IDENTIFICATION OF HISTORICAL POPULATIONS OF COHO SALMON (*Oncorhynchus kisutch*) IN THE OREGON COAST EVOLUTIONARILY SIGNIFICANT UNIT

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Draft

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EXECUTIVE SUMMARY

In 2003, the Oregon Workgroup (Workgroup) of the Oregon Northern California Coast Technical Recovery Team (TRT) convened to review and analyze information that could shed light on historical populations of Oregon Coast coho salmon (*Onchorhynchus kisutch*). This document presents the preliminary conclusions of the Workgroup. A historical perspective describing how these populations functioned is an important first step in assessing viability of present-day populations and in developing de-listing criteria as an overall recovery strategy.

Documentation of life history traits, distribution, or abundance of Oregon Coast coho salmon prior to 1940 is limited. Considerable biological information has been gathered during the past thirty years, and particularly the past twelve years; however, it is difficult to relate the biological characteristics of modern populations to those that existed historically in the same basin. Human activities over the past 200 years have altered every aspect of salmon habitat on the coast, harvest has changed abundance patterns, and hatcheries may have blurred the distinctions among stocks. Coho salmon have adapted their behavior to many of these changes and, as a result, present-day Oregon Coast coho salmon populations function differently than they did historically. Nonetheless, we have tried to address where populations were historically and how these historical populations functioned.

To establish historical population boundaries, we relied on geographical and ecological characteristics of the landscape that have not been greatly altered by human activities. Geographical information was used in calculating the distance between ocean-entry points. Ecological characteristics were utilized in partitioning the Umpqua Basin into two historical populations. A total of 67 historical populations were identified through this analysis.

Our view of the historical population structure of Oregon Coast coho salmon relies on a simple conceptual model of the spatial relationships of 67 populations. We used a rule-based approach to identify populations. Subsequently, we utilized a Relative Independence Model to classify these populations on the basis of two key characteristics: persistence (their relative abilities to persist without input from neighboring populations), and isolation (the relative degree to which they might have been influenced by adult fish from other populations migrating into their spawning areas). The interaction of these two factors across what we believe to have been the historical populations of Oregon Coast coho salmon gives us a measure of Relative Independence. This Relative Independence gives us a basis for classifying the populations as Functionally Independent, Potentially Independent, and Dependent. Nine populations were identified as Functionally Independent, 9 as Potentially Independent, and 48 historical populations were identified as Dependent populations. We will use this classification in the next step—analyzing the viability of populations and ultimately of the ESU in order to identify quantitative goals for recovery. Two other recovery groups (the SONCC Workgroup and the Central California Coast TRT) are also using the Relative Independence Model to classify their populations.

These proposed historical populations are intended to be representative of the range and diversity of populations of Oregon Coast coho salmon, not necessarily an exact reconstruction. In this representation of historical populations, we assume that ocean feeding areas were a shared

resource and that, in the Umpqua Basin, populations probably shared juvenile rearing and migration corridors. Understanding the historical structure of populations in addition to their abundance and life-history characteristics provides a framework for comparing the historical to the present status of populations, the changes that have affected them, and the restoration of processes that may be necessary to recover them.

ACKNOWLEDGEMENTS

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Numerous scientists and fishery managers provided information that aided in preparation of this report on historical populations and deserve special thanks. We particularly want to thank the Independent Multidisciplinary Scientific Team (IMST) for their in-depth analyses on the role of lowlands in coho salmon life history. Thanks are also due to Bridgette Lohrman (OSU CIMRS), Cid Hughes (MES, Inc.), and Justin Mills (ORISE) for their significant contributions to this effort.

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The Oregon Workgroup for Oregon Coast coho salmon consists of Dr. Peter Lawson, Dr. Thomas Wainwright, Dr. Gordon Reeves, Thomas Nickelson, and Charles Huntington. Adjunct members are Mark Chilcote of ODFW and Kelly Moore of OWEB. Heather Stout of NOAA Fisheries NWFSC staffs the Oregon Workgroup.

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)

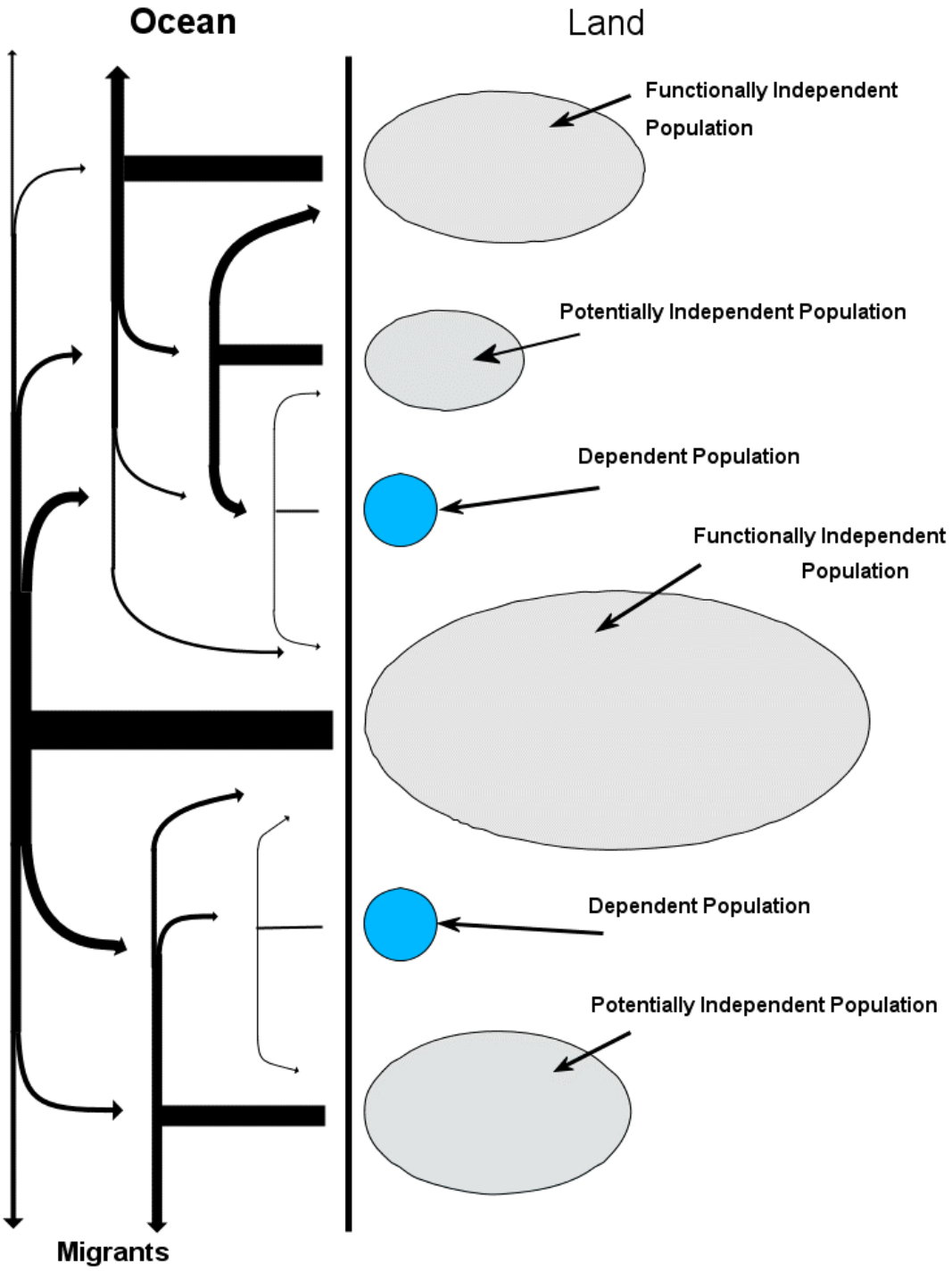

Figure 2. Conceptual model of ESU population structure. Arrow widths are proportional to number of migrants.

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.

METHODS AND RESULTS

In developing the population identification and classification system that reflects the persistence, isolation, and independence of populations of Oregon Coast coho salmon, we sought an approach that had three desirable characteristics: consistency, reproducibility, and transparency. **Consistency** means that the same approach can be applied across ESUs over a broad geographic area, and lead to comparable results in different areas. **Reproducibility** means that conclusions are predictable; in other words, another group of scientists could apply the same methods to the same information and reach essentially the same result. **Transparency** means that methods are reasonably simple and understandable, so that non-specialists can understand the logical connection between information and conclusions. We chose a rule-based approach that we believe meets these criteria.

Criteria for Identifying the Distribution of Historical Populations

The task of identifying historical coho salmon populations within the Oregon Coast Coho Salmon ESU is challenging, because anthropogenic factors such as hatchery operations, stock transfers, harvest effects, and habitat destruction and degradation have significantly influenced the population structure and interactions we observe today. There are no extant populations unaffected by these anthropogenic factors to provide information regarding historical population structure and number. Information about historical abundance and distribution of fish is available only for a few large basins. We have no alternative, therefore, but to examine a suite of characteristics of modern populations and their watersheds in our effort to identify the selective and isolating factors that may have lead to demographically independent historical populations. The factors we have considered include 1) historical use of habitat; 2) geographical isolation; 3) biological characteristics of populations; and 4) ecological characteristics of river, stream, and lake watersheds. This information was considered across the coastal river, stream, and lake basins that may have historically supported coho salmon (Fig. 3).

Documented Historical Use

The extent of historical use of Oregon Coast coho salmon habitat is not very different from the extent of present use in most basins within the ESU (Fig. 4). There are areas, such as the Smith River (Fig. 5) that have had a major barrier removed. There are also new barriers that restrict access to historical habitat. However, large areas of lowland habitat have been cut off or restricted from access by dikes, tidegates, and other hydrologic changes. Therefore, the extent of Oregon Coast coho salmon use does not show much restriction, but what is not shown is the loss of very significant areas that were historically the core of the populations. Because of these changes, the core of many Oregon Coast coho populations have subsequently persisted only in more marginal, less productive areas (IMST 2002).

Figure 3. River and stream basins in the Oregon Coast Coho Salmon ESU.

Figure 4. Potential historical coho salmon distribution in the Oregon Coast Coho Salmon ESU.

Figure. 5. Examples of significant anthropogenic changes to historical coho salmon distribution in the Oregon Coast Coho Salmon ESU.

Geographical Isolation

Geographical isolation is an important factor in the evolution of separate populations within a basin or between basins. The Oregon Coast Coho Salmon ESU, in general, is made up of relatively small basins (Fig. 3). The exception to that general rule is the Umpqua Basin, which is quite large and drains areas of very different vegetation, geology, and distance from the marine influence. Table 1 lists the sizes of the basins that supported what we believe were the historical coho populations on the Oregon Coast and the miles of coho stream miles found within them.

The distance between saltwater entry points of each basin may have a significant effect on the degree of migration among populations. Table 2 shows the locations of the basins and the distances between each successive basin. Some populations may be significantly affected by migrants from larger, or more productive systems. Long-term viability as a population may be affected by the distance from these larger or more productive systems.

Biological Characteristics

The first step in the process of identifying historical population patterns in the Oregon Coast Coho Salmon ESU, was to consider several types of biological evidence. We examined life history traits for naturally spawning coho salmon populations, including smolt size and outmigration timing, age at spawning, river entry and spawn timing, ocean migration patterns based on marine coded-wire-tag (CWT) recoveries, homing fidelity, and genetics. The primary objective of this analysis was to discover patterns in these traits that might indicate how historical populations were structured. Because these traits are believed to have both genetic and environmental bases, similarities among populations could indicate either shared genetic heritage or similar responses to shared environmental conditions.

Several factors make compiling and comparing life history trait information on a basin scale more difficult. First, these traits vary greatly over time and space, presumably due in large part to the highly variable environment. Fish examined in different years or from different locations or habitats within a basin may display different life history characteristics, making it difficult to estimate values that characterize historical or basin-wide populations. Because traits also vary greatly from year to year, study results may be sensitive to the period over which they were conducted. For example, measurements of many life history traits for Oregon coho salmon during the 1983 El Niño were very different from those in the years before and after that event (Johnson 1988). A second factor that has confounded our analysis is the lack of information on life history traits, especially the lack of long-term data sets, from most naturally spawning populations. A third complication is that anthropogenic activities such as land-use practices (Hartman et al. 1984, Holtby 1987) and artificial propagation (Steward and Bjornn 1990, Flagg et al. 1995) may alter life history traits. To help limit this bias, life history trait comparisons in this document have focused on naturally spawning populations. However, because of the practice of releasing hatchery fry and smolts in widespread locations, often outside the basin where the parents originated, many studies of naturally spawning populations probably include first- or second-generation hatchery fish. Information on life history traits from hatchery populations was used only when there was insufficient information available from naturally spawning populations, as in the case of ocean migration patterns. As with environmental

Table 1. Basin areas with stream lengths (1:100,000 scale dataset, Streamnet 2003).

	Basin Sizes			
Name	**Approx. Stream Miles**	**Approx. Stream km**	**Acres**	**Hectares**
Necanicum R.	93	150	53,320	21,578
Indian Cr.	1	2	262	106
Canyon Cr.	2	4	1,127	456
Ecola Cr.	19	30	13,538	5,479
Red Rock Cr.	1	2	149	60
Austin Cr.	1	2	203	82
Asbury Cr.	4	6	1,574	637
Rock Cr.	6	10	3,648	1,476
Arch Cape Cr.	3	5	2,317	938
Short Sand Cr.	6	10	2,950	1,194
Nehalem R.	932	1,502	545,738	220,853
Spring Cr.	4	6	1,874	758
Watseco Cr.	2	4	845	342
Tillamook Bay	622	1,002	358,830	145,214
Netarts Bay	17	27	9,705	3,927
Rover Cr.	2	3	634	257
Sand Cr.	20	32	10,825	4,381
Nestucca R.	381	613	204,119	82,605
Neskowin Cr.	24	38	12,355	5,000
Salmon R.	104	168	47,742	19,321
Devils Lake	20	31	7,799	3,156
Siletz R.	548	882	235,531	95,316
Schoolhouse Cr.	2	3	743	301
Fogarty Cr.	8	12	3,324	1,345
Depoe Bay Cr.	8	12	2,985	1,208
Rocky Cr.	8	13	5,047	2,043
Johnson Cr. (near Siletz)	2	4	712	288
Spencer Cr.	8	13	3,807	1,541
Wade Cr.	4	7	1,709	692
Coal Cr.	4	6	1,527	618
Moolack Cr.	3	6	1,311	530
Big Cr. (near Yaquina)	8	13	3,429	1,388
Yaquina R.	351	566	160,658	65,016
Henderson Cr.	2	3	604	244
Grant Cr.	2	3	366	148
Moore Cr.	2	3	554	224
Thiel Cr.	6	10	2,767	1,120
Beaver Cr.	42	68	21,532	8,714

Table 1 continued. Basin areas with stream lengths (1:100,000 scale dataset, Streamnet 2003).

	Basin Sizes			
Name	**Approx. Stream Miles**	**Approx. Stream km**	**Acres**	**Hectares**
Alsea R.	530	854	301,778	122,126
Little Cr.	1	2	646	262
Big Cr. (near Alsea)	14	22	5,740	2,323
Vingie Cr.	4	6	1,264	511
Yachats R.	59	94	27,845	11,268
Gwynn Cr.	2	4	800	324
Cummins Cr.	11	17	6,282	2,542
Bob Cr.	6	10	3,669	1,485
Tenmile Cr.	24	38	14,963	6,055
Squaw Cr.	3	4	1,086	439
Big Cr. (near Siuslaw)	17	28	10,125	4,097
China Cr.	6	9	2,128	861
Blowout Cr.	2	3	290	118
Cape Cr.	15	24	7,340	2,971
Berry Cr.	6	9	2,442	988
Sutton Cr. (near Mercer Lake)	18	29	10,692	4,327
Siuslaw R.	916	1,474	496,047	200,744
Siltcoos R. (Lake)	84	135	48,632	19,681
Tahkenitch Lake	39	63	23,276	9,420
Threemile Cr.	5	8	2,105	852
Umpqua R. (Total)	4,611	7,424	2,998,976	1,213,647
Lower Umpqua R.	1,218	1,961	640,914	259,370
Upper Umpqua R.	3,393	5,464	2,358,062	954,278
Tenmile Lake	99	159	57,569	23,297
Coos Bay	760	1,223	384,393	155,559
Coquille R.	1,222	1,968	676,342	273,707
Johnson Cr. (near Coquille)	6	9	2,656	1,075
Twomile Cr.	24	38	9,704	3,927
Floras Cr.	133	215	81,414	32,947
Sixes R.	130	209	85,832	34,735

Table 2. Locations of river mouths for basins along the Oregon Coast (Kilgour 2003)[1].

Basin Name	Latitude	Longitude	Distance (km) from Columbia River
Columbia	46.244	124.057	0.0
Necanicum	46.012	123.926	27.7
Indian	45.9307	123.9781	37.6
Canyon	45.9304	123.9779	37.6
Ecola	45.8993	123.9625	41.2
Red Rock	45.845	123.961	47.3
Austin	45.819	123.964	50.2
Asbury	45.815	123.962	50.6
Arch Cape	45.804	123.966	51.9
Short Sands	45.76	123.963	56.8
Nehalem	45.658	123.933	68.4
Spring	45.62	123.937	72.6
Watseco	45.589	123.984	77.6
Tillamook	45.488	123.901	90.5
Netarts	45.403	123.944	100.6
Rover	45.328	123.967	109.1
Sand	45.29	123.937	113.9
Nestucca	45.184	123.956	125.8
Neskowin	45.1	123.986	135.4
Salmon	45.047	124.005	141.5
Devils Lake	44.968	124.016	150.3
Siletz	44.904	124.01	157.4
Schoolhouse	44.873	124.041	161.6
Fogarty	44.839	124.053	165.5
Depoe	44.806	124.058	169.2
Rocky	44.779	124.071	172.4
Johnson	44.738	124.059	177.0
Spencer	44.729	124.059	178.0
Wade	44.716	124.06	179.5
Coal	44.708	124.061	180.4
Moolack	44.703	124.063	180.9
Big Creek (near Yaquina)	44.659	124.058	185.8
Yaquina	44.613	124.017	191.9
Henderson	44.589	124.068	196.7
Grant	44.581	124.068	197.6
Moore	44.572	124.069	198.6
Thiel	44.565	124.07	199.4
Beaver	44.524	124.075	204.0

[1] Columbia and Elk rivers are included to locate the ESU boundary. Tributaries to Tillamook Bay are assumed to harbor a single population.

Table 2 continued. Locations of river mouths for basins along the Oregon Coast (Kilgour 2003)[1].

Basin Name	Latitude	Longitude	Distance (km) from Columbia River
Alsea	44.423	124.08	215.2
Little	44.393	124.088	218.6
Big Creak (near Alsea	44.371	124.088	221.0
Vingie	44.341	124.098	224.5
Yachats	44.309	124.107	228.1
Gwynn	44.271	124.11	232.3
Cummins	44.266	124.108	232.9
Bob	44.244	124.11	235.3
Tenmile	44.226	124.11	237.3
Squaw	44.2086	124.1133	239.3
Rock	44.183	124.114	242.1
Big Creek (near Suislaw)	44.177	124.114	242.8
China	44.169	124.115	243.7
Blowout	44.157	124.117	245.0
Cape	44.134	124.123	247.6
Berry	44.095	124.122	251.9
Sutton (Lake)	44.06	124.127	255.9
Siuslaw	44.017	124.136	260.7
Siltcoos (Lake)	43.874	124.153	276.6
Tahkenitch (Lake)	43.815	124.165	283.3
Threemile	43.748	124.18	290.8
Umpqua	43.669	124.204	299.8
Tenmile (Lake)	43.562	124.231	311.9
Coos	43.429	124.229	326.6
Coquile	43.124	124.429	364.2
Johnson	43.093	124.431	367.6
Twomile	43.044	124.441	373.1
Floras	42.913	124.496	388.3
Sixes	42.854	124.543	395.9
Elk	42.81	124.533	400.9

[1] Columbia and Elk rivers are included to locate the ESU boundary. Tributaries to Tillamook Bay are assumed to harbor a single population.

variability, the effects of anthropogenic activities may confuse the determination of average life history traits and are difficult to factor out.

Because of these potential sources of variability, data were collected from as many sources as possible to give some indication of average results. We especially sought older data sets to indicate coho salmon population traits prior to the 1960s, when technological advances in hatchery practices made it possible to raise large numbers of salmon to juvenile or smolt stages. The resulting proliferation of hatchery release programs has probably decreased local variability among coho populations (Weitkamp 1995, Ford et al. 2004).

The coho salmon life cycle is summarized in Figure 6. Adult coho salmon begin migrating into coastal streams and rivers with the first freshets in the fall. Spawning begins in November, peaks in December or January, and may continue into March. Wild spawners typically migrate and spawn later than hatchery fish in the same area. Eggs hatch in the spring and fry grow rapidly to parr stage by summer or early fall. Parr then seek out areas protected from high flows and spend a second winter in freshwater before migrating to the ocean as smolts in March through June. About 20% of males mature at age 2 and return to freshwater as "jacks" in the same year they entered the ocean as smolts. The remainder of juveniles rear in the ocean for 18 months and return as 3-year-old adults in the following fall (Lawson et al. 2004).

Smolt size and outmigration timing

Recent data do not suggest any population-based pattern for either smolt outmigration timing (Table 3) or smolt size (Table 4) in modern Oregon Coast coho salmon. Regardless of the basin of origin, peak outmigration timing generally occurs in May, with some runs earlier or later, and with most smolts measuring 90-115 mm (3.5-4.5 in.) fork length.

Smolt outmigration timing and smolt size appear to respond to small-scale habitat variability. Smolts residing in ponds or lakes often have different outmigration timing and are a different size than smolts residing in streams within the same basin (Rodgers et al. 1993, Nielsen 1994). For example, large smolts observed in Tenmile Lakes were thought to have resulted from a productive lake-rearing environment (McGie 1970). Both smolt outmigration timing and size exhibit considerable interannual variation; mean smolt sizes from a single system can vary substantially between years (Table 4), whereas peak outmigration timing can vary by several weeks to a month (Table 3).

Because of their responses to small-scale habitat variability, smolt size and outmigration timing have also been shown to be affected by anthropogenic activities, including habitat degradation (Moring and Lantz 1975) and habitat restoration (Johnson et al. 1993, Rodgers et al. 1993). These factors thoroughly complicate the assessment of any basin-linked pattern that may exist for either trait, because these activities have occurred throughout the range of Oregon Coast coho salmon. Sampling design may also influence reported smolt sizes and outmigration timing. It is impossible to discern the historical patterns of smolt size and outmigration timing from the modern patterns cited here. We are unable to predict the effects of anthropogenic activities on these patterns and from this describe the historical condition. Therefore, these characteristics do not appear to be useful in defining historical populations within the Oregon Coast Coho Salmon ESU.

