Appendix A

White Papers

White Paper No. 1[1]

Predicted Fitness Effects of Interbreeding between Hatchery and Natural Populations of Pacific Salmon and Steelhead

1 Introduction

The propagation of Pacific salmon and steelhead (*Oncorhynchus* spp.[2]) in hatcheries has raised concerns for more than 30 years regarding the long-term genetic effects of hatchery-origin fish on the mean fitness of natural populations (Reisenbichler and McIntyre 1977; Campton 1995; Naish et al. 2007). In general, hatchery-origin fish have lower smolt-to-adult survivals (*viability fitness*) and reproductive success (*reproductive fitness*) in nature than do natural-origin fish (Berejikian and Ford 2004; Araki et al. 2008). Environmental effects associated with artificial feeding and rearing in hatcheries are clearly factors contributing to those fitness differences under natural conditions. However, most traits related to fitness (e.g., fecundity, age at sexual maturity) in salmonid fishes have heritabilities[3] greater than zero (Carlson and Seamons 2008), thus providing a genetic mechanism for hatchery populations to respond phenotypically over multiple generations to *domestication selection* in the hatchery environment.[4] Moreover, phenotypic differences between hatchery and wild fish often increase as a function of the number of generations that fish are propagated artificially, consistent with expectations for heritable traits under selection (Araki et al. 2007). Perhaps the best-known example of heritable selection responses in hatchery populations of Pacific salmon and steelhead are

[1] This white paper was prepared by the HSRG to address topics relevant to hatchery reform. It is intended to provide background, documentation and explanations not included in the body of the HSRG's report.

[2] Species include Chinook salmon (*O. tshawytscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), pink salmon (*O. gorbuscha*), sockeye salmon (*O. nerka*), and steelhead (*O. mykiss*).

[3] The *heritability* (h^2)of a trait is defined as the proportion of the total phenotypic variance (V_P) of a trait in a population that is heritable due to *additive* genetic variance (V_A) among individuals within that population ($h^2 = V_A/V_P$; $0 \leq h^2 \leq 1.0$). Most traits are also influenced significantly by environmental and non-inherited sources of genetic variation (i.e., *dominance* and *epistasis*). Indeed, h^2 has been estimated to be less than 0.5 for most traits related to survival or fitness.

[4] Artificial selection in a hatchery environment is often referred to as *domestication selection* (Doyle et al. 1983). Domestication selection includes "natural selection" in the hatchery environment, non-random selection of parents – including non-random culling of progeny - by hatchery personnel (aka "selective breeding"), and random genetic changes resulting from relaxation of natural selection that normally occurs in the "wild" environment (e.g., selection on spawning behavior). Single-generation responses (R) to selection in a population for a particular trait are commonly measured by $R = \mu_P' - \mu_P$, where μ_P' and μ_P are the mean value of the trait in the progeny and parental generations, respectively. This response can be predicted by $\hat{R} = h^2(\mu_S - \mu_P)$, where h^2 is the heritability of the trait in the population, and μ_S is the mean value of the trait for the selected parents (spawners) of the parental generation. In practice, the phenotypic value for each selected parent needs to be weighted by their respective number of progeny. The quantity $\mu_S - \mu_P$ is defined as the *selection differential* (SD) on the trait ($\hat{R} = h^2 \cdot SD$).

shifts in the mean and range of return and spawn dates of adults - as measured by Julian calendar day – relative to natural populations (Mackey et al. 2001; Quinn et al. 2002; Knudsen et al. 2006). Responses to selection for many other traits have been documented or inferred (Berejikian 1995; Fleming et al. 2002; Heath et al. 2003).

The natural spawning of hatchery fish clearly poses genetic risks to natural populations of Pacific salmon and steelhead (Busack and Currens 1995; Currens and Busack 2004). However, those risks and associated effects are difficult to quantify and detect. Based on known phenotypic differences between hatchery and wild fish for heritable traits, the natural spawning of hatchery-origin fish – including the direct interbreeding of hatchery and wild fish in nature – is expected to reduce the mean fitness of natural-origin fish and, hence, reduce the overall productivity[5] of natural populations (Reisenbichler and Rubin 1999; Chilcote 2003; Goodman 2005). Genetic effects are particularly difficult to detect because they are manifested over multiple generations and are usually confounded with other factors that can reduce productivity (e.g., habitat degradation, indirect harvests on wild fish in fisheries targeting hatchery fish, etc.).

The natural spawning of hatchery fish can also increase the total number of fish spawning in a watershed, thus potentially yielding increased numbers of natural-origin smolts and adult recruits in the progeny generation (Bugert 1998; Reisenbichler 2004; Baumsteiger et al. 2008). However, these latter single-generation demographic benefits are sustainable only if they *exceed* the predicted reductions in genetic viability and reproductive fitness of natural-origin fish in subsequent generations. Many hatchery programs for Pacific salmon and steelhead are characterized by large numbers of hatchery-origin adults that, each year, escape fisheries and spawn naturally in watersheds where those fish were released as juveniles. As a consequence, the long-term genetic effects of hatchery fish spawning naturally to natural populations need to be assessed relative to potential demographic benefits when evaluating the benefits and risks of any hatchery program.

The Hatchery Scientific Review Group (HSRG) was tasked with developing hatchery management *solutions* that would allow hatcheries to continue supporting fisheries in a sustainable manner while, at the same time, minimizing or reducing risks to natural populations (Mobrand et al. 2005). The HSRG specifically needed a quantitative method for assessing the long-term fitness effects to natural populations of hatchery fish spawning naturally over multiple generations.

Several theoretical models have been used for assessing the genetic effects of captively-bred animals reproducing in nature with natural populations (Lynch and O'Hely 2001; Ford 2002; Theodorou and Couvet 2004; Goodman 2005). Each of those models has strengths and weaknesses. Of the models currently available, the HSRG adopted the model described by Ford (2002) for its assessments. This model was selected because of its relative simplicity and well-established foundation in quantitative genetics (Bulmer 1985). The HSRG has included the equations of Ford (2002) as algorithmic components

[5] *Productivity* is commonly measured as the mean number of adult recruits (R) of the parental generation per adult spawner (S) of the parental generation, and is often symbolized as "*R/S*". However, *productivity* - in a population dynamics sense - is more precisely defined as the slope at the origin ($S = 0$, $R = 0$) of the spawner-recruitment curve, or function, that defines the empirical mathematical relationship between adult spawner abundance and adult recruit abundance one generation later.

of the *All-H Analyzer* (*AHA*)[6], a hatchery management planning tool designed to assess the combined effects of habitat, hydropower dams, harvest, and hatcheries on the abundance and overall population dynamics of hatchery and wild populations of Pacific salmon and steelhead in the Pacific Northwest.

The paper presented here provides a detailed explanation of the Ford (2002) *phenotypic fitness model* and its direct application to the management of hatchery and wild populations of salmon and steelhead in the Pacific Northwest. Although the mathematical and biological foundations of the model have been thoroughly described elsewhere (Lande 1976; Bulmer 1985; Via and Lande 1985; Ford 2002), the direct application of this model to the complex task of managing hundreds, perhaps thousands, of hatchery and wild populations of Pacific salmon and steelhead has not yet been described. The explanations provided here are intended to serve as a primer for the HSRG's analyses and for entry into the scientific literature.

2 The model: gene flow and selection in two environments (after Ford 2002)

Ford's (2002) *phenotypic fitness model* is a two-population extension of the classic one-population selection model (Bulmer 1985; Appendix). The model assumes the following (after Lande 1976):

- A single trait is under selection with different optimum values, θ_W or θ_H, for fish that are the product of reproduction and early rearing in the wild and hatchery environments, respectively;
- Phenotypic traits are normally distributed and are subject to *Gaussian* selection;
- All adults mate randomly within each environment, not assortatively by origin;
- Populations reproduce as discrete generations;
- Population sizes are large so that random genetic drift, phenotypic plasticity, and other stochastic forces can be ignored;
- All changes in the mean value of a trait between generations are due to the deterministic forces of selection and gene flow;
- Selection does not reduce population sizes, the total genetic variance, or heritability of the trait over time. This form of selection is commonly call "soft selection (Demeeus et al. 1993).

Under the two-population model (Fig. 1), the phenotypic distributions of hatchery and wild fish are assumed to have equal variances (σ^2) but different phenotypic optima, θ_H and θ_W, respectively, resulting from reproduction and early rearing in different environments (Fig. 2). The quantity $|\theta_W - \theta_H|$ measures the *magnitude* of domestication selection in the hatchery environment relative to natural selection in the wild environment.

[6] The *All-H Analyzer* (AHA) tool is a Microsoft Excel® program based on the Beverton-Holt spawner-recruit model. It quantifies the mean number and fate (harvest, hatchery, habitat) of adult recruits each generation. The model and User's Guide are available at *http://www.managingforsuccess.us/site/tools_aha/321/aha.aspx.*

When gene flow occurs between two populations (e.g., hatchery and wild), equation (A6) in the appendix can be extended to the following two, single-generation recursive equations (Ford 2002, eqs. 5 and 6):

$$\overline{P}_W' = p_W\left\{\overline{P}_W + \left[\frac{\overline{P}_W\omega_W^2 + \theta_W\sigma^2}{\omega_W^2 + \sigma^2} - \overline{P}_W\right]h_W^2\right\} + (1-p_W)\left\{\overline{P}_H + \left[\frac{\overline{P}_H\omega_W^2 + \theta_W\sigma^2}{\omega_W^2 + \sigma^2} - \overline{P}_H\right]h_W^2\right\} \quad (1)$$

$$\overline{P}_H' = p_H\left\{\overline{P}_H + \left[\frac{\overline{P}_H\omega_H^2 + \theta_H\sigma^2}{\omega_H^2 + \sigma^2} - \overline{P}_H\right]h_H^2\right\} + (1-p_H)\left\{\overline{P}_W + \left[\frac{\overline{P}_W\omega_H^2 + \theta_H\sigma^2}{\omega_H^2 + \sigma^2} - \overline{P}_W\right]h_H^2\right\} \quad (2)$$

where

$\overline{P}_W'$ and $\overline{P}_H'$ = the mean phenotypic values of wild and hatchery-origin fish, respectively, in the *progeny* generation,

$\overline{P}_W$ and $\overline{P}_H$ = the mean phenotypic values of wild and hatchery-origin fish, respectively, in the *parental* generation,

p_W and $1\text{-}p_W$ = the *proportional genetic contributions* of wild and hatchery-origin parents respectively, to the production of wild (natural-origin) fish in the progeny generation (natural reproduction),

p_H and $1\text{-}p_H$ = the *proportional genetic contributions* of hatchery and wild-origin parents, respectively, to the production of hatchery-origin fish in the progeny generation (hatchery reproduction), and

θ, σ^2, h^2, and ω^2 = the phenotypic optimum, phenotypic variance, heritability, and variance of the fitness function (Fig. 2), respectively, for a quantitative trait, where the subscripts "*W*" and *"H"* for those parameters refer to fish that are the product of natural and hatchery reproduction, respectively.

The parameter p_W can be defined also as the mean proportion of progeny genes in the wild population derived each generation from natural-origin parents. Similarly, the parameter p_H can be defined as the mean proportion of progeny genes in the hatchery population derived each generation from hatchery-origin parents. Equations (1) and (2) are identical to equations (5) and (6) of Ford (2002), except that Ford (2002) assumed that heritabilities in the two environments are equal.

The mean phenotypic value for a trait in each environment (hatchery or wild) is a function of selection acting on each of two components: selection acting on wild and hatchery fish in the wild environment with proportions p_W and $1.0\text{-}p_W$, respectively (eq. 1), and selection acting on hatchery and wild fish in the hatchery environment with proportions p_H and $1.0\text{-}p_H$, respectively (eq. 2). If $p_W = 1.0$, then equation (1) reduces to equation (A6) as a "closed" wild population. Similarly, if $p_H = 1.0$, then equation (2) reduces to equation (A6) as a "closed" hatchery population. When those parameters do not equal 1.0, then selection in one environment can affect phenotypic values and fitness of fish produced via reproduction in the other environment. For a large number of hatchery populations in the Pacific Northwest, p_H equals 1.0 while p_W is less than 1.0 for natural populations. As a result, significant one-way gene flow can occur each generation from a hatchery population to a natural population.

One-way or two-way gene flow between two populations and environments is expected to result in mean phenotypic values for hatchery and/or wild fish that are intermediate to the optimum phenotypic values for each of the two environments (Fig. 2). Stabilizing selection within each environment, coupled with divergent selection between environments, attempts to drive the mean phenotypic value of each population towards their respective optima in each environment. However, gene flow between environments (e.g., hatchery fish spawning naturally) attempts to homogenize populations genetically, thus yielding phenotypic means that are intermediate between the two phenotypic optima. In other words, stabilizing selection drives the mean phenotypic values and underlying gene frequencies of hatchery and wild fish apart towards their respective optima in each of the two environments, whereas gene flow between environments acts to homogenize gene frequencies between them.

If the gene flow parameters ($p_W$and p_H) and phenotypic optima ($\theta_W$and θ_H) are assumed to be constants[7], then - over many generations - a balance between gene flow and selection in the two environments is expected to occur resulting in a *stable equilibrium* in the mean phenotypic values of hatchery and wild fish, respectively. When an equilibrium between selection and gene flow is achieved, then the mean phenotypic values of hatchery and wild fish will not change between generations: $\overline{P}_W' = \overline{P}_W$ and $\overline{P}_H' = \overline{P}_H$.

Setting $\overline{P}_W' = \overline{P}_W = \hat{P}_W$ and $\overline{P}_H' = \overline{P}_H = \hat{P}_H$ in equations (1) and (2) and then solving for $\hat{P}_W$ and $\hat{P}_H$, where $\hat{P}_W$ and $\hat{P}_H$ are the mean phenotypic values of wild and hatchery fish, respectively, at equilibrium, yields the following two equations (after Ford 2002):

$$\hat{P}_W = \frac{\sigma^2\left[\theta_W h^2 + \left(1.0 - h^2\right)\left(\theta_W q_H + \theta_H q_W\right)\right] + \theta_W q_H \omega_H^2 + \theta_H q_W \omega_W^2}{\sigma^2\left[h^2 + \left(1.0 - h^2\right)\left(q_W + q_H\right)\right] + q_W \omega_W^2 + q_H \omega_H^2} \quad (3)$$

$$\hat{P}_H = \frac{\sigma^2\left[\theta_H h^2 + \left(1.0 - h^2\right)\left(\theta_W q_H + \theta_H q_W\right)\right] + \theta_W q_H \omega_H^2 + \theta_H q_W \omega_W^2}{\sigma^2\left[h^2 + \left(1.0 - h^2\right)\left(q_W + q_H\right)\right] + q_W \omega_W^2 + q_H \omega_H^2} \quad (4)$$

where

$q_W = 1.0 - p_W =$ the proportional genetic contribution of hatchery-origin parents to wild progeny each generation (natural reproduction),

[7] In practice, these parameters behave more like random variables than fixed constants, but their variances may vary widely depending on the trait. For example, we might expect the optimum spawn date for a particular natural population to vary widely from year to year depending on seasonal weather conditions. On the other hand, the optimum phenotype for traits related to morphology or egg size may have a relatively low variance and behave more like fixed parameters than random variables. For the purpose of understanding the combined effects of natural selection and gene flow, the aforementioned parameters can be assumed to reflect their long-term averages over many generations.

$q_H = 1.0 - p_H =$ the proportional genetic contribution of wild-origin parents to hatchery progeny each generation (hatchery reproduction),

and σ^2, θ_C, θ_W, h^2, ω_W^2, ω_C^2 are as described previously, but where the heritabilities of the trait are assumed to be equal in the two environments ($h_W^2 = h_H^2 = h^2$).

Equations (3) and (4) are identical to equations (7) and (8), respectively, of Ford (2002) except the terms have been rearranged in equations (3) and (4) above in terms of *1.0-h²* (instead of *h²-1.0*), and with the substitutions $q_W = 1.0 - p_W$ and $q_H = 1.0 - p_H$. These rearrangements show the inherent symmetry of the equilibrium relationships for $\hat{P}_W$ and $\hat{P}_H$: equations (3) and (4) are identical to each other except for the parameter θ_H or θ_W in the first term within brackets in the numerators of the two expressions.

3 Parameterization of the gene flow, selection equations

Equations (3) and (4) are complicated but can be parameterized to yield much simpler expressions. In the classic quantitative genetics model (Falconer and MacKay 1996), the phenotypic distributions of quantitative traits are assumed to be normally distributed ~ $N(\mu, \sigma^2)$ with expected mean value = μ and variance = σ^2 (Note: Non-normal traits can be *normalized* statistically by the appropriate transformation). As noted previously, the magnitude of the difference in the phenotypic optima for any particular trait in the wild and hatchery environments, $|\theta_W - \theta_H|$, is a measure of the strength of domestication selection in the hatchery environment relative to natural selection in the wild environment. Although the exact values of θ_W and θ_H may be unknown for any particular trait, their parameterized difference $\theta_W - \theta_H$ can be set as multiples of σ, the phenotypic standard deviation of the trait, such that $\theta_W - \theta_H = 1.0\sigma$, 2.0σ, or 3.0σ, etc., depending on the trait in question and the amount of domestication selection that may be occurring for any specific or hypothesized trait. If the phenotypic variances (σ^2) are equal for the two populations, then the phenotypic distributions for hatchery and wild fish will overlap by approximately 61%, 32%, or 13% when $\theta_W - \theta_H = 1.0\sigma$, 2.0σ, or 3.0σ, respectively, assuming each population is optimally adapted to the respective environment and no gene flow occurs between them.[8] Consequently, empirical information regarding the amount of overlap between the phenotypic distributions for hatchery and wild fish for one or more traits can be used to establish values of $\theta_W - \theta_H$ relative to σ. Moreover, any normally distributed trait with expected value = μ and variance = σ^2 can be "standardized" by subtracting the expected value of the trait from its observed value and dividing by the square root of the variance (σ = standard deviation). This transformation yields a *standardized* normal distribution with an expected value (μ) = 0 and a variance (σ^2) = 1.0. These latter substitution allowing further simplification of equations (3) and (4) by setting $\sigma^2 = 1.0$, and then establishing values of $\theta_W - \theta_H$ as potential multiples of σ.

[8] The extent of overlap of the phenotypic distributions can be determined easily from tables of the standardized normal distribution when σ^2 is equal in the two populations and the difference in their expected values (means) are expressed as multiples of σ.

If equations (3) and (4) are used to plot $\hat{P}_W$ and $\hat{P}_H$ (y-axis) versus q_W or q_H (x-axis) for various values of $\theta_W - \theta_H$, then one can easily show that the overall shapes of those curves are identical regardless of the actual value of $\theta_W - \theta_H$; only the *scales* (i.e., range of values) of the y-axis for those relationships change.[9] For example, if we assume the value of θ_W is greater than the value of θ_H, then neither $\hat{P}_W$ nor $\hat{P}_H$ can exceed θ_W, nor can they be less than θ_H. Indeed, plots of $\hat{P}_W$ vs. q_W or q_H ($0 \leq q_W$, $q_H \leq 1.0$) will each vary identically between θ_W and θ_H regardless of the actual parameter values of θ_W and θ_H, assuming all other parameters (e.g., h^2) are held constant. This simple relationship between (a) the mean phenotypic values of hatchery and wild fish, respectively, and (b) the gene flow parameters q_W and q_H, allow further simplification of equations (3) and (4). Consequently, for the purpose of evaluating the combined effects of natural selection in the wild environment, domestication selection in the hatchery environment, and gene flow between them, one can set $\theta_W - \theta_H = 1.0\,\sigma$, or simply $\theta_W - \theta_H = 1.0$ for $\sigma^2 = 1.0$. Moreover, one can further set $\theta_W = 1.0$ and $\theta_H = 0$ without changing the *relative values* of $\hat{P}_W$ and $\hat{P}_H$ with respect to each other *or* with respect to the phenotypic optima in the two environments. If heritabilities and selection intensities are further assumed to each be equal in the two environments ($h_W^2 = h_H^2 = h^2$, $\omega_W^2 = \omega_H^2 = \omega^2$), then equations (3) and (4) reduce to the following two simplified expressions:

$$\hat{P}_W = \frac{h^2 + (1.0 - h^2 + \omega^2) \cdot q_H}{h^2 + (1.0 - h^2 + \omega^2) \cdot (q_H + q_W)} \qquad (5)$$

$$\hat{P}_H = \frac{(1.0 - h^2 + \omega^2) \cdot q_H}{h^2 + (1.0 - h^2 + \omega^2) \cdot (q_H + q_W)} \qquad (6)$$

for $\sigma^2 = 1.0$, $\theta_W = 1.0$, and $\theta_H = 0$.

As noted previously, the terms q_W and q_H represent the mean proportional genetic contributions each generation of hatchery and wild fish to natural-origin and hatchery-origin progeny, respectively. In practice, those quantities are very difficult to estimate, particularly for natural populations. Alternatively, one can use the mean proportion of a hatchery broodstock composed of natural-origin fish (*pNOB*) and the mean proportion of naturally-spawning fish composed of hatchery-origin fish (*pHOS*) as approximate

[9] One can easily demonstrate this uniform relationship by setting up plotting routines of $\hat{P}_W$ or $\hat{P}_H$ vs. q_W or q_H, respectively, via equations (3) and (4), and then substituting various values of θ_W and θ_H while holding all other parameters constants. The scale of the y-axis will change, but the shape of the curves will remain constant.

surrogates for q_H and q_W, respectively.[10] These latter substitutions yield the following approximations:

$$\hat{P}_W \approx \frac{h^2 + (1.0 - h^2 + \omega^2) \cdot pNOB}{h^2 + (1.0 - h^2 + \omega^2) \cdot (pNOB + pHOS)} \quad (7)$$

$$\hat{P}_H \approx \frac{(1.0 - h^2 + \omega^2) \cdot pNOB}{h^2 + (1.0 - h^2 + \omega^2) \cdot (pNOB + pHOS)} \quad (8)$$

where

pNOB = mean proportion of a hatchery broodstock composed of natural-origin adults each year, and

pHOS = mean proportion of natural spawners in a watershed or stream composed of hatchery-origin adults each year.

$\hat{P}_W$ and $\hat{P}_H$ in equations (7) and (8) will each vary between $\theta_H = 0.0$ and $\theta_W = 1.0$ depending on the relative values of *pNOB* and *pHOS*. Also, $\hat{P}_W$ will always equal $\theta_W = 1.0$ if *pHOS* = 0, and $\hat{P}_H$ will always equal $\theta_H = 0.0$ if *pNOB* = 0. In other words, a wild population will be optimally adapted to a natural environment if no hatchery fish spawn naturally, and a hatchery population will be optimally adapted to the hatchery environment if no wild fish are included with the broodstock. Equations (7) and (8) quantify those relationships for traits where $\theta_H \neq \theta_W$.

4 Proportionate Natural Influence (*PNI*)

When the phenotypic distributions of hatchery and wild fish are *standardized* with $\theta_H = 0.0$ and $\theta_W = 1.0$, as was done for equations (5) through (8) above, then $\hat{P}_W$ and $\hat{P}_H$ can be interpreted as the *proportional genetic influence* of the natural environment on the mean phenotypic values of wild and hatchery fish, respectively. Thus, equations (7) and (8) can be further generalized to the following two expressions:

$$PNI_{Wild} \approx \frac{h^2 + (1.0 - h^2 + \omega^2) \cdot pNOB}{h^2 + (1.0 - h^2 + \omega^2) \cdot (pNOB + pHOS)} \quad (9)$$

$$PNI_{Hatch} \approx \frac{(1.0 - h^2 + \omega^2) \cdot pNOB}{h^2 + (1.0 - h^2 + \omega^2) \cdot (pNOB + pHOS)} \quad (10)$$

[10] The acronyms *pNOB* (proportion of *natural-origin broodstock*) and *pHOS* (proportion of *hatchery-origin spawners*) were first proposed in 2004 by Craig A. Busack, Washington Department of Fish and Wildlife, Olympia, WA, at an HSRG workshop held in Seattle, Washington, USA.

where *PNI* refers to the *proportionate natural influence* of the wild environment on the mean phenotypic values and genetic constitutions of wild (eq. 9) and hatchery (eq. 10) fish, respectively.[11] *PNI* varies from 0.0 to 1.0, where *PNI* = 0.0 or 1.0 imply that the genetic constitution and mean phenotypic values for a population are influenced only by the hatchery or natural environment, respectively.

PNI values for hatchery and wild fish will not be identical (eqs. 9 and 10). This difference occurs, even at equilibrium with two-way gene flow, because wild fish always have one extra generation of reproduction and selection (*natural*) in the wild environment, while hatchery fish always have one extra generation of reproduction and selection (*domestication*) in the hatchery environment. As a result, PNI_{Wild} will always be greater than zero, and PNI_{Hatch} will always be less than 1.0. For example, if *pHOS* = 1.0 and *pNOB* = 0, then $PNI_{Wild} = h^2/(1.0 + \omega^2)$, which is its lowest possible value (eq. 9). Similarly, if *pNOB* =1.0 and *pHOS* =0, $PNI_{Hatch} = 1.0 - h^2/(1.0 + \omega^2)$, which is its highest possible value (eq. 10).

5 Genetic consequences of gene flow between hatchery and wild populations

The relationships among PNI_{Wild}, PNI_{Hatch}, *pHOS*, and *pNOB* (eqs. 9 and 10) are illustrated in Figures 3 through 8 for various values of h^2 and ω. Two sets of heritabilities were used for generating those graphs: $h^2 = 0.2$ (*moderate* heritability) and $h^2 = 0.5$ (*high* heritability). Similarly, two selection intensities were used to generate Figures 3 through 8: $\omega = 10\sigma$ (*weak* selection) and $\omega = 3\sigma$ (*strong* selection). As noted in Appendix A, $\omega^2 = 100\sigma^2$ ($\omega = 10\sigma$) is considered *weak selection*, and $\omega^2 = 10\sigma^2$ ($\omega = 3.16\sigma$) is considered *strong selection* (Lande 1976; see also Fig. 2). The phenotypic variance (σ^2) was set equal to 1.0 in all plots based on a standardized normal distribution (eqs. 3 and 4).

The first conclusion to be drawn is that relatively small amounts of one-way gene flow between the hatchery and wild populations, continuously over many generations, can have a rather profound genetic effect on the recipient population (Figs. 3 and 4). When *pNOB* = 0 and a hatchery broodstock is composed of only hatchery-origin adults each year, the natural spawning of hatchery fish over many generations can significantly reduce *PNI* for wild fish (PNI_{Wild}), even for relatively low values of *pHOS* (Fig. 3). For example, when *pNOB* equals zero, a value of *pHOS* equal to only 0.05 (5%) results in $PNI_{Wild} < 0.5$ in all cases except when heritabilities and selection intensities are both high ($h^2 = 0.5$; $\omega = 3\sigma$, Fig. 3). Similarly, one-way gene flow from the natural environment to the hatchery environment can significantly increase *PNI* for hatchery-origin fish (PNI_{Hatch}) if *pHOS* equals zero (Fig. 4). Figures 3 and 4 also show that selection intensity has a greater influence than heritability on the shape of the *PNI* curves: as the value of ω decreases, selection intensity increases (Fig. 2), thereby increasing the ability of selection to resist the homogenizing effects of gene flow between populations. Figure 4 is clearly the mirror image of Figure 3, reflecting the symmetry of equations (3) and (4), and equations (9) and (10).

The relationship between PNI_{Wild} and *pHOS* for varying values of *pNOB* is particularly important for assessing long-term genetic risks of hatchery programs to naturally

[11] The term *proportionate natural influence* (*PNI*) was first proposed in 2004 by Craig A. Busack, Washington Department of Fish and Wildlife, Olympia, WA, at an HSRG workshop held in Seattle, Washington, USA.

spawning populations (Figs. 5 and 6). When *pHOS* is greater than 5% (0.05), then wild fish must be included with a hatchery broodstock to achieve $PNI_{Wild} > 0.5$ for traits with moderate heritability and high selection intensity (Figs. 5 and 6). Indeed, increasing the proportion of a broodstock composed of wild fish from *pNOB* = 0 to *pNOB* = 0.1 can increase PNI_{Wild} substantially, but only if *pHOS* is less than 30% (bottom two curves in Fig. 5; Fig. 6). However, *pNOB* must exceed *pHOS* to ensure a value of PNI_{Wild} greater than 0.5, the value at which the hatchery environment is having a 50% influence on the genetic make-up of a naturally spawning population. Moreover, increasing *pNOB* from 0.5 to 1.0 for *pHOS* > 0.3 is not nearly as effective at increasing PNI_{Wild} as increasing *pNOB* from 0 to 0.5 for *pHOS* < 0.3 (Fig. 6). In other words, the effectiveness of including wild fish in a hatchery broodstock to increase PNI_{Wild} decreases rapidly as *pHOS* increases (Figs. 5 and 6). These results indicate that, over a broad range of possible *pHOS* values, decreasing *pHOS* is a much more effective method for increasing PNI_{Wild} than increasing *pNOB*. These graphs also demonstrate the expected result that PNI_{Wild} and PNI_{Hatch} will both equal approximately 0.5 when *pNOB* = *pHOS*.

In practice, the abundance and viability of a naturally spawning population may limit the number of wild fish available for broodstock, further restricting the upper value of PNI_{Wild}. For example, if *pNOB* = 0.1, then the relationship between PNI_{Wild} and *pHOS* approximates a negative exponential such that all values of *pHOS* greater than approximately 30% result in very low *PNI* values (Fig. 5). In this latter situation, a naturally spawning population composed of 30% hatchery-origin fish over many generations is nearly equivalent genetically to a naturally spawning population composed of 100% hatchery-origin fish with no natural-origin spawners. In this case, a 10% gene flow rate from the natural environment to the hatchery environment is unable to compensate genetically for the large proportion of naturally spawning fish composed of hatchery fish. These results further illustrate the need to reduce *pHOS*, not increase *pNOB*, as the most effective way to increase PNI_{Wild}. These results also demonstrate the desirability of maintaining *pHOS* below a maximum value of 20-30% to achieve a value of $PNI_{Wild} > 0.5$, but only if wild fish can be included in the broodstock at a rate that allows *pNOB* to exceed *pHOS* (Fig. 5). Ultimately, the viability and abundance of a naturally spawning population will determine the absolute number of wild fish that can be included in a hatchery broodstock to maintain the desired *PNI* value for both hatchery and natural-origin fish.

