Appendix C
Analytical Methods and Information Sources

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1.0   Overview

The purpose of the analysis was to compare the average, long-term effects of different hatchery strategies on conservation and harvest. Conservation of natural populations was assessed in terms of estimated abundance and productivity as well as via an index of the relative magnitude of natural versus artificial selection pressures on individual populations and their potential impacts on fitness. Harvest was assessed by estimating the average number of hatchery- and natural-origin fish taken in marine, lower Columbia[1], upper Columbia[2], and terminal[3] fisheries. The analysis of these factors entailed the integration of habitat in terms of population-specific productivity and capacity parameters, harvest rates for hatchery- and natural-origin fish in all applicable fisheries, hydrosystem survival for adults and juveniles, and hatchery operations, with special emphasis on broodstock and escapement management and hatchery stray rates. The calculations entailed by these goals were simple in concept, but involved the simultaneous tracking of many populations and their interactions.

The approach used by the HSRG involved an accounting for natural and hatchery reproduction, natural survival, and the fate of fish that survived to be caught the marine fishery or to return to the Columbia River. In turn, the fate of adults returning to the Columbia River was assessed in terms of homing fidelity, the composition of spawning escapement, relative reproductive success, relative contribution to the conservation of Evolutionarily Significant Units (ESUs) in the Columbia River Basin, and relative contributions to harvest by fishery.

2.0   Analytical Methods

This paper describes the analytical methods used by the HSRG. Methods, which depend upon a variety of information, include:

- The basic Beverton-Holt survival function which was assumed to describe recruitment for all fish spawning in nature

- Calculations of broodstock composition in terms of hatchery- and natural-origin adults, survival of hatchery fish by life stage in nature and in the hatchery, and the fate of returning hatchery adults

- Calculations of the mean number of fish taken in each of four fisheries

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[1] Lower Columbia" is defined as the mainstem Columbia River below Bonneville Dam.
[2] "Upper Columbia" is defined as the mainstem Columbia River between Bonneville and McNary dams.
[3] "Terminal" fisheries are those that occur in the mainstem Columbia upstream of McNary Dam, the Snake River mainstem, and inside the subbasin of origin.

- Computations of ecological and genetic interactions between natural- and hatchery-origin fish reproducing in the natural environment

The analysis does not attempt to estimate what might happen in any particular year; rather, it projects the average outcome after many generations. The analysis tracked each hatchery and natural population component over 100 generations.

The methods compute survival and number of recruits of natural and hatchery production. Survival in nature depends on:

- Quantity and quality of habitat used by the population
- Fish passage survival in the Columbia and Snake mainstems
- Estuarine and ocean survival conditions
- Fitness of the natural population
- Relative ability of hatchery fish to spawn and their progeny to survive in nature

Survival of hatchery production depends on:

- Number broodstock collected and spawned
- Pre-spawn survival, fecundity, and sex ratio of the broodstock
- Survival in the hatchery to time of release, including culling
- Post-release survival of hatchery fish

The analysis recognizes and accounts for ecological and genetic interactions between natural and hatchery production. Ecological interactions occur via competition in nature, whereas genetic interactions are expressed in terms of gene flow between the production groups.

Ecological interactions depend on:

- Composition of the naturally spawning population
- Ability of hatchery fish to spawn successfully and the survival of their progeny in nature
- Number of hatchery fish spawning in nature

Genetic interactions depend on:

- Composition of the hatchery broodstock
- Percentage of the hatchery return recovered at the point of release and that spawn in nature
- Composition of the naturally spawning population
- Ability of hatchery fish to spawn successfully and survival of their progeny in nature
- Differences in selection pressure between the natural and hatchery environments

2.1 Natural Production

The abundance of natural progeny from adults spawning in nature is computed using the multi-stage, Beverton-Holt (B-H) survival function (Beverton and Holt 1957; Mousalli and Hilborn 1986). The survival function is based on life parameters for productivity (density-independent survival) and capacity (maximum number of fish that can survive). The two-parameter B-H survival function was assumed for each of the following life stages:

1. Spawning to emergent fry
2. Emergent fry to juveniles leaving the subbasin (smolts)
3. Juvenile mainstem migration in the Snake and Columbia rivers and ocean rearing
4. Adults entering the Columbia River and migration to the mouth of the subbasin
5. Pre-spawning adults, i.e. fish from the point of subbasin entry to the initiation of spawning

The B-H survival function assumed for each life stage was as follows:

$$N_{i+1} = \frac{N_i \cdot p_i}{1 + \dfrac{N_i \cdot p_i}{c_i}} \tag{1}$$

where:

N_i = Number of fish alive at the beginning of life stage i

N_{i+1} = Number of fish alive at end of life stage $i+1$

p_i = Density-independent survival of life stage i

c_i = Capacity of life stage i (maxium number fish survive in life stage)

