DEPARTMENT OF COMMERCE

National Oceanic and Atmospheric Administration

[Docket No. 910248-1255]

Policy on Applying the Definition of Species Under the Endangered Species Act to Pacific Salmon

AGENCY: National Marine Fisheries Service (NMFS), NOAA, Commerce.

ACTION: Notice of policy.

SUMMARY: The Endangered Species Act of 1973, as amended, 16 U.S.C. 1531 *et seq.* (ESA) defines "species" to include any "distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." NMFS announces its final policy on how it will apply this definition of "species" in evaluating Pacific salmon stocks for listing under the ESA. A salmon stock will be considered a distinct population, and hence a "species" under the ESA, if it represents an evolutionary significant unit (ESU) of the biological species. The stock must satisfy two criteria to be considered an ESU: (1) It must be substantially reproductively isolated from other nonspecific population units; and (2) it must represent an important component in the evolutionary legacy of the species. Only Pacific salmon stocks that meet these criteria will be considered by NMFS for listing under the ESA.

EFFECTIVE DATE: November 20, 1991.

FOR FURTHER INFORMATION CONTACT: Patricia Montanio, Protected Species Management Division, NMFS, 1335 East-West Highway, Silver Spring, MD 20910 (301/427-2322), or Rob Jones, Environmental and Technical Services Division, NMFS, Portland, OR 97232 (503/230-5401 or FTS/429-5401).

SUPPLEMENTARY INFORMATION:

Background

The stated purposes of the ESA are to "provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, (and) to provide a program for the conservation of such endangered species and threatened species" (ESA section 2(b)). A review of legislative history indicates that a major motivating factor behind the ESA was the desire to preserve a genetic variability, both between and within species. For example, the House Committee on Merchant Marine and Fisheries described the rationale for H.R. 37, a forerunner to the ESA, in the following terms (H.R. Rep. No. 412, 93d Cong., 1973):

> From the most narrow possible point of view, it is in the best interests of mankind to minimize the losses of genetic variations. The reason is simple: they are potential resources. They are keys to puzzles which we cannot yet solve, and may provide answers to questions which we have not yet learned to ask.

Under the original 1973 Act, a "species" was defined to include "any subspecies of fish or wildlife or plants and any other group of fish or wildlife of the same species or smaller taxa in common spatial arrangement that interbreed when mature." Use of this language established that the ESA protective measures extend to biological units below the subspecies level. Amendments in 1978 provided the current language in the ESA: A "species" is defined to include "* * * 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."

Congress has provided limited guidance for interpreting this definition. In 1979, Congress declined to enact a provision recommended by the General Accounting Office that would have removed the authority to list vertebrate populations. The Senate Report to the 1979 amendments, however, stated that "the committee is aware of the great potential for abuse of this authority and expects the FWS to use the ability to list populations sparingly and only when biological evidence indicates that such action is warranted" (S. Rep. No. 151, 96th Cong., 1979). The ESA also requires that all listing determinations be made solely on the basis of the best scientific and commercial data available (ESA section 4(b)(1)).

Both the U.S. Fish and Wildlife Service (FWS) and NMFS, which share jurisdiction under the ESA, have made listing determinations for populations of vertebrate species; but neither Service has established criteria for determining what qualifies as a distinct population. Joint regulations concerning Listing Endangered and Threatened Species and Designating Critical Habitat (50 CFR part 424) provide that a determination on whether or not a particular population is a "species" under the ESA should rely on the biological expertise of the agency and the scientific community (50 CFR 424.11(a)).

Interim Policy

In 1990, NMFS received petitions to list five stocks of Pacific salmon under the ESA. To address these and other Pacific salmon stocks, NMFS published its "Interim Policy on Applying the Definition of Species Under the Endangered Species Act to Pacific Salmon" (interim policy) on March 13, 1991 (56 FR 10542). In support of this interim policy, the NMFS Northwest Fisheries Center prepared a Technical Memorandum on "Definition of 'species' under the Endangered Species Act: Application to Pacific salmon," (Waples 1991). Comments on the interim policy and supporting paper were requested through June 11, 1991. NMFS used the interim policy in its proposed determinations to list the Snake River sockeye salmon (April 5, 1991; 56 FR 14055), the Snake River fall chinook salmon (June 27, 1991; 56 FR 29547), and the Snake River spring/summer chinook salmon (June 27, 1991; 56 FR 29542), and in its final determination not to list the Lower Columbia River coho salmon (June 27, 1991; 56 FR 29553).

