

**SALMON RECOVERY SCIENCE REVIEW PANEL**  
**Report for the meeting held**  
**August 30-September 2, 2004**  
**Northwest Fisheries Science Center**  
**National Marine Fisheries Service**  
**Seattle, WA**

This introductory material (pp. i-iii) is available on the RSRP web site, but as an aid to the reader we are now including it with individual reports.

<b>Dr. Joe Travis</b>	<b>Florida State University</b>
<b>Dr. Russell Lande</b>	<b>University of California San Diego</b>
<b>Dr. Marc Mangel</b>	<b>University of California Santa Cruz</b>
<b>Dr. Ransom A. Myers</b>	<b>Dalhousie University</b>
<b>Dr. Pete Peterson</b>	<b>University of North Carolina Chapel Hill</b>
<b>Dr. Mary Power</b>	<b>University of California Berkeley</b>
<b>Dr. Dan Simberloff</b>	<b>University of Tennessee</b>

---

<b>Dr. Beth Sanderson</b>	<b>NOAA Fisheries liaison</b> <b>RSRP report coordinator</b>
---------------------------	---

**Recovery Science Review Panel**

**The Recovery Science Review Panel (RSRP)** was convened by NOAA Fisheries to guide the scientific and technical aspects of recovery planning for listed salmon and steelhead species throughout the West Coast. The panel consists of seven highly qualified and independent scientists who perform the following functions:

1. Providing scientific support to Technical Recovery Teams, specifically:
  - a. Reviewing core principles and elements of recovery science;
  - b. Ensuring that well-accepted and consistent ecological and evolutionary principles form the basis for all recovery efforts;
  - c. Encouraging consistent application of core principles across populations, ESUs, and recovery domains;
2. Providing scientific support to scientists at the Northwest and Southwest Fisheries Science Centers who work on Pacific salmon and steelhead;
3. Providing general advice for salmon science.

The panel meets 2-3 times annually, submitting a written review of issues and documents discussed following each meeting.

### Expertise of Panel Members

Panel members have all been involved in local, national, and international activities. They have served on numerous National Research Council committees and have published many papers in prestigious scientific journals.

#### **Dr. Joseph Travis (chair), Florida State University**

- *Field of 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-elect, 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
- *Research:* More than 110 scientific publications

#### **Dr. Russell Lande, University of California-San Diego**

- *Field of expertise:* Evolution and population genetics, management and preservation of endangered species, conservation and theoretical ecology
- *Awards:* Sewall Wright Award from the American Society of Naturalists; Guggenheim Foundation; MacArthur Foundation; Fellow of the American Academy of Arts and Sciences
- *Scientific Leadership:* President of the Society for the Study of Evolution; International recognition; developed scientific criteria for classifying endangered species adopted by the International Union for Conservation of Nature and Natural Resources (IUCN)
- *Research:* More than 116 scientific publications

#### **Dr. Marc Mangel, University of California Santa Cruz**

- *Field of expertise:* Theoretical and mathematical biology
- *Awards:* Koopman Paper Prize, Operations Research Society of America; JASA-Applications Invited Paper, American Statistical Association; Fellow, John Simon Guggenheim Memorial Foundation; Fulbright Senior Fellowship, Oxford University; Distinguished Statistical Ecology, International

Association for Ecology; Fellow, California Academy of Sciences; Fellow, American Association for the Advancement of Science

- *Scientific Leadership*: Founding Director, Center for Population Biology, University of California Davis; Chair, SIAM-AMS Committee on Mathematics in the Life Sciences; Past Editor, Behavioral Ecology; Member, Committee of Scientific Advisors, US Marine Mammal Commission; Member, NMFS Ecosystem Advisory Panel; Member, Science Advisory Board, National Association for Ecological Analysis and Synthesis
- *Research*: More than 200 scientific publications

#### **Dr. Ransom A. Myers, Dalhousie University**

- *Field of expertise*: Ecology, Conservation, and Management of Marine Animals, Modeling and Statistical Ecology, Population dynamics
- *Awards*: The Great Auk Lectureship (1999), Awarded first Killam Chair in Ocean Studies, Dalhousie University (1996)
- *Scientific leadership*: Member of Science Advisory Boards for Sierra Club of Canada (2003), Oceana (2003), and Atlantic Policy Congress (2000), Member of Board of Directors: The International Oceans Institute of Canada (2000) and Natural Resource Modelling Association (1994-1999). Asked to testify at the U.S. Senate Commerce Committee Hearing on Overfishing (2003) and the House of Commons (Canada) Standing Committee on Fisheries and Oceans (2003)
- *Research*: More than 110 scientific publications.

#### **Dr. Charles Peterson, University of North Carolina Chapel Hill**

- *Field of expertise*: Marine community ecology, restoration ecology
- *Awards*: Pew Foundation Scholar in the Environment
- *Scientific Leadership*: Member of many National Research Council panels; Member of several editorial boards; Founding Chair, US GLOBEC Scientific Steering Committee; Past Chair, Scientific Advisory Board, National Center for Ecological Analysis and Synthesis
- *Research*: More than 140 scientific publications

#### **Dr. Mary Power, University of California Berkeley**

- *Field of expertise*: aquatic ecology, food web energetics, ecosystem ecology
- *Awards*: Kempe Award for Distinguished Ecologist, Umea University and Swedish Agricultural University; Jasper Loftus-Hills Prize of the American

Society of Naturalists; John and Margaret Gompertz Chair in Integrative Biology, University of California

- *Scientific Leadership:* Board of Directors, Nature Conservancy, California; Group Leader, Presidential Advisory Commission on Western Water Policy; Director, California Biodiversity Center; Member, Science Advisory Board, National Center for Ecological Analysis and Synthesis
- *Research:* More than 80 scientific publications

**Dr. Daniel Simberloff, University of Tennessee**

- *Field of expertise:* Community ecology, conservation biology, invasion biology
- *Awards:* Fellow, American Academy of Arts and Sciences; Distinguished Statistical Ecologist, International Association for Ecology; Mercer Award of Ecological Society of America (shared)
- *Scientific Leadership:* Member, National Science Board; Former member of Board on Biology of National Research Council and member of several National Research Council panels; Past-President, American Society of Naturalists
- *Research:* More than 250 scientific publications

## **RECOVERY SCIENCE REVIEW PANEL (RSRP)**

**Northwest Fisheries Science Center, Seattle, Washington**

**August 30-September 1, 2004**

### **INTRODUCTION**

One of the major factors affecting the status of listed Pacific salmon is the potential negative effect that hatchery fish exert on populations of wild fish. Ironically, while many hatchery programs were designed to accelerate population recovery of wild fish and stabilize their numbers, there is evidence that many supplementation programs have the opposite effect. To be sure, there is considerable variation among programs in the nature and magnitude of the effort to enhance natural populations and in their effects to date. But the bulk of the evidence indicates that, on the whole, hatchery fish are not equivalent to wild fish, genetically or phenotypically. Despite optimism about improvements in hatchery practices (Brannon et al. 2004), hatchery environments differ substantially from natural environments and create fish that differ from their wild counterparts in developmental trajectories that affect morphology, behavior, physiological responses, and life history. Whether these phenotypic differences are genetically based through domestication (Price 2002) or are induced by early environmental exposure (Travis et al. 1999), they represent inevitable, significant phenotypic alterations. Interbreeding between hatchery fish and wild fish can, through numerical swamping, reduce the fitness of wild fish, which can contribute to the decline of the wild population.

