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Distinct Population Segments

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In reflecting on how the U.S. Endangered Species Act (ESA) has dealt with bio-diversity issues over the past thirty years, it is instructive to review the collection of fifty-seven papers in the 1988 volume by Wilson entitled *Biodiversity* (1988b). Anchored in time midway between enactment of the ESA in 1973 and the present (2006 and counting), Wilson's volume provides a snapshot of the is-sues related to biodiversity that occupied conservation biologists during the first half of these three decades. The vast majority (over 80 percent) dealt with higher levels of biological organization (species or ecosystems), while only two (less than 4 percent) dealt exclusively with diversity at the population level. In sharp contrast, the last decade and a half has seen an explosive interest in con-servation of intraspecific diversity (Rojas 1992; Nielsen 1995; Hughes et al. 1997; Ceballos and Ehrlich 2002). A harbinger of this interest appeared in Wil-son's *Biodiversity* volume in the paper by Ehrlich (1988), who argued that the loss of populations within species was at least as important a problem as the loss of entire species. Much of the recent interest in intraspecific diversity has fo-cused on the concept of *evolutionarily significant units* (ESUs; Ryder 1986), and a variety of approaches to defining ESUs have been proposed (Waples 1991; Di-zon et al. 1992; Vogler and DeSalle 1994; Moritz 1994; Bowen 1998; Crandall et al. 2000).

This chapter considers how these ESA approaches might compare if each were applied to a common conservation problem—how to define conservation units of Pacific salmon (*Oncorhynchus* spp.) from northwestern North Amer-ica. These species have already been the subject of a large-scale application of biological principles to a real-world problem in applied conservation biol-ogy—identifying units that can be considered "species" under the Endangered Species Act. This body of work, based on the ESU framework developed by Waples (1991, 1995), provides a context for evaluating how different the out-comes might be if any of the other most popular ESU approaches were applied to Pacific salmon (see Ford 2004 for a brief example of this type of analysis for one species). Results of this exercise provide insights that may be relevant to

conservation efforts for a wide range of species, both within and outside the aegis of the Endangered Species Act. A general discussion of the strengths and weaknesses of the various ESU approaches can be found elsewhere (Fraser and Bernatchez 2001).

Background on Pacific Salmon

The term "Pacific salmon" is used here to include seven North American anadromous salmonids in the genus *Oncorhynchus*. The five "traditional" species of Pacific salmon—pink (*O. gorbuscha*), chum (*O. keta*), coho (*O. kisutch*), sockeye (*O. nerka*), and chinook (*O. tshawytscha*)—all die after spawning; in contrast, rainbow trout (*O. mykiss*; the anadromous form is known as steelhead) and cutthroat trout (*O. clarki*) can spawn more than once. *O. mykiss, O. clarki*, and other western trout species were formerly considered to be members of the genus *Salmo*, which includes Atlantic salmon and brown trout.

Biology

Pacific salmon have a complex life history that involves spawning and rearing in freshwater streams or lakes and migration (as smolts) to the ocean for growth and maturation in the more productive marine environment. Migratory pathways differ but may include thousands of kilometers in the ocean as well as up to 3,000 kilometers upstream in freshwater. Age at *smoltification* and maturity, timing of juvenile *outmigration*, season of adult entry into freshwater (referred to as *run timing*), and other life history traits vary among species and among populations within species (Groot and Margolis 1991; Waples et al. 2001). Pacific salmon are justifiably renowned for their ability to home accurately to their natal stream. Opportunities for substantial reproductive isolation, together with environmental differences among habitats and a complex life history that requires precise execution of a long sequence of events, have led to a high degree of local adaptation (Ricker 1972; Taylor 1991). Perhaps the best general demonstration of the importance of local adaptation for Pacific salmon is the failure of the vast majority of stock transfer attempts within the historic range of the species to result in new populations (Withler 1982; Wood 1995). Thus, in general Pacific salmon populations are not exchangeable, at least on human time frames.

In spite of the strong homing tendency, some level of natural straying does occur in Pacific salmon, generally into nearby populations (Quinn 1993). Pacific salmon tend to show an isolation by distance pattern of genetic differentiation, provided that distance is measured via a stream network and not as the crow flies. Sharper genetic discontinuities are associated with some geographic

features or historic lineages. Pacific salmon populations are linked in a hierarchical metapopulation network, with interactions between the various hierarchical levels occurring on different temporal scales. Thus, larger geographic/population units may be linked by significant gene flow only on evolutionary time scales.

Evolutionarily Significant Units and the Endangered Species Act

When the first petitions for ESA listing of Pacific Northwest salmon were filed in 1990, they invoked the provision in the act (sec. 3(15)) that allows listing not only of taxonomic species and subspecies, but also *distinct population segments* (DPSs) of vertebrates such as salmon. At that time, neither agency responsible for implementing the ESA (the U.S. Fish and Wildlife Service [USFWS] and the National Marine Fisheries Service [NMFS]) had formal guidance for how to interpret the DPS provision in the act. To address this need, Waples (1991) developed a framework stipulating that a salmon population (or group of salmon populations) would be considered a DPS if it represents an evolutionarily significant unit of the taxonomic species. In this framework, a population unit must satisfy two criteria to be considered an ESU: (1) reproductive isolation, and (2) evolutionary significance. Isolation need not be absolute; it must only be strong enough to allow evolutionarily important differences to accrue in different units. The "significance" criterion is met if the population unit contributes substantially to ecological/genetic diversity of the species as a whole—that is, to its evolutionary legacy. Waples (1995, 9) defined the evolutionary legacy as "genetic variability that is the product of past evolutionary events and that represents the reservoir upon which future evolutionary potential [of the species] depends."

The National Marine Fisheries Service adopted Waples's ESU approach for salmon as a formal policy in 1991 (NMFS 1991). After addressing the initial petitions, NMFS proactively initiated a series of comprehensive status reviews (1994) and used the policy framework to identify ESUs in all seven species of Pacific salmon from Washington, Idaho, Oregon, California, and parts of southern British Columbia (Weitkamp et al. 1995; Hard et al. 1996; Busby et al. 1996; Gustafson et al. 1997; Johnson et al. 1997, 1999; Myers et al. 1998). Reviewing a broad geographic range provided a context for interpreting local patterns of variation, and applying the same approach across seven species, thus providing opportunities to learn from congruent patterns of relationships as well as from species-specific ones. Abundant molecular genetic data are available for Pacific salmon, and these data, together with information from tagging studies and inferences about natural barriers, were the primary factors used to

assess reproductive isolation. Traits that are evolutionarily significant must have a genetic basis and be adaptive, or potentially adaptive, so life history variation was carefully evaluated for the second ESU criterion. However, since most life history traits can be affected by environmental as well as genetic factors, ecological features of the habitat (as a proxy for different selective regimes) were also considered important.