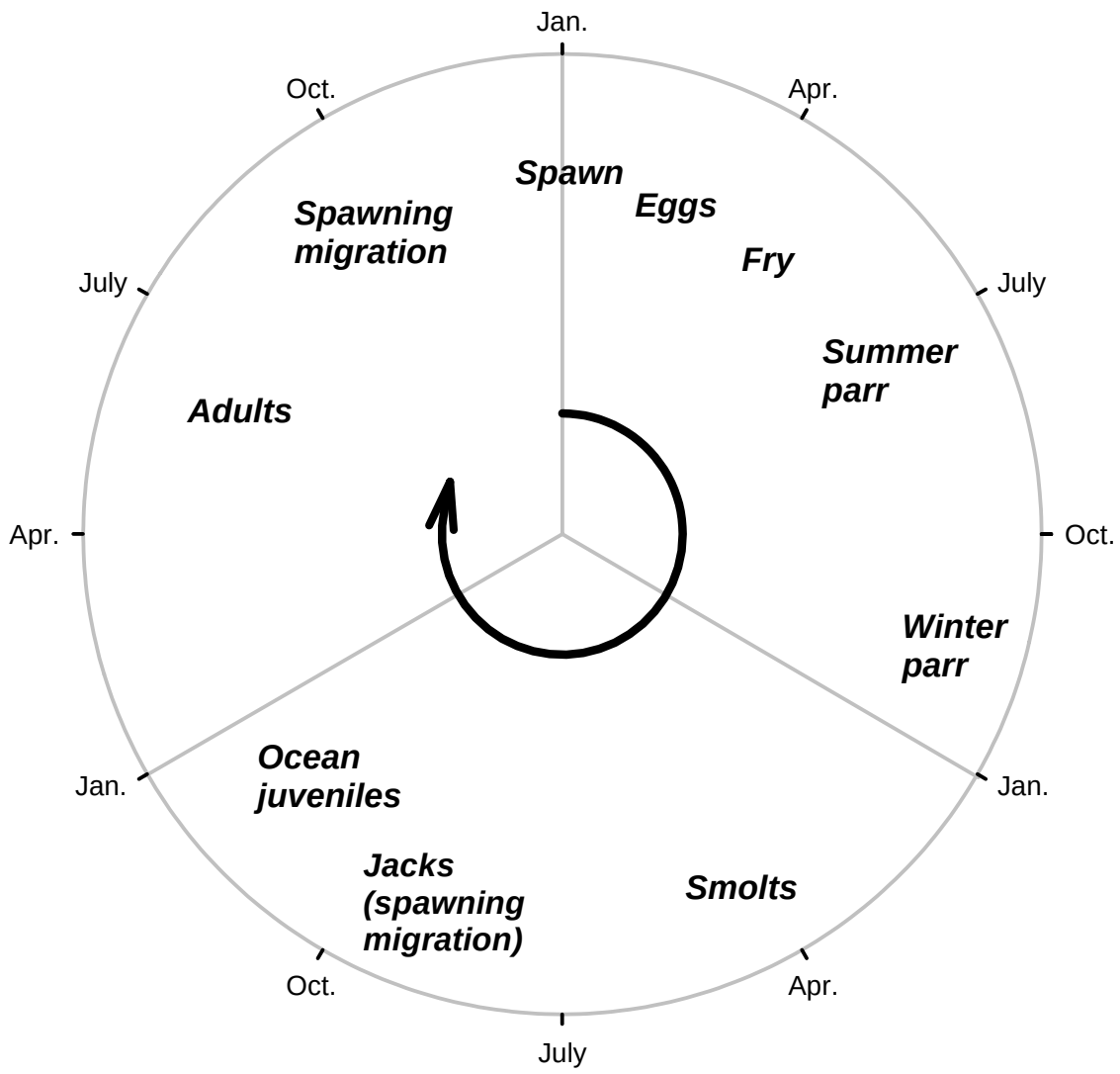

Figure 6. Life cycle of the coho salmon in Oregon (modified from Lawson et al. 2004).

Table 3. Oregon Coast coho salmon smolt outmigration peak timing and duration (after Weitkamp 1995).

River (Tributary)	Smolt Outmigration Duration	Peak Smolt Outmigration	Years Covered	Source
Wilson (Spring Cr.)	Feb-June	Apr	1949-58	Skeesick (1970)
Tillamook (Sand Cr.)	mid Mar-mid June	early May	1946-49	Sumner (1953)
Nestucca (East Cr.)		late April	1988-91	Johnson et al. (1993), Rodgers et al. (1993), Weeks (1994)
Nestucca (Moon Cr.)		late April-early May	1988-91	Rodgers et al. (1993)
Salmon		May	1975-76	McGie (1977)
Alsea	Mar-May	Mar-Apr	1959-73	Moring and Lantz (1975)
Alsea (Lobster Cr.)	Feb-June	late Mar-early Apr	1988-93	Johnson et al. (1993), Rodgers et al. (1993), Weeks (1994)
Alsea (Drift Cr.)	Feb-May			Chapman (1965)
Alsea (Crooked Cr.)		May	1973-79	Weeks (1994)
Tenmile Cr.		May	1992-93	Johnson et al. (1993), Weeks (1994)
Cummins Cr.		late Apr-early May	1992-93	Johnson et al. (1993), Weeks (1994)
Siuslaw	Feb- June	Mid May	1983	Rodgers et al. (1993)
Siuslaw (Triangle Lake)		early May	1973	Weeks (1994)
Tenmile Lake		mid-May	1970-75	McGie (1970-73, 1975)
Floras Lake		mid-May	1973	Weeks (1994)
Coquille		late Apr-early May	1979	Weeks (1994)
Sixes	Mar-June	early-mid May	1969	Reimers (1971)
Nehalem (N. Fk.)		late April-early May	1998-2002	Solazzi et al. (2003)
Tillamook (LS Fk. Kilchis)		late March-early May	1998-2002	Solazzi et al. (2003)
Tillamook (LN Fk. Wilson)		late April-late May	1998-2002	Solazzi et al. (2003)
Siletz (Mill Cr.)		late April-mid-May	1998-2002	Solazzi et al. (2003)
(Bales Cr.)		late March-mid-May	1998-2002	Solazzi et al. (2003)
Yaquina (Mill Cr.)		late April-early May	1998-2002	Solazzi et al. (2003)
Cascade		mid-late April	1998-2002	Solazzi et al. (2003)
Alsea (UM Lobster)		early April-mid-May	1998-2002	Solazzi et al. (2003)
Alsea (E. Fk. Lobster)		early-late April	1998-2002	Solazzi et al. (2003)
Cummins Cr.		late April-late May	1998-2002	Solazzi et al. (2003)

Table 3, continued. Oregon Coast coho salmon smolt outmigration peak timing and duration (after Weitkamp 1995).

River (Tributary)	Smolt Outmigration Duration	Peak Smolt Outmigration	Years Covered	Source
Tenmile Cr.		late April-early June	1998-2002	Solazzi et al. (2003)
Smith (W. Fk.)		mid April-mid-May	1998-2002	Solazzi et al. (2003)
(Fall Cr.)		early April-mid-May	1998-2002	Solazzi et al. (2003)

Table 4. Oregon Coast coho salmon smolt sizes (after Weitkamp 1995).

River (Tributary or Location)	Smolt Size Range (mm)	Mean Smolt Size (mm)	Avg. Length at Peak Migration (mm)	Year(s) Covered	Source
Tillamook (Wilson)	**	100		1949-58	Skeesick (1970)
Tillamook (Sand Cr.)	41-184	105-110		1946-49	Sumner (1953)
Nestucca (East Cr.)	**	100		1988-90	Rodgers et al. (1993)
Nestucsca (East Cr.)	**	116		1991-92	Rodgers et al. (1993)
Nestucca (Moon Cr.)	**	97-102		1988-92	Rodgers et al. (1993)
Yaquina	88-160	118		1980	Nicholas et al. (1982)
Alsea (Lobster Cr.)	**	86		1988-91	Rodgers et al. (1993)
Alsea (Lobster Cr.)	**	91		1992-93	Rodgers et al. (1993), Weeks (1994), Johnson et al. (1993)
					Johnson et al. (1993)
Alsea (E.F.Lobster Cr.)	**	82-83		1988-92	Rodgers et al. (1993)
Alsea (Drift Cr.)	**	80-90		1959-62	Chapman (1965)
Alsea (Deer Cr.)	**	97		1960-73	Knight (1979)
Alsea (Flynn Cr.)	**	95		1960-73	Knight (1979)
Alsea (Needle Cr.)	**	93		1960-73	Knight (1979)
Siuslaw	**	100-107		1983	Rodgers et al. (1987)
Umpqua	**	100		1991	Roper (1994)
Tenmile Lake	**	152		1970-75	McGie (1970-73, 1975)
Sixes	88-150	120		1969	Reimers (1971)
N. Fk. Nehalem	**		101-122	1998-2002	Solazzi et al. (2003)
Tillamook LS Fk. Kilchis	**		99-118	1998-2002	Solazzi et al. (2003)
Tillamook LN Fk. Wilson	**		102-111	1998-2002	Solazzi et al. (2003)
Siletz (Mill)	**		95-117	1998-2002	Solazzi et al. (2003)
Yaquina Bales	**		98-101	1998-2002	Solazzi et al. (2003)
Yaquina Mill	**		122-157	1998-2002	Solazzi et al. (2003)
Alsea Cascade	**		100-140	1998-2002	Solazzi et al. (2003)
Alsea UM Lobster	**		81-98	1998-2002	Solazzi et al. (2003)
Alsea E Fk Lobster	**		77-100	1998-2002	Solazzi et al. (2003)
Cummins	**		105-115	1998-2002	Solazzi et al. (2003)
Tenmile Cr.	**		111-121	1998-2002	Solazzi et al. (2003)
Umpqua (WFk Smith)	**		102-116	1998-2002	Solazzi et al. (2003)
Coos (Fall)	**		100-123	1998-2002	Solazzi et al. (2003)

** No data.

Age at spawning

In the Oregon Coast Coho Salmon ESU, the vast majority of adult fish are 3-year-olds, having spent approximately 18 months in freshwater and 18 months in salt water (Gilbert 1912, Pritchard 1940, Loeffel and Wendler 1968). Exceptions to this pattern are jacks; sexually mature males that return to freshwater to spawn after only 5–7 months in the ocean. A small fraction of adults return at age 4, having spent an extra year in freshwater before spawning (Moring and Lantz 1975).

Drucker (1972) suggested that there is a latitudinal cline in the proportion of jacks in coho salmon populations, with populations in California having more jacks and those in British Columbia having almost none. Although the production of jacks is a heritable trait in coho salmon (Iwamoto et al. 1984), it is also strongly influenced by environmental factors (Silverstein and Hershberger 1992). The proportion of jacks in a given coho salmon population appears to be highly variable through time (Table 5; Zhou 2000), likely as a response of the population to environmental variation.

Some systems have also shown long-term changes in the proportion of jacks produced. The Tenmile Lakes system (Oregon) historically produced large numbers of jacks (Morgan and Henry 1959) but no longer does (Ursitti 1989), presumably because of altered freshwater predation pressures (Reimers et al. 1993). Because of the high level of variability in the relative production of jacks in a population, and its sensitivity to environmental change, the proportion of jacks appeared to be a poor indicator of historical population patterns and was not pursued further.

River entry and spawn timing

In general, river entry and spawn timing show considerable spatial and temporal variability. Most modern Oregon Coast coho salmon enter rivers in October (Mullen 1981a). Spawning occurs from November through January and occasionally into February, depending on the population (Figs. 7a-e). Some coho may spend 1 or 2 months in freshwater before spawning (Flint and Zillges 1980).

Coho salmon river entry timing is influenced by many factors; one of the most important appears to be river flow (Sumner 1953). Coho salmon wait for freshets before entering rivers, so a delay in fall rains delays river entry and spawn timing. Delays in river entry of over a month are not unusual (Eames et al. 1981). Several small Oregon Coast coho salmon systems have sandbars that block their mouths for most of the year except during winter (such as Devils Lake, Sixes River, New River). In these systems, coho and other salmon species are unable to enter the rivers until sufficiently strong freshets breach the sandbars (Sandercock 1991).

These factors make determining and comparing average or peak river entry and spawn timing difficult because of the high spatial and temporal variability exhibited within basins. Compared to normal run times, river entry of some coho salmon populations are exceptionally early or late. It was originally thought that this might be helpful in delineating historical populations. However, the relationship between populations with unusually timed runs is not well understood and exceptional run timing is found in numerous geographical areas.

Table 5. Coho salmon freshwater harvests and terminal runs in Tahkenitch, Siltcoos, and Tenmile Lakes basins 1960-1999. After Zhou (2000).

Tahkenitch			Siltcoos			Tenmile Lakes		
Run year	**Adult Catch**	**Jack Catch**	**Run year**	**Adult Catch**	**Jack Catch**	**Run year**	**Adult Catch**	**Jack Catch**
1960	28	16	1960	340	104	1960	238	1,127
1961	62	12	1961	620	218	1961	462	537
1962	48	6	1962	500	85	1962	366	435
1963	92	49	1963	867	510	1963	658	2,005
1964	31	7	1964	365	60	1964	258	397
1965	28	9	1965	339	167	1965	238	276
1966	89	29	1966	842	93	1966	638	726
1967	21	16	1967	286	128	1967	195	358
1968	100	23	1968	927	205	1968	706	488
1969	69	73	1969	371	461	1969	254	785
1970	23	11	1970	207	52	1970	910	3,467
1971	53	6	1971	100	16	1971	665	307
1972	19	22	1972	373	255	1972	200	102
1973	30	6	1973	280	82	1973	228	148
1974	8	7	1974	244	326	1974	103	71
1975	4	11	1975	413	107	1975	266	380
1976	4	3	1976	210	50	1976	10	9
1977	11	2	1977	134	37	1977	95	83
1978	3	1	1978	153	25	1978	34	30
1979	0	0	1979	3	0	1979	0	0
1980	0	0	1980	286	52	1980	24	31
1981	8	4	1981	485	178	1981	194	185
1982	0	0	1982	360	96	1982	76	117
1983	0	0	1983	272	316	1983	133	125
1984	123	49	1984	1,091	198	1984	287	120
1985	12	8	1985	236	89	1985	67	50
1986	47	22	1986	398	209	1986	102	60
1987	5	3	1987	121	19	1987	15	9
1988	0	0	1988	358	41	1988	90	60
1989	11	12	1989	184	61	1989	373	452
1990	19	17	1990	202	55	1990	108	58
1991	30	6	1991	248	29	1991	144	44
1992	0	0	1992	85	43	1992	50	53
1993			1993			1993	8	4
1994			1994			1994	95	86

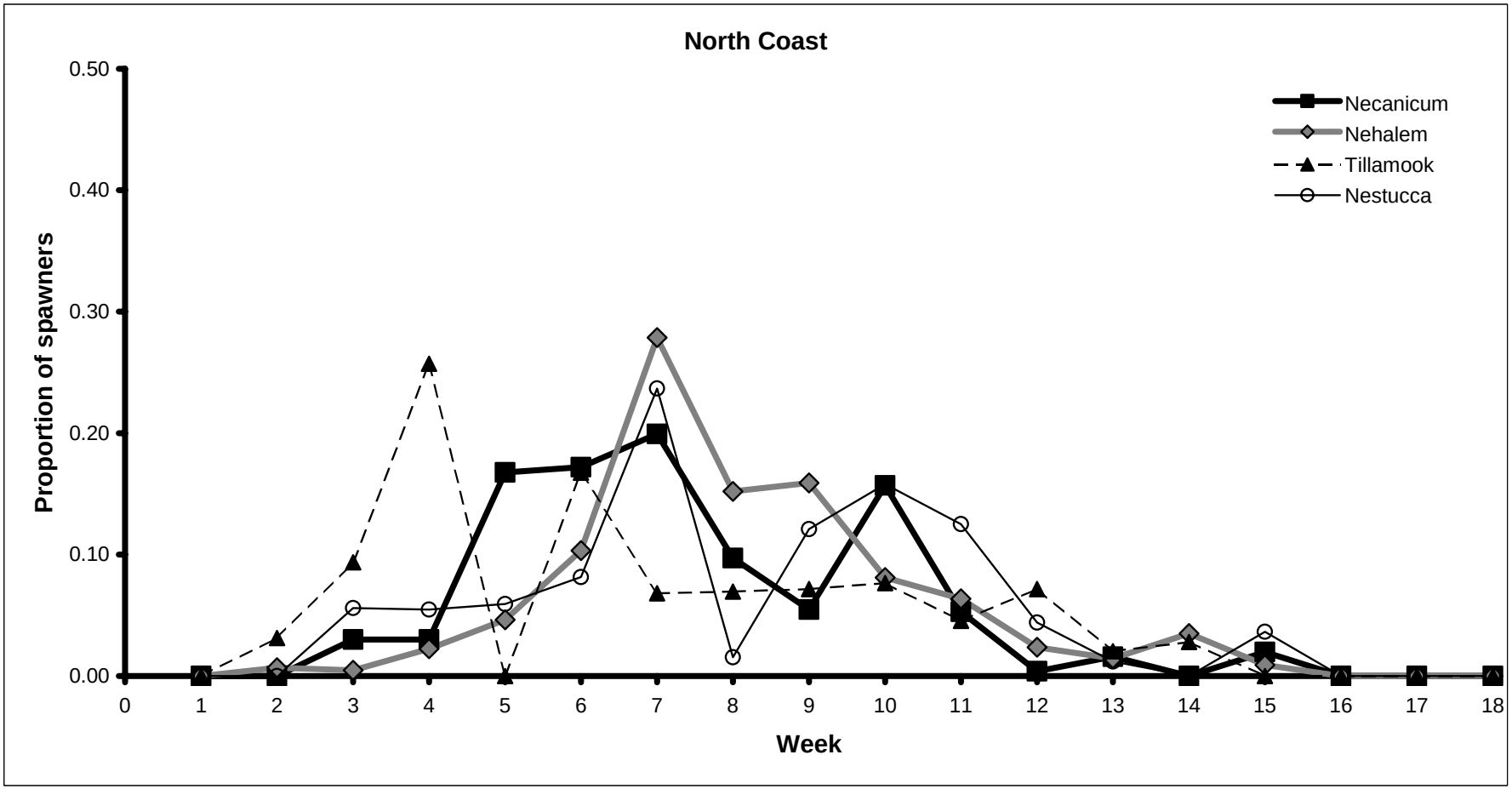

Figure 7a. 2001 North Coast spawn timing for Oregon Coast coho salmon (NOAA 2004)[1].

[1] To convert weeks to calendar dates: week 1 = Oct. 15-21; week 3 = Oct. 29-Nov. 4; week 7 = Nov. 26-Dec. 2; week 11 = Dec. 24-31; week 16 = Jan. 29-Feb. 4, and; week 18 = Feb. 12-18.

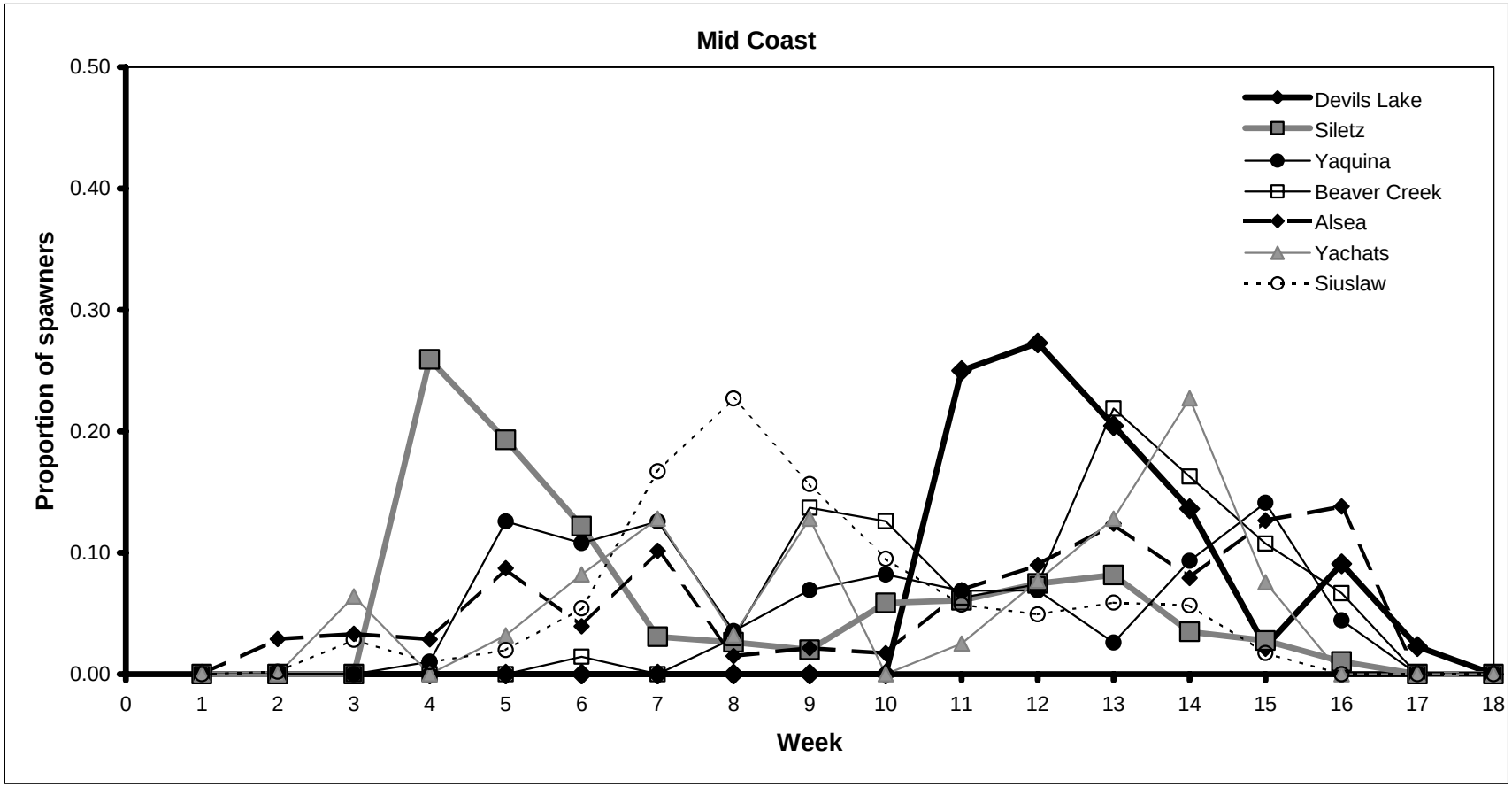

Figure 7b. 2001 Mid-Coast spawn timing for Oregon Coast coho salmon (NOAA 2004)[1].

[1] To convert weeks to calendar dates: week 1 = Oct. 15-21; week 3 = Oct. 29-Nov. 4; week 7 = Nov. 26-Dec. 2; week 11 = Dec. 24-31; week 16 = Jan. 29-Feb. 4, and; week 18 = Feb. 12-18.

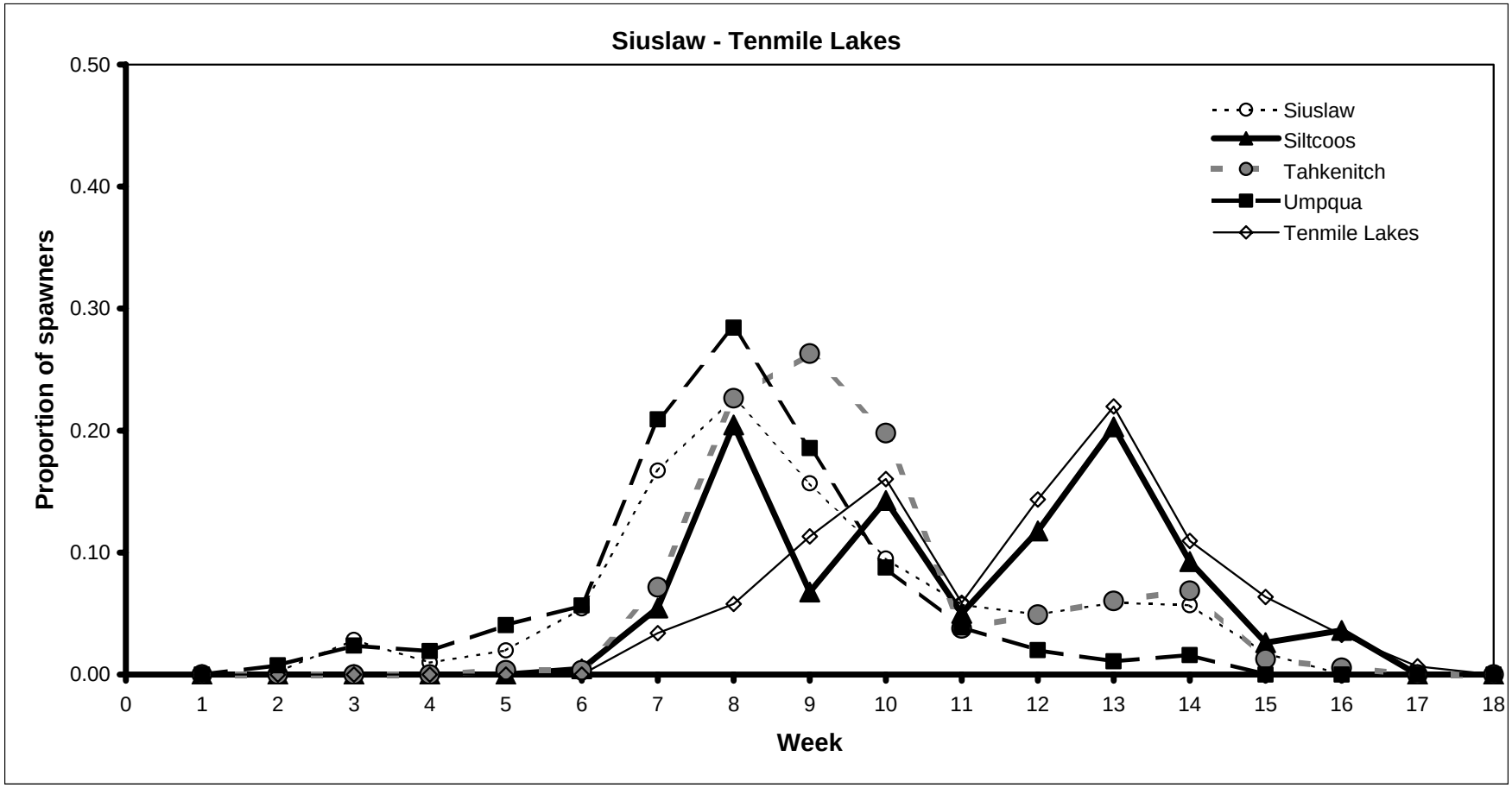

Figure 7c. 2001 Suislaw-Tenmile Lakes spawn timing for Oregon Coast coho salmon (NOAA 2004)[1].