Based on comments received, NMFS issues this final policy. The NMFS Northwest Fisheries Center has also revised the supporting paper "Pacific salmon and the definition of 'species' under the Endangered Species Act" (Waples In press Marine Fisheries Review), which is available upon request (see **FOR FURTHER INFORMATION CONTACT**). This final policy will be used in all Pacific salmon listing determinations until revised or superseded. NMFS has reviewed its "species" determination for the listed Sacramento River winter-run chinook salmon (February 27, 1978, 52 FR 6041; December 9, 1988, 53 FR 49722; August 4, 1989, 54 FR 32085; November 5, 1990, 55 FR 46515) and concludes that consideration of this final policy does not necessitate any change of that determination.

Summary of Comments and Responses

Twenty-one written comments were received. Fourteen respondents agreed with the general framework of the interim policy, although several had suggestions for improvements in specific details. Six respondents disagreed with the framework and believed that substantial changes are needed. Summaries of the major points and responses are provided below.

General

Comment: A number of comments were received on the process NMFS used in developing this policy. Two respondents believed that "distinct population" should be defined by rulemaking; one of these believed it should be subject to formal rulemaking under the Administrative Procedure Act (APA). Others believed the process violated APA because it is based on

material not available to the public, *i.e.*, the results of the 1990 Vertebrate Population Workshop, and because the "not warranted" and the proposed listing determinations on the petitioned stocks did not consider comments on the interim policy.

Response: NMFS believes its process is consistent with the requirements of the APA. Formal rulemaking is required under the APA only "when the rules are required by statute to be made on the record after opportunity for an agency hearing" (5 U.S.C. 553(c)). Developing a policy is not a prerequisite to making proposed or final determinations under the ESA. However, in view of the unique life history characteristics of salmon, NMFS believes a statement of policy is useful. Notice and comment procedures were used in developing this final policy, even though not required by the APA (5 U.S.C. 553(b)(A)). The basis for the interim policy, including concepts discussed at the 1990 Vertebrate Population Workshop, was set forth in the interim policy (56 FR 10542; March 13, 1991) and supporting paper (Waples 1991). Comments were requested and considered in developing this final policy. Future Pacific salmon listing actions, including the final determinations on Snake River sockeye and chinook salmon stocks, will use this final policy to evaluate whether or not the stocks qualify as "species" under the ESA. NMFS has reviewed the "species" determination and all comments received on the Lower Columbia River coho petition and concludes that this final policy does not change that determination.

Comment: One respondent believed that the definition of "species" is a legal interpretation subject to judicial review solely for consistency with Congressional intent and is not a factual "biological" determination subject to judicial deference to the agency expertise.

Response: NMFS recognizes that the definition of "species" under the ESA is in part a legal interpretation subject to judicial review. However, species and populations are biological concepts that must be defined on the basis of the best scientific and commercial data available, just as the decision to list "species" as endangered or threatened (see section 4(b)(1)(A) of the ESA). This final policy is based on all available techniques of statutory interpretation, including legal analysis, scientific usage, and public comments.

Comment: A number of comments were received on the need for a policy. Some respondents believed that a policy was unnecessary, that it would constrain the agency's authority to list populations, and that a straightforward application of the intent of the ESA to preserve genetic diversity should be used. These respondents believed that Congress clearly demonstrated an expansive intent to protect endangered and threatened wildlife, and any policy that narrows the definition of "species" is unwarranted and contrary to the intent of the ESA. One respondent believed that since Pacific salmon present a unique situation that Congress has never considered, language such as in the 1979 Senate Report (S. Rep. No. 151, 96th Cong., 1979) should not be used to limit the agency's authority to list populations.

Other respondents believed that a policy is needed that provides a general framework for determining populations, but leaves flexibility to take into account uncertainties and special circumstances. Some believed that, consistent with the expressed intent of the ESA, the authority to consider distinct populations should be exercised only in those relatively unique circumstances when a population can be shown to be truly distinct. These respondents believed that the management implications of listing each threatened or endangered population would put an enormous strain on agency resources.

Many other respondents believed that a more specific policy is needed to establish clear direction; otherwise definitions of species under the ESA could be subject to different interpretations and could be subject to abuse.

Response: NMFS does not believe that the intent of Congress is clear as to the meaning of "distinct population." The ESA allows vertebrate populations that are "distinct" to be considered "species," but does not explain how distinctness should be measured. Therefore, it is important that NMFS explain and notify the public of its interpretation of the ESA and how it will apply its interpretation to Pacific salmon. This final policy is intended to provide guidance, consistent with the ESA and the intent of Congress.

Further, NMFS does not believe that it is possible to establish highly specific or quantitative standards for determining distinct populations. The process of evolution and differentiation within and between species is manifest in many different ways. Many natural populations show varying degrees of distinctness, and the variations do not always have discrete boundaries. Expert scientific judgment is required in determining what should be considered distinct populations.

