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Article · January 1998

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Southwest Fisheries Science Center
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NOAA Technical Memorandum NMFS-NWFSC-35

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James M. Myers, Robert G. Kope, Gregory J. Bryant[1], David Teel, Lisa J. Lierheimer, Thomas C. Wainwright[2], W. Stewart Grant, F. William Waknitz, Kathleen Neely, Steven T. Lindley[3], and Robin S. Waples

National Marine Fisheries Service
Northwest Fisheries Science Center
Coastal Zone and Estuarine Studies Division
2725 Montlake Blvd. E.
Seattle WA 98112-2097

[1]**National Marine Fisheries Service**
Southwest Region
Protected Species Management Division
501 W. Ocean Blvd., Suite 4200, Long Beach, CA 90802-4213

[2]**National Marine Fisheries Service**
Mark O. Hatfield Marine Science Center
2030 S. Marine Service Dr., Newport, OR 97365-5296

[3]**National Marine Fisheries Service**
Southwest Fisheries Science Center
3150 Paradise Dr., Tiburon, CA 94930-1299

February 1998

U.S. DEPARTMENT OF COMMERCE
William Daley, Secretary

National Oceanic and Atmospheric Administration
D. James Baker, Administrator

NOAA-NMFS-NWFSC TM-35: Chinook Status Review

INTRODUCTION

On 14 March 1994, the National Marine Fisheries Service (NMFS) was petitioned by the Professional Resources Organization-Salmon (PRO-Salmon) to list spring-run populations of chinook salmon (*Oncorhynchus tshawytscha*) in the North Fork and South Fork Nooksack River, the Dungeness River[1], and the White River (Fig. 1) as threatened or endangered species under the Endangered Species Act (ESA) either singly, or in some combination (PRO-Salmon 1994). At about the same time, NMFS also received petitions to list additional populations of other Pacific salmon species in the Puget Sound area. In response to these petitions and the more general concerns for the status of Pacific salmon throughout the region, NMFS announced on 12 September 1994 that it would initiate ESA status reviews for all species of anadromous salmonids in Washington, Oregon, California, and Idaho (NMFS 1994d). This proactive approach was intended to facilitate more timely, consistent, and comprehensive evaluations of the ESA status of Pacific salmonids than would be possible through a long series of reviews of individual populations. Subsequent to this announcement, NMFS was petitioned on 1 February 1995 by the Oregon Natural Resources Council (ONRC) and Siskiyou Project Staff Ecologist Dr. Richard K. Nawa to list 197 stocks of chinook salmon either separately or in some combination.

This document reports results of the comprehensive ESA status review of chinook salmon from Washington, Oregon, California, and Idaho. To provide a context for evaluating these populations of chinook salmon, biological and ecological information for chinook salmon in British Columbia, Alaska, and Asia were also considered. This review thus encompasses, but is not restricted to, the populations identified in the PRO-Salmon and ONRC-Nawa petitions.

Because the ESA stipulates that listing determinations should be made on the basis of the best scientific information available, NMFS formed a team of scientists with diverse backgrounds in salmon biology to conduct this review. This Biological Review Team (BRT) for chinook salmon included: Peggy Busby, Dr. Stewart Grant, Dr. Robert Iwamoto, Dr. Robert Kope, Dr. Conrad Mahnken, Gene Matthews, Dr. James Myers, Philip Roni, Dr. Michael Schiewe, David Teel, Dr. Thomas Wainwright, F. William Waknitz, Dr. Robin Waples, and Dr. John Williams of NMFS Northwest Fisheries Science Center; Gregory Bryant and Craig Wingert of NMFS Southwest Region; Dr. Steve Lindley and Dr. Peter Adams from NMFS Southwest Region (Tiburon Laboratory); Alex Wertheimer of NMFS Alaska Fisheries Science Center (Auke Bay Laboratory); and Dr. Reg Reisenbichler from the USGS Biological Resource Division. NMFS received scientific and technical information from Pacific Salmon Biological and Technical Committees (PSBTCs) convened in Washington, Oregon, and California. Meetings of the PSBTC were not held in Idaho because all chinook salmon populations in Idaho are already listed under the ESA. The BRT discussed and evaluated scientific information gathered at the PSBTC meetings, and also reviewed information submitted to the ESA administrative record for chinook salmon, including specific comments by co-managing agencies on a draft version of this document (CDFG 1997b, HVTC 1997, IDFG 1997, LIBC 1997, NWIFC 1997a, ODFW 1997a, and WDFW 1997a, YTFP 1997a).

In determining whether a listing under the ESA is warranted, two key questions must be addressed:

1) Is the entity in question a "species" as defined by the ESA?

2) If so, is the "species" threatened or endangered?

These two questions are addressed in separate sections of this report. If it is determined that a listing (s) is warranted, then NMFS is required by law (1973 ESA Sec. 4(a)(1)) to identify one or more of the following factors responsible for the species' threatened or endangered status: 1) destruction or modification of habitat, 2) overutilization by humans, 3) disease or predation, 4) inadequacy of existing regulatory mechanisms, or 5) other natural or human factors. This status review does not formally address factors for decline; except insofar as they provide information about the degree of risk faced by the species in the future if current conditions continue. A separate document identifies factors for decline of chinook salmon from Washington, Oregon, California, and Idaho, and is presented subsequent to any proposed listing recommendation.

The "Species" Question

As amended in 1978, the ESA allows listing of "distinct population segments" of vertebrates as well as named species and subspecies. However, the ESA provides no specific guidance for determining what constitutes a distinct population, and the resulting ambiguity has led to the use of a variety of criteria in listing decisions over the past decade. To clarify the issue for Pacific salmon, NMFS published a policy document describing how the agency will apply the definition of "species" in the ESA to anadromous salmonid species, including sea-run cutthroat trout and steelhead (NMFS 1991). A more detailed discussion of this topic appeared in the NMFS "Definition of Species" paper (Waples 1991b). The NMFS policy stipulates that a salmon population (or group of populations) will be considered "distinct" for purposes of the ESA if it represents an evolutionarily significant unit (ESU) of the biological species. An ESU is defined as a population that 1) is substantially reproductively isolated from conspecific populations and 2) represents an important component of the evolutionary legacy of the species.

The term "evolutionary legacy" is used in the sense of "inheritance," that is, something received from the past and carried forward into the future. Specifically, the evolutionary legacy of a species is the genetic variability that is a product of past evolutionary events and that represents the reservoir upon which future evolutionary potential depends. Conservation of these genetic resources should help to ensure that the dynamic process of evolution will not be unduly constrained in the future.

The NMFS policy identifies a number of types of evidence that should be considered in the species determination. For each of the criteria, the NMFS policy advocates a holistic approach that considers all types of available information as well as their strengths and limitations. Isolation does not have to be absolute, but it must be strong enough to permit evolutionarily important differences to accrue in different population units. Important types of information to consider include natural rates of straying and recolonization, evaluations of the efficacy of natural barriers, and measurements of genetic differences between populations. Data from protein electrophoresis or deoxyribonucleic acid (DNA) analyses can be particularly useful for this criterion because they reflect levels of gene flow that have occurred over evolutionary time scales.

The key question with respect to the second ESU criterion is, if the population became extinct, would this represent a significant loss to the ecological/genetic diversity of the species? Again, a variety of types of information should be considered. Phenotypic and life-history traits such as size, fecundity, migration patterns, and age and time of spawning may reflect local adaptations of evolutionary importance, but interpretation of these traits is complicated by their sensitivity to environmental conditions. Data from protein electrophoresis or DNA analyses provide valuable insight into the process of genetic differentiation among populations but little direct information regarding the extent of adaptive genetic differences. Habitat differences suggest the possibility for local adaptations but do not prove that such adaptations exist.

Background of Chinook Salmon under the ESA

On 7 November 1985, NMFS received a petition from the American Fisheries Society (AFS) to list the winter-run chinook salmon in the Sacramento River as a threatened species under the federal ESA. NMFS initially announced its decision not to list this population as threatened or endangered on 27 February 1987 (NMFS 1987). Subsequently, the winter-run chinook salmon population experienced a further decline, and an emergency listing to list the population as threatened was made on 4 August 1989 (NMFS 1989); the listing was extended on 2 April 1990 (NMFS 1990a). A final rule to list the Sacramento River winter-run chinook salmon as threatened was made on 5 November 1990 (NMFS 1990b). The winter run continued to decline and was subsequently listed as endangered 4 January 1994 (NMFS 1994b).

On 7 June 1990, NMFS received a petition from Oregon Trout and five co-petitioners to list Snake River spring-run chinook salmon, Snake River summer-run chinook salmon, and Snake River fall-run chinook salmon under the ESA. A final rule was announced on 22 April 1992 (NMFS 1992), which determined that Snake River chinook salmon should be listed as threatened under the ESA. Furthermore, it was determined that the spring- and summer-run populations collectively constituted a separate ESU from the fall-run chinook salmon under the ESA. As a result of record low adult returns in 1994 and projected returns for 1995, an emergency interim rule was announced 18 August 1994 to reclassify the Snake River spring/summer run and Snake River fall run as endangered (NMFS 1994c); however, both Snake River chinook salmon ESUs were subsequently classified (17 April 1995) in a final ruling as being threatened (NMFS 1995a).

A petition for the listing of summer-run chinook salmon in the mid-Columbia River[2] was submitted to NMFS on 3 June 1993, by the American Rivers and ten co-petitioners. On 23 September 1994, NMFS determined that the mid-Columbia River summer-run chinook salmon stocks petitioned did not constitute an ESU, but belonged to a larger fall- and summer-run chinook salmon ESU located along the mainstem Columbia River between the Chief Joseph and McNary Dams (NMFS 1994a). NMFS concluded that this ESU did not warrant a listing of endangered or threatened.

Summary of Information Presented by the Petitioners

This section briefly summarizes information presented by the petitioners (Professional Resources Organization (PRO)-Salmon 1994, Oregon National Resources Council (ONRC) and Nawa 1995) to support their arguments that specific chinook salmon stocks in Washington, Oregon, Idaho, and California qualify as threatened or endangered species under the ESA. Previous ESA petitions for chinook salmon under the ESA have been evaluated and summarized in elsewhere (NMFS 1987, Matthews and Waples 1991, Waples et al. 1991b, Waknitz et al. 1995).

Distinct Population Segments

The PRO-Salmon (1994) petition requested that NMFS evaluate four stocks of chinook salmon in Washington state for listing as threatened or endangered under the ESA: the North Fork Nooksack River spring run, South Fork Nooksack River spring run, Dungeness River spring run, and White

River spring run. The petitioners presented several alternative groupings of these stocks into one or more ESUs, which might also include stocks not specifically mentioned in their petition. The ONRC and Nawa (1995) petition listed 197 "stocks" in Washington, Oregon, California, and Idaho to be considered for listing as threatened or endangered, either separately or in one or more ESUs. The authors specifically included non-native stocks, such as Clearwater River spring-run chinook salmon, which contains components of other spring-run stocks from the Snake River spring- and summer-run ESU. They argued that if an ESU that contains the original components of a mixed stock is identified and listed as threatened or endangered, then the mixed stock should be included in the ESU.

ONRC and Nawa suggested several alternative scenarios for chinook salmon, specifically, to list:

- chinook salmon and their critical habitat as an ESU in Washington, Oregon, California, and Idaho; or
- spring, summer, fall, and winter chinook salmon and their critical habitat as four distinct ESUs; or
- ESUs which comprise one or more of the 197 stocks of chinook salmon (listed in the petition), the four stocks previously petitioned by PRO-Salmon in addition to stocks which belong to the four existing chinook salmon ESUs identified by NMFS, and their critical habitat; or
- each of the 197 stocks of chinook salmon (listed in the petition) and the 4 stocks previously petitioned by PRO-Salmon as separate ESUs, in addition to the 4 existing chinook salmon ESUs identified by NMFS; or
- regional ESUs: (a) spring- and summer-run chinook salmon in Washington, Oregon, California, and Idaho; (b) coastal fall chinook salmon that spawn in rivers and creeks south of Cape Blanco, Oregon (excluding Rogue River fall chinook salmon); (c) Columbia River fall chinook salmon, which spawn in tributaries below McNary Dam; (d) Puget Sound fall and summer/fall chinook salmon (including Sooes River fall chinook salmon on the Washington Coast); and (e) fall chinook salmon from the Central Valley of California (including "wild" fall chinook salmon that spawn in small tributaries to San Francisco Bay) and their critical habitat.