The RSRP is concerned that including hatchery fish in listing decisions could greatly jeopardize the mandate of long-term recovery of natural, self-sustaining populations. This concern led us to focus our meeting of August 30-September 1, 2004 on an examination of the interactions between hatchery and wild fish, how hatchery fish may be affecting the populations of wild fish, the scientific issues surrounding efforts at habitat compensation and restoration that involve hatchery fish, and the scientific inconsistencies created by the proposed hatchery policy.

In the first section of this report, we review the presentations made during the meeting and offer critical assessments of several supplementation experiments and programs for the analysis of supplementation efforts. In the second part of the report, we address the overarching issues raised by hatchery fish and the burgeoning conflict between the scientific evidence about hatchery fish and the proposed method of addressing hatchery fish in listing policies.

### **PART ONE: REVIEW OF PRESENTATIONS**

#### **A. Basic Interactions Between Hatchery and Wild Salmonids**

##### **1. Hatchery Fish Physiology**

Walt Dickoff from the Northwest Fisheries Science Center reviewed the effects of hatchery environments on the developmental trajectories of fish, specifically the evidence that hatchery environments induce specific physiological and life-historical responses. Conditions in production hatcheries have been designed to promote rapid growth rates, smolting in the first season, and high survival in the migratory, post-smolting stage. In comparison to wild fish, hatchery fish grow more rapidly after hatching, accumulate more lipid stores, and continue growing through the first winter before emigrating. This early developmental trajectory has a number of important consequences for subsequent life-history expression.

These patterns in chinook follow the life history framework developed by Thorpe et al (1998) for Atlantic salmon (using data from Beckman et al. (2003) and Larsen et al. (2004)) and carry three implications about recovery prospects. First, that hatcheries often produce early maturing parr is no surprise; this result follows a natural evolutionary pathway because maturation is essential for reproduction but migration is not. If fish are fed in ways that sustain very high growth rates, then at the appropriate developmental decision points they will elect maturation and may thus mature in freshwater or in the hatchery. Second, even if the growth rates are lowered, which will suppress maturation and lead to smolt metamorphosis in the first spring, the natural life history diversity (which naturally might be 1, 2, 3 or even 4 years in fresh water before migration) will be reduced. Third, because rapid growth early in life has negative long-term consequences for survival (Metcalf and Monaghan 2003), acceleration of developmental processes in hatcheries may lead to reduced survival later in life, even in the absence of genetic effects (cf. Jonsson et al. 2003). It will be very difficult to make fish emerge from hatchery environments with the same potential for future life histories as those expressed in wild fish.

## 2. Ecological and Behavioral Interactions

Barry Berejikian from the Northwest Fisheries Science Center reviewed ecological and behavioral interactions between hatchery and wild salmonids. On release, hatchery fish, which are typically larger, compete with wild fish. This competition, a form of density-dependent mortality, is expected to occur to a greater or lesser extent if juvenile hatchery and wild fish occupy the same habitat. Hatchery fish are typically released at a larger size than wild fish, and they can exert strong mortality on juvenile salmonids of the same, or other, species. Finally, the high local abundance may enhance predator populations with concomitant mortality of wild fish (National Research Council 1996). We recommend that more efforts be made to quantify these ecological interactions between hatchery and wild salmon.

## 3. Genetic Relationships

Mike Ford of the Northwest Fisheries Science Center reviewed experimental data and theoretical models for the genetic interactions between hatchery and wild salmonids. Fish maintained in hatcheries quickly adapt to hatchery conditions through direct selection by hatchery managers and through inadvertent selection, i.e. domestication selection (Einum & Fleming 1997; McGinnity et al. 1997; Fleming et al. 2000). There are two mechanisms that lead to reduced fitness in the wild for hatchery adapted fish: (1) relaxation of selection (Lynch and O'Hely 2001) and (2) adaptation to the hatchery environments that mean lower survival in the wild (Ford 2002). We believe that the loss of fitness in the wild is an inevitable consequence of adaptation to hatcheries and evidence suggests that this loss can occur even in the initial generations of breeding stock (see Part Two, Section A below).

## 4. Disease

Jim Winton from the US Geological Survey reviewed the comparative ecology of infectious diseases in hatchery and wild salmonids. He outlined the basic ecological principles of infectious diseases and the variety of pathologies and diseases affecting salmonids in the northwestern US.

The major issue surrounding disease transmission and the effects of hatchery fish on wild fish is the risk of hatchery fish transmitting disease to wild fish. The major factors contributing to

risk in hatcheries include high densities, adverse environmental conditions, introduced pathogens, the rearing of alien species, and the emergence of drug-resistant pathogens. The major risks to wild fish from hatchery fish are derived from the potential introduction of pathogens that are novel to the resident fish, the amplification of endemic pathogens and their potential evolutionary changes, and the exposure to pathogens at abnormal stages in the life cycle. Whirling disease and infectious hematopoietic necrosis offer two remarkable case histories that illustrated these potential problems and the potential solutions. Improvements in hatchery practice and development of vaccines will enhance disease control; control will also improve if fish moved between watersheds are required to be certified as not carrying pathogens that would be novel at their destination. This issue reflects the general principle that best hatchery practice uses local fish for breeding stock and replenishes stock every generation.

## 5. Straying

Andy Dittman of the Northwest Fisheries Science Center reviewed the current knowledge of straying in anadromous Pacific salmon. This topic is important because straying creates a potential gene flow that connects populations in different systems; this connection can be positive if the populations involved are similar genetically and face similar selective pressures or negative if the populations are adapted to different local conditions. Hatchery fish do not necessarily stray more than wild fish. Some hatchery programs produce high straying rates when hatchery fish are released far off-site. Straying rates vary widely among systems; some hatchery programs have very low straying rates and others produce higher rates despite all efforts to minimize straying. This is an area that deserves more attention in future research.

## B. Effects of Hatchery Supplementation

We received presentations on four different, largely experimental research programs designed to analyze the effects of hatchery supplementation programs. Rigorous experimental evaluations of the effects of hatchery augmentation are critical because they offer the strongest evidence for testing the long-held assumption that hatchery augmentation is effective and beneficial for wild populations. This assumption remains untested because, despite widespread hatchery augmentation, there have been few attempts to exploit hatchery releases in an experimental fashion - meaning treatment and control - to evaluate the effects of augmentation. Given that the results of rigorous testing are vital for informing and supporting science-based policy, each and every opportunity for rigorous testing should be taken.