Figures 11.1 to 11.3 illustrate how these three types of information have been used in ESU determinations for salmon. Ecological data were used to identify twelve major ecological-geographic provinces within the study area (fig. 11.1). Although some diversity occurs within provinces, differences among provinces in environmental conditions (and hence local selective pressures) are much more substantial. Ecological features had a strong influence on ESU determinations, particularly when changes in life history or genetic traits were

A. Georgia Basin
B. Temperate Rainforest
C. North Coast
D. Klamath Mountains
E. North California
F. South California
G. California Central Valley
H. Willamette/Lower Columbia
I. Mid - Columbia
J. Upper Columbia
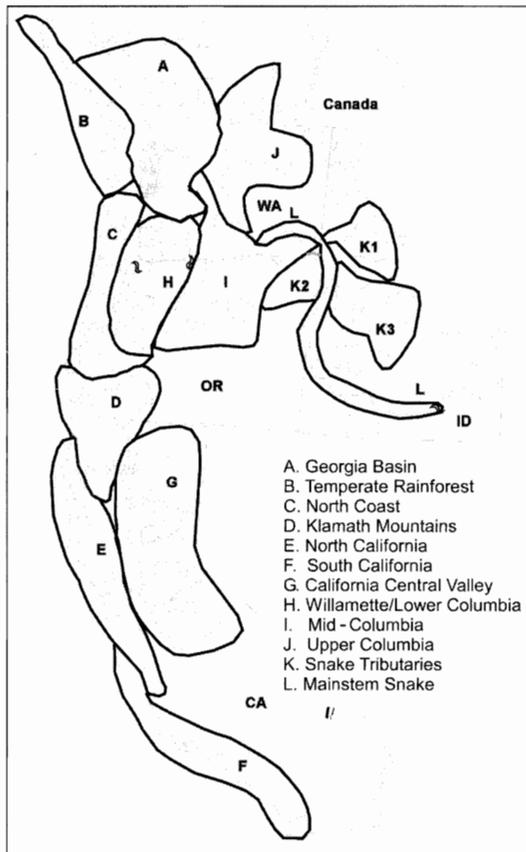K. Snake Tributaries
L. Mainstem Snake

Figure 11.1. Major ecological provinces for Pacific salmon identified by Waples et al. (2001).

congruent with the ecological boundaries (thus providing, respectively, corroboration of evolutionary significance or independent evidence for strong reproductive isolation).

In coho salmon, inferences about ocean ecology are possible based on a two-decade time series of adult size (fig. 11.2). Two patterns are apparent among geographic regions, indicating either a genetically based population difference or substantial environmental differences that can be expected to exert strong selective pressures for local adaptations: (1) Puget Sound populations, but not those from other areas, showed a 50 percent decline in adult size over two decades; and (2) coastal Oregon populations all showed a sharp decrease in adult size in 1983, presumably reflecting the unusually strong El Niño event in 1982.
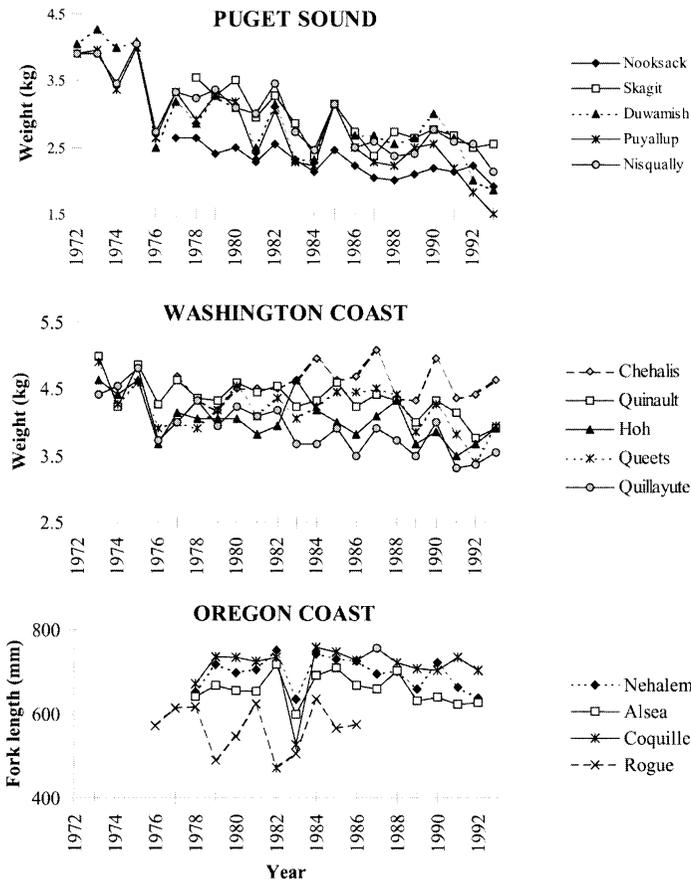

Figure 11.2. Temporal variation in adult size (weight measured in in-river fisheries or length of natural spawners) of coho salmon from populations in Puget Sound and the Oregon and Washington coasts. Source: Weitkamp et al. (1997).

Populations from the Washington coast showed no decline in size during this period, while those in Puget Sound showed a more modest decrease in 1984, a year later. These results indicate substantial variation in the ocean ecology of coho salmon, and this information was important in demonstrating that populations from the three areas met the second criterion to be considered separate ESUs.

