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Evolutionarily Significant Units and the Conservation of Biological Diversity under the Endangered Species Act

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Abstract.—The U.S. Endangered Species Act (ESA) considers "distinct" populations of vertebrates to be "species" (and hence eligible for legal protection) but does not explain how distinctness should be evaluated. A review of the legislative and legal history of the ESA indicates that in implementing the ESA with respect to vertebrate populations, the Fish and Wildlife Service and the National Marine Fisheries Service (NMFS) should strive to conserve genetic diversity scientifically but sparingly. Based on these precepts, NMFS developed a species policy to guide ESA listing determinations for Pacific salmon *Oncorhynchus* spp. According to the policy, a population (or group of populations) will be considered distinct if it represents an evolutionarily significant unit (ESU) of the biological species. The unifying theme of the NMFS species policy is the desire to identify and conserve important genetic resources in nature, thus allowing the dynamic process of evolution to continue largely unaffected by human factors. A review of case histories in which the NMFS policy has been applied shows that it is flexible enough to provide guidance on many difficult issues for Pacific salmon, such as anadromy versus nonanadromy, variation in life history patterns, and the role of hatchery fish in regards to the ESA. Collectively, these case studies also provide insight into approaches for dealing with scientific uncertainty. Some criticisms of the ESU concept (e.g., that it is too subjective and relies too much—or not enough—on genetics) are discussed, as is its applicability to biological conservation outside the ESA.

As amended in 1978 (16 U.S.C. §§ 1532[16]), the U.S. Endangered Species Act (ESA) allows listing of "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" [Section 3(15)]. This language indicates that the scope of the ESA extends beyond the traditional biological definition of species to include smaller biological units. Unfortunately, the ESA does not explain how population distinctness shall be evaluated or measured, and this omission has led to considerable confusion in application of the ESA to vertebrate populations. For example, the Fish and Wildlife Service (FWS) has used a variety of criteria for evaluating population distinctness in species such as grizzly bears, bald eagles, desert tortoises, spotted owls, and alligators.

The issue of vertebrate populations and the ESA is particularly challenging with respect to Pacific salmon *Oncorhynchus* spp. because their strong homing instinct leads to the formation of a large number of local spawning populations that might arguably be considered distinct. Furthermore, recent and widespread declines in Pacific salmon populations have raised the possibility that many might qualify as threatened or endangered "species" under the ESA (e.g., Nehlsen et al. 1991). Following receipt of petitions in 1990 for ESA listing of several Columbia and Snake river salmon populations, the National Marine Fisheries Service (NMFS) published a technical paper (Waples 1991a) and an interim policy (*Federal Register* 56 [13 March 1991]: 10542) on defining distinct population segments of Pacific salmon under the ESA. After a public comment period, the technical paper (Waples 1991b) and the policy (*Federal Register* 56 [20 November 1991]:58612) were revised and published later the same year. The intention of the technical papers and the policy was to provide a biologically sound framework for considering populations under the ESA, with specific guidance for the complex issues involving Pacific salmon.

After briefly summarizing the important concepts in the NMFS species policy, I will explain how the policy has been applied in a number of listing determinations for Pacific salmon. Finally, I will discuss some criticisms of the salmon policy and its applicability to the broader question of defining units for biological conservation outside the ESA.

The National Marine Fisheries Service Salmon Policy

In spite of the failure of the ESA to provide explicit guidance on defining "distinct" populations, an examination of the legislative and legal history of the ESA revealed three guiding principles: (1) an important motivating factor behind the ESA was the desire to preserve genetic variability, both within and between species (e.g., 93rd Congress, 1st Session, 1973. House of Representatives Report 412); (2) the ESA [Section 4(b)(1)(A)] stipulates that listing decisions should be based "solely on the basis of the best scientific and commercial data available"; and (3) a congressional report in 1979 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" (96th Congress, 1st Session, 1979. Senate Report 151). Although not quite self-contradictory, the charge to conserve genetic resources scientifically but sparingly presents a delicate challenge to scientists and policymakers alike.

To balance these themes in a framework consistent with both the letter and intent of the ESA, I adopted as a unifying concept the evolutionarily significant unit (ESU). This term had already seen limited use in the literature (e.g., Ryder 1986), and its usefulness for ESA considerations was suggested by Andrew Dizon of NMFS, who has used an approach based on the ESU for identifying conservation units of marine mammals (Dizon et al. 1992). The framework I developed differs somewhat from that of Dizon et al. and relies on a simple, two-part test for determining whether a population is an ESU (Waples 1991b:12):

> A vertebrate population will be considered distinct (and hence a "species") for purposes of conservation under the Act if the population represents an evolutionarily significant unit (ESU) of the biological species. An ESU is a population (or group of populations) that (1) is substantially reproductively isolated from other conspecific population units, and (2) represents 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 that represents the reservoir upon which future evolutionary potential depends. Some have interpreted this term to mean that NMFS will attempt to determine which populations will play an important role in future evolution of the species. This is not the case; such an attempt would be misguided and probably futile as well. Rather, the intention is to identify the important genetic building blocks of the species as a whole and (because we cannot tell which will be important in the future) conserve as many as possible so that the dynamic process of evolution will not be unduly constrained. In essence, then, the ESU policy of NMFS seeks to implement Aldo Leopold's (1953:147) sage advice: "To keep every cog and wheel is the first precaution of intelligent tinkering."

The NMFS policy identifies a number of types of evidence that should be considered in evaluating each of the two ESU criteria. What follows is only a brief summary of the most important points; readers should consult Waples (1991b) for a more detailed discussion of this topic.

Isolation does not have to be absolute, but it must be strong enough to permit evolutionarily important differences to accrue in different population units. Important types of information to consider include movements of tagged fish, natural recolonization rates, measurements of genetic differences between populations, and evaluations of the efficacy of natural barriers. Each of these measures has its strengths and limitations. Data from protein electrophoresis or DNA analyses can be particularly useful for evaluation of isolation because they reflect levels of gene flow that have occurred over evolutionary time scales.

The key question with respect to a population's evolutionary legacy is, if the population became extinct, would this represent a significant loss to the ecological–genetic diversity of the species? An affirmative answer would lead to a strong presumption that the unit under consideration is an ESU. Again, a variety of types of information should be considered. Phenotypic and life history traits such as size, fecundity, migration patterns, 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 analyses provide valuable insight into the process of 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.

The ESU policy of NMFS provides a framework for addressing several issues of particular concern for Pacific salmon, including anadromous versus nonanadromous population segments, differences in run timing, groups of populations, introduced populations, and the role of hatchery fish. However, although the policy establishes a simple, two-part test for identifying ESUs, it by no means amounts to a simple formula. As illustrated below, application of the policy can be quite complex and often involves professional judgement. This result, however, can be attributed more to the complexities of biological processes than to the policy itself.

Application of the National Marine Fisheries Service Policy in Endangered Species Act Status Reviews

In response to ESA petitions for a number of Pacific salmon populations, NMFS has conducted a series of status reviews to determine whether listings as threatened or endangered species were warranted. By law, a listing determination must be made within 1 year of receipt of an ESA petition. Because the ESA stipulates that these listing determinations should be made on the basis of the best scientific information available, NMFS formed a team of scientists with a background in various aspects of salmon biology to conduct the status reviews. This biological review team (BRT) discussed and evaluated scientific information contained in an extensive public record developed for each of the status reviews. Conclusions of the BRT were used by NMFS in making the formal listing determinations announced in the *Federal Register*, and more extensive scientific reports were published for each of the status reviews as National Oceanic and Atmospheric Administration (NOAA) technical memoranda. The following summary identifies some key issues addressed in status reviews for Pacific salmon completed through mid-1994. Although the status reviews involve evaluation of two questions—is it a species as defined by the ESA? and, if so, is it threatened or endangered?—only the former question is addressed in detail here. For each case study discussed, citations are provided for *Federal Register* notices announcing listing determinations as well as for the NOAA technical memoranda. Geographic features mentioned in the text can be found on Figure 1.

Recent listing determinations by NMFS announced too late to allow discussion in this paper include mid-Columbia River summer chinook salmon *Oncorhynchus tshawytscha* (status review, Waknitz et al. 1995; listing, *Federal Register* 59 [23 September 1994]:48855) and Deer Creek (Puget Sound) summer steelhead *O. mykiss* (*Federal Register* 59 [21 November 1994]:59981).

Snake River Sockeye Salmon

The first of five petitions received by NMFS in 1990 was for Snake River sockeye salmon *O. nerka* (status review, Waples et al. 1991a; listing, *Federal Register* 56 [20 November 1991]:58619). Historically, sockeye salmon occurred in at least six to eight lake systems in the Snake River basin, but by 1990 the only population remaining was in Redfish Lake in Idaho. Extinction of this population also seemed imminent as only 4, 2, and 0 adults returned to spawn in 1988, 1989, and 1990, respectively. Because the nearest sockeye salmon population was over 900 river kilometers away in the upper Columbia River, strong reproductive isolation of Redfish Lake *O. nerka* was not in question. The lengthy freshwater migration and distinctive spawning habitat (almost 1,500 km from the ocean and 2,000 m in elevation, both unequalled by any other sockeye salmon population in the world) provided strong support for the second ESU criterion.

