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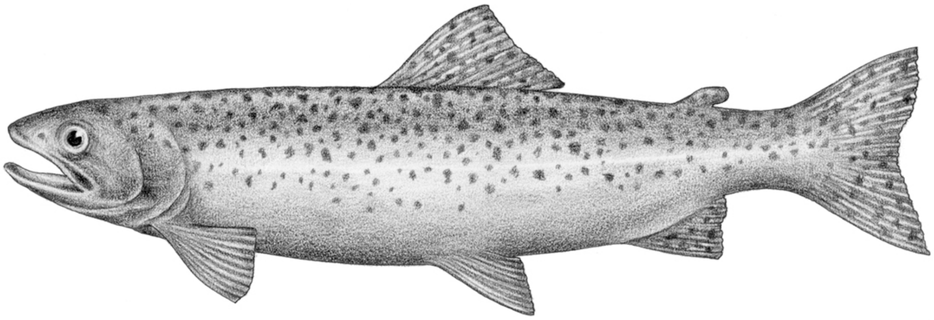
Viability of ESUs Containing Multiple Types of Populations



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Viability of ESUs Containing Multiple Types of Populations

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Viability of ESUs Containing Multiple Types of Populations

Executive Summary

The ISAB has been asked by NOAA Fisheries to answer a series of questions about the viability of ESUs that contain a mixture of hatchery and wild fish and/or resident and anadromous fish. We felt that in order to respond to these questions, the ESU concept required some expansion to include considerations of the elements required for viability. We have termed this expanded definition a “Viable ESU”. To be viable an ESU needs more than simple persistence over time; it needs to be in an ecologically and evolutionarily functional state. Evaluation of ESU viability should not only rest on the numbers of component populations or on the abundance and productivity of those individual populations, but also should be based on the integration of population dynamics within the ecosystem as a whole. This concept of ESU viability does not accommodate the loss of populations or the anadromous or resident life history form from any given ESU, because that loss would represent a loss in diversity for the ESU that would put its long-term viability at risk. This argument is based on evidence that an ESU needs to contain viable populations inhabiting a variety of different habitats, interconnected as a metapopulation, if that ESU is to fulfill the entire complement of ecological and evolutionary interactions and functions.

We consider a Viable ESU to consist of a group of populations existing together as a metapopulation that as an entity is self-sustaining for the foreseeable future. Each population of a viable ESU needs to exhibit the abundance, productivity, diversity, and spatial distribution of natural spawners sufficient to accomplish the following: avoid the loss of genetic and/or life history diversity during short-term losses in abundance that are expected parts of environmental cycles; fulfill key ecological functions that are attributable to the species, such as nutrient cycling and food web roles; and provide for long-term evolutionary adaptability to changing environmental conditions. However, given the high uncertainty in prediction of future environmental conditions, as well as the uncertainty in interpretation of how genetic or other diversity metrics will be expressed in future environments, prudent management would hedge bets by avoiding loss of currently small, peripheral, or in any way seemingly less valuable ESU components.

Establishing the policy boundaries for ESU viability assessment is likely to be as important to the eventual outcome as the method used in the assessment. The natural populations associated with integrated hatchery programs are generally not themselves viable and the habitats upon which they depend are usually inadequate. If the policy decision is made that self-sustaining natural populations are not required for an ESU to be viable, it is likely that the number of extant natural populations will continue to decrease and the impetus behind current efforts to improve habitat conditions will be greatly reduced. We believe that the current science indicates that ESUs dependent upon hatchery production cannot be viable ESUs according to the definition of this term we are using in this report. Therefore, a policy that recognizes such ESUs as viable would need to use a definition of viability much different from the one we are using. The biological validity of such a definition would be questionable.

Summary of ISAB Responses to NOAA Questions

Part I: Hatchery Questions

Question #1A *Are there scientifically sound methods for evaluating the contribution of "in ESU" hatchery stocks to the viability of an ESU?*

At least three different modeling approaches are being used to assess viability of biological entities (i.e., populations, ESUs, DPSs, species), population viability analyses (Beissinger and McCullough 2002), quantitative rule-based systems (Mace and Stuart 1994, Musick 1999), and expert opinion systems (Maquire and Cochrane 2001, Marcot et al. 2001). The population viability analysis entails building a detailed and specific model of the population and its future environment and is the most scientifically rigorous approach. The validity of rule-based systems and expert opinion depends on how closely the rules or opinion are based on accepted scientific theory and empirical facts (e.g., Brown et al. 2004). Regardless of which method is employed, the objectives of the assessment, the questions being addressed, and the policy parameters associated with the objectives need to be stated clearly. Policy parameters that need to be clarified include the time horizons for viability and the likelihood (probability) of viability.

Question #1B *If such methods exist, are they reliable for predicting viability over long-term (centuries or longer), medium-term (decades), and/or short-term (a decade or less) timeframes?*

While methods exist to assess viability, their reliability for application to salmonids is not well understood at present. In general, the accuracy of point predictions is expected to decrease as the time horizon increases. And in general, it is expected that the uncertainty about medium to long term point predictions will be large. For this reason, viability assessments should quantify the uncertainty as well as a point prediction. In this sense, the "reliability" of a viability assessment method is better gauged by the credibility of its quantification of uncertainty than by whether the point predictions (e.g., "best estimate") are uncertain. It is clear that the reliability of viability assessment methods for salmonids could be improved significantly by continued directed research and monitoring.

Question #1C *Are the currently available data for any of the Columbia River salmon ESUs sufficient to enable the application of these methods?*

Some supplementation programs reviewed by the ISAB (2003) are collecting appropriate data for assessment of viability. The Hood River and Yakima supplementation projects have detailed monitoring plans in place and two additional projects, the Northeast Oregon Hatchery (NEOH) and the Johnson Creek Artificial Propagation Enhancement Project, have been proposed. The only ongoing study of which we are aware that could provide some information on the performance of naturally spawning populations after the termination of supplementation is the Idaho Supplementation Study (ISS). However, lack of completeness of the data being collected in the ISS could compromise the application of the results of the study to this question. More subjective assessment methods also have been used. The SHIEER (Salmonid Hatchery Inventory and Effects Evaluation Report) assessment of integrated programs by NOAA Fisheries (NOAA 2004b) is a case-by-case professional judgment review of the effects of hatchery programs on the viability of the natural populations. Professional judgment was used in this effort because data that were needed for a more rigorous assessment were often not available. Even where some of these data were available, the relationship between the reported facts and the conclusions about the effect on viability was not particularly transparent.

Question #2A *In an integrated hatchery-natural system that is operated according to currently accepted best conservation practices (e.g., as described by the Hatchery Scientific Review Group), what does the available scientific information indicate about the probability that the natural component of the population would lose the ability to sustain itself without further augmentation?*

Goodman (2004 and 2005) summarized the demographic and fitness consequences of an integrated natural/hatchery salmon population, and extended this modeling effort by incorporating harvest. Goodman (2004) also drew the following additional conclusions regarding the performance of an integrated system *relative to an unsupplemented population*, and the ISAB concurs with them:

1. Integration will almost certainly increase the potential for harvest that is sustainable as long as the integration continues, but this increase will cease immediately upon termination of supplementation and may be replaced by a decline.
2. Integration will probably increase the number of fish participating in natural spawning for as long as integration continues, but this increase will cease immediately upon termination of integration and may be replaced by a decline.
3. Integration certainly will not increase the natural spawning fitness of the supplemented stock.
4. Integration *may* depress the natural spawning fitness of the stock, and this depression in replacement rate will be manifest for as long as integration continues *and* will continue to express itself for some number of generations after integration is terminated.
5. The probability and magnitude of the depression in natural spawning fitness of the integrated population will increase with the magnitude of the sustainable harvest that is extracted.
6. The probability and magnitude of the depression in natural spawning fitness of the integrated population will increase with the magnitude of the broodstock mining rate.
7. There is a possibility of runaway domestication selection in an integrated breeding program that departs from strict supplementation by drawing some of its broodstock from returning hatchery progeny.
8. The feasibility of adhering to a strict protocol of drawing broodstock only from natural origin fish will depend on the natural spawning and hatchery spawning productivities of the stock, and on limitations of harvest below levels that would otherwise be sustainable.
9. The feasibility of compliance with a cap on the broodstock mining rate and a floor on the fraction of natural origin fish among those spawning naturally will depend on the natural spawning and hatchery spawning productivities of the stock, and on limitation of harvest below levels that would otherwise be sustainable.

Question #2B *What does the available science indicate about how rapidly this might occur?*

Available evidence suggests that fitness declines rapidly with hatchery culture; substantial declines occur after only a few hatchery generations. The current status of integrated hatchery/wild populations also has some bearing on this question. Washington State hatcheries are undergoing a review by the Hatchery Scientific Review Group (HSRG) and Columbia Basin hatcheries are under going a review by the Northwest Power and Conservation Council's Artificial Production Review Evaluation (APRE). The programs range from 2 to 115 years old. Only 2 of 97 natural populations appear to be self-sustaining at this time. In most cases, poor habitat conditions are limiting the recovery of the natural population. Nonetheless, there is little evidence of self-sustaining natural populations in integrated hatchery/natural systems.

***Question** #2C If a naturally spawning population becomes unsustainable without hatchery augmentation, what does the current scientific information say about the likelihood that the population would be able to re-establish self-sustainability, and if so, under what conditions and over what time frame?*

Lynch and O'Healy (2001) and Goodman (2004 and 2005) conclude that a natural population has the potential to readapt to the natural environment once the integration with a hatchery program is terminated. The principal caveat is that if the deleterious effects of integration produce a population that is unable to replace itself, the rate of readaptation must be rapid enough to offset the poor productivity before the population is extirpated. Empirical evidence related to this question can be drawn from efforts to reintroduce coho, spring- and fall-run Chinook, and chum salmon in the Columbia Basin. Results from these programs to date suggest that reestablishing self-sustaining populations is likely to be the exception, rather than the rule unless ecological/habitat/overharvest problems are solved, and augmentation programs have been implemented in a manner that minimizes genetic/adaptive impacts on the natural population.

PART II: Anadromous/Resident Questions

Question #1 *What is known about how resident fish contribute to the long-term viability of ESUs that contain both anadromous and resident fish?*

Although the genetic similarity of sympatric resident and anadromous life histories of rainbow trout does suggest that interbreeding occurs at some level, evidence is not universally conclusive that resident populations play a key role in supporting the productivity or abundance of any steelhead population (or the reverse). The resident life histories may positively influence viability of an ESU that contains sympatric resident and anadromous forms by contributing to the overall abundance and diversity (because residency is an important life history strategy in many circumstances). The role of the resident life history in maintaining population connectivity and spatial structure is unclear, but it undoubtedly differs in timing and extent from the anadromous life history. As a result, the presence of both resident and anadromous life-history forms is critical for conserving the diversity of steelhead/rainbow trout populations and, therefore, the overall viability of ESUs.

Question #2A *Does the loss of anadromy from a population have a sufficient effect on ESU diversity to reduce the likelihood of long-term persistence of the ESU?*

Loss of anadromy will undoubtedly change the structure and connectedness of metapopulations within the ESU. The two life history forms (anadromous and resident) likely play different roles in the maintenance of population structure and the loss of one form may change the population structure by altering patterns of gene flow. When either anadromy or residency is lost, populations will likely become more isolated and vulnerable to loss of genetic diversity. Ultimately, this loss of diversity will reduce the probability of long-term persistence.