[1] To convert weeks to calendar dates: week 1 = Oct. 15-21; week 3 = Oct. 29-Nov. 4; week 7 = Nov. 26-Dec. 2; week 11 = Dec. 24-31; week 16 = Jan. 29-Feb. 4, and; week 18 = Feb. 12-18.

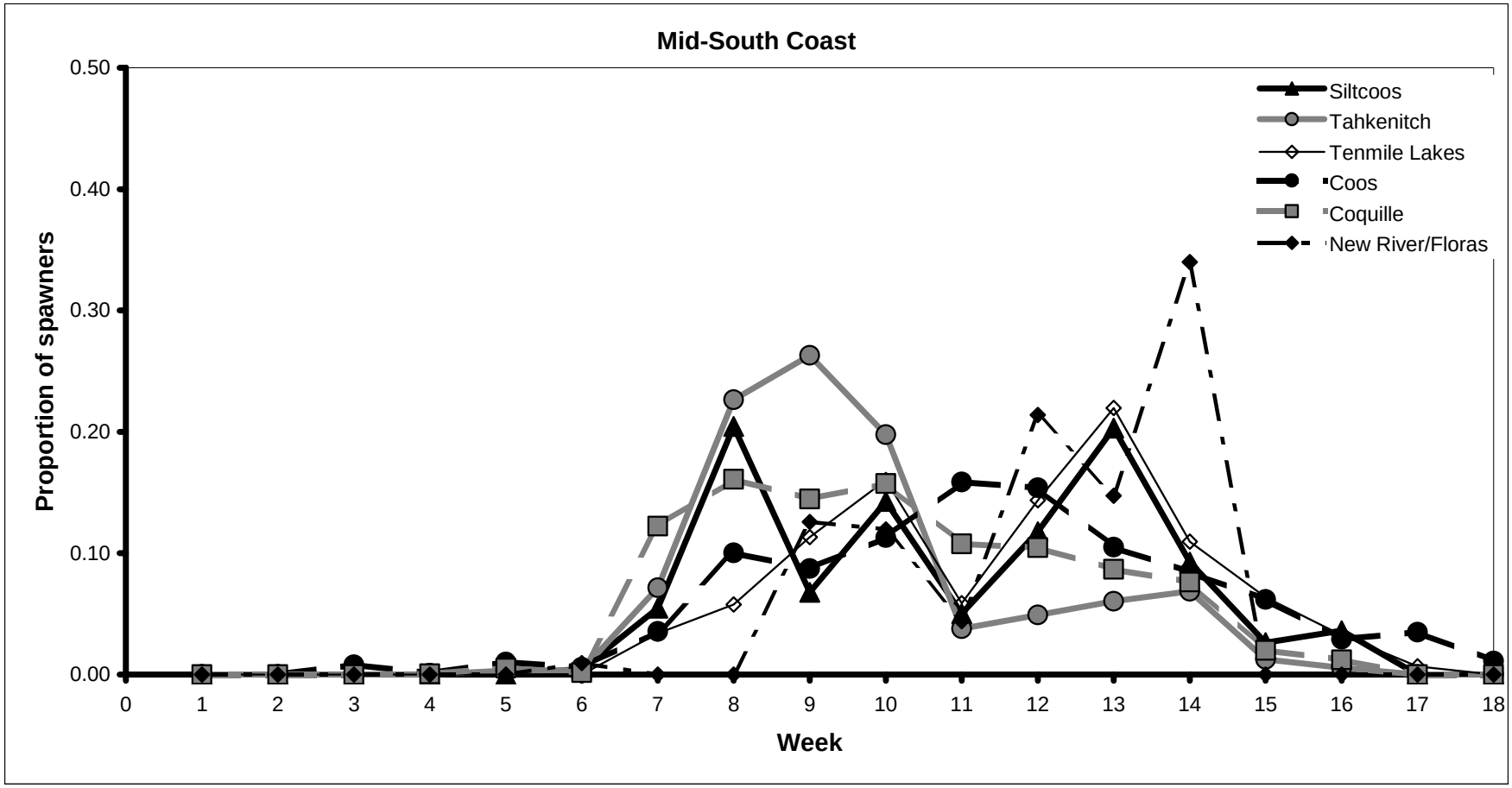

Figure 7d. 2001 Mid-South Coast spawn timing for Oregon Coast coho salmon (NOAA 2004)[1].

[1] To convert weeks to calendar dates: week 1 = Oct. 15-21; week 3 = Oct. 29-Nov. 4; week 7 = Nov. 26-Dec. 2; week 11 = Dec. 24-31; week 16 = Jan. 29-Feb. 4, and; week 18 = Feb. 12-18.

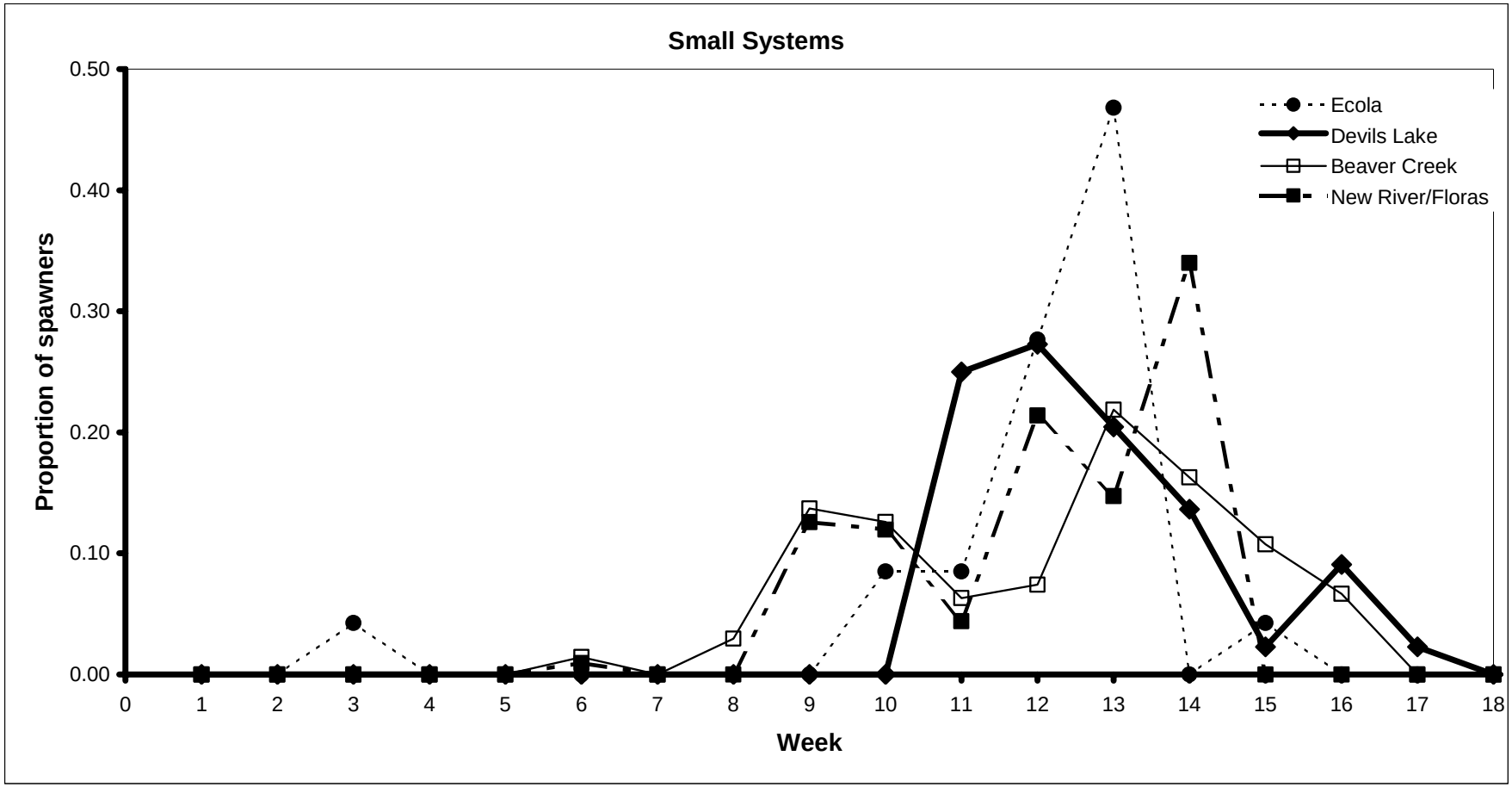

Figure 7e. 2001 Small systems spawn timing for Oregon Coast coho salmon (NOAA 2004)[1].

[1] To convert weeks to calendar dates: week 1 = Oct. 15-21; week 3 = Oct. 29-Nov. 4; week 7 = Nov. 26-Dec. 2; week 11 = Dec. 24-31; week 16 = Jan. 29-Feb. 4, and; week 18 = Feb. 12-18.

Historically, the range of variation might have given clues to population structure in the basins. However, because of the effect of stock transfer and hatchery programs, as well as other anthropogenic effects, it is impossible to discern historical patterns from modern observations. Because there is no evidence to suggest that all runs of a certain type are closely related, we now consider differently timed modern runs to be a component of overall life history diversity within each area and not an indication of historical population structure.

Marine distribution

Coho salmon smolts from the Oregon Coast enter the ocean in the spring and usually encounter a southward-flowing coastal current. Once in the coastal ocean they tend to swim north, but depending on the strength of the currents, may initially be displaced to the south (Pearcy 1992). As juveniles grow larger, swimming speed increases, resulting in a net northward movement. By late summer, juveniles from the coast are distributed off the mouth of the Columbia River and the Washington Coast (Pearcy and Fisher 1988, Brodeur et al. 2004). In the fall, early-maturing males (jacks) return to their natal streams.

Fall and winter distribution of Oregon coastal coho salmon are less well known. Hartt and Dell (1986) report results of tagging experiments conducted from 1956 to 1968. Juvenile salmon in the Gulf of Alaska were tagged at sea and recovered as adults the following year. They estimated that up to 37% of the fish they tagged returned to Oregon and California, with 20% of tags recovered south of the Columbia River. Recent sampling efforts in British Columbia and the Gulf of Alaska confirm the presence of juvenile coho salmon from the Oregon Coast in northern British Columbia (Welch et al. 2004) and the Gulf of Alaska (Weitkamp 2004). However, it doesn't appear that they are as abundant as Hartt and Dell (1986) observed. Pearcy (1992) postulates that ocean conditions may have changed, altering migration patterns. Alternatively, the shift from predominantly wild to predominantly hatchery fish may have affected migration patterns, because the wild fish tend to enter the ocean earlier and migrate further north.

There is a southward migration during the winter or early spring. Maturing fish first appear in ocean salmon fisheries in May off the coast of Northern California, as far south as Monterey (Weitkamp and Neely 2002). There is a northward migration in late spring and summer, with fish arriving in the Coos Bay area in June, and in the ocean off Newport and Tillamook in July. A few adults are caught as far north as Northwest Vancouver Island (Canada), but the majority are caught south of the Columbia River. By August, adults are starting to home to their natal systems, returning to freshwater in September through November.

Coded-wire tags (CWTs) can provide information on marine distribution of specific hatchery populations. They are primarily recovered from marine fisheries or when the salmon return to hatcheries. Consequently, CWT recovery patterns only indicate ocean migration patterns during the last few months of a 1½-year-long migration. Although patterns of movement during earlier stages of ocean migration have been studied (such as Loeffel and Forster 1970, Hartt 1980, Miller et al. 1983, Hartt and Dell 1986, Pearcy and Fisher 1988), the studies are not broad enough in scope to adequately compare early migration patterns for coho salmon released from different areas of the Oregon Coast.

Coded-wire-tag (CWT) recoveries show distinctive differences between regions, as is observed between the SONCC and the Oregon Coast Coho Salmon ESUs (Weitkamp and Neely 2002). Within the Oregon Coast there is a tendency for north-coast fish to be caught in more northerly fisheries, while south-coast fish contribute more heavily to southern fisheries. However, the tendency is not strong enough for us to draw conclusions about neighboring populations within regions, such as between the Yaquina and the Siuslaw rivers. The CWT recovery data provide information at the ESU scale, but are not useful for distinguishing between historical populations.

Genetics

Weitkamp et. al (1995) reviewed the genetics studies available at the time and presented a new analysis of samples collected by NOAA Fisheries. In allozyme studies, coho salmon from the Oregon Coast Coho Salmon ESU consistently showed genetic differences from other groups, including the Columbia River to the north and the Rogue and Klamath rivers to the south (Olin 1984, Solazzi 1986, Hjort and Schreck 1982). One study (Hjort and Schreck 1982) also found that hatchery populations from the north coast of Oregon were distinct from the natural spawners. Studies of DNA patterns concluded there was a unique stock unit south of the Columbia River to Cape Blanco (Currens and Farnsworth 1993, Forbes et al. 1993).

Samples of DNA from California to Alaska (Milner 1993, Johnson et al. 1991) were analyzed for allele frequencies and genetic distances at 6 gene loci (Weitkamp et al. 1995). Cluster analysis identified two overlapping groups on the Oregon Coast: a north-central group (with samples from Alsea, Trask, Siletz, and Nehalem) and a central to south-central group (with samples from the Rogue, Sixes, Eel, Tenmile, New, Coos, Tahkenitch, Alsea, Beaver, Siletz, Salmon, Smith, and Coquille). The Umpqua Basin was in a third group along with Trinity, Rogue, and Elk. The same analysis also grouped Washington Coast and Puget Sound coho salmon separately from Columbia River fish.

Recently, NOAA Fisheries (Ford et al. 2004) analyzed seven microsatellite loci in DNA extracted from coho salmon scales collected from 12 systems on the south-central and central Oregon coast in 2000 and 2001. Additional fin and muscle samples from nearby systems collected between 1991 and 1997 were also used in the analysis. Samples were selected to examine variability within and between three groups of fish. On the central coast, samples from three large basins and one small basin (Siletz, Yaquina, and Alsea rivers, and Beaver Creek) were compared in an attempt to see if the small system (Beaver Creek) had a particular affinity to one of its larger neighbors. Within the Umpqua River, samples were compared from Calapooya Creek, Elk Creek, Smith River, South Fork Umpqua River, and Mainstem Umpqua River. The objective was to look for population structure within this large river basin. The third group of scales was sampled from fish returning to four coastal lakes: Devils Lake, Siltcoos, Tahkenitch, and Tenmile. The lake habitats are distinct from the rivers, and coho from these lakes are thought to be distinct from the coastal river runs.

A phylogenetic tree based on these data (Fig. 8) showed some obvious geographic structure, although the internal branches connecting the geographic groups were relatively short compared to the terminal branches. The samples from the lakes formed a coherent group, as did the samples from the Umpqua Basin. There was some suggestion of structure within each of

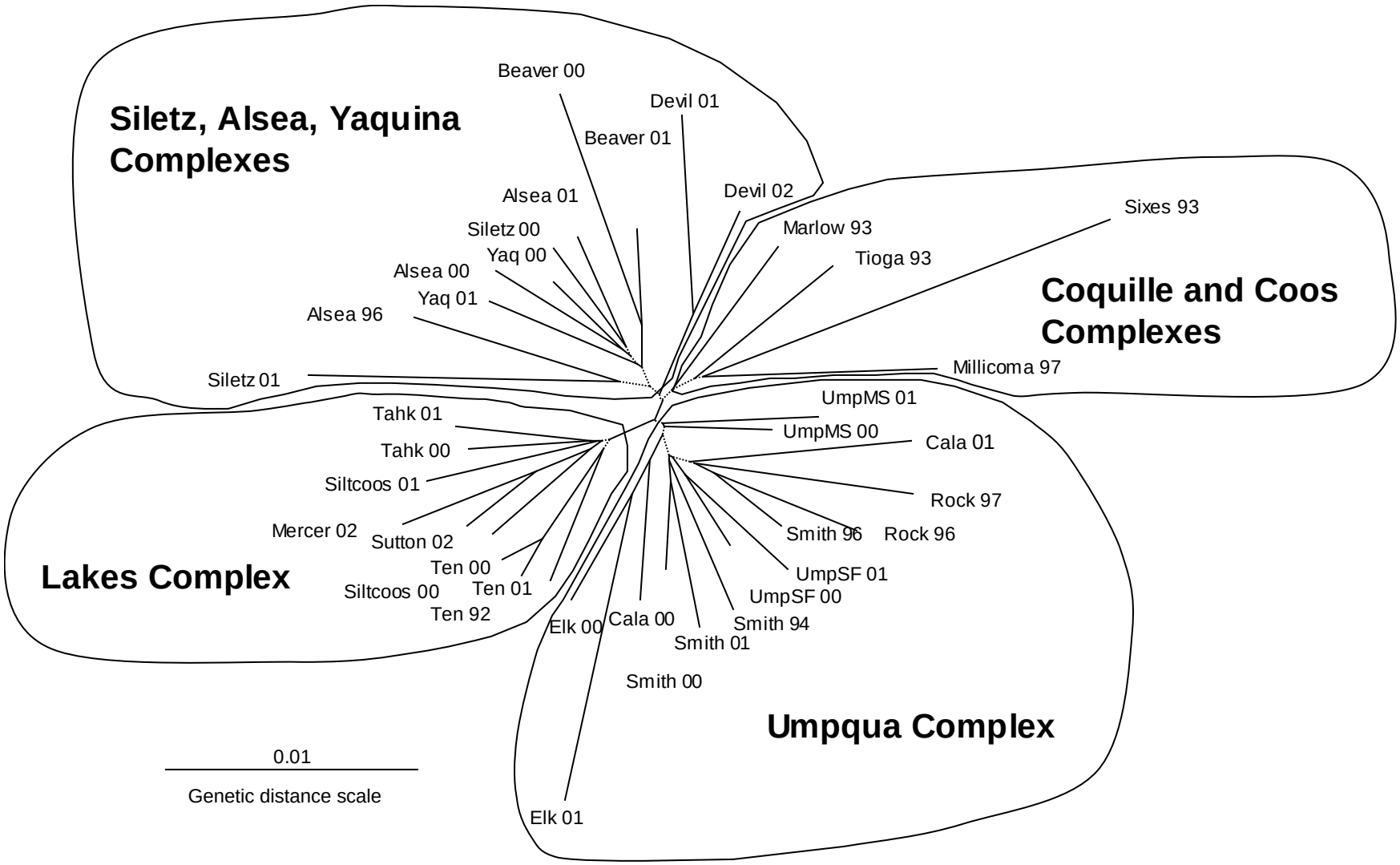

Figure 8. A maximum likelihood tree of Oregon Coast coho salmon genetic samples. Branches not significantly greater than zero are shown with thin dotted lines. Clusters are outlined by heavy curved line. Analysis by M. Ford based on data from Ford et al. (2004).

these groups. The Siletz, Yaquina, and Alsea rivers, and Beaver Creek also grouped together. There was no population structure identified within this group, although the authors stressed that this was not a strong conclusion. More generally, there is no strong evidence whether or not there are independent populations within these groups. Despite sample size limitations, this study was able to use modern genetic techniques to show a finer scale of population structure than had been demonstrated in earlier studies. In particular, this study supports Siltcoos, Tahkenitch, and Tenmile lakes as at least one independent group. Devils Lake clustered with mid-coast rivers rather than the other lakes. The study also supports dividing the modern populations within the Umpqua Basin into more than one population. There was no clear discrimination among the mid-coast basins. This may be due to recent hatchery practices and stock transfers blurring the boundaries between historical populations.

Homing fidelity

The rate of migration between basins is an important component of our population model. Uremovich (1977) found that, over the seven-year period of 1970-1976, 6.5% of the Chinook carcasses in the Sixes River came from the Elk River hatchery, about 5 km to the north. However, he had no data to indicate the proportion of Elk River fish that were straying. Shapovalov and Taft (1954) found that an average of about 20% of coho spawners in two neighboring streams on the California Coast were migrants from the other stream. These two streams, Waddell and Scott creeks, are small systems with ocean entry points about 8.5 km apart. They saw a pattern in migration rates that suggested variability between years in response to abundance. Such variability certainly occurs on the Oregon Coast, but we have no way at the present time to identify this variability or incorporate it in our isolation models.

We examined freshwater CWT recoveries on the Oregon Coast to test assumptions about patterns of migration between basins. For the period of 1990-2003, 52 tagged coho from 17 Columbia River hatcheries were recovered in freshwater areas of coastal basins. Of the 52 tagged fish, 32 were recovered in 2001, including 4 fish from 3 Oregon hatcheries and 28 fish from 9 Washington hatcheries. Twenty-three of these fish were found in basins from the Umpqua to the Rogue. Surprisingly, 6 of the 52 fish were Cowlitz stock, which is typically considered a north-migrating stock. These data would suggest that migration of Columbia River fish in 2001 was episodic and irregular. Because most of the migrants were found in the largest systems on the coast, it may be that fish originating from large systems prefer other large systems.

Migration patterns between hatcheries on the Oregon Coast may be more relevant to the historical behavior of natural fish. For the period of 1990-2003, there were 71 CWTs from 4 Oregon coastal hatcheries recovered outside the basin of hatchery origin. This represents 0.5% of the CWTs recovered. The actual migration rate is almost certainly higher because CWTs are much more likely to be recovered at the hatchery than on the spawning ground or from freshwater fisheries. In any case, modeling with a 0.5% vs. 5% rate would have no effect on our isolation results. More importantly, the pattern of recoveries showed that most fish were recovered from neighboring basins, falling off rapidly with increasing distance. This supports the negative exponential migration distribution assumed in our isolation model.

Summary of biological characteristics

In conclusion, data for comparison of life-history traits of coho salmon populations on the Oregon Coast are not usually collected at the broad geographic scale that would be useful for distinguishing populations. The data that are available show high variability in run timing, smolt outmigration and spawner returns, jacking rate, and homing fidelity that are largely attributable to environmental variation. Genetic data indicate modern population differences on the scale of regions and, to a lesser extent, individual basins. Lake populations appear different from river populations and the large Umpqua Basin shows genetic differentiation within the basin. However, due to the significant anthropogenic impacts to the landscape, none of these biological characteristics were able to shed light on population structure in historical Oregon Coast coho salmon populations.