### 1. Idaho Supplementation Studies (ISS) on Spring and Summer Chinook

These studies, which were presented by Pete Hassemer of the Idaho Department of Fish and Game, reflect thoughtful a priori development of multi-generational tests of impacts of chinook salmon augmentation, using several replicate streams in a comprehensive design. The response variables to be tested seem properly focused on testing success; here, success is defined as maintaining or increasing natural production and maintaining fitness of the wild stock. The history of this study, and other planned experiments, demonstrates the intrinsic difficulty in maintaining commitments to a multi-year experiment involving many localities and interest groups. Long-term studies typically require adaptive re-organization of experimental designs to accommodate unplanned modifications. A very important aspect of the study design for the Idaho program is now being reconsidered. We emphasize the critical importance of the planned termination of ISS juvenile releases for the proper testing of impacts of hatchery augmentation. The management value of the data that will be generated by this termination phase will be tremendous and more than justifies any perceived costs of this planned termination.

## 2. Hood Canal Chum Supplementation

This program, which was reviewed for us by Thom Johnson of the Washington Department of Fish and Wildlife, has been conducted by the Washington Department of Fish and Wildlife, the Point No Point Treaty Tribes, and volunteer groups since 1992 in response to critical declines in chum populations in the Hood Canal and Puget Sound region. The program is especially notable for its dual commitment not only to hatchery and management measures but also to habitat improvement to follow the ESA mandate of restoring numbers of fish and the ability of the natural environment to sustain fish. Specifically, we quote a key premise: "Commensurate, timely improvements in the condition of habitat critical for summer chum salmon survival are necessary to recover the listed populations to healthy levels".

This program has developed a rigorous set of protocols for conservation-driven hatchery programs so as to limit risk of predation on wild stock fish, limit potential competition between hatchery and wild fish, minimize potential disease introduction from hatcheries to the natural system, and maintain genetic variability among and within wild populations. In cases where recovery objectives have been met, hatchery augmentation has ceased. Thus the focus of this restoration program falls unambiguously on promoting recovery of wild stocks and the habitat required to sustain them.

This work is so important, and is of such high quality, that its results deserve wide dissemination in the scientific community. The best path for ensuring that wide dissemination is to publish the results in the primary scientific literature, and so we suggest strongly that papers describing this work and its results be submitted for publication in the primary scientific literature. The design of this program offers a particularly important opportunity for testing key management alternatives. Specifically, this study includes hatchery supplementation and controls in streams with or without high habitat quality (restored or not); the results would test the hypothesis that supplementation is effective only when habitat protection/restoration is also applied. Likewise, the contrast of control streams that had no hatchery supplementation with hatchery-supplemented streams could conceivably allow a powerful test of whether restoration of habitat alone was as effective as the combination of restoration and hatchery augmentation.

## 3. Oregon Unplanned Experiment

Every release of hatchery fish can be considered an 'experiment'. Mark Scheuerell from the Northwest Fisheries Science Center reported results of such unplanned experiments in Oregon (also see Nickelson 2003, which is based on data from 1990-1996 for 14 basins). The work reported here extended Nickelson's analysis with 4 more years of data, during which hatchery production was unchanged in some basins, scaled back in others or highly variable (thus creating the unplanned experiment).

The fundamental idea behind these studies is to estimate productivity from a standard Ricker analysis in which productivity in year  $t$ ,  $P(t)$ , is estimated from spawners in year  $t$ ,  $S(t)$  and recruits in year  $t+1$ ,  $R(t+1)$ , according to  $P(t) = \log(R(t+1)/S(t)) + e$ , where  $e$  denotes a combination of observation error and process uncertainty (sensu Hilborn and Mangel 1997). An ANCOVA model for productivity taking into account site, regime and hatchery releases showed significant results for site, regime, and site by hatchery. The panel recommended that the ANCOVA model be redone to include estimates of carrying capacity; we understand that this is underway.

An alternative to the ANCOVA is a time series analysis of the form  $P(t)=a+bP(t-1)+cH(t)+e$ , where  $H(t)$  is the hatchery release in year  $t$ . The model with hatchery effects ( $c$  estimated) can then be compared to one in which there are no hatchery effects ( $c=0$ ) using Akaike's Information Criterion (AIC; e.g. Hilborn and Mangel 1997). Some of the basins showed strong AIC changes, others weak or none, indicating that hatchery effects occur in some but not all basins.

The conclusions of this study are that 1) hatchery releases have a significant negative effect on the productivity of wild coho and 2) the effects are most prevalent at the basin scale.

#### 4. Yakima Supplementation

Dave Fast from the Yakima Nation reported on the Yakima supplementation project, which is an excellent example of an integrated approach that includes community involvement and education, freshwater habitat restoration, and hatchery supplementation. The results were indeed impressive, in terms of returning adult fish.

However, it is difficult to ascertain whether supplementation was successful. The adjoining watershed, the Naches River, is used as a control for the effects of supplementation. However, the decline of the stocks, implementation of the supplementation program, and subsequent recovery of adult returns coincide with the shift in the North Pacific in about 1975 to a regime of poorer productivity followed by a return in about 1999/2000 to a regime of greater productivity. The trajectories of adult returns coincide with the time course of the north Pacific regime and this effect may overwhelm any differences between the control and treatment watersheds. Moreover, it may be difficult to interpret results that use entire watersheds as either control or treatment (Power et al. 1998); watersheds usually vary widely in many factors beyond the experimentally designated factor and using only two watersheds offers a limited opportunity to isolate the experimental factor as the responsible one.

### C. Presentations on Overarching Recovery and Restoration Efforts

#### 1. Risk Assessment

We considered two presentations on quantitative risk assessment procedures for evaluating the extinction risk for an entire ESU in light of the draft policy to include hatchery-origin fish in listing decisions. We observed that the draft policy (NMFS 2004) makes no reference to restoration, only current viability. Both presentations followed this lead, addressing current viability (immediate extinction risk) almost exclusively. However, we concluded that, even with this limited framework, this direction is not yet proving fruitful and may be misleading.

The presentation by Paul McElhany (Northwest Fisheries Science Center) outlined a straightforward approach for incorporating hatchery-origin fish in a traditional framework for assessing risk of imminent extinction, using Willamette spring-run chinook as an example. The essence of the approach is to include the five hatcheries for this ESU as independent entities, combined with seven existing historical populations, in the calculation of the probability that the entire ESU would disappear. If, for example, a particular population  $i$  (hatchery or natural) had a probability  $P_i$  of going extinct in the next interval, and if the fates of the populations were independent, the probability that all populations (i.e., the entire ESU) would go extinct in the next interval is simply the product of the  $P_i$ s. Because the probabilities of the five hatcheries disappearing in each year are extremely low (arbitrarily taken as 5% for the next hundred years), the product – the total probability of extinction – is dominated by these probabilities and becomes

infinitesimal (0.00003% for all five hatcheries, in this instance). It becomes so infinitesimal that even increased realism in the model (for instance, making the probabilities of extinction for the separate populations dependent on one another) would not change the overall result – an infinitesimal probability of rapid extinction of the entire ESU.

