HSRG Technical Discussion Paper #3

When Do You Start A Conservation Hatchery Program?

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The potential use of hatcheries as a recovery tool for Pacific salmon has consistently raised the following questions: When is it appropriate to start a conservation hatchery program for a declining or imperiled stock? When does the risk of extinction, or negative genetic effects associated with small population size, exceed the risk of hatchery intervention?

Several generalized guides have been published regarding the use of artificial propagation for stocks of Pacific salmon at risk (e.g., Hard et al. 1992, Brannon 1993, Brannon et al. 1998, Flagg and Nash 1999, ISAB 2003, Williams et al. 2003, Flagg et al. 2004). Four key population parameters can be used to assess the viability of salmon populations: *abundance*, *growth rate*, *spatial structure*, and *diversity* (McElhany et al. 2000). However, most current guidelines go little further than suggesting that the best time to intervene with a conservation program depends on the particular stock of fish, its level of depletion, the physical and management limitations of each individual hatchery action, and the biodiversity of the ecosystem.

Biological significance

A key factor in determining the need for a conservation action will be the biological significance of the stock. *Biological significance* is a function of the stock's origin, inherent genetic diversity, biological attributes and uniqueness, local adaptation, and the genetic structure of the population relative to other conspecific populations. A population can be considered highly significant if it exhibits unique genetic and biological attributes that are not shared with other conspecific populations. These attributes may include unique life history, physiological, morphological, behavioral, and/or disease resistance characters, each determined in part by genetic factors.

Genetic diversity

Genetic diversity refers to the magnitude and distribution of genetic variation within and among individuals, as characterized by genetic components of phenotypic variance and population heterozygosities (Falconer and MacKay 1996). Genetic variation is important because it provides the foundation for responses to selection (natural or artificial) and local adaptations. Population viability in dynamic environments is directly related to genetic variation; that is, the fitness and productivity of a population in environments that vary temporally or spatially will be determined largely by the capacity of the population to adapt genetically (e.g., Falconer and MacKay 1996; Franklin 1980). Genetic diversity can be measured by estimating population and quantitative genetic parameters (i.e., allele frequencies at molecular loci and genetic components of phenotypic variance for life history traits).

One of the most important parameters affecting genetic diversity is effective population size (N_e). Effective population size places an upper limit on the amount of genetic diversity that can be maintained in a population or species relative to its pedigree history and potential future losses due to genetic drift. Some general guidelines for maintaining minimum N_e in distinct populations have been proposed:

- $N_e > 50$ to prevent inbreeding depression and a detectable decrease in viability or reproductive fitness of individuals in a population (Franklin 1980).

- $N_e > 500$ to maintain constant genetic variance in a population resulting from a balance between loss of variance due to genetic drift and the increase in variance due spontaneous mutations (Franklin 1980; Soule 1980; Lande 1988)

- $N_e > 5{,}000$ to maintain a constant variance for quasi-neutral genetic variation that can serve as a reservoir for future adaptations in response to natural selection and changing environmental conditions (Lande 1995). The rationale here is that N_e should be large enough to minimize genetic drift and the potential loss of "neutral" alleles that may confer fitness advantages under changing environmental conditions and new selection regimes.

- The $N_e > 5{,}000$ rule applies primarily to an entire ESU or species over evolutionary time scales, whereas $N_e > 50$ applies primarily to closed, local populations over very short time scales (2-5 generations). However, the same basic principles apply to both local populations and entire species in both situations. For example, all individuals of a species with $N_e < 50$ are expected to show reduced viability due to inbreeding depression after a few generations.

Imbalances among parameters affecting N_e can indicate needs for conservation intervention. For example, a detailed analysis of N_e in fluctuating populations may involve a distinction between the inbreeding effective number (N_{eI}) and the variance effective number (N_{eV}) (Crow and Denniston 1988; Simberloff 1988). The inbreeding effective size quantifies the increase in inbreeding – or the probability that two genes are *identical by descent* - over generations, while the variance effective size predicts the amount of genetic drift and the rate of loss of heterozygosity (Ryman et al. 1995). When population numbers are stable, N_{eI} and N_{eV} are nearly identical and constant over time, while in a rapidly declining population N_{eI} may be much larger than N_{eV}.

Age class structure also affects effective population size. The effective population size of a population with overlapping generations is approximately the mean effective number of breeders per year, multiplied by the generation time, or average age of spawners, in years (Waples 1990). A complex age structure, with many overlapping generations tends to diminish the likelihood of a small population going extinct in a particular year in which an environmental disaster occurs.

Population trends

Viable salmon populations, whether natural or hatchery supplemented, exhibit a high intrinsic capacity for population growth. When abundance is reduced (e.g., due to environmental catastrophe or catastrophic harvest) the population can subsequently respond with a rapid increase in abundance, provided habitat of sufficient quantity and quality is available, ocean productivity is favorable, *and* the population has adequate genetic variation to respond demographically and maintain phenotypic resiliency. Extended periods of population depression are evidence either of diminished ecological productivity of habitat (or of the hatchery environment) or reduced genetic viability. Thus, trends of abundance and of variance of abundance over time can be indicators of population viability. More specifically, trends in productivity (adult progeny per parent - recruits/spawner) under stable environmental conditions are good indices of population viability.

