# DEVELOPING RECOVERY OBJECTIVES AND PHASE TRIGGERS FOR SALMONID POPULATIONS

Hatchery Scientific Review Group

December 2020

# TABLE OF CONTENTS

| Executive Summary1 |      |  |            |
|--------------------|------|--|------------|
| 1.0                | Intr | oduction   | 4          |
| 2.0                | Fou  | ndational Concepts   | 5          |
| 2.                 | .1   | Biological Significance of Populations   | 5          |
| 2.                 | 2    | Biological Recovery Phases   | 6          |
| 2.                 | .3   | General Guidelines for Identifying Phase Triggers                              | 8          |
| 2.                 | .4   | Methods for Setting Phase Triggers 1   | 1          |
|                    | 2.4. | 1 Adult Spawning Capacity Method 1   | 1          |
|                    | 2.4. | 2 Available Habitat Method 1   | 12         |
|                    | 2.4. | 3 Empirical Methods 1  | 12         |
| 2.                 | .5   | Key Concepts in Conservation Genetics1   | 13         |
|                    | 2.5. | 1 Loss of Diversity 1  | L4         |
|                    | 2.5. | 2 Within Population Diversity 1  | 17         |
|                    | 2.5. | 3 Among Population Diversity 1   | _9         |
|                    | 2.5. | 4 Domestication Selection 2  | 20         |
|                    | 2.5. | 5 Uncertainties Associated with the Preservation and Recolonization Phases 2   | 21         |
|                    | 2.5. | 6 Guidelines for Hatcheries in Pristine Regions 2                              | 22         |
| 2.                 | .6   | Key Concepts in Population Biology2  | 22         |
|                    | 2.6. | 1 Density Dependence: Why is it Important?2                                    | 23         |
|                    | 2.6. | 2 Density Dependence: Spawner to Smolt Stage 2                                 | <u>'</u> 4 |
|                    | 2.6. | 3 Effects of Hatchery Salmon on Productivity, Local Adaptation, and Harvests 2 | 25         |
| 3.0                | Рор  | ulation Case Studies   | 34         |
| 3.                 | 1    | Snake River Sockeye Salmon   | 36         |
| 3.                 | 2    | Elwha River Chinook Salmon   | 12         |
| 3.                 | .3   | Okanogan Summer/Fall Chinook5  | 50         |
| 3.                 | .4   | Lewis River Spring Chinook Salmon5   | 54         |
| 3.                 | .5   | Elochoman/Skamokawa Fall Chinook Salmon6                                       | 50         |
| 3.                 | .6   | Snow Creek Coho Salmon6  | 56         |
| 4.0                | Con  | clusions and Recommendations7  | /3         |
| 5.0                | Refe | erences  | /4         |

# APPENDICES

Appendix A Implementation of Hatchery Reform in the Context of Recovery Planning Using the AHA/ISIT Tool

# ACKNOWLEDGMENTS

This white paper builds on the work of the Hatchery Scientific Review Group (HSRG) since its inception in 2000. We want to recognize the support of Washington Department of Fish and Wildlife biologists (Joe Anderson, Thomas Buehrens, Kari Dammerman, Bryce Glaser, Elise Olk, Steven VanderPloeg, and Jennifer Whitney) in developing the case studies, as well as the contributions of Idaho Fish and Game, Colville Confederated Tribes (Kirk Truscott and Casey Baldwin), NOAA Fisheries (Craig Busack), PacifiCorp (Erik Lesko), and US Fish and Wildlife Service (Roger Peters). We want to acknowledge the contributions of former HSRG members Andy Appleby and Lars Mobrand, who led the HSRG's efforts to develop the HSRG's 2017 Framework Paper. The HSRG's work products are the result of interactions, data sharing and collaboration with numerous managers and biologists in the region. Credit for final editing and document production goes to Meridian Environmental, Inc.

# **LIST OF FIGURES**

| Figure 1.  | Number of Chinook salmon smolts (A) and smolts per spawner (B) in relation to the number of parent spawners. Approximately 40% of the natural spawners originated from batchery |
|------------|---|
|            | narents Source: ISAB 2015   |
| Figure 2.  | Predicted number of smolts per spawner in relation to total potential spawners. Red line:   |
|            | Beverton-Holt curve fit to the empirical data shown in Figure 1. Blue line: predicted smolts  |
|            | per spawner associated with a 40% reduction (via random harvest) of total spawners. Green   |
|            | line: the combined effect of 40% reduced density and greater intrinsic productivity (3.06x)   |
|            | associated with harvest of all hatchery salmon (40%)  |
| Figure 3.  | Predicted number of smolts produced in response to a 40% reduction in spawner density   |
|            | (blue line) and the combined effect of reduced density and increased intrinsic productivity   |
|            | associated with harvest of all hatchery salmon (green line). Red line is status quo based on  |
|            | the Beverton-Holt fit to data in Figure 1. Lower graph shows the harvest of hatchery salmon   |
|            | (40% of terminal run). The combined effects of reduced density and reduced pHOS (green  |
|            | line) leads to greater not less smolt production after harvesting hatchery salmon over the  |
|            | long term. Managers must consider demographic risks associated with low spawner   |
|            | abundances29  |
| Figure 4.  | Smolt to adult return rate (SAR) needed for sustainability ( $R/S \ge 1$ ) in relation to terminal run  |
|            | size before harvest of hatchery salmon (pHOS = 40%). Under status quo conditions (red line),  |
|            | much greater survival is needed to achieve sustainability and the sustainable spawning  |
|            | population is constrained to ~14,300 fish (maximum equilibrium) or less. In contrast, if  |
|            | hatchery fish are harvested (green line), then terminal run size before harvest (HOR & NOR  |
|            | fish) can grow to ~31,600 fish (~18,960 natural spawners after harvest [maximum   |
|            | equilibrium]) while still enabling a sustainable population at the observed SAR level (1.4%).   |
|            | Thus, harvesting hatchery salmon leads to a larger sustainable population size (maximum   |
|            | equilibrium) at a given level of SAR  |
| Figure 5.  | Location of Redfish Lake and Sawtooth Valley, Idaho   |
| Figure 6.  | Elwha River watershed and location of Elwha and Glines Canyon Dam sites   |
| Figure 7.  | Adult Chinook run size in the Elwha River, 2009-2019. Includes natural spawning escapement  |
|            | and fish collected for hatchery broodstock45  |
| Figure 8.  | Area map showing location of Okanogan River basin   |
| Figure 9.  | Adult summer/fall Chinook escapement from 2009-2019 in the U.S. portion of the Okanogan   |
|            | River below Zosel Dam   |
| Figure 10. | Area map showing locations of Lewis River fish hatcheries, collection facilities, hydroelectric   |
|            | projects and reservoirs   |
| Figure 11. | Adult spring Chinook returns to the North Fork Lewis River Merwin Trap (HORs and NORs   |
|            | shown separately), and adult spring Chinook transported above Swift Dam (HORs and NORs  |
|            | combined) as part of the reintroduction program   |
| Figure 12. | Location of the Elochoman and Skamokawa basins within the Lower Columbia River Basin. 61  |
| Figure 13. | Elochoman River/Skamokawa Creek fall Chinook spawning escapement from 1995-2009,  |
| -          | including unknown proportions of HOR and NOR spawners   |
| Figure 14. | Elochoman/Skamokawa fall Chinook spawning escapement from 2010-2018   |
| Figure 15. | Adult Coho returns to Snow Creek from 1976 to 2011. Breaks in the lines represent years   |
| -          | where adult counts were not made  |

# **LIST OF TABLES**

| Table 1.  | Definitions of biological phases of restoration, in terms of restoration objectives   |
|-----------|---|
| Table 2.  | Example metrics and triggers for moving from Recolonization to Local Adaptation phase10   |
| Table 3.  | Diversity attributes associated with the Preservation phase and desired outcomes during the Recolonization phase. Many of these attributes are interrelated   |
| Table 4.  | Objectives and indicators associated with each restoration phase and triggers to reach the next phase. These natural-origin population characteristics build upon previous HSRG guidelines by emphasizing population capacity, intrinsic productivity, and the maximum spawning population that can replace itself (equilibrium). These metrics can be estimated from spawner-recruit data or approximated from EDT analysis when insufficient data are available |
| Table 5.  | Example of objectives, indicators, and triggers associated with each phase of restoration (Redfish Lake Sockeye Salmon)   |
| Table 6.  | Objectives, indicators, and triggers associated with each restoration phase for Elwha Chinook salmon (Peters et al. 2014)   |
| Table 7.  | Four restoration strategies for Elwha River Chinook salmon (Peters et al. 2014) and benefits and risks associated with each strategy  |
| Table 8.  | Prioritization of restoration strategies during each recovery phase for Elwha River Chinook salmon (1=highest ranked, 4 = lowest ranked; adapted from Peters et al. 2014)   |
| Table 9.  | Objectives, indicators, and triggers associated with each restoration phase for Okanogan summer/fall Chinook salmon   |
| Table 10. | Hypothetical objectives, indicators, and triggers associated with each restoration phase for<br>Lewis River Spring Chinook salmon. Objectives are adapted from Pacificorp and Cowlitz PUD<br>(2020). Indicators and triggers are hypothetical and are intended to provide an example of<br>how these criteria could be developed  |
| Table 11. | Benefits and risks associated with various reintroduction strategies upstream of Swift Dam<br>for North Fork Lewis River spring Chinook salmon  |
| Table 12. | Hypothetical objectives, indicators, and triggers associated with each restoration phase for<br>Elochoman/Skamokawa Fall Chinook salmon. Indicators and triggers are hypothetical and are<br>intended to provide an example of how these criteria could be developed  |
| Table 13. | Benefits and risks associated with various restoration strategies for Elochoman River fall<br>Chinook salmon  |
| Table 14. | Example of objectives, indicators, and triggers associated with each phase of restoration for<br>Snow Creek Coho program. Note: Table is retrospective since triggers were not considered<br>during program   |

# **ACRONYMS AND ABBREVIATIONS**

- AHA All-H Analyzer
- **CWT** Coded-wire tag
- EDT Ecosystem Diagnosis and Treatment
- EIS Environmental Impact Statement
- ESA Endangered Species Act
- **ESU** Evolutionarily Significant Unit
- FSC Floating surface collector
- HOR Hatchery-origin recruit
- IDFG Idaho Department of Fish and Game
- LCRFRB Lower Columbia River Fish Recovery Board
- M&E Monitoring and evaluation
- **NOAA** National Oceanic and Atmospheric Administration
- NMFS National Marine Fisheries Service
- NOR Natural-origin recruit
- **pHOS** Proportion of hatchery-origin fish present on the spawning grounds
- **pNOB** Proportion of natural-origin broodstock used in the hatchery
- **PNI** Proportionate natural influence. Calculated as pNOB/(pNOB+pHOS)
- PUD Public Utility District
- **R/S** Recruits per spawner
- **Rkm** River kilometer
- **SDM** Structured decision making
- **SNP** Single nucleotide polymorphism

- **USFWS** United States Fish and Wildlife Service
- USGS US Geological Survey
- VSP Viable salmonid population
- **WDFW** Washington Department of Fish and Wildlife

# **EXECUTIVE SUMMARY**

The Hatchery Scientific Review Group (HSRG) prepared this white paper at the request of the Washington Department of Fish and Wildlife (WDFW) as an addendum to the HSRG's Framework paper (HSRG 2017). The Framework paper presented an approach for implementing hatchery reform concepts within the context of recovering natural salmonid populations. The purpose of this paper is to assist anadromous fisheries managers with a key step in implementing hatchery reform— the process of identifying recovery phase objectives and phase transition triggers for the four biological recovery phases: Preservation, Recolonization, Local Adaptation, and Full Restoration.

The four phases span the full spectrum of the population recovery process. During the Preservation phase, the primary objective is to preserve the genetic diversity of the natural population and prevent extinction. During the Recolonization phase, habitat continues to be underutilized, but population abundance is increasing. Most fish in the population may be of hatchery origin. During the Local Adaptation phase, natural production is sustainable, but the population is not fully adapted to the local environment. The majority of fish in the naturally spawning population are of natural origin. Productivity and fitness are expected to increase in naturally spawning fish over time as the number of hatchery spawners is reduced and the population becomes locally adapted to the natural environment. When the population meets its recovery goals, it reaches the Full Restoration phase.

We outline an approach and methods to set phase triggers in the various phases. Our approach relies on the methods of Structured Decision Making following the basic steps: framing the decision, developing objectives, and evaluating consequences and tradeoffs of various scenarios. Triggers to transition between the phases should be biologically based (e.g., monitored indicators such as the Viable Salmonid Population (VSP) metrics: abundance, productivity, spatial distribution, and diversity), rather than based on arbitrary management goals or timelines. However, managers should revisit triggers periodically (e.g., every 2-3 generations) to ensure they are realistic and reflect changing conditions. Keeping a program in the early phases indefinitely if triggers are not met suggests that factors causing decline have not been adequately addressed. We describe three methods for setting phase triggers based on natural-origin recruit (NOR) abundance: 1) adult spawning capacity, 2) in the case of habitat restoration programs, the percentage of adult and juvenile habitat within a watershed available or being utilized, and 3) empirical methods (e.g., spawner-recruit analysis).

The HSRG has provided guidelines for pHOS (proportion of hatchery-origin fish on the spawning grounds) and PNI (proportionate natural influence) targets during the four recovery phases. The guidelines vary depending on the Biological Significance of a population (Primary, Contributing, or Stabilizing; LCRFRB 2004). During the early phases, it is critical to understand the genetic diversity risks of operating a conservation hatchery program. Natural spawning populations dominated by hatchery-origin spawners with low

natural recruitment and fitness may linger in the early phases for years (Anderson et al. 2020). Remaining in the Preservation and Recolonization phases could facilitate loss of genetic diversity and other unintended genetic consequences and delay local adaptation (improved fitness), even when habitat is restored (Anderson et al. 2020).

When identifying phase objectives and phase transition triggers, it is also important to consider the carrying capacity of the habitat and the demographic risks of hatchery-origin spawners. In addition to the genetic risks they pose, hatchery-origin spawners can depress productivity of natural-origin spawners through ecological interactions (density effects on productivity) and developmental effects on behavior (e.g., homing back to acclimation sites rather than best habitat). Management of salmon density and pHOS can lead to greater productivity and harvests, improved local adaptation to local environments, and improved viability. This approach does not necessarily involve reducing hatchery production. However, managers must determine how to reduce pHOS by safely harvesting hatchery-origin salmon with little or no harm to natural-origin salmon. If this is not possible, managers may consider adjusting program size by releasing fewer hatchery salmon so that returning hatchery fish do not greatly exceed the maximum equilibrium abundance for naturally spawning salmon.

We use population case studies to illustrate how recovery objectives and phase triggers have been developed for several salmon populations (Snake River Sockeye, Elwha Chinook and Okanogan summer/fall Chinook) or could be applied to populations using established recovery goals and hypothetical phase triggers (Lewis River spring Chinook and Elochoman fall Chinook). All of these populations, with the exception of Okanogan summer/fall Chinook, may be in the early recovery phases (Preservation or Recolonization). Okanogan summer/fall Chinook has met the natural spawner abundance trigger for the Local Adaptation phase during recent years, and has consistently met pHOS, pNOB (proportion of natural-origin broodstock) and PNI objectives for a Primary population. We also present a case study of a fully recovered population, Snow Creek Coho, which met its recovery goals after a hatchery intervention lasting only two generations (six brood years). Each case study also includes a discussion of the trade-offs evaluated when identifying restoration strategies.

The population case studies provide several lessons for salmon restoration programs. When a restoration program is initiated, comanagers and stakeholders should identify the program's purpose and objectives, factors causing decline, and potential recovery actions. If a conservation hatchery is used as part of the recovery program, managers should carefully consider genetic and demographic risks. Recovery phase transitions should occur based on measureable changes in population status (e.g., VSP metrics) and should be revisited every 2-3 fish generations to ensure they are realistic. Managers should have a clear plan to transition to the Local Adaptation phase, which should include reducing pHOS via selective harvest or fewer hatchery releases.

Monitoring and evaluation programs are essential to recovery efforts and should focus on enumeration of spawners (NORs and HORs), estimating natural smolt production, and estimating natural-origin recruitment. These data are needed to refine capacity estimates for the watershed and track progress toward recovery actions. Marking all hatchery-origin fish is essential to managing pHOS and broodstock selection and implementing selective harvest programs. Decision support tools, such as the All-H Analyzer (AHA) and In-season Implementation Tool (ISIT) may be used to help make annual decisions about hatchery and harvest management and evaluate progress toward goals (HSRG 2017, 2020).

# **1.0 INTRODUCTION**

Habitat alteration (including human population infill and hydroelectric development), overharvest, and outdated hatchery management practices (the 4 Hs) along with climate change have had deleterious effects on salmonid populations, which has forced contemporary managers and scientists to confront a suite of issues. Which populations should be prioritized for conservation and which for harvest? Should hatcheries be used as a conservation tool or can natural reproduction accomplish recovery objectives? If hatcheries are used, which broodstock, rearing, release, and tagging strategies should be used? What are the population goals (e.g., escapement and harvest)? Do escapement goals consider the carrying capacity of the habitat (current and future)? How should recovery efforts be monitored and evaluated? Should recovery efforts stop after a predetermined period (e.g., fish generations)? Absent a set of predetermined decision rules and a structured monitoring and evaluation plan, the recovery rate of natural populations may be slowed or jeopardized by undetected intrinsic and extrinsic factors including, for example, failure to minimize genetic and ecological impacts of hatcheries at different stages during recovery.

Two key steps in recovering natural salmonid populations are: 1) identifying the factors preventing the natural spawning population from reaching desired states of abundance and stability, and 2) determining how or if these factors can be addressed and the capacity of the watershed (current and future) to support naturally spawning salmon. The Hatchery Scientific Review Group (HSRG) suggests that managers and stakeholders develop a set of decision rules (phases and triggers) to guide the recovery of salmonid populations. In this white paper, we use case histories to document how recovery phases and triggers have been applied (in the case of Snake River Sockeye, Elwha Chinook and Okanogan summer/fall Chinook) or could be applied to salmonid populations using established recovery goals and hypothetical recovery phase identification and biological triggers for transitioning between phases. The case studies range from small recovery projects to large, complex programs affecting entire drainages and involving multiple co-managers. In addition, we discuss how tools developed by the HSRG may be used to assist in conservation efforts.

Our approach in presenting case studies and outlining the decision process stems from the guidance provided by the HSRG 2017 Framework paper (attached as Appendix A) and the methods of Structure Decision Making (SDM; e.g., Runge et al. 2013). This paper builds on recommendations in the Framework paper, provides guidance to managers on how and when to move between recovery phases based on biological triggers, and revises and clarifies HSRG recommendations for pHOS (proportion of hatchery-origin fish on the spawning grounds) and PNI (proportionate natural influence) targets during the Preservation and Recolonization phases. We describe three methods for setting phase triggers based on adult natural-origin recruit (NOR) abundance: 1) adult spawning capacity, 2) in the case of habitat restoration programs, the percentage of adult and juvenile habitat within a watershed available or being utilized, and 3) empirical methods (e.g., spawner-

recruit analysis). In addition, we discuss the importance of considering genetic and demographic risks when setting phase triggers. By using case studies, we hope that descriptions of the methods and results from past efforts to recover populations, along with current theory, will help guide future recovery efforts.

# **2.0 FOUNDATIONAL CONCEPTS**

This section provides a brief overview of some of the concepts described in the Foundation section of the HSRG's 2017 Framework Paper and applied in the case studies discussed in Section 3. Please refer to Appendix A for the full paper. In addition, several sections contain new information and guidelines. For example, Section 2.2 provides updated pHOS and PNI guidelines for the four recovery phases (particularly during the Preservation and Recolonization phases). Section 2.3 provides updated guidelines for identifying phase triggers. Section 2.4 describes three methods for setting phase triggers based on NOR abundance: 1) adult spawning capacity, 2) in the case of habitat restoration programs, the percentage of adult and juvenile habitat within a watershed available or being utilized, and 3) empirical methods (e.g., spawner-recruit analysis). Section 2.5 gives an overview of key concepts in conservation genetics that are important when identifying recovery phases and triggers. Finally, Section 2.6 provides an overview of key concepts in population biology, with an emphasis on density dependence.

## 2.1 **BIOLOGICAL SIGNIFICANCE OF POPULATIONS**

The HSRG's recovery phase recommendations for broodstock management (pHOS and PNI) vary depending on the biological significance of a natural population to the recovery and sustainability of the Evolutionarily Significant Unit (ESU). Different definitions of biological significance are used by managers throughout the Pacific Northwest. To provide some consistency, the HSRG uses the population designations (Primary, Contributing, and Stabilizing) defined by the Lower Columbia River Fish Recovery Board (LCRFRB) for salmon and steelhead populations (LCRFRB 2004, 2010). The LCRFRB's designations specify that the viability requirements for recovery are highest for Primary and lowest for Stabilizing populations.

The HSRG has adopted the LCRFRB's designations and viability requirements as follows:

- **Primary:** populations must achieve high viability.
  - High priority for recovery of the ESU. Need to be at low risk of extinction.
  - Historically were a large segment (in terms of abundance) of the population structure or contain a unique genetic component of the ESU.
- Contributing: populations must achieve at least medium viability.
  - Second to Primary populations in importance to recovery of the ESU.
  - Historically less abundant than Primary. Contribute to genetic and spatial diversity of the ESU.

- **Stabilizing:** populations must maintain at least current viability.
  - Important to the ESU— viability should not decline.
  - A defined population, but may not have ever been a large segment of the population structure of the ESU. Contribute to genetic and spatial diversity of the ESU.

## 2.2 **BIOLOGICAL RECOVERY PHASES**

We recommend that population recovery proceed through four biologically defined phases. These are the Preservation, Recolonization, Local Adaptation, and Full Restoration phases, as defined in Table 1. In the Preservation phase, the population is severely depressed, and the primary objective is to prevent extinction. During the Recolonization phase, habitat continues to be underutilized, but population abundance is increasing through either natural or artificial means. Most fish in the population may be of hatchery origin. During the Local Adaptation phase, natural production is sustainable, but the population is not fully adapted to the local environment, and reproductive success is below the population's potential. This is a critical phase as it is during this time that productivity and fitness are expected to increase in naturally spawning fish over time in response to fewer interbreeding hatchery salmon that facilitates local adaptations of natural-origin salmon to the natural environment. Most of the fish in the natural spawning population will be of natural origin. During the Full Restoration phase, the population has met its recovery goals and is considered a Viable Salmonid Population (VSP), defined as an independent population with a negligible risk of extinction over a 100-year time frame due to demographic or environmental variation or loss of genetic diversity (McElhany et al. 2000). A VSP is defined in terms of four population attributes: abundance, productivity, population structure, and diversity.

Populations may, over time, move both up and down through the phases. Triggers to determine when to move either back to an earlier phase or forward to the next phase should be developed. The conservation role of a hatchery is different during each phase. For example, during the Preservation and Recolonization phases, hatcheries can help maintain or increase abundance, diversity, and distribution. During the Local Adaptation and Full Restoration phases, hatcheries may serve as demographic safety nets against future sudden or gradual declines in natural productivity.

| Table 1. | Definitions of biological phases of restoration, in terms of restoration |
|----------|--|
|          | objectives.  |

| <b>Biological Phases</b> | Objective   |
|--------------------------|---|
| Preservation             | <ul> <li>Objective - Prevent extinction; retain genetic diversity and identity of existing population or establish founder stock if native population has been extirpated. Increase productivity and abundance.</li> <li>Ecosystem Conditions - Low population abundance; habitat either blocked or unable to support self-sustaining population. Managers should consider the effects of all Hs (habitat, hydro, hatchery and harvest) in limiting population recovery.</li> </ul> |

| Recolonization   | <ul> <li>Objective - Re-populate suitable habitat either with pre-spawning adults or out-<br/>migrating smolts.</li> <li>Ecosystem Conditions - Underutilized habitat; habitat may be expected to<br/>improve through restoration efforts and fish passage improvements. Managers<br/>should consider the effects of all Hs in limiting population recovery.</li> </ul>  |
|------------------|--|
| Local Adaptation | <ul> <li>Objective - Meet and exceed minimum VSP abundance for natural-origin spawners; increase fitness, reproductive success, and life history diversity through Local Adaptation (reduce hatchery influence by managing PNI)</li> <li>Ecosystem Conditions - Habitat capable of supporting abundances that minimize risk of extinction, prevent loss of genetic diversity, and promote life history diversity. Managers should consider the effects of all Hs in limiting population recovery.</li> </ul> |
| Full Restoration | <b>Objective</b> - Maintain viable population, based on all viable salmonid population (VSP) attributes (McElhany et al. 2000) using long-term adaptive management. <b>Ecosystem Conditions</b> - Habitat restored or stable and protected to allow full expression of abundance, productivity, life-history diversity, and spatial distribution   |

#### **Targets for pHOS and PNI during the Recovery Phases**

The HSRG's Framework Paper (2017) did not identify specific pHOS or PNI targets in the Preservation or Recolonization phases because balancing genetic and demographic concerns may occur on a case-by-case basis and may be a policy decision by managers. However, managers pointed out that if there are no pHOS or PNI targets during these phases, there is an incentive to stay in the Recolonization phase indefinitely rather than move to the Local Adaptation phase (e.g., Anderson et al. 2020).