Question #2B *What is the evidence that once the anadromous life history form is lost from an ESU, a self-sustaining anadromous population can be re-established (either naturally or as part of reintroduction effort) from the resident component of the ESU at some time in the future?*

Based on the available information, it seems unlikely that a population of resident trout can consistently reestablish a steelhead population. There is evidence that the capacity to express anadromy is retained in a population of resident trout for many generations after extirpation of the anadromous life history form (Thrower et al. 2005). However, it is uncertain whether the smolting and survival rates exhibited by smolts from resident fish would be sufficient to enable reestablishment of a viable steelhead life history type. One of the few cases of a resident population giving rise to an anadromous component is an example from Argentina (Pascual et al. 2001). In this case, however, the anadromous population that arose from the introduced resident fish did not reestablish an extirpated population but expanded into an unoccupied niche. We conclude that once anadromy is lost from an ESU, resident populations are not likely to regenerate self-sustaining anadromous populations in the short or intermediate term, and that the ESU viability would be largely compromised.

Question #3 *What does current scientific information tell us about the abundance, productivity and diversity of salmon or steelhead ESUs that have lost one or more life-history trajectories?*

The available evidence indicates that the loss of one or more life-history types from an ESU can impact abundance and productivity. The effect on ESU diversity and spatial distribution is less speculative; loss of a life-history type from an ESU clearly impacts these attributes. The ISAB concludes that the maintenance (or restoration, where possible) of all of the naturally occurring life history types of an ESU should be one of the goals of salmon recovery.

Viability of ESUs Containing Multiple Types of Populations

Introduction

At the request of NOAA Fisheries, the ISAB is responding to a series of questions that have arisen in response to recent court cases (e.g., *Alsea Valley Alliance v. Evans* U.S. District Court Ruling September 12, 2001 -- Alsea Decision) and other developments that have emphasized the complexity of evaluating the viability of Evolutionarily Significant Units (ESUs). These questions specifically address the assessment of the viability of ESUs that contain both hatchery and natural populations or steelhead (*Oncorhynchus mykiss*) ESUs that contain both anadromous and resident life-history forms.

Five questions were posed. To help the ISAB answer these questions, a series of presentations were made to the ISAB, and we attended a NOAA Fisheries sponsored workshop held in late March: *ESU Symposium/Workshop: Considering Life History, Behavioral, and Ecological Complexity in Defining Conservation Units and Assessing Viability in Pacific Salmon.*

The presentations made to the ISAB relevant to these questions included:

- Implementation of the NOAA policy regarding inclusion of hatchery fish in ESUs – Rob Jones
- Contribution of resident *O. mykiss* to ESU viability – Jeff Hard
- *O. mykiss* status review update – Robin Waples

Background

The Alsea Decision (Alsea Valley Alliance vs. Evans), which in some ways prompted the management questions that are the subject of this scientific review, was a legal ruling on a procedural issue, not on a scientific one. The Court ruled that because under the ESA an ESU is a legally defined population unit, decisions on whether or not to list an ESU as Endangered or Threatened must be made considering an ESU in its entirety. In contrast to this legal context, conservation biologists consider an ESU in a biological context. That is, an ESU is a demographically and genetically distinct component of a species that because of its past evolutionary history has differentiated from other such components in the process of becoming adapted to its local environment. As such, an ESU represents a component of the species that, if extirpated, is not fully replaceable. Although it is possible that its habitat may at some point in time be recolonized from other ESUs within the species, all or some of the original ESU’s life history characteristics may not become reconstituted. The ISAB has responded to the questions from NOAA using this scientific interpretation of ESUs; comparison to the legal interpretation may not be one to one.

Prior to the Alsea Decision, NOAA Fisheries focused nearly exclusively on naturally spawning populations, both for identifying ESUs and for evaluating their viability. Hatchery stocks were generally included in an ESU if they belonged to the same evolutionary lineage and had not diverged substantially from the natural-origin fish in the ESU. Hatchery-origin components of an ESU whose natural-origin components were listed under the ESA, were themselves listed only if they were considered essential for recovery (see FR 58:17573). In response to the Alsea Decision, NOAA Fisheries has proposed to continue to include hatchery stocks in ESUs in cases where they are genetically similar to natural populations in an ESU. In addition, when making listing decisions, NOAA Fisheries has proposed to consider the contribution that these hatchery stocks make to the viability of the ESU as a whole (*Proposed Policy on the Consideration of Hatchery-Origin Fish in Endangered Species Act Listing Determinations for Pacific Salmon and Steelhead* -- FR 69: 31354).

Resident *O. mykiss* have been considered part of steelhead ESUs because most available data indicate that in areas accessible to anadromous fish, the resident fish are genetically similar to the anadromous fish. Although resident fish generally have not been listed under the ESA, listing the anadromous component of a steelhead ESU, but not the resident component, results in the legal problem identified in the Alsea Decision, i.e., listing only a part of an ESU. In recent status review updates the Biological Review Team (BRT) concluded that the anadromous life-history component of a steelhead ESU was such an important component of the ESU's diversity that it was biologically reasonable to equate the extinction risk of the ESU with the extinction risk of only the anadromous part of the ESU. Legally, a component of an ESU may be designated as essential for recovery (i.e., necessary, but not sufficient).

It is within this context that the ISAB has been asked to answer the five specific questions about the viability of ESUs that contain a mixture of hatchery and wild fish and/or resident and anadromous fish. Because both of these circumstances require determining ESU viability in a specific context, the ISAB begins with a list of our definitions for "hatchery fish", "natural fish", "resident fish", and "anadromous fish". The ISAB follows these definitions with an explanation of our scientific understanding of an ESU, and from that foundation defines a Viable ESU and develops a framework for assessing ESU viability.

There are certain fundamental differences between a "Viable Salmonid Population" (VSP) as defined by NOAA in McElheny et al. (2000), and a viable ESU as we use the term here. To be viable an ESU needs more than simple persistence over time; it needs to be in an ecologically and evolutionarily functional state. Evaluation of ESU viability should not only rest on the numbers of component populations or on the abundance and productivity of those individual populations, but also should be based on the population dynamics within the ecosystem as a whole. For example, populations are needed throughout the landscape to promote the evolutionary diversity needed for adaptation to systematic environmental change (e.g., global warming). This concept of ESU viability does not accommodate the loss of either the anadromous or resident life history form from any given ESU, because that loss would represent a loss in diversity for the ESU that would put its long-term viability at risk. In addition, although this concept of ESU viability may not preclude the presence of hatchery-origin individuals within an ESU, it does preclude the dependence of ESU viability on hatchery-origin individuals and it precludes the replacement of the original wild population with a hatchery derived one.

This argument is based on evidence that an ESU needs to contain viable populations inhabiting a variety of different habitats interconnected as a metapopulation, if that ESU is to fulfill the entire complement of ecological and evolutionary interactions and functions. As a result, there needs to be sufficient connectivity among the spawning habitats of the component populations to allow the migration of individuals to recolonize vacant habitats in the event of local extirpation.

Definitions

Hatchery Fish. Individuals produced from eggs/fry that were incubated/reared in a fish hatchery before release to complete their life-cycle under natural conditions, regardless of the culture history of the parents.

Natural Fish. Individuals produced from eggs that were fertilized by natural spawning and incubated instream in gravel and subsequently from fry reared in natural habitats before migration to the ocean, regardless of the culture history of the parents.

Resident Fish. Individuals that remain in freshwater and do not inhabit marine waters for a portion of their life-cycle. The parents could have been either resident or anadromous.

Anadromous Fish. Individuals produced from eggs that are incubated in freshwater and that subsequently undergo a downstream migration and enter marine waters, before returning as adults from a marine migration to reproduce in freshwater. The parents could have been either resident or anadromous.

Evolutionarily Significant Unit (ESU). We adopt the NOAA Fisheries definition (Waples 1991, 1995) for an ESU: An ESU consists of a group of populations that meets two distinct criteria:

1. an ESU must be substantially reproductively isolated from other conspecific units, and
2. it must represent an important component of the evolutionary legacy of that species.

Expanding beyond these two criteria, the ISAB expects the various component populations within each ESU to be differentiated from one another as a result of adaptation to their local environments, yet linked through occasional gene flow in what is now termed a metapopulation (see Hallerman 2003). A key feature of the metapopulation concept is that natural recolonization from other populations of the same ESA can replace or replenish local populations within the ESU that are extirpated, significantly increasing the likelihood of long-term persistence of the ESU. It is likely that only some of these component populations could at any one time serve as source populations for such recolonization, but it is not possible to predict which component population that will be. Furthermore, the populations serving as sources for recolonization are expected to change over time in response to habitat alterations, harvest pressure, climate change, etc. Finally, it is the genetic and life history diversity within and among these component populations that provides the genetic material (heritable variation) that allows the ESU to adapt to the changing environmental conditions of the future (Noss 1990).

The essential dynamic characteristic of a metapopulation (ESU) is spatially and temporally varying highly abundant and productive source populations providing recruits to less abundant and productive habitats. In the absence of this property, if there are insufficient productive source populations for recruitment to less productive habitats, the less productive sites will become vacant and recolonization would be unlikely in a reasonable timeframe. The failure to maintain sufficient connectivity and source populations within an ESU could have long-range, negative consequences for the entire metapopulation. Because of the interrelationship among the populations within an ESU, the overall viability of the entire ESU is more than the simple sum of the viability of each of its component populations. We emphasize that maintaining the viability of ESUs will also require maintaining the availability of diverse environments that support the full suite of life histories that might be expressed by the component populations. To ensure that this critical linkage between ecological and evolutionary potentials and habitat protection is maintained, it is essential that both ESU and Critical Habitat Policies be consistent.

Viable ESU (VESU). Using our expanded definition of an ESU, we consider a Viable ESU (VESU) to be a group of populations existing together as a metapopulation that as an entity is self-sustaining for the foreseeable future because it has the abundance, productivity, diversity, and spatial distribution of natural spawners sufficient to allow the ESU to:

1. rebound from periods of low abundance that are expected, natural phases of population cycles;
2. avoid the loss of genetic and/or life history diversity during these short-term periods of low abundance;
3. provide colonists, in the form of straying adults, that are capable of establishing new populations in suitable but otherwise vacated habitats;
4. fulfill key ecological and societal functions that are attributable to the species; these can include societal functions such as human harvest;
5. provide for long-term evolutionary adaptability to changing environmental conditions.

Rationale for the Viable ESU Definition

The Viable ESU definition above is intended to expand the concept of viability beyond a narrow focus on measures of near-term persistence (i.e., the probability of extinction in the near-term) to recognize the function that a salmon ESU serves in Pacific Northwest ecosystems. This concept of ESU viability requires both genetic competency of individuals and genetic variation within and between locations, as well as enough suitable habitats to realize the genetic potential of these individuals. Fundamental population principles state that the status of a population, ESU, or species is a function of the genetic constitution of the individuals, the abiotic environment in which those individuals live, and the interaction of those individuals with the rest of the biological community.

