INTRODUCTION

The Oregon Coast Evolutionarily Significant Unit (ESU) of coho salmon (*Oncorhynchus kisutch*) was listed as Threatened under the U.S. Endangered Species Act (ESA) (Fed. Reg. 63:42587-42591) in 1998. The Endangered Species Act requires that a recovery plan be produced for listed species. As part of the recovery planning process, the National Marine Fisheries Service (NOAA Fisheries) has convened a group of scientists to act as the Technical Recovery Team (TRT) for the Oregon and Northern California Coast (ONCC) Recovery Domains (Fig. 1).[1] The two Recovery Domains are composed of the Oregon Coast Coho Salmon and Southern Oregon and Northern California Coast Coho Salmon ESUs. The ONCC TRT is made up of the Oregon Coast and Southern Oregon, Northern California Coho Workgroups. As a team, our goal was to provide a scientific context for identification of necessary actions to help the species recover. The TRT was asked to (1) identify population and ESU de-listing goals; (2) characterize habitat/fish abundance relationships; (3) identify the factors for decline and limiting factors for the ESU; (4) identify early actions that are important for recovery; (5) identify research, evaluation, and monitoring needs; and (6) serve as science advisors to groups charged with developing measures to achieve recovery. This report is the first in a series providing the scientific foundation for biological de-listing goals for the Oregon Coast Coho Salmon ESU. Subsequent reports will discuss population and ESU viability goals, factors limiting the recovery of the ESU, and research and monitoring needs.

Under the ESA, biological de-listing goals define the biological conditions under which the listed species or ESU is no longer in danger of extinction nor likely to become endangered in the foreseeable future in any significant portion of its range. That is, these goals define the conditions necessary for the long-term persistence of the ESU as a whole. An ESU has, by definition, persisted as a unit on an evolutionary time scale. Knowledge of its structure (its component populations, their function, and their interactions) under historical conditions before current threats became substantial provides a background against which to evaluate recent status and minimum conditions needed for long-term persistence. Because the persistence of the ESU depends upon the aggregate performance of its component populations, an essential first step in developing de-listing goals is to identify the historical populations of the ESU and define their interrelationships.

An ESU is composed of numerous constituent populations with varying features and behaviors. Some populations function essentially independently over moderate time scales, while others interact more strongly with nearby populations. In this report we describe what we believe were historical populations in the Oregon Coast Coho Salmon ESU. We draw on a variety of data sources and analyses to estimate the historical size, relative independence, and geographical range for each population.

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[1] A complete description of TRT composition, tasks, and operating principles can be found in the NOAA Fisheries document “Recovery planning guidance for Technical Recovery Teams” (available at http://www.nwfsc.noaa.gov/trt/about.htm).

