Independent Scientific Advisory Board

Review of Salmon and Steelhead Supplementation

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ISAB

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Executive Summary

Supplementation is defined in this report to be a management strategy that uses artificial production for the purpose of attempting to rebuild depressed natural salmon and steelhead populations. The aim of this strategy is to create an integrated natural-origin/hatchery-origin population by allowing at least some of the released hatchery-origin fish that return as adults to spawn in the wild among natural-origin adult fish. The strategy is to use broodstock each generation in the hatchery that is drawn, in whole or in part, from local natural-origin fish. As defined by the Regional Assessment of Supplementation Project (RASP), and adopted here, the primary objective of supplementation is the conservation of the target population, i.e., *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.* Even after many years of conducting various supplementation "experiments", the question still remains, is supplementation an effective strategy to avoid extinction or assist recovery?

Supplementation Objectives. The most basic of the intended objectives of supplementation is to provide a “demographic boost” (i.e., an increase in the number of returning adults) that eventually leads to an increased abundance of natural-origin adults in the target salmon or steelhead population. A necessary condition for realizing this benefit is achieving an increase in the combined hatchery-origin plus natural-origin adult population. The foundation of this desired effect is that the survival advantage for early life stages in the hatchery environment is expected to generate a number of hatchery-origin adults returning from the ocean that is larger than would have resulted from natural spawning by the same number of parents. Then, some of these progeny of hatchery spawning can be allowed to augment the naturally-origin population on the spawning grounds for a net increase on the spawning grounds in that generation. The full list of possible conservation objectives that have been suggested for supplementation is rather long, but includes increasing the speed of rebuilding the size of a naturally spawning population, increasing the size of a natural spawning population, preventing the extirpation of a stock that would continue to decline without supplementation, increasing the genetic effective population size of a stock to avoid inbreeding depression, and allowing for harvest while satisfying conservation goals.

Supplementation Risks. Risks fall into a number of different categories. The primary demographic risk while supplementation is underway is that the number of natural-origin progeny lost due to the removal of natural-origin adults for hatchery broodstock is not replaced by the survival of the hatchery-origin smolts that return as adults and reproduce naturally. The primary genetic risk is that matings in the wild involving one or more hatchery-origin parent(s) result in the production of offspring with reduced fitness through inbreeding depression, outbreeding depression, or domestication. These genetic effects could persist for some number of generations after supplementation is terminated.

The primary ecological risk is that hatchery-origin fish compete with or increase predation on natural-origin fish.

Supplementation Uncertainties. Uncertainties exist regarding potential for both benefits and harm to the target population. As a consequence supplementation in the Columbia River Basin is controversial. Some scientists and managers believe that it is likely that supplementation will produce an increased abundance of natural-origin salmon, and that reformed hatchery practices can reduce the risks from supplementation to acceptable levels. Other scientists and managers not only doubt that the expected increases in abundance will be realized, but also believe that there is a high probability that supplementation will cause significant harm, reducing the productivity and abundance of the natural-origin component of the integrated population. In addition, supplementation (with unmarked hatchery fish) can introduce uncertainty through masking the numbers of natural-origin fish, making a determination of reproductive success difficult (for both natural-origin and hatchery-origin fish).

This report considers 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 tools of benefit-risk assessment used to decide whether to undertake supplementation. Eight general findings are summarized below.

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.

Modeling the Effects of Supplementation:

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.

There are enough streams in the basin already being "treated" with supplementation. Future investment should be in establishing robust experiments with unsupplemented reference streams and rigorous monitoring. Treatments on streams that do not have a matching reference stream should be terminated.

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

1. There is a juvenile survival benefit attributable to the protected hatchery environment; i.e., 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.

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 for 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.
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> 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.
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> 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.
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> 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 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. 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 timeline 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 that a set of supplementation experiments explicitly 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 to the extent possible 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

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 provide the following brief answers to those questions as a summary of our effort. The answers to these questions also appear verbatim in section 8 of the report.

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.

There is a smaller body of empirical studies that document differences in performance and life history attributes of natural-origin and hatchery-origin salmon and trout in situations comparable to supplementation 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 readily by other means that would not expose the population to the risks of supplementation (e.g., nutrient addition).

The five mechanisms that could be harmful 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) and depression of wild spawning productivity because of domestication selection in the hatchery phase (i.e., reduction in population fitness). 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 benefits or losses of supplementation 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 lifecycle, 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 advise 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.