When *pNOB* and *pHOS* are both greater than zero, the shapes of the *PNI* curves for wild and hatchery fish (PNI_{Wild} and PNI_{Hatch}, respectively) will be similar but not identical (Figs. 7 and 8; see also eqs. 9 and 10). The close similarity of PNI_{Wild} and PNI_{Hatch} under conditions of two-way gene flow is somewhat independent of the heritability of the trait. However, PNI_{Wild} and PNI_{Hatch} can differ substantially for traits under *strong selection*, particularly when *pNOB* or *pHOS* equal zero (Figs. 3 and 4).

6 Approximate *PNI* index

The close similarity of PNI_{Wild} and PNI_{Hatch} over a broad range of values for *pHOS* and *pNOB*, particularly when both are greater than zero (Figs. 7 and 8), suggests an approximation for *PNI* that can be used to quickly assess, with very few assumptions, the genetic risks posed by a hatchery population to a natural population:

$$PNI_{Approx} = \frac{pNOB}{pNOB + pHOS} \quad (11)$$

where PNI_{Approx} refers to an approximate value of PNI for both hatchery and wild fish in a particular watershed or geographic area.[12] The elegance of equation (11) is that it requires no assumptions regarding selection intensities or heritabilities associated with any specific trait; it simply approximates the relative influences of the natural and hatchery environments on the genetic constitution and mean phenotypic values of hatchery and wild fish when gene flow occurs between them (Figs. 9 and 10). PNI_{Approx} will be more similar to PNI_{Wild} when $pHOS < pNOB$ and more similar to PNI_{Hatch} when $pHOS > pNOB$ (Figs. 9 and 10). Moreover, PNI_{Approx} will always be slightly lower than PNI_{Wild} for all values of $pHOS$ if $pNOB > 0$.

Equation (11) can be used to calculate an approximate value of PNI_{Wild} (or PNI_{Hatch}) if $pNOB$ and $pHOS$ are both greater than zero. If $pNOB = 0$, then $PNI_{Hatch} = 0$ and equation (9) should be used to calculate PNI_{Wild}, assuming values for h^2 and ω similar to those presented here for this paper. Similarly, if $pHOS = 0$, then $PNI_{Wild} = 1.0$ and equation (10) should be used to calculate PNI_{Hatch}. Situations where $pHOS = 0$ and $pNOB > 0$ – that is, where no hatchery fish are spawning naturally, but wild fish are systematically included in a broodstock each year (or each generation) - are expected to be relatively rare, whereas the converse situations where $pNOB = 0$ and $pHOS > 0$ are known to be common. In these latter situations ($pNOB = 0$), equation (9) should be used to calculate PNI_{Wild} for the purpose of assessing genetic risks of a hatchery program to a natural population. Equation (9) should also be used if hatchery fish spawning naturally represent strays from another watershed, even for $pNOB > 0$ for that out-of-basin hatchery stock. In this latter situation, $pNOB$ should be set equal to zero ($pNOB = 0$) in equation (9) because the naturally-spawning population of interest makes no direct genetic contribution to the out-of-basin hatchery population that is spawning in the recipient watershed.

7 HSRG application of the selection and gene flow model

The HSRG has applied equations (1) and (2) to Beverton-Holt spawner-recruitment equations in the *AHA* model to adjust the number of natural-origin and hatchery-origin adult recruits returning each year to a watershed (see Appendix C of this HSRG report). The mean phenotypic values (eqs. 1 and 2) generated during each iteration of the *AHA* model are used to calculate a mean relative fitness ($\overline{F}$) of wild and hatchery fish each generation according to the following equations (eq. 3 of Ford 2002):

[12] *PNI = pNOB/(pNOB+pHOS)* was first proposed in 2004 by Craig A. Busack, Washington Department of Fish and Wildlife, Olympia, Washington, USA as a working index based on the equations provided by Ford (2002) and computer iterations that converged approximately to that relationship when *pNOB* and *pHOS* were both greater than zero. The HSRG adopted this index as a simple measure to assess the genetic risks of *genetically integrated* hatchery programs where wild fish are included in a broodstock and *pNOB* is greater than zero (Mobrand et al. 2005).

$$\overline{F}_W = e^{-\frac{1}{2}\frac{(\overline{P}_W-\theta_W)^2}{(\omega^2+\sigma^2)}} \quad (12)$$

$$\overline{F}_H = e^{-\frac{1}{2}\frac{(\overline{P}_H-\theta_H)^2}{(\omega^2+\sigma^2)}} \quad (13)$$

where $\overline{F}_W$ and $\overline{F}_H$ are the mean fitnesses of wild and hatchery fish, respectively, in a particular generation. The *AHA* model then apportions those mean fitnesses across each life history stage for each group of fish (hatchery or wild) to yield an adjusted number of hatchery and natural-origin progeny for each of those life history stages (eqs. 3 and 4 of Appendix C). Continued iterations of equations (1), (2), (12) and (13) presented here allow fitness effects in each parental generation to affect the mean fitness and number of adult recruits in each progeny generation via the Beverton-Holt spawner-recruit equations (see Appendix C for details). *AHA* then provides the expected mean number of adult recruits (both hatchery and wild) each year at equilibrium after many generations of iterations. This mode of selection, as implemented in *AHA*, is commonly called *hard selection* because population abundances are adjusted according to their mean relative fitnesses (Demeeus et al. 1993).

The HSRG used parameter values for the fitness functions in *AHA* that simulate traits of high heritability (h^2 = 0.5) and high selection intensity ($\omega^2 = 10\sigma^2$) in both the hatchery and natural environments. These types of traits are expected to undergo the quickest selection responses over the shortest number of generations. The equilibrium trait values resulting from those simulations (Figs. 12 and 13) yield graphs virtually identical to the *PNI* graphs for standardized traits (Figs. 5 and 6). As noted previously, the shapes of the equilibrium curves generated from equations (3) and (4) are largely independent of the optimum phenotypic values (θ_W and θ_H) and variance for the trait; rather, those curves are determined primarily by the relationship between *pNOB* and *pHOS* (q_W and q_H) and secondarily by the heritability and selection intensity of the trait (eqs. 5 and 6). These latter results (Figs. 12 and 13) further justify the use of equations (9) and (10) – and, more generically, equation (11) – to evaluate the genetic risks of hatchery programs to naturally spawning populations of salmon and steelhead in the Pacific Northwest.

8 Discussion

Many traits of anadromous salmonid fishes potentially have very different optimum values for hatchery and wild fish, especially traits subject to selective breeding by hatchery personnel (e.g., return and spawn dates of fish selected for broodstock) and traits related to natural reproduction that are relaxed in the hatchery environment (e.g., spawning behavior; see Quinn 2005 for an excellent discussion of this issue). If no *gene flow* occurs between the hatchery and natural environments, then stabilizing selection in each environment will drive the phenotypic means of each population towards their respective optima; that is, in the absence of gene flow between the two environments, hatchery and wild fish will represent two reproductively distinct populations, each *locally adapted* to their respective environments. However, if hatchery fish spawn naturally and/or wild fish are included with the broodstock each generation, then – over time – the mean phenotypic values of hatchery and/or wild fish will be influenced by the selection,

natural or *domestic*, in the other environment. The net result is that the mean phenotypic values of one or both groups of fish will be intermediate to the phenotypic optima in the two environments. The phenotypic fitness model of Ford (2002) allows assessment of those predicted effects as a function of *pNOB* and *pHOS*.

Lynch and O'Hely (2001) developed an alternative model for assessing the long-term fitness effects of captively bred populations reproducing in natural environments. Their analysis was based on relaxation of natural selection in a captive (hatchery) environment and the accumulation of mutations in the captive population that would otherwise be deleterious and selected against in the natural environment. Despite this different approach, the overall results of Lynch and O'Hely (2001) are amazingly similar to those of Ford (2002), as described here. In the model of Lynch and O'Hely (2001), the relative fitness of the natural population is largely a function of the percent of time that genes spend in the natural environment versus the hatchery environment, a quantity similar to *PNI*. Lynch and O'Hely (2001) also found that increasing the proportion of a broodstock composed of natural-origin adults (*pNOB*) from 0.5 to 1.0 had only a minor genetic benefit - relative to increasing pNOB from zero to 0.5 - at increasing the overall mean fitness of a natural population, a result again similar to that described here based on the model of Ford (2002). Similarly, Lynch and O'Hely (2001) found that reducing *pHOS* from 0.3 to 0.1 had a much greater effect at reducing the segregation load (or increasing mean fitness) of the natural population than reducing *pHOS* from 0.5 to 0.3. These parallel results reinforce the conclusions resulting from the model described by Ford (2002).

Many fishery biologists have suggested that the intensity of domestication selection in the hatchery environment must be low for anadromous salmonid fishes, particularly for species that spend only a few months in captivity prior to their release as smolts (e.g., "ocean-type" Chinook salmon). However, even for species that spend only a few weeks in freshwater prior to release from hatcheries and outmigration to saltwater (e.g., pink and chum salmon, *O. gorbuscha* and *O. keta,* respectively), natural spawning traits related to reproductive fitness have no natural environmental component for hatchery produced fish. Indeed, these latter traits are exactly the kind of traits specifically modeled by Lynch and O'Hely (2001). Artificial spawning in a hatchery can inadvertently impose unknown selection on hatchery populations, eliminate natural selection on traits essential for natural reproduction, while also reducing the genetic effective number of breeders (Campton 2004, 2005; Quinn 2005). Moreover, "natural selection" in a hatchery pond during the freshwater rearing phase can have a significant effect on smolt-to-adult survivorship during the post-release life history phases. For example, the size of fish at the time of release from a hatchery is positively correlated with post-release survival and adult return rates, suggesting that hatchery fish better adapted to hatchery culture have a post-release selective advantage in the wild (Reisenbichler et al. 2004).

The homing instinct of anadromous salmonid fishes provides an evolutionary genetic mechanism for maximizing fitness and development of local adaptations (Quinn 1993; Kinnison et al. 2001; Quinn et al. 2006). Many studies have further demonstrated a genetic component to homing (Bams 1976; McIsaac and Quinn 1988; Pascual et al. 1995; Candy and Beacham 2000; Stewart et al. 2002; Dukes et al. 2004). In general, based on controlled breeding studies, fish reared and released in their natal streams and watersheds exhibit higher homing fidelity than fish of the same population reared and released outside their natal watersheds. These latter results are consistent with *a priori* expectations that homing confers a higher mean fitness to fish that return to spawn in

areas where their parents reproduced successfully compared to fish that "stray" and spawn randomly elsewhere (Hendry et al. 2000). Many biologists have long recognized that subtle variations in the life histories of anadromous salmonid fishes can be attributed to local adaptations that appear to reflect evolutionary responses to stream specific hydrologies, water temperatures during the incubation phase, and geographic location (Hendry et al. 1998; Brannon et al. 2004; Keefer et al. 2004). These traits include date of reentry to freshwater and spawn date of adult fish, age and size at sexual maturity, fecundity and egg size of female parents, pre-hatch developmental rates of embryos, length of freshwater residence prior to outmigration, and marine migration patterns (e.g., Smoker et al. 1998). In some cases, entire geographic races have evolved in response to geographic location, hydrology, and local water temperatures (Waples et al. 2004).

The general results of the Ford (2002) model presented here, and modeled by the HSRG via *AHA*, assumed that heritabilities and selection intensities in the hatchery and wild environments were equal. In practice, the values of these parameters for some traits may differ substantially between the two environments. Selection intensity, as measured by $1/\omega^2$, is proportional to the *force* of stabilizing selection that resists genetic change and maintains phenotypic means as close as possible to the phenotypic optima for each environment. Similarly, heritability is a measure of the *efficiency* of selection acting on phenotypic variation within a population to effect genetic changes between generations. As selection intensity and heritability of a trait in a particular environment increase, the magnitude of gene flow into that population must also increase to achieve the same genetic and phenotypic outcome. For example, if the heritability of a trait is substantially greater in the hatchery environment than in the natural environment, then *pNOB* would need to exceed *pHOS* to achieve $PNI = 0.5$ because the higher efficiency of selection in the hatchery environment will be able to better resist the genetic effects of gene flow from the natural environment. Similarly, if selection intensity in the hatchery environment is greater than selection intensity in the natural environment for a particular trait, then *pNOB* will also need to exceed *pHOS* to achieve a value of $PNI = 0.5$. On the other hand, if the heritability or selection intensity on a trait are greater in the natural environment than in the hatchery environment, then a value of *pNOB* less than *pHOS* could achieve a value of $PNI = 0.5$. In practice, based on our fundamental understandings of population biology and how selection operates, one might predict – for a large number of traits related to fitness - that heritabilities in the hatchery environment may exceed those in the natural environment, but selection intensities in the natural environment may exceed those in the hatchery environment. The counteracting effects of those two unequal forces in the two environments could lead to the situation where a value of *pNOB* approximately equal to *pHOS* yields a value of $PNI \approx 0.5$ for a large number of traits.[13] The following table summarizes the necessary relationships between *pNOB* and *pHOS* to achieve $PNI = 0.5$ when heritabilities (h^2) and selection intensities ($1/\omega^2$) may not be equal in the two environments. As noted previously, the magnitude of selection intensity within each environment is proportional to $1/\omega^2$ (Fig. 2).

[13] Sensitivity analyses performed by Craig A. Busack, Washington Dept. of Fish and Wildlife, Olympia, Washington, indicate that values of *PNI* are fairly robust to violation of the assumption that heritabilities and selection intensities are equal in the two environments.

Table 1. Relative values of *pNOB* and *pHOS* to achieve *PNI* = 0.5 when heritabilities (h^2) and selection intensities (~1/ω^2) differ between natural (*W*) and hatchery (*H*) environments.

	$\omega_H^2 = \omega_W^2$	$\omega_H^2 < \omega_W^2$	$\omega_H^2 > \omega_W^2$
$h_H^2 = h_W^2$	*pNOB = pHOS*	*pNOB > pHOS*	*pNOB < pHOS*
$h_H^2 > h_W^2$	*pNOB > pHOS*	*pNOB >> pHOS*	*pNOB ≈ pHOS?*[14]
$h_H^2 < h_W^2$	*pNOB < pHOS*	*pNOB ≈ pHOS?*	*pNOB << pHOS*

The HSRG has concluded that all hatchery programs for Pacific salmon and steelhead must be classified as either *integrated* or *segregated* (Mobrand et al. 2005). The HSRG defines these terms as follow:

- A hatchery population is defined as *segregated* if it is propagated as a "closed" population where only hatchery-origin fish are used, or are intended to be used, for broodstock;
- A hatchery population is defined as *integrated* if it systematically - and purposefully - includes natural-origin fish in the broodstock, or the intent of the program is to purposefully include natural-origin fish in the broodstock, with the goal of maintaining genetic continuity and phenotypic similarity with a specific natural population.

The segregated and integrated strategies yield very different broodstock goals and propagation protocols. The segregated strategy creates a genetically-distinct, hatchery-adapted population, whereas the integrated strategy attempts to increase the abundance of fish representing an existing natural population.

Both the integrated and segregated strategies have their strengths and weaknesses. If hatchery fish can be precluded from spawning naturally, then the segregated approach may be favored if the primary purpose of the hatchery program is to produce fish for harvest. The segregated strategy will maximize the fitness of hatchery fish adapted to artificial propagation, and the genetic risks of those hatchery fish to natural populations will be minimal if – but only if - *pHOS* is near zero. However, in most instances, the natural spawning of hatchery fish cannot be precluded, and large numbers of fish from segregated hatchery populations escape harvest and broodstock recapture, thus resulting in relatively high values of *pHOS* (>10%) in many watersheds. As noted previously, the long-term genetic effects of hatchery fish spawning naturally over many generations become significant when *pHOS* approaches and exceeds 5%, particularly when pNOB = 0. One goal of the *integrated* strategy is to reduce those risks by increasing the effective *PNI* for hatchery fish where the natural spawning of those fish cannot be precluded. The

[14] The HSRG suggests heritabilities are likely to be greater in the hatchery environment than in the natural environment, but that selection intensities in the natural environment are likely to be greater in the natural environment than the hatchery environment. Under these circumstances, approximately equal levels of gene flow between the two environments may be sufficient to achieve *PNI* = 0.5.

integrated strategy is also favored for hatchery programs intended to assist with the conservation or recovery of natural populations (e.g., Olson et al. 2005). However, integrated hatchery programs inherently impose their own *demographic risks* to natural populations by "harvesting" wild fish for broodstock under the premise that the recruit-per-spawner ratio (*R/S*) is substantially greater for wild fish spawning in a hatchery than in nature. Moreover, natural populations must be viable and self-sustaining to support a "properly-integrated" hatchery population where *pNOB* - at a minimum - exceeds *pHOS*. In general, reducing *pHOS* is a much more effective and efficient method of increasing *PNI* than increasing *pNOB*. For example, increasing *pNOB* above 0.5 is expected to confer a comparatively minor genetic benefit to a naturally spawning population (Lynch and O'Hely 2001; Ford 2002; this paper) but could substantially increase demographic risks to a natural population depending on the size of the hatchery program and the total number of adult fish collected for broodstock. [15]

Minimizing *risks* of hatchery programs to natural populations of salmon and steelhead is a major goal of hatchery reform in the Pacific Northwest (Mobrand et al. 2005). As a consequence, the HSRG has established management guidelines for *PNI*, *pHOS*, and *pNOB* to minimize genetic risks to naturally spawning populations. These guidelines are based primarily on the relationships illustrated in Figs. 3 through 10.

8.1 Management guidelines for segregated hatchery programs (pNOB ≈ 0)

- **Maintain *pHOS* < 5%.**
- When *pHOS* > 5%, either (a) reduce the size of the hatchery program and/or (b) implement new measures to recapture hatchery-origin fish to reduce pHOS to <5%.

8.2 Management guidelines for integrated hatchery programs (pNOB > 0)

- **Maintain *PNI* > 0.5.** *PNI* must exceed 0.5 in order for the natural environment to have a greater influence than the hatchery environment on the genetic constitution of a naturally-spawning population. In general, this guideline requires *pNOB* > *pHOS*.[16]
- **Maintain *pHOS* < 30%.** The effectiveness and efficiency of *pNOB* for maintaining *PNI* > 0.5 decreases significantly for values of *pHOS* > 30%. Consequently, to achieve a desired *PNI* > 0.5, it is much more efficient – and less risky biologically - to reduce *pHOS* than increase *pNOB*. Increasing *pNOB* for high values of *pHOS*, as opposed to decreasing *pHOS*, imposes additional demographic (and potential genetic) risks to naturally spawning populations with comparatively minor increases in *PNI*.
- **Maintain *PNI* > 0.67 for natural populations considered essential for the recovery or viability of an *Evolutionarily Significant Unit* (ESU) of Pacific**

[15] One exception to this generalization might occur when the natural population is highly imperiled or at risk of demographic extinction. In this situation, the demographic risks to the natural population may outweigh the genetic risks, and a value of pNOB = 1.0 may be desired or necessary to reduce those demographic risks.

[16] This guideline and constraint also require a minimum pNOB > 0.10, even for values of pHOS < 0.10 (Figs. 3 and 4). One goal of an integrated hatchery program is to maintain genetic continuity and phenotypic similarity to a naturally-spawning population, and this goal requires a minimum *pNOB* ≥ 10%.

salmon or *Distinct Population Segment* (DPS) of steelhead, as those terms are defined and designated under the U.S. Endangered Species Act (ESA). The HSRG has adopted the term "primary" for natural populations considered by NOAA Fisheries[17] to be essential for the recovery of an ESU or DPS of Pacific salmon or steelhead, respectively. That designation requires a much more stringent constraint on *PNI*.

The HSRG considers the preceding guidelines as *minimal* requirements for minimizing the genetic risks of hatchery programs to naturally spawning populations. For example, a value of *pHOS* = 6% from a segregated hatchery population should not be viewed as exceeding the pHOS < 5% guideline by only 1%; on the contrary, a value of pHOS = 6% for a segregated hatchery population should be viewed as posing a significant, long-term genetic risk to the viability of a naturally spawning population if that potential level of gene flow continues unabated for many generations. Moreover, the aforementioned guidelines should not be interpreted as "benchmarks" or "goals"; rather, they should be interpreted in the context of their presentation here with respect to Figs. 3 through 10: that is, violation of any of those guidelines on a sustained basis over many generations will pose long-term genetic risks to the future viability of naturally-spawning populations.

8.3 Exceptions to the guidelines

The HSRG recognizes that many natural populations of Pacific salmon and steelhead, particularly in watersheds significantly impacted by hydropower and land use practices (e.g., logging, agriculture), may not be viable or self-sustainable at the present time. The HSRG further recognizes that hatcheries and artificial propagation can play critically-important roles at conserving genetic resources and maintaining naturally-spawning populations in areas where significant habitat impacts have occurred. In some instances, the future survival of a naturally-spawning population may require significant increases in natural productivity and recruit per spawner (R/S) ratios, measured as the mean number of natural-origin adult recruits per natural-origin adult spawner in the preceding generation. Such desired increases may not be possible under current conditions.

Consequently, the HSRG acknowledges that some hatchery programs may be required to perform a "life support" function to prevent *functional extirpation* of a naturally spawning population in particular watersheds or geographic areas. Moreover, the abundance of fish representing a natural population must be sufficiently high to allow selection in the natural environment to be an effective deterministic force towards maximizing mean population fitness in view of stochastic forces. Under these exceptional circumstances, maintaining a naturally-spawning component to a hatchery-sustained population – where the number of hatchery fish spawning naturally exceeds HSRG guidelines - may be desirable for both genetic and demographic reasons. In practice, such situations need to be clearly identified and evaluated carefully on a case-by-case basis. Deliberately allowing "surplus" hatchery fish to spawn naturally under the premise of "increasing natural production" (ISAB 2002; Brannon et al. 2004) is not the same justification as preventing local extirpation of an imperiled population; the former poses significant genetic risks whereas the latter confers conservation benefits.

[17]National Marine Fisheries Service, National Oceanic and Atmospheric Administration (NOAA), U.S. Department of Commerce, Washington, DC, USA.

9 Conclusions

Hatchery-origin fish spawning naturally over many generations pose significant long-term genetic risks to natural populations of Pacific salmon and steelhead. Those risks are primarily a function of the mean proportion of a naturally-spawning population composed of hatchery-origin fish each year. Those risks are also a function of the genetic history of the hatchery broodstock over the preceding generations.

When the genetic risk guidelines presented here are violated, the most expeditious and biologically efficient solution is to reduce the number of hatchery-origin fish spawning naturally. This can be accomplished by a number of methods, the simplest of which is to reduce the size of the hatchery program and the number of hatchery-origin fish that are released, at least until other solutions can be implemented (e.g., construction of a weir at a hatchery, implementation of *mass marking* of hatchery fish coupled with intense selective fisheries on hatchery fish).

Genetically-*integrated* hatchery populations can reduce genetic risks to naturally spawning populations, and they can also provide long-term conservation benefits, but they also impose additional *demographic* risks to naturally spawning populations that are not imposed by *segregated* programs. Consequently, reducing *pHOS* should be considered the first management option of choice – rather than increasing *pNOB* - whenever the genetic risk guidelines presented here are violated.

A careful evaluation of the viability of a naturally spawning population, and its biological capability to adequately support a genetically-integrated hatchery program, will be necessary before a segregated hatchery program is converted to an integrated one under the umbrella of "hatchery reform". In most cases, a *sliding scale* may be necessary to adjust the number of natural-origin fish retained for broodstock each year based on the abundance of natural-origin recruits returning to a watershed (e.g., Olson et al. 2005). In all cases, either *pHOS* needs to be maintained at less than 5% (*segregated* programs) or PNI needs to exceed 0.5 to 0.67 (*integrated* programs) to minimize genetic risks to natural populations.

Violations of the guidelines presented here over many generations may jeopardize the future viability and self-sustainability of a natural population. Ultimately, implementation of the HSRG guidelines may represent trade-offs between maintaining benefits and reducing risks of a hatchery program. If resource managers intentionally do not rectify violations of biological guidelines in order to maintain perceived benefits - regardless of whether those guidelines are genetic guidelines, fish health guidelines or other guidelines intended to protect the viability of a biological resource - then those managers need to justify their actions to the scientific community and the general public. Resource managers need to be accountable for their decisions when they contradict established biological principles.

In the long run, resource managers should follow three principles established by the HSRG for hatchery programs: (1) explicitly state the goals of each hatchery program quantitatively in terms of desired or intended benefits; (2) provide scientific justification for each hatchery program through appropriate benefit-risk analyses, including scientific justification of all the methods and protocols (e.g., spawning protocols, rearing protocols) associated with execution of the program; and (3) monitor and evaluate the program annually to determine whether the intended benefits are realized, and whether biological risks exceed established guidelines. The information obtained from (3) should then be used to adjust the program on a regular basis with the goal of increasing benefits and/or

reducing risks. This three step process is nothing less than the foundation of hatchery reform in the Pacific Northwest.

10 Literature cited

Araki, H., Cooper, B., Blouin, M.S. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science 318: 100-103.

Araki, H., Berejikian, B.A., Ford, M.J., and Blouin, M.S. 2008. Fitness of hatchery-reared salmonids in the wild. Evolutionary Applications 1:342-355.

Bams, R.A. 1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (Oncorhynchus gorbuscha). Journal of the Fisheries Research Board of Canada 33: 2716-2725.

Baumsteiger, J., Hand, D.M., Olson, D.E., Spateholts, R., FitzGerald, G., and Ardren, W.R. 2008. Use of parentage analysis to determine reproductive success of hatchery-origin spring Chinook salmon outplanted into Shitike Creek, Oregon. North American Journal of Fisheries Management 28: 1472-1485.

Berejikian, B.A. 1995. The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (Oncorhynchus mykiss) to avoid a benthic predator. Canadian Journal of Fisheries and Aquatic Sciences 52: 2476-2482.

Brannon, E.L. and 10 coauthors 2004. The controversy about salmon hatcheries. Fisheries 29(9): 12-31.

Brannon, E.L., Powell, M.S., Quinn, T.P., and Talbot, A. 2004. Population structure of Columbia River Basin Chinook salmon and steelhead trout. Reviews in Fisheries Science 12: 99-232.

Bugert, R.M. 1998. Mechanics of supplementation in the Columbia River. Fisheries 23: 11-20.

Bulmer, M.G. 1985. The Mathematical Theory of Quantitative Genetics. Clarendon Press, Oxford, UK.

Busack, C.A. and Currens, K.P. 1995. Genetic risks and hazards in hatchery operations: fundamental concepts and issues, p.71-80. In: H.L. Schramm, Jr. and R.G. Piper, eds. Uses and Effects of Cultured Fishes in Aquatic Ecosystems. American Fisheries Society, Bethesda, Maryland.

Campton, D.E. 1995. Genetic effects of hatchery fish on wild populations of Pacific salmon and steelhead: What do we really know?, p.377-353. In: H.L. Schramm, Jr. and R.G. Piper, eds. Uses and Effects of Cultured Fishes in Aquatic Ecosystems. American Fisheries Society, Bethesda, Maryland.

Campton, D.E. 2004. Sperm competition in salmon hatcheries: the need to institutionalize genetically-benign spawning protocols. Transactions of the American Fisheries Society 133: 1277-1289.

Campton, D.E. 2005. Sperm competition in salmon hatcheries - the need to institutionalize genetically-benign spawning protocols: Response to comment. Transactions of the American Fisheries Society 134: 1495-1498.

Candy, J. R., and T. D. Beacham. 2000. Patterns of homing and straying in southern British Columbia coded-wire tagged Chinook salmon populations. Fisheries Research 47:41-56.

Carlson, S.M., and Seamons, T.R. 2008. A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. Evolutionary Applications 1: 222-238.

Chilcote, M.W. 2003. Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (Oncorhynchus mykiss). Canadian Journal of Fisheries and Aquatic Sciences 60: 1057-1067.

Currens, K.P. and Busack, C.A. 2004. Practical approaches for assessing risks of hatchery programs, p.277-289. In: M.J. Nickum, P.M. Mazik, J.G. Nickum, and D.D. Mackinlay, eds. Propagated Fish in Resource Management. American Fisheries Society, Bethesda, Maryland.

Demeeus, T., Michalakis, Y., Renaud, F., and Olivieri, I. 1993. Polymorphism in heterogeneous environments, evolution of habitat selection and sympatric speciation - soft and hard selection models. Evolutionary Ecology 7: 175-198.

Doyle, R.W. 1983. An approach to the quantitative analysis of domestication selection in aquaculture. Aquaculture 33: 167-185.

Dukes, J.P.; R. Deaville, M.W. Bruford, A.F. Youngson, and W.C. Jordan. 2004. Odorant receptor gene expression changes during the parr-smolt transformation in Atlantic salmon. Molecular Ecology 13: 2851-2857.

Falconer, D.S. and Mackay, T.F.C. 1996. Introduction to Quantitative Genetics, 4th ed. Longman, Essex, England.

Fleming, I.A., Agustsson, T., Finstad, B., Johnsson, J.I., and Bjornsson, B.T. 2002. Effects of domestication on growth physiology and endocrinology of Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 59: 1323-1330.

Ford, M.J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. Conservation Biology 16: 815-825.

Goodman, D. 2005. Selection equilibrium for hatchery and wild spawning fitness in integrated breeding programs. Canadian Journal of Fisheries and Aquatic Sciences 62: 374-389.

Heath, D.D., Heath, J.W., Bryden, C.A., Hohnson, R.M., and Fox, C.W. 2003. Rapid evolution of egg size in captive salmon. Science 299: 1738-1740.

Hendry, A.P., Hensleigh, J.E., and Reisenbichler, R.R. 1998. Incubation temperature, developmental biology, and the divergence of sockeye salmon (Oncorhynchus nerka) within Lake Washington. Canadian Journal of Fisheries and Aquatic Sciences 55: 1387-1394

Hendry, A.P., Wenburg, J.K., Bentzen, P., Volk, E.C., and Quinn, T.P. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. Science 290: 516-518.

ISAB (Independent Scientific Advisory Board) 2002. Hatchery surpluses in the Pacific Northwest. Fisheries 27: 16-27.

Keefer, M.L., Peery, C.A., Jepson, M.A., Tolotti, K.R., Bjornn, T.C., and Stuehrenberg, L.C. 2004. Stock-specific migration timing of adult spring-summer Chinook salmon in the Columbia River Basin. North American Journal Fisheries Management 24: 1145-1162.