Population Abundance

Both the PRO-Salmon (1994) and ONRC and Nawa (1995) petitions cited extensive information to document the decline of specific chinook salmon stocks. PRO-Salmon (1994) cited the work of Nehlsen et al. (1991), who considered the four stocks of chinook salmon in the petition to be at a high or moderate risk of extinction, and WDF et al. (1993), who identified the status of the four stocks as "critical," based on "chronically low" escapement or redd counts. The spring run on the White River had declined from 5,432 in 1942 to a low of 66 in 1977, and return numbers have averaged less than 200 fish from 1978-91 (PRO-Salmon 1994). Escapement estimates for the North Fork Nooksack River spring run are less accurate because of unfavorable river conditions for sampling. Spawner/redd surveys nevertheless indicate a considerable decrease in stock size.

ONRC and Nawa (1995) surveyed and categorized 417 stocks of chinook salmon, of which they considered 67 (16.1%) to be extinct, 21 (5.0%) nearly extinct, 95 (22.8%) declining, 75 (18.0%) composite production [in which the hatchery contribution exceeds natural production], and a further 37 (8.9%) of unknown status. Using information from a number of sources, the petitioners presented overall and regional estimates of the decline of chinook salmon stocks. Nehlsen et al. (1991) listed 64 stocks of chinook salmon that they determined to be at a high or moderate risk of extinction or of special concern. WDF et al. (1993) determined the status of 40 of the 108 (37.0%) chinook salmon stocks in Washington State to be "critical" or "depressed." The Wilderness Society (1993) reported that 63% of spring- and summer-run chinook salmon stocks in Washington, Oregon, California, and Idaho were considered to be extinct, with a further 24% being endangered or threatened. Similarly, among fall chinook salmon stocks, 19% were extinct, and 25% endangered or threatened.

On a regional basis, the Central Valley of California had the highest percentage of extinct stocks (40%), with only one wild stock classified as not declining according to ONRC and Nawa (1995). Stocks within the coastal basins south of Cape Blanco, Oregon had also experienced a similar decrease in abundance, with 67% of the stocks classified as extinct, nearly extinct, or declining. Within the Columbia River Basin, chinook salmon stocks below McNary Dam (River Kilometer [RKm] 470) have been heavily influenced by artificial propagation, and only six wild stocks were identified that were not declining. According to ONRC and Nawa, the Columbia River chinook salmon stocks above McNary Dam have experienced the second highest level of extinction (28%), with 44% of the stocks being classified as declining. In the Snake River, the petitioners identified 13 stocks (28%) as being extinct and 22 stocks (47%) to be in decline. No wild stocks were found that were not declining. Among chinook salmon stocks in Puget Sound, 50% of the spring-run stocks were extinct. Only coastal stocks north of Cape Blanco, Oregon were not found to be seriously declining. ONRC and Nawa (1995) presented individual stock historical abundance information for many of the 417 stocks surveyed. This information further documented many of the regional declines noted above.

Causes of Decline for Chinook Salmon

The petitioners identified several factors which they believe have either singly or in combination resulted in the chinook salmon stock declines in abundance described above. Because the petitions cover such a wide geographic area, encompassing several terrestrial and marine ecological regions, and because the populations surveyed have been impacted by varying anthropogenic factors, only a very generalized review of this topic will be given.

PRO-Salmon (1994) and ONRC and Nawa (1995) both cited references indicating that habitat degradation is the major cause for the decline in the petitioned chinook salmon stocks. The influence of dams[3] was most commonly implicated by ONRC and Nawa (1995) as being responsible for the decline or extinction of chinook salmon stocks. Of the stock extinctions surveyed in the coastwide region, 76% were dam related. This was most noticeable in the Central Valley, California where 100% of the extinctions surveyed were dam related (Campbell and Moyle 1990). Furthermore, 48 of the spring- and summer-run stocks found to be in decline were affected by dams. Two of the four chinook salmon stocks petitioned by PRO-Salmon (1994) were impacted to some extent by dam operation, but logging[4] and agricultural land use/water diversion (including diking) also figured as major factors in all four stocks. The Nooksack Technical Group (1987) indicated that sedimentation from logging activities had seriously impacted the quality of the spawning habitats in both the North and South Forks of the Nooksack River. PRO-Salmon (1994) considered water diversion for agricultural use to be a major contributor to the decline of the Dungeness River spring run. Overall, ONRC and Nawa (1995) estimated that logging was responsible, in part, for 60% of the declines and 6% of the extinctions among the stocks surveyed. Similarly, agriculture, water withdrawal, mining and urbanization factors were implicated in 58% of the declines and 9% of the extinctions among the 417 stocks surveyed. Both petitioners also presented evidence that the exploitation rates on the stocks were sufficiently high to have seriously depleted stocks or been partially responsible for the extinction of stocks (Dosewallips, Duckabush, and Mokelumne Rivers spring-run chinook salmon (ONRC and Nawa 1995)).

The other major concern of the petitioners was the impact of introduced and/or artificially propagated fish on indigenous stocks. Potentially deleterious impacts of artificial propagation presented by ONRC and Nawa (1995) include: interbreeding of fall and spring runs in California due to habitat alterations (Campbell and Moyle 1990), interspecies hybridization between chinook and coho salmon (*Oncorhynchus kisutch* Walbaum) (Bartley et al. 1990), competition between hatchery and native stocks, interbreeding between hatchery and native chinook salmon stocks, disease introductions by artificially propagated fish, and the unsustainability of hatchery stocks in general. Finally, ONRC and Nawa (1995) suggested the "inadequacy of existing regulatory mechanisms" was a general reason for the overall decline in abundance of chinook salmon.

INFORMATION RELATING TO THE SPECIES QUESTION

In this section, we summarize biological and environmental information and consider the relevancy of each in determining the nature and extent of West Coast chinook salmon ESUs. ESU boundaries were determined by the BRT on the basis of the team's professional opinion of the degree to which environmental and biological attributes exhibited significant changes with respect to the reproductive isolation and ecological/genetic diversity of West Coast chinook salmon.

General Biology of Chinook Salmon

Chinook salmon, also commonly referred to as king, spring, quinnat, Sacramento, California, or tyee salmon, is the largest of the Pacific salmon (Netboy 1958). The species distribution historically ranged from the Ventura River in California to Point Hope, Alaska in North America, and in northeastern Asia from Hokkaido, Japan to the Anadyr River in Russia (Healey 1991). Additionally, chinook salmon have been reported in the Mackenzie River area of northern Canada (McPhail and Lindsey 1970). Of the Pacific salmon, chinook salmon exhibit arguably the most diverse and complex life history strategies Healey (1986) described 16 age categories for chinook salmon, 7 total ages with 3 possible freshwater ages. This level of complexity is roughly comparable to sockeye salmon (*O. nerka*), although sockeye salmon have a more extended freshwater residence period and utilize different freshwater habitats (Miller and Brannon 1982, Burgner 1991). Two generalized freshwater life-history types were initially described by Gilbert (1912): "stream-type" chinook salmon reside in freshwater for a year or more following emergence, whereas "ocean-type" chinook salmon migrate to the ocean within their first year. Healey (1983, 1991) has promoted the use of broader definitions for "ocean-type" and "stream-type" to describe two distinct races of chinook salmon. This racial approach incorporates life history traits, geographic distribution, and genetic differentiation and provides a valuable frame of reference for comparisons of chinook salmon populations. For this reason, the BRT has adopted the broader "racial" definitions of ocean- and stream-type for this review.

The generalized life history of Pacific salmon involves incubation, hatching, and emergence in freshwater, migration to the ocean, and subsequent initiation of maturation and return to freshwater for completion of maturation and spawning (Fig. 2). Juvenile rearing in freshwater can be minimal or extended. Additionally, some male chinook salmon mature in freshwater, thereby foregoing emigration to the ocean. The timing and duration of each of these stages is related to genetic and environmental determinants and their interactions to varying degrees. Salmon exhibit a high degree of variability in life-history traits; however, there is considerable debate as to what degree this variability is the result of local adaptation or the general plasticity of the salmonid genome (Ricker

1972, Healey 1991, Taylor 1991).

Several types of biological evidence were considered in evaluating the contribution of West Coast chinook salmon to ecological/genetic diversity of the biological species under the ESA. Life-history traits examined for naturally spawning chinook salmon populations included smolt size and outmigration timing, age and size at spawning, river-entry timing, spawn timing, fecundity, and ocean migration. These traits are believed to have both a genetic and environmental basis, and similarities among populations could indicate either a shared genetic heritage or similar responses to shared environmental conditions.

The analysis of life-history trait information is complicated by several factors. Data collected from different locations during different years are confounded by spatial and temporal environmental variability. This variability creates considerable "noise," which may be as large as differences between geographically distant populations, and may mask subtle regional patterns. High interannual variability also complicates the comparison of results from studies conducted during different time periods. For chinook salmon, for which a single broodyear may return from the ocean over a 5- or 6-year period, variations in ocean productivity due to events such as the 1983 El Niño (Johnson 1988b) may bias estimates of age distribution, age-size relationships, and/or age and size-related fecundity estimates. Furthermore, it may be difficult to distinguish between fish from different runs emigrating from, or returning to, the same river system. Direct comparisons of chinook salmon life-history traits between stocks under controlled conditions are limited in number, and the extent to which inference can be made to wild populations is uncertain.

A third confounding complication is that the expression of life-history traits may be altered by anthropogenic activities such as land-use practices (Hartman et al. 1984, Holtby 1987), harvest (Ricker 1981), or artificial propagation (Steward and Bjornn 1990, Flagg et al. 1995b). To help limit any bias introduced by artificial propagation, life-history trait comparisons in this status review have focused on naturally spawning populations. However, because of the widespread practice of off-station plants of hatchery-reared fry and smolts, many studies of naturally spawning populations may have inadvertently included first-generation hatchery fish or fish whose ancestors have been hatchery reared. Life-history trait information from hatchery populations was used only when insufficient information from naturally spawning populations was available, as in the case of ocean migration patterns. As with environmental variability, the effects of anthropogenic activities may confound the expression of life-history traits and are difficult to factor out.

Because of these potential sources of variability, we felt that statistical analyses of life-history trait variability would not be particularly informative. Instead, data were collected from as many sources as possible from each system to give some indication of the mean and range in character traits. Older data sets were especially sought to provide insight into chinook salmon population characteristics prior to the proliferation of hatchery programs, which have produced fish with relatively high juvenile survival and growth rates and modified saltwater entry dates.

Ecological Features

Geological Events

The geologic events of the last 20,000 years have provided mechanisms for genetic isolation, colonization, and population interbreeding. In determining ESU boundaries it is useful to understand the factors that may have shaped present day chinook salmon population distributions. Much of the present distribution of aquatic and terrestrial species in western North America is a legacy of the volcanic, tectonic, and glacial forces that have shaped this region. Events such as headwater transfer or stream capture have altered the flow of major rivers and the aquatic species that inhabit them. The Cordilleran ice sheet was the last major glacial event to affect the distribution of chinook salmon. At its height some 10,000-15,000 years ago, vast areas of Southeast Alaska, British Columbia, Washington, and Idaho were covered with ice (McPhail and Lindsey 1970). This created a discontinuous distribution of chinook salmon stocks. Two major ice-free refugia existed: Beringia, composed of the Bering land bridge connecting Eastern Siberia and Western Alaska; and Cascadia, composed of the lands south of the mid-Columbia River drainage (McPhail and Lindsey 1970). An additional ice-free refuge existed on the coast of the Olympic Peninsula in the area of the Chehalis River. The drop in sea level during the glacial periods may have created minor refugia along the coast of Vancouver Island or the present-day Queen Charlotte Islands (McPhail and Lindsey 1986). As the ice sheet receded, the colonization of newly exposed freshwater habitat began from the two refugia.

