NOAA Technical Memorandum NMFS-NWFSC-2

Pacific Salmon and Artificial Propagation Under the Endangered Species Act

Jeffrey J. Hard,[1] Robert P. Jones, Jr.,[2]
Michael R. Delarm,[2] and Robin S. Waples[1]

[1]National Marine Fisheries Service
Northwest Fisheries Science Center
Coast Zone and Estuarine Studies Division
2725 Montlake Blvd. E.
Seattle WA 98112

[2]National Marine Fisheries Service
Environmental and Technical Services Division
911 N.E. 11th Ave.
October, 1992

U.S. DEPARTMENT OF COMMERCE
Barbara Hackman Franklin, Secretary

National Oceanic and Atmospheric Administration
John A. Knauss, Administrator **National Marine Fisheries Service**
William W. Fox, Jr., Assistant Administrator for Fisheries

CONTENTS

SUMMARY

Artificial propagation, especially the use of production hatcheries, has been a prominent feature of fisheries enhancement efforts for Pacific salmon for several decades. Recently, the decline of many natural populations has prompted the development of another role for artificial propagation: assisting in the conservation of salmon populations. This paper outlines considerations of artificially propagated Pacific salmon during the listing and recovery of threatened and endangered species under the Endangered Species Act (ESA).

The primary objective of the ESA is the conservation of species in their natural ecosystems. Therefore, the evaluation of a species' status for listing or delisting under the ESA focuses on natural populations, which for Pacific salmon are defined as the progeny of naturally reproducing fish. If determined to be similar to the natural spawning population that represents an evolutionarily significant unit

(ESU) of a Pacific salmon species in characteristics believed to have a genetic basis, artificially propagated fish can be considered part of the ESU and used in the recovery of the population. However, a variety of factors may cause appreciable changes in artificially propagated fish relative to a natural population. In such cases, or if substantial uncertainty exists about the effects of artificial propagation, artificially propagated fish will generally not be included in the ESU.

Because of the potential for circumventing the high rates of early mortality typically experienced in the wild, artificial propagation may be useful in the recovery of listed salmon species. However, artificial propagation entails risks as well as opportunities for salmon conservation, and its ability to supplement and restore natural populations of Pacific salmon is largely unproven. Despite the fact that many artificial propagation programs for Pacific salmon have succeeded in producing fish for harvest, supplementation programs involving artificial propagation have generally not increased the abundance of natural fish.

Therefore, the use of artificial propagation for the recovery of Pacific salmon requires careful consideration. The major constraints governing the use of artificial propagation in ESA recovery programs should be the maintenance of genetic and ecological integrity and diversity in listed species. In keeping with these objectives, this paper provides general guidelines for the selection, collection, and mating of broodstock and the rearing and release of artificially propagated fish as part of a recovery program for a listed species. More specific guidelines are difficult to formulate because many critical uncertainties about the effectiveness of supplementation techniques are presently unresolved and because the value of specific guidelines may be highly case-dependent. Intensive monitoring and evaluation of activities associated with artificial propagation are likely to be essential to fully evaluate the impacts of such a program on natural fish.

Artificial propagation of a listed species is not a substitute for remedying the factors causing or contributing to the initial decline, and recovery programs should reflect integrated planning that addresses these factors. In considering recovery options, an objective assessment of potential risks should be undertaken and management techniques requiring less intervention should be evaluated before initiating artificial propagation. As a conservation tool, artificial propagation of salmon should be designed to maintain the inherent distinctiveness of species and protect the viability of threatened and endangered species during the recovery process.

Artificial propagation of unlisted species should be conducted to minimize adverse impacts to listed and unlisted species. The liberation of large numbers of fish genetically distinct from natural fish and the impacts of mixed-stock fisheries associated with this enhancement may have profound consequences for the viability of some distinct populations, including loss of genetic integrity and ecological diversity, increased competition, and elevated levels of harvest and natural predation. Management practices involving widespread transplantation of nonlocal stocks may also further endanger listed species or contribute to the decline of unlisted species. Continued artificial propagation of unlisted species must minimize the potential for deleterious effects on both listed and unlisted species if it is to be consistent with the maintenance of genetic and ecological diversity in Pacific salmon.

I. ARTIFICIAL PROPAGATION AND THE GOALS OF THE ENDANGERED SPECIES ACT

The Endangered Species Act (ESA, Act) of 1973 was enacted in recognition that "various species of fish, wildlife, and plants in the United States have been rendered extinct as a consequence of economic growth untempered by adequate concern and conservation" (ESA, as amended (16 U.S.C. 1531 et seq.), Sec. 2(a)). In passing the ESA, Congress acknowledged that these species are of "esthetic, ecological, educational, historical, recreational, and scientific value to the Nation and its people" (Sec. 2(a)). As stated in the Act, its purposes are

> to provide a means whereby the **ecosystems upon which endangered species and threatened species depend** may be conserved, to provide a program for the conservation of such endangered species and threatened species, and to take such steps as may be appropriate to achieve [these] purposes.... (Sec. 2(b), emphasis added).

The ESA thus mandates the restoration of threatened and endangered species in their natural habitats to a level at which they can sustain themselves without further legal protection. For Pacific salmon (Footnote 1) (*Oncorhynchus* spp.), the ESA's focus is therefore on natural populations--the progeny of naturally spawning fish--and the ecosystems upon which they depend.

Despite this emphasis on maintaining species in their natural habitat, the Act recognizes that conservation of listed species may be facilitated by artificial means. The ESA defines conservation to include

> ...the use of all methods and procedures which are necessary to bring any endangered species or threatened species to the point at which the measures provided pursuant to this Act are no longer necessary. Such methods and procedures include, but are not limited to, all activities associated with scientific resources management such as research,

> census, law enforcement, habitat acquisition and maintenance, **propagation, live trapping, and transplantation....** (Sec. 3(3), emphasis added).

Artificial propagation has been an important element in recovery plans for several species, including plants such as Knowlton's cactus (*Pediocactus knowltonii*) and Kearney's bluestar (*Amsonia kearneyana*), birds such as the peregrine falcon (*Falco peregrinus*) and the California condor (*Gymnogyps californianus*), mammals such as the black-footed ferret (*Mustela nigripes*), and several fishes, including pupfishes (*Cyprinodon* spp.), chubs (*Gila* spp.), and trouts (*Oncorhynchus* spp.). The California condor and the black-footed ferret currently exist largely as captive populations, although some individuals remained in the wild at the time of listing. In the case of the peregrine falcon, interagency cooperation and extensive experience in captively rearing and releasing raptors to the wild contributed to the successful recovery of this species (Cade 1988).

It should not automatically be presumed, however, that artificial propagation will help to conserve a listed species. For example, in *Cayman Turtle Farm v. Andrus* (478 F. Supp. 125 (D.D.C. 1979)), the court rejected the plaintiff's claim that a ban on mariculture is contrary to the ESA mandate to encourage the propagation of protected wildlife under 16 U.S.C. 1532(2) and 1539(a). The court concluded that evidence in the record supported a finding that the expected long-term impact of mariculture "would be detrimental to the prospects for the survival of wild sea turtles" (*Cayman Turtle Farm* 478 F. Supp. 132).

With respect to Pacific salmon, there is considerable experience in the use of artificial propagation for fisheries enhancement. Because Pacific salmon have a moderately high fecundity (typically several thousand eggs per female) and a high natural mortality through the early life-history stages, successful fish hatcheries can generally produce many more juveniles than are produced in the wild. Increased juvenile production may (but does not always) result in increased returns of adult fish. However, the efficacy of artificial propagation as a tool for conserving natural salmon populations has not been clearly demonstrated. Indeed, the success of artificial propagation for supplementation (i.e., the use of hatchery fish to increase the abundance of naturally spawning fish) is highly controversial (Miller et al. 1990, Steward and Bjornn 1990, Cuenco 1991).

The impact of artificial propagation on the total production of Pacific salmon has been extensive. Past management practices have resulted in widespread propagation and transplantation of nonlocal stocks of these fish (Mathews 1980, Washington 1985, Lichatowich and McIntyre 1987), and the impacts of these practices are largely unknown. Although artificial propagation may contribute to the conservation of populations now listed as threatened or endangered, it is unclear whether or how much artificial propagation during the recovery process will compromise the distinctiveness of natural populations. Also unclear is whether or how much ongoing hatchery programs for unlisted species will affect the recovery of listed species or the viability of other unlisted species.

This document considers the possible roles of artificial propagation with respect to the status and recovery of Pacific salmon under the ESA. The next section (Part II) outlines evaluations of the status of artificially propagated species during the listing and delisting processes. The two subsequent sections deal with the scope of artificial propagation during the recovery of threatened and endangered species; Part III discusses factors to consider in contemplating the use of artificial propagation in recovery programs, and Part IV provides guidelines for the implementation of artificial propagation if it is used. Finally, Part V summarizes considerations for the artificial propagation of unlisted species and its potential effects on both listed and unlisted species.

II. STATUS OF ARTIFICIALLY PROPAGATED SALMON IN ENDANGERED SPECIES ACT LISTINGS

To be considered for listing under the ESA, a group of organisms must constitute a "species," which for Pacific salmon and other vertebrates is defined by the Act to include "any distinct population segment...which interbreeds when mature" (ESA, Sec. 3(15)). The National Marine Fisheries Service (NMFS) has determined that, to qualify as a distinct population segment, a Pacific salmon population must be substantially reproductively isolated and represent an important component in the evolutionary legacy of the biological species. A Pacific salmon population meeting these criteria is considered to be an evolutionarily significant unit (ESU: 56 FR 58612, November 20, 1991; Waples 1991a). The ESU concept recognizes that long-term species viability depends on the maintenance of genetic variability within the biological species (Meffe 1986, Nelson and Soul, 1987). The use of artificial propagation to restore salmon abundance should not be allowed to cause the loss of this diversity.