We saw two major problems with this approach. The first is that the probabilities of short-term extinction of each hatchery population cannot be quantified – they depend partly on many socioeconomic and political factors that are neither independent nor remotely quantifiable at this time. Therefore, simply taking (very low) numbers out of a hat is the only way to arrive at a numerical answer. However, simply stating that answer gives the illusion that this is a scientific and quantifiable process, when, in this setting, it is not. This problem with standard risk assessment procedures in resource issues has been recognized previously (e.g., Simberloff and Alexander 1998, O'Brien 2000), but the widespread adoption within the federal government of the principle of quantitative risk assessment as a basis for all regulation induces agencies to attempt this approach even when it is inappropriate. In essence, it becomes a delphic process that substitutes expert belief about probabilities for real scientific data.

The presentation by Ken Currens from the Northwest Indian Fish Commission did not ameliorate this problem because expert judgment was used to estimate certain parameters. The main innovation that Currens discussed is a Bayesian approach to estimating certain initial component probabilities required for estimating total probability of extinction, along with using simulations to improve these estimates. The focus was on one aspect of risk of extinction and risk of failed recovery: risk of domestication. Because the simulation cannot account for many of the factors that might lead to the extinction of particular populations, and it was unclear to which actual data the simulation results would be compared, this approach did not alleviate our concerns about the illusion of quantification for a phenomenon that cannot currently be quantified.

The second major problem with the risk assessment model is that it does not lead to insights on recovery. It targets only the risk of extinction. McElhany alluded to this problem, stating that his analysis suggests that the probability that the Willamette spring-run chinook ESU would become self-sustaining is “very low.” However, this suggestion did not rest on a formal, quantitative procedure. Dr. McElhany ended his presentation with two pertinent questions that seem, to us, to point up the inability of risk assessment to deal with recovery: “Is ability to survive in the natural environment required?” “Is extinction only about zero abundance?” According to the ESA, the answer to the first question is yes. The answer to the second question also appears to be yes. After all, the Amistad gambusia (*Gambusia amstandensis*) and Tecopa pupfish (*Cyprinodon nevadensis calidae*) are both federally listed fish that are classified as having gone extinct, even though, in a sense, both lineages survived: their genetic change was simply so great, in both instances owing to hybridization, that each species is considered to have disappeared, at least as the listed entity (McMillan and Wilcove 1994).

## 2. The Hatchery Reform Project

Don Campton from the US Fish and Wildlife Service reviewed the Hatchery Reform Project and outlined the activities of the Hatchery Science Review Group. The Hatchery Reform Project was created by the US Congress to promote reforms in hatchery practice and scientific oversight of that practice to facilitate assessing how hatcheries could be best used to aid in establishing and rebuilding populations of Pacific salmon. The Project supports a competitive grant program for research on hatchery fish effects and also supports state and tribal efforts to develop and implement hatchery reforms. The Hatchery Scientific Review Group (HSRG) is the independent scientific panel charged with evaluating scientific merits of proposals and proposed

hatchery reforms; this group is composed of five independent scientists (selected from a pool of candidates nominated by the American Fisheries Society) and four agency scientists designated by the Washington Department of Fish and Wildlife (WDFW), the Northwest Indian Fisheries Commission (NWIFC), NOAA Fisheries, and the U.S. Fish and Wildlife Service. The non-profit agency Long Live the Kings is the Project's third-party facilitator charged with providing overall Project management, outreach, and communication of progress to Congress.

The HSRG issued its first report in April 2004. The report featured white papers on emerging issues in hatchery management and outlined a scientific framework for implementing a number of hatchery reforms in light of those issues as well as a framework for assessing the effects of these reforms. The issues on which the HSRG focused, including (but not limited to) effects of ocean conditions on adult survival, the preservation of genetic diversity in hatchery stocks, and the interactions between hatchery and wild fish, have all been considered by the RSRP in previous meetings and reports and especially in this meeting and this report.

### 3. The Minter Creek Experiment

Mike Ford briefly reviewed an ongoing experiment measuring selection and fitness of wild and hatchery coho salmon at Minter Creek using molecular markers for parentage identification of returning adults. This experiment was previously summarized with comments in an earlier report (RSRP July 21-23, 2003). Basic findings from the first year are that no difference in the mean fitness of wild and hatchery fish could be detected. We suggested again, and Ford agreed, that this result is likely attributable to the high gene flow between hatchery and wild stocks that occurred over many generations until the present; the high gene flow means that there is no real hatchery-wild comparison to be made.

Ford confirmed that the current goal of the study is to eliminate gene flow from the hatchery to the wild stock (by controlling fish at the weir) to monitor any potential re-adaptation of the wild population to the natural environment. We commented, again, that analysis of selection on quantitative traits (Lande and Arnold 1983, Morgan and Conner 2001) in this system should separate selection on the hatchery and wild fish, as they experience different environments; this is likely to be a more powerful approach than attempting to find disruptive selection on the pooled population. The panel also notes that curtailing gene flow between the hatchery and wild fish does not eliminate several possible ecological influences of hatchery fish on the wild fish, and is therefore expected to underestimate the overall influence in comparison to an experiment in which the hatchery population was reduced or eliminated at the same time as gene flow was stopped. An outline of approaches to more general experiments assessing the influence of hatchery fish on wild fish appears in earlier RSRP reports.

During this presentation, and one on risk assessment by Currens and Busack, previous theoretical studies of the potential dysgenic effects of hatchery fish on wild populations were mentioned (Adkison 1994, Tufto 2000, 2001; Lynch and O'Healy 2001, Ford 2002). During Currens' presentation, we pointed out that all of these theoretical studies, and the risk assessment, concerned a single quantitative character, and that the predicted dysgenic effects would probably be magnified if, more realistically, multiple characters were included (e.g. using the model of Lande 1980, as was subsequently discussed).

## PART TWO: THE ESU CONCEPT, HATCHERIES, LISTING, AND RECOVERY

### A. Analyzing the Loss of Fitness in Hatchery Fish

The practical question about hatchery fish is how fast fitness in the wild is lost. Evidence for rapid loss in the initial generations would argue strongly against the hypothesis that hatchery fish are ecologically equivalent to wild fish.