Figure 11.3, which depicts genetic relationships among four lineages of chinook salmon from the Columbia River basin, demonstrates how genetic, life history, and geographic information can be integrated into a single analysis.
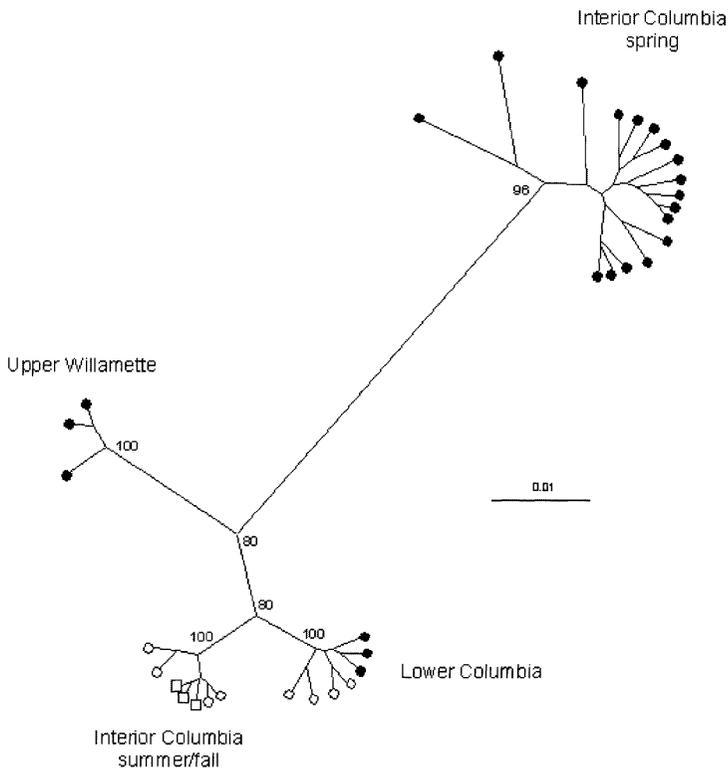
Figure 11.3. Life history variation mapped onto a tree depicting population genetic structure of Columbia River chinook salmon, based on pairwise genetic distances (Cavalli-Sforza and Edwards [1967] chord distance) among populations. Each population is represented by a symbol indicating the peak run timing (time of entry of adults into fresh water on their spawning migration): solid circle = spring; open square = summer; open circle = fall. Support for the four major genetic lineages (two from the interior Columbia River basin, east of the Cascades, and two from west of the Cascades) is indicated by numbers at nodes (percentage of one thousand bootstrap replicates having the identical tree topology). Modified from Waples et al. (2004).

The coherent genetic-geographic groups provide evidence for strong reproductive isolation—the first ESU criterion. Two clusters of populations are restricted to the interior Columbia Basin (east of the Cascades; Provinces I–L in fig. 11.1), and the other two (Lower Columbia and Willamette) are found only west of the Cascades. The four lineages are all in separate ESUs, and the two interior lineages have been further subdivided into ESUs based on geographic isolation and life history and ecological differences among the provinces. In the interior Columbia, all spring-run populations occur in a genetic lineage that is very divergent from all summer and fall-run populations, but spring- and fall-run populations in the lower Columbia River share a common genetic lineage. In the lower Columbia, the run-timing differences thus do not reflect ancient divergence and were considered to represent diversity among populations within a single ESU—consistent with the approach taken with traits showing evidence for parallel evolution (see discussion below).

A total of fifty-eight ESUs/DPSs have been identified in the seven Pacific salmon species (table 11.1), with the number of ESUs per species ranging from two to seventeen. About half of the salmon ESUs are listed as threatened or endangered "species" under the Endangered Species Act (see http://www.nwr.noaa .gov for a current tabulation). Some of the differences among species in number of ESUs are the result of biological differences in the degree of population differentiation and some are explained by geographic distribution (e.g., pink and chum salmon are primarily northern species with relatively few populations in the study area and therefore are represented by fewer ESUs). If these ESU

TABLE 11.1 Number of evolutionarily significant units and major components of diversity in each species of Pacific salmon

| Species | *Number of major diversity groups* | | | | |
	Ecology	*Life history*	*Genetics*	*Total*	*ESUs*
Pink	2	1	2	5	2
Chum	4	1	2	7	4
Sockeye	4	6	9	19	7
Coho	6	1	2	9	7
Chinook	11	7	10	28	17
Steelhead	11	7	7	25	15
Cutthroat	6	2	3	11	6
Total:	44	25	35	104	58

Sources: Major diversity groups for ecology, life history, and genetics were defined by Waples et al. (2001).

designations have successfully accomplished their intent, they represent popula-
tion units that follow essentially independent evolutionary trajectories over
time frames of evolutionary relevance (hundreds or thousands of years). Most
salmon ESUs include populations with diverse genetic, ecological, and life his-
tory traits, but in general the differences among populations within ESUs are
substantially less than differences among ESUs.

Nonsalmonid Distinct Population Segments

Beginning in the 1970s, distinct population segments of vertebrates have been
defined under the Endangered Species Act using a wide variety of criteria. Most
of these DPS determinations were made by the U.S. Fish and Wildlife Service
for terrestrial species such as grizzly bears, bald eagles, and alligators. A desire for
guidelines that would produce more consistent and predictable results moti-
vated the effort to develop a joint USFWS-NMFS policy on interpreting the
DPS language in the act, but it was not until 1996 that such a policy was actu-
ally finalized (USFWS and NMFS 1996e). The joint policy is used to identify
distinct population segments of vertebrate species other than salmon, while the
National Marine Fisheries Service continues to use the more detailed and spe-
cific ESU policy for Pacific salmon. Although the joint policy does not use the
term *ESU*, it is also based on two criteria—discreteness and significance—that
closely parallel those in the salmon ESU policy. Since 1996, the two agencies
have used the joint policy to make DPS determinations for a number of non-
salmonid species, including the gray wolf (USFWS 2003b), Sierra Nevada
bighorn sheep (USFWS 1999b), cactus ferruginous pygmy-owl (USFWS
1997a), barndoor skate (NMFS 2002a), white marlin (NMFS 2002b), and
Puget Sound killer whale (NMFS 2005b).

Alternative ESU Definitions and Application
to Pacific Salmon

Several other frameworks for defining ESUs have been suggested. These frame-
works differ with respect to their underlying philosophy as well as the relative
importance they place on different measures of population distinctiveness.

Phylogeography

Dizon et al. (1992) proposed an approach to defining conservation units based
on principles of *phylogeography* (concordance of genetic lineages with geogra-
phy) developed by Avise (1989). Dizon et al.'s framework is designed to handle
pairwise comparisons of populations or population units, and their examples

are drawn primarily from cetaceans. Population units are compared along two axes: adaptive divergence and reproductive isolation. The authors recognized that, in most cases, practical applications would require use of proxies. They considered distributional data the most suitable proxy for the isolation axis, whereas population response (demographic and behavioral data), phenotype (primarily morphological data), and genotypic data can be useful proxies for adaptation. Each comparison falls into one of four quadrants defined by scores on the two axes: category 1—high scores on both axes; category 2—high on adaptation, low on isolation; category 3—high on isolation, low on adaptation; category 4—low scores on both axes. Dizon et al. did not identify fixed cutoffs between high and low scores on each axis but did provide rough guidelines. Strong reproductive isolation is indicated by physical barriers to dispersal and evidence that the two population units do not intermingle, while mitochondrial DNA (mtDNA) sequence differences greater than 1 percent suggest likely adaptive differences. Firm cutoffs for defining ESUs were not proposed; instead, evidence for stock distinctiveness and evolutionary significance increases as one moves from category 4 to category 1.