Comment: One respondent pointed out that listing of U.S. populations is allowed, citing language from the 1979 Senate Report:

> The U.S. population of an animal should not necessarily be permitted to become extinct simply because the animal is more abundant elsewhere in the world.

(S. Rep. No. 151, 96th Cong., 1979). This respondent also believed that it is not necessary that the U.S. population be reproductively isolated from non-U.S. populations.

Response: NMFS agrees that it may be appropriate to list U.S. populations of species more abundant elsewhere. Under the NMFS policy, a U.S. population could be listed if it is a "distinct population," *i.e.*, an ESU, based on the best scientific evidence available. NMFS believes that the population concept used in the ESA is a biological one, and that political boundaries alone should not be used to define populations. Biological populations must exhibit some degree of reproductive isolation, and, therefore, NMFS disagrees with the second point made by this respondent. However, the entire population (occurring within and outside of the United States) may qualify as an ESU and be considered for listing, particularly if the U.S. portion is a substantial portion of the ESU.

Comment: Two respondents believed that although the interim policy appears to be suitable for Pacific salmon, difficulties might be expended if it were to be applied to some other vertebrates.

Response: This final policy applies only to Pacific salmon, and NMFS will consider these broader comments in developing an overall policy of defining distinct vertebrate population under the ESA.

ESU Concept

Comment: Six respondents agreed that the primary purpose of the ESA is to protect "genetic diversity," "genetic variability," "unique genetic material," or "distinct evolutionary lineages," and one stated that the interim policy adequately addressed ecological concerns. Other respondents stressed the importance of preserving "biodiversity" and the "aesthetic, ecological, recreational, and scientific value" of species. One respondent argued that the interim policy does not adequately take into account the ecological significance of a population and its role in maintaining ecosystems, and another believed that protection of existing distributions of species should be a primary basis for "species" determination.

Response: NMFS recognizes the importance of conserving ecosystems, but this must be accomplished within the limits of what the ESA allows. In general, the ESA provides that the "purposes of the Act are to provide a means whereby the ecosystems upon which endangered and threatened species depend may be conserved * * *" (ESA section 2(b)). The key is the link between threatened and endangered species and their native ecosystems. There may be a number of good reasons for maintaining populations of "keystone" species in ecosystems where they play a key role in fostering diversity, but unless such populations can be shown to be "distinct," such efforts must be accomplished outside the purview of the ESA as presently written.

NMFS believes that its interpretation of the definition of "species" is consistent with the goal of the ESA to conserve genetic resources, both within and between species. If this goal is achieved, then other benefits of biodiversity follow naturally. Attempting to preserve populations for their aesthetic, scientific, or recreational value without regard to the underlying genetic basis for diversity focuses on attributes that are not directly related to long-term survival of the species. While NMFS supports efforts to maintain biological diversity, habitat conservation, and species distributions, NMFS does not believe that the provisions of the ESA provide specifically for these broader objectives.

Comment: Two respondents argued that the ESA allows listing of any geographic population, and that the populations do not have to be reproductively isolated or genetically distinct. One cited the 1987 House Report that states "Any species or subspecies of fish, wildlife, or plants may be listed. In addition, geographically distinct populations of vertebrate species may be listed." (H.R. Rep. No. 467, 100th Cong., 1987). Others argued that a population need only be reproductively isolated, and that the "evolutionary significance" criterion should be deleted. Still other respondents believed that reproductive isolation was not enough to qualify a population as a "species," and that the "evolutionary significance" criterion is appropriate.

Response: Biological populations, by definition, exhibit some degree of reproductive isolation from other populations, whether based on geographic separation or other factors. The reproductive isolation criterion is consistent with the definition of species in the ESA which includes "any distinct population * * * which interbreeds when mature." (ESA section 2(15)).

Further, NMFS does not believe that all populations are included in the ESA definition of "species." The ESA requires that a vertebrate population be "distinct" to qualify as a "species." NMFS believes its interpretation that, to be considered "distinct," a population (or group of populations) must meet the two criteria set out in the interim policy, is consistent with the ESA.

Comment: Several respondents believed that some words or terms should be more clearly defined, including "important component," "evolutionary legacy," "evolutionarily important," "significant loss," "contributes substantially," "substantially reproductively isolated," and some technical terms. Another respondent pointed out that the terms "unique habitat" and "unique adaptation" are not really very meaningful because, when considered on a fine scale, all habitats (and all adaptations) are unique in some way.

Response: NMFS has clarified where possible a number of the terms in the final policy and supporting paper, which provides more extensive explanation of how many of these concepts will be evaluated in practice. NMFS agrees with the respondent regarding use of the word "unique," and has changed the policy to refer to "unusual" or "distinctive" habitat and adaptations. Nevertheless, precise definitions are not possible for many of the terms, as discussed in the next response.