Abundance of hatchery-origin fish spawning in nature and their off-spring were adjusted to include the relative reproductive success of hatchery fish in nature, such that the total number of spawners, N_i, was:

$$N_i = N_{i,Nat} + N_{i,Hatch} \cdot Rel\_Surv_{i,Hatch} \tag{2}$$

where:

$N_{i,Nat}$ = Number of progeny from natural-origin spawners in life stage i

$N_{i,Hatch}$ = Number of progeny from hatchery-origin spawners in life stage i

$Rel\_Surv_{i,Hatch}$ = An estimate of the phenotypic impact of hatchery rearing

on life stage productivity in nature for life stage i

More specifically, $Rel\_Surv_{i,Hatch}$ is a user-provided estimate of the phenotypic depression of the reproductive success of hatchery spawners in nature.

The B-H productivity and capacity[4] parameters were adjusted for the relative fitness, F, of the natural population over the complete (adult-to-adult) life cycle. The formulas used to estimate fitness of the natural population are described in Section 2.4.3 of this appendix. The fitness multiplier was apportioned over each life stage i as follows:

$$f_i = F^{Rel\_Loss_i} \tag{3}$$

where:

$f_i =$ Life-stage specific fitness

$Rel\_Loss_i =$ Assumed proportion of the total fitness effect occuring in life stage i

The overall survival function for life stage i was as follows:

$$N_{i+1} = \frac{p_i \cdot f_i \cdot (N_{i,Nat} + N_{i,Hatch} \cdot Rel\_Surv_{i,Hatch})}{1 + \dfrac{p_i \cdot f_i \cdot (N_{i,Nat} + N_{i,Hatch} \cdot Rel\_Surv_{i,Hatch})}{c_i \cdot f_i}} \tag{4}$$

Cumulative productivity and capacity for a population included an assumed average smolt-to-adult return rate (SAR), calculated at the mouth of the subbasin of origin. Productivity and capacity parameters were adjusted as necessary to ensure that predicted SARs equaled the latest observed SAR by means of the following adjustment:

$$P_{Adj} = P_{Base} \cdot \left(\frac{SAR_{Obs}}{SAR_{Base}} \right) \tag{5}$$

where:

$P_{Adj} =$ Adjusted Spawner-Spawner Productivity

$P_{Base} =$ Baseline period Spawner-Spawner Productivity

$SAR_{Obs} =$ Latest observed subbasin-to-subbasin SAR

$SAR_{Base} =$ SAR assumed in baseline estimate of Productivity

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[4] Capacity is affected by both the quantity of key habitat and productivity by the equation: $C_i = \dfrac{p_i}{(1/C_{i-1} + p_i/c_i)}$.

A comparable adjustment for spawner-to-spawner capacity made use of the multi-stage B-H equation (Moussalli and Hilborn 1986) as follows:

$$C_{Adj} = \frac{p_{Smolt} \cdot SAR_{Obs} \cdot p_{Prespawn}}{\left(\frac{1}{c_{Spawn}} + \frac{p_{Smolt}}{c_{Smolt}} + \frac{p_{Smolt} \cdot SAR_{Obs} \cdot p_{Prespawn}}{c_{Prespawn}} \right)} \tag{6}$$

where:

C_{adj} = Adjusted Spawner-Spawner Capacity

p_{smolt} = Productivity for the period emergent fry to smolt leaving the subbasin

$p_{prespawn}$ = Productivity for the period adult entering subbasin to spawning

c_{spawn} = Life stage capacity from spawner to emgerent fry (relative index)

c_{smolt} = Life stage capacity from emergent fry to smolt leaving subbasin

$c_{prespawn}$ = Life stage capacity from adult entering subbasin to spawning

Productivity and capacity for the pre-spawn and spawner-to-fry life stages were user-supplied input variables. Given these values, productivity (P_{Smolt}) and capacity (c_{Smolt}) for the fry-to-smolt life stage was calculated as follows:

$$p_{Smolt} = \frac{P}{p_{Egg-fry} \cdot SAR_{Obs} \cdot p_{Pre-spawn}} \tag{7}$$

and

$$c_{Smolt} = \frac{1}{\left[\left(p_{Pre-spawn} \cdot SAR_{Obs} \right) \cdot \left(\frac{1}{C} - \frac{1}{c_{Pre-spawn}} \right) \right]} \tag{8}$$

Finally, productivity and capacity of the population from spawner to smolt leaving the subbasin was computed to provide a means of reporting and validating cumulative productivity and capacity parameters and life stage parameters used in the analysis.