Ecological Characteristics

Hydrology

North of Cape Blanco, Oregon, all coastal Oregon rivers, with the exception of the Umpqua River, drain only the west side of the Coast Range. The Oregon Coast Range is relatively low, with peaks at 500-1,000 m (1640-3280 ft) high. Interior portions of the Umpqua Basin, however, drain the east slope Coast Range and the west side of the Cascade Range, which has peaks from 1,000 to 2,000 m (3280-6560 ft) high.

Streamflows in this region follow a similar pattern, with seasonal highs typically experienced in December or January (Fig. 9). Mean annual flows are relatively similar for the basins draining the west slope of the Coast Range. Where they have been measured, these flows have ranged from 0.027 to 0.080 cms per sq. km (Fig. 10). Mean annual flows for the interior drainages within the Umpqua basin have ranged from 0.009 to 0.042 cms per sq. km. Lowest flows generally occur in summer and fall and are a small percentage of the peak flows. Expressed as a percentage of mean flow during the month of greatest runoff, low flows during the month of least runoff range between 1.0% and 5.1% (Fig. 11). The exception to this is the North Umpqua River. The difference in this basin is related to the strong influence of high Cascades geology and hydrology. Duration of high flows range from 4 to 6 months in basins proximal to the coast. In the interior drainages of the Umpqua Basin, high flows can persist for as long as 7 months in unregulated systems (Fig. 12).

Air and stream temperatures

There are few clear broad-scale differences in air or stream temperatures from north to south within coastal areas occupied by the historical Oregon Coast Coho Salmon ESU. Minimum average winter air temperatures are typically around 4ºC (39ºF), whereas minimum average stream temperatures have a range of 4-8ºC (39-46ºF). Maximum average air temperatures are typically around 21ºC (70ºF) and maximum average stream temperatures at selected sites in coastal basins have been observed to range from 15ºC to 21ºC (59-70ºF).

Figure 9. Timing of annual peak flows in rivers of the Oregon Coast Coho Salmon ESU.

Figure 10. Mean annual flow in rivers of the Oregon Coast Coho Salmon ESU.

Figure 11. Seasonality of monthly stream flow in rivers of the Oregon Coast Coho Salmon ESU.

Figure 12. Duration of high flows in the Oregon Coast Coho Salmon ESU. The number of months of duration of peak flow is shown at gauging stations.

Figure 13. Average annual precipitation in watersheds of the Oregon Coast Coho Salmon ESU.

Higher maximum stream and air temperatures have been observed in the South Umpqua River, which is an interior basin.

Precipitation

The Oregon Coast receives high rainfall (120–305 cm [47-120 in.] per year) compared to areas east of the Coast Range (60-120 cm [24-47 in.] per year). Generally, however, it receives less rainfall than the Olympic Peninsula, Washington farther north (>240 cm [95 in.] per year). The exceptions to this are in the Nehalem Basin, the upper areas of the five rivers of the Tillamook Basin, and the upper Salmon and Siletz basins (Fig. 13). Much of the Umpqua Basin receives considerably less rainfall than the areas proximal to the coast, with precipitation averages between 102 cm (40 in.) and 152 cm (60 in.). Because of the relatively low elevation, snowfall in the Coast Range is low, averaging 30-60 cm (12-24 in.) annually, while the higher Cascade Range receives from 250 cm (98 in.) to 760 cm (300 in.) annually. This is important for the Umpqua Basin, as the North and South Umpqua Rivers drain a portion of the west slope of the Cascade Range (Oregon Climate Service 2000).

Vegetation

Dominant vegetation types are a valuable indicator of relative precipitation, temperature, soil type, solar radiation, and altitude because of the specific requirements of different forest communities. Consequently, changes of vegetation types can indicate changes in the physical environment, which may affect the freshwater habitat of salmon. (A more detailed discussion of vegetation has been compiled in Appendix I.) Potential vegetation is similar in most of the basins of the Oregon Coast Coho Salmon ESU with the exception of the Siuslaw and Umpqua rivers, which extend into the interior away from marine influence (Fig. 14).

Ecoregion

Ecoregions, as shown in Figures 15 and 16, are representations of the integrations of vegetation, geology, soils, precipitation, and evaporation potential (ONHP 2001). Level 3 ecoregions of the Oregon Coast Coho Salmon ESU from south of the Columbia River to Cape Blanco show large-scale geologic provinces. Level 4 ecoregions show a finer scale of differences, reflecting areas such as coastal lowlands and volcanics, which often indicate differing potential for development of good coho habitat. Descriptions of each type of level 3 and 4 Ecoregion are found in Appendix II.

The ecological information shows a relative uniformity of conditions throughout the Oregon Coast Coho Salmon ESU. This is not surprising, given the dominant effect of the ocean on coastal climate. Differences relate to the effects of topography on rainfall and of geology on vegetation and slope stability. Inland areas of the Umpqua Basin are drier, with more extreme temperatures than the coastal areas. Ecoregions integrate a variety of biotic and abiotic factors to show patterns of habitat variation that may be important to coho salmon.

Figure 14. Vegetation zones in the watersheds of the Oregon Coast Coho Salmon ESU.

Figure 15. Level 3 Ecoregions of the Oregon Coast Coho Salmon ESU.

Figure 16. Level 4 Ecoregions of the Oregon Coast Coho Salmon ESU.

Summary of potential isolating ecological characteristics

We reviewed a wide range of factors of potential use in distinguishing among populations of coho salmon on the Oregon Coast. Most of the data indicated differences on a broad scale, but there were few data sets useful at the finer scale of individual basins. The most recent genetic analysis indicated that modern populations are probably structured at a smaller scale than broad regions (north coast – south coast). Geographic isolation is potentially useful for defining the degree of interactions among populations, and ecoregions may define habitat divisions significant to life history adaptations that could potentially become isolating factors in population structure. These more enduring ecological characteristics (which include geological history, vegetation, and climate) appear to be more informative when considering the historical population structure of Oregon Coast coho salmon. These were especially useful when considering the Umpqua Basin.

Methods for Population Identification and Classification

We identified two steps for defining populations and their structure: (1) identifying population units, and (2) classifying the units into categories. Identification delineates populations and defines where they occur. Classification categorizes those populations into groups. Based on our conceptual model, we defined three groups: Functionally Independent populations, Potentially Independent populations, or Dependent populations. Both steps are based on simple rules.

Population Identification Method

We used two rules for identifying populations. The first identifies all main basins that encompass the range of one or more populations:

Rule 1: No population will span saltwater; in other words, populations are divided at saltwater entry such that each direct ocean tributary wholly encompasses the range of any populations that spawn within the freshwater basin. For purposes of this rule, estuaries are considered part of the freshwater system, so that multiple streams entering a single bay may contain a single population.

This rule is based on two postulates regarding salmon populations. First, population structure is largely determined by the structure of freshwater spawning and rearing habitats and the migration pathways connecting these habitats. Second, saltwater entry/exit is a major break point in migration pathways, so that migration among habitats within a basin is more likely than migration through saltwater among basins. Coho salmon spawn and rear in freshwater, which allows periods of migration for juveniles before saltwater entry and for adults during spawning migrations.

Applying Rule 1, we identified 66 direct ocean exit basins with coho salmon habitat within the range of the Oregon Coast Coho Salmon ESU (Table 1). These basins range in size from Rover Creek (60 ha [148 ac.]) to the Umpqua River Basin (1.2 million ha [3 million ac.]).

The second rule describes when a basin contains more than one persistent population:

Rule 2: To be considered separate populations, two breeding groups within a basin must be sufficiently isolated to be considered Functionally or Potentially Independent.

Evidence for isolation may include major ecological differences among subbasins, large spatial separation of spawning and rearing habitats, or noteworthy life history or genetic differences. Under Rule 2, we considered subdividing several of the larger basins into multiple populations. These are discussed from north-to-south below.

Population Identification Results

Nehalem River

We considered defining two populations within the basin divided just below the confluence of the mainstem and Humbug Creek. In favor of this split is the geological distinctness of the upper basin, which is largely in the Willapa Hills Ecoregion (Fig. 16). However, there was no apparent isolating mechanism to limit migrations between spawning areas in the upper and lower basins, and the upper basin is ecologically similar to the North Fork, which would have been included in the lower population.

Tillamook Bay

Tillamook Bay drains several moderate-sized rivers—Miami, Kilchis, Wilson, Trask, and Tillamook—each of which could have supported an independent coho population, and thus we considered subdividing the basin into multiple populations. However, we ultimately concluded that historically there probably were not separate populations in this basin. Considerations leading to this conclusion included: (1) habitat is ecologically similar across the rivers, (2) most historical production was in lowland areas, where tributaries are close together and likely merged during floods (Coulton, Williams, and Benner 1996), and (3) most coho habitat is in the Tillamook, Trask, and Wilson Rivers, which are all close together. The Miami River is somewhat separated geographically from the other main tributaries, but was probably not large enough to support a Functionally or Potentially Independent population without input from its neighbors. At present, coho habitat is widely dispersed in the upper reaches of the tributaries; however, this appears to be largely a result of loss of higher quality lowland habitats rather than the natural structure of the population.

Nestucca Bay

Kostow (1995) identified two tributary populations (Nestucca and Little Nestucca Rivers). We found no significant ecological differences or isolating mechanisms between the two tributaries to justify subdividing the population.

Siletz Bay

Kostow (1995) identified three populations entering Siletz Bay. We found no significant ecological differences or isolating mechanisms among the tributaries to justify subdividing the population.

Siuslaw River

Two populations (Siuslaw and North Fork Siuslaw) were identified by Kostow (1995). We considered separating the North Fork from the main river, but found no significant ecological differences, and noted likely historical lowland habitat connections between the two rivers.

Umpqua River

This is a large basin (Table 1) draining a diverse region (Fig. 3). We considered several possible population scenarios with between one and five populations in the basin. The single population scenario was eliminated early, because of the size of the basin, its ecological diversity as indicated by multiple level-three and level-four ecoregions (Figs. 15 and 16), and the apparent genetic diversity within the basin (Fig. 8) (Ford et al. 2004). The finest-scale divisions we considered included independent populations in the North Umpqua River, South Umpqua River, mainstem Umpqua River, lower Umpqua Basin (lower mainstem and bay tributaries), and Smith River. The Smith River, a large tributary entering the Umpqua River below tidewater, was eliminated from consideration as a historically independent population because until 1930 most of the habitat in the basin was inaccessible due to an impassable falls low in the basin. In addition, the lower reaches of the Smith River are geographically close and ecologically similar to other lower basin streams.

Given these considerations, we reduced the likely scenarios to two: (1) dividing the basin geographically into three populations based on 4th-field Hydrologic Units (HUC) (Smith River and mainstem to the forks, North Fork, and South Fork), and (2) dividing the basin into two populations based on dominant level-3 ecoregions (Fig. 15) within subbasins. The HUC-based approach is appealing for simplicity, and recognizes that major tributary branches within basins are possible isolating points for migrating adults. The ecoregion approach focuses more on potential isolation via local adaptation to geology, hydrography, and vegetation differences among regions. The Umpqua Basin spans four level-3 ecoregions: Coast Range, Klamath Mountains, Willamette Valley, and Cascades. However, the latter two historically had little coho salmon habitat (Figs. 4 and 15). The two dominant ecoregions are the Coast Range, which spans the lower tributaries and mainstem, except for Elk and Calapooya Creeks, and the Klamath Mountains, which spans upper Elk Creek, Calapooya Creek, and the lower portions of the North and South Umpqua Rivers.

There are large uncertainties inherent in reconstructing historical population patterns, and there is no clear support favoring one of these scenarios over the other. Recent genetic analysis (Fig. 8) (Ford et al. 2004) supports some division within the basin, but patterns of genetic variation are ambiguous and we do not know to what extent they reflect recent management rather than historical population structure. Pending further evidence, we provisionally identified

two historical populations based on ecoregion differences within the Umpqua River Basin: Lower Umpqua River and Upper Umpqua River (Fig. 15), with the division in the mainstem immediately below the confluence of Elk Creek. The Lower Umpqua River population occupies the Coast Range Ecoregion, while the Upper Umpqua River population inhabits primarily the Klamath Mountains Ecoregion, with some habitat in the Cascades and Coast Range ecoregions. As we develop further analyses regarding viability criteria and recovery actions, we will consider the consequences of different ways of subdividing this basin.

Coos Bay

We considered splitting the South Fork and Millicoma River as separate populations, following the lead of Kostow (1995). However, this was rejected because of lowland habitat connections in the lower basin where much historical production likely occurred, similar to the situation in Tillamook and Siuslaw Bays.

Population Classification

We classified historical populations into the three population categories: Functionally Independent, Potentially Independent, and Dependent, based on relative persistence and degree of isolation. Because no direct measure of persistence was available, we used historical potential population size as a proxy. We reconstructed historical population potential from a landscape-based model (App. III, Burnett et al. 2003). We then used an isolation model based on the distances between the ocean entry points of basins (Bjorkstedt 2004). These models are described in the following sections.

Population Classification Methods

Historical population size (persistence)

We used habitat metrics and recent studies of relationships between habitat and juvenile production to estimate historical abundance. Of course, using current habitat metrics to derive an index of historical abundance requires measuring habitat features that are relatively stable over time. Therefore, we used geomorphic measures of stream conditions that can be calculated from current GIS databases (Coastal Landscape Analysis and Modeling Study [CLAMS]) and digital elevation models (DEMs), adjusted for known changes in the landscape (such as construction or removal of migration barriers) (Burnett et al. 2003). To estimate historical abundance, we combined key geomorphic measures (gradient, valley width, and active channel width) from the DEMs with habitat intrinsic potential (an integrated measure of habitat quality described in Burnett et al. 2003 and illustrated in Figs. III-2 through III-5 in App. III), smolt capacity estimates for different types of habitat, and a smolt-to-adult survival rate based on a good marine survival year. We compared these habitat-based estimates with estimates derived from cannery records from the turn of the century to confirm that our estimates were reasonable (Lichatowich 1989). Appendix III presents a detailed description of the methods used to estimate these potential historical population sizes.

Table 6. Potential historical smolt and adult abundance for 67 putative populations of coho salmon in the Oregon Coast Coho Salmon ESU (App. III).

Population	Potential smolts	Adults @ 10% marine survival	Population	Potential smolts	Adults @ 10% marine survival
Necanicum R.	685,000	68,500	Moore Cr.	1,000	100
Indian Cr.	100	10	Theil Cr.	20,000	2,000
Canyon Cr.	400	40	Beaver Cr.	265,000	27,000
Ecola Cr.	72,000	7,000	Alsea R.	1,628,000	163,000
Red Rock Cr.	100	10	Little Cr.	1,000	100
Austin Cr.	300	30	Big Cr.	34,000	3,000
Asbury Cr.	1,000	100	Vingie Cr.	3,000	300
Arch Cape Cr.	3,000	300	Yachats R.	110,000	11,000
Short Sand Cr.	4,000	400	Gwynn Cr.	1,000	100
Nehalem R.	3,330,000	333,000	Cummins Cr	10,000	1,000
Spring Cr.	5,000	500	Bob Cr.	6,000	600
Watseco Cr.	5,000	500	Tenmile Cr.	28,000	3,000
Tillamook Bay	3,288,000	329,000	Squaw Cr.	100	10
Netarts Bay	15,000	1,500	Rock Cr.	6,000	600
Rover Cr.	2,000	200	Big Cr.	18,000	2,000
Sand Cr.	123,000	12,000	China Cr.	5,000	500
Nestucca R.	1,037,000	104,000	Blowout Cr.	1,000	100
Neskowin Cr.	49,000	5,000	Cape Cr.	15,000	2,000
Salmon R.	168,000	17,000	Berry Cr.	54,000	5,000
Devils Lake	85,500	9,000	Sutton Cr.	84,000	8,000
Siletz R.	1,217,000	122,000	Siuslaw R.	2,674,000	267,000
Schoolhouse Cr.	2,000	200	Siltcoos R.	771,000	77,000
Fogarty Cr.	18,000	2,000	Tahkenitch Cr.	228,000	23,000
Depoe Bay Cr.	7,000	700	Threemile Cr.	22,000	2,000
Rocky Cr.	10,000	1,000	Umpqua (total)	8,199,000	820,000
Johnson Cr.	22,000	2,000	Lwr. Umpqua	1,293,000	129,000
Spencer Cr.	11,000	1,000	Upr. Umpqua	6,906,000	691,000
Wade Cr.	5,000	500	Tenmile Cr.	525,000	53,000
Coal Cr.	4,000	400	Coos Bay	2,058,000	206,000
Moolack Cr.	4,000	400	Coquille R.	4,169,000	417,000
Big Cr.	26,000	3,000	Johnson Cr.	8,000	800
Yaquina R.	1,217,000	122,000	Twomile Cr.	134,000	13,000
Henderson Cr.	1,000	100	Floras Cr.	396,000	34,000
Grant Cr.	400	40	Sixes R.	372,000	37,000

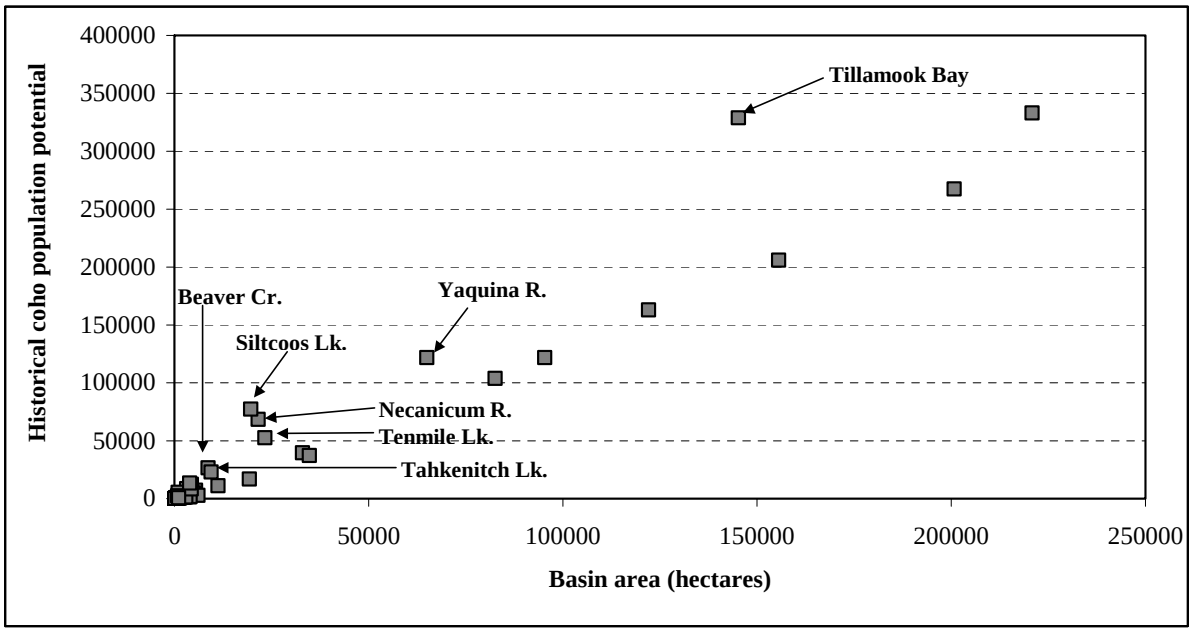

Figure 17. Historical coho population potential versus basin area for Oregon Coast basins (Data sources: Streamnet 2003, App. III).

The advantage of calculating adult abundance from computed GIS data is that estimates can be made for basins where there are no historical fishery data. Table 6 lists the estimated potential historical abundance of coho salmon for the 67 populations in the Oregon Coast Coho Salmon ESU delineated by the process of identification described above. Total adult abundance derived from smolt numbers and a 10% marine survival rate was about 3.3 million adults if all populations peaked in the same year.

Our GIS-based modeling of the historical capacity of Oregon Coast basins to produce coho salmon shows considerable between-basin variation in the ability to produce these fish. Large coastal basins have a greater absolute capacity to produce coho than do smaller basins because they contain a greater abundance of suitable habitat (Fig. 17). However, the potential of Oregon Coast basins to produce coho is influenced by habitat quality as well as quantity. Some basins are inherently more productive for these fish than are others because they have the capacity to form disproportionate quantities of the kinds of complex, low-gradient habitats most favored by coho salmon. These basins, including Tillamook Bay, Yaquina River, Beaver Creek, the lake basins (Siltcoos Lake, Tenmile Lake, Tahkenitch Lake) and others, once produced more coho than would be expected on the basis of their size alone because they contain disproportionately large lowland areas (or lakes) that can provide highly productive rearing environments for juvenile coho.

When compared in terms of their historical capacity to produce coho per unit of basin area, larger basins on the Oregon Coast appear to have been generally more productive than smaller basins because they were more likely to contain relatively extensive lowland areas and complex low-gradient habitats (Fig. 18). Though there were exceptions to this pattern, as

indicated earlier, the lower inherent productivity of the smaller basins tended to make the coho populations within them even smaller than expected on the basis of basin size alone. This made the coho populations within these smaller basins particularly vulnerable to periodic local extinctions unless there was a consistent influx of stray spawners from larger basins. The relatively higher vulnerability of these populations is attributable to demographic risks associated with small population size, to increased sensitivity to fluctuations in marine survival due to lower freshwater productivity, and to the vulnerability of small natal basins to single catastrophic disturbances.

Isolation (proportion of native spawners)

One of the defining properties of salmon is their propensity to undergo a long ocean migration and return with high fidelity to their natal spawning grounds. This is what isolates salmon populations from one another. However, homing is not perfect, and the movement of migrant salmon between populations is also a defining property of salmon populations. The degree of isolation between populations is determined by the proportion of salmon adults that are migrants from another population and the effectiveness of these migrant salmon at placing competetive offspring into the habitat to which they stray. The proportion of migrants into a population also affects the demographic independence of each population. Our rules for classifying a population are based on a calculation of historical abundance and on the proportion of non-migrant or native spawning adults based on distances between populations and the relative sizes of these populations.

We used an isolation model developed by Bjorkstedt (2004) to calculate the relative isolation of each population on the Oregon Coast. Quantitative data on coho salmon dispersal rates are lacking so the model is relatively simple, reducing the number of assumptions at the risk of reducing the descriptive power of the model. Dispersal of migrants among basins separated by saltwater is modeled as a function of distance between the mouths of ocean tributaries. All basins were treated as single units. Thus, the Umpqua Basin, where two populations were delineated, was treated as a single population from the perspective of its neighbors.

In this model, fidelity to native basins (proportion of native spawners) was assumed a constant 95% of potential returning adults. We used our estimates of historical abundance as the number of returning adults for each population. The remaining 5% of the returning population dispersed as migrants along the coast with an exponential decline with distance (Bjorkstedt 2004). After they were dispersed along the coast, they entered the basin nearest to their final location. Distances among watersheds along the Oregon Coast were calculated using the latitude-longitude coordinates for the mouths of each river. The distance between each pair of neighboring river mouths was calculated “as the crow flies.” Distances between non-neighboring rivers were calculated as the sum of all intervening neighbor-pair distances. In this way, the curvature of the coast was included in the distance calculations. Tributaries of Tillamook Bay were considered as a single watershed. Two out-of-ESU systems, the Columbia River, to the north, and Elk River, to the south, were included to allow estimation of migrants across the ESU boundaries. Elk River historical abundance was estimated from Intrinsic Potential. Columbia River abundance was based on Chapman (1986).