We provide the following revised guidelines for the <u>Preservation and Recolonization</u> phases:

- Preservation No specific pHOS or PNI recommendations, but hatchery managers are encouraged to use as many NOR brood as possible. In some cases (e.g., very low R/S values at low spawner abundances or low intrinsic productivity), it may be preferable to use all available NORs in the hatchery brood and allow only extra hatchery-origin recruits (HORs) to spawn naturally.
- 2. Recolonization No specific pHOS or PNI recommendations, but managers are encouraged to continue to use some NOR in broodstock (perhaps 10%-30% of returning NORs), while allowing the majority of NORs to spawn naturally.

Guidelines for the Local Adaptation and Full Restoration phases vary depending on the biological significance of the population. Primary populations have more stringent pHOS and PNI guidelines than Contributing populations, and the HSRG recommends that pHOS and PNI for Stabilizing populations be maintained (at a minimum) at current levels. The reason for the less stringent guidelines for Contributing and Stabilizing populations is that these populations are deemed less important to the ESU. This approach also emphasizes the need to achieve low pHOS and high PNI in Primary populations given that sufficient

resources may not be available to achieve these goals in all three population types while also providing fish for harvest.

Numeric guidelines for the <u>Local Adaptation and Full Restoration</u> phases have not changed from HSRG (2017). However, managers should attempt to keep pHOS as low as possible as this will make PNI targets easier to achieve (fewer NOBs needed).

Primary populations—

- Integrated hatchery programs—PNI  $\geq$  0.67; pHOS  $\leq$  30%
- Segregated hatchery programs—pHOS < 5%

Contributing populations—

- Integrated hatchery programs—PNI > 0.50; pHOS <30%
- Segregated hatchery programs—pHOS < 10%

Stabilizing populations—

- Integrated hatchery programs—maintain or improve upon current pHOS and PNI levels
- Segregated hatchery programs—maintain or improve upon current pHOS and PNI levels

## 2.3 GENERAL GUIDELINES FOR IDENTIFYING PHASE TRIGGERS

Populations move from one phase to the next based on indicators that specific conditions have successfully been met. These observable indicators are referred to as phase triggers.

#### Considerations for defining phase triggers:

- 1. Triggers should be biologically based (e.g., monitored indicators such as the VSP metrics: abundance, productivity, spatial distribution, and diversity), rather than based on arbitrary management goals or timelines.
- Indicators of habitat conditions<sup>1</sup> should be included as triggers to ensure sustainability. For example, triggers could include specific, quantitative habitat improvement milestones (e.g., percent increase in spawning or rearing habitat).
- 3. Triggers should allow movement both up and down through the phases, i.e., the population should be able to advance to the next phase or return to the previous phase (e.g., if NOR abundance or other biological indicators decline).

<sup>&</sup>lt;sup>1</sup> The other 3 H's (hydro, harvest and hatchery) should also be monitored to ensure managers understand their impact on population recovery. See also pHOS and PNI guidelines discussed in Section 2.2.

- 4. Managers should revisit triggers periodically (e.g., every 2-3 generations) to ensure they are realistic and reflect changing conditions. For example, keeping a program in the Preservation phase indefinitely if subsequent recovery triggers are not met suggests additional actions may be required to improve productivity and abundance of the natural spawning population.
- Managers should weigh the tradeoffs of setting high triggers to move from the Recolonization to the Local Adaptation phase. The higher the triggers, the longer Local Adaptation benefits (e.g., increased productivity and fitness as pHOS is reduced and PNI increases) are deferred.
- Triggers should be primarily biological, but also need to consider cultural/societal goals for returning salmon and steelhead to river basins (i.e., Native American and First Nation salmon cultures.)

The distinction between biological targets, phase triggers, and management objectives is important. For example, the biological targets for Recolonization should be the conditions required for entry to the Local Adaptation phase. Thus, the biological targets for each phase are its "end point". Biological targets should be distinguished from management objectives. Management objectives during the Recolonization phase, for instance, might be to populate habitat with salmon, increase abundance, and improve habitat to meet the biological targets, which are expressed in terms of VSP parameters.

Phase triggers may be based on monitored variables such as running averages of NORs, estimated trends in recruits per spawner, or measures of habitat quality or quantity (Table 2). The lower the triggers are set, the sooner the next phase will be reached, but the risk of entering the next phase too soon is that the population may revert to the previous phase. Tradeoffs between high and low trigger thresholds should be evaluated so that informed policy decisions can be made.

| Table 2. | Example metrics and triggers for moving from Recolonization to Local |
|----------|--|
|          | Adaptation phase.  |

| Viability<br>Attribute  | Examples of Biological Targets               | Example of Phase Triggers                                     |
|-------------------------|--|---|
| Abundance               | Mean NOR abundance of 500 adults             | Observed NOR abundance > 600 (5-<br>year running average).    |
| Productivity            | Intrinsic productivity of 2.5                | R/S greater than 1 when spawner abundance is greater than 500 |
| Spatial<br>Distribution | 50% of available habitat occupied            | Surveys indicate < 50% of spawning/rearing habitat is vacant  |
| Diversity               | Genetic effective population size (Ne) > 200 | Observed Ne > 200   |
| Habitat                 | Available spawning or rearing habitat        | 10% increase in available habitat                             |

Phase shifts are generally based on 5-year running averages. For example, if a biological target for Recolonization is an average spawner abundance greater than 500 NORs, then the trigger to shift to the Local Adaptation phase might be 600 NORs. This means that the shift would occur when the 5-year running average reaches 600 NORs, indicating that the long-term abundance is now likely to exceed 500 NORs. This example assumes that 600 NORs can be supported by current habitat conditions.

In addition, we suggest the following general guidelines for initiating the Preservation phase, moving from the Preservation to the Recolonization phase, and moving from the Recolonization to the Local Adaptation phase. For new restoration programs, these guidelines may also be helpful in identifying the population's current phase. Often, establishing triggers will provide insight into the population's current phase. Typically, a recovery goal (usually based on VSP metrics) for the population is established and would be one of the triggers for moving from Local Adaptation to Full Restoration. Then working backwards, triggers for the other phases can be developed.

#### Triggers to initiate the Preservation phase:

- If the population is not self-sustaining and at risk of extinction, consider beginning a hatchery program (anadromous programs are preferred, but captive programs may be required).
- During this phase, the goal is to establish a self-sustaining hatchery program, i.e., no broodstock are imported.

#### **Triggers to move from Preservation to Recolonization phase:**

- Habitat must be capable of sustaining a population in all life stages (spawner to spawner). In degraded habitats, the <u>sustainable</u> population may be smaller than desired.
- Hatchery program is producing extra adults/juveniles that can be used to seed habitat.

#### Triggers to move from Recolonization to Local Adaptation phase:

- Reintroduced population is self-sustaining, spatially distributed to avoid potential catastrophic losses, and has a large enough effective population size to maintain genetic variation and allow local adaptation.
- Potential metrics and examples of thresholds are in Table 2. Program-specific triggers will vary based on the distinct characteristics of the species, habitat, and goals of the program.
- When setting the trigger to move to this phase, it should be expected that the composite spawning population, consisting of both NORs and HORs will likely decrease in abundance, as limits to the number of HORs allowed to spawn naturally should be established using spawner-recruit relationships or other approaches. Since most of the returning NORs are likely F1 hatchery fish, fitness will not be optimal. Recognizing this, the trigger to move back to the Recolonization phase should be set to prevent loss of genetic fitness.
- The number of generations required for the population to develop increased fitness (become locally adapted) is dependent on multiple factors, such as past and current pHOS and PNI, hatchery-stock origin, and the strength of natural selection, and may be difficult to predict.

# 2.4 METHODS FOR SETTING PHASE TRIGGERS

In this Section, we describe three methods for setting phase triggers for adult NOR abundance. The methods are based on the following: 1) adult spawning capacity and 2) percentage of adult and juvenile habitat available (in the case of habitat restoration programs, such as Elwha fall Chinook) or being utilized (in the case of reintroduction programs, such as Lewis River spring Chinook) within a watershed. All phases should include abundance as a trigger (it is readily measurable). In addition, other VSP metrics (productivity and spatial distribution) are often included as triggers. See Table 2 above for examples.

## 2.4.1 Adult Spawning Capacity Method

The adult spawning capacity method identifies adult NOR triggers based on a percentage of the estimated adult capacity of the watershed, adjusted for expected harvest mortality.

Ideally, empirically-based spawner-recruit relationships should be used to estimate the capacity of the watershed to support the population (see Section 2.4.3 for Empirical Methods). However, sufficient data are often not available to conduct these analyses. Therefore, this approach usually relies on habitat-based assessments (e.g., Ecosystem Diagnosis and Treatment (EDT)) of the current and future (if habitat restoration is planned or underway) spawning capacity of the drainage or watershed.

The trigger to move to the Full Restoration phase would typically occur when NOR returns achieve adult capacity (minus expected harvest mortality), based on the future (or intrinsic potential) spawning capacity for a population. Earlier phase triggers are usually expressed as a percentage of the adult spawning capacity. While these percentages are somewhat arbitrary, a value of 30-40% of the above value may be useful as a trigger to move from Recolonization to Local Adaptation. Obviously, such factors as pre-spawning mortality or NORs needed for hatchery broodstock should be considered when setting triggers, as those fish will not be available to spawn in the natural environment.

In the case studies, we describe how this approach was used to identify phase triggers and recovery goals for Snake River Sockeye and Okanogan summer/fall Chinook, and we use this method to identify hypothetical triggers for Lewis River spring Chinook and Elochoman fall Chinook.

# 2.4.2 Available Habitat Method

The available habitat method identifies adult NOR triggers based on the percentage of habitat available in a watershed to adults and juveniles. This method is appropriate where major habitat restoration actions have been taken (e.g., dam removal) or where populations have been reintroduced above migration barriers such as high head dams. The assumption is that over time, fish will recolonize a greater proportion of the total potential spawning and rearing habitat.

In the case studies, we describe how this approach was used to establish phase triggers for Elwha Chinook (Peters et al. 2014) following dam removal. In the Elwha, the assumption is that in each recovery phase, a percentage of the intrinsic (future) habitat potential has been realized. The percent available habitat in each recovery phase is used as a multiplier to calculate the number of natural spawners expected in each phase. For example, in the Preservation phase, 9.5% of habitat is available; 950 naturally spawning fish (NORs and HORs) are expected to use the habitat (9.5% \* 10,000 adult capacity; see Elwha case study in Section 3.2 for details).

# 2.4.3 Empirical Methods

From a conservation perspective, locally adapted hatchery fish on the spawning grounds may provide three primary benefits to wild populations: 1) reducing extinction risk, 2) reducing genetic risks associated with small population size, and 3) providing a "demographic boost" that results in greater utilization of available habitat than would be possible by wild spawners in the absence of supplemental hatchery spawners. As a result, when NOR spawner abundance is sufficient to minimize short term extinction and genetic risks, it is necessary to determine what NOR spawner abundance will make full or near-full use of available habitat. Approaches previously discussed indirectly address this question by estimating spawner capacity and habitat capacity based on extrinsic data, recovery plans, and other non-empirical methods. However, these are ultimately approximations and the surest data to address this question is the observed relationship between recruitment and spawner abundance. As illustrated in Section 2.6, for all populations there exists a point where recruitment (juvenile or adult) will reach an asymptote as a function of spawner abundance, and the number of offspring per spawner will drop below replacement. For many depressed populations, the threshold spawner abundance at which recruitment is maximized or nearly so may be surprisingly low relative to historical abundances or contemporary recovery goals as a result of greatly reduced habitat quality and quantity, reduced NOR fitness, and other factors. Regardless, if recruitment is maximized, or nearly so, by NOR spawners under current conditions, supplemental hatchery spawners cannot provide conservation benefits in the form of a demographic boost, and instead only serve to increase density-dependence, thereby lowering survival of the offspring of NOR spawners. For this reason efforts should be made to empirically assess the relationship between NOR spawner abundance and recruitment.

Modern tools for completing such "stock-recruit" analyses have greatly improved in the form of empirical life cycle models (e.g., Buhle et al. 2018). Many of the best approaches attempt to partition the salmon life cycle between freshwater and marine life stages, thereby separating the density-dependent freshwater life stages from the relatively density-independent ocean phases (e.g., Mousalli and Hilborn 1986, Barrowman 2003, Scheuerell et al. 2005). While establishment of phase triggers in populations lacking NOR spawner-recruit data may necessarily rely on recovery plans and other heuristic or qualitative methods to identify spawner capacity or habitat capacity initially, efforts should be made to collect empirical data on the recruitment relationship, thereby allowing empirical validation of these phase triggers. For example, an appropriate phase trigger for moving between the Recolonization and Local Adaptation phases may be identified as the NOR spawner abundance which produces a substantial portion (for example, 75% or 80%) of the empirically estimated maximum recruitment, or "Rmax".

# 2.5 Key Concepts in Conservation Genetics

The genetic objectives of the early recovery phases, Preservation and early Recolonization, are to preserve existing population genetic diversity while providing the best opportunity to move into the Local Adaptation phase and minimize fitness declines. In the two early phases, decisions to move into advanced recovery phases are often associated with a high level of uncertainty. Further, hatchery programs initially intended as temporary measures may become long-term if the factors causing declines are not adequately addressed (Berejikian and Van Doornik 2018). A review of 260 published case studies of fish

reintroductions showed that failure to address the cause of decline is common and the best predictor of failure (Cochran-Biederman et al. 2015).

However, keeping fish populations under culture while waiting for factors causing declines to be identified and addressed has its own risks. Under these circumstances, programs can linger in the early phases seemingly making little progress towards Local Adaptation. Anderson et al. (2020, see their Appendix 4) recently used a model based on the Ford demographic model (Ford 2002) to investigate two example populations that have shown little progress in advancing to the Local Adaptation phase. Their results suggest that managing an "integrated" hatchery population with relatively high pHOS and low pNOB can result in a situation similar to that of the Kendall Creek Hatchery and the North Fork Nooksack spring Chinook population today – a natural spawning population dominated by hatchery-origin spawners, low natural recruitment and fitness, and a domesticated hatchery population with high fitness in the hatchery, but near zero fitness in the wild (e.g., R/S near 0). Anderson et al. (2020) further suggest that reversing the situation would require a decrease in hatchery production and an extremely low pHOS. Similar to moving to the Local Adaptation phase, this scenario may result in a decrease in the number of natural spawners and a reduction in NORs, at least in the short term. Low recruitment is an outcome managers are trying to avoid in the first place. These examples underscore the need for an understanding of the genetic diversity risks associated with the early phases and the causes of decline. Such an understanding is needed to help guide actions to recover natural salmon populations.

## 2.5.1 Loss of Diversity

Diversity risk, i.e. the risk of loss of diversity, is foundational in the evaluation of the longterm viability of salmonid populations and is one of the four criteria along with abundance, productivity, and spatial structure used by NOAA in assessments of Viable Salmonid Populations (VSP) (e.g., McElhany et al. 2000, Hard et al. 2015). Insights into population diversity typically rely on multiple data sources. Life history parameters such as species distribution, spawn timing, and age distribution provide relatively easily measured metrics of phenotypic diversity and often reflect the underlying genetic diversity. Genetic data from one or several marker types, such as microsatellites or single nucleotide polymorphisms (SNPs), are routinely available and can provide quantitative measures of genotypic diversity and evaluations of diversity risks. These data can inform managers of the risks and benefits of moving from or remaining in the Preservation and early Recolonization phases and the genetic effects of hatchery supplementation. The HSRG and many others have reviewed the genetic risks of hatchery propagation in much detail. Readers are directed to these manuscripts and references therein for detailed descriptions (e.g., Mobrand et al. 2005, Fraser 2008, Naish et al. 2008, Paquet et al. 2011, Christie et al. 2012, Lescak et al. 2019, Anderson et al. 2020, and Waples et al. 2020).

The objective of this section is to specifically highlight potential genetic risks and benefits of advancing to the Recolonization phase as compared to remaining in the Preservation phase.

In evaluating risks and benefits, diversity can be divided into: 1) within-population diversity, 2) among-population diversity, and 3) domestication as a result of hatchery propagation. Each component will be addressed separately in the context of the Preservation and Recolonization phases although it should be noted that many of these attributes are interrelated (Table 3).

# Table 3.Diversity attributes associated with the Preservation phase and desired<br/>outcomes during the Recolonization phase. Many of these attributes<br/>are interrelated.

| Diversity Attribute  | Description  | Conditions Expected<br>During Preservation   | Desired Outcome in<br>Recolonization   |  |
|--|--|--|--|--|
| 1. Within Population Diversity   |  |  |  |  |
| Effective Population Size $(N_e)$ is equivalent to number of breeders $(N_b)$ per year times average age at spawning (g): $N_e = gN_b$ | Direct measure<br>predicts the rate of<br>genetic change in<br>the population.                                     | Hatcheries have the potential<br>to decrease $N_e$ ; strict<br>protocols and use of<br>genotype data can be<br>followed to increase $N_e$ and<br>$N_e/N_c$ , the ratio of $N_e$ to<br>census size. | No specific $N_e$ target but<br>generally > 200 depending on<br>species, generation time, and<br>receiving habitat.  |  |
| Life history and genetic divergence  | Reflects phenotypic<br>diversity of size,<br>age, migration<br>timing, and overall<br>genetic divergence.          | Loss of life history diversity<br>likely from hatchery practices<br>or through amplification of a<br>portion of the broodstock.  | Promotes colonization of<br>underutilized habitats and<br>variability to reduce risks.   |  |
| Total # of alleles and<br>large effect alleles   | Measured by genetic analyses and heterozygosity.   | Loss of alleles likely; small<br>effective number of breeders<br>may result in reduced<br>heterozygosity.  | Maintenance of total # of alleles<br>and frequency of large effect<br>alleles.   |  |
| 2. Among Population Div  | versity  |  |  |  |
| Life history traits  | Phenotypic<br>variability in return<br>time, age of return,<br>size at age; may<br>reflect underlying<br>genotype. | Phenotype and genotype<br>reflect adaptation to hatchery<br>environment.   | Increase potential for local<br>adaptation under varying<br>conditions and habitats,<br>provides ecosystem benefits.   |  |
| Population Structure   | Genetic measures of<br>among population<br>diversity and<br>metapopulation<br>structure.                           | NA   | Increased potential for local<br>adaptation under varying<br>conditions and habitats to buffer<br>varying local conditions;<br>minimize Intentional transfers or<br>straying resulting in<br>homogenizing gene flow and<br>loss of emerging structure. |  |
| 3. Domestication selection   |  |  |  |  |
| Controlling gene flow  | pNOB, pHOS, PNI<br>(determined by<br>pHOS and pNOB)  | pHOS and pNOB may vary depending on hatchery operating plans.  | High pNOB maintains hatchery<br>diversity, reduces fitness loss.<br>Both decreasing pHOS and<br>increasing pNOB provide  |  |

|                 |   |  | fitness benefits. Decreasing<br>pHOS provides greater fitness<br>benefit than increasing pNOB.   |
|-----------------|---|--|--|
| Fitness decline | As measured by<br>Relative<br>Reproductive<br>Success (RRS)                                       | Domestication selection<br>expected. High fitness in<br>hatchery environment.          | Minimize fitness reduction from<br>hatchery practices.<br>Improvement in fitness of<br>naturally-spawning individuals<br>expected assuming habitat<br>availability; increase in RRS<br>expected. |
| Epigenetics     | Fitness traits<br>mediated<br>by epigenetic<br>mechanisms such<br>as DNA methylation<br>patterns. | DNA methylation patterns<br>likely differ between hatchery<br>and natural-origin fish. | Reduced divergence of DNA<br>methylation patterns between<br>hatchery- and natural-origin<br>fish.   |

# 2.5.2 Within Population Diversity

#### **Effective Population Size**

One of the most important parameters affecting genetic diversity is effective population size ( $N_e$ ), a common proxy for genetic diversity. It is the size of an ideal population whose genetic composition is influenced by only random processes. General guidelines have been proposed by Franklin (1980; 50/500 rule) for maintaining minimum  $N_e$  in distinct, or semi-isolated, populations:  $N_e > 50$  to prevent inbreeding depression and a detectable decrease in viability or reproductive fitness of a population, and  $N_e > 500$  to maintain constant genetic variance in a population resulting from a balance between loss of variance due to genetic drift and the increase in variance due spontaneous mutations (Franklin 1980, Lande 1988).

In salmon populations with overlapping generations, effective population size per generation ( $N_e$ ) is equivalent to the effective number of breeders per year ( $N_b$ ) times the average age at spawning or generation length (g). The use of  $N_e = gN_b$  in standard equations for the variance of allele frequencies, loss of heterozygosity, and loss of alleles over time can accurately predict the rate of genetic change in the population as a whole (Waples 1990). Age class structure leads to temporal structuring of populations across years and varies substantially among species; age class structuring is absolute in Pink salmon, with a strict, two-year life cycle, slightly more diverse in Coho salmon, where a three-year life cycle predominates, more complex in Sockeye salmon, Chinook salmon, and Chum salmon, and even more complex in repeat spawners such as steelhead. Importantly  $N_e$  (and  $N_b$ ) are much lower than the census size ( $N_c$ ) (Jamieson and Allendorf 2012); the ratio  $N_b$  /  $N_c$  is also widely used. New tools are now available to simulate, subsample, and estimate  $N_b$  in age structured populations and to quantify the power to detect population declines in  $N_b$  over time (AgeStrucNb; Antao et al. 2020). Similarly, better genetic analyses and data can help estimate gene flow and be used to distinguish between  $N_e$  calculated against inbreeding

loss (e.g.,  $N_e > 50$ ) versus  $N_e$  to estimate evolutionary potential (e.g.,  $N_e > 500$ ), which is the global  $N_e$  based on the metapopulation structure (Jamieson and Allendorf 2012). These analyses will help managers establish genetic monitoring programs, and, with the increasing availability of large genetic data sets and decreasing genotyping costs, these types of analyses are becoming readily available.

Estimates of N<sub>b</sub> can be quite low in the early Preservation and Recolonization phases given the limited number of potential breeders (founders) (reviewed in Fraser 2008) but will vary depending on the particular case and availability of founding broodstock. Skewed sex ratios and variance in family size can further reduce effective sizes (see Naish et al. 2008, Christie et al. 2012), although numerous steps are commonly taken in hatcheries to minimize loss of genetic variation. With these steps, the  $N_b / N_c$  ratio within a captive population can be higher than in the wild, and supplementation may increase the overall effective size of the combined populations (Hedrick et al. 2000). O'Reilly and Kozfkay (2014) review in detail the genetic management of two captive brood programs –Atlantic salmon from the Bay of Fundy and Redfish Lake Sockeye salmon (reviewed in Section 3.1). From the inception of the sockeye salmon program in 1991 through 2012,  $N_b$  ranged from 3 to 528 with an  $N_b / N_c$ ratio in the hatchery ranging from 1.0 to 0.44.  $N_b$  for the Atlantic salmon program ranged from 117 to 328, and ranges for the  $N_b / N_c$  ratio were similar to the Sockeye salmon program. Smaller gains in  $N_b$  were realized for a supplemented population of steelhead over a 17-year period from a harmonic mean of 24.4 in the generation before supplementation to 38.9 after supplementation (Berejikian and Van Doornik 2018).

A well-known risk leading to reductions in  $N_e$  is the Ryman-Laikre effect (Ryman and Laikre 1991); this risk can occur in both the Preservation and Recolonization phases. The Ryman-Laikre effect occurs if a small fraction of the natural adult population is brought into the hatchery and is used as broodstock to produce large numbers of offspring. While release of these individuals can increase population census size, it can also result in a substantial loss of  $N_e$  in the total population. Results emphasize the trade-offs present when hatchery programs attempt to balance multiple goals such as increasing abundance while maintaining genetic diversity.

