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Status Review of Pink Salmon from Washington, Oregon, and California

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Status Review of Pink Salmon from Washington, Oregon, and California

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Contents

EXECUTIVE SUMMARY

The Endangered Species Act (ESA) allows listing of "distinct population segments" of vertebrates as well as named species and subspecies. The policy of the National Marine Fisheries Service (NMFS) on this issue for anadromous Pacific salmonids is that a population will be considered "distinct" for purposes of the ESA if it represents an evolutionarily significant unit (ESU) of the species as a whole. To be considered an ESU, a population or group of populations must 1) be substantially reproductively isolated from other populations, and 2) contribute substantially to ecological/genetic diversity of the biological species. Once an ESU is identified, a variety of factors related to population abundance are considered in determining whether a listing is warranted.

In March 1994, in response to a petition seeking protection under the ESA for two populations of pink salmon in Washington State, NMFS initiated a status review of pink salmon in Washington, Oregon, and California, and formed a Biological Review Team (BRT) to conduct the review. This report summarizes biological and environmental information gathered in that process.

Proposed Pink Salmon ESUs

Pink salmon (*Oncorhynchus gorbuscha*) spawn around the Pacific Rim from 44°N to 65°N in Asia and from 48°N to 64°N in North America. Washington appears to be the southern limit of the spawning distribution of pink salmon in North America; no persistent populations of pink salmon have been documented in Oregon or California, and pink salmon do not occur in Idaho. The BRT examined genetic, life history, biogeographic, physiographic, and environmental information to identify where ESU boundaries for pink salmon should be located. Patterns of genetic differentiation and life history in pink salmon were found to be the most informative for this process. Based on this examination, the BRT identified two pink salmon ESUs in Washington and southern British Columbia. These ESUs, which largely reflect the distinction between even- and odd-year broodlines that are characteristic of pink salmon throughout their natural range, are described as follows:

1) Even-year pink salmon. The only persistent population of even-year pink salmon in Washington occurs in the Snohomish River. Although several attempts were made in this century to transplant even-year pink salmon from Alaska and British Columbia to the Puget Sound region, there is no indication that these attempts were successful. Furthermore, life history and genetic information for Snohomish River even-year pink salmon is consistent with the hypothesis that this population resulted from a natural colonization event. The nearest even-year pink salmon populations occur in British Columbia, at least 130-150 km away. On the basis of available information, the BRT could not resolve with any degree of certainty the extent of the ESU that contains the Snohomish River even-year pink salmon population. After considering all available information, about half of the BRT members concluded that

the Snohomish River even-year population is in an ESU by itself, whereas half judged that the ESU also included populations from British Columbia. In any case, the BRT unanimously agreed that any conclusion about the extent of the even-year pink salmon ESU should be regarded as provisional and subject to revision should substantial new information become available.

2) Odd-year pink salmon. The BRT considered several possible ESU scenarios for odd-year pink salmon. The majority of BRT members concluded that all odd-year pink salmon populations in Washington are part of a single ESU. This ESU includes populations in Washington as far west as the Dungeness River (or the Elwha River, if that population is not already extinct) and in southern British Columbia (including the Fraser River and eastern Vancouver Island) as far north as Johnstone Strait. A minority of BRT members concluded that populations from Washington rivers draining into the Strait of Juan de Fuca are members of a separate ESU. All members agreed that, collectively, odd-year pink salmon in Washington contain a considerable amount of genetic and life history diversity, with populations from the Dungeness, Nooksack, and Nisqually Rivers being the most distinctive in this regard. Several small odd-year populations occur on southwestern Vancouver Island, but little information is available to ascertain the relationship of these populations to the proposed odd-year ESU. Additional information on these populations is needed to resolve the question of whether odd-year pink salmon in Washington and southern British Columbia are in one or more ESUs.

Assessment of Extinction Risk

The ESA (section 3) defines the term "endangered species" as "any species which is in danger of extinction throughout all or a significant portion of its range." The term "threatened species" is defined as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." According to the ESA, the determination whether a species is threatened or endangered should be made on the basis of the best scientific information available regarding its current status, after taking into consideration conservation measures that are proposed or are in place. In this review, the BRT did not evaluate likely or possible effects of conservation measures and, therefore, did not make recommendations as to whether identified ESUs should be listed as threatened or endangered species; rather, the BRT drew scientific conclusions about the risk of extinction faced by identified ESUs under the assumption that present conditions will continue. The resulting conclusions for each ESU follow.

1) Even-year pink salmon. The BRT was unanimous in concluding that this ESU is not presently at risk of extinction. Nevertheless, nearly all BRT members expressed concerns about the status of this ESU. Although available escapement data suggest that the even-year pink salmon population in the Snohomish River has been increasing since 1980, the low abundance and isolation of this population--when coupled with the lack of variable age structure in pink salmon--suggest that the population is at some risk due to demographic or

environmental fluctuations. All BRT members agreed that this population should be closely monitored, even if it is determined to be part of a larger ESU.

2) Odd-year pink salmon. The BRT was unanimous in concluding that this ESU as a whole is not presently at risk of extinction. Most populations appear to be healthy, and overall abundance appears to be close to historical levels. The two most distinctive Puget Sound populations (from the Nooksack and Nisqually Rivers) both show nonsignificant trends in recent abundance, and no other factors were found that would suggest that either of these populations is at immediate risk. However, most BRT members expressed concerns about the status of certain populations within this ESU. For odd-year pink salmon, two of the three U.S. populations along the Strait of Juan de Fuca are in steep decline, and the third may already be extinct. The population nearest to these three occurs in northern Hood Canal and is also declining. However, the remaining odd-year populations in the United States, as well as most of those in southern British Columbia, show no evidence of sustained declines, and many are increasing in abundance. In addition, the other U.S. populations that are the most distinctive based on genetic and life history characteristics appear to be healthy. The majority of BRT members therefore concluded that the odd-year pink salmon ESU is not presently at risk of extinction or endangerment. However, BRT members unanimously expressed concern about the status of the marginal populations along the Strait of Juan de Fuca, and concern that further erosion of these populations might eventually pose risk to a significant portion of the ESU as a whole. In addition, evidence exists for a recent decline in body length of odd-year Washington pink salmon, which increases risk to these populations by limiting their ability to respond to perturbation. A similar decline has also been observed in pink salmon from southeastern Alaska.

ACKNOWLEDGMENTS

The status review for west coast pink salmon was conducted by a team of researchers from the National Marine Fisheries Service (NMFS). This biological review team relied on information in the Endangered Species Act Administrative Record for West Coast Pink Salmon, which was developed pursuant to this review and includes comments, data, and reports submitted by the public and by state, tribal, and federal agencies. The authors acknowledge the efforts of all who contributed to this record, especially the Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, California Department of Fish and Game, U.S. Fish and Wildlife Service, and Northwest Indian Fisheries Commission.

In addition, the authors are grateful to several fishery scientists and managers for assembling and providing information that aided the development of this report and for providing critical reviews of our analyses of this information. Much of the information provided was previously unpublished and represents the most comprehensive body of biological information available on pink salmon in North America south of Alaska and northern British Columbia. Several of these scientists and managers provided their recommendations on the reliability and utility of this information. In particular, the authors thank Jim Ames, Don Hendrick, Dr. James Shaklee, Jim Uehara, and Sewall Young of the Washington Department of Fish and Wildlife; Gary Graves and Keith Lutz of the Northwest Indian Fisheries Commission; Dr. Anthony Gharrett and Dr. William Smoker of the University of Alaska; Dr. Terry Beacham, LeRoy Hop Wo, and Wilf Luedke of the Canadian Department of Fisheries and Oceans; and Frank Thrower of the NMFS Alaska Fisheries Science Center.

The biological review team for this status review included: Dr. Stewart Grant, Dr. Jeffrey Hard, Dr. Robert Iwamoto, Dr. Orlay Johnson, Dr. Robert Kope, Dr. Conrad Mahnken, Dr. Michael Schiewe, William Waknitz, Dr. Robin Waples, and Dr. John Williams, all from the NMFS Northwest Fisheries Science Center (NWFSC), Dr. Peter Dygert from the NMFS Northwest Region, and William Heard from the Auke Bay Laboratory of NMFS's Alaska Fisheries Science Center.

Several NWFSC staff made substantial contributions to the preparation of this status review. JoAnne Butzerin, Sharon Damkaer, and Dr. Robert Iwamoto edited earlier versions of this report and made numerous suggestions to improve its presentation. Peggy Busby and Laurie Weitkamp provided much of the environmental information presented in this review, information that they collected during their preparation of status reviews for west coast steelhead and coho salmon, respectively. Kathleen Neely drafted the maps and assisted in editing the other figures.

INTRODUCTION

Scope and Intent of the Present Document

Pink salmon (*Oncorhynchus gorbuscha*) is a widespread species of Pacific salmon, occurring regularly in most major river basins around the Pacific Rim from Washington State to North Korea, and occasionally in rivers as far south as northern California and the Japanese island of Hokkaido (Heard 1991). Recently published investigations have reported that several local populations of pink salmon in Washington and California have become extinct or are at high risk of extinction, and that the abundance of others is depressed (e.g., Nehlsen et al. 1991, Moyle et al. 1995). These declines led to a petition to the National Marine Fisheries Service (NMFS) to list populations of pink salmon as threatened or endangered "species" under the U.S. Endangered Species Act (ESA; technical terms and abbreviations such as "ESA" are defined in the glossary in the Appendix). Under the ESA, the term "species" is defined rather broadly to include subspecies and "distinct population segments" of vertebrates (such as salmon) as well as taxonomic species.

The National Marine Fisheries Service was petitioned in March 1994 by the Professional Resources Organization-Salmon (PRO-Salmon) to list Elwha River and fall-run Dungeness River pink salmon as threatened or endangered species under the ESA (PRO-Salmon 1994). At about the same time, NMFS also received petitions for several additional populations of Pacific salmon 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 (1994) announced that it would initiate ESA status reviews for all species of anadromous Pacific salmonids. These comprehensive reviews will consider all populations in the states of Washington, Oregon, California, and Idaho and are scheduled for completion in 1996. This proactive approach should facilitate more timely, consistent, and comprehensive evaluation of the ESA status of Pacific salmonids than would be possible through a long series of reviews of individual populations.

This document considers environmental and biological information for pink salmon populations in Washington, Oregon, California, and southern British Columbia (Fig. 1). These populations will be collectively referred to in this document as *west coast pink salmon*. The scope of this review thus encompasses, but is not restricted to, the two populations identified in the PRO-Salmon (1994) petition.

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) discussed and evaluated scientific information presented at two public meetings held in Seattle in December 1994 and February 1995 as well as information gathered independently by the authors of this report. The BRT also reviewed additional information submitted to the ESA administrative record for pink salmon. This document represents the findings and conclusions of the BRT on the status of west coast pink salmon under the ESA.

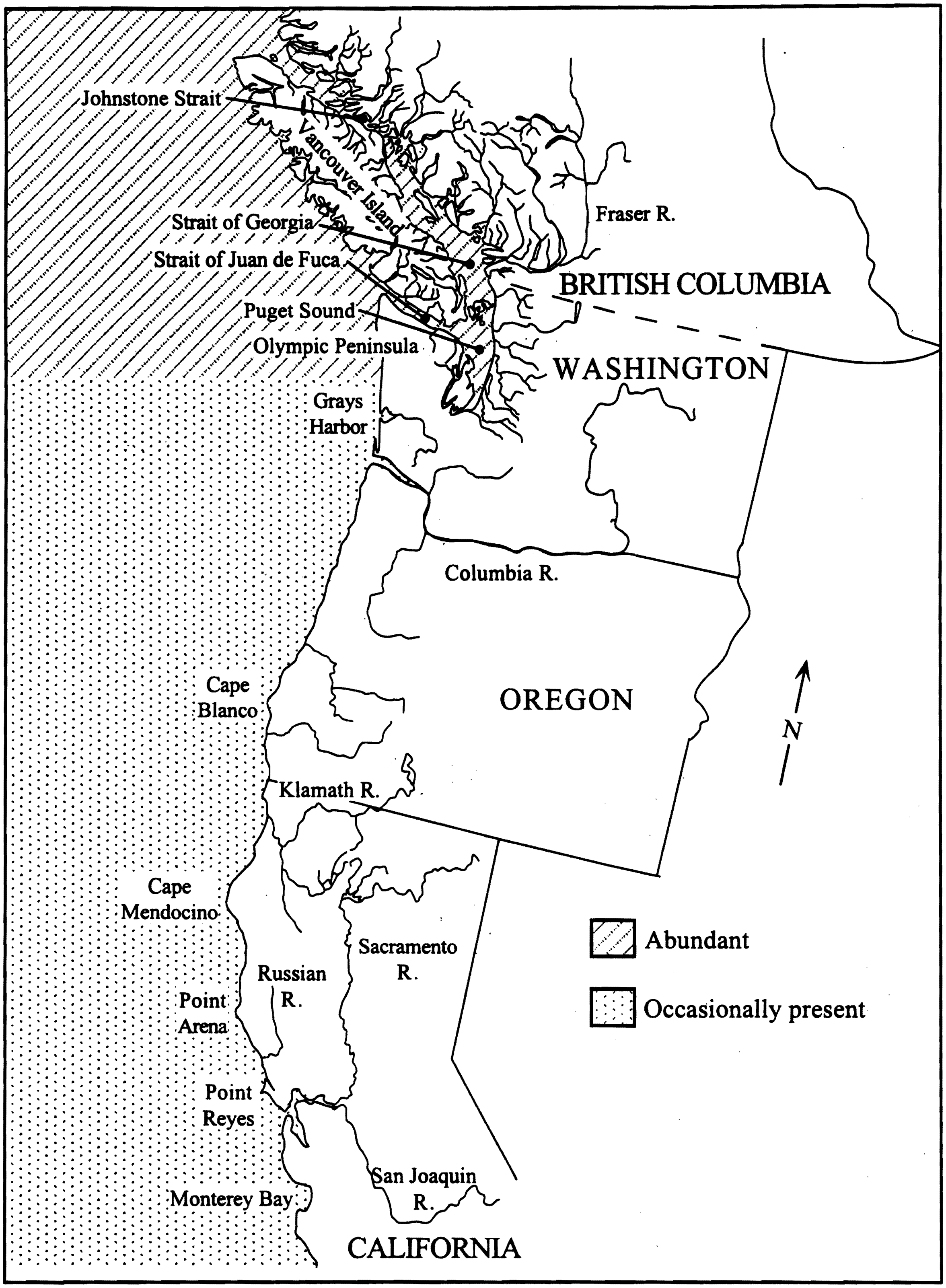

Figure 1. Range of pink salmon populations considered in this status review. Marine abundance patterns modified from Bonar et al. (1989).

Key Questions in ESA Evaluations

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.

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 approaches for considering vertebrate populations. To clarify the issue for Pacific salmon, NMFS published a policy 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 1991a). 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 two criteria (reproductive isolation and evolutionary legacy), 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 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 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.

The "Extinction Risk" Question

The ESA (section 3) defines the term "endangered species" as "any species which is in danger of extinction throughout all or a significant portion of its range." The term "threatened species" is defined as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." NMFS considers a variety of information in evaluating the level of risk faced by an ESU. Important considerations include 1) absolute numbers of fish and their spatial and temporal distribution; 2) current abundance in relation to historical abundance and carrying capacity of the habitat; 3) trends in abundance, based on indices such as dam or redd counts or on estimates of recruit-to-spawner ratios; 4) natural and human-influenced factors that cause variability in survival and abundance; 5) possible threats to genetic integrity (e.g., selective fisheries and interactions between hatchery and natural fish); and 6) recent events (e.g., a drought or a change in management) that have predictable short-term consequences for abundance of the ESU. Additional risk factors, such as disease prevalence or changes in life history traits, may also be considered in evaluating risk to populations.

According to the ESA, the determination of whether a species is threatened or endangered should be made on the basis of the best scientific information available regarding its current status, after taking into consideration conservation measures that are proposed or are in place. In this review, we do not evaluate likely or possible effects of conservation measures. Therefore, we do not make recommendations as to whether identified ESUs should be listed as threatened or endangered species, because that determination requires evaluation of factors not considered by us. Rather, we have drawn scientific conclusions about the risk of extinction faced by identified ESUs under the assumption that present conditions will continue (recognizing, of course, that natural demographic and environmental variability is an inherent feature of "present conditions").

Artificial Propagation

NMFS policy (Hard et al. 1992, NMFS 1993) stipulates that in determining 1) whether a population is distinct for purposes of the ESA, and 2) whether an ESA species is threatened or endangered, attention should focus on "natural" fish, which are defined as the progeny of naturally spawning fish (Waples 1991a). This approach directs attention to fish that spend their entire life cycle in natural habitat and is consistent with the mandate of the ESA to conserve threatened and endangered species in their native ecosystems. Implicit in this approach is the recognition that fish hatcheries are not a substitute for natural ecosystems. Nevertheless, artificial propagation is important to consider in ESA evaluations of anadromous Pacific salmonids for several reasons.

First, although natural fish are the focus of ESU determinations, possible effects of artificial propagation on natural populations must also be evaluated. For example, stock transfers might change the genetic or life history characteristics of a natural population in such a way that the population might seem either less or more distinctive than it was historically. Artificial propagation can also alter life history characteristics such as smolt age and migration and spawn timing.

Second, artificial propagation poses a number of risks to natural populations that may affect their risk of extinction or endangerment. These risks are discussed below in the Assessment of Extinction Risk section. In contrast to most other types of risk for salmon populations, those arising from artificial propagation are often not reflected in traditional indices of population abundance. For example, to the extent that habitat degradation, overharvest, or hydropower development have contributed to a population's decline, these factors will already be reflected in population abundance data and accounted for in the risk analysis. The same is not true of artificial propagation. Hatchery production may mask declines in natural populations that will be missed if only raw population abundance data are considered. Therefore, a true assessment of the viability of natural populations cannot be attained without information about the contribution of naturally spawning hatchery fish. Furthermore, even if such data are available, they will not in themselves provide direct information about possibly deleterious effects of fish culture. Such an evaluation requires consideration of the genetic and demographic risks of artificial propagation for natural populations. The sections on artificial propagation in this report are intended to address these concerns.

Finally, if any natural populations are listed under the ESA, then it will be necessary to determine the ESA status of all associated hatchery populations. This latter determination would be made following a proposed listing and is not considered further in this document.

Summary of Information Presented by the Petitioner

This section briefly summarizes information presented by the petitioner (PRO-Salmon 1994) to support its arguments that two populations of pink salmon on Washington's Olympic Peninsula qualify as a threatened or endangered species under the ESA. We discuss this information and related issues in the following sections, and we evaluate the status of west coast pink salmon in the conclusions of the Assessment of Extinction Risk section.

Distinct Population Segments

A petition to list two pink salmon populations as protected species under the ESA was received by NMFS from PRO-Salmon on 14 March 1994. The status of these two populations, in the lower Dungeness River and the Elwha River, was characterized as "critical" by WDF et al. (1993). In the planned revision of the Washington State Salmon and Steelhead Stock Inventory (SASSI), the Washington Department of Fish and Wildlife (WDFW) is likely to recommend that Elwha River pink salmon be reclassified as extinct (J. Ames[1]). Both petitioned populations are odd-year populations that spawn or have spawned in systems draining into the Strait of Juan de Fuca from the northern side of the Olympic Peninsula. No other rivers along the Strait of Juan de Fuca appear to support persistent pink salmon populations (Williams et al. 1975, WDF et al. 1993).

With respect to the two criteria established by NMFS to define a "species" of Pacific salmon, the petitioner argued that the lower Dungeness and Elwha River populations of pink salmon were both reproductively isolated from other pink salmon populations. Reproductive isolation was inferred primarily on the basis of distance to nearest neighboring population; for lower Dungeness River pink salmon, this distance is approximately 10 km (to the upper Dungeness River population), and for Elwha River pink salmon, this distance is about 25 km (to the lower Dungeness River population). According to the petitioner, genetic data, in the form of allozyme variation, support a hypothesis for at least partial reproductive isolation of the lower Dungeness River population (Shaklee et al. 1991), but no genetic data exist for the Elwha River population (WDF et al. 1993, J. Shaklee[2]).

In its petition, PRO-Salmon provided little information that addresses the "evolutionary significance" criterion. The petitioner argued that spatial and temporal isolation of the lower Dungeness River population from the upper Dungeness River population, due to differences in run timing and spawning location, contribute to the distinctiveness of the lower

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[1]J. Ames, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., January 1995.

[2]J. Shaklee, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., November 1994.

river population. No quantitative data are available to support a hypothesis for the distinctiveness of the Elwha River population.

Population Abundance

The petitioner noted that the run size for lower Dungeness River pink salmon declined from about 11,000 spawners per year between 1969 and 1979 to 6,600 fish in 1981, following severe flooding in January 1980. (The recorded historical high was 210,000 fish in 1963). Recent abundance has ranged from less than 150 to more than 750 spawners, about 5% of pre-flood levels and 0.1% of the historic high (WDF et al. 1993, PRO-Salmon 1994). The run size for Elwha River pink salmon crashed from about 4,800 spawners per year (1969-79) to an estimated 200 fish or less since 1981, following severe flooding in January 1980. (The recorded historical high was 40,000 fish in 1963.) Since 1981, less than 35 pink salmon have been observed in the Elwha River over all of the odd-numbered years combined, and only 4 fish have been observed since 1989 (PRO-Salmon 1994, J. Uehara[3]).

Causes of Decline for Pink Salmon

The petition identified several threats to the viability of lower Dungeness River pink salmon: water withdrawals from the lower river during the holding and spawning periods in late summer and fall, habitat degradation due to increased urbanization along the river, diking for flood control, and possible sewage contamination. Any or all of these factors may be inhibiting natural recovery of pink salmon. In addition, timber harvest near the river and artificial propagation of coho salmon at Dungeness Hatchery may impede recovery (PRO-Salmon 1994; Hiss 1994, 1995).

Finally, harvest in mixed-stock fisheries, especially in fisheries that target Fraser River pink salmon in the Strait of Juan de Fuca, may limit the ability of this population to recover naturally (estimated total exploitation rate on the lower Dungeness River population = 47%, PRO-Salmon 1994). The petitioner suggested that similar factors threaten the viability of Elwha River pink salmon, although urbanization and timber harvest are apparently less significant factors in this drainage, and hatchery production on the river includes chinook salmon and steelhead as well as coho salmon. Unlike the Dungeness River, the Elwha River is obstructed by two dams, the Elwha and Glines Canyon Dams. These structures prevented access by pink salmon to 35 km of the river early in this century, and pink salmon spawning is currently limited to the lowest 5 km of the river. However, the petitioner noted that the Elwha River population did not decline to extremely low levels until the late 1970s (PRO-Salmon 1994). Nevertheless, based on the petitioner's information, the abundance of this population apparently has been depressed since at least the late 1960s.

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[3]J. Uehara, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., February 1996.

INFORMATION RELATING TO THE SPECIES QUESTION

Environmental Features

The spawning populations of west coast pink salmon that are the focus of this review are presently distributed over a small region of the contiguous 48 United States, in northwestern Washington from its border with British Columbia (49°N) south to the Nisqually River (48°N) in southern Puget Sound. Although climatic features do not vary markedly in this region, diverse patterns of vegetation, weather, soils, and water quality exist there. This section summarizes environmental and biological information relevant to determining the nature and extent of ESUs for pink salmon in this region (see also Weitkamp et al. 1995).

Physiography and Geology

Pink salmon inhabit areas in northwestern Washington and southern British Columbia that are represented by several physiographic regions: the Coast Range Province, which extends in the United States from the Strait of Juan de Fuca southward to the Klamath Mountains and from the Pacific Ocean eastward to the lowlands west of the Cascade Mountains, and in Washington includes the Olympic Mountains and Willapa Hills; the Puget-Willamette Lowland, which covers Puget Sound and the Willamette River Valley in the United States; the Coast Mountains of British Columbia, which include in Washington the Cascades North and Cascades South areas; the Coastal Trough, which covers the area surrounding the Strait of Georgia and Johnstone Strait; and the Outer Mountains of Vancouver Island (McKee 1972, Lasmanis 1991). These regions are geologically diverse. Most of the encompassed area, with the exception of the Olympic Mountains and higher elevations in the Cascade Mountains, was glaciated during the Pleistocene Epoch (Booth 1987).

As a result of Pleistocene glaciation, the Puget Sound lowlands contain a thick layer of moraine. The North Cascades along northern Puget Sound and southwestern British Columbia are composed of a wide spectrum of metamorphic rock types. Like the Olympic Peninsula, the coastal mountains of British Columbia are composed of basalt and sedimentary rock as well as volcanic and nonvolcanic rock (McKee 1972). The most unique aspect of the Olympic Peninsula is its massive foundation of marine basaltic flow (McKee 1972). The northern coastal area where pink salmon presently spawn has been heavily influenced by marine sedimentation, as have other lowland areas in the region. In present-day Washington and southern British Columbia, the lowlands surrounding Puget Sound probably have the most complex hydrologic history because of their repeated exposures to alternating glaciation and deposition of marine sediment.

Temperature, Precipitation, and Hydrology

Climate varies primarily with latitude along the west coast of North America, and this region exhibits south-to-north gradients of increasing average precipitation and declining average temperature. The coastal region has a mild climate with warm, relatively dry summers and cool, wet winters.

Pink salmon typically enter fresh water and spawn at a time of year when streamflow is low and water temperature is relatively high. Streamflows are lowest in August and September, and there is some tendency for streamflows to reach their lowest points later in rivers on the Strait of Juan de Fuca and in Hood Canal than in systems on Puget Sound. Water temperatures in northwestern Washington are generally highest in July and August (Hydrosphere Data Products, Inc. 1993). Because run timing and spawn timing are sensitive to these factors, streamflow patterns determine the temporal availability and suitability of spawning and incubation habitat for pink salmon.

The Olympic Peninsula is much wetter (160-380 cm precipitation/yr) than the rest of Washington, with considerable snowfall (over 150 cm/yr) at higher elevations. The abundant precipitation results at least partially from the relatively high elevation of the Olympic Mountains (1,000-2,000 m). Persistent spawning populations of pink salmon are found only in watersheds draining the northern and eastern sides of the Peninsula. Maximum and minimum air and water temperatures are cooler in the Olympic Peninsula than farther south, reflecting effects of both latitude and elevation. Annual maximum and minimum water temperatures are 10°C to 14°C and 2°C to 4°C, respectively, whereas annual maximum and minimum air temperatures are approximately 21°C and 2°C, respectively.

The wet climate of the Olympic Peninsula continues north along the west coast of Vancouver Island and along the British Columbia mainland north of Vancouver Island. Limited hydrographic data (Farley 1979) indicate that water-flow patterns in this area are similar to those on the Olympic Peninsula, with relatively high flows throughout the year. Summer air temperatures generally decrease with increasing latitude--the Olympic coast is a few degrees warmer than the southwestern coast of Vancouver Island, which is a few degrees warmer than the northwestern coast and the mainland north of Vancouver Island.

A smaller gradient of decreasing average precipitation exists from west to east in northwestern Washington. East of the Olympic Peninsula, precipitation rapidly decreases because of the rainshadow caused by the Olympic and Vancouver Island Mountains to the north, and the Willapa Hills to the south. The rainshadow, which becomes apparent along the northern coastline of the Peninsula west of the Elwha River, continues through lowland Puget Sound, up the lowlands bordering the Strait of Georgia, to the south end of Queen Charlotte Strait. Most Washington streams that support pink salmon are found in Puget Sound. Most of this area receives less than 120 cm rain per year, with some areas receiving as little as 50 cm per year (U.S. Dep. Commerce 1968).

A slight summer temperature cline appears to exist within the northern rainshadow region; average maximum air temperatures in Puget Sound and Hood Canal (20°C-24°C) are slightly higher than those in the Strait of Georgia (16°C-20°C), which in turn are higher than those in areas inside Vancouver Island farther north (14°C-16°C). In contrast, winter air temperatures are more uniform and average 0°C-5°C throughout the area. Stream temperatures in the area are generally cool, with a maximum of 12°C-20°C in summer and 0°C-4°C in winter (Hydrosphere Data Products, Inc. 1993).

Marine Upwelling

No major variations in upwelling patterns occur along the coasts of British Columbia and Washington (Smith 1983, Landry et al. 1989). Upwelling in this region is primarily wind driven (Bakun 1973, 1975; Thompson 1981). One exception to this pattern has been observed off the southwestern corner of Vancouver Island where consistent and strong upwelling appears to occur throughout the year (Denman et al. 1981). Upwelling in this area is thought to be caused by current-driven as well as wind-driven events, a condition that leads to relative temporal and spatial stability.

Vegetation

Vegetation patterns in Washington and southern British Columbia are affected by precipitation gradients. Coastal regions in Washington and British Columbia are forested with a Sitka spruce (*Picea sitchensis*)-dominated floral community, which also includes western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), red alder (*Alnus rubra*), and Douglas fir (*Pseudotsuga menziesii*) as major species. This vegetation type is restricted to coastal regions and river valleys extending a few kilometers inland over coastal plains, and to elevations above 150 m in areas immediately adjacent to the ocean (Franklin and Dyrness 1973).

Sitka spruce forests are replaced by western hemlock-dominated forests along the Strait of Juan de Fuca to the north and east. This vegetation type also includes western hemlock, Douglas fir, red alder, and western red cedar. The transition between Sitka spruce and western hemlock along the Strait of Juan de Fuca occurs at about the Elwha River on the Olympic Peninsula and Sooke Inlet on Vancouver Island. Because of Puget Sound's lower precipitation and glacial soils, drought-tolerant western white (*Pinus monticola*), lodgepole (*Pinus contorta*), and occasionally ponderosa (*Pinus ponderosa*) pines, occur more frequently here than elsewhere in the western hemlock zone.

Zoogeography

Along the east coast of the North Pacific Ocean within the range considered in this status review, a distinct faunal boundary for marine fishes occurs off the northern tip of Vancouver Island (approximately 50°N) (Allen and Smith 1988). Within the range of pink salmon in the Pacific Northwest, only one major freshwater ichthyogeographic region has been described: the Columbia (McPhail and Lindsey 1986, Minckley et al. 1986). Thus, no pattern of variation in marine fishes associated with pink salmon is evident in Washington and southern British Columbia.

Estuarine fish assemblages show regional differences based on presence or absence of species, but only a single group exists in northwestern Washington (Monaco et al. 1992). This group, the Fjord Group, occurs within inland estuaries of Puget Sound and Hood Canal. Other estuary groupings are less evident and seem to depend more on characteristics of individual estuaries than on geographic location.

The distribution of marine invertebrates shows transitions between major faunal communities similar to those of marine fishes (Hall 1964, Valentine 1966, Hayden and Dolan 1976, Brusca and Wallerstein 1979). The primary cause of this zonation has been attributed to geographic variation in temperature (Hayden and Dolan 1976), but other abiotic (Valentine 1966) and biotic (Brusca and Wallerstein 1979) factors may also influence invertebrate distribution patterns.

The distributions of many amphibians appear to begin and end at several common geographical areas within the range of pink salmon in Washington; the Strait of Georgia and Vancouver Island are the northern extent of many amphibian distributions (tailed, *Ascaphus truei*, and red-legged, *Rana aurora*, frogs; Pacific giant, *Dicamptodon ensatus*, western long-toed, *Ambystoma m. macrodactylum*, western red-backed, *Plethodon vehiculum*, Oregon slender, *Batrachoseps wrighti*, and brown, *Ambystoma g. gracile*, salamanders) (Cook 1984). In addition, several amphibians are restricted to the Olympic Peninsula (Olympic torrent, *Rhyacotriton olympicus*, and Van Dyke's, *Plethodon vandykei*, salamanders), whereas other species occur in most areas in western Washington and Oregon except in the Olympic Peninsula (Pacific giant and Dunn's, *Plethodon dunni*, salamanders) (Leonard et al. 1993).

Ecoregions

The U.S. Environmental Protection Agency has developed a system of ecoregion classification based on perceived patterns of factors such as climate, topography, potential natural vegetation, and soils (Omernik and Gallant 1986, Omernik 1987). Under this system, the range of pink salmon in Washington covers two ecoregions that border on salt water: the "coast range" ecoregion, which extends from the Strait of Juan de Fuca to Monterey Bay, from the ocean to about the crest of the coastal mountains; and the "Puget lowland" ecoregion, which begins in Washington at about the Dungeness River near the eastern end of the Strait of Juan de Fuca and extends through Puget Sound to the British Columbia border.

Summary

The above information indicates that the Olympic Peninsula is environmentally distinct from the rest of northwestern Washington. However, the gradients in temperature and precipitation within the range of pink salmon in Washington and southern British Columbia are not sharp ones, and, on the basis of the physical and biological factors examined here, the precise geographic boundary separating these two areas is not well defined.

Pink Salmon Life History

Distribution and Life Cycle

Pink salmon occur around the Pacific Rim of Asia and North America north of about 40°N to greater than 70°N (Neave et al. 1967, Takagi et al. 1981). However, the spawning distribution of pink salmon is much more restricted, ranging from 48°N (Puget Sound, Washington) to 64°N (Norton Sound, Alaska) in North America and from 44°N (North Korea) to 65°N (Anadyr Gulf, Russia) in Asia (Heard 1991, Mathisen 1994; Fig. 2). In North America, pink salmon populations regularly occur in marine waters as far south as Washington State and spawn in this area as far south as Puget Sound and the Olympic Peninsula (Williams et al. 1975, WDF et al. 1993; Fig. 1). Between 70 and 80% of the Washington pink salmon spawning escapement occurs in northern Puget Sound (WDF et al. 1993, Big Eagle & Assoc. and LGL Ltd. 1995).

Pink salmon spawn during the late summer and fall in both large and small rivers; they prefer clean, coarse gravel in shallow (10-100 cm) pools and riffles exposed to moderately fast (30-150 cm/s) currents. These fish generally avoid spawning in deep, slow-moving water or on muddy, sandy, or heavily silted substrate (Heard 1991). Water temperatures during peak spawning activity range from about 5°C to 15°C and are generally higher in southern populations. This species tends to spawn closer to tidewater than other species of Pacific salmon, generally within 50 km of a river mouth (Heard 1991, WDF et al. 1993). However, populations returning to large systems such as the Fraser River and Skeena River watersheds in British Columbia migrate up to 500 km upstream to spawn, and a substantial fraction of other populations may spawn intertidally (Hunter 1959, Noerenberg 1963, Jones 1978). Pink salmon mature at the smallest average size of any species of Pacific salmon (1.0-2.5 kg) and show marked sexual dimorphism (Davidson 1935, Pritchard 1937, Beacham and Murray 1985). Spawning populations throughout much of the range of pink salmon may be extremely large, often exceeding hundreds of thousands of adult fish (Heard 1991, WDF et al. 1993).

Mortality of juvenile pink salmon in fresh water is high, ranging from about 75% to over 99%, and most of this mortality occurs before emergence from the gravel (Hunter 1959, McNeil 1966). Upon emerging from the gravel, pink salmon alevins migrate rapidly downstream, generally in schools and usually in darkness (Heard 1991). Juveniles grow most rapidly during their residence in the nearshore marine environment (up to approximately 1 mm per day and 5-6% body weight per day). Preferred prey are small crustaceans, especially euphausiids, amphipods, and cladocerans (McDonald 1960, Bailey et al. 1975). After a few weeks to a few months in estuaries and nearshore habitat, pink salmon move

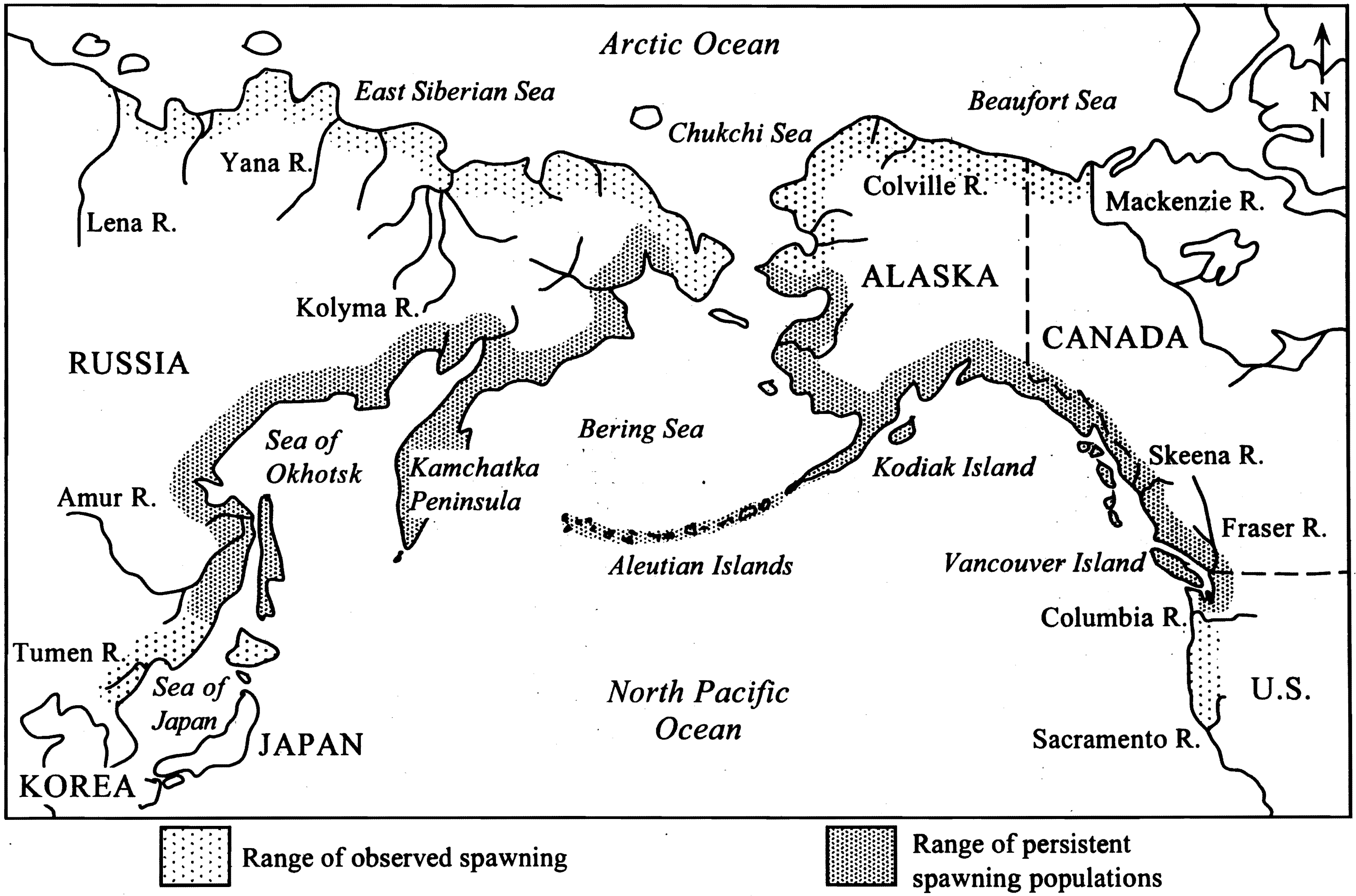

Figure 2. Geographic ranges of observed spawning and of persistent spawning populations of pink salmon in the North Pacific and Arctic Oceans. Figure modified from Heard (1991) and Mathisen (1994).

offshore, where they migrate at sea for 12-16 months (Heard 1991). Tagging studies suggest that southern populations from Washington and British Columbia have a more restricted oceanic migration than Alaskan populations (Takagi et al. 1981, Ogura 1994; Fig. 3).

Pink salmon do not presently occur in Idaho (Heard 1991); it is unknown whether the species occurred there historically. Along the coasts of Washington, Oregon, and California, persistent populations of pink salmon have been documented only in Washington (Ayers 1955, Herrmann 1959, Heard 1991, Mathisen 1994, H. Weeks[4]), although pink salmon have been observed spawning in rivers in central and northern California in the past (Scofield 1916, Evermann and Clark 1931, Snyder 1931, Taft 1938, Smedley 1952, Hallock and Fry 1967). Nehlsen et al. (1991) described pink salmon from the Klamath and Sacramento Rivers in California as extinct and pink salmon from California's Russian River as at high risk of extinction.

