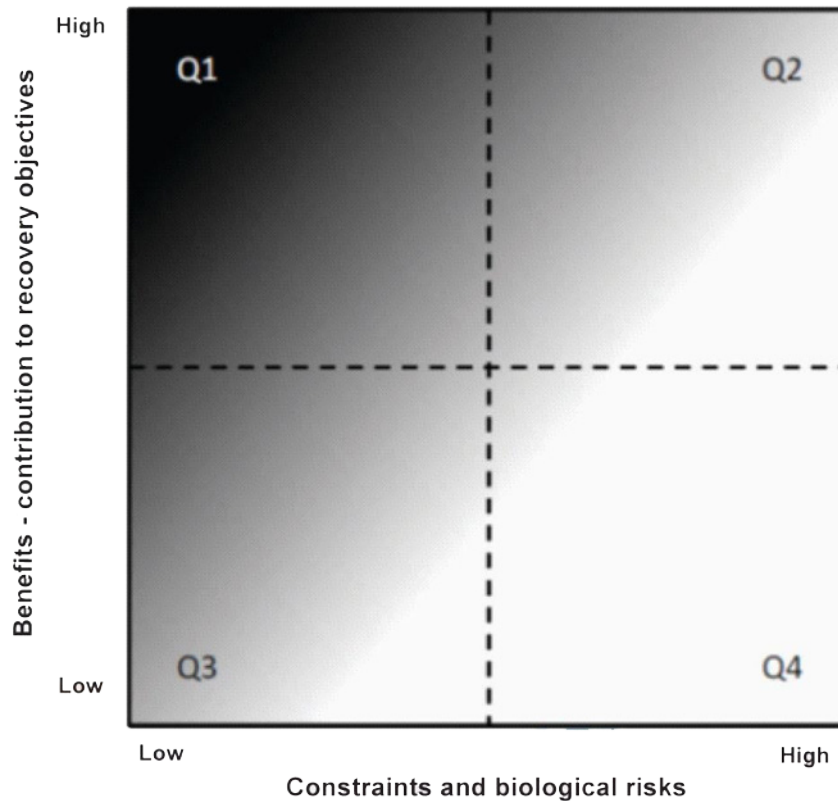


Figure 3. A framework for gauging the net benefit of reintroduction options. Darker shading represents a higher likelihood of contributing to conservation and recovery goals. In each case, the benefits are weighed against the constraints and risks of the project. In quadrant 1, the benefits are high 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 of implementation or the risk of a negative outcome make projects in this region less attractive. Both quadrants 3 and 4 have relatively low benefits; some in quadrant 3 may be selected owing to low risk and ease of execution, whereas those in quadrant 4 will generally be avoided.

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 its 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 the 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, compensatory 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 decouple ecological feedbacks important for healthy, productive salmon populations, such as the 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 is roughly determined by the proportional increase in occupied habitat, and should be evaluated relative to predetermined 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 the extinction risk of the entire ESU (and most rapidly for ESUs with few populations; Ruckelhaus et al. 2003), so the benefits of reintroduction will be greatest in these depauperate regions. Spatial structure is a related viability parameter, as discussed more thoroughly in that section.

Productivity

Productivity is one of the most fundamental drivers of the long-term persistence of a population or metapopulation, and is generally defined as the ratio of the number of animals in general, t , to the number of animals that produced them in the previous 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 (i.e., has net demographic excess) or a sink (i.e., has 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 the colonization of currently unoccupied areas.

Reintroductions can have either positive or negative impacts on the 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) population 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, as discussed under **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 it would 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 a 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. 2011). 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 changes. Analogous to the performance of financial portfolios spread among 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 variability 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:

1. In many cases, dams have truncated diversity by nonrandomly blocking access such that certain landscape features, habitat types, or hydrologic regimes are underrepresented 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.
2. 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., rainbow trout/steelhead [*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 time window 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 a case-by-case basis, and hatchery-related issues are discussed more thoroughly under Execution. Both direct and indirect measures can be used at the population, MPG, and ESU levels. However, more substantive differences in habitat type or other measures are needed to support a large effect at the MPG or ESU level of 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 ways that are 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 the 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 the ability to rapidly colonize habitat made available by the provision of fish passage, restored stream flow, or barrier removal, as significant increases in abundance have been observed within 10 years (Bryant et al. 1999, Kiffney et al. 2009, (Pess et al. 2012). 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 (discussed in detail under Execution). Increasing abundance via reintroduction may take longer in interior populations than in 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 nongenetic 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 (Quinn et al. 2001, Koskinen et al. 2002) 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 will 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 remaining and was sourced from a distantly related population. On the other hand, expansion of an extant population into a new habitat similar to previously occupied areas would offer less opportunity for diversification, but historic patterns of substructure could be realized sooner.

Finally, it is often worth considering the 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 that benefit 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 impact is assessing biological risks and constraints to establishing a self-sustaining population or expanding an existing population. We define risks as unintended negative consequences to nontarget 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).

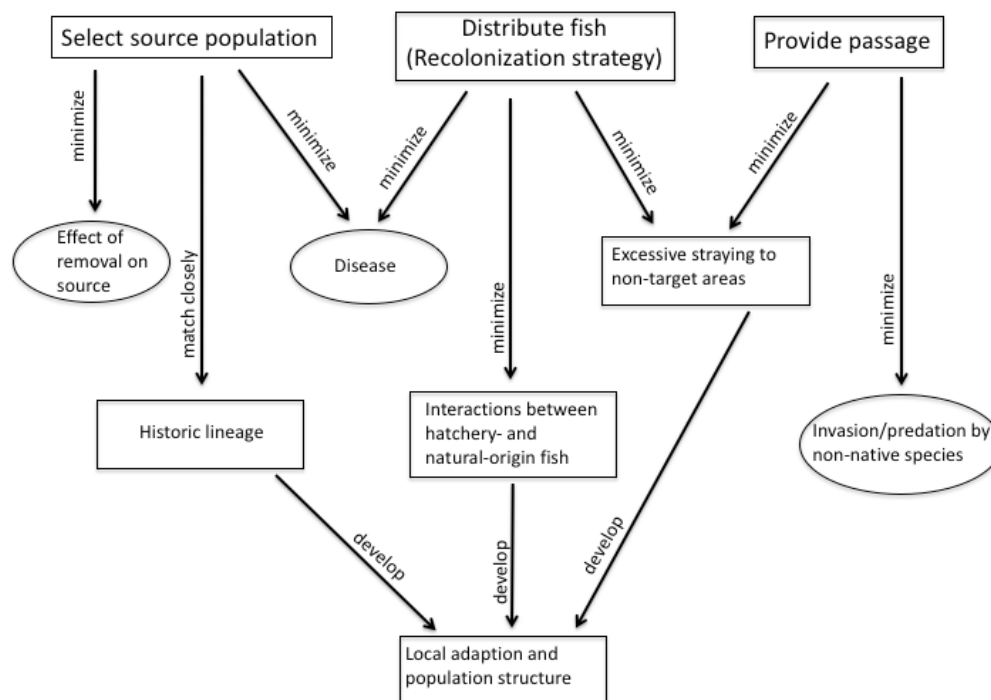


Figure 4. The role of constraints (boxes) and biological risks (ovals) in reintroduction planning.

