ISAB Review of Salmon and Steelhead Supplementation

Introduction

This report represents the ISAB response to requests by the NOAA Fisheries Northwest Fisheries Science Center and the Northwest Power Planning Council to provide an assessment of the risks and benefits of supplementation in the Columbia River Basin.

Northwest Fisheries Science Center Request

In a September 14, 2001 letter, NOAA Fisheries requested that the ISAB consider the benefits and risks of supplementation to natural populations of salmon and steelhead where supplementation was broadly viewed as those salmon and steelhead hatchery programs that intended to integrate natural and hatchery production. With this general request they included eight more specific multi-part questions as samples of issues the ISAB may wish to consider:

1. What do empirical studies of hatchery-wild interaction tell us about the benefits as well as the risks involved in supplementation programs? What are the strengths and limitations of each study, and what is their relevance to the key questions about appropriate use of hatcheries in supplementation? What conclusions can be drawn from the collective body of information?

2. What is the best way to assess the risks and benefits of supplementation to determine the net effects on natural populations? How can this be used to determine whether a supplementation program should be initiated and, if so, on what scale? Under what circumstances is supplementation likely to lead to a net long-term benefit to natural populations, and under what circumstances is it more likely to do more harm than good?

3. What are the empirical results of salmon supplementation to date? What has worked, and what aspects are largely unevaluated? How does evaluation of salmon supplementation depend on the goals of the program?

4. There are two opposing views of the role of natural selection in salmon biology: one that stresses the importance of local adaptation, and one that stresses the flexibility of salmon to respond to different environmental challenges. Both points of view have merit. The real question is the relative importance of these two processes for the recovery efforts, and what are the implications for salmon supplementation. Some key questions related to this complex topic include the following:

   a. What information is needed to determine what spatial and temporal scales are important for local adaptation in salmon and steelhead? How does or can supplementation affect this?

b. What do we need to know to determine how replaceable salmon populations are on ecological and evolutionary time frames? For example, if a local population is lost, how likely is it that another population will replace it, and if so, on what time scale? How does supplementation affect this process?

5. Supplementation programs (as well as conventional hatchery programs) can substantially change the pattern of gene flow between salmon populations. Under what circumstances are these changes likely to be beneficial, and when are they likely to be detrimental to long-term sustainability of natural populations?

6. Even without considering hatcheries, most salmon populations have experienced large perturbations in their ecosystems compared to pre-European influence. How do these changes affect conclusions about the effects of supplementation on sustainability of natural populations?

7. Every supplementation program has unique aspects that need to be evaluated on a case-by-case basis. Nevertheless, it is also important to consider the appropriate use of supplementation on a larger scale (e.g., the Columbia River basin). In this larger context, and given all the uncertainties associated with risks as well as potential benefits of supplementation, what would be an appropriate level of intervention across the basin, and how does this compare with the array of programs that are currently underway or planned?

8. Finally, what are the key scientific uncertainties regarding salmon supplementation, and what are the most profitable lines of research to help resolve them? Do we need a basinwide experiment to assess supplementation impacts?

Northwest Power Planning Council Request

In March 2002 the Northwest Power Planning Council (Council) added an additional question to the developing ISAB supplementation project:

Can artificial production be integrated with natural production to increase capacity and productivity of the combined population in a manner that provides sustained benefits (measured as the abundance and productivity of the integrated population) over the foreseeable future?

The ISAB was requested to consider this question with regard to the following array of circumstances that will likely be faced by subbasin planners:

Scenario 1: There is a healthy naturally self-sustaining population under present and expected future habitat conditions and harvest rates.

Scenario 2: There is a self-sustaining natural population without major habitat limitations that is unable to support present and future desired harvest rates.

Scenario 3: There is a natural population that is weak or declining and not expected to rebuild, given the present and expected future habitat conditions encountered over its life cycle.

The ISAB was requested to delineate for Council the potential benefits and risks of integrating natural and artificial production under each of these scenarios. The ISAB was also asked to describe the types of actions and strategies that could be employed to minimize negative impacts and maximize the likelihood of success. Finally, the ISAB was asked to identify the major scientific weaknesses and uncertainties associated with supplementation and recommend a process for evaluating the success of these types of integrated production programs.

Independent Science Advisory Board Approach

Because the NOAA-Fisheries request was quite broad, the ISAB chose to investigate the following three topics (covering a subset of specific questions) with the intent that these would provide the Columbia River Basin with a useful consideration of the benefits and risks of supplementation:

1. The demographic and population genetic theory underlying our understanding of the benefits, risks, and uncertainties of supplementation.

> *Supplementation programs can substantially alter the demography and gene flow within and among, salmon populations. Under what circumstances are these changes likely to be beneficial, and when are they likely to be detrimental to the long-term sustainability of natural populations?*
>
> *There are differing viewpoints on the importance that natural selection plays in shaping today's salmon population. One viewpoint stresses the importance of local adaptation providing fitness advantages. Another viewpoint favors maximizing the flexibility of salmon to respond to different environmental challenges. What is the relevance of these differing viewpoints for structuring current supplementation programs and for salmon recovery efforts in general?*

2. Case histories of ongoing supplementation experiments and programs within the Columbia River Basin.

> *What are the empirical results of the various supplementation experiments to date?*
>
> *What has worked and what has not, and what aspects are largely unevaluated?*
>
> *How does evaluation of salmon supplementation depend on the goals of the program?*

3. The decision tools used to assess the benefits and risks of supplementation.

What is the best way to assess the benefits and risks of supplementation to determine its net effect on natural populations?

How can this be used to determine whether a supplementation program should be initiated and, if so, on what scale?

Information Resources

A considerable volume of peer-reviewed scientific publications and technical reports exists on the propagation, life histories, and ecological requirements of salmonid fishes. In contrast, there are only a few peer-reviewed scientific publications that document the consequences to natural populations of supplementation programs.

As a first step, we reviewed the peer-reviewed scientific publications concerning supplementation. We also reviewed regional technical reports for background on supplementation, empirical results of ongoing projects, and policy. These reports have typically not undergone peer review. We conducted limited interviews with scientists in the region to clarify specific topics and to address questions about data sets from experiments in the Basin. Finally, we canvassed fisheries professionals both within and outside the region to assess the breadth of ideas on the benefits and risks of supplementation to natural salmon populations and to obtain their input on answers to some of the questions posed by NOAA Fisheries.

Report Structure

Evaluating the benefits and risks of supplementation to natural salmon and steelhead populations could be approached in any one of several ways. This report reviews the genetic and evolutionary theory underlying the genetic risks, summarizes models that provide a quantitative treatment of the anticipated demographic benefits, and describes the parameters that need to be measured to evaluate supplementation. It also presents case histories of supplementation efforts in the Columbia River Basin and reviews benefit/risk assessment tools to decide whether or not to undertake supplementation. The report has eight sections:

Section 1. History of Supplementation in the Columbia River Basin: a brief description of where we are and how we got there.

Section 2. Description of Supplementation: the regional context for supplementation established through a review of supplementation strategy development and a summary of the benefits and risks of supplementation.

Section 3. Genetic/Evolutionary Theory: a summary assessment of the scientific knowledge concerning the risks of using supplementation in attempts to recover natural populations of salmon.

Section 4. Quantitative Expectations of Supplementation: a summary of the models of integrated natural and artificial production providing a framework for the experimental designs needed to address uncertainties associated with supplementation.

Section 5. Recommended Performance Indicators and Experimental Designs: guidance on how to collect data suitable to support statistical assessment of supplementation projects.

Section 6. Case Histories of Ongoing Supplementation Projects: survey of basin supplementation projects, including an assessment of their data adequacy to calculate the recommended performance indicators.

Section 7. Decision Making and Risk Assessment: a review of risk assessment strategies and the limitations of using risk assessments to contain unintended outcomes from supplementation programs.

Section 8. Conclusions and Recommendations: brief answers to NMFS and Council questions.

Section 1. History of Columbia River Basin Supplementation

Salmon and steelhead have been artificially propagated in Columbia River Basin hatcheries for over 100 years. Artificial culture was initiated because it was thought that eggs were wasted in the natural environment, and that increased juvenile fish production would automatically yield more adult fish for harvest (Bottom, 1997). Hatchery production was later used in an attempt to maintain high harvest rates and eventually as a method to provide fish for harvest that had been lost because habitat degradation had reduced natural production (Lichatowich, 1999). It was assumed at that time that these early programs would have little to no negative impacts on natural populations.

At the same time that Columbia River Basin hydroelectric and salmon hatchery systems were expanding (1930s to 1970s), resource managers were becoming more aware of the need to preserve declining wild populations. Advances in the understanding of ecological systems led to a revision of the scientific principles and beliefs that artificial production could unquestionably mitigate for lost natural production (NWPPC 99-15). Scientific principles in the current Northwest Power Planning Council's Fish and Wildlife Program and artificial production policies recognize that salmon and steelhead abundance generated from either natural or artificial production will be constrained by environmental conditions.

Although there now is broad scientific consensus that there are practical limits to the capacity of any watershed to produce salmon, measuring the carrying capacity of a specific watershed with precision remains difficult. There is no formula based on habitat measurements alone for identifying optimal production targets in a given watershed, nor is there a formula for determining the level of artificial production that will not cause detrimental effects on wild production.

Scientific knowledge concerning the impacts of hatchery production on natural populations lags well behind our ability to produce salmon smolts in hatcheries and release them. On either short or long time scales the extent to which natural and artificial production can be integrated successfully is unknown and continues to be debated actively among basin stakeholders.

Although Columbia River Basin management strives to recover salmon, a slate of diverse legal mandates leaves the region struggling with multiple and sometimes conflicting objectives. For example, the Council's Fish and Wildlife Program is obligated to protect, enhance, and mitigate fishery opportunities lost because of hydrosystem development, whereas the National Marine Fisheries Service is obligated to protect species listed under the ESA and to fulfill federal treaty trust obligations to the region's Indian tribes. Salmon harvest and mitigation obligations can conflict with ESA protection mandates. We do not know if fish harvest and species abundance can be recovered simultaneously within a common management framework.

In an effort to meet these multiple objectives, the Council's 1987 Fish and Wildlife Program (FWP) (NWPPC 1987) called for increased fish production to be generated from a combination of enhanced natural production, conventional hatchery production, and supplementation. Conventional hatchery programs were defined as those programs that used technology to replace natural spawning, egg incubation, and freshwater juvenile rearing to produce and release smolts, some fraction of which would survive to adults that would contribute to the fishery. Supplementation was a new idea; it proposed to use hatcheries to increase the number of adults that would spawn naturally. It was hoped that juveniles produced from these hatchery-origin adults spawning naturally would help to restore natural production. It was asserted that supplementation projects would provide approximately 50% of the increased production in the Columbia River Basin (NWPPC 1987).

Using artificial production of salmon and steelhead to rebuild natural production was recognized as experimental and as an activity that was accompanied by substantial genetic and ecological uncertainties. Because of these uncertainties, the Council formed the Regional Assessment of Supplementation Project (RASP) to develop basinwide supplementation theory, project planning, monitoring, and evaluation. In 1992 RASP produced a final report that provided a definition of supplementation and listed its uncertainties and the theory that explained them. The report also contained summaries of project diversity, objectives, and performance standards (RASP 1992).

At least two major experiments designed to assess the efficacy of supplementation for rebuilding natural populations have been initiated under the Council's FWP: the Yakima Fisheries Project (YFP) and the Idaho Supplementation Studies (ISS). A number of other Fish and Wildlife Program projects underway since the mid-1980's were brought under the supplementation umbrella in the early 1990's; e.g., the Hood River Production Program, the Umatilla River Steelhead Supplementation Program, and the Northeast Oregon Hatchery program.

The RASP report (1992), as well as the Council's Artificial Production Review (NPPC 99-15) and the 2000 FWP, explicitly recognized that supplementation was experimental. It was intended that the experimental supplementation programs would be operated within an adaptive management framework to allow for evaluation and adjustment. Although individual projects have undoubtedly undergone modification in response to successes and failures, there has not yet been an overall assessment of the collective contribution of individual supplementation projects to salmon and steelhead production in the Columbia River Basin.

Section 2. Description of Columbia River Basin Supplementation

Supplementation Definition

A common definition of supplementation, together with a suite of clearly defined terms, is necessary not only to develop an unambiguous theoretical framework for guiding supplementation efforts, but also to establish data needs for monitoring and evaluating those efforts.

A number of supplementation definitions have been used (Miller 1990, RASP 1992, Cuenco et al. 1993). The definition of supplementation used in this report and a description of the management and policy framework in which supplementation is applied is provided below. The definition is drawn from RASP (1992). The management and policy context is drawn from Cuenco et al. (1993), Kan-Ush-Mi Wa-Kish-Wit (CRITFC 1995), NWPPC (2000-19), and McElhany et al. (2000).

> *Supplementation is the use of artificial propagation in an attempt to maintain or increase natural production, while maintaining the long-term fitness of the target population and keeping the ecological and genetic impacts on non-target populations within specified biological limits.*

This definition was adopted by RASP at the suggestion of the Scientific Review Group (SRG), a predecessor of the ISAB. The definition was also accepted by the Oregon Independent Multidisciplinary Science Team (IMST) and recommended to the Oregon Department of Fish and Wildlife (ODFW) (IMST 2001). RASP concurred with the Scientific Review Group's determination that when definitions were not specific, they would not be helpful in the design of performance indicators, monitoring systems, or experimental studies.

Management and Policy Framework for Supplementation in the Columbia River Basin

Supplementation has been identified by NOAA-Fisheries as a possible strategy to contribute to recovery and maintenance of some ESA listed populations. In addition, the Council's FWP anticipates that supplementation will contribute to sustained abundance and productivity to support harvest. These expectations are embedded within broader management frameworks. Rebuilding ESA listed species is the charge of NOAA-Fisheries recovery plans developed by Technical Recovery Teams (TRT's) who are guided by the Viable Salmonid Populations (VSP) document (McElhany et al. 2000). Components of the VSP that apply to supplementation are the guidelines being developed to establish abundance and productivity thresholds for naturally spawned population components of listed populations. In contrast, actions to recover fisheries under the

Council's FWP are guided by the program's Scientific Foundation and Scientific Principles and by the policies in the Council's Artificial Production Review (APR) (NPPC 99-15).

The 2000 FWP identifies the following principles for supplementation:

Fish raised in hatcheries for harvest should have a minimal impact on fish that spawn naturally; and

Fish reared in hatcheries or by other artificial means for the purpose of supplementing the recovery of a wild population should clearly benefit that population.

Measures for evaluating supplementation success or failure need to be consistent both with the definition of supplementation and with these Program principles.

Supplementation versus Conventional Hatchery Programs

In the Columbia River Basin management context, supplementation programs lie at one end of an artificial production continuum with conventional hatchery programs at the other. Although supplementation programs differ greatly from conventional hatchery programs in their focus on recovery of wild populations, in the scale of production, and in the mode of its deployment, they differ only subtly in many of the fish culture and husbandry methods used.

Management guidelines constrain supplementation programs through preferential use of local broodstocks, limits on the fraction of wild populations that are allowed to be collected for use as broodstock, and under some circumstances, limits on the proportion of hatchery-origin adults that are allowed to mix with natural-origin adults on spawning grounds. These constraints are intended to produce an artificial production program with reduced levels of genetic and/or demographic risk compared to conventional hatchery programs. The degree of human intervention in the life cycle of Columbia River Basin salmonids by supplementation programs varies greatly from minor additions to a population with substantial natural production to captive broodstock/captive rearing programs.

Because the number of smolts produced and released will be limited by the broodstock management guidelines, supplementation programs are likely, at least initially, to produce fewer harvest opportunities than a conventional hatchery program. If management constraints are relaxed, programs would shift from being supplementation programs toward being conventional hatchery programs, and their impact on wild populations would change accordingly. Management discipline is required to keep supplementation objectives intact.

The RASP definition of supplementation includes two standards for the use of supplementation programs. First, supplementation programs should be directed toward areas where the average annual population growth rates of the naturally producing population is less than or equal to 1.0 (i.e., natural production alone results in a declining or barely stable population) under present or anticipated habitat conditions. Second, when supplementation is used, it should: a) maintain "the long-term fitness of the target population" and b) keep "the ecological and genetic impacts on non-target populations within specified limits." Supplementation is a tool that has been proposed for maintaining salmon populations in areas where they would be marginal or nonexistent under otherwise existing habitat conditions. Supplementation per se does not improve natural habitat conditions. Under adverse habitat conditions supplementation cannot be expected to produce offspring that can sustain themselves without assistance.

Relevant and clearly delineated performance indicators are required to evaluate whether or not these standards are being met and to provide a technically sound basis for management decisions. The combined abundance of natural-origin and hatchery-origin adults spawning in the wild is not a sufficient indicator in itself. The RASP definition implies that performance indicators are needed in three areas: 1) target population production, 2) target population long-term fitness, and 3) non-target population impacts.

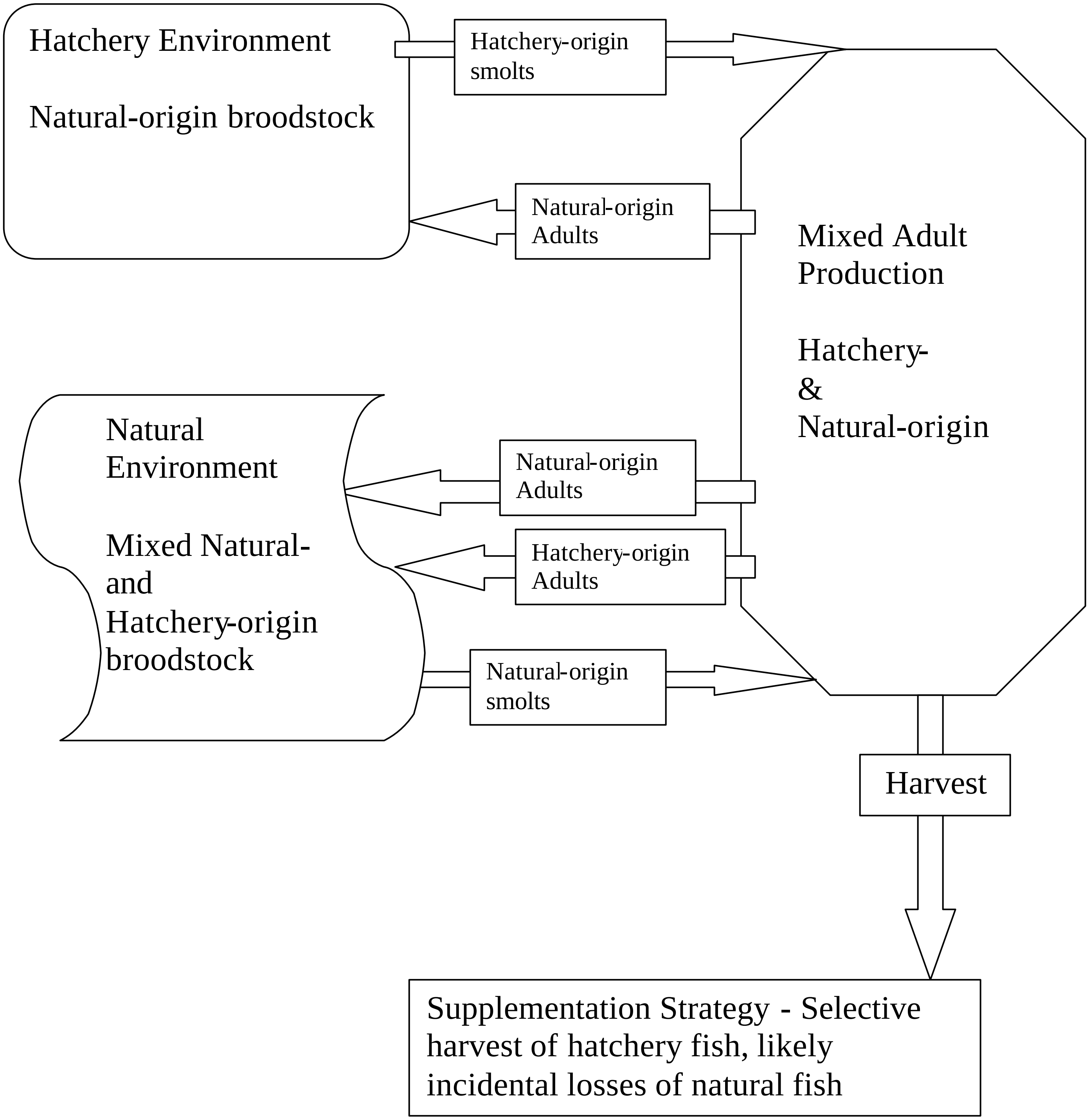

Figure 2a. Schematic representation of the relationship of hatchery spawning, natural spawning, and harvest in an integrated salmon population undergoing supplementation. Ideally, each generation of hatchery production would only use natural-origin adults.

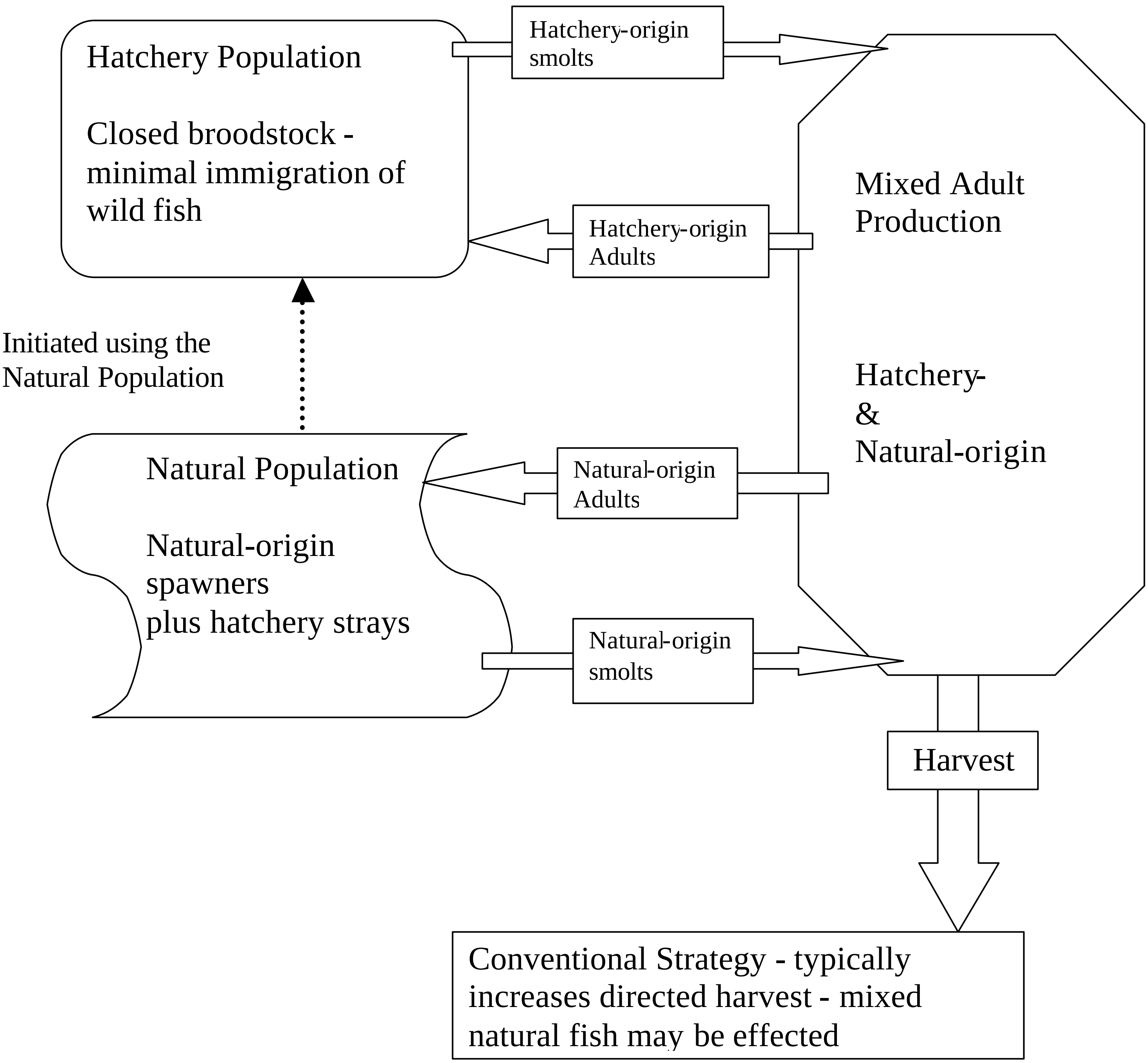

Figure 2b. Conventional artificial production strategy. Diagrammatic representation of the segregation of a natural salmon population and hatchery salmon population, with harvest of the hatchery population.

Supplementation Applications

RASP (1992) listed four general objectives for supplementation:

1. restoration: the restoration of an extirpated native species in specific habitats.
2. introduction: planting a species into habitat where it is not native.
3. rearing augmentation: planting fish in habitat that is underutilized.
4. harvest augmentation: planting fish for the purpose of increasing harvest.

Cuenco *et al.* (1993) identified three uses of supplementation:

1. to assist in rebuilding natural stocks;
2. to replace extirpated stocks;
3. to introduce or establish a stock in a barren habitat.

The ISAB notes that the RASP objectives might be better described as applications for using artificial propagation. The objectives of supplementation are established by its definition: (1) to increase or maintain natural production; (2) to maintain long-term fitness of the target population; (3) to keep ecological and genetic impacts on non-target populations within specified biological limits.

In this review of supplementation, the ISAB focuses on the benefits, risks, and uncertainties of rearing augmentation (assisting to rebuild natural stocks) programs. This consideration also includes the extreme example of captive brood programs. Replacing or reintroducing extirpated stocks and establishing populations in barren habitat are outside the bounds of our review. We emphasize, however, that reintroducing salmon and steelhead into stream systems that formerly supported natural populations or introducing them into historically uninhabited areas include most of the uncertainties, benefits, and risks of programs supplementing natural populations that are below replacement. Finally, we consider the use of artificial production solely for the purpose of harvest augmentation to be outside the definition of supplementation.

Supplementation Program Design Criteria

Design criteria for supplementation programs presented in RASP (1992) and Cuenco et al. (1993) are summarized below. These criteria represent the primary means to contain supplementation risks. They include broodstock selection, mating protocols, escapement management, incubation and rearing practices, release variables, and project scale (the numbers of smolts released and adults returning in relationship to the size of the natural population).

Broodstock selection: The first priority as a source for broodstock collection should be the target population itself. The second priority should be a neighboring population with similar genetics, life history, and ecology. The last priority should be a hatchery stock that best meets the similarity criteria.

Escapement management: After supplementation has been initiated, subsequent hatchery broodstock should be collected from returning adults according to the following order of priority: only natural-origin adults; a mixture of hatchery-origin and natural-origin adults; as a last priority, only hatchery-origin fish (RASP 1992). Cuenco et al. (1993) recommended similar broodstock selection procedures for ongoing supplementation projects. They also recommended limiting collection of natural-origin adults for broodstock to 25% -50% of the returning population.

Project scale: The number of fish released into a stream may be governed by policies that limit the proportion of hatchery-origin and natural-origin fish on the spawning grounds (RASP 1992). Even in the absence of specific policies, the number of fish released into the target stream, combined with fish naturally spawned there, should not exceed the natural stream's carrying capacity (RASP 1992). Numbers of fish stocked should be matched to the biological productivity of the habitat to ensure adequate, but not excessive seeding with respect to carrying capacity (Cuenco et al. 1993).

Benefits and Risks of Supplementation

RASP (1992), Cuenco et al. (1993), Currens and Busack (1995), and Waples and Drake (2002) present frameworks for determining the benefits and risks of supplementation for natural populations of salmon and steelhead. Currens and Busack (1995) consider the detrimental effects of an activity a *hazard*, the probability of the deleterious outcome occurring the *risk*, and the loss that would occur if the hazard is realized. Waples and Drake (2002) pool hazards and risks into a common risk category. We have used the pooled definition of Waples and Drake (2002) throughout this report. Common themes of these frameworks are summarized below:

Summary of Benefits of Supplementation:

1. Primary benefit. Increase in the natural-origin adult population.

2. Secondary benefit. Increase in the combined hatchery-origin / natural-origin adult population.

Summary of Risks of Supplementation:

1. Genetic.

Effective population size (Ne) reduction: Loss of genetic variation within populations and increase in the variance of allele frequencies is affected by the size of the effective breeding population. This risk arises because in some supplementation programs a substantial fraction of the hatchery-origin adults spawning in the wild could be derived from only a few families used in the hatchery phase of the program. This can result in increased inbreeding and inbreeding depression.

Domestication: Domestication is unintentional selection for or adaptation to the hatchery environment. Subsequent interbreeding between hatchery and naturally produced population components could lead to the loss of adaptation to the natural spawning environment.

Loss of among-population diversity: Loss of genetic variation among populations occurs when genetically divergent populations are mixed. In addition, the adaptive genetic differences among these populations can be decreased and the co-adapted gene complexes disrupted by interbreeding between hatchery-origin and natural-origin adults derived from different evolutionary lineages (e.g., ESUs, stocks). This can lead to outbreeding depression.

2. Ecological.

Predation: Juvenile hatchery fish stocked in receiving streams may prey on naturally produced offspring if their size differences are appreciable. These effects could impact both target and non-target species. Release and migration of large numbers of hatchery-origin juveniles may attract avian and mammalian predators, increasing predator population size or increasing the density of predators in an area where hatchery fish are migrating.

Competition: Juvenile hatchery fish stocked in receiving streams may compete for food resources and space with naturally produced juveniles. Hatchery-origin adults spawning in the wild may compete with natural-origin fish for spawning sites and mates. Such competition could be particularly acute when the abundance of hatchery fish is disproportionately large compared to the abundance of the natural population and the carrying capacity of the environment.

Diseases: Disease transmission is possible both from the hatchery population to a wild population and from a wild population to a hatchery population. Hatchery populations that have been infected by natural populations are often destroyed by hatchery staff, reducing the numbers of individuals available for the supplementation program. Diseases introduced from a hatchery can have disastrous effects upon native populations not previously exposed to the pathogen.

3. Demographic.

Poor hatchery fish recruitment rate: The numbers of hatchery-origin adults returning to spawn in the wild may not exceed the number that were removed to produce them or may not be enough to provide for replacement and harvest.

Poor hatchery fish reproductive success: Hatchery-origin adults spawning in the wild may produce fewer adult progeny than their natural-origin counterparts. If the smolt-to-adult survival rate of hatchery-origin adults is insufficient to offset any reduction in reproductive success there will be a net loss of adults in the population.

4. Facility Effects

   Catastrophic failure: Disruption of the water supplies can result in the loss of an entire hatchery annual production, including gametes removed from the wild.

   Passage obstruction: Counting/broodstock collection weirs and other hatchery structures in a water course may disrupt the upstream and downstream migration of target and non-target fish populations and alter spawning and rearing locations within a watershed.

   Intake mortality: If improperly screened, hatchery water intakes can create a significant source of mortality for juveniles of both target and non-target species.

5. Management

   Masking effects: If hatchery-origin and natural-origin adults are not adequately identified and accounted for on the spawning grounds, abundance of the natural population cannot be accurately estimated.

There is uncertainty as to whether the benefits will be realized from supplementation and uncertainty as to whether or not significant harm will materialize from the risks. These two sets of uncertainties underlie the controversy over using supplementation as a management strategy in the Columbia River Basin and elsewhere in the Pacific Northwest. Some scientists and managers believe that demographic benefits are likely to occur and that reformed hatchery practices can reduce the risks from supplementation to acceptable levels. They believe that the risk of extirpation is greater than any genetic risks posed by supplementation. Other scientists and managers are doubtful that the demographic benefits will occur and believe that harmful outcomes have a high probability of being realized, thereby reducing the productivity and abundance of the natural-origin component of the integrated population. Because of the uncertainty associated with these issues, RASP (1992), the Council's Artificial Production Review (NPPC 1999), and the Fish and Wildlife Program (NPPC 2000) recommend that supplementation be implemented in an experimental adaptive management framework.

The remainder of this report addresses these benefits and risks of supplementation in more detail: Section 3 considers the genetic and evolutionary theory underlying the genetic risks; Section 4 summarizes models that provide a quantitative treatment of the anticipated demographic benefits, and describes the parameters needed for evaluating supplementation; Section 5 provides details on collecting the life cycle data needed to estimate parameters for evaluating supplementation; Section 6 assesses case histories of supplementation efforts in the Columbia River Basin; Section 7 reviews tools to assess the benefits and risks of supplementation; Section 8 provides the ISAB's findings on supplementation, recommendations for implementing supplementation, and concise answers to NOAA Fisheries and Council questions; an appendix provides extended summaries of Columbia River Basin supplementation projects.

Section 3. Genetic/Evolutionary Theory

Controversy among Columbia River Basin Scientists

Supplementation of salmon and steelhead involves removing adults from a naturally spawning population, manually stripping gametes from adults to produce offspring *in vitro*, rearing these progeny in an artificial environment very different from the natural environment, and then reintroducing these progeny back into the natural population. The intention is that the salmon and steelhead produced in the hatchery and reintroduced into the wild as smolts will migrate to the ocean and return as adults to interbreed in the wild with the natural-origin returning adult population, thereby producing a sustainable increase in population size. A potential consequence of that interbreeding, however, is the alteration of the genetic characteristics of the target population (Hallerman 2003a; Miller and Kapuscinski 2003). Because these genetic alterations may reduce fitness and productivity, some Columbia River Basin scientists view supplementation as risky (Lichatowich and McIntyre 1987; Nehlsen et al. 1991; Hilborn 1992; Martin et al. 1992; Busack and Currens 1995; Lichatowich 1999;).