The status review, however, was complicated by uncertainty about the relationship between sockeye salmon and kokanee, the latter being a resident, freshwater form of *O. nerka* that was also native to Redfish Lake (Evermann 1896). In 1910, Sunbeam Dam was constructed about 30 kilometers downstream from Redfish Lake, and by all accounts the dam was a serious obstruction to passage of anadromous fish until its partial removal in 1934. According to one view (Chapman et al. 1990), the dam resulted in the extirpation of the original sockeye salmon population, and anadromous *O. nerka* returning since 1934 were derived from kokanee. Because kokanee were relatively abundant (total estimated abundance was approximately 25,000 fish; Bowler 1990), Chapman et al. (1990) argued that no entity was actually endangered: the original sockeye salmon population was extinct (and hence could not be listed under the ESA), and the kokanee presumably could continue to produce a modest number of anadromous fish indefinitely. An alternative view (Waples et al. 1991a) to that proposed by Chapman et al. was that the original sockeye salmon population had persisted, either by achieving limited passage through the dam or by spawning in areas below Sunbeam Dam and recolonizing Redfish Lake after 1934.

Early in the status review for Snake River sockeye salmon, there was considerable uncertainty about how to consider the kokanee population and the effects of Sunbeam Dam in the listing determination. Once the species policy was developed, it was possible to construct the flow diagram shown in Figure 2. From this diagram it is clear that the first key question to be addressed was, are Redfish Lake sockeye salmon and kokanee separate gene pools? A negative answer would lead to consideration of the sockeye salmon–kokanee gene pool as a single unit in ESA evaluations (right branch of flow diagram), whereas an affirmative answer would lead to

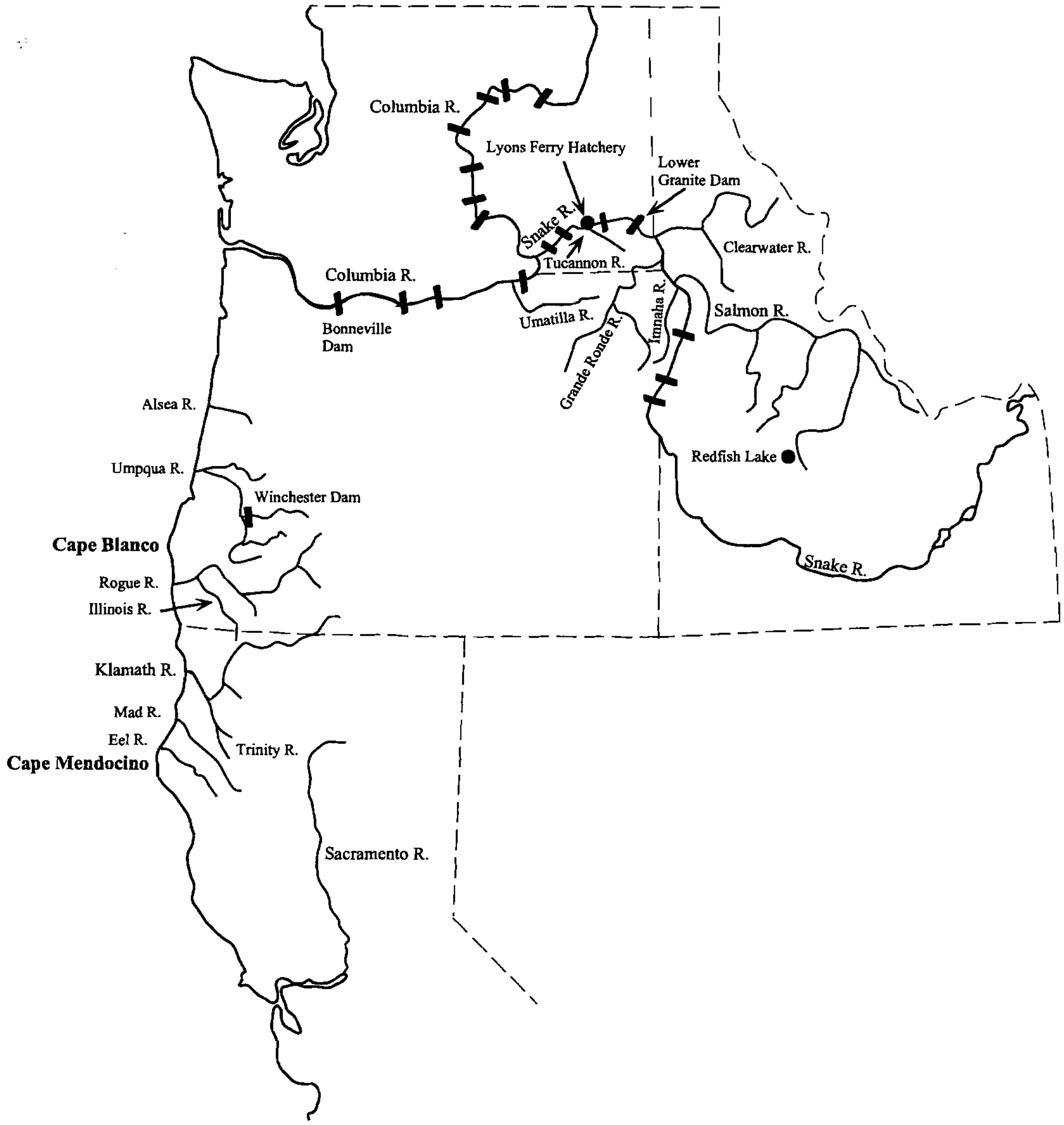

FIGURE 1.—Map of Washington, Oregon, Idaho, and northern California showing location of salmon populations and geographical features discussed in the text.

consideration of the sockeye salmon population as a separate entity (left branch of diagram). For reasons mentioned above, this latter option would presumably lead to recognition of Redfish Lake sockeye salmon as an ESU and, because of its extremely low abundance, eligible for listing as an endangered species under the ESA.

Empirical data could be found to support each of the proposed hypotheses about post-Sunbeam Dam sockeye salmon in Redfish Lake. There is no doubt that the dam was a serious impediment to migration, and it may have completely blocked adult sockeye salmon for as many as 8–10 years (Chapman et al. 1990). Furthermore, it has been observed in several cases (e.g., Foerster 1947; Kaeriyama et al. 1992) that kokanee can produce anadromous offspring, and a study of Redfish Lake in the 1960s found more smolts of *O. nerka* emigrating from the lake in 1 year than could plausibly be explained by the number of anadromous adults spawning in the

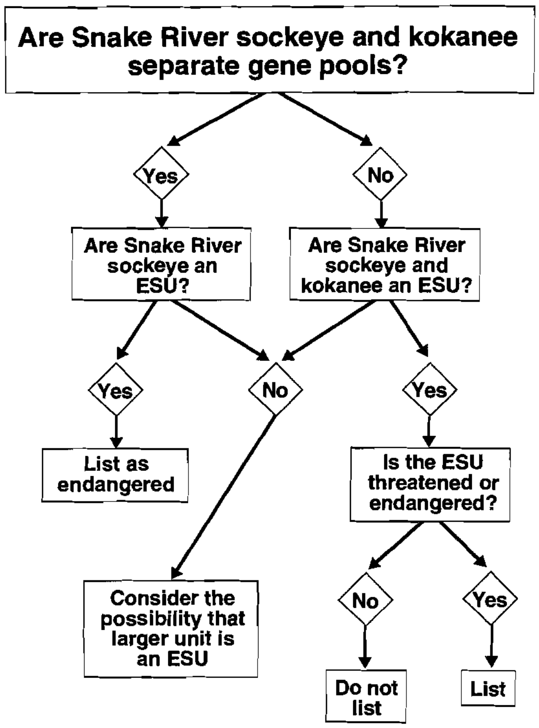

FIGURE 2.—Flow diagram that results from applying the framework of the National Marine Fisheries Service evolutionarily significant unit (ESU) policy (Waples 1991b) to the status review for Snake River sockeye salmon (reproduced from Waples et al. 1991a).

lake the previous year (Bjornn et al. 1968). On the other hand, historical records indicate that anadromous fish passed over Sunbeam Dam in at least some years following the rebuilding of a fish ladder in 1920, and eyewitnesses reported seeing "big redfish" (presumably sockeye salmon and not the smaller kokanee) spawning in Redfish Lake in several years between 1927 and 1933. Therefore, there is no conclusive evidence that the original sockeye salmon population was extirpated. Furthermore, the kokanee population in Redfish Lake spawns in the inlet stream (Fishhook Creek) in August and September, whereas all recent records of sockeye salmon spawning have been on the lake shore in October and November. Thus, substantial reproductive isolation of sockeye salmon and kokanee in Redfish Lake seemed possible, as had been demonstrated between the two forms in several lake systems in British Columbia (Foote et al. 1989).