Recent observations of pink salmon in California have been rare. No pink salmon have been observed spawning in the Russian River in recent years, but a few adult fish are observed occasionally in the Klamath River system (Moyle et al. 1995, P. Moyle[5]). In the last 20 years, only one fish was observed in the Garcia River, and only one or two fish have been caught annually for several years in the Klamath River. Over this same period, three male pink salmon were collected from the American River, and an additional fish was observed there (Moyle et al. 1995). The capture of seven juvenile pink salmon on the Sacramento-San Joaquin River system in March 1990 is evidence that some pink salmon spawned successfully there (Moyle et al. 1995).

Adult pink salmon are rarely observed in Oregon coastal rivers, and none have been recorded in the last several years (H. Weeks[6]). Nevertheless, successful spawning of pink salmon in Oregon has been documented in the past through the collection of juvenile pink salmon from Yaquina Bay near Newport in the late 1950s (C. Bond[7]).

Along the north coast of the Olympic Peninsula and on the outer Washington coast, adult pink salmon are also relatively rare. Small escapements (10-100 adults) have been

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[4]H. Weeks, Oregon Department of Fish and Wildlife, P.O. Box 59, Portland, OR 97207. Pers. commun., September 1994.

[5]P. Moyle, Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616. Pers. commun., September 1994.

[6]H. Weeks, Oregon Department of Fish and Wildlife, P.O. Box 59, Portland, OR 97207. Pers. commun., September 1994.

[7]C. Bond, Department of Fish and Wildlife, Nash Hall, Oregon State University, Corvallis, OR 97331. Pers. commun., September 1994.

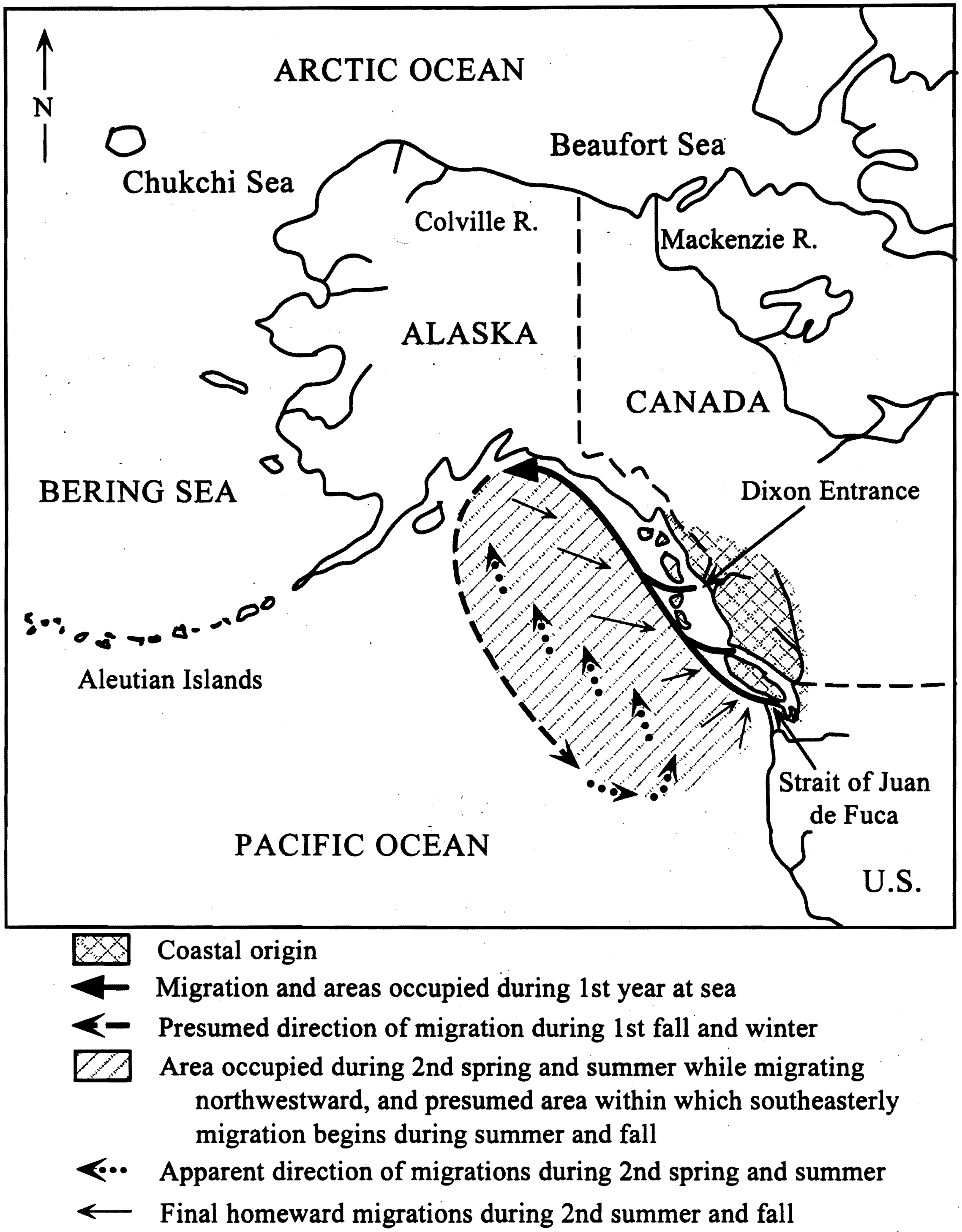

Figure 3. Graphical summary of presumed marine migrations of pink salmon originating from streams in Washington, British Columbia, and southern southeastern Alaska. Figure modified from Takagi et al. (1981) and data in Hartt and Dell (1986) and Ogura (1994).

observed occasionally in the Sekiu, Hoko, and Lyre Rivers. As late as the early 1970s, adult pink salmon were caught in Native American setnets on the Quillayute and Hoh Rivers in both even and odd years, and some spawning (less than 500 adults) was observed a few decades ago in the Quillayute River below the confluence of the Bogachiel and Soleduck Rivers (Williams et al. 1975). At about this same time, relatively large numbers (< 1,500) of adults were observed spawning annually on riffles on both the Queets and Quinault Rivers (the length of this period is unclear). Small numbers have also been observed in several streams in the Chehalis River Basin (Williams et al. 1975).

Pink salmon are rare in the Columbia River Basin, especially upstream of Bonneville Dam. However, adult pink salmon have been observed migrating up the Columbia River past Bonneville and The Dalles Dams in small numbers (Table 1). According to the Army Corps of Engineers' Fish Passage Reports for the Columbia River Basin, no adult pink salmon have been counted at dams upstream of The Dalles Dam (U.S. Army Corps of Engineers 1994). However, Basham and Gilbreath (1978) stated that several adult pink salmon were observed in 1975 at John Day Dam (45) on the Columbia River and at Little Goose Dam (12) and Lower Granite Dam (1) on the Snake River. In the same year, Basham and Gilbreath (1978) recovered five pink salmon carcasses (4 female, 1 male) from the lower Tucannon River between October 18 and November 1. The females appeared to have spawned due to the few remaining eggs in their body cavities and the erosion of the lower lobes of their caudal fins.

In 1991, a record 550 adult pink salmon were observed migrating past Bonneville Dam, and minimum pink salmon abundance for the lower Columbia River that year was estimated at nearly 1,700 adults (H. Fiscus[8]). In that year, approximately 225 pink salmon redds were observed by Washington Department of Fisheries (WDF, now the Washington Department of Fish and Wildlife (WDFW)) biologists in the Cowlitz River, a lower Columbia River tributary. Also in 1991, 32 pink salmon were observed at Cascade Hatchery on the lower Columbia River, and one was observed in the Clackamas River.

Pink salmon have been recovered occasionally in ocean fisheries off the coasts of Oregon and southern Washington (Hubbs 1946, Bonar et al. 1989). At least some of these fish are apparently stray fish from Puget Sound streams (e.g., Van Hyning 1959). A recent review of Pacific salmon populations in Washington (WDF et al. 1993) concluded that pink salmon populations do not exist outside Puget Sound and the northern Olympic Peninsula.

This information suggests that spawning populations of pink salmon no longer occur regularly south of northwestern Washington. The remainder of this report therefore focuses on the status of pink salmon in Washington and southern British Columbia.

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[8]H. Fiscus, Washington Department of Fish and Wildlife, P.O. Box 999, Battleground, WA 98604. Pers. commun., January 1995.

Table 1. Counts of pink salmon over Bonneville and The Dalles Dams, Columbia River, 1938-94. Data from U.S. Army Corps of Engineers (1994).

Year	Bonneville No. fish	The Dalles No. fish	Year	Bonneville No. fish	The Dalles No. fish
1938	0	--	1967	50	4
1939	0	--	1968	21	1
1940	0	--	1969	86	1
1941	4	--	1970	150	4
1942	11	--	1971	176	3
1943	0	--	1972	51	0
1944	1	--	1973	12	1
1945	1	--	1974	2	0
1946	2	--	1975	309	0
1947	3	--	1976	2	0
1948	2	--	1977	0	0
1949	6	--	1978	0	0
1950	8	--	1979	23	4
1951	7	--	1980	0	0
1952	9	--	1981	20	1
1953	10	--	1982	0	0
1954	4	--	1983	52	0
1955	9	--	1984	8	1
1956	4	--	1985	147	5
1957	12	4	1986	23	4
1958	6	5	1987	20	2
1959	22	9	1988	6	0
1960	0	5	1989	12	0
1961	12	4	1990	0	0
1962	27	5	1991	550	103
1963	34	3	1992	24	3
1964	45	5	1993	15	0
1965	64	3	1994	5	0
1966	50	1			

Broodlines

In addition to their small size, extreme sexual dimorphism, and lack of extended residence in fresh water as juveniles, pink salmon differ from other species of Pacific salmon in another important respect. Because essentially all pink salmon mature at 2 years of age (Gilbert 1914, Anas 1959, Bilton and Ricker 1965, Turner and Bilton 1968), this species lacks variable age structure. Two broodlines result from generations spawning in alternate years. Throughout much of the range of this species, many rivers that support pink salmon populations produce both even- and odd-year broodlines which may have arisen independently and have presumably been genetically isolated for hundreds or thousands of generations (Aspinwall 1974, Gharrett and Smoker 1991, Heard 1991). Although 1- and 3-year-old adults have been recorded (Anas 1959, Foster et al. 1981, Alexandersdottir and Mathisen 1983), almost all pink salmon are 2 years of age at maturity (Gilbert 1914, Bilton and Ricker 1965, Turner and Bilton 1968). Fish in the broodline that matures in even-numbered years are referred to as even-year pink salmon; fish in the other broodline, which matures in alternate, odd-numbered years, are referred to as odd-year pink salmon (Aspinwall 1974, Johnson 1979, McGregor 1982, Beacham et al. 1985). Even distinct broodlines in the same river differ for a variety of life history as well as genetic characteristics (Heard 1991).

The geographical distributions of these two broodlines are not random. At the southern extent of the pink salmon range in North America, odd-year pink salmon are most abundant (Atkinson et al. 1967, WDF et al. 1993). Pink salmon in southern British Columbia, including the Fraser River, are dominated by odd-year fish (Aro and Shepard 1967). British Columbia populations north of the Fraser River support both odd- and even-year populations, as do those in southeastern Alaska (Heard 1991). Even-year pink salmon dominate runs in the Queen Charlotte Islands and become more abundant than odd-year pink salmon in western Alaska (Neave 1952, Aro and Shepard 1967, Ricker and Manzer 1974). In Asia, even-year pink salmon generally become more abundant than odd-year pink salmon as latitude increases (Heard 1991). The reasons for this variation in broodline dominance remain a major unsolved problem in pink salmon biology (Ricker 1962, Heard 1991).

The relative abundance of these broodlines can fluctuate dramatically over time, even within the same system (Neave 1952, Ricker 1962). In recent decades, pink salmon south of central British Columbia have been dominated by odd-year fish (Aro and Shepard 1967, Beacham et al. 1985), and even-year fish are almost completely absent from Washington (Atkinson et al. 1967, WDF et al. 1993). Even-year pink salmon in Washington are known only from the Snohomish River on Puget Sound, where spawning escapements have ranged from a few hundred to over 2,000 fish over the last decade (WDF et al. 1993).

With the exception of those in the Fraser River, the sizes of even- and odd-year pink salmon populations in British Columbia generally increase with latitude. In odd-numbered years, large populations (100,000 spawners or more) also occur in some rivers on the east side of Strait of Georgia and Johnstone Strait (Stefanson et al. 1993); in even-numbered years, however, the largest populations occur primarily along Johnstone Strait and farther north (Aro and Shepard 1967; Gould et al. 1988; Stefanson et al. 1989, 1991). Several small populations (less than a few hundred to a few thousand spawners) of pink salmon occur in southern British Columbia, including southern Vancouver Island. On the east coast of Vancouver Island south of the Puntledge and Tsolum Rivers, populations spawning in odd-numbered years are relatively small and probably only rarely exceed a few thousand fish. On the west coast of the island, populations spawning in odd-numbered years probably rarely exceed this size south of Nootka Sound. However, escapement estimates for these populations are probably not very reliable (L. Hop Wo[9], W. Luedke[10]).

Several small populations of pink salmon in southern British Columbia are not well characterized. The even-year pink salmon populations nearest to the Snohomish River appear to spawn in Vancouver Island rivers at least 130-150 km away (and perhaps considerably further), possibly in the lower Fraser River (T. Beacham[11]), along Stuart Channel in the western Strait of Georgia, or between Sooke Inlet and Port San Juan on southwestern Vancouver Island (Aro and Shepard 1967). These areas also support the odd-year populations that appear to be nearest to Washington pink salmon populations (Aro and Shepard 1967).

Run Types

Pink salmon populations vary in timing of adult migration and spawning but often lack the distinct seasonal "runs" observed in several other species of Pacific salmon. The return of maturing pink salmon to fresh water occurs from June to September and tends to advance with increasing latitude (Neave et al. 1967). In North America, pink salmon spawn primarily from August to October, with spawning becoming progressively later at lower latitudes (Heard 1991). Pink salmon runs in some areas can be divided into early and late components, and sometimes these components exhibit spatial separation as well (e.g., southeastern Alaska: Royce 1962, Sheridan 1962, Smoker et al. in press; Fraser River, British Columbia: Ward 1959; Asia: Ivankov 1968).

Davidson et al. (1943) characterized two general strategies of upstream migration and maturation in pink salmon: 1) immediate entry into the stream, where final maturation occurs, and a consequent delay until spawning, and 2) final maturation in the estuary, subsequent entry into the stream (often contingent on flow variation), and immediate spawning. These strategies

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[9]L. Hop Wo, Canadian Department of Fisheries and Oceans, Fisheries Branch, South Coast Division, 3225 Stephenson Point Road, Nanaimo, B.C. V9T 1K3. Pers. commun., May 1995.

[10]W. Luedke, Canadian Department of Fisheries and Oceans, Fisheries Branch, South Coast Division, 3225 Stephenson Point Road, Nanaimo, B.C. V9T 1K3. Pers. commun., March 1995.

[11]T. Beacham, Canadian Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6. Pers. commun., December 1994.

of maturation show some evidence of being genetically based (Davidson et al. 1943; see also Smoker et al. in press). Because spawn timing may influence outmigration timing in pink salmon, and because some evidence indicates that outmigration timing affects marine survival (Taylor 1980, Mortensen et al. 1991), spawn timing is likely to be an important component of local adaptation in pink salmon as well as in other species of Pacific salmon.

In Washington and southern British Columbia, river entry occurs from July to October, and spawning is generally observed from August to October (Neave 1963, Heard 1991, WDF et al. 1993). In Washington, timing of river entry and spawning are generally earliest in northern Puget Sound and in the upper Dungeness River on the Olympic Peninsula (WDF et al. 1993).

Pink Salmon Populations in Washington

Thirteen spawning populations of pink salmon have been identified in Washington (WDF et al. 1993). For 12 of these populations, spawning occurs only in odd years; the sole even-year population exists in the Snohomish River in Puget Sound (Fig. 4).[12] Four odd-year populations occur in the Nooksack, Skagit, Stillaguamish, and Snohomish Rivers in northern Puget Sound, where most pink salmon are produced in Washington. Two odd-year populations occur in southern Puget Sound in the Puyallup and Nisqually Rivers. Three odd-year populations occur in Hood Canal in the Hamma Hamma, Duckabush, and Dosewallips Rivers. In addition, three odd-year populations have been identified by WDF et al. (1993) on the Strait of Juan de Fuca: upper Dungeness ("summer" population), lower Dungeness ("fall" population), and Elwha Rivers (Fig. 4).

Pink salmon have been observed periodically in other Washington rivers, including the Skokomish River on Hood Canal and the Bogachiel River on the western Olympic Peninsula (Williams et al. 1975). Elwha River pink salmon now appear to be extinct, as no adult fish have been observed there since 1989 despite extensive annual surveys for chinook salmon. Because of the temporal overlap in spawning distributions of chinook and pink salmon in the Elwha River, pink salmon should have been observed there if they had been present. Pink salmon apparently occurred historically in the Green/Duwamish River system in Puget Sound;

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[12]Neave (1965, p. 2) reported that Washington state biologists historically observed a persistent, but small (up to a few hundred adults) even-year run of pinks in Day Creek, a Skagit River tributary, and he noted that only one transplant was made into the Skagit River prior to the known presence of these fish, in 1914. He argued that the Day Creek run should be considered endemic because of the poor success of even-year pink salmon transplants to Puget Sound. This run no longer appears to exist (D. Hendrick, Washington Department of Fish and Wildlife, 333 E. Blackburn Rd., Mount Vernon, WA 98273, pers. commun., January 1995).

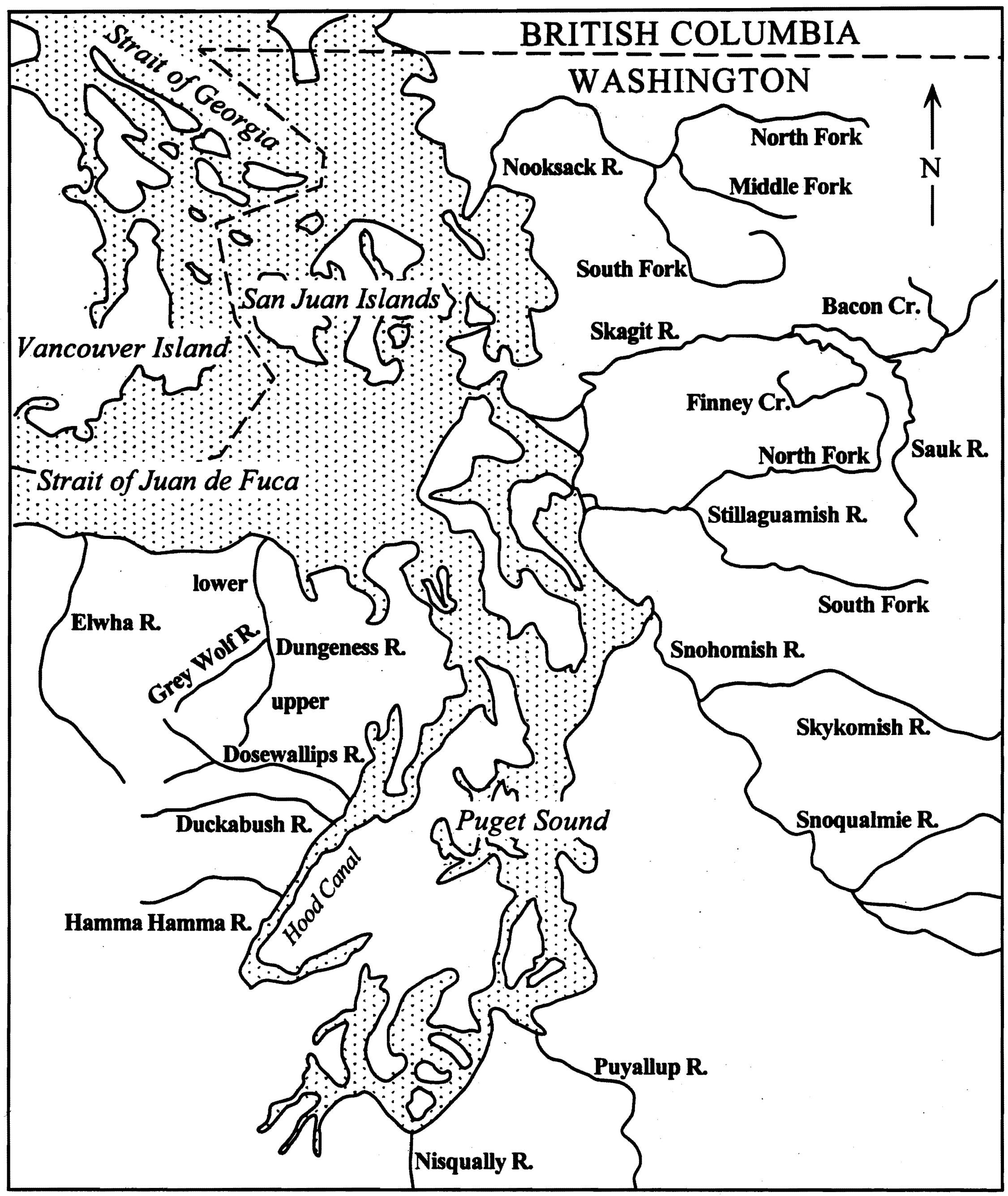

Figure 4. Principal pink salmon spawning streams in northwestern Washington. Stream names are in boldface. Figure modified from IPSFC (1958).

the Washington Department of Fisheries (WDF) (1916-64) reported these fish as "very scarce" in the Green River, and absent from Burns, Newaukum, Spaight, and Soos Creeks. The highest annual number of adult pink salmon observed in the Green River over the last several decades is 13. Up to 16 adults have been observed in the Cedar River in the Lake Washington watershed, but these are believed to be strays (J. Ames[13]).

Several aspects of the life history and ecology of pink salmon in Washington and southern British Columbia are poorly understood in detail. Topics for which data were insufficient to assist the BRT in evaluating possible ESUs for pink salmon include variation in fecundity, development rate, growth and mortality, length of fry residence and migration in the nearshore marine environment, behavior, and physiology, and several aspects of spawning habitat. The remainder of this section concentrates on topics that were important in determining proposed ESUs for pink salmon in Washington and southern British Columbia.

Spawning Habitat

In northwestern Washington rivers, pink salmon generally spawn in relatively fast-flowing shallow water in small, clear water drainages and in both clear water and turbid large drainages (Bonar et al. 1989, WDF et al. 1993). Some intertidal spawning may also occur, but it is probably not extensive in this region. Several populations spawn a considerable distance upstream or under unusual river conditions. For example, "summer" Dungeness River (Strait of Juan de Fuca) pink salmon return earlier than "fall" Dungeness River pink salmon and spawn above RKm 16, about 11 km upstream from the fall fish spawning in the lower river (Johnson 1973, WDF et al. 1993). Some Dosewallips River pink salmon (Hood Canal) migrate more than 15 km upstream to spawn. In southern Puget Sound, pink salmon spawn in the Puyallup River primarily above RKm 20, in South Prairie Creek and in other tributaries as well as the main stem. Spawning by pink salmon in the Nisqually River occurs primarily in the main stem between RKm 35 and RKm 65.

In northern Puget Sound, pink salmon spawning occurs in the following locations: Nooksack River (all three forks), up to RKm 40 in both main stem and tributaries; Skagit River, between RKm 37-149 (especially above RKm 124) and also in the Sauk River up to RKm 64; Stillaguamish River, between RKm 9-54 in the South Fork (primarily RKm 30-48) and throughout the North Fork; and Snohomish River, between RKm 21-34 for both odd-year and even-year populations, especially above RKm 29 (both populations also spawn in the Skykomish River, but use of the river for spawning is more extensive for odd-year fish; only the odd-year fish are known to spawn in the Snoqualmie River) (WDF et al. 1993).

Spawning can occur in water carrying substantial amounts of glacial silt in the Nisqually and Nooksack Rivers. Although the Puyallup River also contains substantial glacial

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[13]J. Ames, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., February 1996.

runoff, nearly all known pink salmon spawning occurs in two clear water tributaries, South Prairie and Kapowsin Creeks (WDF et al. 1993).

Migration, Spawning, and Emergence Timing

Migration--Little detailed information is available on the migration routes and timing of different pink salmon populations from Washington and southern British Columbia. Neave et al. (1967) reported that the return migration of maturing fish in the eastern North Pacific occurs mostly between June and September. The marine migration of pink salmon in this region has been inferred from tagging data to be less extensive than that of fish from more northern populations (Takagi et al. 1981, Ogura 1994). Pink salmon migrating from Washington and British Columbia are believed to remain east of about 150°W longitude and south of about 59°N latitude in the Gulf of Alaska. Thus, they probably overlap at sea with pink salmon originating from southeastern and central Alaska (Takagi et al. 1981). Ogura (1994) summarized recoveries of pink salmon tagged in Washington and southward and found that these recoveries were restricted to the east of 137°W longitude and between 48° and 55°N latitude.

Several early tagging studies were conducted to determine the final migratory pathways of pink salmon returning to British Columbia and Washington (Pritchard and DeLacy 1944, DeLacy and Neave 1948, IPSFC 1958, WDF 1959). A graphical summary of the information gathered in these studies is given in Figure 5. Most pink salmon returning to Washington are believed to travel east through the Strait of Juan de Fuca, but some fish probably also use the Johnstone Strait/Strait of Georgia corridor during their return migration (IPSFC 1958). In addition, returning Fraser River and other southern British Columbia pink salmon may migrate through either corridor.

Although available information is insufficient to discriminate fish from different populations as they migrate into nearshore marine waters in Washington and southern British Columbia to reach spawning grounds, WDF et al. (1993) have outlined some prominent patterns. Generally, differences in migration timing of maturing pink salmon in this region are small; differences among populations within areas can be larger than differences among populations from different areas. Even-year pink salmon returning to the Snohomish River in Puget Sound begin appearing in catches in early June and drop off sharply after mid- to late September. Peak abundance off the river mouth generally occurs in late August (WDF et al. 1993).

For odd-year pink salmon returning to Washington rivers, timing of arrival to terminal areas (i.e., near estuaries and river mouths) shows no clear geographic pattern. Maturing fish returning to streams in northern Puget Sound generally arrive at these areas between mid-August and late September. The earliest run appears to occur to the Nooksack River, the latest to the Skagit River. In southern Puget Sound, fish arrive at terminal areas primarily between mid-July and mid-August. In Hood Canal, fish arrive between mid-July and early September (WDF et al. 1993). Pink salmon appear off the Dungeness River in the Strait of Juan de Fuca

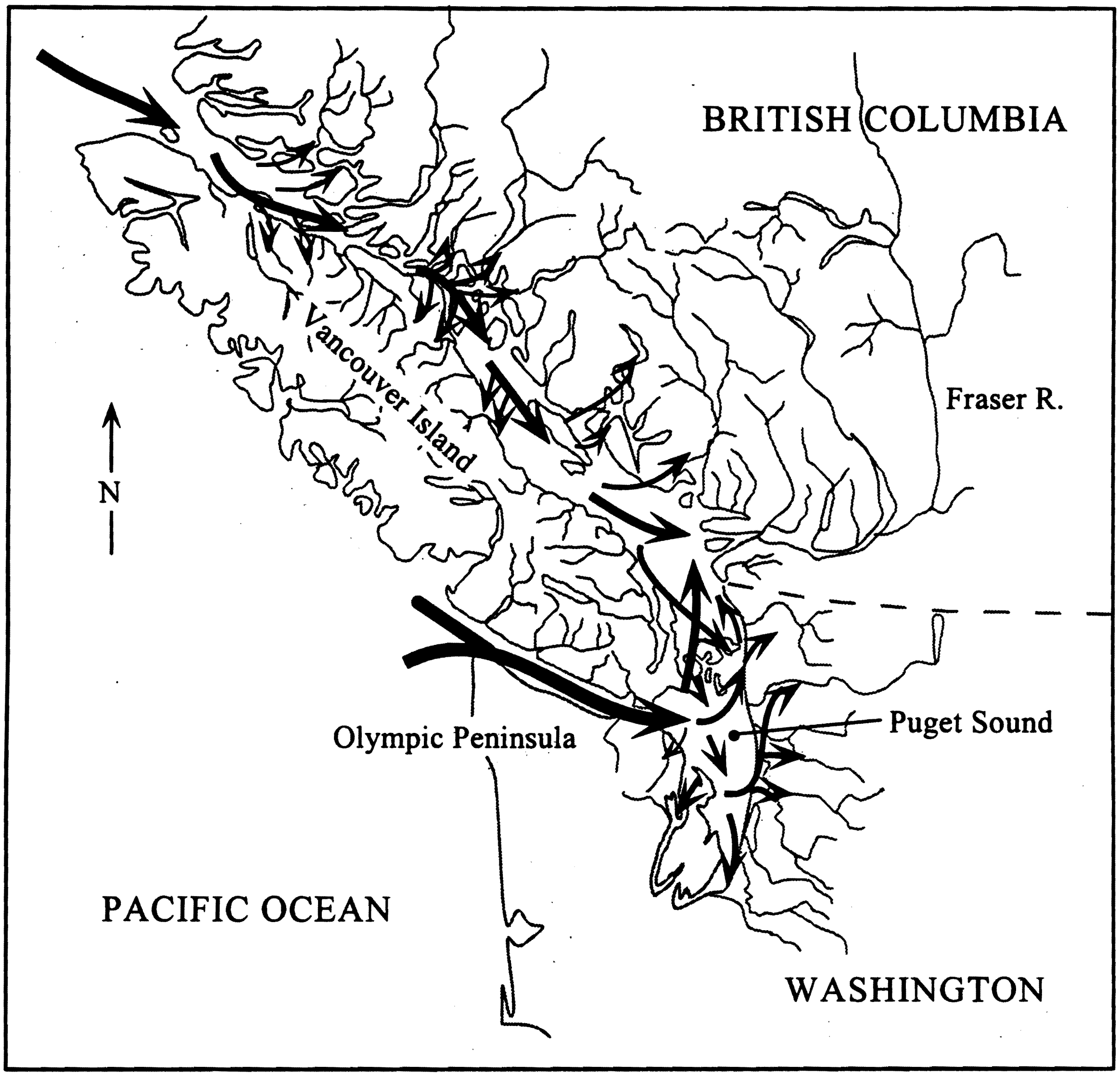

Figure 5. Principal migration routes for adult pink salmon returning to southern British Columbia and Washington. Figure modified from WDF (1959).

earlier than pink salmon returning to other Washington rivers. Fish that migrate to the Dungeness River begin arriving at the river's mouth as early as mid-June and continue to show up until early August, with abundance off the river mouth declining after river entry between late July and early September. These fish constitute the two distinct runs that return to the upper and lower river, respectively, and show considerable temporal differentiation in average spawn timing (WDF et al. 1993).

Spawn timing--Pink salmon populations can vary considerably in their arrival timing at spawning grounds (Sheridan 1962, WDF et al. 1993), and some evidence exists for substantial differences in spawn timing within a single river system. For example, Taylor (1980) and Gharrett and Smoker (1993a) identified early and late spawning populations in Auke Creek, Alaska that were also differentiated by their patterns of fry outmigration timing. These populations have not yet been distinguished by allozymic variation (Lane et al. 1990). Because this sort of life history variability can have consequences for fitness (Taylor 1980, Mortensen et al. 1991), it may be instrumental in maintaining adaptive diversity within and among populations. The fact that such life history variation may not be detected with routine allozyme surveys indicates the importance of considering this variation when attempting to identify distinct population units (Gharrett and Smoker 1993b, Hard 1995a). However, the interpretation of life history variation is complicated because this variation may also be quite sensitive to environmental variation (Waples 1991a, Hard 1995b).

In Washington and southern British Columbia, river entry occurs from July to October, and spawning is generally observed from August to October (Neave 1963, WDF et al. 1993). In their SASSI document, WDF et al. (1993) reported that average timing of river entry and spawning are generally earlier in northern Puget Sound and in the upper Dungeness River on the Olympic Peninsula than elsewhere in northwestern Washington. As noted in an earlier section, the Dungeness River has two populations of pink salmon: "summer" run fish enter the river in ocean-bright condition in July and August, hold in the river for up to a few weeks before final maturation, and spawn above RKm 16 in August and September; "fall" run fish enter the river already exhibiting much of their spawning morphology and coloration in August and September, spawning soon afterward in the lower river. These dark fall-run fish spawn below RKm 5 an average of 2 weeks later than summer-run fish (WDF et al. 1993, J. Uehara[14]).

The Washington Department of Fish and Wildlife has surveyed pink salmon escapement (counts of live and dead adults) in many northwestern Washington rivers since the late 1950s. The Department uses an "area under the curve" method (Ames 1984) to estimate escapement from many of these surveys and from an estimate of spawner life in the stream (generally, 10 or 15 days). Escapement curves generated with this method can also be used to derive median spawn timing for different rivers in various years. One means of deriving an

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[14]J. Uehara, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., January 1995.

estimate of median spawn timing for a given reach or drainage in a particular year is to determine the date at which half the area under the curve is reached. Since these curves are actually a series of connected trapezoids, it is a straightforward matter to calculate this date. This method may be preferable to using peak counts because the median spawn date should be less sensitive than peak count to variation in the shape of the spawning distribution.

Data from WDF spawning surveys conducted between 1983 and 1993 were used to calculate median run timings and examine their patterns. Table 2 summarizes these data and compares them to the range of spawning dates observed in these systems and summarized by WDF et al. (1993). It should be noted that 1) no data were available from Snohomish River even-year pink salmon for this analysis, 2) the Elwha River statistics were based on a single survey in 1985, and 3) few surveys have been made in the Nisqually River. It should also be noted that spawning curves for some river reaches that may contain significant spawning populations are not yet available. In some cases, several surveys within a river and year were combined to determine the median date for that river. For these reasons, data generated from the spawning curves should be examined with caution.

Nevertheless, a complex pattern for odd-year pink salmon run timing is evident from this limited analysis. In general, the run timing estimates derived from spawning curves correspond well to the midranges of spawning reported by WDF et al. (1993); the exceptions are estimated median run timings for Puyallup River and Elwha River pink salmon, which are both earlier than the midranges interpolated from the WDF et al. (1993) report. However, it should be noted that the Puyallup River median timing is within the range reported by WDF et al. (1993), and the Elwha River median timing is based on only a single year.

In general, it appears that pink salmon spawn earliest in the upper Dungeness River (average of the median calendar dates ± SE = 245 ± 0.8, where day 245 = 2 September), followed by the Nooksack River (North Fork, 254 ± 0.8), lower Dungeness River (265 ± 2.7), Hood Canal (major rivers only, 269 ± 6.5), Puyallup River (270 ± 4.1), Skagit River (275 ± 0.8), Stillaguamish River (279 ± 1.3), Snohomish River (280 ± 0.7), and Nisqually River (283 ± 1.3). The general pattern appears to be that peak spawning is earliest for Strait of Juan de Fuca populations and the Nooksack River, with peak spawning in Hood Canal occurring 2-3 weeks later on average, and peak spawning in Puget Sound (excluding the Nooksack and Nisqually Rivers) occurring another week after that.

Run timing for Nisqually River pink salmon is the latest for all Washington populations examined, based on 2 years of surveys. Timing of peak spawning of even-year pink salmon in the Snohomish River is about 3-4 weeks earlier than that of odd-year fish, even though these two groups of fish use some of the same habitat (D. Hendrick[15]). Even-year Snohomish River

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[15]D. Hendrick, Washington Department of Fish and Wildlife, 333 E. Blackburn Rd., Mount Vernon, WA 98273. Pers. commun., January 1995.

Table 2. Comparison of estimates of median run timing for Washington pink salmon (generated from 1983-93 spawning curves; WDFW, unpubl. data) to spawn timing ranges and approximate midranges (WDF et al. 1993). Estimates are in calendar days, where 1 September = day 244 and 15 October = day 288. N refers to the number of spawner surveys in the sample.

	1983-93 Median run timing			Spawn timing[a]		
Drainage	Avg.	SD	N	Start	Midrange	End
			Northern Puget Sound			
Nooksack (NF)	254	3.7	24	233	251	269
Thompson Cr.	254	2.1	6	--	--	--
Cornell Cr.	254	6.4	6	--	--	--
Gallop Cr.	253	2.6	6	--	--	--
Other (pooled)	254	3.2	6	--	--	--
Nooksack (SF)	--	--	--	269	275	281
Skagit	275[b]	3.8	23	238	270	303
Upper Skagit	275	2.5	6	--	--	--
Mid Skagit	270	5.1	6	--	--	--
Lower Skagit	278	4.8	5	--	--	--
Sauk	260	--	1[c]	--	--	--
Other (pooled)	276	3.4	6	--	--	--
Stillaguamish	279	6.1	23	--	--	--
North Fork	273	3.6	6	251	273	296
South Fork	281	9.0	6	256	279	303
Pilchuck Cr. & MS Stillag	287	3.0	6	--	--	--
Other (pooled)	276	8.2	6	--	--	--
Snohomish (odd year)	280	2.5	12	254	278	303
Wallace	276	2.5	5	--	--	--
MS Snohomish	283	4.0	3	--	--	--
Elwell Cr. & other	281	2.1	5	--	--	--
Snohomish (even year)	--	--	--	254	266	278
			Southern Puget Sound			
Puyallup & S. Prairie Cr.	265	3.8	5	251	275	299
Kapowsin	276	5.0	4	--	--	--
Nisqually	283	1.9	2	254	278	303

Table 2. Continued.

Drainage	1983-93 Median run timing Avg.	SD	N	Spawn timing[a] Start	Midrange	End
			Hood Canal			
Dosewallips	272	7.1	5	244	270	298
Duckabush	269	7.5	5	244	270	298
Hamma Hamma	267	6.6	5	244	270	298
Lilliwaup Cr.	271	7.8	5	--	--	--
Skokomish	272	11.1	5	--	--	--
			Strait of Juan de Fuca			
Lower Dungeness	265	6.0	5	244	265	286
Upper Dungeness	245[c]	2.4	9	218	242	265
East Fork	245	2.4	4	--	--	--
Grey Wolf	245	2.7	6	--	--	--
Forks	240	--	1[c]	--	--	--
Elwha	235	--	1[e]	254	268	283

[a] Estimates for the lower and upper Dungeness River are revised from those in the Washington State Salmon and Steelhead Stock Inventory (J. Uehara, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501, pers. commun., April 1995).
[b] Does not include Sauk River data.
[c] 1993 data.
[d] Does not include Forks data.
[e] Based on 87 adults returning in 1985.
WDFW = Washington Department of Fish and Wildlife.
WDF = Washington Department of Fisheries.
NF = North Fork.
SF = South Fork.
MS = main stem.

fish spawn during about the same time that even-year fish spawn farther north in central British Columbia (Aro and Shepard 1967; Gould et al. 1988; Stefanson et al. 1989, 1991).

Emergence timing--WDFW biologists have also collected unpublished observations on development of pink salmon embryos during redd surveys in many of the Washington rivers that support these fish. However, the collection of this information has become infrequent in recent years. Examination of the available information indicates that hatching generally occurs between late January and early March, but the patterns are highly variable both among river systems and within these systems among years. No clear interdrainage patterns are evident from these data. Emergence timing is not directly assessed with these data but would appear to occur primarily in March and April. Because of large gaps in the data and the sensitivity of embryonic development to environmental conditions in the river, the BRT concluded that this information is not likely to be useful in aiding ESU determinations for Washington pink salmon.