The request from NOAA Fisheries asked the ISAB to assess the theoretical framework that underlies the genetic and evolutionary issues associated with supplementation, not only in a general sense, but also as it may pertain to salmon issues specific to the Columbia River Basin:

> *Supplementation programs (as well as conventional hatchery programs) can substantially change the pattern of gene flow among salmon populations. Under what circumstances are these changes likely to be beneficial, and when are they likely to be detrimental to long-term sustainability of natural populations?*

Strategy for Developing Answers to the Question

To make our response to this question as relevant as possible, the ISAB sought to capture the full array of scientific viewpoints on the genetic principles and evolutionary theory that underlie supplementation efforts. The ISAB has used the following sources of information:

1. A survey of 18 Columbia River Basin scientists who have been actively involved with issues of salmon supplementation - each scientist was asked to respond to the question posed to the ISAB;

2. A survey of the 10 Past Presidents of the Genetics Section of the American Fisheries Society - each scientist was asked to respond to the questions posed to the ISAB;

3. Correspondence received by the ISAB in response to our previous reports addressing artificial propagation;

4. Documents produced within the Columbia River Basin that address both supplementation and artificial propagation of salmon (e.g., Final Report to NSF and BPA on Population Structure of Columbia River Basin Chinook and Steelhead - by Brannon, Powell, Quinn, and Talbot (2002); the WDFW Draft Benefit-Risk assessment for Artificial Production; A Scientific Basis for Columbia River Artificial Production Programs – by the Scientific Review Team, Council Document 99-4)

To address the question asked by NOAA Fisheries, we assess the genetic principles and evolutionary theory underlying five subtopics:

1. Adaptation
2. Genetic variation
3. Domestication selection
4. Inbreeding depression
5. Outbreeding depression

The first two subtopics deal with general issues that pertain to the evolutionary history and genetic structure of all natural populations. The final three subtopics deal with how supplementation can impact fitness and genetic structure of the target populations. For each of the five subtopics listed above, we provide the following summary statements:

1. A definition of the subtopic and an explanation of the breadth of viewpoints;
2. A review of the evidence for effects on Columbia River Basin salmonids;
3. A review of the evidence for effects on all salmonids;
4. A review of the evidence for effects on other fish species;
5. A review of the evidence for effects on other plants and animals;
6. An ISAB assessment of how published evidence supports various viewpoints.

Evaluation of the Issues

Issue I - Adaptation

Issue Definition: Adaptation can be characterized as a state, a process, or an individual trait (Amundson 1995; Hallerman 2003a). As a state, adaptation describes the degree to which an individual (or a population) is morphologically, physiologically, and behaviorally competent to survive and reproduce in its environment (Endler 1986). As a process, adaptation represents the evolutionary response of a population to the fact that some organisms (with one specific genotype) are more or less fit relative to others (with different genotypes) in a given environment and at a certain point in time (Fisher 1930). In that way, adaptation acts to change populations through an evolutionary response over successive generations, not by altering the individual, and is a consequence of the historic breeding structure of the population (Dobzhansky 1970). An adaptive trait is the end product of natural selection acting on individuals; i.e., within a specific environment, a trait that confers a fitness advantage to certain individuals within a population (through some combination of increased survival and reproductive success) is selected positively (Hallerman 2003b). That is, individuals possessing that trait produce more surviving offspring per capita than individuals that do not possess it. As a result, over time, the population as a whole consists of more and more individuals with that trait, due to the increased frequency of the relevant alleles.

A trait (i.e., how an individual looks, functions, or behaves) results from the phenotypic expression of a specific genotype within its environment (Falconer and Mackay 1996). The genotype of an individual is determined not only by which alleles that it inherited from its parents (across all genes), but also by which genic arrangements it inherited as well (Lemon and Tjian 2001). Furthermore, there are not only structural genes (portions of the DNA that encode for specific RNA sequences necessary to synthesize proteins), but also regulatory genes (portions of the DNA that control when and to what extent the various structural genes are expressed during the life of that organism) that determine genotype. Control over the expression of structural genes also likely changes depending upon the relative positions of both types of genes within the various genic arrangements that exist among different individuals both within and among populations (Lemon and Tjian 2001). For most traits, there are a large number of different structural and regulatory genes involved in their expression. Selection pressures favor those allelic combinations and genic arrangements whose complex set of expressions results in production of traits that prove adaptive for that individual. Allelic combinations and genic arrangements that provide such a positive fitness benefit evolve as co-adapted gene complexes (Dobzhansky 1948). For example, a correctly shaped fin is produced when a co-adapted gene complex acts by having its set of regulatory genes turn its set of structural genes on and off at the correct time during the development of that individual. Similarly, the time at which an adult salmon chooses to enter the Columbia River for upstream migration is affected by its response to a variety of external stimuli. Those external stimuli trigger that behavior by controlling the expression of a set of genes that have evolved together. That pattern of gene expression is likely the product of one or more co-adapted gene complexes that have been formed over time in response to selection (Templeton 1986).

Range of Columbia River Basin Viewpoints

Although there is reasonable agreement on the fundamental principles associated with adaptation, there are different viewpoints among the scientists within the Columbia River Basin on how adaptation has in fact shaped salmonid populations in the Basin. For example, some scientists believe that the life-history variation observed in Columbia River Basin salmonids reflects the variable expression of a "generalist genotype" in different environments. Others believe that variation represents the specific expression of multiple different genotypes, each the product of an adaptive evolutionary response to past natural selection. There are also differing viewpoints on how declines in salmon abundance and increases in population fragmentation affect the adaptation of breeding populations to current environmental conditions. The role and relative importance of natural selection versus genetic drift and founder effects in determining adaptation is also debated. One view holds that natural selection is the predominant process leading to adaptation and that we cannot predict how genetic manipulation will impact fitness in and adaptation to different environments. Others believe that genetic drift and founding events play a more prominent role, and that active genetic intervention could contribute to recovery. Finally, much of the debate over these issues centers around how quickly adaptation acts to change populations (both historically and currently) and how much human-induced changes in the environment have cancelled out fitness benefits from adaptations to past environments (cf Schramm and Piper 1995).

Body of Evidence

Evidence from Columbia River Basin salmonids:

The Pacific salmon species that inhabit the Columbia River Basin are characterized by extensive life-history variation (e.g., the age at which smolts migrate to the ocean, the age at which adults return to freshwater to spawn, and the extent of their ocean migrations). Many traits have been shown to have a genetic basis, including variation in homing ability (Bams 1976; Quinn 1985; Quinn 1993), migration timing among returning adults (Smoker et al. 1998), fry rheotactic behavior (Brannon 1972), and outmigration timing (Gharrett and Smoker 1993; Smoker et al. 1998). Evidence such as the negative relationship between the distance that hatchery coho salmon are transplanted from their natal stream and relative returns to release sites (Reisenbichler 1988) suggests that life-history variation with a genetic basis reflects local adaptation (Reisenbichler and Rubin 1999).

Coincident with this evidence of a genetic basis for life-history variation and for local adaptive effects, anadromous salmonids also exhibit plasticity in their life histories (Brannon et al. 2002). For example, when steelhead are reared in hatcheries, their diet produces smolts in a single year. Natural-origin steelhead are usually age-2 or 3 when they migrate to the ocean. Hatchery-origin steelhead also return to freshwater to spawn at an earlier age. Chinook salmon exhibit similar alterations in their age of maturity when in hatchery culture. Plasticity in life-history characteristics, particularly when they are exhibited in geographically proximate but environmentally variable conditions, can itself be an inherited local adaptation (Via and Lande, 1985).

Evidence from all salmonids:

A number of studies (reviewed in Taylor 1991c and Waldman and McKinnon 1993) document adaptations and their fitness implications among different salmon species, e.g., alternative life histories among charrs (Skulason et al. 1989) and homing behavior (Quinn 1985; Reisenbichler 1988). Thorpe (1998) summarizes the evidence for adaptation among various salmonids and relates it to stock enhancement, finding that there are numerous reports documenting adaptation within salmonid populations. For example, Sundell et al. (1998) report adaptive differences in various traits involved with parr-smolt transformation between wild and hatchery Atlantic salmon. Simpson and Thorpe (1997) provide evidence for an adaptive link between juvenile Atlantic salmon appetite and seasonal rhythms in food availability. In addition, osmoregulatory ability was shown to vary in an adaptive manner among landlocked and anadromous populations of charr and salmon (Thorpe 1998).

Determining whether life-history variation reflects local adaptation or phenotypic plasticity, as well as evaluating which processes lead to the development of these attributes is not a trivial undertaking. Although rare, successful introductions of Pacific salmon to barren habitats provide an opportunity to understand both the state and process of adaptation. Chinook salmon introduced into New Zealand from California, between 1901 and 1907 colonized their contemporary range in about ten years. Currently, (after approximately 30 generations) the recently established populations exhibit levels of life-history variation comparable to that observed among the North American populations. Quinn et al. (2000) proposed that phenotypic plasticity initially facilitated the observed colonization of multiple river systems, but that subsequently genetic differentiation rapidly occurred in response to natural selection. In support, these authors demonstrated even in New Zealand higher survival was observed for stocks released from their established site than for stocks transferred to a release site (Quinn et al. 2000).

Another example is provided by sockeye salmon introduced from 1951 to 1971 into Frazer Lake (Kodiak Island, Alaska) from three source populations with different life histories – a late-run lake shoreline spawning source, an early-run inlet tributary spawning source, and a late-run outlet spawning source (Burger et al. 2000). Three shoreline locations and four inlet tributaries have become the predominant spawning sites in the colonized lake. Genetic analysis demonstrates that the sockeye population in the lake is subdivided and non-randomly mating. The late-run lake shoreline spawning source was the primary donor for the shoreline spawning sites and the early-run inlet tributary spawning source was the primary donor for the inlet tributary spawning sites. A legacy of the late-run outlet donor source is not apparent (Burger et al. 2000). The varied background characteristics of the donor stocks are believed to have been responsible for providing the essential capabilities for colonizing the lake. Furthermore, the results argue that locally adapted, genetically diverged subpopulations can coexist on spatially contiguous, geographically proximate scales (Burger et al. 2000).

Evidence from other fish species:

Ichthyology texts are replete with examples of adaptations within and among fish species. One well-known example of intraspecific adaptation is the guppy; certain color patterns have been specifically adapted to certain predator faunas (Endler 1978, 1983), providing differential fitness benefits in different environments. In an assessment of adaptation to variable climates, Philipp et al. (2002) used genetically tagged stocks of largemouth bass from different geographic regions to assess the relative reproductive success of native versus non-native stocks in different geographic regions. They found that in each of four cases from Minnesota to Florida, the native stock had greater fitness than all of the non-native stocks of largemouth bass tested. Fitness differences have been observed on a much finer geographic scale as well, i.e., between stocks of largemouth bass from two different tributaries of the Mississippi River (Fox-Illinois and Big Muddy Rivers) within a single state (Philipp and Claussen 1995).

Evidence from other plants and animals:

There are almost limitless examples of adaptations in nature, starting with Darwin's finches in the Galapagos Islands (Darwin 1859). One excellent and well known example of local adaptation (and how to destroy it) was demonstrated by the ibex (Capra ibex). A Czechoslovakian population that went extinct locally was replaced by reintroducing individuals from a neighboring (likely genetically similar) population from Austria (Greig 1979). That population became reestablished and thrived. Some years later, individuals of the same species, but from a population in Turkey (a very different environment) were introduced to that population. Interbreeding was widespread; unfortunately, because the Turkish populations were adapted to a different climate, and their breeding cycle differed, the resulting offspring were born during the winter months and promptly died. The result was that the newly reestablished population was altered genetically, leading to rapid extirpation (Greig 1979).

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There is substantial scientific evidence for local adaptation in Pacific salmon and steelhead in the Columbia River Basin. There is also evidence for phenotypic plasticity, but this evidence does not at all disprove the existence nor discount the importance of genetic divergence and adaptive differences among local populations of these fish within the Columbia River Basin. These two attributes are not mutually exclusive, and in fact, considering them together is likely to be important in designing effective management approaches, including any supplementation efforts. Although chance (i.e., which genotypes were present among initial colonists) is likely an important determinant of initial adaptive value for founded populations, undoubtedly, natural selection has been the driving force behind the historical adaptation among Columbia River Basin populations.

This assessment of the relative importance of the two processes in deriving today's Columbia River Basin salmon and steelhead populations argues for a precautionary approach in designing and using supplementation projects. It is more prudent to assume that historically evolved adaptations have current and future relevance and value than to assume otherwise, even when environmental conditions have been altered. In addition, we cannot currently identify individual selective pressures accurately, nor determine how they interact, much less the ways in which specific environments will change in the future. It would be imprudent to undertake genetic interventions in the hope of producing novel adaptations to the altered environments currently encountered by salmonids in the Columbia River Basin.

The potential for supplementation programs to compromise the adaptive advantages of native salmonid populations located throughout the Columbia River Basin is substantial. We know of no evidence that supports the hypothesis that introducing individuals from a non-native stock would introduce new advantageous adaptations to that stock, even when that native stock's environment has been substantially altered. There is also no evidence to suggest that natural selection will restore adaptations lost through human-induced genetic mixing (e.g., via supplementation efforts) in anything less than an evolutionary timeframe involving many generations. The main issue of concern involving the conservation of local adaptation should center on eliminating all human-induced artificial stock transfers. Although the degree to which past genetic mixing has already erased certain local adaptations within the Columbia River Basin is unknown, eliminating future introductions of non-native alleles and/or genic combinations in all artificial production programs in the Basin should be a clear priority.

Issue II - Genetic Variation

Issue Definition: Genetic variation in a species can be partitioned into two components, the genetic variation among the individuals within each population and the genetic variation among different populations (Wright 1931, 1978). Genetic variation, however, consists not only of the multitude of different alleles encoded in specific genes, but also of the multitude of genic arrangements within the genome as a whole (Dobzhansky 1948; Lynch 1988,1991; Meffe and Carroll 1994). Different species have different levels of overall genetic variation (see Noss 1990), and in addition, that variation is distributed differently within and among populations (see Ryman and Utter 1987). For some species, much of the total genetic variation is present within any single population (e.g., rainbow trout, *O. mykiss*), whereas for other species, different populations vary widely in which alleles or genic arrangements are present or absent (e.g., cutthroat trout, *O. clarki*; Loudenslager and Gall 1980). In either case, within any given species different populations can and do have different levels of genetic variation (see Ryman and Utter 1987; Avise 1994).

The distribution of genetic variation among populations within a species reflects not only that species' evolutionary history (e.g., the pattern of colonization of the habitats within their current range, the level of gene flow among populations over time, the suite of mutations that occurred among various individuals, and the level of differential selection on different populations over time), but also recent changes to their population ecology (e.g., alterations in patterns of historical gene flow, substantial reductions in abundance of mature adults, and major changes to the environment). For this reason the distribution of genetic variation within a species is one source of information used to determine the operational units for management concern, whether they are termed populations, stocks, demes, ESU's, Viable Salmonid Populations, First-order Metapopulations, or something else (Berg 1981; Waples 1991; Nielsen 1995; Grant et al. 1999; Fraser and Bernatchez 2001; Philipp et al. 2002, Brannon et al. 2002).

Maintaining within-population genetic diversity in salmon and steelhead artificial propagation programs depends to a large extent on having sufficiently large spawning populations available to avoid genetic drift and on avoiding strong directional selection for new traits or new adaptations. Maintaining among-population genetic variation in salmon and steelhead artificial propagation programs depends on avoiding the admixture of individuals from different genetic stocks caused by stocking fish from non-native waters.

Range of Columbia River Basin Viewpoints

There is little controversy over the concepts of genetic variation both within and among populations and how they could be affected by fish culture practices. There is, however, a range of viewpoints on the best way to define management units for conservation and recovery. In trying to define the population structure of salmon and steelhead in the Columbia River Basin, the debate centers on how much consideration should be given to the distribution of neutral molecular markers versus functional life-history attributes, as well as to how large a difference is needed for legitimate differentiation.

There are also differing viewpoints on the processes that established the current distribution of genetic variation among Columbia River Basin salmonid populations. One view is that the significant differences in the frequencies of genetic markers among populations are evidence of historical discontinuities in gene exchange among these breeding units. An alternative view suggests that habitat loss has fragmented formerly continuous distributions of these Columbia River Basin salmonid populations, and that the currently observed differences in allele frequencies are attributable to (recent) genetic drift. The implication of the different viewpoints on artificial propagation strategies is substantial; i.e., should broodfish collected from one population be isolated from or intermixed with broodfish from other populations?

Within most, if not all, artificial propagation programs there is agreement on the need for broodstock management practices that maintain extant levels of within-population genetic variation. There is an array of opinions, however, on how detrimental past inattention to broodstock management has been on target and non-target populations.

There is, however, substantial debate over the merits of maintaining the among-population genetic variation. One viewpoint stresses maintaining this variation because empirical evidence within the basin argues that natural interbreeding between distant lineages of chinook salmon (e.g., lower river "fall tule" and upper river spring-run) has not occurred, even though they have been stocked into the same river systems. Another viewpoint believes that there are circumstances (e.g., when rapid changes occur within a local environment) in which inter-stock hybridization should be used to break down co-adapted gene complexes that are currently non-adaptive in that new environment). When these fish would then spawn in the wild, the newly randomized genetic combinations present in this now introgressed genome could be acted upon by the current and future suite of natural selection pressures, thereby providing a better opportunity for adaptation to occur rapidly. The initial fitness cost to the population from that mixing, as well as how much time would be required for that level of adaptation to occur, however, is unknown.

Body of Evidence

<u>Evidence from Columbia River Basin salmonids:</u>

Genetic variation at molecular loci within and among populations of Columbia River Basin steelhead and salmon has been assessed over these species' entire ranges, including detailed reviews of populations in the Basin (cf., Myers et al. 1998; Beacham et al. 1999; Busby et al. 1999; Brannon et al. 2002). Although the levels and patterns of genetic variation are different among these species, substantial genetic differentiation among populations is evident within each of them. Formal analysis of the geographic distribution of most life-history variation is lacking, with the notable exception of the relationship between stream temperature profiles and chinook salmon and steelhead adult and juvenile migration traits in the Columbia River (Brannon et al. 2002).

Steward and Bjornn (1990) reported that although there was indeed evidence for some cases of reduced levels of genetic variability in Columbia River Basin salmonid hatchery stocks, these cases were not overly widespread. The potential for hatchery releases to cause losses of among population genetic variation among Basin stocks, however, is demonstrated by the regional homogenization of lower Columbia River "tule" fall-run chinook salmon populations (Utter et al. 1989) and lower Columbia River coho (Flagg et al. 1995). Unfortunately, because baseline data on the among-population variation prior to the implementation of many hatchery programs is not available, the full extent of its historical loss is unknown (Reisenbichler and Rubin 1999).

<u>Evidence from all salmonids:</u>

A number of studies have shown that salmonid hatcheries outside the Columbia River Basin also have reduced levels of genetic variability compared to wild stocks (Allendorf and Phelps 1980; Ryman and Stahl 1980; Cross and King 1983; Stahl 1983, Vuorinen 1984; Verspoor 1988). Reduced genetic variation in hatchery stocks of Pacific salmon and trout are not uncommon (Allendorf and Phelps 1980, Waples et al. 1990). In addition, feral chinook salmon populations in New Zealand have less variation than their source populations from California (Quinn et al. 1996). Significant year-to-year variation was discovered in Oregon coastal coho hatchery populations, but not in natural populations (Waples and Teel 1990). These genetic changes are attributed to genetic drift due to small broodstock sizes. The negative effects of aquaculture on genetic variability within salmonid populations were summarized by Hutchings (1991), Krueger and May (1991), Utter et al. (1993), and Cloud and Thorgaard (1993). Pacific salmon hatchery populations, however, do not always have lower genetic variation than natural populations (Waples et al. 1990). Recently established sockeye salmon in Frazer Lake, Alaska retain high levels of within population variation and between population life-history variation (Burger et al. 2000). The winter-run chinook salmon supplementation program in the Sacramento River has maintained effective population size by using pedigreed mating, monitored using microsatellite markers (Hedrick et al. 2000a,b). Similarly, mixing stocks of other salmonids has been shown to homogenize them, decreasing the variability among once divergent populations (see Ryman and Uttter 1987; Altukhov and Salamenkova 1990; Skaal et al. 1996).

Evidence from other fish species:

Examples of reduced genetic variation among hatchery stocks were reported for a variety of fish species at the International Symposium on the Ecological and Genetic Implications of Fish Introductions, FIN (Billington and Hebert 1991). Similar concerns were summarized for marine species by Bartley et al. (1995). The Symposium on the Uses and Effects of Cultured Fishes (Schramm and Piper 1995) was filled with examples of reduced genetic variability among hatchery stocks for a variety of freshwater and marine species. Beyond reports that document the occurrence of reduced variability (e.g., Brown et al. 2000), there are a number of examples correlating reduced heterozygosity with reduced survival for a number of different fish species (e.g., Mitton and Koehn 1975; Shami and Beardmore 1978; Mork and Sundnes 1985).

Largemouth bass provide an example of the widespread loss of among population variation over time as a direct consequence of a deliberate stocking program (Philipp and Claussen 1995). In this instance, it is likely that entire stocks of that species across a large part of its southern range have been genetically compromised by the widespread introduction of a different form from Florida.

Evidence from other plants and animals:

In summarizing the theory and data pertinent to the relationship across taxa between genetic variation and fitness, Mitton (1993a,b) concluded that there was overwhelming evidence to support the hypothesis that components of fitness (e.g., fecundity, survival, growth rate, physiological efficiency) decrease as individual heterozygosity decreases (Koehn et al. 1973; Zouros et al. 1983; Kahler et al. 1984a,b; Brotschol et al. 1986). Because few if any non-fish organisms have management programs remotely parallel to hatchery-based supplementation programs, input in that area was lacking.

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It is widely accepted that the conservation of genetic variation is essential for the long-term maintenance of natural populations (Meffe 1986; Gilpin and Soule 1986; Rieman et al.1993). We add that this widespread acceptance includes the conservation of genetic variation within and among populations at both the allelic and genomic levels, but does not include genetic variation among populations that is generated solely as the result of recent human-induced habitat fragmentation and drift.

Simulation modeling (Lacy 1987) has indicated that for artificial propagation programs, genetic drift (due to low Ne of breeding adults) is the dominant cause for the loss of genetic variation within populations. In addition, low Ne values resulting from the use of low numbers of adult breeders can be magnified even further when sex ratios are skewed directly or indirectly, e.g., through the simultaneous mixing of gametes from multiple adults during artificial production activities (Gharrett and Shirley 1985; Withler 1988) or when family lots have unequal representation in the total production of young (Ryman and Laikre 1991; Allendorf 1993; Ryman et al. 1995). Even though many salmonid hatchery programs have historically used low effective numbers of adults as gamete donors to produce hatchery young (Waples and Smouse 1990; Waples and Teel 1990), systematic assessments of the long-term effect on the loss of within-population genetic variation across the Columbia River Basin is not available. It is important to note that genetic variation within a population can also be lost as a consequence of natural selection (see Busack and Currens 1995), and that the rate of genetic change resulting from natural selection increases as the selection pressure increases and is facilitated by a low Ne.

Supplementation programs carry the risk of causing decreases in genetic variation within their target populations (Ryman and Laikre 1991; Waples and Do 1994; Ryman et al. 1995; Duchesne and Bernatchez 2002). That risk results because only a fraction of the adults within the population that could potentially spawn in the wild are used to produce gametes for spawning in the hatchery. As a result, there is always a risk that certain alleles or genic combinations present in the (originally) wild population will not be included in any of the offspring produced in the hatchery. When those hatchery fish are reintroduced to the wild to become part of the year class in combination with those naturally spawned offspring, the frequency of the allele or genic combination that was lost in the hatchery is now (potentially greatly) reduced in the wild. As a result, the likelihood of its being eliminated from future hatchery spawning efforts, as well as from successful natural matings, increases as well. Once an allele or genic combination has been purged from the population as a whole (i.e., both the hatchery and wild components), the possibility for its return through some mutational event is extremely remote.

The question has been raised repeatedly that if heterozygosity is good, then is not more heterozygosity even better? If that were to be the case, then it would be beneficial for almost any population to add additional individuals from another population to introduce new alleles and genic arrangements not previously present, thereby increasing its within population variation (i.e., heterozygosity). The question then becomes, even though heterozygosity is increased as a result of this mixing, does it occur at some expense to that population and/or to the species as a whole? Genetic variation among populations is lost when different populations are mixed (see Ryman and Utter 1987). So, at the species level, any homogenization of the different gene pools that were previously isolated results in a decrease in the among-population genetic variation inherent in that species (Hindar et al. 1991). That scenario is analogous to mixing yellow and blue paint; i.e., the paint that remains is now green, and unless some yellow or blue paint was saved, there is none left, …so if the need for either yellow or blue paint arises, the artist is in trouble. Furthermore, at the population level, additional introduction of new alleles and genic combinations might or might not have negative impacts on the relative fitness of that recipient (now genetically mixed) population in its native environment (Campton 1995), as discussed under Issue V.

Loss of genetic variation, either within populations or among them, clearly can have negative impacts, particularly when the degree of that loss is substantial. In addition, the use of artificially propagated fish to supplement wild Columbia River Basin salmon and steelhead populations can result in the loss of both types of genetic variation. Significant care in implementing appropriate spawning, rearing, and release techniques are needed to decrease the risk of incurring those losses. We would like to stress, however, that even if all recommended hatchery reforms are implemented, it is unlikely that artificially produced fish would be exact equivalents of wild spawned fish; the selection pressures in those two environments will always be different and in many cases, significantly so. As a result, supplementation efforts will always create some risk of losing genetic variation. Any realized reduction of genetic variation within populations of wild Columbia River Basin salmonids (from whatever action) would serve no positive purpose and could have substantial negative impacts (e.g., reduced ability to adapt to changing environmental conditions, reduced ability to fight diseases). In fact, Carson and Templeton (1984) presented evidence suggesting that populations with low levels of genetic variability would be unlikely to respond well to rapidly changing environmental conditions.

Issue III - Domestication

Issue Definition: Domestication is defined as the unintentional selection for traits that affect survival and reproduction in a human-controlled (domestic) environment, i.e., a hatchery (Doyle 1983; Robinson and Doyle 1990). Under domestication, humans control the care and feeding of the target organisms (Hale 1969), and as a consequence, behavior, physiology, and/or morphology becomes altered (Doyle 1983). Domestication selection is often accompanied by a directed, not random, loss of genetic variation within the target population (Busack and Currens 1995).

There are three concerns related to domestication effects with supplementation. The first concern is that domestication selection during hatchery rearing will reduce the fitness of hatchery-reared fish in the wild. The second concern is that if these hatchery fish do spawn in the wild, they will produce fewer smolts than will parents with natural ancestry and perhaps transmit this reduced fitness to their progeny. Finally, selection may act differently on hatchery-origin fish compared to natural-origin fish. For example, even if no selective mortality occurs in the hatchery, hatchery-origin fish are often phenotypically different than wild fish of the same age and life stage. In other words, there could be a genotype by environment interaction, such that a given initial distribution of genotypes results in different phenotypic distributions when placed in the hatchery compared to the wild environment. Because selection only "sees" the phenotype, selection on hatchery fish after release from the hatchery can, in theory, result in a different genetic response from the population than would have been the case had the same selection occurred on a population reared in the wild.

Range of Columbia River Basin Viewpoints

Scientists disagree over the prevalence of domestication in Columbia River Basin salmonid artificial production programs. Some believe that domestication is an unavoidable consequence of rearing under alternative environmental conditions, and as a result that it will always be present to some degree in all hatchery programs. Others believe that it is a rare occurrence, particularly in today's hatcheries, because the salmon and steelhead spend a significant portion of their life cycle in the wild. Scientists also disagree over how domestication selection affects the fitness of the hatchery-origin fish in the wild. Some scientists believe that there is an obligate cost to fitness in the wild that accompanies domestication selection for increased fitness in the hatchery. Others believe that under certain conditions domestication selection can increase both the fitness in the hatchery and fitness in the wild for the same hatchery-origin fish. Some scientists believe that reform of hatchery procedures has eliminated (or at least can in the future) practices that promote domestication.

Some scientists also propose that because the hatchery environment is relatively protected compared to the wild (i.e., egg to smolt survival rates are much higher), selection in the hatchery and, therefore, domestication effects as well, are in fact minimized, not enhanced. Other scientists claim that this assumption is invalid and genetically naïve for several reasons (Busack and Currens 1995). First, mortality of stocked smolts is quite high as well, so that protection from early mortality in the hatchery is basically negated later in their path to maturity and reproduction. Second, domestication selection can occur during the adult sampling phase of gamete collection, and does not require differential survival of more fit individuals within the hatchery environment. Third, if hatcheries are successful in releasing fish from selection pressures normally experienced in the wild (e.g., male-male competition for access to spawning females, mate choice, egg size to gravel size constraints), the resulting shift in the frequencies of surviving genotypes represents selection in and of itself.

Body of Evidence

Evidence from Columbia River Basin salmonids:

Domestication selection within Columbia River Basin salmonids has only been inferred, based on several points. First, many traits have substantial additive genetic variance and respond to directed artificial selection in culture (Tave 1993). Second, there are behavioral, morphological, and life-history differences between hatchery-reared individuals and natural-reared individuals from the same parent stocks (Barton et al. 1986; Olla and Davis 1989; Swain et al. 1991; Maynard et al. 1995; Berejekian et al., 1996). Third, evidence exists that hatchery-origin salmon spawning in the wild produce fewer progeny than their natural-origin counterparts (Reisenbichler and McIntyre 1977; Chilcote et al. 1986; Leider et al. 1990). In addition, natural-origin fish demonstrated lower survival in a hatchery environment than hatchery-origin fish (Reisenbichler and McIntyre 1977).

Evidence from all salmonids:

Morphological, physiological, and behavioral changes resulting from domestication have also been documented in non-Columbia River Basin salmonid populations as well (Vincent 1960; Green 1964; Hager 1964; Moyle 1969; Thomas and Danahoo 1977; Sosiak 1982; Hynes et al. 1981; Bachman 1984; Doyle and Talbot 1986; Woodward and Strange 1987; Jonsson et al. 1991; White et al. 1995). Many of these changes (e.g., excessive surface swimming and increased aggression) result in decreased survival in the wild for juveniles from a number of salmonid species (Johnsson and Abrahams 1991; Mesa 1991; Swain and Riddell 1990, 1991; Holtby and Swain 1992; Riddell and Swain 1991; Ruzzante 1994).

Performance studies on brook trout (Fraser 1981; Keller and Plosila 1981; Lachance and Magnan 1990a,b; Hindar et al. 1991), rainbow trout (Danzmann et al. 1989), and coho salmon (Hjort and Achreck 1982) have shown the negative impacts of domestication once fish are introduced to the wild. Other studies have documented additional domestication impacts on hatchery-origin adults. For example, hatchery-origin males were shown to be less competitive than their natural-origin counterparts in attracting females and spawning with them in the wild (Fleming and Gross 1992, 1993; Chebanov and Riddell 1998; Fleming et al. 2000). In addition, domestication selection was shown to be the cause of changes in a number of important female secondary sexual characteristics (most notably, egg size and number), which could result in reduced reproductive success in the wild (Fleming and Gross 1989; Einum and Fleming 2000a,b; Einum et al. 2002; Heath et al. 2003).

Evidence from other fish species:

Domestication effects have been characterized in other fish species. Most notably, Robinson and Doyle (1990) demonstrated quite substantial phenotypic correlations among behavior and growth parameters for domesticated and wild lines of Tilapia. In addition, Michael Fuhr (The Nature Conservancy, personal communication) has documented that compared to wild largemouth bass *Micropterus salmoides*, the reproductive success of a captive broodstock was significantly greater in artificial hatchery spawning raceways, but significantly lower in natural ponds.

Evidence from other plants and animals:

There are innumerable studies of domesticated plants and animals documenting both performance trait alteration with various levels of domestication - desired and undesired - and a decreased fitness of those organisms to compete in the wild (e.g., Hale 1969; Doyle 1983; Price 1984).

ISAB Consensus Assessment

Domestication selection causes the relative productivity of strains of cultured fish to vary among environments (Doyle et al. 1995). Typically, a strain exhibits superior productivity in its own environment in contrast to its productivity in other environments (Doyle et al. 1995). Because of this documented constraint, and because salmon and steelhead exhibit modifications for many traits when in hatchery culture, it is prudent to anticipate that domestication selection will constrain the benefits of supplementation (e.g., Allendorf 1993; Resienbichler and Rubin 1999; Wang and Ryman 2001; Lynch and O'Hely 2001). Empirical analyses to measure the domestication selection differential for traits within a hatchery, however, are unavailable, as are evaluations of the consequences for fitness in nature for a salmon population following interbreeding with hatchery-origin adults in nature (Campton 1995). The lack of these analyses results from the absence of proper experimental design for Columbia River Basin salmonid hatchery programs. This omission may be remedied by using analyses that track pedigrees among individuals using DNA markers. The usual method to evaluate selection is to maintain a selected line and a reference line, or two selected lines – one selected upwards for the trait of interest and the other downward. The difference between the two lines for a character is a measure of the selection. The challenge to evaluate domestication selection centers around the question of what to use for a control or reference line. Consequently, domestication selection has only been inferred. Ford (2002) discusses in some detail the circumstances under which domestication selection is more or less likely to occur in salmon artificial production programs. To our knowledge, however, there are no studies documenting the absence of domestication selection in Columbia River Basin hatcheries or the absence of negative impacts of hatchery produced fish on the wild populations into which they are introduced.