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 nontarget 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, and 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., continuing to restore habitat and monitor the effects of harvest during reintroduction efforts), but we think this distinction is important to ensure that every effort has a good chance of success prior to removing barriers or actively moving fish.

Biological Risks

The biological risks of 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:

- The transmission of disease from translocated or out-planted fish.
- The mining of a source population.
- Invasion by non-native species.
- Excessive straying.

Disease transmission

Reintroductions can introduce the 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 endemic pathogen strains within the 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 disease monitoring during reintroduction (Brenkman et al. 2008), and screening captively reared or translocated animals prior to release will minimize the risk of spreading disease. Both are important components of reintroduction.

Source population mining

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 the population status below critical thresholds, such as those identified by the ICTRT. This concern primarily applies to natural-origin source populations, because in the context of long-term recovery, maintenance of a hatchery population is of lower concern than developing self-sustaining, viable ESUs. More details are outlined under [Execution](#).

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 may not only reduce the likelihood of reintroduction success, but also threaten pre-existing native species, 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 by a pre-existing fish community to non-native invaders, in general this effect will be less important than habitat factors (Moyle and Light 1996, Benjamin et al. 2007). 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 straying increases, 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 relies heavily 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, as described in more detail under Execution.

Biological Constraints

In some cases, an extirpated area may have great potential to benefit long-term recovery, but immediate circumstances do not support a reintroduction. To have the best chance of success, the 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 to consider (see also Table 1) include, but are not limited to:

- The presence of barriers.
- Habitat quality.
- Out-of-basin factors (or out-of-immediate-area factors, if nonsalmonids), 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 risks 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).

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 a reintroduction effort. 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, some may require amelioration of high mortality along the migration corridor; in general, however, any such actions should occur prior to any movement of fish into a reintroduction site. At the outset of developing a reintroduction plan, there are many interrelated 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.

Table 1. Variables affecting salmonid recolonization, adapted from Pess et al. (2008) and Pess (2009).

Variable	Increase(s) likelihood of dispersal/recolonization	Reduce(s) likelihood of dispersal/recolonization
Barriers to movement	Few, small	Many, large
Habitat type and condition	Similar to source population, Good condition	Different from source population, Poor condition
Habitat area	Large	Small
Interaction with existing fish population(s)	Positive	Negative
Source population size	Large	Small
Source population stray rate	High	Low
Distance from source population	Near	Far
Life-history adaptation to local habitat characteristics	High	Low

Barriers

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

In a sequential arrangement, the order in which barriers are removed will be affected by the order in which they occur (downstream to upstream), the engineering constraints associated with each barrier, sedimentation or other factors related to any reservoirs they form, and the quantity and quality of habitat behind each barrier. In pruned watersheds, the quality and quantity of habitat available behind each barrier 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. Finally, the permitting and engineering processes that are typically required for these efforts are logistically important for sequencing barrier removals.

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 it would to 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 a 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 (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., the Intensively Monitored Watershed Program,² the Integrated Status and Effectiveness Monitoring Program,³ 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, NOAA scientists are beginning to provide quantitative guidelines of physical parameters such as sinuosity and woody debris loadings (Beechie et al. 2017). Qualitative and expert assessments can also be 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 first focus on either habitat restoration in the area targeted for reintroduction, select reintroduction 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 would be passable at higher discharge. Flow reductions also raise stream 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 the expression of the natural flow regime is the primary method of process-based restoration, and 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 river 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,

² <https://wdfw.wa.gov/publications/01398/>

³ <http://isemp.org/>

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 Rivers. 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. Moreover, 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 recolonization (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 among ESUs in the interior Columbia River basin, current harvest restrictions for fisheries that impact Interior Columbia stocks are relatively (and in some cases very) constrained, both 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 2010). In these situations, recolonization planning should include explicit consideration of the effects of the current harvest regime on both the reintroduction area and source populations. Since harvest rates (at least in the mainstem) are set on aggregate stocks, they might differentially affect the natural return rates of spawners from newly colonized, low-density areas. In addition, where natural recolonization would be the preferred strategy, there are potential benefits to modifying harvest schedules to maintain reduced harvest rates on natural source populations to increase straying rates. An evaluation of these options would also need to consider the potential for increased straying from reduced harvest from less-desirable sources, such as hatchery stocks. Thus, it may be necessary 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 the 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), ultimately permitting 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 (*Ptychocheilus oregonensis*) 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 among sympatric natives will also tend to increase at greater densities (Harvey and Nakamoto 1996); 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). Such a result may 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 (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 the high expected mortality of juveniles that must migrate through reservoirs containing abundant non-native populations (see [Providing Passage](#)).

Facultatively migratory species such as rainbow trout or bull trout (*Salvelinus confluentus*) 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 spawned together throughout an entire watershed on Washington State's Olympic Peninsula. Purely resident life-forms of rainbow trout 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 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, the reintroduction of anadromous rainbow trout into areas with isolated resident populations is likely to increase the range of life-history strategies, 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 (Waples et al. 2007, Satterthwaite et al. 2010), so providing ocean access to resident populations previously isolated by barriers does not necessarily ensure the 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 that ameliorate any 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 River basin, hotter summer temperatures 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 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 downscaled 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. 2016, Walters et al. 2013). 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 the resulting habitat conditions can still be included. Uncertainty in these areas is likely to be reduced as our ability to quantitatively model and understand the impacts of climate change 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 that 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 the evolution of traits that are likely to confer fitness advantages in the future by using reintroduction to enhance the viability of populations currently inhabiting watersheds 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 conditions in migration corridors, 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 intraspecific diversity were largely shaped by the 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 as 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 the construction of dams and other barriers have evolutionary consequences for salmon (Waples et al. 2007, McClure et al. 2008a). For example, dams likely introduce 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 the 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 (i.e., over 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 areas will vary substantially in the extent to which their evolutionary legacies are 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, 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 the 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.

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 requires 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 when determining the overall benefit of a project must also 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 the 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 their effects on the viability parameters that will ultimately be used to judge the success or failure of the reintroduction. In general, natural colonization is the most conservative approach with respect to the area being colonized because it minimizes the 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.

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 the 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 may be particularly true for salmon reintroductions, because of both 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; thus, over time, allowing for natural patterns of evolution could benefit these viability parameters.