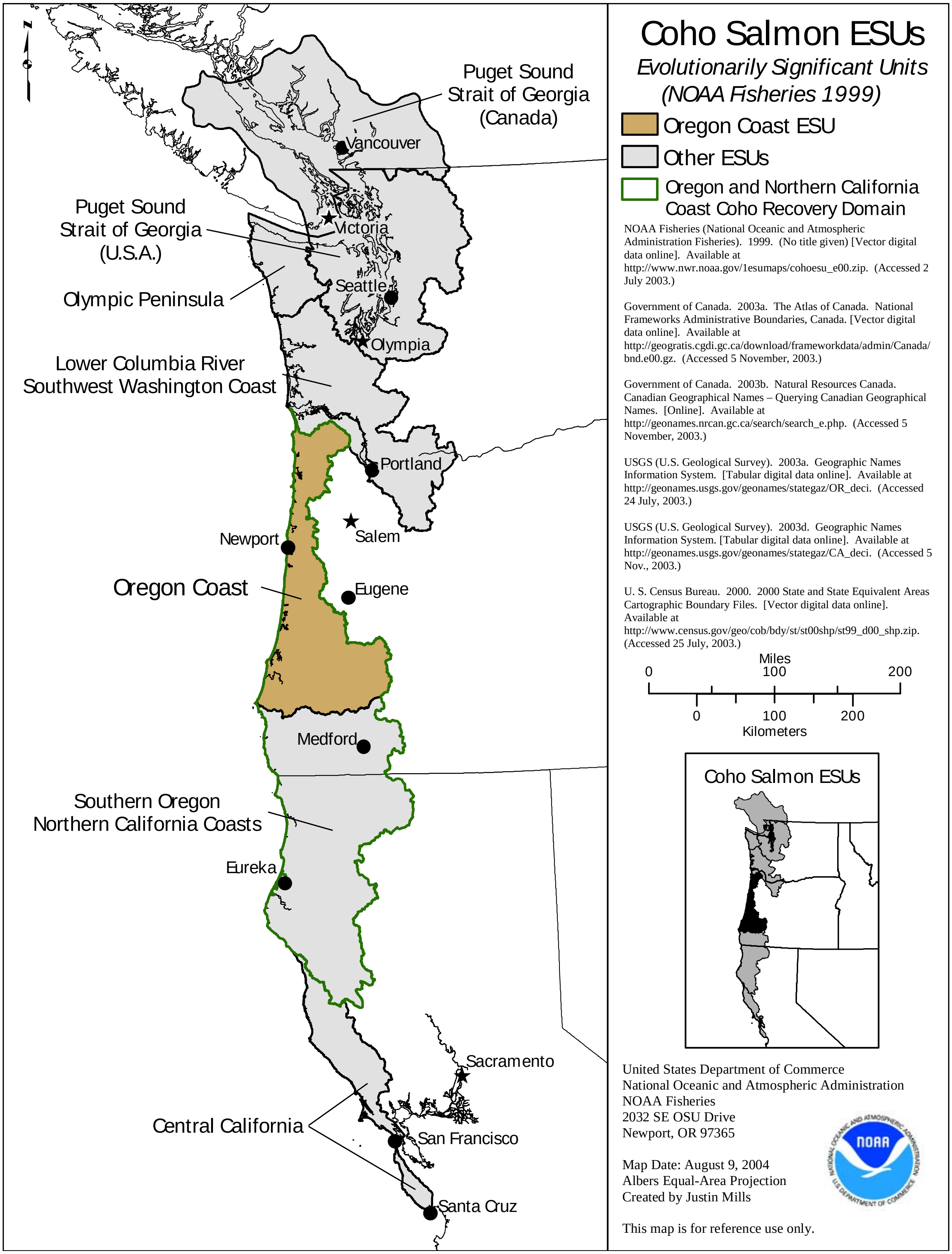

Figure 1. Coho salmon ESUs (NOAA Fisheries 1999).

This document does not attempt to define current populations, or what future populations will look like. It is our view that recovery will require a restoration of process that will enable fish to establish populations in whatever configuration suits them, not necessarily what has existed in the past.

The next part of the TRT deliberation will define population and ESU viability criteria and de-listing goals based initially on these historical populations. However, these proposed populations may change in the future, depending on the viability analysis. This process will continue to feed back to each step if changes are needed.

This proposal divides the ESU into populations, further classifying these populations into Independent (Functionally and Potentially) and Dependent populations. This identification and classification system assumes a model for de-listing criteria that (1) uses geographic strata as a means for ensuring geographical, genetic, and ecological diversity of the recovered ESU, and (2) distinguishes between Independent populations that are the focus of rigorous viability analyses and Dependent populations, which may be less intensively monitored and/or managed. Under this model, ESA de-listing goals would differ among the population classes, with rigorous quantitative productivity, abundance, and habitat goals for Functionally and Potentially Independent populations and more quantitative goals for Dependent populations.

Population Concepts

In the biological literature, the term “population” often refers simply to a group of organisms of the same species that occur in the same area (such as McNaughton and Wolf 1973, Ehrlich and Roughgarden 1987). In a fishery research and management context, Ricker (1972) provided a more specific definition of a local population or “stock” as the “fish spawning in a particular lake or stream (or portion of it) at a particular season, which fish to a substantial degree do not interbreed with any group spawning in a different place, or in the same place at a different season.” This definition has been widely used in assessments of salmon populations (such as WDF et al. 1993, Kostow 1995). McElhaney et al. (2000) based their definition of “independent population” on Ricker’s definition of “stock.” They made the phrase “to a substantial degree” more specific and drew a distinction between independent and non-independent populations. “Independent populations” were described as basic units for assessing population viability in the context of Pacific salmon recovery planning. While we draw heavily from the review of population structure provided by McElhaney et al. (2000), we found that their strict distinction between independent and non-independent populations was overly simplistic when applied to the Oregon Coast Coho Salmon ESU. We therefore have taken a somewhat different approach to classifying populations, starting with Ricker’s (1972) definition of a stock.