#### Life History and Genetic Divergence

The goal of the Preservation phase is to retain sufficient life history diversity and minimize genetic divergence to ensure success during the Recolonization and Local Adaptation phases. However, hatchery-reared salmon commonly differ in a number of life history traits as compared to the progenitor stock, a reflection of both the environment, genotype, and interaction between the two (Knudsen et al. 2006). These trends have been found across numerous studies and species, and evidence suggests that changes can occur rapidly. Even hatchery programs designed to minimize differences between hatchery and naturally-spawning fish may diverge to a certain extent as hatchery fish adapt to their hatchery environment. On a positive note, careful management of gene flow has been shown to minimize divergence. Results of Waters et al. (2015), comparing an integrated hatchery-wild population to a segregated hatchery population showed that following an integrated

approach with managed gene flow using natural-origin broodstock reduced genetic divergence from the source population over the short term compared to one that relied on only hatchery-origin broodstock and a segregated approach.

#### Number of alleles and large effect alleles

To moderate loss of alleles, the goal is to minimize the spawning of close relatives and include those individuals with more unique genotypes potentially carrying low frequency or rare alleles. Various methods can be used to identify which individuals should be chosen for broodstock during the Preservation phase to minimize loss of alleles. These methods include sibship relationships (e.g., Ackerman et al. 2017) and mean kinship information, and a measure of the genetic uniqueness of an individual (O'Reilly and Kozfkay 2014). These approaches have been successful in the short term although there is less evidence to support longer term gains (Fraser 2008).

Advances in genomic research are revealing new challenges facing conservation planning in the Preservation phase as associations are being identified between one or a very few genes and key life history traits (Waples and Lindley 2018). Many of these studies are focused on the recent identification of a GREB1L gene region that explains a large proportion of the variation associated with seasonal timing of adults returning to spawn in steelhead and Chinook salmon (Hess et al. 2016, Prince et al. 2017). Recently, Thompson et al. (2019) found a dramatic allele frequency change at this locus (i.e., spring-run or fall-run) in Chinook salmon from the Rogue River. They hypothesized that a rapid phenotypic shift occurred after dam construction, and their modeling suggests that continued selection against the spring-run phenotype could rapidly lead to complete loss of the spring-run allele. McKinney et al. (2020b) and McKinney et al. (2020a) recently described Ychromosome haplotypes that exhibit associations with size at maturity. These linked portions of the Y-chromosome share similar conservation challenges to the GREB1L situation. The emerging genomic studies suggest a paradigm shift towards not only preserving overall numbers of alleles and neutral variation on a genome-wide level but also preserving frequencies of specific large-effect alleles shown to be important in life history diversity.

## 2.5.3 Among Population Diversity

One of the goals of restoring salmonid populations is local adaptation, which in turn fosters among population diversity and a portfolio of salmon populations. However, restoration efforts may not always prioritize portfolios and among population diversity; rather, hatchery may operate to optimize returns under current conditions. Nelson et al. (2019) reviewed data from the past 65 years and found significant changes in the size and time at which juvenile salmon were released from hatcheries. This increased homogeneity of releases reflects decreases in among population genetic diversity as expressed by life history traits. In addition, Nelson et al. (2019) suggest that current hatchery practices release Chinook salmon in the size range preferred by predatory fish, birds, and marine mammals. With current marine survival rates at chronically low levels, and increasing demand for hatchery subsidies, they argue that modifying existing hatchery programs to reduce homogenization and increase among population diversity may promote improved food web dynamics and better survival with benefits to both hatchery and natural Chinook populations.

Although the portfolio of among population diversity of salmon populations in the Pacific Northwest is truncated compared to historical levels, significant diversity still exists among all species (e.g, Moran et al. 2013, Small et al. 2015). However, the increasing reliance on a single stock continues to threaten existing diversity. Fall Chinook from Green River, which empties into the Puget Sound in Washington (Soos Creek Hatchery) are propagated from several hatcheries throughout Puget Sound. In the mid-1970s the Chinook run in Puget Sound was composed roughly of 50% early (spring and summer) and 50% late (fall) run fish. However, with the wide-scale production of Green River-origin fall Chinook in Puget Sound, the run has become increasingly dominated by late-run, and in 2010 the late-run proportion was roughly 90% (WDFW unpublished data; K. Warheit, pers. comm.). The wide-spread propagation of this single hatchery stock reduced the Chinook portfolio in Puget Sound in less than four decades. Indeed, conservation of the existing among population diversity is the impetus for beginning a program in the Preservation phase; for example, see the case study on Redfish Lake sockeye salmon (Section 3.1).

#### 2.5.4 Domestication Selection

The hatchery environment is markedly different from the wild environment (see section 2.4.2 Life History above), and hatchery fish may become adapted to their hatchery environment through domestication selection. This is to be expected in the Preservation phase. However, the result of both effects may ultimately lead to the release of a genetically altered population in the Recolonization phase. Offspring of the Preservation programs may interact negatively with any naturally-spawning populations present, by decreasing the overall fitness of the combined populations (e.g., Naish et al. 2008, Ford et al. 2016, Willoughby and Christie 2019). The longer the population stays in the Preservation phase, the greater the risk of domestication, and therefore the greater the risk of negatively affecting the naturally-spawning population. Genetic monitoring is critical in these cases as different hatcheries and rearing strategies may have different outcomes (Johnson et al. 2020).

#### **Controlling gene flow**

Monitoring pHOS, PNI, and adjusting pNOB are the primary tools to control gene flow. These concepts have been reviewed extensively in previous HSRG papers (Paquet et al. 2011, HSRG 2017) and more recently by WDFW (Anderson et al. 2020). See also the Case Studies in Section 3.

#### Fitness declines (RRS)

Fitness of hatchery fish released into the wild is commonly measured by Relative Reproductive Success (RRS) (Cuenco 1994). RRS is defined as the reproductive success of

hatchery-origin fish relative to natural-origin fish when both are allowed to spawn in the wild. These studies are multigenerational in design and require extensive genetic sampling through time. Reductions in RRS (i.e., RRS <1) can be substantial depending on factors such as species and broodstock management (HSRG 2017). Results suggests that the fitness loss in the hatchery can be rapid (Fraser 2008), although its magnitude depends on the duration of the Preservation stage and broodstock origin (Ford et al. 2016, Lescak et al. 2019). Newer theoretical and methodological approaches now exist for current and future programs to potentially reduce these effects, but unavoidable trade-offs exist between conserving genetic diversity in the Preservation of supporting self-sustaining populations during the Recolonization phase (Berejikian and Van Doornik 2018). Although expensive to collect, RRS provides an excellent measure of the fitness of the hatchery-origin spawners and important insights into appropriate actions for advancing or returning through the phases.

#### **Epigenetics**

Epigenetics refers to mechanisms that alter gene activity without modifications to the underlying DNA sequence, and recent research suggests that significant differences likely exist between populations in the Preservation phase and those that have advanced to the Recolonization and Local Adaptation phases. In salmon, it is thought that plasticity during early development is likely caused by environmentally-induced and potentially heritable epigenetic change through the processes of DNA methylation (Gavery et al. 2018); these epigenetic changes occur without underlying change to the DNA sequence. Heritable DNA methylation patterns could have lasting effects on growth, metabolism, and other life history traits where the hatchery rearing environment is very different from a future environment when fish are released into the wild (Gavery et al. 2019, Venney et al. 2020).

# 2.5.5 Uncertainties Associated with the Preservation and Recolonization Phases

Rarely do managers have access to complete genetic or other information, which results in considerable uncertainty, and advancing to the Local Adaptation phase may initially result in significant reductions in NOR abundances (e.g., due to low fitness of natural-origin fish, usually F1 hatchery fish) and reductions in hatchery adults spawning naturally (HSRG 2012). Initially, it may seem prudent to remain in the Preservation and Recolonization phases if spawning abundances remain low consistent with the precautionary approach (FAO 1996, Hilborn et al. 2001, González-Laxe 2005). However, the precautionary approach involves the application of prudent foresight— taking account of uncertainties and the need to take action with incomplete knowledge. Remaining in the Preservation and Recolonization phases. Salmon will show local adaptation given appropriate habitat (Fraser et al. 2011, Campbell et al. 2017). The longer a population relies on a high proportion of hatchery-origin spawners (high pHOS), the longer local adaptation (improved fitness) will be delayed, even when habitat is restored (Anderson et al. 2020). Monitoring and evaluation is typically needed to

approximate the number of total spawners that can be supported by the habitat so that the population is not overwhelmed with HORs.

## 2.5.6 Guidelines for Hatcheries in Pristine Regions

Hatcheries are used to boost harvests throughout most of the native range of Pacific salmon, including regions that are relatively pristine and that support sustainable wild salmon populations. HSRG principles and guidelines were developed primarily for the Pacific Northwest region where salmon habitat has been degraded and hatcheries are used to produce harvests and to supplement natural spawning populations. From a science and precautionary perspective, the HSRG recommends that pHOS be zero (or near zero) in regions that are relatively pristine, based on monitoring and evaluation data. In other words, best management practices in pristine regions should ensure that relatively few hatchery-origin salmon spawn in the wild.

# 2.6 KEY CONCEPTS IN POPULATION BIOLOGY

In the Pacific Northwest, artificially produced salmon are frequently used for the dual objectives of restoring natural salmon populations and mitigating for lost fishing opportunity. Considerable research now demonstrates or indicates that domestication selection in hatcheries leads to long-term loss of local adaptations to local environments and to reduced intrinsic productivity of hatchery fish spawning in streams (e.g., Section 2.5, Waples and Do 1994, Anderson et al. 2020, O'Sullivan et al. 2020). Previous guidance by the HSRG focused on minimization of this long-term adverse effect though management of pHOS<sup>2</sup> and pNOB in an effort to maximize the PNI, or to at least maintain a PNI score above 0.5 (Section 2.2, Paquet et al. 2011). In the short-term, however, HORs can also depress productivity of NORs through ecological interactions (density effects on productivity) and developmental effects on behavior (e.g., homing back to acclimation sites rather than best habitat).

In the Columbia Basin, the Independent Scientific Advisory Board for the Northwest Power and Conservation Council (ISAB 2015) concluded that density dependence is now evident in most ESA-listed populations examined and it appears strong enough to constrain their recovery. This was a surprising conclusion for many managers and scientists in the Basin because most of them believed salmon abundance is too low for density effects to constrain recovery (see references in ISAB 2015). Indeed, a key goal of many hatcheries was to replenish spawning grounds with hatchery salmon to jump start depleted natural

<sup>&</sup>lt;sup>2</sup> The influence of the hatchery and natural environments on the adaptation of the composite population is determined by the proportion of natural-origin broodstock in the hatchery (pNOB) and the proportion of hatchery-origin fish in the natural spawning escapement (pHOS). The larger the ratio pNOB/(pHOS+pNOB), the greater the strength of selection in the natural environment relative to that of the hatchery environment. This ratio is known as PNI.

populations and improve their abundance and viability. However, evidence indicates such supplementation has not markedly increased abundance of natural-origin salmon, partly because density-dependence is strong in most areas where data have been collected and evaluated (Venditti et al. 2017). For example, ISAB (2015) reported strong density dependence in 25 of 27 spring/summer Chinook salmon populations, the Snake River fall Chinook salmon population, and 20 interior Columbia steelhead populations, including density dependent growth and survival during the spawner to smolt life stage (e.g., Walters et al. 2013). These relationships led Cooney (2013) to ask: *"At what level of supplementation do genetic and ecological risks outweigh demographic benefits, such that hatchery supplementation should be scaled back?"* 

The goal of this Section is to (1) inform managers, policy makers, and the public about the importance of density dependence to salmon productivity and recovery efforts, (2) illustrate how management of salmon density and pHOS can lead to greater productivity and harvests, improved local adaptation to local environments, and improved viability, and (3) describe salmon recovery phases within a density dependence framework. We address this goal by using spawner and smolt counts for a test population of natural-origin Chinook salmon that exhibits strong density dependence during the spawner to smolt stage (ISAB 2015). The analysis presented here expands upon the analysis by the ISAB.

## 2.6.1 Density Dependence: Why is it Important?

*"If only density-independent causes of mortality exist, the stock can vary without limit, and must eventually by chance decrease to zero"* 

W.E. Ricker 1954

*"Compensatory density dependence must exist for naturally stable populations to persist under harvesting"* 

Rose et al. 2001

"Density dependence is now evident in most of the ESA-listed populations examined and appears strong enough to constrain their recovery"

ISAB 2015

Density dependence occurs when a population's density affects its growth rate by changing one or more vital rates—birth, death, immigration, or emigration. The most common form is compensatory density dependence in which a population's growth rate is highest at low density and decreases as density increases. Compensation is typically caused by competition for limiting resources, such as food or habitat.

Compensatory density dependence is critical to population viability and stability because it tends to restore the abundance of a depleted population to a higher level that fluctuates

around a stable equilibrium, which is the maximum abundance of natural spawners that can replace itself. Typically, when a population declines in abundance, more resources become available to the remaining individuals and their probability of survival and reproduction increases. The stabilizing influence of compensation must occur at some times and places or populations would not persist, as stated by Ricker (1954). Compensation is also fundamental to the concept of sustainable yield in fisheries and wildlife management in that it explains how harvesting an abundant population can increase rather than decrease total production in the next generation (Rose et al. 2001).

#### 2.6.2 Density Dependence: Spawner to Smolt Stage

In salmonids, density dependence is most obvious during the spawner to smolt stage when the population is isolated within a smaller area than in mainstem river areas and the ocean phase where mixed populations may obscure density effects. Nevertheless, competition for prey and resulting effects on growth and survival have been documented between salmon populations and highly abundant species during the ocean phase (e.g., Ruggerone and Irvine 2018). Salmon interactions at sea are important because depleted populations migrate thousands of kilometers at sea and may compete for prey with distant highly abundant populations.

Analysis of the test population of Chinook salmon indicates strong density dependence during the spawner to smolt stage. The number of smolts increases with greater numbers of natural spawners but the rate of increase slows considerably after about 20,000 spawners, and few additional smolts are produced as spawners increase from 40,000 to 100,000 fish (Figure 1A). The population appears to have a maximum smolt production capacity of approximately 1.2-1.8 million smolts. These data show that productivity (smolts per spawner) declines rapidly from approximately 125 smolts per spawner when spawner abundances are low (~5,000 spawners) to 55 smolts per spawner near 20,000 spawners to only 35 smolts per spawner at ~30,000 to 40,000 spawners (Figure 1B). This plot highlights the importance of compensatory density dependence to population viability: productivity increases as population abundance declines (but see Discussion of demographic risks below). However, when restoring a depleted population with hatchery salmon, higher spawner abundances lead to markedly fewer smolts per spawner, as expected from density dependence. Lower productivity at high spawner abundances can be problematic when the high abundance involves a large number of less fit spawners. If both hatchery and wild salmon are equally well-adapted to the local environment, then the concern over high pHOS is less.

A Beverton-Holt curve was fitted to the salmon population data to quantitatively estimate intrinsic productivity (i.e., smolts per spawner when density is low) and capacity. Intrinsic productivity is approximately 219 smolts per spawner and capacity is 1.5 million smolts (Figure 1A). Using these data, and a geometric mean smolt-to-adult survival rate of 1.4%, we estimated the maximum equilibrium value to be 14,300 adults. In other words, the

natural spawning population is expected to stabilize near 14,300 adults, assuming all else remains equal.



Figure 1. Number of Chinook salmon smolts (A) and smolts per spawner (B) in relation to the number of parent spawners. Approximately 40% of the natural spawners originated from hatchery parents. Source: ISAB 2015.

## 2.6.3 Effects of Hatchery Salmon on Productivity, Local Adaptation, and Harvests

#### Methods

We illustrate the benefits of managing salmon density and pHOS on the spawning grounds using two scenarios:

1) Selectively remove all hatchery salmon from spawning areas (40% of total) and estimate survival and abundance benefit related to A) reduced density only, and B) reduced density by removing all hatchery salmon, i.e., the combined effects of fewer hatchery salmon and reduced density.

2) Selectively remove "surplus" hatchery salmon, i.e., hatchery fish that exceed the capacity of watershed to support the population. The target escapement (NORs + HORs) is the maximum number of spawners that can replace itself (equilibrium population)<sup>3</sup>.

These scenarios represent two approaches to what we call the "Sustainable Population Approach to Recovery" (SPAR). Scenario 1 is relevant when the key goals are to maximize adaptation of the population to the local environment and to increase productivity. Scenario 2 is relevant when the goal is to enhance adaptation while also maintaining high spawner abundances within the capacity of the watershed to support spawners and their progeny. Density dependent effects associated with reduced spawner density are predicted from the Beverton-Holt curve fit to the data in Figure 1.

The test population responses to removal (selective harvesting) of hatchery salmon involve the short-term benefits of density reduction (as above) and increased productivity associated with removal of hatchery salmon spawning in less favorable habitats (Williamson et al. 2010, Hughes and Murdoch 2017, but see Chilcote et al. 2011), and the longer-term benefits of increasing PNI and allowing adaptation to local conditions. To account for the long-term benefits of removing hatchery salmon from the spawning grounds, we used the empirical relationship between mean pHOS and intrinsic productivity for 82 populations of Pacific salmon developed by Chilcote et al. (2011, 2013). This relationship involved 28 populations of Chinook salmon, 22 populations of coho salmon, and 32 populations of steelhead. According to Chilcote et al. (2013), the predicted rate of change in intrinsic productivity associated with the level of pHOS did not vary by species, although intrinsic productivity was highest among Chinook salmon populations. The predicted potential increase in intrinsic productivity associated with the removal of all hatchery salmon increased by a factor of 1.8, 3.1, and 5.4 as pHOS prior to removal was 10%, 40%, and 60%, respectively. This prediction assumes that intrinsic productivity will eventually recover to the pre-hatchery level. Adjustments to intrinsic productivity were made within the Beverton-Holt model while retaining constant capacity.

The Chilcote et al. (2013) relationship was used rather than relative reproductive success (RRS) studies of hatchery and natural salmon because RRS studies typically compare productivity of hatchery-origin salmon with natural-origin salmon that have already been influenced by hatchery spawners. The Chilcote et al. (2011, 2013) analysis considered the potential effects of dams, habitat quality, and hatchery fish homing to release sites where habitat quality may have reduced productivity.

<sup>&</sup>lt;sup>3</sup> The spawner abundance leading to maximum recruitment, based on a Ricker curve, could be used but this spawner abundance is less than the equilibrium abundance, i.e., the maximum abundance of natural spawners that can replace itself.

#### **Scenario 1 findings**

Productivity (smolts per spawner) of the test population increased markedly in response to harvest of 40% of the spawning population (<u>random selection of all fish</u>), as expected from the strong compensatory density dependence relationship. For example, predicted smolts per spawner increased from 41 to 61 (49% increase) whereas smolt production declined only ~10% (from 1.2 to 1.1 million smolts) when spawner density was reduced from 30,000 to 18,000 spawners (Figures 2 & 3). Productivity increased more in response to fish removal at lower abundances (Figure 2); however, at lower spawner abundances demographic risks will begin to outweigh the potential benefits of increased productivity.

Demographic risks of low abundance may be offset to some extent by the selective removal of hatchery spawners, which have lower intrinsic productivity than wild salmon when spawning in rivers (e.g., Chilcote et al. 2013). For example, if the 40% reduction in spawners from 30,000 to 18,000 fish involves only the removal of hatchery salmon (pHOS = 40%), then smolts per spawner increases 83% (from 41 to 75 smolts per spawner) and smolt production increases nearly 10% (from 1.23 to 1.35 million smolts) (Figures 2 & 3). Furthermore, smolt production increases by removing all hatchery spawners (40% of the population) throughout the range in potential spawners. Increased smolt production is the predicted long-term response to density dependence plus increased intrinsic productivity associated with removal of less productive hatchery salmon.

Removal of all hatchery salmon (40% in this example) can improve sustainability of the natural population over the long term. In other words, adult returns equal or exceed the abundance of the parent spawning population ( $R/S \ge 1$ ) when supplementation of the natural population with hatchery salmon is terminated. Under status quo, when pHOS is 40% and SAR is 1.4%, the maximum equilibrium spawner escapement is approximately 14,300 fish (Figure 4). If hatchery fish are selectively harvested, then the terminal run size (HOR & NOR fish) can grow to ~31,600 fish (leaving ~18,960 natural spawners after selective harvest of 40%) while still enabling a sustainable population at a SAR level of 1.4% (Figure 4). As shown in Figure 4, reducing density has a greater influence on sustainability than the change in intrinsic productivity associated with harvesting hatchery salmon because fewer progeny are needed to replace the population. Furthermore, if SAR declines below 1.4%, such as from climate change, then a larger sustainable population (maximum equilibrium population) could theoretically be supported by removing hatchery spawners, which contribute to density dependence and overall lower fitness. However, managers must balance this benefit with the demographic risk of low abundance associated with low and variable SAR values.

A key goal of hatchery production is to provide harvests and to improve food security. In this example, approximately 12,000 more hatchery salmon would be harvested if the goal was to remove all hatchery salmon when 40% of the 30,000 spawners are hatchery-origin (Figure 3). Harvests of hatchery salmon in the terminal area increases from zero under status quo conditions to 20,000 fish when the total run to spawning areas increases to 50,000 HOR and NOR salmon and 40% of the HOR are harvested. However, the resulting

30,000 natural spawners would not be sustainable and natural recruitment would fall back to equilibrium (~18,960 natural spawners assuming hatchery fish are consistently harvested). Also, because sustainable harvest rates are dependent on intrinsic productivity (Hilborn and Walters 1992), a reduction in pHOS would improve sustainability of the natural population that may be incidentally harvested in fisheries. Thus, selective harvests of hatchery-origin salmon provide both conservation benefits and social benefits.

#### **Scenario 2 findings**

Managers may choose to maintain the total spawner population near the maximum equilibrium point, such that hatchery salmon would only be harvested when total spawners began to exceed the population equilibrium (~18,960 adults based on the adjusted intrinsic productivity in Scenario 1). When the total population exceeds equilibrium, the productivity and sustainability benefits of this approach would be slightly less than described in Scenario 1, but greater than status quo at all levels. This result stems in part from higher intrinsic productivity relative to status quo but lower intrinsic productivity relative to Scenario 1. Compared with Scenario 1, this approach could reduce potential demographic risk associated with small population size and low SARs. Based on the data in Figure 1, counts of the test salmon population have exceeded 18,960 fish in 40% of the years, indicating the opportunity to apply this approach.



Figure 2. Predicted number of smolts per spawner in relation to total potential spawners. Red line: Beverton-Holt curve fit to the empirical data shown in Figure 1. Blue line: predicted smolts per spawner associated with a 40% reduction (via random harvest) of total spawners. Green line: the combined effect of 40% reduced density and greater intrinsic productivity (3.06x) associated with harvest of all hatchery salmon (40%).


Figure 3. Predicted number of smolts produced in response to a 40% reduction in spawner density (blue line) and the combined effect of reduced density and increased intrinsic productivity associated with harvest of all hatchery salmon (green line). Red line is status quo based on the Beverton-Holt fit to data in Figure 1. Lower graph shows the harvest of hatchery salmon (40% of terminal run). The combined effects of reduced density and reduced pHOS (green line) leads to greater not less smolt production after harvesting hatchery salmon over the long term. Managers must consider demographic risks associated with low spawner abundances.



Figure 4. Smolt to adult return rate (SAR) needed for sustainability (R/S ≥ 1) in relation to terminal run size before harvest of hatchery salmon (pHOS = 40%). Under status quo conditions (red line), much greater survival is needed to achieve sustainability and the sustainable spawning population is constrained to ~14,300 fish (maximum equilibrium) or less. In contrast, if hatchery fish are harvested (green line), then terminal run size before harvest (HOR & NOR fish) can grow to ~31,600 fish (~18,960 natural spawners after harvest [maximum equilibrium]) while still enabling a sustainable population at the observed SAR level (1.4%). Thus, harvesting hatchery salmon leads to a larger sustainable population size (maximum equilibrium) at a given level of SAR.

## Discussion

The illustration of SPAR presented here describes the potential benefits of incorporating HSRG hatchery principles within a density dependence/sustainable fisheries management framework (i.e., the SPAR approach). The SPAR approach was used to develop additional triggers for both initiating recovery programs and for transitioning between the Preservation, Recolonization, Local Adaptation, and Full Restoration phases (Table 4). The illustration demonstrates potentially significant benefits in terms of salmon conservation, viability, and harvests when managing density of hatchery-origin spawners. The magnitude of these benefits will depend on the strength of density dependence, the degree to which intrinsic productivity will increase over the long-term as hatchery salmon are reduced or eliminated from the spawning grounds, and the degree to which the population exceeds the population equilibrium as a result of numerous hatchery salmon.

