

Considering Life History, Behavioral, and Ecological Complexity in Defining Conservation Units for Pacific Salmon

An independent panel report, requested by NOAA Fisheries

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Introduction

This report details the conclusions of a scientific panel that was convened at the request of NOAA Fisheries to summarize scientific thinking on questions regarding the biological relationship between hatchery and wild Pacific salmon populations, and between resident populations of rainbow trout and related steelhead populations. The panel included scientists from a range of specialties that pertain to the questions, including population biology, evolutionary genetics, and especially salmon and fisheries biology. A summary of panel members' backgrounds is provided in appendix 1.

The panel discussions took place on March 30th and 31st, 2005. Prior to the meeting, on March 29th, panel members heard and participated in a day-long symposium that covered many of the biological and evolutionary issues that arise when considering hatchery and wild salmon populations and when considering resident and anadromous life history forms, particularly rainbow trout and steelhead. In addition, in the weeks prior to the meeting, panel members were provided with an extensive body of literature pertaining to the questions at hand. The symposium schedule and bibliography are provided in appendices 2 and 3, respectively.

The body of this report describes the conclusions, with regard to the questions addressed, that were shared by the large majority of panel members. However on some important points there was not full consensus. The minority view is summarized at the end of the report.

The title of this report has been borrowed from the title of the symposium that preceded the workshop deliberations. Michael Ford of NOAA Fisheries served as rapporteur during the workshop.

Background

The panel was convened in light of the district court decision in *Alsea Valley Alliance v. Evans* (161 F. Supp. 2d 1154 [D. Or. 2001]), which held that NMFS's treatment of hatchery fish was inconsistent with the Endangered Species Act (ESA). Since it developed the Evolutionarily Significant Unit (ESU) concept, NMFS had included within ESUs hatchery fish that it determined to be genetically similar to wild runs within ESUs, but only listed those hatchery

populations deemed essential to recovery of the wild stocks. Alsea Valley Alliance held that NMFS could not list only part of a single ESU. NMFS's similar practice of including some resident trout with steelhead in a single ESU, but not listing the resident fish, is likely subject to the same legal problem.

NMFS's rationale for including many hatchery and resident fish in ESUs was rooted in its definition of an ESU, which was focused on genetic distinctions. The ESA permits listing of species, subspecies, and "any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature" (16 U.S.C. 1532(16)). NMFS developed the ESU concept as a way of defining a Distinct Population Segment (DPS) for Pacific salmon and steelhead. In 1991, NMFS issued a policy statement declaring that a salmon stock would be considered a DPS if it qualified as an ESU. An ESU was defined as a population or group of populations that is 1) reproductively isolated from other populations, and 2) consists of an important component of the evolutionary legacy of the species (56 Fed. Reg. 58612 [Nov. 20, 1991]). Reproductive isolation in the ESU definition means that gene flow from other populations must be sufficiently limited to allow evolutionarily important differences to accrue between the two populations. The focus on evolutionary legacy implies that the genetic differences between an ESU and other populations are adaptively important.

The ESU policy did not directly address treatment of hatchery fish. In 1993, NMFS issued a second policy statement specifically dealing with hatcheries, known as the Artificial Propagation Policy (58 Fed. Reg. 17573 [Apr. 5, 1993]). It stated that hatchery fish should be excluded from an ESU if they are of a different genetic lineage than the wild population, if artificial propagation has produced appreciable changes in their characteristics, or if there is substantial uncertainty concerning their relationship to the wild fish. Recently, in many cases hatchery fish were included in ESUs based on origin of the hatchery stock and/or molecular genetic similarity to wild fish, in the absence of information on adaptive phenotypic differences (Salmon and Steelhead Hatchery Assessment Group, NMFS 2003).

Given this history, the panel was charged to address the scientific rationale for alternative approaches to determining when it is biologically appropriate to include hatchery produced fish or resident trout in Evolutionarily Significant Units of anadromous Pacific salmon.

Questions

In a letter from Usha Varanasi Ph.D., Director of the Northwest Science Center of NOAA Fisheries and William Fox Ph.D., Director of the NOAA Fisheries Office of Science & Technology, the panel was provided with four questions. Although the questions were not intended to be either exhaustive or exclusive, the panel chose to follow them fairly closely. They were as follows:

1. Is this focus on evolutionary lineages for considering the status of hatchery fish and resident fish scientifically sound? What other approach(es) are reasonable to consider?
2. Is there reasonable biological justification for excluding from a conservation unit a hatchery stock that is genetically similar to natural populations in that unit? For example, assume that 1) natural populations A, B, and C are part of one biological conservation unit, and 2) hatchery population A' was recently derived from population A and, 3) A and A' are reciprocally each other's closest genetic relative.
3. Is there reasonable biological justification for excluding from a conservation unit resident populations that are genetically similar to anadromous populations in that unit? Consider a scenario similar to that described in the previous question, with anadromous and resident populations within a stream being part of the same lineage.
4. What role should ecological, behavioral, and life history differences between resident/anadromous and hatchery/natural fish play in identification of conservation units? Does the answer depend on the degree to which variation in these factors has a genetic basis?

1. Evolutionary Lineages

Consistent with the idea of biological species, ESUs are identified in part as a population or a group of related populations that exhibit substantial reproductive isolation from other populations. This reproductive criterion is widely recognized by biologists as a primary indicator of whether or not populations are on a common evolutionary trajectory and constitute an evolutionary lineage. Being in the “same lineage” is usually roughly synonymous with “shared phylogenetic ancestry”. Quite generally, organisms that are part of the same lineage can be expected to be more closely related to each other than to organisms in other lineages. It is in this light that a hatchery stock may be considered to be within the same evolutionary lineage as the wild population from which the hatchery stock was founded.

However, because “lineage” typically refers to historical derivation or ancestry, the term can be ambiguous when considering the current biological processes that occur among wild fish and hatchery populations. In practice, biologists often use the more contemporaneous and operational term “population” rather than “lineage”. The distinction is an important one because a key component of evolutionary thinking about the way that species evolve concerns the reproductive and competitive processes that occur among the individuals within populations. Members of the same population are not simply genetically closely related; they are also the product of a shared environment and a common regime of natural selection. Not only do they share a genetic history, but they are also ecologically exchangeable in the sense that the role that is played by one individual of a population, as a competitor and interactor within its environment and ecosystem, can often be approximated by another individual from the same population. Because of this, it can be meaningful to identify a natural population as a biological entity, even when that population regularly receives immigrants from another population or hatchery. Similarly, because of environmental differences, it can be meaningful to identify a hatchery population, even when there is frequent immigration from a wild population.