Because of the focus in the Act on conserving both species and their native ecosystems, an ESU for Pacific salmon is defined on the basis of a natural population (Waples 1991a). A history of hatchery influence does not necessarily preclude protection of a natural salmon population under the ESA, however. Whether a population with hatchery influence qualifies for ESA protection should be determined solely by the two criteria that define an ESU--its reproductive isolation and its contribution to the biological species' evolutionary legacy. See

Waples (1991a) for further discussion of this topic.

Once an ESU has been defined on the basis of a natural population, the status of any hatchery fish (Footnote 2) associated with that ESU must be addressed. This issue will arise frequently because artificial propagation has been such a pervasive factor with Pacific salmon for many years.

A key feature of the ESU concept is recognition of the importance of conserving genetic resources that represent the evolutionary legacy of the biological species. These genetic resources may reside in hatchery fish as well as in naturally reproducing fish. Therefore, hatchery fish may be considered to be part of an ESU defined on the basis of a natural population. If included in the ESU of a listed species, hatchery fish would be protected under the Act and could be used in a recovery program. Alternatively, hatchery fish can be excluded from the ESU, in which case they should be kept as separate as possible from the fish in the ESU to minimize effects on the listed species.

In defining the extent of an ESU with respect to hatchery fish, two types of risk should be evaluated. A too-restrictive definition for an ESU risks excluding important genetic resources and may limit recovery options. Conversely, an overly inclusive definition of an ESU may result in a heterogeneous entity and loss of population distinctiveness. Either type of error may adversely affect the viability or population structure of the listed species. Defining the extent of an ESU in this context is a complex task even under the best of circumstances; in practice, incomplete or ambiguous information often makes the process even more difficult. Nevertheless, the following guidelines provide a general framework for making this determination.

The chief issue in deciding whether or not to include hatchery fish in an ESU is whether, on the basis of all available information, there are appreciable differences between the hatchery and natural fish in characteristics believed to have a genetic basis. In evaluating whether differences are "appreciable," a relevant question to ask is, If the fish in the hatchery were restored to the wild, with the likely result being direct and indirect interactions between the two groups, would this be a benefit or a detriment to the listed species? Appreciable differences between these groups may produce detrimental interactions. The extent and consequences of genetic change in hatchery salmon are imperfectly understood, but important factors to consider in this regard are the length of time the hatchery population has been domesticated; the incidence of straying by hatchery fish into the wild and the degree to which natural broodstock has been regularly used in the hatchery; the stock history of the hatchery population, including evidence for importation of fish or eggs from other stocks; attention to genetic considerations in selecting and mating broodstock; and evidence for divergence of the hatchery population from the wild phenotype in characteristics that are thought to have a genetic basis (e.g., size and age at return, spawning date, etc.). For example, characteristics of fish with hatchery experience may differ from those of their natural counterparts (e.g., Reisenbichler and McIntyre 1977, Swain et al. 1991, Fleming and Gross 1992). If the differences are substantial, hatchery fish should be excluded from the ESU. In considering this issue, the burden of proof should lie in showing that inclusion of hatchery fish is consistent with recovery objectives.

Hatchery fish associated with an ESU that are found to be similar to natural fish in the ESU in characteristics believed to be genetically based can be included in it, in which case they would be protected by provisions of the Act. Progeny of these hatchery fish would also be included in the ESU and protected. The purpose of artificially propagating these fish should be to facilitate recovery of the listed species; therefore, the goal of such a program must be to restore the natural spawning population to the point at which it no longer requires protection under the Act (see Part III).

If an existing hatchery population is not included in the ESU of a listed species because of one or more of the above considerations, isolation of hatchery and natural fish should be as complete as possible. In this case, isolation would include a prohibition against taking natural broodstock from the ESU into the hatchery for use with the current population. Because the adverse consequences of genetic interactions are likely to increase with the degree of genetic divergence between these groups (Hindar et al. 1991, Waples 1991b), such a hatchery should be operated to minimize the possibility of straying into the natural population. Other aspects of hatchery programs that may directly affect a listed species include competition, predation, and disease transfer. Possible indirect effects of hatchery operations include increased harvest rates and increased populations of predators induced by an abundance of hatchery fish (Allendorf et al. 1987, Li et al. 1987, Steward and Bjornn 1990).

In some cases, incomplete or conflicting data will result in a substantial degree of uncertainty about the relationship between a natural population and associated hatchery fish. In that event, hatchery fish should generally be excluded from the ESU unless there is a compelling reason for their inclusion. An example of a compelling reason might be a high imminent risk of extinction or irreversible harm faced by the natural population. This approach maintains the focus of conservation on the viability of the natural population, while permitting the use of existing hatchery fish in a recovery plan if the hatchery fish otherwise qualify as part of the ESU and if circumstances clearly warrant it. Regardless of the relationship of hatchery fish to the ESU, evaluations of the status of the ESU in listing and delisting determinations will depend on the viability of the population in the natural habitat (Waples 1991a) and on the status of ongoing conservation measures.

If possible, the relationship of hatchery fish to the ESU should be determined at the time of listing. Information necessary for making that determination may not be available at listing, however. If information that becomes available after listing (e.g., more comprehensive genetic data) indicates that previously excluded hatchery fish should be incorporated into the ESU, these fish can be included as a component of the listed species and be part of its recovery plan.

III. CONSIDERATION OF ARTIFICIAL PROPAGATION IN ENDANGERED SPECIES ACT RECOVERY PLANS

Artificial propagation of Pacific salmon may be consistent with the purposes of the Endangered Species Act in two situations: 1) when artificial propagation facilitates the recovery of a listed species, or 2) when the enhancement of unlisted populations does not impede the recovery of a listed species or compromise the viability or distinctiveness (and hence be a factor in the listing) of an unlisted species. In either case, the proper management of hatchery operations is essential to minimize adverse effects on listed species. The discussion in this section addresses the question **whether** to use artificial propagation as a recovery tool for listed species. Guidelines for **how** to use artificial propagation in a recovery program (assuming that a decision has been made to do so) are discussed in Part IV. Guidelines for the artificial propagation of unlisted species in relation to the ESA are outlined in Part V.

In deciding whether to use artificial propagation in a recovery program, a key factor to consider is the likelihood that artificial propagation will actually benefit the listed species (Waples 1991b). This evaluation must be made on a case-by-case basis. Although artificial propagation of Pacific salmon has been carried out on a large scale for several decades, almost all these efforts have been directed at fisheries enhancement. Attempts to increase natural production through the use of artificial propagation is a relatively recent enterprise that has, to date, produced mixed results (Miller 1990). Therefore, the use of artificial propagation in ESA recovery plans should be viewed as an experimental technique.

Deliberations over the use of artificial propagation for recovery must also recognize the potential for deleterious direct and indirect effects of this practice on the listed species. Because there is at present considerable uncertainty about the effectiveness of supplementation (see Miller 1990), and because supplementation may have profound consequences for the viability of natural salmon populations, consideration of its use should be based on an objective assessment of potential risks. Genetic risks to listed species from artificial propagation include extinction, loss of genetic variability within and among populations, and domestication (Busack 1990, Riggs 1990). Ecological risks to listed species include disease transfer; increased competition for food, habitat, or mates; increased predation; altered migration; and displacement of natural fish (Steward and Bjornn 1990, see also Regional Assessment of Supplementation Project 1992). Possible consequences of these factors are maladaptive genetic, physiological, or behavioral changes in donor or target populations, with an attendant reduction in natural productivity (e.g., Nickelson et al. 1986, Hindar et al. 1991, Fleming and Gross 1992). Genetic and ecological risks to a listed species are likely to be reduced if a recovery program involving artificial propagation is scaled appropriately for the natural system and if precautions are taken to minimize genetic differentiation between artificially and naturally propagated fish.

The risks to listed species posed by the use of artificial propagation may depend upon the species involved and upon the geographical location of the culture facility. For example, species with extended freshwater residence are likely to face higher risk from domestication, predation, or altered migration than are species that spend only a brief time in fresh water (e.g., pink salmon, *O. gorbuscha*, or chum salmon, *O. keta*). Similarly, hatcheries that require a lengthy freshwater migration for their released and returning fish may face many migration and mortality problems avoided by facilities closer to the ocean. Life history, adult returns, straying rates and patterns, potential disease transfer, and harvest impacts are among the factors that should be considered in evaluating the risks of using artificial propagation for recovery of listed species.

The genetic and ecological risks associated with the use of artificial propagation, together with the inevitable disruption in life-history patterns, must be weighed against risks to the species if artificial propagation is not used in a recovery program. As noted previously (Part I), a successful hatchery program for Pacific salmon can produce many more returning adult fish than are produced naturally. Therefore, the principal risk in not using artificial propagation in a recovery program is in forgoing the possibility of rebuilding the population in the shortest time.

Given the emphasis in the Act on conserving species in their native ecosystems, and given the above-mentioned risks associated with artificial propagation, a guiding principle for an ESA recovery plan should be to restore a viable natural population with the minimum amount of interference in its life history. For Pacific salmon, this means that options such as protecting and restoring natural spawning and rearing habitat, facilitating migrations of juveniles and returning adults, and managing harvest should be given highest priority in recovery plans. Clearly, then, it is essential that all factors responsible for the species' decline be identified as completely and as early as possible. (Kaczynski and Palmisano (1992) catalog several of these potential factors, which include natural phenomena, ecological interactions, management of harvest and escapement, and water and land use, as well as artificial propagation.) Artificial propagation should receive foremost consideration only when it is believed that recovery within an acceptable time is not likely to result from addressing these other factors alone.

The most compelling reason for use of artificial propagation in ESA recovery plans is when extinction of the natural population is likely before natural recovery can occur. If the size of a natural population is very low, then regardless of the amount of genetic variability present, the population may become extinct for demographic reasons (Leigh 1981, Goodman 1987, Lande 1988). In this case, the risks posed by artificial propagation may be outweighed by its potential to rapidly increase abundance and avoid extinction.