SPAR is relevant to many salmon and steelhead populations, at least in the Columbia River Basin, because density dependence is strong and pHOS is high among many salmon and steelhead populations (ISAB 2015). Many populations may now be in the Local Adaptation rather than Recolonization phase of recovery because total spawners may exceed the maximum population at which it can replace itself (equilibrium population). Furthermore, we note that SPAR does not necessarily involve a reduction in hatchery production, rather it simply calls for management of the spawning population within the well-recognized fisheries management framework that stems from the concept of density dependence (e.g., Ricker 1954, Rose et al. 2001) plus hatchery management principles identified by the HSRG. However, if managers recognize that they cannot readily reduce high pHOS by harvesting hatchery salmon with little or no harm to natural-origin salmon, then they may consider adjusting program size by releasing fewer hatchery salmon so that returning hatchery fish do not greatly exceed the maximum equilibrium abundance for naturally spawning salmon.

Table 4.Objectives and indicators associated with each restoration phase and<br/>triggers to reach the next phase. These natural-origin population<br/>characteristics build upon previous HSRG guidelines by emphasizing<br/>population capacity, intrinsic productivity, and the maximum spawning<br/>population that can replace itself (equilibrium). These metrics can be<br/>estimated from spawner-recruit data or approximated from EDT<br/>analysis when insufficient data are available.

| Phase                   | Objectives   | Indicators   | Triggers to Next Phase  |
|-------------------------|--|--|---|
| <u>Preservation</u>     | Secure the genetic identity and<br>diversity of the native<br>population until habitat can<br>support survival at all life<br>stages and population<br>sustainability.<br>Ensure information exists that<br>habitat carrying capacity can<br>support and sustain<br>preservation of population.  | <ul> <li>Fish spawning in habitat<br/>and producing juveniles.</li> <li>Intrinsic productivity near or<br/>below 1 adult per spawner<br/>(or equivalent smolt per<br/>spawner), indicating natural<br/>population may not be self-<br/>sustaining. Low NOR<br/>abundance.</li> </ul> | Intrinsic productivity >1<br>adult per spawner and<br>adequate carrying<br>capacity to move to<br>Recolonization Phase.   |
| Recolonization<br>Phase | <ul> <li>Re-populate suitable habitat, including spawners, juveniles, and outmigrating smolts (all life stages).</li> <li>Establish NOR ranges for optimal productivity in terms of R/S &gt;1 and/or smolts per spawner (S/S), i.e., S/S prior to horizontal asymptote.</li> <li>Establish pHOS ranges that ensure HOR do not markedly decrease intrinsic productivity.</li> </ul> | Intrinsic productivity >1 but<br>HOR continuously needed<br>to replenish spawning<br>population in order to<br>approach maximum<br>equilibrium abundance.  | <ul> <li>Further develop<br/>spawner-recruit<br/>relationships (to smolt<br/>and adult life stages)<br/>and estimate intrinsic<br/>productivity, capacity,<br/>and the maximum<br/>equilibrium value at<br/>which the population<br/>can replace itself.</li> <li>Escapement (NOR &amp;<br/>HOR) continuously<br/>near or exceeding<br/>maximum equilibrium<br/>value to move to Local<br/>Adaptation Phase.</li> </ul> |

| Local<br>Adaptation | <ul> <li>Increase intrinsic productivity<br/>and life history diversity<br/>through local adaptation. Meet<br/>and exceed minimum viable<br/>spawner abundance for<br/>natural-origin spawners.</li> <li>Manage salmon density and<br/>pHOS on spawning grounds<br/>using SPAR approaches either<br/>by:</li> <li>Selectively removing all HOR<br/>from spawning grounds, or</li> <li>Selectively removing "surplus"<br/>HOR above target escapement<br/>(NOR+HOR) for equilibrium<br/>population.</li> </ul> | <ul> <li>Spawning population of<br/>NOR and HOR fluctuating<br/>around maximum<br/>equilibrium point.</li> <li>Intrinsic productivity,<br/>residuals from recruitment<br/>relationship, and<br/>equilibrium abundance<br/>gradually increase over<br/>time as fitness improves.</li> <li>R/S ≥1, and smolts per<br/>spawner produced by<br/>target escapement is<br/>relatively high.</li> </ul> | Intrinsic productivity<br>and abundance lead to<br>a sustainable natural-<br>origin population (R/S<br>>>1) while contributing<br>to fishery harvests. |
|---------------------|---|--|--|
| Full Restoration    | Population recovery. Long-<br>term adaptive management to<br>maintain viable population, in<br>terms of all VSP parameters.   | NOR abundance and<br>intrinsic productivity<br>support a robust fishery.   | Hatchery program<br>minimized or<br>eliminated as a means<br>to eliminate HOR and<br>maintain intrinsic<br>productivity of NOR.                        |

Implementation of the SPAR approach is not straightforward. First, and perhaps foremost, is the current inability or low desire in many watersheds to selectively harvest all or most hatchery-origin salmon. Hatchery salmon must be visually marked so they can be selectively harvested. Salmon in some hatcheries may not be visually marked when the goal is to facilitate survival in non-terminal mark-selective fisheries and allow fish to return to natal areas where they are either harvested or encouraged to spawn in rivers because the belief is that more spawners are needed to enhance future production (e.g., Recolonization Phase). Nevertheless, studies indicate many marked salmon and steelhead remain unharvested and ultimately spawn in watersheds, contributing to strong density dependence and reduced fitness of the natural-origin population (HSRG 2009, Chilcote et al. 2013, ISAB 2015).

Many techniques are available to selectively harvest marked salmon with little or no impact on natural-origin salmon, including traps on rivers and dams, weirs, and purse seines. These techniques have been successfully implemented in some areas by Tribes, such as the Colville Confederated Tribes in the upper Columbia River and in the Okanogan River (Section 3.3, ISAB/ISRP 2016). However, Anderson et al. (2020) describe complications associated with attempts to control pHOS at weirs and dams. Additionally, hatchery managers could improve imprinting and homing of hatchery salmon to specific locations to selectively harvest hatchery salmon. The ability to selectively harvest hatchery salmon is the biggest obstacle to implementation of the Sustainable Population Approach to Recovery. However, if more fishers, hunters, managers, and scientists recognize the substantial benefits of selectively harvesting hatchery salmon, then methods to implement selective harvests will likely improve.

The second obstacle to implementing SPAR involves insufficient data to examine density dependence and estimate the maximum natural spawner abundance that can replace itself (population equilibrium). Key data include counts of NORs and HORs reaching the spawning grounds, smolts per spawner, and recruitment of NOR adults. Empirically-based spawner goals are necessary to fully implement the approach. More effort is needed in most regions to estimate the number of spawners and progeny that the habitat can support. However, in the absence of such data, greater effort could be made immediately by examining existing information or by conducting an Ecosystem Diagnosis and Treatment (EDT) analysis to roughly estimate current spawner capacity and to identify methods to selectively harvest hatchery salmon. Additionally, when implementing Scenario 2, managers could consider an adaptive management approach for reducing uncertainty about the equilibrium population level. Rather than targeting the current estimate of equilibrium population abundance, which may be biased low, managers could temporarily target a spawner abundance that is  $\sim$ 1.5X the equilibrium spawner abundance as a means to reduce uncertainty in the future. This approach is needed if spawning populations contract at low densities and expand into new habitat at higher densities (Isaak et al. 2003, Atlas et al. 2015). Results from such probing must be monitored and evaluated regularly to avoid risking long-term losses in population productivity and sustainability.

A third obstacle to implementing SPAR may occur when a salmon population is small and demographic risk of extinction is moderately-high. As noted above compensatory density dependence is a natural mechanism for reducing risk of extirpation because productivity increases at lower densities. However, if habitat has been degraded (e.g., in the natal river, migration corridor, and ocean), then compensatory density dependence can be insufficient to prevent extirpation. Likewise, strong depensatory predation could overwhelm natural compensatory mechanisms at low abundances and trap populations at low abundances. We encourage managers to produce and evaluate empirical spawner recruit data to develop sustainable spawner goals while also considering demographic risks of extinction. Furthermore, spawner-recruit relationships are essential for evaluating salmonid population responses to restoration and recovery efforts (ISAB 2015). For example, do spawner-recruit analyses indicate intrinsic productivity and capacity are increasing in response to restoration?

Salmon populations are often managed at the stock level, which may include many populations with varying levels of pHOS and productivity. This variability leads to greater uncertainty in sustainable harvest rates when attempting to manage pHOS at the stock level. Ideally, management of pHOS would occur as close as possible to the spawning area to avoid higher demographic risk.

HSRG guidance targets a PNI value of 0.67 or higher for integrated hatchery programs involving Primary populations. The PNI score is not an instantaneous measure of population

condition, rather it approximates the equilibrium point at which the population would arrive after many generations (Busack 2015). Additionally, a PNI score of 0.67, which is often targeted by integrated hatchery programs, should not be considered to represent a population that is well adapted to the natural environment. Rather, this PNI value reflects a population that, at equilibrium, is less adapted to the environment than a wild population, but more adapted to the local environment than a corresponding segregated hatchery salmon population. Furthermore, reducing pHOS leads to greater fitness benefits than increasing natural-origin salmon in the hatchery broodstock (HSRG 2009, Anderson et al. 2020), so that attempts to increase PNI by increasing pNOB while allowing high pHOS are less beneficial than reducing pHOS. For these reasons, the SPAR approach recommends selective harvest of hatchery salmon when those fish produce few or no additional progeny because capacity has been reached.

The two scenarios presented in the SPAR illustration primarily address the Local Adaptation phase of salmon recovery in which total spawner abundance is frequently near the population equilibrium (Table 4). Based on the findings of ISAB (2015) and others, we suspect many salmon and steelhead populations are near or exceeding the population equilibrium and should consider the SPAR approach. Managers of salmon populations that still have some demographic risk of extinction should follow the Scenario 2 approach in which hatchery salmon are selectively harvested when exceeding the natural spawner abundance that can replace itself. Otherwise, managers should consider harvesting and removing all hatchery salmon from the spawning grounds (Scenario 1) to reduce density effects and increase intrinsic productivity over time. Ultimately, the greatest challenge for implementing the SPAR approach is determining how to safely harvest hatchery salmon that contribute little to future natural production.

## **3.0 POPULATION CASE STUDIES**

Managing salmon and steelhead populations can be exceedingly complex with multiple stakeholders, complex jurisdictions, and conflicting objectives. Decision makers, stakeholders, and the public often value different outcomes and hold different interpretations of science. Decisions about managing salmon and steelhead populations require balancing both societal values and science in a transparent way. Ultimately, this requires weighing tradeoffs among a set of competing objectives (e.g., conservation vs. harvest). To illustrate the potential complexity of decisions required by fisheries managers, we present six case studies of salmon populations in the Pacific Northwest: Snake River Sockeye, Elwha Chinook, Okanogan summer/fall Chinook, Lewis River spring Chinook, Elochoman fall Chinook, and Snow Creek Coho.

Our approach in presenting the case studies and outlining the decision process stems from the guidance provided by the HSRG Framework paper (HSRG 2017) and methods of Structure Decision Making (SDM). The general approach of SDM follows these basic steps: frame the decision, elicit objectives, develop alternatives, and evaluate consequences and tradeoffs (PRoACT; e.g., Runge et al. 2013). The exact situation with any program will vary, but these steps add transparency, facilitate objective decisions, and help managers evaluate the consequences of various alternative management actions. In the case studies, we focus on illustrating how to develop phase triggers for individual programs.

We organized the case studies as follows:

#### I. Frame the Decision

- a. Identify the decision makers: stakeholders, co-managers, federal managers, and others. Clarify the roles and responsibilities of those involved in the decisions.
- b. Identify Population Designation
  - 1. Has the population's biological significance been determined (Primary, Contributing, Stabilizing or equivalent)?
  - 2. How long has this population designation been applied to the population? Who made the determination?
- c. Identify Current Population Recovery Phase (this does not have to be identified in a specific Recovery Plan, just agreed to by the managers)
  - 1. Preservation, Recolonization, Local Adaptation, or Full Recovery based on current conditions.
  - 2. Review the phase history. Has the population been in earlier or later phases? If so, when and for how long?

#### II. Formulate objectives

Foremost in formulating objectives is to identify the management goals of the population. This is Principle 1 of the HSRG's recommendations: Develop Clear, Specific, Quantifiable Harvest and Conservation Goals for Natural and Hatchery Populations within an "All H" Context. Unless the goals for the population are clear, it is not possible to develop effective objectives, or monitor and evaluate the success of the management approach. The role of any hatchery program involved will vary depending on the phase of recovery.

- a. Is the purpose conservation, harvest, or both, or education and research?
- b. Is the goal to retain a unique gene pool or the biological diversity associated with a wild selective environment?
- c. What are the biological targets for the natural population during each phase?
- d. What are the harvest goals, if any?
- e. Are there other resource goals?

#### III. Develop alternatives for phase shifts

a. Develop alternatives for biological targets during each phase.

- b. State biological assumptions about the 4 Hs (habitat, harvest, hatchery, and hydro)
   e.g., using the All-H Analyzer/In-season Implementation Tool (AHA/ISIT) (HSRG 2017, 2020).
- c. Develop biological metrics (triggers) to move up or down phases. Instead of linking phase shifts to specific management actions or timelines, we suggest defining phase shifts using biological criteria, e.g. the number of NORs on the spawning grounds. The indicators should reflect progress toward the objectives for each phase and should be measured annually as part of monitoring and evaluation.

## IV. Evaluate consequences and tradeoffs

- a. If a hatchery will be used as a restoration strategy, how will the hatchery program size affect the assumptions about the 4 H's and naturally spawning populations?
- b. What are the potential effects of alternative management strategies on the population?
- c. Will existing habitat support moving to the next recovery phases?
- d. What are the consequences of operating the hatchery as a harvest augmentation program in any of the phases?
- e. What are impacts to other populations/species in the drainage of the various alternatives?
- f. How might climate change and habitat loss affect phase shifts?

## **3.1 SNAKE RIVER SOCKEYE SALMON**

## **Background and Decision Framework**

On the West Coast of the US, 28 populations of Pacific Salmon are listed as Threatened (24) or Endangered (4) under the US Endangered Species Act (ESA). These serve as good examples of recovery planning for Primary Populations. The most critically endangered of these is Snake River Sockeye salmon (*Oncorhynchus nerka*) [ESA-listed November 1991, 56 FR 58619]. The last known remnants of the Snake River Sockeye salmon stock return to Redfish Lake in the Sawtooth Valley in Idaho (Figure 5). Sockeye salmon returning to Redfish Lake travel a greater distance from the Pacific Ocean (1,448 river kilometers) and to a higher elevation (2,138 meters) than any other Sockeye salmon population in the world. Additionally, Redfish Lake supports the species' southernmost population within its recognized range.



Figure 5. Location of Redfish Lake and Sawtooth Valley, Idaho.

Recovery efforts for Snake River Sockeye salmon are continuing along the path described by Kline and Flagg (2014) and coordinated and funded by the Bonneville Power Administration through a Technical Oversight Committee. These efforts are conducted by the Idaho Department of Fish and Game (IDFG) (fish collections, husbandry, and research), NOAA-Fisheries (husbandry), the Shoshone-Bannock Tribes (SBT) (habitat limnology investigations), and other stakeholder groups [hereafter referred to as "the Team"]. In the ensuing decades since ESA-listing, the conservation program for Redfish Lake Sockeye salmon has been perhaps unique in the annals of species conservation in aggressively pursuing both legal protective measures and a holistic science-based approach to recovery including: genetic and behavioral issues; multilevel survival, habitat, and restoration evaluations; comprehensive gene rescue efforts; and full-scale hatchery production (see Table 1 in Kline and Flagg 2014). Fish from the program are tagged for evaluation.

The Redfish Lake Sockeye salmon program is currently in the Recolonization phase (Table 5) after having spent nearly 20 years in the Preservation phase (since 1990).

## **Recovery Objectives and Phase Triggers**

The purpose of the Redfish Lake program is conservation of the Snake River Sockeye salmon population. The objectives for each recovery phase are described in Table 5. The initial program goal was to prevent extinction and retain the genetic diversity of the existing population through a captive broodstock program. The long-term goal is to rebuild stocks to facilitate de-listing and increase population abundance to levels sufficient to sustain sport and tribal harvest. IDFG constructed a new Sockeye salmon hatchery, the Springfield Hatchery, in south central Idaho, capable of producing approximately one million full-term smolts annually to address these needs.

Specific phase triggers based on measures of abundance and productivity were identified by the Team as part of the recovery planning process. Triggers are summarized in Table 5 and described in more detail in the text below.

| Phase  | Objectives  | Indicators  | Triggers to Move to Next Phase   |
|--|---|---|--|
| Preservation, Phase 1<br>Develop and maintain a<br>captive hatchery<br>population to prevent<br>extinction.  | Prevent extinction.<br>Retain genetic<br>diversity and<br>identity of existing<br>population.         | Adult abundance, life<br>history diversity, genetic<br>profile (e.g., allelic<br>diversity, N <sub>e</sub> , metrics of<br>genetic distance from<br>other populations). | No formal/quantitative triggers.<br>Growth and survival of captive<br>broodstocks in culture. Ability of<br>captive broodstocks to produce<br>viable eggs and offspring to<br>amplify population.  |
| Preservation, Phase 2<br>Maintain captive<br>hatchery population to<br>prevent extinction.<br>Begin release of<br>hatchery-produced<br>eggs, juveniles, and<br>adults to habitat to<br>evaluate fitness. | Determine fitness of<br>captive broodstock<br>progeny.  | Adults released spawn<br>in habitat; eyed eggs<br>placed in egg boxes<br>hatch; released<br>hatchery-reared<br>juveniles successfully<br>outmigrate.                    | No formal/quantitative triggers.<br>Initiate Recolonization efforts when<br>adults have returned from ocean<br>from Phase 2 test releases and<br>when facilities are available to<br>produce large numbers of smolts<br>(e.g., upon completion of<br>Springfield Hatchery).            |
| Recolonization Phase<br>Smolt production goal<br>1M smolts produced for<br>release.  | Fish rearing in<br>habitat and<br>outmigrating and<br>adults successfully<br>returning from<br>ocean. | Fish spawning in habitat<br>and producing juveniles.<br>pNOB = 10%; pHOS =<br>not restricted; PNI = not<br>restricted.  | Trigger 1: Begin to phase out<br>NOAA captive bloodstock program<br>when 5-year geometric mean<br>return of anadromous adults<br>>1,000.<br>Trigger 2: Terminate Eagle<br>Hatchery captive broodstock<br>program when 5-year geometric<br>mean return of anadromous adults<br>>2,150.* |

# Table 5.Example of objectives, indicators, and triggers associated with each<br/>phase of restoration (Redfish Lake Sockeye Salmon).

| Phase   | Objectives  | Indicators   | Triggers to Move to Next Phase   |
|---|---|--|--|
|   |   |  | Trigger 3: Initiate the Local<br>Adaptation Phase when 5-year<br>geometric mean return of natural-<br>origin adults >750.<br>* A small captive population may<br>need to be maintained at Eagle<br>Hatchery to buffer against low<br>adult returns due to stochastic<br>environmental events.  |
| Local Adaptation<br>Phase<br>Smolt production goal<br>1M smolts produced for<br>release, phase out<br>captive brood programs. | Increasing<br>abundance and<br>distribution. Fish<br>colonizing additional<br>lake habitats in the<br>Sawtooth Basin. | Fish spawning in habitat<br>and producing juveniles.<br>pNOB = 35%; pHOS =<br>objective <30%; PNI =<br>objective >50%  | Start to phase out the<br>supplementation program at<br>Springfield Hatchery when the 5-<br>year geometric mean of natural-<br>origin adults meets the viability<br>standards and delisting criteria<br>identified by NMFS (1,000 naturally<br>spawning adult fish returning to<br>Redfish Lake and 1,500 combined<br>returning to two other historic<br>Sockeye Salmon lakes in the<br>Sawtooth Valley lakes (2,500<br>total)). |
| Full Restoration<br>Phase<br>Hatchery programs<br>eliminated.   | Population recovery   | Two recovered lakes.<br>The 10-year geometric<br>mean of natural-origin<br>adult returns to Redfish<br>Lake and one additional<br>recovery lake meets<br>NMFS' ESA recovery<br>standards of 1,000<br>NORs.<br>Three recovered lakes.<br>Same standards as in<br>#1, plus 500 NORs in<br>one smaller historic lake<br>(Pettit, Stanley, or<br>Yellowbelly Lake) | Propose ESA downlisting<br>Propose ESA delisting   |

## Phase Shift Alternatives, Tradeoffs and Consequences

## Phase I – Preservation

The Preservation Phase focused on using captive broodstocks to prevent extinction, preserve the gene pool, and increase population numbers. Based on probable extinction scenarios and the pending ESA listing, in May 1991 the Team decided to collect outmigrating smolts and retain any anadromous adults that returned to begin a captive broodstock program. This move was controversial since at the inception of the project in

the early 1990s, the application of captive broodstock technology to Pacific salmon was considered highly experimental and success was uncertain. Nonetheless, the only other alternative at the time appeared to be extinction. The founder population for the preservation effort was the entire 16 adults that returned in 1990 and a few outmigrant and residual juveniles in Redfish Lake (see Kline and Flagg 2014 Table 2). Captive broodstocks are held at multiple facilities and have resulted in the production of more than 10,000 adult descendants. Initially, pedigree information was used to guide spawning. However, as new methods became available, spawning matrices based on full suites of genetic information were developed. The program has retained approximately 95% of the original founding genetic variability of the population (see Kalinowski et al. 2012).

The program has released captive-reared pre-spawning adults, eyed eggs, pre-smolts, and smolts to the ecosystem (see Hebdon et al. 2004, Kozfkay et al. 2019, and Johnson et al. 2020). Estimates of carrying capacity and limnological information developed by program cooperators were used to guide the development of annual reintroduction plans (see Teuscher and Taki 1996; and Griswold et al. 2011). Adult returns from these releases suggested that smolt releases should be sufficient to produce enough adult returns to fully seed the Redfish Lake spawning habitat, and that the juveniles produced by naturally spawning adults should have sufficient fitness to increase smolt-to-adult return rates to a point meeting or exceeding self-sustainability. These data suggest that apparent extinction vortex-type scenarios (Soule 1986) could be reversible for this population. These results led the Team to begin developing estimates of juvenile fish production levels necessary to eventually achieve population stablization and recovery, as described below.

## Trigger status:

- 1. Trigger of gene pool maintenance was met for Phase I.
- 2. Prespawning adults from captive broodstock successfully spawned and produced offspring.
- 3. Hatchery juveniles released to habitat successfully outmigrated.
- 4. Adults from these strategies returned from ocean

## Phases II through IV. Recolonization, Local Adaptation, and Full Restoration

The Team structured the next three phases of the project to: (1) establish parameters for expanding the project and producing enough fish to re-colonize the historic habitat, (2) provide for development of local adaptation and the rebuilding of natural population structure, and (3) meet ESA Recovery goals identified by NMFS. The Team also developed targets for phasing out both the captive broodstock programs and, ultimately, all hatchery intervention components of the program.

The NMFS 2015 ESA Recovery Plan for Snake River Sockeye Salmon identified biological goals of 1,000 naturally spawning adult fish returning to Redfish Lake and 1,500 combined

returning to two other historical Sockeye Salmon lakes in the Sawtooth Valley lakes (2,500 total) (see: <u>https://repository.library.noaa.gov/view/noaa/16001</u>). These are the triggers for moving to the Full Restoration phase (Table 5).

A modification of the HSRG's All-H Analyzer tool (AHA) (HSRG 2009, Paquet et al. 2011) was used to determine the level of juvenile smolt releases required to achieve enough adult returns from the ocean to fully seed Redfish Lake spawning habitats. The Team conservatively estimated Redfish Lake adult spawning capacity of 2,000 pairs and natural smolt production potential of 150,000 juveniles. Calculations indicated that releasing one million hatchery-reared smolts could initially, on average, produce approximately 5,000 returning adult fish (637 NOR and 4,347 HOR). These returns would be targeted primarily for release to Redfish Lake, while additional returns would be released in other nearby lakes (see Table 6 in Kline and Flagg 2014). These return levels are the triggers that will be used to begin to gradually phase out the captive brood programs during the Recolonization phase (Table 5). The captive brood programs would not be fully phased out until the end of the Local Adaptation phase to provide a demographic safety net. Over time, natural spawning could produce more than 1,600 returning adult fish. The juveniles produced from adults spawning naturally in Redfish Lake would presumably develop (through local adaptation) the increased fitness necessary to increase smolt-to-adult return rates to levels that meet or exceed self-sustainability (above 2%).