There are many contexts in which phylogenetic relatedness can be a useful proxy for shared adaptive diversity and ecological exchangeability, but this should be tempered with insights into recent and current evolutionary processes. Genetic relatedness is not a direct determinant of shared adaptive diversity or ecological exchangeability among populations. For example,

individuals that are genetically similar but have been reared under different environments have faced differing selection regimes and may express substantially different phenotypes, particularly those related to physiology, behavior and reproductive capacity. Therefore evidence of phylogenetic relatedness should not be considered a sufficient condition for supposing that two groups are ecologically or physiologically exchangeable or equivalent.

There are significant limitations of a strict phylogenetic perspective in which evidence of a shared genetic history is taken as the sole indicator of which populations meet the reproductive and evolutionary legacy criteria of the ESU standard. In particular, hatchery-reared fish may have experienced a selective regime that shifts their allele frequencies in a direction quite different from what is occurring in the gene pool of a related natural population. Such divergence may not be detectable with randomly selected or neutral molecular genetic markers. A regular process of genetic admixture of hatchery-adapted fish to a wild population can prevent the wild population from evolving to meet changing conditions in the wild. Similarly, the behavior of hatchery-reared fish may differ sufficiently from wild fish such that a mixed group may have reduced reproductive success.

By holding to a phylogenetic criterion and overlooking a population perspective of exchangeability, salmon ESUs are sometimes treated largely as taxonomic units rather than as evolutionary and ecological role players. This can lead to a lumping of hatchery fish with related wild populations when in fact the two groups are biologically different in many ways. In addition, it can lead to reduced reproductive success and viability of wild populations in cases where hatchery-reared fish are admixed at high rates with wild populations.

The important but not sufficient role for phylogenetic relatedness, when defining conservation units, can be seen by considering the question of what source population to use in cases when a wild population has been lost and various possible source populations are considered for reintroduction. Phylogenetic information may indicate one or more populations that are closely related to the original lost population, but it is important to consider ecological exchangeability as well. It is possible that a hatchery stock is the most closely related, as determined by broodstock records or neutral genetic markers such as mitochondrial DNA sequence or

microsatellite markers. However, a different closely related wild population that is somewhat more phylogenetically distant, but that has the behavioral and life history characteristics most similar to the original population, may be more likely to restore a self-sustaining wild population.

Answer to question 1: Is this [NMFS's] focus on evolutionary lineages for considering the status of hatchery fish and resident fish scientifically sound? What other approach(s) are reasonable to consider?

Although a focus on lineage and shared phylogenetic history is a necessary starting point for many questions, important biological processes can be overlooked if it is used to the exclusion of other aspects of the evolutionary process. A strict phylogenetic or taxonomic approach overlooks the fact that even within a single generation, hatchery and wild fish differ because of their responses to dissimilar environments. This response is partly physiological and developmental, but it is also genetic, because the two environments create different selective regimes. It is important that ESUs be considered not just from the perspective of shared phylogenetic history, but also in terms of ecological exchangeability and the short term evolutionary forces.

2. ESUs and Hatchery Produced Fish

The second question addressed by the panel was whether there is reasonable biological justification for excluding from a conservation unit a hatchery stock that is genetically similar to natural populations in that unit. The question, as posed in the letter from Drs. Varanasi and Fox, went on to ask the hypothetical question of whether a hatchery population could be excluded on biological grounds from a conservation unit that includes multiple wild populations, when the hatchery population is more closely related to one of those populations than any of the wild populations are to each other.

A useful starting point for the following discussion on the hatchery/wild contrast, is to recognize that distinction at the level of individual fish. Thus while there may be cases where the term “hatchery population” may seem ambiguous, the same need not be true of “hatchery fish”. In this

report the term “hatchery fish” refers to a fish whose parents were spawned in a hatchery or who has spent a portion of its life-cycle in an artificial environment. Likewise, a “wild fish” (or natural fish) is one whose parents spawned in the wild and which has spent its life in the natural environment. While this distinction may not remove all gray areas (such as in the case of fish that grow in man-made albeit, naturalistic spawning channels), the distinction between hatchery fish and wild fish is one that can help avoid confusion in most situations.

2. A. On Scientific Evidence

For some questions regarding differences between hatchery and wild fish there exists a large scientific literature upon which to draw. For example, it is well known that hatchery stocks, in the absence of regular input from wild populations, rapidly diverge from wild fish in many ways (Alvarez and Nieceza 2003; Berejikian 1995; Berejikian et al. 1996; Fleming and Einum 1997; Glover et al. 2004; Kostow 2004; Petersson and Jarvi 2000; Quinn et al. 2002; Reisenbichler and McIntyre 1977; Sundstrom et al. 2004). Similarly phenotypic differences can arise between genetically similar hatchery and wild fish because of the different rearing environments (Alvarez and Nieceza 2003; Berejikian et al. 2001; Dellefors and Johnsson 1995; Einum and Fleming 2001; Fleming et al. 1994; Fleming et al. 1997; Griffiths and Armstrong 2002; Metcalfe et al. 2003; Rhodes and Quinn 1998). The salmon literature does not resolve all questions, however. For this report three general sources of information have been used to address questions about the biological differences between related hatchery and wild populations. These include empirical evidence from salmon, as well as from other organisms. The third source of evidence is theory. Some kinds of questions may be so difficult to address in salmon and other organisms that the empirical evidence with regard to a particular theoretical concept may not be widely demonstrated. Nevertheless, the foundation of the concept may be sufficiently straightforward, and the conditions under which it is expected to apply may be sufficiently general (or exemplified in salmon populations), that the theory itself carries some weight.

2.B. Biological contrasts between hatchery and wild fish

2.B.1. The direct effect of the hatchery environment on phenotype and behavior

Salmon reared in hatcheries differ for basic morphological and life-history traits from their wild-reared immediate relatives (Kostow 2004), and the hatchery experience has

been shown to cause changes in behavior (Fleming et al. 1997; Olla et al. 1998). Some of those changes are readily reversed once the hatchery fish move into natural streams, and others are not. Similarly, studies of comparative survival through parts of the life cycle in other species have shown reduced survival of hatchery turbot (Iglesias et al. 2003) and Japanese flounder (Tanaka et al. 1998) as well as differential susceptibility to certain predators by hatchery and wild red drum (Stunz and Minello 2001).

2.B.2. The fitness of hatchery-reared fish, relative to wild fish.