Comment: Many respondents argued that the concept of evolutionary significance is too subjective and asked for more definitive guidelines for making this determination. Several others argued that there are no universal markers that will unfailingly define distinct population segments: e.g., "a simple cookbook species definition is not scientifically defensible. Site specific and special-case factors are relevant and must be considered."

Response: NMFS recognizes that the framework of this final policy will not be as easy to apply as would a simple rule. Nevertheless, the wide diversity of views expressed by the respondents on virtually every issue lends credence to NMFS' belief that no simple yardstick will be universally applicable. Inevitably, basing the "species" determination on the best scientific information available will require some judgment.

Reproductive Isolation Criterion

Comment: A number of respondents emphasized the complexity of evaluating the degree of reproductive isolation in Pacific salmon. One stressed that reproductive isolation in these species is seldom absolute; therefore, the task is to identify cases of "significant" reproductive isolation. One, citing an example in which morphologically indistinguishable populations from the same drainage were shown to be chromosomally distinct, argued for caution in assuming that nearby populations are not isolated. Another respondent agreed, arguing that gene flow needs to be documented: "wandering does not equal straying * * * spawned-out fish, or even their offspring rearing in the stream, does not mean that the fish will survive to mature and leave offspring whose genes will enter the population." And, another respondent argued the opposing view, that minor genetic differences between populations should not necessarily be grounds for a finding of reproductive isolation. Another argued that geographic proximity may be irrelevant to the degree of reproductive isolation in Pacific salmon.

Response: NMFS believes that each of these comments has merit. A variety of factors (temporal variation, non-random sampling, etc.) might lead to small genetic (or phenotypic) differences between samples, and care must be used in inferring reproductive isolation from such data. The caveats about wandering and straying mirror those in the Technical Memorandum, and NMFS also recognizes that adjacent populations of anadromous salmonids can sometimes be strongly isolated reproductively. The diversity of comments on this topic illustrates the importance of evaluating each case individually, giving consideration to all available types of scientific information and recognizing the strengths and limitations of each.

Comment: Two respondents pointed out that the exchange of some genetic material (e.g., mitochondrial DNA) between populations or species can occur at a different (often faster) rate than the exchange of nuclear genes, and if this happens, the question of reproductive isolation can be quite complicated.

Response: The respondents are correct to point out this possibility. In the event that different types of genetic analyses lead to different conclusions regarding reproductive isolation, NMFS recommends that all other available lines of evidence be utilized to help clarify the situation.

Comment: One respondent believed that the discussion of recolonization rates in the Technical Memorandum

was overly simplistic, stating that simple replacement of individuals of the same species does not necessarily imply equivalence; the new population might consist of animals less well adapted to the habitat. Another respondent questioned the statement in the Technical Memorandum that, "Presumably, an area that would be repopulated at or near the previous abundance level in a short time would be unlikely to harbor an ESU." The respondent argued that an introduced population might actually do better than the native population, but this does not necessarily mean that the indigenous population is not uniquely suited to its environment.

Response: The passage cited from the Technical Memorandum was meant to refer to natural recolonization, not introductions of exogenous populations. The text in the revised supporting paper has been changed to make this clear. NMFS agrees that replacement does not necessarily imply equivalence; the point here is that if natural replacement is rapid, whether with equivalent individuals or not, one must question whether the population was isolated in the first place. Caveats noted in the Technical Memorandum and by the respondents against drawing casual conclusions from such data will be given appropriate consideration.

Ecological/Genetic Diversity Criterion

Comment: One respondent asked NMFS to clarify whether an affirmative answer to any of the four rhetorical questions relating to the ecological/genetic diversity criterion should be considered strong evidence that the population is an ESU. Another asked whether the fourth of these questions, "If the population became extinct, would this event represent a significant loss to the ecological/genetic diversity of the species?" should be considered from the point of view of the fish species or mankind.

Response: The question of "significant loss" is to be interpreted with respect to the biological species. This question is really at the heart of the "evolutionary significance" concept, and a clear, affirmative answer to this question is a very strong indication that the population in question is an ESU. The other three questions are more specific and address topics that are important to consider (but are not necessarily conclusive) in evaluating evolutionary significance; each of these three questions should be viewed as one part of a larger inquiry. The policy has been clarified to reflect this.

Comment: A variety of views was expressed on the relative importance to attach to different types of data in determining whether populations meet the "ecological/genetic diversity" criterion. Several respondents believed that the interim policy does not provide enough guidance, whereas others emphasized that the most relevant type of information will differ from case to case, and evaluating distinctness will require expert judgment based on all available data. One respondent argued that the different types of data can be ranked as follows: "direct evidence of adaptive differences is most important, followed by evidence of unique alleles (one of two or more forms of a particular gene), large differences in allele frequencies, and lastly perceived differences in selective pressures."