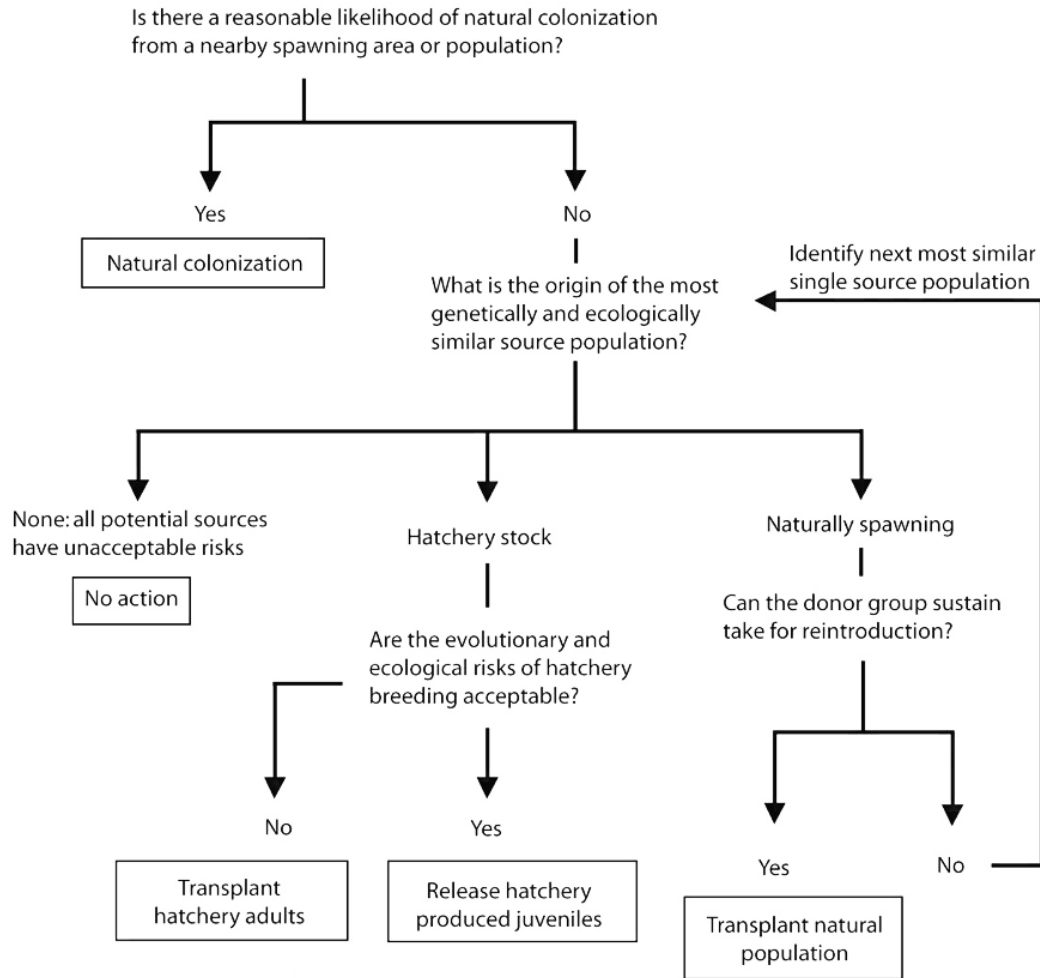


Figure 5. Decision tree for determining colonization strategy.

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 do 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 reopened habitats can occur relatively quickly. Rivers that were left unoccupied due to the eruption of Mount St. Helens, for example, were reoccupied at relatively high density within seven years of the eruption (Lucas and Pointer 1987, Leider 1989, Bisson et al. 2005). Many other studies of newly opened habitat document recolonization within five to thirty years, with most taking between one to two decades (Withler 1982, Bryant et al. 1999, Burger et al. 2000, Glen 2002, Pess et al. 2003, Milner et al. 2007, Kiffney et al. 2009, Pess 2009). 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.

Translocation

For areas that are isolated and distant from extant populations, natural colonization may be unrealistic within the time scales desired by management. In cases where the reintroduction site is so isolated that long-distance dispersal from extant populations is unlikely, translocation 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 translocation, but discuss the selection of the source population separately.

Translocation allows for natural patterns of natural and sexual selection within the new habitat, and thus has many of the same benefits as natural colonization. One difference is that translocation introduces artificial selection of the individuals that reach the reintroduction site. In some cases, natural selection during migration could be important for the evolution of traits (i.e., body morphology or energy reserves) 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 depends on the choice of which individuals are translocated.

Aspects of salmon behavior and ecology may affect the success of translocation. Adult salmon will be naïve in the waters to which they are translocated, and will not recognize the odors they encounter. As demonstrated by experimental translocations, these individuals may eventually depart the reintroduction site without spawning, in search of their natal stream (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 (Wolf et al. 1996, Fischer and Lindenmayer 2000), 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 any fish are taken. Removing large numbers of fish from an already depressed population (as many or most in threatened and endangered ESUs are) increases the risk to that source population. Mining populations in this way can 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 the early-life mortality that occurs in the egg incubation or rearing phases 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 the goals of self-sustaining natural production.

Several issues related to hatchery propagation and release 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 of, 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 that inhabited the site prior to the reintroduction.

In addition, a 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 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 the 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 a 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 has truly increased, or if it has simply been masked by artificial production (McClure et al. 2008b). Some pulsed reintroductions may well fail to establish populations, and this result would indicate either that the donor stock was not appropriately adapted for the reintroduction site, or that there exists some other factor, whether 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 newly-opened area (Pess 2009). Thus, the choice of source population is linked to the method of introduction—whether that method is natural recolonization, translocation, or hatchery release—and is a critical component of implementing a reintroduction effort. Source populations that are most likely to contribute to the long-term success of both the reintroduction and the long-term viability of the population, MPG, or ESU will be:

- Genetically and ecologically appropriate to the area to be reintroduced.
- Abundant enough (with a 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 (Taylor 1991, Quinn 2005); 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 reopened habitats will improve the 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 (Waples 1991, Busby et al. 1996, Myers et al. 1998), using fish from 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 are not relevant), analysis of landscape characteristics can provide a surrogate for ecological similarity. This approach infers that similar habitats promote the 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—populations that have been artificially propagated for many generations will be less like their wild counterparts than those that have been in captivity for fewer generations (Frankham 2008)—increasing their adaptation to the hatchery environment. However, the absolute degree of domestication will obviously depend on how integrated or segregated the hatchery program is from a wild population (Moberg et al. 2005). Thus, an evaluation of hatchery stocks includes considering:

- The original source of the hatchery stock: Local is the least risky, while composite stocks derived from several ESUs are the most risky as they are the most genetically different.
- The period of time and number of generations the stock has been artificially propagated (fewer generations is less risky).
- Whether the hatchery has been operated as an integrated or segregated program: Fully integrated is the least risky, while fully segregated is the most risky, since genes selected for by domestication will accumulate the most in these cases.

Each case will be unique, and in some cases, the benefits of a 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 translocation 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. Translocation 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 provides a useful benchmark for judging the capacity of a potential source population to support the 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 the 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 both the “best” source population and the “best” method for moving it 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 (i.e., with translocation of locally derived hatchery fish that have been bred artificially for only a short time) than recolonized naturally (i.e., 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 for juveniles migrating downstream toward 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 irrigation 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 nontarget populations or spawning areas.

Barrier or dam removal is a special case of volitional passage, in 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 toxin-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 revegetation 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 passing upstream, and would be most appropriate for adult fish ladders that circumvent barriers. Although such structures would increase operation and maintenance costs, they would also 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 both 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 when making a final decision.

A trap-and-haul operation is most appropriate for situations where volitional passage is not logistically, technically, or biologically possible, and fish must be actively moved up- 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 a 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 among 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 translocation strategy may be fuzzy, but will largely depend on the selection of the source population.