COMPARISON WITH OTHER APPROACHES
Dizon et al.'s two axes are roughly comparable to Waples's two ESU criteria (reproductive isolation and contribution to evolutionary legacy), but the proxies are used a bit differently Dizon et al. use molecular genetic data to make inferences about adaptive divergence, whereas Waples's framework places more emphasis on life history and ecology as proxies for adaptation and uses genetic data primarily as an indication of the strength of reproductive isolation.

APPLICATION TO SALMON
Salmon spawn in discrete freshwater areas that might be judged to meet Dizon et al.'s geographic isolation criterion, but some level of straying occurs, so nearby populations are generally not completely isolated. Furthermore, in the migration corridor and especially in the ocean, fish from many populations commingle over large geographic areas. It seems likely that pairwise comparisons of populations from distant geographic areas would meet the Dizon et al. criteria for a high score on the isolation axis, but this would not be true for comparisons involving populations in closer geographic proximity.

Scoring the adaptation axis would also present challenges. Many salmon populations show behavioral or phenotypic differences on the scale of those described in the appendix of Dizon et al. as evidence for genetic discontinuities. On the other hand, very few comparisons of salmon populations would meet the only quantitative criterion for this axis: greater than 1 percent sequence divergence at mtDNA. If phenotypic/behavioral data were weighted most heavily,

most population comparisons would yield high scores on the adaptation axis (hence categories 1 or 2), and a large fraction of existing salmon populations might be considered distinct population segments. Conversely, if mtDNA data were weighted most heavily, most comparisons would yield low adaptive scores (hence category 3 or 4), and the distinct population segments would likely be restricted to the seven named species (table 11.2).

One result seems clear: some salmon population groups would fall into category 2 (strong adaptive differences but little geographic separation), which Dizon et al. and Avise (1989) considered to be a rare combination for most

TABLE 11.2 Application of alternative approaches to defining conservation units of Pacific salmon under the Endangered Species Act

Approach	Number of salmon DPSs[a]	Typical number of populations per DPS
Waples 1991 (ESU = DPS)	58	20–30[b]
Dizon et al. 1992		
If mtDNA heavily weighted	~10	hundreds
If demography/phenotype heavily weighted	~1,000	one
Vogler and DeSalle 1994	7	hundreds
Moritz 1994		
If ESU = DPS	7	hundreds
If MU = DPS	~1,000	one
Bowen 1998		
Using criterion 1 (vicariance) = DPS	a few	a few
Using criteria 2/3 (behavior/ecology) = DPS	~1,000	one
Using criterion 4 (polytypic) = DPS	7?	hundreds?
Using criterion 5 (chromosomal) = DPS	0?	
Crandall et al. 2000		
If only case 1 or 2 = DPS	~10	hundreds
If "distinct population" = DPS	~1,000	one

Note: Results for Waples' method are empirical data current through 2003; estimates for the other methods are best guesses based on likely application of published criteria. A DPS (distinct population segment) is considered a "species" under the ESA. In this analysis, a "population" is defined as described in McElhany et al. (2000) and is roughly equivalent to a "stock." The geographic area considered is Washington, Oregon, Idaho, California, and parts of southern British Columbia, and the seven species are listed in table 11.1.
[a]Gustafson et al. (unpublished data) have identified approximately one thousand separate populations of Pacific salmon in the geographic area under consideration here.
[b]For examples of population identification within salmon ESUs, see http://www.nwfsc.noaa.gov/trt/trtnews.htm.

species. Category 2 would apply to odd- and even-year pink salmon, which often spawn in the same stream in alternative years but are completely isolated reproductively to the extent that they exhibit outbreeding depression when artificially crossed (Aspinwall 1974; Gharrett and Smoker 1991), and to stream- and ocean-type chinook salmon, which can spawn in nearly adjacent areas in the interior Columbia River basin but are separated by large genetic and life history differences (Utter et al. 1995; Waples et al. 2004).

Monophyly of mtDNA

Moritz (1994) proposed what has become one of the most commonly used frameworks for identifying evolutionarily significant units. His approach is simple: ESUs are population groups that exhibit reciprocal monophyly in mtDNA along with substantial frequency differences in nuclear DNA. This criterion in essence requires that all members of one group carry mtDNA haplotypes that are not found in any individual from outside the group (and vice versa). Because Moritz intended his ESUs to complement (rather than replace) traditional taxonomy, formally recognized species are automatically considered ESUs and do not have to meet the reciprocal monophyly criterion. Moritz recognized that his approach would not encompass all units that might be legitimate focus for conservation efforts, so he also proposed recognition of *management units* (MUs), which are populations that do not show reciprocal monophyly for mtDNA but which have "significant divergence of allele frequencies." Management units represent functionally independent populations, are logical units for population monitoring and demographic study, and, ideally, would be managed in a way that promotes conservation of more inclusive ESUs.

COMPARISON WITH OTHER APPROACHES
Moritz's approach differs considerably from the previous two by focusing exclusively on molecular genetic data, primarily mtDNA. This focus was intentional, as Moritz argued that ancient lineages (identified by molecular genetics) are irreplaceable, whereas adaptive differences are more ephemeral on evolutionary time scales and can be regenerated more easily.

APPLICATION TO SALMON
Use of Moritz's criterion to define ESUs of Pacific salmon would be straightforward—no intraspecific population groups identified to date meet the reciprocal monophyly criterion, so no ESUs would be identified within any of the seven taxonomic species. Conversely, most populations or stocks of Pacific salmon would meet Moritz's criteria to be considered MUs, as statistically significant

allele frequency differences are routinely found even between nearby spawning aggregations (e.g., Teel et al. 2000). Therefore, application of Moritz's approach would either lead to recognition of no salmon DPSs other than the taxonomic species (if his ESU = DPS), or many more than are currently identified (if his MU = DPS) (table 11.2).

Phylogenetic Species Concept

In the view of Vogler and DeSalle (1994), tokogenetic lineages (ones that might still be exchanging genes) are not suitable for consideration as separate conservation units; that should be reserved for genetically isolated (phylogenetic) lineages. Accordingly, they proposed that ESUs be defined based on principles of the *phylogenetic species concept* (PSC; Nelson and Platnick 1981; Cracraft 1983). Although several variations of the PSC have been proposed, all are based on the premise that species are distinct entities that are diagnosable based on one or more characters—that is, every individual in taxon A shares one or more characters not found in any individual in taxon B, and vice versa. Vogler and DeSalle proposed that the term ESU be restricted to entities that are completely diagnosable based on one or more characters (e.g., genotypic, phenotypic, behavioral) believed to have a genetic basis.