Kinnison, M.T., A.P. Hendry, T.P. Quinn, and M.J. Unwin. 2001. Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. Evolution 55: 1656-1667.

Knudsen, C.M., Schroder, S.L., Busack, C.A., Johnston, M.V., Pearsons, T.N., Bosch, W.J., and Fast, D.E. 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.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30: 314-334.

Lynch, M. and O'Hely, M. 2001. Captive breeding and the genetic fitness of natural populations. Conservation Genetics 2: 363-378.

Mackey, G., McLean, J.E., and Quinn, T.P. 2001. Comparisons of run timing, spatial distribution, and length of wild and newly established hatchery populations of steelhead in Forks Creek, Washington. North Am. J. Fisheries Management 21: 717-724.

McIsaac, D.O. and Quinn, T.P. 1988. Evidence for a hereditary component in homing behavior of Chinook salmon (Oncorhynchus tshawytscha). Can. J. Fish. Aquat. Sci. 45: 2201-2205.

Mobrand, L.E., Barr, J., Blankenship, L., Campton, D.E., Evelyn, T.T.P., Flagg, T.A., Mahnken, C.V.W., Seeb, L.W., Seidel, P.R., and Smoker, W.W. 2005. Hatchery reform in Washington state: principles and emerging issues. Fisheries 30(6): 11-23.

Naish, K. A., Taylor, J. E., Levin, P. S., Quinn, T. P., Winton, J. R., Huppert, D., and Hilborn, R. 2007. An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. Advances in Marine Biology 53: 61-194.

Olson, D.E., Spateholts, B., Paiya, M., and Campton, D.E. 2004. Salmon hatcheries for the 21st Century: a model at Warm Springs National Fish Hatchery. In: M.J. Nickum, P.M. Mazik, J.G.

Nickum, and D.D. Mackinlay, eds. Propagated Fish in Resource Management. American Fisheries Society, Bethesda, Maryland.

Pasqual, M.A. and Quinn, T.P. 1994. Geographical patterns of straying of fall Chinook salmon, Oncorhynchus tshawytscha (Walbaum), from Columbia River (USA) hatcheries. Aquaculture and Fisheries Management 25: 17-30.

Pasqual, M.A., Quinn, T.P., and Fuss, H. 1995. Factors affecting the homing of fall Chinook salmon from Columbia River hatcheries. Trans. Am. Fish. Soc. 124: 308-320.

Quinn, T.P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fisheries Research 18: 29-44.

Quinn, T.P. 2005. Comment: Sperm competition in salmon hatcheries - the need to institutionalize genetically-benign spawning protocols. Transactions of the American Fisheries Society 134: 1490-1494.

Quinn, T. P. and Dittman, A. P. 1990. Pacific salmon migrations and homing: mechanisms and adaptive significance. Trends in Ecology and Evolution 5: 174-177.

Quinn, T.P., Nemeth, R.S., and McIsaac, D.O. 1991. Homing and straying patterns of fall Chinook salmon in the lower Columbia River. Transactions of the American Fisheries Society 120: 150-156.

Quinn, T.P., Peterson, J.A., Gallucci, V.F., Hershberger, W.K., and Brannon, E.L. 2002. Artificial selection and environmental change: countervailing factors affecting the timing of spawning by coho and Chinook salmon. Transactions of the American Fisheries Society 131: 591-598.

Quinn, T.P., I.J. Stewart, and C.P. Boatright. 2006. Experimental evidence of homing to site of incubation by mature sockeye salmon, Oncorhynchus nerka. Animal Behaviour 72: 941-949.

Reisenbichler, R.R. 2004. Uncertainty and research needs for supplementing wild populations of anadromous Pacific salmon, p.263-275. In: M.J. Nickum, P.M. Mazik, J.G. Nickum, and D.D.

Mackinlay. Propagated Fish in Resource Management. American Fisheries Society. Bethesda, Maryland.

Reisenbichler, R.R. and McIntyre, J.D. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout. Journal of the Fisheries Research Board of Canada 34: 123-128.

Reisenbichler, R.R., Rubin, S., Wetzel, L., and Phelps, S. 2004. Natural selection after release from a hatchery leads to domestication in steelhead, Oncorhynchus mykiss, p.371-384. In M. Leber, S. Kitada, H.L. Blankenship, and T. Svasand, eds. Stock Enhancement and Sea Ranching. Blackwell Publishing Ltd., Oxford pp. 371-384.

Reisenbichler, R.R. and Rubin, S.P. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. ICES J. Marine Sci. 56: 459-466.

Smoker, W.W., Gharrett, A.J., and Stekoll, M.S. 1998. Genetic variation of return date in a population of pink salmon: a consequence of fluctuating environment and dispersive selection? Alaska Fishery Research Bulletin 5: 46-54.

Stewart, D.C., G.W. Smith, and A.F. Youngson. 2002. Tributary-specific variation in timing of return of adult Atlantic salmon (Salmo salar) to fresh water has a genetic component. Canadian Journal of Fisheries and Aquatic Sciences 59: 276-281.

Theodorou, K. and Couvet, D. 2004. Introduction of captive breeders to the wild: harmful or beneficial? Conservation Genetics 5: 1-12.

Via, S. and Lande, R. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. Evolution 39: 505-522.

Waples, R.S., Teel, D.J., Myers, J.M., and Marshall, A.R. 2004. Life-history divergence in Chinook salmon: historic contingency and parallel evolution. Evolution 58: 386-403.

11 Appendix: Quantitative genetic foundations: one population, one environment

Ford (2002) described a deterministic model that is based on the foundation principles of quantitative genetics and modern animal breeding (Bulmer 1985; Falconer and MacKay 1996). Under those principles, the phenotypic distribution of a quantitative trait (e.g., spawn date, run timing, female fecundity, etc.) within a population is assumed to be distributed normally ~N(u, σ^2) with an expected value (population mean) = u and variance = σ^2 (Falconer and MacKay 1996). The phenotypic variation among individuals in a population, measured by σ^2, is assumed to be caused by (a) heritable genetic variation among those individuals, commonly referred to as the *additive genetic variance*, (b) non-heritable genetic variation among individuals associated with interaction effects among alleles within and between loci (e.g., *dominance* and *epistasis*), and (c) environmental variation among individuals, including genotype x environment interaction effects. Under this model, genetic variation is assumed to be caused by allelic (Mendelian) variation at a large number of genes that directly affect the trait in question. The "environment" refers to all non-genetic influences experienced by an individual from the time of fertilization (conception) to the time of death. Variation in those "experiences" is the source of environmental variation.

Under the classic genetic model, the phenotypic value (P) of a trait for an individual is assumed to be sum of the genetic (G) and environmental effects on that trait, plus genetic-environment interaction (I) effects (GxE) for that individual (i.e., $P = G + E + I$). GxE effects occur when the relative phenotypic values of different genotypes vary or change among different environments (e.g., genotype "A" grows faster than genotype "B" in environment "C" but genotype "B" grows faster in environment "D"). Consequently, phenotypic values of individuals are not simply an additive function of genetic and environmental effects. Genetic and environmental variation among individuals within a population, plus variation in the *GxE* interaction effects among individuals (i.e., genotypes), results in measurable phenotypic variation (e.g., spawn date) among individuals, and that variation generally follows a "bell-shaped" curve that closely approximates a normal distribution.

The phenotypic variance among individuals in a population (σ^2) can be partitioned into its causal components:

$$\sigma^2 = \sigma_G^2 + \sigma_E^2 + \sigma_I^2 \qquad \text{(A1)}$$

where σ_G^2 = the *additive genetic variance* among individuals that can respond to artificial or natural selection that can result in a change in the mean value of a trait between the parental and offspring generations, σ_E^2 = the *environmental variance* among individuals, and σ_I^2 = variance in non-additive genetic effects and all genetic-environmental interaction effects.[18]

[18] The covariances between genetic effects and between genetic and environmental effects have been ignored in eq. (1). For example, a covariance between genetic and environmental effects occurs when faster growing genotypes are provided more food than slower growing genotypes, thus resulting in a positive covariance between genotype and environment for the population as a whole.

Another important parameter is the *heritability* (h^2) of a trait ($h^2 = \sigma_G^2 / \sigma^2$) which measures the *proportion of the total phenotypic variance among individuals due to additive genetic variation among those individuals* ($h^2 = \sigma_G^2 / \sigma^2$; $0 \leq h^2 \leq 1.0$). In general, heritabilities of most traits related to fitness (e.g., age and size at sexual maturity, spawn date, etc.) range from approximately 0.1 to 0.3 and rarely exceed 0.5 (Carlson and Seamons 2008).

The heritability of a trait is both population-specific and environment-specific because its value is a direct function of the amount of additive genetic variance within a specific population (numerator of h^2) *and* the amount of environmental variance contributing to the phenotypic variance among those individuals within that population (denominator of h^2). Hence, any reduction in the environmental variance experienced by individuals within a population will increase the heritability of a trait because a greater proportion of the observed phenotypic variation will be due to genetic variation among individuals within that population, all other factors remaining equal. In this context, geneticists have hypothesized that many traits related to fitness in Pacific salmon may have higher heritabilities in hatchery-propagated populations than natural populations because of the potentially lower environmental variances associated with hatchery environments versus natural environments. Also, a low heritability does not necessarily mean that phenotypic variation in the trait is not under significant genetic control because high environmental variation could simply be contributing to the majority of the observed phenotypic variation.

The heritability of a trait, estimable from controlled breeding studies or populations that are pedigreed, can be used to predict a one-generation response (R) to selection (natural or artificial) according to the following expression:

$$R = \overline{P}' - \overline{P} = h^2(\overline{P}_S - \overline{P}) \qquad \text{(A2)}$$

where $\overline{P}$ = mean value of the trait for the population in the parental generation , $\overline{P}'$ = mean value of the trait in the offspring generation, $\overline{P}_S$ = mean value of the trait among the *selected* or *surviving* parents that reproduce where each parent is weighted by the number of adult progeny produced, and h^2 = the heritability of the trait. The term "($\overline{P}_S - \overline{P}$)" is called the "selection differential" (SD) of the trait, and the response to selection ($\overline{P}' - \overline{P}$) - which is defined as the change in mean phenotypic value of the trait between offspring and parents – essentially equals the proportion of the parental SD that is transmitted to the progeny generation as determined by the heritability of the trait. These equations, in more complicated forms, have been the foundation for predicting responses to selection in the agriculture and livestock industries for decades.

The selection component of Ford's (2002) model includes a fitness function that measures the relative fitness[19] (f) of an individual in a particular environment as a

[19] *Fitness* is a commonly used term that is rarely defined precisely. *Individual fitness* can generally be subdivided into two components: *viability fitness* and *reproductive fitness*. Viability fitness measures the probability of individual survival from zygote formation to sexual maturity. Reproductive fitness of an individual measures the number of adult progeny resulting from reproduction. Parents and offspring share 50% of their genes in common (i.e., phenotypes of parents and offspring are highly correlated genetically) and, hence, fitness is correlated

function of (a) an individual's specific phenotypic value (P), (b) the parametric *optimum phenotypic value* (θ) that maximizes fitness of individuals within a particular environment, and (c) the strength or intensity of *stabilizing selection* that results in increasingly reduced fitness of individuals with phenotypic values that deviate increasingly from the phenotypic optimum in the specific environment under consideration. This relative fitness (f_i) of the ith individual with phenotype P_i within a population follows a *quasi-normal distribution* (eq. 2 of Ford 2002):

$$f_i = e^{-\frac{1}{2}\frac{(P_i-\theta)^2}{\omega^2}} \qquad \text{(A3)}$$

where "$(P_i - \theta)$" is the deviation of the ith individual's phenotypic value (P_i) from the *optimum phenotypic value* (θ) in the environment under consideration, and ω^2 is the variance of the probability density function that defines relative fitness as a function of phenotypic values (Fig. 2).

The relative mean fitness of the population is given by the following (eq. 3 of Ford 2002):

$$\overline{F} = e^{-\frac{1}{2}\cdot\frac{(\overline{P}-\theta)^2}{(\omega^2+\sigma^2)}} \qquad \text{(A4)}$$

This mode of selection is called "stabilizing" because it *drives* the mean phenotypic value ($\overline{P}$) of a population each generation towards the optimum phenotypic value (θ) for individuals in the specific environment inhabited by that population. Under this model, θ can have different values in different environments. A population would be considered "locally-adapted" when $\overline{P} = \theta$. The model assumes that θ for a particular environment is constant over multiple generations. However, in practice, the optimum for many traits (e.g., age at sexual maturity) most likely varies stochastically among generations due to varying environmental conditions (e.g., decadal oscillations in marine ocean conditions).

The *intensity* of selection is inversely proportional to the variance of the fitness distribution of phenotypes (i.e., selection intensity $\sim 1/\omega^2$; eq. 3). That is, as ω^2 increases, the selection intensity towards the phenotypic optimum decreases (Fig. 2). In other words, the relative fitness of an individual with a particular phenotypic value (P) in a particular environment will increase as ω^2 increases (when $P \neq \theta$) because the intensity of selection decreases (Fig. 1). According to Ford (2002), $\omega^2 = 10\sigma^2$ ($\omega \approx 3\sigma$, or less) is considered "strong selection", whereas $\omega^2 = 100\sigma^2$ ($\omega \approx 10\sigma$, or greater) would be considered "weak selection" (Lande 1976).

If the mean phenotypic value ($\overline{P}$) for individuals in a population does not equal the phenotypic optimum for that population (i.e., $\overline{P} \neq \theta$), then a population response to stabilizing selection is expected each generation for traits with $h^2 > 0$ until $\overline{P} = \theta$. This predicted response to stabilizing selection (R) follows the following relationship (eq. 4 from Ford 2002):

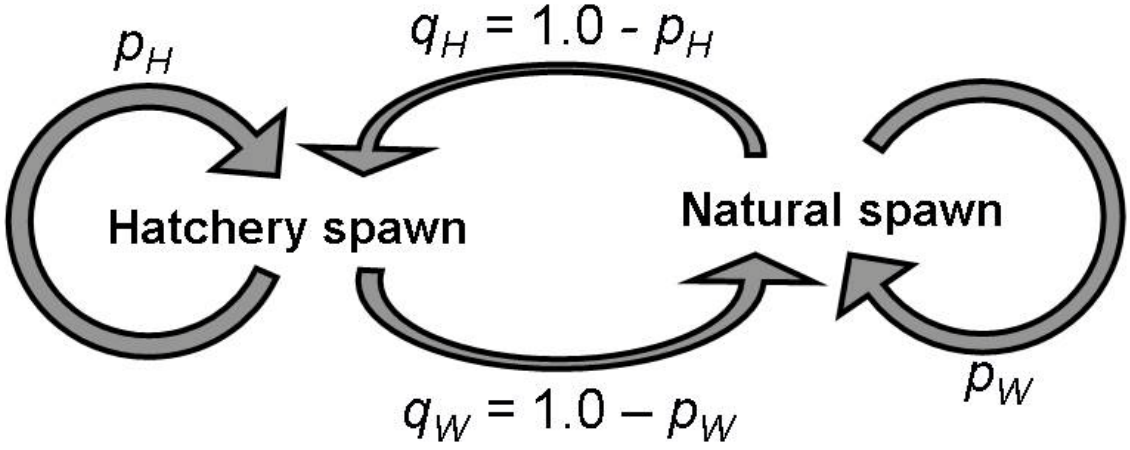
genetically between parents and offspring. For example, increased survival of progeny to sexual maturity (viability fitness) increases the fitness of their parents (reproductive fitness).

$$R = \overline{P}' - \overline{P} = h^2\left[\frac{\overline{P}\omega^2 + \theta\sigma^2}{\omega^2 + \sigma^2} - \overline{P}\right] \quad \text{(A5)}$$

where the quantity in brackets is the selection differential, h^2 is the heritability of the trait, and $\overline{P}'$ is the mean phenotypic value for the population after one generation of selection. The reader should note that the left-hand quantity within brackets is the predicted mean phenotypic value of breeding parents after selection/survival to adulthood (compare eq. A5 to eq. A2). Equation (A5) can be rearranged as a recursive equation which predicts the mean phenotypic value of a population in the offspring generation ($\overline{P}'$) as a function of the mean phenotypic value of the population in the parental generation ($\overline{P}$):

$$\overline{P}' = \overline{P} + h^2\left[\frac{\overline{P}\omega^2 + \theta\sigma^2}{\omega^2 + \sigma^2} - \overline{P}\right] \quad \text{(A6)}$$

These simple relationships are the basis for the two population, selection and gene flow model described by Ford (2002).



p_H = proportional genetic contribution of hatchery-origin adults to hatchery-origin offspring each generation.

p_W = proportional genetic contribution of natural-origin (wild) adults to natural-origin offspring each generation.

Figure 1. Schematic representation of 2-way gene flow between hatchery and wild populations. Each generation, hatchery-origin progeny are composed of a proportion p_H genes from hatchery-origin parents and a proportion 1.0-p_H (= q_H) genes from natural-origin parents. Similarly, natural-origin progeny are composed of a proportion p_W genes from natural-origin parents and a proportion 1.0-p_W (= q_W) genes from hatchery-origin parents. Those proportions are assumed to be constant over time.

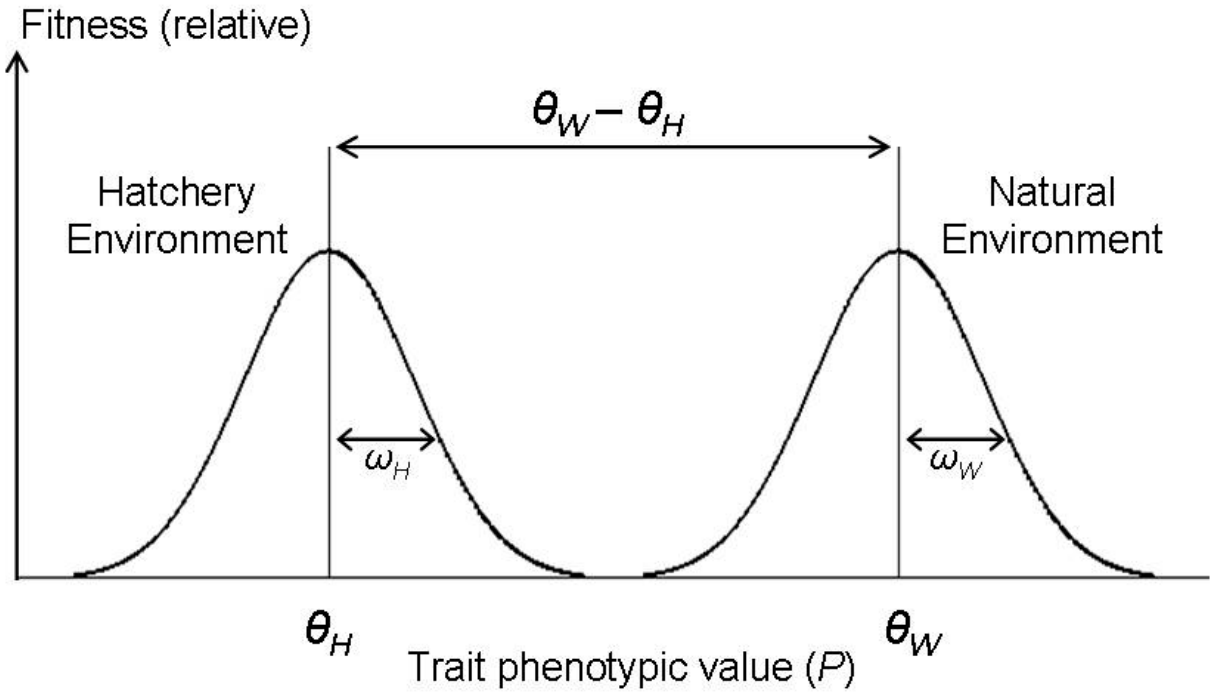


Figure 2. Schematic representation of fitness as a function of phenotypic values for two populations inhabiting different environments where the phenotypic optima (θ_W and θ_H) in the two environments are not equal. Each population is assumed to be under stabilizing selection in each environment. In the absence of gene flow between the two populations, selection in each environment maintains mean phenotypic values for each population equal to the phenotypic optimum for the respective environment. Each distribution is assumed to be distributed as a quasi-normal distribution with mean θ and variance ω^2 where the subscripts "*H*" and "*W*" refer to hatchery and "wild" environments, respectively. The magnitude of the difference $\theta_W - \theta_H$ is a measure of the strength of selective differences between the two environments. For hatchery and wild populations of fish, this difference reflects the strength of domestication selection in the hatchery environment relative to natural selection regimes in the wild environment. The difference in $\theta_W - \theta_H$ depicted here is greater than the actual difference observed for most traits associated with anadromous salmonid fishes. For most traits, the phenotypic distributions for hatchery and wild fish overlap such that a range of phenotypic values have relative fitnesses greater than zero in both environments. (after Ford 2002).

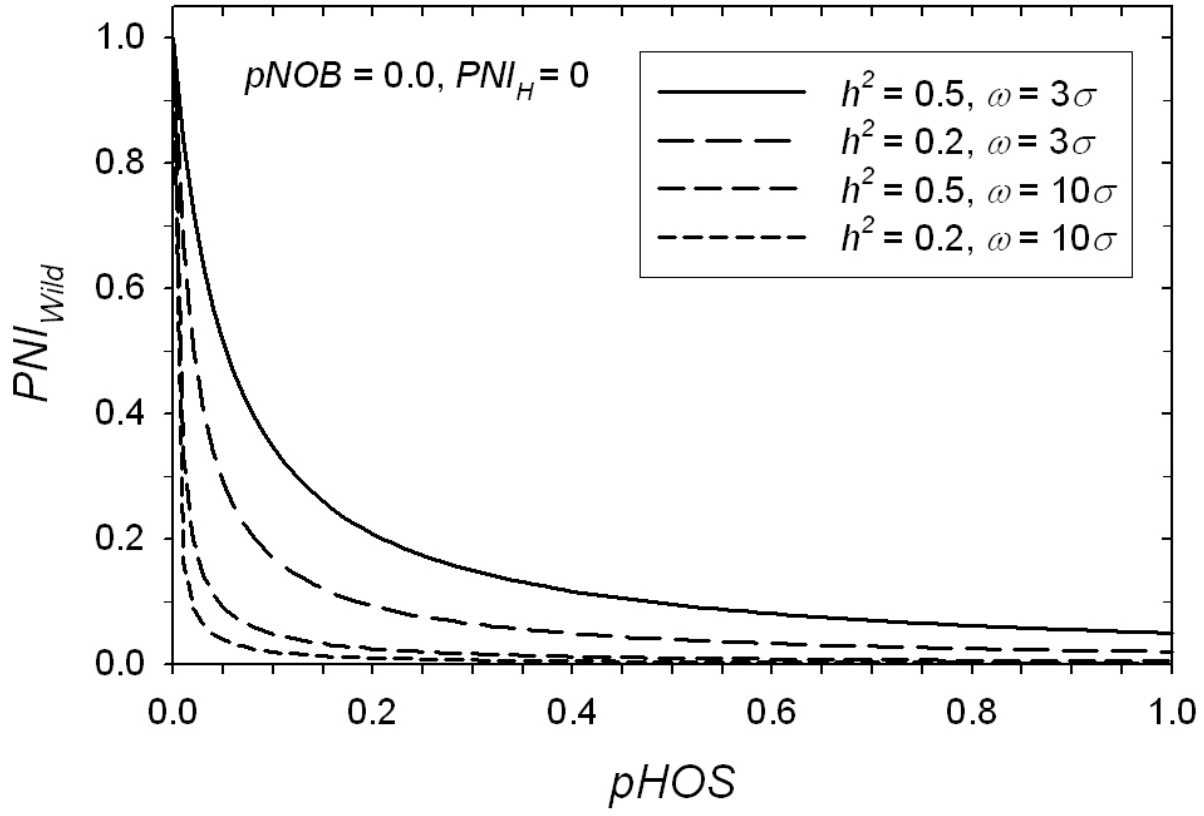


Figure 3. *Proportionate Natural Influence* for wild fish (PNI_{Wild} *or* PNI_W) as a function of the relative genetic contribution of hatchery-origin adults to natural-origin progeny each generation (eq. 9). The proportion of naturally-spawning fish composed of hatchery-origin adults (*pHOS*) is generally used as a management "surrogate" in lieu of empirical estimates of the mean proportional genetic contribution of hatchery-origin fish to a wild population each generation. In this figure, no wild fish are included in the broodstock (*pNOB* =0), thus resulting in $PNI_H = 0$ for hatchery fish (eq. 10). Heritabilities equal to $h^2 = 0.2$ and $h^2 = 0.5$ are considered *moderate* and *high* heritabilities, respectively. Selection intensities equal to $\omega = 3\sigma$ ($\omega^2 = 9\sigma^2$) and $\omega = 10\sigma$ ($\omega^2 = 100\sigma^2$) are considered *strong* and *weak* selection, respectively, where ω^2 = the variance of the distribution function for stabilizing selection about a phenotypic optimum (Fig. 2). Traits are assumed to be normally distributed with optimum values of θ_W =1.0 and θ_H = 0.0 in the wild and hatchery environments, respectively, with standardized phenotypic variances of $\sigma^2 = 1.0$ for both hatchery and wild fish. Heritabilities (h^2) and selection intensities (ω^2) are assumed to be equal in the two environments.

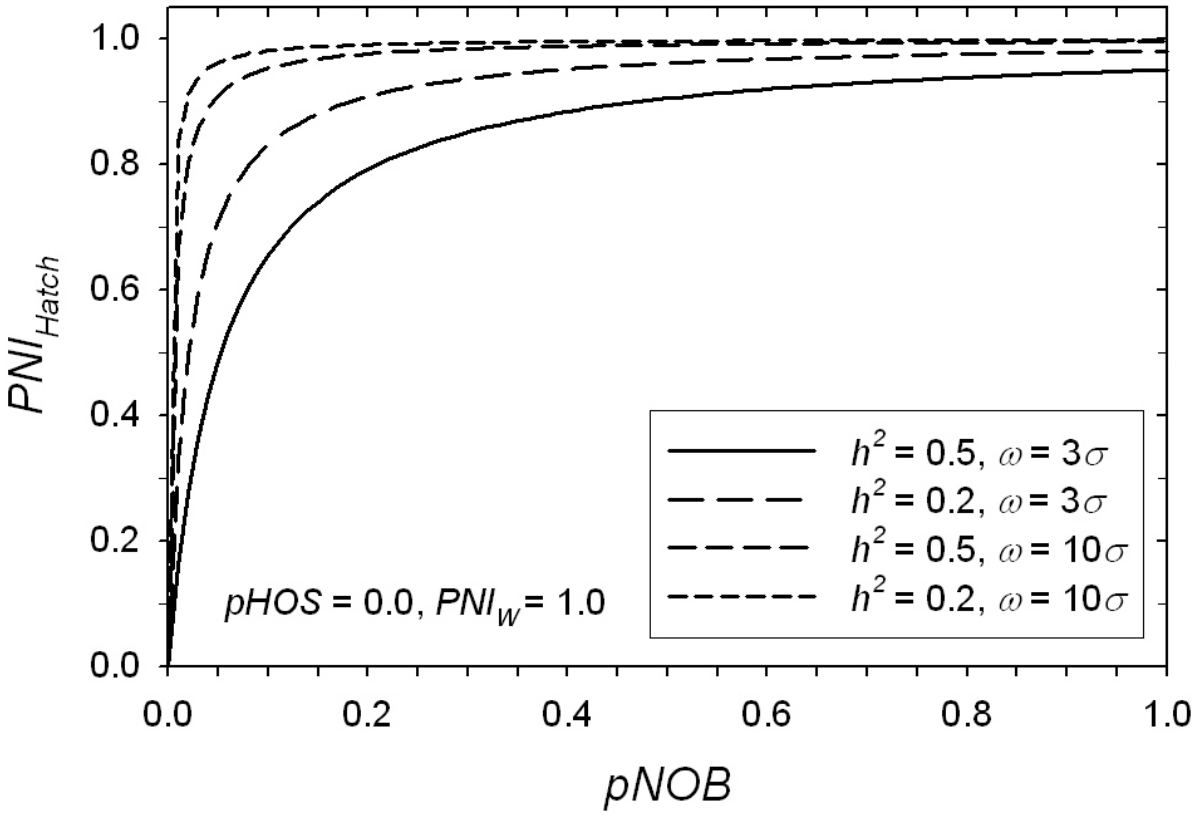


Figure 4. *Proportionate Natural Influence* for hatchery fish (PNI_{Hatch} *or* PNI_H) as a function of the relative genetic contribution of natural-origin adults to hatchery-produced progeny each generation (eq. 10). The proportion of a hatchery broodstock composed of natural-origin adults (*pNOB*) is generally used as a management "surrogate" for the mean proportional genetic contribution of natural-origin fish to hatchery-produced progeny each generation. In this figure, no hatchery fish are allowed to spawn naturally (*pHOS* = 0), thus resulting in $PNI_W = 1.0$ for wild fish (eq. 9).

When pHOS = 0, relatively small amounts of gene flow from the natural environment to the hatchery environment can increase PNI_H substantially. Indeed, when only 20% of a broodstock is composed of wild fish each generation (*pNOB* = 0.2), PNI_H will be greater than 0.75 even under conditions of high heritability and strong selection intensity in the hatchery environment if *pHOS* = 0.