In determining whether to adopt a volitional or a 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 (Williams et al. 1988, IUCN 1998, George et al. 2009). Monitoring ecological systems refers to sampling something in an effort to detect changes in physical, chemical, or biological parameters or processes (Roni 2005). Only by monitoring is it possible to determine whether reintroduction is 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 be 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 changes 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 a 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 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 offers a chance to restore steelhead in one of the few populations that have both a winter and summer run in an ESU (e.g., the 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 affect whether or not reintroduction establishes a self-sustaining population. Although a “build it and they will come” philosophy is appropriate for barrier removals directly above existing productive populations and below high-quality habitat, in other cases, the reasons the population was extirpated in the first place can be both numerous and complex. Consequently, although some limiting factors may have been addressed prior to reintroduction, others may still exist that could curtail project success. In these situations, monitoring is essential to understand the factors that limit reintroduction success, and, if possible, to 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 succeeds or fails. Considering physical processes such as rates of change in water, sediment, wood, and nutrients, rather than just amount, will also provide information on how habitats are functioning. This is especially important if habitat modifications are made as part of the reintroduction effort.

The timeline over which responses are expected and alternative reintroduction strategies are considered is crucial. 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 instead of years) to observe any 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; these may be of conservation concern, or they may support important fisheries. Barrier removal without selective access may also expose streams to invasion by non-native species, and surveys should aim to determine whether invasion occurs so that any 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, which may increase rates of straying to nearby natural spawning areas. Monitoring 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 contemporary populations can offer a unique opportunity to learn about reintroduction ecology and the role that hatchery stocking should play. There are several areas in the interior Columbia River basin 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 the 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 focused monitoring in the natural production areas, such actions could provide crucial information for ongoing and future reintroductions elsewhere.

Conclusion

Reintroductions of extirpated Pacific salmonid populations 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 when determining whether to engage in a reintroduction effort. Program managers must evaluate the potential benefits of a successful effort to the 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 those 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, the risks may outweigh the 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 the 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 and how a reintroduction contributes to overall ESU status.



References

- Abdul-Aziz, O. I., N. J. Mantua, and K. W. Myers. 2011. Potential climate change impacts on thermal habitats of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean and adjacent seas. *Canadian Journal of Fisheries and Aquatic Sciences* 68:1660–1680.
- Allendorf, F. W., and G. Luikart. 2007. *Conservation and the genetics of populations*. Blackwell Publishing, Oxford, UK.
- Angilletta, M. J., E. A. Steel, K. K. Bartz, J. G. Kingsolver, M. D. Scheuerell, B. R. Beckman, and L. G. Crozier. 2008. Big dams and salmon evolution: Changes in thermal regimes and their potential evolutionary consequences. *Evolutionary Applications* 1:286–299.
- Araki, H., B. A. Berejikian, M. J. Ford, and M. S. Blouin. 2008. Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications* 1:342–355.
- Armstrong, D. P., and P. J. Seddon. 2008. Directions in reintroduction biology. *Trends in Ecology and Evolution* 23:20–25.
- Ayllon, F., P. Davaine, E. Beall, and E. Garcia-Vazquez. 2006. Dispersal and rapid evolution in brown trout colonizing virgin sub-Antarctic ecosystems. *Journal of Evolutionary Biology* 19:1352–1358.
- Barbanera, F., O. R. W. Pergams, M. Guerrini, G. Forcina, P. Panayides, and F. Dini. 2010. Genetic consequences of intensive management in game birds. *Biological Conservation* 143:1259–1268.
- Bartz, K. K., K. M. Lagueux, M. D. Scheuerell, T. Beechie, A. D. Haas, and M. H. Ruckelshaus. 2006. Translating restoration scenarios into habitat conditions: An initial step in evaluating recovery strategies for Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 63:1578–1595.
- Battin, J., M. W. Wiley, M. H. Ruckelshaus, R. N. Palmer, E. Korb, K. K. Bartz, and H. Imaki. 2007. Projected impacts of climate change on salmon habitat restoration. *Proceedings of the National Academy of Sciences of the United States of America* 104:6720–6725.
- Beamesderfer, R. C., and B. E. Rieman. 1991. Abundance and distribution of northern squawfish, walleyes, and smallmouth bass in the John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:439–447.
- Beechie, T., E. Buhle, M. Ruckelshaus, A. Fullerton, and L. Holsinger. 2006. Hydrologic regime and the conservation of salmon life history diversity. *Biological Conservation* 130:560–572.
- Beechie, T. J., D. A. Sear, J. D. Olden, G. R. Pess, J. M. Buffington, H. Moir, P. Roni, and M. M. Pollock. 2010. Process-based principles for restoring river ecosystems. *BioScience* 60:209–222.
- Beechie, T. J., O. Stefankiv, B. Timpone-Padgham, J. E. Hall, G. R. Pess, M. Rowse, M. Liermann, K. Fresh, and M. J. Ford. 2017. *Monitoring Salmon Habitat Status and Trends in Puget Sound: Development of Sample Designs, Monitoring Metrics, and Sampling Protocols for Large River, Floodplain, Delta, and Nearshore Environments*. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-137. DOI: 10.7289/V5/TM-NWFSC-137
- Benjamin, J. R., J. B. Dunham, and M. R. Dare. 2007. Invasion by nonnative brook trout in Panther Creek, Idaho: Roles of local habitat quality, biotic resistance, and connectivity to source habitats. *Transactions of the American Fisheries Society* 136:875–888.
- Bisson, P. A., C. M. Crisafulli, B. R. Fransen, R. E. Lucas, and C. P. Hawkins. 2005. Responses of Fish to the 1980 Eruption of Mount St. Helens. Pages 163–182 *in* V. H. Dale, F. J. Swanson, and C. M. Crisafulli, editors. *Ecological Responses to the 1980 Eruption of Mount St. Helens*. Springer, New York.

- Blair, G. R., and T. P. Quinn. 1991. Homing and spawning site selection by sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. *Canadian Journal of Zoology* 69:176–181.
- Brenkman, S. J., S. L. Mumford, M. House, and C. Patterson. 2008. Establishing baseline information on the geographic distribution of fish pathogens endemic in Pacific salmonids prior to dam removal and subsequent recolonization by anadromous fish in the Elwha River, Washington. *Northwest Science* 82:142–152.
- Bryant, M. D., B. J. Frenette, and S. J. McCurdy. 1999. Colonization of a watershed by anadromous salmonids following the installation of a fish ladder in Margaret Creek, Southeast Alaska. *North American Journal of Fisheries Management* 19:1129–1136.
- Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. *North American Journal of Fisheries Management* 22:35–51.
- Burger, C. V., K. T. Scribner, W. J. Spearman, C. O. Swanton, and D. E. Campton. 2000. Genetic contribution of three introduced life history forms of sockeye salmon to colonization of Frazer Lake, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 57:2096–2111.
- Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon and California. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-27.
- Byers, J. E., K. Cuddington, C. G. Jones, T. S. Talley, A. Hastings, J. G. Lambrinos, J. A. Crooks, and W. G. Wilson. 2006. Using ecosystem engineers to restore ecological systems. *Trends in Ecology & Evolution* 21:493–500.
- Carlson, S. M., and T. R. Seamons. 2008. A review of quantitative genetic components of fitness in salmonids: Implications for adaptation to future change. *Evolutionary Applications* 1:222–238.
- Caudill, C. C., W. R. Daigle, M. L. Keefer, C. T. Boggs, M. A. Jepson, B. J. Burke, R. W. Zabel, T. C. Bjornn, and C. A. Peery. 2007. Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: Delayed negative effects of passage obstacles or condition-dependent mortality? *Canadian Journal of Fisheries and Aquatic Sciences* 64:979–995.
- Chapman, D. W. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth century. *Transactions of the American Fisheries Society* 115:662–670.
- Chilcote, M. W., K. W. Goodson, and M. R. Falcu. 2011. Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. *Canadian Journal of Fisheries and Aquatic Sciences* 68:511–522.
- CIG (Climate Impacts Group). 2009. The Washington Climate Change Impacts Assessment. University of Washington, Seattle. Available: ces.washington.edu/db/pdf/wacciareport681.pdf (April 2018).
- Clemento, A. J., E. C. Anderson, D. Boughton, D. Girman, and J. C. Garza. 2009. Population genetic structure and ancestry of *Oncorhynchus mykiss* populations above and below dams in south-central California. *Conservation Genetics* 10:1321–1336.
- Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution* 14:405–410.
- Crozier, L. G., A. P. Hendry, P. W. Lawson, T. P. Quinn, N. J. Mantua, J. Battin, R. G. Shaw, and R. B. Huey. 2008a. Potential responses to climate change in organisms with complex life histories: Evolution and plasticity in Pacific salmon. *Evolutionary Applications* 1:252–270.
- Crozier, L., and R. W. Zabel. 2006. Climate impacts at multiple scales: Evidence for differential population responses in juvenile Chinook salmon. *Journal of Animal Ecology* 75:1100–1109.