Outmigration and Estuarine Use

Juvenile pink salmon generally begin migrating downstream immediately upon emerging from the gravel. Based on work in the Fraser River by Vernon (1966) and in Hooknose Creek, British Columbia by Hunter (1959), pink salmon fry migrate downstream primarily in March and April in this region, although migration can extend into May. Pink salmon outmigrating from rivers draining into Puget Sound and Hood Canal appear to use nearshore areas in these embayments extensively for early rearing (Jewell 1966). The degree of habitat overlap between odd-year populations is unknown.

Little is known about the migratory and feeding habits of juvenile pink salmon outmigrating into the Strait of Juan de Fuca. Hiss (1994) found that juvenile pink salmon began migrating into Dungeness Bay in 1994 by April, peaked in their migration in late April, and had largely left the estuary by the third week in May. Fry ranged in length from 35 to 75 mm over the sampling period; some fry captured in early April were more than 45 mm long, suggesting that they had entered the estuary in March.

In addition, preemergent fry samples collected in the Dungeness River in late February and early March showed that 80-90% of fry were near yolk-sac absorption, suggesting an early outmigration (WDFW, unpubl. data). It was unclear from Hiss' (1994) study whether there was any spatial or temporal separation between juvenile pink salmon from the lower and upper Dungeness River. The study did not address where these pink salmon go after they leave Dungeness Bay; it is unclear whether these fish migrate west through the Strait of Juan de Fuca or (possibly) east and north through the Strait of Georgia.

Resident Fish

Like pink salmon in many populations from more northern regions, pink salmon in British Columbia and Washington often spend an extended period in the nearshore marine environment feeding and growing rapidly before they move offshore (Manzer and Shepard 1962, Phillips and Barraclough 1978, Healey 1980). This period may be as long as 2 to 3 months (reviewed by Heard 1991). However, most pink salmon migrate to the open ocean by late summer or early fall.

An exception to this pattern appears in some pink salmon from Puget Sound (and possibly Hood Canal) that spend their entire marine phase in the nearshore environment. This behavior has been inferred from tagging studies described by Jensen (1956) and Hartt and Dell (1986). Jensen (1956) tagged 873 small (1-1.5 kg) pink salmon in the Tacoma Narrows in June 1955 and sampled these fish in various parts of Puget Sound for the next 4 months to ascertain their origin. These fish were presumed to be resident to Puget Sound on the basis of their small size. Tagged fish remained in the general area for about 1 month, then moved generally north along the eastern shore of Puget Sound. Most of the tags were recovered by sport fishers. The results were largely inconclusive, but three of the four recoveries were made on spawning grounds in the Stillaguamish River, and Jensen suggested the Stillaguamish River population as a possible source of resident pink salmon. Small pink salmon have been repeatedly observed spawning in Pilchuck Creek, a Stillaguamish River tributary, as long as 20 years ago (W. Waknitz[16]).

The Suquamish Tribe sampled immature pink salmon in central Puget Sound in October and November 1976, catching hundreds of them to both the north and south of Bainbridge Island (Hartt and Dell 1986). These fish were about 23 cm long at capture, a size described as "larger than most pinks that had migrated hundreds of miles in the open sea by September" (Hartt and Dell 1986). The captured fish would probably not migrate offshore that late in the year. It is unlikely that this reticence to move to the open ocean is related to their size; Jensen (1956) believed these fish adopted residence in Puget Sound for the marine phase of the life cycle. So far as is known, this unusual practice of forgoing migration on the high seas is not documented for any populations of pink salmon outside Washington (W. Heard[17]). "Resident" chinook and coho salmon also occur in Puget Sound (Haw et al. 1967).

Presumably resident pink salmon (based on their small size of 35-45 cm) supported a sport fishery in Puget Sound in odd-years from the late 1940s until the early 1960s (Haw et al. 1967). These fish were harvested primarily in southern Puget Sound, especially in the Tacoma Narrows and Commencement Bay areas, with gear that incorporated an attractant device composed of a large spinner blade preceded by a rudder to control line twist (known as "shovel and rudder" gear; F. Haw[18]).

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[16]W. Waknitz, NMFS Northwest Fisheries Science Center. Unpubl. observations.

[17]W. Heard, NMFS Alaska Fisheries Science Center Auke Bay Laboratory, 11305 Glacier Hwy., Juneau, AK 99801. Pers. commun., January 1995.

[18]F. Haw, Northwest Marine Technology, Inc., Shaw Island, WA 98286. Pers. commun., January 1995.

Body Morphometry, Fecundity, and Egg Size

Body morphometry--Beacham (1985) and Beacham et al. (1988) observed significant variation in body size and shape both within and among broodlines of British Columbia pink salmon. Variation in morphometric characters (particularly head size, caudal peduncle thickness, and fin size) tended to show greater variation among fish in different broodlines returning to the same river drainage than among fish of different populations within broodlines. Because larger fish with larger heads, thicker caudal peduncles, and larger fins were usually associated with large rivers, the authors interpreted these results as evidence for morphometric adaptation to natal river conditions.

To assist in stock separation analyses, WDFW and its predecessor WDF have been collecting tissue samples from adult pink salmon for protein electrophoresis in several Washington rivers since 1985. Staff biologists have also measured the body lengths of sampled adults (WDFW, unpubl. data). Although these samples may not be representative of the entire spawning populations, sampling in each river was generally conducted in more than 1 year and often in several different locations (S. Young[19]). Early measurements were of snout-to-fork (SF) length (a measure commonly used by U.S. fishery biologists) to the nearest centimeter, but in more recent sampling the measurements have been of postorbital-to-hypural plate (POH) length (a measure more commonly used by Canadian fishery biologists). The POH measurement has the advantage that it is unaffected by snout and tail erosion in spawning adults.

All even-year fish sampled from the Snohomish River were collected in 1990, and all fish measurements were POH lengths. For odd-year populations, fish measurements were either SF or POH lengths, depending on the year of sampling. Separate linear regression equations were necessary to convert SF to POH for both males and females. Regression equations were not available to convert SF to POH; instead, regression equations to convert SF to mideye-to-hypural plate (MEH) length were generated from relationships between SF and mideye-to-fork (MEF) length and between MEF and MEH given for Alaskan pink salmon by Nickerson (1979). Although MEH is smaller than POH, the use of MEH can be justified because 1) MEH and POH are highly correlated, 2) the difference between them is small (< 1 cm), and 3) all measurements analyzed here are rounded to the nearest centimeter. Thus, the practice of using both MEH and POH in this analysis should have little potential to bias the results. The equations (including their correlation coefficients and sample sizes) relating MEH and SF for odd-year pink salmon are

$$\text{males: } MEH = 2.4301 + 0.8179 \times SF;\ r^2 = 0.974\ (n = 27);$$

$$\text{females: } MEH = 0.6777 + 0.8652 \times SF;\ r^2 = 0.972\ (n = 38).$$

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[19]S. Young, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., February 1995.

The results of these manipulations of WDFW's unpublished size data are summarized in Table 3. Analysis of variance of the data indicated highly significant ($P < 0.0001$) effects of sex and sampling year. The sex effect reflects the strong sexual dimorphism that is characteristic of pink salmon. Multiple comparisons (Newman-Keuls test, Sokal and Rohlf 1981) among sampling years, after data among drainages were pooled, indicated a substantial general decline in MEH for odd-year pink salmon over time (1993 < 1991 < 1989 < 1987 < 1985; $P < 0.0001$). The data in Table 3 indicate that the size decline over time is common to all the populations sampled in more than one year. Data are available for Snohomish River even-year pink salmon from only 1 year, but these were the smallest fish observed in all Washington samples (Table 3).

Significant variation among drainages was also observed in odd-year pink salmon when sampling years and sexes were pooled. The relationship among drainages, in order of increasing adult MEH length, was

Nooksack < lower Dungeness < Nisqually < upper Dungeness < [Skagit, Snohomish, Stillaguamish, Dosewallips] < [Puyallup, Duckabush] < Hamma Hamma.

where group differences were significant ($P < 0.05$). Hood Canal Hatchery fish were similar in length to Skagit, Snohomish, Stillaguamish, and Dosewallips River fish. In general, the smallest fish appear to exist in cold, turbid rivers in Puget Sound (Nooksack and Nisqually Rivers) and along the Strait of Juan de Fuca (lower and upper Dungeness River), and the largest fish tend to exist in Hood Canal. Although the Puyallup River is also heavily glacially influenced, all fish were sampled from a clear water tributary, South Prairie Creek, where the majority of spawning in that river is observed (WDF et al. 1993, J. Uehara[20]). No size data are available for Elwha River pink salmon.

Beacham and Murray (1985) and Beacham et al. (1988) calculated POH length data for several even- and odd-year pink salmon populations in British Columbia, and these data provide some basis for comparison with the Washington data. Beacham and Murray (1985) found that even-year fish were shorter ($P < 0.01$) than odd-year fish among the central and southern British Columbia populations they examined, a general result previously reported for body weight by Godfrey (1959). Snohomish River even-year adult pink salmon sampled by WDF in 1990 are similar in size to pink salmon in the even-year populations from the central mainland and northern Vancouver Island described by Beacham and Murray, although the Snohomish River fish tend to be smaller than the even-year British Columbia average. The length estimates for odd-year populations in Washington taken in recent years (Table 3), with the exception of the Snohomish and Skagit River populations, tend to be smaller than the average for odd-year British Columbia populations reported by Beacham and Murray (1985).

[20]J. Uehara, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., January 1995.

Table 3. Means and standard errors (SE) of mideye-to-hypural plate lengths (odd-year fish) and postorbital-to-hypural plate lengths (even-year fish) for adult pink salmon sampled in Washington (WDFW, unpubl. data). For each drainage, multiple samples collected in the same year have been pooled to increase sample sizes; mean sample size was 105.5 fish (range, 18-274). Measurements are in centimeters.

Drainage	Sex	1985 Mean ± SE	1987 Mean ± SE	1989 Mean ± SE	1990 Mean ± SE	1991 Mean ± SE	1993 Mean ± SE
				Odd-year			
Nooksack	m	--	42.4 ± 0.4	--	--	36.7 ± 0.3	36.6 ± 0.6
	f	--	42.9 ± 0.3	--	--	38.7 ± 0.3	37.8 ± 0.6
Skagit	m	48.9 ± 0.8	46.3 ± 0.4	43.9 ± 0.3	--	42.4 ± 0.7	--
	f	46.4 ± 0.5	44.3 ± 0.3	42.4 ± 0.2	--	41.1 ± 0.3	--
Stillaguamish	m	48.8 ± 2.3	46.9 ± 0.5	--	--	--	40.5 ± 0.4
	f	48.2 ± 0.4	44.7 ± 0.3	--	--	--	39.6 ± 0.3
Snohomish	m	52.4 ± 0.5	47.3 ± 0.4	44.4 ± 0.5	--	43.0 ± 0.5	--
	f	46.9 ± 0.4	43.8 ± 0.5	41.9 ± 0.5	--	41.4 ± 0.3	--
Puyallup	m	49.8 ± 0.7	44.2 ± 0.6	--	--	--	--
	f	48.5 ± 0.6	43.9 ± 0.4	--	--	--	--
Nisqually	m	--	--	--	--	41.5 ± 0.5	--
	f	--	--	--	--	40.7 ± 0.2	--
Dosewallips	m	53.2 ± 0.7	47.6 ± 0.7	42.5 ± 0.4	--	43.8 ± 1.5	41.1 ± 0.3
	f	50.6 ± 1.2	43.4 ± 0.3	40.7 ± 0.6	--	42.8 ± 0.7	39.7 ± 0.3
Duckabush	m	49.6 ± 0.8	48.7 ± 0.7	--	--	--	--
	f	45.9 ± 0.8	43.0 ± 0.2	--	--	--	--
Hamma Hamma	m	50.7 ± 0.7	47.8 ± 0.8	--	--	--	--
	f	48.3 ± 0.9	43.9 ± 0.4	--	--	--	--
Upper Dungeness	m	--	46.3 ± 0.4	43.6 ± 0.5	--	--	40.2 ± 0.6
	f	--	43.4 ± 0.4	40.8 ± 0.4	--	--	37.7 ± 0.3
Lower Dungeness	m	--	--	42.0 ± 0.7	--	40.7 ± 0.4	41.3 ± 1.3
	f	--	--	40.2 ± 0.3	--	38.6 ± 0.2	38.4 ± 0.6
				Even-year			
Snohomish	m	--	--	--	37.2 ± 0.4	--	--
	f	--	--	--	37.1 ± 0.7	--	--

WDFW = Washington Department of Fish and Wildlife.

However, many of the lengths taken in 1985 and 1987 in Washington are larger than the British Columbia average, which is based on 1981 and 1983 collections.

Snohomish River even-year pink salmon, based on the 1990 sample, are most similar in length to even-year males sampled from large rivers on the central British Columbia coast and to even-year females sampled from small rivers on Vancouver Island (Beacham et al. 1988). For odd-year males, the greatest length similarities between Washington and British Columbia pink salmon samples are Nooksack River and small Fraser River tributaries; all other Puget Sound rivers and large Fraser River tributaries, except for Nisqually River, which is most similar to large south coast and Vancouver Island rivers; all Hood Canal rivers and large Fraser River tributaries; upper Dungeness River and large Fraser River tributaries; and lower Dungeness River and small Fraser River tributaries.

For odd-year females, the greatest similarities exist between the following: Nisqually River and both large and small north coast rivers as well as small Fraser River tributaries; lower Dungeness River and large Skeena River and Vancouver Island tributaries; and all other Puget Sound rivers and large Fraser River tributaries. These odd-year comparisons are based on Washington collections made in 1985 (the last year sampling was conducted by Beacham et al. 1988), except for the Nooksack (1987), Nisqually (1991), upper Dungeness (1987), and lower Dungeness Rivers (1989). In Washington, there is no apparent relationship between the length of adult pink salmon and river size, as reported for the more comprehensive survey of British Columbia populations by Beacham et al. (1988). No data are available for other morphometric characters in Washington pink salmon.

Two caveats are important to emphasize in interpreting these comparisons. First, the possibility that sampling was not random within drainages cannot be excluded and could bias these results. Second, because much of the Washington and British Columbia length sampling was done in different years, these comparisons should be regarded with caution, as adult pink salmon size can vary significantly between years (Ricker et al. 1978).

Fecundity and egg size--Beacham and Murray (1993) summarized geographic patterns of fecundity and egg size in pink salmon. When fecundity was standardized to a body length of 435 mm, fecundity in both even- and odd-year fish tended to increase with latitude over the range of about 49°N to 61°N in North America. However, available information was meager for Alaskan populations, and considerable variability existed among the British Columbia populations sampled. For odd-year pink salmon in British Columbia, Beacham and Murray (1993) found that fecundity was generally lower in Vancouver Island and upper Fraser River populations than in other British Columbia populations. For even-year British Columbia pink salmon, fish from the Queen Charlotte Islands had the highest fecundities.

Pink salmon egg size (weight and diameter) showed considerable geographic variation within both broodlines but showed no clear relationship with latitude for either broodline. Egg size (when standardized by body length) tended to be larger in even- than in odd-year pink salmon in British Columbia (Beacham et al. 1988, Beacham and Murray 1993). In British

Columbia, egg weight and diameter tended to be largest in Skeena River populations for odd-year fish and in the Queen Charlotte Islands for even-year fish. Southern British Columbia populations showed a considerable degree of scatter in egg size (Beacham and Murray 1993). Among several odd-year populations of British Columbia pink salmon sampled for egg size, populations with larger eggs produced heavier alevins with greater amounts of yolk, but the relationship between egg and alevin size depended on temperature under controlled incubation conditions (Beacham and Murray 1986). No clear relationship between egg or alevin size and embryonic survival was observed by these workers.

Homing and Straying

Homing and straying are prominent features of Pacific salmon biology that can have significant effects on population structure. Consequently, these related behaviors are relevant to ESU determinations for these species. Pink salmon have a widespread reputation for straying at higher rates than other species of Pacific salmon (e.g., Horrall 1981). If true, then if straying pink salmon also reproduce successfully, the elevated rate of gene flow would be expected to result in a less conspicuous population structure and, potentially, reduced opportunity for local adaptations to be maintained in this species. (The analysis of genetic variation provided in the next section sheds some light on the level of population structure in pink salmon.)

Few well-designed studies have been carried out to estimate straying rates in Pacific salmon, and the empirical evidence supporting the hypothesis that pink salmon stray at relatively higher rates than other species of *Oncorhynchus* is mixed (Quinn 1993, Altukhov and Salmenkova 1994). Early work by Davidson (1934) in Washington (Hood Canal) and southeastern Alaska and by Pritchard (1939) in British Columbia produced estimates of straying of about 10%, based on recovery of tagged adults, but Ricker (1962) concluded that this rate was probably rarely exceeded by natural pink salmon.

Helle (1966) moved adult pink salmon from Olsen Creek in Prince William Sound, Alaska to a location 5 km away and recovered 91% of them in Olsen Creek. Gharrett (1985) detected no straying of genetically marked odd-year pink salmon from Auke Creek, Alaska to two other pink salmon streams within 10 km of Auke Creek; however, he did provide some evidence for higher straying of even-year fish to both another run within Auke Creek and another drainage. Altukhov and Salmenkova (1994) reviewed pink salmon straying data from marked fry released from North American and Asian hatcheries and found that estimates ranged from 0.1 to 11.5%. Although most estimates of straying are based on recoveries of adults from streams in the vicinity of the natal stream, Heard (1991) discussed some data that indicate pink salmon can travel several hundred kilometers from the natal stream during their adult migration. Quinn (1993) summarized these studies in this way: “the conclusion that [pink salmon] stray more commonly than other salmon species seems premature.”

Nevertheless, the rapid colonization of systems newly available to pink salmon indicates that this species has an unusual ability to expand into suitable habitat when conditions are favorable. The rapid expansion of pink salmon into the Great Lakes after their accidental introduction (Kwain and Laurie 1981); the recolonization of Sashin Creek, southeastern Alaska, by even-year pink salmon after nearly complete experimental removal of the even-year run (Merrell 1962, Heard 1991); and the immediate recolonization of the upper Fraser River after almost 35 years of blocked access (Vernon 1962) are testaments to this ability. In addition, the reports of pink salmon periodically spawning south of northwestern Washington, in the absence of any evidence for permanent spawning populations in these southern areas, suggest that pink salmon homing behavior is highly plastic. Finally, maturing pink salmon show a strong propensity to move around between neighboring streams, at least in certain areas, prior to spawning (Jones and Thomason 1983).

Straying in pink salmon may depend strongly on spawning location and on conditions at time of spawning. In a recent study in Prince William Sound, Sharp et al. (1994) estimated straying rates between 9 and 53% in coded-wire tagged odd-year wild and hatchery pink salmon. Several factors may contribute to the relatively high straying observed: 1) Prince William Sound is a highly dynamic geological zone, having experienced two major earthquakes in the last century that destroyed many streams and created others; 2) a large fraction of Prince William Sound pink salmon spawn intertidally--approximately 72-77% in even years and 35-57% in odd years prior to the 1964 Good Friday earthquake (Noerenberg 1963); and 3) the southwestern part of Prince William Sound was heavily affected by the 11-million gallon *Exxon Valdez* oil spill in 1989 (S. Rice[21]). In addition, because coded-wire tagging of juvenile pink salmon must occur at the emergent fry stage, some question has been raised as to whether the tagging itself may impair the homing of these fish (Morrison and Zajac 1987; J. Seeb, Alaska Department of Fish and Game, pers. commun., cited in Mathisen 1994).

Levels of natural straying in pink salmon are therefore unclear and may vary widely among populations and within populations under different conditions. More importantly, the genetic consequences of straying in pink salmon are not well understood.

Artificial Propagation of Pink Salmon

Because artificial propagation of Pacific salmonids has been widespread for many years, the influence of hatchery fish needs to be considered in most ESA status reviews. NMFS policy (NMFS 1993) stipulates that in determining whether a population is distinct for purposes of the ESA, attention should focus on natural fish (Waples 1991a). The decision to focus on natural fish is based entirely on ecosystem considerations; the question of the relative merits of hatchery versus natural fish is a separate issue. Fish are not excluded from ESA consideration simply because some of their direct ancestors may have spent time in a fish

[21]S. Rice, NMFS Alaska Fisheries Science Center, Auke Bay Laboratory, Juneau, AK 99801. Pers. commun., March 1995.

hatchery, nor does identifying a group of fish as "natural" as defined here automatically mean that they are part of a listed ESU. For a discussion of artificial propagation of Pacific salmon under the ESA, see Hard et al. (1992).

Transplants into Washington

It is commonly believed that even-year pink salmon historically either were absent from Washington or were at an abundance too low to sustain harvest (Rounsefell 1938, Atkinson 1956, Ellis and Noble 1959). Consequently, WDF made several attempts earlier in this century to establish even-year pink salmon runs in northwestern Washington (WDF 1916-1964, Neave 1965, Roppel 1982). These efforts are summarized in Table 4.

More than 82 million eyed pink salmon eggs were transported from Alaska to various locations in Washington in even-numbered years between 1910 and 1932. In addition, more than one million odd-year Alaskan eggs were brought into Washington from southeastern Alaska in 1929 (Table 5). An estimated 85 million juveniles resulting from these transplanted eggs (see explanation in Table 4) were released between 1911 and 1933; these releases produced no recorded returns of even-year adults to Washington rivers, including the Snohomish River (Ellis and Noble 1959, Neave 1965).

However, Neave (1965) stated that "it appears that streams were not examined for actual escapements," and "in 1924 the traps along the west coast of Vancouver Island, which had never caught pink salmon in the even-numbered, or off years for this variety, reported total catches of more than 20,000 small pinks, resembling the Alaska variety which had been transplanted" (note that in 1923, over 14 million fry from Prince William Sound eggs were released into Washington waters, including nearly a million fry planted in the Skykomish River; Table 4).

Attempts to establish even-year pink salmon in the state were renewed between 1944 and 1956 with the transport of nearly 4 million eyed eggs from the Skeena River drainage in British Columbia (and possibly 200,000 eggs from Alaska in 1948; Table 4). Of the 1.3 million fry released, at least several hundred apparently survived to return as adults, but there is no evidence that returns were sustained beyond one or two generations (Ellis and Noble 1959, Neave 1965). The most substantial return appeared to result from a 1949 release of 299,000 fry (Lakelse River) into the Samish River, where an estimated 300-500 adults returned in 1950 (Neave 1965).

Table 4. Documented transplants of even-year pink salmon into Washington. Data are from WDF (1916-64), Neave (1965), and Roppel (1982). The number of eggs transported to Washington hatcheries is generally that provided by USBF shipping records (Neave 1965, Roppel 1982); the number of fry released into Washington watersheds is generally that provided by WDF planting records (WDF 1916-64, Neave 1965). Note that in some cases the estimated number of juveniles released exceeds the estimated number of eggs transplanted. In addition, it was not always possible to identify the number of fry released from specific broodstocks.

Brood year	Donating agency	Source of broodstock	Eyed eggs transplanted	Juveniles released	Release location
			Alaska		
1910	USBF	Yes Bay H.	100,000	?	Baker Lake
1914	USBF	Afognak H.	5,500,000	4,750,000	Birdsview H.[a]
				1,820,000	Duckabush
				310,000	Big Quilcene
				50,000	Little Quilcene
1916	USBF	Afognak H.	4,106,752	?	Green Lake[b]
			4,000,000	3,729,000	Birdsview H.
			200,000	1,960,000	Duckabush
			2,000,000	1,700,000	Big Quilcene
				225,000	Little Quilcene
1918	USBF	Yes Bay H.	406,000	?	Birdsview H.
		Afognak H.	?	1,969,000	Skagit
				370,000	Duckabush
				386,000	Big Quilcene
1922	USBF	Cordova	14,571,708[c]	492,000	Dungeness
				985,000	Elwha
				4,075,000	Green
				2,171,000	Puyallup
				3,204,000	Samish
				2,536,000	Skokomish
				949,000	Skykomish
1924	USBF	Western Alaska	30,600,000	2,968,000	Big Quilcene
				1,926,000	Chambers Cr.
				10,771,000	Green
				2,316,000	Nooksack
				2,181,000	Pilchuck
				2,452,000	Puyallup
				4,537,000	Samish

Table 4. Continued.

Brood year	Donating agency	Source of broodstock	Eyed eggs transplanted	Juveniles released	Release location
			Alaska, Continued.		
1924	USBF	Western	30,600,000	3,155,000	Skykomish
				2,250,000	SW ponds
1926	USBF	Afognak H.	3,617,000[d]	2,000,000	Big Quilcene
				1,300,000	SW ponds
1928	USBF	Afognak H.	2,300,800[e]	3,304,000	Green & SW ponds
		Yes Bay H.	2,038,000[e]	419,000	Green & SW ponds
1930	USBF	Afognak H.	10,155,776[f]	4,542,000	Green
				2,391,000	Puyallup
				949,000	Samish
				3,335,000	Skykomish
				199,000	SW pond # 2
1932	USBF	Afognak H.	2,228,000[g]	?	?
		Yes Bay H.	379,904[g]	2,478,000[h]	?
1948	USBF	Alaska	200,000[i]	?	?
			British Columbia		
1944	CDF	Skeena R.	?	38,680	Puyallup H.
1948	CDF	Lakelse R.	770,000[j]	298,980	Samish estuary
1950	CDF	Lakelse R.	727,070	57,000	Samish estuary
1952	CDF	Lakelse R.	248,155	?[k]	Samish & Stillaguamish estuary
			331,000	57,625	Dungeness
				103,240[l]	Dosewallips

Table 4. Continued.

Brood year	Donating agency	Source of broodstock	Eyed eggs transplanted	Juveniles released	Release location
		British Columbia, Continued.			
1954	CDF	Lakelse R.	509,688	145,426	Finch Cr.
1956	CDF	Lakelse R.	1,191,200	673,786	Finch Cr.

[a] Satellite facility of Baker Lake H. on Skagit R.
[b] It is possible that this Green Lake entry refers to a transplant to Maine (see O'Malley 1917).
[c] WDF (1916-64) reported 15,290,000 eggs transplanted.
[d] WDF (1916-64) reported 1,500,000 eggs transplanted.
[e] WDF (1916-64) reported a total of 8,889,050 eggs transplanted from all sources.
[f] WDF (1916-64) reported 12,647,476 eggs transplanted.
[g] WDF (1916-64) reported 2,500,000 eggs transplanted.
[h] Apparently this figure from Neave (1965) includes fry from both Alaskan sources.
[i] Reported by Neave (1965), but he noted that this figure could not be confirmed.
[j] Neave (1965) reported 700,000 eggs transplanted.
[k] Neave (1965) reported 249,000 fry released.
[l] Neave (1965) reported 159,000 fry released into "Hood Canal streams."
USBF = U.S. Bureau of Fisheries.
CDF = Canadian Department of Fisheries.
WDF = Washington Department of Fisheries.
SW = salt water.
H = hatchery.

Table 5. Major releases of juvenile pink salmon (fed and unfed fry) in Washington and Oregon. Data from WDF (1916-64), WDF et al. (1993), and NRC (1995).

Brood year	Release year	Agency	Subagency	Release location	Broodstock	Number released
			WASHINGTON			
Nooksack River						
1991	1992	WDF	Tribe	Skookum Cr.	Nooksack R.	46,000
1991	1992	NWIFC	Lummi	Skookum Cr.	Thompson R. & Bear Cr.	46,000
Skagit River						
1950	1951	WDF	WDF	Samish R. & Skagit R.	Lakelse R. (BC)	57,363
1952	1953	WDF	WDF	Bowmans Bay	Unknown	922
1955	1956	WDF	WDF	Bowmans Bay	Dungeness R.	97,081
1957	1958	WDF	WDF	Bowmans Bay	Unknown	22,776
1957	1958	WDF	WDF	Clark Cr.	Unknown	21,107
1959	1960	WDF	WDF	Clark Cr.	Skagit H.	80,870
1971	1972	WDF	WDF	Clark Cr.	Clark Cr.	38,500
1973	1974	WDF	WDF	Clark Cr.	Chambers Cr.	74,730
1973	1974	WDF	WDF	Clark Cr.	Skagit H.	401,486
1975	1976	WDF	WDF	Clark Cr.	Clark Cr.	732,000
1975	1976	WDF	WDF	Clark Cr.	Skagit H.	1,844,817
1977	1978	WDF	WDF	Clark Cr.	Clark Cr.	6,200,000
1977	1978	WDF	WDF	Jones Cr.	Skagit H.	207,000
1979	1980	WDF	WDF	Clark Cr.	Skagit H.	380,000
1981	1982	WDF	WDF	Clark Cr.	Skagit H.	650,000
1983	1984	WDF	WDF	Clark Cr.	Clark Cr.	74,400
1985	1986	WDF	WDF	Clark Cr.	Skagit H.	361,300
1985	1986	WDF	WDF	Clark Cr.	Clark Cr.	2,800
1985	1985	WDF	WDF	Martin Cr.	Skagit H.	210,000
1987	1988	WDF	WDF	Clark Cr.	Clark Cr.	1,033,800
1989	1990	WDF	WDF	Clark Cr.	Clark Cr.	2,800
Samish River						
1952	1953	WDF	WDF	Samish R.	Samish R.	4,335
1953	1954	WDF	WDF	Samish R.	Nooksack R.	16,320
1953	1954	WDF	WDF	Samish R.	Samish R.	18,429
1953	1954	WDF	WDF	Samish R.	Samish R.	1,495
1953	1954	WDF	WDF	Samish R.	Samish R.	1,484
Stillaguamish River						
1951?	1952?	WDF	WDF	Stillaguamish R.	Unknown	Unknown
1952	1953	WDF	WDF	Stillaguamish R.	Unknown	248,155
1953	1954	WDF	WDF	S. Fk. Stillag. R.	Skagit H.	285,674

Table 5. Continued.

Brood year	Release year	Agency	Subagency	Release location	Broodstock	Number released
Stillaguamish River, Continued.						
1963	1964	WDF	WDF	S. Fk. Stillag. R.	Dungeness R.	237,974
1971	1972	WDF	WDF	Asylum Cr.	Stillaguamish R.	100,000
1979	1980	NWIFC	Stillaguamish	Armstrong Cr.	Stillaguamish R.	480,000
1979	1980	WDF	WDF	Jim Cr.	Pilchuck Cr.	517,000
1981	1982	WDF	Tribe	Armstrong Cr.	Stillaguamish R.	105,000
1981	1982	NWIFC	Stillaguamish	Armstrong Cr.	Stillaguamish R.	105,000
1983	1984	NWIFC	Stillaguamish	Stillaguamish R.	Stillaguamish R.	737,000
1983	1984	WDF	Tribe	Stillaguamish R.	Stillaguamish R.	737,000
1985	1986	WDF	WDF	Jordan Cr.	Stillaguamish R.	80,000
1985	1986	WDF	WDF	Navy Base Cr.	Stillaguamish R.	553,500
Skykomish River						
1955	1956	WDF	WDF	May Cr.	Skykomish R.	22,714
1975	1976	WDF	WDF	May Cr.	Skagit R. & Skykomish R.	497,900
1977	1978	WDF	WDF	Wallace R.	Skykomish R. & May Cr.	780,100
1979	1980	WDF	WDF	May Cr.	Skykomish R. & May Cr.	529,000
1981	1982	WDF	WDF	Wallace R.	Skykomish R. & May Cr.	38,125
1985	1986	WDF	WDF	May Cr.	Wallace R.	86,240
1985	1986	WDF	WDF	Wallace R.	Wallace R.	82,240
1987	1988	WDF	WDF	May Cr.	Wallace R.	207,000
1991	1992	WDF	WDF	May Cr.	Skykomish R. & May Cr.	278,100
Lake Washington						
1977	1978	WDF	UW	Portage Bay/ Ship Canal	Unknown	37,400
1979	1980	WDF	UW	Portage Bay/ Ship Canal	Portage Bay	26,635
Puyallup and Green Rivers						
1929	1930	WDF	WDF	Green R.	Yes Bay H. (AK)	Unknown[b]
1929	1930	WDF	WDF	Puyallup R.	Yes Bay H. (AK)	Unknown[b]
1951?	1952?	WDF	WDF	Puyallup R.	Unknown	Unknown
1953	1954	WDF	WDF	Voight Cr.	Voight Cr.	156,400
1955	1956	WDF	WDF	Voight Cr.	Voight Cr.	26,074
1968	1969	WDF	WDF	Voight Cr.	Voight Cr.	1,160
1973	1974	WDF	WDF	Voight Cr.	Chambers Cr.	12,410

Table 5. Continued.

Brood year	Release year	Agency	Subagency	Release location	Broodstock	Number released
Puyallup and Green Rivers, Continued.						
1977	1978	WDF	WDF	Voight Cr.	Hokkaido (Japan)	403,000
1979	1980	WDF	WDF	Voight Cr.	Voight Cr.	302,000
1981	1982	WDF	WDF	Kapowsin Cr.	Voight Cr.	200,000
1989	1990	WDF	WDF	Voight Cr.	Voight Cr.	118,000
Chambers Creek						
1971	1972	WDF	WDF	Chambers Cr.	Stillaguamish R.	50,000
1975	1976	WDF	WDF	Chambers Cr.	Finch Cr.	135,748
1977	1978	WDF	WDF	Chambers Cr.	Finch Cr.	591,700
1977	1978	WDF	WDF	Chambers Cr.	Chambers Cr.	473,468
1979	1980	WDF	WDF	Chambers Cr.	Finch Cr.	982,000
1983	1983	WDF	WDF	Chambers Cr.	Chambers Cr.	2,900
1989	1990	WDF	WDF	Chambers Cr.	S. Prairie Cr.	43,590
1991	1992	WDF	WDF	Voight Cr.	Voight Cr.	10,900
1991	1992	WDF	WDF	Chambers Cr.	Chambers Cr.	15,200
Nisqually River						
1917	1918?	WDF	Unknown	Nisqually R.	Elwha R.	224,000
1977	1978	WDF & NWIFC	WDF & Nisqually	Kalama Cr.	Nisqually R.	212,960
1983	1984	WDF & NWIFC	Nisqually	Nisqually R.	Nisqually R.	39,160
Eld Inlet						
1977	1978	WDF	WDF	Mitchell Cr.	Chambers Cr.	27,500
1977	1978	WDF	WDF	Mitchell Cr.	Finch Cr.	591,700
Minter Creek						
1953	1954	WDF	WDF	Minter Cr.	Minter Cr.	26,650
1955	1956	WDF	WDF	Minter Cr.	Finch Cr.	114,000
1955	1956	WDF	WDF	Minter Cr.	Minter Cr.	219
1959	1960	WDF	WDF	Minter Cr.	Finch Cr.	101,543
1959	1960	WDF	WDF	Minter Cr.	Minter Cr.	85,986
1961	1962	WDF	WDF	Minter Cr.	Finch Cr.	369,312
1973	1974	WDF	WDF	Minter Cr.	Chambers Cr.	22,115
1975	1976	WDF	WDF	Minter Cr.	Minter Cr.	106,797
1977	1978	WDF	WDF	Minter Cr.	Finch Cr.	249,400
1977	1978	WDF	WDF	Minter Cr.	Minter Cr.	435,936
1979	1980	WDF	WDF	Minter Cr.	Finch Cr.	558,000
1979	1980	WDF	WDF	Minter Cr.	Minter Cr.	199,000
1981	1982	WDF	WDF	Minter Cr.	Minter Cr.	77,500
1983	1984	WDF	WDF	Minter Cr.	Minter Cr.	52,500

Table 5. Continued.

Brood year	Release year	Agency	Subagency	Release location	Broodstock	Number released
Minter Creek, Continued.						
1985	1986	WDF	WDF	Minter Cr.	Minter Cr.	4,300
1989	1990	WDF	WDF	Minter Cr.	Minter Cr.	7,800
1989	1990	WDF	WDF	Minter Cr.	S. Prairie Cr.	83,300
1991	1992	WDF	WDF	Minter Cr.	Minter Cr.	102,200
East Kitsap County						
1957	1958	WDF	WDF	Kennedy Lagoon	Finch Cr.	335,000
1963	1964	WDF	WDF	Dogfish Cr.	Finch Cr.	12,472
1963	1964	WDF	WDF	Keyport Lagoon	Finch Cr.	1,539,136
1979	1980	WDF	Tribe	Keyport Lagoon	Finch Cr.	47,000
Hood Canal						
1927	1928	WDF	WDF	Quilcene R.	Dungeness R.	1,000,000[a]
1952	1953	WDF	WDF	Finch Cr.	Unknown	56,039
1953	1954	WDF	WDF	Finch Cr.	Dungeness R.	164,457
1953	1954	WDF	WDF	Finch Cr.	Wild Stocks	18,273
1954	1955	WDF	WDF	Finch Cr.	Unknown	148,240
1954	1955	WDF	WDF	Finch Cr.	Finch Cr.	14,719
1955	1956	WDF	WDF	Finch Cr.	Finch Cr.	280,192
1956	1957	WDF	WDF	Finch Cr.	Unknown	673,786
1956	1957	WDF	WDF	Finch Cr.	Finch Cr.	33,267
1957	1958	WDF	WDF	Finch Cr.	Finch Cr.	254,850
1958	1959	WDF	WDF	Finch Cr.	Finch Cr.	32,400
1959	1960	WDF	WDF	Finch Cr.	Finch Cr.	563,687
1961	1962	WDF	WDF	Dewatto Cr.	Finch Cr.	299,684
1961	1962	WDF	WDF	N. Fk. Skokomish R.	Finch Cr.	504,531
1961	1962	WDF	WDF	Finch Cr.	Finch Cr.	145,665
1963	1964	WDF	WDF	Purdy Cr.	Finch Cr.	535,608
1963	1964	WDF	WDF	Finch Cr.	Finch Cr.	792,875
1965	1966	WDF	WDF	Finch Cr.	Finch Cr.	420,958
1967	1968	WDF	WDF	Finch Cr.	Finch Cr.	602,820
1969	1970	WDF	WDF	Hurd Cr.	Finch Cr.	1,350,674
1969	1970	WDF	WDF	Finch Cr.	Finch Cr.	773,702
1971	1972	WDF	WDF	Big Quilcene R.	Finch Cr.	280,385
1971	1972	WDF	WDF	Finch Cr.	Finch Cr.	1,488,970
1973	1974	WDF	WDF	Finch Cr.	Finch Cr.	708,624
1975	1976	WDF	WDF	Finch Cr.	Finch Cr.	1,533,190
1977	1978	NWIFC	Port Gamble	L. Boston Cr.	Finch Cr.	206,668
1977	1978	WDF	WDF	Gallop Cr.	Finch Cr.	800,000
1977	1978	WDF	WDF	Finch Cr.	Finch Cr.	2,440,100

Table 5. Continued.

Brood year	Release year	Agency	Subagency	Release location	Broodstock	Number released
Hood Canal, Continued.						
1979	1980	WDF	WDF	Gallop Cr. & Hood Canal	Gallop Cr.	200,000
1979	1980	WDF	WDF	Finch Cr.	Finch Cr.	888,485
1979	1980	NWIFC	Port Gamble	Port Gamble Bay Pens	Finch Cr.	47,000
1981	1982	WDF	WDF	Finch Cr.	Finch Cr.	916,675
1983	1984	WDF	WDF	Finch Cr.	Finch Cr.	254,800
1985	1986	WDF	WDF	Finch Cr.	Finch Cr.	974,700
1987	1988	WDF	Tribe	L. Boston Cr.	Finch Cr.	1,772,256
1987	1988	WDF	WDF	Johnson Cr.	Finch Cr.	980,000
1987	1988	WDF	WDF	Finch Cr.	Finch Cr.	4,022,800
1989	1990	WDF & NWIFC	Port Gamble	Port Gamble Bay Pens	L. Boston Cr.	220,000
1989	1990	WDF	WDF	Finch Cr.	Finch Cr.	827,900
1991	1992	WDF	WDF	Finch Cr.	Finch Cr.	1,910,100
Dungeness River						
1957	1958	WDF	WDF	Dungeness R.	Dungeness R.	50,500
1975	1976	WDF	WDF	Dungeness R.	Finch Cr.	499,500
1977	1978	WDF	WDF	Upper Dungeness R.	Dungeness H.	302,400
1987	1988	WDF	WDF	Upper Dungeness R.	Dungeness H.	27,200
Lyre River						
1963	1963	WDF	WDF	Lyre R.	Unknown	1,520,000[a]
Quinault River						
1972	1973	NWIFC	Quinault	Ten O'Clock Cr.	Lover's Cove Cr. (Alaska)	350,000
Willapa Bay						
1973	1974	WDF	Co-op	Johnson Slough	Unknown	5,000
Columbia River						
1957	1958	WDF	WDF	Abernathy Cr.	Finch Cr.	661,500[a]
1973	1974	WDF	Co-op	Chinook R.	Unknown	1,280
Unspecified						
1949	1950	WDF	WDF	Puget Sound	Unknown	28,299
1949	1950	WDF	WDF	N. Puget Sound Streams	Unknown	745,165

Table 5. Continued.