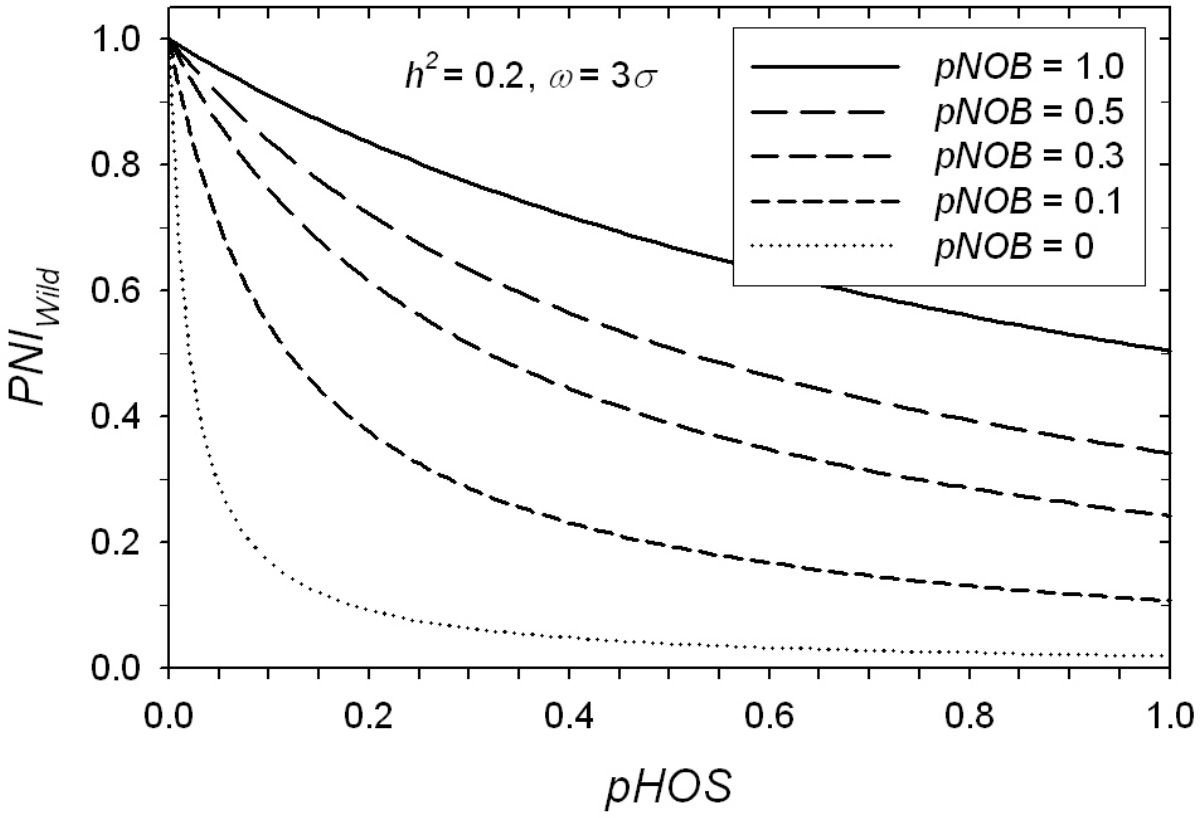


Figure 5. *Proportionate Natural Influence* for wild fish (PNI_W) as a function of the proportion of naturally spawning fish composed of hatchery-origin adults (*pHOS*) for different values of *pNOB*, the mean proportion of the hatchery broodstock composed of natural-origin fish each generation (eq. 9). Heritability and selection intensity in these plots are considered moderate ($h^2 = 0.2$) and strong ($\omega = 3\sigma$), respectively. The variables *pNOB* and *pHOS* are surrogates for the proportional genetic contribution, each generation, of wild fish and hatchery fish to a hatchery broodstock and a naturally spawning population, respectively (see eqs. 5 and 6). Of particular interest here is the long-term genetic effect on PNIW of including wild fish in a hatchery broodstock when pHOS is greater than 0.05.

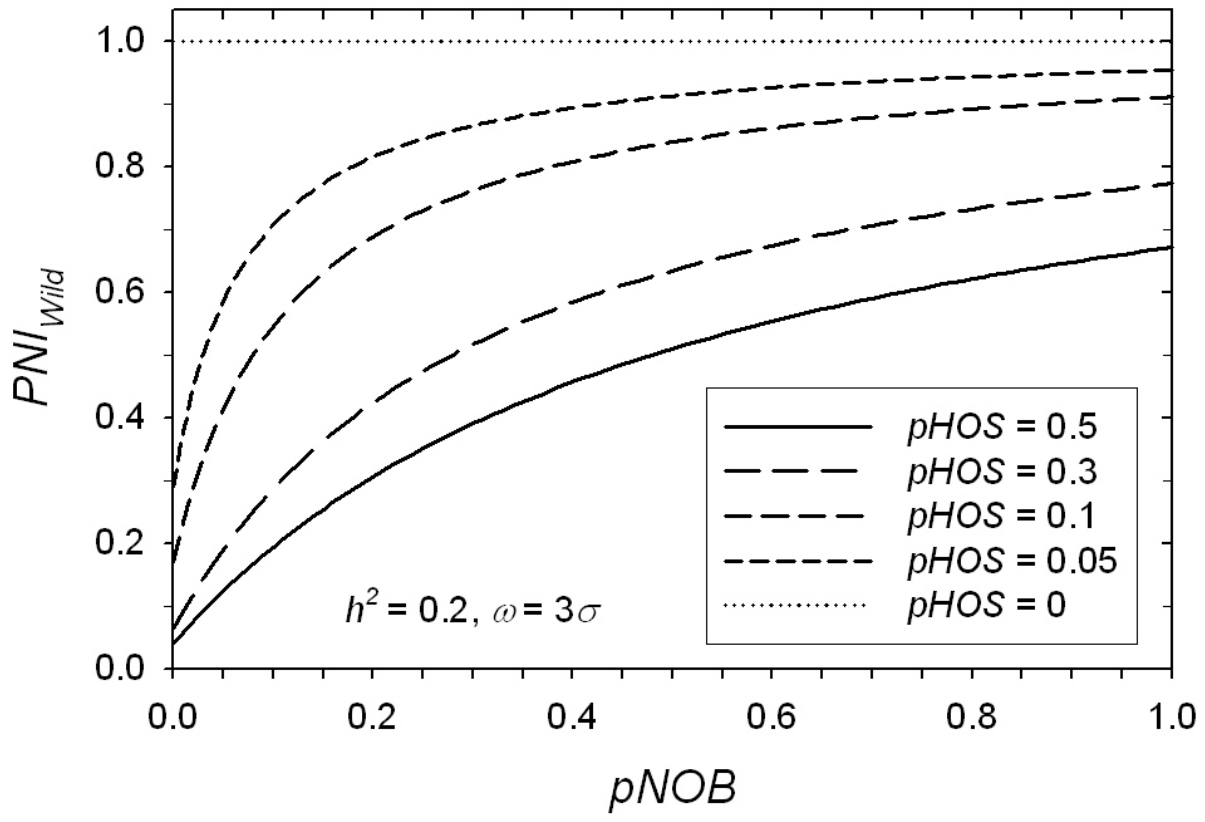


Figure 6. *Proportionate Natural Influence* for wild fish (PNI_W) as a function of the proportion of a hatchery broodstock composed of natural-origin adults (*pNOB*) for different values of *pHOS* (eq. 9). Of particular interest here is the large effect of small amounts of gene flow each generation from the hatchery environment to the natural environment (e.g., *pHOS* = 0.05) when *pNOB* = 0. Increasing *pNOB* = *pHOS* results in $PNI_W \approx$ **0.5 over all values of** *pHOS*. This graph is identical to Fig. 5 (eq. 9) except that PNI_W is plotted as function of *pNOB* instead of *pHOS*.

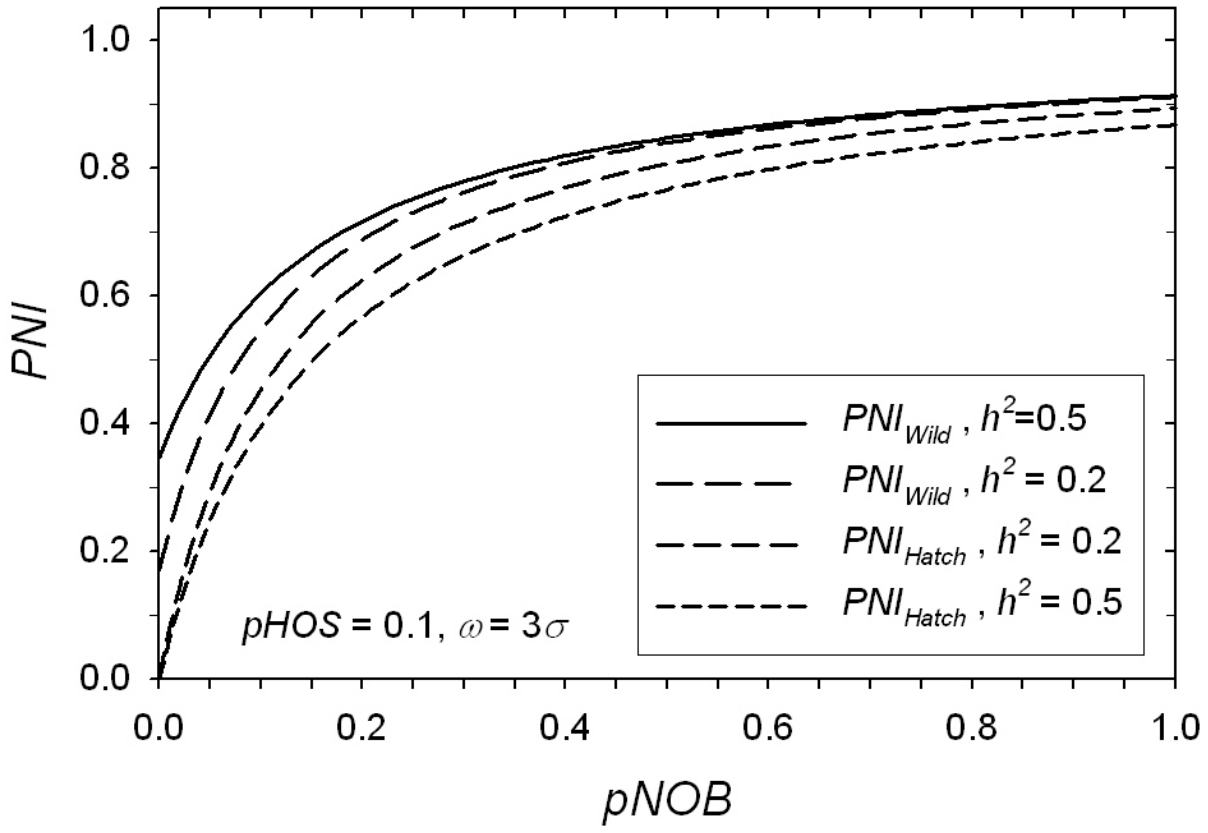


Figure 7. Comparison of *PNI* values for hatchery and wild fish as a function of *pNOB* (eq. 9) when *pHOS* = 0.1, selection intensity is considered strong ($\omega = 3\sigma$), and trait heritabilities are moderate and or high (h^2 = 0.2 and 0.5, respectively). For a given set of parameters, PNI_W will always be greater than PNI_H because wild fish, compared to hatchery fish, represent one extra generation of natural reproduction and selection in the wild environment. Nevertheless, the genetic composition for hatchery and wild fish will be nearly identical when an equilibrium between gene flow and selection is reached (eqs. 5 and 6). The difference between PNI_W and PNI_H increases with increasing heritability, reflecting the increased efficiency of selection and single-generation responses to selection as a function of increasing heritability (eqs. A2 and A4). Conversely, the difference between PNI_W and PNI_H decreases with increasing values of *pNOB*.

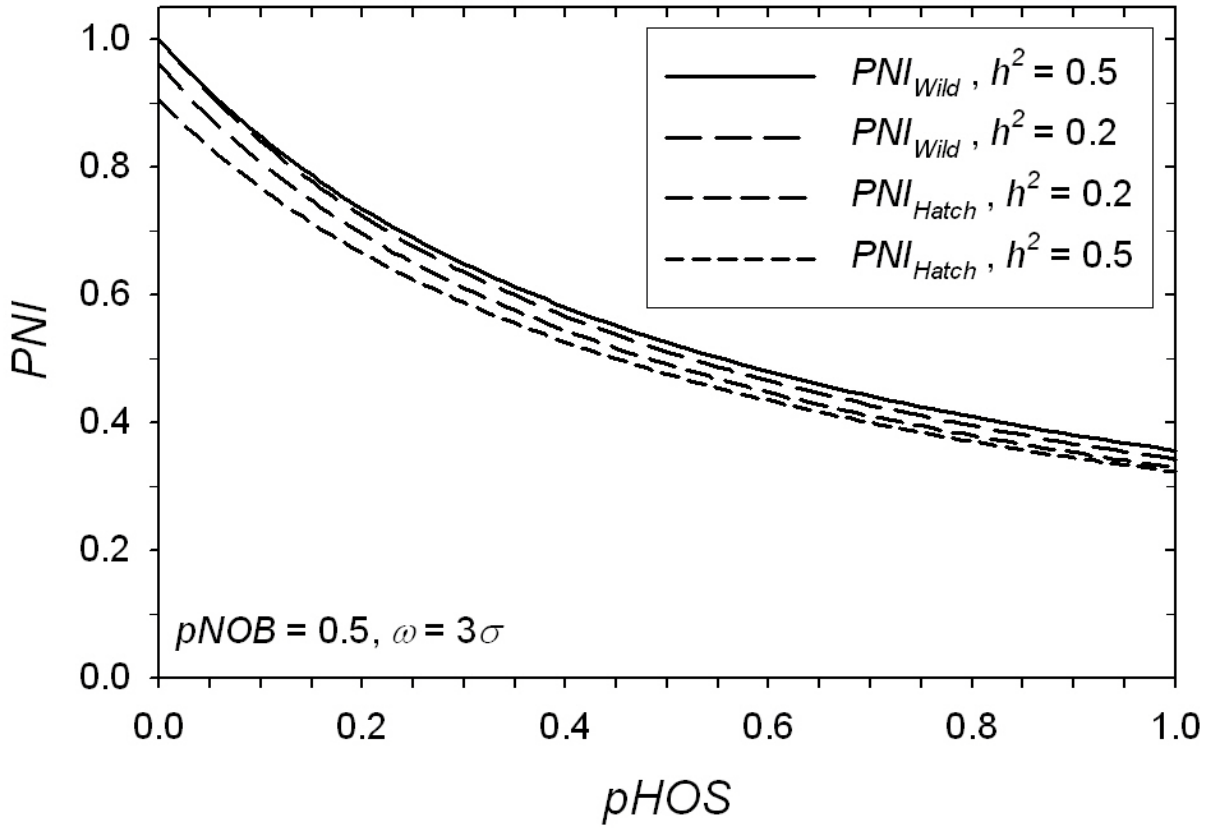


Figure 8. Comparison of *PNI* values for hatchery and wild fish as a function of *pHOS* when 50% of a hatchery broodstock is composed of wild fish each generation (*pNOB* = 0.5) and heritabilities are moderate or high (h^2 = 0.2 or 0.5, respectively). As in Fig. 7, PNI_W will always be greater than PNI_H for a given set of parameter values, although the difference between PNI_W and PNI_H will decrease with increasing values of *pNOB*.

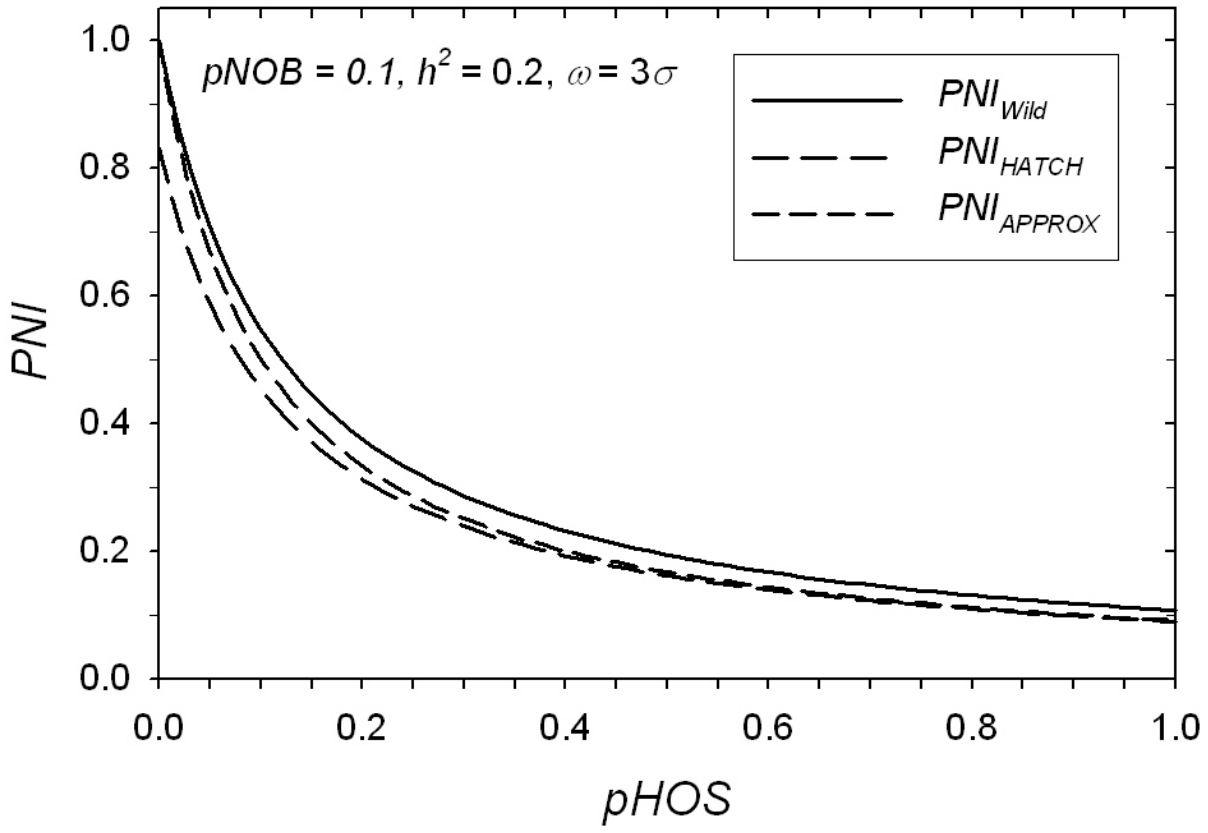


Figure 9. Comparison of the *PNI* index approximation (PNI_{Approx}; eq. 11) to PNI_W (eq. 9) and PNI_H (eq. 10) as a function of *pHOS* when *pNOB* = 0.1 for a trait under strong selection ($\omega = 3\sigma$) with moderate heritability ($h^2 = 0.2$). When *pNOB* is greater than zero, the approximation is very close to the derived value of PNI_W (eq. 9). However, when *pNOB* = 0, which is true for a large number of hatchery broodstocks where only hatchery-origin fish are spawned, then eq. (9) should be used to estimate PNI_W for natural-origin fish. In this latter situation, a range of possible PNI_W values can be generated via eq. (9) assuming heritabilities and selection intensities for traits that are likely to be of greatest concern: that is, traits that can respond quickly to selection over a small number of generations because they are under moderate to high selection intensities ($\omega = 6\sigma$ to $\omega = 3\sigma$)[20] and/or because they have moderate to high heritabilities (h^2=0.2 to h^2 = 0.5, respectively).

[20] Equation (9) assumes that the phenotypic variance of the trait has been standardized to $\sigma^2 = 1.0$.

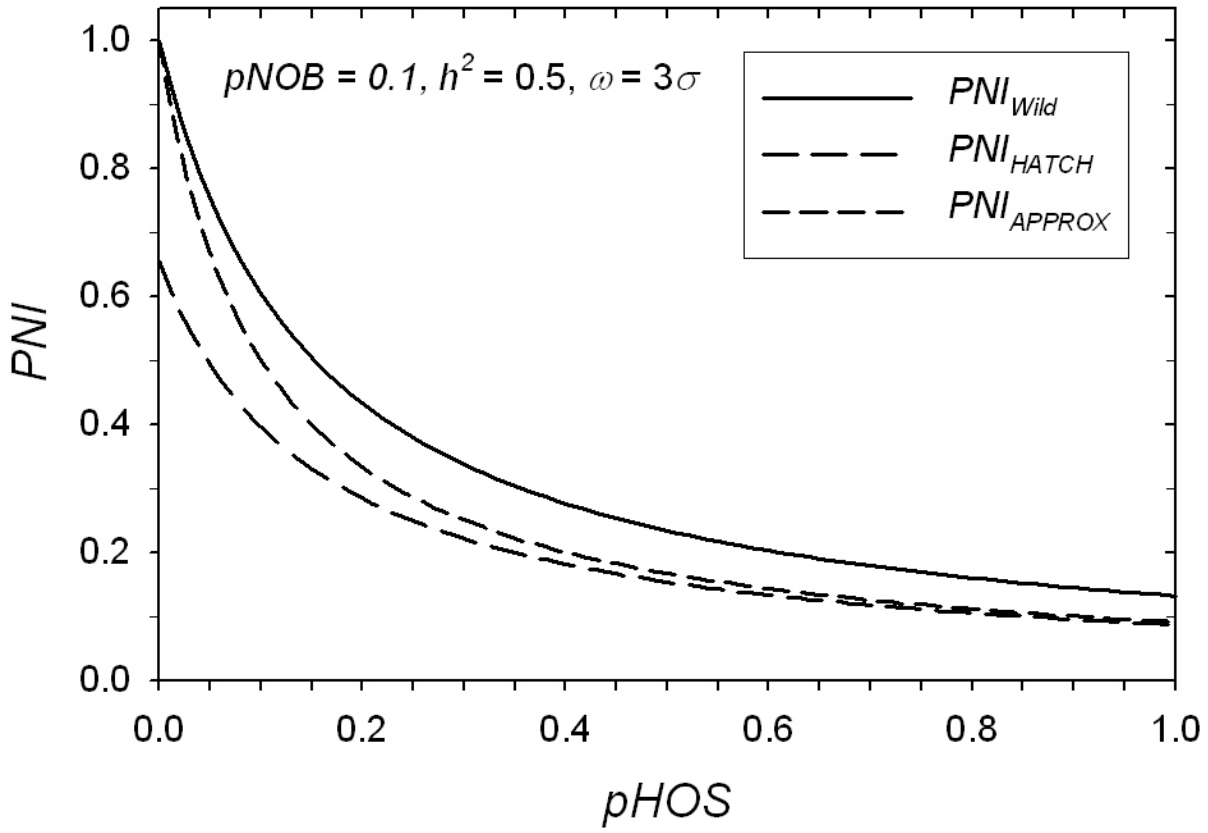


Figure 10. Comparison of the *PNI* index approximation (PNI_{Approx}; eq. 11) to PNI_W (eq. 9) and PNI_H (eq. 10) as a function of *pHOS* when *pNOB* = 0.1 for a trait under strong selection ($\boldsymbol{\omega} = 3\boldsymbol{\sigma}$) with high heritability (h^2 = 0.5; compare graph above to Fig. 9 where h^2 = 0.2). For a trait with high heritability, an extra generation of selection in the respective environments can result a comparatively large difference in the values of PNIW and PNIH at low values of pHOS; however, PNI_{Approx} more closely tracks PNI_W which is the index of greater concern from a natural population perspective. As noted in the caption of Fig. 9, equation (9) should be used to calculate PNI_W, not equation (11), whenever *pNOB* equals zero.

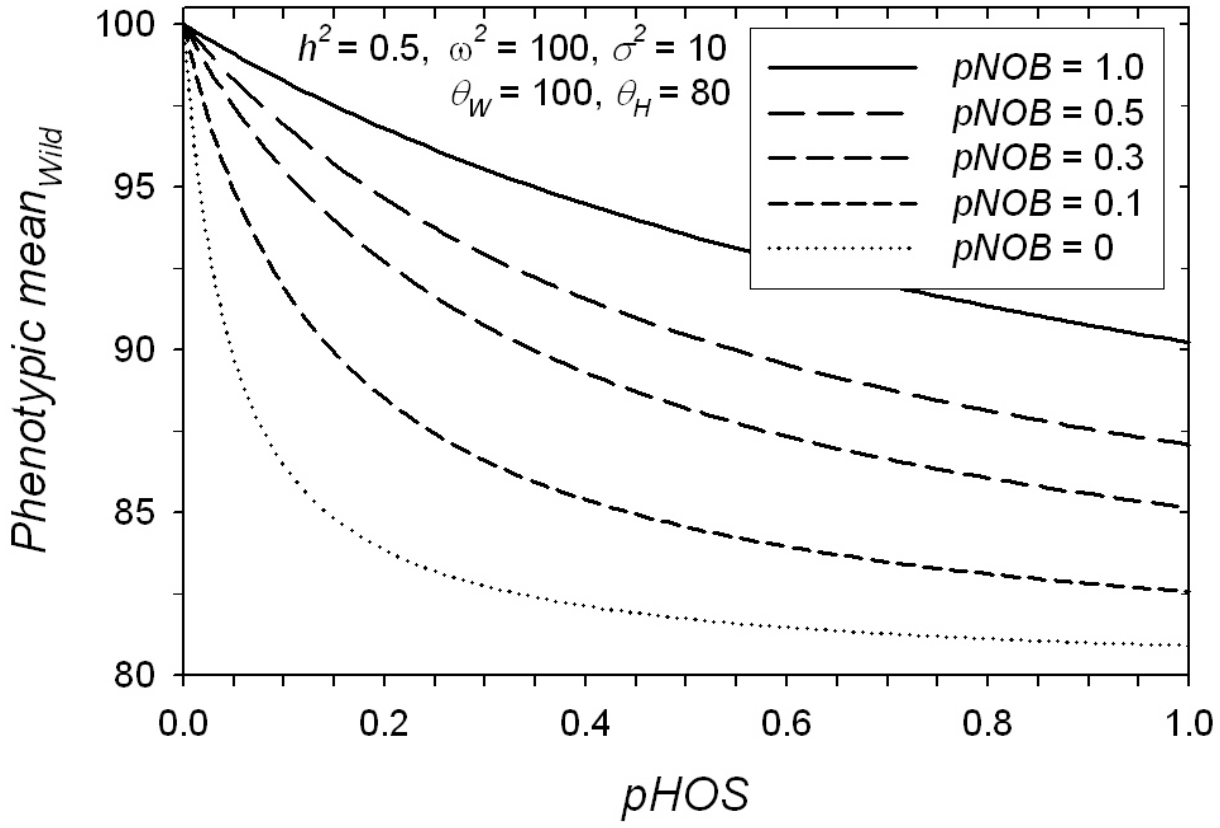


Figure 11. Phenotypic mean of wild fish at equilibrium after many generations of gene flow between hatchery and wild populations as a function of *pHOS*, the mean proportion of a naturally spawning population composed of hatchery-origin fish each generation (eq. 3). The hypothesized trait is assumed to have a heritability (h^2) and phenotypic variance (σ^2) equal to 0.5 and 10, respectively, in both environments. The variance of the fitness function (ω^2) is assumed to be equal to $10 \cdot \sigma^2$ in both environments, which is considered "strong" selection. The trait is further assumed to have phenotypic optima of θ_H = 80 and θ_W = 100 in the hatchery and natural environments, respectively. The values of h^2, ω^2, σ^2, θ_H and θ_W presented here are the same values used by the HSRG in the *AII-H Analyzer* (*AHA*) model to simulate the population dynamics of hatchery and wild fish in the Columbia River Basin. The reader should note that the shapes of the graphs presented here are nearly identical to those presented in Figure 5; slight differences in the shape of the two sets of curves are due primarily to the high heritability (h^2 = 0.5) used here (and in *AHA*) versus the moderate heritability (h^2 = 0.2) used to generate Figure 5. As noted in the text, the shapes of the equilibrium curves for the phenotypic means of wild and hatchery fish ($\hat{P}_W$ and $\hat{P}_H$, eqs. 3 and 4, respectively) are largely independent of specific values of θ_H, θ_W, and σ^2; only the scale of the vertical axis changes as a function different values for the phenotypic optima in each environment. These latter results further warrant the use of equations (9), (10), and (11) to assess the genetic risks of hatchery programs to naturally spawning populations.

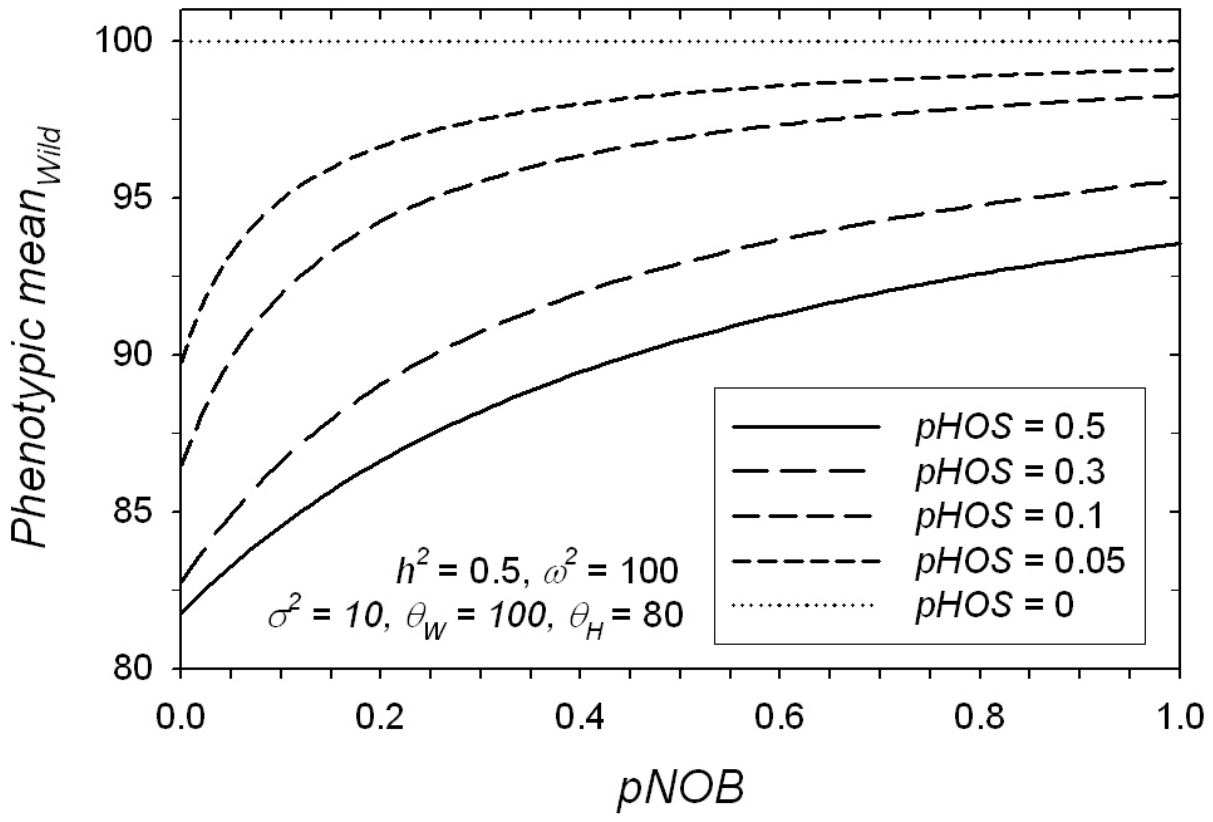


Figure 12. Phenotypic mean of wild fish at equilibrium after many generations of gene flow between hatchery and wild populations as a function of *pNOB*, the mean proportion of a hatchery broodstock composed of natural-origin fish each generation (eq. 3). Parameter values presented here are the same as those described in Figure 11. The reader should note the close similarity between this figure and Figure 6. As noted in Figure 11, the shapes of the curves are largely independent of the specific values of θ_H, θ_W, and σ^2. Variation in the values of θ_H and θ_W only affects the scale of the relationship (vertical axis) without affecting the relative phenotypic values of hatchery and wild fish relative to their optima within each environment.