Salmon biologists may be required to determine the threshold population abundance at which hatchery propagation should be employed to reduce the demographic and genetic risks of extinction, including preventing losses of genetic diversity due to small population size. The threshold is not easy to define because several factors must be considered simultaneously. These factors include (a) the genetic effective size of the declining population, (b) the general trend or mean rate of decline per year over the past 2-5 generations, and (c) the magnitude and frequency of temporal, stochastic variations in abundance, including potential *Allee effects* (Dennis 2002). For example, a regression analysis of trend of abundance may predict extinction within 100 years; however, if the inter-annual variance in abundance exceeds the mean rate of decline, then stochastic fluctuations are likely to result in either earlier extinction or substantial reductions in genetic diversity due to population bottlenecks. Reduction in genetic diversity could further reduce population resiliency and, thus, accelerate the rate of decline in an *extinction vortex* (Tanaka 2000**)**.

Numerical Thresholds

Here, we provide numerical threshold guidelines for initiating hatchery propagation of declining or imperiled populations of Pacific salmon and steelhead. The guidelines are simplistic because they only consider potential losses of genetic variation due to small effective population size. In practice, demographic factors related to the rate of decline and temporal variances in abundance would also be considered. Despite these limitations, the guidelines below are applicable to all situations where a reproductively-distinct, local population – or stock - of high biological significance may be imperiled. The rationale applied here is that some intervention may be desirable when a biologically unique population approaches a threshold level of abundance, below which declines in genetic diversity are expected due to reduced effective population sizes.

Genetic models indicate that populations with genetic effective population sizes (N_e) greater than 500 ($N_e > 500$) can maintain equilibrium levels of genetic diversity by minimizing losses due to genetic drift (Lande and Barrowclough 1987; Lande 1995). Consequently, a minimum threshold effective population size at which artificial propagation might first be considered would be:

$$N_e = 500 \qquad (1).$$

For Pacific salmon and other semelparous species with overlapping generations, the genetic effective size of a population over a single generation equals the product of (a) the mean effective number of breeders per year ($\overline{N_b}$) and (b) the generation time (*g*) or average age of spawners (Waples 2002):

$$N_e = \overline{N}_b \cdot g \qquad (2).$$

Combining equations (1) and (2) yields the following population threshold, measured in terms of the effective number of breeders per year, at which hatchery propagation might be implemented as a conservation measure:

$$\overline{N}_b = 500/g \qquad (3).$$

For Chinook salmon (*O. tshawytscha*) or steelhead (*O. mykiss*), *g* is approximately 4 years. However, for pink salmon (*O. gorbuscha*), $g = 1$ because of their discrete 2-year life history; that is, the entire population spawns in a single year, every other year, and its generations do not overlap.

For naturally spawning populations of Pacific salmon, the best available empirical data indicate that N_b, the effective number of breeders in a single year, is approximately one-tenth (0.10) to one-third (0.33) the observed number, or "census number" (N_c), of adults spawning naturally (Waples 2004). This difference between N_c and N_b results from the naturally high variance of reproductive success among individual fish: many adults produce no progeny, and some males may fertilize eggs from several females. If we assume that the variance of individual reproductive success among adults decreases as a compensatory mechanism for reduced population sizes and lower spawning densities (e.g., Ardren and Kapuscinski 2003), then we can assume that N_b is near the upper range of the estimated values, or approximately one-third the census number of naturally-spawning adults:

$$N_b = 0.33N_c \qquad (4).$$

Combining equations (3) and (4) thus yields the following threshold at which hatchery propagation might be implemented as a conservation measure:

$$\overline{N}_c = 1500/\mathrm{g} \qquad (5),$$

where $\overline{N}_c$ is the mean, census number of spawning adults per year over one full generation (g).

The threshold indicated by equation (5) varies among species depending on the generation time (average age at reproduction) of the population under consideration. For example, if chinook salmon have a generation time of four years, then hatchery propagation of a biologically significant population might be considered when the mean number of spawners per year - over a four-year period – approaches or declines below 375 adults/year (1500/4 = 375).

Numerical effects of hatchery conservation on wild populations

When considering the trapping and removal of natural-origin adults for conservation propagation, biologists and managers must also consider the effective number of breeders in the hatchery and the effective number of breeders remaining in the wild after adults are removed for artificial spawning. In this context, genetic viability and N_b for adult spawners in the hatchery need to follow the same genetic guidelines as those for natural populations (eq. 3). These guidelines for both the naturally-spawning and hatchery-spawned components allow the genetic effective population sizes of both components to each exceed desirable values ($N_e \geq 500$), thus circumventing potential *Ryman-Laikre effects* (Ryman and Laikre 1991; Ryman et al. 1995) *if* the hatchery program is highly successful. Moreover, this strategy reduces the risk of extinction equally between the two components in the event of catastrophic loss or extinction of either component. That is, a minimum effective population size may still be retained if either the hatchery or natural-origin component of the population (or gene pool) suffers a catastrophic loss.