Brood year	Release year	Agency	Subagency	Release location	Broodstock	Number released
Unspecified, Continued.						
1949	1950	WDF	WDF	N. Puget Sound Streams	Unknown	53,342
1951	1952	WDF	WDF	Puget Sound	Unknown	85,576
1951	1952	WDF	WDF	Grays Harbor	Unknown	236,467
1951	1952	WDF	WDF	Puget Sound	Unknown	76,227
			OREGON			
1923	1924	OSFC	OSFC	S. Fk. Coos R.	Alaska	370,985
1977	1978	ODFW	ODFW & OAF	South Beach	Sheldon Jackson H. (Alaska)	2,287,807
1981	1982	ODFW	OSU	South Beach	Sitka (Alaska)	362,180
1982	1983	ODFW	OSU	South Beach	Sitka (Alaska)	839,444
1982	1983	ODFW	OSU	South Beach	Sitka (Alaska)	461,497

Note: "Finch Cr." stock pink salmon are generally Hood Canal Hatchery fish, and "Voight Cr." stock pink salmon are generally Puyallup Hatchery fish.

[a] Neave (1965) reported 513,880 eggs taken to Green River Hatchery and 512,820 eggs taken to Puyallup Hatchery; Roppel (1982) reported 1,021,000 eggs taken to Auburn Hatchery.
[b] Eyed eggs.
WDF = Washington Department of Fisheries.
NWIFC = Northwest Indian Fisheries Commission.
UW = University of Washington.
OSFC = Oregon State Fish Commission.
ODFW = Oregon Department of Fish and Wildlife.
OAF = Oregon Aqua Foods.
OSU = Oregon State University.
USBF = U.S. Bureau of Fisheries.

Artificial Propagation in Washington

A selected review of artificial propagation activity involving pink salmon in Washington is provided in Table 5. This review focuses heavily on historical stock transfers within the state. For about 25 years beginning in the 1950s, pink salmon were produced in Washington hatcheries around Puget Sound in relatively large numbers. Movements of fish among hatcheries and drainages in Puget Sound, Hood Canal, and the Dungeness River on the Olympic Peninsula were common during this period, but very few pink salmon were transplanted to areas outside Puget Sound. Three hatcheries have dominated pink salmon production in the state: Hood Canal Hatchery on Finch Creek in Hood Canal, Puyallup Hatchery on Voight Creek in southern Puget Sound, and Dungeness Hatchery on the Dungeness River on the Olympic Peninsula. In recent years, only Hood Canal Hatchery has maintained an active pink salmon production program. A population of odd-year pink salmon was established in 1953 at Hood Canal Hatchery from the gametes of adults returning to the upper Dungeness River (approximately 90%) and Dosewallips River (approximately 10%). Since then, production of odd-year fish has ranged from a low of less than 15,000 fry (in 1955) to a high of over 4 million fry (in 1988).

Summary

Although major efforts were made several decades ago to increase the abundance of even-year pink salmon in Washington, it is not clear that any of these attempts were successful. Even-year pink salmon are known in Washington only from the Snohomish River (WDF et al. 1993). The origin of this population is uncertain; these fish could be endemic or could have resulted from one or more transplants of even-year fish into the state. Regardless of its origin, however, this population appears to have been naturally self-sustaining for at least the last eight generations (its status prior to 1980 is unclear; WDF et al. 1993).

Most hatchery production of pink salmon in Washington is composed of odd-year fish released from Hood Canal Hatchery in southern Hood Canal. These fish are generally released into Finch Creek, the location of the hatchery, and the hatchery typically uses local broodstock (Table 5). As noted above, however, this broodstock was originally derived from adults returning to the Dungeness and Dosewallips Rivers in 1953. Hood Canal Hatchery production over the last decade has averaged about a million fry released locally every other year into Finch Creek (Table 5). Other recent releases, such as those into the Nooksack River, Voight Creek, Minter Creek, and Chambers Creek, have been relatively small and appear to have used local broodstock. Thus, although artificial propagation of pink salmon in the past--particularly stock transfers from Dungeness and Hood Canal Hatcheries around northwestern Washington--may have affected the population structure of odd-year pink salmon in Puget Sound, recent hatchery production has probably had little effect on this structure.

Stock transfers of pink salmon in British Columbia are summarized elsewhere in Aro (1979) and NRC (1995).

Genetic Information

Differences Between Even- and Odd-year Pink Salmon

Because pink salmon mature and spawn on a strict 2-year cycle, genetic isolation between odd- and even-year spawners is nearly complete, and several genetic and biological variables differ between them. The electrophoretic analysis of enzymatic proteins has been used extensively to measure the genetic differences between odd- and even-year fish and to resolve genetic structure among populations within these groups. One approach for detecting reproductive isolation is to compare frequencies of protein variants (allozymes) among samples. The finding of significant frequency differences between groups can be taken as evidence of reproductive isolation. Another approach to identifying reproductively isolated groups is to estimate genetic distances between samples and to analyze these distances with a clustering algorithm, such as the unweighted pair group method with averages (UPGMA; Sneath and Sokal 1973) or with an ordination technique such as multidimensional scaling analysis (Lessa 1990). When the geographic distribution of genetic variability is continuous and not hierarchical or disjunct, such as in a clinal or reticular pattern, multidimensional scaling is more appropriate than agglomerative clustering (Lessa 1990). Multidimensional scaling is a nonmetric ordination technique that depicts genetic relationships among populations in two or three dimensions and can reduce the distortion that may exist in phenograms because populations are represented in fewer dimensions. When genetic relationships among populations reflect nonhierarchical or semihierarchical geographic variation, multidimensional scaling diagrams are often a more effective means of showing these relationships (Lessa 1990).

Geneticists have used several genetic distance measures (e.g., Cavalli-Sforza and Edwards 1967, Rogers 1972, Nei 1978) to study the population structure of pink salmon as well as other salmonids. A considerable literature has developed on the pros and cons of these measures. For example, an attractive feature of the Rogers' and Cavalli-Sforza and Edwards' distances is that they satisfy the triangle inequality--that is, given three populations (A, B, C), the sum of the distances from A to B and from A to C will always be greater than the distance from A to C. On the other hand, neither of these distance measures employs a correction for sample size, so the distances are biased upwards, especially for small sample sizes. In contrast, Nei's distance is unbiased, but does not always satisfy the triangle inequality. Another important consideration is that both Nei's and Rogers' distance measures can be affected by different levels of heterozygosity between populations, whereas Cavalli-Sforza and Edwards' measure is not. Discussions of these and other features of genetic distances appear in Nei (1987), Hillis and Moritz (1990), and Rogers (1991). Unfortunately, most of this discussion has focused on the merits of the various measures for phylogenetic reconstruction among species and higher taxa. No one has rigorously or quantitatively evaluated the performances of these distances in assessing the genetic population structures of species like salmon, which typically are separated by relatively small genetic distances.

Since it is unclear which distance measure is "best" in any given application, we analyzed each set of data with more than one method to identify results that may not be robust. Nei's unbiased genetic distance has been used in several studies of pink salmon, but we computed all three distance measures for most data sets. In most cases, the different genetic distance measures yielded results that were highly correlated. For simplicity we report only results for Rogers' and Cavalli-Sforza and Edwards' distance measures. Both distance measures range from 0.0 (identity) to 1.0 (complete dissimilarity). Cases in which the results differed substantially among measures are identified in the text.

For many polymorphic enzyme-encoding loci, strong allozyme frequency differences have been reported between even- and odd-year broodlines spawning at the same localities in Alaska (Aspinwall 1974, Johnson 1979, McGregor 1982), Canada (Beacham et al. 1985), and Russia (Salmenkova et al. 1981, Altukhov et al. 1983, Kartavtsev 1991). Shaklee and Varnavskaya (1994) reported a large genetic difference between even- and odd-year pink salmon from the Snohomish River, the only North American locality south of British Columbia that supports a spawning population of even-year pink salmon. The average Nei's genetic distance (Nei 1978) between even- and odd-year pink salmon in British Columbia was 0.018 (Beacham et al. 1988). However, since this estimate was based only on polymorphic loci, it is likely to overestimate the true genetic distance between the two broodlines. The actual distance, which includes monomorphic loci in its estimate, is probably not more than half this value (or about 0.009). This distance is typical of conspecific populations of other animals (Thorpe 1982), and represents an "upper bound" to the largest distance expected to exist between populations within broodlines.

In addition to allozyme frequency differences, other genetic differences have been reported between even- and odd-year spawners. Gorshkova (1983) found that Kamchatka odd-year pink salmon show a chromosomal polymorphism of presumably acrocentric fusions, in which the diploid number is 53 or 54 chromosomes, whereas even-year spawners consistently had only 52 chromosomes.

At Auke Creek in southeastern Alaska, Gharrett and Smoker (1991) made crosses between even- and odd-year spawners to search for possible outbreeding depression in their offspring. Cyropreserved sperm from even-year males was used to fertilize eggs from odd-year females the following year. In the first generation, the number of returning first-generation hybrids and their average date of return were not significantly different from the respective numbers and return times of control fish of the same age, but variability among the hybrids in morphological characters was greater than that among control fish. Second-generation hybrids showed a reduced return rate and greater bilateral asymmetry in meristic characters, which were interpreted as possible genetic effects of outbreeding depression in hybrids between the two broodlines.

Even-year Pink Salmon: Genetic Variability Among Regions

Even-year adult pink salmon spawn throughout much of the species' range but tend to increase in abundance with latitude (Heard 1991). In southern British Columbia and Washington, even-year spawners are less abundant than odd-year spawners, but they are as abundant or more abundant than odd-year spawners in parts of northern British Columbia and western Alaska. Even-year spawners are also abundant in Asia and tend to outnumber odd-year spawners in northern areas. Most genetic studies of even-year spawners have been made in Alaska and British Columbia; the information available for Asian even-year pink salmon is more limited. Several studies indicate that the degree of genetic differentiation among populations of even-year pink salmon is consistently lower than the degree of genetic differentiation between even- and odd-year spawners (McGregor 1983, Beacham et al. 1988, Gharrett et al. 1988, Shaklee and Varnavskaya 1994, Zhivotovsky et al. 1994).

No single study has included samples collected over the entire range of even-year spawners. Zhivotovsky et al. (1994) analyzed allelic frequencies for 20 loci (*sAAT-3**, *ADA-2**, *mAH-3**, *mAH-4**, *CK-A1**, *CK-A2**, *G3PDH-1**, *GPI-B1**, *GPI-B2**, *GPI-A**, *LDH-A1**, *LDH-A2**, *LDH-B2**, *LDH-C**, *sMDH-A1,2**, *sMDH-B1**, *sMDH-B2**, *mMEP-1**, *MPI**, *PEPD-1**, *PEPD-2**, and *sSOD-1**) in samples from southeastern Alaska (McGregor 1982, Lane et al. 1990), northwestern Alaska (Gharrett et al. 1988), and Hokkaido in Japan (Noll et al. 1994). These samples encompassed about three quarters of the geographic range of even-year pink salmon. Zhivotovsky et al. (1994) conducted a gene diversity analysis, which partitions the total genetic diversity observed in a set of samples into its regional components, at five hierarchical levels. The results indicated that 2.7% of the diversity was due to genetic differences between odd- and even-year spawners, and 2.3% was due to differences between Asian and North American samples. About 1.8% of the total diversity was due to regional differences between southeastern Alaska and western Alaska (including the Aleutian Islands). About 2% of the diversity was due to within-region variability, including geographic and run-timing differences in the same river system.

In samples from the Aleutian Islands, northwestern Alaska and Kodiak Island, Gharrett et al. (1988) examined 29 enzymatic loci (21 of which were polymorphic) and found the greatest regional genetic differentiation between the group of Aleutian Island-northwestern Alaska samples and a single sample from southcentral Alaska. Gharrett et al. (1988) then combined allelic frequencies for *sMDH-B1*,sMDH-B2*; PGM-2**, *ME-1**, *G3PDH-1**, and *PGDH** for Alaskan samples with those for samples from Sakhalin Island in Russia (Salmenkova and Omel'chenko 1982, Altukhov et al. 1983). A maximum-likelihood tree based on these frequencies indicated that the Russian samples were most closely related to Alaskan samples from Norton Sound and the Aleutian Islands and more distantly related to samples from Bristol Bay. The sample from southcentral Alaska was most distantly related to the Russian samples. Although these results are consistent with those obtained by Zhivotovsky et al. (1994), it is not clear whether the major genetic discontinuity between eastern and western even-year spawners occurs between Asia and North America across the Bering Sea or across the Alaska Peninsula.

Several allozyme studies have been made of North American even-year spawning populations of pink salmon, but no study has included samples from the entire range of even-year spawners. Populations from northwestern Alaska appear to be most closely allied with Aleutian Island populations (Gharrett et al. 1988), but these authors did not address the relationship between these populations and those farther south. In British Columbia, Beacham et al. (1988) detected three regional groups: 1) populations on the Queen Charlotte Islands (these populations are distinct from all other British Columbia populations), 2) populations in the Skeena River and farther north, and 3) populations in central and southern British Columbia, including Vancouver Island.

An important question in evaluating the status of the Snohomish River even-year population is resolution of its origin. It may be a natural population or it may have originated from eggs translocated from Alaska or British Columbia (Table 4). To address this issue, we analyzed a set of allelic frequencies consisting of a single Snohomish River sample (J. Shaklee[22]) and 34 samples from British Columbia (Beacham et al. 1988). This group of samples had 15 polymorphic loci in common, 9 of which showed common allelic frequencies of 0.95 or less in at least 1 sample. Frequencies for some loci were missing for Cluxewe, Glendale, Kemano, and Puntledge Rivers, so we substituted the average of frequencies in the two nearest populations for these loci. Other loci in these samples did not show strong allelic frequency differences between nearby populations. For odd-year spawning pink salmon, Shaklee et al. (1991) found a consistent difference in the scoring of two loci, *sAAT-3** and *PGDH**, between his laboratory and the laboratory that produced the data presented by Beacham et al. (1988) (see White and Shaklee 1991 for a discussion of this issue). Beacham et al. (1988) reported a 0.105 higher average frequency for the common allele of *sAAT-3** and a 0.060 higher average frequency for the common allele of *PGDH** in his samples than was found by J. Shaklee in samples taken from the same localities in different years. We therefore adjusted allelic frequencies for these two loci in the 34 samples from British Columbia. The adjustment was based on a comparison of allelic frequencies in 13 populations of odd-year pink salmon reported in Beacham et al. (1988) and later studied by Shaklee et al. (1991).

This basic set of data was then combined for analysis with data from Nickerson (1979) for Prince William Sound, and McGregor (1983), Gharrett et al. (1988), and unpublished data provided to us by A. J. Gharrett[23] for western, central, and southeastern Alaska, and the Aleutian Islands (Table 6). We also examined allelic frequencies for Kodiak Island (Johnson 1979), but as only four polymorphic loci were in common with data from British Columbia and Washington, we did not use these results to draw conclusions. We hypothesized that if

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[22]J. Shaklee, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Unpubl. data.

[23]A. J. Gharrett, Juneau Center, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 11120 Glacier Highway, Juneau, AK 99801.

Table 6. Samples used in analyses of even-year pink salmon allozyme variability. Locality numbers appear in Figures 6-13.

Locality No.	Locality Name	Region	Source of data[a]
		Washington	
1.	Snohomish River	Washington	1
		British Columbia	
2.	Read River	Southern BC	2
3.	Wortley River	Southern BC	2
4.	Wakeman River	Southern BC	2
5.	Kakweiken River	Southern BC	2
6.	Glendale River[b]	Southern BC	2
7.	Waukwaas River	Vancouver Island	2
8.	Beer River	Vancouver Island	2
9.	Adam River	Vancouver Island	2
10.	Keogh River	Vancouver Island	2
11.	Puntledge River[b]	Vancouver Island	2
12.	Cluxewe River[b]	Vancouver Island	2
13.	Quinsam River	Vancouver Island	2
14.	Koeye River	Central BC	2
15.	Kairnet River	Central BC	2
16.	Neekas River	Central BC	2
17.	Atnarko River	Central BC	2
18.	Kitimat River	Central BC	2
19.	Kemano River[b]	Central BC	2
20.	Clyak River	Central BC	2
21.	Quaal River	Central BC	2
22.	Khutzeymateen River	Central BC	2
23.	Nakina River	Northern BC	2
24.	Kitwanga River (Skeena River)	Northern BC	2
25.	Babine River (Skeena River)	Northern BC	2
26.	Lakelse River (Skeena River)	Northern BC	2
27.	Kwiramass River	Northern BC	2
28.	Copper River	Queen Charlotte Islands	2
29.	Pallant River	Queen Charlotte Islands	2
30.	Windy Bay	Queen Charlotte Islands	2
31.	Yakoun River	Queen Charlotte Islands	2
32.	Deena River	Queen Charlotte Islands	2
33.	Naden River	Queen Charlotte Islands	2
34.	Security River	Queen Charlotte Islands	2

Table 6. Continued.

Locality No.	Name	Region	Source of data[a]
		Alaska	
35.	Herring Cove Creek (pooled)	Southeastern Alaska	3
36.	Porcupine Creek (pooled)	Southeastern Alaska	3
37.	Sashin Creek (pooled)	Southeastern Alaska	3
38.	Lover's Cove Creek (pooled)	Southeastern Alaska	3
39.	Fish Creek (pooled)	Southeastern Alaska	4
40.	Peterson Creek-mainland (pooled)	Southeastern Alaska	3
41.	Auke Creek (pooled)	Southeastern Alaska	3
42.	Peterson Creek-island (pooled)	Southeastern Alaska	3
43.	Rocky Creek (intertidal)	Prince William Sound	5
44.	Rocky Creek (upper)	Prince William Sound	5
45.	Constantine Creek (intertidal)	Prince William Sound	5
46.	Constantine Creek (upper)	Prince William Sound	5
47.	Zillesenof Creek (intertidal)	Prince William Sound	5
48.	Hartney Creek (intertidal)	Prince William Sound	5
49.	Humpback Creek (intertidal)	Prince William Sound	5
50.	Koppen Creek (intertidal)	Prince William Sound	5
51.	Koppen Creek (upper)	Prince William Sound	5
52.	Olsen Creek (intertidal)	Prince William Sound	5
53.	Olsen Creek (upper)	Prince William Sound	5
54.	Lagoon Creek (intertidal)	Prince William Sound	5
55.	Lagoon Creek (upper)	Prince William Sound	5
56.	Millard Creek (intertidal)	Prince William Sound	5
57.	Duck River (intertidal)	Prince William Sound	5
58.	Cannery Creek (intertidal)	Prince William Sound	5
59.	Swanson Creek (intertidal)	Prince William Sound	5
60.	Mink Creek (intertidal)	Prince William Sound	5
61.	Mink Creek (upper)	Prince William Sound	5
62.	Erb Creek (intertidal)	Prince William Sound	5
63.	Erb Creek (upper)	Prince William Sound	5
64.	Larson Creek (intertidal)	Prince William Sound	5
65.	Kenai River	Cook Inlet	4
66.	Susitna River	Cook Inlet	4
67.	Kodiak Island (pooled)	Kodiak Island	4,7
68.	Unalaska Island	Aleutian Islands	7
69.	Umnak Island	Aleutian Islands	7
70.	Blue Fox Bay, Atka Island	Aleutian Islands	7
71.	Korovin Bay, Atka Island	Aleutian Islands	7
72.	Adak Island	Aleutian Islands	7
73.	Tanaga Island	Aleutian Islands	7
74.	Semisopochnoi (1,2)	Aleutian Islands	7
75.	North Kiska Island	Aleutian Islands	7

Table 6. Continued.

Locality No.	Locality Name	Region	Source of data[a]
		Alaska, Continued.	
76.	Attu Island	Aleutian Islands	7
77.	Naknek River	Bristol Bay	3
78.	Nushagak River	Bristol Bay	3
79.	Kwiniuk River	Norton Sound	3
80.	Nome River	Norton Sound	3

[a] Key to data sources:

1. J. Shaklee, unpubl. data. Washington Dep. Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501.
2. Beacham et al. (1988).
3. McGregor (1983).
4. A. J. Gharrett, unpubl. data. Juneau Center, School of Fisheries and Ocean Sciences, Univ. of Alaska, Fairbanks, 11120 Glacier Highway, Juneau, AK 99801.
5. Nickerson (1979).
6. Johnson (1979).
7. Gharrett et al. (1988).

[b] Missing data estimated by averages of closest localities.

the Snohomish River even-year spawners descended from eggs transplanted from Alaska or British Columbia earlier in this century, they may show genetic affinities to present-day Alaska or British Columbia even-year populations.

In the first analysis, allelic frequencies for populations in Prince William Sound (Nickerson 1979) were included with frequencies for populations in Washington and British Columbia and used to estimate Rogers' (1972) genetic distances based on 10 polymorphic loci (*sAAT-3**, *GPI-A**, *GPI-B1**, *G3PDH-1**, *LDH-B2**, *sMDH-A1**, *sMDH-B1**, *mMEP-1**, *PGDH**, and *PGM-2**). The UPGMA phenogram (Fig. 6) showed two distinct, nonoverlapping clusters: one including Prince William Sound samples (localities 43-64), and the other including British Columbia samples (localities 2-34). The Snohomish River sample (locality 1) fell within the cluster of British Columbia samples. Multidimensional scaling analysis (NTSYS-pc; Rohlf 1993) of these distances (Fig. 7) showed a similar geographical arrangement of the Prince William Sound and British Columbia samples, with the Snohomish River sample appearing at the edge of the British Columbia cluster on the opposite side of the cluster space from the Prince William Sound samples.

The second analysis included Snohomish River (locality 1), British Columbia (localities 2-34), and several localities in southeastern (localities 35-42) and southcentral Alaska (localities 65-67; McGregor 1983, A. J. Gharrett[24]), the Aleutian Islands (localities 68-76; Gharrett et al. 1988), and western Alaska (localities 77-80; McGregor 1983). A UPGMA phenogram (Fig. 8) of Rogers' genetic distances based on 10 polymorphic loci in common among the studies (*sAAT-3**, *ADA-2**, *CK-A1**, *GPI-B1**, *G3PDH-1**, *sMDH-A1**, *sMDH-B1**, *mMEP-1**, *PGDH**, and *PGM-2**) showed 2 major clusters. One cluster included samples from the Aleutian Islands, Kodiak Island and western Alaska, and the other included samples from southeastern Alaska and British Columbia. The sample from the Snohomish River was located within the cluster of British Columbia samples. Multidimensional scaling of Rogers' genetic distances showed close agreement between the geographic locations of the samples and their general positions in the clusters apparent in the multidimensional scaling (Fig. 9). Samples from western Alaska and the Aleutian Islands were located at one end of the multidimensional space; those from southeastern Alaska were placed in an intermediate position, and those from British Columbia were at the other end of the multidimensional space. The Snohomish River sample occupied a position at the extreme end of the multidimensional space, opposite the samples from Alaska.

The results of these analyses demonstrate that the even-year Snohomish River sample is genetically more closely related to even-year populations from British Columbia than to those from Alaska. If this sample is representative of Snohomish River even-year pink salmon, these analyses lend strong support to an argument that this population did not arise from an Alaskan transplant.

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[24]A. J. Gharrett, Juneau Center, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 11120 Glacier Highway, Juneau, AK 99801. Unpubl. data.

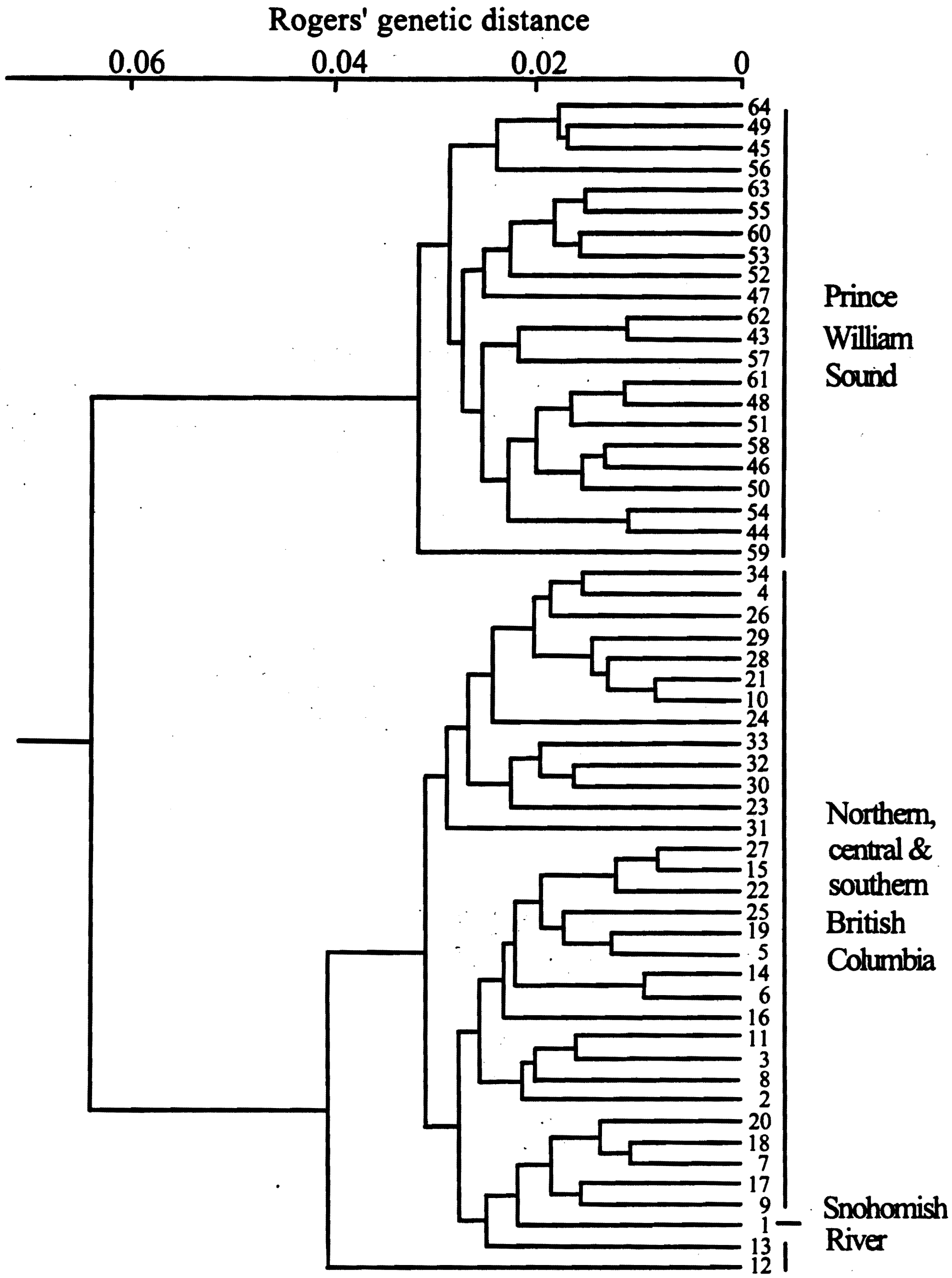

Figure 6. UPGMA phenogram of Rogers' (1972) genetic distances, based on 10 polymorphic loci (see text), between samples of even-year pink salmon collected in Washington (J. Shaklee, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501, unpubl. data), British Columbia (Beacham et al. 1988), and Prince William Sound, Alaska (Nickerson 1979). Locality numbers are given in Table 6.

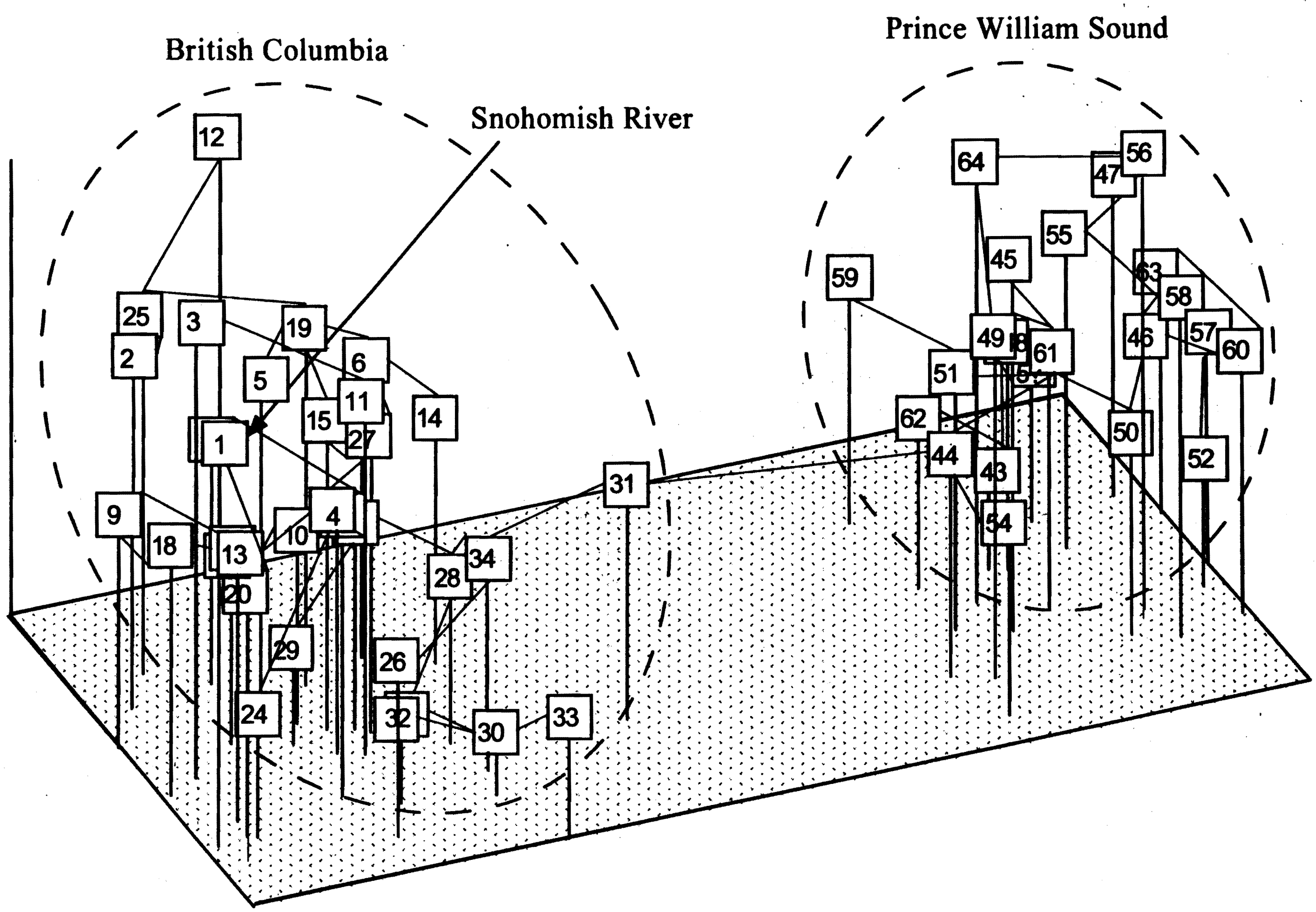

Figure 7. Multidimensional scaling and minimum spanning tree (a tree connecting nearest genetic neighbors) of Rogers' genetic distances, based on 10 polymorphic loci (see text), between samples of even-year pink salmon samples collected in Washington, British Columbia, and Prince William Sound, Alaska. Locality numbers and sources of data as in Figure 6. See text for discussion.

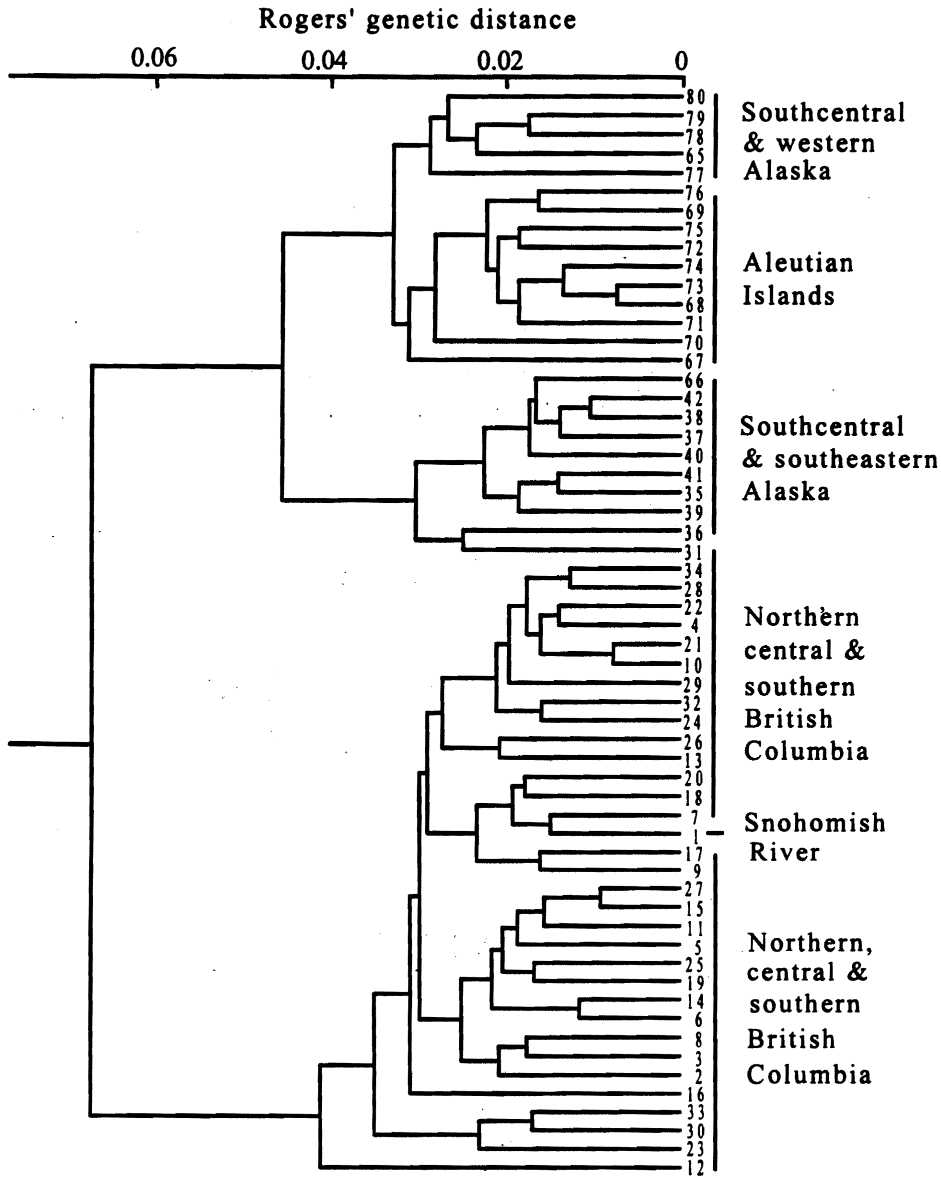

Figure 8. UPGMA phenogram of Rogers' genetic distances, based on 10 polymorphic loci (see text), between samples of even-year pink salmon from central and western Alaska (McGregor 1983), the Aleutian Islands (Gharrett et al. 1988), central and southeastern Alaska (McGregor 1983; A. J. Gharrett, Juneau Center, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 11120 Glacier Highway, Juneau, AK 99801, unpubl. data), British Columbia (Beacham et al. 1988), and the Snohomish River, Washington (J. Shaklee, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501, unpubl. data). Locality numbers are given in Table 6.

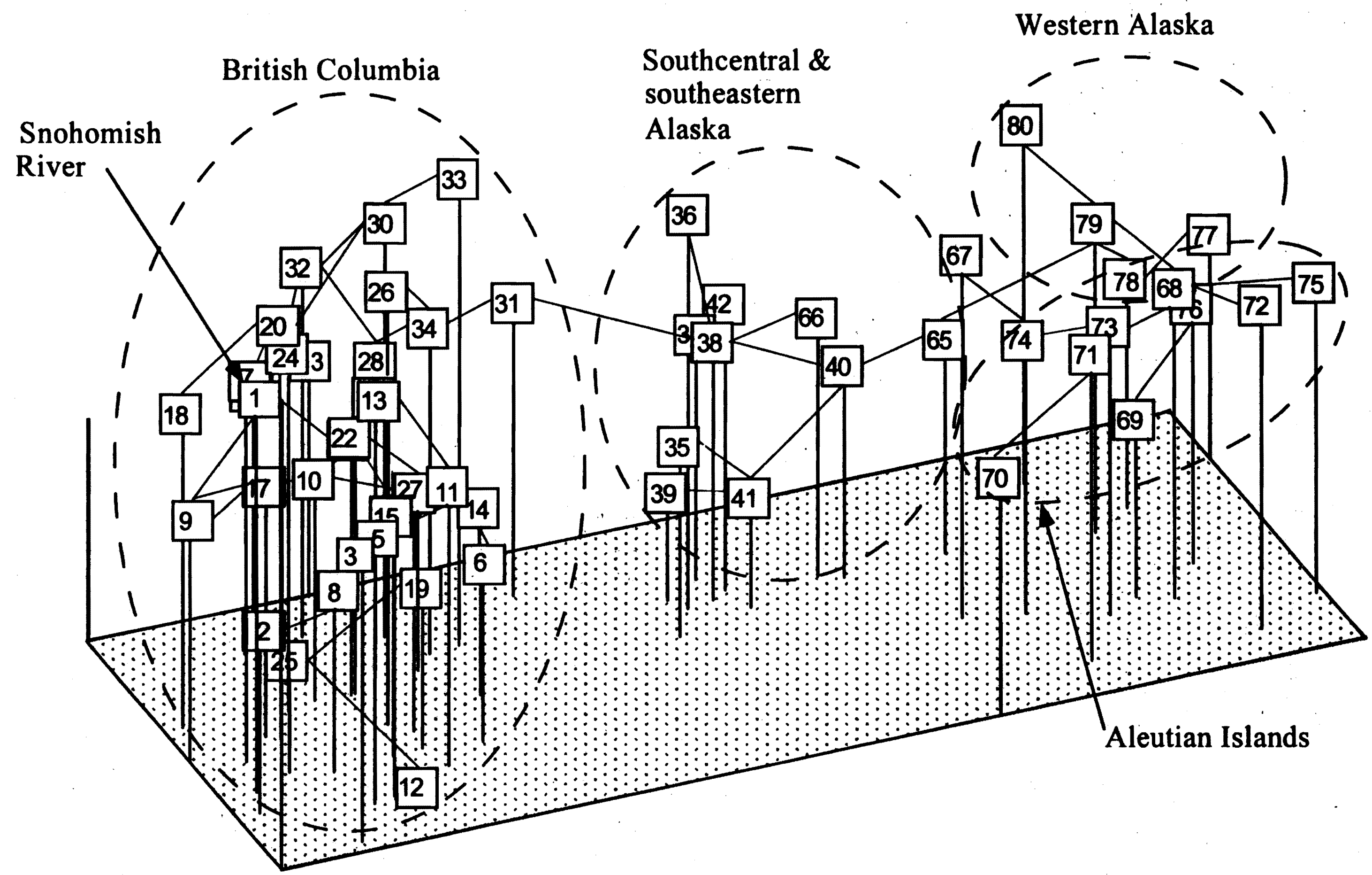

Figure 9. Multidimensional scaling and minimum spanning tree of Rogers' genetic distances, based on 10 polymorphic loci (see text), between samples of even-year pink salmon from western Alaska, the Aleutian Islands, central and southeastern Alaska, British Columbia, and the Snohomish River, Washington. Locality numbers and sources of data as in Figure 8.