Parameters that influence whether or not domestication selection would impact a natural population are discussed in the DRAFT – Benefit-Risk Assessment Procedure for Washington Department of Fish and Wildlife Artificial Propagation Programs (November 30, 2000 revision). Considering these parameters when designing a supplementation project probably would reduce the perceived near-term benefits from supplementation, but might avoid collapse of the population if the concerns about domestication selection are realized. One of these parameters is particularly relevant to this issue, and as a result, the discussion of that parameter in the Draft document is quoted here:

> *"Gene flow between hatchery and wild environments (or proportion of composite population in each environment assuming high gene flow);* Populations connected by gene flow that face different selection regimens have been modeled for both the case of traits controlled by a single locus (e.g. Levene 1953, Karlin and McGregor 1972) as well as traits controlled by many loci (e.g. Barton 1983, Phillips 1996, Lythgoe 1997). The results of these models suggest that high levels of gene flow between hatchery and natural environments (as would be typical for most integrated projects) will make it unlikely that a composite population will become genetically differentiated into two distinct components. This suggests that the continual infusion of wild fish into hatchery broodstocks should at least slow the domestication process. When gene flow occurs in both directions (wild fish into the hatchery and hatchery fish into the wild), however, these models suggest that the potential exists for a composite population to become adapted to the hatchery, rather than remaining adapted to the wild. At this time, it appears impossible to predict the outcome of such composite systems, and no controlled empirical studies have been conducted to address this question in salmonids. For other organisms, Wright (1977) reviewed laboratory experiments involving disruptive selection in *Drosophila* and *Tribolium,* and concluded that the rate of population divergence was negatively correlated with the rate of gene flow between environments. All these experiments were conducted in highly artificial settings. Rice and Hostert (1993), in their review of the literature on attempts at mimicking the speciation process in the laboratory, found considerable experimental evidence demonstrating a relationship between gene flow in different environments and the degree of population divergence under disruptive selection. A reasonable course of action, therefore, to manage the risk of domestication may be to ensure that a large majority of the composite population is naturally propagated."

Issue IV - Inbreeding Depression

Issue Definition: Inbreeding depression (IBD) is defined as the loss in fitness in the offspring of parents that were too closely related (see Fisher 1965; Thornhill 1993, Hallerman 2003c). The loss in fitness is caused by the unmasking of deleterious recessive alleles (e.g., in humans, the alleles for sickle cell anemia or for cystic fibrosis). When the same deleterious recessive allele is inherited from both parents (i.e., the offspring is homozygous at that gene), the fitness of that individual is reduced (sometimes to zero) because the phenotype of that genotype is deleterious (sometimes lethal). The chance of an individual getting two copies of any given deleterious recessive allele increases for offspring that are the product of matings among close relatives. The probability of IBD occurring increases as both the level of prior inbreeding in the group and the genetic load (the number of deleterious recessive alleles in the group) increases (see Gall 1987).

IBD is often manifested as a decrease in fitness-related traits such as viability, growth rate, and reproductive success (Kincaid 1976a,b). IBD also can be manifested as an increased frequency in certain abnormal morphological characteristics such as deformities in spine, jaws, or fins, undeveloped gonads, vision impairment, etc. (Aulstad and Kittleson 1971). Hatchery programs that use hatchery-origin returning adults as gamete donors for producing hatchery offspring are also at increased risk of experiencing IBD (Leary et al. 1987). The risk of IBD increases as the absolute number of adults used for gamete donation decreases, as the number of generations of using hatchery-origin returning adults as gamete donors increases, and as the variation in size of the family lots produced in the hatchery increases. It should be stressed, however, that any population (hatchery-origin or natural-origin) has the potential to experience IBD if the Ne is sufficiently small.

There are a number of questions concerning risks of IBD in Columbia River Basin supplementation efforts. First, how inbred are the hatchery-origin fish relative to natural-origin fish? Second, will mating in the wild between two hatchery-origin adults produce progeny that suffer from IBD? Finally, are there natural populations that are currently suffering from IBD because of low adult abundance?

Range of Columbia River Basin Viewpoints

Differences of opinion exist over the prevalence of IBD in wild or hatchery populations of Columbia River Basin salmon and steelhead, and whether or not supplementation programs elevate the risk of IBD. Some believe it is an actual or at least clearly potential problem, particularly in hatcheries (Allendorf and Ryman 1987). Others do not believe that it is widespread among Basin hatcheries, and even if that were so, that hatchery reform will solve it. Some believe that in natural populations IBD could lead to population level (and maybe even species level) extinctions. Others believe that for the IBD to get that bad, numbers must get so low that extinction would result from demographic catastrophes first; i.e., it is most important to keep numbers of individuals high regardless of their genetic makeup (see Hobbs and Mooney 1998).

Body of Evidence

<u>Evidence from Columbia River Basin salmonids</u>:

There are no completed analyses assessing the level of IBD in Columbia River Basin salmonids, but investigations are underway, and there are some relevant reports. Although Steward and Bjornn (1990) reported that there was little evidence for "extensive inbreeding among hatchery stocks of Pacific salmon used for supplementation", morphological abnormalities observed among hatchery-produced offspring suggest that inbreeding depression may be occurring in some instances (Swain et al. 1991; Maynard et al. 1995). The extremely low numbers of returning adults of Snake River sockeye (Flagg et al. 1995) forced construction of a captive broodstock that very likely experiences some IBD relative to the original wild stock.

Evidence from all salmonids:

Kincaid (1995) summarized what was known about the breeding history of salmonid broodstocks used across the United States. Good historical records were lacking for many of the stocks currently used as broodstock. Beyond that, there was a clear history of past and current inbreeding in a number of stocks. Even though he could not assess directly the occurrence of IBD, he did emphasize its likelihood and the need for much closer genetic monitoring of variation within broodstocks. Inbreeding depression has, however, been demonstrated in a number of cases for rainbow trout and some other salmonids (Ryman 1970; Aulstad and Kittelsen 1971; Kincaid 1976; Kincaid 1983; Gjerde 1988).

Evidence from other fish species:

Considering all fish species, the evidence for IBD is fairly extensive and was summarized by Waldman and McKinnon (1993). These authors state "In fishes, inbreeding depression has been detected in every species for which published data are available…." They go on to add, "The magnitude of inbreeding depression (among fishes) is especially notable given that most studies have been conducted on salmonids, which are derived from a tetraploid ancestor." Concerns over the potential for IBD are particularly acute for artificial production programs that are aimed at supplementing depressed populations of listed species (e.g., razorback suckers, bonytail chub, pallid sturgeon), because access to numbers of adults is often very limited. Extreme efforts are being used in some federal supplementation programs to avoid IBD (Williamson 1994).

Evidence from other plants and animals:

Considering all organisms, evidence for IBD is abundant with the exception of those organisms that self fertilize and those that have developed specific mating systems designed to promote inbreeding (Waser et al. 2000). A survey of numerous examples of IBD across taxa is presented in Thornhill (1993). To illustrate the relevance of IBD, a number of high profile conservation programs have struggled to counteract its negative effects (e.g., programs to conserve Florida panther, American condor, black rhinocerous).

ISAB Consensus Assessment:

Because IBD has been detected in the offspring of matings among related individuals for most animals and plants where data exist (Frankham 1995), IBD is a real concern for captive and integrated populations. It has also been shown that IBD can also be severe in natural populations (Frankham 1995). Because inbreeding increases as the number of breeding adults decreases, IBD only becomes a substantial risk for those wild populations that currently have few returning adults or recently went through such a population bottleneck. Redfish Lake sockeye is such an example (Brannon et al. 2002). Unfortunately, when hatchery programs use hatchery-origin returning adults as gamete donors for producing the next generation of hatchery offspring, the risk of IBD increases (Allendorf and Leary 1988).

Although no natural stocks have been reported to exhibit obvious signs of IBD, it is certainly possible to have the level of inbreeding within a given Columbia River Basin salmon and steelhead population increase to the point of exhibiting IBD. Because the survival of individuals that suffer from IBD is often quite low, however, field observations may not provide us with an accurate assessment of the true incidence of IBD in nature. Those natural populations at the greatest risk for IBD are those that have recently become severely depressed in numbers, ones for which entire year classes of offspring may have resulted from only a few parents.

Unfortunately, those populations are also the ones for which large-scale supplementation is often recommended. Artificial propagation, particularly for fecund organisms like fish, can produce large numbers of highly related individuals that, if stocked, could swamp the few remaining wild-spawned fish in target populations. That scenario, in which mate choice options for that generation of individuals may be limited to for the most part only close relatives, would exacerbate inbreeding problems, not help solve them.

The risk of initiating IBD problems within a naturally spawning population increases when hatchery-produced offspring are introduced into a wild population (Ryman and Laikre 1991; Waples and Do 1994; Ryman et al. 1995; Duchesne and Bernatchez 2002). The potential for supplementation programs to cause IBD depends on the following factors:

1. Source of adults donating gametes. If broodstock adults were collected from the wild and spawned artificially in the hatchery, unless that source population is already highly inbred, the risk that two individuals are closely related is low. Having some or all of the adults that donate gametes be hatchery-origin individuals, however, increases that risk. The level of risk depends upon the history of the hatchery broodstock. If that broodstock was produced through generations of using only hatchery-produced fish as gamete donors, the potential for that broodstock to be already inbred to some degree could be substantial. In addition, if eggs were collected from only a few redds, as may be the case for some captive broodstock programs, a substantial proportion of the reared offspring could be sibs or half sibs.

2. Number of adults donating gametes. Clearly, the fewer the number of adults collected for gamete donation, the fewer the family lots released into the wild, and the greater the chance that any two individuals that return as adults will be closely related. From this standpoint, the use of as many different gamete donors as possible during hatchery production efforts is desirable, even if that means reducing the number of eggs from each family lot produced.

3. Ratio of released hatchery-origin smolts to natural-origin smolts. The risks of causing IBD within a naturally reproducing population as a result of introducing hatchery-origin offspring increases as the number of those individuals released to the wild increases relative to the number of natural-origin offspring already in the wild. When those fish (both natural-origin and hatchery-origin) mature and return

> to the river to spawn, if the numbers of returning hatchery-origin adults are substantially greater than those of natural-origin adults, by chance, most matings in the river could consist of two hatchery-origin adults. If those hatchery-origin adults are closely related, the offspring of those matings could suffer from IBD, expressed either as reduced survival of that year class at any point in their life history or as reduced reproductive success, if and when they return as adults. In either case, the fitness of the naturally spawning population has been decreased.

Besides simply maximizing the Ne of hatchery broodstocks, it is also very important to proceed cautiously with any proposed introductions for the offspring of those broodstocks. Rushing to get a flood of fish into the river could have substantial long-term negative impacts on the target population by introducing huge numbers of closely related individuals.

Issue V - Outbreeding Depression

Issue Definition: Outbreeding depression (OBD) is defined as the loss of fitness in the offspring of parents that were too distantly related (Templeton 1986; Hallerman 2003d). The OBD phenomenon is usually projected as a consequence of the introduction of some non-native stock into an extant native population in its native habitat. The accompanying loss in fitness among offspring resulting from the introgression of these two populations in that environment can be caused by either of two processes or their combination (Templeton 1986). The first process is the response in adaptive value to the introduction of new alleles (at a variety of loci) from the donor (non-native) population that are maladaptive in the recipient population's environment. The second process is the breakdown in co-adapted gene complexes, which are combinations of structural and regulatory genes in specific arrangements within the genome that had evolved within the native stock in response to the selection pressures inherent to its native environment.

The concerns over OBD stem from the potential for impact on the fitness of the target population when hatchery-origin adults return and spawn with natural-origin adults. OBD can occur as a consequence of importing an inappropriate non-target stock to be used as sole broodstock in the artificial production process. It is also possible for OBD to be realized when the hatchery broodstock has been propagated in the hatchery over a number of generations, allowing genetic differentiation from its wild source stock to occur. Although most concerns center around the fate of the offspring produced from natural-origin and hatchery-origin crosses in the wild, OBD can occur directly within supplementation programs if multiple populations were used as a composite source for a single broodstock (each with a different set of co-adapted gene complexes). This could happen by inadvertently (or purposefully) collecting broodfish from more than one stock. An example of that scenario is collecting fall-run and summer-run chinook at the east ladder at Wells Dam, mating them, and using the progeny in the Methow or Similkameen/Okanagon summer-run chinook supplementation programs.

Range of Columbia River Basin Viewpoints

There is substantial divergence in opinion among Columbia River Basin scientists on how great a risk OBD represents for artificial production in general and more specifically for supplementation programs within the Basin. Some scientists argue that the risks from OBD are minimal (cf. Schramm and Piper 1995). This argument is based on several points. First, salmonid populations within the Basin are highly dynamic, with certain levels of historical straying documented among certain watersheds; i.e., it is suggested that each of the Basin salmonid species likely exists as one or a series of metapopulations, not as discrete individual populations. Second, previous stocking efforts over the last hundred or so years have already extensively mixed whatever native stocks existed historically. Third, human impacts on the Basin have so drastically altered the environment and the selection pressures acting on today's fish populations, that adaptations that evolved before those impacts occurred are reasonably irrelevant today. Fourth, in light of the rapid changes of the Basin environment, it may in fact be advantageous for the resident stocks to have their genetic variability artificially elevated through such introductions, thereby allowing natural selection to "redefine" the optimal genotypes of the future.

Other scientists argue that the risk of OBD is perhaps the greatest risk posed by any artificial propagation program, including a supplementation program that uses anything but native fish as broodstock (cf. Schramm and Piper 1995). This argument is based on several issues. First, because of the diversity of habitats across the Basin (and as a correlate, the variety of selective pressures), local populations have become adapted to local environments, similar to local populations of most if not all other species. Furthermore, although there is straying among salmon populations, there is still evidence for substantial levels of divergence among populations within each of the salmonid species extant in the Basin (Utter et al. 1993). Even though Basin salmonids may exist in a metapopulation structure, there is still a multitude of those structures that are differentiated from each other, i.e., there is no change in the argument for conservation of individual stocks, just in how they are organized internally, and what they are called. Second, even though there have been many salmonids stocked throughout the Basin, molecular genetic analyses still show distinct patterns in the distribution of genetic variation (Utter et al. 1993). As a consequence, the assumption that historical levels of among population variation have already been lost through this mixing is not only unsubstantiated, but unlikely. Third, even though humans have altered a great deal of the Basin environment, it is unclear how that activity has affected those selection pressures that may have the greatest impact on driving the evolution of fitness traits. The assertion that historically evolved adaptation may be irrelevant to the present Columbia River Basin environment is entirely speculative. Finally, even if important selection pressures have changed rapidly in response to human activities, a number of scientists believe that having the new selection pressures act on individuals with historically adapted genotypes (i.e., individuals with extant co-adapted gene complexes) will result in more rapid and successful adaptation than having them act on individuals with genotypes resulting from the mixture of different stocks. That is, there is no evidence to support the assumption that natural selection will in fact quickly "redefine" acceptable genotypes for the future when the starting point contains already disrupted co-adapted gene complexes.

Body of Evidence

Evidence from Columbia River Basin salmonids:

There have been a number of arguments made for the existence of OBD in Columbia River Basin salmonids (Emlen 1991; Waples et al. 1991; Gharrett and Smoker 1993), but these have been based on little Columbia River Basin-based empirical data. Reisenbichler and McIntyre (1977), however, did demonstrate that steelhead of pure wild ancestry had better survival in streams than did steelhead with either hatchery or hatchery X wild ancestry; the opposite was true for those steelhead when held in the hatchery environment.

Evidence from all salmonids:

OBD was suggested as the likely mechanism driving an observed decrease in adult return rates among inter-race crosses of pink salmon (Gharrett and Smoker 1991; Gharrett et al. 1999). Because these two races (odd and even year forms) live within the same river systems, presumably with identical environmental conditions across time, these authors concluded that the observed OBD is most likely the result of disruption in co-adapted gene complexes.

Studies on steelhead in western Washington (Leider et al. 1990; Chilcote et al. 1991; Campton et al. 1991) also demonstrated reduced reproductive success in the wild of returning hatchery-origin adults versus returning natural-origin adults, indicating the potential for OBD in interbred offspring. OBD in response to stocking was one potential reason given for the loss of native lake trout reported in an Ontario system (Evans and Willox 1991). Danzmann et al. (1999) reported interaction between genes for thermal tolerance for rainbow trout, providing evidence of potential multi-gene complexes in salmonids.

Evidence from other fish species:

Philipp et al. (2002) used genetically tagged individuals to assess the relative growth, survival, and reproductive success of supplemented and unsupplemented stocks of largemouth bass over several breeding seasons. Supplemental stocking of native Illinois fish with individuals from different geographic regions resulted in the formation of an introgressed population that had genetic contribution from all stocks. That supplementation of the native Illinois stock with non-native individuals of the same species clearly resulted in substantial OBD. The native Illinois (unsupplemented) stock contributed over twice as many genes to successive generations as did the introgressed (supplemented) stock; i.e., supplementation caused a greater than 50% reduction in the relative fitness of the recipient (native) stock. In addition, Cross (2000) provides a general summary of the evidence for the genetic implications of translocations among freshwater fishes in Western Australia.

Evidence from other plants and animals:

Although Waldman and McKinnon (1993) reported ten years ago a lack of data documenting OBD in fish and other ectothermal vertebrates, even then there were no studies showing that OBD did not exist. Most of the early empirical evidence for OBD came from studies with Drosophila (Dobzhansky 1970) plus a few other organisms (Endler 1977; Templeton 1986; Barrett and Kohn 1991). A number of recent empirical studies, however, across a wide array of taxa firmly establish OBD as a real phenomenon throughout nature (e.g., Waser and Price 1994; Fischer and Matthies 1197; Edmands 1999; Aspi 2000; Fenster and Galloway 2000; Keller et al. 2000; Palmer and Edmands 2000; Waser et al. 2000).

ISAB Consensus Assessment

Outbreeding depression, as a byproduct of supplementation, is a potential threat to Columbia River Basin salmonids. We know of no evidence that supports the hypothesis that introducing individuals from a non-native population would increase the fitness of a native population, even when that native population's environment has been substantially altered. Although the degree to which past genetic mixing has already reduced the fitness of some Basin hatchery products is unknown, actions to eliminate future introductions of non-native alleles and/or genic combinations in all artificial production programs in the Columbia River Basin should be a clear priority.

Emlen (1991) developed a model to calculate the loss in fitness incurred as a result of outbreeding depression, and he applied that model to salmon supplementation. The model predicted that OBD is indeed a substantial risk. Based upon those predictions coupled with the empirical data from the large number of recent studies that have been published demonstrating OBD in a variety of species of plants and animals (including some with fish), the ISAB concludes that supplementation can indeed present a significant OBD risk to those wild populations receiving hatchery outplants. In fact, of all of the various relevant genetic issues associated with supplementation, we believe that OBD may provide the greatest potential genetic risk for Columbia River Basin salmonids. Using a broodstock that has all or some individuals that originated from a non-native genetic stock (i.e., one that contains alleles and/or genic combinations not present in the recipient stock targeted for supplementation) presents that risk. Following the broodstock selection recommendations outlined here for supplementation programs would reduce that risk.

Section 4. Quantitative Expectations of Supplementation

Previously, Cuenco (1994) used computer simulations to model the demography of a supplemented system. Goodman (2002) has developed a mathematical matrix model of supplementation that allows mathematical deduction of the essential properties of the system.

In Goodman's model the aggregate productivity and population composition of the supplemented population depend on intrinsic biological parameters of the stock in its environment, on policy constraints, and on management control variables. The two critical biological parameters are the two different per-generation replacement rates, i.e., when a female reproduces in the hatchery and when one spawns naturally. Possible management actions include limitations on the rate of taking natural-origin adults for spawning broodstock, limitations on the rate of taking hatchery-origin adults for broodstock, limitations on the fraction of hatchery-origin adults allowed on the natural spawning ground, and stipulations on the selectivity of the harvest between naturally-origin and hatchery-origin fish. The two broodstock mining rates and the harvest selectivity also constitute management controls.

In the notation of Goodman's model the necessary terms are:

Nww(t) the number of naturally spawning fish in generation t that grew from naturally spawned eggs

Nwa(t) the number of naturally spawning fish in generation t that grew from eggs spawned in the hatchery

Naa(t) the number of fish used as hatchery broodstock in generation t that grew from eggs spawned in the hatchery

Naw(t) the number of fish used as hatchery broodstock in generation t that grew from naturally spawned eggs

Rw the intrinsic replacement rate of a natural spawning generation [(eggs per female) times (egg to smolt survival of naturally spawned fish) times (smolt to adult survival of naturally spawned fish)]

Ra the intrinsic replacement rate of a hatchery spawning generation [(eggs per female) times (egg to smolt survival in the hatchery) times (smolt to adult survival of hatchery-reared fish in nature)]

F the fraction (after harvest) of the adult run of fish grown from naturally spawned eggs that is removed for broodstock

Fa the fraction (after harvest) of the adult run of fish grown from hatchery spawned eggs that is removed for broodstock

H the fraction of the adult run of fish grown from hatchery spawned eggs that is taken in harvest

s the harvest selectivity, as a fraction between 0 and 1, i.e., the fraction (before broodstock removal) of the adult run of fish grown from naturally spawned eggs that is taken in harvest: (1-s) times H

These terms interact to constitute a salmon or steelhead life cycle, integrated between hatchery and natural spawning in a supplementation program (Figure 4.1).

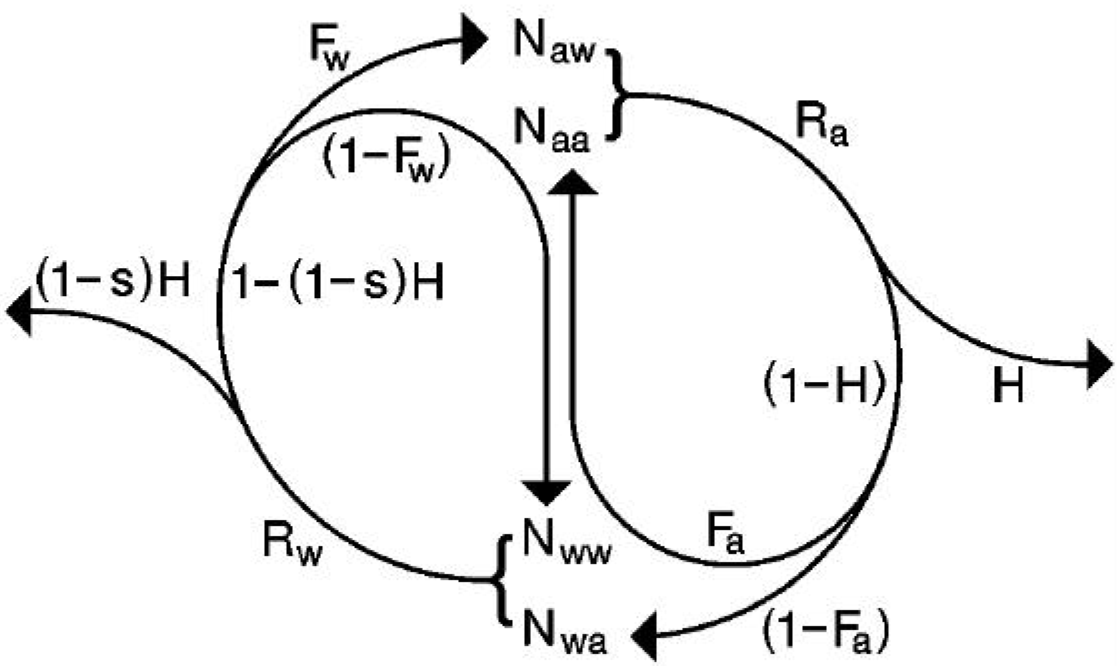

Figure 4.1. Diagrammatic representation of the relationship of intrinsic per capita production, policy constraints, and management control variables when hatchery and natural salmon and steelhead populations are integrated in a supplementation program.

The mathematical relationship among these variables in determining the long-term growth rate and composition of the population is captured in a single matrix equation. A computer implementation of this equation is available on the web at www.esg.montana.edu, and allows one to explore specific scenarios.

With the two replacement rates (Ra and Rw), the two broodstock mining rates (F and Fa), and the harvest selectivity (s) all fixed, there is only one value for the harvest rate (H) that is sustainable. When this level of harvest is realized, the achieved fraction of naturally spawned adults on the natural spawning grounds is fully determined. Thus, for a given stock, with a set hatchery replacement rate and a set natural spawning replacement rate, particular policy constraints (such as limitations on the rate of mining broodstock from hatchery-origin or natural-origin fish, or limitations on the fraction of hatchery-origin fish on the spawning grounds) may or may not be achievable. Similarly, targeted harvest rates may or may not be sustainable, depending on the numbers.

Not all of the actual programs we reviewed specified quantitative objectives or constraints. Of those that did, many, in fact, were not able to meet their objectives. Few programs collected the data necessary to estimate the input parameters for Goodman's model, but of those that did, model results indicate that a substantial fraction of these programs would not be able to meet their objectives.

The genetic effects of supplementation have also been modeled (see below). The analysis of genetic effects of captive propagation in general occupies an enormous literature. There are two distinct classes of genetic effects of supplementation, small-population effects, and evolutionary effects.

Small-population genetic effects of hatchery production result from using too few parents per generation, which increases the potential for genetic drift, fixation of deleterious recessive alleles, the occurrence of inbreeding depression, and the accumulation of deleterious mutations. We believe that these small-population effects can be minimized by good hatchery management. Our recommendations for hatchery practices to minimize this class of genetic effects are given in the executive summary and section 8 of this report.

The second class of genetic effects involves the evolution of adaptations to the conditions of captive propagation and to the post-release consequences of captive rearing. Because natural selection is a universal natural process, adaptation to the altered environment associated with captive propagation is inevitable. It is the general experience in animal breeding that deliberate directional selection for a fitness-related trait leads to erosion of correlated fitness-related traits. For this reason, it is to be expected that natural selection for adaptations to the artificial conditions of the hatchery-spawning phase of the supplementation cycle (including the post-release component) will lead to reductions in the adaptation to the natural-spawning phase of the supplementation cycle.

This phenomenon has been commonly observed, i.e., the poor natural spawning performance of domesticated conventional hatchery stocks. Conventional hatchery stocks, however, are subject only to the unidirectional selection associated with domestication. By contrast, in an integrated breeding program, where there is rapid exchange of genes between the hatchery-spawning and natural-spawning phases, which is a feature of supplementation, there will be countervailing selection pressure during the natural-spawning phase to maintain natural-spawning fitness. It is for this reason that we may reasonably expect that supplementation might cause less extreme domestication and, therefore, less damage to natural-spawning fitness than conventional hatchery programs. Clearly, however, it cannot be concluded that supplementation would cause no deterioration in natural spawning fitness.

The effects of supplementation on the natural-spawning fitness of a population are a critical matter. Supplementation is already being proposed and implemented for some weak wild stocks. In addition, any resulting depression of natural spawning fitness in a supplemented population will persist for some number of generations after the supplementation ceases. Taken together, these issues raise the specter that supplementation might convert a weak but self-sustaining population to one whose existence is dependent on continued supplementation. That outcome runs counter to the assumption that supplementation, as a conservation measure, would be both effective and harmless as a temporary means to maintain the numbers (and perhaps harvest) of a weak wild population, while habitat problems are being rectified.

The historical lack of adequate monitoring and experimental design leaves the empirical record of fitness changes under supplementation (with integrated breeding and local broodstock) inconclusive. This lack of empirical evidence puts more weight, at least for the moment, on the theoretical modeling of the fitness changes that should be expected under supplementation.

These theoretical models include 1-locus 2-allele classical genetic models of selection in the hatchery and natural spawning phases, respectively (Reisenbichler 1984; Byrne et al. 1992; Harada 1992), standard quantitative genetics models (Lande 1976; Lande and Arnold 1983; Roff 1997) quantitative genetics models for traits that are conditionally deleterious in the respective hatchery and natural environments (Hard 1995b; Adkison 1995; Lynch and O'Hely 2001; Ford 2002), and a quantitative model assuming coadaptation of traits (Emlen 1991) in the hatchery and natural spawning phases. These models draw on a more general literature about models of selection in a spatially or temporally subdivided population (Bulmer 1985; Slatkin 1985; Karlin and McGregor 1972; Kawecki 1994; Holt and Gomulkiewicz 1997; Kawecki et al. 1997; Kirkpatrick and Barton 1997: Lythgoe 1997).

Goodman (2002), using the framework of the matrix demographic model, developed an evolutionary analysis without assuming an explicit genetic mechanism. Instead, this model identifies the phenotype at selection equilibrium as an evolutionarily stable strategy (ESS) in a fitness set representation of the trade-off between hatchery fitness and natural spawning fitness. Goodman's extension of the matrix model to represent response to selection requires one more term, quantifying the potential negative correlation between adaptations that increase biological performance in a hatchery breeding life cycle (Ra) and those that increase biological performance in a naturally spawning life cycle (Rw).

Goodman's model for selection equilibrium allows mathematical solutions of considerable generality. Solutions for specific scenarios assuming a linear trade-off between Ra and Rw can be obtained at the same website with the demographic model.

The salient results of the modeling are:

1. Ongoing supplementation can be expected to increase the potential for harvest, and to increase the size of the naturally spawning population

2. The increased population size and any resulting increased harvest attributable to supplementation alone will likely not persist after the termination of supplementation.

3. If habitat improvements are achieved in the interim, these may allow a sustained increase in population size or productivity, but if so, this could have been realized even without supplementation.

4. In a population not subject to genetic drift or inbreeding depression, supplementation cannot give rise to selection that increases the natural spawning fitness. Genetic drift and inbreeding depression are not expected to be problems in populations that are sufficiently large or receive a minimal amount of natural immigration

5. Although supplementation can give rise to selection that decreases the natural spawning fitness; whether it does so, and to what extent, depends on the particular magnitudes of the parameters including the starting hatchery and natural spawning replacement rates, the broodstock mining rates, the harvest selectivity, the degree of the negative correlation between natural spawning and hatchery spawning fitness.

6. All other things being equal, the probability and extent of depression of natural spawning fitness evolved under supplementation will increase with the broodstock mining rate, with the harvest rate, and with an increasing proportion of fish of hatchery spawning origin in the adults taken for broodstock.

7. A supplementation protocol that takes only fish of naturally spawned origin for broodstock would protect the population against runaway domestication selection, and in a plausible family of scenarios will prevent the natural spawning fitness from being reduced by more than 50%.

8. A supplementation protocol that takes some hatchery-origin fish as broodstock can give rise to selection that depresses naturally spawning fitness by more than 50%, can give rise to runaway domestication selection. This effect can occur as an abrupt catastrophic transition as the broodstock mining rate of hatchery spawned fish crosses a critical threshold (which is scenario specific).

9. At present, little is known empirically about the magnitude of the any negative correlation between natural-spawning and hatchery-spawning fitness in actual salmon populations. Nevertheless, modeling shows that this quantity has a large influence on the probability and magnitude of natural-spawning fitness depression in supplementation.

The implications of the modeling analysis are that, for a wild population that is not so small as to be on the brink of imminent extinction or at risk of genetic drift and inbreeding depression, supplementation offers no conservation benefit, and it poses some conservation risk. Supplementation offers the potential for some harvest benefits, but harvest increases the conservation risk even further. The potential harvest benefit of supplementation is smaller than the harvest potential from propagation of a pure hatchery stock.

The theoretical demonstration of risks of supplementation to natural-spawning fitness suggests that the policy to treat supplementation as experimental is prudent, and argues for more and better monitoring of such experiments to generate a robust empirical record.

Section 5. Data Needs and Experimental Designs to Evaluate Supplementation

The objectives of supplementation- *to maintain or increase natural production while maintaining the long-term fitness of the target population, and keeping the ecological and genetic impacts on non-target populations within specified biological limits* -requires performance indicators (response variables) in three areas: 1) target population production, 2) target population long-term fitness, and 3) non-target population impacts. The appropriate performance indicator for target population production is the abundance of natural-origin and hatchery-origin adults and the realized productivity (recruits per spawner, Rw and Ra) for the natural and hatchery population components. Appropriate performance indicators for long-term fitness include the productivity of the integrated natural population following supplementation (Rw) contrasted to productivity in unsupplemented reference populations and estimates of life-history traits that are believed to contribute to fitness (e.g., fecundity, adult population age structure, length and weight, run timing, and spawn timing; see explanatory variables below). If standards are established for these performance indicators, achieving or failing to achieve the standards could provide a mechanism to evaluate supplementation. The following section identifies the data requirements to develop these performance indicators.