Evaluation of ESU viability should rest not only on the numbers of component populations and/or their individual abundances, but also on the population dynamics within integrated metapopulations. There needs to be sufficient connectivity between spawning habitats for migrating individuals to recolonize vacant habitats in the event of extirpation caused by environmental catastrophes (e.g., the eruption of Mount St. Helens or more local disturbances such as fire, sever floods or drought, destructive land use and land development). Component populations of an ESU that are located throughout the landscape promote the diversity in form and function that can provide the genetic resources for adaptation to systematic environmental change (e.g., global warming or climate cycles on various time scales).

Relationship of the ISAB Definition of a Viable ESU to NOAA Fisheries' Definition of a Viable Salmonid Population (VSP, McElhany et al 2000)

NOAA Fisheries adopted a Viable Salmonid Population concept (McElhany et al 2000) to guide their Technical Recovery Teams developing recovery plans for ESA listed Pacific salmon. A VSP is an independent population of any Pacific salmonid (genus *Oncorhynchus*) that has a negligible risk of extinction due to threats from demographic variation (random or directional), local environmental variation, and genetic diversity changes (random or directional) over a 100-year timeframe.

Four parameters are used for evaluating the viability of any given VSP:

1. Abundance (Spawning ground escapements are calculated separately for natural-origin and hatchery-origin returning adults.)
2. Productivity (Spawner-to-spawner ratios or adult replacement rates are calculated separately for natural-origin and hatchery-origin returning adults, and the impacts of hatchery-origin smolts on natural-origin smolts are assessed.)
3. Diversity (Variation in the genetic composition, phenotypic attributes, and life histories are determined separately for natural-origin and hatchery-origin components.)
4. Spatial Distribution (Physical location within the watershed of natural-origin and hatchery-origin returning adults and smolts.)

In determining the condition (risk status) of a single population, each of the four VSP parameters is assessed individually, with the overall result being a synthesis of those assessments, not a simple summation. It might seem logical to define the criteria for assessing the viability of an ESU in a manner directly parallel to that already used to identify a "Viable Salmonid Population" (VSP). In fact, such an approach has been proposed by NMFS (Federal Register – June 15, 2004). The ISAB, however, concludes that such an approach fails to consider adequately a number of attributes needed for long term, self-sustaining persistence of an ESU.

Simply ramping up the current VSP approach to Columbia River Basin ESUs might suggest that some ESU components could be considered expendable if other components had sufficiently high abundance or productivity. The ISAB believes, however, that any effective approach to defining a Viable ESU must explicitly accommodate the high degree of uncertainty about the future states of the environment and about the expression of genotypic or other indirect measures of diversity as phenotypic diversity in those future actual conditions in time and space. Given the high uncertainty in exact prediction of future environmental conditions, as well as the uncertainty in interpretation of how genetic or other diversity metrics will be expressed in future environments (and so how the diversity of phenotypes may interact with and influence one another), prudent management would hedge bets by avoiding loss of currently small, peripheral, or in any way seemingly less valuable ESU components.

Because of the differences between Viable ESUs and VSPs, as explained above, we believe that reliance on the VSP criteria alone is an overly simplistic approach that fails to account for the complex nature of the interactions among the components of ESUs. Because an ESU may incorporate a large amount of ecologically important geographic and genetic structure, any assessment of ESU viability must rest on the integration of the entire group of individual population viability assessments into a logical whole. As a result, the four parameters used to assess population viability, although still relevant for consideration, would need to be considered in a more sophisticated manner, expanded as follows:

1. Abundance - Assessment of abundance cannot simply be determined by the total number of returning spawners across the ESU, but must rely on the integration of component abundances. That is, extraordinary abundances of a single component, either of natural or hatchery-origin, cannot overcome the risks incurred as a result of low abundances among other components within the ESU.
2. Productivity - Similarly, assessment of productivity cannot simply be determined by calculating the adult replacement rate across the ESU, but must rely on the integration of component productivities. That is, one highly productive component cannot overcome the risks associated with a number of the other components having low productivities.
3. Diversity - This assessment needs to consider how the variation in both genetic and ecological (e.g., life history) characters inherent in the ESU as a whole is distributed among its components.
4. Spatial Distribution - This assessment needs to include not only a determination of how the distribution of component populations throughout the ESU would impact risk of catastrophic events, but also how demographic and genetic connectivity is affected.

So, to reiterate our basic ecological/evolutionary premise, a Viable ESU needs to have for each of its component populations the abundance, productivity, diversity, spatial distribution of natural spawners and mutual connectivity among components sufficient to accomplish the following: avoid the loss of genetic and/or life history diversity during short-term losses in abundance that are expected parts of environmental cycles; fulfill key ecological functions that are attributable to the species, such as nutrient cycling and food web roles; and provide for long-term evolutionary adaptability to changing environmental conditions.

Scientists and managers in the Columbia River Basin are facing difficulty devising measures for diversity that can be directly translated into ecological or evolutionary currency, such as absolute and relative demographic performance. There are ways to begin to build understanding of such metrics in nature. For instance, theory of coexistence (of species or populations or phenotypes or components of ESUs) indicates that the independence of demographic response (<u>productivity</u> in the terms of the VSP and new VESU attributes) of components of an ESU over space, time, or both is a significant and useful measure of expressed diversity. Combined with other basic demographic information, such a measure (e.g., complement of covariation of the ESU components productivities) could be used to quantify demographic diversity within the ESU and to analyze how such diversity contributed to persistence in time, space, or both of the entire ESU (Chesson and Huntly 1988, 1989, 1994, 1997; Chesson and Rosenzweig 1991, Chesson 2000). This same body of theory argues that another key metric for understanding persistence of ESU components (stated as populations in the theory, but arguably extended quite naturally to the ESU scenario) and the diversity of ESUs (stated as diversity – species richness in the theory -- but again arguably extended naturally to the ESU scenario) is the tendency for components to rebound when rare. When this is the case, the ESU is expected to persist, i.e., it is viable. Similarly, the same logic and analysis can be applied a step up to look at ESUs within a species or at ESU or populations within a community of interacting species. Beginning to measure comparative productivity over the range of environmental conditions that occur over space and time and to analyze similarity of the productivities of components of ESUs (or ESUs of a regional population, or ESUs of one species with those of other species in the same region) could allow us to better quantify ecologically meaningful diversity. Similarly, we could examine the correlations of genetic diversity or life history diversity with the integrated measure of diversity that is provided by comparative productivity of ESU components in different locations at the same time or over the time-series of conditions in the same place or places.

Active research is needed on the above-described and other approaches to relating measures of diversity to integrated demographic metrics that directly relate to persistence of one or many populations in order to better solve the problems the ISAB is asked to address in this review.

Finally, establishing the policy boundaries for any ESU viability assessment is likely to be as important to the eventual outcome as the method used in the assessment. Deciding on these legal/policy choices will likely determine the trajectory of the natural populations of salmon and steelhead as well as the habitat quality of rivers and streams in the Pacific Northwest. The natural populations associated with integrated hatchery programs are generally not themselves viable and the habitats upon which they depend are usually inadequate (see below). If the policy decision is made that self-sustaining natural populations are not required for an ESU to be viable, it is likely that the number of extant natural populations will continue to decrease and the impetus behind current efforts to improve habitat conditions will be greatly reduced.

In the Artificial Propagation Evaluation Report (NOAA 2004a) Section 3.2 page 27 Clarification of Proposed Hatchery Listing Policy, by contrast, those authors argued that the presence of natural populations was not required for an ESU to be viable. The Hatchery Listing Policy says that it is important to conserve natural populations, but it does not require that natural populations be recovered under all circumstances. This policy conclusion is not consistent with the current understanding of the relevant science, which indicates that a salmon or steelhead ESU should not be considered viable if the natural component of the population is unlikely to persist in the absence of the continued release of hatchery-produced fish.

Answers to Questions

Part I. Hatchery Questions

Question #1A *Are there scientifically sound methods for evaluating the contribution of "in ESU" hatchery stocks to the viability of an ESU?*

Background:
The methods necessary to evaluate effects of "supplementation" on long-term fitness of naturally spawning salmon and steelhead are identical to those needed for an evaluation of the contribution of "in ESU" hatchery stocks to the viability of the naturally spawning proportion of an ESU. As defined by the Regional Assessment of Supplementation Project (RASP), 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.*

A review of salmon and steelhead supplementation was recently completed by the ISAB (2003). Findings 2, 3, and 4 from the ISAB Supplementation report (2003) are applicable to the present questions and are restated here as appropriate:

Finding 2: Contemporary genetic/evolutionary theory, and the literature that supports it, indicate clearly that the natural spawning of progeny of an "in ESU" hatchery stock can present substantial risks to natural populations of salmon and steelhead.

Finding 3: The immediate net demographic benefit or harm to population abundance from natural spawning of progeny of an "in ESU" hatchery stock 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 ESU viability evaluations to date.

Finding 4: Current monitoring and evaluation efforts are inadequate to estimate either benefit or harm from allowing the natural spawning of ESU hatchery stock progeny. The correct parameters are not being measured consistently.

Finding:
At least three different modeling approaches are being used to assess viability of biological entities (i.e., populations, ESUs, DPSs, species), population viability analyses (Beissinger and McCullough 2002), quantitative rule-based systems (Mace and Stuart 1994, Musick 1999), and expert opinion systems (Maquire and Cochrane 2001, Marcot et al. 2001). In addition, analysis of empirical data from "supplementation studies" are of value for evaluation of the contribution of "in ESU" hatchery stocks to the viability of the naturally spawning proportion of an ESU. Each method has strengths and weaknesses. The population viability analysis approach is the most fundamental. It entails building a detailed and specific model of the population and its future environment. Although this effort is a demanding undertaking, it is the most scientifically rigorous. The validity of rule-based systems rests on verification (calibration) against detailed models for a broad enough spectrum of specific cases to establish the generality of the accuracy

of the rules. In the absence of such calibration, the validity of the rules may be open to question. The validity of expert opinion depends on how closely the opinion is founded on accepted scientific theory and empirical facts (e.g., Brown et al. 2004).

A fully detailed population viability analysis for salmonids that accounts for metapopulation phenomena, life history variations, environmental variation, and the influences of hatcheries will require some considerable investment in modeling and in obtaining adequate empirical determinations of the key parameters. Some of the component models are available as mathematical formalisms. For example, Goodman (2004 and 2005) has developed a model that could be used to evaluate whether or not an integrated hatchery and natural population of salmon or steelhead was self-sustaining. That model, however, highlights critically important parameters for which, in fact, empirical estimates are not currently available.

Regardless of which method would be employed, the objectives of the assessment, the questions being addressed, and the policy parameters associated with the objectives need to be stated clearly. For example, addressing the contributions of hatchery individuals to the viability of an ESU could be perceived as the prospects for persistence of natural spawning while the hatchery program continues to operate, the prospects for persistence of the population after termination of the hatchery program, or the prospects for persistence of a particular life history component. These are very different viability assessments. Policy parameters that need to be clarified include the time horizons for evaluating viability and the required likelihood (probability) of viability. In the case of an assessment of the viability of an ESU that includes hatchery programs, the essential policy parameter that needs to be stated clearly is whether or not an ESU can be considered viable if it is maintained only through artificial production. That is, if there are no self-sustaining natural populations, can the ESU be considered viable? If there are self-sustaining natural populations, but the ESU as a whole is judged to not be viable, can it be elevated to "viable" status by including hatchery programs? We believe that the current science indicates that ESUs dependent upon hatchery production cannot be viable ESUs according to the definition of this term we are using in this report. Therefore, a policy that recognizes such ESUs as viable would need to use a definition of viability much different from the one we are using. The biological validity of such a definition would be questionable.