For adults spawning in a hatchery in a particular year, N_b in the hatchery will, most likely, be approximately equal to the actual number of adults spawned (N_H) because mating and reproduction are controlled, and the variance of reproductive success among spawners can be similar to theoretical expectations for an “idealized” population (Campton 2004). Therefore, hatchery managers can protect the genetic viability of the hatchery portion of the population by keeping the number of adults trapped and spawned in the hatchery each year (N_H) above the threshold:

$$N_H > 500/g \qquad (6).$$

Similarly, biologists can protect the viability of the population in the wild by ensuring that the number of adults remaining in the wild to spawn naturally (N_W), *after* adults are removed for hatchery propagation, follows equations 3 and 5. These constraints collectively prescribe a series of minimum population-abundance thresholds at which hatchery propagation might appropriately be implemented as a conservation measure (Table 1).

For a declining population of Chinook salmon, for example, hatchery propagation might first be considered when the mean census number of returning adults declines to near N_c = 500 adults per year. If a hatchery program is implemented, then a *minimum* of N_H = 125 adults per year should be trapped and spawned artificially for four consecutive years, thus leaving a *minimum* of N_W = 375 adults each year to spawn naturally. At these minimum thresholds, the effective population size for each of the hatchery and naturally spawning components over a single generation would be approximately N_e = 500 (assuming no population bottleneck in a preceding generation). Thus, catastrophic loss of either component would still allow a minimum N_e to be retained.

Multiple generations

The objectives of a conservation hatchery program, as outlined here, are to: (1) provide a demographic increase in the total number of returning adults; (2) allow natural spawning by hatchery-origin adults with the goal of increasing natural reproduction and the total number of natural-origin adults returning in subsequent generations; and (3) maintain $N_e > 500$ to minimize potential losses of genetic variation due to small effective population sizes and genetic drift. At least two full generations are necessary to realize these objectives. Consequently, first-generation hatchery-origin fish would be returning and spawning in the wild when a second generation of hatchery propagation would be implemented. This latter situation raises the following question: What number and composition (% hatchery and % wild) of adults should the hatchery remove and spawn during the second generation of hatchery propagation?

Our conclusions regarding this question are: (1) the total number of adults spawned artificially during the second generation should follow the same guidelines presented in Table 1; and (2) the percent composition of natural and hatchery-origin fish in the hatchery broodstock should be the same as the composition of the two groups among all returning adults. Thus, adult fish trapped for broodstock should be selected randomly among all returning fish with the goal of achieving the minimum broodstock sizes (N_H) outlined in Table 1 for each species. This latter approach would result in the same spawner compositions for both the hatchery and natural environments. Such guidelines would automatically reduce the *proportion* of the total number of returning adults taken into the hatchery each year if the hatchery program was successfully meeting its objectives after one generation (i.e., N_H/N_c in generation 2 would be less than the value of this ratio in the initial generation of hatchery propagation if the hatchery program was meeting its objectives). If the objectives of the hatchery program are met after two generations of propagation, then the program could be suspended or terminated, but with monitoring and evaluation (M&E) of adult returns continuing to assess overall extinction risks and the success of hatchery supplementation.

For example, a near-term management strategy might "pulse" hatchery-produced fish into the population for two generations, followed by suspension of hatchery propagation for one to two generations to assess, via M&E, overall population responses and subsequent extinction risks. The hatchery program could be reinstituted at a later date, if necessary, until the causes of the original population declines were rectified. Alternatively, an *integrated* hatchery program could be developed with no immediate "sunset" clause if the factors responsible for the decline were expected to continue indefinitely (e.g., the presence of a hydropower facility).

Overall, we believe the guidelines presented here provide a relatively simple, first-step approach for assessing the potential need for a conservation hatchery program when a population of high biological significance exhibits significant declines in abundance over at least one full generation. When the threshold levels of abundance outlined here are approached (Table 1), then demographic models of population viability could be invoked to predict extinction probabilities and mean times of persistence. However, the approach outlined here assumes that one goal of a conservation hatchery is to prevent significant losses of genetic variation *before* a population is at imminent risk of extinction.

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Table 1. Threshold spawner abundances below which a conservation hatchery program should be considered for a declining natural population. The implicit assumption here is that the mean census number of adults per year will continue decline below the threshold level in the absence of artificial propagation. Thresholds vary by species, depending on generation time and year class overlap. The threshold numbers shown below (N_c) are based on the general principle that the total effective number of breeders over one full generation should be at least 500 ($N_e > 500$) in each of the hatchery and wild components. N_H is the number of adults required for the hatchery program.

Species	No. of years per generation (avg. age of spawners) (g)	Threshold mean census number of adults/year (N_c)	Number of Adults		Resulting effective number of breeders per year in natural environment ($N_b = 0.33N_W$)
			Hatchery (N_H)	Natural Environment ($N_W = N_c - N_H$)	
Chinook salmon	4	500	125	375	125
Chum salmon	4	500	125	375	125
Coho salmon	2.7	750	186	564	188
Pink salmon	1	2000	500	1500	500
Sockeye salmon	3.5	575	144	431	144
Steelhead	4	500	125	375	125