At the time the listing determination had to be made, there was agreement among the BRT on one issue: there was not enough scientific information to determine with any degree of certainty which of the two scenarios was true. Although a protein electrophoretic study conducted by NMFS during the status review demonstrated that kokanee from Redfish and nearby Alturas lakes were genetically distinct from other samples of *O. nerka* from the Pacific Northwest, no adult sockeye salmon returned in 1990, so a comparison of the two forms in Redfish Lake could not be made. Because there was a lack of consensus within the BRT (as well as within the broader community of fishery biologists in the Pacific Northwest) on how to interpret the limited information about the effects of Sunbeam Dam, the listing determination had to be made in the absence of conclusive scientific information. After considerable discussion, it was concluded that the most appropriate approach was to proceed under the assumption that a component of the native sockeye salmon gene pool still persisted in Redfish Lake and was distinct from the kokanee. A factor that weighed heavily in this consideration was the recognition that the consequences of taking the alternate course (i.e., assuming that recent anadromous *O. nerka* in Redfish Lake were derived from kokanee) and being wrong were irreversible, because the original sockeye salmon gene pool could easily become extinct before the mistake was realized.

Accordingly, a proposal to list Snake River sockeye salmon as an endangered species was published in April 1991, with the final rule coming in November of that year. Subsequently, samples taken from sockeye salmon adults that returned in 1991–1993 established that there are large allele frequency differences between sockeye salmon and kokanee within Redfish Lake (about 25–50% at several loci detected by protein electrophoresis [R. S. Waples, G. A. Winans, and P. B. Aebersold, NMFS, Seattle, unpublished data] and about 20% at a nuclear DNA locus [S. Cummings and G. Thorgaard, Washington State University, and E. Brannon, University of Idaho, personal communication]), thus providing strong support for the hypothesis that recent anadromous *O. nerka* returning to Redfish Lake are not merely the product of seaward drift of Fishhook Creek kokanee.

Snake River Chinook Salmon

In 1990, NMFS was petitioned to list three Snake River runs of chinook salmon *O. tshawytscha* as threatened or endangered species: spring-, summer-, and fall-run fish (status reviews, Matthews and Waples 1991; Waples et al. 1991b; listing, *Fed-*

eral Register 57 [22 April 1992]:14653). The different runs are defined by the season during which adults enter freshwater (or can be enumerated as they pass across a dam). According to the ESU policy of NMFS, the first step in evaluating the petitions was to determine whether the different runs were reproductively isolated. If so, they could be considered separately in the species determination; if not, they would be considered together as a single unit in determining whether the larger unit met the second criterion to be an ESU.

Several lines of evidence made it clear that Snake River fall chinook salmon were strongly isolated from spring- and summer-run fish. Whereas the latter two forms spawn in late summer in upper level tributaries (generally at 1,300–2,000 m elevation), Snake River fall chinook salmon spawn later (generally in October and November) in the main stem and its lower tributaries, at elevations of approximately 500 m or less. Genetic data showing substantial allele frequency differences (e.g., 25–50% at multiple loci) between fall chinook salmon and the other two forms in the Snake River supported the evidence for spatial and temporal isolation. Furthermore, juvenile Snake River fall chinook salmon migrate to sea as subyearlings in their first year of life (ocean-type life history; Healey 1991), whereas spring- and summer-run fish in the basin migrate as yearlings (stream-type life history).

The closest relatives to Snake River fall chinook salmon are fall chinook salmon from the Columbia River, which also have an ocean-type juvenile life history. Several years of genetic data from protein electrophoresis showed modest but consistent allele frequency differences between fall chinook salmon from the Columbia and Snake rivers, suggesting the possibility for long-term reproductive isolation (summarized by Waples et al. 1991b). Further evidence of reproductive isolation came from a tagging study of Columbia River fall chinook salmon conducted in the early 1980s that found high homing fidelity for fish from the mid-Columbia region and no evidence of straying into the Snake River (McIsaac and Quinn 1988).

Two lines of evidence were key in evaluating the second ESU criterion—contribution of Snake River fall chinook salmon to the ecological–genetic diversity of the species as a whole. First, the Snake River has greater turbidity, a higher pH and total alkalinity, and a higher and more variable temperature than does the Columbia River. During the summer months, when juvenile fall chinook salmon are rearing or migrating in the river, water temperatures in the Snake River can be as much as 6–8°C warmer than in the Columbia River (Utter et al. 1982). Thus, the Snake River population may have developed physiological tolerance for elevated water temperatures, behavioral strategies to avoid warm water, or both. Second, several years of data from recovery of marked hatchery fish showed that fall chinook salmon from the two rivers differed in their ocean distribution; with Columbia River fish are more commonly taken in Alaskan waters and Snake River fish are more common in waters off California, Oregon, and Washington (Waples et al. 1991b).

As with the Snake River sockeye salmon, however, there was a difficult issue that remained to be resolved: evidence that isolation of the Snake River population began to break down in the 1980s as a result of straying by hatchery fish from the Columbia River. In particular, a large-scale program had been initiated in the early 1980s in an attempt to restore fall chinook salmon to the Umatilla River, the last major tributary of the Columbia River below the confluence with the Snake River. Apparently as a result of poor acclimation of juveniles and inadequate river flows for returning adults, in the late 1980s fish from the Umatilla program began to appear in the Snake River in alarming numbers. At Lyons Ferry Hatchery, a facility designed to provide a means of conserving the genetic diversity of Snake River fall chinook salmon, stray Columbia River hatchery fish constituted almost 40% of the broodstock spawned in 1989. Equally disturbing, a sample of tagged fish taken in 1990 at Lower Granite Dam (the uppermost dam on the Snake River) indicated that stray Columbia River hatchery fish had penetrated some distance into the Snake River, and the presence of strays on the spawning grounds was verified by recovery of carcasses of several tagged fish.

These data raised concerns that the distinctiveness of the Snake River population (i.e., the qualities that made it a species under the ESA) had been compromised by the stray fish from the Columbia River. However, given that (1) there was general agreement that an ESU was present until at least the early 1980s, (2) substantial straying of Columbia River hatchery fish had occurred only within the last generation, and (3) no direct evidence existed for genetic change to wild fall chinook salmon in the Snake River, the BRT felt it would be premature to conclude that the ESU no longer exists. Snake River fall chinook salmon were listed as a threatened species in 1992.

As was the case for fall chinook salmon, life history and genetic data indicated that the closest relatives to the spring and summer chinook salmon

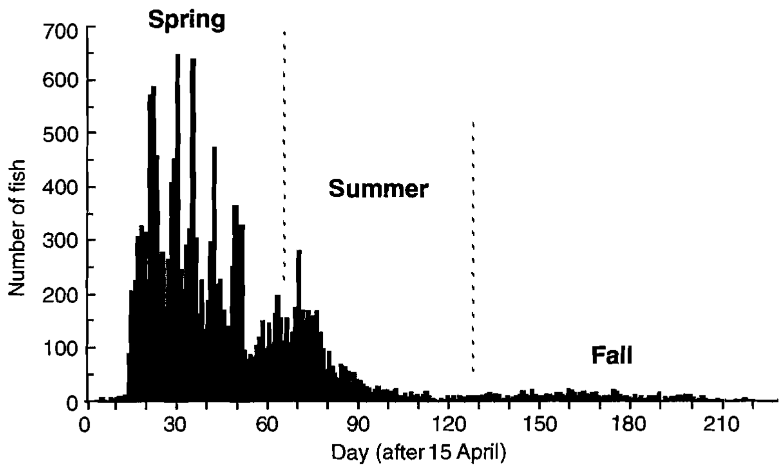

FIGURE 3.—Timing of adult chinook salmon passing Lower Granite Dam on the Snake River, Washington, on their upstream spawning migration in 1989. By convention, fish passing the dam prior to 16 June are considered spring run, those passing between 17 June and 16 August are considered summer run, and those passing from 17 August on are considered fall run.

from the Snake River are found in the Columbia River. However, the upper tributary spawning areas of the two rivers are well isolated from each other geographically. Distinctive habitat features of the upper Snake River basin (similar to those described above for Snake River sockeye salmon) also indicated that Snake River spring and summer chinook salmon were in a different ESU than were the Columbia River populations. Thus, the key issue that remained to be resolved was the relationship between spring- and summer-run fish in the Snake River.