We investigated this question by compiling all 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. We examined all of the studies of salmonids in which hatchery fish came from the same or nearby rivers to the wild fish and did not examine any study in which hatchery fish came from other regions of the species' range. It is well known that the fitness of hatchery fish derived from other regions is almost always well below the fitness of wild fish (McLean, Bentzen and Quinn 2003). We also did not include studies in which most, if not all, of the "wild" fish are derived from prior hatchery escapes (e.g. Dannewitz et al. 2004 and the study coho salmon in Minter creek described by Mike Ford to the panel).

The six studies that met our criteria have their strengths and weaknesses. Hansen's (2002) study on the survival of domesticated brown trout in Denmark was the study with the longest period of hatchery residence (50 years or 12.5 generations). This study compared the expected proportion of domesticated fish returning to a fjord (64%) in Denmark with the observed proportion (6%), using microsatellite DNA markers to distinguish hatchery from wild fish. The ratio of the two can be taken as an estimate of the relative fitness of hatchery fish in the wild to that of wild fish. This approach avoids many of the problems of other studies. This estimate may underestimate the true loss of fitness because the hatchery fish will be exposed to natural selection after release and spawning. The original source for the hatchery stock was a relatively nearby river, less than 100 kilometers away.

Two studies offered results from stocks that had been in hatchery culture from 7 to 9 generations. Leider et al. (1990) estimated the relative survival of summer run steelhead which had been in hatcheries for over 8 generations using electrophoretic markers of eggs produced in hatcheries but transplanted to natural streams. In this case the relative survival was only 12% of the wild fish. Hulett et al. (1986) estimated the relative fitness of hatchery and wild winter run steelhead in the lower Columbia region. The original broodstocks came from the same region of the Columbia River, e.g. within around 50 km of the hatchery (B. Berejikian and M. Ford, personal communication), which represents a distance smaller than most ESU's as they are presently defined. There has been strong directional selection on this steelhead, which may be the reason that their relative survival is so low, i.e. 6% of the wild fish.

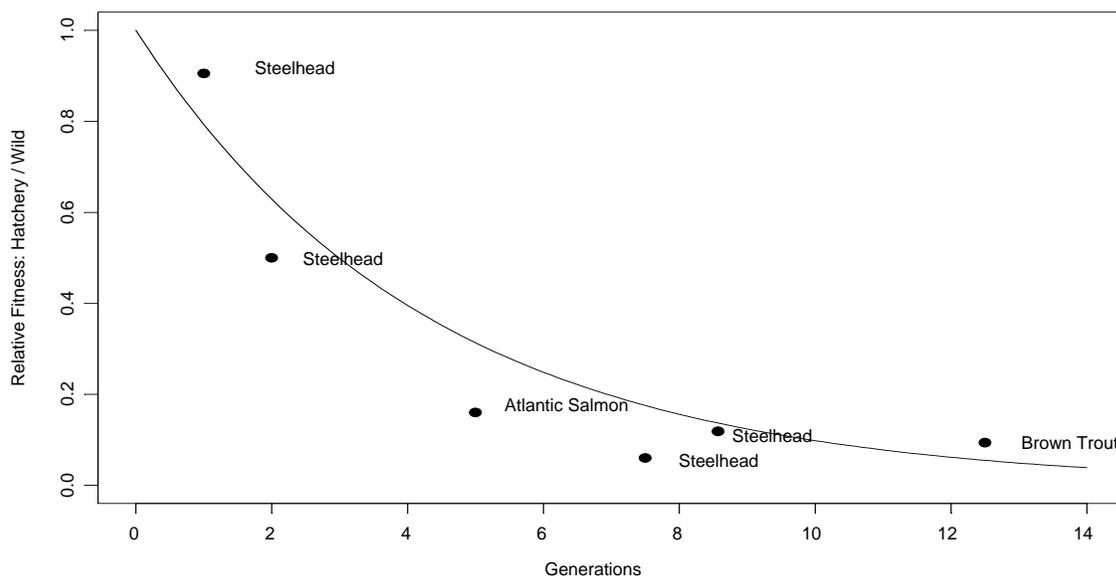
We examined two studies that incorporate hatchery fish that had spent 2-5 generations in the hatchery environment. Fleming et al. (2000) compared the fitness, in the wild, of commercially-farmed Atlantic salmon with brood stock from Norway's national breeding program with the fitness of wild salmon. The fish from this aquaculture strain came originally from the general area of southwestern Norway, but not exactly from the river where the test was carried out. Despite this potential problem, the results are aligned well with the results of the other studies (Figure 1). Most of the fitness loss in the farmed salmon was traced to the deficient breeding ability of males. Reisenbichler and McIntyre (1977) were the first to carry out a study expressly to estimate the relative fitness in the wild of hatchery and wild fish. They planted eggs in 8 streams and monitored the production of seaward migrants using traps. After only two

generations, it was estimated that fitness in the wild of hatchery fish was reduced by roughly half; however, there is large variability among rivers in this decline in survival. In this study, the hatchery fish were derived from local fish.

Finally, we examined a striking study that offered strong evidence for a loss of fitness in a single generation, which is Blouin's (2003) examination of winter run steelhead with molecular genetic markers. For the comparison we make here, we used his data on the "new" hatchery stocks, which had been in the hatchery for only one generation. Those data include estimates for each gender in three brood years (1995-1996, 1996-1997, and 1997-1998). The hatchery fish were less fit in 5 of the 6 comparisons (brood year and gender combinations), with ratios of 0.85, 0.87, 0.90, 0.84, 0.90, and 1.08. We used the delta method to calculate the approximate standard error for each of these ratios and obtained estimated standard errors of 0.16, 0.12, 0.14, 0.10, 0.16, and 0.14, respectively. We carried out a fixed-effect meta-analysis on the 6 estimated relative fitness values (Hedges and Olkin 1985). The meta-analytic average was 0.897 with an approximate standard error of 0.054, yielding an approximate 95% confidence interval for the relative fitness that spanned 0.79 to 1.0. This is reasonably strong evidence for a loss of fitness after only one generation. It is worth noting that Blouin (2003) also included a series of relative fitness estimates for "old" hatchery stock; this stock was an out of basin stock that had been in culture for many generations. The "old" stock exhibited fitness levels that were between 17% and 54% of the fitness of wild fish. We did not use the data from the "old" stock because the number of generations in which this stock had been in culture was not available.

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. These preliminary results should be tested with directed experiments on a diversity of Pacific salmon, and in this light the experimental augmentation studies that we reviewed in Part One, Section B of this report assume great importance.

Independent data support these conclusions. Chilcote (2003) examined the relationship between recruits and spawners of mixed spawning populations of wild and hatchery steelhead; he found survival was reduced in the presence of hatchery fish and his data suggest that a spawning population comprised of equal numbers of hatchery and wild fish would produce 63% fewer recruits, per spawner, than one comprised entirely of wild fish.