Productivity from spawn to smolt was computed by the following expression:

$$p_{Spawn-smolt} = \frac{P}{SAR_{Obs} \cdot p_{Pre-spawn}} \tag{9}$$

Capacity for the spawner-to-smolt life stage ($c_{Spawn-smolt}$) was computed as follows:

$$c_{spawn-smolt} = \frac{C}{\left[\left(SAR_{Obs} \cdot p_{Pre-spawn} \right) \cdot \left(1 - \frac{C}{c_{Pre-spawn}} \right) - \frac{1}{\left(p_{Spawn-smolt} \cdot c_{Spawn-egg} \right)} \right]} \tag{10}$$

Data sources

The cumulative B-H productivity (P) and capacity (C) parameters define the maximum adult recruitment rate (density-independent recruitment) and maximum number of

spawners (adult "carrying capacity") for a population over the complete life cycle (spawner to spawner). The specific parameters used in analyses came from a variety of sources, depending on the population. Most frequently, habitat-based models like Ecosystem Diagnosis and Treatment (EDT) were used to estimate productivity and capacity. In some cases, these parameters were estimated by fitting a B-H function to observed abundance data,; in a few cases, the parameters were based on abundance observed at a mainstem dam, with a subsequent allocation of returns to populations based on the relative quantity and quality of habitat in spawning tributaries above the reference dam.

Life stage specific parameters were obtained from fish passage survival models (FCRPS May 2008), subbasin plans, ESU recovery plans, and hatchery managers.

2.2 Hatchery Production

Hatchery production was evaluated in terms of whether a given hatchery program was segregated or integrated. A hatchery program was considered segregated if the management intent was to create a distinct population that is reproductively isolated from naturally spawning populations. A hatchery program was considered to be integrated if the management intent was to create a composite hatchery/natural population for which the dominant selective pressure was the natural environment. The concepts underlying the computation of net natural vs. artificial selection in integrated programs and the impact of net selective pressure on genetic fitness of the natural population are described in more detail in Section 2.4. In some cases, more than one release strategy was used in a program; for example, some programs release both late summer subyearling parr and spring yearling smolts. In such cases, information was required for both release groups. The combined number of hatchery juveniles produced (H_{Rel}) was computed as follows:

$$H_{Rel} = \sum_a BS_{HOB} \cdot S_{Spawn-egg} \cdot S_{Egg-rel,a} + BS_{NOB} \cdot S_{Spawn-egg} \cdot S_{Egg-rel,a} \cdot Rel\_Surv_{NOB} \quad (11)$$

where:

$$S_{Spawn-egg} = S_{Pre-spawn} \cdot Fecundity \cdot \% Females \cdot (1 - \% EggsCulled)$$

and:

BS_{NOB} = Number of natural-origin adults in broodstock (integrated programs)

BS_{HOB} = Number of hatchery-origin adults in broodstock (local and imported)

$S_{Spawn-rel,a}$ = Survival from egg to release for release group a

$\% R_a$ = Proportion of release comprised of juveniles from release group a

$S_{Pre-spawn}$ = Survival in hatchery of broodstock adults

$Fecundity$ = Average number of eggs per female in broodstock

$\% Females$ = Percent females in broodstock

$\% Culled$ = Percent of eggs in broodstock destroyed, typically for disease management

Survival from release to adult was based on total recruits per hatchery spawner (R/S). Recruits per spawner for hatchery fish (R/S_{Hatch}) is analogous to the productivity value for the natural population. Sometimes called the hatchery return rate, it represents the mean number of hatchery-origin recruits (HORs) produced (harvest plus escapement) per hatchery spawner. Hatchery spawners are the number of adults collected to meet broodstock needs before pre-spawn mortality and culling. The hatchery recruits per spawner value was usually computed from coded wire tag data or other hatchery information and was a user-supplied input variable.

The combined recruits per spawner value (R/S_{Hatch}) for programs that included more than one release strategy was calculated as follows:

$$R/S_{Hatch} = \frac{R/S_{R1} \cdot \%R_1 \cdot S_{R2\_egg-rel} + R/S_{R2} \cdot \%R_2 \cdot S_{R1\_egg-rel}}{\%R_1 \cdot S_{R2\_egg-rel} + \%R_2 \cdot S_{R1\_egg-rel}} \qquad (12)$$

where:

R/S_{R1} & R/S_{R2} = Recruits per spawner for release groups 1 and 2

$S_{R1\_egg-rel}$ = Egg to release survival of hatchery juveniles for group 1, includes eggs culled

$S_{R2\_egg-rel}$ = Egg to release survival of hatchery juveniles for group 2, includes eggs culled

$\%R_1$ & $\%R_2$ = Proportion of program release comprised of release groups 1 and 2

Finally, survival of hatchery fish from release to adult recruitment was computed to provide a means of reporting and validating hatchery inputs for recruit per spawner and in-hatchery survival to release. SAR_{Hat} was calculated by the following expression:

$$SAR_{Hatch} = \frac{R/S_{Hatch}}{\left(S_{Spawn-rel,R1} \cdot \%R_1 + S_{Spawn-rel,R2} \cdot \%R_2\right) \cdot S_{Spawn-egg}} \qquad (13)$$

Finally, SAR_{Hat} was adjusted as necessary to ensure that predicted hatchery SAR equaled the latest observed SAR by means of the following adjustment:

$$SAR_{Hat\_Adj} = SAR_{Hat} \cdot \left(SAR_{Obs} \middle/ SAR_{Base}\right) \qquad (14)$$

where SAR_{Obs} and SAR_{Base} are as previously defined in Equation 5.