In some cases, artificial propagation may also be appropriate for use with populations at less immediate risk of extinction, if factors impeding recovery cannot be remedied in a reasonable time. For example, habitat restoration may be difficult to accomplish, and its effects on abundance may not be seen for many years. In such cases, artificial propagation, in conjunction with efforts to remedy factors responsible for the decline, may be appropriate as a component of a recovery program. In making this determination, however, it must be remembered that supplementation is a largely unproven technique that may not actually contribute to recovery. In general, the lower the risk of imminent extinction or irreparable harm to the species in the absence of artificial propagation, the less attractive this form of intervention is as a potential recovery option.

There are also two special cases in which artificial propagation may warrant high priority among recovery options. First, the outplanting of artificially propagated fish may be necessary to aid recolonization of unutilized but suitable habitat if natural straying is not likely to reseed the habitat within an acceptable time. (This is an example of "transplantation" recognized in the definition of conservation given in the Section 3(3) of the ESA.) Second, artificial propagation may be necessary in recovery when habitat crucial to the viability of a natural population is lost. In this case, artificial propagation provides a temporary means of conserving a natural population until new or reclaimed habitat becomes available.

In any case, if artificial propagation is used as part of a recovery plan, it should not be seen as a substitute for resolving the basic problems that brought the species to the point at which it required protection under the Act. Furthermore, artificial propagation under the ESA should be viewed as a temporary measure, to be discontinued and all recovery options reevaluated if 1) artificial propagation is no longer believed to be necessary for timely recovery, 2) naturally reproducing fish have risen in abundance above levels for delisting, 3) appreciable differences between artificially and naturally propagated fish have emerged during a recovery program, or 4) there is evidence that artificial propagation is impeding recovery.

IV. USE OF ARTIFICIAL PROPAGATION IN ENDANGERED SPECIES ACT RECOVERY PLANS

Once a decision has been made to incorporate artificial propagation into a recovery plan, its implementation involves several important considerations. The intent of such a plan should be to facilitate recovery of the natural population, minimize its risk of further decline, and restrict genetic changes resulting from artificial propagation. To reduce the potential for these risks to arise, the use of artificially propagated fish to supplement a listed natural population should be held to the minimum necessary for sustained recovery. As part of a recovery plan, artificial propagation might require the collection of natural broodstock, the culture of progeny from those adults, and the release of the progeny at appropriate localities to supplement the natural population. Without adequate precautions, these activities may have negative effects on listed species, including deleterious ecological and genetic interactions between hatchery fish and natural fish. This section suggests ways to minimize these effects when relying on artificial propagation as a recovery tool.

A. Choice of Donor Stock

In order to qualify as a "species" under the ESA, a Pacific salmon population must be an evolutionarily significant unit of the biological species. To preserve distinctive characteristics of the ESU, therefore, broodstock for a recovery program must originate from within the ESU. In some cases, significant population structure may occur within an ESU. This structure is reflected by the genetic diversity within and among the spawning aggregations (or populations) that make up the ESU (Footnote 3). For example, Matthews and Waples (1991) recognized the geographical and ecological complexity of the large area occupied by Snake River spring/summer chinook salmon and emphasized that viability of the more comprehensive ESU is dependent on the continued existence of self-sustaining populations throughout the area. To maintain interpopulation diversity in such an ESU, crossbreeding broodstock from separate populations within the ESU should generally be avoided.

The geographic limits to the area that can provide broodstock for supplementing a given population within an ESU must be determined on a case-by- case basis using all available information. In general, broodstock from populations showing clear differences in genetic, phenotypic, or life-history traits, or in habitat characteristics, should not be mixed. A major consideration in such evaluations should be an assessment of the relative degree of risk to the population from inbreeding depression and outbreeding depression (see Definitions). The consequences of inbreeding depression for genetic variability within populations are better understood than the consequences of outbreeding depression for genetic variability among populations (Lynch 1991, Hedrick and Miller 1992). Severe inbreeding (the mating of close relatives) leads to reduced genetic variability and may cause genetic or phenotypic changes that lead to reduced fitness within a population; this, in turn, may limit the ability of an inbred population to adapt to changing environmental conditions. Outbreeding (the mating of distantly related or unrelated individuals) may enhance genetic variability and alleviate reductions in fitness in inbred populations if the populations to be crossed are not too different genetically, but outbreeding between genetically differentiated populations may result in crosses that have reduced fitness due to genetic interactions or loss of important local adaptations.

The nonlinear effect of inbreeding and outbreeding on fitness has suggested to some that there may be an optimal amount of outbreeding for a population (see Lynch 1991). In Pacific salmon, natural straying among populations may provide a general mechanism for the avoidance of inbreeding depression. Although inbreeding depression has been reported in a number of cultured fish populations, similar effects are not well documented for hatchery populations of Pacific salmon, nor is there evidence to show that inbreeding depression is a pervasive problem for natural populations (Allendorf and Ryman 1987, Gall 1987). There also does not appear to be any empirical evidence that outbreeding increases the fitness of natural Pacific salmon populations, whereas there is some theoretical (Emlen 1991) and empirical (Bams 1976; Reisenbichler, unpublished data cited in Emlen 1991; Gharrett and Smoker 1991) evidence for the deleterious effects of outbreeding depression. Therefore, while significant gaps exist in our understanding of the effects of inbreeding depression and outbreeding depression in Pacific salmon, there is ample reason for caution in creating artificial mixtures of populations within an ESU. Nevertheless, outbreeding merits consideration if there is evidence for deleterious effects of inbreeding depression in some local populations or if the size of some local populations is so small that inbreeding is thought to pose a serious risk.

Under extreme circumstances, use of broodstock from outside the ESU may merit consideration. This option might be considered if the species is reduced to individuals of a single sex or if substantial inbreeding depression gives little hope for recovery of the remaining population without additional genetic material.

B. Broodstock Collection and Mating

In choosing fish to make up broodstock for use in supplementing a listed species, a trade-off exists between maximizing the representativeness of the broodstock sample and minimizing the risks to the natural population that result from taking fish for breeding purposes. A large sample of broodstock is more likely to be representative but also reduces the number of actual spawners by a greater amount. This tension between representation and risk suggests that the propagation of hatchery fish for restoration should be appropriately scaled for the system. The potential exists in a supplementation program to overwhelm ecologically or genetically the natural population with fish reared in the hatchery. The scale of supplementation should therefore be guided by the estimated carrying capacity of the ecological system associated with the ESU (taking into account resident fish in the natural habitat that may compete for available resources), the method of supplementation, the number of natural fish, and the number of fish that can be sampled for broodstock without undue risk to the natural population. Furthermore, determination of the appropriate scale should consider the possible genetic consequences of enhancing only a portion of the natural gene pool (Ryman and Laikre 1991).

Limiting the genetic differentiation of hatchery and natural fish is essential to reducing risk to the natural population. Genetic differentiation of hatchery and natural fish has two primary causal agents, one stochastic (genetic drift) and one deterministic (selection). A major opportunity for stochastic effects on genetic variability occurs when broodstock are initially sampled from a population. In deciding what fraction of the population should be sampled, it should be kept in mind that the only way to completely avoid genetic differentiation arising from broodstock collection is to sample the entire breeding population. As this strategy carries a high risk of catastrophic failure and, in any case, will not often be feasible, a systematic subsampling scheme that minimizes risks to the natural population will generally be required. Nevertheless, a comprehensive sampling program merits consideration if the population size is very small or if the sex ratio is highly skewed, if prespawning adults can be sampled without seriously compromising natural reproduction, or if gametes can be sampled safely and adequately after natural spawning.

If a subsampling strategy is used, a primary goal should be to obtain a representative sample of adults for artificial propagation while allowing a representative sample to spawn in the wild. Representativeness of the sample used for artificial propagation is particularly important if progeny of the cultured fish are expected to make up a substantial fraction of the total population. To reduce the potential for directional genetic change and loss of local adaptation, sampled adults should represent the entire return with regard to size, age, and other measurable phenotypic characters that may have adaptive value. For example, adults should be sampled from throughout the run, as spawning date may respond rapidly to selection in salmonids (e.g., Siitonen and Gall 1989). If the number of available natural spawners is large enough to permit a large sample to be taken, random sampling (sampling **without regard to** measurable characters) is likely to ensure that the natural population is represented adequately in the broodstock. If the number of available natural spawners is too small to permit a large sample, however, systematic sampling **on the basis of** measurable characters (particularly run timing and size and age at maturity) may be required to achieve adequate representation. Whatever the sample or population size, ensuring that gametes transferred to the hatchery reflect those in the natural population will help to avoid negative genetic effects due to sampling.

Another major consideration in designing a broodstock sampling program is its consequences for effective population size, N_e (see Definitions). Effective size is important because it determines the rate of genetic change experienced by a population. Populations with small effective size can experience high levels of inbreeding depression and high rates of loss of genetic variability. Artificially propagating a portion of the population via supplementation may reduce N_e by dramatically increasing the contribution of a fraction of the available genotypes to the supplemented population (Ryman and Laikre 1991). Therefore, in determining the number of breeders to be sampled in any year for artificial propagation, the effects on total N_e as well as the representativeness of the sample should be taken into account. Although Ryman and Laikre's study points out the importance of considering N_e for the hatchery/natural population as a whole, it evaluated only one supplementation scenario involving a single generation of enhancement and did not specifically treat age-structured populations (such as Pacific salmon). In a supplementation program designed to increase the abundance of naturally spawning fish, N_e of the hatchery/wild system as a whole depends on a number of factors, including: 1) the absolute number of spawners (and proportion of the population) used for artificial propagation, 2) the life-history stage sampled from the wild (e.g., gametes from pre- or post-spawning adults, eyed eggs, fry, or smolts), 3) the duration of the enhancement program, 4) whether naturally and artificially produced fish can be identified when they return as adults, and 5) harvest, competition, carrying capacity, or other factors that may affect abundance of the enhanced population. This is an active area of research, and more comprehensive guidance may be available in the future about strategies for appropriate scaling of a supplementation program.