We then analyzed a set of data that combined the Washington sample and the samples from British Columbia to estimate the relationship of the Snohomish River sample to its nearest geographic neighbors to the north. However, genetic data for even-year spawners on southern Vancouver Island and in the Fraser River were not available; as noted in an earlier section, such fish are rare in these areas. Excluding the Alaska samples allowed us to include more loci in our analysis. We were aware that in British Columbia, Beacham et al. (1988) found highly significant allelic frequency differences for most polymorphic loci among even-year populations within three areas: 1) the south (localities 2-13 in Table 6) and central (localities 14-22) coasts of British Columbia, 2) the north (localities 23-27) coast of British Columbia, and 3) the Queen Charlotte Islands (localities 28-34). The amount of heterogeneity among areas was substantially greater than that among localities within areas.

In our analysis of unadjusted allelic frequencies, the UPGMA clustering of Rogers' genetic distances (based on 15 loci: *sAAT-3**, *ADA-2**, *CK-A1**, *GPI-B1**, *G3PDH-1**, *mIDHP-1**, *LDH-B1**, *LDH-C**, *sMDH-A1**, *sMDH-B1**, *mMEP-1**, *PEPB-1**, *PEPD-2**, *PGDH**, and *PGM-2**) placed the Snohomish River sample outside the cluster of British Columbia samples (Fig. 10). The Snohomish River sample also appeared as an outlier in the multidimensional scaling of these genetic distances (Fig. 11). In the analysis of adjusted allelic frequencies, the Snohomish River sample was embedded among samples from southern and central British Columbia in the UPGMA phenogram (Fig. 12). The Snohomish River sample showed a closer genetic affinity to samples from eastern Vancouver Island and central British Columbia when the multidimensional scaling was based on adjusted allelic frequencies (Fig. 13) than when the frequencies were unadjusted (Fig. 11). The analysis of Beacham et al. (1988), which used Nei's genetic distance, showed three distinct groups of even-year spawning pink salmon in British Columbia: 1) Queen Charlotte Islands, 2) north and central coasts, and 3) south coast and Vancouver Island. In our analysis using Rogers' distance, groups 2 and 3 were less distinct.

If the Snohomish River population had experienced a strong reduction in population size at or since the time of its founding, a reduction in the amount of genetic variability might be apparent. Average heterozygosities with frequencies adjusted for *sAAT-3** and *PGDH** ranged from 0.134 to 0.171 among the British Columbia even-year pink salmon samples and was 0.134 in the Snohomish River sample. The Snohomish River population is at the lower end of this range of heterozygosities but does not appear to have lost a substantial amount of genetic variability relative to other populations. Therefore, if the Snohomish River even-year population experienced a reduction in population size or a founder effect, it apparently was not severe or protracted.

A hierarchical gene diversity analysis of 15 polymorphic loci (including adjusted frequencies for *sAAT-3** and *PGDH**) indicated that 98.5% of the total genetic diversity in British Columbia and Washington samples of even-year pink salmon was contained on average within populations, 0.9% was due to allelic frequency variability among populations within the areas, and 0.6% was due to differences among the 5 areas. This analysis suggests that the loss

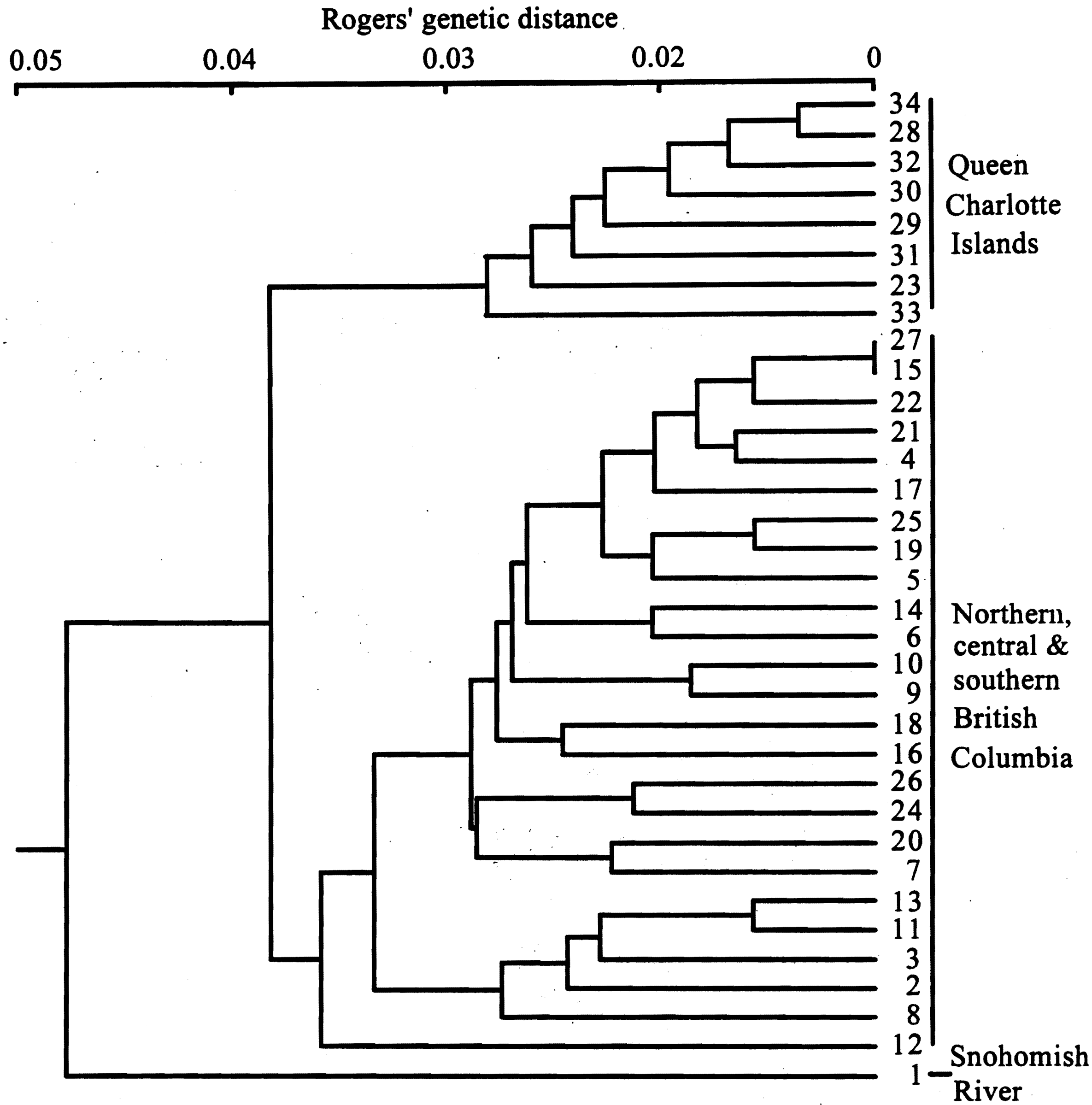

Figure 10. UPGMA phenogram of Rogers' genetic distances, based on 15 polymorphic loci (see text) and unadjusted allelic frequencies for *sAAT-3** and *PGDH** (see text), between samples of even-year pink salmon from British Columbia (Beacham et al. 1988) and the Snohomish River, Washington (J. Shaklee, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501, unpubl. data). Locality numbers are given in Table 6.

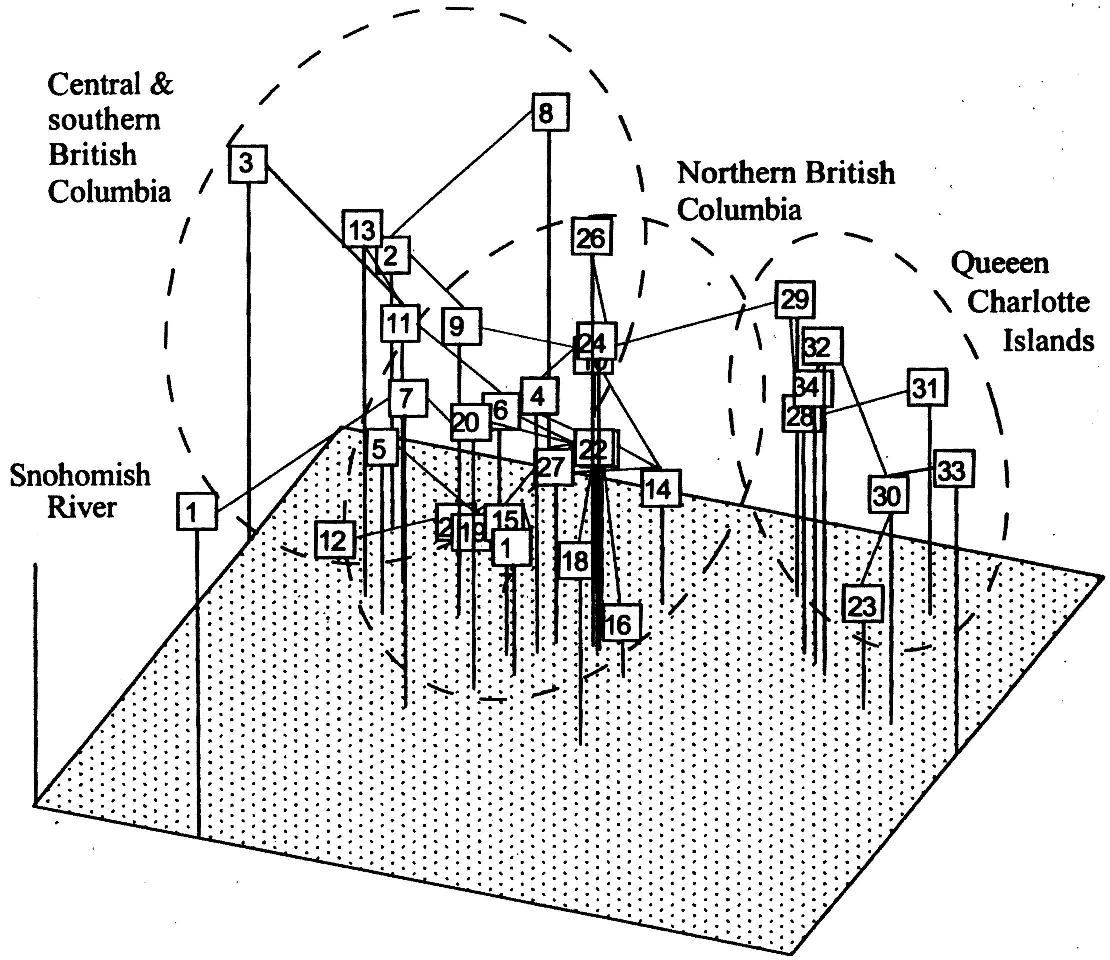

Figure 11. Multidimensional scaling and minimum spanning tree of Rogers' genetic distances, based on 15 polymorphic loci (see text) and unadjusted allelic frequencies for *sAAT-3** and *PGDH**, between samples of even-year pink salmon from British Columbia and the Snohomish River, Washington. Locality numbers and sources of data as in Figure 10.

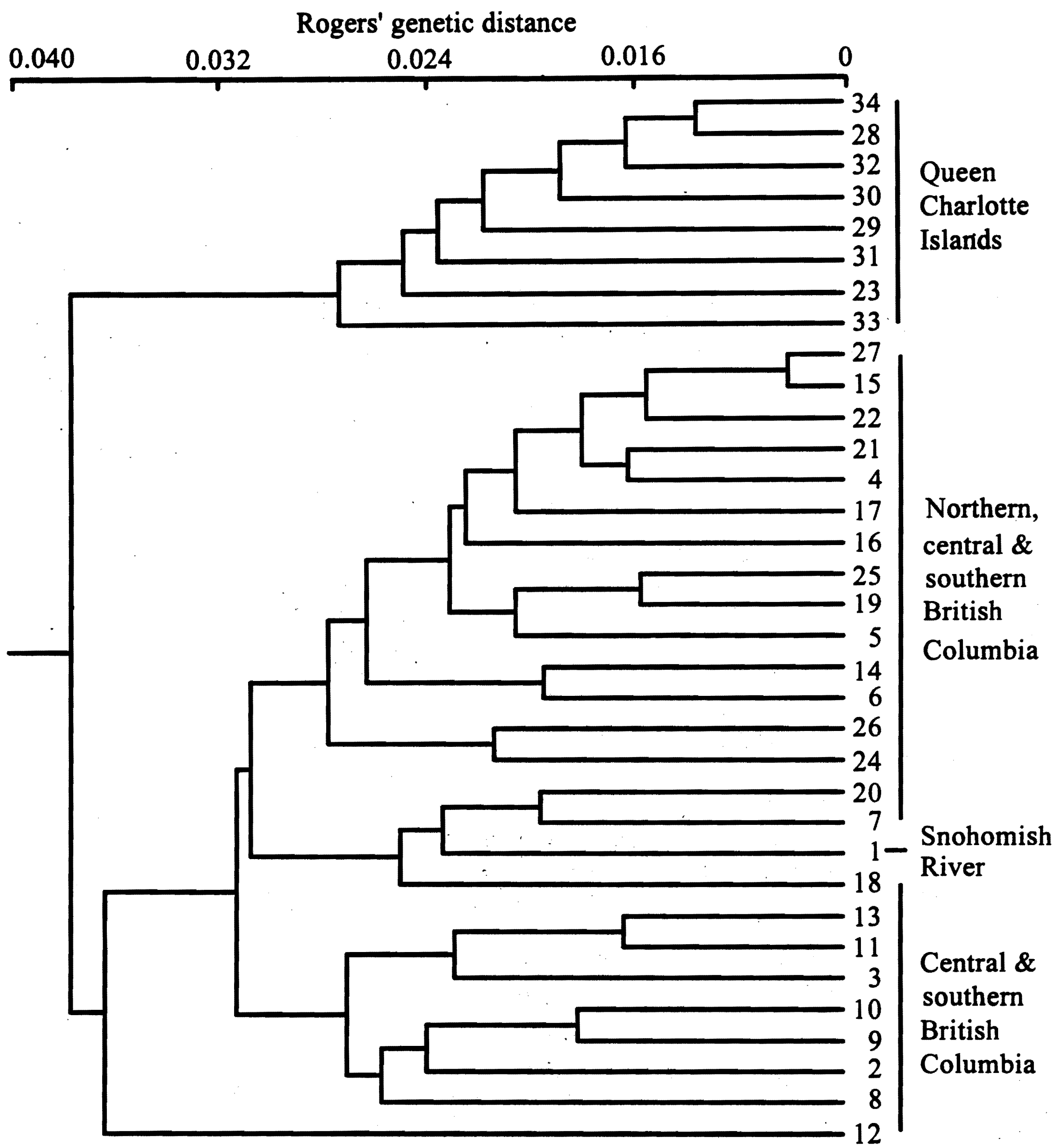

Figure 12. UPGMA phenogram of Rogers' genetic distances based on 15 polymorphic loci (see text) and adjusted allelic frequencies for *sAAT-3** and *PGDH** (see text), between samples of even-year pink salmon from British Columbia and the Snohomish River, Washington. Locality numbers and sources of data as in Figure 10.

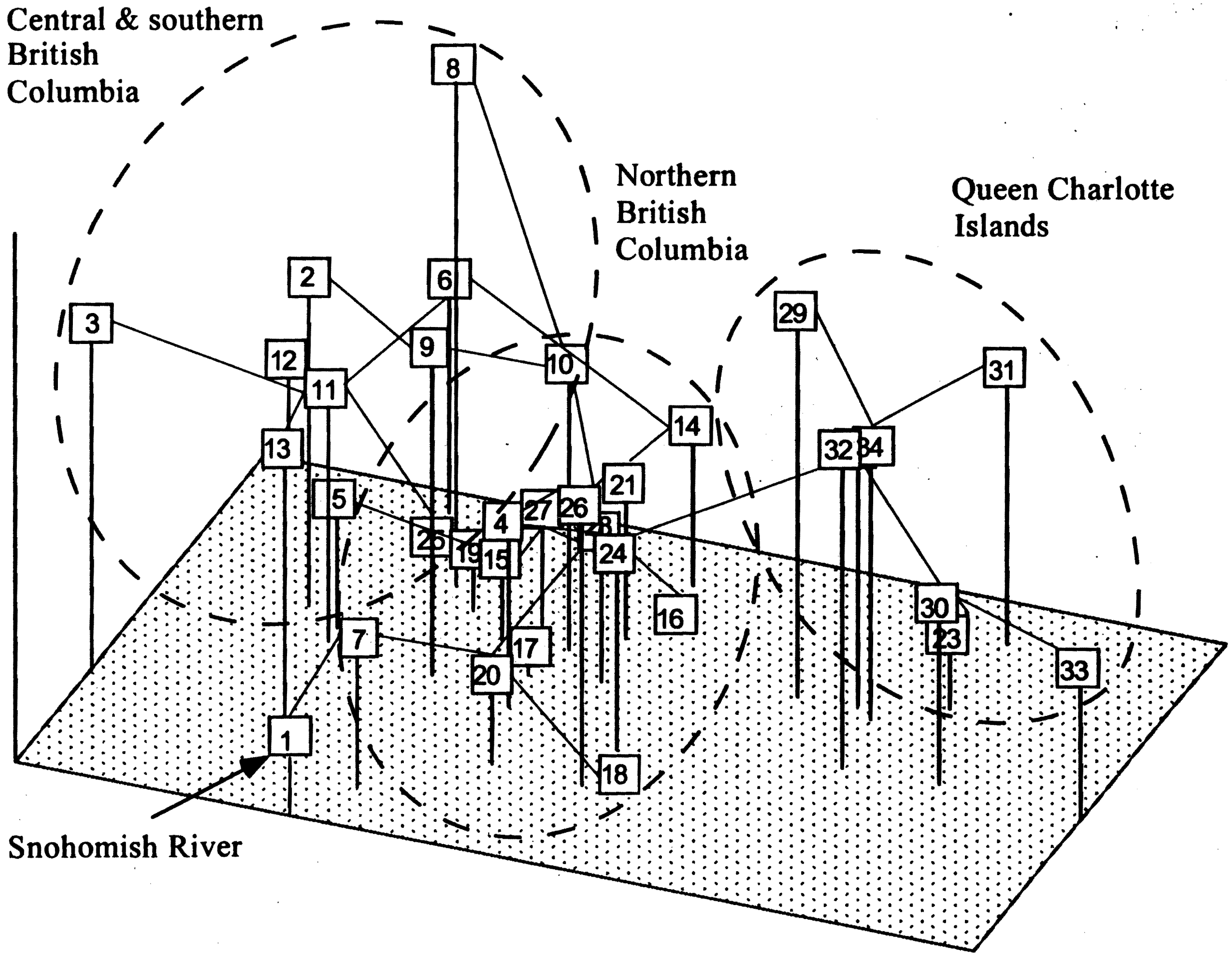

Figure 13. Multidimensional scaling and minimum spanning tree of Rogers' genetic distances, based on 15 polymorphic loci (see text) and adjusted allelic frequencies for *sAAT-3** and *PGDH**, between samples of even-year pink salmon from British Columbia and the Snohomish River, Washington. Locality numbers and sources of data as in Figure 10.

of a single population would not lead to substantial loss of overall genetic diversity as detected by allozymes in even-year pink salmon. The partitioning of genetic variability at other parts of the genome is less well understood, not as easily quantified, and may be different.

Odd-year Pink Salmon: Genetic Variability Among Regions

Odd-year spawners occur throughout the range of pink salmon, but they are more abundant in the southern parts of this range in both Asia and North America. Several researchers have examined the genetic structure of odd-year populations in various regions, and some of these studies have included samples from other geographic regions; thus, a preliminary comparison of within- and among-region variability is possible. Shaklee and Varnavskaya (1994) examined 8 samples of Russian odd-year spawners and compared them with 15 samples of odd-year and 1 sample of even-year pink salmon collected from localities extending from southeastern Alaska, through British Columbia to Washington. Their cluster analyses of genetic distances based on 33 variable loci revealed groups of populations from three geographic areas: 1) Russia, 2) northern North America, including southeastern Alaska and northern British Columbia, and 3) southern British Columbia and Washington. The Russian and northern North American groups were genetically more closely related to one another than either was to the southern North American group. These analyses indicated the existence of a genetic discontinuity between northern and southern odd-year British Columbia populations that is larger than the discontinuity between Alaskan and Russian populations.

Similar results were found by Varnavskaya and Beacham (1992), who combined their allelic frequency data with those of Johnson (1979), McGregor (1983), and Beacham et al. (1988) to calculate genetic distances between samples based on five loci in common to these studies. Varnavskaya and Beacham's cluster analysis of genetic distances indicated that the odd-year spawners of Kodiak Island, southeastern Alaska and northern British Columbia were more closely related to odd-year spawners of the Kamchatka Peninsula than they were to odd-year spawners in southern British Columbia. However, these authors found that genetic distances between these groups were small relative to the distances between odd- and even-year spawners.

Odd-year Pink Salmon: Genetic Variability Within Regions

Asia--Glubokovskii and Zhivotovskii (1986) proposed a fluctuating stock model for the population structure of Russian pink salmon in an attempt to explain variability in genetic differentiation among these populations. They advanced this model as an explanation for periodic changes in population structure that "are due to fluctuations of intensity of [genetic] exchange...between populations which is caused by the appearance of new and the disappearance of old migrational barriers (both natural and anthropogenic)." The model predicts that genetic differences (as measured with allozymes) among these populations are unstable because of shifts in impediments to gene flow. These authors suggested that population structure in pink salmon follows this model for two reasons: 1) the abundances of fish in the same broodline changed markedly over time in an area, especially in the Kurile and

Sakhalin Islands and on the Kamchatka Peninsula (Ivankov 1986); and 2) early genetic studies (Altukhov et al. 1983, Utter et al. 1980) indicated low levels of genetic differentiation among populations. Early genetic studies of Asian pink salmon (Kartavtsev et al. 1981, Salmenkova et al. 1981) failed to find the degree of genetic subdivision among populations that was present in other species of salmon. However, more recent studies of Asian populations (see below), have revealed a degree of genetic subdivision among populations that is similar to that observed among populations in North America. The agreement of the earlier results with the expectations of the fluctuating stock model may be largely due to analyses involving few loci, because the more comprehensive recent analyses are at odds with these expectations.

Four recent studies examined Asian populations in more detail. First, Kartavtsev (1991) studied allozymic variability at 5 loci in samples from 22 Asian rivers over 3 to 5 generations and found little allelic frequency heterogeneity among samples within 4 areas: 1) western Sakhalin Island, 2) eastern Sakhalin Island, 3) the Sea of Okhotsk, and 4) the Kamchatka Peninsula. Kartavtsev found significant differences between some of these areas in some years but not others, and concluded that extensive gene flow between localities was responsible for the genetic homogeneity among populations.

Second, Kartavtsev et al. (1992) extended the analysis of these data and found no significant deviations from expected Hardy-Weinberg genotypic proportions in samples pooled over geographic areas. Although the fit to Hardy-Weinberg proportions in the pooled sample was consistent with a lack of geographic differentiation among populations, this approach for detecting genetic differences among samples is weak.

Third, Varnavskaya and Beacham (1992) studied allozyme variability at 12 loci in pink salmon from 8 rivers on the east coast of the Kamchatka Peninsula. These samples were collected at river mouths, however, and therefore may not represent spawning-ground populations. G-tests detected significant ($P < 0.05$) overall allelic frequency heterogeneity among samples at five loci, and randomization tests detected significant heterogeneity at three loci. Cluster analysis of genetic distances showed that the samples from the Hailula and Uka Rivers were distinct from the other samples, but the genetic distances between these and the remaining samples were small.

Finally, in a larger study, Shaklee and Varnavskaya (1994) examined the products of 44 protein-encoding loci and found variability at 24 loci in 8 samples of odd-year spawners collected in 1991 from 8 localities in the Sea of Okhotsk, the Kamchatka Peninsula, and the western Bering Sea. None of these localities had been represented in the work of Varnavskaya and Beacham (1992). A geographically nested contingency-table analysis of allelic frequencies at 23 loci demonstrated significant total heterogeneity among the 8 samples for 3 loci, but the sum of the G-test statistics over variable loci was not significant. Shaklee and Varnavskaya (1994) detected little heterogeneity within the three regions and found only a single locus that showed significant differences among the three regions. Multidimensional scaling of Cavalli-Sforza and Edwards' (1967) chord genetic distances between samples failed to show any geographically meaningful relationships among samples.

British Columbia--Beacham et al. (1985) collected spawning-ground samples from 4 rivers in British Columbia in 1982 (even-year spawners) and from 21 rivers in British Columbia and Washington in 1983 (odd-year spawners). Samples of odd-year spawners were divided into three geographic areas for analysis: 1) Johnstone Strait and Strait of Georgia (nine localities), 2) Fraser River (seven localities), and 3) Puget Sound (four localities). Significant allelic frequency heterogeneity was detected within each area, but the sums of G-test statistics over loci indicated that the greatest amount of heterogeneity was due to differences among localities in Johnstone Strait and the Strait of Georgia. Cluster analysis of genetic distances based on 14 polymorphic loci detected 3 groups corresponding to the groups used in the contingency-table tests, except that the sample from the south coast Indian River, just north of the Fraser River, was included with the Fraser River samples and not with the Johnstone Strait samples. The Fraser River and Puget Sound samples were more closely related to one another than either was to the samples from northern British Columbia.

Beacham et al. (1988) examined a much larger number of samples at 33 even-year and 47 odd-year spawning sites in British Columbia and 4 odd-year sites in Puget Sound. To test for allelic frequency differences, they divided odd-year spawners into 5 areas and found a significant degree of allelic frequency heterogeneity among localities for most of the 15 polymorphic loci examined. As was the case for even-year pink salmon (see above), on a larger geographic scale they found substantially greater heterogeneity in odd-year pink salmon populations among areas than among localities within areas. Cluster analysis of genetic distances between the British Columbia samples (not all of the loci were examined in Puget Sound samples) showed two somewhat distinct Canadian groups: a cluster including most of the northern island and mainland localities, and a cluster including Fraser River, Vancouver Island, and south coast localities. However, the cluster of northern samples was heterogeneous as it also contained five samples from southern British Columbia.

Washington--Shaklee et al. (1991) examined allelic frequency variability for 21 variable loci in 26 odd-year spawning localities in British Columbia and Washington in 1985, 1987, and 1989. A total of 52 collections were grouped into 26 samples by pooling multiple-year data at several localities, since little temporal variability was present among samples taken from different generations at the same locality. Samples from minor tributaries were also pooled in Hood Canal, the Snohomish River, the Stillaguamish River, the Skagit River, and the Nooksack River, since little variability was present among tributaries within these river systems. An analysis of chord genetic distances between samples revealed three geographic clusters: 1) north coast British Columbia and northern populations from south coast British Columbia; 2) southern populations from south coast British Columbia and Fraser River and Puget Sound (except Nooksack River); and 3) Hood Canal and Washington Strait of Juan de Fuca and Nooksack River (Fig. 1 in Shaklee et al. 1991).

The genetic definitions of groups 1 and 2 by Shaklee et al. (1991) were consistent with those of Beacham et al. (1985, 1988) to the extent that localities in the two studies overlapped. The second group consisted of three geographic subgroups: a) south coast of British Columbia on the Strait of Georgia, b) Fraser River and its tributaries, and c) Puget Sound. The samples from Hood Canal/Strait of Juan de Fuca (Olympic Peninsula) had not been examined by Beacham et al. (1985, 1988), but in the analysis by Shaklee et al. (1991) they appeared to represent a distinguishable cluster lying outside the Puget Sound, Fraser River and southern British Columbia clusters. The sample from the Nooksack River (northern Puget Sound) clustered with those from Hood Canal. Shaklee et al. (1991) hypothesized that the genetic similarity between the Nooksack River and Hood Canal populations reflected a supplementation of the natural Nooksack River population with eggs from the Hood Canal Hatchery in 1977. However, a subsequent analysis suggested that the Nooksack River population may be naturally distinct from other odd-year populations in Washington and southern British Columbia (J. Shaklee[25], Shaklee et al. 1995).

Shaklee et al. (1995) also reported the results of analyses of samples from the upper and lower Dungeness and Nisqually Rivers, so that allelic frequencies are now available for 19 naturally spawning populations in Washington. No genetic data were available for pink salmon from the Elwha River, where they may be extinct, or from the South Fork of the Nooksack River, where odd-year spawners are known to occur. We conducted our own analyses of Washington samples by combining them with British Columbia samples processed in the same laboratory (Shaklee et al. 1991). Allelic identities among these samples are therefore consistent. Since some river systems were represented by a single sample, samples of Washington fish were not pooled by river system; this configuration ensured that the full range of interpopulation variability would appear in the analyses.

Considering the 19 Washington sampling localities alone, we calculated 4 different genetic distances based on 23 polymorphic loci (*sAAT-3**, *sAAT-4**, *ADA-2**, *mAH-4**, *sAH**, *ALAT**, *CK-A1**, *CK-C1**, *GPI-B2**, *GPI-A**, *G3PDH-1**, *FDHG**, *GDA**, *sIDHP-2**, *LDH-A1**, *LDH-B1**, *sMDH-A1,2**, *sMDH-B1,2**, *MPI**, *PEPD-2**, *PEP-LT**, *PGDH**, and *PGM-2**), and used UPGMA cluster analysis and multidimensional scaling analysis to examine relationships among samples. The results distinguished three Washington groups: 1) Dungeness River, 2) Hood Canal, and 3) Puget Sound (Fig. 14, UPGMA). In the UPGMA tree of chord genetic distances, the two samples from the Nooksack River clustered with Hood Canal samples, as found by Shaklee et al. (1991), and the sample from the Nisqually River was positioned outside the Hood Canal and Puget Sound clusters. Multidimensional scaling of chord genetic distances (Fig. 15) showed three groups, but multidimensional scaling of other genetic distances was less successful in distinguishing Hood Canal and Puget Sound samples as separate clusters.

The minimum-spanning tree, in which branches connect nearest genetic neighbors, indicated that samples from both the Nooksack and Nisqually Rivers are probably outliers from the Puget Sound group. None of the populations showed greatly reduced levels of genetic variability relative to the other populations that would indicate strong recent reductions

[25]J. Shaklee, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Unpubl. data.

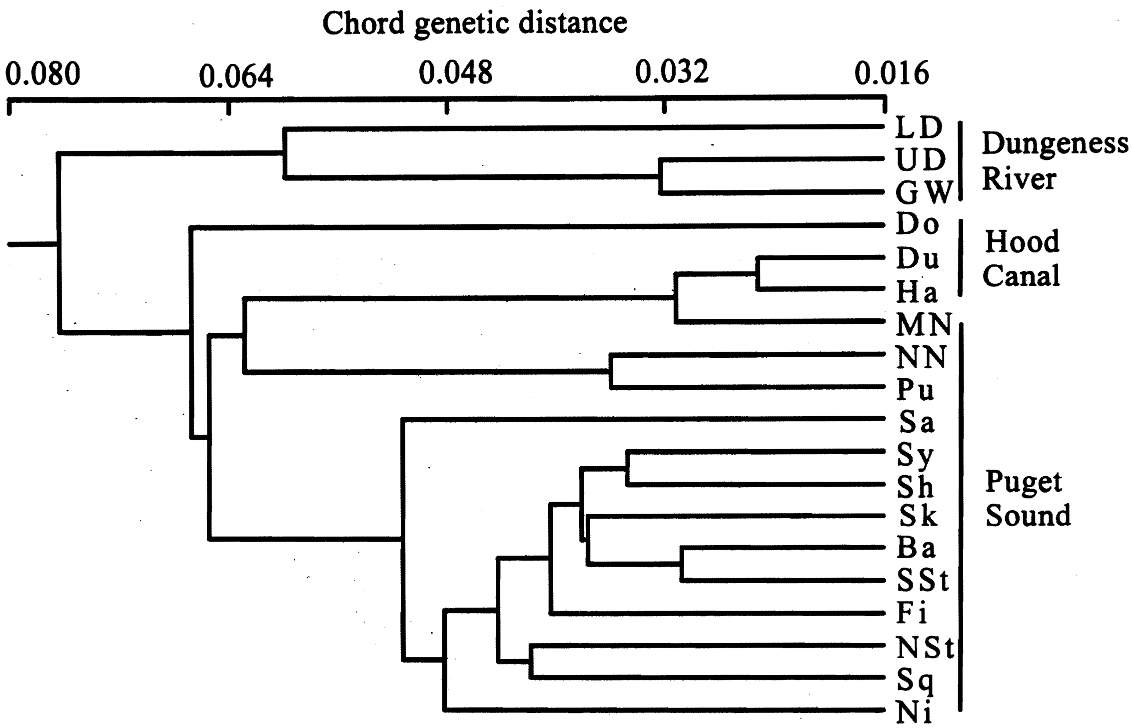

Figure 14. UPGMA phenogram of Cavalli-Sforza and Edwards' (1967) chord genetic distances, based on 23 polymorphic loci (see text), between samples of odd-year pink salmon from Washington (Shaklee et al. 1991; J. Shaklee, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501, unpubl. data). Localities (abbreviation): Lower Dungeness (LD), Upper Dungeness (UD), Grey Wolf (GW), Dosewallips (Do), Duckabush (Du), Hamma Hamma (Ha), Middle Fork Nooksack (MN), North Fork Nooksack (NN), Nisqually (Ni), Puyallup (Pu), Sauk (Sa: Skagit), Skykomish (Sy: Snohomish), Bacon (Bc: Skagit), Snohomish (Sh), South Fork Stillaguamish (SSt), Skagit (Sk: main stem), Finney (Fi: Skagit), North Fork Stillaguamish (NSt), and Snoqualmie (Sq: Snohomish).

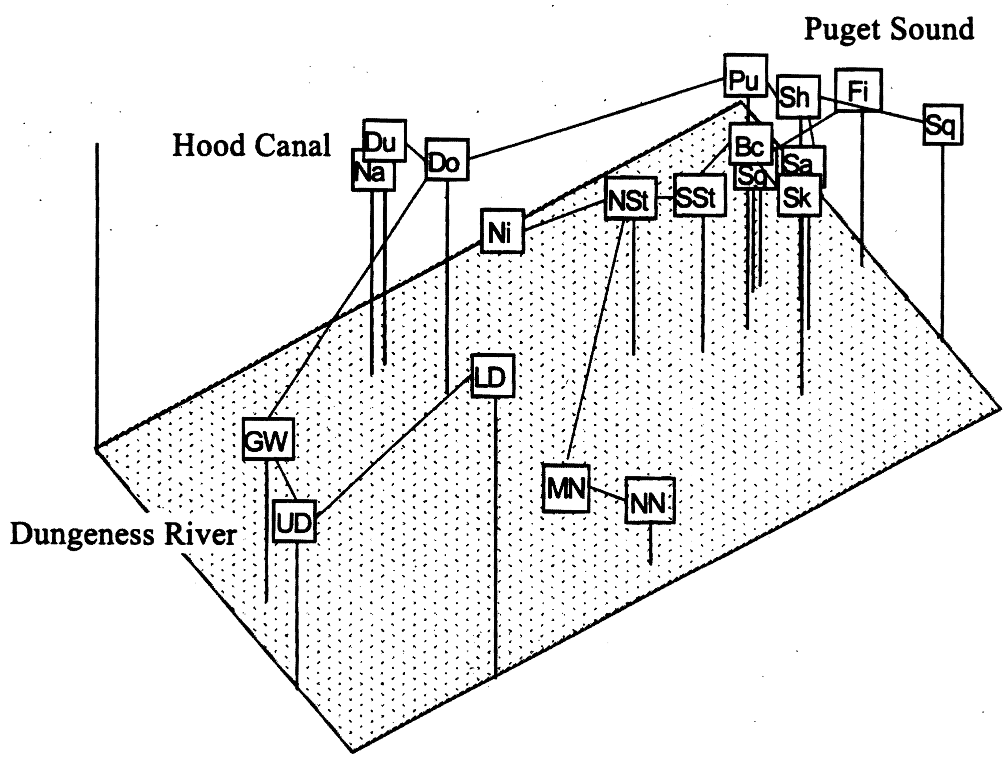

Figure 15. Multidimensional scaling and minimum spanning tree of chord genetic distances, based on 23 polymorphic loci (see text), between samples of odd year pink salmon from Washington. Localities and sources of data as in Figure 14.

in population size. A hierarchical gene diversity analysis of allelic frequencies for the 19 Washington populations indicated that geographic subdivisions accounted for a very small proportion of the total diversity: 98.7% of the total allelic frequency variability was contained on average within populations; 0.3% was due to differences among tributaries within rivers; 0.5% was due to differences among rivers within regions; and 0.5% was due to differences among regions.

To put genetic variability among Washington odd-year spawners into a broader geographic perspective, we conducted additional analyses, adding 17 samples from British Columbia (Shaklee et al. 1991). This combined set of allelic frequencies for 20 polymorphic loci (*sAAT-3**, *sAAT-4**, *ADA-2**, *mAH-4**, *sAH**, *ALAT**, *CK-A1**, *CK-C1**, *GDA**, *GPDH-1**, *FDHG**, *sIDHP-2**, *LDH-A1**, *sMDH-B1,2**, *mMEP-1**, *MPI**, *PEPD-2**, *PEP-LT**, *PGDH**, and *PGM-2**) included 36 populations extending from northern British Columbia to Puget Sound. A UPGMA cluster analysis of chord genetic distances between populations (Fig. 16) again indicated a major subdivision between north coast British Columbia samples and all other southern samples--the same result reported by Beacham et al. (1988) and Shaklee et al. (1991). Four clusters appeared among the southern samples: 1) Olympic Peninsula, 2) south coast British Columbia, 3) Fraser River, and 4) Puget Sound. One difference between this tree and the preceding one was in the positions of the Hood Canal and Nooksack River samples, both of which clustered more closely with the Dungeness River samples in the larger set of data (Fig. 16). Multidimensional scaling of the chord genetic distances (Fig. 17) revealed the major discontinuity between southern and northern British Columbia populations, but southern populations were distributed more or less continuously with small discontinuities between 1) Dungeness River, 2) Hood Canal, 3) Puget Sound, 4) Fraser River, and 5) south and central coasts of British Columbia. In this analysis, the Nooksack River sample was manifest as an outlier from the Hood Canal cluster rather than from the Puget Sound cluster, as it was in the preceding analysis of Washington samples alone. This change in configuration resulted from the use of overlapping but different samples of loci in the two analyses, and indicates that the genetic relationship of the Nooksack River population to other Washington and British Columbia populations is not well resolved.

The results of the gene diversity analysis did not change substantially with the addition of the Canadian samples in the analysis. Most (97.9%) of the variability was contained, on average, within populations; 0.2% was due to variability among localities within rivers; 0.8% was due to differences among rivers within regions; 0.7% was due to differences among regions; and 0.3% was due to differences between north coast British Columbia samples and the other southern samples.