During the Local Adaptation phase, managers will adjust the proportion of natural-origin spawners taken for broodstock (pNOB) and the ratio of hatchery-origin (pHOS) to natural-origin (pNOS) adult Sockeye released to the habitat for natural spawning. The goal is to increase the use of anadromous Sockeye salmon in hatchery spawning designs as well as ensure adequate numbers in the habitat for natural spawning using a sliding scale approach (HSRG 2009). In low abundance years, more HORs would be allowed to reach the spawning grounds to reduce demographic risks. In high abundance years, pHOS would be greatly reduced (through use of existing weir or other methods) and the focus would be on allowing natural-origin fish to make up most of the natural spawners.

In the Recolonization phase, approximately 5,000 anadromous Sockeye salmon (more than 80% HORs) are projected to return to the Sawtooth Valley annually. The program goal is to meet a pNOB of 10%. During this phase of the program, pHOS is not restricted to maximize the number of natural spawners.

The Local Adaptation phase of the program will be initiated when the 5-year geometric mean return of natural-origin adults exceeds 750, an increase from the average of 637 NORs expected during the Recolonization phase (Table 5). As the number of anadromous (hatchery- and natural-origin) adults spawning naturally in Redfish Lake increases, increased numbers of natural-origin adults (produced from in-lake spawning events) will be produced and return to collection sites in the Sawtooth Valley. Natural-origin adult returns are anticipated to be sufficiently abundant to allow a pNOB of 35%. The number of hatcheryorigin adults released to spawn in the habitat (pHOS) will ideally not exceed 30%. The resulting PNI will exceed 0.50, allowing the environment to drive the fitness of the composite population. The HSRG identified that this generally occurs when the number of natural-origin adults incorporated in hatchery spawning designs is greater than the number of hatchery-origin adults released to the habitat to spawn volitionally (HSRG 2009, Paquet et al. 2011). Once the Local Adaptation Phase is fully initiated, both captive broodstock programs will have been terminated. The IDFG Eagle Fish Hatchery will be managed as an integrated conservation program following the guidelines and recommendations discussed above and in HSRG recommendations (Paquet et al. 2011).

Operation of the recovery program during the Recolonization and Local Adaptation phases is expected to have minimal impacts to other species in the Sawtooth Valley basin. Releasing anadromous and captive reared pre-spawning adults into Redfish Lake has led to a positive nutrient flux in this lake (Evans et al. 2020). However, salmon-derived nutrients likely did not play a large role in the primary productivity of Redfish Lake (Selbie et al. 2007). Therefore, it is unlikely that the increase in the number of adults spawning in Sawtooth Valley basin lakes due to this recovery program will greatly affect the nutrient dynamics in these systems. In addition, juvenile releases in the spring result in only a temporary increase in juvenile abundance within the basin. The short duration of this increase probably limits impacts to terrestrial and aquatic piscivores in the Sawtooth Valley during these recovery phases.

The program will enter the Full Restoration phase once the NMFS 2015 ESA Recovery Goals are met (Table 5). The careful step-wise efforts carried out by the Redfish Lake Sockeye salmon program in first containing the immediate extinction threat and then addressing multiple levels of gene rescue, habitat improvements, and carrying capacity issues can be seen as a model for future endeavors. It seems a virtual certainty that without the steps undertaken by the Redfish Lake Sockeye gene rescue program, this ESA-listed endangered stock would be extinct.

Over the course of the recovery program, climate change has a greater chance of negatively impacting the shift between phases than natal habitat loss. Most of the natal watersheds in the Sawtooth Valley lie within the Sawtooth National Recreation Area (NMFS 2015), and Kozfkay et al. (2019) found current freshwater productivity to be similar to what was observed in the mid-20<sup>th</sup> century. However, reduced adult survival has been found to be associated with water temperatures experienced in the migratory corridor (Keefer et al. 2008), indicating that increasing average global temperatures could reduce the smolt-to-adult survival of Snake River Sockeye salmon. This potential reduction in survival could affect the ability of the recovery program to shift between the phases.

## 3.2 ELWHA RIVER CHINOOK SALMON

## **Background and Decision Framework**

The Elwha River is located in the northern Olympic Peninsula in Washington State and empties into the Strait of Juan de Fuca (Figure 6). The Elwha River basin is 833 km<sup>2</sup> with

approximately 123 linear km of habitat for anadromous salmonids. Most of the basin is located within Olympic National Park (NP). More than 90% of salmonid spawning habitat was blocked following construction of the Elwha Dam in 1913 and Glines Canyon Dam in 1927. Salmon were only able to spawn in the 8 km of accessible habitat between the mouth of the Elwha River and Elwha Dam. Removal of the dams was completed in 2014 (though fish passage actions addressing a rock fall located at Glines Canyon continued through 2016), opening 115 km of suitable habitat for anadromous salmonids. Dam removal is the largest step taken to date toward meeting recovery goals for the Elwha River's native salmonid populations (Chinook, Coho, Sockeye, Pink, Chum, steelhead and Bull Trout), three of which are federally listed under the ESA.

The Elwha River Chinook salmon population is part of the Puget Sound Chinook salmon ESU, which is listed as threatened under the ESA (NMFS 2005). Elwha Chinook is genetically distinct from other Chinook populations in the Strait of Juan de Fuca and Puget Sound (Ruckelshaus et al. 2006), and has been identified as a Primary population. Recovery efforts are coordinated by the Lower Elwha Klallam Tribe (hatchery, monitoring and evaluation (M&E), fisheries outside Olympic NP), WDFW (hatchery, M&E, fisheries outside Olympic NP), National Park Service (M&E, fisheries inside Olympic NP), NOAA-Fisheries (research, M&E, ESA recovery), US Fish and Wildlife Service (USFWS), US Geological Service (USGS), and other partners (hereafter, partners). All of the partners have been involved in recovery planning and trigger development.



Figure 6. Elwha River watershed and location of Elwha and Glines Canyon Dam sites.

Hatchery-origin fish comprise the vast majority (>95%) of returning adult Elwha Chinook (Figure 7). The hatchery program has been operating since 1976. Broodstock is collected from the run at large and is comprised largely of hatchery-origin fish. Hatchery releases are 100% otolith marked, and a portion are adipose-clipped. In 2012, the partners approved a 5-year moratorium on fishing in the Elwha River in 2012, which has been extended through 2020, but Elwha Chinook continue to be harvested in the mixed stock ocean fisheries.



Source: WDFW, pers. comm.

# Figure 7. Adult Chinook run size in the Elwha River, 2009-2019. Includes natural spawning escapement and fish collected for hatchery broodstock.

The Elwha Chinook population is currently in the Preservation phase, as defined by the Elwha adaptive management plan, because not all of the triggers to move to the Recolonization phase have been met. Not enough time has elapsed to have four full years of post-dam removal adult to adult returns to evaluate the productivity triggers (Peters et al. 2014; see Table 6 below). All of the triggers for a specific phase must be met before moving to the next phase. However, the program is currently revisiting the phase triggers because of inconsistencies in legal documents (i.e., Biological Opinions, Hatchery and Genetic Management Plans (HGMPs)) and the adaptive management guidelines (Peters et al. 2014)<sup>4</sup>.

## **Recovery Objectives**

The purpose of the Elwha River restoration program is to fully restore the Elwha River ecosystem and its native anadromous fisheries (Elwha River Fisheries and Ecosystem Restoration Act (Public Law 102-495, Section 3(a)). The Elwha River partners developed an adaptive management plan for Chinook and steelhead focusing on recovery of the populations following dam removal (Peters et al. 2014). The objectives for each recovery phase are outlined in Table 6. The plan incorporated recommendations from the HSRG's 2012 review of the Elwha Restoration Plan (HSRG 2012), for example by establishing four recovery phases with biological triggers, rather than basing recovery phases on the dam removal timeline.

<sup>&</sup>lt;sup>4</sup> Roger Peters, USFWS, pers. comm.

The hatchery program plays an important role in the restoration program. Prior to dam removal, the purpose of the Elwha Chinook hatchery program was to provide a safety net for the naturally spawning Chinook population, which had a very limited spawning distribution in the lower Elwha River. Currently, the goal of the hatchery program is to retain the existing genetic diversity of the population and provide a safety net while spawning and rearing habitat in the lower river stabilizes. While dam removal has opened up extensive new Chinook spawning habitat, population recovery has been complicated by the large volume of sediment released during and after dam removal, which has resulted in high turbidity, unstable channels, and filled pools in the lower river.

| Phase  | Objectives  | Indicators   | Triggers for Phase Shifts –<br>Available Spawning Habitat<br>Method*   |  |  |
|--|---|--|--|--|--|
| Preservation<br>Prevent extinction.<br>Retain genetic and life<br>history diversity of<br>native population. | Restore fish passage via dam<br>removal, stabilize conditions in<br>lower river (turbidity, etc.).<br>Hatchery program provides a<br>safety net and HORs help<br>recolonize suitable spawning<br>habitat. | Adult abundance,<br>productivity, spatial<br>distribution                                  | Initiate Recolonization Phase<br>when naturally spawning fish<br>(NORs+HORs) > 950;<br>productivity ≥ 200 juvenile<br>migrants per female spawner,<br>> 1.56 pre-fishing recruits per<br>spawner, > 1.0 spawners per<br>spawner; some spawning<br>above Elwha Dam  |  |  |
| Recolonization<br>Increase natural<br>spawning abundance<br>and spatial<br>distribution.                     | Expand natural spawning to<br>areas above the former dam<br>sites; production of natural-origin<br>smolts. Maintain hatchery<br>program (potential reduction in<br>program size).                         | Adult abundance,<br>pHOS, productivity,<br>spatial distribution                            | Initiate Local Adaptation<br>Phase when naturally<br>spawning fish (NORs+HORs)<br>> 4,340; pHOS < 0.05;<br>productivity ≥ 200 juvenile<br>migrants per female spawner,<br>> 1.56 pre-fishing recruits per<br>spawner, > 1.0 spawners per<br>spawner; > 43% of spawning<br>habitat utilized                           |  |  |
| Local Adaptation<br>Increase abundance,<br>diversity and<br>distribution. Meet or<br>exceed VSP criteria.    | Withdraw hatchery influence.<br>Meet minimum VSP levels of<br>abundance, productivity, and<br>distribution.   | Adult abundance,<br>pHOS, productivity,<br>spatial distribution,<br>life history diversity | Initiate Viable Natural<br>Population Phase when<br>naturally spawning fish<br>(NORs) > 10,000, pHOS = 0,<br>productivity ≥ 200 juvenile<br>migrants per female spawner,<br>> 1.85 pre-fishing recruits per<br>spawner, > 1.0 spawners per<br>spawner; >86% of spawning<br>habitat utilized, diversity<br>increasing |  |  |

# Table 6.Objectives, indicators, and triggers associated with each restoration<br/>phase for Elwha Chinook salmon (Peters et al. 2014).

| Viable Natural<br>PopulationVPopulation<br>Abundance,<br>productivity, diversity,<br>and spatial distribution<br>achieve full potential<br>of the restored<br>habitat.V | Viable natural population which<br>can withstand harvest without<br>hatchery augmentation. | Adult abundance,<br>pHOS, productivity,<br>spatial distribution,<br>life history diversity | Naturally spawning fish<br>(NORs) > 10,000; pHOS = 0:<br>productivity ≥ 200 juvenile<br>migrants per female spawner,<br>> 1.85 pre-fishing recruits per<br>spawner, > 1.0 spawners per<br>spawner;100% of spawning<br>habitat utilized, diversity<br>stable |
|---|--|--|---|
|---|--|--|---|

\*Triggers are based on a 4-year geometric mean.

## Phase Triggers - Available Spawning Habitat Method

The phase triggers in the 2014 adaptive management plan were developed based on an estimate of available spawning habitat in each recovery phase (Table 6; Peters et al. 2014). This method also requires an estimate of adult spawning capacity. Adult Chinook spawning capacity in the fully restored Elwha River was estimated to be 17,000 in the dam decommissioning analysis (FERC 1993) and 31,000 in the final Environmental Impact Statement (EIS) for the Elwha restoration project (DOI et al. 1995), but these are preharvest estimates. Thus, the phase shift triggers were developed based on a goal of 10,000 naturally spawning fish, which is the maximum sustainable yield value for the Elwha River predicted from a spawner-recruit analysis employing empirical data for 25 West Coast Chinook salmon populations with watershed size as a covariate (Liermann et al. 2010). This is the trigger to reach the Viable Natural Population phase (Table 6).

During the Preservation, Recolonization, and Local Adaptation phases, the watershed size is assumed to be less than 100% of the fully restored habitat potential. The adaptive management plan assumed the watershed size to be 9.5% (Preservation phase), 43.4% (Recolonization phase), and 86% (Local Adaptation phase) of its intrinsic potential, which is based on the location of the dams and potential recolonization rates (Peters et al. 2014). These values were used to determine the spawning abundance triggers for each phase (i.e., 9.5% of 10,000 is 950 spawners, the trigger to move from the Preservation to the Recolonization phase; 43.4% of 10,000 is 4,340 spawners, the trigger to move from the Recolonization to the Local Adaptation phase).

As noted above, the Elwha Chinook population is currently in the Preservation phase. Advancing to the Recolonization phase requires meeting a set of triggers (adult abundance, productivity, and spawner distribution; Table 6). The adult abundance and productivity triggers are evaluated based on a 4-year geometric mean. The adult abundance trigger (950 spawners) has been met (Figure 7), and fish are spawning above Elwha Dam, but not enough time has elapsed post-dam removal to evaluate the productivity triggers. The goal of the Recolonization phase is to reestablish a naturally spawning population in > 43% of suitable habitat in the Elwha River. Using the available spawning habitat method, this equates to a trigger of > 4,340 naturally spawning fish. The pHOS objective is 5%, which could be achieved by a combination of actions, including selective harvest,<sup>5</sup> and reducing the hatchery program size (Peters et al. 2014). Finally, three productivity triggers must be met to advance to the Local Adaptation phase. Juvenile productivity must exceed 200 smolts per female spawner, the number of pre-fishing recruits per spawner must exceed 1.56, and the number of spawners per spawner must exceed 1 (Table 6).

Increasing numbers of Chinook are spawning upstream of both the former Elwha and Glines Canyon dams. In fall 2017, a survey of the entire Elwha watershed found 88% of carcasses upstream of the former Elwha Dam site (WDFW 2018). However, the majority (>95%) of spawners are HORs. The hatchery program releases approximately 2.8 million Chinook smolts annually (WDFW 2018), and hatchery-origin returns averaged about 3,600 fish (range: 1,200 – 7,300) from 2009-2019 (Figure 7). Currently, the hatchery program is only authorized under the ESA to take fish for broodstock through the Recolonization phase (WDFW 2012). The hatchery program would either need to be phased out once the Local Adaptation phase is initiated, or ESA consultation would need to be reinitiated to continue the hatchery program. The Elwha co-managers propose phasing out hatchery production during the Recolonization and Local Adaptation phases by reducing the number of hatchery broodstock as the number of natural spawners increases (i.e., a sliding scale approach; Peters et al. 2014, Figure 4). Hatchery production would be completely phased out by the end of the Local Adaptation phase.

Once the program reaches the Local Adaptation phase, pHOS will be substantially reduced (<5%; Table 6), which should promote increased productivity and fitness of the naturally spawning population. When an average of 10,000 Chinook spawn naturally in the Elwha, pHOS is reduced to zero, pre-fishing R/S exceeds 1.85, and spawners per spawner exceeds 1.0 (based on a 4-year geometric mean), the population will reach the Viable Natural Population phase (Table 6).

The adaptive management plan notes that if the program is unable to meet the triggers to move to the next recovery phase, trigger values could be modified (Peters et al. 2014). Phase trigger values will be reevaluated 8 years after dam removal and will be revisited every 4 years. The adaptive management plan also includes a monitoring and evaluation (M&E) component designed to monitor not only the trigger values but also exogenous variables, for example habitat recovery and harvest rates, that directly affect the Elwha Chinook population. M&E data will be used to evaluate trigger values and the assumptions used to develop these values.

## **Restoration Strategies, Tradeoffs and Consequences**

The Elwha River adaptive management plan evaluated four potential restoration strategies for Elwha Chinook (Peters et al. 2014). The benefits and risks associated with each strategy

<sup>&</sup>lt;sup>5</sup> This would require more extensive external marking of Elwha Chinook. Currently, only a limited proportion of Elwha Chinook are externally marked to limit harvest in mixed stock ocean fisheries.

are described in Table 7 (adapted from HSRG 2012). During the Preservation and Recolonization phases, the Elwha Chinook program will primarily use Strategy 1, on-station releases of juveniles, to stabilize the population during and after dam removal and promote recolonization of newly opened spawning habitat. The hatchery program is a requirement of the Elwha River Fisheries Restoration Biological Opinion (NMFS 2006). The adaptive management plan noted that, at the time the plan was developed, otolith data showed the naturally spawning population was not currently self-sustaining, indicating the hatchery program was necessary to preserve the population (Peters et al. 2014). The number of recruits per natural-origin spawner averaged 0.28 for brood years prior to dam removal (2008-2012; WDFW 2018). At the end of the Local Adaptation phase, hatchery production will be terminated and the program will rely on colonization and reproduction by naturally spawning fish (Strategy 4).

|   | Restoration Strategy   | Benefits  | Risks  |  |
|---|--|---|--|--|
| 1 | HORs from on-station releases  | Available immediately—resulting<br>NORs return within a generation<br>Less opportunity for negative<br>ecological interactions <sup>1</sup>                                 | Potentially less optimal spatial distribution of natural spawning  |  |
| 2 | HORs from outplanted adults  | Available immediately—resulting<br>NORs return within a generation<br>Less opportunity for negative<br>ecological interactions  | Transported/volitionally distributed<br>adults may "fall back" or fail to distribute<br>themselves as effectively as those from<br>outplanted juveniles  |  |
| 3 | HORs from outplanted juveniles   | Better spatial distribution of HOR spawners   | NORs will return at least one generation<br>later (i.e., the colonization will occur<br>about 5 years later). Ecological<br>interactions during rearing and<br>outmigration  |  |
| 4 | Spontaneous colonization by<br>NORs or HORs from<br>previous releases. | No additional fitness loss due to<br>domestication effects, resulting in<br>potentially rapid gain in abundance<br>and productivity.<br>No adverse ecological interactions. | If initial population abundance is very<br>low or repeatedly impacted by adverse<br>habitat conditions, colonization may be<br>delayed or hatchery outplants (from the<br>safety net program) may need to be<br>initiated. |  |

# Table 7.Four restoration strategies for Elwha River Chinook salmon (Peters et<br/>al. 2014) and benefits and risks associated with each strategy.

1 Intra-species competition may be particularly significant due to lack of nutrients until ecological functions have been restored.

# Table 8.Prioritization of restoration strategies during each recovery phase for<br/>Elwha River Chinook salmon (1=highest ranked, 4 = lowest ranked;<br/>adapted from Peters et al. 2014).

| Restoration Strategy          | Preservation | Recolonization | Local Adaptation | Viable Natural<br>Population |
|-------------------------------|--------------|----------------|------------------|------------------------------|
| HORs from on-station releases | 1            | 1              | 3                | NA                           |

| HORs from outplanted adults  | 2 | 3 | 2 | NA |
|--|---|---|---|----|
| HORs from outplanted juveniles   | 3 | 4 | 4 | NA |
| Spontaneous<br>colonization by NORs or<br>HORs from previous<br>releases | 4 | 2 | 1 | 1  |

## **3.3 OKANOGAN SUMMER/FALL CHINOOK**

## **Background and Decision Framework**

The Okanogan River extends 185 km from its headwaters in southern British Columbia to north central Washington State and empties into the upper Columbia River near Bridgeport, Washington (Figure 8). The Okanogan River supports populations of spring and summer/fall Chinook, Sockeye, steelhead, Kokanee, Rainbow Trout and Bull Trout. Anadromous fish migrating up the Columbia River must ascend nine dams on the mainstem Columbia River to reach the mouth of the Okanogan River.

Okanogan summer/fall Chinook has been identified as a Primary population by the comanagers (CCT 2009). Management is coordinated by the Colville Tribes (hatchery, M&E, harvest), WDFW (harvest), Okanagan Nation Alliance (Canada), and other partners (hereafter, comanagers). The Colville Tribes operate Chief Joseph Hatchery, located just upstream of the mouth of the Okanogan River and below Chief Joseph Dam. The hatchery releases approximately 2 million summer/fall Chinook subyearlings and smolts into the river annually as part of an integrated conservation and harvest program (1.1 million releases) and segregated harvest program (0.9 million releases). Integrated juveniles are released from acclimation sites along the Okanogan River, and segregated juveniles are released directly from the hatchery.



Source: <u>https://en.wikipedia.org/wiki/Okanogan\_River</u>

## Figure 8. Area map showing location of Okanogan River basin.

The Chief Joseph Hatchery program includes and expands upon the previous hatchery releases into the Okanogan River by the Similkameen Hatchery, which is operated by WDFW. The Tribes operate a selective harvest program using a purse seine at the mouth of the Okanogan designed to capture NORs for broodstock and remove HORs before they reach the spawning grounds. The Colville Tribes also remove summer/fall Chinook HORs at the Chief Joseph Hatchery (CJH) ladder that exceed spawning escapement and broodstock requirements and operate a weir on the mainstem Okanogan River to remove additional HORs and collect broodstock for the hatchery program. Beginning in 2013, WDFW summer/fall Chinook fisheries throughout the mainstem Columbia River began transitioning toward selective fisheries targeting hatchery-origin summer/fall Chinook and conservation of natural-origin summer/fall Chinook, per WDFW Fish and Wildlife Commission's Columbia River Basin Salmon Management Policy C-3620. The combination of the selective harvest program, removal of surplus HORs at the CJH ladder, weir operations and NOR broodstock collection has been successful in reducing pHOS in the Okanogan River and meeting the PNI goal of 0.67. From 2009-2019, NOR spawning escapement averaged 5,269 adults and HOR escapement averaged 2,303 (Figure 9). PNI averaged 0.70 during this period.

The Okanogan River summer/fall Chinook population was in the Recolonization phase when the Chief Joseph Hatchery program was initiated in 2012. In recent years, the program has met the NOR abundance trigger (based on a 5-year running average) as well as the pNOB, pHOS and PNI triggers for transitioning to the Local Adaptation phase (Table 9).



Figure 9. Adult summer/fall Chinook escapement from 2009-2019 in the U.S. portion of the Okanogan River below Zosel Dam.

## **Recovery Objectives**

The Chief Joseph summer/fall Chinook program has both conservation and harvest goals. The purpose of the integrated hatchery program is to provide fish for tribal ceremonial and subsistence fisheries and local recreational harvest, increase the abundance and spatial distribution of the natural spawning population, and preserve the genetic integrity of the population. The segregated hatchery program provides fish for harvest in the ocean and mainstem Columbia River fisheries; very few segregated fish are found on the Okanogan River spawning grounds based on analysis of coded-wire tag (CWT) data. Surplus fish returning to the hatchery (primarily from the segregated program) are distributed to tribal members.

The Colville Tribes, along with the comanagers, developed a set of program phases, objectives, indicators, and triggers for the summer/fall Chinook population (Table 9).

## Phase Shifts: Adult Spawning Capacity Method

In the Okanogan River, summer/fall Chinook adult capacity is estimated to be 16,296 adults (CCT 2009, 2020). Similar to the approach used by the Elwha Chinook program, the program's phase shift goals are based on the potential number of adult returns after

accounting for out-of-basin harvest<sup>6</sup>. The near-term recovery goal is 5,250 NORs (post-harvest returns; CCT 2009, CCT 2020). The long-term recovery goal, as fitness improves and selective fisheries are implemented on the mainstem Columbia River, is 7,000 NORs (post-harvest returns). This is the trigger to reach the Full Restoration phase (Table 9).