Definition of a Population

A population is group of fish of the same species that spawns in a particular locality at a particular season and does not interbreed substantially with fish from any other group.

Our purpose was to describe the historical population structure of the Oregon Coast Coho Salmon ESU. The structure and dynamics of the ESU populations in a historical context represent the conditions under which we are most certain that the ESU was not at risk of extinction. We are increasingly uncertain of the ability of the ESU to persist as the condition of the populations diverges from this baseline. We do not propose that historical conditions are the benchmark for population or ESU viability. Rather, we identify historical population structure as a template against which current and possible future population structures can be compared in the course of developing ESU viability criteria. This document is only concerned with historical populations. There is no attempt to evaluate current population structure or compare current populations with historical populations.

Populations and ESUs

To develop conservation plans, planners must clearly define the organizational units of the organisms of concern (Meffe and Vrijenhoek 1988) and understand how those units behave and interact over time. Two biological units are considered in developing recovery plans for coho salmon listed under the Endangered Species Act: ESUs and populations. In defining units for potential ESA listings of Pacific salmonids (*Oncorhynchus* spp.), NOAA Fisheries adopted the concept of Evolutionarily Significant Units as the definition of listable "species" under the ESA (NMFS 1991, Waples 1991a[1]). ESUs are collections of local populations that share common demographic and genetic features. Over moderate time frames (1 to 10 generations), there may be periodic exchanges of individuals among the populations that make up an ESU, but there is little interaction with populations in other ESUs (Moritz et al. 1995). This document focuses on identifying the structure and relative independence of local populations within the Oregon Coast Coho Salmon ESU.

We acknowledge the link between biological structure and scales of space and time in our approach to identifying and classifying populations. The scale of ESUs was defined in terms of major patterns of genetic and life history diversity (Waples 1991b). Implicit in this definition is the idea that an ESU is made up of a number of populations, so the scales relevant to population structure are smaller than those for ESU structure. Populations are expected to exchange individuals at substantially higher rates within an ESU than between ESUs (Moritz et al. 1995). ESUs are defined primarily with respect to large genetic divergences (Waples 1991a). Populations are demographic units within which individuals interact at time scales of a few days to a few generations, whereas ESUs are genetic units in which relevant variation and structure change on time scales of tens to hundreds of generations.

The genetic structure of salmon ESUs is dynamic, at least on evolutionary time scales. There is no single array of genes (or combination of alleles) that can be said to make up an ESU. Rather, the integrity of an ESU is linked to maintaining the dynamic nature of natural evolutionary processes (gene flow, genetic drift, and adaptation) (Waples 1995). These processes are only imperfectly understood for salmon in general, and this applies as well to the

[1] The term "species" included 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 (ESA section 3).

Oregon Coast Coho Salmon ESU. Nevertheless, within most salmon ESUs a number of natural population units have persisted as largely independent entities for periods that are long on ecological time scales (100 years or more). The effort to identify historical populations of Oregon Coast coho salmon has focused on such units, because they are natural units for assessing viability. In many ESUs, including Oregon Coast coho salmon, the role of small populations and their relationship to larger, historical populations is poorly understood. We would expect that our understanding of Oregon Coast coho salmon population genetics will improve as results from ongoing genetics research and other studies become available. Meanwhile, we consider that a population of any size may play a significant evolutionary role within the ESU.

Viability of an ESU is coupled with the viability and dynamics of its constituent populations. Our approach to these populations defines the relationships among the populations in terms of their interactions; this approach provides us with a basis for comparing historical populations with current populations and for assessing population viability and, subsequently, ESU viability, in a variety of restoration scenarios.

Conceptual Approach to Identifying and Classifying Historical Populations

In preparing for a coast-wide effort to develop recovery plans for all listed Pacific salmon ESUs, NOAA Fisheries developed a general approach to assessing viability of ESUs (McElhaney et al. 2000). The first step involves identifying the historical populations within an ESU and then classifying them in terms of their degree of historical independence. McElhaney et al. (2000) acknowledged that the extinction risk of an entire ESU is a complex function of the dynamics of the ESU's component populations. They also considered that, although the population structure of ESUs is both complex and variable, the problem of ESU risk could be simplified by identifying "independent"[1] populations whose viability[2] could be assessed as individual units. ESU viability can be defined largely in terms of the viability of these independent components. To define and classify historical Oregon Coast coho salmon populations, we have followed the broad concepts outlined by McElhaney et al. (2000). However, we recognize that population independence in this region is more complex, and is relative rather than absolute. We have, therefore, developed a population classification scheme that reflects the properties of individual populations and the interactions among populations. This proposed approach is intended to provide a uniform means of identifying the population structure of coho salmon for coastal ESUs south of the Columbia River. It was developed with collaboration among the Oregon Coast Workgroup of the Oregon and Northern California Coast