It is essential that all current and future supplementation programs be required to collect the data that are needed to assess the production dynamics of the target population. At a minimum this effort should involve estimating the abundance of the adult spawning population, enumerating separately those adults originating from naturally spawning adults in the previous generation (referred to as NORs: Natural-Origin Recruits in Busack et al. 1997, and Ames et al. 2000) and those originating from hatchery production (referred to HORs: Hatchery-origin Recruits). Also important would be a measure of the productivity (adult recruits per spawner) of the naturally spawning (Rw) and hatchery spawning (Ra) population components. How these parameters are used to evaluate specific attributes of different supplementation programs may depend on the goals of those programs. In some circumstances the parameter estimates themselves may be sufficient, and in others contrasts of parameter trend lines in target populations to reference populations will be required. For example, if a hydrosystem BiOp RPA requires a specific lambda (a parameter nearly equivalent to Rw), then these parameter estimates could be used to calculate that performance indicator. Similarly, the Council's FWP anticipates a harvest opportunity from some of the supplementation programs. Achieving these FWP goals is a function of these parameters, and they can be used to assess the likelihood of meeting program objectives. In other circumstances supplementation could be providing a benefit even though population abundance is not increasing. In those cases, supplementation could be reducing the rate of decline. For this type of evaluation, some form of contrast to reference populations is critical. Criteria for success will depend on the goals of individual programs.

Parameters Needed to Assess the Demographic Consequences of Supplementation

The parameters required to assess the production dynamics of supplementation (based on the Goodman model) are defined above. Obtaining the data needed to estimate these parameters, however, can be difficult and expensive. The text below describes these parameters, required data, and concerns related to collection of data. In the notation below, the letter "**w**" designates fish produced naturally and/or it designates a natural environment, and the letter "**a**" designates fish produced in a hatchery and/or it designates a hatchery environment.

Nw(t) designates the number of naturally spawning fish in generation (t) that were produced from naturally spawned parents (i.e., typically unmarked). Data are required to estimate the total population size of natural spawners by stream (or spawning locale), age, and sex. Sampling designs must define the confidence level desired, because high levels of confidence will require extensive sampling efforts. For example, population size by age and sex usually requires sampling for a minimum of six categories in multinomial sampling. While it is not necessarily required, the fecundity by population and age/size categories should also be estimated because it may differ with environmental and genetic background.

In the model, naturally produced fish may subsequently spawn in the natural population (i.e., parameter **Nww(t)**) and some may be removed for broodstock in a hatchery (i.e., parameter **Naw(t)**).

Na(t) designates the number of hatchery origin fish in generation (t) that were produced by hatchery-reared parents (i.e., may be identifiable by mass marking). Data are required to estimate the total population size of returning hatchery fish, including the sampling efforts as defined for **Nw(t**).

In the model, hatchery-produced fish may subsequently spawn in the natural population (i.e., parameter **Nwa(t)**) and some could be used as broodstock in a hatchery (i.e., parameter **Naa(t)**).

For each of the four potential population segments (**Nww, Naw, Nwa, Naa**) estimates of numbers by age and sex categories should be maintained to examine sampling biases. In addition, care must taken as to when sampling and removals occur.

Fw is the fraction of the adult run of fish (after harvest removals) grown from naturally spawned eggs removed for broodstock. Note that **Fw** is expressed as a fraction of the total return of naturally-produced fish in a year, but it may not accurately represent the fraction of the effective spawning population if pre-spawning mortality or unaccounted mortalities occur in the natural population.

Fa is the fraction of the adult run of fish (after harvest removals) grown from hatchery spawned eggs removed for broodstock. As above, **Fa** may not be representative of the effective spawning population of hatchery returns, particularly if the reproductive potential of the hatchery-produced fish is reduced in natural environments.

H designates the portion of the hatchery population removed by harvest (i.e., **Ha**). Fishing mortality on naturally produced fish is accounted for through the parameter "**s**", the **harvest selectivity** relative to **H**. The fraction of the adult run of naturally produced fish that is taken as harvest (estimated before broodstock removal) is estimated as **(1-s)** times **H**.

Unless the harvest selectivity of natural fish equals one (i.e, no differential selectivity or mortality between hatchery and naturally produced fish), then the estimation of "**s**" requires: (a) estimates of the relative encounter rates of hatchery and natural fish, and (b) the expected mortality rate to associate with fish released from the fishing gear. These mortality rates will vary between species, gear types, and handling procedures. Also, if harvest occurs in an area that holds fish and/or fishing occurs over an extended period, then the parameter "**s**" likely needs to be estimated by time interval since the encounter rate or ratio of hatchery: wild fish will change over time.

H also includes the potential mortalities in ocean fisheries. Ocean harvest impacts could be ignored if there were no mass-marked selective fisheries in the ocean. If so, some parameters estimated would be biased low (replacement rate), but the relative error in hatchery and natural sub-populations would be equal. However, if there are selective fisheries for marked-hatchery fish, then the ocean mortalities will not be equal between the hatchery and naturally produced fish. These fisheries would involve direct removal of mass-marked hatchery fish and incidental mortality on natural fish. With selective mass-mark ocean fisheries, an unbiased estimate of ocean exploitation rates for unmarked natural fish cannot be estimated unless there are tagged components (usually CWT) of both stocks (mass-marked hatchery and natural), see SFEC 2002[1]. If there is ocean exploitation or terminal harvest (Ha) that would have associated mortalities on naturally produced fish, then ***a paired tagging program*** is required to estimate the incidental morality rate on the naturally-spawned fish.

The two critical biological parameters for the model are:
Rw, the intrinsic replacement rate for a naturally spawned generation (i.e., adult return rate per spawner from each spawning year). Data needs are:

i. **Nww(t)**, fish that were produced naturally and spawn naturally in the next generation, sex ratio and age of spawners, and fecundity (female eggs per female by age class), pre-spawning mortality rate and effectiveness of spawning;

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[1]Selective Fisheries Evaluation Committee. 2002. Investigation of methods to estimate mortalities of unmarked salmon in mark-selective fisheries through the use of double-index tag groups. TCSFEC(02)-1. 87pg. (Pacific Salmon Commission, Vancouver, BC, website: psc.org).

ii. **Nwa(t)**, fish that spawn naturally but were produce in a hatchery in the previous generation, sex ratio and age of spawners, and fecundity (female eggs per female by age class), pre-spawning mortality rate and effectiveness of spawning;

iii. Effective egg deposition in the natural environment is the sum of (i) and (ii);

iv. Number of emigrating naturally-produced parr and smolts from the population/geographic area of interest; and

v. The number of returning adults by age and sex (also size if varying and affecting fecundity or effectiveness of spawning). Researchers will need to consider how to account for small mature male adults that may return. These fish are typically a year younger than the first age of mature females and can account for a significant portion of the terminal runs in some stocks and years.

We recommend that the enumeration of adults and estimation of Ra and Rw be conducted on females. This would circumvent the conceptual and practical difficulty of treating precocial and jack males in the production model.

Ra, the intrinsic replacement rate for a hatchery-produced generation (i.e., adult return rate per spawner from each spawning year). Data needs are:

i. **Naa(t) and Naw(t)**, by sex and age class, and fecundity (female eggs per female by age/size class)

ii. Number of eggs laid by year

iii. Number of smolts produced from a spawning year

iv. Number of returning adults by age and sex (also size if varying and affecting fecundity or effectiveness of spawning). See comments in paragraph (v) above.

While the parameters identified above (bold) are sufficient for the supplementation model, other variables may influence our ability to estimate the parameter values, or to explain differences between them. These variables may include:

a) Inter-dam loss rates by age/size class or stock
b) Downstream mortality rates by size class or time period
c) Changes in ocean exploitation rates versus marine survival
d) Distribution of hatchery returns (i.e., straying of hatchery releases versus homing fidelity of the natural fish)
e) Accounting for uncertainty in parameter estimates, including the assumption of fixed natural mortality rates between ages in the ocean (typically applies to chinook assessments more than other species).

Assessment Methods

The intrinsic return rates for natural spawning populations (Rw) and hatchery-produced populations (Ra) provide a fundamental basis for assessment of supplementation. However, to estimate the value of Rw or Ra requires that many parameters be evaluated (as listed under each parameter described in the previous section) and that methods for estimating Rw and Ra be developed. A significant amount of information must be collated from each spawning year and the specified population in order to compare the rate of change in population sizes over time. Typically, the estimation of total production attributed to one spawning year begins with estimating the number of mature fish at the oldest age in the population and proceeds backwards to estimate the cumulative production at a specified age and time period. The process "reconstructs" or accumulates the number of fish estimated at each age to estimate total production (i.e., the number of fish alive at a specified time from one brood year and a specific population; the "cohort" size).

The point to which production is reconstructed is an important specification and can have a substantial effect on the data necessary for an analysis. For example, under the Pacific Salmon Treaty, chinook production is frequently estimated back to the first age of recruitment to ocean fisheries and before fishing begins in a year (i.e., total Age-2 for fall Chinook, Age3 for Spring Chinook). Alternatively, production could be estimated as adult returns to river (i.e., mature fish only) and would avoid the need for estimation of fishing mortality in ocean fisheries and natural mortality between year classes. If an assessment was to be based on *relative* return rates of hatchery and natural fish, then adult returns could be a sufficient comparison assuming that ocean exploitation or survivals were not different between the hatchery and natural sub-populations. If this assumption cannot be made, then an unbiased comparison of returns rates can only be achieved by accounting for ocean mortality influences.

In establishing the performance measures to be used in an assessment of supplementation, agreement on this issue is essential before defining the data needs and methods to be applied.

To reconstruct the number of fish surviving to an age, *data are needed for each age from four life stages*: 1. numbers of spawners, 2. catches and incidental mortality in terminal areas, 3. catch and incidental mortality in ocean fisheries, and 4. natural mortality. Different programs are required to acquire each of these data elements.

Numbers of adults spawning: Many methods have been used to estimate the spawning escapement in a population (Table 5.1). Each method requires different assumptions and involves different sampling issues. It is important to recognize that error in the estimated number of spawners affects the accuracy of the entire assessment. Many estimation programs for salmon spawning escapements have a poor statistical basis and unknown accuracy because of the potentially biased selection of index sites. Furthermore, if an assessment requires estimates of the reproductive potential in a stock (hatchery versus natural), then the escapement must be estimated by sex and age (at a pre-determined level of statistical confidence) and contribution by specific parents estimated. Although this has not been possible until recently, the development of DNA parentage methods now provides a means to estimate this value.

Table 5.1. Summary of methods used in the estimation of spawning escapements of Pacific salmon.

Escapement method	Data needs/Assumptions	Unknowns
Redd counts	Redd life for observations, fish/redd by species, expansion of stream reach or habitat to total system	Variability in fish/redd or redd life, how representative a reach is of the total system, etc.
Mark-Recapture program	Standard assumptions concerning randomize tag application or recovery, open or closed population model, tag mortality rate, etc.	Biases in marking and/or recovery (eg. Variable recovery rate by sex and body size), coverage of the entire run period, …
Fence or Weir counts	Fish passing the weir are from that population, total run timing covered, weir was fish tight, etc.	Between year variability due to environment, mortality above the weir, distribution of spawners, …
Visual Indices	Consistency of counting protocols, repeated surveys per year, stream life estimates for extrapolations to total spawners, expansion of stream reach or habitat to total system	Accuracy is stream and weather dependent, usually of unknown accuracy, replication between years is uncertain, how representative a reach is of the total system, etc.?
Biological Sampling needs*	No spawning escapement program is complete without sampling for categories needed in the analysis: Hatchery vs. Wild; mark incidence; numbers by age, size, and sex; pre-spawning mortality rate and/or spawning efficiency	How representative the samples are of the population? Were random samples collected? Variation between years due to recovery conditions.
* Very few escapement sampling programs actually design statistical sampling programs to ensure adequate sampling by category and confidence levels.		

Terminal Mortalities: Mortality in terminal areas refers to any losses that occur from when mature fish emigrate from the ocean fisheries to when they enter the spawning area of their natal stream. These losses may be due to terminal fisheries (commercial in-river, sport, and ceremonial and subsistence) associated with fishing but not reported (incidental mortality), and unaccounted losses (e.g., marine mammal predation). In the Columbia River a prominent unaccounted loss is “Inter-dam” loss or the difference in fish counts between dams, even after accounting for known losses. Pre-spawning mortality of fish that returned to their natal stream, but did not survive to spawn, must also be included. Pre-spawning mortality can be highly variable depending on environmental conditions, and its proper accounting can depend on when the “population size” of the spawners was estimated. For example, if the numbers of spawners was estimated as a count through a fence downstream of the spawning ground, then any pre-spawning mortality should be subtracted from the spawning population to correctly estimate the reproductive potential of that year.

Ocean Fishery Mortalities: Mortality in ocean fisheries includes recorded catches, incidental mortalities associated with the fishing, and unaccounted losses. Incidental mortality by stocks and unaccounted losses are likely to be more poorly estimated in ocean fisheries than in terminal areas. Although catches are usually closely monitored and sampled in ocean fisheries, the coverage of sport fisheries can be more variable due to estimation methods and costs of surveys. Incidental mortality in ocean fisheries is a difficult problem that has become increasingly important in recent years. Encounters of small feeding salmon can be very large in some ocean fisheries, may involve a couple of age-classes, and may vary over time as fish recruit to the size limits. Very little biological sampling of released fish has been conducted in ocean fisheries, and the stocks involved are assumed to be the same as those caught (a largely untested assumption). Furthermore, changes in regulations can substantially change the incidental mortality level compared to the retained catch. For example, the development of mass-mark selective fisheries requires the release of all unmarked fish, but retention of the marked fish (i.e., release natural fish but retain hatchery fish). Selective fisheries will, therefore, substantially increase the incidental mortality of unmarked fish, but will also reduce their retained catch. The extent of unaccounted losses in ocean fisheries is confounded with natural mortality in the marine environments, but to date there have been limited investigations to separate the two sources of mortality. The types of unaccounted losses that may be included are drop-off and mortality from gear before accounting, non-reported catches, and unmonitored fisheries (e.g., small localized sport or Native fisheries). Some allowances for these losses are included by the U.S. Fishery Management Councils and by the Pacific Salmon Commission technical committees, but the accuracy of the estimates is unknown.

Natural Mortality: When natural mortality is included in an assessment, it is frequently based on standard values by age derived from limited and old research programs. Because the supplementation model is to be evaluated based on relative rates of return, these limitations may not influence the comparisons if natural mortality rates are assumed to be equal between the hatchery and natural sub-populations. If this assumption is correct, then natural mortality constants only act as scalars and do not change the relative comparison. Unfortunately, in the Columbia River, natural mortality may not be equal and should be accounted for. For example, if the size and timing of hatchery emigrants differ from the naturally produced fish, then downstream mortality may differ between sub-populations. The importance of such differences though would depend on the basis for comparisons as noted in italic above.

Comment on the Current Accuracy of the Reconstructions

The current information requirements for a quantitative comparison between hatchery (marked) and natural (unmarked) sub-populations have become more demanding in recent years. In years when salmon production was stronger and catches large, the majority of the production from a cohort was accounted for in catches and could be directly sampled. For Chinook and Coho salmon, total exploitation rates were frequently estimated to be 65 to 85%. In those cases, errors in estimates of the spawning escapement had relatively less influence on the vital statistics. Currently though, exploitation rates are greatly reduced, and potentially two-thirds or more of the estimated production from a cohort could be accounted for in spawning escapement and incidental mortality. Consequently, there is a much greater need for accurate estimation of spawners and of incidental mortality, to estimate the uncertainty in current assessment methods and to design appropriate sampling programs. Each of these variables will require estimation procedures with associated levels of uncertainty as opposed to direct observation.

Estimates of production are now likely to be much less precise than was possible in the past, and may involve significant bias in the estimates. These concerns emphasize the need for paired comparisons, uses of references, and direct sampling programs whenever possible (e.g., the use of coded-wire tags for stock identification and estimation of exploitation rates for marked and unmarked populations).

Use of Constants and References

Salmon assessments and annual monitoring programs frequently apply constants to annual observations. For example, a common value of fish/redd is frequently applied to the number of redds observed to estimate the associated number of spawners. In stock-recruitment analyses, it is not uncommon to have a constant age-structure applied to annual terminal runs to allocate annual returns to parental spawning years. The use of such fixed values, or long-term average values, may be expedient but can mask important information about annual variations in production. This issue is particularly important when experimental assessments must be made over relatively short time periods. If annual monitoring of spawning escapements is only concerned with longer term trends and not meant for quantitative assessments, then the application of fixed values maybe acceptable. *However, in assessments of supplementation and estimation of intrinsic rates of return within a limited time period, the use of such constants should be strongly discouraged.*

Similarly, the need to evaluate supplementation and its effect on intrinsic rates of population growth places a significant onus on experimental design of the study. When conducting studies in large-scale, open environments (such as rivers and lakes), strict adherence to experimental design is a major challenge and one that has frequently not been addressed. Although the model above could be studied in a single river system, any results will be confounded with temporal changes in habitat and/or climate, or they may be specific to the particular ecological conditions of that one system. Unless an innovative experimental design has been applied in that system (see below), the investigators have very limited capability to conclude that the supplementation program had any effect on production in that river system. Use of reference river systems for comparison with experimental treatments is an essential experimental design consideration. If paired treatments can be compared over prolonged periods, then results may be inferred from such comparisons. However, to explicitly test the efficacy of supplementation as a production tool, it is necessary to compare the supplementation treatment against a comparable but untreated stock and environment. In the absence of a reference system, changes in production within the treated system may be confounded with environmental trends in habitats and/or climate. References in natural environments can be difficult to design, and their value has been questioned because they are seldom an exact control of the treated situations. The following section considers some of the problems associated with experimental designs in ecological settings.

Experimental Design Considerations

As a general resource for studies conducted in ecological settings, the text by Krebs (1999) is particularly useful. Supplementation studies require large financial investments over prolonged periods and potentially have major policy impacts for resource management and development. As such, a supplementation experiment should involve good experimental design so that there is confidence in the conclusions. Unfortunately though, supplementation studies also involve many of the reasons why there is a history of statistical errors in the ecological literature (Hurlbert 1984, Heffner et al. 1996) and were special features in the journal, Ecology (Matson and Carpenter 1990) on experimental design. Supplementation studies involve:

1. Large open ecological systems (rivers) that have been extensively disturbed through time, plus artificial production systems (hatcheries) that also change;

2. Inherently variable natural systems involving multiple factors in freshwater and marine environments;

3. Long timeframes with expected changes in environments through time (time-treatment interactions, Walters and Holling 1990);

4. Impossibility to truly replicate experimental units in Nature; and

5. Limitations on the allocation of treatment and references experimental units.

These challenges in ecological studies were well described in Hurlbert's (1984) paper. Hurlbert's description of critical features of a controlled experiment identified four design features: controls (i. e., references), replication, randomization, and interspersion.

> "An experiment is successful to the extent that these factors are prevented from rendering its results inconclusive or ambiguous. It is the task of experimental design to reduce or eliminate the influence of those sources [sources of confusion Table 5.2] …"

Hulbert's table provides a useful summary of the sources of confusion in experiments and the role of the features in experimental design.

Table 5.2. Potential sources of confusion in an experiment and means for minimizing their effect[1].

	Source of confusion	Features of an experimental design that reduce or eliminate confusion
1.	Temporal change	Control treatments
2.	Procedure effects	Control treatments
3.	Experimenter bias	Randomization assignment of experimental units to treatments, and other procedures
4.	Experimenter generated variability (random error)	Replication of treatments
5.	Initial or inherent variability among experimental units	Replication of treatments, Interspersion of treatments, Concomitant observations
6.	Intrusions (impingement of chance events on an experiment in progress)	Replication of treatments Interspersion of treatments

1. Adapted from Hulbert 1984 page 191. Hulbert uses the word "control" while we prefer the word "reference".

The reality that a researcher faces when planning a supplementation program is that the classical features of experimental design are nearly impossible to address in large-scale ecological studies. The researcher would need to define the experimental units, randomize the treatment and reference units, replicate each unit, and assess interspersion of treatments over time and space. With large ecological studies such as supplementation, the researcher is often not free to randomize treatments over habitats, the number of replicate treatments and references (if any) are limited, and streams within a region are rarely perfect independent replicates of each other.

Given these limitations, three issues become paramount in designing a supplementation study:

- determine what response variable can be measured, how to compare treatments, and how to estimate the variability in that response variable;

- consider if strict adherence to statistical inference is necessary, and if not, then what evidence will be adequate for comparison of treatments;

- consider whether other experimental designs are appropriate to the study.

The last issue may involve adaptive management designs or temporal interventions (see Walters 1986, Walters et al. 1988) or designs recently presented by Oksanen (2001). Oksanen specifically addressed concerns of "pseudoreplication" discussed by Hurlbert (1984) and identified three designs that may suit ecological studies: use of prediction on system dynamics, comparing a single treatment with replicated references, and conducting an unreplicated experiment (with or without inferential statistics). Each of these options involves trade-offs in information, but continues to allow ecological research while acknowledging the criticisms of Hurlbert.

Oksanen (2001) also presents studies in microcosms as another experimental design. While generally these smaller-scaled "ecosystems" are not suitable to test supplementation as a management tool, they may be useful in studying the production dynamics of hatchery and natural fish, ecological interactions, or density dependent factors (i.e., supplemental or explanatory studies).

We add the observation when randomization and interspersion cannot be fully implemented in large observational ecological studies, it remains critically important to replicate supplementation studies (with the best reference[s] possible) in multiple locations. Such "replicates" do not lend themselves to standard statistical analyses, but information can be gained by careful attention to standardization of methods and data collection procedures.

Assessing the Long-term Fitness Effects of Supplementation

Fitness refers to an individual or a population's ability to produce progeny that survive to adulthood and reproduce. In the strictest sense, fitness is zero until grandchildren are produced. Many biological traits contribute to fitness: production of gametes, gamete quality, ability to mate, and the physiological competence of the progeny produced. Fitness is usually considered relative among individuals with different genotypes or among populations with different breeding histories.

Fitness and the traits that contribute to fitness are not discrete characters that can be assessed by categorizing inspected individuals; they are usually continuously distributed metrics. Fitness and the traits that contribute to fitness are also influenced by an individual's genotype and the environment in which the individual lives. Consequently, fitness and the traits that contribute to fitness are analyzed genetically by contrasting their means and variances in treatment and reference populations.

In salmon and steelhead supplementation programs, productivity metrics such as the adult-to-adult replacement rates (Rw and Ra) are insufficient indicators of a population's intrinsic fitness because they are influenced by the environment and density dependence.

Contrasting such productivity estimates in populations (with different proportions of the naturally spawning population composed of hatchery-origin adults) with unsupplemented reference populations after supplementation has ceased could provide a means of determining the fitness effects of interbreeding between hatchery-origin and natural-origin adults. The challenge in this analysis is to establish a statistical model that removes the environmental influences on the productivity metric. Supplementation programs have been monitoring explanatory traits thought to contribute to fitness. Continuing this approach is worthwhile, but appropriate contrasts of supplementation and reference lines are needed. Moreover, it would be beneficial to employ an experimental design that facilitates evaluating how changes in the traits that contribute to fitness actually affect fitness.

Assessment Data versus Explanatory Data

The section above on “Parameters Needed to Assess the Demographic Consequences of Supplementation” presents a daunting task of monitoring and tagging programs, annual sampling, and data management. These data are the first priority in annual assessment programs and will have to be collected consistently over a number of years. Frequently, however, data to address other topics (e.g., nutrient levels, competition, predation, etc.) is also collected, presumably under the assumption that they will also help evaluate supplementation programs. In ecological studies, investigators may easily be diverted to collecting this additional information but in many cases these data will not be necessary to assess the production dynamics of supplementation. Krebs (1999) identifies one of his first rules of ecological experimentation as "not everything that can be measured should be".

Section 6. Assessment of Columbia River Basin Supplementation

Evaluating whether the strategy of supplementation is providing intended contributions to fishery resources under the Council's Fish and Wildlife Program or to recovery under the Endangered Species Act requires at least three sets of information.

The first is a clear set of constraining management controls; i.e., the proportion of the natural-origin adult population that is permitted to be collected for broodstock, the proportion of natural- and hatchery-origin fish in the hatchery broodstock, and the proportion of hatchery-origin fish permitted on the natural spawning grounds.

Second, for each individual program there must be data collected that effectively assesses the abundance of the natural population and the vital rates of the population both in artificial culture and in the natural environment. Beyond that minimum, SARs and other life-stage specific survival rates for the natural and hatchery components provide additional opportunity to better understand at what points during the life cycle mortality is occurring. Understanding where mortality is occurring in the life cycle has important implications for designing habitat actions outside of the hatchery and modifying rearing practices inside the hatchery.

Third, there needs to be performance standards for the abundance of the natural- and hatchery-origin population components and the vital rates in culture and in nature so that benchmarks can be established for the program.

In this section we provide an assessment of artificial production programs in the Columbia River Basin that are identified by program sponsors as supplementation. This assessment is intended to determine whether each program is likely to provide sufficiently rigorous data for meaningful analysis. We chose to include only programs that were supplementing existing populations. Reintroduction programs followed by supplementation of any naturally spawning adults will have many of the anticipated benefits and risks of programs to supplement existing populations; however, objectives and potential problems in those programs are different from supplementation of existing populations and are not reviewed. The selected programs were:

1. Hood River winter-run steelhead,
2. Umatilla River summer-run steelhead,
3. Yakima River spring-run chinook
4. Wenatchee River-Chiwawa spring-run chinook
5. Okanogan River-Similkameen summer-run chinook
6. Tucannon River spring-run chinook
7. Imnaha River spring-run chinook
8. Imnaha River summer-run steelhead
9. Idaho Supplementation Studies (Spring-run chinook)

A summary of the current status of captive broodstock programs is also included, because these programs can be considered a subset of supplementation. The programs summarized were:

1. Redfish Lake sockeye salmon
2. Grande Ronde River spring-run chinook salmon
3. Tucannon River spring-run chinook salmon
4. Salmon River spring-run chinook salmon

Our specific objective is to assess for each program whether sufficiently transparent management controls existed and whether vital statistics were being estimated and reported. To accomplish this task we reviewed agency program reports, Hatchery and Genetic Management Plans (HGMPs), ESA operating permits, peer reviewed papers, and BPA reports, as well as draft subbasin summaries and BPA project proposals from the CBFWA website. We also used results from these projects to summarize what has been learned about supplementation and what remains largely unevaluated.

Extended summaries of the programs and the data they have collected are provided in appendix A.

ISAB Assessment of the Adaptive Management Information of the Collective Supplementation Projects

Based on the information the ISAB obtained from the various agency reports, subbasin summaries, and HGMPs, we reviewed each program for evidence of guidelines for the primary management constraints (broodstock collections, proportions of natural-origin adults in the hatchery stock, proportion of hatchery-origin adults permitted in the natural spawning population), performance standards (for natural- and hatchery-origin adults abundance, natural- and hatchery- replacement rates, and SARs), facilities to adequately enumerate juvenile and adult salmon and steelhead, and reported estimates of abundance and vital rates. These evaluations for individual programs are summarized in Table 6.1. ISAB conclusions about what is known about supplementation and what is largely unevaluated follows the table. Because of the large number of streams involved in the Idaho Supplementation Study (ISS) it is not included in the table below. An ISAB review of the statistical analysis of the ISS is provided below.

Table 6.1. A summary of Columbia River Basin supplementation programs.

Program Guidelines								
Program	Hood R. Steelhead	Umatilla Steelhead	Wenatchee Chinook	Similkameen Chinook	Imnaha Steelhead	Imnaha Chinook	Tucannon Chinook	Yakima Chinook
Broodstock Source:								
100% target stock	Yes	Yes	Yes		Yes	Yes	Yes	Yes
< 100% target stock				Yes				
Non-Target stock								
Original Brood Collections								
100% Natural Fish	Yes	Yes	Yes		Yes	Yes	Yes	Yes
< 100% Natural Fish				Yes				
Hatchery Fish								
Not Specified								
Subsequent Brood Collections								
100% Natural Fish		Yes						Yes
< 100% Natural Fish	Yes		Yes	Yes	Yes	Yes	Yes	
% Natural Specified, (Y, N, U[1])	Yes	Yes	No	No	Yes	Yes	Yes	
No Guideline								
Proportion of Natural Population that can be collected for broodstock								
Specified (Y, N, U)	Yes	No	Yes	Yes	U	U	Yes	Yes
Proportion of naturally spawning population that must be of natural-origin								
Specified (Y, N, U)	Yes	No	No	No	U	U	No	No

1. U = unclear based on information available to the ISAB

Performance Standards								
Program	Hood R. Steelhead	Umatilla Steelhead	Wenatchee Chinook	Similkameen Chinook	Imnaha Steelhead	Imnaha Chinook	Tucannon Chinook	Yakima Chinook
Hatchery Rearing Survival								
Broodstock Survival (Y, N, U)	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Egg to Release (Y, N, U)	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
SAR (Y, N, U)	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes
Hatchery Production Targets								
Broodstock Collection (Y, N,U)	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Smolt Release (Y, N, U)	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Adult Returns (Y, N, U)	Yes	Yes	No	Yes	Yes	Yes	Yes	Yes
Harvest Contribution (Y, N, U)	Yes	Yes	No	No	No	No	No	No
Spawning Contribution (Y, N, U)	Yes	Yes	No	No	No	No	No	No
Natural Population Production Targets								
Adult abundance (Y, N, U)	Yes	Yes	Yes	Yes	No	No	No	Yes

Facilities to Enumerate Fish								
Adult Counts								
Trap and/or Count Entire Run	Yes	Yes	Yes					Yes
Trap and Count Part of Run					Yes	Yes	Yes	
Spawning Ground Survey/Sample			Yes	Yes	Yes	Yes		Yes
Broodstock Collections								
Weir/Trap below all spawning grounds (Y, N, U)	Yes	Yes	No	No	No	No	No	Yes
Weir/Trap collects only target stocks (Y, N, U)	Yes	Yes	Yes	No	Yes	Yes	Yes	No
Juvenile Trapping/Counting (Y, N, U)	Yes	U	Yes	No	U	U	Yes	Yes
Reference Populations (Y, N, U)	No	No	Yes	No	No	No	No	Yes

Vital Statistics Reported								
Program	Hood R. Steelhead	Umatilla Steelhead	Wenatchee Chinook	Similkameen Chinook	Imnaha Steelhead	Imnaha Chinook	Tucannon Chinook	Yakima Chinook
Hatchery Produced								
No. of natural broodfish collected by sex and age	Yes	U	U	U	U	U	Yes	Yes
No. of hatchery broodfish collected by sex and age	Yes	U	U	U	U	U	Yes	Yes
No. of natural broodfish spawned by sex and age	Yes	U	U	U	U	U	Yes	Yes
No. of hatchery broodfish spawned by sex and age	Yes	U	U	U	U	U	Yes	Yes
Pre-spawning survival	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Egg to release survival	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Smolt to adult return survival (SAR)	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes
Adult recruit per spawner ratio	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes
Naturally Produced							Yes	Yes
No. of natural-origin adults in the spawning escapement by sex and age	Yes	U	U	U	U	U	Yes	Yes
No. of hatchery-origin adults in the spawning escapement by sex and age	Yes	U	U	U	U	U	Yes	Yes
Pre-spawning survival			U				Yes	Yes
Smolt population estimate	Yes	U	U				Yes	Yes
Natural egg to smolt survival	Yes		U				Yes	Yes
Smolt to adult return survival (SAR)	Yes		U				Yes	Yes
Adult recruit per spawner ratio	Yes	Yes	U		Yes	Yes	Yes	Yes

1. U = unclear based on information available to the ISAB

Assessment of Basinwide Organization, Rationale for Management Constraints, Data Collection, and Reporting of Supplementation Programs

Supplementation in the Columbia River Basin is undoubtedly the largest effort to release hatchery-reared individuals in an attempt to recover depressed natural populations ever undertaken, anywhere. As far as we know, using hatchery/captive-reared individuals in this way has not been successful in recovering any other species.

Consequently, supplementation is considered both experimental, because to our knowledge it has never been proven successful, and controversial, because some claims have been made that it could, in fact, further depress the populations it intends to recover. Given the scale of the supplementation effort in the Basin, and the significance of the task it is assigned, more rigor is warranted in establishing and justifying the management constraints of the individual programs, as well as the timely and adequate annual reporting of program results. It is disturbing that there is no evidence of coordination across programs to conduct a meaningful adaptive management experiment or a mechanism to perform meta-analysis. These functions need to be established if supplementation is going to be fully evaluated.

The availabilities of reports and the usefulness of the reporting on individual programs are highly variable. The reports that were most useful to us were those from the Tucannon spring-run chinook salmon program and the Hood River winter-run steelhead program. These reports provided most, but not all, of the data needed in a single volume. The Tucannon River evaluation was easier to work with because it covered only one species and was concise at 52 pages. The Hood River report covered several species/stocks, was over 200 hundred pages, and the recruits/spawner estimates were located in a separate several hundred page steelhead risk-benefit analysis. We recommend that all the basin supplementation programs be required to adopt annual reporting in a standardized format that provides at minimum the details presented in Table 6.1. We suggest that the reports be available through the web and regularly maintained. If data that is collected annually is not processed and examined regularly, the inadequacy of programs, monitoring, and processes will not be exposed, possibly until it is too late to respond and the experiment is compromised.