In the analysis, hatchery recruits included strays, fish taken in the harvest, fish recovered at the point of release, fish recovered at an adult in-river weir, and fish that spawned in nature. Methods to calculate the number of fish harvested are described in more detail in Section 2.3. The following section describes how the escapement, i.e. fish that were not harvested, was distributed.

The number of hatchery adults recovered at the point of release (*#Hatch*) was calculated by the following expression:

$$\#Hatch = H_{Rel} \cdot SAR_{Hat\_Adj} \cdot \left(1 - TotalExploitation\right) \cdot \% \, Hatch \tag{15}$$

where:

$TotalExploitation$ = Total exploitation rate across all fisheries

$\%Hatch$ = Percent hatchery origin escapement recovered and/or that died at the point of release.

The analysis estimated hatchery surplus as the number of hatchery adults collected at the hatchery and other locations such as weirs *(%Weir)*, but not used for broodstock. Hatchery surplus was calculated as follows:

$$Surplus_{Hatch} = H_{Rel} \cdot SAR_{Hat\_Adj} \cdot \left(1 - TotalExploitation\right) \cdot \% \, Weir \cdot \% \, Hatch - BS_{HOB} \tag{16}$$

The number of hatchery returns surviving to spawn in nature (*N_{hat}*) was calculated as follows:

$$N_{Hatch} = H_{Rel} \cdot SAR_{Hat\_Adj} \cdot \left(1 - TotalExploitation\right) \cdot \left(1 - \% \, Hatch\right) \tag{17}$$

The number of hatchery adults spawning in a particular natural population is calculated as follows:

$$N_{Hatch} = \sum_{p=1}^{P} N_{Hatch,p} \cdot \left(1 - \% \, Weir\right) \tag{18}$$

In the previous equation hatchery fish are assumed to originate from one or more hatchery programs *p*. Methods to distribute hatchery fish spawning in nature to natural populations will be described in detail in the Interaction section of this appendix.

Data Sources

Hatchery Genetic Management Plans (HGMPs) were a major information source for hatchery programs. Although HGMPs varied in completeness, comprehensive HGMPs included information on a wide range of parameters including:

- Hatchery type (Segregated/Integrated)
- Broodstock target (number of fish) and hatchery/natural composition in the broodstock
- Broodstock collection procedures
- Contribution of hatchery fish to natural escapement
- Proportion of broodstock imported and/or exported
- Smolt release size and life stage
- Hatchery survival by life stage

- Hatchery return rates
- Hatchery stray rates

Hatchery managers were personally contacted when the pertinent HGMP was out of date or lacked certain types of information. In the majority of cases, sufficient empirical data to assess hatchery programs were obtained through a combination of excerpts from an HGMP and personal contacts with hatchery managers.

2.3 Harvest

Harvest analysis in the methods was relatively simple. Harvest was estimated for four major fisheries (defined by harvest area) as a function of user-supplied harvest rates and the estimated number of HOR and NOR fish available in each fishery. Mark-selective fisheries on hatchery fish were analyzed by imposing differential harvest rates on NORs and HORs. The harvest analysis did not incorporate age-specific harvest rates; harvest rates represent total harvest on a brood over all ages.

The number of *natural* fish surviving to marine fisheries ($N_{Mar, Nat}$) was calculated as follows:

$$N_{Mar,Nat} = N_{Smolt} \cdot S_{Juv} \qquad (19)$$

where:

N_{Smolt} = Estimated number of natural-origin juveniles leaving subbasin.

S_{Juv} = Survival of natural fish during juvenile mainstem passage and in the ocean.

The number of *hatchery* fish surviving to marine fisheries ($N_{Mar, Hat}$) was calculated by a similar expression:

$$N_{Mar,Hatch} = H_{Rel} \cdot S_{Juv,Hatch} \qquad (20)$$

where:

H_{Rel} = Number of hatchery fish released.

$S_{Juv,Hatch}$ = Survival of hatchery fish during juvenile mainstem passage and in the ocean.

The number of fish harvested was calculated sequentially, beginning with the number of fish harvested in marine fisheries ($Harv_{Mar, i}$):

$$Harv_{Mar,i} = N_{Mar,i} \cdot HR_{Mar,i} \qquad (21)$$

where:

$N_{Mar,i}$ = Number of fish surviving to enter marine fisheries for production type i.