Although two or more modes in adult run timing can be observed in any given year (Figure 3), it was clear that the inflexible dates for defining the runs were not sufficient to demonstrate that two independent units existed in the Snake River. Thus, the BRT focused on information for individual spawning populations. Some subbasins are considered to have only one run type; in others, both spring- and summer-run fish are believed to occur. Fish that spawn slightly earlier and at higher elevation are generally considered to be spring-run fish, and those that spawn later and at lower elevation are considered to be summer-run fish. Therefore, a key question was whether summer chinook salmon from a particular stream were more closely related to summer chinook salmon from other streams than they were to spring chinook salmon from the same stream. That is, the BRT looked for evidence to indicate whether the two run types were independent, monophyletic evolutionary units.

After reviewing available phenotypic and life history information, the BRT was unable to find any characters that consistently distinguished spring- and summer-run fish in the Snake River. Genetic data from protein electrophoresis showed a similar pattern. A hierarchical gene diversity analysis (Waples et al. 1993) of samples from both run types found that most (78%) of the total intersample diversity was attributable to geographic differences (between localities within drainages or between drainages within run times). In contrast, differences between Snake River spring- and summer-run fish as a whole accounted for little (8%) of the total intersample diversity (Figure 4). On the basis of the genetic, phenotypic, and life history information, the BRT concluded that Snake River spring/summer chinook salmon should be considered a single ESA species, and they were listed as threatened under the ESA.

In 1994, NMFS published an emergency rule (*Federal Register* 59 [18 August 1994]:42529) that temporarily revised the status of Snake River spring/summer and fall chinook salmon from threatened to endangered. Subsequently (*Federal Register* 59 [28 December 1994]:66784), NMFS initiated a process to finalize the change in status for Snake River chinook salmon.

Lower Columbia River Coho Salmon

Coho salmon *O. kisutsch*, which have become extinct in most upper areas of the Columbia River

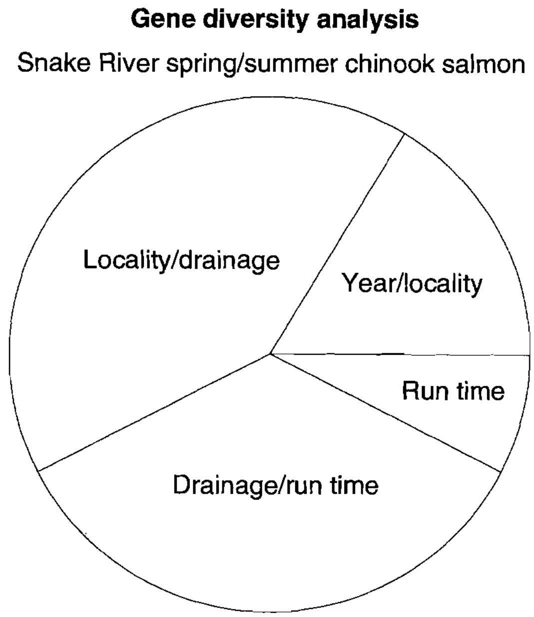

FIGURE 4.—Partitioning total intersample gene diversity (F_{ST} = 0.034) into various hierarchical components for Snake River spring/summer chinook salmon (modified from Waples et al. 1993). The geographic component to the intersample diversity (localities within drainages and drainages within run times) is much larger than that due to run-timing differences.

basin in recent decades, were historically abundant in the lower Columbia River (below Bonneville Dam), with adult returns averaging approximately 1 million fish per year early in this century. By the 1950s, overfishing and habitat degradation had dramatically reduced annual returns to perhaps 5% of their historic levels, and state fishery managers embarked on a large-scale hatchery program in an attempt to restore the runs. Although abundance has been quite variable over the last three decades, adult returns have averaged approximately 500,000 fish in many recent years. However, the number of naturally spawning fish continued to decline, prompting a petition in 1990 to list naturally spawning coho salmon in the lower Columbia River under the ESA (status review, Johnson et al. 1991; listing, *Federal Register* 56 [27 June 1991]:29553).

Although the BRT concluded that there was probably at least one ESU of coho salmon historically in the Columbia River, the difficulty was in determining what remained of this ESU in the 1990s. After declining in the 1950s to a small fraction of their historic abundance, natural populations suffered three decades of extremely high (85–95%) harvest rates directed at the more productive hatchery fish. Furthermore, extensive stock transfers among the hatcheries (Figure 5) and widespread releases of juvenile hatchery fish into virtually every major tributary in the lower Columbia River posed substantial threats to the genetic integrity of the remaining natural populations.

The status review for lower Columbia River coho salmon raised important questions about the role of hatchery fish in ESA evaluations. These issues have played a role in each of the other status reviews conducted to date, but that for Columbia River coho salmon was unusual because of the overwhelming influence of artificial propagation. Because of the emphasis in the ESA on conserving species and their ecosystems, the ESU policy of NMFS focuses on "natural" fish, which are defined as progeny of fish that spawn naturally, whether of wild or hatchery origin (Waples 1991b). This approach directs attention to fish that spend their entire life cycle in natural habitat. Implicit in this approach is the recognition that fish hatcheries are not a substitute for natural ecosystems. More details about NMFS policy regarding artificial propagation of Pacific salmon in relation to the ESA can be found elsewhere (Hard et al. 1992; *Federal Register* 58 [5 April 1993]:17573).

In the lower Columbia River, approximately 25,000 coho salmon spawn naturally each year (Johnson et al. 1991), but the vast majority of these were reared in hatcheries as juveniles and thus are not natural fish. The general consensus of fishery biologists in the region was that if any naturally spawning fish remained that represented the historic legacy of the indigenous populations, they would be found in streams in which spawning occurred much later (post-December) than that of most hatchery populations. However, little biological information was available for the late-spawning populations, and attempts to gather new information during the status review were largely unsuccessful. The NMFS conducted an extensive genetic survey of coho salmon from the lower Columbia River and compared new results with data from previously published studies. The genetic data provided some evidence for reproductive isolation of Columbia River coho salmon from those in other geographic regions but found "no apparent geographical or temporal structuring or separation between hatchery and wild stocks" (Johnson et al. 1991:28).

After considerable discussion, the BRT concluded that they were unable to identify any remaining natural populations of coho salmon in the lower

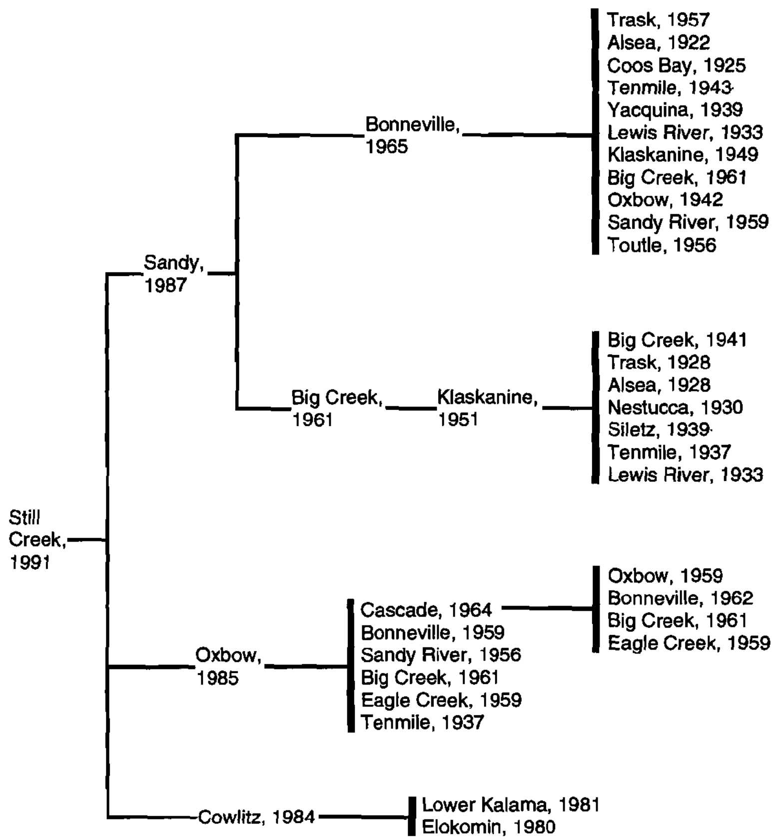

FIGURE 5.—Each of three stocks of coho salmon (Cowlitz, Oxbow, and Sandy) released into Still Creek between 1984 and 1987 are of mixed origin. For example, the Oxbow stock received transfers of eggs or fish from at least six other stocks between 1937 and 1964, and each of these six stocks has a mixed history as well (origins shown for only Cascade stock). Still Creek was identified as one of the sites in the lower Columbia River most likely to have a remnant run of native, naturally spawning coho salmon. Reproduced from Johnson et al. (1991).

Columbia River that warranted protection under the ESA. In 1991, NMFS found the petition for an ESA listing to be unwarranted.