Species	generations	RelSurv	hatcheryFarm	stage	
Atlantic Salmon	5	0.16	Farm	lifetime	Fleming et al. 2000
Steelhead	2	0.5	hatchery	Egg-to parr migration	Reisenbichler and McIntyre 1977
winter run steelhead	7.5	0.06	Hatchery	lifetime	Hulett et al 1996
summer run steelhead	8.6	0.12	Hatchery	lifetime	Leider et al. 1990
winter run steelhead	1	0.897	Hatchery	lifetime	Blouin 2003
Brown trout	12.5	0.094	Hatchery	lifetime	Hansen 2002

## B. Scientific Issues Raised by Habitat Compensation Efforts

In learning about the broad scope of NOAA hatchery regulatory activities, we noted that about 70% of the salmon hatcheries possess the mandate of supplying fish to compensate for a "habitat debt" caused by the construction and presence of dams on streams and rivers used by anadromous fish. The dams degrade habitat upstream and downstream (by altering sediment supply and transport as well as thermal regimes). Depending on management actions and their effectiveness, dams can prevent passage of adult spawners upstream to use any undegraded habitat and impede the outmigration of smolts. In addition, dams or flow diversion structures often eliminate flood peaks from river hydrographs. In rivers of the western United States, seasonal bed-scouring floods provide at least three habitat services: cleansing and renewing of spawning gravels (Lisle 1989), rejuvenating food webs (Wootton et al. 1996, Power 1992), and flushing exotic invasive species downstream of reaches where native species, which are better adapted to winter floods, can persist (Strange et al. 1999, Meffe 1984).

We believe that that the use of hatcheries as a form of compensatory mitigation falls short of the standards applied by other branches of NOAA, specifically by DARP, the Damage Assessment and Restoration Program. If a ship runs aground and physically destroys seagrass habitat in the Florida Keys (Fonseca et al. 2000) or if an oil spill occurs in a coastal region and pollutes the habitat (Burlington 1999), then NOAA requires the responsible party to replace the ecosystem and human services of that injured habitat. This processes requires conducting a "habitat equivalency analysis" (NOAA 1999) to insure compensation in lost ecosystem services. By that standard, the compensation for habitat losses due to dams falls well short of achieving compensation because replacing only the anadromous salmon fails to compensate for the full range of lost habitat services.

In this context, we also draw a lesson from Winton's excellent presentation on disease in hatchery and wild fish populations, specifically on the case of whirling disease. Whirling disease is caused by a protozoan and was introduced into hatcheries through the presence of the protozoan in fish products imported from Europe for hatchery feed. This disease, and other diseases, were actually easier to manage in hatcheries (presumably by purging infected fish and disinfecting the facilities) than in natural environments. Yet natural salmonid populations may prove resilient to diseases if watersheds and river flows are sufficiently unimpaired. For example,

Madison River rainbow trout rebounded from whirling disease in the mid-1990s, either because the fish evolved resistance, or because flushing flows decreased densities of Tubifex worms (an intermediate host for the pathogen) (B. McConnell, cited by Winton). To fulfill the requirements of the Endangered Species Act, watersheds and channel flows must both be managed so that wild salmonids can maintain both evolutionary and ecological resiliency across periods of stress.

To reiterate points made elsewhere in this report, the Endangered Species Act emphasizes that the goal of recovery is to ensure that the natural population will be able to persist. If listing, and especially delisting criteria count hatchery spawned as well as wild fish, Holly Doremus (Professor of Law, University of California-Davis) warned the panel that it will be very difficult to ascertain what recovery means. The major motivation for hatcheries throughout their long history has been to compensate fisheries for production lost to uses of water and watersheds that impair fish habitat. If hatchery spawned fish are counted as part of the ESU, or DPS, for listing and delisting, there may be a tendency to redefine the environment of salmon stocks to include artificial propagation facilities. Despite recent improvements in the practices of some hatcheries (more careful genetic management of brood stock, attempts to mimic features of the natural environment), hatcheries will never produce salmonids with the same evolutionary potential as those spawned and reared in the wild. A perpetual metapopulation between wild and hatchery salmonid populations is not an acceptable recovery for listed salmonids under the ESA. Fish removed from nature to propagate in hatcheries always constitute a loss to the evolutionarily significant natural population. For listed salmonids, this must be done only as a last resort to boost numbers to the point at which the natural population can become self-sustaining, and these hatchery conservation programs need defined termination dates or criteria. Hatcheries managed for harvest production must be viewed as potential or actual threats to listed wild stocks, and must be managed to limit impacts on wild populations so as to not violate the ESA.

### C. Scientific Inconsistencies Created by the Proposed Hatchery Policy

Although most attention focused on the ESA has been on its goal of preventing extinction, the Act has a second mandate: to achieve sufficient self-sustaining wild populations of listed species to ensure their survival in nature (FWS 1992, 2004, NRC 1995). This mandate is spelled out in two sections:

Section 2b. “The purposes of this Act are to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved...”

Section 4f1 – “The Secretary shall develop and implement plans (hereinafter in this subsection referred to as ‘recovery plans’) for the conservation and survival of endangered species and threatened species pursuant to this section unless he finds that such a plan will not promote the conservation of the species.”

Czech and Krausman (2001) see the final clause of Section 4f1 as based on a cynical assumption that publication of a recovery plan might arouse public opposition, and it is true that almost half of all listed species (800 of 1824) still lack recovery plans. However, Congress clearly intended recovery in nature to be the goal of the ESA, and the agencies strongly espouse this goal and provide extensive information on their efforts to achieve it (e.g., FWS 2004).

We remain extremely concerned about scientific implications of the proposed hatchery policy (NMFS 2004), which dictates that when hatchery fish are sufficiently similar to wild fish they should be included in the same ESU as the wild fish. By the terms "hatchery fish" and

"wild fish" we mean fish spawned and reared in a hatchery and in the wild, respectively, regardless of their ancestry.

The criteria for similarity of hatchery fish are summarized in the Hatchery Broodstock Summaries and Assessments for listed ESUs (Salmon and Steelhead Hatchery Assessment Group, NMFS 2003). These are (i) the degree of genetic divergence, based on molecular genetic markers as well as morphology, behavior and fitness, (ii) the origin of the hatchery stock, and (iii) status of the wild population(s). For the great majority of ESUs there is no information on potentially adaptive trait differences between hatchery and wild fish in morphology, behavior or life history (including fitness), and in many cases information on molecular genetic markers is also lacking, so that similarity must be judged solely on the origin of the broodstock and status of the wild population(s). This is a scant basis for a clear assessment of similarity. Even when substantial data exist to support similarity with respect to quasi-neutral molecular genetic markers, in the absence of information on morphology, behavior and life history, it is not valid to conclude that there are no adaptive differences between hatchery and wild fish.