Chinook salmon colonization during the postglacial period (approximately beginning 10,000 years ago) occurred through a number of possible pathways. Straying adults could invade coastal river systems, as could salmon that moved farther upriver to headwaters exposed by the receding glaciers. Ice dams and land expansion after the retreat of glacial ice sheets caused rivers to alter course and change watersheds. Watershed capture has resulted in the exchange of aquatic organisms between several major river systems. Parts of the present day Fraser River drainage flowed into the Columbia River via the Okanogan River and Shuswap Creek during the last deglaciation (McPhail and Lindsey 1986). Species that moved into the Upper Fraser River from the Columbia River also gained access to southeastern Alaskan coastal rivers. The Stikine, Skeena, and Nass Rivers at various times drained east into the Fraser River Basin relative to their current westerly flow to the Gulf of Alaska (McPhail and Lindsey 1986). Similarly, the Alsek River in Alaska, which also flows to the Gulf of Alaska, drained what is now part of the Yukon River headwaters (Lindsey and McPhail 1986). Presently, the headwaters of the Taku, Stikine, and Yukon Rivers lie within 50 miles of one another. Chinook salmon populations from Beringia also had access to the Mackenzie River in Canada during the deglaciation, which may explain recurring reports of chinook salmon in that river system (McPhail and Lindsey 1970).

Ecoregions

The fidelity with which chinook salmon return to their natal stream implies a close association between a specific stock and its freshwater environment. The selective pressures of different freshwater environments may be responsible for differences in life-history strategies among stocks. Miller and Brannon (1982) hypothesized that local temperature regimes are the major factor influencing life-history traits. If the boundaries of distinct freshwater habitats coincide with differences in life histories it would suggest a certain degree of local adaptation. Therefore, identifying distinct freshwater, terrestrial, and climatic regions may be useful in identifying chinook salmon ESUs. The Environmental Protection Agency (EPA) has established a system of ecoregion designations based on soil content, topography, climate, potential vegetation, and land use (Omernik 1987). These ecoregions are similar to the physiographic provinces determined by the Pacific Northwest River Basins Commission (PNRBC 1969) for the Pacific Northwest. Historically, the distribution of chinook salmon in Washington, Oregon, California, and Idaho would have included 13 of the present day EPA ecoregions (Fig. 3). Similarly, there is a strong relationship between ecoregions and freshwater fish assemblages (Hughes et al. 1987). We have retained the ecoregion names and numbers used by Omernik (1987) and included physiographic information presented by PNRBC (1969), present day water use information (USGS 1993), river flow information

(Hydrosphere Products, Inc. 1993), and climate data from the U.S. Department of Commerce (1968) into the appropriate ecoregion description (Omernik and Gallant 1986, Omernik 1987). Additional information for British Columbia (Environment Canada 1977, 1991) and Alaska (Hydrosphere Products, Inc. 1993) is included for comparative purposes. The following ecoregions are wholly or partially contained within the historical natural range of chinook salmon in Washington, Oregon, California, and Idaho.

Coastal Range (#1)

Extending from the Olympic Peninsula through the Coast Range proper and down to the Klamath Mountains and the San Francisco Bay area, this region is influenced by medium to high rainfall levels due to the interaction between marine weather systems and the mountainous nature of the region. Topographically, the region averages about 500 m in elevation, with mountain tops under 1,200 m. These mountains are generally rugged with steep canyons. Between the ocean and the mountains lies a narrow coastal plain composed of sand, silt, and gravel. Tributary streams are short and have a steep gradient; therefore, surface runoff is rapid and water storage is relatively short term during periods of no recharge. These rivers are especially prone to low flows during times of drought. Regional rainfall averages 200-240 cm per year (Fig. 4), with generally lower levels along the southern Oregon coast. Average annual river flows for most rivers in this region are among the highest found on the West Coast when adjusted for watershed area (Fig. 5). River flows peak during winter rain storms common in December and January (Fig. 6). Snow melt adds to the surface runoff in the spring, providing a second flow peak, and there are long periods when the river flows are maintained at least 50% of peak flow (Fig. 7). During July or August there is usually no precipitation; this period may expand to 2 or 3 months every few years. River flows are correspondingly at their lowest (Fig. 8) and temperatures at their highest during August and September (Fig. 9). Oregon coastal rivers have the largest relative difference in minimum and maximum flows, where minimum flows are 2-5% of the maximum flows.

The region is heavily forested primarily with Sitka spruce, western hemlock, and western red cedar. Forest undergrowth is composed of numerous types of shrubs and herbaceous plants.

Puget Lowland (#2)

Situated between the Coast Range and Cascade Range Ecoregion, this region experiences reduced rainfalls (50-120 cm) from the rainshadow effect of the Coast Mountains. The area is generally flat with high hills (600 m) at the southern margin of the ecoregion. Soils are composed of alluvial and lacustrine deposits. These deposits are glacial in origin north of Centralia, Washington. This area tends to have large groundwater resources, with groundwater from the bordering mountain ranges helping sustain river flows during drought periods. Peak river flow varies from December to June depending on the contribution of snowpack to surface runoff for each river system. Rivers tend to have sustained flows (5 to 8 months of flows at 50% of the peak or more), and low flows are generally 10-20% or more of the peak flows.

Douglas fir represent the primary subclimax forest species, with other coniferous species (lodgepole, western white, and ponderosa pines) locally abundant. Prairie, swamp, and oak, birch, or alder woodlands are also common. The land is heavily forested, and wood-cutting activities (including road building, etc.) contribute to soil erosion, river siltation, and river flow and temperature alteration.

The region is heavily urbanized, and domestic and industrial wastes impact local water systems.

Urban run-off and sewage treatment influence water quality west of the Cascade Mountains, with the exception of the Olympic Peninsula coastal and northern Puget Sound rivers. Glacial sediment also influences water quality, especially in the Skagit, North Fork Nooksack, Nisqually, and Puyallup/White River Basins.

Willamette Valley (#3)

Adjoining the southern border of the Puget Sound Lowland Ecoregion at the Lewis River, this region was not glacially influenced. A rainshadow effect, similar to the one influencing the Puget Sound Lowlands, limits rainfall to about 120 cm per year. River flows peak in December and January and are sustained for 6 or 7 months of the year. Low flows occur in August and September, although the volume is generally 20% of the peak flow.

Much of the land has been converted to agricultural use, with Douglas fir and Oregon white oak stands present in less-developed areas. Irrigation is commonly employed, and stream flows, especially in the southern portion of this region, can be significantly affected. Agricultural and livestock practices contribute to soil erosion and fertilizer/manure deposition into stream systems.

Water quality is impacted by agricultural and urban activities. Many water quality problems are exacerbated by low water flows and high temperatures during the summer. Pulp and paper mill discharges of dioxin into the Columbia and Willamette Rivers were cited as another water quality concern, although this situation has been much more serious in the past (USGS 1993).

Cascades (#4)

This region is composed of the Cascade Range in Washington and Oregon and the Olympic Mountains in Washington state. Peaks above 3,000 m are distributed throughout the region. The crest of the Cascade Range (averaging 1,500 m) captures much of the ocean moisture moving eastward in addition to providing a biological barrier. Rainfalls can average 280 cm per year (up to 380 cm in the Olympic Mountains), much of which is in the form of heavy snowpack. Intensive rainstorms, those depositing more than 2.5 cm per hour, are rare. Rainfall is generally spread over the year with the majority occurring between October and March. Except where porous rock substrate exists, there is little capacity for long-term groundwater storage. In these porous rock areas, streams receive 75-95% of their average discharge as groundwater, and are able to maintain their flows during dry periods. Surface water flow originating in the Cascades and Olympic Mountains influences river flows throughout this region.

Currently the area is primarily forested with Douglas fir, noble fir, and Pacific silver fir (all subclimax species), whereas western hemlock and red cedar are common climax species. At higher elevations, these trees are replaced by Englemann spruce, whitebark pine, and mountain hemlock. Forest undergrowth tends to be dense on the western slopes of this region and rather sparse on the eastern slopes. Heavy rainfall, combined with woodcutting activities, has resulted in increased soil erosion.

Sierra Nevada (#5)

To the south of the Cascades Ecoregion lies a similar mountainous ecoregion, comprised of portions of the Klamath, Sierra, Trinity, and Siskiyou Mountains. Annual rainfall varies considerably, from 40 cm to over 150 cm, depending on elevation and the degree of rainshadowing. Most of the rain comes in the winter months, with summers being hot and dry. Topographically, the region rises to over 2,000 m with an average elevation of 1,000 m. This region contains the headwaters for the Rogue, Klamath, and Sacramento Rivers. Peak flows occur in February, with low flows in August, September, or October. As a result of water diversion and impoundment activities, flows are now more evenly apportioned throughout the year. This has occurred primarily through irrigation/flood mitigation-related reductions in peak flows and less so through increased spillage during the historical time of minimum flows.

Douglas fir is the predominant tree species, but mixed coniferous-oak stands are common. Soils tend to be unstable, and timber harvest or livestock grazing can result in severe erosion. Hydraulic placer mining has had a considerable impact on stream quality and hillslope stability.

Southern and Central California Plains and Hills (#6)

To the east and in the rainshadow of the Coastal Mountain range, the tablelands and hills of this region have generally low levels of annual rainfall (40-100 cm). Tributary rivers to the Sacramento and San Joaquin Rivers flow through this region. Vegetation is composed of California oaks and manzanita chaparral with extensive needlegrass steppe. Livestock grazing in the open woodlands is the predominant land use.

Central California Valley (#7)

The Sacramento and San Joaquin Rivers are the key features of the Central California Valley Ecoregion. The broad flat lands that border the river naturally support needlegrass and marshgrasses, although much of the region has been extensively converted to agricultural use. The annual rainfall for the region is 40-80 cm. The Sacramento and San Joaquin Rivers peak in February with a 6-month period of high flows (>50% of peak flow). Low flows occur in September and October. Changes in the hydrology of tributaries and irrigation withdrawals from the mainstem rivers have drastically altered the flow characteristics of these rivers over the course of the last 100 years. An estimated 90% of the surface water withdrawals were used for irrigation in 1990 (USGS 1990). The maintenance of livestock and cultivation, irrigation, and chemical treatment of crop land has resulted in increases in fecal coliform, dissolved nitrate, nitrite, phosphorus, and sulfate concentration levels (USGS 1993). Industrial and mining runoff from sites, such as the copper mines near Spring Creek in the Sacramento River Basin, also impact water quality in the immediate area.

Eastern Cascades Slopes and Foothills (#9)

This ecoregion marks the transition between the high rainfall areas of the Cascades Ecoregion and the drier basin ecoregions to the east. The area receives 30 cm to 60 cm of rainfall per year. Streamflow is intermittent, especially during the summer dry season. Surface and groundwater contributes to flows in the Yakima, Deschutes, Klickitat, and White Salmon Rivers.

Ponderosa and lodgepole pine are common throughout the region, with little forest undergrowth. Soils tend to be volcanic, young, and highly erodible. Primary land uses are timber harvest and mixed grazing/timber areas. Agriculture is limited to valleys and irrigation is commonly employed.

Columbia Basin (#10)

This ecoregion is typified by irregular plains, tablelands, and high hills/low mountains. The plateau spans from the Cascade Mountains to the Blue Mountains in the south and southeast. Much of the basin is covered with glacial and alluvial deposits. The loose surface substrate is prone to erosion. There is little rainfall and the majority of the water discharge comes from the mountains that border the basin. Because tributaries to the mid- and upper Columbia River receive much of their water from snowmelt, peak river flows are in May and June, except for the Deschutes, John Day, and Umatilla Rivers, which peak in April. Peak flows are not as sustained as on the coast, generally lasting 2-3 months. Annual rainfalls of 20-60 cm support sagebrush and wheatlands. Most smaller streams are ephemeral, partially due to irrigation withdrawals (Omernik and Gallant 1986). The Columbia Plateau experiences a prolonged drought of 1 to 3 months every year, with longer events occurring frequently. Low river flows occur during the late summer and early fall, August-October, when irrigation demand is heavy. Nitrates, sulfites, and pesticides commonly associated with crop irrigation are found in most of the rivers in the Columbia River Basin. Heavy metal contamination from Canadian mining operations has been detected at several downstream sites on the Columbia River (USGS 1993).

Sagebrush and wheatgrass constitute the primary natural vegetation for this region. Much of the land has been converted to dryland wheat agriculture, with smaller irrigated areas supporting the cultivation of peas and potatoes. Irrigation and agriculture have changed the flow and course of smaller rivers and streams (Omernik and Gallant 1986).

Blue Mountains (#11)

The Blue, Wallowa, Ochoco, Strawberry, and Aldrich Mountains are contained in this ecoregion. The mountains are a mix of older sedimentary and younger volcanic peaks. Mountainous regions contain ponderosa pine, grand fir and Douglas fir, and Englemann spruce stands. Rainfall varies from 25-50 cm in the lowlands, and as much as 100 cm in the mountains, most of which falls as snow. The aquifers that develop in these mountains feed into numerous river systems: the John Day, Umatilla, and Walla Walla Rivers, which flow into the Columbia River, and the Tucannon, Grande Ronde and Imnaha Rivers, which flow into the Snake River. Peak flows occur from April to June, but only last 2 to 4 months; however, flood events historically have occurred from December through February as rain on snow events (WDFW 1997a). Minimum flows occur predominantly in August or September, except in the mountains where flows are at a minimum in January and February.