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[1] An independent population, according to McElhaney et al. (2000), is "any collection of one or more local breeding units whose population dynamics or extinction risk over a 100-year time period is not substantially altered by exchanges of individuals with other populations" (p. 3).
[2] A viable salmonid population (McElhaney et al. 2000) is an independent population of any Pacific salmonid (genus *Onchorhynchus*) that has a negligible risk of extinction due to threats for demographic variation (random or directional), local environmental variation, and genetic diversity changes (random or directional) over a 100-year time frame (p. 2).

Technical Recovery Team (ONCC TRT) and the Central California Coast TRT, but has had additional input from the full ONCC TRT and staff from other coastal TRTs.

Conceptual Approach to Identifying Populations

Our approach to identifying populations differs somewhat from the approach taken by other TRTs (Meyers 2004, Puget Sound Technical Recovery Team 2003). This is due to differences among the listed salmon species. Along the linear Oregon Coast, there are many basins of all sizes, each with a separate ocean entry point. This landscape contrasts with the river networks of the Columbia Basin, and with the hub and spoke geography of Puget Sound, where populations distribute themselves from a central basin or hub into contributing river basins, or spokes. These differences in the geometric patterns of rivers result in different patterns of movement of fish between rivers and, hence, different population structures and population dynamics. We sought a population definition that would be relevant to the geography and population dynamics on the Oregon Coast and would accommodate rivers and streams of vastly different sizes. While the role of large basins in ESU viability is obvious, it was also clear to the TRT that smaller basins are also an important part of the ESU. Our approach was designed to reflect this structure and to elucidate the historical role of each population in the demographic functioning of the ESU.

One of the problems in describing the historical population structure for Oregon Coast coho salmon was that this region of coast is composed of basins with a wide range of sizes. In this ESU, direct ocean tributaries range from less than 1 to greater than 4,600 stream miles (less than 1.6 to over 7400 km). Large basins may have multiple populations. Smaller basins that drain directly into the ocean probably did not support enduring populations, but are not necessarily a part of a single larger unit. We had no basis for combining smaller basins with larger ones, and we thought it was important to reflect the full range of coho salmon habitats on the Oregon Coast. Spawners have a strong tendency to return home to their basin of origin, so each basin would naturally form a separate population. We have, therefore, defined historical populations based on their points of salt water entry.

Conceptual Approach to Classifying Populations

In order to classify historical populations of Oregon Coast coho salmon, we first had to explain our view of the population dynamics historically operating in this ESU. Our approach to this problem is somewhat different from the other TRTs because of the linear nature of the Oregon Coast (Puget Sound Technical Recovery Team 2003, Myers 2004). We based our conceptual model of population dynamics for this ESU on existing literature regarding the functioning of complex populations in general and salmon populations in particular (Rieman and Dunham 2000). Two assumptions we made were: 1) populations interact through the exchange of individuals, and 2) movement of individuals in salmon populations is strongly influenced by the physical relationship of ocean entry points (Fig. 2). None of the published literature exactly matched the patterns of connectivity implied by the geography of the Oregon Coast or population interactions of coho salmon. Consequently, we adapted concepts from the published literature (see, for example, Hanski and Gilpin 1997) to develop our own population classification system, with quantitative support from the Bjorkstedt Relative Independence Analysis (Bjorkstedt 2004)