Two respondents believe that the interim policy placed too much emphasis on genetic characteristics, and three believed that genetic traits should be accorded more importance. Two respondents argued that phenotypic or life history traits should weigh heavily in favor of finding a population to be distinct; two others argued that such characteristics are inherently unreliable because of the potential for strong environmental influence. One respondent commented that although analysis of morphological characteristics is complicated by environmental and size effects, these characteristics might be relatively more useful for groups of vertebrates with determinate growth (e.g., birds and mammals). Several respondents expressed the view that more work is necessary to sort out the genetic and environmental effects on phenotypic characteristics. One respondent argued that habitat characteristics should be "heavily weighted in favor of finding a population to be distinct;" another believed that, because of uncertainty about the selective importance of habitat differences, such data "are less useful than other information that can be collected."

Response: NMFS agrees that the task of sorting out genetic and environmental effects on phenotypic characteristics is a difficult but important one. Although caution must be used in interpreting data for such characteristics, they should not be dismissed out of hand. There is a strong evidence for a genetic basis for some phenotypic and life history characteristics in some Pacific salmon populations. NMFS continues to recommend that judgments regarding evolutionary significance be made based on all available scientific information, weighted as deemed most appropriate for the particular case.

A major concern regarding unique alleles (those found in only one population or one geographic region) is sampling error; that is, the failure to find the alleles in other localities may be due to inadequate sampling. Nevertheless, alleles that have been found in only one area and occur there at moderate or high frequency suggest a substantial degree of reproductive isolation. The same inference may be drawn from the occurrence of a number of unique alleles at low frequency. Further, although unique alleles do not necessarily reflect adaptation, they may, if numerous or at high frequency, provide an indication of likely adaptive differences elsewhere in the genome (see also next response).

Comment: Two respondents cautioned against automatically assuming that all electrophoretically detectable variation is selectively neutral. One also argued that such variation is evolutionarily important in the sense that it provides the raw material upon which selection may act in the future. Another respondent argued that because electrophoretically detectable variation is largely neutral, it provides little information relative to the question of evolutionary significance beyond the insights it may provide regarding reproductive isolation.

Response: NMFS agrees with the respondents that there is persuasive evidence in a number of organisms for adaptive variation at some gene loci detected by protein electrophoresis. The key questions are: (1) How much of the electrophoretically-detectable variation is neutral, and (2) How much is influenced by natural selection? This issue has been debated by evolutionary biologists for over 2 decades, without a complete resolution of opposing views. Nevertheless, the majority opinion seems to be that most such variation is effectively neutral. That is, if selection is occurring, it is weak enough that the behavior of genotype and allele frequencies is dominated by random genetic drift. This does not rule out strong selection at some electrophoretically detectable gene loci, and this possibility should always be kept in mind in evaluating such data.

NMFS also agrees that, even if essentially neutral at present, genetic variation at protein-coding loci provides a reservoir of raw material upon which natural selection may act at some future time. Thus, such variation may play an important role in evolution. The Technical Memorandum stressed that the bulk of evidence for adaptive differences must come from sources other than protein electrophoresis. However, the magnitude of presumably neutral differences can also provided insight into the likelihood that adaptive

differences are present at other parts of the genome, and in this respect such data can be useful in drawing inferences about evolutionary significance.

Comment: One respondent agreed with the statement in the interim policy that "failure to find (genetic) differences (or the absence of genetic data) would * * * place a greater burden of proof on data for other characters." Another disagreed, arguing that this would shift emphasis to the most subjective characteristics, and therefore the inability to detect genetic differences might be used to exclude populations from ESA consideration. Three other respondents expressed the view that the lack of demonstrable genetic differences should not weigh heavily against finding a population distinct. One of these asked that NMFS affirm that the absence of genetic data "would not preclude consideration of that population as an ESU."

Response: There are really two separate, albeit related, issues here: (1) How to proceed in the absence of any direct genetic information? and (2) How to proceed if there are some genetic data, but they fail to show significant differences between populations? Regarding the first question, NMFS recognizes that the majority of "species" determinations under the ESA have been made without the aid of any direct genetic evidence. Data from protein electrophoresis or DNA analyses can be very useful in determining population "distinctness," but they are not essential. NMFS believes that, to be considered an ESU, a population must be genetically distinct from other conspecific populations—because population characteristics that are evolutionarily significant must have a genetic basis. This does not mean, however, that the genetic differences must be (or can be, in every case) detected by any particular analytical technique. Thus, NMFS agrees that a lack of direct genetic information does not preclude consideration of a population as an ESU. However if no direct genetic information is available, evidence to support an ESU must be found elsewhere, which inescapably places a greater burden of proof on other characteristics.