Our criticism of reporting does not imply that data have not been collected for the other programs we reviewed. We believe that the way the data are made available could be improved. For example, three different BPA projects collect the data needed for an analysis of the Umatilla River summer-run steelhead supplementation program. Based on the reported data, independent calculation of the recruit/spawner ratios is not possible. The Imnaha River spring-run chinook salmon and summer-run steelhead program reports provided graphs of progeny-per-parent ratios (recruits/spawner: Rw and Ra), but did not provide the numbers themselves nor the data that were used to calculate the ratios. It is not clear whether or not the data collections for the mid-Columbia summer-run chinook salmon programs on the Okanogan-Similkameen are sufficient to calculate the necessary performance indicators.

Of the programs we reviewed, only the Wenatchee River-Chiwawa, Yakima, and ISS spring-run chinook salmon programs had identified reference populations (called controls in the ISS). Without populations to serve as references, the inferences that can be made about the success of supplementation are limited. Although it would be possible without reference streams to measure progress toward numerical targets for adult abundance and to estimate whether a project was sustainable (the product of natural and hatchery replacement rates being greater than 1.0), it would not be possible to establish that supplementation was increasing natural-origin adult abundance or even slowing the decline in natural-origin adult abundance. Populations that serve as references are needed urgently. It will be necessary to exclude hatchery-origin adults from these reference populations and the suite of performance indicators measured in the supplemented streams will also need to be measured in the reference streams. Even though we sometimes use the word "control" stream, they are more correctly referred to as reference streams, because it is impossible to obtain perfect matches on all environmental variables.

Some supplementation programs are experimenting to determine if different captive-rearing conditions or fry or smolt release protocols can affect smolt-to-adult survival of hatchery-reared individuals. Although these fish culture experiments are worth conducting, they do not constitute a test of the efficacy of supplementation. Survival of hatchery-reared juveniles to mature adults that return to spawn naturally is a necessary, but not sufficient, component of supplementation. The needed experiment would test whether supplementation can increase the abundance of natural-origin spawning adults in a manner that also maintains the fitness of the natural-origin adult population component within specified limits and maintain the enhanced numbers of naturally spawning adults after supplementation has stopped.

The ISS aims to test for a single ESU of Columbia River Basin salmon, whether or not supplementation increases the abundance of natural-origin adults and whether this increase is maintained once supplementation is stopped. As summarized below, the experimental design for that study has been compromised and as a result, interpretation of the results will be difficult. Although the ISS and Yakima supplementation studies are geographically large-scale environmental studies, they are limited in scope compared to the size of the Columbia River Basin. In addition, maintaining the study designs over a long period of time may be extremely difficult (and has proven difficult with the ISS). Consequently, the Basin cannot rely on the ISS or the Yakima supplementation studies alone to provide a test of supplementation with results that generalize throughout the basin. There currently is no sufficiently rigorous experimental test of the overall supplementation strategy. The region will have to depend on weight of evidence and judgment to reach conclusions for multiple species over varying habitat and environmental conditions. One option to rectify this deficiency would be to use the existing supplementation programs within the basin as an adaptive management experiment that assesses the general efficacy of supplementation. That experiment would require the control/reference populations that we suggested above, better data collection efforts and perhaps some adjustments in the parameters under management control.

The management constraints (i.e. the proportion of natural-origin adults used in the hatchery or allowed to escape to the natural spawning grounds and the proportion of the natural-origin adult population that can be collected as broodstock) are variable from program to program. The rationale for the different sets of constraints for individual programs is not clear but if coordinated, they could be a component of a basinwide supplementation experiment. Unfortunately, the constraints that are in place now are regularly relaxed to facilitate producing more juveniles for release. Relaxing constraints to facilitate producing such an abundance of hatchery-origin juveniles, when natural-origin adult abundance is decreasing, is ill-advised because this removes the mechanism for managing risk.

Statistical Analysis of the Idaho Supplementation Studies

It is very difficult to design, implement, and maintain the integrity of large field supplementation studies. When the integrity of the experiment is compromised a long-term field study may lose much of the basic justification required for experimental determination of cause and effect relationships. Inferences are often limited to correlation and regression methods, and uncontrolled confounding factors often limit the interpretation of study results. For example, the Idaho Supplementation Studies (ISS) apparently included random selection of streams for "treatment" and "control" in the original plans. The ISS refers to control streams and we adopt that terminology in our review of the ISS; however, reference streams is a better phrase because it is recognized that the streams are not perfectly matched on all important factors and in the end, randomization was not implemented. Substantial changes have been made in the assignment of treatment and control status to study streams limiting statistical inferences. Variation (noise) introduced by *de facto* supplementation by strays from conventional hatcheries may over shadow treatment effects in the ISS.

Variations of the prototype statistical analyses for the ISS (Lutch et al. 2003) are appropriate. One criticism that we have of the prototype statistical analysis is that relatively too much emphasis is placed on statistical testing of null hypotheses and classical analysis of covariance instead of modeling and point estimation. As recognized by the ISS sponsors, statistical significance does not imply that results may be of practical importance and insignificance does not imply that results are not of practical importance. However, the temptation is strong to overstate the conclusions of statistical tests of null hypotheses.

In the current ISS data set, only one "control" stream was reported to have no strays, namely Bear Valley Creek in the Salmon River Basin. With the possible exception of White Cap Creek (where there are no data), all "control" streams in the Clearwater had *de facto* supplementation with substantial levels of strays (apparently both ISS and non-ISS fish). The annual abundance of strays in the streams varies and the levels are not controlled by the study design. The annual abundance of supplementation fish on the spawning grounds also varies so that consideration of "treatment" or "partial treatment" as fixed categories in the analysis of covariance seems to be inaccurate. Regardless of the best intentions, the study has characteristics of an observational study that limits inferences to correlation and regression methods.

Point estimation of effects with measures of precision and fitting of models for prediction of effects are a natural part of the prototype statistical analysis, and we grant that the report contains tables of point estimates adjusted for the fitted models. However, we recommend that point estimation of effects with measures of precision and modeling of effects play the dominant role in the statistical analyses. The analyses should also consider building models using criteria such as Akaike's Information Criterion (AIC) (Burnham and Anderson 2002) in addition to classical hypothesis testing in analysis of covariance. For example, in the section entitled Straying Effect Results and Conclusions, point estimates and measures of precision might be reported instead of simply stating that certain effects were not significant at a certain significance level (p-value). We also suggest that the actual linear models be written out with an explicit list of accompanying assumptions.

Emphasis on modeling and estimation may also make it possible to more realistically incorporate the effects of *de facto* supplementation arising from strays (both ISS fish and strays from conventional hatcheries). An alternate point of view that the investigators should investigate for the design and analysis of Phase III is that there are no "controls" in the ISS, i.e., there are simply streams with various levels of two types of supplementation, at levels ranging from 0% to somewhat less than 67% for non-ISS strays and 0% to some unreported level X% for ISS fish. The effects of other predictor variables such as harvest and measures of primary productivity might also be modeled.

In Phase III, the design calls for stopping supplementation with ISS fish. The investigators should consider the merits of changing the design in Phase III to also include stopping *de facto* supplementation by non-ISS fish in some of the streams (control, partial treatment, and/or treatment), perhaps by building additional weirs on some of the streams or by continuing supplementation with ISS fish on some streams. For example, perhaps Johnson Creek and some other treatment streams should continue to receive supplementation by ISS fish during **Phase III**. Abundance of redds and other dependent variables in streams within groups (e.g., Lower Lochsa, Lower Salmon, etc.), might be modeled by multiphase regressions over the three Phases of the study (Seber and Wild 1989) to provide inferences concerning the effects of stopping or changing the levels of supplementation, non-ISS strays, and/or ISS strays during Phase III. Investigation of these possible changes in the design of Phase III and ramifications of these suggested alternatives are beyond the charge of the ISAB in the current report. This recommendation does not call for a major change in the prototype statistical analysis, but rather a change in emphasis to modeling of an observational study and in methods for communication of the statistical results.

Finally, we note that the data necessary to conduct the protocol statistical analysis or modifications are apparently not being collected (Lutch et al. 2003). Only a subset of the ISS streams has annual carcass data sufficient to estimate the abundance of strays and the abundance of ISS adults (i.e., adults from ISS hatchery produced juveniles) on the spawning grounds. Unless the redd counts and carcass data are collected annually on all ISS streams it will not be possible to analyze even one measure of success, namely abundance of redds.

What is known about supplementation, and largely undisputed?

1. The broodstock collected for supplementation programs are spawned successfully and the resulting fry survive and are released in proportions exceeding the survival rate of progeny spawned in the wild; i.e., there is a juvenile survival benefit attributable to the protected hatchery environment. In the projects for which data were reported, pre-spawning mortality of the broodstock averaged from 2% in Wenatchee River spring-run chinook salmon to 18% in Umatilla River summer-run steelhead. Survival from green egg to smolt (or fry) release ranged from mid-80% in Wenatchee River and Yakima spring-run chinook programs to 60% in Umatilla River summer-run steelhead. In contrast, the survival rate for naturally produced Hood River winter-run steelhead was only 1.2% and only 4.2% for Tucannon River spring-run chinook salmon.

2. Where evaluated, the survival to returning adults (SARs) for smolts released from the hatchery environment is less than that for natural-origin smolts. For hatchery-origin smolts, SARs ranged from 0.13% for Wenatchee spring-run chinook salmon to 5.85% for Yakima spring-run chinook. SARs for naturally produced smolts were available only for Hood River winter-run steelhead and the Tucannon and Yakima River spring-run chinook salmon. Hatchery rates have exceeded wild rates in one year in the Yakima River spring-run chinook program. SARs for the three locations where both hatchery and naturally produced smolts are estimated are presented in table 6.2.

Table 6.2. Smolt-to-Adult survival for hatchery and wild spawning Columbia River Basin salmon and steelhead.

	% Smolt-to-Adult Survival (SAR)	
	Hatchery	Wild
Hood River -Steelhead	0.68	3.80
Tucannon R - Chinook	0.22	1.63
Yakima R - Chinook	5.85	6.50

3. *Because of the juvenile survival advantage provided by the hatchery before release, hatchery spawning often generates a higher adult recruits-per-spawner rate than natural spawning even though the SAR for hatchery-origin smolts is lower than natural-origin smolts.* Recruits-per-spawner are available for hatchery and natural spawning from five of seven projects. Wenatchee River spring-run chinook and Similkameen River summer-run chinook estimates were absent. Recruits-per-spawner for hatchery and natural spawning in Tucannon spring-run chinook (figure 6.1) is representative of the year-to-year variation observed in Columbia River Basin salmon. The average recruits-per-spawner for hatchery spawning ranged from 2.52 in Tucannon River spring-run chinook to 8.49 in Hood River winter-run steelhead. In contrast the average recruits-per-spawner for natural spawning ranged from under

0.50 in Imnaha River summer-run steelhead to 0.94 in Hood River winter-run steelhead. There was a hatchery: natural advantage of almost nine-fold in the Hood River winter-run steelhead. During the late 1980s and 1990s many naturally spawning populations were not replacing themselves even though supplementation was underway (i.e., Rw < 1.0) while most hatcheries were (but not all every year). Based on only two spawning years (1997 and 1998 broods), the Yakima River spring-run program demonstrates that large values are possible in very good production years. Adult-to-adult production for hatchery culture was 22 and 33: 1, compared to approximately 3 and 8: 1 from a supplemented natural and reference populations.

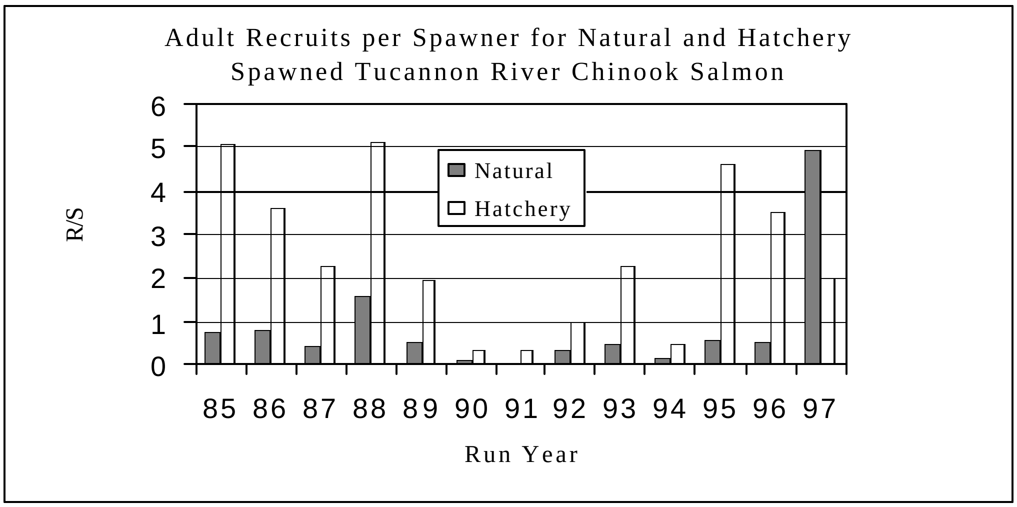

Figure 6.1. Recruits-per-spawner for hatchery and natural spawning spring-run chinook salmon in the Tucannon River from 1985 through 1997.

4. *The ability of individual supplementation projects to consistently achieve their smolt production goals is variable.* The Imnaha, Tucannon, and Wenatchee River spring-run chinook salmon have generally not achieved smolt production goals because adult broodstock were unavailable. Because of broodstock availability, the Hood River winter-run steelhead smolt production goal was reduced from 85,000 to 60,000, and this reduced production goal has been largely met. To try to improve smolt quality by decreasing hatchery rearing densities, the Umatilla summer-run steelhead smolt production was reduced from 210,000 to 150,000 and these reduced production targets have largely been met. The Imnaha summer-run steelhead has regularly met the 330,000 smolt production goal since 1987, but to do so required using 90% hatchery-origin females in the broodstock. The Similkameen summer-run chinook project has met its smolt release targets. But as with Imnaha steelhead, hatchery-origin adults have been an appreciable proportion of the broodstock.

5. Because SARs for hatchery-produced smolts is substantially lower than program target figures, the yield of adult fish has not typically achieved performance standards in the late 1980s through the mid 1990s. Table 6.3 below provides SAR performance standards and the actual SAR values achieved, including the performance standards for the numbers of returning adults, and those achieved for several projects.

Table 6.3. SAR and adult abundance performance standards and those achieved for Columbia River Basin salmon and steelhead.

	SAR		Adult Production	
	Standard (%)	Observed[1]	Standard	Observed[1]
Hood - SH	4.5	0.68	3800	320
Umatilla - SH	2.7	0.40	1500	592
Imnaha - Ch	0.65	------	3210	462
Imnaha - SH	0.61	0.27	2000	849
Tucannon - Ch	0.87	0.15	1152	432

1. Based on different sets of years for different projects. See summaries in the Appendix for additional details.

6. Among the programs that we assessed, the presence of appreciable numbers of hatchery-origin adults on the spawning grounds in the late 1980s and early 1990s did not prevent declines in the abundance of natural-origin spawning adults in the mid 1990s. In a summary assessment of supplementation in 22 Pacific salmon populations, including 12 in the Columbia River Basin, Waples et al. (2002) came to a similar conclusion. Ten of the populations continued to decline following supplementation, nine increased, while for three there were no data. Supplemented and unsupplemented reference populations had similar trends in abundance in four of six comparisons. In one comparison the reference performed better than the supplemented treatment and in another the treatment performed better than the reference. It is not clear whether natural-origin or total salmon population abundance was evaluated in the assessment. In our review Tucannon, Imnaha, and Wenatchee spring-run chinook and Imnaha summer-run steelhead (Figure 6.2) natural populations declined despite large numbers of hatchery-origin adults available for spawning.

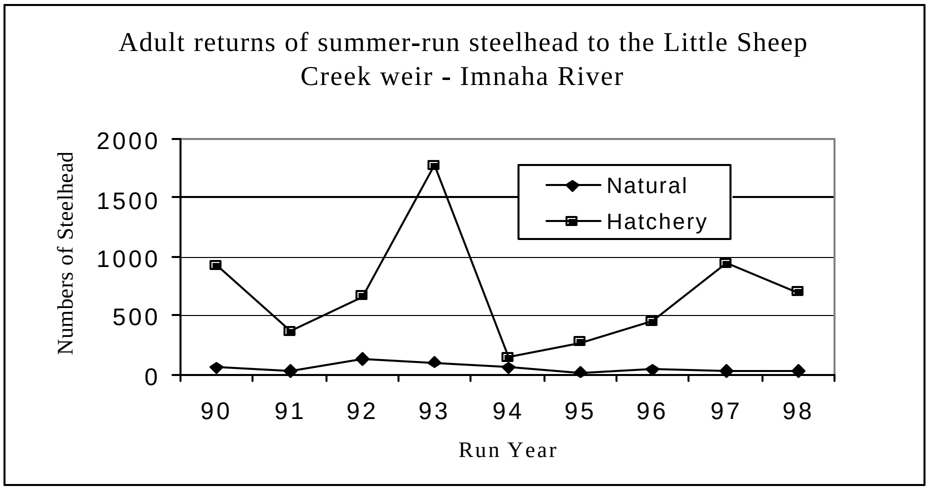

Figure 6.2. Adult returns of summer-run steelhead remain low throughout the 1990s.

7. Beginning with the 2000 run-year, and in some locations perhaps as early as the 1999 run-year, there has been a basinwide increase in the abundance of adult salmon and steelhead in the Columbia River Basin. These increased returns are not uniformly reflected in the assessment above because the data are not yet processed and in reports. Data that have been made available indicate that the increases are not uniform in all programs, every year, or for every stock.

Some of the best evidence of both the increased production and variability among populations is from Yakima River spring chinook (Figure 6.3). Between the 1981 and 1995 spawning years the average smolt to adult survival for Yakima spring-run chinook was 2.2%. For the 1996 spawning year survival increased to 8.4%. In 2000 there was a total return of 12,327 chinook to Roza Dam, more than in any recorded year since 1940. These were predominately naturally produced fish. Similarly, in 2001 substantial numbers of natural-origin adult spring-run chinook returned to Johnson Creek in the Salmon River. Other streams in the subbasin did not see similar increases in adult abundance. In the programs we reviewed, hatchery-origin spring-run chinook salmon increased more dramatically than natural-origin salmon in the Chiwawa River and the opposite was observed in the Tucannon River (Figure 6.4). In general natural-origin steelhead increased more than hatchery-origin steelhead in both the Hood and Umatilla rivers.

Because salmon spend a portion of their life cycle in freshwater and a portion in the ocean, changes in adult spawning recruitment can be affected by natural environmental conditions (drought in freshwater and shifts in ocean productivity in the sea) and management activities (land use practices in freshwater and harvest in the sea) in either environment. Poor marine survival of coho salmon in the Strait of Georgia, Puget Sound, and off the coast from California to Washington after 1989 improved abruptly in 1998 (Beamish et al. 2000). The change in marine survival was largely synchronous over the southern area of coho distribution in the Northeast Pacific suggesting a common environmental cause. Similar recent increases in the abundance of steelhead and chinook salmon are being reported from California north to at least Washington, including the Columbia River Basin. Because of the nearly synchronous and widespread increase, these reported increases are most likely to be attributable to changes in marine productivity rather than to management actions in freshwater.

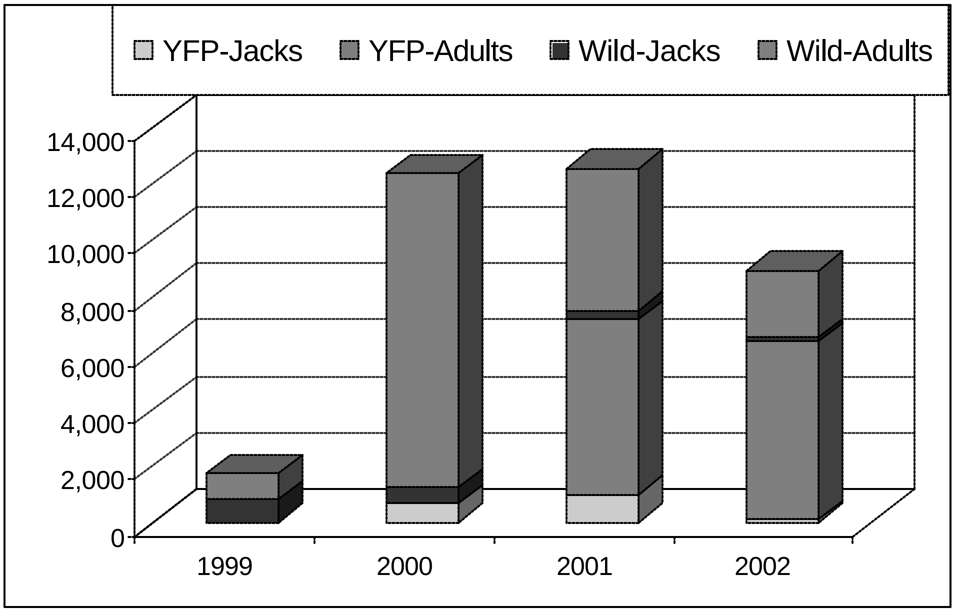

Figure 6.3. Total return of upper Yakima spring chinook at Roza Dam, 1999 to 2002. Returns are identified by naturally spawning (Wild-Jacks and Wild-Adults) chinook and Cle Elum supplementation program (YFP-Jacks and YFP-Adults) chinook. YFP-Jacks for 2002 do not show on the scale, actual value was 86 Jacks, and Wild-Jacks was 133.

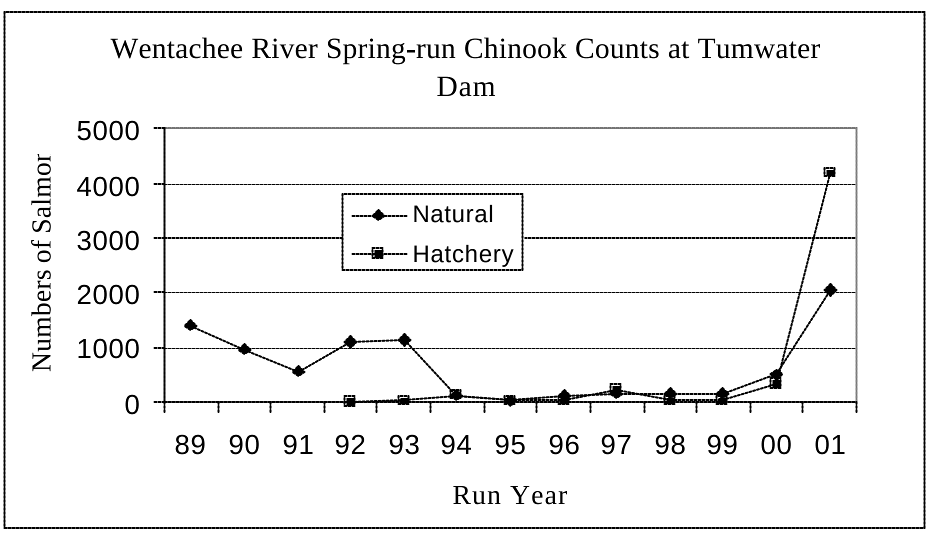

Figure 6.4. Increased spring-run chinook salmon adult returns in the Wenatchee beginning in 2001.

8. Stray hatchery-origin adults from conventional production hatchery programs constitute the majority of adult salmon and steelhead in some locations. This may compromise assessing supplementation projects. As emphasized above in the discussion of the Idaho Supplementation Study statistical design, hatchery-origin adults from conventional production hatcheries routinely stray into a number of both treatment and reference streams in the Clearwater subbasin (Table 6.4). These challenge maintaining an appropriate experimental design to fully evaluate supplementation. These sorts of strays apparently occur throughout the Columbia River Basin. Table 6.5 shows the increase in both the numbers of steelhead strays and their percent of the total run in the Deschutes River in recent years. This type of straying can be controlled in the Hood River and is minimal in other locations such as the Yakima River.

Table 6.4 Average percent of non-ISS chinook salmon carcasses recovered in ISS study streams in the Clearwater subbasin during carcass surveys.1

Stream	Category	Number of Years	Percent Stray Hatchery Adults
American River	Treatment	7	61
Big Flat Creek	Treatment	7	63
Brushy Fork Creek	Control	7	44
Clear Creek	Treatment	7	31
Colt Killed Creek	Treatment	6	64
Crooked Fork Creek	Control	7	58
Crooked River	Treatment	7	30
Eldorado Creek	Control	3	22
Herd Creek	Treatment	4	8
Lolo Creek	Treatment	7	38
Newsome Creek	Treatment	5	44
Papoose	Treatment	7	41
Pete King Creek	Treatment	1	0
Red River	Treatment	7	43
Squaw Creek	Treatment	3	33
White Cap Creek	Control		ND

1. From Lutch et al. (2002).

Table 6.5. Estimated numbers of wild, subbasin hatchery, and out-of-subbasin stray hatchery steelhead migrating past Sherars Falls, Deschutes River, Oregon 1977 - 2000.

Run Year	Wild	Round Butte Hatchery	Stray Hatchery	Total	Percent Out-of-Subbasin Hatchery Stray
1977-78	6,600	6,100	900	13,600	6.62
1978-79	2,800	3,200	300	6,300	4.76
1979-80	4,200	5,400	600	10,200	5.88
1980-81	4,100	5,500	500[a]	10,100	4.95
1981-82	6,900	3,800	1,200[a]	11,900	10.08
1982-83	6,567	3,524	1,249[a]	11,340	11.01
1983-84	8,228[b]	7,250	7,684[a]	23,162	33.18
1984-85	7,721[b]	7,563	3,824[a]	19,108	20.01
1985-86	9,624[b]	7,382	5,056[c]	22,062	22.92
1986-87	6,207[b]	9,064	9,803[c]	25,074	39.10
1987-88	5,367[b]	9,209	8,367	23,943	34.95
1988-89	3,546	3,849	3,909	10,304	37.94
1989-90	4,278	2,758	3,659	10,695	34.21
1990-91	3,653	1,990	2,852	8,495	33.57
1991-92	4,826	3,778	8,409	17,049	49.32
1992-93	904	2,539	4,261	7,704	55.31
1993-94	1,487	1,159	4,293	6,936	61.89
1994-95	482	1,781	4,391	6,654	65.99
1995-96	1,662	2,708	11,855	16,225	73.07
1996-97	3,458	5,932	23,618	33,008	71.55
1997-98	1,820	5,042	17,703	24,465	72.36
1998-99	3,800	3,527	11,110	18,437	60.26
1999-2000	4,790	2,628	13,785	21,203	65.01

a. May include some AD CWT marked steelhead that originated from Warm Spring NFH;
b. May include some unmarked hatchery steelhead outplanted as fry into the Warm Springs River.
c. May include adults from a release of 13,000 smolts from Round Butte Hatchery that were accidentally marked with the same fin clip as steelhead released from other Columbia River Basin hatcheries.

What is largely unevaluated?

1. *Recent contributions of supplementation are largely unevaluated.* Although natural populations that were being supplemented with hatchery-origin adults through the mid-1990s exhibited a continued downward trend in natural-origin adult abundance, supplementation program reports assert that the programs still aided the natural population by providing additional adults for spawning. They conclude that as a consequence these populations were declining more slowly than unsupplemented populations. The validity of that assertion is unassessed, and that would require an experimental design employing unsupplemented reference populations. The ISAB is not aware that any of these programs have been subjected to such an analysis at this time.

2. *The reproductive performance of hatchery-origin adults spawning in the wild is largely unevaluated*. An assumption of supplementation is that the yield of viable offspring from hatchery-origin adults is the sufficient to replace natural-origin adults subtracted to provide broodstock. If hatchery-origin adults produce fewer progeny in comparison to their natural-origin counterparts, the effectiveness of supplementation will be diminished (under certain circumstances supplementation could actually deplete the natural-origin adults). The production of offspring from the hatchery-origin adults must be sufficient to offset the offspring that would have been produced as descendents of the natural-origin adults collected for broodstock in the previous generation.

Breeding generates intense competition among males for mates and among females for spawning sites (Fleming and Petersson, 2001). Natural selection as a consequence of this competition affects morphological traits like body shape and size and life history traits like age of maturation and egg size. Competition between females for spawning sites can delay breeding, displace females to less suitable spawning sites, and destroy redds by superimposition (Fleming and Petersson, 2001). The outcome of this competition can be the production of fewer progeny.

There are demonstrable differences in body shape between hatchery-origin and natural-origin adults. In Columbia River Basin supplementation programs (as elsewhere) hatchery rearing often produces younger but larger smolts compared to the naturally produced cohort. This in turn produces younger and smaller adults with different reproductive traits, a scenario that is observed in the spring-run chinook supplementation programs. Most comparisons of mating between hatchery-origin and natural-origin adults are available only from experimental stream channels.

Because of recent advances in the utility of gene markers, it has become technically feasible to estimate the parentage of large numbers of progeny with good accuracy. Several projects, some underway and others proposed (i.e., BPA Project Proposal 35041 Title: Monitoring the reproductive success of naturally spawning hatchery and natural spring chinook salmon in the Wenatchee, Tucannon, and Kalama Rivers) are beginning to compare the reproductive performance in the wild of hatchery-origin adults with that of natural-origin adults (Table 6.6). These assessments can measure the relative reproductive success of hatchery-origin and natural-origin salmon in both natural and hatchery settings. Furthermore, they can attempt to determine if traits such as run timing, morphology or behavior explain differences in reproductive success between hatchery-origin and natural-origin salmon.

Table 6.6[1.] -- Proposed or ongoing research to evaluate the reproductive success of hatchery-origin adults

Species	Location	Principle Investigator(s)	Status	BPA funded?
steelhead	Kalama R., WA	Hulett, Sharpe – WDFW	Ongoing	No
steelhead	Imnaha R., OR	Moran – NMFS	Ongoing	Yes
steelhead	Hood R., OR	Kostow -- ODFW, Blouin – OSU	Ongoing	No
steelhead	Clearwater R., ID	Reisenbichler – USGS	Ongoing	Yes
steelhead	Wenatchee R., WA	Murdoch, Pearsons, WDFW	Proposed	No
steelhead	Forks Cr., WA	Quinn – UW	Ongoing	No
coho	Minter Cr., WA	Ford – NMFS, Fuss – WDFW	Ongoing	No
coho	Rogue R., OR	Kostow -- ODFW, Blouin – OSU	Proposed	No
chinook	Deschutes R., OR	Reisenbichler – USGS, Young, WDFW	Ongoing	Yes
chinook	Lostine R., OR	Moran – NMFS	Proposed	Yes
chinook	Catherine Cr., OR	Moran – NMFS	Proposed	Yes
chinook	Yakima R., WA	Knudsen, Schroder, Young, Pearsons – WDFW	Ongoing	Yes
chinook	Tucannon R., WA	Bugert, Mendel, Busack, Young – WDFW	Ongoing	Yes

1. Table taken from BPA Project Proposal 35041

Even if hatchery-origin adults are reproductively competent, supplementation could replace, rather than add to, the natural production if carrying capacity limits freshwater production. Assessing whether supplementation is adding to, rather than replacing, natural production requires an experimental design with not only supplemented treatments but also references that exclude hatchery salmon and steelhead.

3. *The longer-term fitness consequences to the naturally spawning population that results from interbreeding with individuals reared as juveniles in a hatchery are largely unevaluated*. This is a legitimate and scientifically fascinating problem facing supplementation. Because only limited experimental work is available to support these theoretical concerns, risk tolerant parties remain optimistic about the efficacy of supplementation. Nevertheless, if the predicted negative fitness consequences are indeed realized, there are two distinct but related impacts. First, the integrated natural-artificial

population would have reduced natural productivity. Columbia River Basin salmon are currently managed under the Endangered Species Act and the performance standard to fulfill the obligations of the 2000 BiOp is population productivity. If a long-term decrease in natural productivity is realized, then the decrease will compromise the improvements in habit needed to reestablish productivity levels as required by the BiOp RPAs. Second, the integrated natural-artificial population is likely to have reduced productivity in the hatchery phase relative to a conventional hatchery program. Consequently, the harvest benefits anticipated from the hatchery production phase may not achieve the levels established during basin planning.

4. *Ecological interactions are largely unevaluated.* The primary focus of the debate on the uncertainty of whether or not supplementation can increase the abundance of natural origin adult recruits has been the reproductive competence of hatchery-origin adults when spawning in the wild. The ecological conditions required to achieve benefits from supplementation have received considerably less conceptual development or programmatic experiments to address them, with the notable exception of the Yakima species interaction studies (BPA project No.199506424). RASP (1993) and others, including the Council's Fish and Wildlife Program (NPPC 2000), acknowledge that supplementation will not work unless the factors limiting productivity and abundance are addressed. If insufficient attention is given to evaluating ecological interactions, there will be an inability to discriminate whether it was intrinsic biological attributes of the species being supplemented, biotic ecological interactions, or habitat limitations that constrained the anticipated increases in natural-origin adult recruits. The ecological interactions need to consider not only habitat carrying capacity within the stream reaches and subbasins where supplementation is being conducted, but also survival through migration routes and species interactions such as competition and predation.