White Paper No. 2[1]
Antibiotics in Salmonid Aquaculture: Does Their Use Justify the Risks?

1 Introduction

1.1 Antibiotics in Aquaculture

Antibiotics, both natural and synthetic, have been successfully used for decades in aquaculture to control bacterial diseases. There is general agreement, however, that the use of antibiotics for this purpose should be held to a minimum because they have the potential to cause harmful effects. The danger with this approach is that in minimizing the use of antibiotics, treatments for detected sub-clinical infections may be delayed or even withheld, leading to disease outbreaks that may otherwise have been avoided.

Whereas underuse of antibiotics in aquaculture might result in disease outbreaks, overuse or misuse may produce harmful environmental effects. The goal of this paper is to summarize existing literature on aquacultural use of antibiotics with the objective of aiding managers and other interested parties make informed decisions. The specific areas of interest covered by the literature review and this paper are:

- The mechanisms involved in development of antibiotic resistance
- Risks to human and fish health of using antibiotics in aquaculture
- Potential ecological effects of using antibiotics in aquaculture
- Recommendations for minimizing harmful effects of antibiotic use in aquaculture

1.2 Methods of Enquiry

This paper is primarily concerned with antibiotic use during the freshwater rearing of salmon and steelhead in the Pacific Northwest. In this region, the antibiotics currently approved for use are oxytetracycline (OTC) and Romet, a potentiated sulfa drug. Other antibiotics, such as erythromycin and florfenicol, are also used under veterinary license. In order to obtain a fuller appreciation of the consequences of using antibiotics in cold water (salmonid) aquaculture, the relevant published literature on both freshwater and marine aquaculture use of antibiotics was reviewed.

2 Antibiotic Use in Aquaculture

2.1 Mechanisms of development of antibiotic resistance

Most antibiotics used in salmonid aquaculture are not mutagenic. It seems likely, then, that antibiotic treatments simply provide the environment in which cells of a bacterial fish pathogen that have undergone chance mutations conferring resistance to one or more

[1] White papers were prepared by the HSRG to address topics relevant to hatchery reform. They are intended to stimulate discussion and provide background, documentation and explanations not included in the body of the HSRG's report.

antibiotics, can multiply to the stage where they become the dominant cells in the bacterial population. Normally, such cells would occur as an extremely small fraction of the cell population. However, if antibiotic treatments go on for long enough or are too frequently used, the opportunity is provided for the antibiotic resistance selection process to occur, the end result being an antibiotic resistant fish pathogen.

Genes responsible for antibiotic resistance can be transferred between bacteria by any of three processes:

- A gain of genes from the uptake of naked DNA (Transformation)
- A gain of genes through infection with viral DNA (Transduction)
- A gain of genes by cell-to-cell mating (Conjugation)

All three of these processes are thought to occur in soil and aquatic systems (Trevors, Barkay, and Bourquin 1987; Coughter and Stewart 1989).

2.2 Risks to human and fish health of using antibiotics in aquaculture

2.2.1 *Risk of producing fish pathogens resistant to antibiotics*

One of the concerns in treating fish with antibiotics is the potential for producing fish pathogens that are resistant to the antibiotics. Studies of Japanese aquaculture convincingly support the conclusion that increased aquacultural use of antibiotics was responsible for the increase in single and multiple-drug resistance shown by various bacterial fish pathogens, including *Aeromonas salmonicida* (Aoki et al. 1983; Aoki 1988). Similar findings have been reported in other countries for other bacterial fish pathogens following the use of antibiotics to control diseases in cultured salmonids. When antibiotic resistance occurs, the effectiveness of the antibiotics in treating fish diseases is compromised.

2.2.2 *Risks of producing human pathogens resistant to antibiotics*

Genes that encode for drug resistance may be contained in the cells of bacterial fish pathogens or in the cells of other types of bacteria associated with fish or present in their environment. These genes can end up on mobile bits of DNA, e.g., plasmids, which are also present in the same cells. The plasmids bearing the resistance genes can then be transferred to other bacteria, including bacteria of public health significance. The recipient bacteria subsequently become resistant to the particular antibiotics encoded for by the transferred resistance genes.

Plasmid-borne resistance genes have been transferred by conjugation from the fish pathogen *A. salmonicida* to *Escherichia coli*, a bacterium of human origin, some strains of which are pathogenic for humans (Aoki et al. 1983; Kruse and Sorum 1994; Adams et al.1998). Plasmid-borne drug resistance genes have also been transferred from the fish pathogen, *Vibrio anguillarum*, to the causative bacterium of cholera in humans, *Vibrio cholera* (Nakajima et al. 1983). Plasmid-borne antibiotic resistance genes present in the cells of various groups of bacteria isolated from cultured rainbow trout also proved transferable to *E. coli* (Toranzo et al. 1984).

2.2.3 *Risk and significance of producing environmental bacteria resistant to antibiotics*

Fish contain a multiplicity of bacteria in their gastrointestinal tracts. When diseased fish are treated with antibiotics contained in feed, the cells of non-pathogenic gastrointestinal

bacteria and cells of environmental bacteria can come in contact with the antibiotics present in fish farm and hatchery wastes. The number of cells containing genes encoding for resistance may be increased due to the addition of the non-pathogenic and environmental bacteria. The risk is that such cells may serve as a source of resistance genes that could be transferred to fish and human pathogens with which they might come in contact.

Treatment of salmonids with various antibiotics (including OTC) has, in fact, been shown to result in significant increases in the proportion of the gut micro-flora showing resistance to the antibiotics (Austin and Al-Zahrani 1988; Herwig, Gray, and Weston 1997). The same is true for environmental bacteria coming in contact with wastes containing antibiotics such as OTC. In such wastes under marine salmon farms in Norway and Ireland, the proportion of OTC-resistant environmental bacteria ranged from 16 to 26 % (Nygaard et al. 1992; Kerry et al. 1994 and 1996) and, in one exceptional case, all of the bacteria in the OTC-containing farm sediments proved resistant to OTC (Samuelsen et al. 1992b).

In comparison, in sites not affected by marine salmon farms, the OTC-resistant proportions were lower, ranging from less than 1% to 5% (Torsvick, Sorheim, and Goksoyr 1988; Nygaard et al. 1992; Samuelsen, Torsick, and Ervik 1992; Kerry et al. 1994 and 1996. In Puget Sound, Washington, the proportion of micro-flora showing OTC resistance under a marine salmon farm that relied heavily on the use of antibiotics, including OTC, was 3% to 9%. Analogous values were 0.2% to 1.6% for samples from sites in Puget Sound which were thought to be unaffected by salmon farms (Herwig, Gray and Weston et al 1997). Although not all of the bacteria in marine salmon farm sediments showing resistance to OTC contain resistance genes transferable to other bacteria via plasmids (Kapetanaki et al. 1995; Kerry et al. 1996), those that do have been shown to be capable of transferring resistance genes to bacteria of human origin, e.g., *E. coli* (results of R.A. Sandaa cited by Husevag et al.1991). Similar results have been found for ubiquitous freshwater bacteria isolated from a Danish trout farm; antibiotic resistance in these bacteria was readily transferred to *E. coli* in the laboratory (Schmidt et al. (2001).

2.2.4 *Risk of exposing non-target animals that might serve as food for humans to antibiotics*

Antibiotics may end up in non-target fauna associated with fish culture sites. Reports on this topic relating to freshwater salmonid hatcheries appear to be lacking; however, the opposite is true with marine salmon farms. Wild fish, crustaceans, and mollusks living in the vicinity of marine salmon farms have been shown to accumulate measurable levels of antibiotics in their tissues as a result of feeding on waste medicated feed and feces.

Samuelsen et al. (1992) thought it possible that drug residues in non-target fauna might represent a pathway by which antibiotics could enter human populations. In this connection, four studies have been conducted with respect to OTC:

- In the first study, farmed blue mussels (*Mytilus edulis*) in Norway were found to contain 7.0 µg OTC/g tissue while those collected 80 meters from the farm contained only trace levels (Moster 1986 as reported by Coyne, Hiney, and Smith 1997).
- In the second study, Bjorklund, Bondestam, and Bylund (1990) detected OTC levels of 0.2 µg/g to1.3 µg/g in samples of muscle from bleak (A*burnus*

alburnus) in Norway. Their samples were obtained from a location near a salmon farm on the final day of antibiotic therapy.

- The third study was conducted in Puget Sound, Washington. Samples of non-target organisms were taken from the vicinity of, and under, a salmon farm during, and within 12 days of, an OTC treatment. No more than trace levels of OTC (0.1 µg/g) were found in oysters (*Crassostrea gigas*) and Dungeness crabs (*Cancer magister*), but about half of the sampled red rock crabs (*Cancer productus*) contained OTC at levels ranging from 0.8µg/g to at least 3.8 µg/g muscle (Capone et al. 1996).
- In the fourth study, mussels sampled 20 meters from a salmon farm in Ireland on the last day of an OTC treatment contained no detectable OTC, but those sampled from under the farm contained 10.2 µg/ OTC/g of soft tissue (Coyne, Hiney, and Smith1997). OTC levels in the mussel tissues declined rapidly following the treatment (the half-life was approximately 2 days). The authors concluded that residues present in filter-feeding bivalves as a result of therapeutic use of OTC are unlikely to present a significant human health hazard.

Studies have also been conducted with other antibiotics and non-target fauna. Samuelsen et al. (1992) sampled wild fishes in the vicinity of two Norwegian marine salmon farms treated with oxolinic acid. The samples were obtained on the last day of treatment. The mean levels of oxolinic acid found for the muscle samples that proved positive for the drug were 4.38 µg/g at one farm and 0.42 µg/g at the other. The highest oxolinic acid concentration (12.51 µg/g) was in a coalfish, *Pollachius virens*. In mussels near the farm, oxolinic acid levels of 0.65 µg/g were found.

In a similar Norwegian study, Ervik, Samuelsen, et al. (1994) tested muscle samples from wild fish living in the vicinity of six salmon farms treated with quinolone drugs (oxolinic acid and flumequine). Samples were taken on the last day of treatment or one day after treatment. Most or all of the fish sampled at each farm were positive for the antibiotics. Mean muscle concentrations ranged from 0.95 µg/g to 4.89ug/g. Ervik, Thorsen, et al. (1994) reported in a follow-up study on two devices that reduced feed waste on salmon farms. They found that using the devices resulted in reduced drug residues in wild fish sampled near treated farms. The authors recommended, however, that, in addition to using such devices, fishing should not be conducted in the vicinity of fish farms during and after medication.

2.3 Ecological effects of using antibiotics in aquaculture

The long-term environmental impacts of using antibiotics in aquaculture are still uncertain. In some cases, short-term decreases in the size of gastrointestinal bacterial populations of fish during treatment with erythomycin have been noted (Moffit and Mobin 2006). The same has been found for bacterial populations in hatchery effluents during separate treatments with OTC, oxolinic acid, and a potentiated sulfonamide (Austin 1985). In other cases, the use of antibiotics has had no appreciable effect on the sizes of the aquatic bacterial populations; if any size changes occurred, they were masked by temporal variations in the microbial densities (Samuelsen et al. 1992; Herwig, Gray, and Weston 1997). During separate treatments with three antibiotics, increases in the proportion of the hatchery effluent populations resistant to each of the antibiotics occurred; however, these increases were soon reduced after conclusion of the treatments (Austin 1985).

Antibiotics in general should be efficacious, readily absorbed from the intestinal tract, and have short half-lives once they are voided to the environment. OTC, one of the most commonly used antibiotics in fish farms and hatcheries, does not exhibit all of these characteristics. It is poorly absorbed from the intestinal tract (Cravedi, Choubert, and Delous 1987). An estimated 70% to80% of it is voided intact in the feces (Samuelsen 1989). Also, while OTC can apparently undergo degradation in seawater (Samuelsen 1989), it appears, under certain conditions, to be virtually indestructible in the sediments under marine salmon farms. Following 13 treatments with OTC, OTC levels in farm sediments ranged from 0.1 µg/g to 11 µg/g (in one exceptional case, it ranged up to 285 µg/g) and the half-lives for persistence were estimated to range from 9 to 415 days (Smith and Samuelsen 1996). The high proportions of OTC-resistant bacteria that persist in these sediments may provide a threat to fish farms since they can serve as sources of OTC-resistance genes for fish pathogens in the vicinity of the farms. Whether the OTC-induced changes in the micro-flora of the sediments interferes in any way with the rates of decomposition of organic matter in the sediments and with re-colonization of the seabed by organisms displaced by sediment deposition has apparently not been investigated.

The fate of OTC in freshwater sediments appears not to have been studied. However, the persistence of OTC resistance in ubiquitous freshwater bacteria, such as the motile *Aeromonas* spp. (aeromonads) reported by Schmidt et al. (2001), might be explained if the antibiotic is also stable in freshwater sediments. Schmidt et al. (2001) studied antibiotic resistance of the aeromonads in a Danish river in which trout hatcheries had earlier used OTC without restriction, but which were no longer permitted to do so as a result of recent restrictions on its use in Danish aquaculture. It was proposed that the aeromonads might serve as reservoirs of transferable OTC-resistance genes.

In another study on the same river, Schmidt et al. (2000) examined the antibiotic sensitivities of a large number of isolates of two bacterial fish pathogens (*Flavobacterium psychrophilum* and *Yersinia ruckeri*) and of the motile aeromonads. In tests with five antibiotics, they found that fish farming on the river had exerted a heavy impact on the flavobacteria and aeromonads in the river; these bacteria showed high levels of individual and multiple antibiotic resistances. In addition, in comparing aeromonad samples from the hatchery inlets and outlets, it was found that the proportions of the populations showing antibiotic resistance were significantly higher in the hatchery outlet samples.

Spangaard et al. (1993), also working on a freshwater system in Denmark, reported the prevalence of resistance to the antibiotics OTC and oxolinic acid in an unpolluted river to be 6% and 16%, respectively. In comparison, the prevalence of resistance to these antibiotics in samples from three fish hatcheries was somewhat higher (15% and 27%, respectively). It was not made clear whether the resistances found in the unpolluted river were due to intrinsic, non-transferable resistance or whether they were due to antibiotic-specific, transferable genes that resulted, perhaps, from unrecognized prior exposures to the two antibiotics. In any event, in comparing the total counts of bacteria and the composition of the micro-flora in the unpolluted river with the analogous findings in samples from the three fish farms, the authors concluded that the farms had exerted no adverse impacts on the bacterial populations. The differences in the prevalence of antibiotic resistance in the unpolluted river and fish farm environments were found not to be statistically significant.

The majority of studies indicate that increased levels of antibiotic resistance can be expected to occur for as long as antibiotics are used in aquaculture. It might be expected,

however, that if the use of a given antibiotic in aquaculture is discontinued or if the frequency with which it is used is reduced, the advantage of possessing resistance to the antibiotic would disappear. Under such circumstances, the wild-type, non-resistant bacterial cells might regain their numerical dominance in the population unless, of course, continued inputs of the antibiotic to the aquatic system from other sources interfere to prevent this reversion. Results from human medicine support the foregoing idea (Forfar et al. 1966).

One means of reducing the use of antibiotics in aquaculture is to use vaccines for controlling disease problems whenever possible. In Norwegian salmon farming, the use of antibiotics was dramatically reduced in 1992 from a high of almost 50,000 kg of active drug in 1987 to a low of approximately 1000 kg (Markestad and Grave 1997). This decrease was almost entirely due to implementing the large-scale use of vaccination and occurred despite the fact that the tonnage of salmon being produced on the farms was increasing at the time. Vaccination plays only a very small part in disease control in the freshwater salmon and steelhead hatcheries of the Pacific Northwest despite the fact that at least three of the cultured species may be reared for a year or so before their release to the sea. The problem is that vaccines effective against the bacterial diseases of greatest concern in the Pacific Northwest, e.g., bacterial kidney disease and bacterial cold water disease, are still lacking. While efforts to develop an anti-BKD vaccine have thus far led to less-than-satisfactory protection in Pacific salmon, these efforts should be continued. In addition, the prognosis for an effective anti-BCWD is good (Madetoja et al. 2006). Clearly, support for developing vaccines against these diseases should be encouraged.

A second means of reducing antibiotic use in aquaculture is to implement rearing practices that minimize the level of stress on the fish being reared and that reduce the likelihood that infections requiring antibiotic treatment will occur. With regard to the latter practice, many salmon hatcheries in the Pacific Northwest do not normally use eggs derived from brood Chinook found to be infected with the causative agent of bacterial kidney disease (BKD), *Renibacterium salmoninarum* (Rs), because the agent is transferable to their progeny via their eggs. This practice has greatly reduced the prevalence of BKD problems in Chinook hatcheries and has reduced the frequency with which antibiotic treatments are needed.

3 Conclusions

Alderman and Hastings (1998) reviewed the literature on the use of antibiotics in aquaculture and came to the conclusion that “although there is evidence that antibiotic resistance can be selected for in normal therapeutic use in aquaculture, the risks of transfer of such resistance to human consumers by any of the possible routes appear to be low”. This, they considered, was particularly true for cultured cold- and cool-water fishes. Since the Alderman and Hastings review was published, there has been no new information to warrant a change in the above conclusion.

Alderman and Hastings’ conclusion is supported by the findings of Moffit and Mobin (2006) on the gut micro-flora of cultured spring Chinook salmon. They found no evidence in the salmon they tested of human pathogens or of animal disease agents transmissible to man. Since the gut micro-flora of fish tends to reflect the environment they inhabit and the food they eat, salmonids cultured in the Pacific Northwest are not likely to be carrying such pathogens. Thus, in the Pacific Northwest, one need not hesitate to use antibiotics when it is absolutely necessary to do so.

For example, there are many situations in the Pacific Northwest in which salmonid hatcheries are forced to operate on untreated river water. Such water is a potential source of fish pathogens, including Rs, the causative agent of BKD. As mentioned above, there are currently no vaccines available for controlling BKD in Pacific salmon. Some of the hatcheries relying on untreated river water rear species, such as spring Chinook salmon and steelhead, that require long-term rearing. For much of the rearing period, water temperatures in some of the hatcheries are below 10o C, thus compromising any potential cell-mediated resistance the fish might have against Rs (Hamel 2005). The use of appropriate chemotherapy would be justified in such situations if infection with Rs were detected. It would be ill advised not to treat such fish in a timely manner since failure to use antibiotics would run the risk of poor survival which is unacceptable especially for hatchery programs whose goals are conservation. The fish should also be treated because of enhanced risk that they would pose to other salmonids that share the waterway. In these cases, the benefits of treating the infected fish would outweigh the risks.

4 Recommendations

The HSRG concludes that antibiotics will likely always be needed in the operation of fish-rearing facilities. However, these compounds must be used with care in order to minimize risks to humans and the environment.

Recommendations are as follows:

- In setting up and operating new freshwater or marine aquaculture facilities, consideration should be given to the following questions raised by Ahne, Winton, and Kimura (1989) :
  - Will the facility's water supply permit pathogen avoidance?
  - Will the culture environment suit the needs of the species to be reared?
  - Will, the species to be reared be resistant to the pathogens likely to be encountered?
  - Are vaccines available to combat any pathogens encountered?
- The quantities of antibiotics used in operating the facilities will be minimal if most or all of these questions can be answered in the affirmative.
- Antibiotic use should be as infrequent as possible to avoid enriching the numbers of antibiotic-resistant bacteria in the hatchery or farm environment.
- Bacterial infections in fish hatchery populations should be treated without delay when detected. If treatment is via medicated feed, the feeding rate should be adjusted so that all medicated feed is eaten and none (or very little) sinks to the bottom. This will not only maximize the effectiveness of the treatment, but will reduce the problem of accumulating large amounts of waste in hatchery and fish farm environments. In hatcheries, uneaten medicated feed and fecal material should be removed from hatchery effluents using filters, settling ponds, or both as these materials are likely to be associated with the antibiotics being used (Smith et al. 1994).
- Tests for detecting pathogens in hatchery populations should be conducted on a regular basis and, to maximize the chances of detecting infections, the samples used should not be collected at random. Rather, the samples selected for testing

should consist of freshly dead and moribund specimens and of fish showing other signs of abnormality including lesions, darkened pigmentation, loss of appetite, and sluggish behavior.

- Treatments of hatchery-reared Pacific salmon and steelhead intended for natural rearing at sea must be timed so that any antibiotics in their tissues are at acceptably low levels by the time they are released as smolts. Similarly, treatments of farmed salmon and trout intended for human consumption must be timed so that any antibiotics in their tissues (particularly the flesh) are at acceptably low levels by the time they are marketed. Proper timing is important if bacteria in the gastrointestinal tracts of animals preying on released smolts or of humans eating marketed salmon and trout products are to avoid unnecessary exposure to the antibiotics. Because water temperature and the type of antibiotic being used are major factors affecting the rate of antibiotic clearance from fish tissues, these factors must be taken into account in the timing of treatments (Namdari, Abedini, and Law 1996; Fairgrieve et al. 2005).
- Agencies operating salmon and steelhead hatcheries and private firms operating fish farms are strongly urged to support research in vaccine development. When vaccines effective against the bacterial diseases of the greatest concern become available, the use of antibiotics in affected facilities should decrease significantly.

5 References

Adams, C.A., B. Austin, P.G. Meaden, and D. McIntosh. 1998. Molecular characterization of plasmid-mediated oxytetracycline resistance in *Aeromonas salmonicida*. *Applied and Environmental Microbiology* **64**: 4194-4201.

Ahne, W., J.R. Winton, and T. Kimura. 1989. Prevention of infectious diseases in aquaculture. *Journal of Veterinary Medicine **B***: **36**: 561-567.

Aoki, T. 1988. Drug resistant plasmids from fish pathogens. *Microbiological Sciences* 5: 219-223.

Aoki, T., N. Kitso, Y. Lemurs, and T. Nomura. 1983. The susceptibility of *Aeromonas salmonicida* isolated in cultured and wild salmonids to various chemotherapeutics. *Bulletin of the Japanese Society of Scientific Fisheries* 49: 17-22.

Alderman, D.J. and T.S. Hastings. 1998. Antibiotic use in aquaculture: development of antibiotic resistance – potential for consumer health risks. *International Journal of Food Science and Technology* 33: 139-155.

Austin, B. 1985. Antibiotic pollution from fish farms: effects on aquatic microflora. *Microbiological Science* 2: 113-117.

Austin, B. and A.M.J. Al-Zahrani. 1988. The effect of antimicobial compounds on the gastrointestinal microflora of rainbow trout, *Salmo gairdneri*. *Journal of Fish Biology* 32: 1-14.

Bjorklund, H., J. Bondestam, and G. Bylund. 1990. Residues of oxytetracycline in wild fish and sediments from fish farms. *Aquaculture* 86: 359-367.

Capone, D.G., D.P. Western, V. Miller, and C. Shoemaker. 1996. Antibacterial residues in marine sediments and invertebrates following chemotherapy in aquaculture. *Aquaculture* 145: 55-75.

Coughter, J.P. and G.J. Stewart. 1989. Genetic exchange in the environment. Antonie van Leeuwenhoeck *55: 15-22*.

Coyne, R., M. Hiney, and P. Smith. 1997. Transient presence of oxytetracycline in blue mussels (*Mytilus edulis*) following its therapeutic use at a marine Atlantic salmon farm. *Aquaculture* 149: 175-181.

Cravedi, J-P, G. Choubert, and G. Delous. 1987. Digestibility of chloramphenicol, oxolinic acid and oxytetracycline in rainbow trout and influence of these antibiotics on lipid digestibility. *Aquaculture* 60: 133-141.

Ervik, A., O.B. Samuelsen, J.E. Juell, and H. Sveier. 1994. Reduced environmental impact of antibacterial agents applied in fish farms using the LiftUp feed collector or a hydroacoustic feed detector. *Diseases of Aquatic Organisms* 19: 101-104.

Ervik, A. B. Thorsen, V. Eriksen, B.T. Lunestad, and O.B. Samuelsen. 1994. Impact of administering antibacterial agents on wild fish and blue mussels *Mytilus edulis* in the vicinity of fish farms. *Diseases of Aquatic Organisms* 18: 45-51.

Fairgrieve, W.T., C.L. Masada, W.C. McAuley, M.E. Peterson, M.S. Meyers, and M.S. Strom. 2005. Accumulation and clearance of orally administered erythromycin and its derivative, azithromycin, in juvenile fall Chinook salmon *Oncorhynchus tshawytscha. Diseases of Aquatic Organisms* 64: 99-106.

Forfar, J.O., A.J. Keay, A.F. McCabe, J.C. Gould, and A.D. Bain. 1966. Liberal use of antibiotics and its effect on neonatal staphylococcal infection with particular reference to erythromycin. *Lancet ii*, 295: 295-300.

Hamel, O.S. 2005. Immunosuppression in progeny of Chinook salmon infected with *Renibacteriunm salmoninarum*: re-analysis of a brood stock segregation experiment. *Diseases of Aquatic Organisms* 29: 29-41.

Herwig, R.P., J.P. Gray, and D.P. Weston. 1997. Antibacterial resistant bacteria in surficial sediments near salmon net-cage farms in Puget Sound, Washington. *Aquaculture* 149: 263-283.

Husevag, B., B.T. Lunestad, P.J. Johannessen, O. Enger, and O.B. Samuelsen. 1991. Simultaneous occurrence of *Vibrio salmonicida* and antibiotic resistant bacteria in sediments at abandoned aquaculture sites. *Journal of Fish Diseases* 14: 631-641.

Kapetanaki, M., J. Kerry, M. Hiney, C. O'Brien, R. Coyne, and P. Smith. 1995. Emergence in oxytetracycline-free marine mesocosms, of microorganisms capable of colony formation on oxytetracycline-containing media. *Aquaculture* 134: 227-236.

Kerry, J., R. Coyne, D. Gilroy, M. Hiney, and P. Smith. 1996. Spatial distribution of oxytetracycline and elevated frequencies of oxytetracycline resistance in sediments beneath a marine salmon farm following oxytetracycline therapy. *Aquaculture* 145: 31-39.

Kerry, J., M. Hiney, R. Coyne, D. Cazabon, S. NicGabhainn, P.Smith. 1994. Frequency and distribution of resistance to oxytetracycline in micro-organisms isolated from marine fish farm sediments following therapeutic use of oxytetracycline. *Aquaculture* 123: 43-54.

Kerry, J., M. Hiney, R. Coyne, S. NicGabhainn, D. Gilroy, D. Cazabon, and P. Smith. 1995. Fish feed as a source of oxytetracycline-resistant bacteria in sediments under fish farms. *Aquaculture* 131: 101-113.

Kruse, H. and H. Sorum. 1994. Transfer of multiple drug resistance plasmids between bacteria of diverse origins in natural microenvironments. *Applied and Environmental Microbiology* 60: 4015-4021.

Madetoja, J., L-G Lonnstrom, C. Bjorkblom, G. Ulukoy, G. Bylund, C. Syvertsen, K. Gravningen, E-A Norderhus, and T. Wiklund. 2006. Efficacy of injection vaccines against *Flavobacterium psychrophilum* in rainbow trout. *Journal of Fish Diseases* 29: 9-20.

Markestad, A. and K. Grave. 1997. Reduction of antibacterial drug use in Norwegian fish farming due to vaccination. Pages 365-369 *in* R. Gudding, A. Lillihaug, P. J. Midtlyng, and F. Brown, editors. Fish Vaccinology. Developmental Biological Standards. Basel, Karger, Volume 90.

Moffit, C.M. and S.M.A. Mobin. 2006. Profile of microflora of the posterior intestine of Chinook salmon before, during, and after administration of rations with and without erythromycin. *North American Journal of Aquaculture* 68: 176-185.

Nakajima, T., M. Suzuki, K. Harada, M. Inoue, and S. Mitsuhashi. 1983. Transmission of R plasmids in *Vibrio anguillarum* to *Vibrio cholera*. *Microbiology and Immunology* 27: 195-198.

Namdari, S. Abedini, and F.C.P. Law. 1996. Tissue distribution and elimination of oxytetracycline in seawater Chinook and coho salmon following medicated-feed treatment. *Aquaculture* 144: 27-38.

Nygaard, K., B.T. Lunestad, H. Hektoen, J.A. Berg, and V. Hormazabal. 1992. Resistance to oxytetracycline, oxolinic acid and furazolidone in bacteria from marine sediments. *Aquaculture* 104: 31-36.

Samuelsen, O. B. 1989. Degradation of oxytetracycline in seawater at two different temperatures and light intensities, and the persistence of oxytetracycline in the sediment from a fish farm. *Aquaculture* 83: 7-16.

Samuelsen, O.B., B.T, Lunestad, B. Husevag, T. Holleland, and A. Ervik. 1992. Residues of oxolinic acid in wild fauna following medication in fish farms. *Diseases of Aquatic Organisms* 12: 111-119.

Samuelsen, O.B., V. Torsvik, and a. Ervik. 1992. Long-range changes in oxytetracycline concentration and bacterial resistance towards oxytetracycline in a fish farm sediment after medication. *Science of the Total Environment* 114: 25-36.

Schmidt, A.S., M.S. Bruun, I. Dalsgaard, K. Pedersen, and J.L. Larsen. 2000. Occurrence of antibacterial resistance in fish-pathogenic and environmental bacteria associated with

four Danish rainbow trout farms. *Applied and Environmental Microbiology* 66: 4908-4915.

Schmidt, A.S., M.S. Bruun, I. Dalsgaard, and J.L. Larsen. 2001. Incidence, distribution, and spread of tetracycline resistance determinants and integron-associated antibiotic resistance genes among motile aeromonads from a fish farming environment. *Applied and Environmental Microbiology* 67: 5675-5682.

Smith, P., J. Donlon, R. Coyne, and D. Cazabon. 1994. Fate of oxytetracycline in a freshwater fish farm: Influence of effluent treatment systems. *Aquaculture* 120: 319-325.