In the absence of substantial information on potentially adaptive differences between specific hatchery fish and the wild fish in an ESU, a highly precautionary approach to the assessment of their similarity ought to be taken. The wisdom of a precautionary approach is suggested by well-known behavioral differences, e.g. in feeding and predator avoidance (Olla et al. 1998), the recent finding of greatly diminished brain size in hatchery fish (Marchetti and Nevitt 2003), and by several reports of substantially reduced fitness in hatchery fish (e.g. Blouin 2003, Kostow et al. 2003, McLean et al. 2004, Berejikian and Ford 2004; see also Part Two, Section A of this report). Yet in all cases with extant wild population(s), even those with no data on either quasi-neutral molecular markers or potentially adaptive traits or fitness, a determination of the degree of similarity was made. This does not appear justified to us; we believe that in the majority of cases there is insufficient evidence on which to make a reliable assessment of similarity, and most of the specific determinations should have been "unknown" or "data deficient". Alternatively, the precautionary principle, combined with the expectation that hatchery influence is usually detrimental to wild fish populations, could have been used to exclude hatchery fish from an ESU in specific cases with inadequate information to make a strongly supported determination of similarity. The scientific justification for including hatchery fish in an ESU in such cases is extremely weak.

Even clear evidence of minimal genetic differences between wild and hatchery fish should be interpreted cautiously. In many situations, e.g. for some ESUs listed as threatened or endangered under the ESA, hatchery strays constitute a substantial or overwhelming fraction of fish spawning the the wild. In such situations, even though genetic and fitness differences between wild and hatchery fish may not be statistically significant, it is possible, or even likely, that adaptation to the hatchery environment has reduced the fitness of fish spawning in the wild, and if hatchery influences continue unabated, evolution of the ESU will be substantially impeded or altered in direction, to the detriment of its long-term viability. For this reason, the RSRP suggests that in such situations hatchery fish, either should not be included as part of the ESU, or if included in the ESU should not be used to justify delisting from the ESA. This highlights the importance of conducting experiments on the genetic and ecological effects of hatchery fish on wild fish, as recommended in previous RSRP reports.

The Hatchery and Broodstock Summaries and Assessments classified the degree of similarity only on a 1 to 4 scale based on the available information. Final determination of the degree of similarity for including hatchery fish in a listed ESU was made by the fisheries management branch of NMFS rather than by the science branch. This sets an inappropriate

precedent for what is fundamentally a scientific determination. As explained to the panel, the science branch agreed to this procedure because of the extreme time pressure for the determinations to be made in response to recent court decisions, and uncertainty in the science branch about how to interpret the working draft of the proposed hatchery policy.

Myers et al (2004) suggested that hatchery fish should never be included in an ESU. The main justification for this point of view is that hatchery fish experience a different environment than wild fish during their early life and inevitably undergo natural selection in a different direction than wild fish. Adaptation to the hatchery environment is similar to the well-understood process of domestication (Price 2002), which in the presence of gene flow from hatchery to the wild, generally reduces the fitness of the wild population and their ability to adapt to future changes in the natural environment. Except for extreme cases when a temporary conservation hatchery is necessary to prevent extinction of a small (possibly inbred) and declining wild population, hatchery fish should be regarded as impeding the future evolution of an ESU. For this reason Myers et al. (2004) recommended that NMFS scientists should revisit the definition and application of the ESU concept. In the context of restoring wild self-sustaining populations of salmon, placing increased emphasis on the future adaptation and continued persistence of an ESU in a changing environment would justify the categorical exclusion of hatchery fish from most ESUs.

Our suggestions in the previous paragraphs are consistent with Waples' (1991) arguments that hatchery fish should not be included in an ESU based solely on origin of the hatchery stock and that a burden of proof must be met for determining similarity to the wild stock(s). The Artificial Propagation policy (NMFS 1993) likewise stated that hatchery fish should be excluded from an ESU if they are a different genetic lineage, have undergone major changes, or if there is substantial uncertainty. To the panel it appears that the proposed hatchery policy directly violates the thinking of leading NMFS scientists.

We believe that the scientific considerations indicate clearly that NMFS should redefine the ESU concept. We discussed the history of Endangered Species Act, its implementation, and the history of legal argument in the courts over the Act with Prof. Holly Doremus, in particular the case law precedent that might inform the ESU concept and hatchery fish. She indicated that there should be no legal impediment to NMFS scientists redefining the ESU concept if they felt this was scientifically justified. We believe that there is strong scientific justification for redefining the ESU concept and suggest - that in the immediate future NMFS convene a scientific workshop to revisit the issue of ESU definitions in relation to hatchery fish.--

## REFERENCES

- Adkison, M. D. 1994. Application of mathematical modeling to problems in salmon biology and management. Ph. D. Dissertation. University of Washington, Seattle.
- Beckman, B. R., D. A. Larsen, and W. W. Dickhoff. 2003. Life history plasticity in chinook salmon: relation of size and growth rate to autumnal smolting. *Aquaculture* **222**:149-165.
- Berejekian, B. and M. Ford. 2004. Review of relative fitness of hatchery and natural salmon. NWFSC Report of May 25, 2004.
- Blouin, M. S. 2003. Relative reproductive success of hatchery and wild Steelhead in the Hood River. BPA and ODFW Final Report Contract 9245 (Bonneville Power Administration).

Brannon, E., 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* 29:12-31.

Burlington LB. 1999. Ten-year historical perspective of the NOAA damage assessment and restoration program. *Spill Science Technology Bulletin* 5: 109-116.

Chilcote, M. W. 2003. Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1057–1067.

Czech, B., and P.R. Krausman. 2001. *The Endangered Species Act*. Baltimore: Johns Hopkins University Press.

Dannewitz, J., E. Petersson, J. Dahl, T. Prestegard, A-C Lof, and T. Jarvi. 2004. Reproductive success of hatchery-produced and wild-born brown trout in an experimental stream. *Journal of Applied Ecology* 41: 355–364.

Fleming, I. A., K. Hindar, I. B. Mjølnerod, B. Jonsson, T. Balstad, and A. Lamberg. 2000. Lifetime success and interactions of farm salmon invading a native population. *Proc. Roy. Soc. Lond. B* 267:1517-1523.

Fonseca M.S., B. E. Julius, and W. J. Kenworthy. 2000. Integrating biology and economics in seagrass restoration: how much is enough and why? *Ecological Engineering* 15:227-237.

Ford, M. J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. *Conservation Biology* 16: 815-825.

Hansen, M.M. 2002. Estimating the long-term effects of stocking domesticated trout into wildbrown trout (*Salmo trutta*) populations: an approach using microsatellite DNA analysis of historical and contemporary samples. *Mol. Ecol.* 11:1003-101.

Hedges, L. V., and I. Olkin. 1985. *Statistical methods for meta-analysis*. Academic Press, San Diego, California, USA.