The island model of migration can be used to estimate the number of migrants between each population in this analysis by assuming that allelic frequencies at all loci reflect an equilibrium between the differentiating effect of random genetic drift and the homogenizing effect of gene flow (Wright 1951). The F_{ST} value (a measure of genetic differentiation among populations), averaged over all loci, was 0.021 and yielded an estimate of 11-12 migrants into

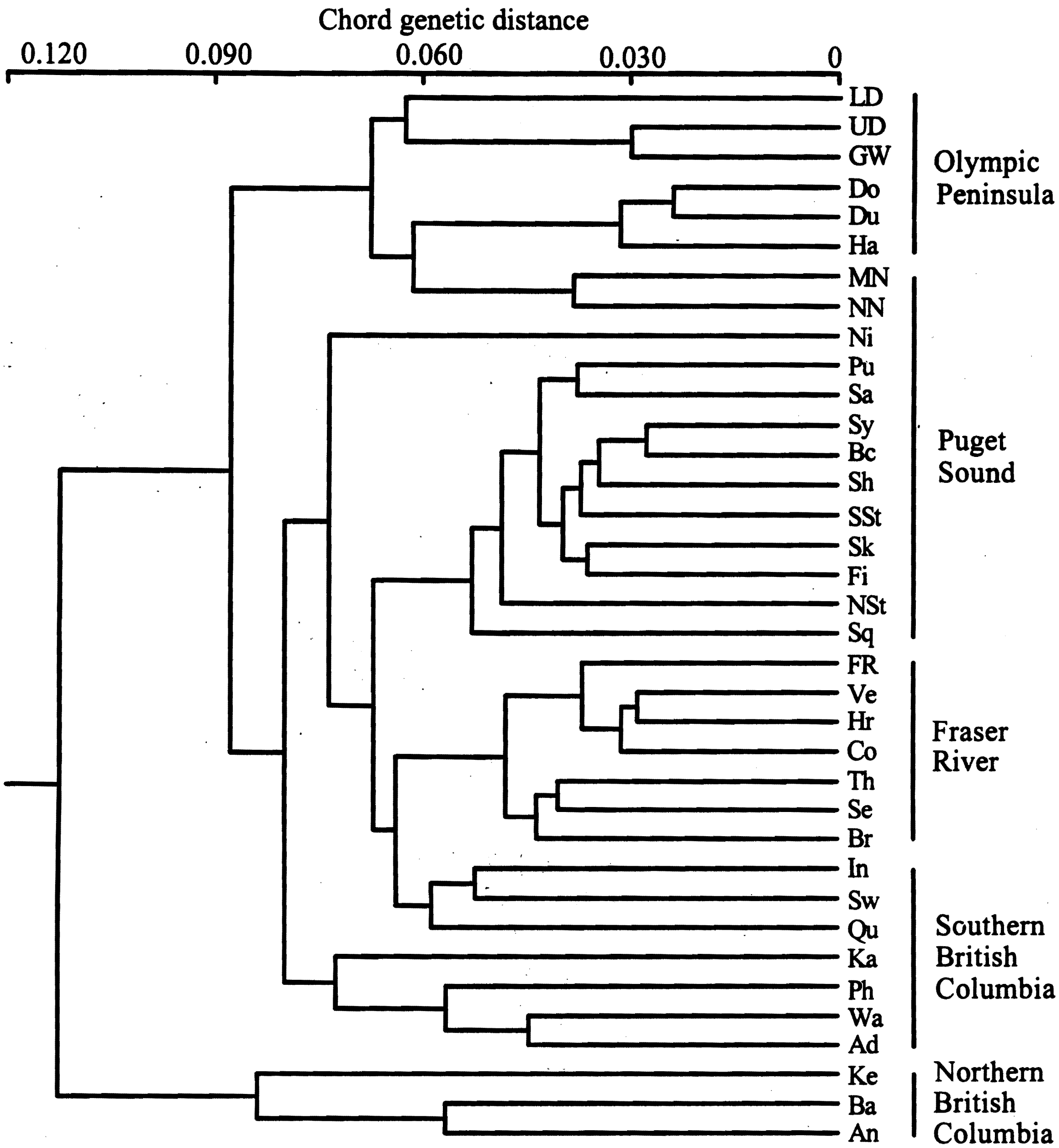

Figure 16. UPGMA phenogram of chord genetic distances, based on 20 polymorphic loci (see text), between samples of odd-year pink salmon in Washington and British Columbia. Localities and sources of data as in Figure 14, with the following additional localities from British Columbia (abbreviation): Fraser River (FR: main stem), Vedder (Ve), Harrison (Hr), Coquihalla (Co), Thompson (Th), Seton (Se), Bridge (Br), Indian (In), Skwawka (Sw), Quinsam (Qu), Kakweiken (Ka), Phillips (Ph), Wakeman (Wa), Adam (Ad), Keogh (Ke), Babine (Ba), and Andesite (An).

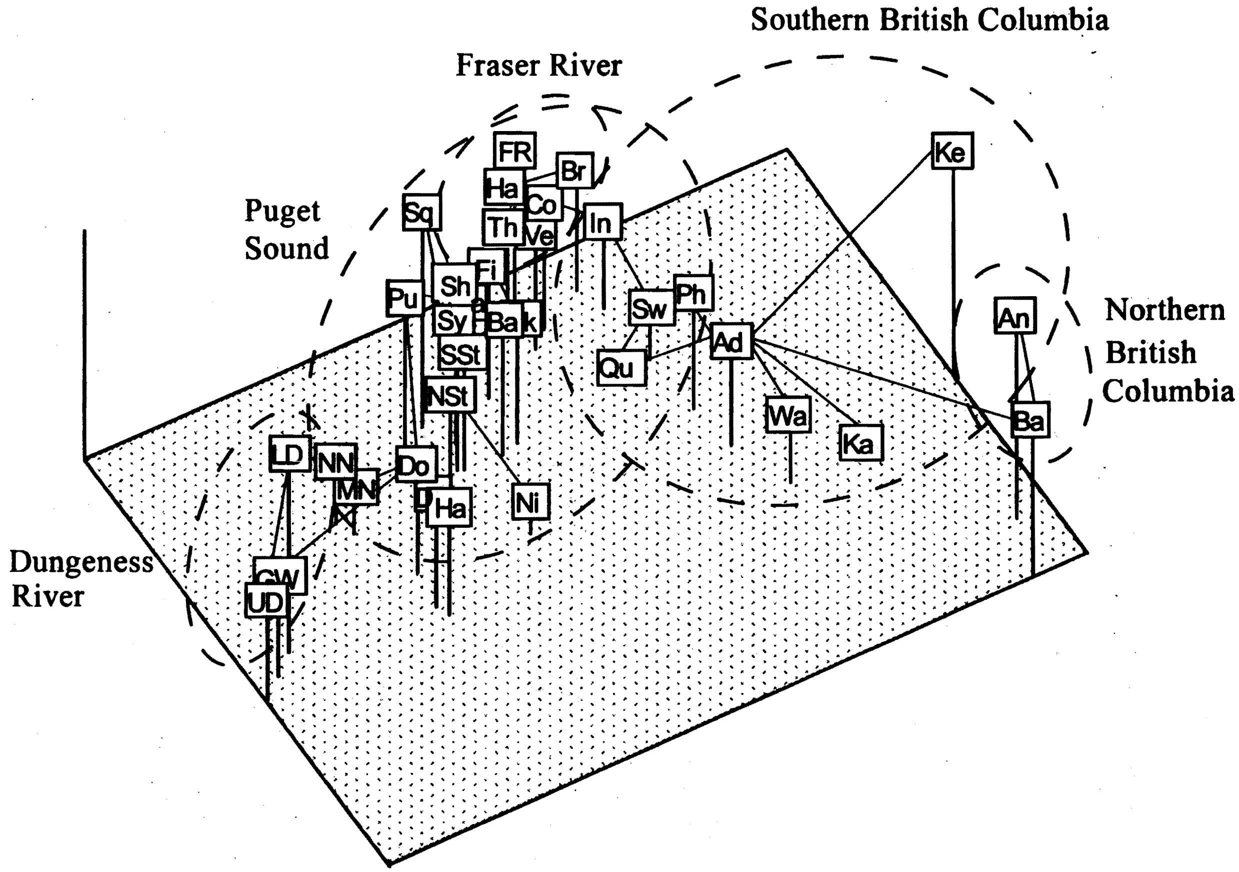

Figure 17. Multidimensional scaling and minimum spanning tree of chord genetic distances, based on 20 polymorphic loci (see text), between samples of odd-year pink salmon in Washington and British Columbia. Localities and sources of data as in Figure 16.

each population per generation. This measure provides a rough estimate of the level of intermixing between populations. However, if the populations are not at equilibrium (i.e., if insufficient time has elapsed since population expansion during the current interglacial period), then this statistic overestimates gene flow between populations. On the other hand, this approach may underestimate the number of migrants into salmon populations because salmon straying does not strictly follow the island model of migration.

Conclusions

Genetic data do not show a close affinity between the single population of even-year pink salmon in the Snohomish River in Washington and any known source of eggs translocated to Washington from northern British Columbia and Alaska. The analysis of available data indicates that the Snohomish River even-year pink salmon population is genetically most closely related to central and south coast British Columbia populations and is a peripheral population at the southern extreme of the geographic distribution of even-year spawners. However, genetic data are not available for even-year spawners from southern Vancouver Island and the Fraser River, and the Snohomish River population may be closely related to these populations.

Odd-year pink salmon populations located around the Pacific Rim can be divided into three major genetic groups: 1) Asia, 2) Alaska and northern British Columbia, and 3) southern British Columbia and Washington. Populations in the first two groups are more closely related to one another than they are to populations in the third group. These major divisions may have resulted from the formation of glacial barriers during the last ice age (Beacham et al. 1988). The populations within each region are also genetically subdivided to some degree, and the degrees of subdivision among populations within each of the three regions are about the same.

Four subgroups of odd-year spawners are distinguishable within southern British Columbia and Washington: 1) Olympic Peninsula, 2) south coast of British Columbia, 3) Puget Sound, and 4) Fraser River. Groups 3 and 4 are most closely related to each other, and groups 2 and 1 are progressively more distantly related to groups 3 and 4. Within Washington, the populations of the Nooksack and Nisqually Rivers are genetic outliers and do not fall within expected geographic clusters in the analyses. The relationship of the Nooksack River population to other populations depended on the sample of loci and populations used in the analyses: in analyses limited to samples from Washington, it was genetically closest to Puget Sound populations, but when analyses included British Columbia samples and a different set of loci, it tended to show greater affinity to Hood Canal populations. Consequently, the relationship of this population to other populations in the region is unclear.

It should be recognized that the conclusions drawn from these analyses must be tempered by the fact that the analyses were generated with data from several studies with different sets of loci and different means of generating and interpreting electrophoretic data. Some of the analyses involved an implicit assumption that the different sets of data are compatible, an assumption that has been shown to be invalid for some pink salmon studies (White and Shaklee 1991).

Discussion and Conclusions on ESU Determinations

Based on the genetic, life history, and ecological information presented above, the Biological Review Team identified two ESUs for North American pink salmon in Washington and southern British Columbia. In the following discussion we describe these ESUs and outline the issues that were valuable to the BRT in making each ESU determination.

Even-year Pink Salmon

A single population of even-year pink salmon occurs in the United States south of Alaska, in the Snohomish River. This population is genetically much more similar to even-year pink salmon from British Columbia and Alaska than it is to odd-year pink salmon from Washington. This pattern of similarity is also found in life history traits such as body size and run timing. This result is consistent with numerous other studies that have found large genetic differences between even- and odd-year pink salmon from the same area, with the magnitude of the differences roughly comparable to that found between coastal and inland steelhead, *Oncorhynchus mykiss* (Okazaki 1984, Reisenbichler et al. 1992). The BRT concluded, therefore, that Snohomish River even-year pink salmon are in a different ESU than odd-year pink salmon from Washington.

The origin of the Snohomish River even-year population and its relationship to other even-year populations in British Columbia and Alaska is less certain. Although several concerted efforts were made between 1910 and 1956 to introduce even-year pink salmon from Alaska and British Columbia into Puget Sound, no direct evidence indicates that any were successful in producing sustained returns. The allozyme studies described here also failed to show a similarity of the Snohomish River sample to any of the putative sources of stock transfers for which data are available.

Although available data do not provide evidence to support the hypothesis that the Snohomish River population has resulted from a human-mediated stock transfer in this century, this possibility cannot be excluded entirely. Not all sources of even-year stock transfers are known, and some of those that are known have not been characterized genetically. The genetic distinctiveness of the current Snohomish River population might have resulted from genetic change (founder effect or subsequent genetic drift or both) associated with a natural colonization event, but it might also have occurred relatively recently as a result of similar processes in an introduced population. In addition, available genetic information for the Snohomish River sample is based on a single year's collection.

Nevertheless, the BRT concluded that even-year pink salmon in the Snohomish River should be presumed to be a native population in the absence of more convincing evidence that it is not. This decision was reached because 1) observed genetic and life history traits of this population are consistent with what might be expected from a natural colonization, and 2) this population has apparently been naturally self-sustaining in the Snohomish River for at least 8 generations (and possibly for 25 or more).

At present, the Snohomish River population is relatively small (up to a few thousand adults per generation), and this raises the issue of the importance of historical population size in considering and defining ESUs. Because ESUs are intended to represent units that are largely independent from other such units over evolutionarily important time frames, Waples (1991a, p. 19) argued in the NMFS "Definition of Species" paper that

> A Pacific salmon population should not be considered an ESU if the historic size (or historic carrying capacity) is too small for it to be plausible to assume the population has remained isolated over an evolutionarily important time period. In making this evaluation, the possibility should be considered that small populations observed at present are still in existence precisely because they have evolved mechanisms for persisting at low abundance.

The small size of the current Snohomish River even-year population suggests that it may be part of a larger geographic unit on evolutionary time scales (hundreds or thousands of years). However, the Snohomish River odd-year population, which has the same spawning habitat available, is 1-2 orders of magnitude larger, so it is possible that the even-year population was also larger in the past. If so, long-term persistence of the even-year population in isolation from other even-year populations would be easier to explain.

The Snohomish River even-year pink salmon population is geographically isolated by several hundred kilometers from other even-year populations of appreciable size. However, life history features of the Snohomish River even-year population are similar to those in other even-year populations from central British Columbia. For example, peak spawning time of Snohomish River even-year pink salmon is comparable to that of some British Columbia even-year pink salmon, yet it is about 2 weeks earlier than that of Snohomish River odd-year pink salmon. This timing differs despite spatial overlap in habitat use by even- and odd-year adults in that system. Results of genetic analyses depend heavily on whether an adjustment is made for possible differences between laboratories in methods for recording the data. A comparison of published data suggests that the Snohomish River even-year population is genetically the most distinctive of any sample from the United States or southern British Columbia. However, the Snohomish River population is much less distinctive in analyses of adjusted allelic frequencies.

The BRT could not resolve with any degree of certainty the extent of the ESU that contains the Snohomish River even-year pink salmon population. This issue was particularly difficult because it is not clear which analyses--those with or without the adjustment for possible bias--should be preferred. After considering all available information, about half the BRT members concluded that the Snohomish River even-year population belongs in an ESU by itself, and half concluded that it belongs in an ESU with populations from British Columbia. Most of those favoring the latter scenario felt that the ESU probably includes all even-year pink salmon from streams entering the Strait of Georgia and Johnstone Strait.

In any case, the BRT was unanimous in agreeing that any conclusion about the extent of the even-year pink salmon ESU should be regarded as provisional and subject to revision should substantial new information become available on 1) the Snohomish River population, 2) the history and success of transplanting even-year pink salmon into northwestern Washington, or 3) small populations of even-year pink salmon in southern British Columbia that are at present poorly understood.

Odd-year Pink Salmon

Genetic, life history, and environmental data were the most important factors in consideration of ESUs for odd-year pink salmon. Environmental and ecological characteristics generally show a strong north-south trend, but no substantial differences were identified that consistently differentiated Washington and British Columbia populations. An east-west gradient, separating populations along the Strait of Juan de Fuca from those to the east, was considered more important for evaluating pink salmon populations. In addition, three U.S. rivers supporting odd-year pink salmon populations (the Nisqually, Nooksack, and Puyallup Rivers) are dominated by glacial runoff, which may promote special adaptations in spawning populations. However, glacial rivers are also common in most other areas of pink salmon distribution throughout the Pacific Rim.

Although odd-year pink salmon show considerable variation in body size among populations in Washington, the range of this variation does not exceed that found in British Columbia. Among U.S. populations, Nooksack River fish average the smallest and Hood Canal fish the largest in body size. Time of peak spawning varies over about a 4- to 5-week period in northwestern Washington; spawning occurs earliest in the Nooksack and Upper Dungeness Rivers, followed by Hood Canal and then Puget Sound (excluding the Nooksack and Nisqually Rivers), with the latest spawning occurring in the Nisqually River.

Some pink salmon appear to reside in Puget Sound during their marine phase rather than migrating to the open ocean (Jensen 1956, Hartt and Dell 1986). This behavior has not been documented for pink salmon in other areas, but this may simply reflect a lack of appropriate studies. Furthermore, resident Puget Sound fish have not yet been associated with any particular freshwater population(s), so the importance of this trait in helping to define odd-year pink salmon ESUs is not clear.

Comprehensive genetic analyses show that odd-year pink salmon from southern British Columbia and Washington are clearly in a different evolutionary lineage than nearby even-year populations and more northerly odd-year populations. Within the southern British Columbia-Washington group, there is also evidence of geographic population genetic structure, with some differences among populations from the Dungeness River, Hood Canal, Puget Sound, the

Fraser River, and southern and central British Columbia. In some analyses, samples from the Nisqually and Nooksack Rivers were both genetic outliers but were not similar to each other. However, none of the genetic differences found within the southern British Columbia-Washington group are very large in absolute magnitude. For example, the F_{ST} value (averaged over all loci) for all odd-year samples of pink salmon from Puget Sound to central British Columbia was only 0.021, considerably smaller than the value found among populations within the ESU for Snake River spring/summer chinook salmon (*O. tshawytscha*) (F_{ST} = 0.034; Waples et al. 1993) or among populations of steelhead (*O. mykiss*) within the Klamath Mountains Province ESU (F_{ST} = 0.033; NMFS, unpubl. data[26]).

Although genetic differences (as determined by protein electrophoresis) among odd-year pink salmon populations in the Puget Sound/British Columbia area are relatively modest, the general geographic coherence of the structure that does exist indicates that there has been some reproductive isolation among pink salmon populations within this larger area. The BRT next considered whether any of these individual groups of populations (Dungeness River, Hood Canal, Puget Sound, Fraser River, southern and central British Columbia) might represent a substantial contribution to ecological/genetic diversity of the species as a whole. As noted above, the BRT did not find strong environmental or ecological differences among these areas. Two of the U.S. rivers dominated by glacial runoff (Nooksack and Nisqually) also have pink salmon populations that are genetically somewhat distinctive. However, the two populations are not similar to each other, either on the basis of genetic or life history characteristics, so it seems unlikely that they are evolving together as a unit independent from other odd-year pink salmon populations. A minority of the BRT believed that these two populations were distinctive enough to each be separate ESUs, but most members thought that they simply represented part of the natural variability within a larger ESU.

There was somewhat stronger concurrence among BRT members that odd-year pink salmon populations from the Strait of Juan de Fuca (i.e., those in the Dungeness and Elwha Rivers) were in a separate ESU from other Puget Sound and British Columbia odd-year populations. Evidence to support this view is based on genetic differences detected by protein electrophoresis, geography and habitat differences, and the fact that recent declines (including the possible extinction of the Elwha River population) are shared by Strait of Juan de Fuca populations but not Puget Sound populations. Notably, the upper Dungeness River population shows an extraordinarily early run timing for the region and an apparently unique maturation strategy. However, no life history data are available for the Elwha River population, and the lower Dungeness River population has life history features similar to those of other Puget Sound populations. Furthermore, although there are some habitat and ecological differences between the Dungeness and Elwha Rivers and others in the Puget Sound area, a stronger environmental transition is found west of the Elwha River, where much wetter areas typical of the Olympic Peninsula are encountered (Weitkamp et al. 1995). The majority of the BRT

[26]Modified from the value reported by Busby et al. (1993) by omitting samples from outside the ESU.

therefore concluded that the populations of the Dungeness and Elwha Rivers (if the latter still exists) are part of the larger Puget Sound/British Columbia ESU for odd-year pink salmon.

Based on currently available information, the BRT concluded that the northern boundary of the Puget Sound/southern British Columbia ESU corresponds to the geographic location where a strong genetic discontinuity was observed in the Johnstone Strait region of British Columbia. The ESU does not include northern British Columbia, Alaskan, or Asian populations. In Washington, the westernmost populations in this ESU are both found in the Dungeness River, but the ESU presumably would also include the Elwha River population, if a remnant still exists. The BRT felt there was insufficient information to determine whether other populations on the Olympic Peninsula or farther south (if any such populations exist) would be included in this ESU. Also uncertain is the relationship of odd-year populations from southwestern Vancouver Island to this ESU.

It is clear that pink salmon populations within the Puget Sound/southern British Columbia ESU contain a substantial amount of genetic and life history diversity. Much of this diversity is contained within the "marginal" populations in Washington, which represent the southernmost regularly spawning populations of North American pink salmon and are likely to be important for colonizing available habitat in this region when conditions are favorable to do so (Scudder 1989, Lesica and Allendorf 1995). The ESU has representatives that are distinctive on the basis of run timing and maturation strategy, and may include an unknown population or populations that lack an oceanic migration, using instead a protected embayment for the marine phase of development and growth. In addition, the ESU has populations that spawn far from tidewater, in stream reaches heavily influenced by glacial runoff.

ASSESSMENT OF EXTINCTION RISK

Background

As outlined in the Introduction above, NMFS considers a variety of information in evaluating the level of risk facing an ESU. Aspects of several of these risk considerations are common to all pink salmon ESUs. These are discussed in general below; more specific discussion of factors for each of the ESUs under consideration here can be found in the following sections. Because we have not taken future effects of conservation measures into acount (see Introduction), we have drawn scientific conclusions about the risk of extinction faced by identified ESUs under the assumption that present conditions will continue. Future effects of conservation measures will be taken into account by the NMFS Northwest and Southwest Regional Offices in making listing recommendations.

Absolute Numbers

The absolute number of individuals in a population is important in assessing two aspects of extinction risk. For small populations that are stable or increasing, population size can be an indicator of whether the population can sustain itself into the future in the face of environmental fluctuations and small-population stochasticity; this aspect is related to the concept of minimum viable populations (MVP) (Gilpin and Soulé 1986, Thompson 1991). For a declining population, present abundance is an indicator of the expected time until the population reaches critically low numbers; this aspect is related to the concept of "driven extinction" (Caughley 1994).

In addition to total numbers, the spatial and temporal distribution of adults is important in assessing risk to an ESU. Spatial distribution is important both at the scale of river basins within an ESU and at the scale of spawning areas within basins ("metapopulation" structure). Temporal distribution is important both among years, as an indicator of the relative health of different brood-year lineages, and within seasons, as an indicator of the relative abundance of different life history types or runs.

Traditionally, assessment of salmon populations has focused on the number of harvestable or reproductive adults, and these measures comprise most of the data available for Pacific salmon. In assessing the future status of a population, the number of reproductive adults is the most important measure of abundance, and we focus here on measures of the number of adults escaping to spawn in natural habitat. However, total run size (spawning escapement + harvest) is also of interest because it indicates potential spawning in the absence of harvest. Data on other life history stages (e.g., freshwater smolt production) can be used as a supplemental indicator of abundance.

Because the ESA (and NMFS policy) mandates a biological review that focuses on viability of natural populations, we attempted to distinguish natural fish from hatchery produced fish. All statistics are based on data that indicate total numbers or density of adults that spawn in natural habitat ("naturally spawning fish"). The total of all naturally spawning fish ("total escapement") is divided into two components: "Hatchery produced" fish are reared as juveniles in a hatchery but return as adults to spawn naturally; "natural" fish are progeny of naturally spawning fish.

Historical Abundance and Carrying Capacity

The relationship of current abundance and habitat capacity to that which existed historically is an important consideration in evaluating risk for several reasons. Knowledge of historical population conditions provides a perspective of the conditions under which present stocks evolved. Historical abundance also provides the basis for establishing long-term population trends. Comparison of present and past habitat capacity can also indicate long-term population trends and problems of population fragmentation.

Although the relationship of present abundance to present carrying capacity is important for understanding the health of populations, the fact that a population is near its current capacity does not in itself mean that it is healthy. If a population is near capacity, there will be limits to the effectiveness of short-term management actions to increase its abundance, and competition and other interactions between hatchery and natural fish may be important considerations because hatchery supplementation will further increase population density in a limited habitat.

Quantitative assessments of habitat are quite rare, although rough estimates of carrying capacity are frequently made for setting management goals. From the evidence available, overall natural production of pink salmon does not appear to be below historical levels for the odd-year ESU considered here, and production in the even-year ESU has been generally increasing over the last 15 years. In the odd-year ESU, however, abundance in some individual populations appears to be severely depressed, and some of these declines could be due in part to habitat degradation in individual drainages (e.g., Dungeness River pink salmon; Lichatowich 1993).

Trends in Abundance

Short- and long-term trends in abundance are a primary indicator of risk in salmonid populations. Trends may be calculated from a variety of quantitative data, including dam or weir counts, stream surveys, and catch data. These data sources and methods are discussed in more detail below, under Approach. When data series are lacking, general trends may be inferred by comparing historical and recent abundance estimates, or by considering trends in habitat quantity or condition.

The role of artificial propagation (in the form of hatcheries) for Pacific salmon requires careful consideration in ESA evaluations. Artificial propagation has implications both for evaluating production trends and in evaluating genetic integrity of populations. Waples (1991a,b) and Hard et al. (1992) discussed the role of artificial propagation in ESU determination and emphasized the need to focus on natural production in the threatened or endangered status determination. Because of the ESA's emphasis on ecosystem conservation, this analysis focuses on naturally reproducing salmon. A fundamental question in ESA risk assessments is whether natural production is sufficient to maintain the population without the constant infusion of artificially produced fish. A full answer to this question is difficult without extensive studies of relative production and interactions between hatchery and natural fish.

When such information is lacking, the presence of hatchery fish in natural populations leads to substantial uncertainty in evaluating the status of the natural population. For Washington pink salmon, hatchery production is small relative to natural production and is localized in southern Hood Canal. Therefore, the presence of hatchery fish among naturally spawning pink salmon is not likely to have a substantial effect on our attempts to evaluate the sustainability of natural production for individual populations in this review.

Factors Causing Variability

Variations in the freshwater and marine environments are thought to be a primary factor driving fluctuations in salmonid run size and escapement (Pearcy 1992, Beamish and Bouillon 1993, Lawson 1993). Recent changes in ocean condition are discussed below. Habitat degradation and harvest have probably made stocks less resilient to poor climate conditions, but these effects are not easily quantifiable.

Threats to Genetic Integrity

In addition to being a factor in evaluating natural replacement rates, artificial propagation can substantially affect the genetic integrity of natural salmon populations in several ways. First, stock transfers that result in interbreeding of hatchery and natural fish can lead to loss of fitness in local populations and loss of diversity among populations. The latter is important to maintaining long-term viability of an ESU because genetic diversity among salmon populations helps to buffer overall productivity against periodic or unpredictable changes in the environment (Fagen and Smoker 1989, Riggs 1990). Ricker (1972) and Taylor (1991) summarized some of the evidence for local adaptations in Pacific salmon that may be at risk from stock transfers.

Second, because a successful salmon hatchery dramatically changes the mortality profile of a population, some level of genetic change relative to the wild population is inevitable, even in hatcheries that use local broodstock (Waples 1991b). These changes are unlikely to be beneficial to naturally reproducing fish.

Third, even if naturally spawning hatchery fish leave few or no surviving offspring, they still can have ecological and indirect genetic effects on natural populations. On the spawning grounds, hatchery fish may interfere with natural production by competing with natural fish for territory or mates. If they successfully spawn with natural fish, they may divert production from more productive natural-by-natural crosses. The presence of large numbers of hatchery juveniles or adults may also alter the selective regime faced by natural fish.

For smaller stocks (either natural or hatchery), small-population effects (inbreeding, genetic drift) can also be important concerns for genetic integrity. Inbreeding and genetic drift are well understood at the theoretical level, and researchers have found inbreeding depression in various fish species (reviewed by Gall 1987 and Allendorf and Ryman 1987). Other studies (e.g., Simon et al. 1986, Withler 1988, Waples and Teel 1990; see also Campton 1995) have shown that hatchery practices commonly used with anadromous Pacific salmonids have the potential to affect genetic integrity. However, we are not aware of empirical evidence for inbreeding depression or loss of genetic variability in any natural or hatchery populations of Pacific salmon or steelhead.

For Washington pink salmon, genetic concerns, particularly those related to stock transfers and small-population effects, are relevant primarily to Snohomish River even-year pink salmon and Hood Canal odd-year pink salmon.

Recent Events

A variety of factors, both natural and human-induced, affect the degree of risk facing salmon populations. Because of time-lags in these effects and variability in populations, recent changes in any of these factors may affect current risk without any apparent change in available population statistics. Thus, consideration of these effects must go beyond examination of recent abundance and trends. Unfortunately, forecasting future effects is rarely straightforward and usually involves qualitative evaluations based on informed professional judgment. A key question regarding the role of recent events is: Given our uncertainty regarding the future, how do we evaluate the risk that a population may not persist?

For example, climate conditions are known to have changed recently in the Pacific Northwest, and Pacific salmon stocks south of British Columbia have been affected by changes in ocean production that occurred during the 1970s (Pearcy 1992, Lawson 1993). Much of the Pacific coast has also been experiencing drought conditions in recent years, which may depress freshwater salmon production. However, at this time we do not know whether these climate conditions represent a long-term change that will continue to affect stocks in the future or whether these changes are short-term environmental fluctuations that can be expected to be reversed in the near future. Possible future effects of recent or proposed conservation measures have not been taken into account in this analysis.

Other Risk Factors

Other risk factors typically considered for salmonid populations include disease prevalence, predation, and changes in life history characteristics such as spawning age or size. We have not found evidence that any of these factors are widespread throughout any pink salmon ESU, except for the apparent decline in body size of adult pink salmon previously discussed under Pink Salmon Populations in Washington. Factors that may be important for individual populations are noted in the ESU summaries below.

Approach

Previous Assessments

In considering the status of ESUs, we evaluated both quantitative and qualitative data. Among the qualitative data considered were previous reviews of the status of pink salmon (Nehlsen et al. 1991, WDF et al. 1993). These reviews used different definitions of population and different criteria to assess the status of the populations. Nehlsen et al. (1991) classified populations as at high risk of extinction, moderate risk of extinction, or of special concern. They considered populations at high risk of extinction to have likely reached the threshold for classification as endangered under the ESA. Populations were placed in this category if they had declined from historical levels, were continuing to decline, or had spawning escapements less than 200. Populations were classified as at moderate risk of extinction if they had declined from historical levels but presently appear to be stable at a level above 200 spawners. Nehlsen et al. (1991) felt that populations in this category had reached the threshold for threatened status under the ESA. Populations were classified as of special concern if a relatively minor disturbance could threaten them, if insufficient data were available for them, if they were influenced by large releases of hatchery fish, or if they possessed some unique character. Nehlsen et al. (1991) also listed some populations that they considered as possibly extinct, but did not discuss populations not considered to be at some risk. They classified pink salmon in the Skokomish (southern Hood Canal) and Elwha Rivers as at high risk of extinction, and pink salmon in the Dungeness River as at moderate risk of extinction (Table 7). They listed California runs in the Klamath and Sacramento Rivers as extinct, and the run in the Russian River as possibly extinct.

WDF et al. (1993) classified populations as to origin ("native," "non-native," "mixed," or "unknown"), production ("wild," "composite," or "unknown"), and status ("healthy," "depressed," "critical," or "unknown"). Status categories were defined as healthy, "experiencing production levels consistent with its available habitat and within the natural variations in survival for the stock"; depressed, "production is below expected levels...but above the level where permanent damage to the stock is likely"; and critical, "experiencing production levels that are so low that permanent damage to the stock is likely or has already occurred."

Of the 15 populations of pink salmon identified by WDF et al. (1993; see Table 7), 9 were classified as healthy, 2 as critical, 2 as depressed, and 2 as unknown. They classified all runs as wild production and all except those in the North and Middle Forks of the Nooksack River as native origin. Pink salmon spawning in these two forks of the Nooksack River are likely to be designated as native runs in the 1995 revision of SASSI, based on new sample collections and interpretation of genetic data (J. Ames[27], J. Shaklee[28]). Nine of the Puget Sound and Hood Canal populations were classified as healthy and two in the Nooksack River were of unknown status. Populations in the Dosewallips and upper Dungeness Rivers were classified as depressed, and populations in the lower Dungeness and Elwha Rivers were classified as critical (Table 7).

Various problems arise in applying results of these studies to ESA evaluations. One major problem is that the definition of "stock" or "population" varied considerably in scale

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[27]J. Ames, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., April 1995.

[28]J. Shaklee, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., April 1995.

Table 7. Status of pink salmon populations assessed in previous reviews.

		WDF et al. (1993)		
Population[a]	Nehlsen et al. (1991)[b]	Origin[c]	Production Type[d]	Status[e]
	EVEN-YEAR Washington			
Snohomish		N	W	H
	ODD-YEAR Washington			
Nooksack				
North Fork/ Middle Fork		M	W	U
South Fork		N	W	U
Skagit		N	W	H
Stillaguamish				
North Fork		N	W	H
South Fork		N	W	H
Snohomish		N	W	H
Puyallup		N	W	H
Nisqually		N	W	H
Skokomish	A			
Hamma Hamma		N	W	H
Duckabush		N	W	H
Dosewallips		N	W	D
Dungeness	B			
Upper		N	W	D
Lower		N	W	C
Elwha	A	N	W	C
	California			
Klamath	X			
Russian	A+			
Sacramento	X			

[a] Tributaries and minor drainages combined.
[b] A+ = possibly extinct, A = high risk of extinction, B = moderate risk of extinction, X = extinct.
[c] N = native, M = mixed.
[d] W = wild.
[e] H = healthy, D = depressed, C = critical, U = unknown.

among studies, and sometimes among regions within a study. Identified units range in size from large river basins to minor coastal streams and tributaries. A second problem is the definition of categories used to classify population status. Only Nehlsen et al. (1991) used categories intended to relate to ESA threatened or endangered status, and they applied their own interpretations of these terms to individual populations, not to ESUs as defined here. WDF et al. (1993) used general terms describing the status of populations that cannot be directly related to the considerations important in ESA evaluations. For example, the WDF et al. (1993) definition of healthy could conceivably include a population that is at substantial extinction risk due to loss of habitat, hatchery fish interactions, and/or environmental variation, although this does not appear to be the case for any pink salmon population. A third problem is the selection of populations or stocks included in the review. Nehlsen et al. (1991) did not evaluate (or even identify) populations not perceived to be at risk, so it is difficult to determine the proportion of populations they considered to be at risk in any given area. WDF et al. (1993) included all natural Washington populations of pink salmon in their assessment, as they considered all of these to be substantially "wild."

Data Evaluations

Quantitative evaluations of data included comparisons of current and historical abundance of pink salmon, calculation of recent trends in escapement, and evaluation of the proportion of natural spawning attributable to hatchery fish. Historical abundance information for these ESUs is largely anecdotal. Time-series data are available for many populations, but the amount and quality of the data varied among ESUs. We compiled and analyzed this information to provide several summary statistics of natural spawning abundance, including (where available) recent total spawning run size and escapement, percent annual change in total escapement, recent naturally produced spawning run size and escapement, and average percentage of natural spawners of hatchery origin.

Although our evaluation used the best data available, these data have several limitations, and not all summary statistics were available for all populations. For example, we generally did not measure spawner abundance directly for all populations; rather, we often had to estimate abundance from catch (which itself may not always have been measured accurately) or from limited survey data. In many cases, it was difficult to separate hatchery production from natural production.

Quantitative methods--Information on population abundance was compiled from a variety of state, federal, and tribal agency records. We believe it to be complete in terms of long-term adult abundance records for pink salmon in the region covered here. Principal data sources were fishery statistics and stream surveys. Neither of these provides a complete measure of abundance for any of the streams. Specific problems are discussed below for each data type.

Data types--There are two primary sources of abundance data for pink salmon: fishery statistics and spawning escapement surveys. Fishery data span a longer series, but landings in

Washington, Oregon, and California are dominated by Fraser River fish and do not accurately reflect abundance of local pink salmon populations. In addition, fisheries harvest mixed populations and no systematic marking or tagging programs can be used to attribute fishery landings to streams of origin consistently. Landings from areas covered by the Pacific Salmon Treaty (PST) have been partitioned by country of origin with genetic stock identification (GSI) techniques since 1985, and prior to that were allocated by assuming that U.S. populations provided a constant percentage of the landings in treaty catch areas (J. Woodey[29]). These GSI techniques are used to estimate landings of fish originating from 23 stocks, but harvest management is currently based on the analysis of contributions from 3 major groups--Fraser River, non-Fraser River British Columbia, and Puget Sound (B. White[30]). Landings within Puget Sound and the U.S. origin catches from U.S. PST catch areas are allocated among individual populations on the basis of the location of the fisheries and the relative abundance of the populations believed to contribute to each catch area.

Implicit in this methodology is the assumption that populations contribute to fisheries in direct proportion to their run size. However, shifts in the timing and migratory pathways of returning populations can substantially alter their contribution rate to preterminal fisheries. Because the Fraser River typically produces many more pink salmon than Puget Sound, this system of run reconstruction inaccurately estimates fishery exploitation rates on individual populations, especially for smaller populations. For these reasons, spawning escapement estimates are the most reliable estimates of population abundance, although they also have inaccuracies and reflect abundance only after the populations have been subjected to variable domestic exploitation and foreign interception rates.

Fishery landings of pink salmon are summarized in the Northwest Indian Fisheries Commission (NWIFC) run reconstruction database (Big Eagle & Assoc. and LGL Ltd. 1995). Run reconstruction attributes catches to stream of origin on the basis of geographic location and assumed migration pathways, but the process is an approximation at best and can provide only reasonably accurate estimates for individual populations. Nevertheless, estimates of Puget Sound exploitation rates for individual populations can be constructed from these data.

The most comprehensive attempt to attribute historical harvest to area of origin was made by Canadian Department of Fisheries and Oceans (CDFO) biologists who reconstructed estimates of landings from many sources using a variety of methods and synthesized a time series of harvest for the United States that spans the period from 1889 through 1981 (Shepard et al. 1985). They also estimated the harvest of U.S. (excluding Alaska) pink salmon from U.S. landings by adding in Canadian interceptions of U.S. salmon and subtracting U.S.

[29]J. Woodey, Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, B.C. V6E 1B5. Pers. commun., March 1995.

[30]B. White, Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, B.C. V6E 1B5. Pers. commun., February 1996.

interceptions of Canadian salmon. Since there is practically no domestic production of pink salmon outside of Puget Sound, these landings can be attributed to Puget Sound production. However, the partitioning of U.S. and British Columbia landings by country of origin requires a number of assumptions and is therefore imprecise. It is possible to calculate exploitation rates on Puget Sound pink salmon by dividing catch by catch plus escapement for the entire Puget Sound for the years in which both estimates are available. These estimated exploitation rates show an increasing trend with a low of about 35% in 1969 to a high of about 90% in 1981, but the accuracy of these estimates is questionable.

In Puget Sound, most spawning escapement estimates have been made with a few standard methods (see Vernon et al. 1964, Hourston et al. 1965). In the early 1960s an intensive effort was made to estimate the size of pink salmon runs in Puget Sound. Pink salmon were captured near the mouths of rivers and marked with external tags. Spawning grounds were surveyed and spawners were sampled throughout the river systems; effort was concentrated in areas of heaviest spawning. The spawner distribution was used to establish index areas. Carcasses were examined for tags, and Petersen mark-recapture estimates (Ricker 1958) of the total numbers of spawners were made. The Petersen estimate simply expands the number of tags applied to fish by the ratio of unmarked to marked fish observed in the carcass surveys to estimate the number of unmarked fish in the spawning run (Caughley 1977). This procedure assumes that the marked fish are randomly distributed in the spawning population, that they have the same survival rate as unmarked fish or that spawners have an equal probability of being in the sample, that no tags are lost, and that all marked fish encountered in the carcass surveys are recognized.