Smith, P. and O.B. Samuelsen. 1996. Estimates of the significance of out-washing of oxytetracycline from sediments under Atlantic salmon sea-cages. *Aquaculture*144: 17-26.

Spangaard, B., F. Jorgensen, L. Gram, and H.H. Huss.1993. Antibiotic resistance from three freshwater fish farms and an unpolluted stream in Denmark. *Aquaculture* 115: 195-207.

Toranzo, A. E., P. Combarro, L.M. Lemos, and J.L. Barja. 1984. Plasmid coding for transferable drug resistance in bacteria isolated from cultured rainbow trout. *Applied and Environmental Microbiology* 48: 872-877.

Torsvik, V.L., R. Sorheim, and J. Goksoyr. 1988. Antibiotic resistance of bacteria from fish farm sediments. International Council for the Exploration of the Sea, Mariculture Committee F: 10, 9 pp.

Trevors, J.T., T. Barkay, and W. Bourquin. 1987. Gene transfer among bacteria in soil and aquatic environments: a review. *Canadian Journal of Microbiology* 33: 191-198.

White Paper No. 3[1]

Global Climate Change and its Effects on the Columbia River Basin

1 Introduction

The purpose of this white paper is to describe possible impacts of climate change on the anadromous fish populations of the Columbia River Basin and to discuss the implications these changes may have on hatchery facilities used to produce fish for both conservation and harvest purposes. The primary concern in the Pacific Northwest regarding climate change is the increase in ambient temperature, i.e., global warming.

Global warming is accepted by the majority of the scientific community as a fact, though the pace and severity cannot be predicted with certainty[2]. Global warming is expected to cause sea levels to rise, alter marine productivity, change precipitation levels and timing, and increase the severity and frequency of extreme weather events such as flooding[3]. The productivity of both natural and hatchery salmon is highly dependent upon the freshwater and marine environments. Any perturbation or degradation of water quality and/or quantity has the potential to negatively impact anadromous fish.

If the pace of global change is slow enough (over decades rather than years), salmon populations may be able to adjust to changes in their environment. The larger the change and the faster the pace, the less likely wild salmonid populations will be able to adapt. Hatcheries, with their ability to tightly control at least the freshwater component of the salmon life cycle, could play a positive role in conserving salmon populations if the pace of warming is rapid.

The information presented in this paper is not an exhaustive review of the pertinent scientific literature on the topic of global warming, but is rather an overview aimed at educating the layperson as to the effects on wild and hatchery salmon populations and the implications for hatchery production and operations in the Columbia River Basin.

Several documents formed the basis for this report, including:

- Climate Change 2007- Synthesis Report. A Report of the Intergovernmental Panel on Climate Change (IPCC 2007)
- Potential impacts of global warming on salmon production in the Fraser River watershed. Canadian Technical Report of Fisheries and Aquatic Sciences (Levy 1992).

[1] White papers were prepared by the HSRG to address topics relevant to hatchery reform. They are intended to stimulate discussion and provide background, documentation and explanations not included in the body of the HSRG's report.

[2] (http://www.ipcc.ch/)

[3] (http://archive.greenpeace.org/climate/arctic99/reports/salmon.html),

- Natural Climate Insurance for Pacific Northwest Salmon and Salmon Fisheries: Finding Our Way through the Entangled Bank (Mantua and Francis 2004)
- Climate Change Impacts on Columbia River Basin Fish and Wildlife (ISAB 2007)
- On the decline of Pacific salmon and speculative links to salmon farming in British Columbia (Noakes et al. 2000)
- Projected impacts of climate change on salmon habitat restoration (Battin et al. 2007)

2 Problem Statement and Concerns

Climate records show that the Pacific Northwest has warmed about 1.0 ºC since 1900 which is about, 50% more than the global average warming over the same period. The warming rate for the Pacific Northwest over the next century is projected to be in the range of 0.1-0.6° C/decade. Projected precipitation changes for the region are relatively modest and unlikely to be distinguishable from natural variability until late in the 21st century. Most models project long-term increases in winter precipitation and decreases in summer precipitation. Salmon are expected to be affected by changes in the freshwater, terrestrial, and marine environments. These impacts include: increased rainfall, decreased snowfall, increases in peak river flows, increases in stream temperatures, indirect effects from increases in terrestrial temperatures on riparian and terrestrial communities, and warmer ocean temperatures.

2.1 Warmer temperatures should result in more precipitation falling as rain rather than snow

In the Pacific Northwest, rain-dominated streams exhibit the highest stream flows in the fall, compared to the spring and early summer for snowmelt-dominated streams. The change in peak flow timing from spring to fall may affect the species of salmonids and the runs present in each stream. For example, spring Chinook run timing has evolved to coincide with spring freshets resulting from snow-melt in the mountains. The large amount of cool water present at this time allows spring Chinook to migrate long distances to spawning grounds where they hold in large deep pools until spawning in the late summer and early fall. As spring-time flows decrease due to global warming, spring Chinook may not be able to access spawning grounds and, if they do, water temperatures may be too high, causing increased mortality and reduced productivity. If the change in flow and stream temperature is too severe, spring Chinook runs may disappear from affected streams.

2.2 Snow pack should diminish and stream flow timing should be altered

Juvenile salmon of multiple species migrate to the ocean during the spring and early summer. As was the case with spring Chinook adults, juveniles take advantage of the snow-melt-freshet to migrate hundreds of miles in a relatively short time. The coldwater and turbidity associated with systems dominated by snowmelt reduces the ability of natural predators to find and consume juvenile migrants. A decrease in snow-pack

decreases the magnitude and duration of the spring freshet which will likely increase predator success and change the run-timing of the juveniles migrating from the system.

For the Columbia River, reduced snow pack may lead to a reduction in the amount of stored water available to fish managers for increasing spring and summer flows during key salmon migration periods. Lower flow and higher stream temperatures may lower juvenile migration survival rates through the system due to migrational delay, increased predation, and disease incidence.

2.3 Peak river flows should increase

Fall precipitation levels will likely increase due to global warming. The result will likely be increased flood frequency and magnitude. This is especially true for streams substantially located in the snow zone. These systems are highly susceptible to rain-on-snow events where rainfall rapidly melts the early winter snow pack, resulting in large-scale flooding in the months of November and December. Flooding causes scouring of the streambed where salmon lay their eggs, effectively destroying that year's salmon production. Salmon populations are usually able to withstand these flood events because portions of the run spawn at different times and because large flood events occur infrequently. More frequent and larger floods will negatively impact salmon survival.

2.4 Stream temperatures should continue to rise

All phases of the salmon life cycle are impacted by water temperature. For example, fry emergence timing is based on the daily stream temperature, to which eggs are exposed, with higher temperatures stimulating fry to emerge after a shorter incubation period. A change in emergence timing may expose fish to unfavorable environmental conditions (such as flooding) that reduce survival. Higher summer stream temperatures may stress rearing juveniles and increase their susceptibility to disease. This same effect could occur for adult salmonids as well. Additionally, increased stream temperatures may favor the production of other native or non-native species that prey on juvenile salmon, again reducing juvenile salmon survival.

Bull trout are particularly at risk if stream temperatures rise. This species requires cold (less than 10.0 ^{o}C) headwater streams for spawning. An analysis of the effects of temperature increases associated with climate change predicts a substantial loss of current bull trout habitat in the Columbia River Basin.

2.5 Warmer temperatures may affect riparian and terrestrial communities

Several habitat types and vegetative communities in the Columbia River Basin are likely to decrease greatly in area or disappear regionally as a result of global warming. These types are: alpine habitats, subalpine spruce-fir forests, aspen communities, and sagebrush communities. Resulting shifts in vegetation type may alter nutrient inputs to the stream and reduce the amount of riparian habitat that shades and cools streams.

2.6 Global warming will also alter marine water temperatures and sea levels

Global warming will also affect the marine environment where salmon spend a considerable amount of their life history. New research suggests that ocean temperature and associated sea level increases between 1961 and 2003 were 50 percent larger for the upper 700 meters of oceans than estimated in the 2007 IPCC report (Domingues et al.

2008). Changing ocean temperatures may alter the behavior, distribution, and migration patterns and distances that salmon have to travel from their home streams to ocean feeding areas and back. Energy demands are increased at warmer temperatures, requiring increased consumption of prey to maintain a given growth rate. Ocean temperature also influences the distribution and abundance of species that prey on salmon. Impacts from predators may be positive or negative depending on which species are most susceptible to ocean temperature changes.

Sea level rise from melting ice pack, in conjunction with higher winter river flows, could cause the degradation of estuary habitats due to increased wave damage during storms. This in turn could reduce food production in the estuary environment where salmon spend critical portions of their life history. In addition to increases in ocean temperature and rises in sea levels, other physical changes in the ocean associated with warming include increased stratification of water column, acidification, and changes in the intensity and timing of coastal upwelling. Such changes can affect the ocean food web, resulting in reduced coastal productivity and salmon survival.

3 Implications for Hatchery Management

Hatcheries require abundant sources of cold-water to rear quality juvenile salmonids. Groundwater is a key source of water for many of the hatcheries in the Columbia River Basin. A reduction in snow pack may reduce the amount of cold water entering the water table. This, in turn, could decrease the amount of water available for hatchery use. Hatcheries may have to reduce production or use expensive mechanical water chilling devices to produce high quality juveniles. Additionally, because water temperature affects the growth rate of cultured fish, any change in temperature alters the ability of managers to produce fish of sufficient size to meet size-at-release targets that have been shown to increase hatchery fish survival.

Hatcheries which rely on river water may also experience similar problems. Both the quality and quantity of water used by hatcheries for culture purposes may be seriously altered as stream flows change. Higher fall flood flows may increase the amount of sediment entering the hatchery facility or damage hatchery intake structures. Decreased summer flows mean that the proportion of a stream's water used to rear fish increases which will negatively impact the natural environment and salmon survival in stream reaches downstream of the intake.

Many common microbial diseases of cultured fish are exacerbated as temperatures in the rearing environment increase. Both the frequency and severity of these diseases may increase as temperatures in the hatchery and the natural environment increase. Infections of salmon by the parasite, *Ceratomyxa shasta*, are also likely to increase in areas such as the Cowlitz River where this organism is present.

4 HSRG Conclusions and Recommendations

Global warming is expected to result in substantial, and possibly rapid, changes to salmon habitat and population response. How fish populations will respond to this environmental change is currently unknown. Salmon life histories that were successful in the past at maintaining healthy populations may no longer be viable under a warming climate. New life histories may be expressed that have not been previously seen in each

watershed. In addition, some races of salmon may disappear from the watershed and be replaced by other native or non-native species.

The scientific literature indicates that salmon are able to adapt to environmental changes if those changes are not too extreme or occur too rapidly. A good example of this is the Clearwater fall Chinook population which has responded to the decrease in stream temperatures associated with coldwater releases from Dworshak Dam by switching from a sub-yearling to a yearling life history that over-winters in mainstem Columbia and Snake River pools.

The ability of salmon to adapt to changes in the natural environment reinforces the HSRG conclusion that hatcheries should be operated so that the natural, rather than the hatchery, environment drives adaptation. This can be achieved by keeping the proportion of natural spawners (pNOS) and proportion of natural-origin fish used as hatchery broodstock (pNOB) high and the proportion of hatchery-origin fish on the spawning grounds (pHOS) low. Managers are encouraged to maintain a proportion of natural influence (PNI) for integrated hatchery programs larger than 0.67 and a pHOS of less than 0.05 for segregated programs.

Hatchery managers need to be aware that natural population life histories may change with the changing climate and respond accordingly. For example, the timing of juvenile releases from the hatchery may need to be altered to reflect different river run-off patterns and temperatures as the climate warms. Observing and monitoring the success of wild populations will help better direct hatchery programs in the future. Additionally, the size or number of fish released may need to be reduced if data collected in key areas, e.g., the Columbia River estuary, indicates substantial decreases in food production. This can be accomplished by tying hatchery production levels to wild fish abundance in the receiving watershed and the Columbia River Basin.

Because of climate change and continued degradation of habitat from human population growth, some salmon populations may not survive in the face of global climate change because their habitat is also being degraded by human population growth. Hatchery programs may be able to play a maintenance role in preserving these populations by operating as well-run integrated programs with high PNI values. The focus of these hatcheries may need to shift from emphasizing harvest to an emphasis on conservation.

5 References

Bates, B.C., Z.W. Kundzewicz, S. Wu and J.P. Palutikof [Eds.]. 2008. Climate Change and Water, Technical Paper of the Intergovernmental Panel on Climate Change, IPCC Secretariat. Geneva, Switzerland. 210 pp.

Battin, J., M.W. Wiley, M. H. Ruckelshaus, R. N. Palmer, E. Korb, K. K. Bartz, H. Imaki. 2007. Projected impacts of climate change on salmon habitat restoration. *Proceedings of the National Academy of Sciences* 104(16): 6720-6725.

Domingues, C.M., J.A. Church, N.J. White, P.J. Gleckler, S.E. Wijffels, P.M. Barker, and J.R. Dunn. 2008. Improved estimates of upper-ocean warming and multi-decadal sea-level rise. Nature 453**:**1090-1093.

Independent Scientific Advisory Board. 2007. Biological Climate Change Impacts on Columbia River Basin Fish and Wildlife. Document No. ISAB 2007-2, Northwest Power and Conservation Council. Portland, Oregon. 146 pp.

Intergovernmental Panel on Climate Change. 2007. Climate Change 2007 – Synthesis Report.

Levy, D.A. 1992. Potential impacts of global warming on salmon production in the Fraser River watershed, Canadian Technical Report of Fisheries and Aquatic Sciences 1889.

Mantua, N. J. and R. C. Francis. 2004. Natural climate insurance for Pacific Northwest salmon and salmon fisheries: Finding our way through the entangled bank. *In*: Sustainable Management of North American Fisheries, E. E. Knudsen, D. D. MacDonald, and Y. K. Muirhead [Eds.], *American Fisheries Society Symposium* 43:218pp.

Noakes, D.J., R.J. Beamish, M.L. Kent. 2000. On the decline of Pacific salmon and speculative links to salmon farming in British Columbia *Aquaculture* 183 (3), p.363-386.

White Paper No. 4[1]

Framework for Monitoring and Evaluating Hatchery Programs

1 Introduction and Background

Recent studies have raised questions about the influence of hatchery programs on naturally producing salmon populations. The result is increased pressure on hatchery operators to assess the effectiveness of hatchery programs through monitoring and evaluation, then improve programs, or terminate those where risks exceed benefits. Through its review, the HSRG has concluded that hatchery programs can significantly increase the likelihood of meeting harvest and conservation goals if the programs are designed and operated consistent with clearly stated biological objectives and in a manner that is compatible with expected habitat and harvest conditions.

To aid in achievement of biological objectives, it is important that hatchery programs be operated under a theoretical rationale or "working hypothesis." The working hypothesis for each program will be unique and will form the basis for the biological objectives.

The HSRG has demonstrated that working hypotheses can be developed for hatchery programs using tools such as the All "H" Analyzer (AHA). AHA is a modeling approach that identifies and defines assumptions about harvest, habitat, and survival of hatchery fish for individual hatchery programs. The assumptions constitute the unique theoretical rationale, i.e., the working hypothesis, for the hatchery program.

The validity of the working hypothesis is determined through monitoring and evaluation (M&E). The HSRG has formulated an approach to M&E which will aid in making this determination. The M&E approach is designed to:

- assure that conservation and harvest goals are stated with sufficient detail to evaluate the hatchery program (*population goals),*
- determine if the hatchery program is achieving its stated biological objectives in terms of program size, broodstock selection (pNOB), and release strategy (*implementation monitoring*),
- determine program effectiveness in terms of survival and reproductive success of hatchery fish (*effectiveness monitoring*)
- determine progress toward conservation and harvest goals for all populations affected by the hatchery program, i.e., natural escapement trends in abundance and composition, catch, and verification of habitat and harvest assumptions) (*validation monitoring*)

[1] White papers were prepared by the HSRG to address topics relevant to hatchery reform. They are intended to stimulate discussion and provide background, documentation and explanations not included in the body of the HSRG's report.

It is important that the various regional entities involved in monitoring and evaluating the hatchery programs within the Columbia River Basin adopt consistent and cost effective approaches to prioritization of research investments, management of data and information, and reporting of results. This paper outlines the HSRG's recommended approach to hatchery program monitoring and evaluation and discusses a regional framework for M&E.

2 HSRG Proposed Hatchery Monitoring and Evaluation Framework

2.1 Statement of Population Goals

The HSRG review requires that the conservation goal for a population is designated by the managers as Primary, Contributing, or Stabilizing. A set of standards based on the contribution of hatchery fish to natural spawning (PNI and pHOS) has been proposed for each category. These standards represent tolerance limits for hatchery influence on natural populations and serve as guidelines for the design and operation of hatchery programs. In addition to the population designation, the conservation goal should also identify escapement abundance and composition targets. Harvest goals should include catch contribution targets by fishery for both the natural and hatchery population components.

2.2 Implementation Monitoring

Implementation monitoring can also be termed Best Management Practices (BMPs). As described in Section I, the HSRG used AHA to design a hatchery program that would contribute to conservation and/or harvest goals and would be compatible with all other management goals. The analysis is based the working hypothesis for the program, i.e., assumptions concerning habitat productivity, expected harvest patterns, and hatchery fish survival and reproductive success.

Inherent in the working hypothesis is a subset of assumptions about the facilities and operation of the hatchery program including the assumption that BMPs are being employed. The HSRG has detailed BMPs for the salmonid culture process in the Scientific Framework document (HSRG 2004). The Research, Monitoring and Evaluation section of this document presents an extensive list of monitoring questions that should be addressed with any hatchery program. This template continues to represent the basic Monitoring and Evaluation Plan for the HSRG. The framework document also explains how the practices are linked to effects on the affected salmon populations and the environment. It should be noted that BMPs are not the same for all hatchery programs, but rather depend upon the hatchery program type (integrated or segregated) and purpose (conservation, harvest, or both).

At the implementation level, M&E should track compliance with BMPs and should record the following:

- hatchery program type (integrated or segregated)
- program purpose (conservation, harvest, or both)
- hatchery brood (number of adults spawned and pNOB)
- number of smolts released

- in-hatchery survivals
- number of fish marked and type of mark
- methods used to obtain all information, e.g., means and variances of estimates
- external conditions and events that might affect hatchery performance, e.g., environmental events (floods, droughts, fish kills, etc.) and annual variations in harvest

2.3 Effectiveness Monitoring

Effectiveness monitoring targets the effectiveness of hatchery programs in the short-term. A hatchery program can be deemed a success if the BMP in-hatchery performance targets and post-release performance targets, such as assumed survival and reproductive success, are met in an average harvest and habitat year. The post-release performance targets are part of the program's working hypothesis developed through AHA. Post-release survival parameters that should be estimated annually include:

- survival of hatchery fish from release to fisheries and escapement
- proportion of returning hatchery fish that escape to natural spawning grounds
- the reproductive contribution of hatchery fish spawning in the wild and the number of adult recruits produced per hatchery spawner

Reproductive success will most likely be obtained from multi-year studies; the status of any such studies should be reported annually.

2.4 Validation Monitoring

Validation monitoring tracks the long-term effectiveness of hatchery programs. It involves annual reporting of parameters including population viability, status of habitat conditions, and trends in harvest patterns. The annual monitoring report should include documented conclusions about the status of populations relative to the stated goals (conservation and/or harvest) and updated habitat assumptions and harvest patterns (harvest rates by fishery). Any new research results affecting the assumptions contained in the current working hypothesis (as captured in AHA) should also be reported.

3 Regional Coordination of Monitoring and Evaluation

It is essential that data collection methodologies and information management approaches be standardized throughout the region. A well-integrated regional approach will allow comparison of similar hatchery programs in different watersheds in order to evaluate successful trends in achievement of management objectives. Consistent data collection and information management will result in greater cost effectiveness for region-wide M&E programs. There are currently several different forums that are attempting to design integrated monitoring and evaluation programs for hatcheries in the Columbia River Basin. These forums include the Independent Scientific Review Panel, the Independent Scientific Advisory Board, the Collaborative Systemwide Monitoring and Evaluation Project (CSMEP) Hatchery Subgroup, the Ad Hoc Supplementation Monitoring and Evaluation Workgroup (AHSWG), and the Pacific Northwest Aquatic Monitoring Partnership (PNAMP). Native American Tribes, Pacific Northwest State

agencies, Upper Columbia Public Utility Districts, Federal agencies, and other entities have prepared M&E plans for their proposed hatcheries.

3.1 ISRP and ISAB

In a report prepared for Northwest Power and Conservation Council, the ISRP and ISAB reviewed the types of demographic, genetic, and ecological risks that could be associated with supplementation and concluded that currently available information was insufficient to provide an adequate assessment of the magnitude of these effects under alternative management scenarios (ISRP and ISAB 2005). The ISAB and ISRP concluded in this report that monitoring and evaluation of supplementation projects are critically important to successful hatchery programs. They recommended that an interagency working group be formed to design an approach for evaluating hatchery supplementation at the basin-wide level. This recommendation resulted in the formation of the *Ad Hoc* Supplementation Workgroup discussed below.

3.2 Collaborative Systemwide Monitoring and Evaluation Project

Created in 2003, CSMEP is a multi-agency effort designed to develop a coordinated regional monitoring and evaluation program for fish populations in the Columbia River Basin. Project participants were divided among several work groups including: Status and Trends, Harvest, Hydrosystem, Habitat, Hatcheries, and Integration. As a test case to refine design methods and analytical tools, CSMEP initially focused their plans on M&E of spring/summer (stream-type) Chinook salmon populations in the Snake River Basin Evolutionary Significant Unit (ESU). The results were summarized in the Snake River Basin Pilot Report (Marmorek et al. 2007a and 2007b).

3.3 Ad Hoc Supplementation Workgroup

Subsequent to the CSMEP's work, the *Ad Hoc* Supplementation Workgroup (AHSWG) was created. The AHSWG sponsored three workshops in which different approaches for monitoring and evaluating the impacts of supplementation on wild populations were reviewed, as well as the data types and time frames that would be required to implement potential M&E designs. AHSWG had many of the same agency representatives as the ongoing CSMEP group and built upon previous efforts to develop an integrated monitoring plan. AHSWG presented their consensus view that a three-pronged approach is required to achieve the basin-wide evaluation requested by the ISRP and ISAB (*Ad Hoc* Supplementation Monitoring and Evaluation Workgroup 2008). This approach involves:

1. investigating the long-term trends in the abundance and productivity of supplemented populations relative to un-supplemented populations
2. conducting a series of relative reproductive success studies to quantify short-term impacts
3. developing a request for proposals to fund several intensive small-scale studies designed to elucidate various biological mechanisms by which introduction of hatchery-produced fish may influence natural population productivity.

The AHSWG report includes appendices which:

- clearly define the various management scenarios under which hatchery-reared fish may influence natural populations (Appendix A)
- describe AHSWG activities and those of other regional processes which have addressed similar issues (Appendix B)
- describe a framework within which hatchery monitoring and evaluation (M&E) activities may be standardized and the different types of M&E programs organized for assessment of long-term and short-term effectiveness (Appendix C)
- describe a preliminary regional analysis of available abundance and productivity trends among a subset of Columbia basin supplemented and un-supplemented populations (Appendix D)

Appendix C, "Framework for Integrated Hatchery Research, Monitoring and Evaluation", describes three categories of research, monitoring, and evaluation associated with hatchery programs:

1. Implementation and Compliance Monitoring
2. Hatchery Effectiveness Monitoring, at both project and regional scales
3. Uncertainty Research

Basic monitoring and evaluation activities and projects that address Implementation and Compliance Monitoring should be conducted on all hatchery programs. An increased intensity of M&E activities/projects addressing Hatchery Effectiveness Monitoring (both regionally and locally) should be conducted on a subset of programs. A limited number of research projects would focus intensively on M&E projects/activities addressing Uncertainty Research.

This approach employs a common set of standardized performance measures established by the Collaborative System-wide Monitoring and Evaluation Project (CSMEP). Adoption of this suite of performance measures and definitions across multiple study designs will facilitate coordinated analysis of findings from regional monitoring and evaluation efforts aimed at addressing management questions and critical uncertainties associated with supplementation and ESA-listed stock status/recovery.

3.4 Pacific Northwest Aquatic Monitoring Partnership

The Pacific Northwest Aquatic Monitoring Partnership (PNAMP) was established to provide a forum to evaluate the various programs implemented or proposed under the Northwest Power and Conservation Council's Fish and Wildlife Program (www.pnamp.org). It is the key forum for implementing a regional framework for monitoring habitat and fish and wildlife programs. Through PNAMP, the Council, Bonneville Power Administration, and the fish and wildlife managers are working to implement the Fish and Wildlife Program within a regional network of monitoring efforts aimed at achieving common objectives and monitoring needs.

PNAMP contends that a regional approach to monitoring will fail without the support of a data management system that can provide regional access in a timely fashion to the data sets developed through monitoring efforts. They also recommend that the region develop consistent data standards and protocols within and across each of the types of monitoring. Several plans and strategies have been developed by PNAMP including "Recommendations for Coordinating State, Federal, and Tribal Watershed and Salmon

Monitoring Programs in the Pacific Northwest" (PNAMP 2004) and "Monitoring Strategy for Coordinating Monitoring of Aquatic Environments in the Pacific Northwest" (PNAMP 2005).

PNAMP observed that monitoring the effects of artificial production on population health is currently conducted project-by-project, yet it constitutes a significant component of the current Columbia River Basin monitoring budget. Some ongoing artificial production projects have included monitoring planning and/or research elements. These elements are being developed along with programmatic research, monitoring, and evaluation activities.

A number of groups have either developed plans and/or instituted monitoring, evaluation and research activities, including:

- Northeast Oregon Hatchery (Hesse, Harbeck, and Carmichael 2006)
- Yakima Fishery Project (Busack, Pearsons, Knudsen, Phelps, and Watson 1997)
- Nez Perce Tribal Hatchery (Johnson, Larson, and Walker 2000)
- U.S. Fish and Wildlife Service's Hatchery Review (U.S. Fish and Wildlife Service 2007)
- Recommendations for broad scale monitoring to evaluate the effects of hatchery supplementation on the fitness of natural salmon and steelhead populations.
- (AHSWG2008)
- Monitoring Section of ISRP's Retrospective Report (ISRP 2005)
- Salmonid Hatchery Inventory and Effects Evaluation (NMFS 2004)
- Conservation of Columbia Basin Fish; Final Basinwide Salmon Recovery Strategy (Federal Caucus 2000)
- Research, Monitoring, and Evaluation (RME) Plan for the NOAA Fisheries 2000 Federal Columbia River Power System (FCRPS) Biological Opinion (Action Agencies and NOAA 2003)
- Research, Monitoring and Evaluation in the Updated Proposed Action for the FCRPS Biological Opinion Remand (Action Agencies 2004)
- ISAB and ISRP Review of the Action Agencies and NOAA Fisheries' Draft Research, Monitoring & Evaluation Plan for the NOAA-Fisheries 2000 Federal Columbia River Power System Biological Opinion (RME Plan) (ISAB and ISRP 2004)
- Plan for Research, Monitoring and Evaluation of Salmon in the Columbia River Estuary (PNNL, COE, BPA, and NOAA 2004)
- Research Plan for the Columbia River Basin (NPCC 2006)
- Proposed Design and Evaluation of Preliminary Design Templates (CSMEP 2004)

- Data Quality Objectives for Decisions Relating to Status and Trend of Fish Populations, as well as Action Effectiveness of Habitat, Hatchery, Harvest and Hydrosystem Actions (PNAMP and CSMEP 2006)
- Scope of Work for Implementation of the Northwest Environmental Data Network Project (Northwest Environmental Data Network 2005)

The HSRG recommends that all hatchery programs in the Columbia Basin continue to work together to develop and coordinate monitoring methods and metrics, analytical methods, and reporting formats to maximize information for evaluation of hatchery programs.

4 Uncertainties

A number of "critical uncertainties" have been identified through review of existing hatchery programs and associated M&E. These uncertainties must be addressed in order to evaluate the success of hatchery programs.

4.1 Accuracy and precision of data

Monitoring the results of best management practices employed in the culture phase of the hatchery program is relatively straightforward when compared to the post-release phase. For the culture phase, hatchery operators can enumerate natural and hatchery fish in the broodstock, fecundity, eggs taken, survival through various life stages in the hatchery, etc. Monitoring released fish in the ocean or returning to their natal freshwater system is more difficult. However, it is very important to be able to collect accurate and precise data on survival, harvest, and straying of hatchery and natural stocks throughout their migration routes as well as determining the number of hatchery and natural fish returning to spawning areas. Marking hatchery fish is vital for accurate monitoring of these parameters.

4.2 Long-term fitness of populations with natural and hatchery components

Long-term fitness of mixed populations of hatchery and natural salmon is an important consideration in determining the success of hatchery programs. To gather this information, river systems with mixed hatchery programs should ideally be compared to a control system with no hatchery influence. The Yakima/Klickitat Fisheries Program is currently conducting this type of research to monitor numerous life stages in the populations of the Upper Yakima and Naches (www.ykfp.org). Other programs designed to address this question are discussed in the AHSWG Final Report (AHSWG 2008).

4.3 Relative reproductive success of hatchery and natural adults

Another critical uncertainty involves the reproductive success rates of natural and hatchery fish of various stocks including both integrated and segregated populations. This information is very important in determining the relative risks and benefits associated with hatchery fish spawning with natural fish. The research should be conducted in conjunction with fitness research described above.

5 Conclusions and Recommendations

Monitoring and evaluation is a key component of successful hatchery programs, but only if it is correctly targeted and consistently implemented. The HSRG concludes that:

- Hatchery programs must be designed and operated consistent with clearly stated biological objectives.
- Biological objectives for hatchery programs must be based upon the assumptions contained in a working hypothesis.
- The working hypothesis must address the 4 "Hs".
- The All "H" Analyzer is currently the best tool for defining assumptions.
- Monitoring and evaluation programs must be established to determine if the assumptions are valid and if the biological objectives are being met.
- Monitoring and evaluation programs and the data and information generated by the programs must be coordinated and standardized (to the extent possible) throughout the Columbia River Basin.
- Critical uncertainties including accuracy and precision of data, long-term population fitness, and relative reproductive fitness of hatchery and natural fish should be addressed through Columbia Basin-wide research and coordination.