5. *Another source of uncertainty is interaction with other salmon restoration programs in the basin.* Artificial propagation, both conventional production and supplementation, has increased throughout the Columbia River Basin. As more fish are released, and releases are made in new areas, the complexities of interactions increase. For example, in the Salmon River drainage in Idaho, conventional mitigation production releases continue within the watershed where the ISS experiment is being conducted. The extent to which these releases confound the reference and treatment streams is largely undefined. Along with the challenges presented by the confounding effects of other artificial production programs, the streams that are being used for supplementation are also being modified as part of various habitat improvement projects. If great care is not exercised in the choice of location for these activities, the adaptive management opportunities of both the habitat and supplementation activities will be compromised.

There is accumulating evidence of the consequences of the interaction between fish species in the Columbia River Basin. In Salmon River tributaries inhabited by introduced brook trout (*Salvelinus fontinalis*), survival of hatchery-origin chinook salmon juveniles is only half that of the survival in tributaries where brook trout are absent (Levin et al. 2002). The numbers of hatchery steelhead smolts released into the Salmon River is negatively correlated with smolt-to-adult survival of natural spring-run salmon (Levin and Williams 2002). On a basinwide scale, the smolt-to-adult survival of salmon and steelhead is negatively associated with the numbers released during the years when ocean productivity indices are low (Levin et al. 2001). In summary, there is evidence of interactions with deleterious consequences for wild salmon and steelhead at the tributary, subbasin, and basinwide scales.

Captive Broodstock Programs

Since the early 1990s several "captive broodstock" programs have emerged for Pacific salmon populations in the Columbia River basin, and elsewhere in western North America. These programs are appropriately considered a subset of possible supplementation options, since they are intended to integrate natural and artificial production and increase the abundance of naturally spawning fish. In these programs, naturally produced juvenile life stages (e.g., eyed eggs pumped from redds or out-migrating smolts) are collected, reared in captivity to adult hood and then these reproductive adults are used to produce progeny. In some programs adults are returned to the wild to spawn, in others the adults are spawned in captivity and subsequent progeny are released into the natural environment similarly to standard supplementation programs.

Outside of the Columbia River Basin captive broodstock programs have been established for Sacramento winter-run chinook salmon, White River (coastal Washington) spring-run chinook salmon, Dungeness River spring-run chinook salmon and Hood canal coho salmon (Flagg et al. 1995). Within the Columbia River Basin captive broodstock programs are established for Redfish Lake sockeye salmon, and Salmon River (IDFG), Grande Ronde River (ODFW), Tucannon River spring-run chinook salmon in the Snake River and the Wenatchee River (White River) spring-run chinook salmon in the Columbia Cascade province. The Redfish Lake sockeye captive broodstock program was initiated in the early 1990s when less than 10 adult sockeye were returning to the Stanley basin annually. The remaining Snake River spring-run chinook salmon captive broodstock programs are operated in parallel with supplementation programs and were initiated because of the failure of existing supplementation programs to compensate for the rapid decline in salmon abundance.

Captive broodstock programs should be evaluated using the same performance indicators as standard supplementation programs. The anticipated benefits of captive broodstock programs are identical to supplementation, as should be the consideration of genetic risks. The comparative risk of captive broodstock programs and standard supplementation programs will be case specific. For example, the risk of loss of within population genetic variation might be greater for captive broodstock programs because of the low numbers of families represented in the juvenile collections that established the broodstock. However, the ability to genotype individual adults and perform pedigreed mating permits some compensation for this constraint.

Captive broodstock programs are faced with artificial culture obstacles not encountered in traditional supplementation programs. Since the salmon are maintained during their entire life cycle in captivity, the nutritional and cultural requirements to facilitate reproduction must be provided. These are daunting challenges. Nonetheless, for populations like the Redfish Lake sockeye and Sacramento River winter-run chinook *ex situ* captive propagation may be necessary.

Redfish Lake Sockeye Salmon Captive Broodstock Program

Precipitous declines of Snake River sockeye salmon prompted the Idaho Department of Fish and Game (IDFG) to initiate a captive broodstock program in 1991 to attempt to avoid the species extinction.

Broodstock was developed using 16 wild, anadromous adult sockeye salmon that returned to the Stanley Basin and were captured from 1991 to 1998; 26 residual sockeye salmon adults captured in 1992, 1993, and 1995; and 886 wild, outmigrating smolts from Redfish Lake captured from 1991 to1993. Adults are produced at the IDFG Eagle Fish Hatchery and at NOAA-Fisheries facilities in Washington State. The program generates hatchery-produced eggs, juveniles, and adults for supplementation to Stanley Basin waters. Fish culture attributes, juvenile out-migrations and adult returns are monitored and evaluated.

Through 2002 , the IDFG and NOAA Fisheries hatchery programs produced in excess of 860,000 pre-smolts, 158,000 smolts, 880 adults, and 325,000 eyed-eggs for reintroduction to Stanley Basin lakes and tributary streams. From this production, approximately 300,000 hatchery-produced, juvenile sockeye salmon have emigrated from Stanley Basin waters.

Hatchery-produced adult sockeye salmon have been spawned yearly since 1994. Egg survival to the eyed stage of development has been variable (39% to 73%) averaging 55%.

Four strategies to reintroduce sockeye to Stanley Basin lakes are being tested: maturing adults released to spawn naturally, eyed eggs planted in lake shore gravel, pre-smolts released into lakes for over wintering prior to a natural spring migration, and smolts released into the Salmon River.

Six hatchery-produced age-3 jack males and one age-3 jill sockeye salmon returned to Idaho in August and September 1999. All originated from smolts released to the upper Salmon River and to Redfish Lake Creek on April 28 and May 4, 1998.

In 2000, 257 anadromous sockeye salmon returned to the Sawtooth Basin. Traps on Redfish Lake Creek and the upper Salmon River at the Sawtooth Fish Hatchery intercepted 119 and 124 adults, respectively. Additionally, 14 adult sockeye salmon were observed immediately downstream of the Sawtooth Fish Hatchery trap. Fish were captured between July 22, and September 15, 2000. These adult sockeye salmon originated from a variety of release strategies including: 1) 1996 pre-spawn adult and eyed-egg releases in Redfish Lake, 2) 1997 pre-smolt releases in Redfish, Alturas, and

Pettit lakes, and 3) 1998 smolt releases in Redfish Lake Creek and the upper Salmon River.

One hundred-ninety of the 243 fish examined in 2000 were produced from spawning performed at the Big Beef Creek Hatchery. Eyed-eggs were transferred to the Oregon Department of Fish and Wildlife Bonneville Fish Hatchery for hatch and rearing to release. Fish were released to Redfish Lake Creek and the upper Salmon River as smolts in 1998.

In 2001, 26 sockeye salmon returned to the Stanley basin and in 2002, 22. Seven salmon were captured at Sawtooth, eight at Redfish Lake Creek, and seven were observed below the Sawtooth trap but not collected.

Ten, four, and six, un-marked adults have returned to the Redfish Lake Creek weir or Sawtooth trap in 2000, 2001, and 2002 respectively. The origin of the un-marked adults is yet to be validated. Tissue samples have been collected from all adults spawned in Idaho and Washington hatcheries as well as from anadromous adults released for natural spawning. Beginning in 2000, tissue samples have been collected from all un-marked outmigrants from Stanley Basin lakes. Parentage assignment using DNA markers should begin to be available in FY2004.

The strategy of maintaining the broodstocks, and rearing progeny for reintroduction, at multiple locations is to avoid catastrophic loss owing to mechanical failures or diseases at a hatchery. This risk management strategy was useful in 2002 when more than 43,000 sockeye salmon smolts being reared at Bonneville Hatchery near Cascade Locks were destroyed because INH (infectious hematopoietic necrosis) virus was detected in fingerling pre-smolts in April.

Grande Ronde Spring-run Chinook Salmon

In response to severely declining runs of chinook salmon in the Grande Ronde Basin, a captive broodstock program was initiated in 1995 to prevent extirpation of endemic chinook populations in the Lostine River (LR), upper Grande Ronde River (GR) and Catherine Creek (CC).

In this captive broodstock program up to 500 naturally-produced parr are collected annually from each stream. Eight cohorts (1994-2001) have been collected from Catherine Creek and Lostine River. Only six cohorts have been collected from Grande Ronde River (1994, 1996-1998, 2000, 2001) because of a lack of fish in the river in 1996 and 2000. These juveniles are reared to the smolt stage at Lookingglass Fish Hatchery (LFH) under either an accelerated or simulated natural pre-smolt growth regime. For the 1994-1999 cohorts, two-thirds of these smolts were transferred to Bonneville Fish Hatchery (BOH) and reared in freshwater and one-third to NOAA-Fisheries Manchester Marine Laboratory (MML) and reared in saltwater. Beginning with the 2000 cohort, one half of the fish have been sent to each post-smolt rearing facility.

At maturity, saltwater adults are transported from MML to BOH where all fish are spawned. Eggs are incubated at Oxbow Fish Hatchery (OFH) to the eyed stage when they are transferred to Irrigon Fish Hatchery (IFH), where they hatch. Fry are transported to LFH for rearing to the smolt stage. Resulting F_1 smolts are acclimated at and released into the stream of parental origin.

Juveniles reared in captivity to adults have been spawned from 1998-2002. Full production is intended to provide sufficient smolts to ensure threshold escapement levels of 150 spawners in each parental stream. Therefore, release levels are based on management goals and the number of wild spawners present. Other potential release strategies include outplanting of adults, eggs or parr produced in excess of smolt needs, directly into unseeded historic production areas within the Grande Ronde basin. Parr were released in 2002 and 2003 and probably will be released in 2004.

In March, Captive Broodstock offspring are transported to acclimation facilities located within the area of their parent's natal stream where wild fish spawn. In April, after a 14-30 day period of acclimation, fish are released into the stream, volitionally at first, with the remaining fish being forced out. Four cohorts of F_1's have been released and two groups of age 3 fish (jacks) have returned (2001 and 2002) and one group of age 4 fish (2002). Additional years of fish returning to the streams are necessary to evaluate survival rates. However, the return rates of 0.2-0.8% of 1998 cohort fish (ages 3 and 4, only) are viewed as encouraging.

The sponsor's summary conclusions of the Grande Ronde captive rearing efforts todate follow:

Initial Field Collections for establishing broodstock

1. Parr collections of 500 fish per stream generally were met.
2. Accelerated growth pre-smolts produced larger smolts but grew slower than expected.
3. Parr-to-smolt survival was above 95%.

Broodstock Performance

1. Smolt-to-spawn survival was variable but slightly above 55%.
2. Sex ratio was 1:1.
3. Saltwater groups grew slower than freshwater groups.
4. Pre-smolt rearing regime affected age at maturity but not size at maturity.
5. Males matured earlier than expected - most at age 3.
6. Females matured later than expected - fewer age 4 and more age 5.
7. Captive broodstock spawn about 3 weeks later than wild fish.
8. Mean fecundity and the number of eyed eggs was lower (~ 50%) than expected for ages 4 and 5 females.

F_1 Captive Broodstock Performance

1. Survival to eye-up was greater than the 75% expected.
2. Egg-to-smolt survival was generally lower than the 80% expected.
3. Smolt production was generally below the 150,000 expected but smolt production has been limited at times by management objectives.
4. Outmigration timing of captive broodstock progeny was similar to that of wild salmon, but survival to Snake/Columbia River dams was lower than wild salmon.
5. F_1 (ages 3 and 4, only) return rate ranged from 0.2% (Grande Ronde) to 0.8% (Lostine River) for 1998 cohort.

Tucannon Spring-run Chinook Salmon

Adult returns of spring-run chinook salmon to the Tucannon River ranged from 400 - 750 between 1985 and 1993. In 1994 adult escapement was under 150, and in 1995 was estimated to be only 54 salmon. In 1997, WDFW and the co-managers believed that extreme intervention (captive broodstock) was called for to prevent extinction. This captive broodstock project was planned to be short-term (ending in 2008) to reduce potential negative genetic risks.

This intent of this program is to produce additional hatchery smolts for release into the Tucannon River between 2002 and 2008, concurrently with the existing supplementation program begun in 1985. The supplementation program requires collection of 100 salmon from the Tucannon River (50 natural and 50 hatchery), to produce 132,000 smolts for release at 15 fish/lb. Alone, the Tucannon River supplementation program has not been able to prevent the continued decline in abundance of Tucannon River spring-run chinook.

The captive broodstock program is projected to produce approximately 290,000 eggs on an annual basis once three brood years have obtained maturity. With an estimated egg viability of 70% and estimated fry to smolt survival rate of 70-80%, WDFW has estimated 150,000 smolts (15 fish/lb) will be available for release into the Tucannon River from Curl Lake Acclimation Pond. Smolt production of that magnitude could double the current spring chinook smolt releases into the Tucannon River. Based on smolt to adult survival rates of hatchery spring chinook in the Tucannon River, WDFW estimates that 240-280 adult fish will return from each brood year. Combined with the standard supplementation program, hatchery origin spring chinook runs in the Tucannon River could reach 500-600 fish/year between 2005 and 2010. These returning captive brood origin adults will be left in the river to spawn naturally to increase natural production in the Tucannon River.

In this captive broodstock program 80 progeny from between 15-30 distinct family groups (1200 individuals/brood year (BY)) generated by the standard supplementation program will be retained and reared to maturity at Lyons Ferry Hatchery. At one year of age, 30 fish/family will be retained for final rearing (450/brood year). Wild x wild, and wild x hatchery crosses will be selected over hatchery x hatchery crosses. Captive broodstock collections are intended from the 1997-2001 brood years. As of January 1, 2003, there were 11 BY 1998, 194 BY 1999, 314 BY 2000, and 447 BY 2001 fish rearing at Lyons Ferry hatchery.

The 2002 eggtake from the 1997 BY (Age 5) was 13,176 eggs from 10 ripe females. Egg survival was 22%. Mean fecundity based on the 5 fully spawned females was 1,803 eggs/female. The 2002 eggtake from the 1998 brood year (Age 4) was 143,709 eggs from 93 females. Egg survival was 29%. Mean fecundity based on the 81 fully spawned females was 1,650 eggs/female. The 2002 eggtake from the 1999 BY (Age 3) was 19,659 eggs from 18 ripe females. Egg survival was 55%. Mean fecundity based on the 18 fully spawned fish was 1,092 eggs/female. These progeny will be marked for evaluation and then released in the Tucannon River. Gamete quality is apparently insufficient to provide the target egg viability of 70%.

The first adult returns (jacks) from the captive broodstock program are expected to return to the Tucannon River in 2003.

Captive Rearing Initiative for Salmon River Chinook Salmon

The IDFG initiated the Captive Rearing Project for Salmon River Chinook Salmon to investigate using an adult reintroduction strategy rather than the juvenile introduction strategy used in the Grande Ronde River and Tucannon River captive-rearing projects.

The project requires developing culture techniques to produce adult salmon with behavioral, morphological, and physiological characteristics to successfully interact with and breed with wild individuals. Field monitoring is used to document behavioral interactions, spawn timing, success of redds spawned by captive-reared individuals, and to assess if changes in culture technique result in the desired changes in reproductive behavior or performance. The chinook project was initiated in 1995 with the collection of parr from the Lemhi, East Fork Salmon, and West Fork Yankee Fork Salmon Rivers. Because of disease, parasite infestations, and slow growth in wild caught juveniles, eyed-eggs have been hydraulically pumped from natural redds to provide ongoing broodstock for the program since 1999. Through brood year 2002, 1143 Lemhi River, 1950 West Fork Yankee Fork Salmon River, and 2071 East Fork Salmon River parr or eggs have been collected for rearing to adulthood.

Juvenile fish or eggs are reared in freshwater at the Eagle Fish Hatchery until they reach the smolt stage. At the smolt stage a portion of each cohort is transferred to NOAA Fisheries Manchester Marine Laboratory seawater rearing facility in Manchester, Washington.

Captive-reared adult chinook salmon are smaller in size, compared to either their anadromous counterparts or conventionally reared hatchery-origin individuals with an anadromous component to their life-cycle. For example, growth rates of brood year 1994 chinook salmon reared in freshwater and saltwater were similar, but maturing fish from each group were generally smaller than their ocean reared conspecifics. Inventories conducted between June and September 1996-1998 indicated that captive-reared fish had grown to approximately 200, 380, and 520 mm fork length in each year, respectively. In contrast, ocean reared spring/summer chinook salmon returning to the Columbia River basin between 1991 and 1996 generally averaged 740-800 mm fork length (Fryer 1998).

To evaluate reproduction (e.g., maturation timing, gamete quality, egg survival to eyed stage of development) by captive-reared adult chinook salmon, individuals were spawned at the Eagle Fish Hatchery. Captive-reared adult chinook salmon produced fewer eggs, and had reduced fertilization relative to than their anadromous counterpart. Egg quality is greater in saltwater reared individuals than in freshwater reared individuals and sperm quality was greater in fresh milt than in cryo-preserved milt.

Chinook salmon have been reintroduced into the Lemhi, West Fork Yankee Fork, or East Fork Salmon River(s) or tributary streams in 1997 (9 males), 1998 (28 males, 84 females), 1999 (30 males, 39 females), 2000 (24 males, 48 females), 2001 (43 males, 46 females), and 2002 (247 males, 91 females, 9 unknown). Based on behavioral observations, inspection of carcasses, and excavation of redds to search for viable eggs, several limitations associated with the reintroduced captive-reared chinook salmon have been identified:

1. the limited availability of age 4 and age 5 captive-reared males,

2. asynchronous spawn timing for captive-reared and wild/natural chinook salmon, and incomplete or arrested maturation and ovulation in captive-reared females,

3. questionable gamete quality,

4. insufficient physical ability of captive-reared adults to negotiate natural stream conditions, construct successful redds, and compete with other species for spawning privileges.

In culture, greater proportions of age 2 and age 3 males mutature than age 2 and 3 wild/natural males counterparts.

Physical performance deficiencies in captive-reared adult chinook salmon were present. Based on observations during spawning, captive-reared adults were less robust physically than their wild/natural counterparts. As a result, the selection of appropriate spawning habitat was likely compromised as fish "settle" for locations that suit their physical limitations. Associated with this suspected dysfunction was the potential for adults to build shallow or poorly armored redds that place deposited eggs in jeopardy of being "scoured out".

The following are examples of the information documenting the reduced vigor of captive-reared adult salmon. In 1998, four redds constructed by captive-reared adults were identified in the West Fork Yankee Fork Salmon River between September 3 and September 27. Wild/natural chinook salmon were observed in and above the study section but appeared to have completed spawning prior to the release of captive-reared adults. Five female carcasses were recovered, four appeared to have not ovulated and spawned while the fifth female appeared to have successfully spawned (<10% retained eggs; Hassemer et al. 1999). In the Lemhi River in 1998 seven captive-reared female chinook salmon carcasses were recovered. Three had failed to ovulate and spawn while the remaining four fish appeared to have partially spawned. Egg retention for these four females was estimated at approximately 50%.

In Bear Valley Creek in 1999, 11 female carcasses were recovered from captive-reared adults. Nine were examined for retained eggs. Five (56%) appeared to have spawned and deposited the majority of their eggs (the mean number of retained eggs for these five females was 17.2; range three to 30 eggs). One partially spawned female was recovered with 698 retained eggs and three females were recovered that appeared to have died before spawning (mean retained eggs = 1,536, range 1,175 to 1,933)

Eggs recovered from redds in Big Springs Creek in 2000 verifed that captive-reared adults deposited eggs successfully in 13 of the 15 redds. However, only 21% of the 440 eggs were viable. A large percentage of eggs were found to be unfertilized.

ISAB Summary Assessment of Captive Broodstock/Rearing

The BPA funded captive broodstock/rearing programs in the Columbia River Basin have had some noteable successes. In general however, positive outcomes from captive rearing have been constrained by technological and biological limitations. The successes include collecting fry and eggs and rearing these life-stages to adult hood, release of juveniles and their return as adults, and release of adults with some evidence of their subsequent reproduction in the wild. Fish culturists and managers involved in these projects are understandably encouraged by these results. The technological and biological limitations have included smaller adult size and lower egg viability, asynchronous maturation of sexes, delayed age of maturation, water supply disruptions, diseases in wild caught juveniles, and destruction of several thousand smolts because of a viral infection.

From a fish culture perspective the successes are gratifying and the limitations are challenges to further develop technological capabilities. As a management tool to delay extinction of lineages that can not be replaced by migration or transplanting from other extant populations, the strategy has merit. Clearly in the case of Redfish Lake sockeye or Sacramento River winter-run chinook the lack of other options makes captive rearing a reasonable solution. Depending on captive rearing as a primary recovery tool would be premature. The longest running captive broodstock program has returned 7, 257, 26, and 22 adult sockeye salmon to Idaho's Stanley basin. This level of abundance is barely enough to assert that the ESU is not quasi extinct - even as a partially captive population. The ESU could be considered quasi-extinct in the wild. The reasons egg-to-smolt and smolt-to-adult survival are insufficient to rebuild populations above adult-to-adult replacement must be corrected for recovery.

Section 7. Benefit-Risk Assessment and Decision Making

This section addresses questions about how risks and benefits of supplementation are assessed and the application of that assessment to decision making. Specifically, the section responds to the following question posed by NOAA Fisheries.

What is the best way to assess the risks and benefits of supplementation to determine the net effects on natural populations? How can this be used to determine whether a supplementation program should be initiated and if so, on what scale?

Motivation for Risk-Benefit Analyses

The 1994 Fish and Wildlife Program contains language requiring that artificial production programs in the Columbia River Basin meet minimum standards. The Artificial Production Review, which appears as a technical appendix to the Fish and Wildlife Program, contains two recommendations related to the risks of artificial production. The first is that artificial production be implemented within an experimental adaptive management design that aggressively evaluates risks and benefits and addresses scientific uncertainties. The second is that in using artificial propagation, appropriate risk management must be maintained (NPPC 1994; NPPC 1999).

The Washington Department of Fish and Wildlife (WDFW), in implementing the statewide strategy for salmonid recovery, also requires risk-benefit assessments. The WDFW has developed an action plan intended to transform hatcheries from being a risk factor for wild salmon to being a tool for wild stock recovery. The agency recognizes that for hatcheries to be effective recovery tools, managers must be provided with information on the risks and benefits of each proposed hatchery program. They must also operate in a policy context that articulates the level of risks from artificial propagation that are acceptable (WDFW 2000).

As part of its Wild Fish Conservation Policy (now the Native Fish Conservation Policy (ODFW 2002a)) the Oregon Department of Fish and Wildlife (ODFW) reports on the status of wild fish populations every two years. The biennial report updates the list of wild fish populations, presents the first provisional list of gene conservation groups, and assesses the status of each group. The status assessment categories include population size, stability, extinction, fragmentation and isolation, losses of genetic variation, breeding and survival failure, impacts of hatchery programs including both within species interactions and species introductions, risks due to harvest and habitat management problems, and identification of species and subspecies with limited world distribution (ODFW 1995).

In a March 2002 discussion of the Native Fish Conservation Policy, an Oregon Fish and Wildlife Commission Subcommittee attempted to determine the appropriate default position when information is inadequate to accurately predict the effect of a management action. In that discussion, the Subcommittee recognized that perfect information will never be available for management decisions. Instead, ODFW staff will be expected to provide the best scientific information available to evaluate the risks. Balancing risk in the face of uncertainty is the Commission's job (ODFW 2002b). Here a clear distinction is made between risk assessment and risk management.

The federal Endangered Species Act sets a stringent burden of proof to demonstrate that a perceived threat (identified as a potential cause of "jeopardy") will not cause harm. In other words, the default position in a Biological Opinion is that in the absence of strong evidence it is assumed that the perceived threat will cause harm to the listed population.

Definition and Conceptual Origins of Risk-Benefit Analysis

Terms describing components and variants of risk assessment are often used interchangeably. However, distinctions between the various types are relevant to understanding the approach and scope of the analysis. Risk assessment and its variants are usefully defined by Suter (1993) and Wilson and Crouch (2001).

Analysis: formal, usually quantitative determination of effects of an action.
Assessment: combination of analysis with policy-related activities such as identification of issues and comparison of risks and benefits.
Ecological risk analysis: determination of probability and magnitude of adverse effects of environmental hazards on non-human biota.
Ecological risk assessment: Process of defining and quantifying risks to no-human biota and determining the acceptability of those risks.
Environmental impact assessment: assessment of the consequences of proposed government action as an aid to decision making. Required of federal agencies by the National Environmental Policy Act of 1970 (NEPA).
Risk-benefit analysis: a systematic comparison of the risks of a given action to its related benefits (Wilson and Crouch 2001).
Risk management: process of deciding which actions to take in response to a risk.

Common usage of "risk", found elsewhere in this report, defines risk as the probability and magnitude of adverse effects. A risk-benefit analysis defines and measures both risks and expected benefits so that the tradeoffs among them may be evaluated. This evaluation is intended to inform a management decision as to whether an action is likely to impose greater or fewer risks than the benefits it will generate; i.e., whether the risk of taking that action is acceptable. Risk-benefit analysis is an amalgam of risk assessment and cost-benefit analysis now required for various environmental management actions in the Columbia River Basin.

Risk-benefit analysis is an extension of risk assessment, which is a process of assigning probabilities and magnitudes to the adverse impacts of human actions (Suter et al.1995). The subjects of risk assessments are many, ranging from human health effects of exposure to chemicals to transportation safety rules. Ecological risk assessment, more specifically, is a process of estimating the probability of undesired effects of human actions on animals and their ecosystems. Developed in the mid-1980s to provide a basis for environmental decision-making, it was derived from methods used in human risk assessment, environmental hazard assessment, and environmental impact assessment (Suter et al. 2000.)

Risk-benefit analyses comprise not only assessment of existing risks but also predictions of future risks under different environmental management assumptions. They also contain an assessment of the economic and other consequences of alternative risk management strategies (Hampshire Research Institute n.d).

The use of risk assessment as a tool for environmental decision-making is an acknowledgement of uncertainty about the impacts of actions, the risks that are contained in those actions, and the costs of preventing or remediating those actions. The purpose of ecological risk assessment is to provide scientifically credible evaluations of the effects of human activities. To evaluate effects requires that the aspect of the environment in question and the nature and significance of changes to the environment be defined in operational terms (Suter 1993.)

Because it is quantitative, systematic, transparent and formalized, risk assessment can improve the rigor of environmental decision-making. It offers the advantages of a quantitative basis for comparing and prioritizing risks, it provides a systematic framework to prioritize research, it explicitly acknowledges uncertainty about future environmental states, it focuses on clear measurable endpoints, it estimates probabilities and magnitudes of effects according to formal quantitative methods that allow comparison and replication, and it separates the estimation of risks from the management of those risks (Suter et al. 1995.)

A standard framework for conducting ecological risk assessments has evolved from a National Research Council framework for human health risk assessment to the EPA version represented in Guidelines for Ecological Risk Assessment issued in 1998 (Suter et al. 2000; EPA 1998). Various documents on ecological risk analysis tools and applications developed at the Oak Ridge National Laboratory are available on their website [www.esd.ornl.gov/programs/ecorisk/ecorisk.html].

Reports issued in the mid-1990s by National Research Council Committees and the Commission on Risk Assessment and Risk Management [an EPA advisory group established under the 1990 Clean Air Act amendments; disbanded in 1997 (www.riskworld.com)] responding to criticisms that risk assessment as practiced was incomprehensible and biased, recommended that these criticisms be addressed, in part, through greater public involvement in the process (Bell and Wilson 2000.)

It is widely recognized that environmental risk cannot be eliminated. Risk assessment has continued to evolve in the direction of a mechanism to represent the best available scientific information about risks of alternative actions to those who represent public values in decision making. It is policy makers, not risk assessors, who decide about acceptable levels of risk (Adams and Hairston 1995; Bell and Wilson 2000.)

Research on the psychology of risk has added insights into strategies for risk communication (Hance et al. 1998). Risks, from the human perspective, can be catastrophic, or pervasive, voluntary or involuntary. Catastrophic risks tend to attract the greatest attention, while involuntary risks are often the least palatable (Adams and Hairston 1995). Risks difficult to observe and without immediate impact on people, such as those represented by supplementation, require more studied approaches to communication.

Many environmental problems are characterized by uncertainty and unclear risks, where remediation costs are high and the benefits in investment not necessarily obvious. Risk analysis has helped environmental policymakers evaluate alternate approaches to solving these complex problems (Tversky and Kahneman 1981). For example, the EPA developed a risk analysis to assess the risk of using chlorine gas to disinfect drinking water (Bell and Wilson 2000.)

Probability and Risk

In this section we use risk according to its more formal definition. Risk is the relationship between the probability of a harmful effect and the magnitude of that effect. Probability is a central feature of risk: with certainty that the adverse effect will or will not occur ($p = 1$; $p = 0$) there is no need to make the decision on the basis of risk, since the decision can simply be based on a reliable prediction (Suter 1993). However, probability alone does not constitute risk. Risk is also a function of the severity (cost) associated with the adverse effect. This means that there are always two components to uncertain management action: the probabilities of each outcome and the costs of each possible outcome (Wilson and Crouch 2001; Goodman 2002).

Risks can only be estimated, not measured. Risk analysis differs from impact assessments by its formal quantitative consideration of uncertainties and the expression of the final estimated effect as a probability (Bartell et al. 1992). Goodman (2002) describes the different schools of thought concerning the meaning of probability:

Subjectivist, or Subjective Bayesian: probability is an expression of the strength of a belief. Because it is subjective, it cannot form the basis of any but private decision making.

Frequentist: under imagined repeated sampling, a frequency distribution of outcomes for the universe of cases is what gives meaning to the probability of a single case. Since it is an imagined distribution, it fails to correspond to actual frequencies. Suter (1993) agrees with the limitations of frequentist concepts of risk, noting that they have limited applicability to ecological risk assessments where endpoints are levels of effects on populations or ecosystem properties, rather then on individual components.

Empirical Bayes: a universe of empirical cases is narrowed to data representing the case of interest using Bayesian calculations, combining the best of the frequentist and Bayesian inference approaches.

Goodman argues for the utility of this approach to probability in the case of environmental decision-making because it stresses a probability distribution inferred from data. Correctly calculated probabilities are then conditional on data and on the extent of knowledge.

Suter et al. (2000) note that a reason Bayesian statistics is appealing in assessing risk is the assumption concerning the relationship between the data and the model. The use of frequentist statistics assumes that repeated samples vary but the model is fully specified.

Bayesian statistics, in contrast, assumes that the sample is fixed, but the model is uncertain. This is effectively the situation presented by data from a sample for which there is uncertainty about the population distribution and the variability of that distribution. With simulation models, the specification of variability and associated uncertainty is done by nested Monte Carlo analysis (Suter et al. 2000).

Distinguishing risk analysis from impact assessments is its formal quantitative consideration of uncertainties and the expression of the final estimated effect as a probability. The estimation of ecological risk is influenced by a number of uncertainties, the most crucial of which may be the difficulty in identifying critical endpoints and the incomplete understanding of ecosystem processes. Incomplete understanding limits the ability to model the dynamics of ecological systems, a factor that constrains confidence in risk assessments (Bartell et al. 1992).

Measuring Benefits

The benefits of an environmental action are conceptually similar to risks in that they also have some degree of uncertainty associated with them. Benefits are expected positive outcomes associated with an action, meaning that benefits are estimated as the relationship between the probability of a positive outcome and the magnitude of the effect. For both benefits and costs, the value of the outcome can be measured in economic terms or in policy terms (e.g. % increase in habitat use) (Wilson and Crouch 2001; Goodman 2002).

It is generally the case in ecological risk assessments and in risk-benefit analyses that far more attention is paid to estimating the risks of an action than to estimating the potential benefits of an action. The primary interest remains in categorizing risks according to their magnitude. In ecological risk assessment this appears to be either because the benefits of restoration or mitigation are unquestioned and assumed to be obvious on their face or that the action is dictated by a policy derived from an expected benefit, and the analytical task remains assessing the risks of alternative actions taken to achieve the policy objective. The latter approach was taken by the Northwest Power Planning Council's Independent Economic Analysis Board (IEAB) in its recent economic analysis of artificial production, in which it analyzed the cost-effectiveness of artificial production facilities, rather than the costs and benefits of artificial production (IEAB 2002).

In the case of an uncertain prospect like supplementation, uncertainty surrounds both risks and benefits. The policy question is whether the potential benefits of a proposed action are large enough to outweigh the risks. From the policy perspective, an efficient action – one that makes the best use of public resources – is one that maximizes net benefit. Acceptable actions are those for which expected benefits are larger than the expected costs (Tietenberg 1988).

There is a time element to benefit, as there is for risk. There is usually a time lag between the time of the action and the cost or benefit of the outcome. There will be a stream of risks and benefits over time that, for the purpose of decision-making, it is useful to express in a common currency. Conceptually, the value of a particular action becomes the value of the future net benefits of that action (benefits reduced by costs and risks) expressed in terms discounted to the present. This is the net present value, which, over the time horizon of analysis, is discounted by some rate at which we hold future costs and benefits to be less valuable than those in the present. In the simplest possible case the criteria for decision-making becomes a positive net present value (Wilson and Crouch 2001).