COMPARISON WITH OTHER APPROACHES

In its focus on diagnosability, Vogler and DeSalle's approach is similar to Moritz's, except that it would recognize ESUs based on any heritable character, not just mtDNA. In theory, many of the characters considered in evaluating salmon ESUs (e.g., morphological or life history traits) could also form the basis of ESU determinations under Vogler and DeSalle's framework.

APPLICATION TO SALMON

Application of the Vogler and DeSalle approach to salmon would yield results similar to those of Moritz's (table 11.2). Although many salmon populations differ in mean values of eligible traits, few if any meet the diagnosability criterion when species-wide ranges of these traits are considered. For example, run-timing diversity is extensive in most salmon species, including chinook salmon (Healey 1991; Myers et al. 1998). Within any particular population, individuals return to spawn over a period of perhaps four weeks to four months (fig. 11.4). Although many pairs of populations have nonoverlapping distributions of run timing (e.g., Hoko and Willamette; Pistol and Nooksack), collectively North American chinook salmon can return to spawn during every month of the year. Thus, no population has a run timing that doesn't overlap with that of some other populations, and none would be completely diagnosable—not even
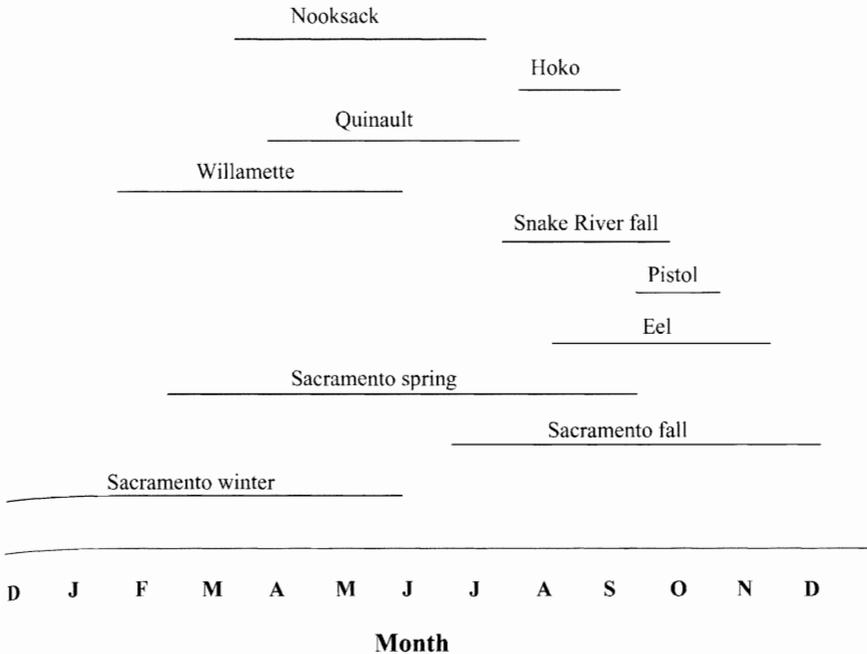
Nooksack

Hoko

Quinault

Willamette

Snake River fall

Pistol

Eel

Sacramento spring

Sacramento fall

Sacramento winter

| D | J | F | M | A | M | J | J | A | S | O | N | D |

Month

Figure 11.4. Variation in run timing in selected chinook salmon populations. Width of line indicates duration of run timing for each population. Some population pairs have nonoverlapping run timing, but this trait is not diagnostic for any single population when considering all other populations in the species. Source: Myers et al. (1998) and unpublished data.

the Sacramento River winter-run population, which is considered to have "unique" run timing.

Geminate Evolutionary Units

Bowen (1998) discussed the relevance for conservation of both evolutionary history and future evolutionary potential. He felt that Waples's (1995) definition of "evolutionary legacy" (cited above) captured the importance of both factors but that when put into practice the various ESU definitions had focused primarily on the former and had not effectively considered the latter. To address this shortcoming, Bowen proposed a new concept, that of the *geminate evolutionary unit* (or GEU). In Bowen's view, recognizing GEUs would afford conservation recognition and status to units that might play an important role in future speciation events.

Although identifying GEUs is challenging, Bowen suggested several criteria that might be useful: (1) recent isolation by vicariant events (e.g., marine species

isolated by closing of the Isthmus of Panama near the end of the Pliocene); (2) behavioral barriers to gene flow, such as breeding at different times of the year; (3) ecological speciation—invasion of a new habitat or niche with novel selective pressures can lead to rapid divergence from the parent population; (4) polytypic species characterized by a high diversity in morphological, ecological, or genetic traits; and (5) morphological differentiation (especially that associated with chromosomal duplications or rearrangements) coupled with minimal divergence at molecular markers.

COMPARISON WITH OTHER APPROACHES
Bowen views the GEU as a complement to, rather than a substitution for, ESUs defined by other criteria. Although in principle the National Marine Fisheries Service ESU approach is both backward- and forward-looking, Bowen is correct that in application the primary focus has been on identifying components of diversity that are the result of past evolutionary events. Waples (1995) argued that this focus was appropriate because of the difficulty in identifying which particular populations will play a significant future role in evolution.

APPLICATION TO SALMON
To evaluate how his framework might apply to Pacific salmon, we can consider Bowen's criteria individually:

1. The most recent major vicariant event for Pacific salmon was the series of Pleistocene glaciations that fragmented populations, leading to separate glacial refugia (McPhail and Lindsey 1986). In the past ten thousand years, at least some of these vicariant separations have broken down. Some populations have been isolated much more recently by anthropogenic factors, such as dams or habitat degradation and fragmentation, but it is not clear whether Bowen would propose that such units be considered GEUs. A few peripheral populations (e.g., Snake River sockeye salmon, and steelhead in Southern California) may be undergoing a more natural process of isolation due to climate change and range constriction, and these would appear to be the best candidates to meet Bowen's first criterion.

2 and 3. Behavioral barriers to gene flow, such as differences in run or spawn timing, are common in salmon, so a large number of populations would meet this criterion. However, expression of these traits in salmon is known to be influenced by environmental as well as genetic factors, so the evolutionary significance of the differences cannot easily be evaluated without detailed information or experiments. Even if the differences weren't genetically based, however, they would appear to meet Bowen's third criterion (i.e., expansion into a new niche with different selective regimes).