Violation of these assumptions reduces the accuracy of estimates and tends to bias the estimates upward. Attempts were made by WDF to reduce biases due to mortality of tagged fish and tag loss by rounding down the Petersen estimates (D. Hendrick[31]; see Vernon et al. 1964, Hourston et al. 1965). These Petersen estimates of total spawning escapement are the best estimates available for Puget Sound, and they became the base-year data for subsequent escapement estimates (Johnson et al. 1968, J. Ames[32]). In years following the Petersen estimates, spawning escapement has typically been estimated by multiplying the base-year spawning escapements by the ratio of counts of total live plus dead fish observed at the peak of the run (peak counts) in index reaches to peak counts in the base years. Historical estimates for northern Puget Sound rivers were usually generated by comparing the total number of carcasses counted in index areas to the total number of carcasses in the same areas

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[31]D. Hendrick, Washington Department of Fish and Wildlife, 333 E. Blackburn Rd., Mount Vernon, WA 98273. Pers. commun., April 1995.

[32]J. Ames, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., December 1994.

during the tagging studies. (Except for the Nooksack River, consistent live counts were not made during the tagging years; D. Hendrick[33]).

Since the mid-1970s, area-under-the-curve (AUC) estimates have been used instead of peak counts to scale the base-year Petersen estimates (Ames 1984). These estimates are currently compared for the Nooksack and Stillaguamish Rivers (D. Hendrick[34]). These AUC estimates are made from repeated surveys of the spawning grounds; the sequential counts are plotted against time and used to generate an escapement curve. The area under the curve is calculated to provide an estimate of the number of fish-days composing the spawning run in an index reach.

Computed statistics--To represent current run size or escapement where recent data were available, we have computed the geometric mean of the most recent 5 years reported (or fewer years if the data series is shorter than 5 years). We tried to use only estimates that reflect the total abundance for an entire river basin or tributary, and avoided index counts or dam counts that represent only a small portion of available habitat.

As an indication of overall trend in pink salmon populations in individual streams, we calculated average (over the available data series) percent annual change in adult spawner indices within each river basin. Trends were calculated as the slope (a) of the regression of $\log_e$(abundance) against years corresponding to the biological model $N(t) = be^{at}$, where $N(t)$ is population size in year t, b is a scalar coefficient, and e is the base of the natural logarithm. Slopes significantly different from zero ($P < 0.05$) were noted. The regressions provided direct estimates of mean instantaneous rates of population change (a); these values were subsequently converted to percent annual change, calculated as $100(e^a - 1)$. No attempt was made to account for the influence of hatchery produced fish on these estimates, so the estimated trends included any supplementation effect of hatchery fish.

In reviewing the status of individual ESUs of pink salmon in Washington and southern British Columbia, we considered the risks posed by artificial propagation to be less important than other risk factors, such as habitat degradation, indicating declines in abundance. This factor was a consideration in the BRT's conclusions that the ESUs for pink salmon are not at risk of extinction or endangerment. However, the BRT's conclusions on this issue should be regarded as preliminary because information about the degree of interactions that actually occur between hatchery and natural fish is still incomplete.

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[33]D. Hendrick, Washington Department of Fish and Wildlife, 333 E. Blackburn Rd., Mount Vernon, WA 98273. Pers. commun., April 1995.

[34]D. Hendrick, Washington Department of Fish and Wildlife, 333 E. Blackburn Rd., Mount Vernon, WA 98273. Pers. commun., April 1995.

Analysis of Extinction Risk by ESU

Several data series of pink salmon spawner abundance in northwestern Washington exist, but the ultimate sources for all quantitative estimates of spawning escapements are WDFW for data from Washington and CDFO for data from British Columbia. These data have been compiled in an electronic database and submitted to the ESA administrative record (Big Eagle & Assoc. and LGL Ltd. 1995). These data are summarized for even- and odd-year pink salmon in Figures 18-20. Trends and recent averages for spawning escapements of even- and odd-year pink salmon populations in Washington and British Columbia are given in Tables 8 and 9. Additional information on individual pink salmon streams is summarized below.

Even-year ESU

Snohomish River--There are anecdotal and sporadic accounts of even-year runs for some northern Puget Sound rivers (D. Hendrick[35], W. Waknitz[36]), but the only river for which an even-year population has been documented is the Snohomish River (WDF et al. 1993). The run sizes were estimated by aerial counts of redds, and these estimates were used to scale Snohomish River base-year estimates from odd-year runs. This run has been documented every even year since 1980, but no run-size estimate was made in 1982. The distribution of spawning is thought to be far more restricted for even-year pink salmon than for odd-year pink salmon, with most spawning activity occurring in the mainstem Snohomish River. Scattered redds have been observed in the Skykomish River as far upstream as Sultan. In general, this run has been increasing since 1980. Estimated escapement for 1994 was approximately 1,600 fish, which is less than 1990 and 1992 estimates but greater than those for 1986 and 1988. A few adults are occasionally reported in even years in the Nooksack, Stillaguamish, and Skagit Rivers, but the numbers are very small, and surveys are not conducted in these systems in even years.

British Columbia--All of the Canadian even-year populations for which we received escapement estimates are located in rivers draining into the northern Strait of Georgia or Johnstone Strait. Additional populations may occur on the west coast of Vancouver Island as far south as the Strait of Juan de Fuca (Aro and Shepard 1967), but if so these populations are probably very small.

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[35]D. Hendrick, Washington Department of Fish and Wildlife, 333 E. Blackburn Rd., Mount Vernon, WA 98273. Pers. commun., January 1995.

[36]W. Waknitz, NMFS Northwest Fisheries Science Center. Unpubl. observation.

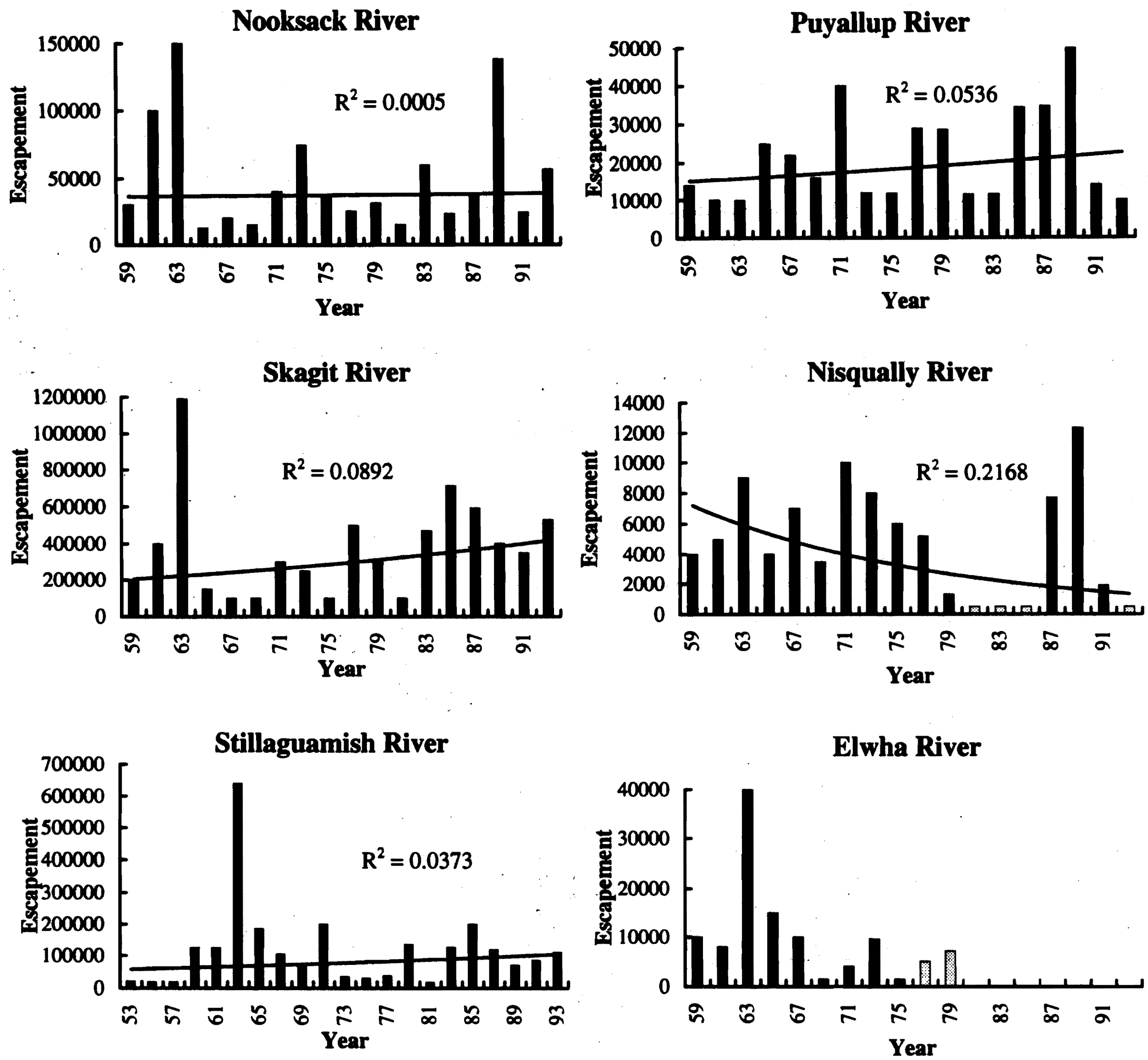

Figure 18. Spawning escapements for odd- and even-year pink salmon populations in Washington. For each population, an exponential trend line is fitted to the spawning escapements (see Tables 8 and 9 for statistical significance of trend estimates). All populations are odd-year except for Snohomish River pink salmon. In the Nisqually River from 1981 to 1985 and in 1993, escapements were not estimated and a value of 500 was assigned for each of these years for run reconstruction. Escapements in the Elwha River in 1977 and 1979 were assumed to be 14.25% of the Dungeness River escapement (see text for discussion).

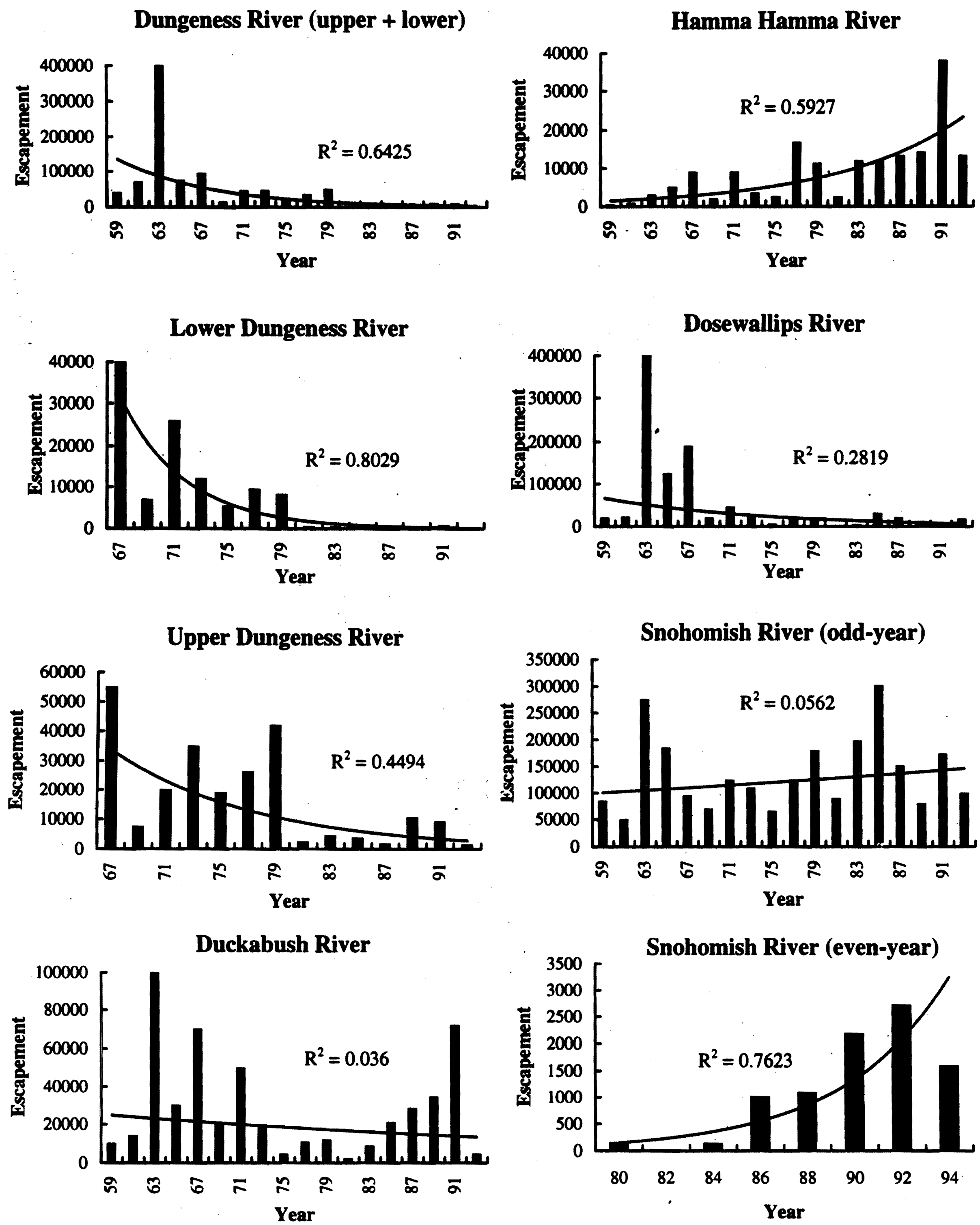

Figure 18. Continued.

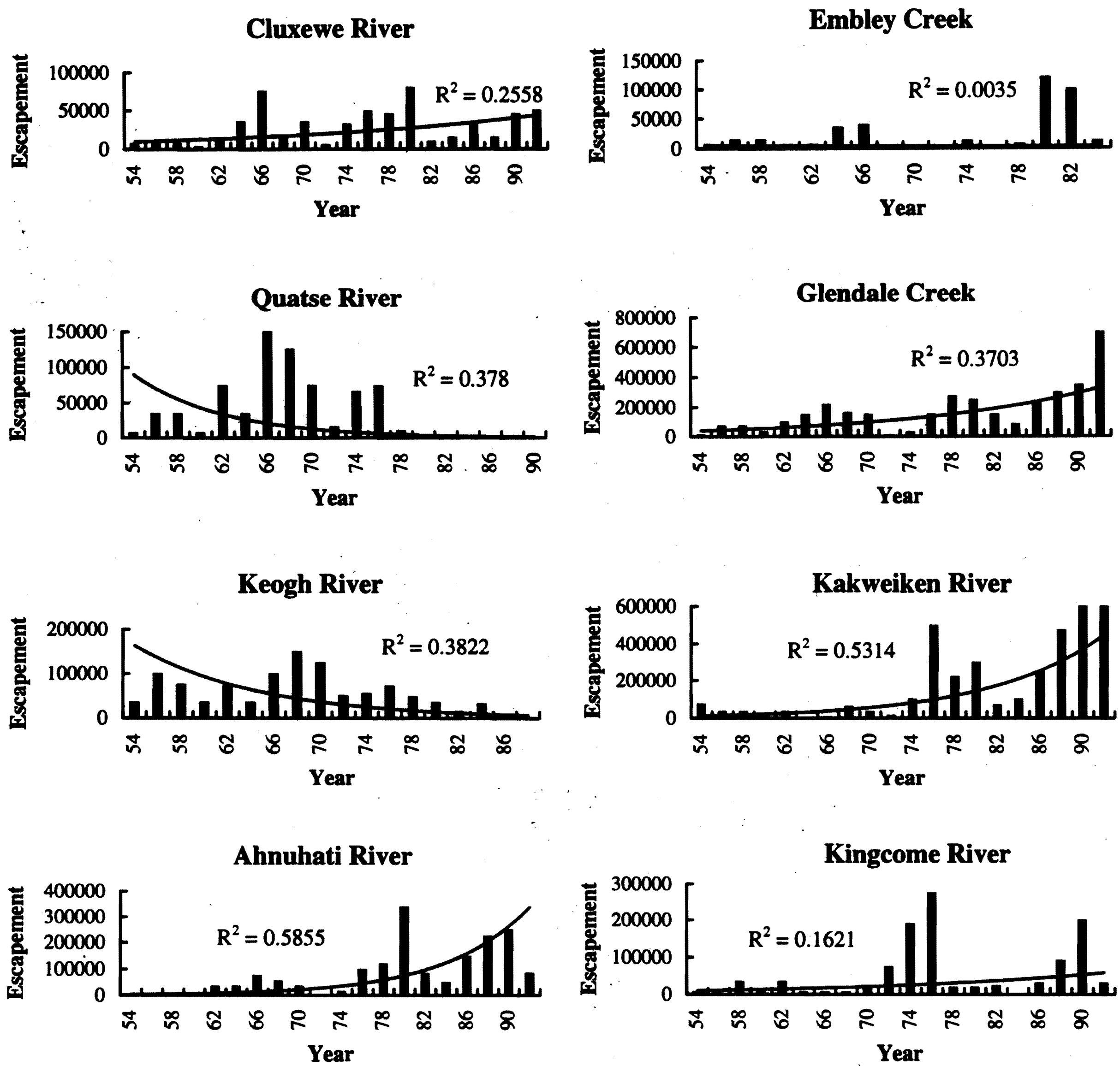

Figure 19. Spawning escapements for selected even-year pink salmon populations in British Columbia. For each population, an exponential trend line is fitted to the spawning escapement (see Table 8 for statistical significance of trend estimates).

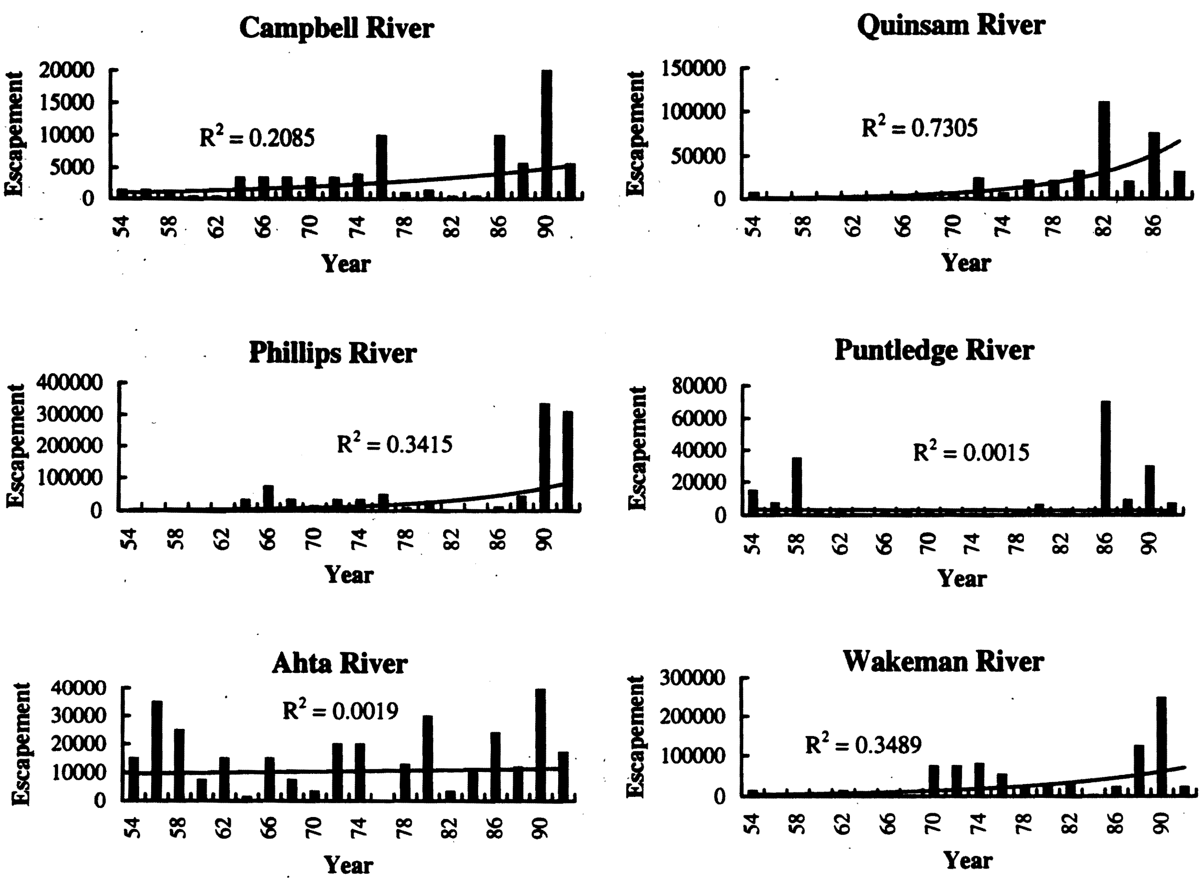

Figure 19. Continued.

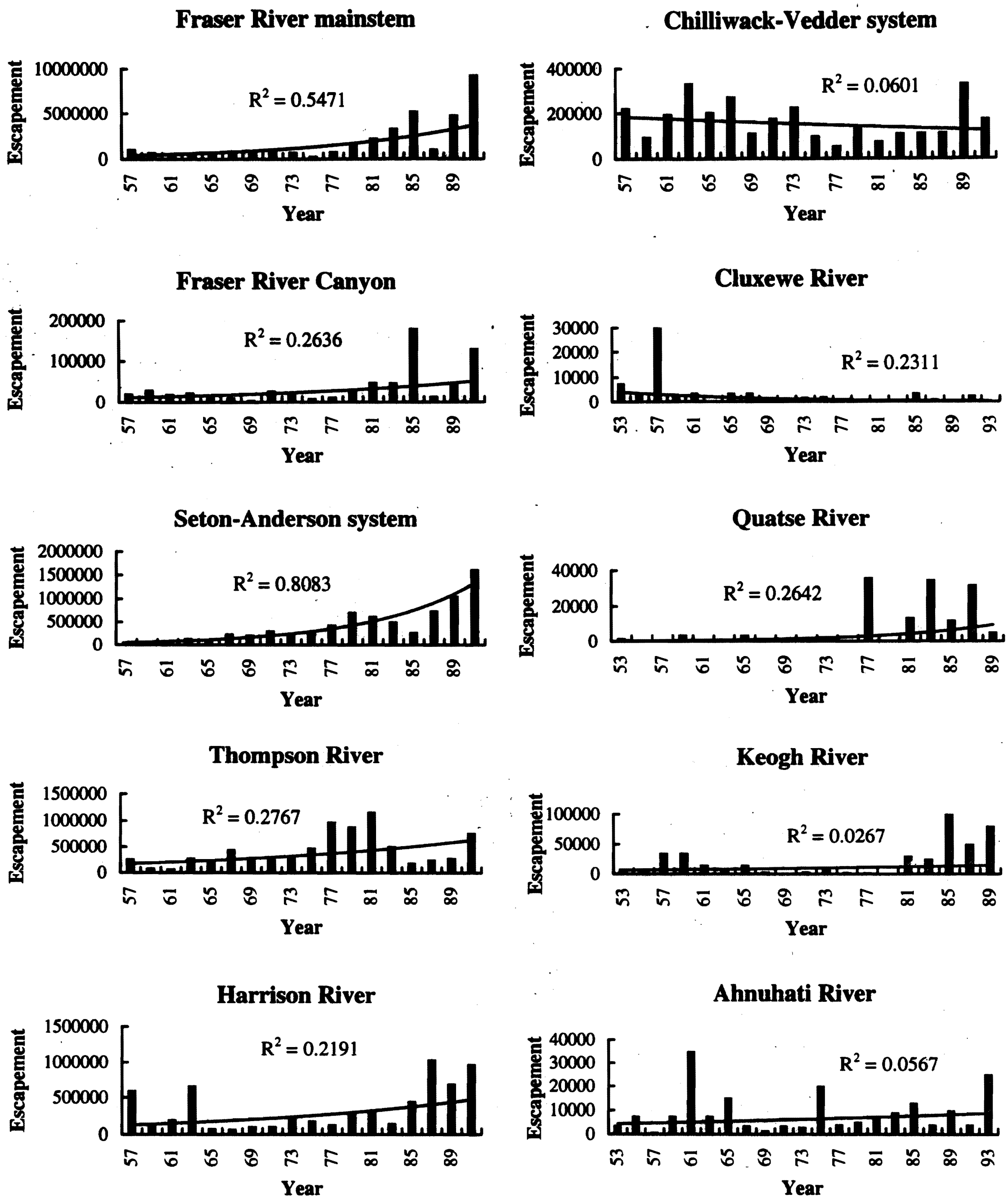

Figure 20. Spawning escapements for selected odd-year pink salmon populations in British Columbia. For each population, an exponential trend line is fitted to the spawning escapement (see Table 9 for statistical significance of trend estimates).

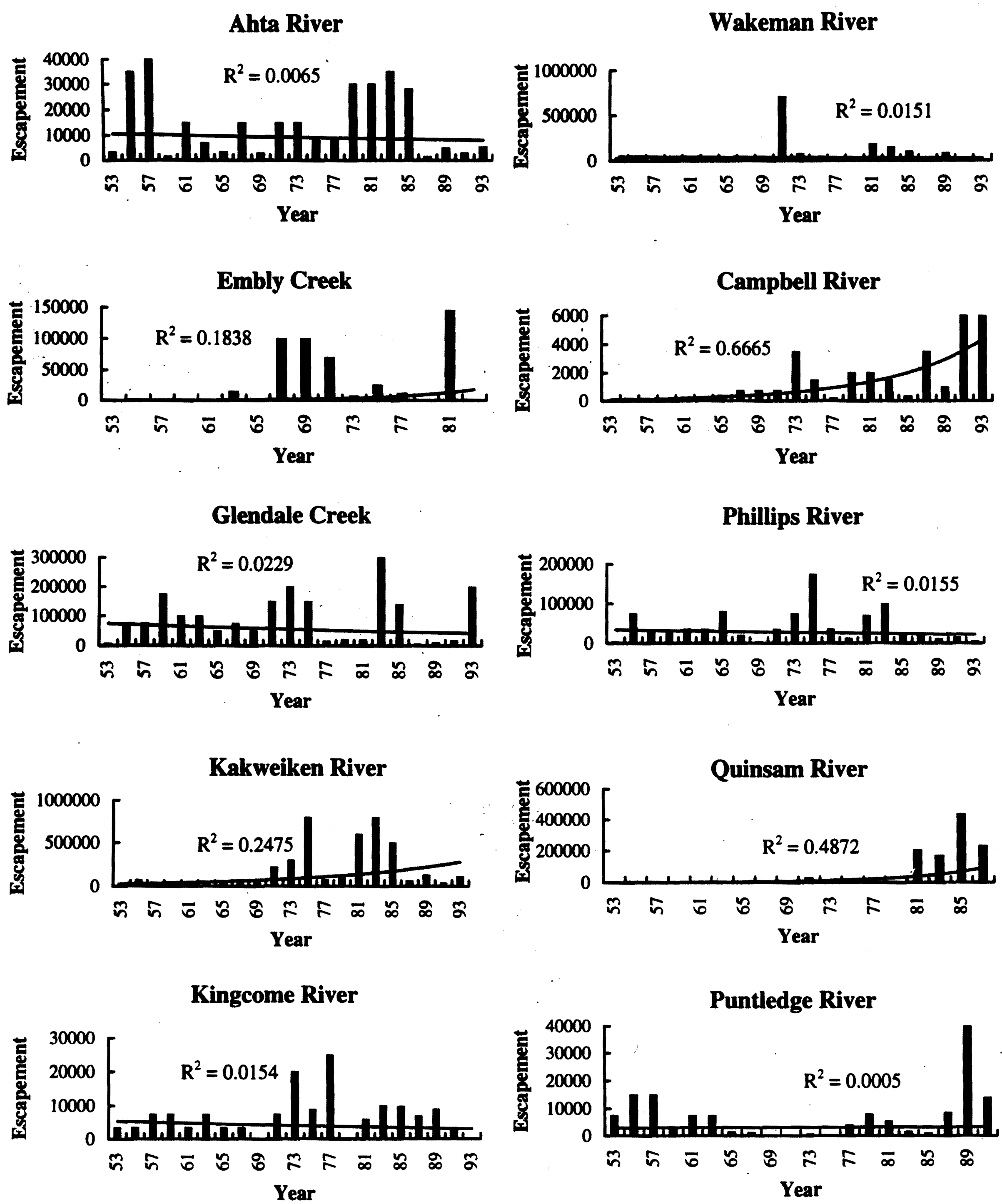

Figure 20. Continued.

Table 8. Average spawning escapement estimates and trends for even-year pink salmon populations in Washington and British Columbia. Average escapements are geometric means calculated from the five most recent spawning escapement estimates. For each system, annual percentage change is calculated for the periods shown in Figures 18-20. See text for further explanation.

Population	Production	Average escapement	Annual % change
		Washington	
Snohomish	natural	1,604	+25.6
		British Columbia	
Cluxewe	natural	28,163	+3.3
Quatse	natural	1,316	-14.8*
Keogh	natural	1,961	-11.3*
Ahnuhati	natural	129,310	+8.5*
Ahta	natural	18,161	+2.2
Embley Creek	natural	13,000	+0.6
Kingcome	natural	33,066	+3.0
Wakeman	natural	37,279	+8.7*
Phillips	natural	40,735	+10.0*
Campbell	mixed	5,021	+5.3*
Glendale Creek	mixed	272,385	+5.1*
Kakweiken	mixed	335,882	+13.2*
Quinsam	mixed	36,110	+16.4*
Puntledge	hatchery	5,847	+1.9

* Denotes trends that differ significantly ($P < 0.05$) from zero.

Table 9. Average spawning escapement estimates and trends for odd-year pink salmon populations in Washington and British Columbia. Average escapements are geometric means calculated from the five most recent spawning escapement estimates. The annual percentage change, calculated for the periods shown in Figures 18-20, includes the effect of the unusually high odd-year escapements observed in 1963 in Washington. See text for further explanation.

Population	Production[a]	Average escapement	Annual % change
		Washington	
Nooksack	natural	43,573	+0.2
Skagit	natural	500,125	+2.1
Stillaguamish	natural	109,650	+1.5
Snohomish	natural	144,958	+1.1
Puyallup	natural	24,142	+1.2
Nisqually	natural	2,141	-0.5
Dosewallips	natural	16,024	-6.3
Duckabush	natural	23,272	-1.2
Hamma Hamma	natural	17,651	+7.3
South Hood Canal	natural	181	+0.2
Upper Dungeness	natural	3,981	-8.6
Lower Dungeness	natural	340	-17.0[b]
Elwha	natural	53	--[c]
Hood Canal Hatchery	hatchery	2713	+0.4
		British Columbia	
Lower Fraser	natural	3,828,815	+6.6[b]
Fraser Canyon	natural	59,390	+4.4[b]
Thompson	natural	352,460	+3.8[b]
Cluxewe	natural	1,223	-6.6[b]
Quatse	natural	16,101	+12.9[b]
Keogh	natural	56,234	+2.6
Ahnuhati	natural	7,153	+1.8
Ahta	natural	7,391	-0.7
Embley Creek	natural	500	+12.7
Kingcome	natural	7,145	-1.4
Wakeman	natural	36,651	-1.3
Phillips	natural	23,571	-1.1
Seton-Anderson	mixed	705,877	+10.0[b]
Harrison	mixed	540,953	+3.9
Chilliwack-Vedder	mixed	150,291	-1.2
Glendale Creek	mixed	33,798	-1.4
Kakweiken	mixed	163,260	+6.0[b]
Campbell	mixed	1,616	+10.1[b]
Quinsam	mixed	258,749	+15.2[b]
Puntledge	hatchery	6,069	+0.3

[a] According to the corresponding management agency.
[b] Denotes trends that differ significantly ($P < 0.05$) from zero.
[c] Exponential trend cannot be calculated when recent spawning escapements are zero.

Odd-year ESU

Nooksack River--Because the Nooksack River is fed by glacial meltwater and the fish cannot be counted reliably in the main stem because of the high turbidity, escapement estimates for the Nooksack River are the least reliable in northern Puget Sound. Data collection began in 1959, and Petersen estimates were made in 1959, 1961, and 1963. These base-year estimates have subsequently been scaled by peak counts and AUC estimates. In the base years, most fish spawned in the main stem. This may still be the case, as tributary spawning alone cannot account for total production from the system, but only clear water tributaries are surveyed due to the difficulty observing spawners in the main stem. Because these tributaries contain a relatively small and variable fraction of the spawning escapement, the escapement estimates have potentially large errors.

Skagit River--Skagit River run sizes were estimated in the main stem by comparing total carcasses in mainstem index areas to the number of carcasses sampled during tagging to construct the Peterson estimates in the base years 1959 through 1963. AUC estimates were used in tributaries. Since the base years, the distribution of spawners has shifted somewhat. There is presently more spawning in upper reaches of the river than occurred in the base years, so recent runs may be underestimated. However, this bias should be minimal because tagging-year data are available for the entire main stem and because WDFW currently surveys nearly 65 km of the river's length (D. Hendrick[37]).

Stillaguamish River--Escapement estimates are again based on AUC estimates of observed live spawners. Base years are 1959 through 1965, with additional Petersen estimates from 1967 and 1987. In the original base years the majority of fish spawned in the North Fork Stillaguamish River. This remained the case until 1987, when the Washington Department of Fisheries (WDF) conducted a mark-recapture study on the Stillaguamish River (D. Hendrick[38]). Drought conditions in that year limited spawning in the North Fork, and substantial numbers of fish spawned in the South Fork. WDF biologists did not realize where the fish were until after the peak of spawning occurred, so their use of the 1987 AUC estimate for the South Fork in scaling subsequent escapements is questionable. Since 1989, the run in the North Fork has been rebuilding, but the South Fork still has the majority of spawning activity.

Snohomish River--Runs were estimated by AUC scaling of base-year Petersen estimates for 1959 through 1963 and 1967. Index reaches were in the Snohomish River and the Skykomish River, with a few observational surveys made in the Snoqualmie River. The

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[37]D. Hendrick, Washington Department of Fish and Wildlife, 333 E. Blackburn Rd., Mount Vernon, WA 98273. Pers. commun., January 1995.

[38]D. Hendrick, Washington Department of Fish and Wildlife, 333 E. Blackburn Rd., Mount Vernon, WA 98273. Pers. commun., January 1995.

portion of the run using the Snoqualmie River is unknown but may be increasing. In some years, considerable numbers of spawners have been reported in the Tolt River, but the run is inconsistent and is therefore believed to be just a component of the Snoqualmie River run. Spawning distribution has expanded since the base years. There is presently more spawning in intertidal areas, the Snoqualmie River, and in upper reaches of the Skykomish River and its tributaries (D. Hendrick[39]). Because of this shift, the index reaches may contain a smaller fraction of the escapement than they did in the base years, and recent estimates may be biased downward.

Lake Washington--There is no evidence of sustained runs of pink salmon in the Lake Washington watershed.

Southern Puget Sound and Hood Canal--Recent spawning escapement estimates for southern Puget Sound and Hood Canal are based on AUC estimates of total live spawners. Data series are of variable length, and early estimates were the sum of live and dead fish observed during the peak of the spawning run. Except for the Nisqually River, which is surveyed by Nisqually tribal biologists, spawning ground surveys are generally conducted by WDFW biologists, and the AUC estimates are made by WDFW from WDFW and tribal data. Data are generally reliable, except for those from surveys in the Nisqually River for 1981-85 and 1993 (see below).

The Nisqually River is glacially influenced with a few clear water tributaries, and consequently has presented some special problems in estimating escapement. Escapements have been estimated with several methods. Before 1981, escapements were estimated from visual surveys in the main stem and tributaries. From 1987 to 1991, estimates were made from a combination of mark-recapture studies, visual surveys in tributaries, and fishery catches. Estimates from the tributary surveys are expanded, somewhat arbitrarily, to account for mainstem spawning. In 1981, 1983, and 1985, conditions were unfavorable in the tributaries and the vast majority of fish spawned in the main stem. The number of spawners in the main stem was unknown, but very few fish were seen in the tributary surveys. Peak counts in those years ranged from three to nine fish. In 1993, no pink salmon data were recorded during stream surveys. Thus, for odd years from 1981 to 1985 and for 1993, an escapement of 500 was assigned as a placeholder for run reconstruction (J. Ames[40], J. Uehara[41]). For all four of these years, actual spawning escapement is unknown and should be considered missing values.

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[39]D. Hendrick, Washington Department of Fish and Wildlife, 333 E. Blackburn Rd., Mount Vernon, WA 98273. Pers. commun., January 1995.

[40]J. Ames, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., April 1995.

[41]J. Uehara, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., April 1995.

Dungeness River--The Dungeness River supports two different populations of pink salmon: an early run that enters the river in July and August and ascends to areas above RKm 16, and a late run that enters the river in late August and September and spawns below RKm 5. Until 1981, a hatchery rack at about RKm 16 was used to enumerate the early run. The lower (late) run was not surveyed regularly and was assumed to be a fixed proportion of the early run in some years. When the rack was removed in 1981, WDF had to change their estimation method, a change that coincided with the effects of a major winter flood in 1980 on the incubating 1979 brood. WDFW biologists do not believe that the visual survey method significantly underestimates the run size in this case, and it seems unlikely that underestimation could fully account for the observed drop in run size. Survey conditions are consistently good in the Dungeness River when spawner counts are made (J. Ames[42]).

Since 1981, the spawning ground surveys have attempted to estimate the entire run by AUC estimates. Runs were relatively stable until 1981, when 1979-brood fish affected by the 1980 winter flood returned[43]. Both runs have been depressed since that time, with the lower run exhibiting a continued decline. Both runs on the Dungeness River exhibit statistically significant downward trends in spawner abundance.

Elwha River--Data extend back to 1959 and tend to become less reliable in recent years. Estimates in 1959, 1961, and 1963 were based on visual surveys made by WDF as part of an extensive marking program at that time (J. Ames[44]). In 1975, the escapement estimate of 1,500 was based on a single float survey in which it was estimated that 300 spawners were seen. In 1977 and 1979, the Elwha River was not surveyed, but its escapement was estimated to be 14.25% of the total escapement to the Dungeness River. This was based on the average ratio of escapements to the two rivers in the preceding five spawning runs. As did the Dungeness River, the Elwha River experienced severe flooding in the winter of 1979-80. Since 1981, the Elwha River has been surveyed every run year with 5 to 18 surveys conducted each year. These surveys, which were made primarily for chinook salmon, incorporated multiple breakout counts for different river sections. More intensive surveys in 1991 and 1993 failed to find any pink salmon in the Elwha River. As noted earlier in this report, WDFW's management biologists for this area believe the Elwha River run of pink salmon to be extinct.

British Columbia--Data on run sizes for Fraser River populations and populations in the Strait of Georgia and Johnstone Strait have been received from CDFO (Big Eagle &

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[42]J. Ames, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., April 1995.

[43]A large slide on Gold Creek, a tributary of the upper Dungeness River, during the winter of 1968-69 apparently reduced productivity of the upper Dungeness River population during the early 1970s (Johnson 1973).

[44]J. Ames, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., January 1995.

Assoc. and LGL Ltd. 1995). Spawning escapements were estimated with a variety of methods, and managers have been required to provide escapement numbers regardless of the quality of the estimates (Big Eagle & Assoc. and LGL Ltd. 1995). In addition, escapement data from western Vancouver Island may be collected only incidentally during surveys for other species. For these reasons, several escapement estimates for British Columbia populations are of questionable quality. Nevertheless, pink salmon escapement data collected over the last several years by Canadian Department of Fisheries and Oceans staff suggest that western Vancouver Island escapements have declined significantly since the 1970s. Current escapement levels on the west coast of the island are typically small, that is, a hundred to a few thousand adults. Indirect evidence points to declining trends in some populations along the southwestern coast of Vancouver Island, but this evidence is weak because the escapement data are not robust (W. Luedke[45]). Tables 8 and 9 summarize the escapement data that Canadian biologists felt were the most reliable for runs in central and southern British Columbia.