Of course, decisions are never that simple. The approach outlined above ignores the fact that those who bear costs and receive benefits are likely to be different people over different periods of time, particularly if we are talking about ecological long time horizons. So there is a question of distributional equity among generations because the rate at which future benefits or costs is discounted is a major determinant of how resources are allocated over time. The choice of discount rate for public actions like environmental decisions is a controversial matter, with the extreme position being that future claims to benefits and costs are equal to those in the present, so a discount rate of zero should apply. For benefit-cost analyses of public projects the discount rate is usually standardized by administrative requirement (Tietenberg 1988).

Ecological Risk Assessment in Practice

Concepts Underlying Ecological Risk Assessment

Conceptual models: A conceptual model summarizes the planned assessment approach, hypothesizing ecological risks by describing how actions may affect different ecosystem components, relationships among endpoints, data, methods, and data collection protocols. The development of a conceptual model summarizes the nature of the problem and the type and quantity of information needed to conduct the assessment (Barnthouse and Brown 1994). Investigators at the Environmental Sciences Division of Oak Ridge National Laboratory have developed guidelines for conceptual models for ecological risk assessment (Suter 1996.)

Uncertainty: Uncertainties in risk assessment have three basic sources: stochasticity of natural world; ignorance (imperfect knowledge); and error (mistakes in execution of assessment activities). Uncertainty increases with the hierarchical level of the endpoint because the specificity of knowledge declines. The emphasis on characterizing and quantifying uncertainty is what distinguishes risk assessments from impact assessments (Suter 1990; Bartell et al. 1992; Smith and Shugart 1994).

Smith and Shugart (1994) discuss a large number of uncertainties that can compromise an ecological risk assessment. These include: poor knowledge of the ecological system; incorrect choice of scale, endpoints, or models; extreme variability; unexpected effects; errors in data collection; poor quality control protocols; statistical errors, unknown interactions, misapplication of literature based model parameters; inappropriate extrapolations across endpoints; and poor statistical design.

Suter (1993) describes three types of uncertainty that are of particular interest in ecological risk assessment because they undermine the credibility of a predicted value: natural stochasticity, parameter error, and model error. The first two – variability and parameter error from measurement imprecision – can be addressed in a relatively straightforward way using statistical or mechanistic models, but model error is far more problematic (Suter 1993). Model errors resulting from misspecification are not subject to analysis using straightforward statistical techniques. To deal with uncertainties of this type, Suter notes, requires one of two approaches: first, testing the model through collection of field data or experimentation; or second, comparing alternative model predictions to observed data. The presence of model error is a reason for alternative approaches to ecological risk assessment that take advantage of available data.

Endpoints: An assessment endpoint is a formal expression of the ecological components likely to be affected by the action - the environmental values to be protected - defined in either deterministic or probabilistic terms. Defining an endpoint requires identifying attributes of the environment that are considered at risk and specifying those attributes in measurable terms (Suter 1993). The best assessment endpoints are those for which there are well-developed test methods, field measurement techniques, and predictive models (Suter 1989). According to Suter et al. (2000), any ecological assessment endpoint can be expressed as a probability, given either variability or uncertainty about exposure or effects, but ecological risk assessment endpoints have typically been too poorly specified for probabilistic considerations to arise. A notable exception is Population Viability Analysis (PVA), in which the endpoint is the probability of extinction of a population given certain management actions.

Scale: Temporal and spatial scale, as well as the level of organization, are strong influences on the usefulness and relevance of a particular endpoint. The mismatch of scale between the action taken and the response of an endpoint of influence can be an important hindrance to assessing effects. The ecological significance of the endpoint rests in large part on the choice of appropriate scale (Harwell et al. 1994).

Effects characterization: Response relationships of the direct and indirect effects of actions on endpoints, or the patterns of response to one or more actions, are a major part of an ecological risk assessment. The conceptual model forms the basis for approaches to developing stressor-response profiles used in an ecological response analysis (Sheehan and Loucks 1994).

Steps of an Ecological Risk Assessment

Problem formulation: developing the conceptual model. Problem formulation is the initial planning and scoping process that defines the feasibility, scope and objectives of the risk assessment. It also, through a systematic process of considering the objectives and scope of the assessment, establishes information needs. Problem formulation begins with establishing the regulatory and physical context within which the assessment will take place. It articulates the management issues of concern. It then defines the boundary of the assessment consideration, the actions of concern, the hypothesized effects, measures of those effects and the assessment endpoints (EPA 1993).

The exercise in problem formulation involves several activities. The scale – both temporal and spatial – over which the assessment will take place must be chosen. What is the spatial unit of analysis (individual, stock, population)? What are the spatial boundaries of concern (stream reach, watershed, subbasin)? What is the hypothesized relationship between actions and effects (the “dose-response” relationship; the vulnerabilities)? Are there multiple stressors that may confound the evaluation of effects? Are there likely to be indirect effects? What are the relevant and possible measures of risk (Currens 1992; EPA 1993; Suter et al. 2000)?

The specification of data quality objectives is a useful device for the development of a decision-oriented problem statement, decision rules, acceptable levels of decision error and assessment design (Quality Assurance Management Staff 1994, cited in Suter et al. 2000).

The selection of assessment endpoints is motivated by the environmental values to be protected. Endpoints may be selected according to different criteria ranging from policy goals, to ecological relevance; susceptibility; or other practical considerations such as operational practicality. Some common problems with ecological endpoints are that they are often vague, not directly related to the action to be taken, and misrepresent the value of concern (Currens 1992; EPA 1998; Suter et al. 2000).

Problem formulation also includes the development of a plan for analyzing effects. Suter et al. (2000) identify a number of considerations in selecting measures of effects: do they correspond to an assessment endpoint? Can they be quantitatively related to an assessment endpoint? Do data already exist, or are they readily obtainable? Are effects measured at the appropriate temporal and spatial scale? Are they appropriate to the actions taken? Do effects have low enough natural variability to be able to isolate the effect of an action? Are they broadly applicable across reference sites and standardized across studies?

Analysis: Analysis includes the technical evaluation of the management action (exposure) and its effects. To characterize exposure, the spatial and temporal distribution of the management action and its interaction with the ecological components of concern is measured or predicted, using life history or other available biological information. How exposure is modeled depends on the purpose of the risk assessment and the information resources available. Life history and other information on the ecological component of concern can be used to characterize exposure. Uncertainty about exposure estimates can be reduced through model validation. To characterize effects, effects are measured and quantitatively related to the causal management action (EPA 1993).

Reference sites - sites without treatment - are necessary as baselines against which to compare the effects of treatment. The properties of endpoints at a reference site serve as reference information for evaluating effects. Reference information can be obtained empirically from a specified reference site, or, in the case of limited site-specific information, from model estimations or from empirical studies of similar sites (Suter et al. 2000). Criteria for the selection of reference sites should be clearly specified (EPA 1993).

Suter (1993) identifies three general categories of assessment methods: physical models, statistical models, and mechanistic models. Physical models are based on laboratory test systems. These could include physical transport models of contaminants or lethality tests of toxic exposure. Statistical models use experimental or observational data to explain the sources of variation through techniques such as regression or principal components analysis. Statistical models are used to estimate functional relationships in order to test hypotheses and extrapolate results. Mechanistic models, describe in quantitative terms the relationship between some phenomenon and its underlying cause in cases where data are insufficient to support statistical estimation. Examples are models of fate and effects, models of population dynamics, and simulations of ecosystems.

Suter et al. (2000) describe a number of techniques for handling uncertainty in the analysis. Safety factors are numerical adjustments to either model parameters or output as insurance against the underestimation of risk. The distribution of parameter values can represent the degree of variability in a parameter. Monte Carlo analysis, an iterative technique that generates a distribution of results is used to obtain information about uncertainty in simulation models. Nested Monte Carlo analysis attempts to separate the influence of variability and uncertainty in the estimation of the probability of an effect. Sensitivity analysis estimates the relative contribution of various parameters to the estimation of effects. Analysis of model uncertainty that arises from the selection of models is conducted by estimating the variance among results of multiple credible models or, in the case of a single model, estimating changes in variance due to changes in model assumptions. Model validation is a process of selecting among alternative approximations (Suter 1993).

Risk Characterization: the third step in risk assessment uses the results of the analysis of the exposure-effects analysis to evaluate the likelihood that adverse effects will occur. The risk characterization includes a summary of the important properties of the analysis: its scale, critical assumptions, key uncertainties and overall strengths and weaknesses in estimating causal linkages and measuring effects. Risks are often characterized qualitatively when quantitative information is lacking. Expert judgment can be used if quantification is infeasible, but this source of information is inherently subjective (Suter 1993). Whatever methodology is used, it should be well specified and documented so that it can be replicated by other analysts, and, ideally, it should allow refinement of risk estimates based on new knowledge (Bartell et al. 1992). The risk characterization concludes with a discussion of the ecological significance of the risks in terms of the types, magnitudes and distribution of effects (Currens 1992; EPA 1993).

The EPA has developed guidelines for the use of probabilistic analysis in risk assessment (EPA 1997b). It recommends a tiered approach to risk assessment that progresses from simpler (deterministic) to more complex (probabilistic) analyses as the risk management situation requires. Monte Carlo analysis, as described above, is the most frequently encountered probabilistic tool for analyzing variability and uncertainty in risk assessments. If employed, the EPA has listed guiding principles for conditions that must be met by the assessment (EPA 1997a). Further guidance for the use of Monte Carlo analysis is found in a special issue of *Human and Ecological Risk Assessment* (Callahan 1996).

Risk-Benefit Assessments of Columbia River Basin Supplementation

We reviewed one concept paper, one risk assessment and four risk-benefit assessments of supplementation projects in the Columbia River Basin. The concept paper is "Toward a Risk/Benefit Analysis for Salmon Supplementation" (Waples and Drake 2002). The risk assessment is "Genetic Variability of the Yakima Fishery Project: A Risk Assessment" (Currens 1993). The risk-benefit assessments are "Nez Perce Tribal Hatchery Benefit Risk Analysis" (Beasley et al. 1999), "Johnson Creek Artificial Propagation and Enhancement Project (JCAPE) Benefit Risk Analysis" (Beasley et al. 2000), "Hood River Steelhead Hatchery Programs Goals, Risk/Benefit Analysis and Assessment of Alternative Operational Protocols" (Kostow et al. 2000), and "Summer Chum Salmon Conservation Initiative: An Implementation Plan to Recover Summer Chum in the Hood Canal and Strait of Juan de Fuca Region" (Ames et al. 2000).

Waples and Drake

Waples and Drake (2002) present a framework for comprehensive risk-benefit analysis for salmon supplementation. Regarding the question of whether to use artificial propagation to supplement natural populations, the authors argue that preceding this decision should be a comprehensive evaluation of potential risks and benefits of proposed action to assess whether the potential benefits of supplementation outweigh the risks. The document outlines the types of risks and benefits that should be considered, makes observations about risks and benefits, and suggests factors to be considered in combining benefits and risks into overall assessment.

The authors use findings from a wide range of literature on supplementation to reach some key conclusions: risks and benefits must be evaluated in the context of particular program goals; it is possible for risks of supplementation to outweigh potential benefits even for populations that face significant demographic and/or genetic risk; risks can be reduced but generally not eliminated; some risks are inversely correlated, so reduction of one may lead to an increase in another; a cautious approach to supplementation is dictated by the unknown effects of fish culture on natural populations, uncertainty about supplementation effects on permanent increases in natural populations and by the difficulty of terminating supplementation; supplementation should be regarded as experimental and carried out within adaptive management framework; methods less invasive than artificial propagation should be used when possible; and supplementation should be integrated with other recovery measures to provide maximum benefit.

The Yakima Fishery Project

Currens (1995) performed a genetic risk assessment of the Yakima supplementation project in 1992. The framework to analyze genetic vulnerability is a tool intended for use as a part of monitoring and evaluation for supplementation. It formed the basis of the guidelines for risk-benefit assessment procedures later developed by the Washington Department of Fish and Wildlife (2000).

Currens uses a different terminology in his discussion of risk. He defines an adverse effect as a hazard, risk as the probability of a hazard, and vulnerability = risk * hazard. The definition of vulnerability is qualitatively the same as other definitions of risk: the relationship between the probability of a harmful effect and the magnitude of that effect.

He uses the framework of various genetic hazards to assess the performance of the supplementation program with regard to genetic components. He calculates resilience and reliability scores for various genetic hazards.

Currens found three major factors in the Yakima project contributed to the expected low performance of supplementation compared to unsupplemented populations: operating procedures and protocols for implementing conservation guidelines did not exist, were inconsistent, or were superficial; decision trees to indicate contingency plans for failure or unanticipated results were few; and there was an absence of training to avoid technical errors.

Currens concludes that although investments have been made in the development of experimental designs to test supplementation methodologies, the lack of explicit well-developed operating guidelines, monitoring and evaluation plans, decision trees or contingency plans result in an absence of safeguards against failure of these experiments. He further concludes that the risk assessment vocabulary has been incorporated into fishery management in such a loose way that multiple definitions and inconsistent usage are common.

Nez Perce Tribal Hatchery Benefit-Risk Analyses

Beasley et al. (1999) list three goals of the Nez Perce tribal hatchery: to preserve genetic, ecological and behavioral attributes of Snake River fall chinook; stimulate the restoration of early-returning fall chinook life history; and, build a naturally-sustaining, fall-early returning fall chinook population capable of supporting sustainable fisheries. The motivation for doing the risk-benefit analysis is the consideration of supplementation as an experimental approach to restoration.

The approach taken in this document is to identify a suite of genetic and ecological risks using Waples (1996) as a guide. Analysis was influenced by conclusions of the Waples paper that if two criteria are met: 1) there is a high short-term risk of extinction; 2) if restoration to habitat is to be accomplished in a short time frame, then the risk-benefit analysis should focus on the choice of appropriate donor stock and on efforts to minimize adverse effects on nearby populations.

The relative importance of the risks is assessed on the basis of a literature review of similar issues. Absence of scientific findings in literature related to various risks is noted. In recognition of the absence of data relevant to evaluate either risks or benefits, a number of experimental studies are proposed.

The analysis also notes that many of the risks outlined by Waples are of a theoretical nature lacking data to estimate the probability of their occurrence. The authors took the approach of analyzing a suite of possible hazards and impacts posed by the hatchery supplementation program by examining experimental and theoretical studies in the context of related management actions. On the basis of the literature review and information on the methods of hatchery operation such as broodstock management and a proposed monitoring and evaluation plan, each risk topic was assigned a value of high, medium, or low in relation to the population of fall chinook within Snake River ESU, and all stocks within the Columbia River Basin.

The authors recognize that some genetic and behavioral changes among population components will occur. They estimate the extent to which losses in fitness will have to occur for supplementation to be detrimental to population and conclude that changes from hatchery rearing are temporary and reversible. The general conclusion of the document is that with some notable exceptions (a potential for variance in reproductive success, artificial selection on direct production traits, indirect artificial selection on fitness traits) there is little or no genetic and ecological risk associated with the Nez Perce Tribal Hatchery program.

The document asserts as substantial benefits of supplementation the reduced risk of extirpation, maintenance of genetic and phenotypic variability within populations, and an increased potential for adaptive radiation into habitat in the Clearwater.

Specifically, for the various risks of supplementation considered by the authors, they conclude:

- Outbreeding depression: unlikely to occur
- Inbreeding depression: low risk
- Loss of within-population diversity: low risk
- Loss of genetic diversity between populations: indeterminate, but likely to have little effect
- Artificial selection: risk minimized by hatchery practices
- Competitive interaction between hatchery-reared and wild: low risk
- Long-term viability: little to no detrimental effect
- Disproportionate survival: low

The analysis contains a paragraph questioning the burden of proof, asking whether proponents of supplementation should be required to provide evidence that supplementation will not harm wild populations, or whether opponents should have to prove that supplementation is unnecessary. The authors conclude that scientific method does not offer absolute proof under any circumstances and state that the real question is what management alternatives are available.

Johnson Creek Artificial Propagation and Enhancement Risk-Benefit Analysis

The Johnson Creek Artificial Propagation and Enhancement (JCAPE) risk-benefit analysis (Beasley et al. 2000) is very similar in approach to the Nez Perce Tribal Hatchery analysis. The document lays out the goals of the Johnson Creek artificial production program, which are to prevent extirpation of the summer-run chinook spawning aggregate in Johnson Creek, preserve the genetic, behavioral and ecological attributes in Johnson Creek summer-run chinook, and to build a naturally sustaining summer-run chinook population once factors contributing to initial decline are addressed.

Potential benefits of the JCAPE are related to achieving recovery goals, maintaining genetic diversity, reducing the short-term risk of extinction, addressing uncertainty through experimentation, and restoring functional ecosystems.

The authors define the risk factors related to the JCAPE, guided by the risk factors outlined by Waples (1996). Then, on the basis of a literature review, they assign a risk level of low, medium, or high to most of the risk factors representing a qualitative assessment of likelihood of detrimental impacts being realized.

Specifically, for the various risks of supplementation considered by the authors, they conclude:

- Fitness differences between hatchery reared from wild: unknown
- Adequate proxies for fitness: undefined
- Loss of within-population diversity: moderate
- Artificial selection: moderate
- Disproportional survival: moderate
- Formation of captive broodstock: moderate
- Outbreeding depression: low
- Inbreeding depression: low
- Loss of between population diversity: low
- Straying: low
- Competition: low
- Incorporating surplus adult returns: low

Hood River Steelhead Hatchery Programs Risk/Benefit Analysis

Kostow et al. (2000) developed a draft document that evaluates management protocols to optimize biological benefits and manage risks to listed steelhead. The goals of the hatchery program are to serve as an artificial reserve for the listed Hood River steelhead, to serve as a tool to increase the abundance of wild steelhead, and to evaluate the use of hatchery fish to increase natural production.

Acknowledging that the benefit of hatchery supplementation in recovery is highly uncertain, the document proposes an experimental approach to a strategy of supplementation in the Hood River subbasin. The existence of the Powerdale Dam fish trap below the natural production area allows capture and experimentation with all naturally produced steelhead. This situation would allow monitoring and evaluation of the effects of supplementation through reference and treatment sites, and replication.

The document presents an array of scenarios, goals and alternatives for each of the three stocks. The document extensively reviews the history of the hatchery programs in the Hood River subbasin, discussing origin and age of broodstocks, broodstock and wild donor population sizes since founding, relative survivals of hatchery and wild fish, historical mixing of hatchery and wild fish, degrees of success in maintaining "wild-type" hatchery fish, disease outbreaks and other catastrophic events, releases of hatchery juveniles and deposition of hatchery adults.

A series of three benefit tests are performed to assess whether the hatchery programs could be expected to achieve benefits outlined in the hatchery program goals for the STS50 and STW50. Because the Hood River STS24 hatchery program is not intended to benefit wild fish, the test is not applied to it. Each of the benefit tests includes a background discussion of the issues and the identification of explicit measures of success required for the benefit to be accomplished by a particular action. It also identifies the risks introduced by taking the action and develops measures for evaluating risk. Likely benefits and risks are discussed on the basis of historic performance, and options for operational protocols and monitoring to assess achievement of benefits and minimization of risks are listed. Alternative approaches are evaluated in terms of their likely contribution to benefits and risks.

Benefit Tests

Test 1: Demonstrating the value of an artificial reserve
Test 2: Demonstrating the ability of a hatchery program to increase the abundance of wild steelhead
Test 3: Demonstrating the research value of these programs

The document addresses risks explicitly and introduces decision points for assessing risks and evaluating whether to proceed. A series of 10 tests comprise the assessment of risks. For each test (for example, "modification of species structure"), a background discussion introduces the issues. Risks are identified and discussed, with operational protocols and a monitoring plan developed for alternative options.

Risk Tests

Test 4: Modification of species structure
Test 5: Broodstock sampling selectivity
Test 6: Size and degree of isolation of broodstock
Test 7: Risk to wild donor population of using wild fish in the broodstock
Test 8: Rearing and release selectivity
Test 9: Risks associated with the deposition of returning hatchery adults
Test 10: Risk of intraspecific and interspecific hybridization
Test 11: Ecological risks (modification of community structure and ecosystem dynamics)
Test 12: Other associated management risks (e.g. mixed-stock harvest)
Test 13: Operational risks

The summary risk-benefit analysis and final conclusions are incomplete, pending decisions on the choice of alternatives.

Summer Chum Salmon Conservation Initiative for the Hood Canal and Strait of Juan de Fuca Region

The goal of the Summer Chum Salmon Conservation Initiative (Ames et al. 2000) is to protect, restore and enhance the productivity, production and diversity of Hood Canal summer chum salmon and their ecosystems to provide surplus production sufficient to allow future directed and incidental harvests of summer chum salmon. The implementation plan contains an assessment of factors contributing to decline ranked according to "impact ratings" ranging from major to undetermined. Part three of the plan, Evaluation and Mitigation of Factors for Decline, contains an assessment of the risks and benefits of supplementation for summer chum salmon. Extinction risks are rated (high, medium, low or special concern) for each of nine existing stocks.

The anticipated benefit of supplementation is the alleviation of the risk of extinction through rapid boosts in population abundance, increases in natural spawner densities, and the seeding of usable habitats. The document uses Quilcene and Salmon Creek supplementation programs as examples of six potential benefits of summer chum supplementation: reduce short-term extinction risk, preserve the population while factors for decline are being addressed, speed recovery, establish a reserve population for use in case of catastrophic loss of the natural population, reseed vacant habitat capable of supporting salmon, and provide scientific information regarding the use of supplementation in conserving natural populations.

Five categories of ecological and genetic hazards to remaining wild summer chum populations are discussed: partial or total hatchery failure leading to catastrophic loss, ecological effects, genetic effects, risks to donor stocks such as numerical reduction or selection effects, and risks to other salmonid populations and species, for example redd superimposition impacts on wild pink salmon. Strategies are proposed to manage the risks associated with these hazards.

The plan is driven by an urgency to preserve and restore the at-risk summer chum stocks. The plan, while recognizing the need to systematically assess the risks and benefits of supplementation, also recognizes the need to act without prolonged consideration of the risks and benefits. Monitoring and evaluation proposals are included to allow for learning and adaptation as supplementation proceeds. The plan recognizes the need for criteria to determine when to modify or stop supplementation. The method proposed in the plan is to use an adaptive approach to assess progress toward objectives of genetic impact reduction and numerical return goals.

General risk assessments are conducted for nine existing stocks and seven recently extinct stocks. Each assessment includes a consideration of extinction risks, potential population size, stream habitat impacts, broodstock availability, and operational resources and project siting. Each category is rated, with a total rating score calculated.

A detailed assessment of the likelihood of hazards is presented for each of the three hazard categories: hatchery failure (egg loss, fish loss, disease, flood damage to incubation), ecological hazards (predation, competition, disease), and genetic hazards (reduction in effective population size, within-population diversity loss, among-population diversity loss, masking of population status). The likelihood of meeting the criteria to minimize or avoid hazards is rated high, medium or low. Actions to be taken to reduce losses if hazards occur are outlines.

On the basis of the assessment of likelihoods of hazards occurring and risk management actions associated with these hazards, conclusions are reached for each potential supplementation stock and reintroduction stock regarding whether a supplementation project should be begin, continued, ended, or not begun. The project selection summary lists those projects recommended to continue and those recommended with qualification, and those not recommended.

Implementation plans for those stocks recommended for supplementation or reintroduction contain specific performance objectives. A detailed section on ecological interactions assesses the potential predation, competition and disease impacts of supplemented summer chum on other salmonid species, and potential impacts of other salmonid species on summer chum. Risks associated with each of these interactions are ranked according to detailed ranking criteria. Specific risk management, monitoring and evaluation measures are proposed for each stock to reduce the risks of hazards associated with hatchery operations, predation, competition, behavioral modification, and disease.

ISAB Summary Assessment of Risk and Risk-Benefit Analyses

The five risk and risk-benefit analyses reviewed incorporate various degrees of quantification and analytical structure.

Currens' analysis (1993) is limited in scope to genetic risks of a single supplementation project. He develops a framework of various genetic hazards and uses it to assess the performance of the supplementation program with regard to genetic components. He identifies components of broodstock sampling and develops a fault tree to calculate hypothetical probabilities of successful completion of each component. Resilience and reliability scores for various genetic hazards are calculated. He develops conclusions and recommendations about the major sources of vulnerability in this supplementation project and recommends actions to reduce that vulnerability. Among those recommended actions are the development of protocols that employ decision trees for contingencies, training personnel in appropriate protocols, and establishment of monitoring and evaluation procedures.

The Nez Perce and Johnson Creek risk-benefit analyses take the approach of constructing a list of risk factors based on Waples (1996). They conduct a literature review to determine the degree of empirical support for the relevance of each risk factor to the particular supplementation activity being analyzed. Findings of the literature review combined with plans for the conduct of supplementation activities are used to assign a qualitative ranking of low, medium or high to each risk factor. Benefits are not explicitly identified or ranked according to likelihood but are asserted to be substantial in consideration of the high short-term risk of extinction, extirpation from locations, unused habitat capacity, and insufficiency of returns to support harvest. Each analysis discusses how each risk factor will be addressed and then moves from being an assessment document to a decision document by forming conclusions about the acceptability of these risks on the basis of the considerable benefits expected from the conservation effects of supplementation.

The Hood River Steelhead Hatchery Programs Risk/Benefit Analysis (Kostow et al. 2000) makes explicit acknowledgment of the uncertainty surrounding the benefits and risks of hatchery supplementation to recovery. To reduce some of these uncertainties, the document proposes an experimental approach to a strategy of supplementation in the Hood River subbasin that includes reference and treatment sites, replication, and monitoring and evaluation. A series of three benefit tests and 10 risk tests were performed to assess whether the hatchery programs could be expected to achieve benefits outlined in the hatchery program goals. The tests include the definition of key uncertainties and the development of protocols to allow learning about these uncertainties and modification of operations in response to learning.

The Hood Canal and Strait of Juan de Fuca Summer Chum Salmon risk assessment (Ames et al. 2000) takes a detailed and systematic approach to the assessment of whether the risk to target populations of using supplementation outweighs the risk of foregoing supplementation. Despite incomplete data, the plan uses expert opinion to rank a large number of potential hazards of supplementation of nine existing stocks and reintroduction of seven recently extinct stocks. Detailed risk management strategies and plans for monitoring and evaluation are also developed. On the basis of the rankings, conclusions are reached for each stock regarding whether supplementation is recommended, and under what conditions.

Application of Risk Assessment to Decision Making

Risk assessment is a formal process based on science and objectivity. Risk assessment helps decision makers be more effective in an environment of risk and uncertainty by increasing their understanding of how uncertainties affect the scientific information on which their decisions will be based. The benefit provided by risk assessment is the information to avoid both excessive risk-taking and excessive risk aversion.

Risk assessment is ideally separate from risk decisions and risk management. Making use of the risk assessment in deciding how much risk is acceptable is subjective and is normally a matter for policy. Risk management involves a number of considerations, only one of which is the risk assessment.

Goodman (2002) addresses the process of decision-making under uncertainty. He notes that although uncertainty cannot be eradicated from environmental decision-making, decision-making can be exact if uncertainty is addressed in a formal, systematic way. Decision-making will be effective if, over the long run, the probabilities are evaluated well enough that gains exceed losses. The mathematical discipline of statistical decision theory addresses this type of decision problem as a formal optimization problem (Berger 1985, cited in Goodman 2002).

The goal for decision-making under uncertainty is to have a risk assessment procedure that estimates uncertainties in a formal reproducible way and a decision process that makes rational use of the probability distribution that represents the uncertain prediction (Goodman 2002). The decision to take an action is then driven by the determination of acceptable risk, set by policy. When risks are calculated according to formal statistical data-based process described by Goodman, this calculation represents "true risk" – including the effects of ignorance as well as the effects of variation. The greater the ignorance about a factor, the wider will be the distribution representing its parameter (Goodman 2002). As Goodman notes, this mathematically rigorous as well as empirically objective approach creates a cleaner separation between science and policy, allowing both to function better.

Although risk assessment is conceptually straightforward and is the most widely used analytic approach to evaluate environmental policy options, it is not without controversy. According to Lackey (2002) the most heated debates revolve around delineating the specific meaning of risk in context and framing the risk question to be answered. There is a tradeoff between the narrowness and tractability of a risk question and the breadth and policy relevance of the assessment. There may be disagreement on the appropriate policy question to be asked. Even asking questions about acceptable levels of ecological risk is abhorrent to some. Analysts may misuse the process by introducing their personal values into risk calculations (Lackey 2002). Suter (1993) notes a common tendency for risk assessors to use conservative assumptions in place of more formal estimates of uncertainty. This subjective approach creates problems for decision-making because it is inconsistent, it hides uncertainty and error from the decision makers, and ignores the cost of taking over-conservative action. The decision maker needs to fully understand the uncertainties associated with the scientific information on which the decision will be based.

ISAB Findings Regarding Risk Assessments of Supplementation

Salmon recovery is a race between the time a population or group of populations will be extirpated and the time habitat to support those populations can be recovered. Whether supplementation is appropriate for a population depends on the anticipated time to extirpation compared to the time required for habitat recovery. Supplementation could be considered appropriate if a population would be extirpated before habitat could be recovered, and if the habitat could be recovered in the extended time frame that supplementation could provide. Supplementation would not be considered appropriate if habitat could be recovered before a population were extirpated or if habitat couldn't be recovered in the extended time frame afforded by supplementation. If spawning or rearing habitat is not likely to be available, it may not be cost-effective to supplement. If habitat is available, it would have to be substantially under-seeded to ensure that there would be habitat available for population expansion. Driving the supplementation decision are habitat recovery rates balanced against the rate of population decline. Risk assessment is a systematic approach to evaluating this balance.

Much of the debate about supplementation is based on differing perceptions of the status of the natural population: is the population on a rapid trajectory to zero or is it small but relatively stable? We recognize that it is not easy to come to a consensus on risks facing a population, nor is it always straightforward to balance the risks of supplementing against the risks of not supplementing. In light of this uncertainty, supplementation should be limited to cases where the population is declining and supplementation can contain the risks.

Determining whether these conditions are met is done through a risk-benefit assessment. Columbia River Basin data are not adequate for complete risk assessments, but limited data and expert opinion are available. Conducting risk assessments with limited data is uncomfortable but necessary to be as informed as possible about the conditions under which supplementation will take place.

In conditions of data paucity, qualitative risk assessments provide useful information for decision-making by presenting checklists for systematic assessments of potential risks before experimentation begins. The list does not comprise a risk assessment, but the information and the reasoning that go into the evaluation of items on the list do comprise a limited qualitative risk assessment which can form the basis for a risk management plan.

The risk assessments we reviewed are distinguished not by their qualitative versus quantitative ranking of risks but rather by the degree to which the qualitative evaluation is approached systematically, thoroughly and objectively rather than presenting information to justify a foregone conclusion.

The experimental nature of supplementation means that recommendations can neither be made to never use it nor to always to use it. The conditions under which supplementation could be used are those in which it plausibly could help recovery, and where implementation monitoring will generate information to assess whether it is having the intended effect. Because it is an experiment, supplementation should be implemented only in half the cases that meet these conditions in order to spread risk and to set up a system of references. The design of the experiment and the identification of the data to be collected are outlined elsewhere in this report.

Section 8. ISAB Findings, Recommendations and Answers to NOAA Fisheries and Council Questions.

The basis of this report is the response to a series of questions asked by NOAA Fisheries and the Northwest Power Planning Council concerning the efficacy of past, current, and future supplementation programs for salmon and steelhead in the Columbia River Basin. Although the detailed answers to these complex questions comprise the body of the report, we conclude the report with the following findings, recommendations, and brief answers to those questions as a summary of our effort. This section appears verbatim in the executive summary of the report.

ISAB Findings

Finding 1: Hatchery programs in the Columbia River Basin provide some salmon harvest and reintroduction opportunities. Those hatchery programs which are based on hatchery broodstock lines, and which allow the hatchery products to interact intensively with natural populations, almost certainly impose a large cost on the affected natural populations. For hatchery programs where the hatchery and natural population are integrated, the empirical basis is inadequate for determining the cost to the natural population.

Hatchery programs in the Columbia River Basin release nearly 200 million salmon and steelhead smolts into the natural environment annually. These releases of hatchery-reared juveniles can return large numbers of adult fish, providing commercial, sport, and tribal harvest. Hatchery-reared juveniles are also beginning to be used to reintroduce salmon into areas where they had become extirpated. Most of the hatchery programs are not integrated with natural production because they rely extensively on fish of hatchery-origin for their broodstock. Nevertheless, the hatchery productions from these programs are present in large numbers on the breeding grounds of many natural spawning stocks. In some cases this is deliberate, in others it is inadvertent. Either way, this constitutes a supplementation action.

The impacts of these hatchery programs on the extinction risk to (or recovery of) the remaining natural populations of salmon and steelhead have not been determined empirically. These knowledge gaps need to be filled. They may be addressed by Reasonable and Prudent Alternatives (RPA)-184 and -182 of the 2000 Columbia River Hydrosystem Biological Opinion.

Finding 2: Contemporary genetic/evolutionary theory, and the literature that supports it, indicate clearly that supplementation presents substantial risks to natural populations of salmon and steelhead.

Supplementation can affect the *adaptation* of natural populations to their environment by altering *genetic variation within and among populations,* a process that can negatively affect a population's fitness through *inbreeding depression*, *outbreeding depression*, and/or *domestication selection*.

Based on this finding, the ISAB concludes:

1. It would be imprudent to undertake genetic interventions in the hope of producing novel (and presumably beneficial) adaptations to the altered environments currently encountered by salmonids in the Columbia River Basin.