4. All Pacific salmon species are polytypic, showing considerable varia-
    tion in morphological, ecological, and genetic traits. A recent compi-
    lation (Waples et al. 2001) of major components of diversity (ecology,
    life history, genetics) in Pacific salmon found that the number of ma-
    jor diversity categories ranged from a low of five in pink salmon and
    seven in chum salmon to a high of twenty-five in steelhead and
    twenty-eight in chinook (table 11.1). Would all of these species, or
    only the most diverse, meet Bowen's criterion to be considered poly-
    typic? If the criterion was met, would the whole species be considered
    a GEU, or would various subcomponents be separate GEUs?
5. Salmon are ancestrally tetraploid (Allendorf and Thorgaard 1984), so
    all extant populations share this feature. Some intraspecific variation
    in chromosome number does occur (e.g., Thorgaard 1983), but there
    is no evidence that variation in chromosome number leads to rapid
    reproductive isolation, as would be expected of units that meet this
    criterion.

In summary, a few peripheral populations in some species might meet
Bowen's first criterion to be considered ESUs, but most are already considered
ESUs. Still, identifying such populations as GEUs might call attention to pop-
ulation units that otherwise would be lumped in larger, more inclusive ESUs. A
large number of populations would appear to meet Bowen's second and/or third
criteria to be considered GEUs in their own right, whereas few if any would
meet the fifth criterion (table 11.2),

Exchangeability

In reaction to Moritz (1994) and others who consider only molecular genetic
markers for defining ESUs, Crandall et al. (2000) proposed a framework de-
signed to place equal emphasis on adaptive diversity. They felt the ESU debate
was too constrained by the either-or question, "Is it an ESU or not?" Instead,
they outlined a framework involving eight separate cases, each reflecting differ-
ent levels of evidence for genetic and ecological exchangeability. Exchangeabil-
ity is assessed currently as well as historically.

Evaluation of ecological exchangeability focuses on traits believed to have a
genetic basis. The ultimate criterion is whether a population can be moved to
another geographic area and occupy the same ecological niche. In practice, var-
ious proxies are used for this criterion because direct tests of exchangeability are
rare. Evidence for lack of genetic exchangeability can include occurrence of
unique alleles, low estimates of gene flow, or genetic divergence concordant
with geographic barriers. The proposed gene flow criterion (number of mi-
grants per generation [*Nm*] less than one) corresponds to a measure of genetic
divergence of approximately $F_{ST} = 0.2$. Crandall et al. (2000) did not specify a

time scale for historical analyses, noting instead that the appropriate time frame would vary depending on the conservation issue and data at hand.

The eight cases are described by different patterns in a 2 × 2 matrix, with each cell represented by either a plus sign (+) (evidence to reject exchangeability) or a minus sign (−) (null hypothesis of exchangeability is not rejected). The left column represents genetic exchangeability and the right column ecological exchangeability; the top row represents current status and the bottom row historical conditions.

COMPARISON WITH OTHER APPROACHES

Crandall et al.'s (2000) framework is similar to that of Waples and Dizon et al. in that it focuses on both adaptive and isolation factors but provides more alternative scenarios. It also explicitly considers both historic and current characteristics of populations, which Moritz (1994) accomplishes to some extent by considering MUs as well as ESUs. Crandall et al. provide a separate management recommendation for each case.

APPLICATION TO SALMON

As most salmon populations do not appear to be ecologically exchangeable (direct test = transplants), they would have a plus (+) in the upper right sector. Conversely, F_{ST} values for most Pacific salmon are less than 0.1, suggesting Nm is greater than 2 (twice as high as Crandall et al.'s criterion). Most genetic differences among salmon populations are not diagnostic, and unique alleles, if present, usually occur at relatively low frequencies. Therefore, most salmon populations would receive a minus (−) for current genetic exchangeability. The stream- and ocean-type chinook salmon populations in the interior Columbia River basin (fig. 11.3) and many sockeye salmon populations from the Pacific Northwest (Winans et al. 1996) have F_{ST} values in the range 0.15–0.2, and these population groups might therefore score a plus (+) on the genetic exchangeability axis.

Lacking any clear guidance regarding a historical time frame, I will assume for the purposes of this example that "historical" represents conditions near the end of the Pleistocene, when the last episode of glaciation was ending but before salmon had expanded into the areas freed by receding glaciers (e.g., virtually all of British Columbia, Puget Sound, and parts of the upper Columbia River basin). In the bottom row, therefore, populations from areas subject to glaciation would have a minus (−) (or perhaps a blank) in both cells. Historic exchangeability of populations not directly affected by glaciation is largely speculative.

Taken together, the above considerations suggest that most salmon populations would fall into one of the following cases (current status/historical status):

+,+/+,+ (case 1; lack of exchangeability currently and historically). This might apply to the divergent chinook salmon lineages and at least some sockeye populations.

–,+/+,+ (case 3; recent loss of genetic distinctiveness). This might apply to ancient lineages that experienced some level of mixing following post-glacial dispersal. Possible examples include chinook salmon in British Columbia (Beacham et al. 2003; Waples et al. 2004) and inland and coastal subspecies of *O. mykiss.*

–,+/–,+ (case 5b; exchangeable genetically but not ecologically, both currently and historically). This is probably the most common situation for salmon populations.

–,+/–,– (case 6; recent evolution of ecological divergence). Evidence exists for repeated, parallel evolution (see discussion below) of some life history traits in Pacific salmon, perhaps over relatively short evolutionary time frames. However, it is difficult to distinguish differences that have evolved recently in isolation from differences that result from a long-term balance between divergence opposed by ongoing gene flow.

Like Dizon et al., Crandall et al. did not provide specific thresholds to be considered an ESU; in fact, they suggested that the term *evolutionarily significant unit* be abandoned, pointing out that various authors have used the term to represent each of the eight cases they identified. Crandall et al. (2000) recommend treating case 1 as long-separated species and cases 3, 5b, and 6 as distinct populations. However, there is no indication that they intended this latter term to equate to "distinct population segments" under the Endangered Species Act. It is reasonable to assume that any salmon populations falling in case 1 would be considered at least DPSs (if not full species) under the ESA, but these would be relatively few. On the other hand, if case 5 and 6 populations were also considered DPSs, there would be a large number of salmon DPSs (table 11.2).

Parallel Evolution

A phenomenon that complicates efforts to define conservation units is *parallel evolution*—the repeated evolution of the same trait (generally, a morphological or life history trait). Pacific salmon provide ample evidence for parallel evolution of life history traits. For example, in *Oncorhynchus nerka* repeated evolution of a freshwater resident form (kokanee) has occurred from the anadromous form (sockeye) (Taylor et al. 1996); in *O. tshawytscha* repeated evolution of run-timing differences has occurred among chinook salmon populations in coastal basins (Waples et al. 2004); and in *O. mykiss* parallel evolution has been documented for two life history traits: run-timing differences (summer-run populations

presumably evolving from the more common winter-run; Busby et al. 1996) and anadromy/residency (the resident form [rainbow trout] apparently having evolved repeatedly from the anadromous [steelhead] form; Docker and Heath 2003). Parallel evolution of life history traits has also been described in a wide range of other taxa (e.g., Rundle et al. 2000; Briscoe 2001; Nosil et al. 2002), so how this topic is dealt with in defining conservation units is of general relevance.