Rather than a complete absence of genetic information, the second issue involves how to proceed if available genetic data do not provide evidence for population distinctness. Caution is required in drawing a conclusion of "no difference" on the basis of such data, as there are numerous examples in the scientific literature of well-differentiated populations or species that cannot be reliably distinguished using available genetic techniques, as well as cases in which further analysis has shown previously in distinguishable populations to be genetically different. Again, NMFS agrees that a finding of "no significant difference" on the basis of protein electrophoresis or DNA analysis does not rule out consideration of a population as an ESU. On the other hand, the possibility must also be considered that the available data accurately reflect a lack of overall genetic differences between populations. This hypothesis should be evaluated in terms of the comprehensiveness of the genetic analyses and the observed pattern of genetic variation in the species. Studies that have used large samples and a large number of genetic markers without revealing population differences place a clear burden of proof on other characteristics to satisfy the two criteria for an ESU.

Comment: Several respondents questioned the focus on the past implied by the term "evolutionary legacy." Two of these argued that recent isolates (including those populations isolated as the result of human activities) should be considered "species" under the ESA because every such isolate holds the potential to become evolutionarily important to the species (possibly even become a new species) at some point in the future. Another respondent argued that some populations that have been evolutionarily important to the species in the past may be "dead ends" in terms of future evolutionary potential.

Response: NMFS believes that considering recently isolated stocks to be ESUs simply on the basis of their isolation is not appropriate. The loss of such isolates, whether resulting naturally or from human activities, would generally not represent an irreversible loss of diversity to the species because presumably most of the genetic diversity contained in the isolates would still reside in the parent population. The isolate might eventually become an ESU if the isolation were to persist for a long enough period of time. If, however, fragmentation into isolated segments poses a threat to a larger population unit as a whole, the entire unit may be considered for protection, as discussed under "Groups of Populations" below.

The term "evolutionary legacy" was not meant to be construed only in a historical sense. Rather, the term is used in the sense of "inheritance"—that is, something received from the past and carried forward into the future. This reflects the concern expressed in the ESA "to better safeguarding * * * the Nation's heritage in fish, wildlife, and plants." (ESA section 2(a)(5)). Specifically, the evolutionary legacy of a species is the genetic variability that is a product of past evolutionary events and that represents the reservoir upon which future evolutionary potential depends. In evaluating vertebrate populations, NMFS cannot predict which ones will play major evolutionary roles in the future. Rather, NMFS believes that efforts should focus on conserving genetic resources of species (their "evolutionary legacy") so that the dynamic process of evolution will not be unduly constrained in the future.

Anadromy/Nonanadromy

Comment: One respondent argued that for an anadromous/nonanadromous unit to be considered an ESU, it is not necessary to show both (1) that there is a genetic basis for the anadromy and (2) that the anadromous component makes the population distinct; demonstration of either should be sufficient. Another respondent expressed the fear that under the interim policy, the anadromous portion of a population could become extinct without triggering any ESA protection. A third respondent believed that the key question is, "What is the likelihood of the nonanadromous form giving rise to the anadromous form after the latter has gone locally extinct."

Response: NMFS believes that anadromous and nonanadromous traits should be considered in the same way as other traits in determining whether a population is an ESU. Traits that contribute to evolutionary significance must have a genetic basis, but not all genetically-based traits will make a population an ESU. It is also necessary to ask whether loss of the trait would compromise the distinctiveness of the population. Thus, both conditions must be met. NMFS agrees that the question posed by the third respondent is relevant to the key issue—does the anadromous trait make the population distinct?

Differences in Run-Time

Comment: One respondent argued that differences in run-timing are sufficient to establish ecological/genetic diversity between reproductively isolated populations. Another respondent argued that run-timing distinctions "should be taken into account from a purely biological perspective" and should not be a factor in evaluating distinctiveness unless a link can be shown between run-time differences and the overall health of the biological species.

Response: Run-time differences can provide information relevant to each of the two criteria for an ESU. Timing differences that contribute to reproductive isolation are relevant to the first criterion, and timing differences that also contribute substantially to ecological/genetic diversity are relevant to the second criterion. In both cases, it is first important to establish that the timing differences have an inherent biological basis and are not largely artifacts of past or present management practices. NMFS believes that run-timing differences should be considered in the same fashion as other characteristics in evaluating the two criteria. A demonstration of timing differences does not automatically lead to a firm conclusion regarding either criterion; rather, such information should be considered together with all other available data. Note that it is possible for run-timing differences to be sufficient to establish reproductive isolation between population segments that do not differ enough ecologically/genetically to be considered separate ESUs.