Question #1B *If such methods exist, are they reliable for predicting viability over long-term (centuries or longer), medium term (decades), and/or short term (a decade or less) timeframes?*

Finding:

While methods exist to assess viability, their reliability for application to salmonids is not well understood at present. In general, the accuracy of point predictions is expected to decrease as the time horizon increases. And in general, it is expected that the uncertainty about medium to long term point predictions will be large. For this reason, mature methods for viability assessment quantify the uncertainty as well as delivering a point prediction. In this sense, the "reliability" of a viability assessment method is better gauged by the credibility of its quantification of uncertainty than by whether the point predictions (e.g., "best estimate") are uncertain. Prudent decision systems take uncertainty into account, so credible quantification of uncertainty leads to better decisions. It is clear that the reliability of viability assessment methods for salmonids could be improved significantly by continued directed research and monitoring. The reliability of a fully detailed population viability analysis can be evaluated one case at a time by considering the comprehensiveness and realism of the model and the empirical basis for the parameter values used. The reliability of alternative methods could be evaluated by comparison to a portfolio of validated population viability analyses or by retrospective application to a set of empirical case studies with known outcomes. This evaluation has not been attempted systematically for situations with the complexity of the salmonid ESUs under consideration here. Sufficient time has not elapsed since scientists began predicting the likelihood that a salmonid population (or ESU) would lose viability to develop confidence in alternative methods. Elapsed time must be coupled with appropriate monitoring to establish whether or not the viability changed as predicted by the assessments.

Question #1C *Are the currently available data for any of the Columbia River salmon ESUs sufficient to enable the application of these methods?*

Background:
The ISAB has previously recommended monitoring that could evaluate the effects of supplementation (ISAB 2003). These same recommended parameters should be monitored to answer the questions concerning the contribution of "in ESU" hatchery stocks to the viability of an ESU. We strongly support the funding of adequate monitoring for these supplementation projects.

In addition to our review of supplementation (ISAB 2003), an inspection of both the HSRG and APRE reports reveals that the vital statistics needed to assess the sustainability of an integrated hatchery (natural population, the abundance of hatchery and natural adults, hatchery and natural replacement rates, broodstock mining rate, proportion of hatchery fish on the natural spawning grounds, harvest rates, and harvest selectivity) are lacking for many programs. Assessing the contribution of integrated (and segregated) hatchery programs to ESU viability using expert systems may be possible in the absence of rigorous data, but the results are highly uncertain.

Finding:
Some supplementation programs reviewed by the ISAB (2003) are collecting appropriate data for assessment of viability. For example, the Hood River and Yakima supplementation projects have detailed monitoring plans in place. Since our 2003 review, two additional projects, the Northeast Oregon Hatchery (NEOH) and the Johnson Creek Artificial Propagation Enhancement Project, have proposed monitoring that would help evaluate the benefit of ESU hatcheries for maintaining the viability of naturally spawning populations in the ESU. The proposed increases in monitoring, however, are not currently being funded.

The only ongoing study of which we are aware that could provide some information on the performance of naturally spawning populations after the termination of supplementation (i.e., ESU hatchery affect) is the Idaho Supplementation Study (ISS). Supposedly, supplementation was stopped in 2004 on treated streams in the ISS and the study is entering Phase III where data collections (and analysis) are intended to address critical uncertainties about the efficacy of supplementation. If useful data are collected, some answers could be available within two to three generations of spring/summer Chinook salmon. Unfortunately, the ISS may not have the level of specificity needed to fully evaluate many hypotheses about the effects of supplementation on naturally spawning populations. Based on the recent ISRP review of the ISS (ISRP 2003), only one basic parameter, redds per mile, was analyzed to relate various levels of supplementation to production. Critical questions about the relationship of ESU hatchery stocks to the naturally spawning segment of the ESU cannot be answered if only redds per mile are evaluated in Phase III of the ISS, or if proposed genetic and environmental monitoring is not included in the NEOH and Johnson Creek studies

In addition, the SHIEER (Salmonid Hatchery Inventory and Effects Evaluation Report) assessment of integrated programs by NOAA Fisheries (NOAA 2004b) appears to have been a case-by-case professional judgment review of the effects that a given hatchery program has on the viability of the natural population. The application of professional judgment was used because data that were needed for a more rigorous assessment for most of the programs were not available. Even where some of these data were available, the relationship between the reported facts and the conclusions about the effect on viability was not particularly transparent.

Question #2A *In an integrated hatchery-natural system that is operated according to currently accepted best conservation practices (e.g., as described by the Hatchery Scientific Review Group -- http://www.longlivethekings.org/HRP_Publications.html), what does the available scientific information indicate about the probability that the natural component of the population would lose the ability to sustain itself without further augmentation?*

Background:

The following definition of Integrated Conservation Hatchery Programs is incorporated from HSRG documents to provide a context for our response.

> An integrated **conservation** (emphasis added) hatchery program is associated with a specified natural population from which gene flow occurs. The goal of an integrated program is to demographically increase the abundance of fish representing a natural population (two environments, one gene pool) with the natural environment driving the adaptation and fitness of a composite population of fish that spawns both in a hatchery and in the wild.

Some of the HSRG Management Guidelines for Integrated Programs are:

1. Use natural-origin adults in the hatchery broodstock. The percentage of natural-origin adults in the broodstock should be a minimum of 10% to avoid divergence of the hatchery population from the natural component.

2. The proportion of natural-origin fish in the broodstock must exceed the proportion of the hatchery-origin fish spawning in the wild for the natural environment to drive adaptation.

3. A general rule of thumb is that the total number of adults (hatchery- and natural-origin) used for broodstock cannot exceed the total number of natural-origin escapement.

These broodstock management guidelines impose limitations on the size of the program. These limitations depend on the ability to control the mix of hatchery- and natural-origin fish both on the spawning grounds and in the hatchery. They also depend on the number of natural spawners available for hatchery broodstock – i.e., the productivity of the natural environment and the harvest rate of natural fish.

The primary scientific foundation for the integrated program's management guidelines is drawn not only from the well developed theory and practice in population genetics and animal breeding concerning natural selection and optimum phenotypes when a population is exposed to two or more environments (either spatially or temporally), but also from the theory of the effect of gene flow on fitness of populations exposed to different environments (Hedrick 1985, Lande 1980, Lande and Arnold 1983). In general, when two population components experience different natural selective forces, if the rate that genes move from one population component to another exceeds the difference in natural selection, the phenotype of that population component will predominate in both environments. That is, gene flow overwhelms the difference in natural selection, and the individuals occupying both environments resemble the individuals from the dominating environment.

This general theory has been explored for the specific case of integrated (supplemented, supported) hatchery and natural salmon populations (Lynch and O'Healy 2001, Ford 2002, Goodman 2004 and 2005). Allele frequencies can change in the hatchery component of the integrated population due to relaxed selection as a result of the increased egg to smolt survival (Lynch and O'Healy 2001), domestication selection in the hatchery (Ford 2002), and strong selection in the wild on the hatchery products after release (Reisenbichler et al. 2004). When natural selection is relaxed, alleles that are deleterious in the wild, and consequently kept at low frequencies, can predominate or even become fixed in the hatchery component of the population. This condition becomes progressively more deleterious for the naturally spawning component when the hatchery population receives only few natural-origin fish as broodstock, and makes a large contribution to natural spawning. Lynch and O'Healy (2001) conclude that under a broad range of gene exchanges between the hatchery and natural components, an equilibrium reduction in fitness of 50% is reached in 10-20 generations. When the hatchery population is nearly closed, with very relaxed selection, fitness is lost much more rapidly.

Natural selection that occurs in the captive population component is termed *domestication selection* (Campton 1995). Selection that occurs in captivity can be deleterious to the natural component because alleles that are advantageous in captivity may not be advantageous in the wild (Ford 2002). Interbreeding between hatchery-origin and natural-origin individuals can alter the phenotype of the natural population and produce reduced relative reproductive performance (aka reduced fitness). The rate of decline in the fitness of the natural population component is a function of the strength of the selection difference in the two environments, the proportion of natural-origin fish in the hatchery broodstock, and the proportion of hatchery-origin fish spawning in the wild. When selection is strong, there can be a 50% reduction in natural-spawning fitness in less than 20 generations under a broad range of broodstock management conditions (Ford 2002). Ford (2002) also coupled a model of fitness reduction in a natural population owing to domestication selection in the hatchery environment with a model of the carrying capacity of the natural environment and the reproductive rate of the natural population. Fitness reduction in the natural population was larger when the carrying capacity of the natural population and the natural spawning replacement rate was less. Ford (2002) concluded that naturally spawning individuals of natural-origin were essential to reduce the change in the phenotype of the natural population component, and that improving habitat to increase the carrying capacity of the natural environment and the replacement rate of the natural spawning population component may be the most effective way to minimize phenotype change in a natural population, even when those improvements are insufficient to permit the population to sustain itself. Strong selection on the hatchery component, different from the selection operating on the natural population, can occur after release in the natural environment, because the hatchery products enter the natural environment at a different size, age, and physiological state, and possibly at a different season, than their natural counterparts. This can lead to the evolution of a different post-release life history, one that is adaptive for hatchery-reared fish, but maladaptive for natural spawning (Reisenbichler et al. 2004, Goodman 2004 and 2005).

Finding:

Goodman (2004 and 2005) summarized the demographic and fitness consequences of an integrated natural/hatchery salmon population, and extended this modeling effort by incorporating harvest. Goodman (2004) also drew the following additional conclusions regarding the performance of an integrated system *relative to an unsupplemented population*, and the ISAB concurs with them:

1. Integration will almost certainly increase the potential for harvest that is sustainable as long as the integration continues, but this increase will cease immediately upon termination of supplementation and may be replaced by a decline.

2. Integration will probably increase the number of fish participating in natural spawning for as long as integration continues, but this increase will cease immediately upon termination of integration and may be replaced by a decline.

3. Integration certainly will not increase the natural spawning fitness of the supplemented stock.

4. Integration *may* depress the natural spawning fitness of the stock, and this depression in replacement rate will be manifest for as long as integration continues *and* will continue to express itself for some number of generations after integration is terminated.

5. The probability and magnitude of the depression in natural spawning fitness of the integrated population will increase with the magnitude of the sustainable harvest that is extracted.

6. The probability and magnitude of the depression in natural spawning fitness of the integrated population will increase with the magnitude of the broodstock mining rate.

7. There is a possibility of runaway domestication selection in an integrated breeding program that departs from strict supplementation by drawing some of its broodstock from returning hatchery progeny.

8. The feasibility of adhering to a strict protocol of drawing broodstock only from natural origin fish will depend on the natural spawning and hatchery spawning productivities of the stock, and on limitations of harvest below levels that would otherwise be sustainable.

9. The feasibility of compliance with a cap on the broodstock mining rate and a floor on the fraction of natural origin fish among those spawning naturally will depend on the natural spawning and hatchery spawning productivities of the stock, and on limitation of harvest below levels that would otherwise be sustainable.

Question #2B *What does the available science indicate about how rapidly this might occur?*

Finding:

Loss of Fitness in Hatchery-Origin Salmon and Steelhead

The RSRP reviewed and analyzed empirical evidence of whether or not, and how fast, hatchery fish lose fitness for natural spawning (RSRP 2004). The major evidence they identify is adopted for this report.