Illinois River Winter Steelhead

In May 1992, NMFS received a petition for ESA listing of winter-run steelhead *O. mykiss* from the Illinois River, a tributary of the Rogue River in southern Oregon (status review, Busby et al. 1993; listing, *Federal Register* 58 [20 May 1993]:29390). In the Pacific Northwest, steelhead are generally considered to be either summer or winter run, based (as in chinook salmon) on the timing of adult entry into freshwater. The petitioners argued that Illinois River winter steelhead were an ESA species because of phenotypic and life history differences in comparison with other steelhead populations from the Rogue River.

Although Busby et al. (1993) found some evidence that Illinois River steelhead differed from other populations in the Rogue River in traits such as smolt age and age and size at spawning, the differences were small and the biological significance unclear. Furthermore, in none of these traits did Illinois River steelhead differ substantially from other coastal steelhead populations; if anything, the Rogue River populations were the ones that were somewhat distinctive. A protein electrophoretic survey of 15 steelhead populations from Oregon and northern California conducted by NMFS found evidence for genetic heterogeneity among populations, but no evidence for distinctiveness of steelhead from the Illinois River (Busby et al. 1993). In fact, in pairwise comparisons using genetic distance values, three of the four Illinois River samples were genetically more similar to a population from out of the basin than they were to any of the other Illinois River samples.

On the basis of this information, NMFS concluded that Illinois River winter steelhead did not by themselves constitute an ESA species, and the petition was found to be not warranted. However, NMFS also recognized that the petitioned population was part of a larger ESU whose boundaries remained to be determined. Accordingly, a broader status review was initiated to determine the boundaries of that ESU and whether it was threatened or endangered. That broader status review has recently been completed (Busby et al. 1994), and it provides a good example of how multiple lines of evidence can be used to define ESUs.

A prominent physical and ecological feature of the west coast of the United States is the Klamath Mountains Geological Province, which extends from the vicinity of Cape Blanco in southern Oregon to include the Klamath River basin in northern California. Geologically, the province is distinctive in that it includes northern extensions of formations typical of the California Coastal Ranges and the Sierra Nevada. Ecologically, the province includes areas that are warmer and drier than are coastal regions to the north and south; interior valleys receive less precipitation than does any other location in the Pacific Northwest west of the Cascade Range. The vegetation combines elements from California, the northern coast, and eastern Oregon, including a large number of endemic species (Whittaker 1960). Zoogeographic studies have also found similarities between the freshwater fish faunas of the Klamath and Rogue rivers, the two major rivers draining the Klamath Mountains Geological Province.

The "half-pounder" life history form of steelhead also appears to be restricted to southern Oregon and northern California, having been described from the Rogue, Klamath, Eel, and Mad rivers. Following their smolt migration, half-pounders spend only a few months at sea before returning to freshwater at a size that inspired their name. After overwintering in freshwater, half-pounders return to sea before their spawning migration the following fall or winter. Although the factors responsible for this life history strategy are poorly understood, expression of this trait is likely due to a combination of genetic and environmental factors.

The nearshore ocean environment in this region is strongly affected by seasonal upwelling. The strength and consistency of upwelling south of Cape Blanco yields highly productive waters. The area of increased upwelling extends, with some local variations, as far south as 33°N.

Patterns of ocean migration of salmon and steelhead may reflect reproductive isolation of spawning populations. Chinook salmon populations from south of Cape Blanco are generally considered south migrating (e.g., to ocean areas off southern Oregon and California), whereas most stocks from north of Cape Blanco are considered north migrating (Nicholas and Hankin 1988). Other studies (see Pearcy 1992) suggest that coho salmon and steelhead from south of Cape Blanco also may not be strongly migratory, remaining instead in the productive oceanic waters off southern Oregon and California.

Several lines of evidence (geology, ecology, life history, zoogeography, and genetics) thus suggest that Cape Blanco forms the northern boundary for the ESU that contains Illinois River winter steelhead. To the south, Cape Mendocino is a natural landmark associated with changes in ocean currents and represents the approximate southern limit of summer steelhead and the half-pounder life history strategy. However, the Klamath River basin forms the southern boundary of the Klamath Mountains Geological Province as well as the Klamath–Rogue freshwater zoogeographic zone. Furthermore, genetic data compiled by NMFS showed a sharp transition between steelhead populations from the Klamath River basin and those farther south (Busby et al. 1994). Therefore, the BRT concluded that the geographic boundaries of the ESU that contains Illinois River steelhead extend from Cape Blanco in the north to include the Klamath River basin in the south. In early 1995, NMFS proposed that Klamath Mountains Province steelhead (including summer-, fall-, and winter-run fish) be listed as a threatened species under the ESA (*Federal Register* 60 [16 March 1995]:14253).

Umpqua River Cutthroat Trout

In April 1993, NMFS was petitioned to list sea-run cutthroat trout *O. clarki* from the North and South Umpqua rivers under the ESA (status review, Johnson et al. 1994; listing, *Federal Register* 59 [8 July 1994]:35089). Because *O. clarki*, like *O. mykiss* and *O. nerka*, has both anadromous and resident life history types, the first issue to address was the relationship between the two forms in the Umpqua River. In this case, the situation was complicated by the possibility that a third (potamodromous) life-history type occurs in the Umpqua River, consisting of fish that migrate extensively in freshwater but do not enter the ocean.

This potamodromous life history type provides a possible link between anadromous and resident fish that may act to retard divergence between the life history forms. Sea-run cutthroat trout also have other distinctive life history traits that may have a similar effect. Unlike sockeye salmon, sea-run cutthroat trout do not necessarily die after spawning, and it is generally believed that the incidence of repeat spawning is higher than it is in steelhead. Sea-run cutthroat trout are also distinctive among anadromous salmonids in that they do not overwinter at sea; rather, it is believed that each year after only a few months at sea they return to freshwater and overwinter there. In addition, it is thought that a cutthroat trout that has gone to sea and returned may spend an entire year (or more) in freshwater before migrating to the sea again.

In combination, these traits suggest that opportunities for reproductive isolation between the different life history forms are not as great as in other *Oncorhynchus* species. Therefore, the BRT concluded that, at least until better information is developed, all life history forms of *O. clarki* in the Umpqua River should be considered part of the same ESU. The BRT also concluded that cutthroat trout from the Umpqua River probably were substantially reproductively isolated from other coastal cutthroat trout populations.

On three other key issues, however, the BRT concluded that there was insufficient information to allow a completely scientific determination. First, there remains some uncertainty about the geographic boundaries of the ESU. There are some distinctive features of the Umpqua River drainage, which originates in the Cascade Mountains rather than in the Coast Range, where most other coastal rivers originate. Anadromous cutthroat trout in the Umpqua River migrate farther inland than do cutthroat trout in most other coastal rivers, and the petitioners (ONRC et al. 1993) suggested that elevated water temperatures may have promoted adaptations in Umpqua River cutthroat trout. However, it is not clear whether water temperatures were historically elevated, and virtually no biological information was available during the status review on resident or potamodromous forms of Umpqua River cutthroat trout.

Second, the evolutionary lineage of present-day anadromous cutthroat trout in the Umpqua River is uncertain. Counts of adult (presumably sea-run) fish crossing Winchester Dam (river kilometer 190) are probably the most reliable data for Umpqua River cutthroat trout, and these records show that the number of fish declined to very low levels in the mid-1950s, increased dramatically from about 1960 to 1975, and rapidly declined again after about 1976. The period of increase coincides almost exactly with releases into the Umpqua River of sea-run cutthroat trout from the Alsea River Hatchery on the Oregon coast. The most parsimonious explanation for the sudden increase in adults passing Winchester Dam in 1960–1975 is that they represent predominantly Alsea River Hatchery fish. Alsea River fish have a later run timing than the Umpqua River fish, and a shift toward later run timing in fish returning to Winchester Dam occurred after 1960 (Johnson et al. 1994). There is some evidence of a shift back toward the original run timing after cessation of the hatchery program. The unresolved issue is, what do the few remaining anadromous fish represent: remnants of the original Umpqua River gene pool, descendants of the Alsea River Hatchery fish, or a mixed lineage?

Finally, although the precarious status of the remaining sea-run fish in the Umpqua River was not in question, the status of the other two forms of *O. clarki* was essentially unknown. The existence of potamodromous fish in the Umpqua River was still largely a hypothesis, and the total information available to the BRT on abundance of resident *O. clarki* in the Umpqua River drainage amounted to a list of lakes believed to contain cutthroat trout.