Lowlands contain sagebrush, wheatgrass, and bluegrass. Land-use activities correspond to vegetation, with timber harvest more prevalent in the mountains and grazing prevalent in the lowlands. Both of these activities have led to considerable localized stream-side erosion.

Snake River Basin/High Desert (#12)

This region spans southeastern Oregon, southern Idaho, northeastern California, and northern Nevada. Passage of chinook salmon into most of the region has been blocked by dams, but the region still exerts a considerable influence on downstream habitat. This area is geologically very new and contains extensive areas of lava and other volcanic material. The rock substrate is very permeable, streams tend to lose much of their flow through percolation and evaporation, and only the larger rivers that lie below the water table contain substantial flows year round. Rainfalls are generally less than 30 cm annually, but may be as high as 60 cm on the borders of the ecoregion. Extended dry intervals are very common in the Snake River Plateau.

Sagebrush and wheatgrass are prevalent with much of the area utilized as rangeland. Agriculture (potatoes, corn, grains) is sustained where water resources are available. Rivers in the southern half of Idaho are affected by agricultural and urban development. Irrigation return flows, livestock grazing, and urban activities were associated with high nutrient concentrations in the Boise and Snake Rivers (USGS 1993).

Northern Rockies (#15)

Forming the northeast boundary of the Columbia Basin Ecoregion, this region is a mosaic of mountain crestlines (up to 2,500 m) and valleys. Rainfall varies accordingly from 50 to 150 cm or more per year, some of which falls in intense local storms. Winter snowpack is the major contributor to the streamflows; river flows peak with the spring melt in May or June lasting only 2-3 months. One- and 2-month drought periods are fairly common; however, longer periods are quite rare, especially in the higher mountains, where drought periods of even 1 month are rare (once in 5 years). Low flows correspond with low periods of precipitation in August and September except in the higher elevations, where winter temperatures limit flow. In many areas, soil and subsoil development have created important areas for water storage. Seepage is an important water source for major rivers in this area. The Salmon and Clearwater Rivers drain the southern portion of this region and are the only major tributaries to which chinook salmon still have access. The Spokane, Kootenai, and Pend Oreille Rivers drain into the Columbia River from the eastern and northern portions of this ecoregion; however, runs that historically existed on these rivers have been eliminated by impassable dams (Fulton 1968).

Forests are dominated by conifers: western white pine, lodgepole pine, western red cedar, western hemlock, western larch, Englemann spruce, subalpine fir, and Douglas fir. Prairie and mixed forest/grassland are also common. Forestry is the primary land-use activity, although mining and grazing activities are commonplace. Water systems in the northern half of Idaho, the Coeur d'Alene and Clearwater Rivers, are impacted by mining and logging operations; however, containment ponds appear to limit metal concentrations downstream (USGS 1993).

Marine Habitat

The marine habitat can be subdivided into three general regions--estuary, coastal, and ocean. Chinook salmon with different life-history strategies use these regions to different extents; therefore, changes in the conditions in one region may selectively affect some populations more than others.

Ocean-type chinook salmon reside in estuaries for longer periods as fry and fingerlings than do with yearling, stream-type, chinook salmon smolts (Reimers 1973, Kjelson et al. 1982, Healey 1991). The diet of outmigrating ocean-type chinook salmon varies geographically and seasonally, and feeding appears to be opportunistic (Healey 1991). Aquatic insect larvae and adults, *Daphnia*, amphipods (*Eogammarus* and *Corophium spp.*), and *Neomysis* have been identified as important food items (Kjelson et al. 1982, Healey 1991). Rivers with well developed estuaries are able to sustain larger ocean-type populations than those without (Levy and Northcote 1982). Juvenile chinook salmon growth in estuaries is often superior to river-based growth (Rich 1920a, Reimers 1971, Schluchter and Lichatowich 1977). Stream-type chinook salmon move quickly through the estuary, into coastal waters, and ultimately to the open ocean (Healey 1983, Healey 1991). Very limited data are available concerning the ocean migration of stream-type chinook salmon; they apparently move quickly offshore and into the central North Pacific, where they make up a disproportionately high percentage of the commercial catch relative to ocean-type fish (Healey 1983, Myers et al. 1987). The Stikine, King Salmon, and Chilkat Rivers are notable exceptions to this general stream-type migration pattern.

Apparently, a portion of fish from these stocks remain in the coastal waters of southeast Alaska throughout their lives (ADFG 1997). In contrast, throughout their ocean residence ocean-type chinook salmon inhabit coastal waters, where coded-wire tag (CWT)-marked fish are recovered in substantial numbers (Healey and Groot 1987).

The utilization of estuaries by ocean-type chinook salmon makes them more susceptible to changes in the productivity of that environment than stream-type chinook salmon. Estuaries may be "overgrazed" when large numbers of ocean-type juveniles enter the estuary en masse (Reimers 1973, Healey 1991). The potential also exists for large-scale hatchery releases of fry and fingerling ocean-type chinook salmon to overwhelm the production capacity of estuaries (Lichatowich and McIntyre 1987). The loss of coastal wetlands to urban or agricultural development may more directly impact ocean-type populations. Dahl (1990) reported that California has lost 94% of its wetlands. Furthermore, an estimated 80-90% of the undiked tidal marshlands in the Sacramento River Delta area, the major nursery area for Central Valley chinook salmon stocks, has been lost (Nichols et al 1986, Lewis 1992). A similar reduction has been reported in Washington and Oregon wetlands: a 70% loss in the Puget Sound, 50% in Willapa Bay, and 85% in Coos Bay (Refalt 1985).

The ocean migrations of chinook salmon extend well into the North Pacific Ocean. The productivity of various ocean regions has been correlated with the degree of wind-driven upwelling (Bakun 1973, 1975). Under normal conditions this upwelling decreases along the coast from California to Washington and British Columbia (Bakun 1973). Changes in wind directions related to sea level pressure (SLP) systems, most notably the Aleutian low pressure (ALP) or Central North Pacific (CNP) pressure indices, can greatly alter upwelling patterns (Ware and Thompson 1991, Beamish and Bouillon 1993). Upwelling brings cold, nutrient-rich waters to the surface, resulting in an increase in plankton and ultimately salmon production (Beamish and Bouillon 1993). Strong ALP measurements (high pressure readings) tend to result in minimal upwelling in the North Pacific. Similarly, atmospheric pressure systems in the Central Pacific can alter trade wind patterns to bring warmer water up along the California coast; this occurrence is better known as an El Niño. El Niño events suppress coastal upwelling off the Washington, Oregon, and California coasts and tend to bring warmer water and warm-water species northward (McLain 1984). One difference between El Niño events and ALP events is that the northerly flow of warm waters associated with El Niño events may stimulate ocean productivity off Alaska (McLain 1984). Ocean migratory pattern differences between and within ocean- and stream-type chinook salmon stocks may be responsible for fluctuations in abundance. Moreover, the evolution of life-history strategies has, in part, been a response to long-term geographic and seasonal differences in marine productivity and estuary availability.

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Chinook Salmon Life History and Ecology

Juvenile Life History

The most significant process in the juvenile life history of chinook salmon is smoltification, the physiological and morphological transition from a freshwater to marine existence. The emigration from river to ocean is thought to have evolved as a consequence of differences in food resources and survival probabilities in the two environments (Gross 1987). Salmon juvenile life-history patterns are usually deduced by examining the developmental pattern of circuli on juvenile and adult fish scales (Gilbert 1912, Rich 1920a, Koo and Isarnkura 1967). Within the ocean-type (subyearling) and stream-type (yearling) migrant designations, several subtypes have been described (Gilbert 1912, Reimers 1973, Schluchter and Lichatowich 1977, Fraser et al. 1982). Ocean-type juveniles enter saltwater during one of three distinct phases. "Immediate" fry migrate to the ocean soon after yolk resorption at 30-45 mm in length (Lister et al. 1971, Healey 1991). In most river systems, however, fry migrants, which migrate at 60-150 days post-hatching, and fingerling migrants, which migrate in the late summer or autumn of their first year, represent the majority of ocean-type emigrants. When environmental conditions are not conducive to subyearling emigration, ocean-type chinook salmon may remain in freshwater for their entire first year. Stream-type chinook salmon migrate during their second or, more rarely, their third spring. Under natural conditions stream-type chinook salmon appear to be unable to smolt as subyearlings. The underlying biological bases for differences in juvenile life history appear to be both environmental and genetic (Randall et al. 1987). Distance of migration to the marine environment, stream stability, stream flow and temperature regimes, stream and estuary productivity, and general weather regimes have been implicated in the evolution and expression of specific emigration timing.

The success of different juvenile life-history strategies is linked to the coordinated expression of other traits. Gilbert (1912) noted that ocean-type fish exhibited a faster growth rate relative to stream-type fish. The growth difference between ocean- and stream-type juveniles has also been observed by other researchers (Carl and Healey 1984, Cheng et al. 1987, Taylor 1990a). Some of this difference may be related to differences in rearing environment, although under standardized conditions there was still a significant growth difference between ocean- and stream-type juveniles (Taylor 1990b). Clarke et al. (1992) demonstrated that the growth of stream-type juveniles was strongly associated with photoperiod, while ocean-type juvenile growth appeared to be independent of photoperiod. Juvenile life history appears to be a heritable trait. Hybridization experiments indicated that the stream-type smoltification and growth pattern are recessive relative to the ocean-type pattern (Clarke et al. 1992). Juvenile stream-type chinook salmon have also been shown to be more aggressive than ocean types. This may be a territorial defense mechanism for resource limited freshwater systems (Taylor and Larkin 1986, Taylor 1988, Taylor 1990b). Morphometric differences, such as larger and more colorful fins, observed in some stream-type populations may be related to social displays that maintain territories (Carl and Healey 1984, Taylor and Larkin 1986). Thus, the timing of parr-smolt transition appears to be associated with the expression of a number of other traits in order to maximize individual survival.

Juvenile stream- and ocean-type chinook salmon have adapted to different ecological niches. Ocean-type chinook salmon tend to utilize estuaries and coastal areas more extensively for juvenile rearing. In general, the younger (smaller) juveniles are at the time of emigrating to the estuary, the longer they reside there (Kjelson et al. 1982, Levy and Northcote 1982, Healey 1991). There is also an apparent positive relationship between rivers with large estuary systems and the number of fry migrants (Fraser et al. 1982). Brackish water areas in estuaries also moderate physiological stress during parr-smolt transition. The development of the ocean-type life-history strategy may have been a response to the limited carrying capacity of smaller stream systems and glacially scoured, unproductive watersheds, or a means of avoiding the impact of seasonal floods in the lower portion of many watersheds (Miller and Brannon 1982). In the Sacramento River and coastal California rivers, subyearling emigration is related to the avoidance of high summer water temperatures (Calkins et al. 1940, Gard 1995). Ocean-type chinook salmon may also use seasonal flood cycles as a cue to volitionally begin downstream emigration (Healey 1991). Migratory behavior in ocean-type chinook salmon juveniles is also positively correlated with water flow (Taylor 1990a).

Stream-type juveniles are much more dependent on freshwater stream ecosystems because of their extended residence in these areas. A stream-type life history may be adapted to those watersheds, or parts of watersheds, that are more consistently productive and less susceptible to dramatic changes in water flow, or which have environmental conditions that would severely limit the success of subyearling smolts (Miller and Brannon 1982, Healey 1991). Stream-type chinook salmon juveniles exhibit downstream dispersal and utilize a variety of habitats during their freshwater residence. This dispersal appears to be related to resource allocation and migration to overwintering habitat and is not associated with saltwater osmoregulatory competence (Hillman et al. 1987, Levings and Lauzier 1989, Taylor 1990a, Healey 1991). For example, the migration of subyearling juvenile spring-run chinook salmon in the Wenatchee River (a stream-type population) may be due to competition with hatchery releases or the interspecific interaction between steelhead and chinook salmon juveniles (Hillman and Chapman 1989). There was a tendency for juveniles to move into deeper water, farther from the bank shelter, as they grew older. If suitable overwintering habitat, such as large cobble, is not available then the fish will tend to migrate downstream (Bjornn 1971, Bustard and Narver 1975, Hillman et al. 1987). At the time of saltwater entry, stream-type (yearling) smolts are much larger, averaging 73-134 mm depending on the river system, than their ocean-type (subyearling) counterparts and are therefore able to move offshore relatively quickly (Healey 1991).