6 References

Action Agencies (U.S. Army Corps of Engineers, the Bureau of Reclamation, Bonneville Power Administration). 2004. Updated Proposed Action for the FCRPS Biological Opinion Remand.

Action Agencies and National Oceanic and Atmospheric Administration. 2003. Research, Monitoring, and Evaluation (RME) Plan for the NOAA Fisheries 2000 Federal Columbia River Power System (FCRPS) Biological Opinion.

Ad Hoc Supplementation Monitoring and Evaluation Workgroup. 2008. Recommendations for broad scale monitoring to evaluate the effects of hatchery supplementation on the fitness of natural salmon and steelhead populations.

Busack, C., T. Pearsons, C. Knudsen, S. Phelps, and B. Watson. 1997. Yakima Fisheries Project Spring Chinook Supplementation Monitoring Plan.

Federal Caucus. 2000. Conservation of Columbia Basin Fish; Final Basinwide Salmon Recovery Strategy.

Hager, R. C. and R. J. Costello (eds.). 1999. Optimal Conventional and Semi-Natural Treatments for the Upper Yakima Spring Chinook Salmon Supplementation Project: Treatment Definitions and Descriptions and Biological Specifications for Facility Design. Final Report to BPA. Project 95-06404. BPA Report DOE/BP-64878-2. 84 pp.

Hatchery Scientific Review Group 2004. *Hatchery Reform: Principles and Recommendations of the HSRG*. Long Live the Kings, 1305 Fourth Avenue, Suite 810, Seattle, WA 98101. Available at www.hatcheryreform.us

Hesse, J. A., J. R. Harbeck and R. W. Carmichael. 2006. Monitoring and evaluation plan for Northeast Oregon hatchery Imnaha and Grande Ronde subbasin spring Chinook salmon, 2006 Technical Report, Project No. 198805301, 160 electronic pages, (BPA Report DOE/BP-00004034-1) (http://pisces.bpa.gov/release/documents/documentviewer.aspx?doc=00004034-1.

Independent Scientific Review Panel. 2004. Review of the final review draft Comprehensive Research, Monitoring, and Evaluation Plan for Umatilla Subbasin Summer Steelhead and Chinook Salmon (for projects 48 49 199000500 and 199000501). ISRP 2004-17. (http://nwcouncil.org/library/isrp/isrp2004-17.htm).

_____. 2005. Retrospective Report 1997-2005. ISRP 2005-14. Northwest Power and Conservation Council, Portland, Oregon. (http://www.nwcouncil.org/library/isrp/isrp2005-14.pdf).

Independent Scientific Advisory Board and Independent Scientific Review Panel. 2004. Draft Research, Monitoring & Evaluation Plan for the NOAA-Fisheries 2000 Federal Columbia River Power System Biological Opinion.

_____. 2005. Monitoring and Evaluation of Supplementation Projects. ISRP&ISAB Report 2005-15. Northwest Power and Conservation Council, Portland, Oregon. (http://www.nwcouncil.org/library/isrp/isrpisab2005-15.pdf).

Johnson, D. B., R. E. Larson, and G. Walker. 2000. Nez Perce Tribal Hatchery Project Annual Report 1998, Report to Bonneville Power Administration, Contract No. 00004504, Project No. 198335000, 28 electronic pages (BPA Report DOE/BP-00004504-2).

Marmorek, D. R., M. Porter, D. Pickard and K. Wieckowski (editors). 2007a. Snake River Basin Pilot Study: Volume 1. Prepared by ESSA Technologies Ltd., Vancouver, B.C. on behalf of the Columbia Basin Fish and Wildlife Authority, Portland, OR. 2007. Collaborative Systemwide Monitoring and Evaluation Project (CSMEP) Snake Basin Pilot Report. Prepared by ESSA Technologies Ltd., Vancouver, B.C. on behalf of the Columbia Basin Fish and Wildlife Authority, Portland, OR. 47 pp.

(http://www.cbfwa.org/csmep/web/documents/general/Documents/Volume%201%20FINAL.pdf).

Marmorek, D. R., M. Porter, D. Pickard and K. Wieckowski. 2007b. Collaborative Systemwide Monitoring and Evaluation Project (CSMEP) Snake River Basin Pilot Study: Volume 2. Prepared by ESSA Technologies Ltd., Vancouver, B.C. on behalf of the Columbia Basin Fish and Wildlife Authority, Portland, OR. 216 pages. (http://www.cbfwa.org/csmep/web/documents/general/Documents/volume%202_Draft_FINAL.pdf).

National Marine Fisheries Service. 2004. Salmonid Hatchery Inventory and Effects Evaluation Report Technical Memorandum NMFS-NWR/SWR.

Northwest Environmental Data Network. 2005. Scope of Work for Implementation of the Northwest Environmental Data Network Project.

Northwest Power and Conservation Council. 1999. Review of Artificial Production of Anadromous and Resident Fish. Northwest Power and Conservation Council. Portland OR. Council Document 99-4.

_____. 2006. Research Plan for the Columbia River Basin. Northwest Power and Conservation Council. Portland OR. Council Document 2006-3.

Pacific Northwest Aquatic Monitoring Partnership. 2004. Recommendations for Coordinating State, Federal, and Tribal Watershed and Salmon Monitoring Programs in the Pacific Northwest.

_____. 2005. Strategy for Coordinating Monitoring of Aquatic Environments in the Pacific Northwest. Pacific Northwest Aquatic Monitoring Partnership.

Pacific Northwest Aquatic Monitoring Partnership and the Collaborative Systemwide Monitoring and Evaluation Project. 2006. Second Annual Research, Monitoring and Evaluation (RME) Workshop for Decision Makers, Program Managers, Scientists and Field Practitioners.

U.S. Fish and Wildlife Service Columbia Basin Hatchery Review Team. 2007. Columbia Gorge NFHs Assessments and Recommendations Report. www.fws.gov/pacific/fisheries/hatcheryreview/reports.html/.

White Paper No. 5[1]

Transition of Hatchery Programs

1 Introduction and Background

Hatchery programs, in order to be successful, need clearly stated goals and biological objectives as well as scientifically defensible operational guidelines. They must be designed to achieve either specific harvest or conservation purposes. Hatchery programs targeted at producing fish primarily for harvest must be consistent with conservation goals established by managers for populations that may be affected by the program in order to avoid unacceptable ecological and genetic interactions with naturally produced fish

In 2004, the Puget Sound and Coastal Washington Hatchery Scientific Review Group (HSRG) developed two technical discussion papers with the Washington Department of Fish and Wildlife (WDFW), the Northwest Indian Fisheries Commission (NWIFC), and regional treaty Tribes. The papers included definitions, theoretical premises, and operational guidelines for implementing integrated and segregated hatchery programs (HSRG, WDFW, and NWIFC 2004a and 2004b). The premises, definitions, and recommendations of the Puget Sound HSRG have been adopted by the Columbia River HSRG. Some of the conclusions found in HSRG, WDFW, and NWIFC 2004a and 2004b have been included in this document.

Expanding the HSRG hatchery review into the Columbia River Basin has allowed further consideration of the implications of hatchery reform. This has, in turn lead to additional recommendations, presented in this document, to better accomplish harvest and conservation goals. The recommendations focus on facilitation of properly integrated and segregated programs and providing guidelines for hatchery programs whose primary goal is re-introduction. Re-introduction programs were not addressed by the Puget Sound HSRG in the 2004 documents.

This paper presents a series of "scenarios" to guide establishment of integrated and segregated hatchery programs. The scenarios address establishment of new integrated and segregated programs as well as the transition from fully and partially segregated to integrated programs and vice versa. The scenarios are based on a stated set of existing conditions within the affected watershed; recommendations and considerations are presented for each scenario.

[1] White papers were prepared by the HSRG to address topics relevant to hatchery reform. They are intended to stimulate discussion and provide background, documentation and explanations not included in the body of the HSRG's report.

2 Integrated Hatchery Programs

2.1 Implications and Constraints of Broodstock Management Guidelines for Integrated Hatchery Programs

Broodstock management guidelines for an integrated hatchery program impose limitations on the program's size. The limitations are dependent upon controlling the mix of hatchery- and natural-origin fish on the spawning grounds and in the hatchery and on factors affecting the number of natural spawners available for broodstock, i.e. the productivity of the natural environment and the harvest rate on natural fish. Identification of the options available to implement integrated programs such as i.e., changing the ratio of pNOB to pHOS and/or the size of the hatchery program, requires case-by-case analyses. Currently, few hatchery programs are meeting the broodstock guidelines recently developed by HSRG for integrated hatcheries.

2.2 Implementing an Integrated Hatchery Program

Once it is determined that an integrated program is the best method to achieve resource goals, design and implementation of the program must be addressed. Program design will depend upon:

- The genetic makeup of the current hatchery and natural population components
- Risk tolerance which varies depending on the viability of and goals for the natural population

In a recovery program, it may be necessary to rely on hatchery propagation to secure genetic resources until the receiving habitat is capable of supporting a fully integrated program. Initially, this type of program may have to be developed from one where the composite population is highly influenced by the hatchery environment, but where a detailed management plan has been structured to transition to a population dominated by the natural environment. Similarly, integrated harvest programs with goals to maintain or improve the biological significance of the stock should be operated to ensure that selective forces in the natural environment dominate. There may be circumstances where one or more elements of these approaches are not applicable.

2.2.1 Scenario 1: New Integrated Program

Initial Conditions:

- No hatchery program currently exists.
- Natural population been minimally influenced by hatchery fish.

Recommended approach:

- Initiate hatchery program by collecting representative sample of natural fish.
- Size program consistent with conservation goals, the ability of the natural population to support hatchery broodstock requirements, and gene flow limitations to the natural population.
- At a minimum, ensure that gene flow from the natural to the hatchery population is greater than gene flow from the hatchery to the natural population (PNI > 0.5; pNOB > pHOS).

- Limit contribution of hatchery fish to less than 30% of the natural spawning population (pHOS < 30%).
- For stocks of moderate or high biological significance and viability (or goals to maintain or improve the biological significance and viability of the stock), PNI should be greater than 0.67
- Collect a number of brood that allows for an effective population size of the composite population (natural plus hatchery) in excess of 500 fish.
- If a long-term goal of the hatchery program is to provide a conservation benefit, or if the natural spawning of hatchery-origin fish will be difficult to control, then the effective population size of the hatchery component should also be greater than 500 fish.

Considerations:

- *Likelihood of achieving natural adaptation:* There is a high likelihood of attaining population goals (developing a program where the natural environment drives the adaptation of the composite hatchery and natural population), as long as broodstock collection is feasible and gene flow is maintained within recommended guidelines for the goals of the population. Some loss of productivity from the natural population is expected.
- *Cost:* There is additional program cost compared to segregated programs, primarily for natural broodstock collection.
- *Effect on Harvest:* Changes in harvest contribution are dependent on productivity of the natural component of the population, as well as productivity of the hatchery component. If the recommended approach is followed, harvest can generally be increased at the cost of some loss of productivity from the natural population.

2.2.2 Scenario 2: Transition from a segregated program to an integrated program

Initial Conditions:

- Hatchery broodstock has had no systematic gene flow from the natural population.
- Natural spawning population has had little influence from hatchery fish.

Recommended Approach #1: This approach should be employed if harvest goal attainment can be interrupted during the transition to an integrated program.

- Terminate segregated harvest program.
- Initiate a new hatchery program by collecting a representative sample of natural fish.
- Size program consistent with conservation goals and the ability of the natural population to support hatchery broodstock requirements and gene flow limitations to the natural population.
- At a minimum, ensure that gene flow from the natural population to the hatchery population is greater than gene flow from the hatchery to the natural population (PNI > 0.5; pNOB > pHOS).

- Limit contribution of hatchery fish to less than 30% of the natural spawning population (pHOS < 30%).
- For stocks of moderate or high biological significance and viability (or goals to maintain or improve the biological significance and viability of the stock), PNI should be greater than 0.67.
- Collect a number of brood that allows for an effective population size of the composite population (natural plus hatchery) in excess of 500 fish.
- If a long-term goal of the hatchery program is to provide a conservation benefit, or if the natural spawning of hatchery-origin fish will be difficult to control, then the effective population size of the hatchery component should also be greater than 500 fish.

Considerations for Approach #1

- *Likelihood of achieving natural adaptation*: There is a high likelihood of attaining stock goals as long as broodstock is feasible and gene flow is maintained within recommended guidelines. Some loss of productivity from the natural population is expected.
- *Cost*: The increase in cost incurred for broodstock collection appears similar for all approaches.
- *Effect on Harvest*: A loss of contribution would be expected between termination of the segregated program and achieving the final size of the new integrated program. In the long term, if the recommended approach is followed, harvest can generally be increased at the cost of some loss of productivity from the natural population.

Recommended Approach #2: This approach should be used if harvest goal attainment cannot be interrupted during transition to an integrated program.

- Initiate new hatchery program by collecting representative sample of natural fish.
- Size program consistent with population goals and the ability of the natural population to support hatchery broodstock requirements and gene flow limitations to the natural population.
- At a minimum, ensure that gene flow from the natural population to the hatchery population is greater than gene flow from the hatchery to the natural population (PNI > 0.5; pNOB > pHOS).
- Limit contribution of hatchery fish to less than 30% of the natural spawning population (pHOS < 30%).
- For stocks of moderate or high biological significance and viability (or goals to maintain or improve the biological significance and viability of the stock) PNI should be greater than 0.67.
- Collect a number of brood that allows for an effective population size of the composite population (natural plus hatchery) to be in excess of 500 fish.
- If a long-term goal of the hatchery program is to provide a conservation benefit, or if the natural spawning of hatchery-origin fish will be difficult to control, then

the effective population size of the hatchery component should also be greater than 500 fish.

- Differentially mark and release offspring of old/new broodstock. Preferentially use returns that represent the natural origin broodstock. Phase out use of old broodstock as new broodstock returns.

Considerations for Approach #2:

- *Likelihood of achieving natural adaptation*: There is a high likelihood of attaining stock goals, as long as broodstock collection is feasible and gene flow is maintained within recommended guidelines. Some loss of productivity from the natural population is expected.
- *Cost*: The increase in cost incurred for broodstock collection appears similar for all approaches. Under this scenario, an additional cost for differentially marking the two hatchery broodstocks would be incurred. Cost in terms of operational complexity is high, but should be no greater than rearing an additional species.
- *Effect on Harvest*: The loss of contribution to harvest in Scenario 2, Approach #1, above, could be avoided during transition with additional marking cost. In the long term, if the recommended approach is followed, harvest can generally be increased at the cost of some loss of productivity from the natural population.

2.2.3 Scenario 3: Transition from a partially segregated program to an integrated program[2]

Initial Conditions:

- Hatchery broodstock has had no systematic gene flow from the natural population
- Natural spawning population has had significant influence from hatchery fish.

Approach #1: This approach is recommended if the program goal is to return the natural population to its highest level of productivity as rapidly as possible.

- Take steps to reduce the number of hatchery fish in the natural population to less than 5% through reduction in hatchery programs, selective harvest to limit strays, installation of weirs, or other measures.
- Allow a minimum of 3 to 4 generations to promoted adaptation of naturally spawning fish.
- Initiate a new hatchery program by collecting representative samples of naturally spawning fish.
- The program size should be consistent with conservation goals and the natural population's ability to support hatchery broodstock requirements while limiting gene flow to the natural population.
- At a minimum, ensure that gene flow from the natural population to the hatchery population is greater than the gene flow from the hatchery to the natural population. PNI should be greater than 0.5 and pNOB should be greater than pHOS.

[2] This is the most common scenario in many places within the Columbia River Basin.

- Limit the contribution of hatchery fish to less than 30% of the natural spawning population, i.e. pHOS should be greater than 30%.
- For stocks of moderate of high biological significance and viability or to achieve goals to maintain/improve the biological significance and viability of a stock, the PNI should be greater than 0.67.
- Collect sufficient broodstock to achieve a composite (natural and hatchery components) population in excess of 500 fish.
- The effective population size of the hatchery component should be greater than 500 fish if the long-term goal of the hatchery program is to provide a conservation benefit or if the natural spawning of hatchery-origin fish is difficult to control.
- Terminate segregated harvest program.

Considerations for Approach #1:

- *Likelihood of achieving natural adaptation*: There is a moderate likelihood of attaining population goals because of the uncertainty of adaption to the natural environment after 3 or 4 generations. The likelihood of meeting population goals increases with the amount of time allowed before initiating the new program. The approach allows the most rapid adaptation to the natural environment and improved productivity of the natural population is expected.
- *Cost*: The increased costs incurred for broodstock collection are expected to be similar for all approaches. An additional cost for differentially marking two hatchery broodstocks would be incurred if the phased approach is adopted (see Effects on Harvest)
- *Effect on Harvest*: There is a high likelihood of losing contributions to harvest since the segregated program would likely be reduced to allow adaptation of the natural stock. A phased approach during broodstock transition (including differential marking) as described in Approach 2, Scenario 2, could be used to reduce loss of the harvest contribution.

Approach #2: Recommended approach if productivity of natural population can be allowed to improve over an extended period of time.

- Take steps to reduce the number of hatchery fish in the natural population through measures such as reducing the hatchery program, employing selective harvest to limit strays, installing weirs, etc. Initiate a new hatchery program by collecting a representative sample of natural fish for broodstock (NOB) in accordance with the limitations described below.
- The program size should be consistent with conservation goals and the natural population's ability to support hatchery broodstock requirements while limiting gene flow to the natural population.
- At a minimum, ensure that gene flow from the natural population to the hatchery population is greater than the gene flow from the hatchery to the natural population. PNI should be greater than 0.5 and pNOB should be greater than pHOS.

- Limit the contribution of hatchery fish to less than 30% of the natural spawning population, i.e. pHOS should be greater than 30%.
- For stocks of moderate of high biological significance and viability or to achieve goals to maintain/improve the biological significance and viability of a stock, the PNI should be greater than 0.67.
- Collect sufficient broodstock to achieve a composite (natural and hatchery components) population in excess of 500 fish.
- The effective population size of the hatchery component should be greater than 500 fish if the long-term goal of the hatchery program is to provide a conservation benefit or if the natural spawning of hatchery-origin fish is difficult to control.

Considerations for Approach #2:

- *Likelihood of achieving natural adaptation*: There is a moderate likelihood of achieving population goals will increase over time and as the PNI increases through reduction in hatchery fish spawning naturally and/or through the incorporation of additional natural fish into the hatchery broodstock. A PNI of greater than 0.5 is necessary to regain fitness and should be the minimum broodstock management goal even during transition between hatchery programs.
- *Cost*: Increased costs incurred for broodstock collection are expected to be similar for all approaches. An additional cost for differentially marking two hatchery broodstocks would be incurred if the phased approach is adopted (see Effects on Harvest)
- *Effect on Harvest*: High likelihood of losing contributions to harvest unless the contribution of hatchery fish to the natural spawning population can be controlled without reducing the program. A phased approach during broodstock transition (including differential marking) as described in Approach 2, Scenario 2, could be used to reduce loss of the harvest contribution.

2.2.4 Scenario 4: New Integrated Re-introduction Program

Initial Conditions:

- The natural population has been extirpated.
- A hatchery stock from another watershed is available as a donor.

Recommended Approach:

- Managers should have a defensible premise that re-introduction will be successful, i.e. the conditions that led to extirpation have been corrected.
- Managers should choose the stock most likely to succeed from among the available donor stocks. Stocks with similar genetic and life history characteristics from watersheds with similar habitat should be chosen.
- If an out-of-basin hatchery stock is used, the following guidelines should be followed.
    - Continue working to develop a locally adapted (in-basin) hatchery stock as a donor.

- Cease using the out-of-basin stock once a locally adapted stock has been developed. Allow broodstock in excess of hatchery needs to spawn naturally.
- Initiate an integrated re-introduction program once there is evidence of natural production. Representative samples of naturally spawning fish should be collected for broodstock.
- The program's size should allow the natural population to support hatchery broodstock requirements while limiting gene flow to the natural population.
- Ensure that gene flow from the natural to the hatchery population is greater than that from the hatchery to the natural population, i.e. PNI should be greater than 0.5 and pNOB should be greater than pHOS.
- The program should be terminated once the naturally spawning population reaches a size that is resistant to stochastic changes (recommended 500 to 1,000 natural spawners per year).
- Monitor the population for self-sufficiency.

Considerations:

- Successful re-introduction depends on the conditions that led to extirpation being corrected to the point that the hatchery program can produce a self-sustaining stock.
- Habitat productivity and capacity should be sufficient to support the population.
- Current or expected exploitation rates should not hinder re-introduction.
- The preferred donor stock in most cases will be a naturally reproducing stock from a nearby watershed with similar habitat characteristics.
- In many cases where natural stocks have been extirpated, other local natural stocks are also depressed and hatchery stocks are the only available donors.
- Re-introduction of adults, rather than juveniles, eliminates hatchery influence at all life stages and can simplify operational problems associated with juvenile releases.

2.3 Implementing a Segregated Hatchery Program

Segregated programs are generally managed to maximize productivity of the hatchery population without regard to the ability of returning adults to reproduce naturally. As a result, segregated programs often represent major trade-offs between minimizing biological risks to naturally spawning populations and maximizing efficiency and harvest benefits of the hatchery program. These types of programs are often used to meet only harvest goals and, as such, have few operational constraints other than limiting the contribution of adults from these programs to natural spawning populations. The degree to which segregated hatchery programs are successful depends significantly on the degree to which genetic and ecological risks to natural populations can be minimized (HSRG, WDFW and NWIFC 2004b).

2.3.1 Scenario 1: New Segregated Program

Initial Conditions:

- No hatchery program exists.
- The status of the natural population in terms of past influences from hatcheries is not important.

Recommended Approach:

- Initiate the program with sufficient fish to provide a minimum effective population size of 500 fish.
- Identify HORs and NORs. Avoid unintentional inclusion of NORs in the broodstock.
- Operate the program to avoid significant genetic and/or ecological interactions with natural populations. Methods include selecting the appropriate program size in terms of the number of juveniles to be released, selective removal of adults through fisheries to limit strays, adult collection facilities or weirs, long-term acclimation at the point of release, and other measures to control straying.
- Ensure that the contribution of hatchery-origin fish spawning naturally is less than five percent of the natural spawning population.

2.3.2 Scenario 2: Transition from a partially segregated or integrated program

Initial Conditions:

- Hatchery broodstock has had no systematic gene flow from the natural population.
- The naturally spawning population has had significant influence from hatchery fish.

Recommended Approach:

- Identify HORs and NORs. Avoid unintentional inclusion of NORs in the broodstock.
- Operate the program to avoid significant genetic and/or ecological interactions with natural populations. Methods include proper sizing of hatchery program, selective removal through fisheries to limit strays, adult collection facilities or weirs, long-term acclimation at the point of release, and other measures to control straying.
- Ensure that the contribution of hatchery-origin fish spawning naturally is less than 5% of the natural spawning population

2.3.3 Scenario 3: Transition from a well-integrated program to a segregated program

Initial Conditions:

- There has been systematic gene flow to hatchery broodstock from the natural population.
- Gene flow from the natural population to the hatchery population has been greater than from the hatchery to the natural population.

Recommended Approach:

- Identify HORs and NORs. Avoid unintentional inclusion of NORs in the broodstock.
- Operate the program to avoid significant genetic and/or ecological interactions with natural populations. Methods include proper sizing of hatchery program, selective removal through fisheries to limit strays, adult collection facilities or weirs, long-term acclimation at the point of release, and other measures to control straying.
- Ensure that the contribution of hatchery-origin fish spawning naturally is less than 5% of the natural spawning population

3 References

Hatchery Scientific Review Group, Washington Department of Fish and Wildlife, and Northwest Indian Fisheries Commission. 2004a. Technical Discussion Paper #1: Integrated Hatchery Programs. (Available from www.hatcheryreform.us).

_____. 2004b. Technical Discussion Paper #2: Segregated Hatchery Programs. (Available from www.hatcheryreform.us).

White Paper No. 6[1]

Nutrient Enhancement of Freshwater Streams to Increase Production of Pacific Salmon

1 Introduction

The purpose of this paper is to inform resource managers about the use of stream nutrient enhancement as a tool for increasing survival of juvenile salmonids. Nutrient enhancement is widely recognized as a benefit to natural salmonid stocks. Lack of sufficient stream nutrients can be a limiting factor in the recovery of salmonid populations. In-stream nutrients are usually derived from the disintegration of spawned-out salmon carcasses. In the absence of sufficient naturally occurring carcasses, additional nutrification may be needed. The HSRG advocates nutrient enhancement of streams while recognizing that some methods, such as the use of salmon carcasses, carries the risk of disease transmission. This paper contains a review of existing literature on the development, use, and evaluation of stream nutrient enhancement. Recommendations based on the literature review are presented.

2 Background

Pacific salmon and steelhead once contributed large amounts of marine-derived carbon, nitrogen, and phosphorus to freshwater ecosystems in the Pacific Northwest. These nutrients are no longer available in the historic quantities because fewer adult fish are returning to freshwater systems.

To compensate for reduced nutrient load and resultant lowered stream productivity, recent mitigation efforts have focused on addition of nutrients to freshwater systems. The two methods for adding nutrients are 1) allocation of larger fish escapements and 2) artificial nutrient enhancement.

1. *Larger Escapement Allocation.* The concept behind larger allocations is that more adult salmonids returning to the streams will result in a higher natural nutrient load. Re-evaluation of escapement goals would generally require escapements that are 2 to 15 times higher than those currently allocated (Bilby et al. 2001; Knudsen, Symmes, and Margraf 2003; Michael 1998; Michael 2003; Peery, Kavanagh, and Scott 2003). Nonetheless, this method should be considered during the decision-making process. A possible added benefit of larger escapements would be reduction in stream siltation because more fish would dig more spawning redds.[2] However, increasing escapements with only hatchery-origin fish will negatively affect the reproductive success of wild fish, and therefore must be considered in the context of other HSRG broodstock management recommendations.

[1] White papers were prepared by the HSRG to address topics relevant to hatchery reform. They are intended to stimulate discussion and provide background, documentation and explanations not included in the body of the HSRG's report.

[2] Digging redds disturbs silted substrates, allowing fines to be washed away. Redds which are not affected by siltation are generally more successful.

2. *Artificial nutrient enhancement*. There are three methods of artificially enhancing nutrient loads: direct application of fertilizers, the application of "carcass analogs", and the distribution of salmonid carcasses from fish hatcheries.

The first method involves application of fertilizer to increase wild fish production. This method has been used in the Pacific Northwest for years. Currently, there are two methods in use. One involves the introduction of liquid fertilizer into the water, either through large "slug" doses or through low level drip. The second involves the placement of solid fertilizer pellets that dissolve at a predetermined rate, releasing nutrients over a period of months. Both methods have been shown to cause substantial increases in fish growth, survival, condition factors, etc. Water quality monitoring has shown that the fertilizers are rapidly taken up into the food chain and are generally not detectable in the water column outside of the treatment area/reach. This method of fertilization is widely used and described in the literature.

The remainder of the discussion in this paper is focused on nutrient enhancement using carcass analogs and salmonid carcasses.

3 Findings

3.1 Why Nutrient Enhancement

Returning anadromous salmon are an important source of marine-derived nutrients (MDN) and serve as the primary method of nutrient transport for freshwater ecosystems in the Pacific Northwest (Cederholm et al. 1999; Naiman et al. 2002). MDN have been detected in a variety of aquatic and terrestrial plants and wildlife (Gende et al. 2002; Hicks et al. 2005) including aquatic insects (Lessard and Merritt 2006), mosses and liverworts (Wilkinson, Hocking, and Reimchen 2005), and birds and mammals (Jauquet et al. 2003). It is clear that MDN are an integral part of properly functioning anadromous ecosystems. The level of MDN in an anadromous system depends upon the returning salmon runs: the reduced run sizes have decreased the nutrient input to the streams. Today, most ecosystems with anadromous salmon are considered to be in a "nutrient deficit" (Gresh, Lichatowich, and Schoonmaker 2000). This lack of nutrients could be one of the factors limiting recovery either directly and indirectly in many salmon streams. Nutrient enhancement may, therefore, be an important component of a holistic recovery program.

3.2 Benefits of Nutrient Enhancement

Studies have shown that addition of salmon carcasses has little effect on primary production in nutrient-rich streams. In oligotrophic (nutrient-poor) systems, however, primary production often increases in response to the addition of nitrogen and phosphorus, two of the main nutrients transported by salmonids. Increased primary production has a cascading effect through the food chain (Kline et al. 1990; Kohler, Rugenski, and Taki 2008). Invertebrate production increases in response to the increased food, and these in turn provide more food for fish and other aquatic animals. Marine derived nutrients from salmon carcasses have been detected in many species of birds and mammals, and some seem to rely heavily on salmon carcasses (Ben-David 1997; Ben-David et al. 1997; Cederholm et al. 1999; Jauquet et al. 2003). Carcass dispersal and scavenging can facilitate the transfer of MDN to riparian environments (Meehan, Seminet-Reneau, and Quinn 2005).

The increase in food through invertebrate production and direct consumption of the salmon carcasses and eggs results in significant increases in growth of juvenile salmonids (Bilby et al. 1998; Lang et al. 2006) and other fishes (Wipfli et al. 2003). Larger size seems to confer some over-winter survival advantage, although the relationship between larger size and survival is complicated by size-independent factors that affect survival, such as water flow, winter temperature, and food availability (Connolly and Petersen 2003; Ebersole et al. 2006; Lang et al. 2006; Quinn and Peterson 1996). Larger juvenile salmonids also tend to survive to maturity at higher rates than smaller juveniles (Bilton, Alderdice, and Schnute 1982; Henderson and Cass 1991; Holtby, Andersen, and Kadowaki 1990; Koenings, Geiger, and Hasbrouck 1993; Tipping 1986; Tipping 1997; Ward et al. 1989), although this is also a relationship complicated by other factors that affect survival, most notably ocean conditions.

While these findings imply that the addition of MDN to streams would improve the survival (and subsequent run size) of anadromous salmon, this hypothesis has not yet been tested. In addition, it is likely that the effects would be complicated by other factors. It is also clear that the reduced MDN is usually only one of many issues limiting the recovery of anadromous salmon, all of which would likely need to be addressed for successful recovery.