- Crozier, L. G., R. W. Zabel, and A. F. Hamlett. 2008b. Predicting differential effects of climate change at the population level with life-cycle models of spring Chinook salmon. *Global Change Biology* 14:236–249.
- Deredec, A., and F. Courchamp. 2007. Importance of the Allee effect for reintroductions. *Écoscience* 14:440–451.
- Dias, P. C. 1996. Sources and sinks in population biology. *Trends in Ecology & Evolution* 11:326–330.
- Dittman, A.H., D. May, D. A. Larsen, M. L. Moser, M. Johnston, and D. Fast. 2010. Homing and spawning site selection by supplemented hatchery- and natural-origin Yakima River spring Chinook salmon. *Transactions of the American Fisheries Society* 139:1014–1028.
- Durkin, J. T., D. L. Park, and R. F. Raleigh. 1970. Distribution and movement of juvenile salmon through Browlee Reservoir, 1962–65. *Fishery Bulletin* 68:219–243.
- Einum, S., K. H. Nislow, S. Mckelvey, and J. D. Armstrong. 2008. Nest distribution shaping within-stream variation in Atlantic salmon juvenile abundance and competition over small spatial scales. *Journal of Animal Ecology* 77:167–172.
- Fausch, K. D. 1988. Tests of competition between native and introduced salmonids in streams—what have we learned? *Canadian Journal of Fisheries and Aquatic Sciences* 45:2238–2246.
- Fausch, K. D., B. E. Rieman, J. B. Dunham, M. K. Young, and D. P. Peterson. 2009. Invasion versus isolation: Trade-offs in managing native salmonids with barriers to upstream movement. *Conservation Biology* 25:859–870.
- Ferguson, J. W., B. P. Sandford, R. E. Reagan, L. G. Gilbreath, E. B. Meyer, R. D. Ledgerwood, and N. S. Adams. 2007. Bypass system modification at Bonneville Dam on the Columbia River improved the survival of juvenile salmon. *Transactions of the American Fisheries Society* 136:1487–1510.
- Fischer, J., and D. B. Lindenmayer. 2000. An assessment of the published results of animal relocations. *Biological Conservation* 96:1–11.
- Ford, M. J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. *Conservation Biology* 16:815–825.
- Ford, M. J., editor. 2010. Status Review Update for Pacific Salmon and Steelhead Listed under the Endangered Species Act: Pacific Northwest. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-113.
- Frankham, R. 2008. Genetic adaptation to captivity in species conservation programs. *Molecular Ecology* 17:325–333.
- Fraser, D. J. 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications* 1:535–586.
- Fullerton, A. H., S. T. Lindley, G. R. Pess, B. E. Feist, E. A. Steel, and P. McElhany. 2011. Human influence on the spatial structure of threatened Pacific salmon metapopulations. *Conservation Biology* 25(5):932–944.
- Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. *Bioscience* 52:917–928.
- George, A. L., B. R. Kuhajda, J. D. Williams, M. A. Cantrell, P. L. Rakes, and J. R. Shute. 2009. Guidelines for propagation and translocation for freshwater fish conservation. *Fisheries* 34:529–545.
- Gibson, R. J., R. L. Haedrich, and C. M. Wernerheim. 2005. Loss of fish habitat as a consequence of inappropriately constructed stream crossings. *Fisheries* 30:10–17.
- Glen, D. 2002. Recovery of salmon and trout following habitat enhancement works: Review of case studies 1995–2002. Pages 93–112 *in* M. O’Grady, editor. Proceedings of the 13th International Salmonid Habitat Enhancement Workshop, Westport, County Mayo, Ireland, September 2002. Central Fisheries Board, Dublin, Ireland.

- Good, T. P., J. Davies, B. J. Burke, and M. H. Ruckelshaus. 2008. Incorporating catastrophic risk assessments into setting conservation goals for threatened Pacific Salmon. *Ecological Applications* 18:246–257.
- Greene, C. M., J. E. Hall, K. R. Guilbault, and T. P. Quinn. 2010. Improved viability of populations with diverse life-history portfolios. *Biology Letters* 6:382–386.
- Griffiths, A. M., J. S. Ellis, D. Clifton-Dey, G. Machado-Schiaffino, D. Bright, E. Garcia-Vazquez, and J. R. Stevens. 2011. Restoration versus recolonisation: The origin of Atlantic salmon (*Salmo salar* L.) currently in the River Thames. *Biological Conservation* 144(11):2733–2738.
- Gustafson, R. G., R. S. Waples, J. M. Myers, L. A. Weitkamp, G. J. Bryant, O. W. Johnson, and J. J. Hard. 2007. Pacific salmon extinctions: Quantifying lost and remaining diversity. *Conservation Biology* 21:1009–1020.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, UK.
- Harvey, B. C., and R. J. Nakamoto. 1996. Effects of steelhead density on growth of coho salmon in a small coastal California stream. *Transactions of the American Fisheries Society* 125:237–243.
- Hendry, A. P., V. Castric, M. T. Kinnison, and T. P. Quinn. 2004. The evolution of philopatry and dispersal: Homing versus straying in salmonids. Pages 52–91 in A. P. Hendry and S. C. Stearns, editors. *Evolution Illuminated: Salmon and Their Relatives*. Oxford University Press, Oxford, UK.
- Hendry, A. P., J. K. Wenburg, P. Bentzen, E. C. Volk, and T. P. Quinn. 2000. Rapid evolution of reproductive isolation in the wild: Evidence from introduced salmon. *Science* 290:516–518.
- Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the United States of America* 100:6564–6568.
- Honea, J., M. McClure, J. Jorgensen, and M. Scheuerell. 2016. Assessing freshwater life-stage vulnerability of an endangered Chinook salmon population to climate change influences on stream habitat. *Climate Research* 71(2):127–137.
- Huff, D. D., L. M. Miller, and B. Vondracek. 2010. Patterns of ancestry and genetic diversity in reintroduced populations of the slimy sculpin: Implications for conservation. *Conservation Genetics* 11:2379–2391.
- Hutchings, J. A. 2011. Old wine in new bottles: Reaction norms in salmonid fishes. *Heredity* 106:421–437.
- ICTRT (Interior Columbia Technical Recovery Team). 2003. Independent populations of Chinook, steelhead, and sockeye for listed evolutionarily significant units within the Interior Columbia River domain. Available: www.nwfsc.noaa.gov/research/divisions/cb/genetics/trt/col/trt_viability.cfm (April 2018).
- ICTRT (Interior Columbia Technical Recovery Team). 2007. Viability criteria for application to Interior Columbia basin salmonid ESUs. Available: www.nwfsc.noaa.gov/research/divisions/cb/genetics/trt/col/trt_pop_id.cfm (April 2018).
- IUCN (International Union for Conservation of Nature and Natural Resources). 1998. *IUCN guidelines for re-introductions*. Information Press, Oxford, UK.
- Kareiva, P., M. Marvier, and M. McClure. 2000. Recovery and management options for spring/summer Chinook salmon in the Columbia River basin. *Science* 290:977–979.
- Keefer, M. L., C. C. Caudill, C. A. Peery, and S. R. Lee. 2008. Transporting juvenile salmonids around dams impairs adult migration. *Ecological Applications* 18:1888–1900.
- Kiffney, P. M., G. R. Pess, J. H. Anderson, P. Faulds, K. Burton, and S. C. Riley. 2009. Changes in fish communities following recolonization of the Cedar River, WA, USA, by Pacific salmon after 103 years of local extirpation. *River Research and Applications* 25:438–452.
- Kinnison, M. T., and N. G. Hairston. 2007. Eco-evolutionary conservation biology: Contemporary evolution and the dynamics of persistence. *Functional Ecology* 21:444–454.