The variability in the time of emigration to the marine environment among stocks of chinook salmon, combined with geographic and yearly differences in freshwater productivity, make comparisons of the sizes of smolts among different stocks difficult. Size data may be confounded by the presence within a watershed of multiple native stocks that exhibit different life-history strategies. The possible inclusion of hatchery-reared fish in smolt samples is a further confounding factor. Smolt size, therefore, was not emphasized among the life-history traits used to determine ESU boundaries.

Ocean- and stream-type chinook salmon populations exhibit a geographical distribution that further underscores the ecological adaptation of these two races. Chinook salmon stocks in Asia, Alaska, and Canada north of the 55th parallel, and in the headwaters (upper elevations) of the Fraser River and the Columbia River Basins, exhibit a stream-type life history: emigrating to sea in their second or third spring and generally entering freshwater several months prior to spawning (Healey 1991). A notable exception to this trend includes populations in the Situk River and several Yakutat foreland River Basins in Alaska, which emigrate primarily as subyearlings (Johnson et al 1992a, ADFG 1997). Ocean-type chinook salmon are predominant in coastal regions south of 55N, in Puget Sound, in the lower reaches of the Fraser and Columbia Rivers, and in California's Central Valley (Gilbert 1912, Rich 1920a, Healey 1983, Taylor 1990b). One analysis of principal components influencing life-history type (distance to the sea, daylight hours during the growing season and air temperature) accounted for 96% of the total observed variation in age at smoltification (Taylor 1990a). However, the abrupt change between stream- and ocean-type life histories at 55N occurs in the absence of a similarly abrupt change in environmental conditions (Healey 1983) and may be related to patterns of colonization following deglaciation (Taylor 1990b).

Stream-type life histories are most commonly associated with early timed runs of fish (Rich 1920a, Healey 1983). This is partially because the headwater regions south of 55N are only accessible during peak spring stream flows, additionally, temperatures in more northerly streams and headwater areas are much colder than in other areas and require early deposition of eggs to allow for proper developmental timing. Overall, juvenile smoltification strategies are one expression of a more complicated, genetically based life-history adaptation to ecological conditions (Taylor 1990a, Clarke et al. 1992). Differences in juvenile life-history strategies among chinook salmon stocks were a useful component in helping to determine boundaries between ESUs.

Ocean Distribution

Coastwide, chinook salmon remain at sea from 1 to 6 years (more commonly 2 to 4 years), with the exception of a small proportion of yearling males which mature in freshwater or return after 2 or 3 months in salt water (Rutter 1904, Gilbert 1912, Rich 1920a, Mullan et al. 1992). Differences in the ocean distribution of specific stocks may be indicative of resource partitioning and may be important to the success of the species as a whole. Current migratory patterns may have evolved as a balance between the relative benefits of accessing specific feeding grounds and the energy expenditure necessary to reach them. If the migratory pattern for each population is, in part, genetically based, then the efficiency with which subsequent generations reach and return from their traditional feeding grounds will be increased.

The vast majority of CWT-marked chinook salmon come from hatchery populations; therefore, the migratory routes of many wild fish stocks must be inferred from their corresponding hatchery populations. Furthermore, CWT ocean recoveries are obtained through commercial and sport fishery samples; therefore, the relative intensity of each fishery can bias the interpretation of the oceanic distribution of each stock. Comparisons of oceanic distributions across years can also be influenced by changes in fishing regulations and ocean conditions (such as during an El Niño). Confounding effects were considered in the interpretation of CWT recoveries, and small differences in CWT ocean recoveries between stocks were not considered as a distinguishing factor.

The genetic basis for ocean distribution has been supported by a number of different studies involving the monitoring of CWT-marked fish caught in the ocean fisheries. The relative influence of genetic vs. environmental factors on migratory pattern can be deduced from transplantation studies. Transplanted Elwha River chinook salmon continued to follow their traditional migratory pattern after being reared and released at a site 150 km to the east, except that the actual route had also been shifted 150 km eastward (Brannon and Hershberger 1984). Additionally, hybrids between the Elwha River and Green River (University of Washington) stocks exhibited an intermediate ocean migration pattern. Transplantation studies with coastal stocks in Oregon have yielded similar results (Nicholas and Hankin 1988). Chinook salmon whose natal stream lies south of Cape Blanco tend to migrate to the south, while those to the north of Cape Blanco tend to migrate in a northerly direction. Transplants of south migrating stocks to release sites north of Cape Blanco do not alter the basic southerly direction of ocean migration (Nicholas and Hankin 1988). Recoveries of CWT-marked fish from ocean fisheries indicate that fish stocks follow predicable ocean migration patterns, and that these are based on "ancestral" feeding routes (Brannon and Setter 1987).

Ocean- and stream-type chinook salmon are recovered differentially in coastal and mid-ocean fisheries, indicating divergent migratory routes (Healey 1983, 1991). Ocean-type chinook salmon tend to migrate along the coast, while stream-type chinook salmon are found far from the coast in the central North Pacific (Healey 1983, 1991; Myers et al. 1984). Studies of CWT-marked prerecruit (<71 cm) fish in the marine fisheries off of Southeastern Alaska indicated that differences in migration speed, timing, and growth were related to the life history, age, and general geographic origin of the stocks (Orsi and Jaenicke 1996). The causal basis for this difference in migration pattern is unknown, but may be related to poor coastal feeding conditions during past glacial events for the more northerly (stream-type) populations.

The freshwater component of the adult returning migratory process is also under a significant genetic influence. In one experiment, "upriver bright" chinook salmon were captured, spawned, and the subsequent progeny reared and released from a downriver site (McIsaac and Quinn 1988). A significant fraction of the returning adults from the "upriver bright" progeny group bypassed their rearing site and returned to their "traditional" spawning ground 370 km further upriver. The high degree of fidelity with which chinook salmon return to their natal stream has been shown in a number of studies (Rich and Holmes 1928, Quinn and Fresh 1984, McIsaac and Quinn 1988). Returning to the "home stream" provides a mechanism for local adaptation and reproductive isolation.

Ocean migration patterns represent an important form of resource partitioning and are important to the evolutionary success of the species; therefore, differences in ocean migratory pattern were an important consideration in the determination of ESU boundaries.

Size and Age at Maturation

The age at which chinook salmon begin sexual maturation and undertake their homeward migration is dependent on a number of different factors. Age, body size and composition, and fecundity traits in salmonids have all been shown to be partially under genetic control (Ricker 1972) and genetically and phenotypically correlated (Gall 1975). Because of genetic correlations between these traits, natural selection on one or more of these traits may affect the expression of other traits. The confounding effects of correlated traits make it difficult to identify specific selective (ecologically important) criteria that influence size and age at maturity.

Adult body size in chinook salmon does not appear to be strongly correlated to latitude; however, there appears to be a slight negative correlation between adult body size and length of migration (Roni and Quinn 1995). The relationship between size and length of migration may also reflect the earlier timing of river entry and the cessation of feeding for chinook salmon stocks that migrate to the upper reaches of river systems. Juvenile life history has an apparent influence on the size of returning spawners. Ocean-type fish that have been at sea from 1 to 2 years are generally larger than their respective stream-type counterparts (Roni and Quinn 1995). This may reflect the more productive feeding conditions that exist in the marine environment and/or the additional 3 to 5 months that ocean-type fish remain in the marine environment before beginning their spawning migration.

Body size, which is correlated with age, may be an important factor in migration and redd construction success. Beacham and Murray (1987) reported a correlation between body size and large (< 100 km^2 watershed area) and small river size in chum salmon (*O. keta*). Roni and Quinn (1995) reported that under high density conditions on the spawning ground, natural selection may produce stocks with exceptionally large-sized returning adults. Spawning aggregations may select for large body size in males due to competition between males for females and the "attractiveness" of large males to females (Foote 1990). Large body size may be advantageous for females because of the success of larger fish in establishing, digging, and protecting their redds (Healey and Heard 1984). Competition for redd sites, stream flow, and gravel conditions are also thought to influence adult size in coho salmon (Holtby and Healey 1986).

An alternative strategy for chinook salmon is for males to mature at an early age. "Mini-jack" or "jack" chinook salmon males mature in their first or second ocean years, respectively. Early maturation among male chinook salmon was first described by Rutter (1904). Early maturation offers a reduced risk of mortality, but younger (smaller) males may be at a competitive disadvantage in securing a mate (Gross 1987). The incidence of jack males has underlying genetic determinants and appears to be, in part, a response to favorable growing conditions. A variant of this life-history strategy is maturation without emigrating to the ocean. Rich (1920a) estimated that 10-12% of the juvenile males on the McCloud River were maturing without leaving the river. Mullan et al. (1992) found that early maturing resident males were common in both hatchery and wild populations in the Wenatchee River. Non-migrating mature males have also been observed in the Snake River Basin (Gebhards 1960, Burck 1967, Sankovich and Keefe 1996), Methow and Yakima Rivers (Hubble[5]), and the Deschutes River. Resident males have been observed among some stream- and ocean-type chinook salmon stocks in the Fraser River above Hell's Gate, which would have historically been a potential barrier to small migrating early maturing males, but not among lower river or coastal populations (Taylor 1989, Foote et al. 1991). The location and physical characteristics of each river may determine the expression of this life-history trait. It is unlikely that small jack males would be physically able to undertake the arduous return migration to many upriver areas (Mullan et al. 1992) or that sufficient time exists for the completion of the smolt emigration and return migration. Nonmigrating early maturing males may have a good chance of mating success, especially during poor return years when there may be a shortage of large males on the spawning grounds. The modification of smoltification, a major physiological process, to produce early maturing males in a population is indicative of the importance of this life-history trait to the reproductive success of specific populations.

The heritability of body size and age has been more extensively studied in chinook salmon than have other traits. Crosses between different aged parents have demonstrated that the ages of maturity for parents and progeny were strongly correlated (Ellis and Noble 1961, Donaldson and Bonham 1970, Hershberger and Iwamoto 1984, Withler et al. 1987, Hankin et al. 1993). The expression of early maturation in chinook salmon was found to have a significant genetic component; moreover, different stocks exhibited different levels of early maturation in response to environmental changes (Heath et al. 1994). The positive response of chinook salmon to selective breeding experiments is indicative of a significant genetic component to body size (Donaldson and Menasveta 1961). Chinook salmon stocks exhibit considerable variability in size and age of maturation, and at least some portion of this variation is genetically determined.

From an evolutionary standpoint, the potential increases in size, fecundity, and egg size gained from remaining on the marine feeding grounds an additional year must be weighed against the chances of mortality during that year (Healey and Heard 1984, Healey 1986). The specific conditions that exist in each river must also influence, in part, the expression of these characteristics. The size and age of spawning chinook salmon in any given population may have a significant impact on their survival, and trends in size and age were utilized in determining ESU boundaries. However, the large environmental influence (on a regional and annual basis) on chinook salmon size and age, as well as possible biases resulting from different fishery harvest techniques and the inclusion of hatchery reared fish, would suggest that available size and age data be used with caution.

Run Timing

Early researchers recorded the existence of different temporal "runs" or modes in the migration of chinook salmon from the ocean to freshwater. Two major influxes of chinook salmon were observed returning to the Sacramento-San Joaquin River system, although "...there is no definite distinction between spring and fall runs; there is no time during the summer when there are no salmon running" (Rutter 1904, p. 122). It was also reported that spring-run fish tended to migrate to the upriver portions of the Sacramento River and spawn earlier than the fall run, which spawned in the lower regions of tributaries and in mainstem river areas. A similar distinction was made between spring, summer, and fall or "snow" salmon runs in the Klamath River (Snyder 1931). The underlying genetic influence on run timing was initially demonstrated by Rich and Holmes (1928), when spring-run chinook salmon from the MacKenzie River were reared, marked, and released from a predominantly fall-run watershed. The transplanted chinook salmon displayed no apparent alteration in their normal time of return or spawning, although there was an increase in straying. Subsequent stock transplantations have further substantiated the heritable nature of run timing. Heritability estimates for return timing among early- and late-returning pink salmon (*Oncorhynchus gorbuscha*) runs in Alaska were 0.4 and 0.2 for females and males, respectively (Gharrett and Smoker 1993).