The RSRP compiled studies of salmonids for which the relative fitness of hatchery fish in the wild can be compared to that of wild fish and for which there is information on the number of generations the fish have been in hatcheries. They chose only those studies in which hatchery fish came from rivers that were the same as or nearby to the origin of the wild fish and those in which hatchery fish came from other regions of the species' range. They also excluded studies in which most, if not all, of the "wild" fish were derived from prior hatchery escapes.

Six studies met their criteria. A study with Danish brown trout had the longest period in culture, about 12.5 generations (50 years) (Hansen 2002). Columbia River basin winter- and summer-run steelhead studies provided contrasts from populations that had been in culture from 7 to 9 generations (Hulett et al. 1996, Leider et al. 1990). Commercially farmed Atlantic salmon provided populations that had spent 2-5 generations in the hatchery environment (Fleming et al. 2000). Estimates of relative reproductive success for each gender in three brood years (1995-1996, 1996-1997, and 1997-1998) of Hood River winter-steelhead provide evaluations of populations in culture for a single generation.

The RSRP concluded: "despite the limitations of each study, there is a relationship between the relative fitness of hatchery fish and the number of generations in hatchery culture (Figure 1). Relative fitness of hatchery fish declines regularly with the number of generations in culture. An exponential curve fit to the data indicates that fitness is lost in excess of 20% per generation. Even if the actual loss rate is overestimated by these data (recall that Blouin's results indicated approximately a 10% loss in one generation), they suggest that fitness is lost rapidly in hatcheries."

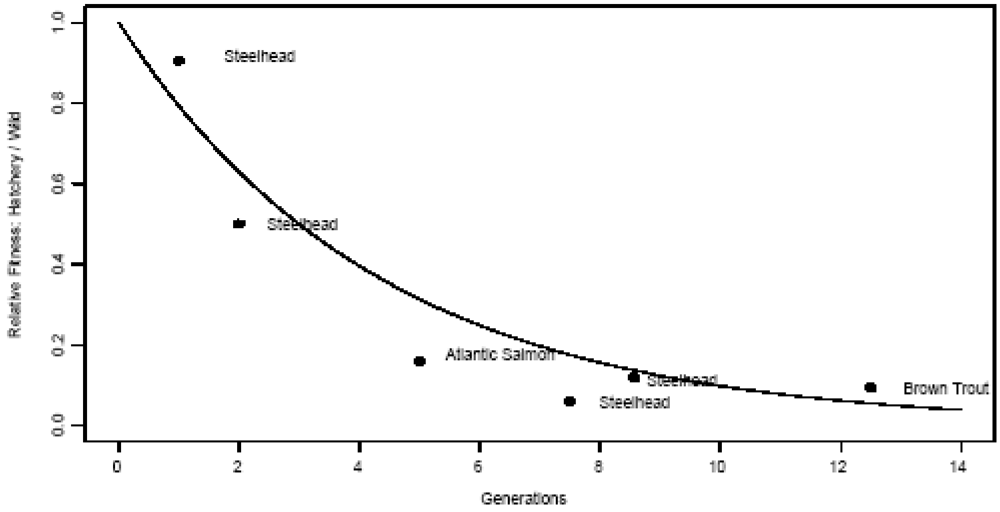

Figure 1. Relative fitness of hatchery to wild salmonids (From RSRP 2004).

The analysis in the RSRP report includes only iteroparous salmonid species. While unlikely, semelparous species – those that die after spawning – might exhibit a different rate of change in reproductive fitness associated with the number of generations under hatchery culture. Also, the RSRP did not use a few studies that showed equal or greater fitness for hatchery fish, arguing that “wild” populations in these cases were really just feral hatchery populations. The ISAB concurs with this approach and analysis.

Status of Natural Populations Integrated with Pacific Northwest Hatchery Programs
Directed by the United States Congress, Washington State hatcheries are undergoing a review by the Hatchery Scientific Review Group (HSRG) and Columbia Basin hatcheries are under going a review by the Northwest Power and Conservation Council’s Artificial Production Review Evaluation (APRE). Both of these reviews categorized each hatchery program as either integrated or segregated. NOAA Fisheries identified which of these integrated programs were associated with natural populations for each of the listed ESUs (NOAA Fisheries 2004a: SHIEER Report). In their review the HSRG reported the status of the viability of the natural population integrated with a hatchery population and the status of the habitat used by the natural population. In the review by the APRE, the status of the natural population and habitat was also reported, but in this case the status was the combined natural and artificial components. The NOAA Fisheries SHIEER Report compiled a list of programs and evaluated whether they believed hatchery fish were contributing to the natural population. This evaluation did not report on the status of the natural population or the habitat.

Using the HSRG, APRE, NOAA Fisheries SHIEER, and the NOAA-Fisheries Biological Review Team status report (NOAA Fisheries 2004b), the ISAB assigned one of three status categories to each natural population: critical (generally referring to populations in low abundance with productivities less than 0.90), at risk (populations in low abundance with productivities 0.90 - 1.0), or healthy. The ISAB also assigned one of three categories to the habitat: inadequate, limiting, or healthy.

This assessment is compiled into Table 1, for steelhead, chinook, coho, and chum salmon.

Species/ESU/Subbasin	River Basin	Program/Stock	Date of Culture	Status of Natural Population	
				Viability	Habitat
Steelhead					
Lower Columbia Steelhead ESU					
Cowlitz	Cispus River	Cowlitz Winter Run	1996	At Risk	Inadequate
Cowlitz	Tilton River	Cowlitz Winter Run	2002	At Risk	Inadequate
Cowlitz	Upper Cowlitz	Cowlitz Winter Run	1996	At Risk	Inadequate
Cowlitz	Lower Cowlitz	Cowlitz Winter Run	1967	At Risk	Limiting
Kalama	Kalama	Kalama Winter Run	1998	At Risk	Limiting
Kalama	Kalama	Kalama Summer Run	1999	At Risk	Limiting
Clackamas	Clackamas	Clackamas Winter Run	1991	At Risk	Limiting
Sandy	Sandy River	Sandy River Late Winter Run	2000	At Risk	Limiting
Hood River	Hood River	Hood River Winter Run	1991	At Risk	Limiting
Hood River	Hood River	Hood River Summer Run	1998	Critical	Limiting
Middle Columbia Steelhead ESU					
Umatilla	Umatilla	Umatilla Summer Steelhead	1992	At Risk	Limiting
Walla Walla	Touchet River	Touchet Summer Steelhead	2000	At Risk	Limiting
Deschutes	Deschutes	Deschutes Summer Steelhead	1974	At Risk	Limiting
Yakima	Yakima	Yakima Summer Steelhead	2000	Critical	Inadequate

Species/ESU/Subbasin	River Basin	Program/Stock	Date of Culture	Status of Natural Population	
				Viability	Habitat
Upper Columbia Steelhead ESU					
Wenatchee	Wenatchee	WDF Wenatchee Program	1996	Critical	Inadequate
Methow	Methow	Wells Hatchery	1982	Critical	Inadequate
Methow	Methow	Winthrop Hatchery	1982	Critical	Inadequate
Okanogan	Omak Creek	Methow/Sp-Methow	2003	Critical	Inadequate
Snake River Steelhead ESU					
Clearwater	Clearwater	Dworshak B-run Steelhead	1969	At Risk	Inadequate
Imnaha	Imnaha	Summer Steelhead	1982	At Risk	Limiting
Tucannon	Tucannon	Summer Steelhead	2002	Critical	Inadequate
Chinook					
Puget Sound Chinook ESU					
	Nooksack	Kendall Creek/Spring	1979	Critical	Inadequate
	Skagit	Marblemount/Spring	1978	Critical	Inadequate
	Skagit	Marblemount/Summer	1995	Healthy	Limiting
	Skagit	Marblemount/Fall	1999	At Risk	Limiting
	Tulalip Bay	Tulalip/Summer	1999		
	Stillagamish	N.F.Stillagamish/Su	1980	Critical	Inadequate
	Snohomish	Wallace/Summer	1973	Critical	Limiting
	Green	Soos Ck/F	1901	At Risk	Limiting
	Green	Keta Ck/F	1987	At Risk	Limiting
	Puyallup	Voights Ck/F	1917	At Risk	Inadequate

Species/ESU/Subbasin	River Basin	Program/Stock	Date of Culture	Status of Natural Population	
				Viability	Habitat
Puget Sound Chinook ESU (cont.)	Puyallup	Diru Ck/F	1979	At Risk	Inadequate
	Puyallup	White R/Su	1989	Critical	Inadequate
	Nisqually	Clear/Kalama/F	1979	At Risk	Limiting
	Dungeness	Dungeness/Sp	1992	At Risk	Limiting
	Elwha	Elwha/F	1953	At Risk	Inadequate
Lower Columbia ESU					
Columbia Estuary	Chinook River	Sea Resources/Fall	1982	At Risk	Limiting
Columbia Estuary	Big Creek	Fall Chinook/Tule	1941	At Risk	Limiting
Cowlitz	Cowlitz	Cowlitz/Fall	1963	Unclear	Inadequate
Cowlitz	Cowlitz/Sp	Cowlitz/Spring	1968/1999	Unclear	Inadequate
Cowlitz	Toutle/Sp	Toutle/Sp	1950/1985	Unclear	Inadequate
Kalama	Kalama	Kalama/Spring*	1959	Unclear	Limiting
Kalama	Kalama	Kalama/Fall	1895	Unclear	Limiting
Elochman	Elochman	Elochman/Fall	1956	Unclear	Limiting
Lewis	Lewis	Lewis/Spring	1960	Unclear	Healthy
Washougal	Washougal	Washougal/Fall	1955	Unclear	Healthy
White Salmon	White Salmon	Spring Creek NFH/Fall	1901	Unclear	Limiting
Sandy	Sandy River	Sandy River/Spring	2002	Unclear	Limiting
Upper Willamette ESU					
Willamette	N.F. Santiam River	N.F. Santiam/Spring	1950	Critical	Inadequate
	M.F. Willamette	Willamette/Spring	1957	Critical	Inadequate

Species/ESU/Subbasin	River Basin	Program/Stock	Date of Culture	Status of Natural Population	
				Viability	Habitat
	McKenzie	McKenzie/Spring	1930	At Risk	Limiting
	S.F. Santiam	S.F. Santiam/Spring	1968	Critical	Inadequate
	Clackamas	Clackamas/Spring	1979	Healthy	Limiting
Upper Columbia ESU	Wenatchee	Chiwawa/Sp	1989	Critical	Inadequate
	Wenatchee	White R/Sp	1999	Critical	Inadequate
	Methow	Twisp/Sp	1992	Critical	Inadequate
	Methow	Chewuch/Sp	1992	Critical	Inadequate
	Methow	Methow/Sp-Methow	2001	Critical	Inadequate
	Methow	Methow/Sp-Winthrop	2001	Critical	Inadequate
Snake River Fall ESU	Snake River	Lyons Ferry/Fall	1984	At Risk	Inadequate
Snake River Sp/Su ESU	Salmon	McCall S.F./ Su	1974	At Risk	Inadequate
	Salmon	McCall Johnson Ck/Su	1998	At Risk	Inadequate
	Salmon	Sawtooth/Sp	1985	At Risk	Inadequate
	Salmon	Pahsimeroi/Su	1980	Critical	Inadequate
	Grande Ronde	Catherine Ck/Su	1995	Critical	Inadequate
	Grande Ronde	Up Grande Ronde/Su	1995	Critical	Inadequate
	Grande Ronde	Lostine R/Su	1995	Critical	Inadequate
	Imnaha	Imnaha/Sp-Su	1982	At Risk	Limiting
	Imnaha	Big Sheep Creek/Sp-Su	1997	At Risk	Limiting
	Tucannon/Sp	Tucannon/Sp	1985	Critical	Limiting