Nevertheless, one strategy for sampling broodstock can be identified that has a dual benefit in a recovery program for a listed species: in general, returning adults that were produced artificially should not be used for broodstock. This strategy will avoid unnecessary reductions in N_e (by avoiding repeated enhancement of the same segment of the population) while also limiting to a single generation the exposure of any natural fish to artificial conditions (thus minimizing possibilities for selective genetic change). In very small populations, however, this strategy may not be possible or even desirable. In such cases, judicious use of returning hatchery fish for broodstock may be considered. Exclusive use of natural fish for broodstock may also create an unacceptably high risk for the natural population. This is particularly true for an unsuccessful or marginally successful hatchery program, in which case artificial propagation may contribute directly to the decline of the listed species by taking adults for broodstock. This possibility argues strongly for a cautious approach, with attention to appropriate scaling, for a supplementation program for a listed species.

Various authors (e.g., Franklin 1980, Lande and Barrowclough 1987) have suggested that the effective size of a population should be on the order of several hundred per generation to avoid long-term problems associated with loss of genetic variability. For Pacific salmon, this is equivalent to a minimum effective number of breeders per year (N<,sub>b) of approximately 50-100 (Waples 1990 - Footnote 4) . It is also generally believed that, in the short term, a population can experience a substantially smaller bottleneck (N_e of perhaps 50 per generation or so) with little risk of inbreeding depression. These are useful guidelines in formulating a recovery plan for a listed species. However, in some cases (e.g., when total abundance is very low) it may not be possible to achieve the desired effective size regardless of whether artificial propagation is used. In such cases, the general strategy for sampling and mating broodstock should be to maximize effective size for the hatchery/wild system as a whole (as described above), while maintaining representativeness of the adults used for broodstock.

Maintaining genetic characteristics of a population during artificial propagation may also depend on how broodstock are mated. In theory, there may be some advantages for a cultured population to mimicking mating strategies that occur in the wild. However, mimicking natural spawning behavior might lead to large inequalities in reproductive success among individuals (particularly males) and a consequent reduction in N_e. Furthermore, the understanding of patterns of reproductive success in natural populations is so incomplete that it would be difficult to mimic natural conditions even if one wanted to.

Therefore, the mating design should be chosen to equalize as much as possible the contributions of parents to the next breeding generation. This procedure will maximize N_e for a given number of breeders and minimize the effects of selection (Falconer 1981, Simon et al. 1986, Lande and Barrowclough 1987). If possible, parents should be mated at random with regard to phenotypic characters that may have adaptive value (e.g., age and size at maturity). Mating designs may include matings of single pairs, matings of single females to overlapping pairs of males, or factorial designs involving crosses between all possible parents. These different designs are outlined by Becker (1984) and Gharrett and Shirley (1985). A modified single-pair design is generally preferable to simple matings of single pairs because it reduces the risk of loss due to infertile males. A factorial design, assuming that the realized variance in progeny number is small, increases the probability of unique genetic combinations in the progeny. However, a complete factorial design will generally be feasible only with very small populations; the benefits derived from a factorial design rapidly decrease (and the logistical difficulties rapidly increase) with increasing numbers of adult spawners.

Gametes from different individuals should not be mixed prior to fertilization; mixing would decrease the contribution of some individuals if variation in potency of milt exists (Withler 1988). In very small populations, a fraction of the milt from each male should be cryopreserved to maintain a "sire bank." These gametes can provide additional male "breeders" in years when the number of available males is low. Moreover, such crosses between brood years can help to preserve long-term genetic variability if severe population bottlenecks have been frequent or persistent.

C. Husbandry Techniques

There are two fundamental considerations in developing strategies for artificially rearing fish in an ESA recovery plan: 1) how to produce the most fish in the shortest possible time (and therefore speed the recovery process), and 2) how to produce fish as similar as possible genetically and ecologically to natural fish in the ESU. Although these considerations are not necessarily contradictory, it is clear that there may be situations in which it will be difficult to accomplish them both simultaneously. In such cases, the appropriate emphasis in husbandry techniques should be dictated by the nature and degree of risk faced by the natural population. For example, if the population is small enough that the short-term risk of extinction is high, then it may be appropriate to place primary emphasis on producing enough fish to rapidly expand the population size beyond the high-risk level. If the necessity for expanding population size is less urgent, attention should focus on husbandry techniques that are likely to produce fish with characteristics as similar as possible to those of the natural fish. Some additional guidelines to consider during culture of listed Pacific salmon species are discussed below.

There are some clear advantages to minimizing mortality in cultured fish to be used in supplementation. If relatively high survival carries through to the adult stage, substantial progress toward recovery is possible. Furthermore, by coupling minimal genetic drift with low hatchery mortality due to disease and other agents, a recovery program involving artificial propagation can, in principle, minimize genetic change in a hatchery salmon population. However, with anadromous fish such as Pacific salmon, mortality that operates after release (which typically represents the bulk of total mortality) may also depend on culture conditions. These conditions may affect subsequent mortality (Leider et al. 1990) by limiting ability to forage, evade predators, and resist pathogens. Therefore, even if genetic change is minimized in the hatchery, it may be difficult to avoid after release. For example, selection for rapid growth or other factors during culture may result in fish that tend to return at smaller sizes and younger ages, even in the absence of selective forces in nature such as size- selective predation and harvest. However, the latent effects of selection in captivity on subsequent survival, phenotype, and reproductive success of salmonids are poorly understood. All that is known about latent effects of selection in captivity is that culturing fish in the hatchery environment, where they are protected from many sources of natural mortality, will not eliminate natural selection that occurs after the fish are released. Rather, it will postpone selection to a later life-history stage. Only if this delayed selection removes the same genotypes that would naturally be removed earlier will the cultured fish be genetically equivalent to their natural counterparts (Waples 1991b). Since the selective regime in nature cannot be duplicated, the best that can realistically be attained is the minimization of differences between the hatchery and natural environments. Efforts to simulate prominent features of the natural environment in the hatchery should help to reduce the ability of domestication selection (Doyle 1983) to produce genetic change.

Nonetheless, selection in the hatchery is to some degree unavoidable. Unknown genetic correlations between traits can easily confound the detection and measurement of selection (Falconer 1981). The most effective ways to limit domestication selection in the hatchery are unknown, but they are thought to include restricting the use of artificial propagation to a very few generations, maintaining quasi-natural culture regimes, and minimizing mortality in the hatchery.

A few general practices may help to enhance the survival and adaptive potential of hatchery-reared salmon subsequently released to the wild. It should be understood, however, that some of these practices are untested and warrant further investigation. For the successful culture of Pacific salmon, what does **not** work is often better known than what **does** work.

First, conservation facilities should develop procedures that provide adequate safeguards for fish health. Adults contributing gametes should be regularly sampled for pathogens (H†stein and Lindstad (1991) describe some of the more common salmonid diseases). Incubation facilities should be sterilized before gametes are transported there. Gametes brought into the facility should be isolated from all others and the resulting fertilized eggs disinfected. To avoid horizontal disease transfer, progeny should if possible be isolated by full-sib family until cleared through pathological testing and then monitored regularly during culture. Infected fish should be isolated and treated. However, it should be recognized that some incipient level of disease is natural and also probably essential for immunological readiness for episodic outbreaks. If necessary, the hatchery water supply and effluent should be treated to minimize the transfer of pathogens to and from the natural population.

Second, environmental conditions in the hatchery such as photoperiod, water quality (temperature, pH, dissolved oxygen, dissolved solids and metabolites, etc.), water flow, and substrate composition that attempt to simulate natural conditions are likely to reduce typical differences between hatchery and natural fish. Additional strategies that should be considered include use of low incubation and rearing densities, provision of cover and structural heterogeneity for holding facilities, and use of more variable feeding schedules and rates to better simulate those experienced in nature. Emphasis should be placed on maintaining natural variation in cultivated fish rather than on producing uniform fish of large size, a more typical practice in production hatcheries. Feeding from the raceway bottom and exposing fish periodically to model predators may help to avoid conditioning fish to the presence of large animals above the water's surface, perhaps enhancing their ability to detect and evade predators after release.

As a safeguard against catastrophic events, fish or gametes from a listed species should be distributed between two or more facilities to "spread the risk," especially if the entire population is brought into captivity. Progeny from the different facilities could then be combined upon release into the natural habitat.

The details of various aspects of husbandry practices for conservation are not found in standard salmon culture handbooks. Meffe (1986), Allendorf and Ryman (1987), and Nelson and Soul, (1987) provide some guidelines for the maintenance of genetic variability in artificially propagated fishes. Steward and Bjornn (1990) summarize genetic and ecological factors to consider when supplementing natural salmon populations with hatchery fish. However, a comprehensive review of practices appropriate for a salmon facility designed specifically for stock conservation is not available. Critical uncertainties exist in several areas, including the effects of domestication on genetic variability within and between population; the latent effects of selection on realized progeny number and genetic change; the consequences of artificial propagation for performance traits such as survival, growth, reproduction, and migration; and the consequences of quasi-natural variability in culture conditions for these performance traits. Research in these areas is needed before more specific guidelines for recovery can be recommended.

D. Release Strategies

The release of juvenile salmon into the natural environment is a critical stage in the artificial propagation of salmon for recovery. The survival of released juveniles depends heavily on their physiological status and ecological competency. In turn, this readiness depends not only on their size at release and the timing of their release, but also on the capability of hatchery fish to rapidly acclimate to conditions in the wild. There is probably no single most effective release strategy for purposes of salmon recovery; almost certainly, this will vary among the biological species of Pacific salmon and among populations within species. However, traditional releases of cultured salmon for enhancement seldom resemble what is known about natural outmigrations of juvenile salmon. The preservation of natural variability in artificially propagated fish is likely to be better maintained by reproducing as much as possible the spatial and temporal patterns of movement and colonization found in the natural habitat. This approach should thus help to preserve population fitness and long-term productivity. Its possible costs include reduced survival of released fish and, consequently, lowered efficiency of supplementation.