In Pacific salmon, the different life history forms typically are more closely related to the opposite form in the same drainage than to the same form in another drainage. For example, summer steelhead from the South Fork Umpqua River are more closely related to nearby winter-run steelhead than to summer steelhead from other river basins. This general pattern of evolutionary relationships is shown schematically in figure 11.5, panel 1. Three different schemes for identifying conservation units are consistent with these evolutionary relationships (panels 2A–C), with the schemes differing in the degree to which populations are lumped within conservation units. It is not possible to determine which of these approaches is "best" based on biology alone. Based on congressional and legal guidance regarding the Endangered Species Act, life history variants believed to result from parallel evolution have generally been considered to be part of the same Pacific salmon ESUs (Busby et al. 1996; Myers et al. 1998). As most salmon ESUs contain populations from multiple river drainages, they typically follow the pattern shown in panel 2C.

It is not entirely clear how parallel evolution would be considered under the other ESU scenarios. Presumably the different life history types would be considered ESUs by Vogler and DeSalle or Moritz only if they achieved diagnosability or reciprocal monophyly. In Pacific salmon, the observed genetic differences among populations with different life history types are generally much less than this threshold (for example, Waples et al. [2004] found a mean F_{ST} of only about 0.01 for comparisons of spring and fall chinook in the same coastal basins). However, the separate forms presumably represent local adaptations and probably are not ecologically exchangeable, at least in human time frames. Therefore, application of the approaches of Dizon et al., Bowen, or Crandall et al. could lead to identification of conservation units that follow the pattern shown in figure 11.5, panel 2A. If Moritz's MU criteria were applied to salmon, the result would probably also follow this pattern. It is possible that one or more of the ESU approaches might "downgrade" the differences resulting from parallel evolution, resulting in a pattern that followed panel 2B in figure 11.5, but whether this would be the case is not easy to determine from published criteria.

ESUs and the Continuum of Biological Diversity

Except for Waples (1991, 1995), none of the ESU approaches considered above was designed specifically to conserve biological diversity under the legal frame-
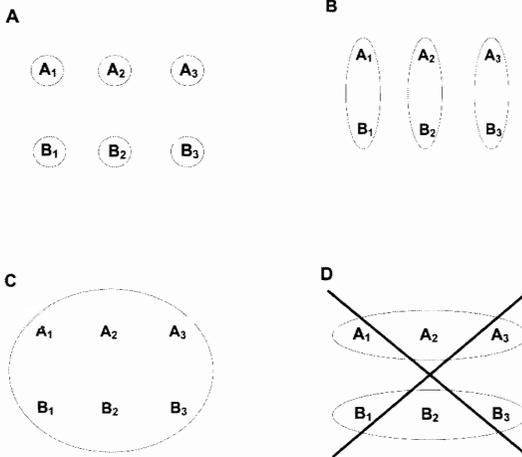
panel 1
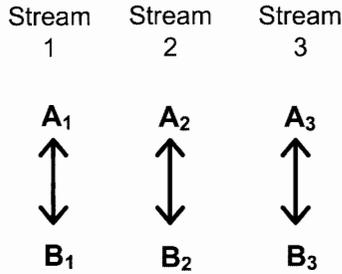
panel 2

Figure 11.5. Schematic diagram of parallel evolution of life history traits and ESU delineation. Pairs of populations occur in three different geographic areas (e.g., different river basins). Within each area, the same two life history types are found (A and B). In Pacific salmon, genetic data (e.g., Waples et al. 2004) indicate that, in general, A and B within an area are more closely related than either is to the same form in a different area (panel 1; genetic relationships indicated by arrows). Three different approaches to defining conservation units (ESUs) are consistent with this pattern of evolutionary relationships: each population a separate ESU (panel 2A); each river basin a separate ESU (panel 2B); or the entire system a single ESU (panel 2C). One approach that would not be consistent with the evolutionary relationships would be to create an artificial ESU uniting all the type-A populations and another uniting all the type-B populations (panel 2D).

work of the Endangered Species Act. In particular, none of the other approaches have attempted to define the ESA term "distinct population segment" in a biological framework. Therefore, when we ask the question, How many salmon DPSs would there be under an alternative framework?, the answer will of necessity be speculative.

Nevertheless, it is clear from the above analysis that application of several published ESU approaches would lead to widely divergent outcomes for Pacific salmon. The number of salmon DPSs identified would range from none or virtually none beyond the seven taxonomic species (Vogler and DeSalle; Moritz, assuming his ESU = DPS), to a few in some species (Crandall et al., assuming only case 1 or 2 = DPS; Dizon et al. if mtDNA is most heavily weighted as a proxy; Bowen under criterion 1) to very many (Moritz, assuming his MU = DPS; Dizon et al., assuming demographic and phenotypic data are heavily weighted; Crandall et al. if each of their "distinct populations" is considered to be a DPS; Bowen under criteria 2 or 3) (table 11.2). Thus, only for the Vogler and DeSalle approach is the outcome clear: as expected, application of the phylogenetic species concept would not be useful for recognizing diversity of Pacific salmon below the species level. For each of the other approaches, the number of conservation units recognized as "species" under the ESA could range from few or none to a large number, depending on how the criteria are interpreted. (Moritz [pers. comm., October 2003] has clarified that he did not intend that his MUs be equated with DPSs.)

One interesting result of this analysis is that it does not seem likely that any of the other approaches would result in ESUs/DPSs of approximately the same geographic scale as currently recognized salmon ESUs. Instead, the units would either be larger (perhaps only one for each of the seven taxonomic species) or much smaller (with a large fraction of local populations or stocks being recognized as separate DPSs) (table 11.2). That is, the other ESU approaches would appear to focus conservation attention at either of the two extremes in the continuum of biological diversity—the taxonomic species or the local population. Between these two extremes, however, there typically exist several additional levels of biological diversity in Pacific salmon—each of which has potential relevance for conservation. For example, it is possible to identify at least eight separate hierarchical levels in *O. mykiss* from the Oregon coast:

    1 Species (*O. mykiss*)
        2 Subspecies (*O. mykiss mykiss*) (coastal)
            3 ESU (Oregon coast)
                4 Gene Conservation Group (mid- and North Coast)
                    5 Major River Basin (Umpqua River)
                        6 Major tributary (South Fork Umpqua River)
                            7a Life history form (resident)
                            7b Life history form (anadromous)
                                8a Life history form (summer run)
                                8b Life history form (winter run)

Level 8 is generally considered a "population" or "stock," which is a natural unit for routine fishery management. The National Marine Fisheries Service has

identified level 3 as a unit (Oregon coast ESU) that it believes is biologically meaningful and also consistent with the legislative and legal framework of the ESA. In contrast, application of other published approaches would appear to result in recognition of salmon DPSs at either extreme of this continuum of diversity (i.e., either levels 1–2 or 7–8).