There is clear evidence for lifetime fitness differences between fish of hatchery/domesticated origin and wild fish through tag-recapture studies in the field that used molecular markers to assign fish from one generation to parental types in the preceding generation (Blouin 2003; Chilcote 2003; Fleming et al. 2000; Hansen et al. 2002; Leider et al. 1990; McGinnity et al. 2003; McGinnity et al. 1997). A study based on microsatellite markers found differences in fitness between wild steelhead and hatchery steelhead, including differences for hatchery fish from an integrated breeding practice (Blouin 2003). In addition, several tag-recapture studies that surveyed part of the life cycle have shown reduced survival rates in hatchery stocks compared to wild fish (Chilcote 2003; Einum and Fleming 2001; Hansen et al. 2002; Kostow 2004; Reisenbichler and McIntyre 1977).

Taken together, the evidence that hatchery fish have reduced fitness when released to the wild, relative to wild fish, is quite strong. Despite considerable research by a number of investigators, studies that do not show such a difference are difficult to come by.

Although one of Blouin's (2003) six comparisons does not show a difference, the other five comparisons show the typical effect. The findings of Dannewitz et al. (2004), suggesting similar fitness of hatchery and wild fish, are partly obscured by the fact that the "wild" fish appear to have had a high degree of hatchery ancestry. Even studies that are questionable because of small sample sizes, such as McLean et al. (2003), suggest a decreased fitness (per capita production of adults) or decreased components of fitness in hatchery-origin fish.

2.B.3. The evolutionary response of salmon to the hatchery environment

Hatchery stocks rapidly evolve and diverge from related wild populations, without regular input from wild populations (Alvarez and Nicieza 2003; Berejikian 1995; Berejikian et al. 1996; Fleming and Einum 1997; Glover et al. 2004; Kostow 2004; Petersson and Jarvi 2000; Quinn et al. 2002; Reisenbichler and McIntyre 1977; Sundstrom et al. 2004). Wild salmon populations can evolve rapidly in the wild (Kinnison et al. 2001; Hendry 2001; Koskinen et al. 2002), potentially compounding the rate of divergence between hatchery and wild populations. Indeed, salmonids show rates of contemporary evolution in the wild that are every bit as “rapid” as any other taxa (Kinnison and Hendry 2004).

2.B.4. The effect of admixture of hatchery fish on the evolutionary potential of wild populations.

Several theoretical treatments have examined the consequences of mixing genotypes adapted to different conditions when the less-fit genotypic class is overwhelmingly more abundant than the more fit class. The original motivation behind these treatments was to examine the consequences of mixing individuals from differently sized populations (Bulmer 1972) and the idea was extended into several areas, including estimating the “migration load” from the influx of maladapted individuals (Felsenstein 1977) and the probability of successful adaptation to a novel habitat (Kirkpatrick and Barton 1997). The general phenomenon has been termed “gene swamping” (Lenormand 2002) and has been applied to the mixing of hatchery and wild stocks by many authors (see e.g. Adkison 1995; Emlen 1991; Ford 2002; Goodman 2005; Harada 1992; Hard 1995; Lynch and O'Hely 2001; Tufto 2001). This work indicates that “gene swamping” by hatchery stocks has the capability of driving wild stocks to extinction, even in integrated breeding programs if there are genetic covariances between traits conferring high fitness in the hatchery environment and low fitness later in life in the wild environment. These effects occur over a broad range of parameter values and the fitness differences required

for those effects to occur fall well within the range of fitness differences that are estimable from tag-recapture comparisons of wild and hatchery fish.

2.C. On the relationship of hatchery and wild populations

A discussion framework that readily arises when considering the distinction between ESUs of wild populations and their related hatchery populations is to consider the hatchery populations, not as part of the conservation unit, but as a potential *tool* for conservation or recovery of a wild population. Within this framework it must be appreciated that some hatchery populations may play a critical role in maintaining wild populations, particularly where habitat conditions may preclude the ability of natural populations to sustain themselves. In those cases where careful study of the critical factors affecting the viability of the wild population leads to the conclusion that a hatchery is a critical resource for sustaining or assisting the recovery of that wild population, then that hatchery resource needs to be maintained and optimized for that purpose. While the biological distinction between hatchery-raised, and wild-bred fish may be recognized when defining conservation units, the role of particular hatcheries as conservation tools needs to be assessed on a case-by-case basis.

The kinds of biological and short-term evolutionary differences that are summarized here can necessarily be expected to vary on a continuum as a function of the differences between the environments experienced by hatchery and wild populations. To the extent that hatchery circumstances mirror the natural environment, selective differences as well as the developmental differences that lead to changes in physiology and behavior will be reduced. However, as long as artificial propagation can be recognized as such, then there is biological justification for exclusion of artificially propagated fish from ESUs. As the boundary between artificial propagation and habitat improvement/restoration blurs (in naturalistic spawning channels for example), then the situation can be reevaluated.

2.D. Regarding the conservation of hatchery stocks

Some hatchery stocks are likely to be useful or essential in future recovery and restoration activities, particularly if they are managed to retain as much of their genetic and phenotypic similarity to the wild populations from which they were derived and to minimize other kinds of biological differences that can affect the wild population when hatchery-reared fish spawn in the

wild. Domestication selection, genetic drift and inbreeding should be minimized through proper hatchery design and operation. This objective may also require, in some circumstances, breeding designs that are seldom used in fish hatcheries but are commonplace in other contexts, such as minimal kinship selection to recover or maximize founder diversity and reduce domestication selection (Ballou and Lacy 1995; Caballero et al. 1996; Doyle et al. 2001; Fernández et al. 2003; Fiumera et al. 2004; Sánchez et al. 2003). Another example is the production of multiple inbred lines for maintaining genetic diversity and minimizing domestication selection with reconstitution of wild genotypes from interline hybrids (Dobzhansky 1951; Lande 1995). Notwithstanding such efforts, it must be recognized that well-executed designs will not be able to eliminate domestication selection, only reduce it.

Given a biological distinction between hatchery and wild fish, the question arises whether a categorical exclusion of hatchery origin fish from ESUs would negatively affect the preservation of hatchery stocks that are deemed essential for conservation efforts of related wild populations. In such cases it seems reasonable that some kind of ESA or other legal protection be afforded these artificially propagated fish. For example, in artificial propagation programs designed explicitly to assist with the conservation and recovery of an ESU, hatchery-produced offspring of wild fish should have some protected status. The details of how this would be done, if hatchery fish are in general excluded from ESUs, were beyond the scientific questions addressed by the panel. It does seem clear, however, that practical and logistical considerations, along with biological considerations, may be necessary for developing a workable policy on when and how to ensure conservation of artificially propagated fish.