During the Recolonization phase, the goal is to increase the number of natural-origin spawners and increase the spatial distribution of spawners in the river. The integrated hatchery program uses 100% NOR broodstock when possible, with a PNI target of >0.67. The program has also identified triggers to return to the previous phase if NOR abundance declines substantially (based on a five-year running average). For example, the program advances to the Local Adaptation phase if the 5-year NOR average exceeds 5,250 adults, and would return to the Recolonization phase if the 5-year NOR average is less than 3,000 adults (Table 9).

| Table 9. | Obje | ctives, indicators, and | triggers associat | ed with each restoration |
|----------|------|-------------------------|-------------------|--------------------------|
|          | phas | e for Okanogan summ     | er/fall Chinook s | almon.                   |
|          |      | 0                       |                   |                          |

| Phase  | Objectives  | Indicators  | Triggers for Phase Shifts:<br>Adult Capacity Method   |
|--|---|---|---|
| Preservation<br>Prevent extinction.<br>Retain genetic and life<br>history diversity of<br>existing population. | Hatchery program<br>provides a safety net.<br>Preserve genetic identity<br>of this summer/fall<br>Chinook stock.  | Adult abundance,<br>productivity, spatial<br>distribution                                   | Initiate Recolonization phase<br>when hatchery program is self-<br>sufficient and habitat is capable<br>of supporting all life stages<br>(egg-spawning adult); NORs ><br>1,000.                               |
| Recolonization<br>Increase natural<br>spawning abundance<br>and spatial distribution.                          | Recolonize suitable habitat<br>with all life stages (pre-<br>spawning to smolt).  | Adult abundance,<br>pHOS, productivity,<br>spatial distribution                             | Initiate Local Adaptation Phase<br>when NORs > 5,250. Maintain<br>pNOB of 100%, pHOS < 30%,<br>PNI > 0.67. Increase spatial<br>distribution, diversity. Return to<br>Preservation phase if NORs <<br>800.     |
| Local Adaptation<br>Increase abundance,<br>diversity and<br>distribution. Meet or<br>exceed VSP criteria.      | Meet and exceed minimum<br>VSP abundance for NORs;<br>increase fitness,<br>reproductive success, and<br>life history diversity<br>through local adaptation. | Adult abundance,<br>pHOS, productivity,<br>spatial distribution,<br>life history diversity. | Initiate Full Restoration Phase<br>when NORs > 7,000. Maintain<br>pNOB of 100%, pHOS < 30%,<br>PNI > 0.67. Increase spatial<br>distribution, diversity. Return to<br>Recolonization phase if NORs<br>< 3,000. |

<sup>&</sup>lt;sup>6</sup> Smolt capacity for Okanogan River summer/fall Chinook is estimated to be 3.7 million. Adult capacity is calculated as smolt capacity \* SAR (smolt-to-adult survival rate), which is 0.44%. However, this SAR does not account for out-of-basin harvest. The expected number of returning adults must therefore be adjusted to account for harvest. This is why the near-term recovery goal is 5,250 NORs (post-harvest returns) even though adult capacity is 16,296.

| Phase   | Objectives  | Indicators   | Triggers for Phase Shifts:<br>Adult Capacity Method  |
|---|---|--|--|
| <b>Full Restoration</b><br>Abundance,<br>productivity, diversity,<br>and spatial distribution<br>achieve full potential of<br>the restored habitat. | Maintain viable population<br>based on all VSP<br>attributes. | Adult abundance,<br>pHOS, productivity,<br>spatial distribution,<br>life history diversity | Return to Local Adaptation<br>phase if NORs < 6,000. |

## **Restoration Strategies, Tradeoffs and Consequences**

Several alternative restoration strategies for summer/fall Chinook and spring Chinook were evaluated in the Chief Joseph Hatchery Program Master Plan (CCT 2004). The analysis evaluated the ability of different strategies to: 1) meet the Colville Tribes' conservation and harvest goals, 2) address specific limiting factors (e.g., nine mainstem Columbia River dams and inadequate distribution throughout historical habitat), and 3) meet federal mitigation requirements. The Master Plan also considered the ecological risks of the various alternatives to other salmonid populations and the economic costs of the proposed approaches.

In the long term, the hatchery program size will be adjusted to protect the naturally spawning summer/fall Chinook population and promote local adaptation, while continuing to provide tribal and recreational harvest opportunities. Broodstock for the segregated program come from integrated program HORs, which reduces the genetic impact of segregated program strays that spawn in the Okanogan River. A set of Decision Rules help managers achieve performance criteria (natural-origin spawners, pHOS and PNI) during each program phase. An Annual Program Review is used to identify in season management targets for the upcoming year, which are finalized when the July 15<sup>th</sup> run forecast is available. The program makes adjustments to broodstock collection, weir operations, and selective harvest (purse seine) operations based on the in-season run forecast, and has been highly successful in meeting the program's biological targets despite challenging conditions during some years (e.g., lower than expected run sizes and less than ideal conditions for brood collection due to warm water). Finally, the monitoring and evaluation (M&E) program is a critical component of the program and ensures coordination among hatchery production, harvest management, and escapement, and helps managers track progress toward conservation goals.

## 3.4 LEWIS RIVER SPRING CHINOOK SALMON

## Background and Decision Framework

The North Fork Lewis River is located in southwestern Washington State and empties into the lower Columbia River (Figure 10). The North Fork Lewis River basin is approximately 2,709 km<sup>2</sup>, and the river supports populations of spring and fall Chinook, Coho, Chum, steelhead, Kokanee, Rainbow Trout, cutthroat trout and Bull Trout. Virtually all spring

Chinook spawning habitat was blocked following construction of Merwin Dam in 1931, Yale Dam in 1953 and Swift Dam in 1958. As part of the federal relicensing process for the dams, a program to reintroduce spring Chinook, Coho and late winter steelhead above Swift Dam was initiated in 2013. Upstream reintroduction is the largest step taken to date toward meeting recovery goals for Lewis River spring Chinook.



Source: Pacificorp and Cowlitz PUD 2020.

## Figure 10. Area map showing locations of Lewis River fish hatcheries, collection facilities, hydroelectric projects and reservoirs.

The Lewis River spring Chinook salmon population is part of the Lower Columbia River Chinook salmon ESU, which is listed as threatened under the ESA (NMFS 2005). Lewis River spring Chinook has been identified as a Primary population (LCFRB 2004 and NMFS 2013). Restoration efforts are coordinated by the Aquatic Coordination Committee (ACC), which consists of PacifiCorp and Cowlitz Public Utility District (PUD; hatchery, M&E, fish passage), WDFW (hatchery, M&E, fisheries management), NOAA-Fisheries (ESA recovery), Tribes, and other partners (hereafter, comanagers).

Prior to initiation of the upstream reintroduction program, the naturally spawning spring Chinook population in the North Fork Lewis River had been essentially eliminated (a few fish continued to spawn below the dam) and the remaining population consisted of adult returns from hatchery releases below Merwin Dam. The reintroduction program opened up 119 linear km of potentially accessible salmonid habitat above Swift Dam, and in the future may also include areas above Merwin and Yale dams (Figure 10), pending review by NOAA Fisheries and U.S. Fish and Wildlife Service (USFWS) pursuant to the Settlement Agreement (Pacificorp and Cowlitz PUD 2020).

From 2013-2019, an average of 1,603 spring Chinook returned to the Merwin adult trap and Lewis Hatchery ladder (Figure 11). The average run size was comprised of <50 natural-origin fish (range: 16-42) and 1,571 hatchery-origin fish (range: 547-2,871) from 2013-2019 (Pacificorp and Cowlitz PUD 2020). After hatchery broodstock needs are met (about 1,400 adults, including adults returning to the hatchery ladder), the number of adults available for the upstream reintroduction program has failed to meet the program goal of 3,000 adults (NORs + HORs). In several years, zero adults were transported upstream (Figure 11). This shortfall, in addition to low success in capturing and transporting naturally produced juveniles from the upper watershed to below the dams, has prevented the program from moving past the Recolonization phase.



Source: Pacificorp and Cowlitz PUD 2020.

## Figure 11. Adult spring Chinook returns to the North Fork Lewis River Merwin Trap (HORs and NORs shown separately), and adult spring Chinook transported above Swift Dam (HORs and NORs combined) as part of the reintroduction program.

The North Fork Lewis River spring Chinook population has been in the Recolonization phase since the upstream reintroduction program was initiated in 2013 (Pacificorp and Cowlitz PUD 2020). Prior to 2013, the program was in the Preservation phase.

## **Recovery Objectives**

Prior to initiation of the reintroduction program above Swift Dam, the primary purpose of the Lewis River spring Chinook hatchery program was to provide fish for harvest in the lower river below Merwin Dam as well as preserve the genetic integrity of the population.

Currently, program goals are to provide harvest opportunities in the lower river, broodstock for the hatchery program, and adults for the reintroduction program above Swift Dam. The hatchery program releases 1.35 million smolts into the lower river below Merwin Dam. The long-term goal of the upstream reintroduction program is to rebuild the naturally spawning population above Swift Dam (and potentially areas above Merwin and Yale Dams) so that it is self-sustaining (i.e., sufficient numbers of natural-origin adults return to the adult trap at Merwin Dam to fully utilize the available spawning habitat above the dams). Achieving this goal will require a substantial increase in the efficiency of the floating surface collector at Swift Dam, which is used to trap outmigrating smolts for transport and release below Merwin Dam.

The North Fork Lewis River Hatchery and Supplementation Plan (PacifiCorp and Cowlitz PUD 2020) notes,

"Although North Fork Lewis River hatcheries will continue to produce juveniles needed for the supplementation programs for the foreseeable future, there are many key questions that need to be addressed over the next five years to develop criteria for determining when these populations move from the Recolonization to the Local Adaptation phase, and how populations will be managed once they are in the Local Adaptation phase."

Because the program has not yet addressed phase transitions, the HSRG developed a set of hypothetical program phases, objectives, indicators, and triggers for Lewis River spring Chinook using the adult capacity method (Table 10). As noted above, the program has been in the Recolonization phase since the upstream reintroduction program was initiated in 2013, even though there were only a few naturally spawning spring Chinook in the North Fork Lewis River at that time.

Table 10.Hypothetical objectives, indicators, and triggers associated with each<br/>restoration phase for Lewis River Spring Chinook salmon. Objectives<br/>are adapted from Pacificorp and Cowlitz PUD (2020). Indicators and<br/>triggers are hypothetical and are intended to provide an example of<br/>how these criteria could be developed.

| Phase   | Objectives<br>(Hypothetical)  | Indicators<br>(Hypothetical)                              | Triggers for Phase Shifts:<br>Adult Capacity Method<br>(Hypothetical)  |
|---|---|---|--|
| Preservation<br>Prevent extinction.<br>Retain genetic and<br>life history diversity<br>of existing<br>population. | Hatchery program<br>provides a safety net.<br>Preserve genetic identity<br>of this spring Chinook<br>stock. | Adult abundance,<br>productivity, spatial<br>distribution | Initiate Recolonization phase<br>when upstream reintroduction<br>program initiated and hatchery<br>program is self-sufficient; new<br>habitat is capable of supporting<br>all life stages (egg-spawning<br>adult); and smolts can get out of<br>upper watershed. |

| Phase   | Objectives<br>(Hypothetical)  | Indicators<br>(Hypothetical)   | Triggers for Phase Shifts:<br>Adult Capacity Method<br>(Hypothetical)  |
|---|---|--|--|
| Recolonization<br>Increase natural<br>spawning<br>abundance and<br>spatial distribution.  | Repopulate suitable<br>habitat with all life stages<br>(pre-spawning to smolt).<br>The upstream<br>reintroduction program<br>prioritizes NORs but uses<br>HORs as needed to<br>recolonize available<br>habitat. | Adult abundance,<br>productivity, spatial<br>distribution  | Initiate Local Adaptation Phase<br>when NORs > 500, 50% of<br>spawning habitat utilized; R/S<br>>1.0 (requires improvements to<br>smolt capture facilities at dams).                         |
| Local Adaptation<br>Increase<br>abundance,<br>diversity and<br>distribution. Meet or<br>exceed VSP<br>criteria.   | Meet and exceed minimum<br>VSP abundance for NORs;<br>increase fitness,<br>reproductive success, and<br>life history diversity<br>through local adaptation.   | Adult abundance, pHOS,<br>productivity, spatial<br>distribution, life history<br>diversity (requires<br>improvements to smolt<br>capture facilities) | Terminate transport of HORs to<br>upstream spawning areas and<br>initiate Full Restoration Phase<br>when NORs > 1,500. Reduce<br>pHOS to <5%; 75% of spawning<br>habitat utilized; R/S >1.0. |
| <b>Full Restoration</b><br>Abundance,<br>productivity,<br>diversity, and<br>spatial distribution<br>achieve full<br>potential of the<br>restored habitat. | Maintain viable population<br>based on all VSP<br>attributes.   | Adult abundance, pHOS,<br>productivity, spatial<br>distribution, life history<br>diversity   |  |

## Phase Shifts: Adult Spawning Capacity Method

Adult spring Chinook spawning capacity in the North Fork Lewis River upstream of Swift Dam was estimated by EDT to be 2,981 under current (baseline) habitat conditions (PacifiCorp and Cowlitz PUD 2020). This is the program goal for the number of adult ocean recruits produced, but it does not account for harvest. The Minimum Viability Goal for North Fork Lewis River spring Chinook is 1,500 NORs, with a PNI > 0.67 (WDFW 2015). Thus, the phase shift triggers were developed based on a NOR target of 1,500 adult natural-origin returns. This is the trigger for the Full Restoration phase (Table 10).

The goal of the Recolonization phase is to reestablish a naturally spawning spring Chinook population upstream of Swift Dam. Currently, the hatchery program uses only hatcheryorigin broodstock. In the long-term, the plan is to integrate the hatchery program once the reintroduced population upstream of Swift Dam contributes more NORs than are needed for the transport program. The HSRG recommends using NORs (e.g., pNOB of 10%) as soon as possible in reintroduction programs, or initiating a small, well integrated program (separate from the current segregated harvest program) and using those returning fish to recolonize new habitat.

The program could move into the Local Adaptation phase when a five-year average of >500 NORs (33% of spawning capacity) return to the adult trap at Merwin Dam on the North Fork Lewis River (Table 10). When an average of 1,500 NORs return to the North Fork Lewis River, the population would be considered Fully Restored.

Modifications to overall hatchery production may be made as natural production from reintroduction efforts increases (as described in the Settlement Agreement). As natural production of spring Chinook upstream of Merwin Dam exceeds its threshold level (2,977 adults, based on the number of adult ocean recruits, or pre-harvest recruitment), hatchery production would be reduced on a 1:1 basis (Pacificorp and Cowlitz PUD 2020).

## **Reintroduction Strategies, Tradeoffs and Consequences**

The Hatchery and Supplementation Plan considered three strategies for reintroducing spring Chinook above Swift Dam, each of which is associated with benefits and risks (Table 11). Initially, the program focused on strategy 3, releasing hatchery juveniles upstream of Swift Dam. The goal was to allow juveniles to imprint on the spawning habitat above Swift Dam and migrate downstream naturally, where a Floating Surface Collector (FSC) at the head of Swift Dam would be used to capture juveniles. Juveniles would then be transported and released downstream of Merwin Dam. The FSC efficiency has been much lower than the target level (95%), resulting in far fewer hatchery juveniles being transported below Merwin than expected. Consequently, juvenile outplants have been suspended, and the program is instead releasing hatchery juveniles downstream of Merwin Dam and using strategies 1 and 2 to transport HOR and NOR adults upstream of Swift Dam.

| Sannon.                 |   |  |  |  |
|-------------------------|---|--|--|--|
| Reintroduction Strategy |   | Benefits   | Risks  |  |
| 1                       | Adult HORs from on-station releases transported upstream of Swift Dam                                       | Available immediately—resulting<br>NORs return within a generation.<br>Less opportunity for negative<br>ecological interactions <sup>1</sup> | Potentially less optimal spatial distribution of natural spawning. |  |
| 2                       | Adult NORs from juveniles<br>produced upstream of Swift<br>Dam; adults transported<br>upstream of Swift Dam | Initiate local adaptation process.<br>Less opportunity for negative<br>ecological interactions.  | Potentially less optimal spatial distribution of natural spawning. |  |

# Table 11.Benefits and risks associated with various reintroduction strategies<br/>upstream of Swift Dam for North Fork Lewis River spring Chinook<br/>salmon.

| Reintroduction Strategy |   | Benefits   | Risks  |  |
|-------------------------|---|--|--|--|
| 3                       | Juvenile HORs outplanted<br>upstream of Swift Dam | Potentially better spatial distribution of returning HOR spawners. | Downstream passage mortality due to<br>inefficiency of Floating Surface<br>Collector. NORs will return at least one<br>generation later (i.e., the colonization<br>will occur about 5 years later).<br>Ecological interactions during rearing<br>and outmigration. |  |

1 Intra-species competition may be particularly significant due to lack of nutrients until ecological functions have been restored.

The drawback to transporting adults upstream continues to be the low juvenile capture rate at the FSC at the head of Swift Dam. While spawning adults provide an ecosystem function by contributing nutrients to the upper watershed, and naturally produced juveniles imprint on the area, too few juveniles survive during outmigration to produce a meaningful number of natural-origin adult returns. Should collection of upper river juveniles improve, there is a real possibility of moving into the Local Adaptation phase. One trigger could be reaching a specific juvenile collection rate at the FSC to allow the reintroduced population to be sustainable. This would be reflected in an improving R/S value. In the meantime, any excess hatchery returns allow for fishing in the lower Lewis River.

The program prioritizes hatchery broodstock collection over the reintroduction program. Due to low numbers of adult returns, the adult transport goal for the reintroduction program has not been met. The upstream reintroduction program is part of the recovery strategy for spring Chinook identified by NMFS (NMFS 2013).

## 3.5 ELOCHOMAN/SKAMOKAWA FALL CHINOOK SALMON

## **Background and Decision Framework**

The Elochoman River and Skamokawa Creek are located in southwestern Washington State and empty into the lower Columbia River (Figure 12). The Elochoman and Skamokawa basins comprise 190 km<sup>2</sup>, and fall Chinook spawn in approximately 48 linear km of habitat in the lower Elochoman River and Skamokawa Creek (WDFW, pers. comm.). The Elochoman and Skamokawa fall Chinook salmon population is part of the Lower Columbia River Chinook salmon ESU, which was listed as threatened under the ESA in 1999 and has been identified as a Primary population (NMFS 2013). Restoration efforts are coordinated by WDFW (hatchery, M&E, fisheries management), NOAA-Fisheries (ESA recovery), and other partners (hereafter, comanagers).

Historically, the Elochoman River had a substantial fall Chinook population, which was estimated to be 2,000 fish in 1950 (WDF 1951). The Elochoman Hatchery was constructed in 1953, and since then, the naturally spawning population has been dominated by hatchery-origin fish. The hatchery released about 4 to 6 million fall Chinook smolts annually into the Elochoman River from 1995-1997, and 2 million smolts from 1998-2008 (WDFW 2015). In

the early 2000s, the run size (including returns to the Elochoman River and Skamokawa Creek) averaged more than 5,000 fish (Figure 13) and consisted mostly of hatchery-origin returns. The spawning escapement included many strays from other Lower Columbia River hatcheries, including Youngs Bay, which has a history of using out-of-basin (Rogue River) broodstock (HSRG 2009). The HSRG recommended that because of the importance of this Primary population to the ESU<sup>7</sup>, the hatchery program should be reduced in size to about 200,000 smolts (HSRG 2009). Following consideration of several hatchery reform alternatives, including renovating the Elochoman Hatchery, WDFW decided to discontinue the hatchery program in 2009 to allow the naturally spawning population to rebuild.



Source: LCRFRB 2004.

## Figure 12. Location of the Elochoman and Skamokawa basins within the Lower Columbia River Basin.

A recovery phase was not designated in WDFW's Lower Columbia plan (WDFW 2015) or in the Mitchell Act EIS (NMFS 2014, 2017). More recently, WDFW identified the Elochoman as being in the Local Adaptation phase (Murdoch and Marston 2020), based on NOR spawners occupying all expected usable habitat. However, empirical analysis of the relationship

<sup>&</sup>lt;sup>7</sup> Designated as a Primary population in the Recovery Plan (NMFS 2005) and WDFW's Lower Columbia plan (WDFW 2015).

between spawner abundance and recruitment is not yet complete, and the population remains at a severely depressed abundance. For the purposes of this case study, we suggest the Elochoman/Skamokawa fall Chinook population may be somewhere between the Preservation phase and Local Adaptation phase due to very low abundance of natural-origin spawners.



# Figure 13. Elochoman River/Skamokawa Creek fall Chinook spawning escapement from 1995-2009, including unknown proportions of HOR and NOR spawners.<sup>8</sup>

## **Recovery Objectives**

WDFW (2015) identified Minimum Viability goals for the Elochoman population of 1,500 naturally spawning fish and pHOS < 5%. Reaching this pHOS goal would likely depend on removing hatchery-origin strays using a weir in the lower Elochoman River. From 2012-2018, total spawning escapement to the Elochoman and Skamokawa drainages averaged 391 (range: 59-223), and pHOS averaged 63% (Figure 14). The majority of hatchery strays to Skamokawa Creek come from the Clatskanie Hatchery program (Oregon). Additionally, a conservation hatchery program could be considered to facilitate achieving recovery goals. The purpose of an Elochoman/Skamokawa recovery program would be to reestablish a selfsustaining naturally spawning fall Chinook population in the basin. The HSRG developed a set of hypothetical program phases, objectives, indicators and triggers for Elochoman/Skamokawa fall Chinook based on population goals identified by WDFW (2015) (Table 12). Although we have identified interim phase triggers based on the recovery plan, WDFW initiated intensive adult monitoring of this population in 2010 and could use the results of this monitoring program to implement the empirical methods described in Section

<sup>&</sup>lt;sup>8</sup> Source: <u>https://fortress.wa.gov/dfw/score/score/species/population\_details.jsp?stockId=1508</u>



2.4.3 to update phase triggers by determining the NOR spawner abundance needed to maximize recruitment, particularly through the freshwater life stages.

- Figure 14. Elochoman/Skamokawa fall Chinook spawning escapement from 2010-2018.<sup>3</sup>
- Table 12.Hypothetical objectives, indicators, and triggers associated with each<br/>restoration phase for Elochoman/Skamokawa Fall Chinook salmon.<br/>Indicators and triggers are hypothetical and are intended to provide an<br/>example of how these criteria could be developed.

| Phase  | Objectives<br>(Hypothetical)  | Indicators<br>(Hypothetical)                                     | Triggers for Phase Shifts: Adult<br>Capacity Method ( <i>Hypothetical</i> )  |
|--|---|--|--|
| Preservation<br>Prevent extinction.<br>Retain genetic and life<br>history diversity of<br>existing population. | Preserve genetic identify<br>of this Tule fall Chinook<br>stock. Develop appropriate<br>sized conservation<br>hatchery program. | Adult abundance,<br>productivity in the<br>hatchery.             | Initiate Recolonization phase when<br>excess adults/juveniles are<br>available and habitat can sustain<br>all life stages (adult to adult).  |
| Recolonization<br>Increase natural<br>spawning abundance<br>and spatial distribution.                          | Repopulate suitable<br>habitat with all life stages<br>(pre-spawning to smolt).   | Adult abundance,<br>pHOS, productivity,<br>spatial distribution. | Adopt interim Local Adaptation<br>Phase trigger when NORs > 500,<br>50% of spawning habitat utilized,<br>R/S >1.0. Implement monitoring<br>and empirical methods to validate<br>interim phase trigger. |

| Phase   | Objectives<br>(Hypothetical)  | Indicators<br>(Hypothetical)  | Triggers for Phase Shifts: Adult<br>Capacity Method (Hypothetical)  |
|---|---|---|---|
| Local Adaptation<br>Increase abundance,<br>diversity and<br>distribution. Meet or<br>exceed VSP criteria.   | Meet and exceed minimum<br>VSP abundance for NORs;<br>increase fitness,<br>reproductive success, and<br>life history diversity<br>through local adaptation. | Adult abundance,<br>pHOS, productivity,<br>spatial distribution, life<br>history diversity. | Initiate Full Restoration Phase<br>when NORs > 1,500. Reduce<br>pHOS to <5%; 75% of spawning<br>habitat utilized, R/S >1.0. |
| <b>Full Restoration</b><br>Abundance,<br>productivity, diversity,<br>and spatial distribution<br>achieve full potential of<br>the restored habitat. | Maintain viable population<br>based on all viable<br>salmonid population (VSP)<br>attributes.   | Adult abundance,<br>pHOS, productivity,<br>spatial distribution, life<br>history diversity. |   |

## Phase Triggers: Adult Spawning Capacity Method

The phase shift triggers were developed based on a recovery goal of 1,500 natural spawners, which is the Minimum Viability goal identified by WDFW (2015). This is the trigger to reach the Full Restoration phase (Table 12).

In its 2009 Columbia Basin Review, the HSRG recommended that a small conservation hatchery (~200,000 smolts), along with reduced harvest rates on unmarked (NOR) fish and removal of strays using a weir in the lower Elochoman River, were the most appropriate tools to restore the naturally spawning population (HSRG 2009). As discussed below, we suggest this may still be an appropriate strategy to restore the natural spawning population, which has declined sharply since the hatchery program was discontinued in 2009.