- Koskinen, M. T., T. O. Haugen, and C. R. Primmer. 2002. Contemporary Fisherian life-history evolution in small salmonid populations. *Nature* 419:826–830.
- Kostow, K. 2009. Factors that contribute to the ecological risks of salmon and steelhead hatchery programs and some mitigating strategies. *Reviews in Fish Biology and Fisheries* 19:9–31.
- Kostow, K., and S. Zhou. 2006. The effect of an introduced summer steelhead hatchery stock on the productivity of a wild winter steelhead population. *Transactions of the American Fisheries Society* 135:825–841.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911–927.
- Leider, S. A. 1989. Increased straying by adult steelhead trout (*Salmo gairdneri*) following the 1980 eruption of Mount St. Helens. *Environmental Biology of Fishes* 24:219–229.
- Lichatowich, J. 1999. *Salmon without rivers: A history of the Pacific salmon crisis*. Island Press, Washington, D.C.
- Liebold, A., W. D. Koenig, and O. N. Bjornstad. 2004. Spatial synchrony in population dynamics. *Annual Review of Ecology Evolution and Systematics* 35:467–490.
- Liermann, M., and R. Hilborn. 2001. Depensation: Evidence, models and implications. *Fish and Fisheries* 2:33–58.
- Lindsey, P. A., R. R. Alexander, J. T. du Toit, and M. G. L. Mills. 2005. The potential contribution of ecotourism to African wild dog *Lycaon pictus* conservation in South Africa. *Biological Conservation* 123:339–348.
- Lucas, B., and K. Pointer. 1987. Wild steelhead spawning escapement estimates for southwest Washington streams—1987. Washington Department of Game, Fisheries Management Division 87–6. Olympia, Washington.
- Mantua, N., I. Tohver, and A. Hamlet. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. *Climatic Change* 102:187–223.
- Martinez, A., J. C. Garza, and D. E. Pearse. 2011. A Microsatellite Genome Screen Identifies Chromosomal Regions under Differential Selection in Steelhead and Rainbow Trout. *Transactions of the American Fisheries Society* 140:829–842.
- Matala, A. P., J. E. Hess, and S. R. Narum. 2011. Resolving Adaptive and Demographic Divergence among Chinook Salmon Populations in the Columbia River Basin. *Transactions of the American Fisheries Society* 140:783–807.
- McClure, M. M., S. M. Carlson, T. J. Beechie, G. R. Pess, J. C. Jorgensen, S. M. Sogard, S. E. Sultan, D. M. Holzer, J. Travis, B. L. Sanderson, M. E. Power, and R. W. Carmichael. 2008a. Evolutionary consequences of habitat loss for Pacific anadromous salmonids. *Evolutionary Applications* 1:300–318.
- McClure, M. M., F. M. Utter, C. Baldwin, R. W. Carmichael, P. F. Hassemer, P. J. Howell, P. Spruell, T. D. Cooney, H. A. Schaller, and C. E. Petrosky. 2008b. Evolutionary effects of alternative artificial propagation programs: Implications for viability of endangered anadromous salmonids. *Evolutionary Applications* 1:356–375.
- McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-42.
- McMillan, J. R., S. L. Katz, and G. R. Pess. 2007. Observational evidence of spatial and temporal structure in a sympatric anadromous (winter steelhead) and resident rainbow trout mating system on the Olympic Peninsula, Washington. *Transactions of the American Fisheries Society* 136:736–748.
- McPhee, M. V., F. Utter, J. A. Stanford, K. V. Kuzishchin, K. A. Savvaitova, D. S. Pavlov, and F. W. Allendorf. 2007. Population structure and partial anadromy in *Oncorhynchus mykiss* from Kamchatka: Relevance for conservation strategies around the Pacific Rim. *Ecology of Freshwater Fish* 16:539–547.

- Milner, A. M., C. L. Fastie, F. S. Chapin, D. R. Engstrom, and L. C. Sharman. 2007. Interactions and linkages among ecosystems during landscape evolution. *Bioscience* 57:237–247.
- Mobrand, L. E., J. Barr, L. Blankenship, D. E. Campton, T. T. P. Evelyn, T. A. Flagg, C. V. W. Mahnken, L. W. Seeb, P. R. Seidel, and W. W. Smoker. 2005. Hatchery reform in Washington state: Principles and emerging issues. *Fisheries* 30:11–23.
- Moore, J. W., M. McClure, L. A. Rogers, and D. E. Schindler. 2010. Synchronization and portfolio performance of threatened salmon. *Conservation Letters* 3:340–348.
- Moore, J. W., D. E. Schindler, and M. D. Scheuerell. 2004. Disturbance of freshwater habitats by anadromous salmon in Alaska. *Oecologia* 139:298–308.
- Moyle, P. B., and T. Light. 1996. Biological invasions of fresh water: Empirical rules and assembly theory. *Biological Conservation* 78:149–161.
- Mueter, F. J., B. J. Pyper, and R. M. Peterman. 2005. Relationships between coastal ocean conditions and survival rates of northeast Pacific salmon at multiple lags. *Transactions of the American Fisheries Society* 134:105–119.
- Myers, J. M., R. G. Kope, G. J. Bryant, D. J. Teel, L. J. Lierheimer, T. C. Wainwright, W. S. Grant, F. W. Waknitz, K. Neely, S. Lindley, and R. S. Waples. 1998. Status review of Chinook salmon from Washington, Idaho, Oregon, and California. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-35.
- Naish, K. A., J. E. Taylor III, P. S. Levin, T. P. Quinn, J. R. Winton, D. Huppert, and R. Hilborn. 2008. An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology* 53:61–194.
- NMFS (National Marine Fisheries Service). 1997. Endangered and Threatened Species; Listing of Several Evolutionarily Significant Units (ESUs) of West Coast Steelhead. *Federal Register* 62:159(18 August 1997):43937–43954.
- NMFS (National Marine Fisheries Service). 1999. Endangered and Threatened Species; Threatened Status for Three Chinook Salmon Evolutionarily Significant Units (ESUs) in Washington and Oregon, and Endangered Status for One Chinook Salmon ESU in Washington. *Federal Register* 64:56(24 March 1999):14308–14328.
- NMFS (National Marine Fisheries Service). 2005. Endangered and Threatened Species: Final Listing Determination for 16 ESUs of West Coast Salmon, and Final 4(d) Protective Regulations for Threatened Salmonid ESUs. *Federal Register* 70:123(28 June 2005):37160–37204.
- NPPC (Northwest Power Planning Council). 1986. Compilation of information on salmon and steelhead losses in the Columbia River basin. Portland, Oregon.
- NRC (National Research Council). 1996. *Upstream: Salmon and society in the Pacific Northwest*. National Academy Press, Washington, DC.
- Ostberg, C. O., S. L. Slatton, and R. J. Rodriguez. 2004. Spatial partitioning and asymmetric hybridization among sympatric coastal steelhead trout (*Oncorhynchus mykiss irideus*), coastal cutthroat trout (*O. clarki clarki*) and interspecific hybrids. *Molecular Ecology* 13:2773–2788.
- Pess, G. R. 2009. *Patterns and processes of salmon colonization*. University of Washington, Seattle.
- Pess, G. R., T. J. Beechie, J. E. Williams, D. R. Whitall, J. I. Lange, and J. R. Klochak. 2003. Watershed assessment techniques and the success of aquatic restoration activities. Pages 185–201 *in* R. C. Wissmar and P. A. Bisson, editors. *Strategies for Restoring River Ecosystems: Sources of Variability and Uncertainty in Natural and Managed Systems*. American Fisheries Society, Bethesda, Maryland.