Consideration of the role of some hatcheries as important conservation tools should not imply that hatchery fish are automatically useful for conservation purposes or should automatically be “counted” toward ESU viability goals. Indeed, in many cases hatchery fish may be a threat to the ESU. Clearly, if conservation units are constituted from wild populations then the assessment of viability of an ESU should be based only on the viability of the natural populations in the ESU.

Answer to Question 2. Is there reasonable biological justification for excluding from a conservation unit a hatchery stock that is genetically similar to natural populations in that unit?

Yes there are biological differences between hatchery and wild fish that arise because of the differences between artificial and natural environments. These differences could be used to justify the exclusion of hatchery fish from an ESU even when they are phylogenetically related to wild fish and even when the hatchery fish are progeny of wild fish that belong to an ESU. This exclusion need not preclude the use of hatcheries as a conservation tool and the justification for exclusion is clearest for hatchery fish that are not required for conservation and recovery of the ESU. In those cases where hatchery origin fish are deemed of critical importance for the conservation of the wild populations, the hatchery fish need protection as well. While recognizing that ESUs can, on biological grounds, be identified as including only wild populations, the maintenance of those hatcheries that are deemed necessary for the preservation of an ESU is also important.

3. Resident and anadromous populations of *Oncorhynchus mykiss* (rainbow trout and steelhead, respectively)

The relationship between resident populations and related anadromous populations of *O. mykiss* have been considered under a three case system by NOAA-Fisheries and the U.S. Fish and Wildlife Service (USFWS):

- 1) When resident rainbow trout inhabit the same spawning and rearing habitats as steelhead and there is no evidence of reproductive isolation between the two types.
- 2) When resident trout are separated from steelhead by a long standing natural barrier (e.g. a waterfall).
- 3) When resident trout are separated from steelhead by a manmade barrier (e.g. an impassable dam). In this case, it is also common for reservoirs and other areas upstream of the barrier to be stocked with non-native rainbow trout from domesticated hatchery strains.

The capacity of *O. mykiss* to exhibit two quite different life histories is an interesting and important evolutionary feature of the species. The anadromous life history appears to be the ancestral condition in salmonids (McDowall 2002). Resident populations of *O. mykiss* have often been established from resident, steelhead, and mixed stock sources (Behnke 1992). However, even though resident populations can be established easily behind migration barriers, the reverse process has been documented to have occurred just once (Pascual et al. 2001). In this case anadromy has evolved from a stock introduced to the Santa Cruz River, however it is unclear whether the introduced stock was composed of pure resident genotypes (Behnke 2002; Pascual et al. 2002; Rossi et al. 2004).

An imbalance, in which anadromous populations can quickly give rise to resident stocks but evolution in the reverse direction is rare, is expected and consistent with basic ideas on the evolutionary loss of functions. In brief, anadromous populations are steadily selected for viability in fresh and saltwater at different parts of the life cycle, whereas resident populations are not, and so the resident populations are expected to lose the ability to survive in seawater because of the absence of selective pressures to maintain that capacity (Cooper and Lenski 2002; Darwin 1859, pp. 134-139; Pannebakker et al. 2004).

For case (1) populations in which anadromous and resident fish appear to be exchanging genes and in which some parents produce progeny exhibiting both life history paths, the two life history alternatives occur as a kind of polymorphism. In these cases there is little justification for putting the resident and anadromous life history types into different conservation units. The situation is more complex for 'pure' resident populations that have no genetic exchange with anadromous fish that sometimes occupy the same river, because in these cases it may be best to consider them as two separate wild populations. Regardless of how the conservation unit is defined, however, it is important to conserve the evolutionary potential of the anadromous component of the conservation unit because of the highly asymmetrical transition rate between the two life-history types.

In cases (2) and (3) resident and anadromous populations are separated and are adapting to different life styles and circumstances. Notwithstanding that they may have a history of being

closely related (i.e. a case (2) or (3) may have been a case (1) in the past), the fact of separation and the biological differences that extend from that and from the different life styles do constitute biological justification for excluding resident fish in cases (2) and (3) from a conservation unit of anadromous fish in the same watershed. In cases where anadromous populations regularly receive input from upstream case (2) or (3) resident populations, it is still possible for the resident populations to have diverged with regard to important life-history traits (e.g. by loss of anadromy in the resident populations). The occurrence of regular input to anadromous populations from physically separated resident populations is similar to the case where wild salmon receive regular input from a hatchery, and it does not mean that the populations need be considered as one (see Question 2). In cases where a manmade barrier is removed, the ESU status of the resident fish above the barrier could be reassessed. Like the hatchery case, exclusion of case (3) resident fish from an ESU need not preclude their future use for conservation purposes if this is deemed biologically necessary.

It is also noted that recognition of a distinction between case 2 or 3 resident populations, from downstream “anadromous” populations, does not mean that case 2 and 3 populations are evolutionarily equivalent to each other. For example, an anadromous population isolated in freshwater due to anthropogenic influences (i.e. case 3), is unlikely to have the same extent of adaptations to a fully freshwater existence as natural resident populations that have existed for millennia. Some resident fish populations may be sufficiently evolutionarily unique to merit their own conservation unit.

Answer to Question 3: Is there reasonable biological justification for excluding from a conservation unit resident populations that are genetically similar to anadromous populations in that unit?

Yes, in those cases where a resident population is cut off by natural or manmade barriers from an anadromous population, there is biological justification for excluding them from the conservation unit composed of that that anadromous population. In those cases where the two populations co-occur and the lifestyle variation is present as a polymorphism, then it would be biologically justified for the conservation unit to include both the resident and anadromous fish.

4. The Role of ecology versus genetics in defining conservation units

The final question addressed by the panel was: *What role should ecological, behavioral, and life history differences between resident/anadromous and hatchery/natural fish play in identification of conservation units? Does the answer depend on the degree to which variation in these factors has a genetic basis?*

This question was largely answered in the course of addressing the other questions. It is important to consider that the different environments of hatchery versus wild fish, and resident versus anadromous fish, do lead to different selection pressures, as well as to ecological, behavioral and life history differences. In addition this answer does not depend on there being genetic differences between populations. The degree of genetic relatedness is a major factor for considering which hatchery, or resident, populations may play a constructive role in the conservation of a wild population. However, important biological differences occur between hatchery and wild fish, and between anadromous and resident fish, even though they may be very recently descended from the same individuals.