The Oregon coast ESU covers a relatively large geographic area (coastal streams from Cape Blanco to the Columbia River—about 500 kilometers of coastline) and includes a substantial number of largely independent populations. Collectively, however, these populations share genetic, ecological, and life history traits that distinguish Oregon coast steelhead from those from other areas (Busby et al. 1996). The State of Oregon has made a systematic effort to identify major components of salmon diversity within Oregon (Kostow 1995) and recognizes three *gene conservation groups* of *O. mykiss* along the Oregon coast that are nested within the Oregon coast ESU. The State of Washington (Busack and Shaklee 1995) has also used biological criteria to define hierarchical levels of diversity within its salmon species, generally at smaller scales than ESUs.

How might these alternative ESU frameworks play out if applied to species other than salmon? Although it is beyond the scope of this chapter to consider such a question in any detail, some general observations can be made. Salmon have a natural proclivity for hierarchical population structure, fostered by the hierarchical design of stream networks and the complicated life cycle that lends itself to strong local adaptations. Still, many other species have complex population structures and more than one level of diversity below the taxonomic species, and if the analysis here is correct, patterns of diversity not at either extreme of the continuum might be overlooked in many of the commonly used approaches for defining ESUs.

Whether this is a desirable result is not a question that can be answered by science alone. The merits of any particular conservation approach can be evaluated properly only in the context of the goals one is trying to accomplish. Deciding where on the continuum of biological diversity to focus conservation efforts involves a trade-off between various societal goals. Defining DPSs and hence ESA species on a very fine scale (e.g., the level of a local population or stock) could provide legal protection for units that might otherwise receive little attention. This approach also could provide increased flexibility in recovery planning—for example, by allowing delisting of local populations that recover faster than others. On the other hand, it likely would lead to recognition of a very large number of ESA "species," with attendant increases in regulatory and administrative burdens for the agencies and the public alike. Some recovery options might be precluded if each subunit were required to be maintained in complete isolation of other subunits. If almost every biological population were a separate DPS/ESU, it would also be difficult for the U.S. Fish and Wildlife

Service and the National Marine Fisheries Service to determine how best to prioritize allocation of scarce resources for conservation. Finally, if DPSs were recognized on too fine a scale, there would be a risk of conferring ESA protection on units that would not persist in nature over evolutionary time frames—in which case the ESA would be attempting to preserve a rather ephemeral product of evolution.

Defining ESUs and DPSs to be more inclusive would alleviate many of these concerns and is arguably more consistent with the direction from the U.S. Senate that the two agencies use the ability to list vertebrate populations "sparingly" (96th congr., 1st sess., 1979, senate report 151). However, defining ESUs on too coarse a scale also has societal and biological costs. Under an extreme lumping scenario, distinctive populations might be overlooked and lost without triggering ESA protection. Flexibility would also be reduced, as the entire DPS must be listed or delisted as a unit. Larger and more inclusive DPSs would also be more likely to include a diverse and heterogeneous collection of local populations, which can greatly complicate extinction risk analysis and recovery planning. Defining conservation units on a large scale is most likely to yield successful results if other mechanisms exist to address diversity among the subunits.

Identifying conservation units is only the first step in a conservation program, and it might not even be necessary. Many feel that the ultimate goal should be the conservation of "normal" evolutionary processes (Rojas 1992; Bowen 1999; Crandall et al. 2000; Fraser and Bernatchez 2001; Moritz 2002; Naeem et al., this volume). According to this view, the focus on defining conservation units is somewhat unfortunate because it puts too much emphasis on identifying (and therefore conserving) specific types, when in reality evolution is a dynamic process, and population traits in evidence today might not even be adapted to current conditions, let alone be adaptive in the future (see Lomolino, this volume). Less consensus exists regarding how best to accomplish the goal of conserving evolutionary processes. The concept of ecosystem-based management has a certain cachet, because by conserving whole ecosystems one would by definition also be conserving many natural biological processes. Nevertheless, this concept remains poorly defined and few examples exist in which it has been applied to real-world conservation problems.

Moritz (2002) suggested that overall conservation goals can be achieved through attention to two major axes of diversity: long-term or vicariance (the focus of his 1994 paper) and adaptive divergence (emphasized in particular by Crandall et al. 2000). These two axes correspond closely to the two ESU criteria of Waples (1991, 1995) and the two axes of Dizon et al. (1992). According to Moritz, the vicariance axis is best considered as an index of representativeness (of unique evolutionary lineages), whereas the adaptation axis relates most directly to population fitness and persistence. In the view of Moritz (2002), a bi-

ologically sound conservation strategy would include a focus both on products of evolution (representation of divergent lineages, because these units cannot be replaced if lost) and evolutionary processes (which should allow the more ephemeral products of adaptive divergence to be regenerated naturally).

Since the legal framework of the Endangered Species Act is organized around protection of units that can be considered ESA "species," an emphasis on defining conservation units is unavoidable. Within this legal framework, it is still possible to make important contributions toward conserving evolutionary processes, as illustrated by experience with Pacific salmon. The overall approach to defining salmon ESUs follows Aldo Leopold's sage advice: unless you have a perfect understanding of how a complex system works, save all the pieces if you tinker with it (Leopold 1953). If most or all salmon ESUs are conserved (so the thinking goes), then adequate diversity will remain for the future evolutionary trajectory of the species to unfold largely unaffected by humans. These considerations have also informed ESA recovery planning for Pacific salmon, where regionally based technical teams are developing new methods to address the considerable genetic, ecological, and life history diversity that exists within most salmon ESUs (for example, see the Northwest Salmon Recovery Planning Web site at http://www.nwfsc.noaa.gov/trt/index.html) (Ruckelshaus and Darm, this volume). If recovery plans can be developed that conserve the essential fabric of this diversity, ample raw material should remain for the processes of evolution to act on in the future. This dual focus both on products and processes of evolution is consistent with the conservation strategy proposed by Moritz (2002).