- Pess, G. R., R. Hilborn, K. Kloehn, and T. P. Quinn. 2012. The influence of population dynamics and environmental conditions on pink salmon re-colonization after barrier removal in the Fraser River, British Columbia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 69(5):970–982.
- Pess, G. R., M. L. McHenry, T. J. Beechie, and J. Davies. 2008. Biological impacts of the Elwha River dams and potential salmonid responses to dam removal. *Northwest Science* 82:72–90.
- Petrosky, C. E., and H. A. Schaller. 2010. Influence of river conditions during seaward migration and ocean conditions on survival rates of Snake River Chinook salmon and steelhead. *Ecology of Freshwater Fish* 19:520–536.
- Platts, W. S. 1972. The effects of heavy metals on anadromous runs of salmon and steelhead in the Panther Creek drainage, Idaho. *Proceedings of the Annual Conference, Western Association of State Game and Fish Commissioners* 52:582–600.
- Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Prendergast. 1991. Feeding of predaceous fishes on outmigrating juvenile salmonids in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:405–420.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *Bioscience* 47:769–784.
- Poff, N. L., and D. D. Hart. 2002. How dams vary and why it matters for the emerging science of dam removal. *Bioscience* 52:659–668.
- Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States of America* 104:5732–5737.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Quinn, T. P. 2005. *The behavior and ecology of Pacific salmon and trout*. University of Washington, Seattle.
- Quinn, T. P., M. T. Kinnison, and M. J. Unwin. 2001. Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: Pattern, rate, and process. *Genetica* 112–113:493–513.
- Reeves, G. H., F. H. Everest, and J. R. Sedell. 1993. Diversity of juvenile anadromous salmonid assemblages in coastal Oregon basins with different levels of timber harvest. *Transactions of the American Fisheries Society* 122:309–317.
- Ricker, W. E. 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada* 11:559–623.
- Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in the John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:448–458.
- Rogers, L. A., and D. E. Schindler. 2008. Asynchrony in population dynamics of sockeye salmon in southwest Alaska. *Oikos* 117:1578–1586.
- Roni, P. 2005. *Monitoring stream and watershed restoration*. American Fisheries Society, Bethesda, Maryland.
- Roni, P., K. Hanson, and T. Beechie. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. *North American Journal of Fisheries Management* 28:856–890.
- Ruckelshaus, M., P. McElhany, and M. J. Ford. 2003. Recovering species of conservation concern: Are populations expendable? Pages 305–329. *in* P. Kareiva and S. Levin, editors. *The Importance of Species: Perspectives on Expendability and Triage*. Princeton University Press, Princeton, New Jersey.
- Ruzycki, J. R., L. R. Clarke, M. W. Flesher, R. W. Carmichael, and D. L. Eddy. 2009. *Performance of Progeny from Steelhead and Rainbow Trout Crosses: Final Report*. Oregon Department of Fish and Wildlife, Salem, Oregon. Available: www.fws.gov/lsnakecomplan/Reports/ODFW/Eval/Breeding%20Expt.%20Final%20Report.pdf (April 2018).

- Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K.A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 32:305–332.
- Sanderson, B. L., K. A. Barnas, and A. M. W. Rub. 2009. Nonindigenous species of the Pacific Northwest: An overlooked risk to endangered salmon? *Bioscience* 59:245–256.
- Satterthwaite, W. H., M. P. Beakes, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2010. State-dependent life history models in a changing (and regulated) environment: Steelhead in the California Central Valley. *Evolutionary Applications* 3:221–243.
- Schaller, H. A., and C. E. Petrosky. 2007. Assessing hydrosystem influence on delayed mortality of Snake River stream-type Chinook salmon. *North American Journal of Fisheries Management* 27:810–824.
- Schindler, D. E., X. Augerot, E. Fleishman, N. J. Mantua, B. Riddell, M. Ruckelshaus, J. Seeb, and M. Webster. 2008. Climate change, ecosystem impacts, and management for Pacific salmon. *Fisheries* 33:502–506.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465:609–U102.
- Schtickzelle, N., and T. P. Quinn. 2007. A metapopulation perspective for salmon and other anadromous fish. *Fish and Fisheries* 8:297–314.
- Seddon, P. J., D. P. Armstrong, and R. F. Maloney. 2007. Developing the science of reintroduction biology. *Conservation Biology* 21:303–312.
- Sims, C. W. 1970. Emigration of juvenile salmon and trout from Brownlee Reservoir, 1963–65. *Fishery Bulletin* 68:245–259.
- Spalton, J. A., M. W. Lawrence, and S. A. Brend. 1999. Arabian oryx reintroduction in Oman: Successes and setbacks. *Oryx* 33:168–175.
- Stanley, E. H., and M. W. Doyle. 2003. Trading off: The ecological effects of dam removal. *Frontiers in Ecology and the Environment* 1:15–22.
- Stüwe, M., and B. Nievergelt. 1991. Recovery of alpine ibex from near extinction: The result of effective protection, captive breeding, and reintroductions. *Applied Animal Behaviour Science* 29:379–387.
- Tallmon, D. A., G. Luikart, and R. S. Waples. 2004. The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology and Evolution* 19:489–496.
- Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* 98:185–207.
- Tear, T. H., P. Kareiva, P. L. Angermeier, P. Comer, B. Czech, R. Kautz, L. Landon, D. Mehlman, K. Murphy, M. Ruckelshaus, J. M. Scott, and G. Wilhere. 2005. How much is enough? The recurrent problem of setting measurable objectives in conservation. *Bioscience* 55:835–849.
- USOFR (U.S. Office of the Federal Register). 1996. Policy Regarding the Recognition of Distinct Vertebrate Population Segments Under the Endangered Species Act (96–2639). *Federal Register* 61:26(7 February 1996):4722–4725.
- Vettorazzo, E., A. Borgo, and N. Martino. 2009. Communication activities about alpine marmot reintroduction in the Dolomiti Bellunesi National Park project (Italy). *Ethology Ecology & Evolution* 21:349–353.
- Viggers, K. L., D. B. Lindenmayer, and D. M. Spratt. 1993. The importance of disease in reintroduction programs. *Wildlife Research* 20:687–698.
- Walker, S. F., J. Bosch, T. Y. James, A. P. Litvintseva, J. A. O. Valls, S. Pina, G. Garcia, G. A. Rosa, A. A. Cunningham, S. Hole, R. Griffiths, and M. C. Fisher. 2008. Invasive pathogens threaten species recovery programs. *Current Biology* 18:R853–R854.