$HR_{Mar,i}$ = Marine harvest rate on adults for production type i.

The number of fish harvested in the Lower Columbia, the upper Columbia, and inside subbasins of origin was then calculated sequentially with each successive harvest making use of the fish remaining after previous harvests. Thus, Lower Columbia (below Bonneville) harvests of production type i ($HARV_{LCol, i}$) were calculated by the following expression:

$$Harv_{LCol,i} = N_{Mar,i} \cdot \left(1 - Harv_{Mar,i}\right) \cdot HR_{LCol,i} \tag{22}$$

Upper Columbia (Bonneville Dam to McNary Dam) harvests of production type i ($Harv_{UCol,i}$) were calculated by a similar expression,

$$Harv_{UCol,i} = N_{Mar,i} \cdot \left(1 - HR_{Mar,i}\right) \cdot \left(1 - HR_{LCol,i}\right) \cdot HR_{UCol,i} \tag{23}$$

and terminal harvest ($Harv_{Term, i}$), the number of fish harvested in the Columbia mainstem upstream of McNary Dam, Snake mainstem and inside the subbasins of origin) was calculated as:

$$Harv_{Term,i} = N_{Mar,i} \cdot S_{Adult-pass} \cdot \left(1 - HR_{Mar,i}\right) \cdot \left(1 - HR_{LCol,i}\right) \cdot \left(1 - HR_{UCol,i}\right) \cdot HR_{Term,i} \tag{24}$$

In equations 21 through 23, $HR_{LCol, i}$, $HR_{UCol, i}$, and $HR_{Term, i}$, are harvest rates in the Lower Columbia, upper Columbia, and terminal areas, respectively, and $S_{Adult-pass}$ is the survival of adults through the mainstem Columbia and Snake Rivers.

Data Sources

Harvest rate is the number of fish harvested divided by the total number of fish available to the fishery. Harvest rates are taken from recent brood year averages or from target harvest rates described in management plans. Future harvest rates applied to the analysis came from proposed harvest plans or recommendations.

2.4   Interactions – (Ecological and Genetic)

The analytical methods evaluated interactions between hatchery and natural fish in two ways: 1) through ecological interactions between progeny of naturally spawning hatchery and natural-origin parents and 2) through long-term genetic interactions resulting from hatchery adults spawning with natural fish. The methods to compute effects of these interactions for each of these ways are described in the following sections. The sections describe the quantitative assessment of ecological and genetic interactions in the analysis. First, however, an overview of methods to compute the number of hatchery fish spawning in nature and their distribution among natural populations is presented, followed by descriptions of methods to compute effects of ecological and genetic interactions.

2.4.1   Distribution of Hatchery Adults Spawning in Nature

Hatchery returns may be recovered at the point of release, at a weir, on the spawning grounds within the subbasin of origin, on spawning grounds outside the subbasin of

origin, or they may die after escaping the fisheries, but before spawning. The analytical methods included assumptions about the fate of all hatchery return escaping fisheries. The procedure tracked the eventual fate of all returning hatchery adults from every population/program.

All hatchery adults not recovered in fisheries or at hatchery racks or weirs at their point of release are considered strays. Strays were allocated to a natural population within their respective basin of origin (within-basin strays), to natural populations outside of the originating basin (out-of-basin strays), or designated as adults returning to areas with no spawning populations. The purpose of the straying component in the analysis is to account for the effect of reproductive interactions between natural populations ("recipient populations") and hatchery programs ("donor populations").

The proportion and source of hatchery strays in the natural spawning escapement is used to estimate relative genetic fitness (see following section) of recipient natural populations. Recall from equation 17, the number of hatchery strays (N_{Hatch}) spawning in nature from the donor population p was calculated as follows:

$$N_{Hatch} = H_{Rel} \cdot SAR_{Hatch} \cdot (1 - TotalExploitation) \cdot (1 - \% Hatch) \tag{25}$$

The number of strays from donor hatchery p to a particular recipient natural population was calculated as follows:

$$Recip_{Hatch,p} = N_{Hatch,p} \cdot \% Recip \tag{26}$$

where *%Recip* is an estimate of the proportion of the adults that stray to the recipient natural population.

Generally the *%Recip* would sum to 100% for a donor population, i.e. all strays were assumed to spawn with a natural population. However, information suggested that, in some cases, a portion of the hatchery return not recovered at the hatchery does not attempt to spawn with a natural population (e.g., programs that release fish a long distance away from natural populations).

The actual number of hatchery fish spawning in a recipient natural population is the sum of hatchery fish from all donor populations:

$$Strays_{Hatch} = \sum_{p=1}^{P} Recip_{Hatch,p} \cdot (1 - \% Weir) \tag{27}$$

where *%Weir* is the proportion of the hatchery adults destined to spawn with the natural population, but are recovered at an adult weir either below the population or within the boundaries of the natural population.