Effects of Supplementation

Comment: One respondent agreed with the statement in the interim policy that evidence merely of the release of exogenous fish is not sufficient to disqualify a population from consideration as an ESU; the important question is whether the introduced fish have successively reproduced and contributed to later generations. The respondent believed, however, that in cases where successful mixing can be documented, it is better simply to apply the two-criteria test for an ESU than to ask (as suggested in the Technical Memorandum) whether stock mixing has compromised evolutionarily important adaptations in the indigenous population.

Response: NMFS agrees with the respondent that meeting the two criteria is the real test of whether a population affected by artificial propagation is an ESU. In making this evaluation, however, it may be useful to consider whether the population was likely to have been an ESU in the past and ask whether stock mixing has compromised the evolutionarily important adaptations that distinguished the original population.

Historic Population Size

Comment: One respondent stated that, with respect to historic population size, the interim policy considers only genetic factors as a cause of extinction. The respondent further stated that the question of historic population size should be considered "only if more direct methods of evaluating the evolutionary importance of a population are inconclusive." Another respondent questioned whether NMFS is likely to be in the position of artificially maintaining units that might naturally undergo periodic episodes of extinction/recolonization, given that ESA protection presumably would extend only to manmade (and not environmental) disturbances.

Response: The Technical Memorandum noted that demographic and evironmental variability poses risks for small populations, and concluded that "such fluctuations may place greater constraints on the long-term survival of small populations than do genetic factors associated with inbreeding." NMFS agrees with the respondent that theoretical considerations about the likely persistence time of small populations should not be used to dismiss strong evidence for long-term reproductive isolation. Historic population size is only one consideration in determining whether a population is an ESU.

It is not likely that NMFS will be artificially maintaining populations that would naturally go extinct because such small populations are unlikely to be considered ESUs, although a collection of them might be. Absent other compelling information, a Pacific salmon population will not be considered an ESU if the historic size is too small to assume that the population has remained isolated over an evolutionarily important time period. Evaluating the historic population size is useful in focusing attention on populations with the greatest probability of representing ESUs. NMFS notes, however, that the ESA allows a "species" to be listed based on natural or manmade threats to its continued existence.

Groups of Populations

Comment: One respondent believed that the topic of groups of populations is very important and should be addressed more thoroughly. One respondent believed that the statement in the Technical Memorandum, "In general * * * ESUs should correspond to more comprehensive units unless there is clear evidence that evolutionarily important differences exist between smaller population segments," is an inappropriate reversal in the burden of proof from the intent of Congress. Another respondent commented that:

> a trade-off must be resolved between the evolutionary significance of that level of population structure and the stability of individual units * * * Groups of spawning aggregations which experience highly reduced gene flow between groups, relative to gene flow within groups, should be considered evolutionary units under the ESA process.

Response: As anadromous species, Pacific salmon spawn in a freshwater environment that is often naturally organized in a hierarchical fashion—major river systems may contain several large tributaries, each with numerous streams fed by smaller creeks, etc. Other areas may be characterized by numerous smaller streams, each entering directly into a tidewater area. In both cases, geographical, environmental, or other factors may naturally lead to genetic structuring of the various spawning aggregations into more or less discrete units. NMFS agrees with the last respondent that the first step in determining the appropriate hierarchical level for consideration as an ESU is to identify units within which levels of gene flow are high relative to the rate of exchange between neighboring units. Often, however, there will be more than one hierarchical level for which this is true. Therefore, it is also important to identify such reproductively isolated units that contribute substantially to the ecological/genetic diversity of the species as a whole.

The statement about "more comprehensive units" was not intended to diminish the level of protection afforded to distinct populations. Rather, it reflects (1) the view that population "distinctness" should be supported by positive scientific evidence, and (2) the concern that fragmenting groups of populations into multiple ESUs on the basis of insufficient data may create artificial units without a biological basis.

Comment: Two respondents believed that the interim policy would not provide sufficient protection for ESUs fragmented by habitat degradation or loss. One of these respondents expressed particular concern for species "exhibiting clinal gradations of certain characters rather than discrete, separate units," arguing that the interim policy might allow destruction of an important component of the population (or its habitat) because it was not sufficiently discrete. Another respondent requested clarification on the linkage between the definition of "species" and the determination of thresholds for "threatened" and "endangered" status, arguing that "the threshold must ensure protection for such smaller populations in order to maintain the long-term viability of the overall ESU."

Response: NMFS believes that "distinctness" as it pertains to the ESA

is an evolutionary attribute of a population; therefore, recent human-influenced events resulting in fragmentation of habitat are unlikely to have created "distinct" populations. Similarly, there may be little biological basis for treating populations showing gradual transition along a geographic or environmental cline as multiple distinct populations.