A release strategy that attempts to mimic natural outmigration should have several features. Upon release, the size and developmental profiles of artificially propagated juveniles (including size and developmental variation among individuals) should be similar to wild juveniles of equivalent age. It is important that no attempt be made to reduce natural variation in size at release. While hatchery fish released at larger sizes may survive to return at higher rates than smaller hatchery fish (e.g., Martin and Wertheimer 1989), juvenile natural fish are typically smaller than hatchery fish of the same age and developmental stage. Releasing many larger fish may harm the smaller natural fish, perhaps even displacing them from the habitat (Nickelson et al. 1986). Increasing the size at release may also affect other life-history traits in the hatchery fish themselves, such as age and size at maturity (Bilton et al. 1982), particularly if the supplementation program exceeds a single generation.

Timing of release may be significant in determining how well hatchery fish survive at sea to return (Bilton et al. 1982, Hard et al. 1985). Release timing may also be important in reducing negative interactions between hatchery fish and natural fish (Nickelson et al. 1986). A large body of research on anadromous salmonids focuses on seasonal development and the factors affecting the physiological transition from fresh water to seawater. It is now well documented that seasonal cues such as photoperiod trigger endocrine processes that facilitate the transition to seawater (Folmar and Dickhoff 1980, Hoar 1988). However, this transition is also affected by other environmental factors such as water temperature (Holtby et al. 1989), and while considerable research has focused on the physiological state of fish slated for release, many of the factors that maintain temporal variation in saltwater adaptability remain elusive. To develop natural release strategies reliable enough for recovery purposes, these and other factors that explain observed variation in natural outmigrants must be more clearly defined.

In developing release strategies for artificially propagated juveniles, managers of hatcheries intended for salmon conservation should keep in mind that much of the mortality resulting from selection in the wild has already been avoided. Although it is tempting to try to reduce additional mortality, the immediate objective is to minimize genetic change in the cultured fish while facilitating recovery. In the absence of definitive information on how natural selection acts on natural outmigration, an attempt should be made to release fish in a manner that recognizes the importance of natural variation. One option to be considered is the release of juveniles before smoltification is complete in fresh water in a spatial and temporal pattern that simulates the natural distribution of juvenile outmigration and downstream movement. The spatial pattern of such a release should depend on the estimated densities of natural fish in the watershed and should be used to colonize underutilized (but suitable) rearing habitat. However, it should be recognized that quasi-natural spatial and temporal patterns of outmigration may result in ecological interactions that have deleterious consequences for the viability of natural fish. For example, releasing large numbers of presmolts might increase competitive interactions among juveniles or elevate predation rates on natural fish. Little information is available to provide firm guidelines on natural release strategies, and considerable research is needed to resolve uncertainties in the factors limiting juvenile survival in natural habitats.

Despite the possibility of reduced survival and negative ecological interactions, release strategies that take natural variability in size, timing, and related factors into account may have several advantages. In addition to limiting genetic change resulting from selection in the hatchery, natural release strategies that involve more naturally cultured presmolts should permit released fish to acclimate more completely to their natural surroundings. A more extended residence in the natural habitat should provide greater opportunity for outmigrants to learn to cope with natural predators (Olla and Davis 1989) and perhaps reduce their propensity to stray to other sites at maturity (Reisenbichler 1988). It may also help to alleviate reduced reproductive success that has been observed in natural habitats following supplementation (Chilcote et al. 1986, Campton et al. 1991). Furthermore, release practices that incorporate temporal and spatial variation should help to spread the risk of catastrophic loss due to natural selection or chance environmental events.

Except in cases in which currently unutilized habitat is seeded, spatial variation in releases should avoid the release of fish into habitats outside an ESU's range (stock transfers). Stock transfers have several potential undesirable effects (as described in previous sections) and are inconsistent with the maintenance of existing population structure. The guiding principle for a release strategy, like all other aspects of a recovery program, should be the preservation of genetic and ecological diversity.

E. Monitoring and Evaluation

Monitoring the effects of artificial propagation on the restoration of a threatened or endangered species should be a hallmark of a well-designed recovery plan. Supplementation is an experimental technique with a largely unproven record. The primary objectives of a monitoring and evaluation program administered under the ESA should be to estimate the contribution of artificially propagated fish to the natural population during the recovery process, to monitor changes in the genetic and phenotypic characteristics of the listed species, to evaluate and suggest ways of improving supplementation activities, and to determine when artificial propagation is no longer necessary or appropriate to assist in recovery. Careful monitoring can also aid in identifying factors impeding recovery and may assist in the development of effective supplementation strategies for unlisted species as well as measures to prevent other declining populations from relying on the ESA "safety net" for protection and recovery.

To estimate the relative contribution of hatchery and natural fish during recovery, these two groups of fish must be distinguishable. Permanently marking all cultured fish is essential to accurately monitor trends in relative abundance. To identify juveniles in the natural environment as well as adults returning to spawn, all cultured fish should be unambiguously marked each generation with a unique, permanent mark such as the commonly used combination of an adipose fin clip and coded wire tag implant. Visual marks (i.e., brands or fin clips) are likely to prove useful in monitoring fish in natural habitats, but managers must weigh this advantage against possible costs in survival of fish marked in these ways. In some cases, routine screening for genetic markers may allow more sensitive assessment of direct genetic effects such as introgression (Skaala et al. 1990).

If possible, full-sib families should be kept separate until they can be uniquely marked. This is most important for very small broodstocks, for which it is also most feasible. For these broodstocks, the pedigreeing of families with the use of unique marks should be considered to better monitor their genetic contribution to successive generations.

Ideally, detectable genetic differences between hatchery and natural fish should not exist in a successful recovery program. Monitoring genetic variation in hatchery and natural fish to ensure their similarity is important to evaluate the techniques used to sample and culture fish (Waples et al. 1990). Because genetic relationships are at the foundation of ESA decisions involving Pacific salmon (Waples 1991a), monitoring for genetic changes should be an integral part of the evaluative process.

Evaluation of artificial propagation as part of a recovery program should assess long-term as well as short-term effects of artificial propagation on genetic and ecological interactions between hatchery and natural fish. At a minimum, a monitoring and evaluation program should regularly estimate survival to outmigration and to subsequent adult return for both hatchery and natural fish. A comprehensive monitoring and evaluation program would include the regular estimation of genetic composition of artificially and naturally propagated fish; of survival, rearing, and migratory success of juveniles; and of reproductive success of adults returning to spawn naturally, as well as periodic evaluations of fish health, behavioral assays, statistical analyses of morphological/phenotypic characters of hatchery and natural adults, and estimates of introgression. The evaluative process should be responsive enough to provide information that will allow rapid adjustments in the recovery plan, such as changes in the size of broodstock collections or juvenile releases, or modifications to the culture regime to reduce the effects of domestication selection.

The most important functions of a monitoring and evaluation program are determining whether artificial propagation is facilitating recovery and when artificial propagation is no longer necessary for recovery. In general, once artificial propagation is initiated as a component of an ESA recovery plan, it may continue as long as ongoing management efforts that include artificial propagation are not resulting in a stable increase in population size or in appreciable differences between artificially propagated and natural fish. As stated in Part III, artificial propagation should be terminated if there is reason to believe that artificial propagation is actually impeding recovery. Cessation of artificial propagation for recovery should also be considered if the naturally reproducing fish have increased in abundance to levels appropriate for delisting or if artificial propagation is no longer believed to be necessary for timely recovery. In such events, all recovery options and their associated risks should be reevaluated. Successful recovery does not preclude the use of artificial propagation for enhancement purposes so long as enhancement is not likely to cause relisting or new listings.

F. Captive Broodstock Programs

Situations may arise that require greater reliance on artificial propagation to facilitate the recovery of a threatened or endangered salmon population. The most prominent of these situations is when the natural population is dangerously close to extinction. One option to consider in this case is a captive broodstock program, a special case of supplementation. A captive broodstock program typically involves taking gametes or fish from the natural population, rearing them to maturity in the hatchery, breeding them, and releasing their progeny into the natural habitat. A captive broodstock program thus involves rearing fish in captivity for an entire life cycle, rather than releasing them as fry or smolts as is done in a traditional salmon hatchery. The potentially high survival of salmon in protective culture affords a unique opportunity to produce large numbers of juveniles for supplementation in a single generation. If proper precautions are taken to minimize genetic change during the collection, mating, and rearing of captive broodstock, these programs may provide the ability to rapidly restore severely depleted stocks.

However, it should be recognized that although captive broodstock programs hold promise for some species, they are unproven as a conservation measure for Pacific salmon and may involve considerable risk to the population. Therefore, as with other types of artificial propagation for recovery, captive broodstock programs for Pacific salmon should be regarded as experimental. Nonetheless, a captive broodstock program may be the preferred option if the imminent risk of extinction is high. If implemented as part of a recovery plan, a captive broodstock program should be integrated with other measures intended to address population viability, such as habitat protection and restoration (Povilitis 1990).

If sufficient adults are available for a captive broodstock program, it may be desirable to allow some of the captive adults to spawn in the wild. Captive broodstock may be collected as adults, as deposited eggs, or as juveniles from the natural habitat. The choice of life stage to collect affects how much natural selection occurs in the broodstock sample before it is established in the hatchery and may also affect the representativeness of the sample. The later the life stage, the greater the opportunity for natural selection to occur and, consequently, the more closely the resulting broodstock is likely to resemble the natural spawning population. However, potential disadvantages of collecting older life stages for use as broodstock include difficulties in acclimating older juveniles to the hatchery environment and, if adults are used, prespawning (holding) mortality. Any losses that occur that alter the original genetic composition would reduce the efficacy of supplementation in rebuilding the natural population.