Freshwater entry and spawning timing are generally thought to be related to local temperature and water flow regimes (Miller and Brannon 1982). Temperature has a direct effect on the development rate of salmonids (Alderdice and Velsen 1978). Only one run timing for chinook salmon is found in most rivers in Alaska and northern British Columbia, where summers are short and water temperatures cold (Burger et al. 1985). The Kenai River in Alaska is an exception to this trend, having mid-June and mid-July runs that ultimately spawn in areas with distinct thermal regimes (Burger et al. 1985). Asian rivers are thought to contain only one run of chinook salmon, with the possible exception of the Kamchatka and Bol'shaya Rivers (Vronskiy 1972, Smirnov 1975). Among stream-type stocks, the King Salmon River in Alaska differs from the general trend in that adults return in a relatively mature condition and spawn in the lower river, extending down to the intertidal area (Kissner 1985, ADFG 1997). The majority of multiple run rivers are found south from the Bella Coola and Fraser Rivers.

Runs are designated on the basis of adult migration timing; however, distinct runs also differ in the degree of maturation at the time of river entry, thermal regime and flow characteristics of their spawning site, and actual time of spawning. Early, spring-run chinook salmon tend to enter freshwater as immature or "bright" fish, migrate far upriver, and finally spawn in the late summer and early autumn. Late, fall-run chinook salmon enter freshwater at an advanced stage of maturity, move rapidly to their spawning areas on the mainstem or lower tributaries of the rivers, and spawn within a few days or weeks of freshwater entry (Fulton 1968, Healey 1991). Summer-run fish show intermediate characteristics of spring and fall runs, spawning in large and medium-sized tributaries, and not showing the extensive delay in maturation exhibited by spring-run chinook salmon (Fulton 1968). Winter-run chinook salmon (which presently exist only in the Sacramento River) begin their freshwater migration at an immature stage and travel to the upper portions of the watershed to spawn in the spring. All stocks, and especially those that migrate into freshwater well in advance of spawning, utilize resting pools. These pools provide an energetic refuge from river currents, a thermal refuge from high summer and autumn temperatures, and a refuge from potential predators (Berman and Quinn 1991, Hockersmith et al. 1994). Furthermore, the utilization of resting pools may maximize the success of the spawning migration through decreases in metabolic rate and the potential reduction in susceptibility to pathogens (Bouck et al. 1975, Berman and Quinn 1991). In the Stilliguamish River, there was a high correlation between the location of pools and redds, suggesting that the pool abundance may limit the amount of spawning habitat available (PSSSRG 1997).

Run timing is also, in part, a response to streamflow characteristics. Rivers such as the Klickitat or Willamette Rivers historically had waterfalls which blocked upstream migration except during high spring flows (WDF et al. 1993). Low river flows on the south Oregon coast during the summer result in barrier sandbars which block migration (Kostow 1995). The timing of migration and, ultimately, spawning must also be cued to the local thermal regime. Egg deposition must be timed to ensure that fry emerge during the following spring at a time when the river or estuary productivity is sufficient for juvenile survival and growth. The strong association between run timing and ecological conditions made this trait useful in considering potential ESU boundaries.

Straying

The high degree of fidelity with which chinook salmon return to their natal stream has been shown in a number of studies (Rich and Holmes 1928, Quinn and Fresh 1984, McIsaac and Quinn 1988). Returning to one's natal stream may have evolved as a method of ensuring an adequate incubation and rearing habitat. It also provides a mechanism for reproductive isolation and local adaptation. Conversely, returning to a stream other than that of one's origin is important in colonizing new areas and responding to unfavorable or perturbed conditions at the natal stream (Quinn 1993). High rates of straying by returning Umatilla River fall chinook salmon (an introduced upriver bright stock) into the Snake River in 1987-89 were apparently related to poor acclimation, high water temperatures, and lack of water in the Umatilla River (Waples et al. 1991b). Straying coho salmon (*O. kisutch*) and sockeye salmon have rapidly colonized newly deglaciated habitat (Milner and Bailey 1989), and summer-run chinook salmon may have recolonized the Okanogan River following the cessation of trapping operations at Rock Island Dam, which blocked entry from 1939-43 (Waknitz et al. 1995). The degree of straying in wild populations determines the extent of reproductive isolation and the potential for the formation of ESUs.

Available information on straying rates primarily involves hatchery-reared, transplanted, or transported fish. Rich and Holmes (1928), in one of the earliest studies of homing, released marked chinook salmon juveniles from a number of hatcheries along the lower Columbia River. Of the 104 chinook salmon that were recovered in spawning areas or at hatchery racks, only 5 (4.8 %) had strayed to areas other than their release sites (Rich and Holmes 1928). Quinn and Fresh (1984) reported that only 1.4% of the returning spring-run chinook salmon from the Cowlitz River Hatchery were recovered outside of their natal watershed, and it was suggested that straying was more frequent in older fish and in years when the run-size was low. Olfactory cues provided by conspecifics on spawning grounds, especially large aggregations, may be a powerful attractant to returning salmon (Duker 1981). If these spawning aggregations are an attractant, it may explain the negative correlation between run-size and straying as well as explaining the observed straying of naturally-produced salmon into hatcheries. Chapman et al. (1991, 1994) suggested that straying is more common among fall-run fish than among spring-run fish. Quinn et al. (1991) found that straying rates differed considerably (10-27.5%) between hatcheries releasing fall chinook salmon on the lower Columbia River.

The adult returning migratory process has been shown to be under a significant genetic influence. In one experiment, "upriver bright" chinook salmon were captured, spawned, and the subsequent progeny reared and released from a downriver site (McIsaac and Quinn 1988). A significant fraction of the returning adults from the upriver bright progeny group bypassed their rearing site and returned to their "traditional" spawning ground 370 km further upriver.

Hatchery rearing and release procedures may increase the rate of straying. Wild chinook salmon had significantly lower straying rates than did hatchery-reared fish from the Lewis River (McIsaac 1990). Releasing fish even a short distance from the hatchery can dramatically increase the straying rate (Quinn 1993, Heard 1996). Straying rates as high as 86% resulted from the long-distance transportation and release of fall chinook salmon in the Sacramento River (Cramer 1989). Unfavorable conditions (high water temperature and low flow) at hatchery return facilities may further increase straying rates (Quinn 1993). The use of hatchery stocks founded from a composite of wild stocks (e.g., upriver bright fall chinook salmon) may increase straying if the genetic component to homing is more important than the olfactory (learned) component. Chapman et al. (1994) indicated that Columbia River fall chinook salmon upriver bright hatchery stocks did have a relatively high straying rate. However, Pascual and Quinn (1994) found similar homing success rates for local and introduced stocks of chinook salmon released in the Columbia River.

Any interpretation of straying rates should consider the way in which strays were enumerated. Chapman et al. (1991) made a distinction between "legitimate" strays and "wanderers," those fish that enter non-native streams as a part of their homing search or as a temporary refuge from unfavorable river conditions. Wanderers will normally retreat from these non-native streams and continue their return migration; however, where weirs or hatchery traps are present, wanderers will be unable to return and are often considered strays. Additionally, straying rates can be influenced by the effort placed on surveying sites other than the release site.

The use of cut-off dates by hatcheries to separate run-times can result in "temporal" straying. Cope and Slater (1957) found that 16% of the fish returning as "spring-run" adults to Coleman NFH were produced from fall-run parents, and 19% of the returning "fall-run" adults came from spring-run parents. The use of fixed return or spawning dates to distinguish runs at adult collection facilities may have resulted in the introgression of previously distinct stocks (Mullan 1987, WDF et al. 1993, Waknitz et al. 1995).

Straying by hatchery fish, especially those from non-native hatchery stocks, increases the potential for interbreeding and genetic homogenization. This may result in the loss of regionally distinct life-history characteristics.

Fecundity and Egg Size

Fecundity and egg size differences between stocks of salmon occur on a geographic basis. In salmon, fecundity tends to increase while egg size decreases with latitude (Healey and Heard 1984, Kaev and Kaeva 1987, Fleming and Gross 1990). Variation between and within regions can be considerable.

The anadromous life history of salmon is thought to be a response to the relatively poor productivity of glacially influenced or unstable freshwater environments relative to the nearby marine habitat (Neave 1958, Miller and Brannon 1982). In order to maximize the success of their emigration to saltwater, salmon juveniles must obtain a relatively large size in productivity-limited freshwater environments. One strategy for accomplishing this is through the production of large eggs and thereby large embryos (Taylor 1991, Kreeger 1995). Larger eggs produce larger fry (Fowler 1972), which may be more successful at migrating to saltwater than smaller fry (Kreeger 1995). Ocean-type chinook salmon stocks in British Columbia were reported to have larger eggs than stream-type stocks (Lister 1990). Rich (1920b) found that some chinook salmon returning to coastal streams in Oregon and Washington had larger eggs than fish returning to the Columbia River. In general, Smironov (1975) suggested that latitudinal differences existed in egg size, with southern stocks having larger eggs. Furthermore, he speculated that this was because embryonic development at higher temperatures is less efficient; southern stocks need more energy stores (larger eggs) to complete development. Alternatively, this trend may be related to the need for more southerly, predominantly ocean-type, chinook salmon to produce larger-sized fry for migration to estuary areas. In general, stream-type stocks of chinook salmon have smaller eggs than ocean-type stocks. However, there is no apparent latitudinal cline in egg size among stream-type nor ocean-type stocks (Appendix C).

Older (larger) year classes of salmon tend to produce larger sized eggs but not proportionately larger numbers of eggs than their younger (smaller) counterparts; this may be a life-history strategy to improve the survival of individual progeny rather than producing more of them (Gray 1965, Iwamoto 1982, Beacham and Murray 1985, Healey 1986, Nicholas and Hankin 1988). Factors affecting egg size in chinook salmon appear to be operating on a between- and within-population basis. Variability in egg size within populations appears to be most directly related to fish size and, to a lesser extent, age (Healey and Heard 1984, Hankin and McKelvey 1985), whereas between-population differences may represent an adaptation to regional environmental and geographic conditions.

Physiological and ecological factors have been identified that may limit the potential minimum and maximum egg sizes, 0.12 and 0.47 g, respectively (Quinn and Bloomberg 1992). The physical limitations of large eggs in absorbing oxygen due to a reduced surface area-to-volume ratio and the generally high physiological oxygen demands of salmonids may limit the maximum size of chinook salmon eggs. Stream flow, gravel quality, and silt load all significantly influence the survival of developing chinook salmon eggs. Therefore, behavioral traits such as spawning site selection would need to be correlated with physical fecundity traits. Healey (1991) showed that suboptimum habitat conditions delay or discourage spawning at a specific site.

Variation in fecundity and egg size among different stocks of chinook salmon appears to be related to geography and life-history strategy. Chinook salmon females sampled from the Sacramento River had 68% more eggs than females from the Klamath River, after adjusting for differences in body size (Snyder 1931, Healey and Heard 1984). Fecundity is related to body size, although this relationship is also dependent on a number of other factors--age, migration distance, latitude--and varies between stocks (Healey and Heard 1984, Kaev and Kaeva 1987, Fleming and Gross 1990). Galbreath and Ridenhour (1964) found that linear length-fecundity regressions for the Columbia River chinook salmon stocks were not significantly different when compared on a seasonal (monthly) run timing, total age, or smolt age basis; however, differences in body size and a small sample size may have obscured racial differences in fecundity. A further complication in the analysis of fecundity traits is the difference in body weight devoted to gonadal tissue in coastal and inland populations. Populations which undertake extended migrations may not be able to devote the same percentage of body weight toward gonad (especially ovary) development (Lister 1990). Linley (1993) found a significant negative correlation for adult sockeye salmon between the percentage of body weight devoted to gonads and the length and duration of the freshwater migration. Ivankov (1983) determined that differences in the fecundity of masu salmon (*O. masu*) females within and among rivers were correlated with juvenile growth rate and the rate of gonadal development prior to saltwater emigration, although he did not specifically evaluate the relative contributions of genetic and environmental effects.

Correlations between fecundity and body size and age, in addition to environmental fluctuations over several years, complicate the interpretation of fecundity differences. Furthermore, the majority of fecundity information comes from hatchery populations. Differences in selection on fecundity and egg size traits under hatchery conditions relative to the natural environment may limit the representative value of hatchery populations for their wild counterparts (Fleming and Gross 1990).