3.3 Carcasses vs. Carcass Analogs

The generally positive ecosystem responses to the addition of salmon carcasses has prompted resource managers to begin distributing carcasses of adults returning to hatcheries into rivers and streams of the Pacific Northwest. In its regional hatchery reviews, the HSRG observed inconsistent use of carcass distribution among and within agencies. Some hatcheries distributed all of their available carcasses while others buried them all in landfills. For hatcheries that do distribute salmon carcasses, volunteer groups have been found to be a cost-efficient and effective distribution method.

Because sufficient carcasses may not be available, and because they can be relatively inconvenient to distribute, and represent a source of disease transmission (see below), researchers have developed carcass analogs as a substitute. Carcass analogs are essentially pellets made from dried spawned-out salmon (Pearsons, Roley, and Johnson 2007) which are treated to kill disease organisms. The fish pellets lack the variety of tissues available from carcasses, and may be consumed more quickly than carcasses. Therefore, analogs may not benefit as many organisms as carcasses. However, analogs are much easier to transport and distribute, they can be stored as needed, and, because they are disease-free, they can be transferred between watersheds. The few studies focusing on carcass analog use compared to fish carcasses have found the analogs to be effective and convenient (Mesa et al. 2007; Wipfli, Hudson, and Caouette 2004; Zendt and Bill 2006).

3.4 Risks Associated with Nutrient Enhancement

Enhancement appears to be a useful tool for raising the nutrient level in freshwater systems. It is, however, not without its risks. The primary risks are disease transmission (with carcasses), introduction of contaminants, and over-nutrification.

3.4.1 Disease transmission

The distribution of salmon carcasses represents a potential vector for disease transmission. To reduce this risk, the HSRG recommends the following:

- Certify that adult broodstock is free of viral pathogens before planting. The adult sampling level should be a minimum of 60 fish for carcass plantings within the same watershed and 150 fish for plantings in different watersheds within the same fish health management zone.
- Freeze carcasses before planting to reduce the infectious titers of pathogenic organisms in the salmon carcasses. This measure will decrease the risk of transmission of certain disease organisms (Evelyn 2001; Margolis 1977).
- Plant carcasses only within the historic range of the species being used for nutrient enhancement.
- Do not plant adults or juveniles which may have died of infectious disease. This includes pre-spawning adult mortalities and juvenile mortalities from hatchery ponds.

3.4.2 *Contaminant deposition*

There is growing evidence that adult salmon transport contaminants from the marine environment back into freshwater. For example, it has been shown that large numbers of spawning salmon can increase the levels of PCBs in a stream well above background levels (Compton et al. 2006; Krummel et al. 2005; Krummel et al. 2003; Missildine 2005). The risk of introducing contaminants along with nutrients needs to be considered for each stream system.

3.4.3 *Over-nutrification*

Though the level of marine-derived nutrients has dropped in many streams, some nutrients are entering streams as a result of human activity. Phosphorus in particular can be increased by human activity adjacent to streams. Therefore, nutrient enhancement, particularly in the spring and summer when temperatures are warmer and there are more hours of sunlight, could exacerbate algal blooms and negatively affect fish production (Compton et al. 2006). Furthermore, the nutrient additions may cause the receiving waters to exceed guidelines established in the Clean Water Act.

4 Recommendations

The literature indicates that artificial enhancement can be of great benefit in raising the level of nutrients in freshwater systems. The methods endorsed by the HSRG are distribution of adult hatchery carcasses or carcass analogs. Certain guidelines and protocols should be applied to all nutrient enhancement projects. Nutrification projects require careful planning and evaluation to ensure that the resources are used wisely and that the risks to the resource are understood. There is widespread agreement in the published literature that haphazard distribution of carcasses or analogs does not optimize this management tool and may, in some cases, be counter-productive. Opportunities to understand the effects of distribution programs will be missed without including evaluation as part of the projects.

Comprehensive protocols and guidelines for nutrient enhancement have been developed by Ashley and Stockner (2003), Washington Department of Fish and Wildlife3 and Fisheries and Oceans Canada4. These protocols and guidelines can be adapted to local

[3] http://wdfw.wa.gov/hab/ahg/shrg_t11.pdf
[4] http://www-heb.pac.dfo-mpo.gc.ca/publications/pdf/carcass_guide_e.pdf

needs. Programs should be followed up with a thorough evaluation to ensure the intended goals are being met.

5 References

Ashley, K. I., and J. G. Stockner. 2003. Protocol for applying limiting nutrients to inland waters. Pages 245-258 *in* Nutrients in salmonid ecosystems: Sustaining production and biodiversity.

Ben-David, M. 1997. Timing of reproduction in wild mink: The influence of spawning Pacific salmon. *Canadian Journal of Zoology* **75**(3):376-382.

Ben-David, M., T. A. Hanley, D. R. Klein, and D. M. Schell. 1997. Seasonal changes in diets of coastal and riverine mink: The role of spawning Pacific salmon. *Canadian Journal of Zoology* **75**(5):803-811.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **55**(8):1909-1918.

Bilby, R. E., B. R. Fransen, J. K. Walter, C. J. Cederholm, and W. J. Scarlett. 2001. Preliminary evaluation of the use of nitrogen stable isotope ratios to establish escapement levels for Pacific salmon. *Fisheries* **26**(1):6-14.

Bilton, H. T., D. F. Alderdice, and J. T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon *Oncorhynchus kisutch* on returns at maturity. *Canadian Journal of Fisheries and Aquatic Sciences* **39**(3):426-447.

Cederholm, C. J., M. D. Kunze, T. Murota, and A. Sibatani. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries* **24**(10):6-15.

Compton, J. E., C. P. Andersen, D. L. Phillips, J. R. Brooks, M. G. Johnson, M. R. Church, W. E. Hogsett, M. A. Cairns, P. T. Rygiewicz, B. C. McComb, and C. D. Shaff. 2006. Ecological and water quality consequences of nutrient addition for salmon restoration in the Pacific Northwest. *Frontiers in Ecology and the Environment* **4**(1):18-26.

Connolly, P. J., and J. H. Petersen. 2003. Bigger is not always better for overwintering young-of-year steelhead. *Transactions of the American Fisheries Society* **132**(2):262-274.

Ebersole, J. L., P. J. Wigington, Jr., J. P. Baker, M. A. Cairns, M. R. Church, B. P. Hansen, B. A. Miller, H. R. LaVigne, J. E. Compton, and S. G. Leibowitz. 2006. Juvenile coho salmon growth and survival across stream network seasonal habitats. *Transactions of the American Fisheries Society* **135**(6):1681-1697.

Evelyn, T. T. P. 2001. The effects of chilling, freezing and cold-smoking on the infectious titre of certain microbial fish pathogens that may occasionally be present in marketed salmon flesh. Pages 225-229 *in* C. J. Rodgers, editor. Risk Analysis in Aquatic Animal Health. Proceedings of an International Conference, Paris, France, 8-10 February 2000.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. *BioScience* **52**(10):917-928.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries* **25**(1):15-21.

Henderson, M. A., and A. J. Cass. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake British Columbia Canada sockeye salmon *Oncorhynchus nerka*. *Canadian Journal of Fisheries and Aquatic Sciences* **48**(6):988-994.

Hicks, B. J., M. S. Wipfli, D. W. Lang, and M. E. Lang. 2005. Marine-derived nitrogen and carbon in freshwater-riparian food webs of the Copper River Delta, southcentral Alaska. *Oecologia* **144**(4):558-569.

Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon *Oncorhynchus kisutch*. *Canadian Journal of Fisheries and Aquatic Sciences* **47**(11):2181-2194.

Jauquet, J., N. Pittman, J. A. Heinis, S. Thompson, N. Tatyama, and J. Cederholm. 2003. Observations of chum salmon consumption by wildlife and changes in water chemistry at Kennedy Creek during 1997-2000. Pages 71-88 *in* Stockner, J., editor. Nutrients in salmonid ecosystems: Sustaining production and biodiversity. Symposium 34. American Fisheries Society, Bethesda, Maryland.

Kline, T. C., J. J. Goering, O. A. Mathisen, P. H. Poe, and P. L. Parker. 1990. Recycling of elements transported upstream by runs of Pacific salmon .1. Delta-N-15 and Delta-C-13 evidence in Sashin Creek, Southeastern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **47**(1):136-144.

Knudsen, E. E., E. W. Symmes, and F. J. Margraf. 2003. Searching for a life history approach to salmon escapement management. Pages 261-276 *in* Stockner, J., editor. Nutrients in salmonid ecosystems: Sustaining production and biodiversity. Symposium 34. American Fisheries Society, Bethesda, Maryland.

Koenings, J. P., H. J. Geiger, and J. J. Hasbrouck. 1993. Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*): Effects of smolt length and geographic latitude when entering the sea. *Canadian Journal of Fisheries and Aquatic Sciences* **50**(3):600-611.

Kohler, A. E., A. Rugenski, and D. Taki. 2008. Stream food web response to a salmon carcass analogue addition in two central Idaho streams. *Freshwater Biology* **53**(3):446-460.

Krummel, E. M., I. Gregory-Eaves, R. W. Macdonald, L. E. Kimpe, M. J. Demers, J. P. Smol, B. Finney, and J. M. Blais. 2005. Concentrations and fluxes of salmon-derived polychlorinated biphenyls (PCBs) in lake sediments. *Environmental Science & Technology* **39**(18):7020-7026.

Krummel, E. M., R. W. Macdonald, L. E. Kimpe, I. Gregory-Eaves, I. M. J. Demers, J. P. Smol, B. Finney, and J. M. Blais. 2003. Delivery of pollutants by spawning salmon - Fish dump toxic industrial compounds in Alaskan lakes on their return from the ocean. *Nature* **425**(6955):255-256.

Lang, D. W., G. H. Reeves, J. D. Hall, and M. S. Wipfli. 2006. The influence of fall-spawning coho salmon (*Oncorhynchus kisutch*) on growth and production of juvenile coho salmon rearing in beaver ponds on the Copper River Delta, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **63**(4):917-930.

Lessard, J. L., and R. W. Merritt. 2006. Influence of marine-derived nutrients from spawning salmon on aquatic insect communities in southeast Alaskan streams. *Oikos* **113**(2):334-343.

Margolis, L. 1977. Public health aspects of codworm infection: a review. *Journal of the Fisheries Research Board of Canada* **34**(7):887-898.

Meehan, E. P., E. E. Seminet-Reneau, and T. P. Quinn. 2005. Bear predation on Pacific salmon facilitates colonization of carcasses by fly maggots. *American Midland Naturalist* **153**(1):142-151.

Mesa, M. G., C. D. Magie, T. C. Robinson, E. S. Copeland, and P. J. Connolly. 2007. Nutrient assessment in the Wind River watershed: Report of phase III activities in 2006. Prepared for Lower Columbia Fish Enhancement Group and Lower Columbia Fish Recovery Board.

Michael, J. H. Jr. 1998. Pacific salmon spawner escapement goals for the Skagit river watershed as determined by nutrient cycling considerations. *Northwest Science* **72(**4):239-248.

Michael, J. H., Jr. 2003. Toward new escapement goals: Integrating ecosystem and fisheries management goals. Pages 277-282 *in* J. Stockner, editor. Nutrients in salmonid ecosystems: Sustaining production and biodiversity. Symposium 34. American Fisheries Society, Bethesda, Maryland.

Missildine, B. 2005. Salmon carcass deployment: A potential pathway for PCB contamination. *Fisheries* **30**(1):18-19.

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific Salmon, Nutrients, and the Dynamics of Freshwater and Riparian Ecosystems. *Ecosystems* (2002)5: 399-417.

Pearsons, T., D. Roley, and C. Johnson. 2007. Development of a carcass analog for nutrient restoration in streams. *Fisheries* **32**(3):114-124.

Peery, C. A., K. L. Kavanagh, and J. M. Scott. 2003. Pacific salmon: setting ecologically defensible recovery goals. *BioScience* **53(**7):622-623.

Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* **53**(7):1555-1564.

Tipping, J. 1986. Effect of release size on return rates of hatchery sea-run cutthroat trout. Progressive Fish-Culturist 48(3):195-197.

_____, J. M. 1997. Effect of smolt length at release on adult returns of hatchery-reared winter steelhead. *Progressive Fish-Culturist* **59**(4):310-311.

Ward, B. R., P. A. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout *Oncorhynchus mykiss* back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River British Columbia Canada. *Canadian Journal of Fisheries and Aquatic Sciences* **46**(11):1853-1858.

Wilkinson, C. E., M. D. Hocking, and T. E. Reimchen. 2005. Uptake of salmon-derived nitrogen by mosses and liverworts in coastal British Columbia. *Oikos* **108**(1):85-98.

Wipfli, M. S., J. P. Hudson, and J. P. Caouette. 2004. Restoring productivity of salmon-based food webs: Contrasting effects of salmon carcass and salmon carcass analog additions on stream-resident salmonids. *Transactions of the American Fisheries Society* **133**(6):1440-1454.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies in freshwater ecosystems: Salmon carcasses increase the growth rates of stream-resident salmonids. *Transactions of the American Fisheries Society* **132(**2):371-381.

Zendt, J., and B. Sharp. 2006. Influences of stocking salmon carcass analogs on salmonids in Klickitat River tributaries. 2001-2005 Completion Report, Project No. 200105500, 25 electronic pages (BPA Report DOE/BP-00007534-1).

White Paper No. 7[1]

Outplanting and Net Pen Release of Hatchery-Origin Fish

1 Introduction

In general, most salmon and steelhead (*Oncorhynchus* spp) hatcheries in the Columbia River Basin and the Pacific Northwest operate in a similar manner: upstream-migrating adults are trapped for broodstock and spawned when they reach sexual maturity. The fertilized eggs are incubated and hatched and the resulting progeny are reared to the smolt stage prior to release from the facility into a freshwater stream. Age at smoltification varies among species of Pacific salmon and steelhead, ranging from a few weeks after yolk absorption for pink and chum salmon (*O. gorbuscha* and *O. keta*, respectively) to approximately 15–20 months post-fertilization for steelhead (*O. mykiss*), coho salmon (*O. kisutch*), and spring Chinook salmon (*O. tshawytscha*).

The standard method of hatchery propagation is to release juvenile fish into stream areas where returning adults can be recaptured for broodstock. The homing and recapture of returning adults may be maximized if smolt releases occur where adults are trapped for broodstock and where the progeny fish are reared, e.g., at a hatchery. Fish that do not return to a hatchery or release site are commonly called "strays". Recapture and removal of unharvested, hatchery-origin adults at a hatchery (or other release site) reduces the potential for genetic and ecological risks to naturally spawning populations.

However, smolts are often released at sites where adult collection facilities do not exist, but where managers desire fisheries on returning adults to occur. In many situations, smolts are transported by hatchery truck—oftentimes into other watersheds and sometimes over relatively large distances, e.g., more than 100 km—prior to release. In general, adult salmon and steelhead transported to other watersheds return to areas where they were released as smolts. The stray rate for these fish is higher than for those released "on-station" (Quinn 1993).

Releasing smolts into streams geographically removed from a hatchery or adult collection facility is commonly called "outplanting." Steelhead programs in the Pacific Northwest have often used outplanting to support recreational fisheries in a large number of small streams or release locations where adult collection facilities do not exist. The often-stated rationale for such outplanting is to "spread out" the fishing effort of recreational fishers or to respond to specific requests by anglers. More recently, freshwater and saltwater "net pens" have increasingly been used to acclimate and release salmon smolts in areas where a targeted fishery on returning adults is desired. Significant harvests on returning adult fish can then occur in freshwater and marine areas in the general vicinity of the net pens.

[1] White papers were prepared by the HSRG to address topics relevant to hatchery reform. They are intended to stimulate discussion and provide background, documentation and explanations not included in the body of the HSRG's report.

A common feature of outplanting and net pen programs is the release of smolts into areas where no facilities exist to trap returning adults that escape target fisheries. In these situations, non-harvested adults may spawn in streams far-removed from the source hatchery or geographic location where their parents were trapped for broodstock.

Outplanting juvenile and/or adult salmonids also occurs in reintroduction and recovery programs where natural spawning by hatchery-origin adults is explicitly desired. These programs, however, are specifically designed to restore extirpated or imperiled natural populations and are generally not intended to support harvest.

Outplanting and net pen releases can pose significant genetic and ecological risks to natural populations by promoting high stray rates to freshwater areas where interbreeding and competition with naturally spawning populations are undesirable. Among the problems associated with outplanting are delayed downstream migration for smolts, potentially high genetic divergence between hatchery and natural populations, and reduced homing instinct in hatchery fish.

2 Findings and Discussion

Homing to natal streams is an important biological characteristic of salmonid fishes, allowing evolution of local adaptations in life history and other fitness traits (Quinn 1993; Altukhov and Salmenkova 1994; Kinnison et al. 2001; Quinn, Kinnison, and Unwin 2001). Homing precision to a particular stream appears to be under very strong response to stream-specific olfactory cues. Stock-specific, and thus stream-specific, genetically-based adaptations include age and size at sexual maturity, within-season return and spawn timing of adult fish in response to geographic location and water temperatures of the home stream, pre-hatch developmental rates, length of freshwater residence prior to outmigration, and marine migration patterns (Smoker, Garrett, and Stekoll 1998). Despite the biological importance of homing, natural straying of anadromous salmonid fishes plays an important role related to colonization of new habitats and maintaining connectivity between geographically adjacent populations (Shapovalov and Taft 1954; Milner 1997; Quinn 1997).

Many studies have shown that salmon and steelhead seek alternative spawning habitats if no appropriate habitat is immediately available (Pasqual and Quinn 1994). Such behavior is most apparent when natal streams are blocked by catastrophic environmental events. For example, siltation resulting from the 1980 eruption of Mount St. Helens resulted in significant numbers of Chinook salmon and steelhead straying from the Cowlitz River to the Kalama and Lewis rivers (Leider 1989; Quinn, Nemeth, and McIsaac 1991).

Physiological and behavioral studies indicate that environmental cues used by salmon for homing are acquired throughout freshwater life stages, but are particularly sensitive during the smoltification and outmigration period (Brannon 1972; Dittman, Quinn, and Nevitt 1996; Quinn, Stewart, and Boatright 2006). These observations indicate that salmon transported away from their incubation and nursery freshwater environments will have reduced homing fidelity as adults.

Tagging and genetic studies have shown that outplanting and net pen programs promote stray rates that far exceed natural levels (Candy and Beacham 2000; Mackey, McLean, and Quinn 2001). The absence of freshwater imprinting by fish released from saltwater net pens can lead to unpredictable straying by large numbers of unharvested adults to streams where natural spawning is not desired. Similarly, significant numbers of adults

returning to outplanted streams typically escape targeted fisheries and most likely spawn with natural-origin fish in non-target streams.

Outplanted smolts often have delayed downstream migration rates compared to fish released on-station from their culture facilities. This can result in the increased probability of ecological interactions with wild fish (Hawkins and Tipping 1999; Pearsons and Fritts 1999). For example, in separate studies, mean downstream migration rates of outplanted steelhead smolts were 2.9 km/day (Tipping and Byrne 1996) and 1.6 km/day (Tipping et al. 1995), respectively, whereas mean downstream migration rates for smolts released on-station were 33 km/day (Dawley, Sims, and Ledgerwood 1978; Harza 1999).

Outplanting and net pen releases from segregated hatchery programs can be especially problematic because of the potentially high level of genetic divergence between the hatchery stock and natural populations where straying and natural spawning may occur. Although the natural spawning success of hatchery-origin fish is generally less than that of natural-origin fish when they occur in the same stream, those same data indicate that significant numbers of hatchery-origin fish – even those from non-native or long-standing "domesticated" populations - do indeed spawn successfully and can contribute significant numbers of progeny to naturally spawning populations (Chilcote, Leider, and Loch 1986; Campton et al. 1991; Mackey, McLean, and Quinn 2001; Kostow, Marshall, and Phelps 2003; McLean, Bentzen, and Quinn 2003; Araki et al. 2007). Kostow, Marshall, and Phelps (2003) presented data supporting a conclusion that hatchery summer steelhead adults and their offspring may have contributed to wild winter steelhead population declines through competition for spawning and rearing habitats.

Many studies have further indicated a genetic component to homing (Bams 1976; McIsaac and Quinn 1988; Pasqual, Quinn, and Fuss 1995; Candy and Beacham 2000; Stewart, Smith, and Yougson 2002; Dukes et al. 2004), suggesting that native fish have higher genetic sensitivity to detect home stream odors than non-native fish reared and released under identical conditions. These characteristics could further compound the potential genetic risks associated with straying by increasing the stray rates among natural-origin progeny of stray hatchery-origin fish that reproduced successfully in nature.

Based on the scientific information available, the HSRG has concluded that outplanting and net pen releases of hatchery-origin salmon and steelhead smolts pose significant genetic and ecological risks to naturally spawning populations. The simplest way to reduce these risks is to reduce the number and/or size of existing outplanting and net-pen release programs.

However, it is recognized that many of net-pen and outplanting programs support important tribal, commercial and/or recreational fisheries. As a result, significant trade-offs may be needed between the fishery benefits of such programs and the risks they pose to naturally spawning populations. Comprehensive assessments of the benefits and risks of each program, on a case-by-case basis, are necessary to understand the potential trade-offs and make informed decisions.

3 Recommendations

The HSRG has formulated guidelines in an effort to reduce the biological risks of outplanting and saltwater net pen programs. The guidelines encompass program implementation as well as program management and monitoring and evaluation. It is the

HSRG's belief that these guidelines and recommendations should be implemented as soon as possible to reduce the biological risks of outplanting and net pen programs.

- Mark all net pen-released and outplanted fish each year and tag a statistically significant proportion of released fish with coded-wire tags.
- This will allow assessment of the direct contribution of those fish to targeted fisheries and assessment of stray rates and biological risks to natural populations. Systematically tagging a portion of the released fish each year, coupled with marking all outplanted and net pen-released fish, will allow fishery co-managers to assess the degree to which these programs minimize risks to natural populations while meeting harvest goals.
- Conduct intensive harvest of hatchery-origin fish and/or use adult traps to reduce potential natural spawning of unharvested, hatchery-origin fish.
- Restrict releases of hatchery-origin fish to areas where adult collection facilities exist or can be easily developed. In some cases, adult traps can be added to existing smolt release ponds. In other cases, release sites can be restricted to streams with existing adult collection facilities.
- Use locally-adapted and genetically integrated hatchery populations for net pen releases and outplanting wherever possible.
- In other words, minimize or eliminate the use of "out-of-region" populations and fish from genetically segregated hatchery populations in regions supporting natural populations. Fish released for harvest programs should be obtained from genetically integrated hatchery populations and/or populations native to the region or watershed where net pen or outplanting programs occur. One possible exception would be hatchery populations that have been selectively bred, or otherwise genetically or phenotypically manipulated to obtain certain reproductive traits, such as spawn timing, that result in low probabilities of successful natural reproduction in the specific streams or geographic area where smolts are released.
- Monitor and evaluate high-risk hatchery programs annually to ensure that adverse effects to wild populations are minimal, that straying risks are appropriately managed, and that off-station releases are appropriately located so that non-harvested, hatchery-origin adults do not spawn in undesirable locations.
- Develop area-wide risk management guidelines and protocols for outplanting and net pen programs.
- Evaluate fishery benefits and biological risks of each outplanting and net pen program annually or not less than every three years. Programs imposing significant risks relative to benefits should be reduced in size or terminated.

4 References

Altukhov, Y.P. and E.A. Salmenkova. 1994. Straying intensity and genetic differentiation in salmon populations. Aquaculture and Fisheries Management 25: 99-120.

Araki, H., W.R. Ardren, E. Olsen, B. Cooper, and M.S. Blouin. 2007. Reproductive success of captive-bred steelhead trout in the wild: evaluation of three hatchery programs in the Hood River. *Conservation Biology* 21:181-190.

Bams, R.A. 1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbuscha*). *Journal of the Fisheries Research Board of Canada* **33**: 2716-2725.

Brannon, E.L. 1972. Mechanisms controlling migration of sockeye salmon fry. International Pacific Salmon Fisheries Commission Bulletin XXI. IPSFC, New Westminster, BC, Canada. 86pp.

Campton, D.E., F.W. Allendorf, R.J. Behnke, F.M. Utter, M.W. Chilcote, S.A. Leider, and J.J. Loch. 1991. Reproductive success of hatchery and wild steelhead. *Transactions of the American Fisheries Society* **120**: 816-827.

Candy, J. R., and T. D. Beacham. 2000. Patterns of homing and straying in southern British Columbia coded-wire tagged Chinook salmon populations. *Fisheries Research* **47**:41-56.

Chilcote, M.W., S.A. Leider, and J.J. Loch. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. *Transactions of the American Fisheries Society* **115**: 726-735.

Dawley, E., C. W. Sims, R. D. Ledgerwood. 1978. A study to define the migrational characteristics of Chinook and coho salmon and steelhead trout in the Columbia River estuary. Coastal Zone and Estuarine Studies Annual Report.

Dukes, J.P.; R. Deaville, M.W. Bruford, A.F. Youngson, and W.C. Jordan. 2004. Odorant receptor gene expression changes during the parr-smolt transformation in Atlantic salmon. *Molecular Ecology* **13**: 2851-2857.

Dittman, A.H., T. P. Quinn, and G. A. Nevitt. 1996. Timing of imprinting to natural and artificial odors by coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci*. **53**: 434–442.

Griffith, J.N., A.P. Hendry, and T.P. Quinn. 1999. Straying of adult sockeye salmon, *Oncorhynchus nerka*, entering a non-natal hatchery. *Fishery Bull*. **97**: 713-716.

Harza Engineering Company. 1999. The 1997 and 1998 Technical Study Reports, Cowlitz River Hydroelectric Project Volume 2. Tacoma Power, Tacoma, WA.

Hasler, A.D. and A.T. Scholz. 1983. Olfactory imprinting and homing. Springer-Verlag, Berlin. 134 p.

Hawkins, R. S., and J. M. Tipping. 1999. Predation by juvenile hatchery salmonids on wild fall Chinook salmon fry in the Lewis River, Washington. *California Fish and Game* **85**(3):124-129.

Kinnison, M.T., A.P. Hendry, T.P. Quinn, and M.J. Unwin. 2001. Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. *Evolution* **55**: 1656-1667.

Kostow, K. E., A. R. Marshall, and S. R. Phelps. 2003. Naturally spawning hatchery steelhead contribute to smolt production but experience low reproductive success. *Transactions of the American Fisheries Society* **132**:780-790.

Leider, S.A. 1989. Increased straying by adult steelhead trout, *Salmo gairdneri*, following the 1980 eruption of Mt. St. Helens. Environ. *Biol. Fishes* **24**: 219-229.

Mackey, G., J.E. McLean, and T.P. Quinn. 2001. Comparisons of run timing, spatial distribution, and length of wild and newly established hatchery populations of steelhead in Forks Creek, Washington. *North Am. J. Fisheries Management* **21**: 717-724.

McIsaac, D.O. and T.P. Quinn. 1988. Evidence for a hereditary component in homing behavior of Chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* **45**: 2201-2205.

McLean, J. E., P. Bentzen, and T. P. Quinn. 2003. Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead trout through the adult stage. *Canadian Journal of Aquatic Sciences* **60**:433-440.

Milner, A. M. 1997. Glacial recession and freshwater ecosystems in coastal Alaska, pages 303-330. *In* Milner, A.M. and Oswood, M.W. (editors), Freshwaters of Alaska. Ecological Studies: Analysis and Synthesis. 97. Springer-Verlag, Berlin.

Nevitt, G.A. and A.H. Dittman. 1998. A new model for olfactory imprinting in salmon. *Integrative Biology: Issues, News, and Reviews* **1**: 215-223

Pasqual, M.A. and T.P. Quinn. 1994. Geographical patterns of straying of fall Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), from Columbia River hatcheries. *Aquaculture and Fisheries Management* **25**: 17-30.

Pasqual, M.A., T.P. Quinn, and H. Fuss. 1995. Factors affecting the homing of fall Chinook salmon from Columbia River hatcheries. *Trans. Am. Fish. Soc.* **124**: 308-320.

Pearsons, T. N., and A. L. Fritts. 1999. Maximum size of Chinook salmon consumed by juvenile coho salmon. *North American Journal of Fisheries Management* **19**:165-170.

Quinn, T.P. 1997. Homing, straying, and colonization, pages 73-85. *In* W.S. Grant (editor), Genetic effects of straying on non-native hatchery fish into natural populations. Proceedings of the Workshop, June 1-2, 1995, Seattle, Washington. NOAA Technical Memorandum NMFS-NWFSC-30. U.S. Dept. of Commerce, National Marine Fisheries Service, Seattle, Washington.

Quinn, T.P. 1993. A Review of Homing and Straying of Wild and Hatchery-Produced Salmon. *Fisheries Research* **18**: 29-44.

Quinn, T.P., M.T. Kinnison, and M.J. Unwin. 2001. Evolution of Chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* **112**: 493-513.

Quinn, T.P., R.S. Nemeth, and D.O. McIsaac. 1991. Homing and straying patterns of fall Chinook salmon in the lower Columbia River. *Transactions of the American Fisheries Society* **120:** 150-156.

Quinn, T.P., I.J. Stewart, and C.P. Boatright. 2006. Experimental evidence of homing to site of incubation by mature sockeye salmon, *Oncorhynchus nerka*. *Animal Behaviour* **72**: 941-949.

Shapovalov, L. and A.C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhychus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. *Calif. Dept. Fish Game Fish. Bull.* **98**: 1-375.

Smoker, W.W., A.J. Gharrett, and M.S. Stekoll. 1998. Genetic variation of return date in a population of pink salmon: a consequence of fluctuating environment and dispersive selection? *Alaska Fishery Research Bulletin* **5**: 46-54.

Stewart, D.C., G.W. Smith, and A.F. Youngson. 2002. Tributary-specific variation in timing of return of adult Atlantic salmon (*Salmo salar*) to fresh water has a genetic component. *Canadian Journal of Fisheries and Aquatic Sciences* **59**: 276-281.

Tipping, J. M., R. V. Cooper, J. B. Byrne, and T. H. Johnson. 1995. Length and condition factor of migrating and non-migrating hatchery-reared winter steelhead smolts. *Progressive Fish-Culturist* **57**:120-123.

Tipping, J. M., and J. B. Byrne. 1996. Reducing feed levels during the last month of rearing enhances emigration rates of hatchery-reared steelhead smolts. *Progressive Fish-Culturist* **58**:128-130.

Tipping, J. M., and T. D. Hillson. 2002. Adult recoveries of winter and summer steelhead by release location on the Lewis River, Washington. *California Fish and Game* **88**(2):49-56.