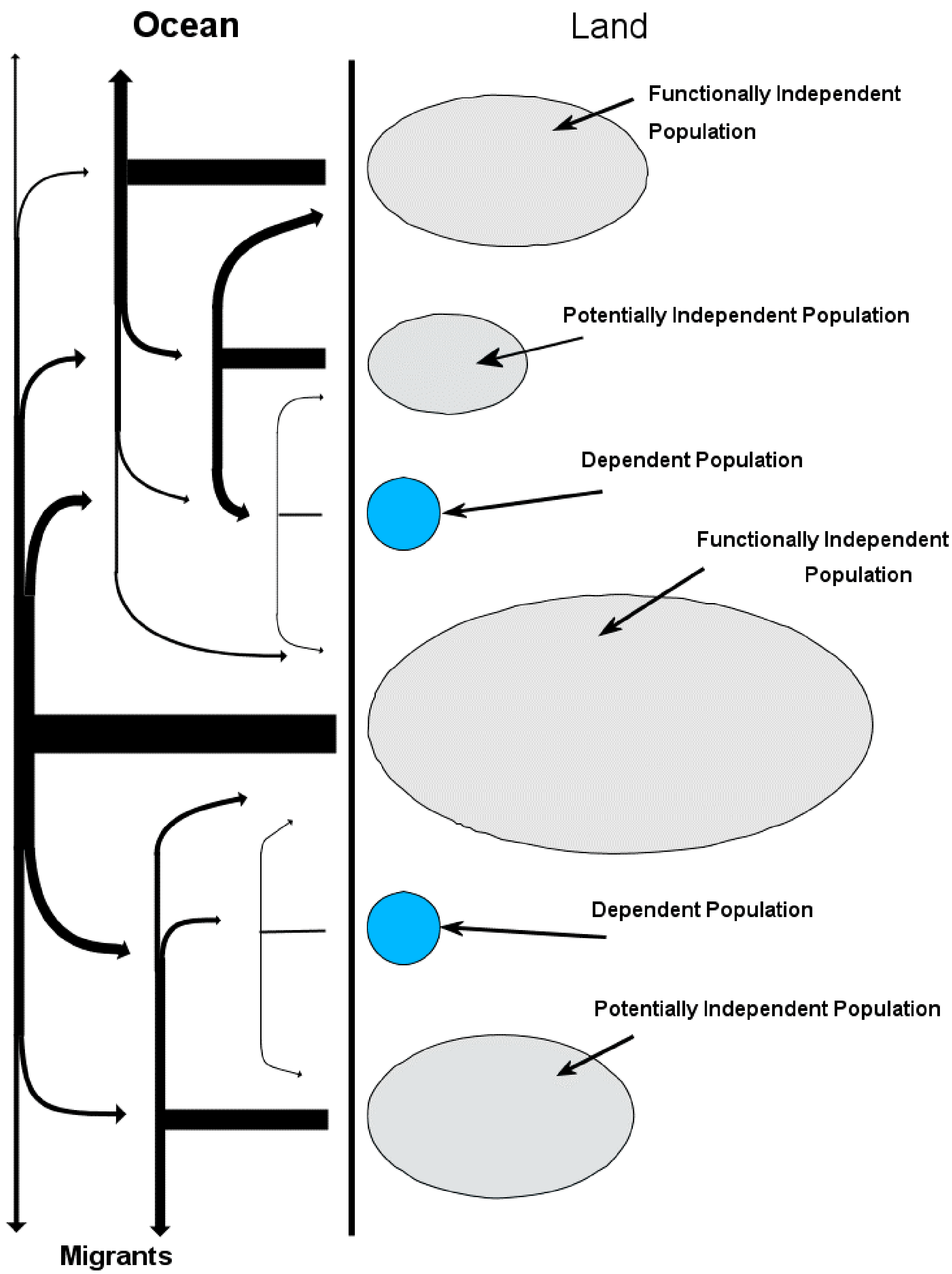

Figure 2. Conceptual model of ESU population structure. Arrow widths are proportional to number of migrants.

and estimates of historical population size based on a new synthesis of physical habitat features (Intrinsic Potential) and historical population abundance calculations (App. III and IV).

Persistence, isolation, and independence in population classification

In developing the classification system for historical Oregon Coast coho salmon populations, we utilized three key population characteristics: persistence, isolation, and independence.

Persistence is the ability of a population to sustain itself through time without inputs from other populations. We use persistence to refer to the sustainability of a population in isolation; we reserve the more common term "viability" for the sustainability of populations in the context of other populations. Thus, a population that is not persistent may be viable within a larger (ESU-level) context.

Isolation is the degree to which a population is unaffected by immigration to and from other populations: as the influence of immigration decreases, a population's isolation increases.

Independence reflects the interaction between isolation and persistence; a persistent population that is highly isolated is highly independent.