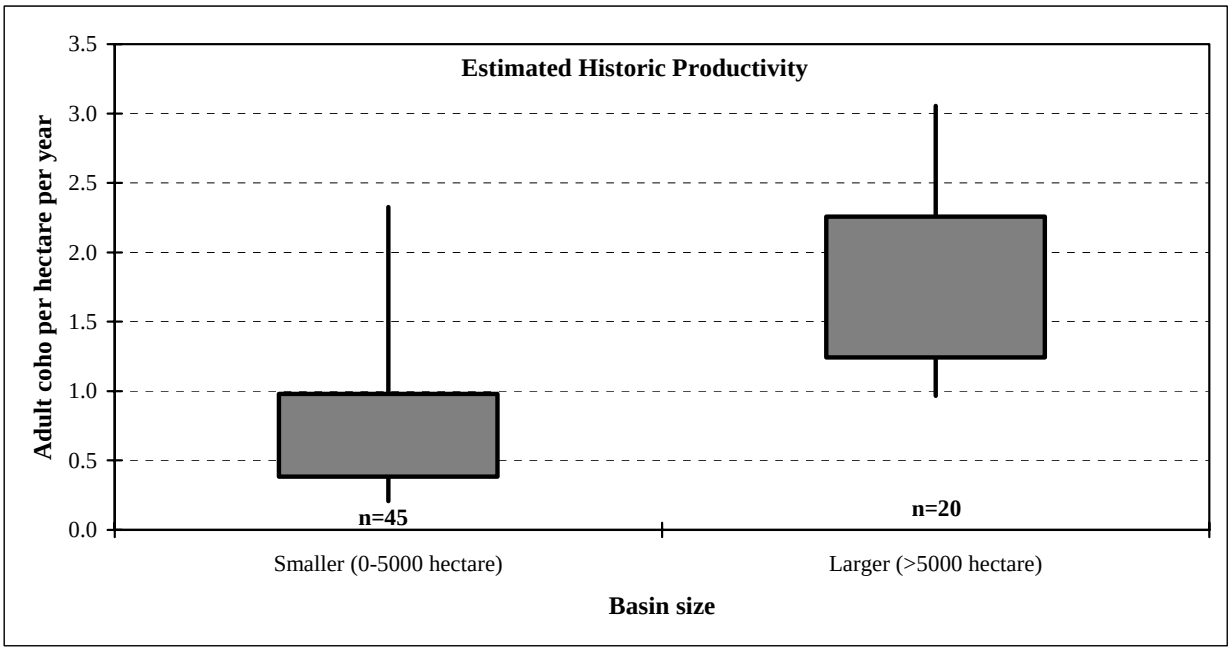

Figure 18. Box-whisker plots of estimated historical coho productivity (adults per hectare of basin area per year) for Oregon Coast basins smaller and larger than 5000 hectares. Boxes depict the 25th to 75th percentile productivity values for basins of a given size; whiskers extend to the 10th and 90th percentile values (Data source: Streamnet 2003, App. III).

Population Classification Results

The isolation model reports the proportion of spawners in each stream that originated from that stream (proportion of native return). Streams with a higher proportion of native return are more isolated. Figure 19 is an analysis of Relative Independence based on the isolation of each population in the ESU and the historical population size (persistence). It shows a continuum from small, dependent populations to large, independent populations. Defining the relative roles of populations on this continuum required us to create divisions that were, to some extent, artificial and arbitrary. We focused on understanding the axes of isolation and historical population size in terms of the analytical techniques used and the population dynamics. We were concerned with finding criteria for these break points that were realistic and defensible in terms of existing analyses.

Establishing a horizontal line to distinguish the Functionally Independent populations was straightforward because of the model structure. The native return rate used in the model was 95%. Thus, all populations with greater than 95% proportion native return were net donors, and those with fewer than 95% proportion native return were net receivers. The horizontal line at [0.95] in Figure 19 depicts this division.

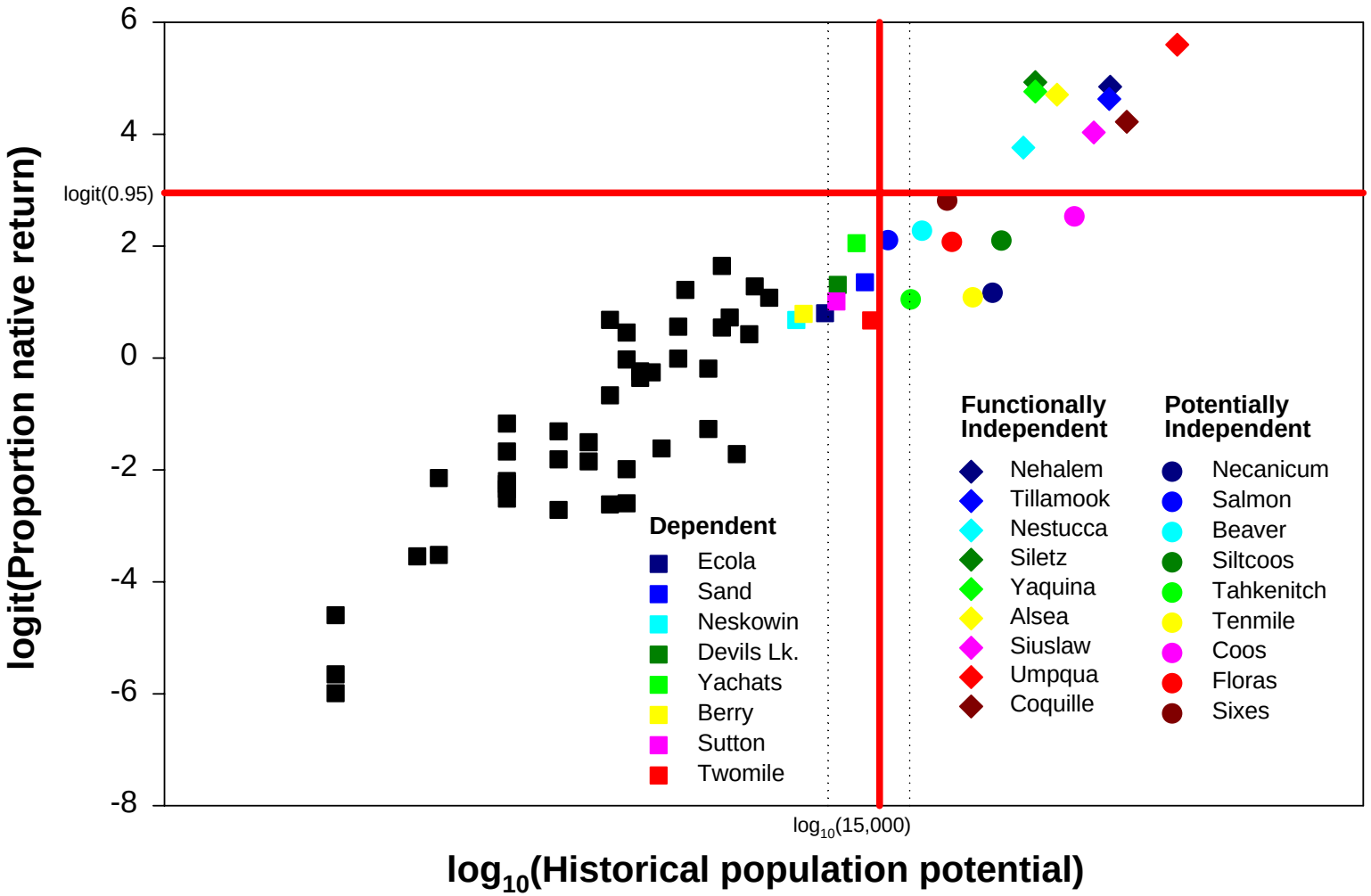

Figure 19. Isolation analysis for Oregon Coast coho salmon using estimates of potential historical coho salmon abundance and a dispersal model in which fidelity is fixed at 95% and dispersers are spread across neighboring watersheds according to an exponential decline with distance (decay parameter = 0.05). This includes the influence of the Columbia and Elk rivers. The solid horizontal line represents the isolation criterion of 95% native spawners. The solid vertical line represents the persistence criterion of 15,000 adult coho at 10% marine survival. The dotted vertical lines represent +/- 50% of 15,000.

Establishing a vertical line to distinguish between persistent and non-persistent populations was more difficult. As population abundance, or their habitat areas (or capacity), gets smaller, the probability of extinction rises. It is, however, harder to quantify that probability than it is to characterize the functional relationship between habitat size and extinction probability. The stochastic life-cycle model (Nickelson and Lawson 1998) produces quantitative extinction probabilities. However, these probabilities are sensitive to many of the model parameters, including patterns of freshwater production, density dependence, straying, and marine survival. As a consequence, we were unwilling to use the absolute extinction probabilities from the model to define the vertical line criterion. We were, however, more comfortable with the qualitative model result; as habitat quantity decreases, extinction probability increases exponentially. We chose as our criterion for persistence the point where the probability of extinction started to increase rapidly (Fig. 20). We considered 24 km (15 miles) of habitat as the break point. The resulting habitat quantity would be expected to produce 15,000 adult spawners at 10% marine survival, so we set the vertical line at 15,000 adult spawners on the historical population potential axis. This does not mean that populations to the left of this point would necessarily go extinct in 100 years without input from other populations. It does mean that the probability of such extinctions is high enough so that on an evolutionary time scale of tens to thousands of years, we expect such extinctions to be a normal part of the populations' dynamics and reflected in the genetic population structure.

We explored the effect of increasing or decreasing this number by 50% (7,500 or 22,500), as represented by the vertical dotted lines in Figure 19. If our estimate is low only one basin, the Salmon River, would be reclassified as Dependent. With a high estimate, five of the larger Dependent populations (Twomile, Sand, Yachats, Devils Lake, and Sutton Lake) would be reclassified as Potentially Independent.

Fifteen thousand adult spawners sounds, at first, like a high threshold for persistence. However, the historical population potential was calculated as a maximum, assuming 10% marine survival. In years with 1% marine survival, as we have experienced recently, these populations would have been below 1,500 adults. These estimates assume the best possible production from these populations, a condition that probably occurred only rarely. The smallest populations were probably composed of 10 to 100 spawners during periods of poor ocean conditions.

Using Figure 19, we can assign each population a classification according to our conceptual model. All populations to the left of the vertical line had a relatively low probability of persistence and were classified as Dependent (non-viable *sensu* McElhaney et. al 2000). Their long-term existence depended on input from larger, neighboring populations. Populations to the right of the vertical line were capable of persistence over longer periods. The populations above the horizontal line were considered Functionally Independent, with demographics not greatly influenced by neighboring populations. Those persistent populations below the horizontal line were classified Potentially Independent, capable of sustaining themselves without input from neighboring populations, but with demographics influenced by their larger neighbors. Populations in the upper-left quadrant would be both isolated from other populations and unlikely to persist over a time frame of 100 years. These could be considered ephemeral populations. Such populations would experience periodic extinctions with low probability of

recolonization from other populations. None of our historical populations fell into this category. This lends some support to the break points we chose for the horizontal and vertical lines.

Forty-eight (slightly over 70%) of the 67 populations we identified were classified as Dependent populations. Altogether they inhabited less than 6% of the coho salmon habitat in the Oregon Coast Salmon ESU. Based on our models, these populations probably would have experienced periodic extinction and recolonization events on a time frame of 10 to 1000 years. There is a wide range of basins in this category, ranging from Twomile Creek, supporting up to 13,000 adults at 10% marine survival, to Indian Creek, Red Rock Creek, and Squaw Creek, each estimated to produce only 10 adults under good marine survival. The larger dependent populations are expected to be occupied most of the time, while many of the smaller systems probably do not have spawning coho in most years. Some of the smaller systems we have identified may never have supported coho, while there may be other small systems not on our list where coho occasionally spawn.

Figure 21 is a map of proposed populations and Table 7 is the list of populations and their proposed classification. Table 8 allows a comparison between population classification and the distance to the nearest Functionally Independent population. Ten of the 67 populations were classified as Functionally Independent, including the two in the Umpqua Basin. An additional nine populations were classified as Potentially Independent, including the populations in the three large lake basins and the Coos Basin. The Coos population is a good illustration of the distinction between Functionally and Potentially Independent populations. Although this is the sixth largest historical population on the coast, it is flanked by the two largest; the Umpqua Basin (here treated as a single population) to the north and the Coquille to the south. These two large populations would have provided enough adult migrants into the Coos Basin to affect its demographics, even though the Coos is certainly large enough to sustain itself in the absence of input from other populations. It must be remembered that these classifications are for historical populations, and do not reflect the current functioning of this ESU.

Forty-eight (slightly over 70%) of the 67 populations we identified were classified as Dependent populations. Altogether they contained less than 6% of the coho salmon habitat in the Oregon Coast Coho Salmon ESU. Based on our models, these populations probably would have experienced periodic extinction and recolonization events on a time frame of 100 to 1000 years.

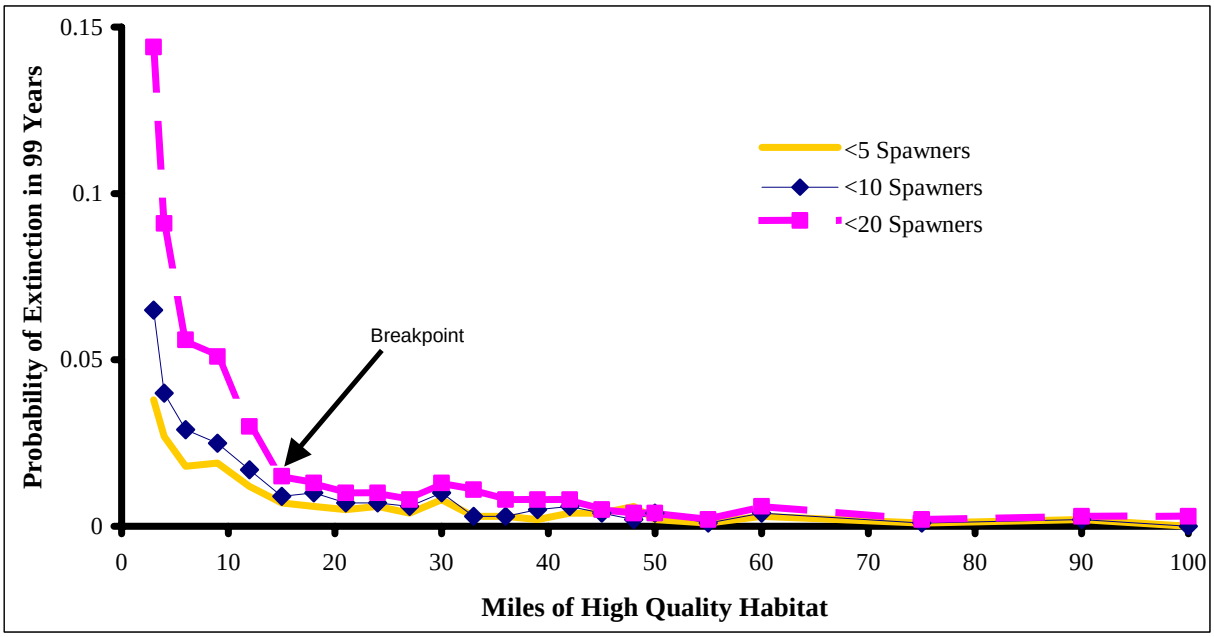

Figure 20. The relationship between the quantity of high-quality habitat (habitat that will support populations of coho salmon when marine survival is 3%) and probability of extinction defined as the number of spawners less than 5, 10, or 20 (from Nickelson 2001).

Figure 21. Proposed historical coho populations in the Oregon Coast Coho Salmon ESU. Dependent-population basins are identified in Figure 3.

Table 7. Proposed historical populations, listed north-to-south, with classification (App. III, Bjorkstedt 2004).

Population	Population type	Population	Population type
Necanicum R.	Potentially Independent	Moore Cr.	Dependent
Indian Cr.	Dependent	Theil Cr.	Dependent
Canyon Cr.	Dependent	Beaver Cr.	Potentially Independent
Ecola Cr.	Dependent	Alsea R.	Functionally Independent
Red Rock Cr.	Dependent	Little Cr.	Dependent
Austin Cr.	Dependent	Big Cr.	Dependent
Asbury Cr.	Dependent	Vingie Cr.	Dependent
Arch Cape Cr.	Dependent	Yachats R.	Dependent
Short Sand Cr.	Dependent	Gwynn Cr.	Dependent
Nehalem R.	Functionally Independent	Cummins Cr	Dependent
Spring Cr.	Dependent	Bob Cr.	Dependent
Watseco Cr.	Dependent	Tenmile Cr.	Dependent
Tillamook Bay	Functionally Independent	Squaw Cr.	Dependent
Netarts Bay	Dependent	Rock Cr.	Dependent
Rover Cr.	Dependent	Big Cr.	Dependent
Sand Cr.	Dependent	China Cr.	Dependent
Nestucca R.	Functionally Independent	Blowout Cr.	Dependent
Neskowin Cr.	Dependent	Cape Cr.	Dependent
Salmon R.	Potentially Independent	Berry Cr.	Dependent
Devils Lake (lake)	Dependent	Sutton Cr. (Mercer Lake)	Dependent
Siletz R.	Functionally Independent	Siuslaw R.	Functionally Independent
Schoolhouse Cr.	Dependent	Siltcoos R. (lake)	Potentially Independent
Fogarty Cr.	Dependent	Tahkenitch Cr. (lake)	Potentially Independent
Depoe Bay Cr.	Dependent	Threemile Cr.	Dependent
Rocky Cr.	Dependent	Lower Umpqua	Functionally Independent
Johnson Cr.	Dependent	Upper Umpqua	Functionally Independent
Spencer Cr.	Dependent	Tenmile Cr. (lake)	Potentially Independent
Wade Cr.	Dependent	Coos Bay	Potentially Independent
Coal Cr.	Dependent	Coquille R.	Functionally Independent
Moolack Cr.	Dependent	Johnson Cr.	Dependent
Big Cr.	Dependent	Twomile Cr.	Dependent
Yaquina R.	Functionally Independent	Floras Cr.	Potentially Independent
Henderson Cr.	Dependent	Sixes R.	Potentially Independent
Grant Cr.	Dependent		

Table 8. Locations of river mouths and distance to the nearest Functionally Independent population for basins along the Oregon Coast (Kilgour 2003)[a].

Basin Name	Latitude	Longitude	Population Type[b]	Distance (km) from Columbia River	Distance (km) to Nearest FI Population
Columbia	46.244	124.057	N/A	0.0	--
Necanicum	46.012	123.926	PI	27.7	40.7
Indian	45.9307	123.9781	D	37.6	30.8
Canyon	45.9304	123.9779	D	37.6	30.8
Ecola	45.8993	123.9625	D	41.2	27.2
Red Rock	45.845	123.961	D	47.3	21.1
Austin	45.819	123.964	D	50.2	18.2
Asbury	45.815	123.962	D	50.6	17.8
Arch Cape	45.804	123.966	D	51.9	16.5
Short Sands	45.76	123.963	D	56.8	11.6
Nehalem	45.658	123.933	FI	68.4	0.0
Spring	45.62	123.937	D	72.6	4.2
Watseco	45.589	123.984	D	77.6	9.2
Tillamook	45.488	123.901	FI	90.5	0.0
Netarts	45.403	123.944	D	100.6	9.9
Rover	45.328	123.967	D	109.1	18.6
Sand	45.29	123.937	D	113.9	23.4
Nestucca	45.184	123.956	FI	125.8	0.0
Neskowin	45.1	123.986	D	135.4	9.6
Salmon	45.047	124.005	PI	141.5	15.7
Devils Lake	44.968	124.016	D	150.3	7.1
Siletz	44.904	124.01	FI	157.4	0.0
Schoolhouse	44.873	124.041	D	161.6	4.2
Fogarty	44.839	124.053	D	165.5	8.1
Depoe	44.806	124.058	D	169.2	11.8
Rocky	44.779	124.071	D	172.4	15.0
Johnson	44.738	124.059	D	177.0	14.9
Spencer	44.729	124.059	D	178.0	13.9
Wade	44.716	124.06	D	179.5	12.4
Coal	44.708	124.061	D	180.4	11.5
Moolack	44.703	124.063	D	180.9	11.0
Big Creek (near Yaquina)	44.659	124.058	D	185.8	6.1
Yaquina	44.613	124.017	FI	191.9	0.0
Henderson	44.589	124.068	D	196.7	4.8
Grant	44.581	124.068	D	197.6	5.7
Moore	44.572	124.069	D	198.6	6.7

[a] Columbia and Elk rivers are included to locate the ESU boundary. Tributaries to Tillamook Bay are assumed to harbor a single population.
[b] D = Dependent; FI = Functionally Independent; PI = Potentially Independent

Table 8 continued. Locations of river mouths and distance to the nearest Functionally Independent population for basins along the Oregon Coast (Kilgour 2003).

Basin Name	Latitude	Longitude	Population Type	Distance (km) from Columbia River	Distance (km) to Nearest FI Population
Thiel	44.565	124.07	D	199.4	7.5
Beaver	44.524	124.075	PI	204.0	11.0
Alsea	44.423	124.08	FI	215.2	0.0
Little	44.393	124.088	D	218.6	3.4
Big Creak (near Alsea	44.371	124.088	D	221.0	5.8
Vingie	44.341	124.098	D	224.5	9.3
Yachats	44.309	124.107	D	228.1	12.9
Gwynn	44.271	124.11	D	232.3	17.1
Cummins	44.266	124.108	D	232.9	17.7
Bob	44.244	124.11	D	235.3	20.1
Tenmile	44.226	124.11	D	237.3	22.1
Squaw	44.2086	124.1133	D	239.3	21.4
Rock	44.183	124.114	D	242.1	18.6
Big Creek (near Suislaw)	44.177	124.114	D	242.8	17.9
China	44.169	124.115	D	243.7	17.0
Blowout	44.157	124.117	D	245.0	15.7
Cape	44.134	124.123	D	247.6	13.1
Berry	44.095	124.122	D	251.9	8.8
Sutton (Lake)	44.06	124.127	D	255.9	4.8
Siuslaw	44.017	124.136	FI	260.7	0.0
Siltcoos (Lake)	43.874	124.153	PI	276.6	15.9
Tahkenitch (Lake)	43.815	124.165	PI	283.3	16.5
Threemile	43.748	124.18	D	290.8	9.0
Umpqua	43.669	124.204	FI	299.8	0.0
Tenmile (Lake)	43.562	124.231	PI	311.9	12.1
Coos	43.429	124.229	PI	326.6	37.6
Coquille	43.124	124.429	FI	364.2	0.0
Johnson	43.093	124.431	D	367.6	3.4
Twomile	43.044	124.441	D	373.1	8.9
Floras	42.913	124.496	PI	388.3	24.1
Sixes	42.854	124.543	PI	395.9	31.7
Elk	42.81	124.533	N/A	400.9	--

[a] Columbia and Elk rivers are included to locate the ESU boundary. Tributaries to Tillamook Bay are assumed to harbor a single population.
[b] D = Dependent; FI = Functionally Independent; PI = Potentially Independent

DISCUSSION

Our view of the historical population structure of Oregon Coast coho salmon relies upon a simple conceptual model of the spatially-dependent demographics of 67 populations we consider likely to have been present within the ESU. This model classifies populations on the basis of two key characteristics: persistence (their relative abilities to persist in isolation from one another) and isolation (the relative degree to which they might have been influenced by adult fish from other populations straying into their spawning areas). The interaction of these two factors across what we believe to have been the historical populations of Oregon Coast coho salmon gives us a measure of Relative Independence.

Our model of the interplay between the persistence and isolation of historical coho populations within the Oregon Coast ESU provided us a clear method for classifying the relative independence of individual populations. Historical populations were classified into three distinct groups: Functionally Independent, Potentially Independent, and Dependent. In general, Oregon Coast drainage basins of intermediate to large size (whose coho populations fell to the right of a persistence threshold in Figure 19) are thought to have each supported a coho population capable of persisting indefinitely in isolation, though some of them (seen below a horizontal line representing an isolation threshold in Figure 19) may have been demographically influenced by adult coho straying into spawning areas from elsewhere in the ESU. Those persistent populations with minimal demographic influence from adjacent populations were classified as Functionally Independent (9 populations), while populations that appeared likely to have been capable of persisting in isolation but were demographically influenced by adjacent populations were classified as Potentially Independent (9 populations). Small coho populations would have been found in 48 smaller coastal basins (seen falling both to the left of the persistence line and below the isolation line in Figure 19) and may not have been able to maintain themselves continuously for periods as long as hundreds of years without the demographic boost provided by migrating spawners from other populations. For this reason, these populations were classified as Dependent.