This does not mean, however, that threats posed by habitat fragmentation should be neglected under the ESA. The underlying concern should be whether important genetic resources of the biological species are at risk because of the fragmentation. If so, then the appropriate action would be to protect the larger population as a whole, rather than the individual fragments. In this context, NMFS recognizes that thresholds for threatened and endangered status must be flexible enough to deal with threats to groups of populations (metapopulations) and clinal populations, as well as more discrete population units. Just as there is no simple formula for determining evolutionary significance, there is no universally applicable numerical threshold for a listing determination; in both types of evaluation, a variety of factors must be considered.

Statistical Considerations

Comment: Several respondents commented on statistical issues. One argued that the statement in the interim policy, "In general * * * the appropriate null hypothesis to test is that no differences exist between the populations being compared," leads to bias against a listing determination. Another cautioned against considering modest, but statistically significant, allele frequency differences as sufficient proof of evolutionarily important differences between populations. A third respondent pointed out that the interim policy does not stipulate a significance level (*e.g.*, the 5-percent or 1-percent level) that should be used for statistical tests.

Response: NMFS was careful in the Technical Memorandum to point out that statistical significance and evolutionary significance are different concepts. The above quotation regarding the "appropriate null hypothesis" referred to a test for statistical signficance. Adopting an initial hypothesis of "no difference" and testing for differences by attempting to reject this "null" hypothesis as implausible is the foundation of most statistical tests. NMFS acknowledges that formal hypothesis testing may play an important role in ESA considerations, but also recognizes that not all types of information relevant to the "species" determination are easily quantifiable in this way. Because of the lack of direct connection between statistical and evolutionary significance, and because different tests used on the same data may give different results, NMFS does not endorse (or recommend) any particular significance level for statistical tests. Instead of setting up an arbitrary cut-off for significance such that (for example) a test result at the $P=0.04$ level triggers a listing and one at the $P=0.06$ level does not, NMFS recommends that the approximate significance level of statistical tests be taken into consideration along with other factors in making the "species" determination. The question of minor but significant genetic differences is addressed above under "Reproductive isolation."

Policy Statement

A stock of Pacific salmon will be considered a distinct population, and hence a "species" under the ESA, if it represents an evolutionarily significant unit (ESU) of the biological species. A stock must satisfy two criteria to be considered an ESU:

(1) It must be substantially reproductively isolated from other conspecific population units; and

(2) It must represent an important component in the evolutionary legacy of the species.

The first criterion, reproductive isolation, does not have to be absolute, but it must be strong enough to permit evolutionarily important differences to accrue in different population units. Insights into the extent of reproductive isolation can be provided by movements of tagged fish, recolonization rates of other populations, measurements of genetic differences between populations, and evaluations of the efficacy of natural barriers. Each of these methods has its limitations. Identification of physical barriers to genetic exchange can help define the geographic extent of distinct populations, but reliance on physical features alone can be misleading in the absence of supporting biological information. Physical tags provide information about the movements of individual fish but not the genetic consequences of migration. Furthermore, measurements of current straying or recolonization rates provide no direct information about the magnitude or consistency of such rates in the past. In this respect, data from protein electrophoresis or DNA analysis can be very useful because they reflect levels of gene flow that have occurred over evolutionary time scales. NMFS will use all available lines of evidence for and against reproductive isolation, recognizing the limitations of each and taking advantage of the complementary nature of the different types of information.

To be considered an ESU, the population must also represent an important component in the evolutionary legacy of the species. The evolutionary legacy of a species is the genetic variability that is a product of past evolutionary events and which represents the reservoir upon which future evolutionary potential depends. This second criterion would be met if the population contributed substantially to the ecological/genetic diversity of the species as a whole. In other words, if the population became extinct, would this event represent a significant loss to the ecological/genetic diversity of the species? In making this determination, the following questions are relevant:

1. Is the population genetically distinct from other conspecific populations?

2. Does the population occupy unusual or distinctive habitat?

3. Does the population show evidence of unusual or distinctive adaptation to its environment?

Several types of information are useful in addressing these questions. Again, the strengths and limitations of the information will be considered in making the determination. Phenotypic/life-history traits such as size, fecundity, and age and time of spawning may reflect local adaptations of evolutionary importance, but interpretation of these traits is complicated by their sensitivity to environmental conditions. Data from protein electrophoresis or DNA analysis provide valuable insight into levels of overall genetic differentiation among populations but little direct information regarding the extent of adaptive genetic differences. Habitat differences suggest the possibility for local adaptations but do not prove that such adaptations exist.

NMFS will use the best scientific and commercial data available and will rely on the biological expertise of the agency and the scientific community in making "species" determinations under the ESA. A "species" determination must be supported by scientific evidence. However, the lack of direct genetic or any other type of information does not preclude consideration of a population as a "species" under the ESA if such a finding is supported by other information.

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William W. Fox, Jr.,

Assistant Administrator for Fisheries.

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