A population's persistence relies on the quantity and quality of habitat which, in turn, influences potential population size. Habitat quantity and quality can be expressed in terms of the habitat's capacity to produce fish (in other words, the potential population size supported by the habitat). All else being equal, persistence is related to population size, with large populations tending to have a greater probability of persistence than small populations.

Small populations are affected differently by processes that influence population dynamics than are larger ones (McElhaney et al. 2000). These processes include density effects, variation in environmental conditions, genetic processes, demographic stochasticity, and catastrophic events. Density effects can be positive or negative for small populations. As population numbers decline below carrying capacity, population production may increase because more resources are available to the remaining individuals. This gives a population resilience as productivity increases when numbers decline. If numbers decline below a critical point, reproduction may start to decline because individuals are unable to secure mates (Hilborn and Walters 1992). Environmental variation may result in periods of unfavorable conditions for a population. If the duration of unfavorable conditions persists longer than the reproductive cycle of the species, then populations may decline (Dennis et al. 1991, Lande 1993). Small populations may produce poor-quality offspring through the effects of genetic processes such as loss of diversity, and inbreeding depression (accumulations of deleterious genes that reduce their ability to survive). Demographic stochasticity includes non-genetic changes in fecundity, mortality, and sex ratios. Changes in the reproductive potential and capacity that result from these factors are much more pronounced in small populations than in larger ones (Lande 1998). Catastrophic events, either natural or man-made, may result in large mortality in a short time period. Through a combination of genetic and demographic factors, population numbers may be reduced below the level at which the population is able to maintain itself (Mangel and Tier

1994). Taken together, the various processes that cause small populations to lose productivity are termed "depensation."

Better-quality habitats produce more individuals per unit area than poor habitats because the quality of habitat is defined by the number of fish it produces. Watershed size also influences population size. Larger watersheds in general will be expected to support more fish than smaller watersheds. Additionally, larger watersheds will be composed of smaller subwatersheds. Larger populations may, therefore, contain subunits. This resulting structure within larger systems provides a buffer against infrequent catastrophic events, which historically were fires and floods on the Oregon Coast (Reeves et al. 1995). These events generally affected only parts of the landscape. Some subunits may have been lost temporarily while unaffected subunits continued to produce fish. Smaller populations, without the buffering effect of subunits, may have been lost in such cases. Larger populations may also have a greater genetic diversity, which increases the potential for a population to respond to unfavorable or changing conditions (Waples 1990, Waples and Teel 1990).

There is a theoretical lower limit to the size of (or habitat required for) a persistent population (reviewed in Soulé 1987); below this minimum, random events and depensation cause the risk of extinction to increase substantially. This concept informs our consideration of independence; any extant population occupying a basin with sufficient habitat to support a minimum population size is likely to persist continuously. Populations with less habitat are likely to persist only if there is significant immigration from other populations. If we knew the minimum habitat capacity necessary to support a persistent population, we could separate those populations that can function independently in isolation from those that cannot simply on the basis of habitat capacity. Even if we do not know the theoretical lower limit to the population abundance or habitat capacity required to produce that minimum population size, we may be able to use habitat capacity as a proxy measure for the relative ability of a population to persist without immigration.

A population's isolation reflects the degree to which immigration from other populations affects its dynamics: as the influence of immigration decreases, a population's isolation increases. This concept can also be thought of in terms of the ratio of native spawners to spawners from other basins. This is influenced by the rate that spawners from other populations migrate in, and the size of the other populations. A small population next to a large one is apt to have a high proportion of spawners from the larger population even if migration rates are low. It only takes a few fish from a large population spawning in a small population to lower the smaller population's degree of isolation.

McElhany et al. (2000) suggest that, for the purposes of recovery planning, a particular population should be considered independent if exchanges of individuals with other populations do not substantially affect the dynamics of that population over a 100-year time frame. However, in our view, independence is relative and reflects the interactions between isolation (in other words, proportion of native spawners returning to a population) and persistence. When we consider whether a population is independent in the context of this analysis we do not base our consideration on the current state or predicted fate of that population (in other words, the population's historical persistence or whether the population has a high likelihood of persisting for 100 years into the future). Instead, we combine the degree of isolation of a population with the historical abundance to compare the relative independence of each population in relation to others in the ESU, regardless of its likely persistence.