Other Life-History Traits

Information concerning the variability, adaptiveness, and heritability of other life-history traits in salmon is extremely limited. Genetically based differences in the rate of Pacific salmon embryonic and alevin development between run times in the same river (Tallman 1986), and between rivers (Iwamoto 1982, Beacham and Murray 1987, 1989) represent important adaptations to ensure emergence occurs at a time for optimal survival. The heritability estimates for embryonic development to hatch in chinook salmon range from 0.25 to 0.40 (Hickey 1983). Smirnov (1975) suggested significant differences in the embryonic development exist between Asian and North American stocks of chinook salmon.

Pathogen resistance is another locally adapted trait. Chinook salmon from the Columbia River drainage exhibited reduced susceptibility to *Ceratomyxa shasta*, an endemic pathogen, relative to stocks from coastal rivers where the disease is not known to occur (Zinn et al. 1977). Differences in susceptibility to the infectious hematopoietic necrosis virus (IHNV) were detected between Alaskan and Columbia River stocks of chinook salmon (Wertheimer and Winton 1982). Variability in temperature tolerance between populations is also probably due to adaptation to local conditions; however, information on the genetic basis of this trait is lacking (Levings 1993).

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Regional Variation in Life-History Traits

Comparisons of life-history traits among chinook salmon populations revealed regional differences in many traits. The definition of geographic regions which contained populations with similar life-history attributes was an important step in the establishment of tentative ESU boundaries. The following discussion includes information on anthropogenic changes in habitat quality, stock transfers, and artificial propagation efforts. The impacts of these activities on genetic integrity, abundance, and other potential risks to chinook salmon populations are discussed in later sections in more detail and are included here only to the extent that these activities may have altered the expression of life-history traits in presumptive native populations.

Puget Sound to the Strait of Juan de Fuca

Chinook salmon are found in most of the rivers in this region. WDF et al. (1993) recognizes 27 distinct stocks of chinook salmon: 8 spring-run, 4 summer-, and 15 summer/fall- and fall-run stocks. The existence of an additional five spring-run stocks has been disputed among different management agencies (WDF et al. 1993). The Skagit River and its tributaries--the Baker, Sauk, Suiattle, and Cascade Rivers--constitute what was historically the predominant system in Puget Sound containing naturally spawning populations (WDF et al. 1993). Spring-run chinook salmon are present in the North and South Fork Nooksack Rivers, the Skagit River Basin, the White, and the Dungeness Rivers (WDF et al. 1993). Spring-run populations in the Stillaguamish, Skokomish, Dosewallips, and Elwha Rivers are thought to be extinct (Nehlsen et al. 1991). Summer-run chinook salmon are present in the Upper Skagit and Lower Sauk Rivers in addition to the Stilliguamish and Snohomish Rivers (WDF et al. 1993). Fall-run stocks (also identified by management agencies as summer/fall runs in Puget Sound) are found throughout the region in all major river systems. The artificial propagation of fall-run stocks is widespread throughout this region. Summer/fall chinook salmon transfers between watersheds within and outside the region have been commonplace throughout this century; thus, the purity of naturally spawning stocks varies from river to river. Captive broodstock/recovery programs for spring-run chinook salmon have been undertaken on the White River (Appleby and Keown 1994), and the Dungeness River (Smith and Sele 1995b). Supplementation programs currently exist for spring-run chinook salmon on North Fork Nooksack River and summer-run chinook salmon on the Stillaguamish and Skagit Rivers (Marshall et al. 1995, Fuss and Ashbrook 1995). Hatchery programs also release Suiattle River spring-run chinook salmon and Snohomish River (Wallace River) summer-run chinook salmon (Marshall et al. 1995, Fuss and Ashbrook 1995). The potential impacts of artificial propagation and rearing programs (especially delayed-release programs) on the expression of life-history traits were taken into account when comparing the characteristics of each stock.

Adult spring-run chinook salmon in the Puget Sound typically return to freshwater in April and May (Table 1) and spawn in August and September (Fig. 10) (Orrell 1976, WDF et al. 1993). Adults migrate to the upper portions of their respective river systems and hold in pools until they mature. In contrast, summer-run fish begin their freshwater migration in June and July and spawn in September, while summer/fall-run chinook salmon begin to return in August and spawn from late September through January (WDF et al. 1993). Studies with radio-tagged fish in the Skagit River indicated that river-entry time was not an accurate predictor of spawning time or location (SCC 1995). In rivers with an overlap in spawning time, temporal runs on the same river system maintain a certain amount of reproductive isolation through geographic separation. For example, an 18-km river section (at river kilometer (RKm) 35-53) of poor spawning habitat separates the spawning areas for summer and spring runs on the Sauk River (Williams et al. 1975).

The majority of Puget Sound fish emigrate to the ocean as subyearlings. Many of the rivers have well-developed estuaries that are important rearing areas for emigrating ocean-type smolts. Puget Sound stocks also tend to have relatively large eggs, with average diameter being greater than 8.0 mm, which may be an adaptation for their subyearling smolting strategy. In contrast, the Suiattle and South Fork Nooksack Rivers have been characterized as producing a majority of yearling smolts (Fig. 11) (Marshall et al. 1995). Analysis of scales from adults returning to the South Fork Nooksack in 1994 and 1995 indicated that 69.1% of the fish had emigrated as yearlings (WDFW 1995); however, analysis of adults returning in 1980-85 showed only 16.4% of the fish had emigrated as yearlings and 75% of these were hatchery fish (WDFW, unpublished). The reason for this difference is unknown. Glacially influenced conditions on the Suiattle River may be responsible for limiting juvenile growth, delaying smolting, and producing a higher proportion of 4- and 5-year-olds compared to other chinook salmon stocks in Puget Sound, which mature predominantly as 3- and 4-year-olds (Fig. 12). Puget Sound stocks exhibit a similarity in marine distribution based on CWT recoveries in ocean fisheries. Tagged fish have been primarily captured in Canadian coastal and Puget Sound waters (Fig. 13). Marine recoveries of CWTs from Nooksack River spring-run chinook salmon have occurred to a lesser extent in the Puget Sound fishery than in other Puget Sound stocks. This may be due to the geographical position of the Nooksack River Basin at the northern end of Puget Sound and/or the allocation of effort by fishers in Puget Sound. Additionally, Elwha River summer/fall chinook salmon CWT recoveries in Alaska and Puget Sound appear to be intermediate in their frequencies between Puget Sound stocks and Washington coast stocks.

Anthropogenic activities have limited the access to historical spawning grounds and altered downstream flow and thermal conditions. Water diversion and hydroelectric dams haveprevented access to portions of several rivers. Furthermore, the construction of Cushman Dam on the North Fork Skokomish River may have resulted in a residualized population of chinook salmon in Lake Cushman. Watershed development and activities throughout Puget Sound, Hood Canal, and Strait of Juan de Fuca regions have resulted in increased sedimentation, higher water temperatures, decreased large woody debris (LWD) recruitment, decreased gravel recruitment, a reduction in river pools and spawning areas, and a loss of estuarine rearing areas (Bishop and Morgan 1996). These impacts on the spawning and rearing environment may also have had an impact on the expression of many life-history traits and masked or exaggerated the distinctiveness of many stocks.

Life-history similarities--emigration timing, age at maturation, and ocean migration--among spring-, summer-, and fall-run chinook salmon may be related to the relatively recent deglaciation (10,000 b.p.) of the Puget Sound region. It is unclear when suitable freshwater habitats for chinook salmon became available in the Puget Sound area following deglaciation (Busack and Marshall 1995). However, chinook salmon in Oregon coastal rivers, which were not glaciated, also show little differentiation in life-history characteristics, except for run timing. The life history exhibited may instead represent an optimized strategy for stocks in the Puget Sound area regardless of run timing or simply the homogenization of stocks due to artificial propagation.

Washington and Oregon coasts (Hoko River to Cape Blanco)

Fall-, summer-, and spring-run chinook salmon are found in this region. Rivers in this region tend to be short with low gradients near the coast. These low gradient areas are preferred spawning sites for chinook salmon. The relatively small size of the rivers limits the amount of spawning habitat available and minimizes the likelihood of spatial separation of run times. The Chehalis and Umpqua Rivers are physically much larger than any of the other basins, although they do not maintain proportionately larger chinook salmon runs. WDF et al. (1993) recognized 2 spring-run, 4 summer-run, 4 spring/summer-run, and 23 fall-run "stocks" on the Washington coast. According to the Oregon Department of Fish and Wildlife (ODFW), the Oregon coast from the mouth of the Columbia River to Cape Blanco contains 11 spring-run, 1 summer-run, and 33 fall-run populations (Kostow 1995). Peak spawning periods for spring, spring/summer, and summer-run populations occur from mid-September to early October which is somewhat later than in Puget Sound and the Strait of Juan de Fuca. Peak river-entry times for spring- and summer-run stocks range from May to August. In general, populations considered spring, spring/summer, and summer runs return to the river at an immature stage and hold in the river for an extended period before spawning. In contrast, fall-run fish enter freshwater at an advanced stage of maturation. Peak spawning periods for coastal fall runs occur from late-October to early-December, with a tendency for later spawning in more southerly rivers. The existence of multiple runs on many of the smaller coastal river systems is associated with low summer flows that physically limit access or result in high summer water temperatures in the lower river reaches (Nicholas and Hankin 1988).

Chinook salmon from the Washington and Oregon coasts emigrate to saltwater primarily as subyearlings and utilize the productive estuary and coastal areas as rearing habitat. The limited size of many coastal watersheds mandates the reliance on extended estuary or coastal rearing by juveniles. Furthermore, high summer water temperatures and related low flows may be responsible for early emigration. Chinook salmon from coastal populations (ocean-type) tend to have much larger eggs than inland, predominantly stream-type, populations (Rich 1920b , Nicholas and Hankin 1988, Lister 1990). Larger eggs result in larger juveniles and may enable an earlier and more successful emigration to marine rearing habitat (Fowler 1972, Kreeger 1995). The Washington and Oregon coasts contain numerous large estuary areas: Grays Harbor, Willapa Bay, Tillamook Bay, Coos Bay, Winchester Bay (Umpqua R.), and Yaquina Bay. Emigrating juveniles from rivers without well-developed estuary systems may undertake coastal migrations to estuary feeding areas or find sufficient rearing habitat in coastal areas, but it is unclear which strategy they undertake. Coastal chinook salmon from this region also mature at a later age than stocks from Puget Sound, the lower Columbia River and southern Oregon coastal areas (Nicholas and Hankin 1988, SCC 1995, QFD 1995, WDFW 1995). The majority of the runs are composed of 4- and 5-year-old fish, with a small proportion of 6-year-olds. The numerically large populations of chinook salmon on smaller coastal rivers may create competition for mates and select for larger (older) male chinook salmon (Roni and Quinn 1995).

Marine recoveries of CWTs indicate a similar ocean migration distribution for Washington and northern Oregon coastal stocks. The majority of the recoveries are from 4- and 5-year-old fish in British Columbia and Alaska fisheries. This is a more northerly oceanic distribution than is observed for Puget Sound, Lower Columbia River, and Southern Oregon and California stocks. A proportion of fish from stocks in the vicinity of Cape Blanco tend to exhibit a "north-and-south" migration pattern, with a proportion of recoveries occurring in Oregon and California coastal waters (Nicholas and Hankin 1988). The existence of a transition zone in migratory patterns may be due to natural and/or anthropogenic factors. CWT ocean recoveries of Umpqua River spring-run chinook salmon, specifically Rock Creek Hatchery fish, show a north and south distribution. The mouth of the a single ESU. Contrasting minority viewpoints were that: 1) Spring-run fish are part of the same ESU that includes the fall and late-fall runs; 2) fall and late-fall runs constituted separate ESUs; and 3) fall-run fish in the San Joaquin River Basin constituted their own ESU.

4) Southern Oregon and California Coastal ESU

All coastal spring and fall chinook salmon spawning from Cape Blanco (south of the Elk River) to the southern extent of the current range comprise this ESU. The Cape Blanco region is a major biogeographic boundary for numerous species. The Southern Oregon and California Coastal ESU extends to the southern limit of the Coastal Range Ecoregion. Populations from the Central Valley and Klamath River Basin upstream from the Trinity River confluence are in separate ESUs. Chinook salmon in this ESU exhibit an ocean-type life-history; ocean distribution (based on marine CWT recoveries) is predominantly off the California and Oregon coasts. Life-history information on smaller populations, especially in the southern portion of the ESU, is extremely limited. Additionally, there was anecdotal or incomplete information on the existence of several spring-run populations, including the Chetco, Winchuck, Smith, Mad, and Eel Rivers. Allozyme data indicate that this ESU is genetically distinguishable from the Oregon Coast, Upper Klamath and Trinity River, and Central Valley ESUs.