Species/ESU/Subbasin	River Basin	Program/Stock	Date of Culture	Status of Natural Population	
				Viability	Habitat
Coho					
Lower Columbia Coho ESU					
Grays	Grays River	Type - S Coho Program	1961	Critical	Inadequate
Grays	Grays River	Sea Resources Type - S	1996	Critical	Inadequate
Grays	Grays River	Deep River Type - S Coho	1993	Critical	Inadequate
	Big Creek	Big Creek Hatchery Coho	1941	Critical	Inadequate
Elochoman	Elochoman River	Type - S Coho Program	1954	Critical	Inadequate
Elochoman	Elochoman River	Type - N Coho Program	1954	Critical	Inadequate
Cowlitz	Uper Cowlitz	Type - N Coho Program		Critical	Inadequate
Cowlitz	Lower Cowlitz	Type - N Coho Program	1967	Critical	Inadequate
Cowlitz	Toutle River	Type - S Coho Program	1951	Critical	Inadequate
Lewis	N.F. Lewis R.	Type - S Coho Program	1991	Critical	Inadequate
Lewis	N.F. Lewis R.	Type - N Coho Program		Critical	Inadequate
Lewis	Cedar Creek	Fish First Wild Coho		Critical	Inadequate
Lewis	N.F. Lewis R.	Fish First Type - N Coho		Critical	Inadequate
Clackamas	Clackamas River	Eagle Creek NFH Coho	1957	At Risk	Limiting
Sandy	Sandy River	Sandy River Coho Program		At Risk	Limiting
Washougal	Washougal River	Type - N - Coho	1985	Critical	Inadequate
Columbia Gorge	Lower Gorge Tribs	Bonneville/Cascade/Oxbow Coho		Critical	Inadequate

Species/ESU/Subbasin	**River Basin**	**Program/Stock**	**Date of Culture**	**Status of Natural Population**	
				Viability	**Habitat**
Chum					
Lower Columbia Chum ESU					
Columbia Estuary	Chinook River	Sea Resources/ Fall	1996	At Risk	Inadequate
Grays	Grays River	Grays River/ Fall	1997	At Risk	Inadequate
Washougal	Washougal River	Washougal-Duncan Creek/ Fall	2002	At Risk	Inadequate
Hood Canal Summer Chum ESU					
Bio Quilcene River	Big Quilcene	Quilcene NFH/ Summer	1992	At Risk	Inadequate
Western Hood Canal	Hamma Hamma	Hamma Hamma H/ Summer	1998	At Risk	Inadequate
Southwestern Hood Canal	Lilliwaup Creek	Lilliwaup Creek/ Summer	1992	At Risk	Inadequate
Union River	Union River		2000	At Risk	Inadequate
North Hood Canal	Big Beef Creek	Big Beef Creek Hatchery/ Su	1996	At Risk	Inadequate
Discovery Bay	Salmon Creek	Salmon Creek Hatchery/ Su	1992	At Risk	Inadequate
Port Townsend Bay	Chimacum Creek	Chimacum Creek Hatchery/ Su	1996	At Risk	Inadequate
Sequim Bay	Jimmycomelately C	Jimmycomelately C H/ Su	1999	At Risk	Inadequate

Based on this compilation from the Columbia River Basin and Puget Sound domains, there are approximately 97 integrated hatchery programs for steelhead (21), Chinook (48), coho (17), and chum (11) salmon. For steelhead, 14 populations are categorized as at risk and seven as critical; all have limiting or inadequate habitat. For Chinook salmon, 17 populations were categorized as at risk, 19 as critical, and two as healthy (Clackamas in the Upper Willamette Chinook ESU and Marblemount Summer - Skagit R in the Puget Sound Chinook ESU). Only two locations, the Lewis River and the Washougal River, in the lower Columbia River Basin had healthy habitat. The remaining 46 Chinook programs had inadequate or limiting habitat. For coho salmon, two populations (Clackamas and Sandy Rivers) were at risk and the remaining 15 critical. Habitat was rated as limiting in streams of the two at risk populations and inadequate in the remaining 15. For chum salmon, three Lower Columbia Chum ESU populations were rated as at risk with inadequate habitat and eight Hood Canal Summer Chum ESU populations were rated as at risk with inadequate habitat.

From a brief scanning of the narratives of these programs, most appear to fall short of achieving the HSRG criteria for having 10% or more of the broodstock be of natural-origin and having less than 5% of the natural spawning adults be of hatchery-origin. The programs range from 2 to 115 years old. The question of how long these programs can operate before the natural-origin population is no longer self-sustaining appears to be moot. Only 2 of 97 natural populations appear to be self-sustaining at this time, primarily because of limited habitat. To move toward the recommendations of the HSRG and the theoretical work of both Ford (2002) and Goodman (2004 and 2005), the first step toward improving these programs is to improve the carrying capacity of the environment and the productivity of the natural-origin salmon and steelhead. Nonetheless, there is little evidence of self-sustaining natural populations in integrated hatchery/natural systems.

Question #2C *If a naturally spawning population becomes unsustainable without hatchery augmentation, what does the current scientific information say about the likelihood that the population would be able to re-establish self-sustainability, and if so, under what conditions and over what time frame?*

Background:
If a naturally spawning population becomes unsustainable for ecological reasons, such as degraded habitat or imposed mortality, the only prospects for re-establishing self-sustainability are to correct the ecological problems. Hatchery augmentation may be used to “buy time” for a short duration while ecological problems are being addressed, but during this period the cumulating (probably compounding) genetic/adaptive problems caused by the hatchery phase reduces the ability of eventual reestablishment. Theoretical consideration of the genetic/adaptive aspects of this question is addressed by Lynch and O’Healy (2001) and Goodman (2004 and 2005). Empirical evidence to address this question can be drawn from efforts to reintroduce coho, spring- and fall-run Chinook, and chum salmon.

Lynch and O’Healy (2001) and Goodman (2004 and 2005) conclude that a natural population has some potential to readapt to the natural environment once the integration with a hatchery program is terminated. The principal caveat is that if the deleterious effects of integration produce a population that is unable to replace itself, readaptation will also have to offset the consequences of demographic failure. If the rate of readaptation cannot offset the poor productivity, the population could become extirpated before it readapts. Under these conditions, when the natural population component receives substantial gene flow from the hatchery component, it may require several dozens of generations to recover lost fitness (Lynch and O'Healy). The rate of recovery will depend on the average selection coefficient against the deleterious alleles that had accumulated under conditions of relaxed selection. If a proportion of the deleterious alleles became fixed in the natural population during integration, the time to recovery may be substantially greater. This would require new, or back, mutations and/or the migration of wild-type alleles from other population sources.

In the Columbia River basin, coho salmon have been reintroduced into the Wenatchee, Yakima, Umatilla, and Clearwater subbasins. Spring Chinook have been reintroduced into the Umatilla and Hood River subbasins, and fall Chinook into the Umatilla River subbasin. In the Hood Canal, summer-run chum have been reintroduced into two streams. The success of these programs has been variable, but none has reestablished self-sustaining runs. These reintroduction programs have taken eggs from one location, reared them at a hatchery, and then released them into a foreign environment. These programs are challenged both by the number of generations that the hatchery fish have been under culture and by the environmental differences between the donor and recipient environments. A few of the programs (Umatilla spring-run Chinook and Yakima coho) have been sufficiently successful in returning first generation hatchery-origin adults that eggs to continue the programs are taken *in-situ*, rather than from the origin donor stock location. Other programs (Hood River spring-run Chinook) have not achieved that level of success and rely on continued importation of fish or eggs. The recent Umatilla subbasin plan did not anticipate that either the fall-run Chinook or coho reintroduction programs would become self-sustaining in the foreseeable future.

Finding:
Based on these observations, reestablishing self-sustaining populations is likely to be the exception, rather than the rule unless ecological/habitat/overharvest problems are solved and augmentation programs have been implemented in a manner that minimizes genetic/adaptive impacts on the natural population.

Part II. Anadromous/Resident Questions

Question #1 *What is known about how resident fish contribute to the long-term viability of ESUs that contain both anadromous and resident fish?*

Background:
The long-term viability of an ESU depends to a substantial degree on the conservation of the diversity of the various life histories inherent within it. As a result, when considering the question of how fish with one life history strategy (e.g., residency) contribute to the viability of an ESU containing at least two life history strategies (residency and anadromy), we need to consider how resident fish influence the four viability parameters (abundance, productivity, diversity, spatial distribution) of both life histories. Such an assessment needs to consider gene

flow between forms, its resulting impact on fitness, and the role of each form in metapopulation processes. This assessment must recognize that the two forms may or may not be reproductively isolated. Empirical evidence supports anadromy and residency in the same gene pool (partial anadromy, Jonsson and Jonsson 1993, Docker and Heath 2003), reproductive isolation of sympatric populations exhibiting the alternative migratory forms (Zimmerman and Reeves 2000), and genetic differentiation between the migratory forms on a small spatial scale (e.g., Narum et al. 2004).

Abundance:
The assessment of abundance as a viability parameter must integrate individual population abundances of both forms. Nevertheless, the presence of viable, natural spawning, populations of resident *O. mykiss* will positively influence ESU viability simply by increasing the overall abundance (resident + anadromous). Evolutionary theory suggests the abundance of anadromous and resident rainbow trout in an ESU (here we consider only resident fish below migration barriers) will depend largely on the habitat characteristics that influence the relative fitness of each strategy (Hendry et al. 2004, Jonsson and Jonsson 1993). Therefore, as the habitat characteristics change (as a result of natural or anthropogenic factors), we expect the relative abundance of the two migratory forms to change (Jonsson and Jonsson 1993). For example, habitat alterations (e.g., dams) have caused a decline in anadromous populations in some ESUs (e.g., Upper Columbia River, NOAA Fisheries 2003). Consequently, the resident form is the major source of abundance. The viability of these ESUs is positively influenced by the abundance of resident rainbow trout. In general, however, viability is likely diminished because of the levels of lost productivity, diversity, and spatial distribution that accompany loss of the anadromous form (see below).

Productivity:
It has been clear since the 1940's that resident rainbow trout are the major (if not exclusive) source of production of resident fish, and that steelhead are the major (if not exclusive) source of production of anadromous fish. Neave (1944) collected eggs from resident x resident and steelhead x steelhead crosses from the Cowichan River in British Columbia in 1938 and 1939. The resulting parr were marked and released back into the river and adults from the crosses were recaptured through 1944. He found that all recaptured adult fish of steelhead parents were anadromous and all recaptured offspring of resident trout crosses remained in freshwater, suggesting a strong genetic component to life history. In fact, Neave (1944) suggested that these results indicated that resident rainbow trout and steelhead should be considered separate species.