Data Sources

Assumptions regarding strays were developed from data provided by managers where available. This was generally in the form of a time series of coded wire tagged releases from the originating hatchery and adult recoveries at the originating hatchery adult trap, at adult traps, at hatchery adult traps other than the originating hatchery, and from spawning ground surveys. Recoveries of hatchery adults at hatchery traps other than the release hatchery were used to provide a measure of straying outside of the basin of origin. Observations of the number of hatchery adults on the spawning grounds or at weirs were used to validate or revise default assumptions. Default stray assumptions were developed using coded wire tag recovery data for several populations in the Columbia Basin. The information used in that analysis can be separated into five types.

1. The proportion of strays assumed to spawn within the originating subbasin and the reciprocal of this fraction, the proportion of strays spawning outside the originating subbasin. Tag recovery data were available for several population groups in the Columbia Basin. For example, recoveries of coded wire tags from fall Chinook released from Lower Columbia hatcheries reported in Meyers et al. (2006) indicates that about 85% of the tags are recovered within 5 km of the release location. This information is the basis of the assumption that 85% of un-recovered Lower Columbia hatchery fall Chinook would stray to spawning areas within the subbasin with the remaining 15% straying to areas outside the subbasin.

   The distribution of strays from hatchery programs not associated with a Subbasin, such as the Youngs Bay net pens, was determined on a case-by-case basis. In most cases, it was assumed that most of the adult escapement would stray to recipient populations in nearby subbasins. However, it was assumed that a small fraction did not stray, but rather remained in the general vicinity of the release site.

2. The proportion of out-of-subbasin strays that spawn in subbasins upstream and downstream of the natal watershed.

3. The distance of potential recipient populations from each donor program. For example, Meyers et al. (2006) reported few recoveries beyond 105 km from the release location.

4. The relative sizes of the subbasins with potential recipient populations. Larger subbasins provide greater attraction flows and therefore may receive a higher proportion of out-of-subbasin strays (Quinn, Nemeth, and McIsaac 1991). Although the actual mechanism of this relationship probably involves mean monthly discharge in the recipient subbasin during the spawning run, there is a good correlation between mean discharge and watershed area. The relationship used in the analysis is based on subbasin area because these data are readily available.

5. The influence of water temperature was considered to affect stray rates to potential recipient populations upstream of Bonneville Dam. The analysis adjusted stray rates based on the relative mean monthly water temperatures of the mainstem Columbia or Snake Rivers and potential recipient subbasins during the spawning run. This was especially important when developing stray rates for steelhead and fall Chinook (Keefer et al. 2005).

2.4.2 Ecological Interactions

The analysis considered the effect of hatchery fish in nature on survival of natural fish through competitive interactions (reviewed in Kostow 2008). While the number of hatchery fish that "effectively" interbreed may be low, the census number of fish present may be very large and may have a significant ecological effect (Kostow 2003, Kostow 2004, Kostow 2006). The concern is that hatchery fish may compete effectively at the juvenile stage, but have inferior reproductive success.

The analytical approach computed an adjusted survival of progeny of natural-origin spawners based on estimates of productivity and competition factors for hatchery fish relative to natural-origin fish.

The number of fish from natural-origin parents surviving to the next life stage was adjusted based on the quantity of fish from hatchery-origin parents. In other words, Equation 4 described previously was modified to account for competition between the progeny of hatchery and natural spawners in nature. The following equation was used to compute number of fish surviving to the next life stage from natural-origin parents ($N_{i,Nat}$):

$$N_{i+1,Nat} = \frac{p_i \cdot f_i \cdot N_{i,Nat}}{1 + \dfrac{p_i \cdot f_i \cdot (N_{i,Nat} + N_{i,Hatch} \cdot Rel\_Surv_{i,Hatch} \cdot Rel\_Comp_{i,Hatch})}{c_i \cdot f_i}} \tag{28}$$

The number of fish surviving to the next life stage from hatchery-origin parents ($N_{i,Hatch}$) was computed by the following:

$$N_{i+1,Hatch} = \frac{p_i \cdot f_i \cdot Rel\_Surv_{i,Hatch} \cdot N_{i,Hatch}}{1 + \dfrac{p_i \cdot f_i \cdot (N_{i,Hatch} \cdot Rel\_Surv_{i,Hatch} + N_{i,Nat})}{c_i \cdot f_i}} \tag{29}$$

In the previous equations, $N_{i,Nat}$ is the number of natural progeny from natural-origin parents and $N_{i,Hatch}$ is the number of natural progeny from hatchery-origin parents. The competition effect of offspring from hatchery spawners may be adjusted based on the $Rel\_Comp_{i,Hatch}$ parameter. A value of 1.0 results in equal competition between the off-spring of hatchery spawners and natural spawners. Values less than 1.0 signify that off-spring from hatchery fish are less competitive in nature.