We do not suggest a specific NOR abundance trigger to move out of the Preservation phase. Rather, the program could move into the Recolonization phase once the habitat supports all life stages and surplus adults/juveniles from the hatchery program are available (i.e., the hatchery program is self-sustaining using local broodstock). During the Recolonization phase, naturally spawning fish are expected to produce increasing numbers of NORs. The program could move into the Local Adaptation phase when a five-year average of >500 NORs (33% of the Minimum Viability goal) return to Elochoman/Skamokawa subbasins. This is an interim trigger for moving between Recolonization and Local Adaptation phases. However, the intensive monitoring program implemented in the basin should allow WDFW to empirically revisit this trigger to verify the number of spawners needed to maximize the use of available habitat. When an average of 1,500 NORs return to the spawning grounds, the population would be considered Fully Restored.
#### **Restoration Strategies, Tradeoffs and Consequences**

The Lower Columbia Conservation and Sustainable Fisheries Plan (WDFW 2015) considered several hatchery reform actions, each of which addresses various VSP parameters and impacts the restoration process (Table 13). Actions 1, 2, 3, 6 and 7 have been completed. Action 5 has not yet been addressed.

Action 4, which would establish a small supplementation program to enhance conservation of the population, is being considered. The HSRG's Columbia Basin Review (2009) considered an alternative to establish a small integrated conservation hatchery with 190,000 smolts released annually. The HSRG's analysis found this approach would result in almost twice as many NORs as the no hatchery alternative (923 NORs with the small conservation hatchery vs. 540 NORs with no hatchery).

In addition to the hatchery reform actions, the Plan considered seven harvest reform actions. Completed actions include reducing the harvest rate from historical levels of up to 60%. The harvest rate is now adjusted annually based on abundance, which protects natural-origin fish from incidental harvest mortality in low abundance years. Mark-selective fisheries have been implemented in the ocean and lower Columbia River in some years, and alternative gear studies are underway. The terminal fishery is also mark-selective.

High harvest rates on lower Columbia River fall Chinook may make it difficult to transition to the Local Adaptation phase. First generation NORs (F1 generation progeny of naturally spawning HORs) have not realized the benefits of local adaptation and are unlikely to be very productive in the watershed. Without a reduced harvest rate, any surviving fish cannot return to begin the adaptation process.

| Table 13. | 213. Benefits and risks associated with various restoration strategi |  |  |  |
|-----------|--|--|--|--|
|           | Elochoman River fall Chinook salmon.                                 |  |  |  |
|           |  |  |  |  |

| Hatchery Reform Actions |   | Abundance | Productivity | Spatial<br>Distribution | Diversity |
|-------------------------|---|-----------|--------------|-------------------------|-----------|
| 1                       | Establish Elochoman Basin as a refuge for wild fall<br>(tule) Chinook   | Х         | Х            | Х                       | х         |
| 2                       | Eliminate hatchery fall (tule) Chinook smolt releases<br>in Elochoman Basin to improve juvenile productivity        |           | Х            | Х                       | Х         |
| 3                       | Annually operate temporary weir in lower Elochoman<br>River to control hatchery fish on natural spawning<br>grounds |           | Х            |                         | Х         |

| Hatchery Reform Actions |  | Abundance | Productivity | Spatial<br>Distribution | Diversity |
|-------------------------|--|-----------|--------------|-------------------------|-----------|
| 4                       | Evaluate and determine whether emergency juvenile supplementation program is necessary   | Х         | Х            | Х                       | Х         |
| 5                       | Investigate feasibility of capturing naturally produced<br>juvenile fall Chinook for transport and release into the<br>mainstem Columbia River to reduce predation | Х         | Х            |                         |           |
| 6                       | Provide adult passage at hatchery barrier at<br>Elochoman River to improve escapement of wild fish   | Х         | Х            | Х                       |           |
| 7                       | Improve adult passage at hatchery intake on Beaver<br>Creek to improve escapement of wild fish   | Х         | Х            | X                       |           |

### 3.6 SNOW CREEK COHO SALMON

#### **Background and Decision Framework**

The hatchery component of the Snow Creek Coho restoration program was conducted from 1998 to 2005 and is an example of a cooperative effort between State, Federal, and Tribal entities. WDFW partnered with two volunteer groups, Wild Olympic Salmon (WOS) and North Olympic Salmon Coalition (NOSC), to carry out the Coho recovery effort at Snow Creek. The Point No Point Treaty and Jamestown S'Klallam tribes assisted in program planning.

Snow Creek is located in the northeastern part of the Olympic Peninsula in Washington State. The stream empties into the southern end of Discovery Bay on the Strait of Juan de Fuca. The Snow Creek basin is approximately 50 km<sup>2</sup> with 16 linear kilometers of habitat accessible to anadromous salmonids. Andrews Creek in the Crocker Lake subbasin is a major tributary and has wild populations of steelhead, cutthroat, Chum, and Coho salmon.

In 1976, Washington Department of Game installed a weir in Snow Creek at rkm 1.3 to monitor adult returns. From 1976 through the early 1980s, 600 to 1,400 adult Coho

returned annually to the stream (Figure 15)<sup>9</sup>. An alarming decline in abundance of Coho returning to Snow Creek was observed in the early 1990s. Because of this decline, WDFW listed the Snow Creek Coho population as "critical" in its 1992 Salmon and Steelhead Stock Inventory (SASSI). It was the only Puget Sound or coastal Coho population given this designation.



# Figure 15. Adult Coho returns to Snow Creek from 1976 to 2011. Breaks in the lines represent years where adult counts were not made.

#### **Recovery Objectives and Phase Triggers**

The purpose of the Snow Creek Coho restoration program was conservation and rebuilding of the naturally spawning population. Although not formalized at the time, retrospective objectives for each recovery phase as they might have been construed are described in Table 14. The initial program goal was to prevent extinction and retain the genetic diversity of the existing population through a hatchery-based effort. The long-term goal was to rebuild stock abundance to a healthy abundance. Specific potential phase triggers based on measures of abundance and productivity are summarized in Table 14 and described in more detail in the text below.

<sup>&</sup>lt;sup>9</sup> In Figure 15, the designations for the brood year lines are based on the first year that adult Coho originating from an individual brood line were counted at the Snow Creek weir. The solid green line represents the 1976 line, the dashed red line equals the 1977 line, and the black line equals the 1978 line.

| Tett ospective since triggers were not considered |  |   |   |   |  |
|---|--|---|---|---|--|
|   | Phase  | Objectives  | Indicators  | Retrospective Triggers  |  |
| Preservation, Phase 1<br>Determine preservation   |  | Prevent extinction  | Adult abundance and life history.   | Population declared critical in<br>1992 SASSI   |  |
|   | need and support   |   |   | <ul> <li>Information available on<br/>population constraints</li> <li>Weir in place for monitoring</li> <li>Agreement and participation of<br/>co-managers</li> </ul>   |  |
|   | Preservation,<br>Phase 2<br>Establish regulatory<br>protections. establish<br>hatchery population<br>to prevent extinction | Secure the genetic<br>identity and diversity of<br>the native population<br>until habitat can support<br>survival of all life stages  | <ul> <li>Establish regulatory<br/>protections</li> <li>Establish hatchery<br/>program. Limit program to<br/>nine generations,<br/>pNOB=100%.</li> <li>Establish habitat<br/>improvements</li> </ul> | <ul> <li>Harvest reductions<br/>implemented through<br/>US/Canada Salmon Treaty</li> <li>Habitat improvements including<br/>removal of non-native species<br/>in Crocker Lake</li> <li>Ability to isolate and spawn<br/>adults in Snow Creek habitat</li> <li>Availability of Hurd Creek<br/>hatchery for incubation/rearing</li> </ul> |  |
|   | Recolonization<br>Begin release of<br>hatchery-produced<br>eggs to habitat to<br>evaluate fitness.                         | Re-populate suitable<br>habitat from eyed egg to<br>smolt outmigration (all<br>life stages)   | <ul> <li>Successful spawning and incubation of eggs.</li> <li>Successful thermal marking of eggs.</li> <li>Successful (blank) coded wire tagging of pre-smolt release groups</li> </ul>             | Release of eyed eggs and<br>juveniles to habitat; 2/3rd to<br>RSIs, 1/6th to fry release in<br>October, 1/6th as pre-smolts in<br>February.   |  |
|   | Local Adaptation   | <ul> <li>Meet and exceed<br/>projected spawner<br/>abundance for natural-<br/>origin spawners.</li> <li>Increase fitness,<br/>reproductive success<br/>and life history diversity<br/>through local adaptation</li> </ul> | Fish spawning in habitat<br>and producing juveniles.<br>pNOB = 100%; pHOS = 0;<br>PNI =1.0  | <ul> <li>Local Adaptation Phase to<br/>include passage of all adults<br/>not needed for broodstock<br/>above weir to spawn naturally.</li> <li>Spawned adults surveyed<br/>(otoliths and scales) to<br/>determine success of release<br/>strategies.</li> </ul>   |  |
|   | Full Restoration   | Population recovery.<br>Long-term adaptive<br>management to<br>maintain viable<br>population, in terms of<br>all VSP parameters   | Intervention program<br>scheduled to last three<br>generations with<br>monitoring of smolt<br>outmigration and adult<br>returns for all release<br>strategies.                                      | <ul> <li>Monitoring showed all life-stage release strategies to be successful.</li> <li>Adult returns were above preprogram level</li> <li>Intervention terminated at two generations</li> </ul>  |  |

# Table 14.Example of objectives, indicators, and triggers associated with each<br/>phase of restoration for Snow Creek Coho program. Note: Table is<br/>retrospective since triggers were not considered during program.

#### **Recovery Strategies and Monitoring and Evaluation Approach**

WDFW and Tribal co-managers identified three factors that appeared to be responsible for the temporal collapse of Snow Creek Coho: (1) over-harvest in US and Canadian fisheries, (2) presence of warm water fishes in Crocker Lake including illegally introduced northern pike, and (3) degraded freshwater habitat. The Coho recovery effort at Snow Creek began in 1998. From the initial SASSI (1992) report to 1998, a series of events and management decisions furthered the preservation and eventual enhancement of this stock. First, marine harvests of naturally produced Coho were substantially reduced due to the US/Canada Pacific Salmon Treaty and the advent of mass marking and associated selective fisheries. Second, WDFW adopted the Wild Salmonid Policy, which committed the agency to preserve and rebuild wild stocks to self-sustaining and harvestable levels. Third, several habitat restoration projects in the Andrews Creek subbasin were completed. And fourth, WDFW took emergency action to eradicate illegally planted northern pike from Crocker Lake.

The Snow Creek Coho population was chosen as a target stock for recovery actions for three principal reasons. First, adult returns from 1990-1997 (SASSI 1992; and Figure 15) showed the population was headed toward extinction without some form of intervention. Second, the permanent weir in the lower portion of the stream made it possible to evaluate population responses to any implemented recovery actions. This was an important consideration because other Coho populations in southern Puget Sound, coastal Washington (e.g., Willapa Bay) and in the Lower Columbia were also depressed and possibly in jeopardy of extirpation. Managers concluded that if carefully monitored and evaluated, the efficacy of strategies used at Snow Creek could provide insights into how Coho recovery actions could be conducted elsewhere. And third, the support and participation of two salmon restoration groups; Wild Olympic Salmon (WOS), and North Olympic Salmon Collation (NOSC) meant that volunteers were available to help perform monitoring and data collection tasks under WDFW supervision. Such public support is crucial, and given the scarcity of monetary resources that can be used for salmonid preservation and conservation, the labor and contributions of motivated public citizens is often essential.

**Hatchery Intervention**. Several key decisions were made prior to the inception of the Snow Creek hatchery program. One was to use hatchery incubation and rearing conditions to enhance egg-to-juvenile survival rates. Another was to exclusively use Snow Creek Coho as broodstock. Importing Coho eggs or adults from nearby stocks was prohibited. A time limit of three-generations of hatchery intervention (9 brood years) was also established. Because of the precarious status of the stock's three brood lines, a decision was made to use every adult returning to the stream in 1998 (77 Line), 1999 (78 Line), and 2000 (76 Line) as broodstock. There was some speculation that the 76 Line was already extinct and that no adults would return to the stream in 2000. Even under that circumstance, the rule of no imports from outside stocks was to be enforced. Fortunately, adults from the 76 Line did return and their offspring were incorporated into the program. An objective of using 25 males and 25 females as broodstock during each spawning year was also established. Jacks (2-yr-old males) were incorporated into the broodstock (~10%) to facilitate genetic exchange among the brood lines. When adult abundance levels exceeded 100 fish,

individuals not saved for broodstock purposes were passed over the weir and allowed to spawn in nature. At this abundance level (i.e.,  $\geq$  100 returning adults) attempts were made to obtain brood fish throughout the entire migration period.

**Mating Protocol**. There is no hatchery or incubation facility at Snow Creek. To meet pathogen transmission concerns raised by State and Tribal staff, gametes were collected at Snow Creek. Fish selected for broodstock were captured at the weir and held in 20-cm diameter x 92 cm long perforated PVC tubes (1 fish/tube) that were placed in the weir's adult trap. The maturation status of each fish was regularly evaluated by WDFW fish culturists. Using a factorial mating scheme rather than a single-pair mating scheme maximized the likelihood of preserving the genetic diversity of the population. Gametes were placed into insulated coolers with ice for transfer and eventual fertilization at WDFW's Hurd Creek Hatchery located 23 miles away from Snow Creek.

Three recovery treatments were implemented, each having a different level of hatchery intervention. About 64% of the eyed eggs obtained from every female were placed into Remote Site Incubators (the RSI treatment). Two RSIs were established in Snow Creek and one was installed in Andrews Creek above Crocker Lake. Upon emergence, fry directly entered Snow or Andrews Creek. The leftover eggs from each female (~36%) remained at Hurd Creek to complete the incubation period. Half of the fry produced from those eggs were reared at the hatchery for seven months and then released into Crocker Lake as presmolts in October. This is hereafter referred to as the "OCT" treatment. Releasing the fish in October allowed the fish to acclimate for an extended period in a natural setting, experience the winter solstice in the basin, and completely recover from any stresses due to transfer or release. The remaining fish were reared for an additional three months and released as pre-smolts into Crocker Lake in early February, the "FEB" treatment. Because they were released as pre-smolts, fish in the FEB treatment were expected to fully recover from stresses due to their release into Crocker Lake, acclimatize to natural conditions, and imprint on Snow Creek waters prior to emigration. Crocker Lake was chosen as the release site for fish in both the OCT and FEB treatments because it was known to be an important over-wintering and rearing location for Coho.

**Marking and Tagging.** All fish incubated at the Hurd Creek Hatchery received thermal marks in their otoliths. Separate pre-hatch codes were induced into the eyed eggs destined for Snow and Andrews Creek RSIs. Eggs used for the OCT and FEB treatments received the same thermal mark, which differed from the ones applied to the RSI fish. Blank coded-wire tags (CWTs) were used to differentiate fish representing the OCT and FEB treatments. CWTs were applied to the snout of every fish receiving the OCT treatment and tags were applied to the adipose fin area of the FEB fish. Separate sets of thermal marks were used on fish originating from different brood years.

In combination, the presence of thermal marks and the use of CWTs on the program's fish made it possible to estimate the freshwater survival, abundance, migration timing, size (FL), and age-at-smolting of the juvenile fish originating from each treatment. The tags and

thermal marks were also utilized to identify the origin of adult Coho returning to Snow Creek. The sex, FL, and arrival timing of each fish captured at the weir was recorded. Otoliths were collected on all the fish used as broodstock, and extensive stream surveys were performed above and below the weir to collect additional otoliths from as many carcasses as possible. Scales were obtained from adults as they were passed over the weir. Data from otoliths and scales were used to assign ages, identify life history strategies used by project fish, and as the project proceeded, detect the occurrence and abundance of natural-origin adults—progeny from the program's RSI, OCT, and FEB treatments.

#### **Results of the Recovery Program**

Originally, the hatchery intervention program was scheduled to last for nine years, or three generations. However, Coho returns produced from the program's first three brood years (411 to 580 fish) were abundant enough that in 2001, 2002, and 2003 any Coho not used as hatchery broodstock were passed upstream and allowed to spawn in nature. Because the abundance of adults returning from all three brood lines continued to increase (Figure 15), hatchery intervention was terminated after the 2003 brood year, one generation or three years earlier than expected.

The long-term effects of the Snow Creek Coho restoration effort on smolt abundance by out-migration year are shown in Figure 16. The removal of northern pike and warm water fishes from Crocker Lake and possible beneficial effects of habitat restoration in the basin created conditions that allowed Coho to become, once again, self-sustaining in the basin.



# Figure 16. The number of smolts leaving Snow Creek from 2000 to 2012. Smolts from the Remote Site Incubator (RSI), OCT, and FEB treatments were present in out-migration years 2000-2006. Natural-origin smolts were present in out-migration years 2003-2012.

The proliferation of smolt life histories in the early brood years (1998, 1999, and 2000) of the recovery program generated a diverse array of adult life histories and ages at return. The predominant life histories in Puget Sound Coho are the 1.0 (jack) and 1.1 (3-year old) strategies. Adult Coho using alternative strategies (e.g., 0.1, 2.0, 2.1, and 3.0) were generated by the recovery treatments. Their occurrence, however, decreased in tandem with decreases in age at smolting. Starting in 2001, conditions favoring the production of 2.0 and older smolts had changed, and <2% of the smolts produced from a brood year, regardless of treatment origin, emigrated at age 2.0 or older. The occurrence of the 0.1, 1.0, 2.1, and 3.0 strategies provide potential avenues of genetic exchange among the three brood lines returning to Snow Creek. The presence of these types of adults may increase the effective population size (N<sub>e</sub>) and the effective number of breeders (N<sub>b</sub>) in a brood line— important attributes in populations with few returning adults. The three treatments implemented at Snow Creek each contributed to the recovery of the population and acted as important backups to one another in case one or more experienced a catastrophic failure.

#### Some Lessons to Consider from the Snow Creek Coho Program

- *A priori* identification of limiting factors is critical. All else being equal, recovery actions should be implemented where management or administrative actions can alleviate impediments preventing the maintenance of self-sustaining populations.
- Hatcheries can serve as important agents in salmonid conservation.
- Stock recovery is possible but depends upon public support.
- Monitoring and evaluation are essential. Parentage-based tagging, thermal marks, and other tags and marks should be applied to all hatchery-origin fish used in recovery programs. The path to improved recovery methods depends upon empirical data.
- If limiting factors prove to be intractable, it may be a better to use scarce recovery resources elsewhere. Consider placing time limits on recovery efforts.
- Utilize multiple recovery treatments if possible. Employ the same strategies across multiple years to allow statistical comparisons among the treatments.
- Use native fish in recovery actions, even if they are at extremely low levels. Resist the temptation to import non-native conspecifics. If native fish are not available, use mixtures of adjacent conspecific populations that can accept continued adult gamete removals.
- Although still under debate, when making artificial crosses, the factorial design, as
  opposed to the one-to-one mating strategy, provides the best chance for every
  broodfish to contribute to succeeding generations. As noted above, even Puget Sound
  Coho that largely use the 1.1 life history strategy appear to have an innate capacity to
  take up alternative maturation schedules that facilitate genetic exchanges across brood
  year lines. This capacity will increase the effective population size and effective breeding
  number in populations undergoing restoration. Polyploidy will also help reduce the
  effects of inadvertent inbreeding that the one-to-one strategy is designed to prevent.
- Do not underestimate the resiliency of salmonids—their capacity to express unexpected life-history strategies is robust and key in recovery actions.

• Anticipate the effects of climate change on populations targeted for restoration. Will modeled changes in precipitation patterns and water temperatures be untenable in the near future for salmonid populations targeted for recovery?

## 4.0 CONCLUSIONS AND RECOMMENDATIONS

In this white paper, we provide updated pHOS and PNI recommendations and outline an approach and methods to set phase triggers for the four recovery phases. Previous HSRG reports did not recommend specific pHOS or PNI targets in the Preservation or Recolonization phases. The HSRG reasoned that balancing genetic and demographic concerns would likely occur on a case by case basis and, to some extent, reflect policy decision by managers. However, it became apparent that if there were no pHOS or PNI targets during these phases, there could be an incentive to stay in the Recolonization phase indefinitely rather than move to the Local Adaptation phase. Remaining in an early phase has the potential to increase the time to Local Adaptation as well as facilitate unintended genetic consequences.

Our approach to setting phase triggers relies on the methods of Structured Decision Making following the basic steps: framing the decision, developing objectives, and evaluating consequences and tradeoffs of various scenarios. We describe three methods for setting phase triggers based on adult NOR abundance: 1) adult spawning capacity, 2) in the case of habitat restoration programs, the percentage of adult and juvenile habitat available or being utilized, and 3) empirical methods (e.g., spawner-recruit analysis).

These approaches and methods are illustrated using case studies to document how recovery phases and triggers have been applied or could be applied to salmonid populations using established recovery goals and hypothetical recovery phase identification and triggers. The case studies range from small recovery projects to large, complex programs affecting entire drainages and involving multiple co-managers. We also present a case study of a fully recovered population which met its recovery goals after a hatchery intervention. Each case study includes a discussion of the trade-offs evaluated when identifying restoration strategies.

Anadromous fisheries managers overseeing population recovery programs face a range of ecological conditions and management challenges. Despite these differences, the population case studies provide several lessons for salmon restoration programs:

• The purpose and objectives of restoration programs should be clearly defined by comanagers and stakeholders. This includes identifying factors causing decline and potential recovery actions.

- If a conservation hatchery is used as part of the recovery program, it should be operated consistent with the overall recovery goals for the population and should consider genetic and demographic risks.
- Phase transitions should occur based on measureable changes in population status (e.g., VSP metrics). Revisiting phase triggers every 2-3 fish generations helps ensure program objectives and management strategies are realistic and are addressing factors causing decline.
- Populations dominated by hatchery-origin spawners often remain in the Preservation and Recolonization phases for many years, resulting in loss of genetic diversity and reduced productivity and fitness, even when habitat is restored. Managers should have a clear plan to transition to the Local Adaptation phase, which includes reducing pHOS via selective harvest or fewer hatchery releases.
- Monitoring and evaluation programs that provide information to evaluate progress toward meeting phase triggers are essential. Marking all hatchery-origin fish is essential to managing pHOS and broodstock selection and implementing selective harvest programs. Enumeration of spawners (NORs and HORs), smolt production, and natural-origin recruitment is needed to refine capacity estimates for the watershed and track progress toward recovery goals.

Once managers complete the process of identifying management objectives, indicators, and triggers for the four recovery phases, the next step is to develop a decision-making framework to make annual decisions about hatchery and harvest management and evaluate progress toward goals. The HSRG suggests using decision support tools such as the All-H Analyzer (AHA) to capture assumptions about the four Hs: habitat, harvest, hatcheries, and passage through the hydrosystem (HSRG 2020). The AHA tool allows managers to explore the potential outcomes of a variety of hatchery and harvest management strategies and assumptions about the Hs. In addition, tools such as the HSRG's In Season Implementation Tool (ISIT) help managers organize status and trends data and set management targets for the upcoming year (HSRG 2017).

# **5.0 References**

- Ackerman, M. W., B. K. Hand, R. K. Waples, G. Luikart, R. S. Waples, C. A. Steele, B. A. Garner, J.
   McCane, and M. R. Campbell. 2017. Effective number of breeders from sibship
   reconstruction: empirical evaluations using hatchery steelhead. Evol Appl 10:146-160.
- Anderson, J. and A. Hoffmann. 2017. Elwha River dam removal, fish status update, and fishing moratorium. Presentation to the Washington Fish and Wildlife Commission.
   <u>https://wdfw.wa.gov/sites/default/files/about/commission/meetings/2017/09/sep0817</u>
   <u>14 presentation.pdf</u>

 Anderson, J. H., K. I. Warheit, B. E. Craig, T. R. Seamons, and A. H. Haukenes. 2020. A review of hatchery reform science in Washington State. Washington Department of Fish and Wildlife; Final report to the Washington Fish and Wildlife Commission, January 23, 2020. Available at: https://wdfw.wa.gov/sites/default/files/publications/02121/wdfw02121\_0.pdf.

Antao, T., T. Cosart, B. Trethewey, R. S. Waples, M. W. Ackerman, G. Luikart, and B. K. Hand. 2020. AgeStrucNb: Software for Simulating and Detecting Changes in the Effective Number of Breeders (N<sub>b</sub>). Journal of Heredity.