More recent work on this topic has used the Sr/Ca ratios in the primordia of otoliths to indicate whether the maternal parent of that fish was reared in salt or fresh water. Phelps et al. (1997) applied this technique to 16 returning steelhead from the Kalama River and found that all of these fish were the offspring of anadromous females. Unfortunately, no resident rainbow trout were analyzed in this study. This technique, however, was later applied to assess the parentage of resident and anadromous rainbow trout in both the Deschutes River, Oregon and the Babine River, British Columbia (Zimmerman and Reeves 2000). Otoliths from 20 steelhead and 38 resident rainbow trout were collected from the Deschutes River. All steelhead examined had anadromous maternal parents and all resident trout were produced by resident mothers. The maternal parentage of the Babine River fish was not as consistent. Of the 24 steelhead examined from this system, one had a resident maternal parent. Of the nine resident trout examined, two had otolith chemistry indicating that the maternal parent was anadromous. The authors attributed the high degree of segregation of the resident and anadromous rainbow trout populations in the Deschutes River to a difference in spawning time and spawning habitat characteristics; steelhead spawn about 9-10 weeks earlier than resident fish and select spawning habitat in deeper water with larger substrate size.

There is some additional evidence in California river systems that resident rainbow trout can produce anadromous offspring. Otolith chemistry of steelhead smolts from the central California coast indicated these fish were the offspring of both resident and anadromous mothers (Zimmerman, unpublished data as cited in Zimmerman and Reeves 2000). Similarly, a small number of smolts emigrating from Sespe Creek, a tributary of the Santa Clara River, have been traced to resident rainbow trout stocked in this stream (Entrix Inc., 1996). There is no evidence, however, that any of the smolts produced by the resident trout in these streams have contributed to the very few adult steelhead that currently return to these California systems. Although it is clear that the each of the two life history forms can produce offspring that apparently initiate the alternative form, the degree at which this occurs, much less its impact, is most likely population, or even location, specific.

Diversity and Spatial Distribution:
Even though the breeding and otolith studies cited above found limited evidence to suggest cross contributions of the two life history forms, molecular genetic studies have found evidence for a reasonable amount of historical geneflow. For example, genetic characterization of resident and anadromous forms of rainbow trout in the Deschutes and Walla Walla Rivers found few distinctions between the two life history forms. Chilcote (1976) used protein electrophoresis to examine 13 polymorphic loci of resident and anadromous fish from five sites in the Deschutes and found that only a single resident population, one that was isolated above two impassable waterfalls, exhibited significant deviation in allele frequencies from the other populations. In a subsequent study of *O. mykiss* in the Deschutes River, differences in protein and meristic characters were found between resident populations isolated above waterfalls and downstream fish, but no differences were found in sympatric populations of resident and anadromous rainbow trout (Currens et al. 1990). Narum et al. (2004) found evidence of weak but significant genetic differentiation between sympatric resident and anadromous rainbow trout in the mainstem Walla Walla River, but not the Touchet River. Narum et al. (2004) suggest the two life history forms may mate assortatively by size or spawning time in the Walla Walla River. Alternatively, evidence of reproductive isolation could reflect the stocking of out-of-basin steelhead of Snake River origin in the mainstem Walla Walla River. Collectively, these results suggest that significant genetic exchange occurs at least sporadically between resident and anadromous forms of rainbow trout in the Deschutes and Walla Walla systems (Chilcote 1976). The more recent otolith work appears to indicate, however, that this level of geneflow may not be consistent.

Both “anadromous” and “resident” forms may be highly migratory, and the two migratory forms may play geographically distinct roles in colonization and the maintenance of genetic diversity and population structure. Resident rainbow trout in large freshwater systems can be highly migratory (Meka et al. 2003) and may contribute more to gene flow on a fine spatial scale than do steelhead. Steelhead may contribute more to gene flow on a broad spatial scale (between distant watersheds and across saltwater), thereby providing a mechanism for genetic connection among isolated populations of resident rainbow trout. There is some support for such an anadromous/nonanadromous dichotomy in gene-flow pattern if one compares across species. Castric and Bernatchez (2004) found that nonanadromous brook charr exhibit a higher rate of fine-scale dispersal than co-occurring anadromous Atlantic salmon (*Salmo salar*), consistent with the different migratory behaviors of the two species. As a result, resident and anadromous fish may both play key roles in recolonization efforts within an ESU, with the relative importance of each form varying with environmental circumstances.

There are few if any examples of the diversity and spatial structure of resident and anadromous populations of *O. mykiss* in pristine rivers in the western US, largely because most river basins have been extensively altered by human development. There is evidence, however, that broad life history diversity exists in some rivers of the Kamchatka Peninsula of eastern Asia where environmental impacts have been far fewer. The following figure illustrates the variation in life histories of *O. mykiss* inhabiting adjacent river basins in relatively pristine ecosystems.

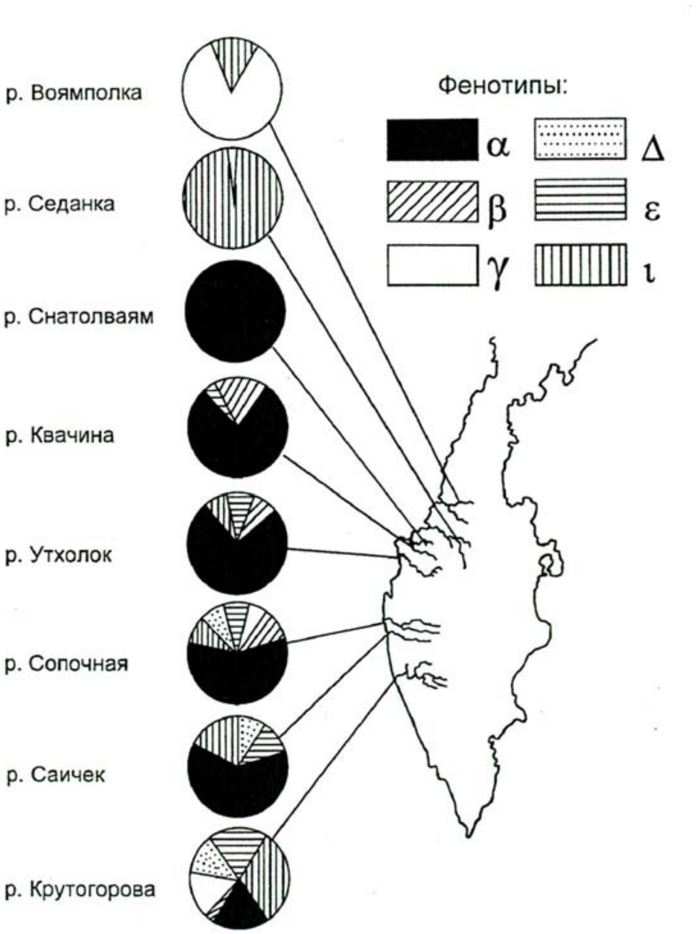

Figure 2. Variation in the proportion of different life history strategies in *O. mykiss* [*Parasalmo mykiss*, according to Russian authors] in eight rivers on the west coast of the Kamchatka Peninsula. Six life history strategies were recognized from scale analysis: two different

patterns of anadromy, estuarine residency, riverine-estuarine migrants, “half-pounders” (<1 year at sea), and strict freshwater residency. Each strategy is represented by a different shading pattern (from Pavlov et al. (2001).

This figure illustrates two important points. First, considerable life history diversity, including multiple variations of anadromy and residency, tends to be expressed in this species where the freshwater environment contains the full range of habitats to which the species has adapted over time. Second, the relative importance of different life histories can vary markedly in adjacent rivers and in different parts of the drainage system, suggesting that local conditions strongly influence which life history will predominate. Life history variation may also occur within a river system over both short- and long-term temporal scales. Pavlov et al. (2001) found that the relative contribution of different life histories to the population varied in a continuum along a river from headwaters to mouth, rather than being expressed as discrete resident and anadromous populations. Such variation may be essential for long-term population persistence in changing environments.

Finding:

Although the genetic similarity of sympatric resident and anadromous life histories of rainbow trout does suggest that interbreeding occurs at some level, there is little information for specific populations on the extent to which resident rainbow trout contribute to the abundance of the anadromous life history component. That is, evidence is not universally conclusive that resident populations play a key role in supporting the productivity or abundance of any steelhead population (or the reverse). On the other hand, the resident life histories may positively influence viability of an ESU that contains sympatric resident and anadromous forms by contributing to the overall abundance and diversity (because residency is an important life history strategy in some circumstances). The role of the resident life history in maintaining population connectivity and spatial structure is unclear, but it undoubtedly differs in timing and extent from the anadromous life history. As a result, the presence of both resident and anadromous life-history forms is critical for conserving the diversity of steelhead/rainbow trout populations and, therefore, the overall viability of ESUs.

Question #2A *Does the loss of anadromy from a population have a sufficient effect on ESU diversity to reduce the likelihood of long-term persistence of the ESU?*

Background:

Loss of anadromy will undoubtedly change the structure and connectedness of metapopulations within the ESU. The two life history forms (anadromous and resident) likely play different roles in the maintenance of population structure (as suggested above), and the loss of one form may change the population structure by altering patterns of gene flow. In particular, long distance migrations between major watersheds and through saltwater can only be accomplished by anadromous *O. mykiss*. When either anadromy or residency is lost, populations will likely become more isolated and vulnerable to loss of genetic diversity.

Finding:
Based on the evidence presented below, the ISAB concludes that the likelihood of long-term persistence would be substantially compromised by the loss of anadromy in *O. mykiss* ESUs.

Question #2B *What is the evidence that once the anadromous life history form is lost from an ESU, a self-sustaining anadromous population can be re-established (either naturally or as part of reintroduction effort) from the resident component of the ESU at some time in the future?*

Background:
Once anadromy has been lost from a population or ESU, it is unclear whether or not this life history could be reestablished within a population of entirely resident fish; evidence on this is equivocal. The potential for reestablishment of anadromy by resident fish most likely depends greatly upon which resident fish population is being considered. Unfortunately, there is no reliable method to predict where and when resident populations are capable of this process at all, much less within a timeframe important to recovery.

One way to assess this question is to weigh the evidence that anadromous and nonanadromous forms can be derived from one another. There are some reports in the literature of resident rainbow trout populations establishing anadromy. Rainbow trout from several sources, including some fish from California that were derived at least partly from steelhead, were introduced into numerous rivers in Argentina starting in the early 20th century. Populations of resident rainbow trout were established in many of these systems. Anadromy, however, was not reported from this region until 2001, when it was determined that a population in the Santa Cruz River had developed an anadromous form (Pascual et al. 2001). Microsatellite evaluation indicated that the now sympatric resident and anadromous forms from this river were genetically indistinguishable and appeared to be most closely related to the fish from California. The newly established Argentine anadromous population may, however, exhibit some differences from steelhead populations in California.

The capacity for a resident rainbow trout population to reestablish an anadromous form also may be influenced by the environment. In both the Yakima and the Willamette Rivers, there are resident *O. mykiss* populations in headwater tributaries and cool upper reaches of the mainstem rivers. Steelhead spawning in these rivers are spatially segregated from resident trout spawning. Cramer et al. (2003) propose that *O. mykiss* juveniles migrate from spawning and rearing tributaries when flows are reduced in the late summer/fall. If these migrating individuals arrive at mainstem habitats that have sufficient flow and low temperature, they halt their migration and become residents. If flows in the mainstem are low and temperatures high, they continue a downstream migration until they reach the ocean. Even in river systems like the Deschutes, where both life history types occur in sympatry, anadromous and resident life history types use different tributaries and river habitats (Zimmerman and Reeves 2000).