Categories of historical populations

As a specific criterion for relative persistence, we chose to define "high-persistence populations" as those that would have a high likelihood of persisting with no migrants from neighboring populations for 100 years. The boundary between high persistence and low persistence reflects the abundance (or habitat capacity) below which persistence begins to decline rapidly (Nickelson 2001). Those populations that did not meet this criterion were classified as "Dependent populations." These low-persistence populations would probably not be in existence if they were not receiving migrants from neighboring populations. As a next step, high-persistence populations were further divided into two types ("Potentially Independent" and "Functionally Independent") on the basis of their historical interaction with other populations (isolation). The boundary between Functionally and Potentially Independent populations reflects the likelihood of influence from other nearby populations (the proportion of native spawners returning to a population). Functionally Independent populations on average provide more migrants to other populations than they receive, so their demographics are not greatly influenced by outside migrants.

We separated historical populations into three categories based first on their relative persistence and then on their degree of isolation:

Functionally Independent populations: high-persistence populations whose dynamics or extinction risk over 100-year time frame is not substantially altered by exchanges of individuals with other populations. These populations are net "donor" populations that may provide migrants for other types of populations. This category is analogous to the "independent populations" of McElhaney et al. (2000).

Potentially Independent populations: high-persistence populations whose population dynamics may be substantially influenced by periodic immigration from other populations. In the event of the decline or disappearance of migrants from other populations, a Potentially Independent population could become a Functionally Independent population.

Dependent populations: low-persistence populations that rely upon immigration from other populations. Without these inputs, Dependent populations would have a lower likelihood of persisting over 100 years. They are "receiving" populations that are dependent on sufficient immigration from surrounding populations to persist.

Isolation depends primarily on two factors: (1) the size and potential productivity of a population relative to nearby populations, and (2) the effective migration (migrants who contribute to the next generation) among nearby populations. The effective migration among nearby populations is a function of the size of the donor population, the distance from the donor to the receiving population, and the ability of the migrants to contribute offspring to the receiving population. The larger the donor population and the closer it is to the receiving population, the greater the rate of effective migration. Functionally Independent populations, in that they are highly persistent and, hence, larger populations, are more likely to have individuals that stray to other populations. Thus, populations closest to large Functionally Independent populations will have a greater potential for receiving migrants than will populations that are farther away from larger donor populations (Fig. 2). A population that is classified as Potentially Independent due to its proximity to a very large Functionally Independent population might function at some other time as Functionally Independent if the very large neighboring population experienced a significant population crash. Dependent populations are very likely to rely on immigration from both Functionally and Potentially Independent populations. Seldom would Dependent populations be expected to contribute directly to the long-term persistence of other population types.

Both Functionally and Potentially Independent populations tend to be larger than Dependent populations (Fig. 2). Large numbers of individuals, usually spread over a large area within each river or lake system, buffer larger populations from the impacts of catastrophic flood and fire events. Catastrophic events on the scale of a large watershed are rare (Reeves et al. 1995). In addition, these larger populations often occur in larger watersheds with greater variety of habitats including areas of stable, lowland habitat that is most productive for coho salmon. Dependent populations are smaller and thus more vulnerable to periodic declines resulting from events in the freshwater and marine environments.

All population types, in varying degrees, contribute to the persistence and productivity of the ESU. Functionally Independent populations are the foundation of the ESU. Because of their large size, these populations make the greatest contribution to the productivity and persistence of the ESU. The Potentially Independent populations are also important sources of productivity that may function as "giver" populations to the Dependent populations. A Potentially Independent population may play an important role in the persistence of a Functionally Independent population if the productivity of that system declines due to disturbance in freshwater or estuarine habitats. Dependent populations contribute to the overall health of the ESU by increasing the total productive area, and may provide reservoirs of potentially adaptive diversity for the ESU (Buckling et al. 2003). They may also be important for maintaining the integrity of a given watershed. For example, returning adults provide nutrients that are used by a wide array of other aquatic and terrestrial organisms and vegetation (Cedarholm et al. 1999).

One task of the TRT is to determine the modern population structure necessary to restore the aspects of life-history diversity, distribution of populations, and abundance needed to provide for a sustainable Oregon Coast Coho Salmon ESU into the future. Understanding the number, abundance, life-history diversity, and distributions of historical populations of Oregon Coast coho salmon is an important first step in determining viability criteria and recovery scenarios. The historical organization and abundance of these populations were dynamic (Hanski and Gilpin 1997). However, the static picture of historical structure we have reconstructed here provides a template for sustainability.