Ecologically, the majority of the river systems in this ESU are relatively small and heavily influenced by a maritime climate. Low summer flows and high temperatures in many rivers result in seasonal, physical, and thermal barrier bars that block movement by anadromous fish. The Rogue River is the largest river basin in this ESU and extends inland, into the Sierra Nevada and Cascades Ecoregions.

A minority of the BRT felt that coastal chinook salmon from south of the Klamath River should be considered a separate ESU. Allozyme data, which show some level of genetic divergence between coastal chinook salmon populations north and south of the Klamath River, support this argument, as do the establishment of ESU boundaries for steelhead south of the Klamath River and for coho salmon south of Punta Gorda. A nearly total lack of biological information for chinook salmon south of the Eel River makes this issue difficult to resolve.

The BRT also considered arguments for the creation of separate fall- and spring-run ESUs in this and other coastal regions, but the consensus of the BRT was that this was not warranted.

5) Upper Klamath and Trinity Rivers ESU

Included in this ESU are all Klamath River Basin populations from the Trinity River and the Klamath River upstream from the confluence of the Trinity River. These populations include both spring- and fall-run fish that enter the Upper Klamath River Basin from March through July and July through October and spawn from late August through September and September through early January, respectively. Body morphology (vertebral counts, lateral-line scale counts, and fin-ray counts) and reproductive traits (egg size and number) for populations from the Upper Klamath River differ from those of populations in the Sacramento River Basin. Genetic analysis indicated that populations from the Upper Klamath River Basin form a unique group that is quite distinctive compared to neighboring ESUs. The Upper Klamath River crosses the Coastal Range, Sierra Nevada, and Eastern Cascades Ecoregions, although dams prevent access to the upper river headwaters of the Klamath River in the Eastern Cascades Ecoregion.

Within the Upper Klamath River Basin, there are statistically significant, but fairly modest, genetic differences between the fall and spring runs. The majority of spring- and fall-run fish emigrate to the marine environment primarily as subyearlings, but have a significant proportion of yearling smolts. Recoveries of CWTs indicate that both runs have a coastal distribution off the California and Oregon coasts. There was no apparent difference in the marine distribution of CWT recoveries from fall-run (Iron Gate and Trinity River Hatcheries) and spring-run populations (Trinity River Hatchery). The BRT discussed at some length the proposition that spring- and fall-run populations should be in separate ESUs based on differences in run timing and habitat utilization and reproductive isolation. The majority of the BRT concluded that both run types should be considered part of the same ESU; a minority felt that separation into two ESUs was warranted; and some BRT members were undecided on this issue. The BRT was concerned that the only estimate of the genetic relationship between spring and fall runs in this ESU is from a comparison of hatchery stocks that may have undergone some introgression during hatchery spawning operations. The BRT acknowledged that the ESU determination should be revisited if substantial new information from natural spring-run populations becomes available.

6) Oregon Coast ESU

This ESU contains coastal populations of spring- and fall-run chinook salmon from the Elk River north to the mouth of the Columbia River. These populations exhibit an ocean-type life history and mature at ages 3, 4, and 5. In contrast to the more southerly ocean distribution pattern shown by populations from the lower Columbia River and farther south, CWT recoveries from populations within this ESU are predominantly from British Columbia and Alaska coastal fisheries. There is a strong genetic separation between Oregon Coast ESU populations and neighboring ESU populations. This ESU falls within the Coastal Ecoregion and is characterized by a strong maritime influence, with moderate temperatures and high precipitation levels.

A minority of the BRT felt that, because of similarities in life-history traits and environmental features, populations from the Oregon and Washington coasts were part of a single ESU. A separate minority felt that, based primarily on genetic information, the Oregon Coast ESU should be divided into two units, with populations north of the Umpqua River being in separate ESUs.

7) Washington Coast ESU

Coastal populations spawning north of the Columbia River and west of the Elwha River are included in this ESU. These populations can be distinguished from those in Puget Sound by their older age at maturity and more northerly ocean distribution. Allozyme data also indicates geographical differences between populations from this area and those in Puget Sound, the Columbia River, and the Oregon coast ESUs. Populations within this ESU are ocean-type chinook salmon and generally mature at ages 3, 4, and 5. Ocean distribution for these fish is more northerly than that for the Puget Sound and Lower Columbia River ESUs. The boundaries of this ESU lie within the Coastal Ecoregion, which is strongly influenced by the marine environment: high precipitation, moderate temperatures, and easy migration access. As noted above, a minority of the BRT felt that this ESU should be combined with chinook salmon from the Oregon coast.

8) Puget Sound ESU

This ESU encompasses all runs of chinook salmon in the Puget Sound region from the North Fork Nooksack River to the Elwha River on the Olympic Peninsula. Chinook salmon in this area all exhibit an ocean-type life history. Although some spring-run chinook salmon populations in the Puget interbasin transfers that were common in earlier decades (CDNR 1931). The Russian River is a notable exception to this rule, having received artificially propagated fall-run chinook salmon from a variety of sources, most commonly Sacramento River stocks and the Great Lakes (which were stocked with a myriad of populations from Washington, Oregon, and California) (Appendix D). In the absence of existing permanent native runs of chinook salmon, local enhancement efforts south of San Francisco Bay in this area have generally used Sacramento River fall-run chinook salmon, although stocks from Washington, Oregon and the Great Lakes have been released there as well (NRC 1996). Spring-run chinook salmon artificial propagation has been very limited in the coastal river basins of California, with the exception of the Klamath River Basin (see ESU #5).

5) Upper Klamath and Trinity Rivers ESU

Early artificial propagation efforts in the Upper Klamath and Trinity Rivers began at the turn of the century. In 1896, over a million chinook salmon fry were introduced into the Klamath River from the Sacramento River (Snyder 1931). In 1890, a fish hatchery at Fort Gaston on Minor Creek, a tributary to the Trinity River, was established (Kirk 1994). During the operation of this hatchery (1890-98) eggs were collected from the Trinity and Sacramento (Baird NFH) Rivers and Redwood Creek, and the majority of the 2 million fry produced from this facility were released into the Trinity River and Redwood Creek (Snyder 1931). Several canneries near the mouth of the Klamath River also operated small hatcheries on an intermittent basis. The U.S. Fisheries Commission Hornbrook Hatchery (later known as the Klamathon Racks) on Cottonwood Creek (a tributary of the Klamath River) initially trapped rainbow trout and coho salmon, but in 1914 trapping operations were relocated on the Klamath River to intercept chinook salmon (Snyder 1931). On average, several million eggs were collected at this site annually. By 1916, nearly 17 million chinook salmon fry had been released into the Klamath River Basin (Cobb 1930). Surplus eggs were normally transferred to the CDFG hatchery at Sisson, California (later named the Mt. Shasta Hatchery) for incubation and rearing (Snyder 1931).

To mitigate the loss of spawning habitat caused by the construction of COPCO Dam (RKm 320) on the Klamath River in 1917, a CDFG hatchery was constructed on Fall Creek (RKm 316) and supplied with eggs from the Klamathon egg collection site (Shebley 1922). From 1916 to 1928, over 118 million chinook salmon eggs had been collected from the Klamath River (Snyder 1931). Although a substantial proportion of the fry and fingerlings produced from these eggs were returned to the Klamath River Basin, millions of eggs and fry were transferred to the Sacramento, Eel, and Mad Rivers (Shebley 1915 1922; Snyder 1931). The disposition of many millions of additional eggs is unclear. The Fall Creek Hatchery was closed in 1948, and although egg collections continued, no rearing facilities existed on the Klamath until 1966 (KRBFTF 1991).

The construction of Iron Gate Dam on the Klamath River (1962) resulted in the construction of the Iron Gate Hatchery (1965). Eggs for the Iron Gate Hatchery have primarily been collected from adults returning to the hatchery, although the hatchery has occasionally relied on spawners captured in the nearby Bogus Creek. Similarly the impact of the completion of the Lewiston Dam (RKm 249) on the Trinity River (1964) was mitigated by the construction of the Trinity River Hatchery (RKm 247) in 1963. Prior to the completion of the hatchery (1958-62), returning adult chinook salmon had been trapped downstream from the dam construction site, spawned, and their eggs incubated at Mt. Shasta Hatchery.

Iron Gate Hatchery has released primarily fall-run chinook salmon. Attempts to maintain a spring run from adults returning to the hatchery were intermittent and eventually abandoned. The Trinity River Hatchery has successfully maintained both fall and spring runs of chinook salmon. Both hatcheries have relied on returning adults to maintained their runs. Since 1965, the upper Klamath River has received about 7.3 million fall-run chinook salmon juveniles per year; almost all have been Klamath River stock (Appendix D). Since 1964, about 2.6 million fall-run chinook salmon and 1.5 million spring-run chinook salmon have been released in the Trinity River each year (Appendix D), all of which have been of Trinity or Klamath River origin.

Pathogens, specifically infectious hematopoietic necrosis virus (IHNV) and bacterial kidney disease (BKD), which are caused by *Renibacterium salmoninarum*, have been detected in juvenile and returning adult spring-run chinook salmon from the Trinity River Hatchery (PFMC 1994). These pathogens may have significantly limited the success of hatchery programs in the Klamath River Basin; for example, IHNV was associated with the loss of 20% of the spring-run chinook juveniles held at the Trinity River Hatchery (PFMC 1994). Another consequence of artificial propagation in this ESU has been the inadvertent hybridization of chinook and coho salmon at the Iron Gate Hatchery (Bartley et al. 1990). However, because this interspecies hybrid is sterile (Johnson 1988a), the long-term genetic effects of this hybridization are minimal while ecological effects would depend on the hybridization rate.

6) Oregon Coast ESU

Artificial propagation efforts for chinook salmon in this ESU began in the late 1890s. By the early 1900s, there were hatcheries or egg-taking stations on most of the larger streams along the Oregon coast, especially the Yaquina, Alsea, Siuslaw, Umpqua, Coos, and Coquille Rivers (Cobb 1930, Wahle and Smith 1979). Before 1960, a substantial portion of the chinook salmon introduced into river basins in this ESU came from lower Columbia River (LCR) fall- and spring-run chinook salmon stocks--mostly from the Bonneville and Clackamas Hatcheries (Appendix D).

Chinook salmon populations in this ESU were considered to be mostly wild prior to 1960, based on the relatively low number of hatchery fish contributing to naturally spawning populations (Kaczynski and Palmisano 1993). However, the contribution of hatchery-reared fish relative to naturally spawning fish in this ESU has apparently increased since that time (ODFW 1995). Declining numbers of wild salmon prompted an increase in artificial propagation efforts. Improvements in hatchery rearing and release practices, feed formulation, and disease treatment have allowed hatcheries to produce fish that are larger, more fully-smolted, and healthier than fish produced before the mid-1960s (McGie 1980). Releases of larger smolts, in turn, have yielded a higher survival to adulthood than previous releases of fry and parr-stage fish (CBFWA 1990a). Furthermore, legislation enacted in the mid-1970s allowed the establishment of privately operated, for-profit hatcheries in Oregon (Wahle and Smith 1979). Private facilities operated in the Coos River and Yaquina River Basins until 1988 and 1989, respectively (NRC 1996). These salmon ranching operations released millions of smolts produced from spring- and fall-run broodstock primarily obtained from Oregon coastal rivers, such as the Rogue, Trask, and Yaquina (NRC 1996). In addition, a number of smaller cooperative hatcheries, built to restore depleted populations, are responsible for a substantial proportion of the current hatchery production (Appendix D).

Currently, most of the fall-run chinook salmon populations in this ESU are thought to have been minimally influenced by hatchery fish, which made up less than 10% of the spawning population (Kostow 1995). However, hatchery fish are thought to comprise up to 50% or more of the naturally spawning fish in the Salmon and Elk Rivers (ODFW 1995); Kaczynski and Palmisano (1993) estimated that 78% of natural spawners in the Elk River were of hatchery origin. Although fall-run chinook salmon hatchery programs are currently in operation in a number of basins, ODFW (1995)