Minority Viewpoint

The primary conclusions of this report represent the scientific judgment of the large majority of the workshop panel members. The minority view on the questions addressed by the panel is summarized here.

Question 1. With regard to the focus on evolutionary lineages for considering potential conservation units, the minority opinion is that focusing on the evolutionary lineages of hatchery and resident fish is scientifically sound, if there has been no intentional alteration for some other management objective inconsistent with the biological needs of the wild component. Ecological exchangeability is an important element in the success of hatchery fish, but much of the behavioral alterations they may display are conditioned responses, short-term in the wild, and not transferable to progeny (Brannon et al. 2004a).

Question 2. On the second question, the minority opinion is that if biologically meaningful differences exist between the hatchery and wild components of a population, there may be biological justification for exclusion. It is suggested, however, that the genetic legacy of the donor population is retained in the hatchery fish, and these fish are generally most compatible with the wild fish of the same origin (Brannon et al. 2004b). With regard to having separate conservation measures for important hatchery fish, including them in the conservation unit with the wild counterpart would be the most effective and manageable way to protect them.

Question 3. The minority and majority opinions are in agreement on question 3, with an exception. The minority proposes that resident fish isolated upstream from the anadromous component of the population could reasonably be considered part of the conservation unit as long as the resident fish contribute to the polymorphic gene pool below the separating barrier.

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Appendix 1 - Workshop Panel - Biographical Information

Ernest L. Brannon (University of Idaho)

Distinguished Research Professor, Aquaculture Research Institute
Professor Emeritus Fisheries Resources and Animal Sciences

B.S., Fisheries, University of Washington; Ph.D., Fisheries, University of Washington

Former Director of the Aquaculture Research Institute, and former Professor at the School of Fisheries, University of Washington, Seattle. Current research interests include *Development of American Indian Science Education Model*, *Development of Engineered Streams for Salmon Production*; finding new methods of wastewater treatment for Idaho's aquaculture and confined animal industries; and *Genetic Analysis of Oncorhynchus nerka*.

SELECTED PUBLICATIONS:

- Brannon, E.L., D.F. Amend, M.A. Cronin, J.E. Lannan, S. LaPatra, W.J. McNeil, R.E. Noble, C.E. Smith, A.J. Talbot, G.A. Wedemeyer, and H. Westers. 2004. The controversy about salmon hatcheries. *Fisheries* 29(9): 12-31.
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- Brannon, E.L., D.A. Beauchamp, D.E. Campton, C.V.W. Mahnken, and J.R. Winton. (Special Scientific Advisory Panel). 2001. The Cedar River sockeye salmon hatchery plan. For City of Seattle. Aquaculture Research Institute, University of Idaho, Moscow, Idaho.

Donald E. Campton (U.S. Fish & Wildlife Service, Abernathy, WA)

Senior Scientist

Don received a BS degree in Genetics from UC Berkeley in 1974, an MS in Fisheries from the University of Washington in 1981, and a PhD in Genetics from the University of California, Davis in 1986. He worked also as a Fisheries Geneticist for the Washington State Department of Wildlife (Mt. Vernon, WA), 1978-1980. After completing his PhD degree in 1986, he was an Assistant Professor in the Department of Fisheries and Aquatic Sciences at the University of Florida (Gainesville, FL), 1986-1992, and an Associate Professor in the same department, 1992-1997. He left the University of Florida in 1997 to accept employment as the Regional Fish Geneticist (Pacific Region) for the U.S. Fish and Wildlife Service at the Abernathy Fish Technology Center, Longview, WA, where he currently works today as a Senior Scientist (2004-present). He has authored or co-authored over 30 peer-reviewed journal articles and book chapters.

SELECTED PUBLICATIONS

- Campton, D.E. 1987. Natural hybridization and introgression in fishes: methods of detection and genetic interpretations, p.161-192. *IN: N. Ryman and F. Utter (eds.), Population Genetics and Fishery Management.* Washington Sea Grant College Program and University of Washington Press, Seattle, Washington.
- Campton, D.E. 1995. Genetic effects of hatchery fish on wild populations of Pacific salmon and steelhead: What do we really know?, p. 337-353. *IN: H.L. Schramm, Jr., and R.G. Piper (eds), Uses and Effects of Cultured Fishes in Aquatic Ecosystems,* American Fisheries Society Symposium 15, American Fisheries Society, Bethesda, Maryland.
- Burger, C.V., K.T. Scribner, W.J. Spearman, C.O. Swanton, and D.E. Campton. 2000. Genetic contribution of three introduced life history forms of sockeye salmon to colonization of Frazer Lake, Alaska. *Can. J. Fish. Aquat. Sci.* 57: 2096-2111.
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- Mobrand, L.E., J. Barr, L. Blankenship, D.E. Campton, T.T.P. Evelyn, T.A. Flagg, C.V.W. Mahnken, L.W. Seeb, P. Seidel, and W.W. Smoker. 2005. Hatchery Reform in Washington state: principles and emerging issues. *Fisheries* 30: in press.

Holly Doremus (University of California, Davis)

Professor of Law

Holly Doremus is a Professor of Law and Chancellor's Fellow at the University of California, Davis. Her teaching and research experience includes environmental law; natural resources law; science and law; endangered species and biodiversity; and conservation policy. Before entering law school, she conducted basic research on the metabolic pathways of plants. She finds that environmental law offers the same sort of intellectual stimulation as science, with a more direct connection to the policy-making arena.

SELECTED PUBLICATIONS

- Environmental Policy Law: Problems, Cases and Readings, (4th ed.) (with Thomas J. Schoenbaum & Ronald H. Rosenberg) (Foundation Press 2004).
- The Purposes, Effects, and Future of the Endangered Species Act's Best Available Science Mandate, 34 Environmental Law 397 (2004)
- Fish, Farms and the Clash of Cultures in the Klamath Basin, 30 Ecology Law Quarterly 279-350 (2003) (with A. Dan Tarlock).
- Why Listing May Be Forever: Perspectives on Delisting Under the U.S. Endangered Species Act, 15 Conservation Biology 1258 (2001) (with Joel Pagel).
- The Rhetoric and Reality of Nature Protection: Toward a New Discourse, 57 Wash. & Lee L. Rev. 11 (2000).

Roger W. Doyle (Genetic Computation Limited)

Dalhousie University, Retired

Ph.D. Yale University (Biology); M.Sc. Dalhousie University (Oceanography); B.Sc. Dalhousie University (Biology and Physical Chemistry).