This status review was thus distinctive in the lack of reliable information on virtually every key aspect of cutthroat trout biology, both for the species in general and for Umpqua River sea-run cutthroat trout in particular. Given this reality, and the legal obligation to decide whether to propose a listing within 1 year, NMFS was faced with two general options: (1) reject the petition because either (a) the petitioned entity is not an ESA species, or (b) the species is not threatened or endangered; or (2) propose a listing. Option 1b would require that an ESA species be defined and found not to be threatened or endangered. This, clearly, was not what the BRT concluded. Because the BRT concluded that all life history forms of cutthroat trout in the Umpqua River were part of the same ESU, option 1a was feasible but not particularly satisfactory and would not have represented a resolution of the issue. Option 2, however, also was problematical because it would presume that an ESU was identified and determined to be threatened or endangered, determinations the BRT concluded could not be made from a purely scientific standpoint. Option 2 would therefore require that NMFS adopt a conservative approach on each of the three unresolved issues: geographic extent of the ESU, the effects of introduced hatchery fish, and the abundance of resident and potamodromous fish. In the end, NMFS elected to take this approach and propose a listing of Umpqua River cutthroat trout as an endangered species.

Sacramento River Winter-Run Chinook Salmon

The winter run of chinook salmon from the Sacramento River was the first salmon population listed as a "distinct population segment" under the ESA (listing, *Federal Register* 55 [5 November 1990]: 46515). Although this action preceded the development of the ESU policy of NMFS, the listing determination did discuss biological characteristics of the population (e.g., unique run timing within the species and temporal isolation from other chinook salmon runs in the river) that are relevant to ESU evaluations.

Smith et al. (1995, this volume) express concern that although the winter run is listed, the other runs of chinook salmon in the Sacramento River (spring, fall, and late-fall) may not qualify for ESA protection under the NMFS ESU policy. Because the ESA status of these populations have not been formally considered by NMFS, it would be premature to speculate whether any or all of the other runs should be listed. Although NMFS has not yet determined how many ESUs include Sacramento River chinook salmon, each of these runs belongs to some ESU, and the ESU (or ESUs) as a whole could be listed if determined to be threatened or endangered. Even if it were concluded that an ESU contained more than one nominal run type, conservation of the diversity within the ESU could still be accomplished by following a procedure similar to that for Snake River spring/summer chinook salmon.

Atlantic Salmon

Following receipt of a petition to list all U.S. populations of Atlantic salmon as a threatened or endangered species under the ESA, NMFS and the FWS conducted a joint status review (Anonymous 1995) that used the ESU policy of NMFS as the basis for addressing the species issue. The status review concluded that, because Atlantic salmon had been extirpated from many rivers in southern New England as far back as the eighteenth century, populations of mixed, nonnative origin that had been reintroduced into these streams did not qualify for protection under the ESA (*Federal Register* 60 [17 March 1995]:14410). However, NMFS and the FWS also concluded that populations from seven rivers in Maine did represent an historic ESU of Atlantic salmon and announced an intention to issue a proposed rule regarding the status of this ESU in the near future.

Comprehensive Status Reviews

The status reviews discussed above were all initiated by ESA petitions. Ideally, of course, status reviews should be conducted proactively on a comprehensive basis, because ESUs can best be identified in the broader context of the range of variation found within the entire species. Toward this end, NMFS recently announced (*Federal Register* 59 [12 September 1994]:46808) that it was initiating comprehensive ESA status reviews for all Pacific salmon and anadromous trout (cutthroat trout and steelhead). The status reviews will cover all populations in California, Oregon, Idaho, and Washington and are scheduled for completion in 1996. Recently, NMFS announced results of the first of these comprehensive status reviews, that for coho salmon (status review, Weitkamp et al., in press; listing, *Federal Register* 60 [25 July 1995]:38011). The status review identified six ESUs of coho salmon from central California to southern British Columbia, and NMFS proposed listing the three southernmost ESUs as threatened species and declared that two of the remaining ESUs should be considered candidate species for future listing.

Discussion of Case Studies

The listing determinations described above illustrate how the ESU policy of NMFS has been applied in a variety of case studies. Two recurring themes are worth noting.

Life history diversity.—Two of the more common traits contributing to life history diversity in anadromous Pacific salmonids are run timing and anadromy versus nonanadromy. In applying the ESU policy of NMFS to these issues, the first question to address is whether the different forms are reproductively isolated. Results of the status reviews conducted to date indicate that there is no universal answer to that question. Substantial evidence for reproductive isolation led to separate ESA consideration for Snake River fall versus spring/summer chinook salmon and for Redfish Lake sockeye salmon versus kokanee, although conclusive evidence in the latter case was not obtained until after the final listing determination. On the other hand, inability to find consistent biological differences between spring and summer chinook salmon in the Snake River, summer, fall, and winter steelhead in the Klamath Mountains Geological Province, and resident, potamodromous, and anadromous cutthroat trout in the Umpqua River led to inclusion of multiple life history forms within these ESUs. These results show that ESA evaluations of life history diversity in Pacific salmonids will have to continue to be guided strictly by biological considerations and not by convention.

Uncertainty.—Collectively, the listing determinations described above provide considerable insight into how NMFS has addressed the issue of scientific uncertainty, which can be expected to arise to some extent in virtually every attempt to define conservation units. In general, NMFS has demonstrated a strong inclination to give the benefit of the doubt to the resource in these situations. Thus, NMFS proceeded with a listing of Snake River sockeye salmon in spite of uncertainty about the relationship between sockeye salmon and kokanee in Redfish Lake and has proposed a listing of Umpqua River cutthroat trout in spite of substantial uncertainty on several key issues. With Snake River fall chinook salmon, NMFS also elected to go forward with a listing in spite of evidence for a high level of straying by Columbia River hatchery fish in recent years and considerable uncertainty about the effects of this straying on the remaining natural population in the Snake River.

How far should the benefit of the doubt extend to the resource in cases of uncertainty? This is not primarily a scientific question, but some insight into how NMFS has dealt with this issue can be gained by considering the status review for Lower Columbia River coho salmon. Considerable uncertainty also existed about the status of naturally spawning coho salmon in the lower Columbia River, but NMFS did not propose a listing. In this case, the evidence for massive and long-term effects on natural coho salmon populations from overharvest, habitat degradation, and artificial propagation was overwhelming. Given that reality, the BRT looked for tangible evidence that coho salmon which retained the distinctive characteristics of the original population still existed in the lower Columbia River. Lacking convincing evidence for this, the BRT concluded that it could not identify a population or populations that warranted protection under the ESA.

Criticism of the Evolutionarily Significant Unit Concept and the National Marine Fisheries Service Species Policy

Because scientists often cannot even agree on how to define taxonomic or biological species, it is not surprising that a framework for formally recognizing smaller units should be controversial. This section briefly reviews some of the criticisms of the ESU concept and the ESU policy of NMFS that have been raised in the nearly 4 years since it was published. Many of the comments were made in public meetings or in submissions to the ESA administrative record, but formal literature references are provided as available.

Comment: Defining "distinct" populations under the ESA is primarily a legal and policy issue rather than a biological one (Rohlf 1994).

The ESA is concerned with avoiding extinctions. Because extinction is a biological process, it makes little sense to discuss extinction of units that do not have an underlying biological basis. Although legal and policy issues have a legitimate role in establishing the general context under which populations are considered (hence the admonition of the 1979 Senate report [96th Congress, 1st session, 1979. Senate Report 151] to use the ability to list vertebrate populations "sparingly"), it would be inconsistent and contrary to the goals of the ESA to abandon fundamental biological principles in defining units for conservation.

Comment: The ESA [Section 2(a)(3)] states that species are of "esthetic, ecological, educational, historical, recreational, and scientific value to the Nation and its people," and these qualities should be considered in evaluating population distinctness.

These are all good reasons why it is important to conserve biological diversity in general, but they are not necessarily good reasons for deciding which units to conserve. Because extinction is irreversible, effective conservation of biological diversity must be based on long-term considerations. In contrast, society's view of which species are of recreational or aesthetic value is subject to change, and many species that will be economically or scientifically important in the future may not be recognized as such today. Coggins (1991:64) described one of the remarkable features of the ESA.

> In 1918, Congress acted to protect birds because they sang prettily; in 1940, Congress singled out the bald eagle for preservation as the living national symbol. By

1973, Congress had dispensed with species-by-species evaluations of good and bad in terms of value to *Homo sapiens*. It simply said that all fauna and flora species of whatever utility were entitled to continued existence.

Comment: The ESU policy of NMFS would allow fragmentation and loss through attrition of large, composite ESUs. It does not adequately consider population viability and ignores metapopulation structure.

The first concern is understandable: if NMFS were to make determinations of threatened and endangered status largely on the basis of absolute abundance levels, it might be possible to avoid listing a large ESU even if it faced pervasive declines throughout its geographic range. In practice, however, this is not how NMFS has approached the issue. The NMFS status reviews (e.g., Matthews and Waples 1991; Waples et al. 1991b; Busby et al. 1993) have identified a number of factors that should be considered in evaluating the level of risk faced by an ESU, including (1) absolute numbers of fish and their spatial and temporal distribution; (2) current abundance in relation to historical abundance and current carrying capacity of the habitat; (3) trends in abundance; (4) natural and human-influenced factors that cause variability in survival and abundance; (5) possible threats to genetic integrity; and (6) recent events that have predictable short-term consequences for the ESU.