The guidelines recommended for artificial propagation regarding collection and mating of broodstock, rearing and releasing strategies, and monitoring may be even more critical to the success of a captive broodstock program. In such a program, natural selection on fish brought into the hatchery can be minimized if mortality during captivity is low. If so, the main genetic consequences to be assessed are the consequences of broodstock sampling, mating, and progeny release strategies, and the effects of enhancing particular genotypes (Ryman and Laikre 1991). Note that this latter effect does not occur if the entire population is enhanced through artificial propagation.

Of paramount importance for a threatened or endangered species is protection of the captive broodstock from catastrophic loss or high mortality. This is especially true if all natural gametes have been removed from the wild to establish a captive broodstock program. Consequently, the broodstock gametes should be divided between at least two independent facilities. Broodstock should be isolated from all other fish and kept under security with safeguards against environmental perturbation (including equipment failure). Because a release strategy is the pivotal last element in a recovery attempt involving a captive broodstock, timing of releases should be based on the behavior of any remaining natural fish, or on knowledge of the life-history characteristics of the natural fish if none are present.

Finally, captive broodstock programs are most appropriate as temporary recovery measures. For the purposes of recovery under the ESA, a captive broodstock program should, if possible, be limited to one complete life cycle, at which time the progeny of these broodstock would be released into the wild. Determination of whether such a program should be extended beyond a single generation will depend on the performance of these fish in captivity and the wild and on the viability of the natural component being supplemented.

V. ARTIFICIAL PROPAGATION OF SPECIES NOT LISTED UNDER THE ENDANGERED SPECIES ACT

For several decades, artificial propagation of Pacific salmon has been used in an attempt to mitigate detrimental impacts, such as destruction of habitat or blockage of migratory routes, to natural populations. Artificial propagation of Pacific salmon is now widespread throughout much of their natural range, and in many cases it has been instrumental in sustaining or increasing harvest. Nonetheless, although the potential of artificial propagation to increase salmon abundance holds promise for facilitating recovery of listed species, this capability also creates the possibility for undesirable impacts on both listed and unlisted species (e.g., Johnson et al. 1991). Such impacts must be minimized to avoid conflicts with recovery of listed species and additional listings of currently unlisted species. Such a result is likely unless adequate precautions are taken to minimize interactions between listed and unlisted species.

Artificial propagation of unlisted species may have indirect effects on listed species (see Parts III and IV for specific examples) by reducing their abundance or altering the selection regime affecting them (Waples 1991b). Interactions between unlisted hatchery fish and listed natural fish may result in greater competition for food, habitat, or mates; an increase in predation or harvest pressure on natural fish; and potential transmission of disease between populations (Steward and Bjornn 1990). In addition, artificial propagation can entail habitat changes with detrimental impacts on natural fish. Examples of potential problems include effects of hatcheries on water quality and effects of weirs or diversion structures on migration of natural fish.

While interactions between unlisted and listed salmon species are more likely for hatcheries in geographic proximity to listed species, more distant hatcheries may also pose problems for listed species. Perhaps the most notable of these problems is harvest of listed species in mixed-stock fisheries attempting to target artificially propagated fish. Additionally, attempts to capture artificially propagated spawners that stray may hinder the ability of listed fish to migrate to and spawn in their natural habitat. Therefore, to reduce the potential for deleterious effects on listed species, artificial propagation procedures for unlisted species in areas that may be important to the viability of listed species should be coordinated to minimize these effects and monitored to ensure that this is the case.

For situations in which genetic interactions between unlisted and listed species are a possibility, genetic changes attributable to artificial propagation should be limited as much as possible to reduce the severity of these interactions. Direct effects include straying and subsequent crossbreeding with listed fish, which may result in loss of genetic variability between populations and depressed fitness in population crosses. Low rates of natural straying may be beneficial in maintaining genetic variability in natural populations, but these rates may become elevated through artificial propagation (Bams 1976, Reisenbichler 1988), with potentially serious consequences for local adaptation in listed species. These effects have already been discussed in some detail with regard to artificially propagating a listed species for recovery in Parts III and IV, but they are likely to be even more serious when they involve a listed species and unlisted hatchery fish from outside the ESU.

Because of the prevalence of hatchery programs throughout the Pacific Northwest, for listed species genetic interactions with unlisted hatchery populations will often be a possibility. In such cases, one means to help limit this genetic contact is to regularly evaluate and if necessary modify culture practices so that their activity does not contribute to the loss of genetic integrity of natural fish. Hatcheries involved should restrict their choices of broodstock to local populations. The origin of broodstock either returning to hatcheries or collected off-site should be verified before spawning. Stock transfers between propagation facilities that increase the possibility for adverse genetic interactions with listed species should be avoided. Conditions or procedures associated with artificial propagation that result in differentiation of phenotypic traits between cultured and natural fish should be identified and generally avoided. Collection of returning hatchery fish should be designed to restrict opportunities for these fish to interfere with the natural breeding of listed fish. Monitoring the effects of interactions on natural fish is essential to ensure that artificial propagation of unlisted species remains compatible with conservation efforts directed at listed species (discussed further in Part IV).

The effects described above resulting from artificial propagation of unlisted species may constitute a "take" of a listed species as defined in the Act (see Definitions). Take of all salmon species currently listed under the ESA is prohibited without specific authorization. However, two specific types of take of listed species that can result from activities associated with artificial propagation may be authorized under the ESA. **Directed** or intentional take of a listed species may be permitted under Section 10(a)(1)(A) of the ESA only if it "would further a bona fide and necessary or desirable scientific purpose or enhance the propagation or survival of the endangered species, taking into account the benefits anticipated to be derived on behalf of the endangered species" (50 CFR 222.23(c)). Directed take of individuals of a listed Pacific salmon species to fulfill broodstock needs for conservation of the listed species, as discussed in Part IV of this document, is an example of an activity that might be permitted under Section 10(a)(1)(A) of the ESA. Collection of a listed species for the purpose of enhancing a population that is not part of the ESU is an example of a directed take that is not permissible under the Act.

Incidental take is take that results from, but is not the purpose of, an otherwise lawful activity. Incidental take is the form of take likely to arise most commonly during the artificial propagation of unlisted species. Direct and indirect effects on listed species discussed earlier in this section are examples of incidental take of listed Pacific salmon. Incidental take can legally occur only after fulfilling the requirements of Sections 7 or 10 of the ESA, depending on whether or not there is Federal involvement in the activity. For Federal actions, incidental take of listed species is subject to the requirements of Section 7 of the ESA. Section 7(a)(2) requires that "each Federal agency shall, in consultation with and with the assistance of...[NMFS], ensure that any action authorized, funded, or carried out by such agency is not likely to jeopardize the continued existence of (Footnote 5) any endangered species or threatened species...." If consultation determines that the action is not likely to jeopardize any listed species, then an incidental take statement under Section 7(b)(4) may be issued. The incidental take statement specifies those "reasonable and prudent measures...necessary or appropriate to minimize...impact" and specifies other "terms and conditions (including, but not limited to, reporting...) that must be complied with" (Section 7(b)(4)). In addition to the operation of propagation facilities, Federal funding or authorization (permitting or licensing) of such facilities or associated activities constitute "agency actions" which require compliance with Section 7 standards. Coordination with non-Federal entities (e.g., state or tribal agencies) that operate or manage such facilities is encouraged to ensure that the Section 7 consultations are conducted with the best available information.

Non-Federal activities (i.e., activities not directly influenced by Federal agency actions) that are likely to result in the incidental take of a listed species can be conducted only if a conservation plan is prepared and an incidental take permit issued pursuant to Section 10(a)(1)(B) of the ESA. In this case, the conservation plan must comply with the Act by specifying: 1) impacts that will likely result from the take, 2) steps the applicant will take to minimize and counter such impacts (as well as the resources available to implement these steps), 3) alternatives to the take and the reasons why these alternatives have been dismissed, and 4) other measures that may be required by NMFS (in the case of Pacific salmon) for the conservation plan (50 CFR 222.22).

In addition to potential effects on listed species, the artificial propagation of an unlisted species may contribute to its own decline or to the decline of other unlisted species. There is a growing perception that this has been the case for many Pacific salmon enhancement programs in the Pacific Northwest (e.g., Goodman 1990, Hilborn 1992). The considerations outlined above for interactions between listed and unlisted species generally apply to interactions between different unlisted species as well. Many of the general guidelines for recovery of listed species described in Part IV of this document provide a working foundation for the operation of existing and future salmon hatcheries that may enhance their longevity in the face of increasing conservation activities. The future of artificial propagation for unlisted species of Pacific salmon in the presence of conservation activities hinges on the ability of artificial propagation to operate under the constraints of the ESA and, ultimately, on its compatibility with the conservation of natural salmon populations in their natural settings.

Return to Table of Contents

VI. DEFINITIONS

Allele - An alternative form of the same gene at a particular gene locus (the location of the gene on a chromosome).

Artificial propagation - Any assistance provided by man in the reproduction of Pacific salmon. This assistance includes, but is not limited to, spawning and rearing in hatcheries, stock transfers, creation of spawning habitat, egg bank programs, captive broodstock programs, and cryopreservation of gametes.

Bottleneck - A sharp reduction of a breeding population's size to a few individuals. The genetic consequences of a bottleneck, especially the loss of genetic variability, depend on both its magnitude and its duration.

Captive broodstock program - A form of artificial propagation involving the collection of individuals (or gametes) from a natural population and the rearing of these individuals to maturity in captivity. For listed species, a captive broodstock is considered part of the evolutionarily significant unit (ESU) from which it is taken.

Crossbreeding - Reproduction between two distinct conspecific gene pools (compare with "hybridization," which generally refers to reproduction between distinct species or higher taxa). With respect to listed species of Pacific salmon, crossbreeding generally refers to interbreeding between individuals from different evolutionarily significant units (ESUs).

Cryopreservation - Preservation of gametes at very low temperature (e.g., use of liquid nitrogen to freeze sperm for later propagative use).