Professor of Biology and Founding Director of the Marine Gene Probe Laboratory at Dalhousie University, until early retirement in 1997. Former President of the International Association for Aquaculture Genetics, and former Co-coordinator of the Aquaculture Genetics Network in Asia. Extensive research, development and commercial experience in genetic conservation and aquaculture genetics in North and South America, the Middle East, Africa and Asia. Founding C.E.O. and Chairman of two private research & development companies in applied genetics. Many publications, invited lectures, consultancies and visiting professorships in aquaculture, fisheries management and fisheries genetics.

RESEARCH INTERESTS include: Effect of long-term domestication on genetic variance-covariance matrices of commercially important fitness traits in aquaculture. Maintenance of founder genome diversity in aquacultural broodstocks using incomplete pedigree and marker information. Commercial breeding civilities in shrimp, Atlantic salmon and tilapia.

SELECTED PUBLICATIONS

2005. A farmer-oriented Nile tilapia (*Oreochromis niloticus*) breed improvement program in the Philippines. Basiao, Z. U., A. L. Arago, and R. W. Doyle. *Aquaculture Research* 36:113-119.
2003. Li, K., C.A. Field, and R.W. Doyle. Estimation of additive genetic variance components in aquaculture populations selectively pedigreed by DNA fingerprinting. *Biometrical Journal* 45: 61-72.
2002. Doyle, R.W. Contribution of genetics to aquaculture: a socio-economic critique. *Fisheries Science* 68: 708-713.
2001. Doyle, R.W., R. Perez-Enriquez, M. Takagi, and N. Taniguchi. Selective recovery of founder genetic diversity in aquaculture broodstocks and captive endangered fish populations. *Genetica* 111: 291-304.
2001. Ruzzante, D.E., C.T. Taggart, R.W. Doyle, and D. Cook. Stability in the historical pattern of genetic structure of Newfoundland cod (*Gadus morhua*) despite the catastrophic decline in population size from 1964 to 1994. *Conservation Genetics* 2 (3): 257-269.

Ian A. Fleming (Memorial University of Newfoundland)

Director, Ocean Sciences Centre

Ian Fleming's research integrates perspectives from ecology and evolution with fishery and conservation biology, and his areas of expertise include fish behavioral and evolutionary ecology, reproduction, life history, maternal effects and population biology. He has worked extensively on the conservation of wild salmon populations and their ecological/genetic interactions with cultured fish (hatchery and farmed). He has also served in a number of capacities related to fisheries research and policy, including the review panel of the National Research Council (US) on the Status of Atlantic Salmon in Maine (2002-4), Co-chair of the Scientific Advisory Board of the Cooperative Institute for Marine Resources Studies at Oregon State University, the Northwest Power Planning Council's Artificial Propagation Assessment Committee and the Steering Committee of the Norwegian Institute for Nature Research's

program on Effects of Ecosystem Changes on Biodiversity. Ian has previously held academic/research positions at the Hatfield Marine Science Center of Oregon State University (2001-04) and the Norwegian Institute for Nature Research (1991-2001), and continues to hold adjunct status at both institutes, as well as at the University of Siena.

SELECTED PUBLICATIONS

- Fleming, I.A., Einum, S., Jonsson, B. and Jonsson, N. 2003. Comment on “Rapid Evolution of Egg Size in Captive Salmon”. *Science* 302: 59b.
- Fleming, I.A. and Petersson, E. 2001. The ability of released, hatchery salmonids to breed and contribute to the natural productivity of wild populations. *Nordic Journal of Freshwater Research* 75: 71-98.
- Einum, S. and Fleming, I.A. 2001. Implications of stocking: ecological interactions between wild and released salmonids. *Nordic Journal of Freshwater Research* 75: 56-70.

Jody Hey (Rutgers, the State University of New Jersey)

Professor, Department of Genetics

Ph.D. 1987 SUNY Stony Brook. Senior Research Fellow, University of Edinburgh. 1998-99; Guggenheim Fellow, 1998; SMBE Council Member 03-05; NIH Genetics Study Section Member 1997-01; Computer Programs Authored and Distributed: IM, SITES, WH. RESEARCH INTERESTS include Divergence Population Genetics; Genetics of Human Origins; Population Genetics of *Caenorhabditis elegans*; Speciation in Lake Malawi Cichlids; and the Species Problem.

SELECTED PUBLICATIONS

- Won, Y. J., and J. Hey. 2005. Divergence population genetics of chimpanzees. *Molecular Biology and Evolution* 22:297-307.
- Hey, J., and R. Nielsen. 2004. Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of *Drosophila pseudoobscura* and *D. persimilis*. *Genetics* 167: 747-760.
- Hey, J., R. S. Waples, M. L. Arnold, R. K. Butlin and R. G. Harrison. 2003 Understanding and confronting species uncertainty in biology and conservation. *Trends in Ecology and Evolution* 18: 597-603
- Hey, J. and C. A. Machado. 2003. The study of structured populations – new hope for a difficult and divided science. *Nature Reviews Genetics* 4: 535-543
- Hey, J. 2001 Genes, Categories and Species: the evolutionary and cognitive causes of the species problem. Oxford University Press, New York.

Michael T. Kinnison (University of Maine)

Assistant Professor of Biological Sciences

Dr. Kinnison is a cooperating member of the School of Marine Sciences and also involved in the Ecology and Environmental Sciences and Conservation Biology programs at the University of Maine. He serves as a member of the Maine Atlantic Salmon Technical Advisory Committee where he provides advising on conservation genetics of endangered salmon. He is an evolutionary/population ecologist who focuses on adaptation and other processes influencing diversity within and among populations of fishes and other organisms. Much of his work

surrounds evolutionary mechanisms operating over contemporary or ecological time scales, in both natural and introduced populations. Some of his primary areas of investigation include tempo and mode of contemporary evolution in the wild, the role of contemporary evolution in conservation, and the interaction of local adaptation with other micro-evolutionary processes. Examples of this work include: theoretical reviews on quantification and interpretation of evolutionary rates, empirical studies of evolution in introduced populations of salmonids, evaluation of trait diversity and selection in endangered Atlantic salmon, and testing of models of gene flow- adaptation interactions with wild populations of Trinidadian guppies.