We believe that the Dependent populations relied at times upon the strength of adjacent larger populations for their continuous historical presence in the Oregon Coast's smaller basins. As long as the larger persistent populations within the ESU remained strong, the smaller (Dependent) populations would rarely if ever have disappeared from their basins. However, if some form of broad-scale environmental change triggered a substantial decline in one or more of the larger populations, the reduction in migrants would have increased the possibility that the same environmental change, perhaps coupled with local disturbances, would have resulted in the intermittent disappearances of the Dependent populations found in some of the smaller basins.

Uncertainties

Despite the simplicity of the conceptual model we used to classify the Relative Independence of historical coho populations within the Oregon Coast Coho Salmon ESU, it should be emphasized that analytical components of our model are no different from those of other mathematical models of populations or habitat. Our model produces results that we

consider a reasonable but uncertain approximation of an imperfectly understood biological phenomenon: the interactions of historical Oregon Coast coho salmon populations.

We are confident in the way our modeling has arrayed 67 historical populations of Oregon Coast coho salmon on the basis of their potential abundance. The abundance levels assigned to the populations reflect what is known about how the species uses its habitat and are consistent with patterns evident in both recent and historical data on coho abundance. However, the specific coho population size we used to define our persistence (threshold) line in Figure 19 was based on results from a simple habitat-based model of coastal coho populations developed by Nickelson and Lawson (1998). That model fits data on the recent performance of Oregon Coast coho salmon populations, but habitat available to these populations has been substantially altered from that which supported historical populations, and is of lower quality (IMST 2002). Historical habitats may have been somewhat more stable and productive than those we can study today, raising the possibility that historical coho populations may have been able to persist on smaller quantities of relatively higher quality habitat than recent data on coho abundance and population performance might suggest. There are also inherent between-basin differences in the stability or aggregate productivity of coho habitat that could affect the persistence of some smaller populations but that were only weakly accounted for when we used absolute coho abundance as a proxy for population persistence. Taking these things into account, we assessed the sensitivity of our population classifications to a 50% reduction in the coho population size used as a persistence threshold and found that only 5 of 49 coho populations otherwise classified as Dependent (Twomile Creek, Sand Lake, Devils Lake, Sutton Lake, and Yachats River) would be reclassified as Potentially Independent. Similarly, a 50% increase in the persistence threshold would have resulted in only one Potentially Independent population (Salmon River) being reclassified as Dependent. Most of our classifications of populations would thus be unaffected by what we might consider as reasonable changes to our persistence threshold.

Another area of uncertainty within our classification model is the dispersal pattern used to simulate migration between coho populations, and thus to distinguish between Functionally Independent and Potentially Independent populations in the historical ESU. The pattern that we used assumes an exponential decline in migration rate with increasing distance from the natal basin and does not account for a variety of environmental gradients that may (or may not) affect the relative attractiveness of non-natal basins to straying coho. A more complex pattern might be more realistic, but we are not aware of any data or studies that would provide us a sufficient basis for structuring such a pattern. This creates uncertainty about the degree to which the results of our model reflect the true isolation of individual coho populations. Sensitivity analyses by Bjorkstedt (2004) have shown that changes in the assumed dispersal pattern of migrant coho tend to have only minor effects on the apparent isolation of the larger coho populations within the historical Oregon Coast Coho Salmon ESU, but variable effects on the apparent Isolation of intermediate-sized to smaller populations. This is a topic worthy of further investigation.

Other Applications of the Relative Independence Model

Our model-based approach to classifying the Relative Independence of coho salmon populations within the Oregon Coast Coho Salmon ESU may be of interest to other NOAA Fisheries Technical Recovery Teams because it provides a structured way to delineate

independent salmon populations within geographically linked coastal areas. At present, the general model is being used to help identify historically independent coho salmon populations within two additional ESUs, both along the California coast. The model may also prove useful in examining recent changes in the interactive demographic behavior of geographically linked salmon populations and in establishing a conceptual framework for the development of ESU recovery goals.

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GLOSSARY

A

Abundance. The number of fish in a *population*.

Active channel width. The distance across a stream or channel as measured from bank to bank at bankful flow.

Allelle. Any one of a number of alternative forms of a gene that can occur at the same location (*locus*) on a chromosome. A *population* can have many alleles for a particular locus, but an individual can carry no more than two alleles at a *diploid* locus.

Allozymes. Alternative forms of an enzyme that have the same function, are produced by different *alleles*, and are often detected by *protein electrophoresis*.

Anthropogenic factor. A circumstance or influence caused or produced by human action.

Artificial propagation. *Hatchery* spawning and rearing of salmon, usually to the *smolt* stage.

AUC (Area Under the Curve). A statistical technique for estimating an annual total number of *spawners* from periodic spawner counts.

B

Barrier. A blockage such as a waterfall, culvert, or rapid that impedes the movement of fish in a stream system.

Biological Review Team (BRT). The team of scientists who evaluate scientific information for the National Marine Fisheries Service (NMFS) status reviews.

C

Carrying capacity. The number of individuals that the resources of a habitat can support.

Catastrophic events. Sudden events that disastrously alter large areas of landscape. These can include floods, landslides, forest fires, and volcanic eruptions.

Channel gradient. The slope of a stream reach.

CIMRS (Cooperative Institute for Marine Resources Studies). A cooperative project between Oregon State University and NOAA Fisheries.

CLAMS (Coastal Landscape Analysis and Modeling Study). A cooperative project between the Oregon State University Department of Forestry and the U.S. Forest Service Pacific Northwest Forest Science Laboratory.

Co-managers. Federal, state, and tribal agencies that cooperatively manage salmon in the Pacific Northwest.

Coded-wire tag (CWT). A small piece (0.25 x 0.5 or 1.0 mm) of stainless steel wire that is injected into the snouts of juvenile salmon and steelhead. Each tag is etched with a binary code that identifies its release group.

D

De-listing. Taking a species off of the endangered species list.

Demographic stochasticity. "Chance events in the survival and reproductive success of a finite number of individuals" (Shaffer 1981).

DEM (Digital Elevation Model). A digital data set representing a topographic map that can be used for computer analysis. We used DEMs to calculate the *intrinsic potential* of stream systems.

Density effects. Survival of juvenile salmon may be influenced by their density. Survival is usually higher when density is low.

Dependent populations. Populations that rely upon immigration from surrounding populations to persist. Without these inputs, dependent populations would have a lower likelihood of *persisting* over 100 years.

Depensation. The effect where a decrease in spawning stock leads to reduced survival or production of eggs through either (1) increased predation per egg given constant predator pressure, or (2) the "Allee effect" (the positive relationship between population density and the reproduction and survival of individuals) with reduced likelihood of finding a mate.

Diploid. Having two complete chromosome pairs in a nucleus.

Distinct population segment (DPS). A *population*, or group of populations of a vertebrate species that is "discrete" from other populations and *significant* to the biological species as a whole.

DNA (deoxyribonucleic acid). A complex molecule that carries an organism's heritable information. The two types of DNA commonly used to examine genetic variation are *mitochondrial DNA* (mtDNA), a circular molecule that is maternally inherited, and *nuclear DNA*, which is organized into a set of chromosomes (see also *allele* and *electrophoresis*).

Donor populations. These are *Functionally Independent* or *Potentially Independent populations* that are large enough to "donate" *migrant* adults to *Dependent populations*.

E

Ecoregion. An integration of physical and biological factors such as geologic history, climate, and vegetation.

Effective migration rate. The proportion of successfully spawning adults that migrate to a new *population*. (Excludes *migrants* that do not successfully reproduce.) (See also *Migration rate*.)

Electrophoresis. The movement of charged particles in an electric field. This process has been developed as an analytical tool to detect genetic variation revealed by charge differences on proteins or molecular weight in DNA.

Endangered species. A species in danger of extinction throughout all or a significant portion of its range.

ESA. U.S. Endangered Species Act.

Escapement. Usually refers to adult fish that "escape" from both fisheries and natural *mortality* to reach the spawning grounds.

Estuarine habitat. Areas available for feeding, rearing, and smolting in tidally influenced lower reaches of rivers. These include marshes, sloughs and other backwater areas, tidal swamps, and tide channels.

Evaporation potential. The maximum depth of water that could evaporate in a year. Evaporation potential is principally determined by temperature and relative humidity. It is a measure of how much moisture "stress" plants are under due to dry conditions.

Evolutionarily Significant Unit (ESU). An ESU represents a *distinct population segment* of Pacific salmon under the *Endangered Species Act* that 1) is substantially reproductively isolated from conspecific populations and 2) represents an important component of the evolutionary legacy of the species. See also *Distinct population segment*.

Exploitation rate. The proportion of adult fish from a *population* that die as a result of fisheries.

Extinction. The loss of a species, or ESU. May also be used for the extirpation of local populations.

F

Factors for decline. These are factors identified that caused a species to decrease in *abundance* and *distribution* and become threatened or endangered.

Fecundity. The number of offspring produced per female.

Fourth-Field and Fifth-Field Hydrologic Units. In the United States Geological Survey (USGS), hydrologic units have been divided at different scales. The area of a fourth-field hydrologic unit is 440,000 acres and a fifth-field hydrologic unit is between 40,000 and 250,000 acres.

Freshwater habitat. Areas available for spawning, feeding, and rearing in freshwater.

Fry. Young salmon that have emerged from the gravel and no longer have an egg sack.

Functionally Independent population**.** A high-*persistence population* whose dynamics or extinction risk over a 100-year time frame is not substantially altered by exchanges of individuals with other populations (*migration*). Functionally independent 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).

G

Genetic distance. A quantitative measure of the genetic difference between a pair of samples, based on *allele* frequencies at multiple loci.

Genetic drift. Random changes in gene frequencies of *populations*.

Gradient. The slope of a stream system.

H

Habitat quality. The suitability of physical and biological features of an aquatic system to support salmon in the freshwater and estuarine system.

Hatchery. A facility where *artificial propagation* of fish takes place.

Historical abundance. The number of fish that were produced before the influence of European settlement.

Homing fidelity. The propensity of an adult salmon to return to its natal stream.

Hydrology. The distribution and flow of water in an aquatic system.

I

Independent Multidisciplinary Science Team (IMST). A scientific advisory body to the Oregon Legislature and Governor on Watershed, Forestry, Agriculture, and Fisheries Science issues.

Inbreeding depression. Reduced survival rates of individuals in a *population* suffering from the effects of harmful recessive genes through matings between close relatives. Inbreeding depression may become a problem when populations get very small.

Independence. Reflects the interaction between *isolation* and *persistence*. A persistent population that is highly isolated is highly independent.

Intrinsic potential. A modeled attribute of streams that includes the *channel gradient*, *valley constraint* and *mean annual discharge of water*. Intrinsic potential in this report refers to a measure of potential coho salmon habitat quality (Burnett et al. 2003).

Isolating mechanisms. Things that reduce the ability of *populations* to interbreed. These could include physical mechanisms such as distance, and behavioral mechanisms such as *run timing*.

Isolation. The degree to which a *population* is unaffected by *migration* to and from other populations. As the influence of migration decreases, a population's isolation increases.

J

Jack. A coho salmon that matures at age 2 and returns from the ocean to spawn a year earlier than normal. Jacks are all male fish.

Jacking rate. The proportion of adult coho salmon from a brood that return as *jacks*.

Juvenile. A fish that has not matured sexually.

L

Latitudinal cline (also known as a latitudinal diversity gradient.) A change in a biological trait that occurs across latitudes. For example, *jacking rate* generally increases from north to south.

Life history. The specific life cycle of a fish from egg to adult.

Limiting factors. Factors that limit survival or *abundance*. They are usually related to habitat quantity or quality at different stages of the life cycle. Harvest and predation may also be limiting factors.

Listed species. Species included on the "List of Endangered and Threatened Species" authorized under the *Endangered Species Act* and maintained by the *U.S. Fish and Wildlife Service* and *NOAA Fisheries*.

Littoral zone. In lakes, the area of lake bottom that receives enough light for rooted plants to grow. In the ocean, the marine ecological realm that experiences the effects of tidal and longshore currents and breaking waves to a depth of 5 to 10 m (16 to 33 feet) below the low-tide level, depending on the intensity of storm waves. (Encyclopædia Britannica 2004).

Locus. Location on a chromosome that holds a specific gene. Plural is loci.

Lowland habitat. Low-gradient stream habitat with slow currents, pools, and backwaters used by fish. This habitat is often converted to agricultural or urban use.

M

Marine survival rate. The proportion of smolts entering the ocean that return as adults.

Mean annual discharge of water. A single value or average that summarizes or represents the annual discharge amount, typically expressed in cubic meters per second.

MES, Inc. Manufacturing Engineering Systems, Inc.

Metric. A unit of measure.

Microsatellite. A class of repetitive DNA used for estimating genetic distances.

Migrant. A fish that is born in one *population* but returns to another population to spawn.

Migration. Movement of fish from one *population* to another.

Migration rate. The proportion of *spawners* that migrate from one population to another. See also *Effective migration rate*.

Mitochondrial DNA (mtDNA). The *DNA* genome contained within mitochondria and encoding a small subset of mitochondrial functions. Only female mtDNA is transmitted to the next generation.

Mortality. Death.

N

NMFS. National Marine Fisheries Service, also known as NOAA Fisheries.

NOAA. National Oceanic and Atmosphere Administration.

NOAA Fisheries. The fisheries branch of NOAA, also known as NMFS.

Nuclear DNA (nDNA). The DNA contained in the chromosomes within the nucleus of eukaryotic cells. The nuclear genome in Pacific salmon is approximately 4.6 billion base pairs in size.

NWFSC. NOAA Fisheries Northwest Fisheries Science Center.

O

ODFW. Oregon Department of Fish and Wildlife.

ONCC. Oregon Northern California Coho Salmon Technical Recovery Team.

ORISE. Oak Ridge Institute for Science and Education.

OWEB. Oregon Watershed Enhancement Board.

P

Parr. The life stage of salmonids that occurs after *fry* and is generally recognizable by dark vertical bars (parr marks) on the sides of the fish.

Persistence. A *population's* relative ability to sustain itself without input from neighboring populations.

Phylogenetic tree. The genetic distances and relationships among *populations*, frequently represented with a branching or tree-like diagram.

Population. A 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.

Population classification. The grouping of *populations* into *Functionally Independent*, *Potentially Independent*, and *Dependent* classes.

Population dynamics. Changes in the number, age, and sex of individuals in a *population* over time, and the factors that influence those changes. Five components of populations that are the basis of population dynamics are birth, death, sex ratio, age structure, and dispersal.

Population identification. Delineating the boundaries of *historical populations*.

Population structure. This includes measures of age, density, and growth of fish populations.

Potentially Independent populations. *High-persistence populations* whose *population dynamics* are 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.

Production. The number of fish produced by a *population* in a year.

Productive capacity. Maximum possible *production* from a given area.

Productivity. The rate at which a *population* is able to produce fish.

Protein electrophoresis. An analytical laboratory technique that measures differences in the amino acid composition of proteins from different individuals. See also *Electrophoresis*.

R

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

Recovery domain. The area and species that the Technical Recovery Team is responsible for.

Recovery plan. A document identifying actions needed to make *populations* of naturally produced fish comprising the Oregon Coast Coho Salmon *ESU* sufficiently *abundant*, *productive*, and diverse so that the ESU as a whole will be self-sustaining and will provide environmental, cultural, and economic benefits. A recovery plan will also include goals and criteria by which to measure the ESU's achievement of recovery, and an estimate of the time and cost required to carry out the actions needed to achieve the plan's goals.

Recovery scenarios. Various sequences of events expected to lead to *recovery* of Oregon Coast Coho Salmon.

Run timing. The time of year (usually identified by week) when spawning salmon return to the spawning beds.

S

Salmonids. Any of the species included in salmon, trout, and char.

Significant. Biological significance refers to an effect that has a noteworthy impact on health or survival.

Smolt. A life stage of salmon that occurs just before the fish leaves freshwater. Smolting is the physiological process that allows salmon to make the transition from fresh to salt water.

Smolt capacity. The maximum number of smolts a basin can produce. Smolt capacity is related to habitat quantity and quality.

Spawners. Adult fish on the spawning grounds.

Species. Biological definition: A small group of organisms formally recognized by the scientific community as distinct from other groups. Legal definition. Refers to joint policy of the USFWS and NMFS that considers a species as defined by the ESA to include biological species, subspecies, and *DPSs*.

Stock transfer. The practice of moving fish between basins or *populations*.

Stray rate. As used in this document, the stray rate refers to the number of spawning adults that return to a stream other than their natal stream within a basin. (See also *Migration rate*.)

Sustainability. The ability of a stock to *persist* or sustain itself over long periods of time.

SWFSC. NOAA Southwest Fisheries Science Center.

T

Threatened species. A species not presently in danger of extinction but likely to become so in the foreseeable future.

TRT. Technical Recovery Team.

U

USFS. United States Forest Service.

USGS. United States Geologic Survey.

V

Valley constraint. The valley width available for a stream or river to move between valley slopes.

Viability. The likelihood that a *population* will *sustain* itself over a 100-year time frame.

Viability criteria. A prescription of a *population* conservation program that will lead to the *ESU* having a negligible risk of extinction over a 100-year time frame.

W

Warmwater fish. Spiny-rayed fish such as sculpins, minnows, darters, bass, walleye, crappie, and bluegill that generally tolerate or thrive in warm water.

APPENDIX I: VEGETATION

Because of the specific requirements of different plant communities, dominant vegetation types are a valuable indicator of relative precipitation, temperature, soil type, solar radiation, and altitude. Therefore, changes of vegetation types can indicate changes in the physical environment, which may affect freshwater salmon habitat. The following discussion of vegetation was compiled from studies by Franklin and Dyrness (1973), Barbour and Major (1977), and Hickman (1993).

Sitka Spruce Zone—Coastal regions in Oregon are forested with a Sitka spruce-dominated plant community: Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), red alder (*Alnus rubra*), and Douglas fir (*Pseudotsuga menziesii*) are major species that occur there. This vegetation type is restricted to coastal regions and river valleys and only on the coastal plains does it extend farther than a few kilometers inland. The Sitka Spruce Zone reaches elevations above 150 m (490 ft) only in areas immediately adjacent to the ocean. However, where mountains are adjacent to the coast, the zone may extend to 600 m (1970 ft). This vegetation type only occupies areas with a uniformly wet and mild climate. Sitka spruce forests could be considered a variant of western hemlock forests of higher elevations and inland areas, but they are distinguished by frequent summer fogs and proximity to the ocean (Franklin and Dyrness 1973).

Western Hemlock Zone—Along the Oregon coast, the western hemlock-dominated plant community replaces Sitka spruce at elevations above 150 m (490 ft). This zone includes western hemlock, Douglas fir, red alder, and western red cedar as major tree species. South of the Columbia River, the Western Hemlock Zone extends southward along the Coast Range to the Klamath Mountains and southward along the Cascade Mountains to the Umpqua River.

Alpine and Subalpine Zones—The headwaters of rivers draining higher mountains, such as the Cascade Mountains and Oregon Coast ranges, begin in alpine meadows and subalpine parklands, before they change to western hemlock-dominated forests below 700-1,000 m (2300-3280 ft). The higher alpine regions appear as a mosaic of meadows and tree patches with long-lasting and deep snow cover. The Subalpine Zone is dominated by mountain hemlock (*Tsuga mertensiana*) and subalpine fir (*Abies lasiocarpa* var. *lasiocarpa*) and is wetter and colder than areas at lower elevations, but has less extended snow cover than the higher alpine areas. With the exception of some of the higher peaks in the Coast Range, the majority of this zone is found in the drainage of the North Umpqua River.

Umpqua Valley—The interior Umpqua Valley area is a complex of many different vegetation types. These include coniferous tree associations including Douglas fir, Ponderosa pine (*Pinus ponderosa*) and Incense Cedar (*Calocedrus decurrens*), oak forest stands, woodlands and savannas with Oregon oak (*Quercus garryana)*, California black oak (*Quercus kelloggii*) and madrone (*Arbutus menziesii*), grasslands with Kentucky bluegrass (*Poa pratensis*), orchard grass (*Dactylis glomerata*), and Idaho bent (*Agrostis Idahoensis*), sclerophyllus hillside communities dominated by Douglas Fir, tan oak (*Lithocarpus densiflora*), canyon live oak (*Quercus chrysolepis*), madrone, chinquapin (*Chrysolepis chrysophylla*), and riparian communities with black cottonwood (*Populus balsamifera* ssp. *trichocarpa*), many willow species (*Salix rigida, S.*

lasiandra, *S. fluviatilis*, and *S. sessilifolia*), Oregon oak, and California laurel (*Umbellularia california*).

Mixed Conifer and Evergreen Forest Zones—The Klamath Mountain Province (ONHP 2003) extends into the Umpqua Basin in the region of the South Umpqua and mainstem Umpqua Rivers. This section of the province is the northern Siskiyou Mountains. In the western Siskiyou Mountains, the dominant vegetation is a mixed forest of evergreen-needle-leaved trees and broad-leaved evergreen sclerophyllous trees. Dominants in these mixed evergreen forests are Douglas fir, tan oak, madrone, and chinquapin. These species are more allied with forests found to the south than those in the more mesic coastal areas.

APPENDIX II: ECOREGIONS OF THE OREGON COAST COHO SALMON ESU FROM SOUTH OF THE COLUMBIA RIVER TO CAPE BLANCO

Level 3 ecoregions are shown in Figure 15; level 4 ecoregions are shown in Figure 16. These descriptions are compiled from Thorson (2003) and ONHP 2003b.

Level 3 Ecoregion Descriptions

Klamath Mountain Ecoregion—The Klamath Mountain Ecoregion within the Oregon Coast Coho Salmon ESU is found in the Interior Umpqua River Basin, encompassing systems such as Cow Creek, South Umpqua River, and a portion of the North Umpqua River. This area is the most northerly of a system of mountains that extend into northwestern California (the Siskiyou Mountains). These are the oldest landscapes in Oregon, due to their origin as ocean crust or island archipelago environments that were carried eastward on a tectonic plate that collided with the continent of North America. These terranes (exotic pieces of landscapes) were then welded to the continent by granitic intrusives (Orr and Orr 2000). This area is a very diverse geological landscape, which includes serpentine, limestone, and gabbro, as well as granite and basalt. The Umpqua portion of the Klamath Mountains Ecoregion is less rugged than others found in the Rogue Basin just to the south. Precipitation in this portion of the ecoregion tends to be drier than the more coastal portions of the Klamath Mountains and summer high temperatures can average more than 32ºC (90ºF). Vegetation is diverse in this area and is described in the level 4 ecoregion descriptions for the Siskiyou foothills, Umpqua Interior foothills, and Coastal Siskiyous.

Oregon Coast Range Ecoregion—The entire coast of Oregon is included within the Oregon Coast Range Ecoregion, and extends eastward to include the northern and central Oregon Coast Range Mountains. Geology is a mix of sedimentary sandstones, siltstones, and mudstones, with areas of volcanic activity. Elevations range from sea level to 1200 m (4,000 ft). The marine climate moderates temperatures, which average 10ºC (50ºF). Average annual rainfall may vary from 152 to 460 cm (60 to 180 in.) per year. The soils in this region are generally deep and mature and vegetation is dominated by giant Sitka spruce, Douglas fir and western hemlock forests. In the southern end of the range, Coast redwood, Port Orford cedar, red alder, and tan oak also become co-dominants.

West Cascade Ecoregion—The West Cascades Ecoregion within the Oregon Coast Coho Salmon ESU is found in the Umpqua Basin, specifically in the North Umpqua and South Umpqua drainages). Geology is closely related to volcanic actitivity of the Cascade Crest. The ecoregion is dominated by Douglas fir-western hemlock forests to about 1,000 m (3,300 ft). Above that, silver fir/mountain hemlock forests dominate. Very little of the area within the Oregon Coast Coho Salmon ESU is alpine area. This drier portion of the West Cascades Ecoregion is subject to lightning-caused fire regimes similar to the Klamath Mountains. Snows are not as heavy as in the northern portion of the West Cascades Ecoregion in Oregon.

Level 4 Ecoregion Descriptions

Descriptions below refer to areas mapped in Figure 16.