An example of application of this approach to a large ESU is the listing determination for Snake River spring/summer chinook salmon. Although total abundance for the ESU averaged about 20,000–30,000 adults per year in the decade preceding the listing determination, this represented only a fraction of historical levels. Furthermore, a substantial proportion of the total run was hatchery fish, and the remaining natural spawners were thinly spread over a large geographic area. Finally, recent trends in abundance were uniformly downward throughout the ESU, and this pattern was not expected to improve in the near term because a series of drought years had adversely affected juveniles that would form the basis for subsequent years' adult returns. After considering all these factors, NMFS listed the ESU as a threatened species in 1992. However, NMFS also pointed out that considerable diversity exists within the ESU, in habitat as well as population characteristics, and indicated that conservation of this diversity was important to maintaining viability of the ESU (Matthews and Waples 1991). A draft recovery plan (Bevan et al. 1994) submitted to NMFS by an independent recovery team also recognized this diversity and identified about 40 subpopulations within the ESU that are important to conserve as separate management units.

Recognition of multiple management units in no way limits the ability of those units to function as a metapopulation. Neither NMFS nor the recovery team has suggested that natural dispersal among subpopulations be restricted in any way. If efforts to address the root causes of the decline of Snake River spring/summer chinook salmon are effective, then natural processes should lead to reestablishment of a population structure approximating that which occurred historically.

The ESU policy of NMFS is inherently hierarchical and, far from ignoring metapopulation structure, is easily compatible with this concept. For example, Waples (1991b) discussed how the ESU concept can be applied to groups of populations as well as individual populations. The key is to focus on units that are largely independent from other population units over evolutionary time scales. Populations within such larger groups might exchange individuals on a regular basis, in which case the group might be considered a metapopulation in the sense that term is commonly used. Alternatively, populations within an ESU might experience gene flow only sporadically, with years or decades during which little or no exchange occurs. In any case, however, the ESU policy of NMFS does not focus on subpopulations recently isolated by human factors. Rather, ESU evaluations are based on inferences about historical levels of gene flow that have occurred over evolutionary time scales.

Comment: The ESU policy of NMFS relies too heavily on genetic information. It cannot be used in situations in which genetic data are not available.

It is true that genetics plays a central role in the NMFS ESU concept. However, this is a natural and inevitable consequence of focusing on the conservation of biological units. Extinction of a biological unit is irreversible because it involves the permanent loss of genetic resources capable of regenerating that unit; therefore, a program aimed at avoiding extinction must focus on conserving genetic resources. The ESU concept of NMFS is firmly rooted in genetic principles; it could not be otherwise and still accomplish the goals of the ESA.

The term genetics, however, is often used in a much more restrictive sense—that is, to refer to traits that can be detected by genetic procedures such as protein electrophoresis or DNA analyses. As noted above, genetic data of this type can be instrumental in making ESU determinations, but primarily by providing information about reproductive isolation. The second ESU criterion focuses on adaptive genetic differences that generally must be inferred from nongenetic information. This point is clearly articulated in the species definition paper (Waples 1991b), and much of the effort in the status reviews conducted to date has been directed toward compiling and evaluating phenotypic, life history, and habitat information relevant to the criterion of ecological–genetic diversity.

It is not clear what has spawned the apparently common misconception that ESU determinations cannot be made in the absence of biochemical genetic data; certainly this idea is not supported by an examination of the ESA record of NMFS. For example, when Snake River sockeye salmon were listed as an endangered species in 1991, no genetic data were available for the population because no anadromous adults returned to spawn in 1990. Similarly, no genetic data were available for cutthroat trout from the Umpqua River when they were proposed for listing as an endangered species in 1994. Furthermore, the species definition paper (Waples 1991b) and *Federal Register* notice announcing the final NMFS species policy (*Federal Register* 56 [20 November 1991]:58612) state clearly that such data are not required for an ESU determination. Notably, the vast majority of listing determinations made by the FWS since the ESA was adopted in 1973 have been made in the absence of genetic data. If genetic data are not available, however, evidence to support an ESU must be found elsewhere, which inevitably places a greater burden of proof on other characters. Because data for other characters are often open to multiple interpretations, lack of genetic data may add complexity and contribute uncertainty to ESU determinations.

As can be seen from the discussion that follows, others feel that genetic characteristics are the only traits that should be considered in defining ESUs.

Comment: The concept of evolutionary significance is too subjective to apply in practice.

Biological processes are complex and do not easily lend themselves to tidy categorizations. In recognition of this, the ESU policy of NMFS adopts a holistic, multidisciplinary approach to defining units for conservation under the ESA. Because this approach involves evaluations based on scientific judgement, it has been criticized as being too subjective. Subjectivity can come into play in ESU determinations in two principal ways: in determining how to synthesize diverse types of information and in determining the level of differentiation required for evolutionary significance.

One approach to avoiding subjectivity would be to adopt an objective yardstick for defining units of conservation and apply it uniformly. This approach, however, has its problems as well. First, although it might be possible to identify a number of essentially objective standards for this purpose, the choice of which standard to adopt would necessarily be somewhat subjective (if not arbitrary). Second, even if there were consensus on an appropriate method to use, it would still be necessary to choose threshold values that would guide the identification of conservation units. As Moritz et al. (1995, this volume) point out, "there is no theoretically sound answer to the question 'How much difference is enough?' "; hence, this aspect of the "objective" approach would involve subjectivity as well.

In response to the latter difficulty, some have suggested that ESUs should be stringently diagnosable on the basis of reciprocal monophyly of mitochondrial DNA (Moritz 1994; Moritz et al. 1995) or any heritable trait (Vogler and DeSalle 1994). This approach focuses on qualitative rather than quantitative differences between conservation units, thus avoiding the problem of determining how much difference is enough. The goal of identifying ESUs that are monophyletic is reasonable, because otherwise the ESUs would be of doubtful biological value. However, this approach has several other drawbacks. First, one of the more lively topics in evolutionary biology involves arguments over the various methods that have been used for constructing phylogenies (e.g., Swofford and Olsen 1990; Hillis and Huelsenbeck 1992). One result seems clear: there is no single method that uniformly produces the "best" phylogeny in all situations. Thus, an approach that depends upon inferring phylogenetic relationships is not immune to subjectivity.

Second, the proposal to require that ESUs be uniquely defined by characteristics not found in other ESUs confuses the problem of identifiability with the goals of conservation; the result is a criterion that is overly restrictive. For example, Vogler and DeSalle (1994) would consider a biological unit an ESU only if all individuals in the unit shared at least one heritable trait not found in any individuals from any other unit. Most units that would meet this criterion would typically be recognized as species or subspecies already, which raises the question, what additional conservation benefits would be derived from identifying such units as ESUs? Moreover, Moritz et al. (1995) admit that if their criterion were followed, a number of widely accepted fish species (e.g., many African cichlids and desert pupfish) would not even be recognized as ESUs. They argue that this result does not really cause a conservation problem because such species would generally be recognized and protected through other means, perhaps through recognition of what they term management units. The whole point of the ESA, however, is to prevent extinction of taxa that have not been adequately conserved by other methods, and there is no shortage of these.

If Moritz et al.'s ESU criterion were applied to anadromous Pacific salmonids, the answer would be fairly clear and very simple: the only ESUs would be the recognized species of *Oncorhynchus*. Although Vogler and DeSalle's method allows characters other than mitochondrial DNA to be considered, I believe the result would be essentially the same. Regardless whether one thinks this is a reasonable outcome, it would result in the failure to recognize considerable ecological–genetic diversity within each of the salmon species, diversity which provides the raw material for evolution and which the ESA mandates be conserved.

In the final analysis, whether the concept of evolutionary significance is too subjective to apply in practice should be determined by examining case histories of its application. A number of such examples have been described in this paper, and I believe that collectively they demonstrate the ESU concept can be applied successfully to real biological problems.

Comment: The ESU concept may work for salmon, but it is not applicable to other organisms.

There are several levels at which the relevance of the ESU concept might be considered, all of which are discussed to some extent in papers in this proceedings. Unfortunately, the level at which the ESU concept is being considered is often not clearly articulated, which contributes to confusion in the discussion of its usefulness. Below, I identify four possible levels for approaching biological conservation and briefly discuss the relevance of the ESU concept to each.

The first level is identification of "distinct population segments" of salmon under the ESA. This is the specific purpose for which the ESU concept of the NMFS was developed, and much of this paper has been devoted to a discussion of its usefulness on this level.