Hatchery and natural fish can potentially interact after release when returning as pre-spawners and as spawners on the spawning grounds. The methods did not quantitatively evaluate these potential effects. The analysis considered these potential effects by considering a variety of factors such as the number of fish released, life stages at release, release strategies, and the percent of the natural spawning abundance that is comprised of hatchery-origin fish.

Data Sources

The analysis assumed a relative survival of 0.80 for hatchery Chinook and coho, and integrated and Upper Columbia River hatchery steelhead. Many of the hatchery releases in the Lower Columbia River and Willamette River are outplant programs based on domesticated hatchery stocks (e.g., early winter-run, and Skamania summer-run). Hatchery fish from these programs make a relatively small direct genetic contribution to the naturally spawning populations because of differences in spawn timing and behavior (Lieder et al. 1984). The analysis assumed 11% relative survival of domesticated winter steelhead in nature and 18% relative survival of domesticated summer steelhead in nature.

2.4.3   Genetic Interactions

The analysis of genetic interactions comprises the long-term effects on fitness of hatchery adults spawning with natural populations. A more detailed description of the basis for these equations is described in the HSRG white paper on Fitness and Local Adaptation (Appendix B). The application of the Ford (2002) model in the analytical methods is described below.

The Ford model is based on gene flow between hatchery and natural fish. Two parameters represent the mean proportional genetic contributions in each generation of hatchery and natural fish to natural-origin and hatchery-origin progeny. The proportion of hatchery broodstock composed of natural-origin adults (proportion of natural-origin broodstock or *pNOB*) was calculated as the following:

$$pNOB = \frac{BS_{NOR}}{BS_{NOR} + BS_{HOR}} \tag{30}$$

The proportion of naturally spawning fish composed of hatchery-origin spawners (proportion of effective hatchery-origin spawners or *pHOS_Eff*) was calculated as the following:

$$pHOS_{Eff} = \frac{N_{HOS} \cdot Rel\_Surv_{HOS}}{\left(N_{HOS} \cdot Rel\_Surv_{HOS}\right) + N_{NOS}} \tag{31}$$

where N_{HOS} and N_{NOS} were the number of natural spawning hatchery and natural adults, respectively. Effective hatchery spawners were those that successfully produced progeny that survived to spawn to the next generation.

The proportional influence of the natural environment on the mean phenotypic values (and genetic constitutions) of natural and hatchery fish is referred to as *PNI* [5] (proportionate natural influence). An approximate index of *PNI* for natural and hatchery fish when *pNOB* and *pHOS* were both greater than zero was calculated as the following:

$$PNI_{Approx} = \frac{pNOB}{\left(pNOB + pHOS\right)} \tag{32}$$

When *pHOS* or *pNOB* were zero, the calculated *PNI* depends on assumptions regarding selection intensities and "heritabilities" associated with a specific trait. If *pNOB* = 0 then $PNI_{Hatch} = 0$ and the following equation was used to calculate PNI_{Nat}:

$$PNI_{Nat} = \frac{h^2 + (1.0 - h^2 + \omega^2) \cdot pNOB}{h^2 + (1.0 - h^2 + \omega^2) \cdot (pNOB + pHOS)} \tag{33}$$

where:

h^2 = Heritability of the trait ≡ proportion of the total phenotypic variance resulting from heritable genetic variance among individuals $(0 < h^2 < 1.0)$

ω^2 = Variance of the probability distribution of fitness as a function of phenotypic values for individuals in the population

The analysis assumed σ^2 and ω^2 to be equal between natural and hatchery fish. Note that the inverse of ω^2, i.e. $1/\omega^2$, is the intensity selection towards the phenotypic optimum. In other words, as ω^2 increases the selection intensity decreases. According to Ford (2002), $\omega^2 = 10\sigma^2$ is considered "strong selection", whereas $\omega^2 = 100\sigma^2$ would be considered "weak selection".

Fitness is computed for each generation (*g*) in the analysis based on *pHOS* and *pNOB* in the parent generation (*g-1*).

Population fitness in generation *g* is calculated as the following:

$$F_g = e^{-\frac{1}{2}\left(\frac{\bar{P}_{Nat,g} - \theta_{Nat}}{\omega^2 + \sigma}\right)^2} \tag{34}$$

where:

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[5] The term *proportionate natural influence* (*PNI*) was first coined by C. Busack, Washington Department of Fish and Wildlife, Olympia, WA.