SELECTED PUBLICATIONS

- Kinnison, M.T., and A.P. Hendry. 2004. From Macro to micro: tempo and mode in salmon evolution. In A. Hendry and S. Stearns eds. *Evolution Enlightened: Salmon and their Relatives*. Oxford University Press.
- Stockwell, C.A., A.P. Hendry and M.T. Kinnison. 2003. Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution*. 18:94-101.
- Kinnison, M.T. and A.P. Hendry. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* 112-113:145-164
- Kinnison, M.T., M.J. Unwin, A.P. Hendry and T.P. Quinn. 2001. Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. *Evolution* 55:1656-1667.

Russell Lande (University of California San Diego)

Professor of Biology

EXPERTISE

Evolution and population genetics, management and preservation of endangered species, conservation biology and theoretical ecology

AWARDS

Sewall Wright Award from the Society of American Naturalists; MacArthur Foundation Fellow, Member of the American Academy of Arts and Sciences.

SCIENTIFIC LEADERSHIP

Past President of the Society for the Study of Evolution; International Recognition: coauthored scientific criteria for classifying endangered species adopted by the International Union for Conservation of Nature and Natural Resources (IUCN)

PUBLICATIONS

More than 140 scientific publications

Jeffrey Olsen (U.S. Fish and Wildlife Service, Anchorage, AK)

Geneticist

Ph.D. 1999 University of Washington, B.S. 1981 University of Washington

My general focus is on applying principles of population genetics to conservation and management of Pacific salmon in Alaska. Current projects include evaluating population structure and dispersal in steelhead and resident rainbow trout and examining sex ratio bias and effective population size in chinook salmon. Prior to doing my dissertation, I was operations manager for a private non-profit salmon hatchery program in Prince William Sound, Alaska.

SELECTED PUBLICATIONS:

- Olsen, J.B., W.J. Spearman, G.K. Sage, S.J. Miller, B. Flannery, J.K. Wenburg. 2004. Variation in the population structure of Yukon River chum and coho salmon: evaluating the potential impact of localized habitat degradation. *Transactions of the American Fisheries Society* 133: 476-484.
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- Olsen, J.B., C. Busack, J. Britt, and P. Bentzen. 2001. The aunt and uncle effect: an empirical evaluation of the confounding influence of full sibs of parents on pedigree reconstruction. *Journal of Heredity* 92: 243-247.
- Bentzen, P., J.B. Olsen, J. McLean, T.R. Seamons, and T.P. Quinn. 2001. Kinship analysis of Pacific salmon: insights into mating, homing and timing of reproduction. *Journal of Heredity* 92: 127-136.
- Olsen, J.B., P. Bentzen, M.A. Banks, J.B. Shaklee, and S. Young. 2000. Microsatellites reveal population identity of individual pink salmon to allow supportive breeding of a population at risk of extinction. *Transactions of the American Fisheries Society*. 129: 232-242.

David P. Philipp (Illinois Natural History Survey)

Principal Scientist

CURRENT RESEARCH INTERESTS

Natural resource conservation genetics; factors controlling reproductive success in fishes; evolution of reproductive behaviors in fishes; evolution of gene regulatory mechanisms; developmental and biochemical genetics of fishes.

SERVICE

Board of Directors, Fisheries Conservation Foundation

Scientific Advisory Board, Bonefish-Tarpon Unlimited

Member, Independent Scientific Advisory Board (NPCC, NOAA-Fisheries, CRITFC)

PUBLICATIONS (SELECTED)

- 2001 Cooke, S.J., T.K. Kassler, and D.P. Philipp. Physiological performance of largemouth bass related to local adaptation and interstock hybridization: implications for conservation and management. *Journal of Fish Biology* 59A: 248-268.
- 2002 Philipp, D.P., J.E. Claussen, T. Kassler, and J.M. Epifanio. Mixing stocks of largemouth bass reduces fitness through outbreeding depression. *American Fisheries Society Symposium* 30: 349-363.
- 2004 Cooke, S.J. and D.P. Philipp. Behavior and mortality of caught-and-released bonefish (*Albula* spp.) in Bahamian waters with implications for a sustainable recreational fishery. *Biological Conservation* 118: 599-607.
- 2004 Aday, D.D., D.H. Wahl, and D.P. Philipp. 2004. Assessing population-specific and environmental influences on bluegill life histories: a common garden approach. *Ecology* 84:3370-3375

Joseph Travis (Florida State University)

Professor of Biology

EXPERTISE

Population ecology and genetics, physiological ecology, ichthyology

AWARDS

Fellow, American Association for the Advancement of Science; Dennis Chitty Lecturer, University of British Columbia; Distinguished Visiting Scholar, University of Zurich; Robert O. Lawton Distinguished Professorship, Florida State University

SCIENTIFIC LEADERSHIP

President American Society of Naturalists; Past Chair, Science Advisory Board, National Center for Ecological Analysis and Synthesis; Past Editor, The American Naturalist; Member of several editorial boards; Member of scientific advisory boards on state and local conservation and management activities

PUBLICATIONS

More than 110 scientific publications

Chris C. Wood (Canadian Department of Fisheries and Oceans, Nanaimo, BC)

Head, Conservation Biology Section, Pacific Biological Station

Dr. Chris C. Wood received a B.Sc (Honours) in Biology from Simon Fraser University (1977) and a Ph.D in Zoology from the University of British Columbia (1984). He has been a research scientist with Fisheries and Oceans Canada since 1984 and has over 20 years experience in research on population and evolutionary biology of marine and anadromous fish. He was head of the North Coast Salmon Section (1994-1997), and chaired the DFO Science Branch team that prepared the Wild Salmon Policy Discussion Paper. He has been head of the Conservation Biology Section at the Pacific Biological Station in Nanaimo since its formation in 2001. He has adjunct faculty status in the Department of Biology at the University of Victoria (since 1995), in the School of Resource and Environmental Management at Simon Fraser University (since 2003), and visiting professor status in the Department of Zoology at the University of Toronto (in 2005). He has been a member of the Marine Fishes Species Specialist Subcommittee of COSEWIC since 2000. Dr. Wood has authored over 50 primary publications and 40 secondary publications, and co-edited two books.

Appendix 2 Symposium Held Prior to the Workshop

March 29, 2005

Seattle, NOAA Sand Point Auditorium

8:00 Registration

8:45 Welcome Usha Varanasi, Director, Northwest Fisheries Science Center

I. Background (Session Chair: John Stein)

Goal: Review background information, regulatory language and policies and history of their application, and provide broader context for thinking about conservation units.