On a second level, one can ask whether the ESU concept could be applied to all vertebrate populations under the purview of the ESA. Some issues covered by the ESU policy of NMFS (e.g., anadromy versus nonanadromy) have little direct relevance for most other species. However, other issues that might appear to be esoteric to salmon have clear analogues in other organisms. For example, the biological consequences of straying in salmon are similar to the consequences of migration or dispersal in other species. Similarly, although run timing is not a concept commonly applied to organisms other than anadromous fish, differences in mating season and other life history traits may be equally important for other vertebrates. More generally, any attempt to define biologically meaningful units for conservation should consider the same types of information identified in the NMFS ESU policy: migration, gene flow, and factors affecting reproduction; physical and ecological features of the habitat; and genetic, phenotypic, and life history characteristics. The basic framework of the ESU concept of NMFS is thus in no way specific to salmon and could be applied to other vertebrates under the ESA.

On a third level, one can ask whether the ESU concept could be applied more broadly to the problem of biological conservation in general. Again, I believe the basic framework is flexible enough to provide guidance on this issue for most organisms. There are two caveats, however. First, the concept of reproductive isolation is not particularly useful with organisms that reproduce clonally or by parthenogenesis. Reproductive isolation is briefly discussed below under "Other Species Concepts." Second, the concept of evolutionary significance is truly meaningful only when placed in an appropriate context. The ESA provides a legislative and legal context for interpreting the term "evolutionary significance," the basic precepts of which are, in essence, "conserve genetic diversity, do it scientifically, but do it sparingly." Outside the ESA, conservation efforts might be guided by any of several alternative contexts for interpreting evolutionary significance. For example, at one extreme, every individual might be considered evolutionarily significant because each potentially contributes to the future evolutionary trajectory of the species. Alternatively, evolutionary significance might be interpreted in terms of much larger units (Figure 6). The key factor is how conservative one wants to be (or can afford to be) in attributing evolutionary significance to a biological unit.

Finally, a fourth level of consideration may be appropriate for cases in which the struggle to obtain basic human necessities (food, water, and shelter)

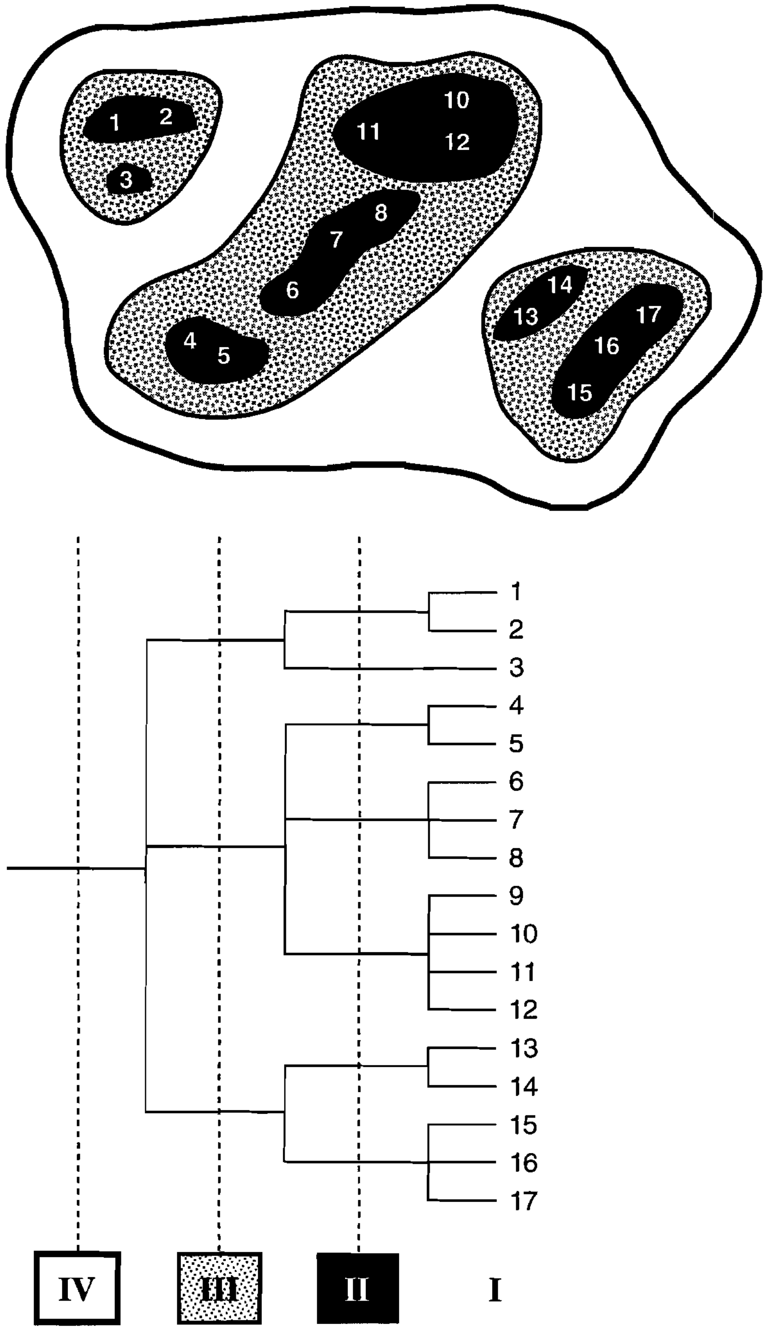

FIGURE 6.—Identifying units for conservation involves two essentially independent steps. First, one or more types of data are used to estimate evolutionary relationships among biological units (e.g., populations), as depicted here in a schematic diagram (top) and a phylogenetic tree (bottom). Additional data might resolve some of the uncertainties apparent in these diagrams (e.g., the relationships among populations 9, 10, 11, and 12). Second, a decision must be made regarding the appropriate hierarchical level on which to focus conservation efforts. In the example shown, approaches focusing on 1 all-inclusive unit, 3 units (stippled shading), 7 units (dark shading), or 17 individual populations all would be consistent with the biological data. Determining the appropriate hierarchical level may involve considering social, economic, and legal factors in addition to scientific ones.

precludes many conservation options (e.g., Mina and Golubtsov 1995, this volume; Stauffer et al. 1995, this volume). Societies in this situation often do not have the luxury of being concerned with the loss of biological populations, and even conservation of individual species may be beyond reach. Although the general concept of evolutionary significance might still be useful in guiding conservation efforts in such situations, the specific framework of the ESU concept as outlined here has little direct relevance to consideration of biological units above the level of species.

Other Species Concepts

In recent years, there have been a number of alternatives suggested to the traditional biological species concept of a group of actually (or potentially) interbreeding populations isolated from other such groups (e.g., Otte and Endler 1989; Avise 1994; see also discussions by Mayden and Wood 1995, this volume; Smith et al. 1995, this volume). In general, discussions of alternative species concepts have focused on a higher level of biological organization than that considered by the ESU concept of NMFS. That is, although the ESA considers distinct populations of vertebrates to be species, that legal definition does not change the biological reality that, in an evolutionary sense, populations are different entities than species. This is true whether species are defined according to biological, phylogenetic, evolutionary, recognition, or cohesion species concepts.

Nevertheless, the issue of reproductive isolation deserves a brief discussion here because it plays a central role in both the biological species concept and the ESU concept of NMFS. Critics of the biological species concept have pointed out that use of reproductive isolation to identify species has two limitations: (1) the test is difficult, if not impossible, to apply to strictly allopatric populations, and (2) many "good" species are not completely isolated reproductively from other species.

Neither of these difficulties represents a real problem for the NMFS ESU concept. First, consideration of allopatric populations as possible ESUs need only focus on the strength and duration of isolation that has actually occurred, not whether the allopatric units are hypothetically capable of reproducing successfully. Second, there is no requirement in the ESU concept of NMFS that reproductive isolation be absolute; rather, it need only be strong enough to allow important differences to develop in different population units. Factors affecting the level of differentiation may include pre- and post-mating isolating mechanisms and selection for locally adapted genes or genotypes. Thus, the NMFS ESU concept takes a functional approach that focuses on the evolutionary consequences of reproductive isolation rather than on the isolation itself.

Joint Interagency Policy

As this paper was being finalized, the FWS and NMFS announced a draft, joint policy on recognition of distinct vertebrate population segments under the ESA (*Federal Register* 59 [21 December 1994]:65884). The joint policy is intended to be consistent with the NMFS salmon policy but will be applicable to all vertebrate species. Although the joint policy does not focus on evolutionary significance, it, like the NMFS salmon policy, proposes a two-part test for determining whether populations are distinct under the ESA. The first criterion (discreteness) is similar to the reproductive isolation criterion in the NMFS salmon policy, and the second (significance to the biological species) is roughly analogous to the contribution to ecological–genetic diversity criterion of the NMFS salmon policy. It is anticipated that NMFS will continue to use the salmon policy for Pacific salmon, and the joint policy will be used for other vertebrates.

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