Hulett, P.L., C.W. Wagemann, and S.A. Leider. 1996. Studies of hatchery and wild steelhead in the lower Columbia region. Progress report for fiscal year 1995, report no. RAD 96-01. (Available from Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, Washington 98501-1091).

Hilborn, R. and M. Mangel. 1997. *The Ecological Detective. Confronting models with data*. Princeton University Press, Princeton, NJ.

Jonsson, N., B. Jonsson, and L. P. Hansen. 2003. The marine survival and growth of wild and hatchery-reared Atlantic salmon. *Journal of Applied Ecology* 40:900-911.

Kostow, K. E., A. R. Marshall, and S. R. Phelps. 2003. Naturally spawning hatchery steelhead contribute to smolt production but experience low reproductive success. *Trans. Am. Fish. Soc.* 132:780-790.

- Lande, R. 1980. Genetic variation and phenotypic evolution during allopatric speciation. *American Naturalist* 116: 463-479.
- Lande, R. and S.J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210-1226.
- Larsen, D. A., B. R. Beckman, K. A. Cooper, D. Barrett, M. Johnston, P. Swanson, and W. Dickoff. 2004. Assessment of high rates of precocious male maturation in a spring chinook salmon supplementation hatchery program. *Transactions of American Fisheries Society* **133**:98-120.
- Leider, S.A., P.L. Hulett, J.J. Loch, and M.W. Chilcote. 1990. Electrophoretic comparison of the reproductive success of naturally spawning transplanted and wild steelhead trout through the returning adult stage. *Aquaculture* 88:239-252.
- Lisle, T. E. 1989. Sediment transport and resulting deposition in spawning gravels, North Coastal California. *Water Resources Res.* 25:1303-1319.
- Lynch, M. and M. O'Healy. 2001. Captive breeding and the genetic fitness of natural populations. *Conservation Genetics* 2: 363-378.
- Marchetti, M. P. and G. A. Nevitt. 2003. Effects of hatchery rearing on brain structures of rainbow trout, *Oncorhynchus mykiss*. *Environmental Biology of Fishes* 66: 9-14.
- Meffe, G. K. 1984. Effects of abiotic disturbance on coexistence of predator-prey fish species. *Ecology* 65:1525-1534.
- McLean, J. E., P. Bentzen and T. P. Quinn. 2004. Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead, *Oncorhynchus mykiss*. *Env. Biol. Fishes* 69:359-369.
- McMillan, M., and D. Wilcove. 1994. Gone but not forgotten: Why have species protected by the Endangered Species Act become extinct? *Endangered Species UPDATE* 11:5-6.
- Metcalf, N., and P. Monaghan. 2003. Growth versus lifespan: perspectives from evolutionary ecology. *Experimental Gerontology* **38**:935-94
- Morgan M. T. and J. K. Conner. 2001. Using genetic markers to directly estimate male selection gradients. *Evolution* 55: 272-281.
- Myers, R. A., S. A. Levin, R. Lande, F. C. James, W. W. Murdoch and R. T. Paine. 2004. Hatcheries and endangered salmon. *Science* 303: 1980.
- National Marine Fisheries Service. 1993. Interim policy on artificial propagation of Pacific salmon under the Endangered Species Act. *Fed. Reg.* 58:17573-17576.
- National Marine Fisheries Service. 2003. Hatchery Broodstock Summaries and Assessments for Chum, Coho, and Chinook Salmon and Steelhead stocks within Evolutionarily Significant Units listed under the Endangered Species Act. May 12, 2003. Salmon and Steelhead Hatchery Assessment Group, NOAA NMFS NWFSC/SWFSC.

National Marine Fisheries Service. 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. Fed. Reg. 69:31354-31359.

National Oceanic and Atmospheric Association. 1999. Habitat equivalency analysis: an overview. NOAA Damage Assessment Center, Silver Spring, MD.

National Research Council. 1995. Science and the Endangered Species Act. National Academy Press, Washington, DC.

National Research Council. 1996. Upstream: Salmon and Society in the Pacific Northwest. National Academy Press, Washington, D.C.

Nickelson, T. 2003. The influence of hatchery coho salmon (*Oncorhynchus kisutch*) on the productivity of wild coho salmon populations in Oregon coastal basins. Canadian Journal of Fisheries and Aquatic Sciences 60:1050-1056

O'Brien, M. 2000. Making Better Environmental Decisions: An Alternative to Risk Assessment. Cambridge, Massachusetts: MIT Press.

Olla, B. L., M. W. Davies and C. H. Ryer. 1998. Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. Bull. Mar. Science 62:531-550.

Power, M. E. 1992. Hydrologic and trophic controls of seasonal algal blooms in northern California rivers. Archivs fur Hydrobiologie 125:385-410.

Power, M. E., W. E. Dietrich, and K. O. Sullivan. 1998. Experimentation, observation, and inference in river and watershed investigations. Pp. 113-132 in W. J. Resitarits, Jr. and J. Bernardo, eds., Experimental Ecology: Issues and Perspectives. Oxford University Press, New York.

Price, E.O. 2002. Animal domestication and behavior. CABI Publishing, New York.

Reisenbichler, R.R. and J.D. McIntyre. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. J. Fish. Res. Board Can 34: 123-128.

RSRP 2003. Report from meeting of July 21-23, 2003. <http://www.nwfsc.noaa.gov/trt/rsrp.htm>

Simberloff, D. and M. Alexander. 1998. Assessing risks to ecological systems from biological introductions (excluding genetically modified organisms). Pp 147-176 in P. Calow, ed., Handbook of Environmental Risk Assessment and Management. Oxford: Blackwell.

Strange, E. M., K. D. Fausch, and A. P. Covich. 1999. Sustaining ecosystem services in human-dominated watersheds: Biohydrology and ecosystem processes in the South Platte River Basin. Environmental Management 24:39-54.

Thorpe, J. E., M. Mangel, N. B. Metcalfe, and F. A. Huntingford. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology 12:581-600.

- Travis, J., M. G. McManus, and C. F. Baer. 1999. Sources of variation in physiological phenotypes and their evolutionary significance. *American Zoologist* 39:422-433.
- Tufto, J. 2000. Quantitative genetic models for the balance between migration and stabilizing selection. *Genetical Research* 76: 285-293.
- Tufto, J. 2001. Effects of releasing maladapted individuals: a demographic-evolutionary model. *American Naturalist* 158: 331-340.
- United States Fish and Wildlife Service. 1992. Report to Congress, Endangered and Threatened Species Recovery Program. Washington, DC: U.S. Government Printing Office.
- United States Fish and Wildlife Service. 2004.  
<<http://endangered.fws.gov/recovery/recovery.pdf>>
- Waples, R. S. 1991. Pacific salmon, *Oncorhynchus spp.*, and the definition of “species” under the Endangered Species Act. *Marine Fisheries Review* 53:11-21.
- Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. *Science* 273:1558-1560.