- Walters, A., K. Bartz, and M. McClure. 2013. Interactive impacts of water diversion and climate change for juvenile Chinook salmon in the Lemhi River. *Conservation Biology* 27(6):1179–1189.
- Waples, R. S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of “species” under the Endangered Species Act. *Marine Fisheries Review* 53:11–22.
- Waples, R. S. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. *American Fisheries Society Symposium* 17:8–27.
- Waples, R. S., T. Beechie, and G. R. Pess. 2009. Evolutionary history, habitat disturbance regimes, and anthropogenic changes: What do these mean for resilience of Pacific salmon populations? *Ecology and Society* 14(1):3. Available: digitalcommons.unl.edu/usdeptcommercepub/453/ (April 2018).
- Waples, R. S., G. R. Pess, and T. Beechie. 2008. Evolutionary history of Pacific salmon in dynamic environments. *Evolutionary Applications* 1:189–206.
- Waples, R. S., R. W. Zabel, M. D. Scheuerell, and B. L. Sanderson. 2007. Evolutionary responses by native species to major anthropogenic changes to their ecosystems: Pacific salmon in the Columbia River hydropower system. *Molecular Ecology* 17:84–96.
- Welch, D. W., E. L. Rechisky, M. C. Melnychuk, A. D. Porter, C. J. Walters, S. Clements, B. J. Clemens, R. S. McKinley, and C. Schreck. 2008. Survival of migrating salmon smolts in large rivers with and without dams. *PLoS Biology* 6:2101–2108.
- Williams, J. E., D. W. Sada, and C. D. Williams. 1988. American Fisheries Society guidelines for introductions of threatened and endangered fishes. *Fisheries* 13:5–11.
- Williams, J. G., R. W. Zabel, R. S. Waples, J. A. Hutchings, and W. P. Connor. 2008. Potential for anthropogenic disturbances to influence evolutionary change in the life history of a threatened salmonid. *Evolutionary Applications* 1:271–285.
- Withler, F. C. 1982. Transplanting Pacific salmon. Canadian Technical Report of Fisheries and Aquatic Sciences 1079:1488–5379.
- Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: Update and reanalysis of 1987 survey data. *Conservation Biology* 10:1142–1154.
- Young, K. A. 2001. Habitat diversity and species diversity: Testing the competition hypothesis with juvenile salmonids. *Oikos* 95:87–93.

Recently published by the Northwest Fisheries Science Center

NOAA Technical Memorandum NMFS-NWFSC-

- 140 Buhle, E. R., M. D. Scheuerell, T. D. Cooney, M. J. Ford, R. W. Zabel, and J. T. Thorson. 2018.** Using Integrated Population Models to Evaluate Fishery and Environmental Impacts on Pacific Salmon Viability. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-140. NTIS number pending. <https://doi.org/10.7289/V5/TM-NWFSC-140>
- 139 Harvey, C., N. Garfield, G. Williams, K. Andrews, C. Barceló, K. Barnas, S. Bograd, R. Brodeur, B. Burke, J. Cope, L. deWitt, J. Field, J. Fisher, C. Greene, T. Good, E. Hazen, D. Holland, M. Jacox, S. Kasperski, S. Kim, A. Leising, S. Melin, C. Morgan, S. Munsch, K. Norman, W. T. Peterson, M. Poe, J. Samhour, I. Schroeder, W. Sydeman, J. Thayer, A. Thompson, N. Tolimieri, A. Varney, B. Wells, T. Williams, and J. Zamon. 2017.** Ecosystem Status Report of the California Current for 2017: A Summary of Ecosystem Indicators Compiled by the California Current Integrated Ecosystem Assessment Team (CCIEA). U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-139. NTIS number PB2018-100477. <https://doi.org/10.7289/V5/TM-NWFSC-139>
- 138 Kamikawa, D. J. 2017.** Survey Fishes: An Illustrated List of the Fishes Captured during the Northwest Fisheries Science Center's Fishery Resource Analysis and Monitoring Division's West Coast Surveys. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-138. NTIS number PB2018-100308. <https://doi.org/10.7289/V5/TM-NWFSC-138>
- 137 Beechie, T. J., O. Stefankiv, B. Timpane-Padgham, J. E. Hall, G. R. Pess, M. Rowse, M. Liermann, K. Fresh, and M. J. Ford. 2017.** Monitoring Salmon Habitat Status and Trends in Puget Sound: Development of Sample Designs, Monitoring Metrics, and Sampling Protocols for Large River, Floodplain, Delta, and Nearshore Environments. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-137. NTIS number PB2017-102556. <https://doi.org/10.7289/V5/TM-NWFSC-137>
- 136 Keller, A. A., J. R. Wallace, and R. D. Methot. 2017.** The Northwest Fisheries Science Center's West Coast Groundfish Bottom Trawl Survey: History, Design, and Description. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-136. NTIS number PB2017-101432. <https://doi.org/10.7289/V5/TM-NWFSC-136>
- 135 Mongillo, T. M., G. M. Ylitalo, L. D. Rhodes, S. M. O'Neill, D. P. Noren, and M. B. Hanson. 2016.** Exposure to a Mixture of Toxic Chemicals: Implications for the Health of Endangered Southern Resident Killer Whales. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-135. NTIS number PB2017-101431. <https://doi.org/10.7289/V5/TM-NWFSC-135>
- 134 Leonard, J. 2016.** Washington and Oregon Charter Vessel Survey: Methodology and Results. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-134. NTIS number PB2017-100472. <https://doi.org/10.7289/V5/TM-NWFSC-134>
- 133 Duffield, D., J. K. Gaydos, S. Raverty, K. Wilkinson, B. Norberg, L. Barre, M. B. Hanson, P. Foreman, A. Traxler, D. Lambourn, J. Huggins, J. Calambokidis, T. McKlveen, S. Dennison, and H. Brubaker. 2016.** Wild Animal Mortality Investigation: Southern Resident Killer Whale L-112 Final Report. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-133. NTIS number PB2017-100471. <https://doi.org/10.7289/V5/TM-NWFSC-133>

NOAA Technical Memorandums NMFS-NWFSC are available at the Northwest Fisheries Science Center website, <https://www.nwfsc.noaa.gov/index.cfm>.