A striking example of the potential for a resident population to reestablish anadromy was reported from Alaska (Thrower et al. 2004). Juvenile trout were captured in 1926 from a stream that contained steelhead and transported to a lake that was isolated from the ocean by several barrier waterfalls. These stocked fish established a resident population in this lake. In 1996, a study (Thrower et al. 2004) was undertaken to determine the propensity for fish from the lake population to produce smolts after 70 years of selection against this life history trait. The proportion of juvenile fish smolting was compared with the smolting rate of offspring from steelhead captured in the lower river. Not surprisingly, the smolting rate of the lake fish was lower than that of the steelhead. Even after 70 years of selection against anadromy, however, nearly half the fish produced from a cross of a resident male with a resident female smolted. These smolts were subsequently released from the hatchery where the crosses were produced, and marine survival was evaluated. Offspring from the lake fish survived at a lower rate than smolts from anadromous parents (0.7% versus 2.8%). This is one of the only experiments where the production of smolts and subsequent marine survival of a resident population of rainbow trout has been quantified.

There is also evidence that resident rainbow trout populations are unlikely to reestablish an anadromous form. Steelhead in California historically occurred south to nearly the Mexican border (BRT 2003). Anadromy has been lost in many of these watersheds despite the presence of resident rainbow trout populations. It is not clear whether or not the failure to reestablish anadromy is due to an inability of the extant resident populations to express this life history trait or the loss of habitats critical to support of steelhead.

We conclude from these various observations that there are likely both genetic and environment determinants for the expression of anadromous and resident *O. mykiss* life-history variation. Whether the underlying genetic mechanisms generate life-history plasticity (the production of different life-history types by a single genotype under different environmental conditions) or polymorphism (the production of different life-history types by different genotypes), or a combination of both, is not known. Regardless of the genetic mechanism, however, maintaining the anadromous population component is likely very important. Empirically this is demonstrated by the experiments with resident *O. mykiss* in Alaska (Thrower et al. 2004), where the resident fish have reduced performance after isolation from the anadromous component of the population. Theoretically, both plasticity (Kingsolver et al. 2002) and polymorphism (Meyers and Bull 2002) are maintained by evolution in spatially or temporally variable environments with gene exchange between individuals in the different environments.

We feel that in addressing this question, it is also important to consider the reciprocal situation, i.e., whether or not a self-sustaining resident population can be re-established (either naturally or as part of a reintroduction effort) from the anadromous component of the ESU at some time in the future. Although the effect of the diversity introduced into a rainbow trout ESU by anadromy on the long-term viability of that ESU is difficult to assess directly, there are examples where the existence of an anadromous life history form has clearly aided in the recovery of depressed populations. Large catastrophic disturbances are relatively common in many of the areas occupied by these fish in western North America. Large wildfires, volcanic eruptions, and earthquakes all have the potential to reduce or extirpate trout populations in freshwater. Because a substantial proportion of a steelhead population is in the ocean at any given point in time, that portion is immune from such large disturbances. These fish can later serve to recolonize areas impacted by the disturbance. Perhaps the most striking example of this situation occurred following the eruption of Mt. St Helens in 1980. Steelhead that were at sea during the 1980 eruption rapidly reoccupied areas of the South Fork Toutle River and Green River (a tributary of the North Fork Toutle River) where adequate habitat remained after the eruption. As a result of the availability of these colonizing fish, steelhead populations in the affected area rebounded rapidly with populations achieving fishable levels by the mid 1980s (Lucas 1985). Whether resident populations were re-established by steelhead is less certain, however. Some rainbow trout were present above migration barriers in upper Toutle River tributaries before the eruption, but these fish may have originated from resident trout stocked in headwater lakes. Hatchery steelheads were widely stocked in Toutle River tributaries to accelerate the recovery of naturally spawning fish after the eruption. In one stream, a resident rainbow trout population was established as a result of steelhead supplementation; over a 20-year period the rainbow trout population completely displaced the native coastal cutthroat trout population that lived there (Bisson et al. 2005, in press).

Finding:
Based on the available information, it seems unlikely that a population of resident trout can consistently reestablish a steelhead population. The only clear evidence of a resident population giving rise to an anadromous component is the example from Argentina (Pascual et al. 2001). In this case, however, the anadromous population that arose from the resident fish did not reestablish an extirpated population but expanded into an unoccupied niche. If shifts in life history are common in steelhead generated by resident parents, reestablishment of a self-sustaining anadromous component of a population or ESU could be very difficult. The work of Thrower et al. (2005) suggests that the capacity to express anadromy is retained in a population of resident trout for many generations. In this study, the smolting rate and marine survival of the smolts produced by the resident fish were lower than that of the offspring of steelhead. In addition, it remains uncertain whether or not the smolting and survival rates exhibited by the resident fish would be sufficient to enable reestablishment of a viable steelhead life history type. Based on the various empirical observations of *O. mykiss* life-history variations and on principles from theory, we conclude that once anadromy is lost from an ESU, resident populations are not likely to regenerate self-sustaining anadromous populations in the short or intermediate term, and that the ESU viability would be largely compromised.

Question #3 *What does current scientific information tell us about the abundance, productivity and diversity of salmon or steelhead ESUs that have lost one or more life-history trajectories?*

Background:
For this discussion, we consider the term “lost” to mean loss of a significant number of populations and not necessarily complete elimination. We consider the phrase “life-history trajectory” to include traits other than anadromy/nonanadromy. Life-history trajectory also refers to the variation (within a species or ESU) in the season and amount of time that different runs of fish occupy the freshwater, estuarine, and ocean environments. Life-history variation can be dramatic, as in the difference between resident kokanee and anadromous sockeye salmon (both *O. nerka*) and as in the difference between odd and even year pink salmon (*O. gorbuscha*). It can also be subtle, as in the variation in adult run timing in lower Columbia River Chinook salmon that return in the spring, early fall (tules), and late fall (lower river brights) to different tributary spawning streams. Sometimes these life-history trajectories are placed in the same ESU (e.g., the Lower Columbia River Chinook ESU), and at other times they are placed in their own

ESU (e.g., Sacramento River Chinook salmon are placed in separate fall, winter, and spring-run ESUs).

The loss of a life-history trajectory will likely result in a decline in population abundance and productivity, as well as lost diversity. As a result, a decline in ESU viability is expected. This conclusion is based on a large body of literature showing that life history trajectories are the outcome of generations of selection, allowing for local adaptation and maximum use of heterogeneous habitat (Taylor 1991). Pacific salmon have evolved a large array of unique life history types that allow them to persist in dynamic and volatile environments. Many examples have been reported that reveal the importance of life history variation to the resilience and long-term persistence of Pacific salmon. Hilborn et al. (2003) described the importance of multiple life history strategies to the resilience and sustainability of sockeye salmon in Bristol Bay, Alaska. Here, as in other areas (e.g. Fraser River basin, Wood 1995), the sockeye have evolved beach and tributary spawning subpopulations that exhibit distinct morphological and behavioral differences specific to the two environments (Quinn et al. 2001). These sockeye also exhibit a bi-modal timing in adult returns (mid- and late-summer) that appears to be linked to the thermal regime of the incubation habitat (Quinn et al. 2001). Hilborn et al. (2003) show that these and other life history traits allow the Bristol Bay sockeye complex to persist despite major changes in climatic conditions affecting the freshwater and marine environments. They show that life history strategies that dominate during one climatic regime are minor producers during others.

Another example of how life history strategies are linked to local adaptation and increased use of the environment was presented by Brannon (1967). Brannon demonstrated that sockeye salmon spawning in lake outlets have evolved a juvenile migratory strategy that differs from populations that spawn in lake tributaries. Specifically, the juveniles emerging from gravel at the outlet must swim upstream to reach lake rearing environment, whereas the juveniles emerging from gravel in the tributaries must swim downstream (Brannon 1967).

Adult run timing is also an important life history strategy linked to the environment and local adaptation. Chinook salmon exhibit perhaps the greatest diversity of adult run schedules (Healy 1991). For example, the Lower Columbia River ESU consists of spring run chinook, fall (tule) chinook, and late fall (bright) chinook. The different runs have likely evolved to utilize unique habitat, increasing the resilience of the chinook in this area. The importance of maintaining all run times was recognized by the BRT in assessing viability (NOAA 2003). They concluded the decline and loss of some spring-run populations contributed to the finding that this ESU was likely to become endangered in the foreseeable future.

Loss of one or more life histories from an ESU certainly has an effect on ESU diversity and often on spatial distribution. As noted above, steelhead provide a mechanism of genetic connection among populations of resident rainbow trout. This genetic interchange may have a significant impact on the evolutionary pathway of the resident populations. Thus, the presence of both resident and anadromous life history forms likely plays a key role in determining the diversity of rainbow trout populations and ESUs.

There is less empirical evidence regarding the effect of a reduction in life history diversity on productivity or abundance. As noted above, however, there is the theoretical basis to expect that a decrease in life-history diversity could impact abundance and productivity. For example, the existence of an anadromous form in a population or ESU does provide a mechanism for the recolonization of habitats where populations were extirpated by a catastrophic disturbance event or human actions. Typically, these types of extirpations do not affect an entire ESU. Nonetheless, if steelhead were not available to recolonize areas of habitat that were depopulated by such disturbances, recovery of abundance and productivity could take much longer.

The significance of multiple life history types in the support of ESU viability also has been recognized by the BRTs in the recent status reviews (NOAA 2003). For example, the Lower Columbia Chinook ESU consists of a combination of fall run (tules), late fall run (brights), and spring run life history trajectories inhabiting coastal, western Cascade, and Columbia gorge ecological zones (Myers et al. 2003). The loss of many of the spring Chinook populations from the Lower Columbia River ESU was one of the factors supporting their decision to list these ESUs as threatened (NOAA 2003). The same situation applies to the Puget Sound Chinook ESU, where early-returning (spring) fish have been greatly reduced from historical levels. In both cases, the differential impact on the spring life history form is due, in part, to dams blocking access to the high-elevation habitat that historically supported these fish. The Chinook salmon populations in these ESUs have low abundance and productivity, in part due to the loss of the spring life history type and the habitats that supported these fish.

This loss of spring-run biodiversity has ramifications beyond increasing the probability that the entire ESU will become extinct. Salmon are keystone species in the watersheds that they historically have inhabited. Their presence contributes to the diversity of life by cycling nutrients and modifying habitats. Their extinction would increase the risk of extirpation for other species. Keystone species support the ecosystem (entire community of life) of which they are a part. The ISAB emphasized in our definition of a Viable ESU that viability included having sufficient abundance and diversity to continue to provide the ecosystem functions typically attributed to salmon. Loss of life-history trajectories will undoubtedly reduce the resilience of not only the ESU, but also the community to which these fish belonged.

Finding:

The available evidence indicates that the loss of one or more life-history types from an ESU can impact abundance and productivity. The effect on ESU diversity and spatial distribution is less speculative; loss of a life-history type from an ESU clearly impacts these attributes. The ISAB concludes that the maintenance (or restoration, where possible) of all of the naturally occurring life history types of an ESU should be one of the goals of salmon recovery.

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