2. To conserve the local adaptations present within salmon populations, human-induced exchange of individuals among divergent salmon populations should be eliminated.

3. Supplementation programs carry the risk of causing decreases in the genetic variation present within their target populations which can lead to inbreeding depression.

4. Supplementation programs carry the risk of homogenizing previously distinct gene pools, thereby causing a decrease in the genetic variation among salmon populations.

5. Mixing divergent populations can lead to outbreeding depression.

6. Because many of the adults from conventional hatcheries stray across the basin, and because collection of adults for broodstock often occurs before populations segregate into spawning groups, hatchery broodstocks can easily contain individuals from multiple populations.

7. Domestication selection alters the relative productivity of strains of cultured fish. Typically, a strain exhibits superior productivity in its own environment in contrast to its productivity in other environments.

8. Domestication selection causes the natural spawning performance of strains of cultured fish to decline. Because of this documented constraint, and because salmon and steelhead exhibit modifications for many traits when in hatchery culture, it is prudent to anticipate that domestication selection will constrain the benefits of supplementation.

9. A reasonable course of action to manage the risk of domestication is to ensure that a large majority of the composite population is naturally propagated and to require that the hatchery broodstock in each generation is drawn only from the products of natural spawning.

These genetic risks of supplementation suggest that it would be prudent to continue to treat supplementation as experimental, that supplementation should only be deployed on a limited scale, and that better and more extensive monitoring of such experiments be required to generate an empirical record capable of evaluating those experiments.

Finding 3. The immediate net demographic benefit or harm to population abundance from supplementation depends on three things: intrinsic biological parameters of the stock in its environment; policy constraints; and management control variables. The integration of these factors, much less their measurement, has not been adequately considered in supplementation evaluations to date.

Two intrinsic biological parameters affect supplementation success: the individual replacement rates for fish reproducing in the hatchery and the individual replacement rates for fish reproducing naturally in the river. Policy constraints that impact the efficacy of supplementation include limitations on the removal of natural-origin adults for broodstock, limitations on the rate of taking hatchery-origin adults for broodstock, limitations on the fraction of hatchery-origin adults allowed on the natural spawning ground, and stipulations on the selectivity of, and harvest between, natural-origin and hatchery-origin fish. Management control variables that impact supplementation include the broodstock mining rates for both hatchery-origin and natural-origin adults (proportion of the population removed for use as broodstock in the hatchery) and the harvest selectivity for hatchery-origin versus natural-origin adults.

Demographic Modeling:

The ISAB used a mathematical matrix model of these intrinsic biological parameters, policy constraints, and management control variables to describe theoretically the aggregate productivity and population composition of the supplemented population. This matrix model was then extended to theoretically model the fitness consequences of integrating the breeding of hatchery-origin and natural-origin adults.

The salient results of the theoretical modeling exercise include the following:

1. Supplementation can be expected to increase the potential for harvest and to increase the number of salmon spawning naturally in the target river system.

2. The increased population size and any resulting increased harvest attributable to supplementation alone will likely not persist after the termination of supplementation.

3. If habitat improvements are achieved in the interim, these may allow a sustained increase in population size or productivity, but if so, this could have been realized even without supplementation.

4. In a population not subject to genetic drift and inbreeding depression, supplementation cannot give rise to selection that increases the fitness of the target population. Genetic drift and inbreeding depression are not expected to be problems in populations that are sufficiently large or receive a minimal amount of natural immigration.

5. Supplementation can result in decreased fitness of the target population. Whether it does so, and to what extent, depends on the particular magnitudes of the pertinent parameters, e.g., the initial hatchery and natural spawning replacement rates, the broodstock mining rates, the harvest selectivity, as well as the degree of the negative correlation between natural spawning and hatchery spawning fitness.

6. All other things being equal, the probability and extent of a decrease in fitness of the target population following supplementation will increase with increases in the broodstock mining rate, in the harvest rate, and in the proportion of hatchery-origin versus natural-origin adults taken for broodstock.

7. A supplementation protocol that takes only natural-origin fish for broodstock will protect the population against runaway domestication selection and prevent the natural spawning fitness from being reduced by more than 50%.

8. A supplementation protocol that takes some hatchery-origin fish as broodstock can give rise both to selection that depresses naturally spawning fitness of the target population by more than 50% and to runaway domestication selection. This effect can occur as an abrupt catastrophic transition as the broodstock mining rate for hatchery-spawned fish crosses a critical threshold (which is scenario specific).

9. At present, little is known empirically about the magnitude of any correlation between natural spawning fitness and hatchery spawning fitness in actual salmon populations. Nevertheless, modeling shows that this relationship has a large influence on the probability and magnitude of the depression in natural spawning fitness as a consequence of supplementation.

The implications of theoretical modeling analyses are that for a wild population that is not so small as to be on the brink of imminent extinction or at risk of genetic drift and inbreeding depression, supplementation not only offers little chance for conservation benefit, but also poses some conservation risk. Supplementation may offer the potential for some harvest benefits, but it should be noted that harvest also increases the conservation risks even further.

Finding 4. Current monitoring and evaluation efforts are inadequate to estimate either benefit or harm from ongoing supplementation projects. The correct parameters are not being consistently measured.

The objective of supplementation (as defined by RASP) is *to maintain or increase natural production, while maintaining the long-term fitness of the target population and keeping the ecological and genetic impacts on non-target populations within specified biological limits*. This definition illustrates that performance indicators (response variables) are needed in three areas:

1. target population abundance, hatchery productivity and natural spawning productivity during supplementation, compared to unsupplemented controls;

2. target population long-term fitness after supplementation is terminated, compared to unsupplemented controls;

3. non-target population impacts (e.g., effects of steelhead supplementation on the abundance and productivity of chinook populations in the target areas, compared to unsupplemented controls).

Once a set of standards has been established for these performance indicators, measuring progress toward achieving those standards would then provide a mechanism to evaluate supplementation. The supplementation models identify those parameters that need to be estimated to assess supplementation.

Finding 5. Columbia River Basin supplementation projects are considered to be "experimental". Unfortunately, inadequate replication and widespread failure to include unsupplemented reference streams coupled with a lack of coordination among projects make it unlikely that these projects (as currently conducted) will provide convincing quantification of the benefits or harm attributable to supplementation.

Enough streams exist in the basin that are already being "treated" with supplementation. Future investment should be in establishing robust experiments with unsupplemented reference streams, and implementing rigorous monitoring and evaluation practices. Treatment streams without adequate unsupplemented reference streams for comparison should be considered for termination of supplementation and reallocation of funds.

Finding 6. The following operational conclusions emerged from our review of case histories of Columbia River Basin supplementation programs:

1. The broodstocks that are collected for supplementation programs are spawned successfully and the resulting fry survive and are released as smolts with rates exceeding the survival rates of progeny spawned in the wild; i.e., there is a juvenile survival benefit attributable to the protected hatchery environment.

2. Where evaluated, the survival to returning adults (SARs) for smolts released from the hatchery environment is usually less than that for naturally produced smolts.

3. Even though the SAR for hatchery-origin smolts is usually lower than natural-origin smolts, hatchery spawning often generates a higher adult recruits-per-spawner rate than natural spawning because of the juvenile survival advantage provided by the hatchery before release.

4. It has been difficult for some supplementation projects to consistently achieve their smolt production goals because of the limited number of returning salmon available for broodstock. There is no evidence that similar problems will not occur in the future.

5. Because SARs for hatchery-origin smolts have been substantially lower than program target figures, the yield of adult fish has not typically achieved performance standards. There is no evidence that similar problems will not occur in the future.

6. Among the programs that we assessed, the presence of appreciable numbers of hatchery-origin adults on the spawning grounds in the late 1980s and early 1990s did not prevent declines in the abundance of natural-origin spawning adults. There is no evidence that similar problems will not occur in the future.

7. Straying and interbreeding of conventional hatchery fish with naturally spawning populations are occurring at rates much higher than planned in some supplementation programs. Strays on the spawning grounds are often in the range of 20 to 60% of the total numbers of spawners (e.g. spring/summer chinook in reference streams in the Idaho Supplementation Study and steelhead in the Deschutes River basin) and are progeny of broodstock not derived from local populations. The risks of detrimental effects of this *de facto* supplementation to naturally spawning populations are real and likely far more serious than the risks involved in a well-designed supplementation program.

Finding 7. Many hypotheses and conjectures concerning supplementation are largely unevaluated. This finding is based on our review of case histories of Columbia River Basin supplementation programs. Three examples are provided.

Assertion 1. Even though natural populations supplemented with hatchery-origin adults through the mid-1990s exhibited a continued downward trend in natural-origin adult abundance, it has been claimed that supplementation still aided the natural populations by providing additional adults for spawning. The validity of this assertion is unsubstantiated. A test of this claim would have required an experimental design employing unsupplemented reference populations.

Assertion 2. It has been claimed that supplementation will provide a net "demographic boost" to a target population, because the total production of offspring from natural spawning of the hatchery-origin adults is larger than the production of offspring that would have occurred if the broodstock in the previous generation had been allowed to spawn naturally.

This assertion has not been tested because the reproductive performance of hatchery-origin adults spawning in the wild has not been adequately compared to that of natural-origin adults.

Assertion 3. It has been claimed that the long-term fitness of progeny that result from the in-river breeding of hatchery-origin individuals with hatchery-origin or with natural-origin individuals is comparable to the fitness of progeny from two natural-origin individuals. This assertion is unevaluated in programs following an integrated breeding protocol, and it is contradicted by empirical evidence on the natural spawning performance of domesticated hatchery strains.

The ecological conditions required to expect to achieve benefits from supplementation have received little conceptual development or programmatic experimentation. RASP (1993) and others, including the Council's Fish and Wildlife Program (NPPC 2000), acknowledge that supplementation will not work unless the factors that currently limit productivity and abundance are addressed. If insufficient attention is given to evaluating ecological interactions, it will be impossible to determine if it was intrinsic biological attributes of the species being supplemented, biotic interactions, or habitat limitations that constrained the anticipated increases in natural-origin adult recruits. Habitat carrying capacity needs to be assessed, not only within the stream reaches and subbasins where supplementation is being conducted, but also throughout the required migration route. In addition, the role that species interactions (e.g., competition, predation and disease transmission) play in determining survival needs to be determined.

Finding 8. With our current knowledge base, a technically valid risk-benefit analysis of supplementation is dominated by the high level of scientific uncertainty about the possible magnitudes of the potential beneficial and detrimental effects.

Although a conceptual framework for risk-benefit assessment has been developed in the abstract and analytical methods for performing these assessments exist, the data required to parameterize such models in application to supplementation are insufficient. Estimates of the magnitudes and probabilities of demographic benefits and of ecological and genetic alteration are unavailable. Furthermore, the demographic consequences of such a genetic or ecological alteration are not sufficiently understood. How a decrease in the fitness of natural-origin adults due to interbreeding with hatchery-origin adults translates into a reduction in population abundance is unknown.

Recovering depressed populations is a race between the time it would take a population to become extirpated and the time it would take to restore needed habitat. In considering whether or not to supplement a population, the risk of extirpation has to be balanced against the likelihood of habitat recovery. Before supplementing a population, three conditions should be met. First, the expected time to extirpation should be less than the time it would take to recover habitat with a good faith effort. Second, the expected benefit of supplementation should extend the timeline to extirpation beyond the time to restore the necessary habitat. Third, a credible plan should be in place, and resources committed, to restore the habitat on that timetable.

As a result of the scientific uncertainties, the prudent response would be to carry out supplementation on a limited experimental scale and only when an effective monitoring program is in place to determine if the potential beneficial/detrimental effects do or do not materialize. In addition, it is imperative that there be enough programmatic flexibility to terminate any given project if serious detrimental effects are detected. All projects should have a predetermined timeline. Those projects that achieve a supplementation target within the time line should move to a monitoring phase with a planned cessation of supplementation. Those projects that are showing detriment should be terminated. Supplementation should not proceed independent of programs to restore habitat and improve the productivity of the population in its natural environments. This consideration of habitat includes downstream passage.

Primary ISAB Recommendations

Based on the substantial uncertainty that is likely to remain for the foreseeable future concerning the efficacy and risks of supplementation, *and recognizing that the objective of supplementation is to increase natural production while maintaining the long-term fitness of the population*, the ISAB recommends that all supplementation projects be implemented with the following conservative approach:

1. Only natural-origin adults should be used as broodstock in each generation of hatchery supplementation operations. This restriction will reduce the potential for domestication selection and create motivation to implement habitat improvements that will increase the abundance of the natural-origin adults.

2. Performance standards for natural-origin and hatchery-origin adult abundance and per capita production rates should be established for each project.

3. To reduce uncertainty and to contain the risk of long-term impacts, all supplementation programs should be conducted within an explicit experimental design that is accepted by all affected parties. That design should contain:

    a. Limits to the proportion of the adult natural population that can be collected as broodstock. Those limits should reflect a balance between maintaining a reasonable population in the wild and collecting sufficient adults to minimize genetic drift. For example, it could be stipulated that broodstock collected for supplementation should not exceed 50% of the natural population of female spawners. We recommend explicitly that a set of supplementation experiments should test different proposed limits (i.e., different percentages not to exceed 50%).

       When an extremely low number of adults return (as occurred in many locations in 1995), the choice of whether to leave all the fish in the wild or collect all of them for broodstock is not adequately informed by the current scientific evidence. The uncertainty is too great to allow a firm conclusion. The region should select and test different options in different locations to learn if there is a distinction between the alternatives.

    b. Allowance for the numerical abundance of hatchery smolt releases to vary with environmental changes and juvenile production in the natural population. When natural abundance is limited, recommendation 3(a) protects the natural population, but when productivity increases, the numbers of hatchery-origin smolts released (combined with the number of natural-origin smolts) should be based on the carrying capacity of the natural environment. Part of the carrying capacity calculation should include an escapement goal. Each year the program should try to reach as large a fraction of that escapement goal as possible with natural-origin adults.

c. Operational guidelines and performance standards that respond to changes in the ratio of natural-origin and hatchery-origin adult abundance. For example, the proportion of hatchery-origin adults permitted to spawn with natural-origin adults should be established as part of the experimental design and should be regulated so as not to exceed a specified level in each treatment. The treatments should represent a spectrum of values for that ratio from zero to 50%. A set of supplementation experiments should then test different limits.

d. Commitment to a specified monitoring and assessment program that includes an unsupplemented reference population(s) evaluated in parallel with each of the supplemented populations. Monitoring requires measuring the adult-to-adult return rate for natural spawning of hatchery-origin fish and for natural-origin fish in the supplemented treatment, and for natural-origin fish in the unsupplemented control.

e. A schedule of annual reporting that ensures that the data collected are being analyzed, reviewed, and utilized on a timely basis. We recommend that all the basin supplementation programs be required to adopt annual reporting in a standardized format that provides at minimum the details presented in Table 6.1.

4. For ongoing supplementation programs to be continued or new supplementation programs to be initiated, it is imperative that requisite reference populations be established and that adequate levels of monitoring and evaluation be included as part of the basinwide adaptive management experiment. Adequate controls should be streams that as far as is known are interchangeable with the treatment. When such pairs are identified, the assignment of one to the treatment and one to the control should be random to eliminate any systematic bias resulting from unavoidable differences.

5. Program plans must contain an objective means to assess when supplementation should be terminated (due to either success or failure) and should commit to a decision rule to do so.

6. Multiple supplementation projects should be coordinated across the Columbia River Basin so that in aggregate they constitute a basinwide adaptive management experiment, maximizing the information collected and attempting to reduce uncertainty. For ongoing supplementation programs to contribute to the experiment, adequate monitoring needs to be instituted, and reference populations need to be designated or established.

7. The Fish and Wildlife Program should include mechanisms to ensure that supplementation projects are collecting the data necessary to test their effectiveness. Project analysis and reporting should be required. Regional (basinwide) coordination and responsibility for a meta-analysis of the multiple experiments are necessary.

8. Supplementation should be used sparingly, focusing on a subset of the locations where natural spawning salmon or steelhead populations are not replacing themselves, where habitat capacity is believed to be able to accommodate additional production, and where the landscape conditions are suited to the experimental design (i.e., similar habitat for the treatment and reference populations and a means to prevent mixing of the two populations).

Specific Review Questions and Brief Answers

NOAA Fisheries Questions

1. What do empirical studies of hatchery–wild interactions tell us about the benefits as well as the risks of supplementation programs? What are the strengths and limitations of each study, and what is their relevance to the key questions about appropriate use of hatcheries in supplementation? What conclusions can be drawn from the collective body of information?

Answer: An extensive peer-reviewed literature documents differences in the performance and life history attributes of natural-origin and hatchery-origin salmon and trout. Much of this literature is based on the large North Atlantic aquaculture programs that use highly domesticated strains. Many of the differences between wild and farmed fish include traits that are linked to fitness, such as size and age at maturity. In Norway occasional catastrophic large-scale releases of farm fish have caused genetic and demographic swamping of local indigenous Atlantic salmon populations, which has led to genetic interbreeding and reductions in fitness to wild populations.

A smaller body of empirical studies documents differences in performance and life history attributes of natural-origin and hatchery-origin salmon and trout in situations comparable to supplementation plans in the Pacific Northwest. Some of those studies assessed supplementation broodstock that was derived from local wild fish (e.g., Yakima Fisheries Project on chinook) or from an admixture of local wild fish and a regional semi-domesticated hatchery strain (e.g., Idaho Supplementation Study on chinook). These studies also document that there can be fitness differences between the hatchery-origin and natural-origin fish.

These studies of hatchery–wild interactions reveal three potentially beneficial mechanisms to the wild segment of the population, and five potentially harmful mechanisms. Some of these mechanisms can operate with different intensities in supplementation programs (or other "integrated programs") compared to a system in which there is no appreciable gene flow between the wild and hatchery components of a population.

The three mechanisms that create potential benefits of hatchery-wild interactions are: (1) increased nutrient supply to the freshwater system resulting from the increased number of carcasses; (2) increased aggregate productivity of the population owing to the much higher egg to smolt survival rate in the hatchery phase; (3) increased genetic effective population size caused by the larger total number of adults. Potential benefits (2) and (3) are significant only for very small populations, those that we might characterize as on the brink of extirpation. Potential benefit (1) could be achieved by other means that would not expose the population to the risks of supplementation.

The five potentially harmful mechanisms are: (1) depression of genetic diversity because of over representation of small numbers of parents in the hatchery phase; (2) increased exposure to disease; (3) increased predation; (4) exceeding the carrying capacity of the habitat; (5) depression of wild spawning productivity because of domestication selection in the hatchery phase. Potential harm (1) is unlikely to be significant in a population that is not small, but the other four potential harms represent mechanisms that do not diminish in intensity as the size of the population increases.

The expected magnitudes of these positive and negative effects cannot be predicted from the existing empirical studies because of two primary limitations. First, the available results are from studies that generally were not carried out in a context of a true supplementation protocol. Second, many of them employed a design that was geared toward detecting the existence of an effect rather than quantifying the size of that effect. Nevertheless, the existing empirical studies are relevant for their identification of mechanisms that certainly will operate at some level in supplementation.

The conclusions that can be drawn from the collective body of existing empirical information relevant to supplementation is that there is credible potential for a benefit to very small wild populations and credible potential for harm at any population size. Current information, however, does not allow accurate prediction of the magnitudes of the harm and benefit or of the net balance.

2. What is the best way to assess the risks and benefits of supplementation to determine the net effects on natural populations? How can this be used to determine whether a supplementation program should be initiated and, if so, on what scale? Under what circumstances is supplementation likely to lead to a net long-term benefit to natural populations, and under what circumstances is it more likely to do more harm than good?

Answer: The best way to assess the benefits and risks of supplementation is to monitor the abundance and natural spawning productivity of a supplemented population, compared to the abundance and vital rates of unsupplemented reference populations. Unfortunately, within the context of Columbia River Basin supplementation, measurements of abundance and vital rates are usually collected only after a project has begun, and frequently there are no reference populations in the design (there are however some notable exceptions to these generalities). As a result, there is an insufficient empirical record of accomplishment to provide statistically significant probabilities of either achieving the desired benefits or causing harm to the target population. Consequently, we conclude that any benefit-risk assessment that attempts to predict the magnitude of the benefit of supplementation and then subtract from that benefit the predicted losses likely from genetic, ecological, and managerial causes will largely be driven by uncertainties rather than by predictive power of the data. Because of these limitations on performing risk-benefit assessments, we recommend that supplementation be undertaken only as an explicit experiment, on a limited scale, with rigorous design, valid controls, and intensive monitoring. In recognition of the uncertainty involved, the Columbia River Basin needs to be prepared for the possibility that supplementation, as it is currently conceived, may not provide sufficient net benefit and, therefore some supplementation projects should be terminated or greatly modified.

3. What are the empirical results of salmon supplementation to date? What has worked, and what aspects are largely unevaluated? How does evaluation of salmon supplementation depend on the goals of the program?

Answer: A number of supplementation projects are underway in the Columbia River Basin. It is clear that they have been successful in producing and releasing salmon and steelhead into the Columbia River system, although the adult production from these hatchery releases has not achieved program expectations largely due to poor smolt-to-adult survival rates prior to 2000. Data collected on these populations subsequent to initiation of smolt releases for supplementation are largely inadequate to make any conclusion as to whether or not additional natural-origin recruits have resulted from the natural spawning of hatchery-origin adults prior to 2000. Furthermore, data assessing the in-river reproductive performance of hatchery-origin adults and their progeny remain unavailable despite the fact that this information is vital for determining the success or failure of supplementation. We recommend that all ongoing supplementation projects, together with projects that may be developed in the future, be incorporated into a basinwide adaptive management experiment designed to thoroughly assess and evaluate the strategy of supplementation. That general assessment of supplementation will require estimating the abundance of both the hatchery-origin and natural-origin adult populations, as well as the productivity of both of these population components separately and in comparison to the abundance and productivity of an unsupplemented reference population.

4. There are two opposing views of the role of natural selection in salmon biology: one that stresses the importance of local adaptation, and one that stresses the flexibility of salmon to respond to different environmental challenges. Both points of view have merit. The real question is the relative importance of these two processes for the recovery efforts, and the corresponding implications for salmon supplementation. Some key questions related to this complex topic include the following:

a) What information is needed to determine what spatial and temporal scales are important for local adaptation in salmon and steelhead? How does or can supplementation affect this?

b) What do we need to know to determine how replaceable salmon populations are on ecological and evolutionary time frames? For example, if a local population is lost, how likely is it that another population will replace it, and if so, on what time scale? How does supplementation affect this process?

Answer: Much of the debate within the region over these issues centers on how quickly adaptation acts to change populations (both historically and currently), and to what degree human-induced changes in the environment have cancelled out fitness benefits from adaptations to past environments. There is substantial scientific evidence for local adaptation in Pacific salmon and steelhead in the Columbia River Basin. There is also evidence for phenotypic plasticity, which is not discordant with the existence of adaptive differences among local populations of Columbia River Basin salmon; these two attributes are not mutually exclusive. How quickly adaptation occurs in response to selection is unknown, but it likely varies widely depending upon the organisms and the environment being considered. Similarly, the limits of short-term adaptive changes compared to long-term adaptation are not known. The difficulty of introducing, or reintroducing, a certain life-history form, such as anadromous sockeye, suggests that there are such limits.

5. Supplementation programs (as well as conventional hatchery programs) can substantially change the pattern of gene flow between salmon populations. Under what circumstances are these changes likely to be beneficial, and when are they likely to be detrimental to long-term sustainability of natural populations?

Answer: If supplementation programs are conducted using the endemic natural population, then relating supplementation with gene flow seems misleading. Supplementation may vary gene frequencies between generations, especially in very small populations, but is unlikely to involve exchange of genes unless through straying or the unlikely event of mutation. Genotypic frequencies may also vary due to non-random mating in the hatchery environment. Genes may still be lost during supplementation programs simply through stochastic events, but if productivity of the population is increased then negative risks associated with gene flow would seem to be unlikely.

However, if supplementation involves mixing of non-local stocks, then altering patterns of gene flow is a euphemism for mixing stocks. Except in conditions of extreme pre-existing inbreeding, all existing experimental evidence on the outcome of mixing stocks indicates that the result is a fitness loss incurred as a result of outbreeding depression. No experimental evidence exists to document a different result. Until results to the contrary are forthcoming, we should assume that there are no circumstances except for extreme pre-existing inbreeding when altered patterns of gene flow would likely be beneficial. In the special case of extreme inbreeding, this can be rectified by a small amount of gene flow, so even in this case there would be no advantage to a large continuing amount of gene flow.

6. Even without considering hatcheries, most salmon populations have experienced large perturbations in their ecosystems compared to pre-European influence. How do these changes affect conclusions about the effects of supplementation on sustainability of natural populations?

Answer: It is clear that there have been a number of substantial changes in the various aquatic habitats within the Columbia River Basin, including those critical to all freshwater life stages of salmonids. What is unclear, however, is how those changes relate to changes in the key selective pressures that drive the adaptations and the life history strategies that have evolved and continue to evolve in Columbia River Basin salmonids. It is often asserted that salmon populations, having evolved over evolutionary time, now find themselves having to cope with recently degraded habitats and may not be as fit in the current environments as they once were. That clearly may be the case, but it has no bearing on the associated assumption that haphazardly altering the genetic structure of the extant population by stock mixing, or directionally altering the genetic structure through domestication selection may help it evolve new, more appropriate adaptations. That assumption is not supported by empirical evidence or evolutionary theory. In fact, as indicated in the answer to the previous question, all empirical evidence and evolutionary theory points to the opposite conclusion. If supplementation increases the variability in gene frequencies over time, it is possible that these programs could retard adjustment to new environmental conditions, depending on the selection pressures on different traits.

7. Every supplementation program has unique aspects that need to be evaluated on a case-by-case basis. Nevertheless, it is also important to consider the appropriate use of supplementation on a larger scale (e.g., the Columbia River Basin). In this larger context, and given all the uncertainties associated with risks as well as potential benefits of supplementation, what would be an appropriate level of intervention across the basin, and how does this compare with the array of programs that are currently underway or planned?

Answer: Currently available empirical information is inadequate to predict the outcome of a thoughtful conservative supplementation effort for any potential target population or on collective populations in subbasins or the entire Columbia River Basin. Given the overwhelming uncertainties, it is critical that future supplementation efforts be carried out within an adaptive management framework that not only copes with uncertainties by spreading risk and avoiding irreversible outcomes, but also puts a priority on using these experiments in a coordinated fashion so that the results contribute to reducing the uncertainties. Programmatically, this approach argues for limiting the scale of supplementation and for ensuring that a considerable fraction of the populations not be supplemented initially, but rather serve as a "reference" for the supplemented "treatments", an experimental component that is crucial for the ability to draw the needed conclusions.

8. ***Finally, what are the key scientific uncertainties regarding salmon supplementation, and what are the most profitable lines of research to help resolve them? Do we need a basinwide experiment to assess supplementation impacts?***

Answer: The following is what the ISAB believes to be the key uncertainties regarding salmon supplementation. It has been adapted from RASP (1992) by Lichatowich and Watson (1993).

1. Under what set of conditions will supplementation efforts add to rather than reduce the total natural production of salmon, steelhead, or other targeted fishes over the long term?

2. How prevalent is domestication in the artificial production programs associated with supplementation, and how does that domestication translate into decreased fitness and performance in the wild?

3. How widespread is the phenomenon of outbreeding depression, and how detrimental are the consequences of losing co-adapted gene complexes in wild stocks?

4. How rapidly do hatchery-origin stocks adapt to the natural environment, and how rapidly do natural-origin stocks adapt to the hatchery environment?

5. Relative to natural-origin fish, what level of reproductive success do hatchery-origin fish have in the wild?

6. To avoid deleterious genetic effects, what should be the maximum allowable ratio on the spawning grounds of hatchery-origin to natural-origin spawners?

7. How much competition with or predation of natural-origin offspring results from supplementation efforts, and can that level prevent a depressed population from responding to supplementation?

8. What scale of habitat improvement in estuary, migration corridor, and tributary spawning and rearing habitats is required for supplementation to contribute to increasing the abundance of recovering salmon stocks?

The FCRPS 2000 BiOp's RPA 182 and RPA 184 address the need for evaluating many of the uncertainties listed above. Initiating the implementation of those RPAs would be a logical and productive first step in addressing these uncertainties.

Finally, because all the supplementation programs in the Columbia River Basin interact with one another during significant portions of the salmon life cycle, the basin does need a "grand experiment". It would be much more productive to incorporate all of them into a comprehensive program now than to try to disentangle confounding effects later.

Northwest Power Planning Council Question

Can artificial production be integrated with natural production to increase capacity and productivity of the combined population in a manner that provides sustained benefits (measured as the abundance and productivity of the integrated population) over the foreseeable future?

The ISAB was requested to consider this question particularly in regard to the following circumstances that will likely be faced by subbasin planners:

Scenario 1: There is a healthy naturally self-sustaining population under present and expected future habitat conditions and harvest rates.

Scenario 2: There is a self-sustaining natural population without major habitat limitations that is unable to support present and future desired harvest rates.

Scenario 3: There is a natural population that is weak or declining and not expected to rebuild given the present and expected future habitat conditions encountered over its life cycle.

Answer: The capacity and productivity of a population with integrated natural and artificial production will depend on the habitat quality and quantity in both the natural environment and in the hatchery. It will also depend on the productivity of both population components, the harvest rates of each component, and any negative correlations of fitness generated by breeding in alternate environments. Improving population productivity will require management of natural habitat quality and quantity (in the Columbia River Basin this habitat would include tributary spawning and early life-stage habitat, parr and smolt habitat, juvenile migration habitat, and returning adult habitat), managing harvest rates and harvest selectivity of the natural and artificial production, and managing the integration of the two populations (establishing the broodstock collection rates for the hatchery component, and the natural: hatchery ratio of parents for both the hatchery and natural spawning subpopulations.)

At present we are unable to adequately estimate capacity and productivity of the natural habitat in the Columbia River Basin; – this is a complicating uncertainty in the current subbasin planning process. The supplementation experiments necessary to develop recommendations for how an integrated population should be managed are not yet underway or are not complete (e.g. Yakima Fisheries Project).

One of the serious uncertainties attendant upon using artificial production to bolster the abundance of any given target population is our ignorance of whether that action diminishes or enhances natural production. This uncertainty is not likely to be resolved easily. In fact, the question of whether artificial production augments or simply replaces natural production is debated beyond the Columbia River Basin, (e.g., for commercially harvested species like pink salmon in Alaska). While preparing the FCRPS BiOp and biological opinions for hatchery operations throughout the Pacific Northwest, NOAA-Fisheries has made qualitative, not quantitative judgments of the effects of hatchery operations on listed salmon and steelhead. The FCRPS BiOp RPA 184 calls on the federal action agencies to undertake research to evaluate whether hatchery reforms can reduce the risk of extinction for Columbia River Basin salmonids. Given all of these uncertainties, providing a scientifically defensible answer as to whether or not capacity and productivity can be increased in an integrated population is not now possible.

Prior to industrial development of the Columbia River Basin in the late 19th Century, most of the basin would have had conditions described in scenario 1. We believe, however, that only scenarios 2 and 3 exist in the Columbia River Basin at this time. As an example, it is unclear if even the Hanford fall chinook population is a healthy naturally self-sustaining because of the regular addition of hatchery-origin adults from Priest Rapids Hatchery.

Supplementation as defined in this report has a credible potential for benefit to very small wild populations falling in scenario 3, and a credible potential for harm at any population size under any of the scenarios. Current information, however, does not allow accurate prediction of the magnitudes of the harm and benefit or of the net balance.

Developing and using the hatchery system to maintain harvest during the 20th Century industrialization of the Columbia River Basin was a *de facto* experiment to determine whether capacity and productivity could be increased using artificial production. Even with the large hatchery returns of the last few years, the Columbia River Basin is producing less than half of the runs that were achieved prior to development. This retrospective view informs us that we have not been able to maintain salmon and steelhead abundance and productivity using an *ad hoc* amalgam of integrated and segregated artificial production programs.

Clearly, a great deal has been learned during the last century. Expectations for resource use and manipulations are more realistic. Nonetheless, the scientific knowledge and managerial skills required to integrate hatchery-origin and natural-origin populations for increased capacity and productivity are not available. Attempting to integrate natural and artificial populations exhibiting the capacity and productivity in scenario 2 and 3 above is likely to follow patterns observed in fisheries around the globe. Initially, numerical abundance will increase owing to the artificial production. Large natural variation in abundance will preclude determining the extent to which the artificial production is subtracting from the natural production. The abundance of the artificial production will provide the rationale for harvest. In species like salmon with variable production, harvest rates established during periods of abundance usually continue when production returns to more modest conditions. This situation leads to excessive exploitation. For salmon this dilemma is duplicated by habitat needs in freshwater. The productive hatchery population component provides the opportunity to use some of the stream course or water for other uses. This use pattern is intensified during periods of coincidently high freshwater and marine productivity. When the productivity of one or both of the environments decreases, the salmon populations are not viable. This situation is what the Columbia River Basin faces today. Given the variation evident in marine survival rates, the time required to address freshwater habitats, and the evidence from past hatchery and supplementation programs, we must advice that it is unlikely that increased capacity and productivity of integrated populations (the stated goal of supplementation) will provide sustained benefits over the foreseeable future.