Coastal Lowlands – elevations sea level to 90 m (300 ft)—Estuaries within the Oregon Coast Coho Salmon ESU are all drowned river mouths. (Good 2000). They are mainly of three types: well-flushed drowned rivers, seasonally open to the ocean (such as Sixes, New River); well-flushed drowned rivers, predominantly freshwater input (e.g., Coquille, Umpqua, Siuslaw); and well-flushed drowned rivers with predominantly oceanic input (such as Coos, Sand Lake, Yaquina, Nestucca). Many of these areas historically had relatively large areas of salt, brackish, and freshwater marshes; sloughs; and swamps. Most, however have suffered losses of these areas of up to 80% of these tidally-influenced systems through diking and channelization.

Sand dune sheets are part of the Pacific Northwest Coastal Region (Terrel 1979, Proctor et al. 1980) between the Strait of Juan de Fuca in Washington State to Cape Mendocino in California. Two hundred and twenty-five kilometers of the Oregon Coast is covered by these dune systems. Some are found as isolated areas associated with bays and river mouths between headlands (such as Netarts Bay). Others are extensive dune sheets found on broad terraces (such as Coos Bay Dune Sheet and Sand Lake). These broad terraces may have extensive dune systems and may also harbor extensive freshwater lakes, bogs, fens, and blackwater streams (Wiedemann 1984, ONHP 2003b).

Coastal Uplands– elevations to about 150 meters (500 ft)—This ecoregion is characterized by uplifted marine consolidated and semi-consolidated sediments. These include sandstones and siltstones. Also included are some volcanics.

Volcanics—Volcanic geology is found at elevations from 300 to 1200 m (1,000 to 4,000 ft). These volcanics are of various origins: these include the Columbia River Basalts, the Siletz River, and the Yachats series of basalts. Some of the mountains found in this ecoregion may have been off-shore seamounts buried by continental sediments (ONHP 2003b, KCM 1983)

Willapa Hills—These low-lying hills are a continuation of a larger area north of the Columbia River (WDNR 2003). These are in the Western Hemlock Zone.

Mid-Coastal Sedimentary—The Mid-Coastal Sedimentary Ecoregion is underlain by siltstone and sandstone. The mountains are more rugged (dissected and higher) than the Willapa Hills. These sedimentary mountains are very prone to landslides if the vegetation is removed. Stream gradients and fluvial erosion rates can be high in these rugged areas, but are lower in the higher order streams that occupy the lowlands. Many of these areas have deep soils, and most are in the Western Hemlock Zone (ONHP 2003b).

Southern Oregon Coastal Mountains—These are mountainous areas in the south portion of the Oregon Coast Coho Salmon ESU with ocean-modified climate. They are transitional between the Siskiyou and Coast ranges. These areas are underlain by Jurassic sandstone, metmorphosed sediments, granite, and serpentine (metamorphosed ocean sediments). Soils are dependent upon parent material. This is a complex much like the Inland Siskiyous, but the ruggedness is less and elevations are lower. This is an area of very high plant diversity. The northern distribution

limits of southern plant and animal species and southern limit of northern plant species are one reason for the diversity. Also, the area's unusual geology and stable climate have lead to the evolution of local endemic plants. The Mixed Conifer and Evergreen Zones are found in this subregion (Orr and Orr 2000, Barbour and Major 1977, ONHP 2003b).

Inland Siskiyous—This area encompasses the Umpqua and Rogue valleys and is very complex vegetationally. These vegetation types include Douglas fir forests, oak woodlands and savanna, mixed evergreen forest, mixed conifer forests, and Ponderosa pine woodlands. Grasslands and chapparal are found in the valley bottoms. Geology is complex with large areas of metamorphosed rocks such as serpentine and gabbro, sedimentary rocks such as limestone, as well as granite and basalt. Floristic elements of the Sierra Nevada Mountains, Sacramento Valley, Cascade Mountains, and Great Basin are all found in this ecoregion and contribute to the high plant diversity found here. Because of its unusual geology, and stable climate, it is also a major locality of vascular plant species evolution as well. Conifers are especially diverse in the Oregon section of the Inland Siskiyou subregion with 18 species. This area has major climatic extremes ranging from 254 cm (100 in.) of precipitation per year to 50 cm (20 in.) (Orr and Orr 2000, Barbour and Major 1977, ONHP 2003b).

Valley Foothills—This subregion is an extension of the Willamette Valley on the west side, and is transitional between the Cascade Mountains and the Coast Range. This area has lower rainfall than adjacent mountainous subregions due to a rainshadow effect. Oregon white oak and Douglas fir are potentially dominant in this area, but agricultural conversion has substantially reduced the native forests (ONHP 2003b).

Umpqua Interior Foothills—This is an area of narrow interior valleys, terraces, and foothills with elevations from about 120 to 460 m (400 to 1500 ft). Vegetation is a mix of Oregon white oak woodlands and coniferous forests with pastureland, vineyards, row crops, and orchards replacing the native vegetation. Other dominant tree species found are Douglas fir, Ponderosa pine, and madrone (ONHP 2003b).

Umpqua Cascades—This portion of the Cascades is dryer than the western Cascades. Grand fir, white fir, western hemlock, Pacific silver fir, Douglas fir, and Shasta red fir dominate. The diversity of vegetation is greater than the western Cascades subregions due to warmer summer temperatures and a longer growing season, as well as floristic elements from both northern and southern floristic provinces (ONHP 2003b).

APPENDIX III: POTENTIAL HISTORICAL ABUNDANCE OF COHO SALMON

Having estimates of potential historical abundance of coho salmon populations is useful for a number of reasons. Such estimates can be used to compare with current abundance, they could be useful for developing an understanding of limiting factors, and they can be used in modeling the independence of individual populations. Here we use two independent approaches to estimate historical abundance of coho salmon in the Oregon Coast Coho Salmon ESU for the purpose of modeling the independence of individual populations.

Calculating Adult Abundance from Catch

Lichatowich (1989) estimated historical abundance of adult coho salmon based on in-river catch records. Mullen (1981a) compiled catch records for individual coastal basins within the Oregon Coast Coho Salmon ESU and converted pounds landed to estimated number of adult salmon. Both Mullen (1981b) and Lichatowich (1989) divided total number of fish landed coast-wide by an assumed exploitation rate of 40% to estimate total abundance. Mullen (1981b) estimated mean annual abundance for 5-year intervals from 1892 to 1940. Lichatowich (1989) estimated mean annual abundance for the five peak years between 1892 and 1920, which he considered a conservative measure of production because of the many problems associated with the accuracy of the early cannery records.

The methods of Mullen (1981b) and Lichatowich (1989) were adopted here with the exception that they were applied to the peak year of catch in each of 10 coastal basins during the period of 1882-1925 as estimated by Mullen (1981a). Because maximum catch of coho salmon in individual basins did not occur in a single year, this approach gives a better estimate of potential historical abundance. Peak catches in the 10 basins actually occurred in six different years. However, like the earlier estimates, these estimates of abundance only apply to streams where fisheries took place. The 10 basins included represent about 89% of the coho salmon distribution in the Oregon Coast Coho Salmon ESU.

Calculating Adult Abundance from GIS Data

Data from CLAMS used to calculate intrinsic potential for coho salmon (Burnett et al. 2003) (Figs. III-2 through III-5) were converted to an estimate of historical potential smolt abundance for each population in the Oregon Coast Coho Salmon ESU. The estimated smolt potential was then converted to adult potential by applying a marine survival rate.

Stream reaches were divided into two categories based on their gradient. Those reaches with a gradient less than or equal to 0.5% were assumed to be associated with wetlands and an expansive floodplain (Rosgen 1994, 1996; Buffington et al. 2002; Montgomery and Buffington 1997), which would provide winter habitat for coho salmon outside the active channel. For reaches with a gradient greater than 0.5%, the assumption was made that coho salmon smolts were produced primarily within the active channel.

For each population, potential smolt production was calculated as the sum of the potential of all reaches with intrinsic potential greater than 0. For each reach with a gradient less than or equal to 0.5%, potential smolt production was calculated from the equation

$$S = 0.0741\ L\ (V\text{-}W)\ P$$

where S is the potential number of smolts produced in the reach, L is the length of the reach (m), V is the valley width (m), W is the active channel width (m), P is the intrinsic potential of the reach (an index without units), and 0.0741 is the number of smolts per square meter (741/ha) based on data from NMFS et al. (1983).

Potential smolt production was calculated for each reach with a gradient greater than 0.5% from the equation

$$S = (0.3405)\ (0.5)\ L\ W\ P$$

where 0.3405 is the number of smolts per square meter in main channel pools based on data from Nickelson (1998), and 0.5 is the proportion of the area in pools based on an assumed 50:50 pool:riffle ratio.

For lake populations, potential smolt production was estimated by multiplying the lake area by 741 smolts/ha. This is a deviation from the approach used in Washington (NMFS 1983), where only a 30-m- (100-ft-) wide littoral zone is considered. However, Oregon coastal lakes are shallow, with littoral zones that cover most if not all of their area.

Potential historical adult abundance was estimated for each population by applying a 10% marine survival rate to the smolt estimates. These estimates were capped for two stream populations and several lake populations at 1,500 adults per mile of spawning habitat based on current estimates of the miles of stream in each basin that would be available for spawning. The value of 1,500 adults per mile is consistent with the maximum level observed in a lake system tributary in 2001, a high-survival year (ODFW 2003e), and the density of coho observed in Tenmile Lakes in the 1955 (Morgan and Henry 1959) before warmwater fish became a problem.

Results

The results of the two different approaches used to estimate potential historical abundance of coho salmon in the large basins of the Oregon Coast Coho Salmon ESU produced surprisingly similar results (Table III-1). Differences between the two estimates ranged from 1% for the Yaquina Basin to 73% for the Umpqua Basin. There is a strong correlation between the estimates derived by the two methods (Figure III-1).

The advantage of calculating adult abundance from computed intrinsic potential is that estimates can be made for basins where there are no historical fishery data. Table III-2 lists the estimated potential historical abundance of coho salmon for 67 putative populations of coho salmon in the Oregon Coast Coho Salmon ESU. Total adult abundance derived from smolt numbers and 10% marine survival was about 3.5 million adults if all populations peaked the same year.

Discussion

Historical abundance of coho salmon was estimated for the purpose of modeling the effects of relative abundance on population independence. For this exercise, marine survival was assumed to be 10% for all populations. This assumption resultes in an unrealistically high total abundance for the Oregon Coast Coho Salmon ESU when all populations are aggregated. This aggregate estimate of 3.3 million adult coho salmon is higher than the 978,000 for the peak 5-year of Mullen (1981b) and the 1,385,000 (1,915,000 if you use the peak year) of Lichatowich (1989), both of which also included the Rogue River in the Southern Oregon Northern California ESU. The primary reasons for this result is that the populations are asynchronous; in other words, the peak abundance of the various populations did not occur in the same year as was assumed for this analysis. Thus it is a mistake to conclude that historical abundance was 3.3 million adult coho salmon. One example of an approach to use this information to come up with a more realistic ESU abundance estimate is to assume that only 60% of the coastal habitat was productive at any given time (Reeves 2003). This would yield an estimate of 2.0 million fish, which may be on the low side because most fish are produced from the lowlands, which were likely more stable than the uplands where the Reeves (2003) analysis applies. More work is needed to convert the smolt capacity estimates generated here into estimates of historical adult abundance.

It is interesting to note that the basins with the greatest discrepancy between peak adult abundance estimated from catch and that estimated from intrinsic potential are the basins with the greatest effects from splash damming at the turn of the 20th century (Sedell and Duvall 1985). In each case, the abundance of adults estimated from intrinsic potential was at least 30% greater than that estimated from catch. Thus, it could be that even as early as 1900, coho salmon populations had been significantly reduced by habitat destruction in some basins which would result in underestimates of abundance derived from harvest data.

Table III-1. Estimate of potential historical abundance of coho salmon in large basins of the Oregon Coast Coho Salmon ESU using methods based on peak historical catch and based on estimated habitat capacity (based on data from Lichatowich 1989, Chapman 1986, Burnett 2003).

	Estimated Potential Historical Abundance			
Basin	**Based on catch (a)**	**Based on IP (b)**	**Difference**	**(b-a)/a**
Nehalem	240,000	333,000	93,000	39%
Tillamook	292,500	329,000	36,500	12%
Nestucca	115,000	104,000	-11,000	-10%
Siletz	125,000	122,000	-3,000	-2%
Yaquina	120,000	122,000	2,000	2%
Alsea	150,000	163,000	13,000	9%
Siuslaw	292,500	267,000	-25,500	-9%
Umpqua	585,000	820,000	235,000	40%
Coos	150,000	206,000	56,000	37%
Coquille	310,000	417,000	107,000	35%

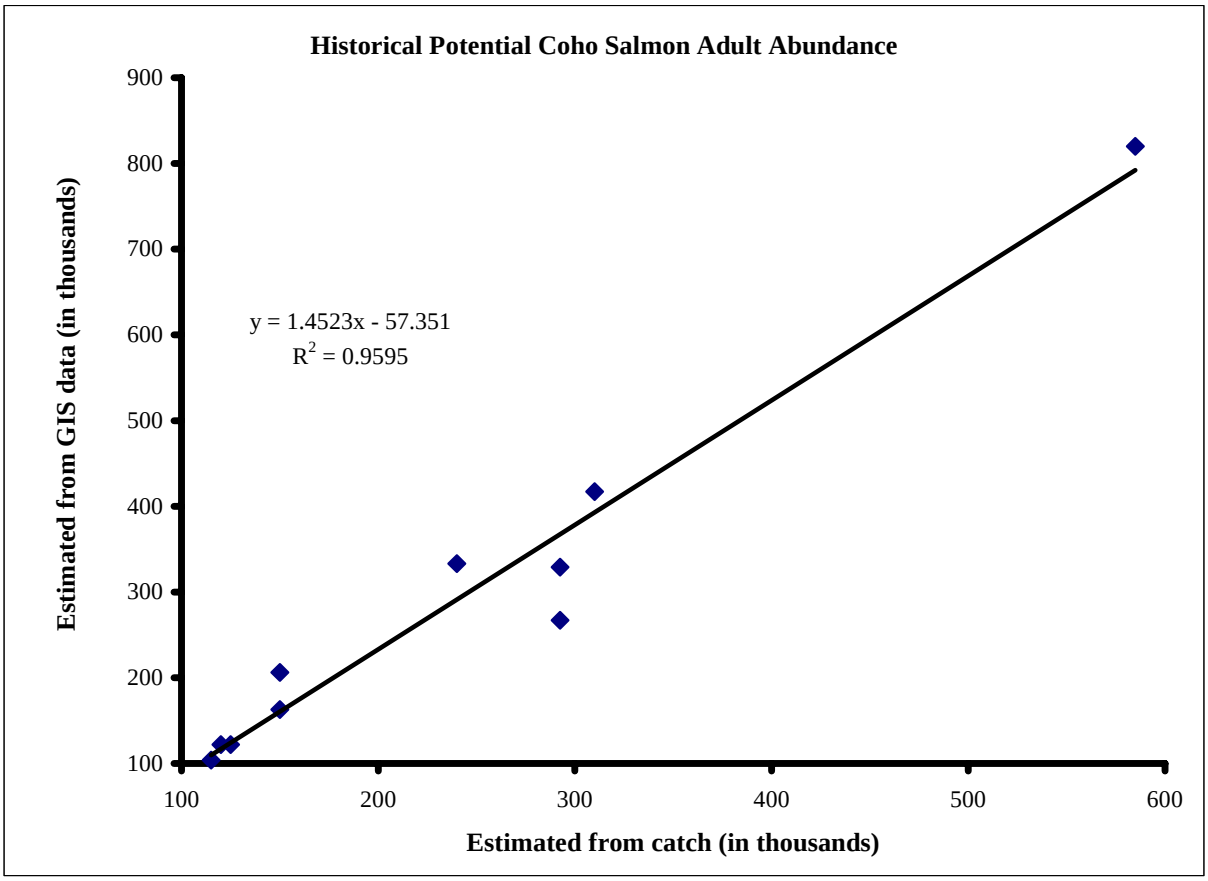

Figure III-1 The relationship between historical potential coho salmon adult abundance estimated by historical catch records and adult abundance calculated from GIS data (data from Table III-1).

Table III-2. Potential historical smolt and adult abundance for 67 putative populations of coho salmon in the Oregon Coast Coho Salmon ESU (based on data from Burnett 2003, NMFS 1983).

Population	Potential smolts	Adults @ 10% marine survival	Population	Potential smolts	Adults @ 10% marine survival
Necanicum R.	685,000	69,000	Moore Cr.	1,000	100
Indian Cr.	100	10	Theil Cr.	20,000	2,000
Canyon Cr.	400	40	Beaver Cr.	265,000	27,000
Ecola Cr.	72,000	7,000	Alsea R.	1,628,000	163,000
Red Rock Cr.	100	10	Little Cr.	1,000	100
Austin Cr.	300	30	Big Cr.	34,000	3,000
Asbury Cr.	1,000	100	Vingie Cr.	3,000	300
Arch Cape Cr.	3,000	300	Yachats R.	110,000	11,000
Short Sand Cr.	4,000	400	Gwynn Cr.	1,000	100
Nehalem R.	3,330,000	333,000	Cummins Cr	10,000	1,000
Spring Cr.	5,000	500	Bob Cr.	6,000	600
Watseco Cr.	5,000	500	Tenmile Cr.	28,000	3,000
Tillamook Bay	3,288,000	329,000	Squaw Cr.	100	10
Netarts Bay	15,000	1,500	Rock Cr.	6,000	600
Rover Cr.	2,000	200	Big Cr.	18,000	2,000
Sand Cr.	123,000	12,000	China Cr.	5,000	500
Nestucca R.	1,037,000	104,000	Blowout Cr.	1,000	100
Neskowin Cr.	49,000	5,000	Cape Cr.	15,000	2,000
Salmon R.	168,000	17,000	Berry Cr.	54,000	5,000
Devils Lake	85,500	9,000	Sutton Cr.	84,000	8,000
Siletz R.	1,217,000	122,000	Siuslaw R.	2,674,000	267,000
Schoolhouse Cr.	2,000	200	Siltcoos R.	771,000	77,000
Fogarty Cr.	18,000	2,000	Tahkenitch Cr.	228,000	23,000
Depoe Bay Cr.	7,000	700	Threemile Cr.	22,000	2,000
Rocky Cr.	10,000	1,000	Umpqua	8,199,000	820,000
Johnson Cr.	2,000	200	Lower Umpqua	1,293,000	129,000
Spencer Cr.	11,000	1,000	Upper Umpqua	6,906,000	691,000
Wade Cr.	5,000	500	Tenmile Cr.	525,000	53,000
Coal Cr.	4,000	400	Coos Bay	2,058,000	206,000
Moolack Cr.	4,000	400	Coquille R.	4,169,000	417,000
Big Cr.	26,000	3,000	Johnson Cr.	8,000	800
Yaquina R.	1,217,000	122,000	Twomile Cr.	134,000	13,000
Henderson Cr.	1,000	100	Floras Cr.	396,000	40,000
Grant Cr.	400	40	Sixes R.	372,000	37,000

Figure III-2. Intrinsic Potential of rivers and streams on the North Coast segment of the Oregon Coast Coho Salmon ESU.

Figure III-3. Intrinsic Potential of rivers and streams on the Mid-Coast segment of the Oregon Coast Coho Salmon ESU.

Figure III-4. Intrinsic Potential of rivers and streams on the Umpqua River Basin segment of the Oregon Coast Coho Salmon ESU.

Figure III-5. Intrinsic Potential of rivers and streams on the Mid-South Coast segment of the Oregon Coast Coho Salmon ESU.

APPENDIX IV: COMMENTS AND RESPONSES TO CO-MANAGERS' DRAFT

17 May 2004

Dr. Peter Lawson
ONCC-TRT Co-chair
NOAA Northwest Fisheries Science Center
2032 SE OSU Drive
Newport , OR 97365

Dear Pete:

Thank you for the opportunity to review "Identification of Historical populations of coho salmon...in the Oregon Coast Evolutionary Significant Unit". This is a well-researched document that should be useful for your recovery planning.

In general I found the report to be scholarly, well-grounded theoretically, and clearly written. I offer the following comments constructively; I suspect that they are things that have already been considered by the TRT.

1 1. One of my main problems in thinking about the ESA listing or delisting process is with the ESU concept. Theoretically it can make sense, but in practice it is very difficult to define precisely. This confounds things then when it comes to classification of populations into your three categories. For example, if a population is "Functionally Independent", then why is it not an independent ESU since it would be a "distinct population segment"?

I appreciate that you do not rely just on allozyme or DNA analyses. With these, unfortunately, we can only look at such a small, perhaps uninformative, part of the genome.

2 2. The assumptions in the report appear reasonable. It would be useful to include some justification for some. For example, why is using 100 year's persistence as a criterion (page 10) appropriate. Would it change things if the criterion were 150 of 200 years? Likely not.

3 Similarly, how precise is the break-point on figures 20 and 21 [new figure numbers 19 and 20] allowing separation of persistent from non-persistent populations. Are the data in these figures really best described by more than one model. In other words, do populations in "miles of high quality habitat" play by dissimilar ecological rules than those in systems with few mile of good habitat? Hence, if so, the data should not be thought of as continuous. Perhaps there two models that could best describe the data and their intersections best identify the breakpoint.

4 It would also be good if justification for using 95% proportion native return rate could be provided. Would any classification change if 90% or 99% were used?

5 I think that the important thing would be to use values for criteria that are conservative; i.e., sufficiently large so that any conclusion would not result in an error relative to fish protection.

6 Given that the conclusions are based on multiple assumptions, has any analysis been done about the potential for compounding errors? In other words, if each assumption had only a small probability of being wrong and if several of these were indeed wrong, then the confidence in resultant conclusions could be quite low since the probability of being wrong for each would be multiplicative in total.

7 3. I agree with the decision not to use size as a criterion for smolts. One question would be if the timing of smolt migrants are based on in-river migrant traps, how far upstream are those traps and are these fish really headed straight out to sea from the lower river or do they "hang out", perhaps in the estuary.

8 4. The figures of spawning timing are not intuitive. Are these the means of spawn timing of estimates over time? Is there some variation associated with these data?

Again, I appreciate the chance to look at this document. I suspect that the synthesis presented will be useful by agencies far beyond federal listing issues.

Cheers,

Carl B. Schreck, Leader

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April 26, 2004

Ms. Heather A. Stout NOAA-Fisheries
Northwest Fisheries Science Center \
2032 SE OSU Drive
Newport, OR 97365

RE: Identification of Historical Populations of Coho Salmon (*Oncorhynchus kisutch)* in the Oregon Coast Evolutionarily Significant Unit

Dear Heather:

Thank you for the opportunity to comment on the above referenced document. I would like to compliment the Technical Review Team (TRT) on producing a clear and readable product. I found the description and analysis used to be transparent and understandable. I found the population characterization (dependent, potentially independent, functionally independent) to be a very useful framework for understanding the populations that comprise the ESU. The analysis that supports the distinctions was very clearly described and not hidden in modeling jargon that I have seen from other TR T products.

The population characterization creates an excellent framework for the development of management strategies for recovery .As the TR T develops recovery goals and strategies it appears that hatchery stocks can be considered as dependent populations. The only substantive comment I have is that Table 2 could be reconstructed as below:

Table 2. Locations and distances of river mouths for basins along the Oregon Coast

9

Basin Name	**Latitude**	**Longitude**	**Population Type**	**Distance to Nearest Functionally Independent Population** *(For Dependent and Potentially Independent Populations)*

Thank you very much for the opportunity to comment.

Sincerely,

Kenneth F. Bierly
Deputy Director

Subject: Re: TRT Report
Date: Mon, 17 May 2004 14:40:29 -0700
From: peter lawson <peter.w.lawson@noaa.gov>
To: William Pearcy <wpearcy@coas.oregonstate.edu>
CC: Heather Stout <Heather.Stout@noaa.gov>,
Thomas Wainwright <Thomas.Wainwright@noaa.gov>

Hi Pete,

Thanks for sending the hard cc of the report on Identification of historical populations of Oregon coho.