9:00 Why are we here? Background to the issues at hand (Mike Ford, NWFSC, Seattle)

9:30 Review of NMFS ESU concept, other published ESU concepts, and application to salmon, including hatchery and resident fish (Robin Waples, NWFSC Seattle)

10:10 Break

II. Reality check: practical questions that any DPS/ESA framework must be able to address (Session Chair: Robin Waples)

Goal: Make sure everyone understands the kinds of practical problems that any proposed framework will have to deal with.

10:40 Hatchery/wild fish (Rob Jones, NMFS NW Regional Office, Portland)

11:00 Resident/anadromous fish (Pete Adams, SWFSC, Santa Cruz)

III. Evolutionary theory (Session Chair: Robin Waples)

Goal: Summarize current thinking by evolutionary biologists on two key topics related to the questions at hand.

11:20 Selection in two environments, within and/or between generations (Sara Via, U. Maryland). *Dr. Via was unable to attend. The presentation was made by Joseph Travis and Russell Lande.*

11:50 Tempo and mode of contemporary evolution: a review of the empirical record (Michael Kinnison, U. Maine)

12:20 Lunch

IV. State-of-the-science reviews of hatchery/resident fish issues (Session chair: Mike Ford)

Goal: provide a common empirical and theoretical background for considering hatchery fish and resident fish in identifying conservation units. The NMFS policy has focused on evolutionary/genetic relationships and lineages, but some other possible frameworks focus more on ecological/behavioral factors.

- 1:30 Genetic/evolutionary relationships between hatchery and wild fish
(Ken Currens et al., Northwest Indian Fisheries Commission, Olympia)
Ecological/behavioral relationships between hatchery and wild fish
(Ian Fleming, Memorial University of Newfoundland)
- 2:15 Genetic/evolutionary relationships between resident and anadromous fish
(Don Campton, US Fish and Wildlife Service, Abernathy, WA)
Ecological/behavioral relationships between resident and anadromous fish
(Sue Sogard, Southwest Fisheries Science Center, Santa Cruz)
- 3:00 Break
- V. Panel Discussion of alternative frameworks for considering hatchery fish and resident fish in conservation unit determinations (Session Chair: Tom Quinn, U. Washington)
Goal: Summarize alternative ways for dealing with hatchery fish and resident fish under the DPS provision in the ESA. Discuss pros and cons of each approach in light of material covered in Sessions I-IV.
- Panel members: Russ Lande, UC San Diego; Ernie Brannon, U. Idaho; Rich Carmichael, Oregon Department of Fish and Wildlife, La Grande; Chris Wood, Canada Department of Fisheries and Oceans, Nanaimo, B.C.; Roger Doyle, Dalhousie U., (emeritus)
- 3:20 Brief presentations (~ 15 minutes each)
Russ Lande
Ernie Brannon
- 3:50 Remarks by Chair and other panel members
- 4:15 Panel and audience discussion
- 5:15 Adjourn

Appendix 3

Background documents provided to speakers and panelists at the symposium/workshop,
“Considering Life History, Behavioral, and Ecological Complexity in Defining Conservation
Units for Pacific Salmon”

Policy and legal documents

- Alsea Valley Alliance v. Evans. 2001. 161 F. Supp. 2d 1154 (D. Or. 2001) (“Alsea decision”)
- NMFS. 1991. Policy on applying the definition of species under the Endangered Species Act to Pacific salmon. FR 56, 58612, 20 November 1991.
- NMFS. 1993. Interim Policy on Artificial Propagation of Pacific Salmon under the Endangered Species Act. FR 58, 19573, 5 April 1993.
- NMFS. 2004. Endangered and Threatened Species: Proposed Policy on the Consideration of Hatchery-Origin Fish in Endangered Species Act Listing Determinations for Pacific Salmon and Steelhead. 69 FR, 31354 3 June 2004.
- USFWS-NMFS. 1996. Policy regarding the recognition of distinct vertebrate population segments under the Endangered Species Act. FR 61, 4722, 7 February 1996.

Scientific papers and reports

- Brannon, E., and 10 coauthors. 2004. The controversy about salmon hatcheries. *Fisheries* 29(9):12-31.
- Docker, M. F., and D. D. Heath. 2003. Genetic comparison between sympatric anadromous steelhead and freshwater resident rainbow trout in British Columbia, Canada. *Cons. Genet.* 4:227-231.
- Myers, R. A, S. A. Levin, R. Lande, F. C. James, W. W. Murdoch and R. T. Paine. 2004. Hatcheries and endangered salmon. *Policy Forum. Science* 303:1980.
- Salmon Recovery Science Review Panel. Report for the meeting held August 30-September 2, 2004. Available at <http://www.nwfsc.noaa.gov/trt/rsrp.htm>.
- Waples, R. S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. *Mar. Fish. Rev.* 53(3):11-22.
- Waples, R. S. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. pp 8-27 in: J. L. Nielsen, ed. *Evolution and the aquatic ecosystem: defining unique units in population conservation*. American Fisheries Society, Bethesda, MD.
- Waples, R. S. 1999. Dispelling some myths about hatcheries. *Fisheries* 24(2):12-21.
- West Coast Salmon Biological Review Team. 2003. Introduction and Methods. In: *Updated Status of Federally Listed ESUs of West Coast Salmon and Steelhead*. July 2003. Available at <http://www.nwfsc.noaa.gov/trt/brtrpt.htm>.
- Wood, C. C., and C. J. Foote. 1996. Evidence for sympatric genetic divergence of anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). *Evolution* 50:1265-1279.
- Zimmerman, C. E., and G. H. Reeves. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. *Can. J. Fish. Aquat. Sci.* 57: 2152–2162.

Public and peer review comments submitted to the ESA administrative record (Available from NOAA Fisheries, Protected Resources, Portland, OR).

California Department of Fish and Game. 2004. Comments on proposed rule on listing determinations for 27 ESUs of West Coast salmonids. 12 November 2004.

Great Lakes Fishery Commission. 2004. Comments on the proposed hatchery listing policy. 1 September 2004.

Lannon, J., and 11 coauthors. 2004. Response to NOAA Fisheries Proposed Hatchery Policy Under the Endangered Species Act.

Quinn, T. 2004. Peer review comments on proposed rule on listing determinations for 27 ESUs of West Coast salmonids. 13 October 2004.

Trout Unlimited and co-petitioners. 2002. Petition to list the Oregon Coast coho salmon as a threatened species under the federal Endangered Species Act. [Section III, hatchery and DPS issues] 25 April 2002.

Washington Department of Fish and Wildlife. 2004. Comments on proposed hatchery listing policy. 4 November 2004.