Domestication selection - Natural selection that operates on a population during artificial propagation to produce adaptations to the culture environment (Doyle 1983). Domestication selection typically requires more than one complete life cycle to produce a permanent phenotypic response. Domestication selection tends to eliminate fish that cannot adapt well to the captive environment, which may include some fish that are well-adapted to their natural environment.

Effective population size (N_e) - A mathematical construct that takes into account skewed sex ratio and variance in progeny number, as well as the actual number of breeders, to estimate the number of effectively breeding individuals in a population. Ne is the size of an idealized population (i.e., one in which sexes are equally represented, parents are randomly mated, and numbers of progeny are randomly distributed among families) that shows the same rate of loss of genetic variability as the observed population (Falconer 1981, Lande and Barrowclough

1987).

Evolutionarily significant unit (ESU) - A population or group of populations that is considered distinct (and hence a "species") for purposes of conservation under the Endangered Species Act. To qualify as an ESU, a population must 1) be reproductively isolated from other conspecific populations, and 2) represent an important component in the evolutionary legacy of the biological species (Waples 1991a). (In this document, the term "stock" is synonymous with "population.")

Fitness - An individual's contribution, relative to other individuals, to the breeding population in the next generation. Measures of an individual's reproductive success such as its survival, fertility, and age at reproduction, are typically used as indicators of fitness. The fitness of a group of individuals (e.g., a population) may be defined as the group's ability to maintain itself in its environment. It is therefore a composite measure of individual reproductive success. Endler (1986) discusses the fitness concept further.

Full-sib family - A group of individuals that shares the same two parents (i.e., brothers and sisters). Members of a half-sib family, by contrast, share only one parent.

Genetic drift - The stochastic process of genetic change through random shifts in allele frequencies. These changes can lead to loss (or, alternatively, fixation) of alleles. Genetic drift can eliminate gene polymorphisms and thereby erode genetic variability, and its effects are greatest in populations of small size.

Hatchery - An artificial propagation facility designed to produce fish for harvest or spawning escapement. A conservation hatchery differs from a production hatchery in that it specifically seeks to supplement or restore naturally spawning populations.

Inbreeding depression - A reduction in fitness resulting from mating between close relatives that occurs by chance in small populations or by assortative mating in large populations. Inbreeding depression is a consequence of the expression of deleterious recessive alleles as homozygosity increases; therefore, it depends largely on dominance, or interactions between alleles within loci (Falconer 1981, Lynch 1991).

Introgression - Incorporation of genetic material from one gene pool into another by hybridization or crossbreeding, followed by backcrossing between crossbred individuals and fish from the parental population(s).

Jeopardy - The National Marine Fisheries Service and U.S. Fish and Wildlife

Service have defined the phrase "jeopardize the continued existence of [a listed species]" to mean "to engage in an action that reasonably would be expected, directly or indirectly, to reduce appreciably the likelihood of both the survival and recovery of a listed species in the wild by reducing the reproduction, numbers, or distribution of that species" (50 CFR 402.02).

Listed species/listed population/listed evolutionarily significant unit (ESU) - For Pacific salmon, any ESU that has been determined to be threatened or endangered under Section 4 of the Endangered Species Act.

Natural fish - Fish that are progeny of naturally spawning parents (Waples 1991a). Natural fish thus spend their entire life cycle (except perhaps for brief periods in conservation facilities such as fish ladders or transportation barges) in natural habitat. (See Bjornn and Steward (1990) for a suggested distinction between the terms "natural" and "wild" fish.)

Outbreeding depression - A reduction in fitness that results from mating between unrelated or distantly related individuals (see crossbreeding). Outbreeding depression may result from loss of local adaptation (see Taylor 1991 for a review of local adaptation in salmon) or from the breakup of gene combinations favored by natural selection; in the latter case, the effects of outbreeding depression are thought to depend on epistasis, or interactions between different loci (Lynch 1991).

Recovery/restoration - The reestablishment of a threatened or endangered species to a self-sustaining level in its natural ecosystem (i.e., to the point where the protective measures of the Endangered Species Act are no longer necessary).

Recovery program - A strategy for the conservation and restoration of a threatened or endangered species. An Endangered Species Act recovery plan refers to a plan prepared under Section 4(f) of the Act and approved by the Secretary, including 1) a description of site-specific management actions necessary for recovery, 2) objective, measurable criteria that can be used as a basis for removing the species from threatened or endangered status, and 3) estimates of the time and cost required to implement recovery. (For Pacific salmon, "Secretary" refers to the Secretary of Commerce.)

Self-sustaining population - A population that perpetuates itself, in the absence of (or despite) human intervention, without chronic decline, in its natural ecosystem. A self-sustaining population maintains itself at a level above the threshold for listing under the Endangered Species Act. In this document, the terms "self-sustaining" and "viable" are used interchangeably.

Species - "Any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature" (Endangered Species Act, Sec. 3 (15)). For Pacific salmon, this includes any distinct population segment that meets the qualifications of an ESU (Waples 1991a). A listed species is one determined to be threatened or endangered under the Endangered Species Act.

Stock transfer - Transfer of fish from one location to another. This includes any fish originating outside the geographical boundary of an ESU and transferred into it, any fish transferred out of an ESU's range or between areas occupied by different ESUs, or any fish transferred into vacant habitat.

Supplementation - The use of artificial propagation to reestablish or increase the abundance of naturally reproducing populations (c.f. recovery/restoration).

Take - To "harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in such conduct" (Endangered Species Act, Sec. 3(18)). See Part V for the regulation of take during artificial propagation.

ACKNOWLEDGMENTS

The ideas in this paper have drawn heavily from the documents by Utter (1981), Thompson (1991), and Waples (1991a), and from public comments on those documents. The critical reviews provided by a number of scientists and agencies were instrumental in improving an earlier version of this paper.

CITATIONS

Allendorf, F. W., and N. Ryman. 1987. Genetic management of hatchery stocks. *In* N. Ryman and F. Utter (editors), Population genetics & fishery management, p. 141-160. Univ. Washington Press, Seattle.

Allendorf, F. W., N. Ryman, and F. M. Utter. 1987. Genetics and fishery management: Past, present, and future. *In* N. Ryman and F. Utter (editors), Population genetics & fishery management, p. 1-19. Univ. Washington Press, Seattle.

Bams, R. A. 1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbuscha*). J. Fish. Res. Board Can. 33:2716-2725.

Becker, W. A. 1984. Manual of quantitative genetics, 4th ed. Academic

Enterprises, Pullman, WA, 196 p.

Bilton, H. T., D. F. Alderdice, and J. T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Can. J. Fish. Aquat. Sci. 39:426-447.

Bjornn, T. C., and C. R. Steward. 1990. Concepts for a model to evaluate supplementation of natural salmon and steelhead stocks with hatchery fish. *In* W. H. Miller (editor), Analysis of salmon and steelhead supplementation, Part 3. Report to Bonneville Power Administration (Proj. 88-100). (Available from Bonneville Power Administration, P. O. Box 3621, Portland, OR 97208.)

Busack, C. 1990. Yakima/Klickitat production project genetic risk assessment. Unpubl. manuscr., 21 p. Genetics Unit, Washington Department of Fisheries, 115 General Administration Building, Olympia, WA 98504.

Cade, T. J. 1988. Using science and technology to reestablish species lost in nature. *In* E. O. Wilson and F. M. Peter (editors), Biodiversity, p. 279-288. National Academy Press, Washington, DC.

Campton, D. E., F. W. Allendorf, R. J. Behnke, F. M. Utter; M. W. Chilcote, S. A. Leider, and J. J. Loch. 1991. Reproductive success of hatchery and wild steelhead. Trans. Am. Fish. Soc. 120:816-827.

Chilcote, M. W., S. A. Leider, and J. J. Loch. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. Trans. Am. Fish. Soc. 115:726-735.

Cuenco, M. L. 1991. Examples where supplementation has successfully resulted in increasing naturally-reproducing fish populations. Unpublished report submitted to the Endangered Species Act Administrative Record for petitioned salmon stocks, February 1991, 18 p. (Available from Environmental and Technical Services Division, NMFS, Portland, OR 97232.)

Doyle, R. W. 1983. An approach to the quantitative analysis of domestication selection in aquaculture. Aquaculture 33:167-185.

Emlen, J. M. 1991. Heterosis and outbreeding depression: A multi-locus model and an application to salmon production. Fish. Res. 12:187-212.

Endler, J. A. 1986. Natural selection in the wild. Princeton Univ. Press, Princeton, NJ, 336 p.

Falconer, D. S. 1981. Introduction to quantitative genetics, 2nd ed. Longman, London, U.K., 340 p.

Fleming, I. A., and M. R. Gross. 1992. Reproductive behavior of hatchery and wild coho salmon (*Oncorhynchus kisutch*): Does it differ? Aquaculture 103:101- 121.

Folmar, L. C., and W. W. Dickhoff. 1980. The parr-smolt transformation (smoltification) and seawater adaptation in salmonids: A review of selected literature. Aquaculture 21:1-37.

Franklin, I. R. 1980. Evolutionary changes in small populations. In M. E. Soul, and B. A. Wilcox (editors), Conservation biology: An evolutionary-ecological perspective, p. 135-149. Sinauer Associates, Sunderland, MA.

Gall, G. A. E. 1987. Inbreeding. *In* N. Ryman and F. Utter (editors), Population genetics & fishery management, p. 47-87. Univ. Washington Press, Seattle.

Gharrett, A. J., and S. M. Shirley. 1985. A genetic examination of spawning methodology in a salmon hatchery. Aquaculture 47:245-256.

Gharrett, A. J., and W. W. Smoker. 1991. Two generations of hybrids between even- and odd-year pink salmon (*Oncorhynchus gorbuscha*): A test for outbreeding depression? Can. J. Fish. Aquat. Sci. 48:1744-1749.

Goodman, D. 1987. The demography of chance extinction. *In* M. E. Soulé (editor), Viable populations for conservation, p. 11-34. Cambridge Univ. Press, Cambridge, U.K.