θ_{Nat} = Phenotypic optimum or expected value (mean) of the
phenotypic probability distribution for the natural population

θ_{Hatch} = Phenotypic optimum or expected value (mean) of the
phenotypic probability distribution for the hatchery population

σ^2 = Phenotypic variance for the trait in question

$\bar{P}_{Nat,g}$ = Mean phenotypic value of the natural population in generation g

$\bar{P}_{Nat}$-θ_{Nat} = Deviation from the optimum phenotypic value for the natural environment

The mean phenotypic value of the natural population ($\bar{P}_{Nat,g}$) and hatchery population
($\bar{P}_{Hatch,g}$) in generation g is calculated as the following:

$$\bar{P}_{Nat,g} = \left(1 - pHOS_{g-1}\right) \cdot \left[\bar{P}_{Nat,g-1} + \left(\left(\left(\bar{P}_{Nat,g-1} \cdot \omega^2 + \theta_{Nat} \cdot \sigma^2\right)/\left(\omega^2 + \sigma^2\right)\right) - \bar{P}_{Nat,g-1}\right) \cdot h^2\right]$$
$$+ pHOS_{g-1} \cdot \left[\bar{P}_{Hatch,g-1} + \left(\left(\left(\bar{P}_{Hatch,g-1} \cdot \omega^2 + \theta_{Nat} \cdot \sigma^2\right)/\left(\omega^2 + \sigma^2\right)\right) - \bar{P}_{Hatch,g-1}\right) \cdot h^2\right] \tag{35}$$

and:

$$\bar{P}_{Hatch,g} = \left(1 - pNOB_{g-1}\right) \cdot \left[\bar{P}_{Hatch,g-1} + \left(\left(\left(\bar{P}_{Hatch,g-1} \cdot \omega^2 + \theta_{Hatch} \cdot \sigma^2\right)/\left(\omega^2 + \sigma^2\right)\right) - \bar{P}_{Hatch,g-1}\right) \cdot h^2\right]$$
$$+ pNOB_{g-1} \cdot \left[\bar{P}_{Nat,g-1} + \left(\left(\left(\bar{P}_{Nat,g-1} \cdot \omega^2 + \theta_{Hatch} \cdot \sigma^2\right)/\left(\omega^2 + \sigma^2\right)\right) - \bar{P}_{Nat,g-1}\right) \cdot h^2\right] \tag{36}$$

Data sources

The analytical methods applied by the HSRG used the following parameter values in all
analyses in order to model the long-term genetic effects of the natural population of
hatchery-origin fish spawning naturally:

$$\sigma_{Nat}^2 = \sigma_{Hatch}^2 = 10.0$$
$$\theta_{Hatch} = 80.0$$
$$\theta_{Nat} = 100.0$$
$$h_{Nat}^2 = h_{Hatch}^2 = 0.5$$
$$\omega^2 = 10 \cdot \sigma^2 = 100.0 \text{ (Strong selection)}$$

3.0 Analysis Tool

The calculations described above are contained within "All H Analyzer" (AHA)
analytical tool. The AHA tool is a Microsoft Excel-based application to evaluate salmon
management options in the context of the four "Hs"—**H**abitat, [passage through the]
Hydroelectric system, **H**arvest, and **H**atcheries. The AHA calculator integrates the four

"Hs" using the methods described previously to estimate equilibrium natural escapement, broodstock requirements, and harvest by fishery for natural- and hatchery-origin fish.

Most importantly, AHA estimates reflect a measure of hatchery influence on natural populations that is a function of both the percent hatchery-origin spawners in the natural escapement and the percent of natural-origin broodstock incorporated into the hatchery program. The assumptions underlying these fitness impacts are based on recently published work (Ford 2002, Lynch and O'Hely, 2001) and further development of these ideas by Campton, Busack, and Currens (personal communication 2002).

The AHA tool consists of a battery of interconnected modules for each H incorporating the equations described previously to estimate total recruits, escapement, and harvest for populations and hatchery programs. A critical feature of the analytical tool is the distribution of hatchery recruits to harvest, those recovered back at the point of release, and those straying to spawn in natural populations in the Columbia Basin. In turn, the number of strays to natural populations affects the degree of hatchery influence in all natural populations receiving strays, and thus the fitness, abundance, and harvest potential for each population.

The purpose of the AHA tool is to allow managers to explore the implications of alternative ways of balancing hatcheries, harvest, habitat, and hydrosystem constraints. This tool is not used to make decisions nor to judge the "correctness" of management policies. Rather, it illustrates the implications of alternative ways of balancing the four "Hs" so that informed decisions can be made.

AHA should not be viewed as a new tool to predict habitat, harvest, or hydro effects to populations, but rather as a platform for integrating existing analyses. AHA makes relatively few new assumptions; instead, it brings together the results of other models, such as EDT for habitat, SIMPASS, or CriSP for Columbia River hydroelectric passage, and others. It does not replace these other models but instead relies on them for input. AHA is thus a relatively simple aid to regional decision making which, by incorporating the results of other models, can rapidly explore the impacts of very detailed scenarios relating to one or more of the "Hs".

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