- Atlas, W. I., T. W. Buehrens, D. J. F. McCubbing, R. Bison, and J. W. Moore. 2015. Implications of spatial contraction for density dependence and conservation in a depressed population of anadromous fish. Canadian Journal of Fisheries and Aquatic Sciences 72:1682-1693.
- Barrowman, N. J., R.A. Myers, R. Hilborn, D.G. Kehler, and C.A. Field. The variability among populations of coho salmon in the maximum reproductive rate and depensation. Ecological Applications, 13(3), 2003, pp. 784–793.
- Berejikian, B. A., and D. M. Van Doornik. 2018. Increased natural reproduction and genetic diversity one generation after cessation of a steelhead trout (*Oncorhynchus mykiss*) conservation hatchery program. Plos One 13:e0190799.
- 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. DOI: 10.7289/V5/TMNWFSC-140.
- Busack, C. 2015. Extending the Ford Model to three or more populations. NMFS Sustainable Fisheries Division, Portland, OR.
- Campbell, N. R., C. Kamphaus, K. Murdoch, and S. R. Narum. 2017. Patterns of genomic variation in Coho salmon following reintroduction to the interior Columbia River. Ecol Evol 7:10350-10360.
- CCT (Confederated Tribes of the Colville Reservation). 2004. Chief Joseph Dam Hatchery Program Master Plan. Vol. 1, 203 p. Confederated Tribes of the Colville Reservation, Nespelem, Washington.
- CCT. 2007. Chief Joseph Dam Hatchery Program Step 2 Submittal. 166 p. Confederated Tribes of the Colville Reservation, Nespelem, Washington.
- CCT. 2009. Chief Joseph Dam Hatchery Program Monitoring and Evaluation Plan for Summer/Fall Chinook Salmon. November 2009. 102 p. Confederated Tribes of the Colville Reservation, Nespelem, Washington.

- CCT. 2020. Chief Joseph Dam Hatchery Program In-season Implementation Tool (ISIT). July 2020. Confederated Tribes of the Colville Reservation, Nespelem, Washington.
- Chilcote, M.W., K.W. Goodson, and M.R. Falcy. 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.
- Chilcote, M.W., K.W. Goodson, and M.R. Falcy. 2013. Corrigendum: Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. Canadian Journal of Fisheries and Aquatic Sciences 70:513-515.
- Christie, M. R., M. L. Marine, R. A. French, R. S. Waples, and M. S. Blouin. 2012. Effective size of a wild salmonid population is greatly reduced by hatchery supplementation. Heredity (Edinb) 109:254-260.
- Cochran-Biederman, J. L., K. E. Wyman, W. E. French, and G. L. Loppnow. 2015. Identifying correlates of success and failure of native freshwater fish reintroductions. Conservation Biology, 29:175-186.
- Cooney, T. 2013. Snake River fall Chinook population status update. PowerPoint presentation at the Lower Snake River Compensation Program review, August 2013. NOAA Fisheries.
- Cuenco, M. L. 1994. A model of internally supplemented population. Trans. Am. Fish. Soc. 123:277-288.
- DOI (U.S. Department of the Interior), NMFS (National Marine Fisheries Service), and Lower Elwha Klallam Tribe. 1995. Elwha River ecosystem restoration. Final Environmental Impact Statement, June 1995. Olympic National Park, Port Angeles, Washington. Online at http://www.nps.gov/olym/elwha/docs/eis0695/eis-0695toc.htm.
- Evans, M. L., A. E. Kohler, R. G. Griswold, K. A. Tardy, K. R. Eaton, and J. D. Ebel. 2020. Salmonmediated nutrient flux in Snake River Sockeye salmon nursery lakes: the influence of depressed population size and hatchery supplementation. Lake and Reservoir Management 36(1):75-86.
- FAO. 1996. Food and Agriculture Organization. Precautionary approach to capture fisheries and species introductions. Elaborated by the technical consultation on the Precautionary Approach to capture fisheries (including species introductions), 6–13 June 1995, Lysekil, Sweden. FAO Tech. Guidelines Responsible Fish. No 2. Garcia, S. http://www.fao.org/3/W1238E00.htm.
- FERC (Federal Energy Regulatory Commission). 1993. Proposed Elwha (FERC No. 2683) and Glines Canyon (FERC No. 588) hydroelectric projects, Washington. Office of Hydropower Licensing (now Division of Hydropower Licensing within the FERC Office of Energy Projects). Federal Energy Regulatory Commission, Washington, D.C.

- Ford, M. J. 2002. Selection in Captivity During Supportive Breeding May Reduce Fitness in the Wild. Conservation Biology 16:815-825.
- Ford, M. J., A. R. Murdoch, M. S. Hughes, T. R. Seamons, and E. S. LaHood. 2016. Broodstock History Strongly Influences Natural Spawning Success in Hatchery Steelhead (Oncorhynchus mykiss). Plos One 11:e0164801.
- Franklin, I. R. 1980. Evolutionary change in small populations. Pages 135-149 in M. E. Soule and B. A. Wilcox, editors. Conservation biology: An evolutionary-ecological perspective. Sinauer Assoc., Sunderland, MA.
- Fraser, D. J. 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. Evolutionary Applications 1:535-586.
- Fraser, D. J., L. K. Weir, L. Bernatchez, M. M. Hansen, and E. B. Taylor. 2011. Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. Heredity 106:404-420.
- Gavery, M. R., K. M. Nichols, B. A. Berejikian, C. P. Tatara, G. W. Goetz, J. T. Dickey, D. M. Van Doornik, and P. Swanson. 2019. Temporal Dynamics of DNA Methylation Patterns in Response to Rearing Juvenile Steelhead (*Oncorhynchus mykiss*) in a Hatchery versus Simulated Stream Environment. Genes (Basel) 10:356.
- Gavery, M. R., K. M. Nichols, G. W. Goetz, M. A. Middleton, and P. Swanson. 2018.
   Characterization of Genetic and Epigenetic Variation in Sperm and Red Blood Cells from Adult Hatchery and Natural-Origin Steelhead, *Oncorhynchus mykiss*. G3:
   Genes Genomes Genetics 8:3723-3736.
- González-Laxe, F. 2005. The precautionary principle in fisheries management. Marine Policy 29:495-505.
- Griswold, R. G., D. Taki, and S. Letzing. 2011. Snake River Sockeye salmon habitat and limnological research: 2010 annual progress report. Bonneville Power Administration final report, Portland, OR. (https://pisces.bpa.gov/release/documents/documentviewer.aspx?doc=P122997)
- Hard, J. J., J. M. Myers, E. J. Connor, R. A. Hayman, R. G. Kope, G. Lucchetti, A. R. Marshall, G. R. Pess, and B. E. Thompson. 2015. Viability criteria for steelhead within the Puget Sound distinct population segment. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-129. doi:10.7289/V5/TM-NWFSC-129.
- Hebdon, J., P. Kline, D. Taki, and T. Flagg. 2004. Evaluating reintroduction strategies for Redfish
   Lake Sockeye Salmon captive broodstock progeny. American Fisheries Society
   Symposium 44:401- 413. American Fisheries Society, Bethesda, MA.

- Hedrick, P. W., D. Hedgecock, S. Hamelberg, and S. J. Croci. 2000. The Impact of Supplementation in Winter-Run Chinook Salmon on Effective Population Size. Journal of Heredity 91:112-116.
- Hess, J. E., J. S. Zendt, A. R. Matala, and S. R. Narum. 2016. Genetic basis of adult migration timing in anadromous steelhead discovered through multivariate association testing. Proceedings of the Royal Society of London B: Biological Sciences 283.
- Hilborn, R., J. J. Maguire, A. Parma, and A. Rosenberg. 2001. The Precautionary Approach and risk management: can they increase the probability of successes in fishery management? Canadian Journal of Fisheries and Aquatic Sciences 58:99-107.
- HSRG (Hatchery Scientific Review Group). 2009. Columbia River hatchery reform system-wide report. Peter Paquet (chair), Andrew Appleby, John Barr, Lee Blankenship, Don Campton, Mike Delarm, Trevor Evelyn, David Fast, Tom Flagg, Jeffrey Gislason, Paul Kline, Des Maynard (alternate), George Nandor, Paul Seidel, Stephen Smith. <u>http://hatcheryreform.us/</u>
- HSRG. 2012. Review of the Elwha River Fish Restoration Plan and Accompanying HGMPs. A. Appleby, H. Bartlett, H. L. Blankenship, D. Campton, K. Currens, T. Evelyn, D. Fast, T. Flagg, J. Lichatowich, C. Mahnken, L. Mobrand, P. Paquet, L. Seeb, and S. Smith.
   Prepared for the Lower Elwha Klallam Tribe and Washington Department of Fish and Wildlife. January 2012. <u>http://hatcheryreform.us/</u>
- HSRG. 2014. On the Science of Hatcheries: An updated perspective on the role of hatcheries in salmon and steelhead management in the Pacific Northwest. <u>http://hatcheryreform.us/</u>
- HSRG. 2017. Implementation of hatchery reform in the context of recovery planning using the AHA/ISIT tool. <u>http://hatcheryreform.us/</u>
- HSRG. 2020. All-H Analyzer Guide and Documentation. May 2020. 53 p. http://hatcheryreform.us/
- Hughes, M. S., and A. R. Murdoch. 2017. Spawning habitat of hatchery spring Chinook salmon and possible mechanisms contributing to lower reproductive success. Transactions of the American Fisheries Society 146:1016-1027.
- Isaak, D. J., R. F. Thurow, B. E. Rieman, and J. B Dunham, J.B. 2003. Temporal variation in synchrony among Chinook salmon (*Oncorhynchus tshawytscha*) redd counts from a wilderness area in central Idaho. Canadian Journal of Fisheries and Aquatic Sciences 60:840-848.
- ISAB (Independent Scientific Advisory Board). 2015. Density dependence and its implications for fish management and restoration programs in the Columbia River Basin. ISAB Document 2015-1. Prepared for the Northwest Power and Conservation Council. Available online at: http://www.nwcouncil.org/fw/isab.

- ISAB/ISRP (Independent Scientific Advisory Board and Independent Scientific Review Panel). 2016. Critical uncertainties for the Columbia River Basin Fish and Wildlife Program. ISAB/ISRP Document 2016-1. Prepared for the Northwest Power and Conservation Council. Available online at: http://www.nwcouncil.org/fw/isab.
- Jamieson, I. G., and F. W. Allendorf. 2012. How does the 50/500 rule apply to MVPs? Trends in Ecology & Evolution 27:578-584.
- Johnson, E. L., C. C. Kozfkay, J. H. Powell, M. P. Peterson, D. J. Baker, J. A. Heindel, K. E. Plaster, J. L. McCormick, and P. A. Kline. 2020. Evaluating Artificial Propagation Release Strategies for Recovering Endangered Snake River Sockeye Salmon. North American Journal of Aquaculture 82:331-344.
- Kalinowski, S. T., D. M. Van Doornik, C. C. Kozfkay. 2012. Genetic diversity in the Snake River Sockeye Salmon captive broodstock program as estimated from broodstock records. Conservation Genetics 13(5):1183-1193.
- Keefer, M. L., C. A. Peery, and M. J. Heinrich. 2008. Temperature-mediated en route migration mortality and travel rates of endangered Snake River Sockeye salmon. Ecology of Freshwater Fish 17(1):136-145.
- Kline, P., and T. Flagg. 2014. Putting the red back in Redfish Lake Twenty years of progress towards saving the Pacific Northwest's most endangered stock of salmon. Fisheries 39(11):488-500.
- Knudsen, C. M., S. L. Schroder, C. A. Busack, M. V. Johnston, T. N. Pearsons, W. J. Bosch, and D.
   E. Fast. 2006. Comparison of Life History Traits between First-Generation Hatchery and Wild Upper Yakima River Spring Chinook Salmon. Transactions of the American Fisheries Society 135:1130-1144.
- Kozfkay, C. C., M. Peterson, B. P. Sandford, E. Johnson, and P. Kline. 2019. The productivity and viability of Snake River Sockeye Salmon hatchery adults released into Redfish Lake, Idaho. Transactions of the American Fisheries Society 148:308-323.
- Lande, R. 1988. Genetics and demography in biological conservation. Science 241:1455-1460.
- Lescak, E. A., K. R. Shedd, and T. Dann. 2019. Relative productivity of hatchery pink salmon in a natural stream NPRB project 1619. <u>https://www.adfg.alaska.gov/index.cfm?adfg=fishingHatcheriesResearch.findings\_updat\_es</u>.
- Liermann, M. C., R. Sharma, and C. K. Parken. 2010. Using accessible watershed size to predict management parameters for Chinook salmon, *Oncorhynchus tshawytscha*, populations with little or no spawner-recruit data: a Bayesian hierarchical modelling approach. Fisheries Management and Ecology 17:40-51.

- LCRFRB (Lower Columbia River Fish Recovery Board). 2004. Lower Columbia Salmon Recovery and Fish & Wildlife Subbasin Plan. LCRFRB, Longview, WA.
- LCRFRB. 2010. Washington Lower Columbia Salmon Recovery and Fish & Wildlife Subbasin Plan. LCFRB, Longview, WA.
- McElhany, P., M. J. Ruckleshaus, M. J. Ford, T. C. Wainwright, and E. Bjorkstedt. 2000. Viable Salmon Populations and the Recovery of Evolutionarily Significant Units. U. S. Department of Commerce, National Marine Fisheries Service, Northwest Fisheries Science Center, NOAA Technical Memorandum NMFS-NWFSC-42. 156p. http://www.nwfsc.noaa.gov/publications/techmemos/tm42/tm42.pdf.
- McKinney, G. J., K. M. Nichols, and M. J. Ford. 2020a. A mobile sex-determining region, malespecific haplotypes, and rearing environment influence age at maturity in Chinook salmon. bioRxiv:2020.2004.2023.056093.
- McKinney, G. J., J. E. Seeb, C. E. Pascal, D. E. Schindler, S. E. Gilk-Baumer, and L. W. Seeb. 2020b. Y-chromosome haplotypes are associated with variation in size and age at maturity in male Chinook salmon. Evolutionary Applications.
- 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.
- Moran, P., D. J. Teel, M. A. Banks, T. D. Beacham, M. R. Bellinger, S. M. Blankenship, J. R. Candy, J. C. Garza, J. E. Hess, S. R. Narum, L. W. Seeb, W. D. Templin, C. G. Wallace, C. T. Smith, and E. Taylor. 2013. Divergent life-history races do not represent Chinook salmon coastwide: the importance of scale in Quaternary biogeography. Canadian Journal of Fisheries and Aquatic Sciences 70:415-435.
- Murdoch, A., and G. Marston. 2020. WDFW Hatchery and Fishery Reform Policy Implementation Assessment Draft Progress Report, 2009-2019. WDFW, Olympia WA. <u>https://wdfw.wa.gov/sites/default/files/publications/02133/wdfw02133.pdf</u>
- Moussalli E. and R. Hilborn.1986. Optimal stock size and harvest rate in multistage life-history models. Can. J. Fish. Aquat. Sci. 43, 135–141. (doi:10.1139/f86-014).
- Naish, K. A., J. E. Taylor, 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. Pages 61-194 in D. W. Sims, editor. Advances in Marine Biology.
- Nelson, B. W., A. O. Shelton, J. H. Anderson, M. J. Ford, and E. J. Ward. 2019. Ecological implications of changing hatchery practices for Chinook salmon in the Salish Sea. Ecosphere 10:e02922.

- NMFS (National Marine Fisheries Service). 2005. Endangered and threatened species: final listing determinations for 16 evolutionarily significant units of West Coast salmon, and final 4(d) protective regulations for threatened salmonid ESUs. Final rule. Federal Register 70:123 (28 June 2005):37160-37204.
- NMFS. 2006. Elwha River and Fisheries Restoration Biological Opinion. NMFS, Washington State Habitat Office, NWR-2005-07196.
- NMFS. 2013. ESA Recovery Plan for Lower Columbia River Coho Salmon, Lower Columbia River Chinook Salmon, Columbia River Chum Salmon, and Lower Columbia River Steelhead. June 2013. 1051 p.
- NMFS. 2014. Final EIS to Inform Columbia River Basin Hatchery Operations and the Funding of Mitchell Act Hatchery Programs. September 2014. 2120 p.
- NMFS. 2017. Record of Decision for the Selection of Policy Direction for the Funding of Mitchell Act Hatchery Programs. January 2017. 24 p.
- NMFS (National Marine Fisheries Service). 2015. ESA Recovery Plan for Snake River Sockeye Salmon (*Oncorhynchus nerka*). Federal Register 80(109):32365-32367.
- NOAA Fisheries. 2014. Final Environmental Impact Statement to Inform Columbia River Basin Hatchery Operations and the Funding of Mitchell Act Hatchery Programs. NOAA Fisheries, NMFS, West Coast Region, Seattle, WA.
- O'Reilly, P. T., and C. C. Kozfkay. 2014. Use of microsatellite data and pedigree information in the genetic management of two long-term salmon conservation programs. Reviews in Fish Biology and Fisheries 24:819-848.
- O'Sullivan, R. J., T. Aykanat, S. E. Johnston, G. Rogan, R. Poole, P. A. Prodoh, E. de Eyto, C. R. Primmer, P. McGinnity, and T. E. Reed. 2020. Captive-bred Atlantic salmon released into the wild have fewer offspring than wild-bred fish and decrease population productivity. Proceedings of the Royal Society B 287: 20201671.
- Pacificorp and Cowlitz PUD (Public Utility District). 2020. Lewis River Hatchery and Supplementation Plan. Version 3.
- Paquet, P., T. Flagg, A. Appleby, J. Barr, L. Blankenship, D. Campton, M. Delarm, T. Evelyn, D. Fast, J. Gislason, P. Kline, D. Maynard, L. Mobrand, G. Nandor, P. Seidel, and S. Smith. 2011. Hatcheries, conservation, and sustainable fisheries achieving multiple goals: results of the hatchery scientific review group's Columbia River Basin review. Fisheries 36(11):542-561.
- Peters, R. J., J. J. Duda, G. R. Pess, M. Zimmerman, P. Crain, Z. Hughes, A. Wilson, M. C.Liermann, S. A. Morley, J. R. McMillan, K. Denton, D. Morrill, and K. Warheit. 2014.Guidelines for Monitoring and Adaptively Managing Restoration of Chinook Salmon

(Oncorhynchus tshawytscha) and Steelhead (O. mykiss) on the Elwha River. USFWS, 112 p.

- Prince, D. J., S. M. O'Rourke, T. Q. Thompson, O. A. Ali, H. S. Lyman, I. K. Saglam, T. J. Hotaling, A. P. Spidle, and M. R. Miller. 2017. The evolutionary basis of premature migration in Pacific salmon highlights the utility of genomics for informing conservation. Science Advances 3.
- Ricker, W.E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11:559-623.
- Rose, K.A., J.H. Cowan Jr., K.O. Winemiller, R.A. Myers and R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries 2:293-327.
- Ruckelshaus, M. H., K. P. Currens, W. H. Graeber, R. R. Fuerstenberg, K. Rawson, N. J. Sands, and J. B. Scott. 2006. Independent populations of Chinook salmon in Puget Sound. U.S. Dept. Commerce, NOAA Tech. Memo. NMFS-NWFSC-78, 125 p.
- Ruggerone, G.T., and J.R. Irvine. 2018. Numbers and biomass of natural- and hatchery-origin pink, chum, and sockeye salmon in the North Pacific Ocean, 1925-2015. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 10:152-168.
- Runge, M. C., J. B. Grand, and M. S. Mitchell. 2013. Structured decision making. Pages 51-72 in
   P. R. Krausman and J. W. I. Cain, editors. Wildlife Management: Contemporary Principles and Practices. John Hopkins University Press, Baltimore, MD.
- Ryman, N., and L. Laikre. 1991. Effects of supportive breeding on the genetically effective population size. Conservation Biology 5:325-3329.
- Scheuerell, M.D., R. Hilborn, M.H. Ruckelshaus, K.K. Bartz, K.M. Lagueux, et al. 2006. The Shiraz model: a tool for incorporating anthropogenic effects and fish–habitat relationships in conservation planning. Canadian Journal of Fisheries and Aquatic Sciences 63 (7), 1596-1607.
- Selbie, D. T., B. A. Lewis, J. P. Smol, and B. P. Finney. 2007. Long-term population dynamics of the endangered Snake River Sockeye salmon: evidence of past influences on stock decline and impediments to recovery. Transactions of the American Fisheries Society 136:800-821.
- Small, M. P., S. D. Rogers Olive, L. W. Seeb, J. E. Seeb, C. E. Pascal, K. I. Warheit, and W. Templin. 2015. Chum Salmon Genetic Diversity in the Northeastern Pacific Ocean Assessed with Single Nucleotide Polymorphisms (SNPs): Applications to Fishery Management. North American Journal of Fisheries Management 35:974-987.

- Soule, M. E. (Ed.). 1986. Conservation biology, the science of scarcity and diversity. Sinauer, Sunderland, MA, 584p.
- Teuscher, D., and D. Taki. 1996. Salmon River Sockeye salmon habitat and limnological research. Pages 1-50 in Teuscher, D. and D. Taki (editors), Snake River Sockeye salmon habitat and limnological research: 1995 annual progress report. U.S. Department of Energy, Bonneville Power Administration, Portland, OR. Project number 91-71. (https://pisces.bpa.gov/release/documents/documentviewer.aspx?doc=22548-4)
- Thompson, T. Q., M. R. Bellinger, S. M. O'Rourke, D. J. Prince, A. E. Stevenson, A. T. Rodrigues, M. R. Sloat, C. F. Speller, D. Y. Yang, V. L. Butler, M. A. Banks, and M. R. Miller. 2019.
   Anthropogenic habitat alteration leads to rapid loss of adaptive variation and restoration potential in wild salmon populations. Proc Natl Acad Sci U S A 116:177-186.
- Venditti, D. A., R. N. Kinzer, K. A. Apperson, B. Barnett, M. Belnap, T. Copeland, M. P. Corsi, and K. Tardy. 2018. Effects of hatchery supplementation on abundance and productivity of natural-origin Chinook salmon: two decades of evaluation and implications for conservation programs. Canadian Journal of Fisheries and Aquatic Sciences 75:1495-1510.
- Venney, C. J., K. W. Wellband, and D. D. Heath. 2020. Rearing environment affects the genetic architecture and plasticity of DNA methylation in Chinook salmon. Heredity.
- Walters, A.W., T. Copeland, and D.A. Venditti. 2013. The density dilemma: limitations on juvenile production in threatened salmon populations. Ecology of Freshwater Fish 22:508-519.
- Waples, R. S. 1990. Conservation Genetics of Pacific Salmon. III. Estimating Effective Population Size. Journal of Heredity 81:277-289.
- Waples, R.S., and C. Do. 1994. Genetic risk associated with supplementation of Pacific salmonids: captive broodstock programs. Canadian Journal of Fisheries and Aquatic Sciences 51(Supplement 1):310–329.
- Waples, R. S., and S. T. Lindley. 2018. Genomics and conservation units: The genetic basis of adult migration timing in Pacific salmonids. Evolutionary Applications 11:1518-1526.
- Waples, R. S., K. A. Naish, and C. R. Primmer. 2020. Conservation and Management of Salmon in the Age of Genomics. Annual Review of Animal Biosciences 8:null.
- Ward, L., P. Crain, B. Freymond, M. McHenry, D. Morrill, G. Pess, R. Peters, J. A. Shaffer, B.
   Winter, and B. Wunderlich. 2008. Elwha River Fish Restoration Plan–Developed pursuant to the Elwha River Ecosystem and Fisheries Restoration Act, Public Law 102-495. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-90, 168 p.

- Waters, C. D., J. J. Hard, M. S. O. Brieuc, D. E. Fast, K. I. Warheit, R. S. Waples, C. M. Knudsen, W.
   J. Bosch, and K. A. Naish. 2015. Effectiveness of managed gene flow in reducing genetic divergence associated with captive breeding. Evolutionary Applications 8:956-971.
- WDFW (Washington Department of Fish and Wildlife). 2012. Hatchery and genetic management plan - Elwha Channel Hatchery Chinook salmon subyearlings and yearlings. Fish Program, WDFW. Olympia, Washington. 46p.
- WDFW. 2015. Lower Columbia Conservation and Sustainable Fisheries Plan. WDFW in partnership with the Lower Columbia Fish Recovery Board. December 2015.
- Weinheimer, J., J. Anderson, R. Cooper, S. Williams, M. McHenry, P. Crain, S. Brenkman, and H. Hugunin. 2018. Age structure and hatchery fraction of Elwha River Chinook salmon: 2017 carcass survey report. June 2018. WDFW, Lower Elwha Klallam Tribe, and Olympic National Park. 32 p.
- Williamson, K.S., A.R. Murdoch, T.N. Pearsons, E.J. Ward, and M.J. Ford. 2010. Factors influencing the relative fitness of hatchery and wild spring Chinook salmon (*Oncorhynchus tshawytscha*) in the Wenatchee River, Washington, USA. Canadian Journal of Fisheries and Aquatic Sciences 67:1840-1851.
- Willoughby, J. R., and M. R. Christie. 2019. Long-term demographic and genetic effects of releasing captive-born individuals into the wild. Conservation Biology 33:377-388.