Goodman, M. L. 1990. Preserving the genetic diversity of salmonid stocks: A call for federal regulation of hatchery programs. Environ. Law 120:111-166.

Hard, J. J., A. C. Wertheimer, W. R. Heard, and R. M. Martin. 1985. Early male maturity in two stocks of chinook salmon (*Oncorhynchus tshawytscha*) transplanted to an experimental hatchery in southeastern Alaska. Aquaculture 48:351-359.

Håstein, T., and T. Lindstad. 1991. Diseases in wild and cultured salmon: Possible interaction. Aquaculture 98:277-288.

Hedrick, P. W., and P. S. Miller. 1992. Conservation genetics: Techniques and fundamentals. Ecol. Appl. 2:30-46.

Hilborn, R. 1992. Hatcheries and the future of salmon in the Northwest. Fisheries 17(1):5-8.

Hindar, K., N. Ryman, and F. Utter. 1991. Genetic effects of cultured fish on natural fish populations. Can. J. Fish. Aquat. Sci. 48:945-957.

Hoar, W. S. 1988. The physiology of smolting salmonids. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology Vol. XIB, p. 275-343. Academic Press, New York.

Holtby, L. B., T. E. McMahon, and J. C. Scrivener. 1989. Stream temperature and inter- annual variability in the emigration timing of coho salmon (Oncorhynchus kisutch) smolts and fry and chum salmon (*O. keta*) fry from Carnation Creek, British Columbia. Can. J. Fish. Aquat. Sci. 46:1396-1405.

Johnson, O. W., T. A. Flagg, D. J. Maynard, G. B. Milner, and F. W. Waknitz. 1991. Status review for lower Columbia River coho salmon. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-202, 94 p.

Kaczynski, V. W., and J. F. Palmisano. 1992. A review of management and environmental factors responsible for the decline and lack of recovery of Oregon's wild anadromous salmonids. Technical report prepared for the Oregon Forest Industries Council, 292 p. (Available from Oregon Forest Industries Council, P. O. Box 12519, Salem, OR 97309.)

Lande, R. 1988. Genetics and demography in biological conservation. Science 241:1455-1460.

Lande, R., and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. *In* M. E. Soulé (editor), Viable populations for conservation, p. 87-123. Cambridge Univ. Press, Cambridge, U.K.

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.

Leigh, E. G. 1981. The average lifetime of a population in a varying environment. J. Theor. Biol. 90:213-239.

Li, H. W., C. B. Schreck, C. E. Bond, and E. Rextad. 1987. Factors influencing changes in fish assemblages of Pacific Northwest streams. *In* W. J. Matthews and D. C. Hein (editors), Community and evolutionary ecology of North American stream fishes, p. 193-202. Univ. Oklahoma Press, Norman.

Lichatowich, J. A., and J. D. McIntyre. 1987. Use of hatcheries in the management of Pacific anadromous salmonids. Amer. Fish. Soc. Symp. 1:131-136.

Lynch, M. 1991. The genetic interpretation of inbreeding depression and outbreeding depression. Evolution 45:622-629.

Martin, R. M., and A. C. Wertheimer. 1989. Adult production of chinook salmon reared at different densities and released at two smolt sizes. Prog. Fish-Cult. 51:194-200.

Mathews, S. B. 1980. Trends in Puget Sound and Columbia River coho salmon. *In* W. J. McNeil and D. C. Himsworth (editors), Salmonid ecosystems of the North Pacific, p. 133-145. Oregon State Univ. Press, Corvallis.

Matthews, G. M., and R. S. Waples. 1991. Status review for Snake River spring and summer chinook salmon. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-200, 75 p.

Meffe, G. K. 1986. Conservation genetics and the management of endangered fishes. Fisheries 11(1):14-23.

Miller, W. H. (editor). 1990. Analysis of salmon and steelhead supplementation. Report to Bonneville Power Administration (Proj. 88-100). (Available from Bonneville Power Administration, P. O. Box 3621, Portland, OR 97208.)

Miller, W. H., T. C. Coley, H. L. Burge, and T. T. Kisanuki. 1990. Emphasis on unpublished and present programs. *In* W. H. Miller (editor), Analysis of salmon and steelhead supplementation, Part 1. Report to Bonneville Power Administration (Proj. 88-100). (Available from Bonneville Power Administration, P. O. Box 3621, Portland, OR 97208.)

Nelson, K., and M. Soulé. 1987. Genetical conservation of exploited fishes. In N. Ryman and F. Utter (editors), Population genetics & fishery management, p. 345-368. Univ. Washington Press, Seattle.

Nickelson, T. E., M. F. Solazzi, and S. L. Johnson. 1986. Use of hatchery coho salmon (*Oncorhynchus kisutch*) presmolts to rebuild wild populations in Oregon coastal streams. Can. J. Fish. Aquat. Sci. 43:2443-2449.

Olla, B. L., and M. W. Davis. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. Aquaculture 76:209-214.

Povilitis, T. 1990. Is captive breeding an appropriate strategy for endangered species conservation? Endang. Spec. Update 8:20-23.

Regional Assessment of Supplementation Project (RASP). 1992. Supplementation in the Columbia Basin. RASP Summary Report Series, Part I. Background, description, performance measures, uncertainty, and theory. Unpublished report submitted to the Bonneville Power Administration (Proj. 85-62), 39 p. (Available from Bonneville Power Administration, P.O. Box 3621, Portland, OR, 97208.)

Reisenbichler, R. R. 1988. Relation between distance transferred from natal stream and recovery rate for hatchery coho salmon. N. Am. J. Fish. Manage. 8:172- 174.

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.

Riggs, L. A. 1990. Principles for genetic conservation and production quality: Results of a scientific and technical clarification and revision. Unpubl. rep. prepared for the Northwest Power Planning Council (Contract No. C90-005), 20 p. (Available from GENREC (Genetic Resource Consultants), P. O. Box 9528, Berkeley, CA 94709).

Ryman, N., and L. Laikre. 1991. Effects of supportive breeding on the genetically effective population size. Conserv. Biol. 5:325-329.

Siitonen, L., and G. A. E. Gall. 1989. Response to selection for early spawn date in rainbow trout, *Salmo gairdneri*. Aquaculture 78:153-161.

Simon, R. C., J. D. McIntyre, and A. R. Hemmingsen. 1986. Family size and effective population size in a hatchery stock of coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 43:2434-2442.

Skaala, ., G. Dahle, K. E. J rstad, and G. N‘vdal. 1990. Interactions between natural and farmed fish populations: Information from genetic markers. J. Fish. Biol. 36:449-460.

Steward, C. R., and T. C. Bjornn. 1990. Supplementation of salmon and steelhead stocks with hatchery fish: A synthesis of published literature. *In* W. H. Miller (editor), Analysis of salmon and steelhead supplementation, Part 2. Report to Bonneville Power Administration (Proj. 88-100). (Available from Bonneville Power Administration, P. O. Box 3621, Portland, OR 97208.)

Swain, D. P., B. E. Riddell, and C. B. Murray. 1991. Morphological differences between hatchery and wild populations of coho salmon (Oncorhynchus kisutch): Environmental versus genetic origin. Can. J. Fish. Aquat. Sci. 48:1783- 1791.

Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185-207.

Thompson, G. G. 1991. Determining minimum viable populations under the Endangered Species Act. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-198, 78 p.

Utter, F. 1981. Biological criteria for definition of species and distinct intraspecific populations of anadromous salmonids under the U.S. Endangered Species Act of 1973. Can. J. Fish. Aquat. Sci. 38:1626-1635.

Waples, R. S. 1990. Conservation genetics of Pacific salmon. II. Effective population size and the rate of loss of genetic variability. J. Hered. 81:267-276.

Waples, R. S. 1991a. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. Mar. Fish. Rev. 53(3):11-22.

Waples, R. S. 1991b. Genetic interactions between hatchery and wild salmonids: Lessons from the Pacific Northwest. Can. J. Fish. Aquat. Sci. 48 (Suppl. 1):124-133.

Waples, R. S., G. A. Winans, F. M. Utter, and C. Mahnken. 1990. Genetic approaches to the management of Pacific salmon. Fisheries 15(5):19-25.

Washington, P. J. 1985. Survey of artificial production of anadromous salmonids in the Columbia River basin. Final report to the Bonneville Power Administration, 221 p. (Available from Bonneville Power Administration, P. O. Box 3621, Portland, OR 97208.)

Withler, R. E. 1988. Genetic consequences of fertilizing chinook salmon (*Oncorhynchus tshawytscha*) eggs with pooled milt. Aquaculture 68:15-25.

Return to Table of Contents

Footnotes

1. The term "Pacific salmon" has traditionally referred to species of the genus *Oncorhynchus*, five of which (*O. gorbuscha, O. keta, O. kisutch, O. nerka*, and *O. tshawytscha*) occur in North America. The recent decision to move the western trouts from the genus *Salmo* to *Oncorhynchus* calls this usage into question. In this document, "Pacific salmon" is used to include anadromous forms of *O. clarki* and *O. mykiss*, as well as the five above-mentioned species (Waples 1991a).

2. Defined in this context as fish that are in a hatchery (see Definitions) or have spent part of their life cycle prior to maturity in a hatchery.

3. ALthough such spawniung aggregations may exhibit genetic and phenotypic differences sufficient to discriminate among different populations, the evolutionary significance of these differences may be uncertain (Waples 1991a).

4. This estimate of Nb is appropriate for species of Pacific salmon with several year classes represented in the spawning population and an average age at maturity of 3-5 years (pink salmon excluded).

5. The phrase "jeopardize the continued existence of" has a strict legal meaning in the context of the ESA: "[To] engage in an action that reasonably would be expected, directly or indirectly, to reduce appreciably the likelihood of both the survival and recovery of a listed species in the wild by reducing the reporduction, numbers, or distribution of that species" (50 CFR 402.02).

Return to Table of Contents