It is well written and I thought an excellent analysis of existing information to assess historical populations and classify stocks into the three categories of independence. Good work by a good team!

I had a few minor comments:

I had the most difficult time, as a ocean type, with the section on Population Classification Results. Specifically the relationship between historical population sizes and proportion of native returns. I think the basis for historical populations, with all its assumptions, is fine, but you assume that the proportion of returns is directly related to population size, which is related to degree of isolation (are we getting circular here?).

Has this been tested?

10 What is the empirical evidence that straying is less for large populations?

Uremovich (1977) found higher straying among broods of chinook poorest overall returns, suggesting the ocean conditions that were related to homestream fidelity. And for coho, Shapovalov and Taft (1954) noted a positive relationship between the amount of straying and the number of outmigrants; they hypothesized that "conditions existing at the time of migration to the ocean determine the amount of straying that will take place one or two years seasons later." This makes intuitive sense if overseeding and density dependent survival occurs for large populations. In any event, I doubt that the relationship between straying and population size is linear!

I think that the team may underestimate the importance of small populations to the long-term adaptablility and evolution of OCN coho. You state that small populations may produce poor-qualilty offspring through loss of genetic diversity, depensation, and inbreeding, hence they have higher probabilities of extinction than large populations. But you also say that small populations may provide reserviors for adaptive diversity. This is important.

11 My recollections of metapopulation theory, which the TRT buys for coho, harkens back to papers by Sewall Wright in the 40s. He thought that partial isolation of local populaitons is favorable for new alleles to develop from inbreeding and drift, favoring rapid evolution in a changing environment, Lcal adaptations are hence the stuff that allow for adaptive radiation and

provide resilence against events such as future climatic changes. So some of your dependent or potentially depend populations may be crucial to long-term viability. As the IMST has said in the past, from the management perspective, don't write off the importance of small coho populations.

12 On Marine Distribution: Do coho encounter a "warm California Current" when they enter the ocean in the spring? The California Current is that major sluggish offshore current. It is warm relative to subarctic waters and the cool upwelled waters along the coast, and it is the latter that the fish enter. Fig 8 gives the impression that coho enter this broad current up to 100 miles offshore! In reality, few juveniles are caught beyond the shelf break and coastal water influences by upwelling during the spring-fall periods. You could add that during periods of a strong coast jet, some fish entering the ocean in May or June may be advected to the south before they swim to the north.

13 Also, as I have said several times (see my little book), (Is it in the OSU bookstore?) it is curious that many of the juvenile coho that Hartt and Dell tagged in the Gulf of Alaska in the 50s and early 60s were recaptured or returned as adults to Oregon and Washington before there were large scale hatchery releases, suggesting the wild fish migrated much farther to the north than we suspect they do today.

Bill

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Comments on:

IDENTIFICATION OF HISTORICAL POPULATIONS OF COHO SALMON *(Oncorhynchus kisutch*) IN THE OREGON COAST EVOLUTIONARY SIGNIFICANT UNIT

(Prepared by Dr. Wayne Hoffman, Midcoast Watershed Council, transmitted through Oregon Watershed Enhancement Board)

Clearly historical data are insufficient to give a clear picture of Oregon Coastal Coho productivity and population structure before the recent major habitat modifications, increased harvests, and hatchery programs. Therefore, taking a modeling approach to construct a story about historical coho populations is a reasonable endeavor, provided the story is not given more credibility than deserved. The modeling approach used is a reasonable one, but necessarily is based on some assumptions that are reasonable but not strongly substantiated by experiment or other data. The report does an admirable job of making these assumptions explicit. I have several suggestions of ways to analyze the data that are available and thus refine the story, but am more concerned that the initial assumptions may be wrong in ways that will tend to push the whole recovery planning effort in inappropriate directions.

If this report were merely to be used as an historical basis for numerical recovery targets, the approach would be fine. I am greatly concerned, however, that it will be used as the basis for policy decisions in recovery planning, that are highly dependent on the assumptions used, and that this document will come to be seen as justifying use of those assumptions where they really matter.

The central questions in Oregon Coastal Coho recovery planning have to do with population structure and the extent, depth, and importance of local adaptation. The authors of this document begin by assuming a position on these questions, and proceeding within constraints imposed by that initial position. Specifically, the authors assume that stream mouths are the most important focus in discussions of straying, that straying is governed by an exponentially declining distance function, and that persistence of local populations is a positive function of amount and quality of freshwater habitat. Again, these assumptions are reasonable, but are essentially unproven at the scales used here.

The consequence of the emphasis on stream mouths in straying analyses is to divert attention from the possibilities of intra-basin population subdivision. By assuming that they do not need to look at patterns of fidelity and wandering within basins, the authors have an easier time justifying neglect of local adaptation within basins. Considerable research on other salmonids demonstrates capabilities for rapid population subdivision and local adaptation in the face of considerable genetic interchange. The likely outcomes of such adaptation include higher local carrying capacities and greater production overall, so this issue is relevant to the goals of returning Coho populations to economically important levels. Overall, the analyses of possible intra-basin subdivision appear superficial and driven by a desire to minimize complexity. A few years ago I assembled a list of rather anecdotal examples of morphological and life history differences among Oregon Coastal Coho that lead me to suspect a greater degree of local adaptation within as well as between stream systems than is admitted here.

14 The assumption of an exponentially declining distance function for population exchange is not only not proven, but a fair body of data are available contradicting it. Two examples: in fall 2001 substantial numbers of fin-clipped coho were found in coastal rivers on spawning surveys and at traps, including the one at Siletz Falls. Coded wire tags were found in some of these fish, and indicated they were from Columbia River hatcheries. I have not seen a detailed analysis, but my impression of the raw data was not of a decline-with-distance function. Hatchery Steelhead seem to have a higher stray rate than Coho, and streams without hatchery programs often have 15% or more fin-clipped fish. My impression, from discussions with people catching these fish, is that very often clip patterns indicate these are not fish from the closest streams with hatchery programs. For example, this winter (2004), hatchery Steelhead in the Yachats River were apparently from the south coast, not from the Alsea or Siuslaw.

15 The second assumption (exponentially declining distance function for population exchange among ocean entry points) has implications about the still poorly known ocean navigation and homing systems in salmon. If this assumption is correct and applies at the scale indicated here, then salmon presumably are responding to global cues (magnetic field, elevation of the sun, etc.) rather than primarily to chemosensory clues. A century of hatchery acclimation practice assumes the opposite, and has good enough results to justify continuation. Further, the assumption implies that navigation system failures are essentially de-tuning rather than complete failure. At some level this is probably true (the strays we see have found their way back to the west coast), but I am not confident it applies well enough to validate an exponentially declining distance function.

16 I would like to suggest some alternatives that have at least some support, and that I think need consideration. First, I suggest revisiting the hypothesis that choice of freshwater entry point is influenced by chemosensory clues. This would mean that strays tend to enter streams that "taste" somewhat like their native streams. Obviously, we know little about how freshwater entering the ocean tastes to salmon, but a little speculation may be worthwhile. I believe most of this is ground that has been gone over in the salmon literature, at least speculatively. Underlying geology should provide chemosensory clues. In the context of the ESU, this could mean that streams in basalt areas give different clues than streams in exclusively sedimentary geology, and the Umpqua and Coquille should be really different from the rest. Lakes systems likely have substantially different water chemistry than lake-less streams. Outflow from streams with extensive estuaries undoubtedly has a different chemical signature than outflow from streams without estuaries. And, there likely are chemical signals that are correlated to stream size, at least categorically. Small streams as a group probably lack certain chemical constituents that result from extended weathering or decompositional processes in larger systems. If this chemosensory alternative applies, then straying might tend to be biased toward stream mouths more similar to the source system in whatever chemical clues are most important to the fish. Lake system fish might tend to stray into other lake systems, and fish from small streams into other small streams.

17 Second, incidents such as the widespread straying of Columbia Coho in 2001 suggest a more catastrophic failure of the navigation system. These fish may have lacked the ability to find their source river, and so entered whatever stream was convenient when they were physiologically ready. Or they may have sorted somewhat according to secondary clues (e.g., preferentially picked larger rivers over small creeks).

18 Third (and this suggestion leads to some refinements that can be done to the analysis) the attractiveness of stream mouths to salmon likely varies temporally. The report documents this for some extreme cases (p. 26 for Devil's Lake, Sixes River, New River), but is likely more widespread. In particular, access to many smaller streams is difficult until after the first substantial fall rains, while the larger rivers may be accessible much earlier. I suggest that an analysis can be done to test the effects of this on model results of population dependence by overlaying a function of the overlap in spawn timing graphs (as in Fig. 7) on the exponentially declining distance function. I suspect that this would, for example, move the New River/Floras system from Potentially Independent to Functionally Independent on the basis that the bulk of the Coquille River fish would already be inland before the New River mouth opened. Actually, using spawn-timing graphs would be conservative because in general the fish in large systems spend more time in fresh water before spawning than fish in smaller streams, so their "decision time" leaving the ocean is even earlier.

The third assumption, that persistence of local populations is a positive function of amount and quality of freshwater habitat has to be true at some level, but I would challenge the levels set in this document. I consider the level (capacity to produce 150,000 smolts - vertical line on Figure 20 [new figure number 21]) unreasonably high. Note the text on p. 56 explaining this choice:

"The stochastic life-cycle model (Nickelson and Lawson 1998) produces quantitative extinction probabilities. However these probabilities are sensitive to many of the model parameters including patterns of freshwater production, density dependence, straying, and marine survival. As a consequence we were unwilling to use the absolute extinction probabilities from the model to define the vertical line criterion. We were, however, more comfortable with the qualitative model result; as habitat quantity decreases, extinction probability increases exponentially. We chose as our criterion for persistence, the point where the probability of extinction started to increase rapidly (Fig. 21[new figure number 20])."

19 I understand the authors' reluctance to use the model extinction probabilities. However, the break (inflection) points in the graphs are subject to the same sources of error as the probabilities, and using them instead does not buy any robustness. In my opinion, the model has several properties that makes it unsuitable for this kind of use, either with the probabilities or with the inflection points. First, it undervalues density-dependence. In reasonably good habitat juvenile Coho grow larger before smolting when at low densities, and much hatchery and other research demonstrates that larger smolts have higher ocean survival rates. Second, the freshwater life cycle stage limiting Coho smolt production differs from stream to stream, making total miles of habitat a poor metric of productivity. For example, the Devils Lake system is considered by the model too small to be potentially independent, but the lake itself would have been such good rearing habitat before introduction of bass, etc. that smolt production should have been very high. Third, the model results presented do not consider the buffering effects of

inter-cohort genetic exchange on the effects of poor years on small streams. Very small returns in years of poor ocean survival have a potential for genetic impoverishment in small populations, but inter-cohort exchange, through jacks and four-year-olds can buffer this effect. Devils Lake and other lake systems have appreciable numbers of fish remaining in fresh water an extra year before smolting. This increases probability of persistence in two ways. These older, extra-large smolts should have much higher ocean survival, and their longer life contributes to inter-cohort exchange.

20 What using the inflection points does, is push the line to the right, qualifying fewer systems as potentially or functionally independent. Actually, the authors have pushed the line even farther to the right than warranted by the inflection points. On Figure 21 [new figure number 20], the marked break points are actually around 15 miles of habitat, rather than the 20 selected for use in this analysis (In a previous version of this analysis Nickelson used 14 miles).

21 The report as a whole builds an illusion of a population structure in which a few large systems with undivided large populations are key to survival of the ESU, and in which smaller systems lack the capacity to maintain independent populations long enough to evolve significant local adaptations. The policy consequences of this illusion are enormous. This approach will lead to a recovery strategy in which population status in smaller systems is considered not very relevant to overall recovery, or to regulation of ocean harvest. If these assumptions are wrong, the likely consequence is a “recovery” strategy leading to reduction in genetic diversity and less local adaptation, leading to chronically reduced productivity and complete loss of some smaller streams as Coho producers.

Oregon

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June 2, 2004

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Dear Pete,

The Oregon Department of Fish and Wildlife (ODFW) has reviewed the April 16, 2004 Co-Manager's Draft of "Identification of Historical Populations of Coho Salmon in the Oregon Coast Evolutionarily Significant Unit" and provides the following comments. In general, ODFW approves of the process taken to identify the historical populations and commends the Oregon Northern California Coast Technical Recovery Team (ONCC TRT) for bringing significant new knowledge to the coho recovery planning process. The State of Oregon has already begun using this population structure in the State's assessment of the Oregon Plan for Salmon and Watersheds as it relates to coastal coho salmon.

The Oregon Workgroup of the ONCC TRT has done a laudable job of attempting to identify and classify historical populations of coho salmon along the Oregon coast. The draft document, however, does not describe at any length how the results of these efforts will be used in the recovery planning process. Thus providing the necessary context for the review. ODFW is well aware of the limited information available to assist in this exercise and the need to make reasoned assumptions on historical population structure and interactions. However, because assumptions must be made and it is not clear how these populations will be used, ODFW recommends that the ONCC TRT be cautious in making those assumptions. The ONCC TRT should describe how they envision this information being used in future aspects of this process and seek to ensure that any errors in assumptions do not significantly increase the risk to the recovery and sustainability of the ESU and also do not lead to unreasonable recovery expectations. Areas where ODFW believes the ONCC TRT should review their assumptions and use caution are identified below.

Identification of Populations

22 The identification of historical populations that comprised the Oregon Coast Coho Salmon ESU is one of the more important tasks that the ONCC TRT was charged with undertaking. Populations identified in the document under review will likely be the basis for decisions on ESU viability and recovery. There is the potential within the conceptual model used to identify populations, for some of the historical populations to be overlooked or misidentified. Because a level of certainty cannot be placed on the methods used in identifying populations, caution needs to be taken in defining potential populations. Caution should also be taken in applying the results of any identification method chosen to the definition of a viable and persistent population, and ultimately, a viable and persistent ESU. ODFW recommends that the ONCC TRT consider strategies in upcoming viability analyses that ensure that the potential misidentification of populations will not pose a significant risk to the recovery of the Oregon Coast coho salmon ESU and minimize the potential for unforeseen and unintended consequences.

Classification of Dependent Populations

23 ODFW agrees that it is likely that some populations in smaller basins relied upon immigration from other populations to persist. We believe caution needs to be taken in classifying those populations that were likely to have been dependent populations. Since the desired future status of the ESU will likely be based on historical population dynamics, it is important to categorize each population as accurately as possible. ODFW recommends that the ONCC-TRT describe how they intend to use these classifications and what measures will be taken to re-evaluate their accuracy and importance as new information and analyses become available.

Historical Abundance Estimate

24 ODFW is concerned with the estimated historical abundance of 3.3 million adults described in Appendix III in the Co-Manager's Draft. This estimate appears to represent a best possible modeled historical abundance and is misleading. Overestimating historical abundance for the recovery planning process underway could create unrealistic expectations of what viable and sustainable population levels should be. An overestimate will also suggest that the habitat can be more productive than it may actually be. The estimate is based on maximum production from each population at the same time – an unrealistic situation. ODFW suggests developing a range of abundances based on the approach that not all habitats are productive at any given time. Creating upper and lower limits that capture the uncertainties in the data would be more appropriate. The ONCC-TRT should also describe how this estimate would be used in their future work.

25 ODFW also questions a suggestion made in the Discussion section of Appendix III. In this section the authors suggest that the 30% difference between the intrinsic potential estimate of abundance and the estimate made from cannery records could be evidence that significant habitat destruction occurred at the turn of the century. To use a comparison of two different abundance estimation methods to infer significant habitat loss is just one plausible explanation. There are many possible explanations for the difference in the two estimates; not the least of which is that

one or both of the estimates could be in error. ODFW suggests the ONCC TRT be cautious in speculating about factors for decline before the TRT has completed their analyses into the causes of decline. The success of the recovery planning process depends on the scientific products being accepted by the public. It is important for the ONCC TRT to produce reports for the recovery planning process that are scientifically defensible. ODFW suggests the above-mentioned portion of the Discussion section be expanded to include other possible explanations for the results described.

26 ODFW would like to thank the ONCC TRT for allowing us an opportunity to review and comment on the Co-Manager's Draft. The document is well written and should allow even non-technical readers to understand the concepts and decision processes described in it. The methods used to identify and classify historic populations are well reasoned. The inexact nature of the methods, however, needs to be clearly identified. ODFW suggests it may be useful to describe in this document how the decisions made in the document will be used in subsequent reports and what precautions are being taken to reduce any risk to the viability of the ESU that could result from inadvertently misidentifying populations and their interactions. It will be important to continually remind reviewers how each product of the TRT fits into the overall work of the group, as we currently lack the ability to review the sum of the parts. The ONCC-TRT should also incorporate a feedback loop that can be used throughout their work to look back at previous assumptions and decisions and assess if they are still valid and do not impose unnecessary risk. ODFW staff would be more than happy to meet with the ONCC TRT to discuss our comments if clarification is needed.

Sincerely,

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Responses to Comments

1. The discussion on page 4, paragraph 3 presents the concept that ESUs (also known as Distinct Population Segments, which is the way the ESA is written, but the terminology is confusing) are defined primarily by large genetic divergences operating on time scales of tens to hundreds of generations. Populations are demographic units (measured by survival and reproductive success) where individuals interact at time scales of a few days to a few generations. We presume that the Functionally Independent populations are more similar to each other than to populations in a different ESU.

2. The use of 100 years persistence is seen frequently in the conservation literature as a benchmark. Even though we don't have methods that give differentiation for fine scale differences, for example, between 100 and 90 years, it is useful as a rhetorical tool for visualizing the time scale we are talking about. We are also attempting as much as possible, to be consistent with the McElhaney (2000) Viable Salmonid Population Document.

3. The model used to define the breakpoint includes two sets of ecological rules. At higher densities, a density-dependent production rule dominates. At lower densities, a depensation rule is more important. The breakpoint in Figure 20 (previously Figure 21) shows where the transition between the two rules occurs.

   Two recent examples of the effects of small population size in small habitats are Cummins Creek, a direct ocean tributary, and Cascade Creek, an Alsea River tributary. In Cummins Creek, the 1995 brood which produced 730 smolts evidently returned no adult spawners in 1998, as no juveniles were found in summer 1999 and there were only 7 smolts estimated in 2000 (likely leftovers from the 1994 brood). In Cascade Creek, the 1998 brood consisted of 1 male, 7 females, and 7 jacks. This brood produced only 13 smolts.

4. See the discussion on page 54, paragraph 2. Changing the native return rate to 90% or 99% simply changes the position of points on the y-axis without changing the relative position of the populations.

5. We did perform sensitivity analysis on these values and found the results that were discussed in response #4.

6. We performed a sensitivity analyses by scaling migration probabilities to the degree of overlap in migration timing and found that the results were not sensitive to that change. We also did a + or – 50% on the arithmetic scale to see if that affected the vertical (Independence) line. Only a few populations were affected. We have revised Figure 19 (previously Figure 20). to include the +/- 50% lines. As we continue to develop the viability criteria, we will continue to reexamine the location of the "independence line."

   The highest conservation risk occurs if there are more populations, and more independent populations, than we define. In this case we would underestimate the number of

populations needed for a viable ESU. In developing our viability criteria we recognize this risk and will be stipulating that in each historical population as defined in this document there be a distribution of spawners throughout the population. This recognizes that the populations we have defined are large enough to have considerable substructure, and this substructure is important to population viability.

There is also the risk of defining too many populations. In this case we could impose an unnecessary burden on regulatory agencies, resource use, and development. In our view the Independent populations we have defined are about the largest divisions on the Oregon Coast that are consistent with a conservation goal. Also, remember that we are defining historical population, not the present situation.

7. We agree with your comment: the smolt traps are in substantially different locations within the basins. There may be a substantial migration from trap to estuary during which growth can occur. Also, these fish may be hanging out in the estuary to gain weight and size before they make the transition to the ocean.

8. The figures of spawn timing are from the year 2001, which was chosen as a somewhat "normal" year with no substantial drought , El Niño, or excessively low adult abundance.

9. See Table 8, a new table to present this information in a more readable format.

10. We have revised the Homing fidelity section, on page 36.

11. Other TRTs have practically ignored smaller populations. Our scheme, which defines everything with an independent ocean entry point as a population, was developed specifically because we felt these small populations were important to the functioning of the ESU. We will revisit the role of small populations in our viability criteria and analysis. This may result in changes to our historical population discussion as well.

12. We have deleted Figure 8.

13. We have revised the Marine distribution section, based upon your comments. See page 33.

14. We draw a distinction in the report between migration (movement between basins) and straying (movement within a basin). We have reviewed the CWT data for evidence of migration patterns of Columbia River and coastal hatchery fish. Migration of hatchery fish between basins tends to be strongly centered around the basin of origin (see text in Homing fidelity section, page 36).

15. We did not postulate whether global or chemosensory cues were responsible for the migration patterns we modeled.

16. These ideas about the nature of the "taste" of basins are very interesting and worthy of study, but as far as we are aware, are untested.

17. We do not consider straying or migration as necessarily a "failure of the navigation system" but, rather an adaptation to variable environmental conditions.

18. We used spawn timing as an additional isolating mechanism in several of our isolation analyses. The results were not greatly influenced. In particular, New River/Floras did not change status.

19. Perhaps we were not clear on how the models were used. The Nickelson – Lawson model was used to estimate the 15 miles of habitat as a cutoff for 100-year independence. At low population levels, egg-to-parr survival is at a maximum of 44%. The curve is driven by depensatory factors related to the difficulty of finding mates at low densities. The data used to determine independence came from an analysis of the Intrinsic Potential of each system to produce coho salmon. Lake areas were incorporated in this calculation. This was subsequently input into the Relative Independence Model described in Bjorkstedt 2004.

    Although smolts at low densities sometimes show faster growth rates and higher marine survival rates, and these are certainly of biological interest, the effects are probably not important at the resolution of modeling we are doing here.

20. The value used in the analysis was 15 miles. We have corrected the text.

21. We appreciate that the reviewer is concerned that we are undervaluing small populations. In fact, we consider them to be important to the health of the ESU and very probably in genetic divergence of some populations, but they play a different role from the large populations. We are at this time building the theoretical framework for including both large and small systems in our viability definition. Our assessment of historical coho salmon habitats may be revised as we proceed with our viability analysis.

22. This document does not attempt to define current populations, or what future populations should look like. It is our intention that recovery will specify restoration of processes that will enable fish to establish populations in whatever configuration suits them – not necessarily what has existed in the past. This document is an attempt to define how historical populations worked, but we are not locked into the populations that are defined here. Current and future populations will probably look different and be dealt with during the viability analysis.

23. We recognize that populations are not necessarily monolithic units and they they may have internal structure, even though we may not know what that structure is (see response 6). Therefore there may be the need for spawning aggregations within populations. The future status of the ESU will not necessarily be based on historical population dynamics. The historical populations defined here are being used only as a template of how Oregon Coast coho salmon populations operated before their structure was so significantly affected by European fisheries and land use practices. This definition and classification of historical populations is not an implementation plan, it is only the first step to define how we believe historical populations worked, so we can utilize that in our viability analysis. Again, it is the intent of recovery to restore the ability of populations to

function properly. In the viability report we will reevaluate the dependent/independent classifications and current population genetics should be available for use in the next report.

24. Production estimates are higher than those observed in recent times due to the inclusion of habitat that has not been in production for 100 years. Much of this lowland habitat was diked, filled, or ditched for agricultural purposes early in the process of European settlement, but was an integral part of historical Oregon Coast coho salmon population dynamics. See Appendix III for an expanded discussion of this analysis.

25. Historical abundance of coho salmon was estimated for the purpose of modeling the effects of relative abundance on population independence. See Appendix III for an expanded discussion of this analysis.

26. It is our intention to revisit our conclusions with every new analysis and not be constrained by our original definition of historical populations, or even our original definition of viability. This is intended to be a feedback loop where if our original definitions or classifications don't make sense in the context of the next steps, we will change them. We look forward to working with ODFW staff throughout the TRT process to produce useful, scientifically defensible reports that contribute to our understanding of recovery and what that means for Oregon Coast coho salmon. See also response #6.

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