Conclusions

There is no evidence of strong or sustained recent declines in abundance for most pink salmon populations in Washington and southern British Columbia. However, both odd-year pink salmon populations in the Dungeness River are depressed, and the lower river population shows a strong declining trend. Although this latter population also declined substantially from 1973 to 1979, major flooding during the winter of 1979-80 appears to have been an important factor leading to its current, severely depressed state. This flooding in fact appears to have influenced all the Washington odd-year pink salmon populations along the Strait of Juan de Fuca, including the Elwha River population. The single U.S. population of even-year pink salmon in the Snohomish River is small, and although it has been increasing in size over the last decade, the estimated 1994 escapement was a substantial drop over that in 1992.

In addition to abundance, two ecological factors relating to the status of pink salmon populations were of concern to the BRT: low-water conditions upon river entry and spawning, which can limit spawner distribution to suboptimal center-channel areas; and subsequent high-water conditions, which can erode the quality of spawning and incubation habitat and may adversely affect embryonic development. These factors may have been exacerbated by water withdrawals for irrigation and by structures erected for flood control, particularly on the lower Dungeness River (Lichatowich 1993, K. Lutz[46]). In addition, flooding can reduce substrate

[45]W. Luedke, Canadian Department of Fisheries and Oceans, Fisheries Branch, South Coast Division, 3225 Stephenson Point Road, Nanaimo, B.C. V9T 1K3. Pers. commun., March 1995.

[46]K. Lutz, Northwest Indian Fisheries Commission, 6740 Martin Way E., Olympia, WA 98516. Pers. commun., April 1995.

stability and permeability and subsequent pink salmon productivity (Wickett 1962). Extensive severe flooding in several Puget Sound rivers caused by heavy rains in winter 1995-96 may have substantially reduced the productivity of the 1995 brood in these systems through the mortality of embryos and hatchlings.

Other possible threats to pink salmon in the Puget Sound region include predation on juvenile pink salmon by wild (Hiss 1994) and hatchery (Hiss 1995) coho salmon, and, perhaps in some locations, predation by marine mammals (Knudsen et al. 1990, J. Ames[47]). In addition, the population dynamics of pink salmon are not well understood, and may be affected by intra- and interspecific interactions involving pink and chum salmon (Gallagher 1979, Smoker 1984, Heard 1991). Consequently, the possibility that hatchery production of pink and chum salmon can limit the viability of some Washington populations of pink salmon cannot be excluded.

Finally, oceanic conditions may also affect pink salmon abundance (Davidson and Vaughan 1941; Mysak et al. 1982; Blackbourn 1985, 1990; Mysak 1986; Heard 1989). The widespread declines observed in pink salmon body size (Ricker et al. 1978, Ricker 1981, Marshall and Quinn 1988, Ricker 1989; Table 3) may have resulted from increased salmon density, reduced ocean productivity, or directional selection on body size in both net and troll fisheries. From analysis of the southeastern Alaska pink salmon fishery between 1895 and 1940, Davidson and Vaughan (1941) identified an inverse relationship between the abundance (measured as total pack) of these fish and adult body size, and they suggested that this relationship resulted from greater competition for marine prey. Small adult body size is a cause for concern because it limits reproductive potential (Skud 1973), and there is some evidence for a strong genetic component to body size (Smoker et al. 1994). Growth at sea or the subsequent body sizes of adults may also affect the timing of their spawning migration (Davidson and Vaughan 1941), which in turn may affect fry recruitment. Skud (1973) suggested that the interaction between these factors tends to yield higher fry survival in years when spawners are larger and spawn earlier than in years when spawners are smaller and spawn later. Conclusions for each of the proposed ESUs are summarized below.

Even-year ESU

Because it is unclear whether populations other than that in the Snohomish River are in the even-year pink salmon ESU, the BRT first considered the status of this ESU under the assumption that it included only the single U.S. population. Based on available information, which shows a relatively small population with a generally increasing trend in abundance in recent years, the BRT concluded that this ESU is not at risk of imminent extinction or endangerment. Because even-year populations in British Columbia are generally stable or increasing and are apparently not at low levels compared to historical abundance, the BRT also

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[47]J. Ames, Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501. Pers. commun., October 1994.

concluded that an ESU that included populations in British Columbia would not currently be at risk of extinction or endangerment.

However, three factors prompted considerable concern among BRT members about risks the Snohomish River population might face in the near future: 1) it may be strongly isolated from all other even-year populations; 2) although the population has generally been increasing in recent years, it remains at low abundance; and 3) the invariant age structure in pink salmon, coupled with considerable interannual variability in abundance, increases risks faced by small, isolated populations. Clearly, these concerns would be greatest for an ESU that included only the single U.S. population; however, it is also likely that the Snohomish River population would be considered an important part of a larger ESU that contained populations from British Columbia. Therefore, the BRT concluded that the Snohomish River even-year pink salmon population should be closely monitored so that if any factors arise that substantially increase risk faced by this population, they can be identified at an early stage.

Odd-year ESU

Most populations in the odd-year pink salmon ESU appear to be healthy, and overall abundance appears to be close to historical levels. The two most distinctive Puget Sound populations (from the Nooksack and Nisqually Rivers) both show nonsignificant trends in recent abundance (Nooksack River slightly increasing, Nisqually River slightly decreasing), and no other factors were found that would suggest that either of these populations is at immediate risk. The BRT therefore concluded that the ESU for odd-year pink salmon as a whole is not at significant risk of becoming extinct or endangered.

However, two populations on the Strait of Juan de Fuca are clearly at risk, and an additional population (in the Elwha River) already appears to be extinct. These populations contribute substantially to the ecological and genetic diversity of the ESU, and the BRT expressed concern that further erosion of individual populations might result in future risk to a significant portion of the ESU as a whole.

The BRT also identified risk factors that should be monitored in the future. Some evidence exists for recent declines in body length of odd-year fish in Washington, which raises concern about the ability of natural populations (notably those in the Strait of Juan de Fuca) to recover naturally. The BRT was unable to review data on body size in odd-year British Columbia pink salmon since the studies by Ricker et al. (1978) and Ricker (1989) to ascertain whether body size in these populations has been declining to levels similar to those observed in Washington fish in recent years. However, the decline in body length of odd-year Washington pink salmon indicated by the data in Table 3 is qualitatively similar to a decline in length observed in pink salmon returning to Auke Creek, Alaska over the last 20 years

(W. Smoker[48]). Data estimated from catches of southeastern Alaska pink salmon suggest similarly declining trends over an even longer period (Marshall and Quinn 1988). Collectively, these patterns suggest that pink salmon from populations over wide geographic areas have been experiencing conditions at sea that restrict adult body size and, consequently, reproductive potential.

[48]W. Smoker, Juneau Center School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 11120 Glacier Hwy., Juneau, AK 99801. Pers. commun., March 1995.

CITATIONS

Alexandersdottir, M., and O. A. Mathisen. 1983. Life history of pink salmon (*Oncorhynchus gorbuscha*) and implications for management. Univ. Wash., Fish. Res. Inst. FRI-UW-8313, 72 p.

Allen, M. J., and G. B. Smith. 1988. Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 66, 151 p.

Allendorf, F. W., and N. Ryman. 1987. Genetic management of hatchery stocks. *In* N. Ryman and F. Utter (editors), Population genetics & fishery management, p. 141-159. Univ. Washington Press, Seattle.

Altukhov, Yu. P., and E. A. Salmenkova. 1994. Straying intensity and genetic differentation in salmon populations. Aquacult. Fish. Manage. 25(Suppl. 2):99-120.

Altukhov, Yu. P., E. A. Salmenkova, V. T. Omel'chenko, and V. N. Efanov. 1983. Genetic differentiation and population structure of pink salmon of the Sakhalin-Kurile region. Biol. Morya. 2:46-51. (Engl. Transl. Sov. J. Mar. Biol. 9:98-102.)

Ames, J. 1984. Puget Sound chum salmon escapement estimates using spawner curve methodology. Can. Tech. Rep. Fish Aquat. Sci. 1326:133-148.

Anas, R. E. 1959. Three-year-old pink salmon. J. Fish. Res. Board Can. 16:91-94.

Aro, K. V. 1979. Transfers of eggs and young of Pacific salmon within British Columbia. Can. Dep. Fish. Oceans, Fish & Mar. Serv. Tech. Rep. 861, 147 p.

Aro, K. V., and M. P. Shepard. 1967. Salmon of the North Pacific Ocean--Part IV. Spawning populations of North Pacific salmon. 5. Pacific salmon in Canada. Int. North Pac. Fish. Comm. Bull. 23:225-327.

Aspinwall, N. 1974. Genetic analysis of North American populations of the pink salmon, *Oncorhynchus gorbuscha*, possible evidence for the neutral mutation-random drift hypothesis. Evolution 28:295-305.

Atkinson, C. E. 1956. Review of the pink salmon fishery of Puget Sound and the Gulf of Georgia. U.S. Dep. Interior, Fish Wildl. Serv., Pacific Salmon Investigations, Seattle, WA, 33 p.

Atkinson, C. E., J. H. Rose, and T. O. Duncan. 1967. Salmon of the North Pacific Ocean--Part IV. Spawning populations of North Pacific salmon. 4. Pacific salmon in the United States. Int. North Pac. Fish. Comm. Bull. 23:43-223.

Ayers, R. J. 1955. Pink salmon caught in Necanicum River. Oreg. Fish Comm. Res. Briefs 6(2):20.

Bailey, J. E., B. L. Wing, and C. R. Mattson. 1975. Zooplankton abundance and feeding habits of fry of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *Oncorhynchus keta*, in Traitors Cove, Alaska, with speculations on the carrying capacity of the area. Fish. Bull., U.S. 73:846-861.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.

Bakun, A. 1975. Daily and weekly upwelling indices, west coast of North America, 1967-73. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-693, 114 p.

Basham, L., and L. Gilbreath. 1978. Unusual occurrence of pink salmon (*Oncorhynchus gorbuscha*) in the Snake River of southeastern Washington. Northw. Sci. 52:32-34.

Beacham, T. D. 1985. Meristic and morphometric variation in pink salmon (*Oncorhynchus gorbuscha*) in southern British Columbia and Puget Sound. Can. J. Zool. 63:366-372.

Beacham, T. D., and C. B. Murray. 1985. Variation in length and body depth of pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) in southern British Columbia. Can. J. Fish. Aquat. Sci. 42(2):312-319.

Beacham, T. D., and C. B. Murray. 1986. Comparative developmental biology of pink salmon, *Oncorhynchus gorbuscha*, in southern British Columbia. J. Fish Biol. 28:233-246.

Beacham, T. D., and C. B. Murray. 1993. Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). J. Fish Biol. 42:485-508.

Beacham, T. D., R. E. Withler, and A. P. Gould. 1985. Biochemical genetic stock identification of pink salmon (*Oncorhynchus gorbuscha*) in southern British Columbia and Puget Sound. Can. J. Fish. Aquat. Sci. 42:1474-1483.

Beacham, T. D., R. E. Withler, C. B. Murray, and L. W. Barner. 1988. Variation in body size, morphology, egg size, and biochemical genetics of pink salmon in British Columbia. Trans. Am. Fish. Soc. 117:109-126.

Beamish, R. J., and D. R. Bouillon. 1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. 50:1002-1016.

Big Eagle & Associates and LGL Ltd. 1995. Pink salmon catch, escapement and historical abundance data. Electronic database of pink salmon abundance, containing data from WDF et al. (1993), Northwest Indian Fisheries Commission run reconstruction, and Coordinated Information System (CIS) escapement data. Report to U.S. Department of Commerce, NOAA, NMFS, January 1995, 16 p. + Appendices. (Available from Environmental and Technical Services Division, National Marine Fisheries Service, 525 NE Oregon St., Portland, OR 97232.)

Bilton, H. T., and W. E. Ricker. 1965. Supplementary checks on the scales of pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*). J. Fish. Res. Board Can. 22:1477-1489.

Blackbourn, D. J. 1985. The "salinity" factor and the marine survival of Fraser River pinks and other stocks of salmon and trout. *In* B. G. Shepard (editor), Proceedings of the 1985 Northeast Pacific pink and chum salmon workshop, p. 67-75. Can. Dep. Fish. Oceans, Vancouver, B.C.

Blackbourn, D. J. 1990. Comparison of size and environmental data with the marine survival rates of some wild and enhanced stocks of pink and chum salmon in British Columbia and Washington State. *In* P. A. Knudsen (editor), Proceedings of the 14th Northeast Pacific pink and chum salmon workshop, p. 82-87. Wash. Dep. Fish., Olympia, WA.

Bonar, S. A., G. B. Pauley, and G. L. Thomas. 1989. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)--pink salmon. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.88).

Booth, D. B. 1987. Timing and processes of deglaciation along the southern margin of the Cordilleran ice sheet. *In* W. F. Ruddiman and H. E. Wright, Jr. (editors), North America and adjacent oceans during the last deglaciation. Geology of North America Series, Vol. K-3. Geological Society of America, Boulder, CO.

Brusca, R. C., and B. R. Wallerstein. 1979. Zoogeographic patterns of idoteid isopods in the Northeast Pacific, with a review of shallow water zoogeography of the area. Bull. Biol. Soc. Wash. 3:67-105.

Busby, P. J., O. W. Johnson, T. C. Wainwright, F. W. Waknitz, and R. S. Waples. 1993. Status review for Oregon's Illinois River winter steelhead. U.S. Dep. Commer., NOAA Tech. Memo. NMFS NWFSC-10, 85 p.

Campton, D. E. 1995. Genetic effects of hatchery fish on wild populations of Pacific salmon and steelhead: What do we really know? Am. Fish. Soc. Symp. 15:337-353.

Caughley, G. 1977. Analysis of vertebrate populations. Wiley, London, U.K., 234 p.

Caughley, G. 1994. Directions in conservation biology. J. Anim. Ecol. 63:215-244.

Cavalli-Sforza, L. L., and A. W. F. Edwards. 1967. Phylogenetic analysis: Models and estimation procedures. Evolution 21:550-570.

Cook, F. R. 1984. Introduction to Canadian amphibians and reptiles. National Museum of Natural Sciences, National Museums of Canada, Ottawa, 200 p.

Davidson, F. A. 1934. The homing instinct and age at maturity of pink salmon (*Oncorhynchus gorbuscha*). U.S. Bur. Fish., Bull. 48(15):27-39.

Davidson, F. A. 1935. The development of the secondary sexual characters in the pink salmon (*Oncorhynchus gorbuscha*). J. Morphol. 57(1):169-183.

Davidson, F. A., and E. Vaughan. 1941. Relation of population size to marine growth and time of spawning migration in the pink salmon (*Oncorhynchus gorbuscha*) of southeastern Alaska. J. Mar. Res. 4:231-246.

Davidson, F. A., E. Vaughan, S. J. Hutchinson, and A. L. Pritchard. 1943. Factors influencing the upstream migration of the pink salmon (*Oncorhynchus gorbuscha*). Ecology 24:149-168.

DeLacy, A. C., and F. Neave. 1948. Migration of pink salmon (*Oncorhynchus gorbuscha*) in southern British Columbia and Washington in 1945. Wash. Dep. Fish. Biol. Rep. 47A, 11 p.

Denman, K. L., D. L. Mackas, H. J. Freeland, M. J. Austin, and S. H. Hill. 1981. Persistent upwelling and mesoscale zones of high productivity off the west coast of Vancouver Island, Canada. *In* F. A. Richards (editor), Coastal upwelling, p. 514-521. Am. Geophys. Union, Washington, DC.

Ellis, C. H., and R. E. Noble. 1959. Even year-odd year pink salmon. Wash. Dep. Fish. Annu. Rep. 69 (1959):36-29.

Evermann, B. W., and H. W. Clark. 1931. A distributional list of the species of freshwater fishes known to occur in California. Calif. Dep. Fish Game Fish Bull. 35, 67 p.

Fagen, R., and W. W. Smoker. 1989. How large-capacity hatcheries can alter interannual variability of salmon production. Fish. Res. 8:1-11.

Farley, A. L. 1979. Atlas of British Columbia. Univ. British Columbia Press, Vancouver, 136 p.

Foster, R. W., C. Ragatell, and H. J. Fuss. 1981. Return of one-year-old pink salmon to a stream in Puget Sound. Prog. Fish-Cult. 43:31.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S.D.A. Forest Service General Tech. Rep. PNW-8, 417 p. (Available from Superintendent of Documents, U.S. Gov. Printing Office, Washington, DC 20402, Stock 0101-00329.)

Gall, G. A. E. 1987. Inbreeding. *In* N. Ryman and F. Utter (editors), Population genetics & fishery management, p. 47-87. Univ. Washington Press, Seattle.

Gallagher, A. F., Jr. 1979. An analysis of factors affecting brood year returns in the wild stocks of Puget Sound chum (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*). Master's Thesis, Univ. Washington, Seattle, 152 p.

Gharrett, A. J. 1985. Genetic interaction of Auke Creek Hatchery pink salmon with natural spawning in Auke Creek. Univ. Alaska, Juneau. Alaska Sea Grant Rep. No. 85-9. SFS UAJ8509, 40 p.

Gharrett, A. J., and W. W. Smoker. 1991. Two generations of hybrids between even- and odd-year pink salmon (*Oncorhynchus gorbuscha*): A test for outbreeding depression? Can. J. Fish. Aquat. Sci. 48:1744-1749.

Gharrett, A. J., and W. W. Smoker. 1993a. Genetic components in life history traits contribute to population structure. *In* J. G. Cloud and G. H. Thorgaard (editors), Genetic conservation of salmonid fishes, p. 197-202. Plenum Press, New York.

Gharrett, A. J., and W. W. Smoker. 1993b. A perspective on the adaptive importance of genetic infrastructure in salmon populations to ocean ranching in Alaska. Fish. Res. 18:45-58.

Gharrett, A. J., C. Smoot, A. J. McGregor, and P. B. Holmes. 1988. Genetic relationships of even-year northwestern Alaskan pink salmon. Trans. Am. Fish. Soc. 117:536-545.

Gilbert, C. H. 1914. Age at maturity of the Pacific coast salmon of the genus *Oncorhynchus*. U.S. Bur. Fish., Bull. 32 (1912):1-22.

Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: Processes of species extinction. *In* M. E. Soulé (editor), Conservation biology: The science of scarcity and diversity, p. 19-34. Sinauer Assoc., Sunderland, MA.

Glubokovskii, M. K., and L. A. Zhivotovskii. 1986. Population structure of pink salmon: System of fluctuating stocks. Sov. J. Mar. Biol. (Engl. Transl. Biol. Morya) 12(2):92-97.

Godfrey, H. 1959. Variations in annual average weights of British Columbia pink salmon, 1944-1958. J. Fish. Res. Board Can. 16:329-337.

Gorshkova, G. V. 1983. Comparative morphological characteristics of pink salmon of closely related generations in Utka River (west coast of Kamchatka). *In* Morphology, population structure, and problems of rational exploitation of salmonidae, p. 43-44. Naula, Leningrad. (In Russian, cited in Ivankov 1986.)

Gould, A. P., A. P. Stefanson, and L. Hop Wo. 1988. The 1978, 1980, 1982, and 1984 returns of even year pink salmon stocks to the Johnstone Strait study area. Can. Manuscr. Rep. Fish. Aquat. Sci. 1629:53 p.

Hall, C. A. 1964. Shallow-water marine climates and molluscan provinces. Ecology 45:226-234.

Hallock, R. J., and D. H. Fry, Jr. 1967. Five species of salmon, *Oncorhynchus*, in the Sacramento River, California. Calif. Fish Game 53(1):5-22.

Hard, J. J. 1995a. A quantitative genetic perspective on the conservation of intraspecific diversity. *In* J. L. Nielsen (editor), Evolution and the aquatic ecosystem: Defining unique units in population conservation, p. 304-326. Am. Fish. Soc. Symp. 17, Bethesda, MD.

Hard, J. J. 1995b. Genetic monitoring of life-history characters in salmon supplementation: Problems and opportunities. *In* R. G. Piper and H. L. Schramm (editors), Uses and effects of cultured fishes in aquatic ecosystems, p. 212-225. Am. Fish. Soc. Symp. 15, Bethesda, MD.

Hard, J. J., R. P. Jones, M. R. Delarm, and R. S. Waples. 1992. Pacific salmon and artificial propagation under the Endangered Species Act. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWFSC-2, 56 p.

Hartt, A. C., and M. B. Dell. 1986. Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. Int. North Pac. Fish. Comm. Bull. 46, 105 p.

Haw, F., H. O. Wendler, and G. Deschamps. 1967. Development of Washington state salmon sport fishery through 1964. Wash. Dep. Fish. Res. Bull. 7, 192 p.

Hayden, B. P., and R. Dolan. 1976. Coastal marine fauna and marine climates of the Americas. J. Biogeogr. 3:71-81.

Healey, M. C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. *In* W. J. McNeil and D. C. Himsworth (editors), Salmonid ecosystems of the North Pacific, p. 203-229. Oregon State Univ. Press, Corvallis.

Heard, W. R. 1989. Importance of the initial marine period in overall ocean survival of pink and chum salmon. Unpubl. manuscr., 29 p. Presented at the International Symposium on Problems of the Pacific Salmon Biology, Yuzhno-Sakalinsk, Sakhalin Isl., U.S.S.R., 11-15 September 1989. (Available from Alaska Fisheries Science Center Auke Bay Laboratory, 11305 Glacier Hwy., Juneau, AK 99801.)

Heard, W. R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). *In* C. Groot and L. Margolis (editors), Pacific salmon life histories, p. 121-230. Univ. British Columbia Press, Vancouver.

Helle, J. H. 1966. Behavior of displaced adult pink salmon. Trans. Am. Fish. Soc. 95:188-195.

Herrmann, R. B. 1959. Occurrence of juvenile pink salmon in a coastal stream south of the Columbia River. Oreg. Fish Comm. Res. Briefs 7(1):81.

Hillis, D. M., and C. Moritz (editors). 1990. Molecular systematics. Sinauer Assoc., Sunderland, MA.

Hiss, J. M. 1994. Migration of juvenile pink salmon (*Oncorhynchus gorbuscha*) through Dungeness Bay, Clallam County, Washington. Unpubl. manuscr., 21 p. (Available from U.S. Fish and Wildlife Service, Western Washington Fishery Resource Office, 2625 Parkmont Lane SW, Bldg. A, Olympia, WA 98502.)

Hiss, J. M. 1995. Environmental factors influencing spawning escapement of Dungeness River pink salmon (*Oncorhynchus gorbuscha*) 1959-1993. Unpubl. manuscr., 33 p. (Available from U.S. Fish and Wildlife Service, Western Washington Fishery Resource Office, 2625 Parkmont Lane SW, Bldg. A, Olympia, WA 98502.)

Horrall, R. M. 1981. Behavioral stock-isolating mechanisms in Great Lakes fishes with special reference to homing and site imprinting. Can. J. Fish. Aquat. Sci. 38:1481-1496.

Hourston, A. S., E. H. Vernon, and G. A. Holland. 1965. The migration, composition, exploitation and abundance of odd-year pink salmon runs in and adjacent to the Fraser River Convention Area. Int. Pac. Salmon Fish. Comm. Bull. 17, 151 p.

Hubbs, C. L. 1946. Wandering of pink salmon and other salmonid fishes into southern California. Calif. Fish Game 81-86.

Hunter, J. G. 1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16:835-886.

Hydrosphere Data Products, Inc. 1993. Hydrodata Regional CD-ROMs: U.S. Geological Survey Daily values, Vols. West 1, West 2. (Available from Hydrosphere Data Products Inc., 1002 Walnut, Suite 200, Boulder, CO 80302.)

International Pacific Salmon Fisheries Commission (IPSFC). 1958. A preliminary review of pertinent past tagging investigations on pink salmon and proposal for a co-ordinated research program for 1959. Pink Salmon Co-ordinating Committee, Rep. No. 1, 17 p.

Ivankov, V. N. 1968. Pacific salmon in the region of Iturup Island (Kuril Islands). Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 65:49-74. (English transl. Fish. Res. Board Can. Transl. Ser. 1999.)

Ivankov, V. N. 1986. Peculiarities of specific population structure of pink salmon and its rational exploitation. Sov. J. Mar. Biol. (Engl. Transl. Biol. Morya) 12(2):98-103.

Jensen, H. M. 1956. Migratory habits of pink salmon found in the Tacoma Narrows area of Puget Sound. Wash. Dep. Fish., Fish. Res. Pap. 1:21-24.

Jewell, E. D. 1966. Forecasting pink salmon runs. *In* W. L. Sheridan (editor), Proceedings of the 1966 Northeast Pacific pink salmon workshop, p. 93-110. Alaska Dep. Fish Game Inf. Leafl. 87.

Johnson, K. R. 1979. Genetic variation in populations of pink salmon (*Oncorhynchus gorbuscha*) from Kodiak Island. Master's Thesis, Univ. Washington, Seattle, 94 p.

Johnson, R. C. 1973. 1973 Upper Dungeness River pink salmon escapement. Unpubl. rep., 4 p. (Available from Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501.)

Johnson, R. C, R. Gerke, D. Heiser, R. Orrell, and J. Olds. 1968. Pink and chum salmon investigations 1967. Progr. Rep., Puget Sound Stream Studies. Wash. Dep. Fish., Res. Div., Olympia, WA.

Jones, D. 1978. Pink salmon stock predictions--S.E. Alaska. Tech. Rep. for Period July 1, 1977 to June 30, 1978, Anadromous Fish Conservation Act Proj. No. AFC-59-1, 27 p. Alaska Dep. Fish Game, Juneau, AK.

Jones, J. D., and G. Thomason. 1983. Southeast Alaska pink salmon secondary tagging and escapement enumeration studies, 1982. *In* Final report--1982 salmon research conducted in southeast Alaska by the Alaska Department of Fish and Game inconjunction with joint U.S.-Canada interception investigations, p. 1-13. Alaska Dep. Fish Game, Comm. Fish. Div., Juneau, AK.

Kartavtsev, Yu. F. 1991. Temporal and spatial variability in allele frequencies in populations of pink salmon, *Oncorhynchus gorbuscha*. Vopr. Ikhtiol. 31(3):487-495. (English transl. J. Ichthyol. 31(3):87-98.)

Kartavtsev, Yu. F., V. V. Efremov, E. A. Salmenkova, and V. T. Omel'chenko. 1981. Genetic morphological variability of pink salmon populations in Maritime Territory. *In* Genetics, selection, hybridization of fishes, p. 126-127. AzNIIRHh, Rostov-on-Don. (In Russian, cited in Ivankov 1986.)

Kartavtsev, Yu. F., V. V. Efremov, M. V. Smirnov, E. V. Ivankova, and N. E. Polyakova. 1992. Analysis of genotype distributions at allozyme loci in populations of pink salmon, *Oncorhynchus gorbuscha*. J. Ichthyol. (Engl. Transl. Vopr. Ikhtiol.) 32(4):102-115.

Knudsen, E. E., J. Calambokidis, and A. Erickson. 1990. Predation of salmonid smolts by Harbor Seals in Quilcene Bay, Washington. Unpubl. rep. (Available from U.S. Fish and Wildlife Service, Western Washington Fishery Resource Office, 2625 Parkmont Lane SW, Bldg. A, Olympia, WA 98502.)

Kwain, W., and A. H. Laurie. 1981. Pink salmon in the Great Lakes. Fisheries 6(2):2-6.

Landry, M. R., J. R. Postel, W. K. Peterson, and J. Newman. 1989. Broad-scale distributional patterns of hydrographic variables on the Washington/Oregon shelf. *In* M. R. Landry and B. M. Hickey (editors), Coastal oceanography of Washington and Oregon, p. 1-40. Elsevier, New York.

Lane, S., A. J. McGregor, S. G. Taylor, and A. J. Gharrett. 1990. Genetic marking of an Alaskan pink salmon population, with an evaluation of the mark and the marking process. Am. Fish. Soc. Symp. 7:395-406.

Lasmanis, R. 1991. The geology of Washington. Rocks and Minerals 66:263-277.

Lawson, P. W. 1993. Cycles in ocean productivity, trends in habitat quality, and the restoration of salmon runs in Oregon. Fisheries 18(8):6-10.

Leonard, W. P., H. A. Brown, L. L. Jones, K. R. McAllister, and R. M. Storm. 1993. Amphibians of Washington and Oregon. Seattle Audubon Society, Seattle, WA, 168 p.

Lesica, P., and F. W. Allendorf. 1995. When are peripheral populations valuable for conservation? Conserv. Biol. 9:753-760.

Lessa, E. P. 1990. Multidimensional analysis of geographic genetic structure. Syst. Zool. 39:242-252.

Lichatowich, J. 1993. Dungeness River pink and chinook salmon historical abundance, current status, and restoration. Unpubl. rep. to Jamestown S'Klallam Tribe, August 1992 (revised October 1993), 55 p. (Available from Jamestown S'Klallam Tribe, 305 Old Blyn Hwy., Sequim, WA 98382.)

Manzer, J. I., and M. P. Shepard. 1962. Marine survival, distribution and migration of pink salmon (*Oncorhynchus gorbuscha*) off the British Columbia coast. *In* N. J. Wilimovsky (editor), Symposium on pink salmon, p. 113-122. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

Marshall, R. P., and T. J. Quinn II. 1988. Estimation of average weight and biomass of pink, chum, sockeye and coho salmon in Southeast Alaska commercial harvests. Alaska Dep. Fish Game Fish. Res. Bull. 88-07, 52 p.

Mathisen, O. A. 1994. Spawning characteristics of the pink salmon (*Oncorhynchus gorbuscha*) in the eastern North Pacific Ocean. Aquacult. Fish. Manage. 25(Suppl. 2):147-156.

McDonald, J. 1960. The behavior of Pacific salmon fry during their downstream migration to freshwater and saltwater nursery areas. J. Fish. Res. Board Can. 17:655-676.

McGregor, A. J. 1982. A biochemical genetic analysis of pink salmon (*Oncorhynchus gorbuscha*) from selected streams in northern Southeast Alaska. Master's Thesis, Univ. Alaska, Juneau, 94 p.

McGregor, A. J. 1983. A biochemical genetic analysis of pink salmon (*Oncorhynchus gorbuscha*) from selected streams in northern Southeast Alaska. Alaska Dep. Fish Game Inf. Leafl. 213, 70 p.

McKee, B. 1972. Cascadia. The geologic evolution of the Pacific Northwest. McGraw-Hill Book Co., New York, 394 p. (Reprinted 1992 by TechBooks, Fairfax, VA.)

McNeil, W. J. 1966. Effect of the spawning bed environment on reproduction of pink and chum salmon. Fish. Bull., U.S. 65:495-523.

McPhail, J. D., and C. C. Lindsey. 1986. Zoogeography of the freshwater fishes of Cascadia (the Columbia system and rivers north to the Sitkine). *In* C. H. Hocutt and E. O. Wiley (editors), Zoogeography of North American freshwater fishes, p. 615-637. Wiley Intersci. Publ., New York.

Merrell, T. R. 1962. Freshwater survival of pink salmon at Sashin Creek. *In* N. J. Wilimovsky (editor), Symposium on pink salmon, p. 59-72. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

Minckley, W. L., D. A. Hendrickson, and C. E. Bond. 1986. Geography of western North American freshwater fishes: Description and relationships to intracontinental tectonism. *In* C. H. Hocutt and E. O. Wiley (editors), Zoogeography of North American freshwater fishes, p. 519-613. Wiley Interscience Publications, New York.

Monaco, M. E., T. A. Lowery, and R. L. Emmett. 1992. Assemblages of U.S. west coast estuaries based on the distribution of fishes. J. Biogeogr. 19:251-267.

Morrison, J., and D. Zajac. 1987. Histologic effect of coded wire tagging in chum salmon. N. Am. J. Fish. Manage. 7:439-441.

Mortensen, D., J. Landingham, A. Wertheimer, and S. Taylor. 1991. Relationship of early marine growth and survival of juvenile pink salmon to marine water temperature and secondary production in Auke Bay, Alaska. *In* Proceedings of the 15th Northeast Pacific pink and chum salmon workshop, p. 38-49. Pac. Salm. Comm. and Can. Dep. Fish. Oceans. (Available from Pacific Salmon Commission, Canadian Department of Fisheries and Oceans, 600-155 Robson St., Vancouver, BC V6E 1B9.)

Moyle, P. B., R. M. Yoshiyama, J. E. Williams, and E. D. Wikramanayake. 1995. Fish species of special concern in California, 2nd ed. Calif. Dep. Fish Game, Sacramento, CA, 272 p.

Mysak, L. A. 1986. El Niño, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 43:464-497.

Mysak, L. A., W. W. Hsiah, and T. R. Parsons. 1982. On the relationship between interannual baroclinic waves and fish populations in the Northeast Pacific. Biol. Oceanogr. 2(1):63-103.

National Marine Fisheries Service (NMFS). 1991. Notice of policy: Policy on applying the definition of species under the Endangered Species Act to Pacific salmon. Federal Register [Docket 910248-1255, 20 November 1991] 56(224):58612-58618.

National Marine Fisheries Service (NMFS). 1993. Interim policy on artificial propagation of Pacific salmon under the Endangered Species Act. Federal Register [Docket 921186-2286, 5 April 1993] 58(63):17573-17576.

National Marine Fisheries Service (NMFS). 1994. Listing endangered and threatened species and designating critical habitat: Initiation of status reviews for pink salmon, chum salmon, sockeye salmon, chinook salmon, and sea-run cutthroat trout populations in Washington, Oregon, Idaho, and California. Federal Register [I.D. 081694D, 12 September 1994] 59(175):46808-46810.

Natural Resource Consultants (NRC). 1995. Artificial propagation of anadromous Pacific salmonids, 1950 to present. Pink salmon. Contract report to U.S. Department of Commerce, NOAA, NMFS, January 1995. Includes electronic database. (Available from Environmental and Technical Services Division, National Marine Fisheries Service, 525 N.E. Oregon St., Portland, OR 97232.)

Neave, F. 1952. "Even-year" and "odd-year" pink salmon populations. Trans. R. Soc. Can. 46, Ser. 3, Sec. 5:55-70.

Neave, F. 1963. Life history of the pink salmon of British Columbia. Int. N. Pac. Fish. Comm. Doc. 665, 15 p.

Neave, F. 1965. Transplants of pink salmon. Fish. Res. Board Can. Manuscr. Rep. Ser. (Biol.) 830, 37 p.

Neave, F., T. Ishida, and S. Murai. 1967. Salmon of the North Pacific Ocean. Part VII. Pink salmon in offshore waters. Int. North Pac. Fish. Comm. Bull. 22, 39 p.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: Stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4-21.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 76:583-590.

Nei, M. 1987. Molecular evolutionary genetics. Columbia Univ. Press, New York.

Nickerson, R. B. 1979. Separation of some pink salmon (*Oncorhynchus gorbuscha* Walbaum) sub-populations in Prince William Sound, Alaska by length-weight relationships and horizontal starch gel electrophoresis. Alaska Dep. Fish Game Inf. Leafl. 181, 36 p.

Noerenberg, W. A. 1963. Salmon forecast studies on 1963 runs in Prince William Sound. Alaska Dep. Fish Game Inf. Leafl. 21, 17 p. + Appendices.

Noll, C., N. V. Varnavskaya, E. Matzak, S. Hawkins, V. V. Midyanaya, O. Katugin, C. Russell, G. S. Fesunova, N. M. Kinas, C. M. Guthrie, III, H. Mayama, F. Yamazaki, and A. J. Gharrett. 1994. Genetic relationships among even-year pink salmon (*Oncorhynchus gorbuscha*) from Asia and Alaska. Unpubl. manuscr. (Cited in Zhivotovsky et al. (1994).)

Ogura, M. 1994. Migratory behavior of Pacific salmon (*Oncorhynchus* spp.) in the open sea. Bull. Nat. Res. Inst. Far Seas Fish. 31:1-139.

Okazaki, T. 1984. Genetic divergence and its zoogeographical implications in closely related species *Salmo gairdneri* and *Salmo mykiss*. Jpn. J. Ichthyol. 31:297-310.

O'Malley, H. 1917. The distribution of fish and fish eggs during the fiscal year 1917. U.S. Bur. Fish. Doc. 846, 99 p.

Omernik, J. M. 1987. Ecoregions of the conterminous United States. Ann. Assoc. Am. Geogr. 77(1):118-125.

Omernik, J. M., and A. L. Gallant. 1986. Ecoregions of the Pacific Northwest. U.S. Environ. Protec. Agen. Rep. EPA/600/3-86/033, 39 p. (Available from U.S. Environmental Protection Agency, Environmental Research Laboratory, 200 SW 35th St., Corvallis, OR 97333.)

Pearcy, W. G. 1992. Ocean ecology of North Pacific salmonids. Univ. Washington Press, Seattle, 179 p.

Phillips, A. C., and W. E. Barraclough. 1978. Early marine growth of juvenile Pacific salmon in the Strait of Georgia and Saanich Inlet, British Columbia. Can. Fish. Mar. Serv. Tech. Rep. 830, 19 p.

Pritchard, A. L. 1937. Variation in the time of run, sex proportions, size and egg content of adult pink salmon (*Oncorhynchus gorbuscha*) at McClinton Creek, Masset Inlet, B.C. J. Biol. Board Can. 3(5):403-416.

Pritchard, A. L. 1939. Homing tendency and age at maturity of pink salmon (*Oncorhynchus gorbuscha*) in British Columbia. J. Fish. Res. Board Can. 4:233-251.

Pritchard, A. L., and A. C. DeLacy. 1944. Migration of pink salmon (*Oncorhynchus gorbuscha*) in southern British Columbia and Washington in 1943. Fish. Res. Board Can., Bull. 66, 23 p.

Professional Resource Organization-Salmon (PRO-Salmon). 1994. Petition for a rule to list nine Puget Sound salmon populations as threatened or endangered under the Endangered Species Act and to designate critical habitat. Unpubl. manuscr., 86 p. Document submitted to the USDOC NOAA NMFS Northwest Region, Seattle, Washington, September 1993. (Available from PRO-Salmon, Washington Public Employees Association, 124 10th Ave. S.W., Olympia, WA 98501.)

Quinn, T. P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fish. Res. 18:29-44.

Reisenbichler, R. R., J. D. McIntyre, M. F. Solazzi, and S. W. Landino. 1992. Genetic variation in steelhead of Oregon and northern California. Trans. Am. Fish. Soc. 21:158-169.

Ricker, W. E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119, 300 p.

Ricker, W. E. 1962. Regulation of the abundance of pink salmon populations. *In* N. J. Wilimovsky (editor), Symposium on pink salmon, p. 155-201. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. *In* R. C. Simon and P. A. Larkin (editors), The stock concept in Pacific salmon, p. 19-160. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

Ricker, W. E. 1981. Changes in the average body size and average age of Pacific salmon. Can. J. Fish. Aquat. Sci. 38:1636-1656.

Ricker, W. E. 1989. History and present state of the odd-year pink salmon runs of the Fraser River region. Can. Tech. Rep. Fish. Aquat. Sci. 1702, 37 p.

Ricker, W. E., H. T. Bilton, and K. V. Aro. 1978. Causes of decrease in size of pink salmon (*Oncorhynchus gorbuscha*). Can. Fish. Mar. Serv. Tech. Rep. 820, 93 p.

Ricker, W. E., and J. I. Manzer. 1974. Recent information on salmon stocks in British Columbia. Int. North Pac. Fish. Comm. Bull. 29:1-24.

Riggs, L. A. 1990. Principles for genetic conservation and production quality: Results of a scientific and technical clarification and revision. Unpubl. rep. to Northwest Power Planning Council (Contract No. C90-005), 20 p. (Available from Genetic Resource Consultants, P.O. Box 9528, Berkeley, CA 94709.)

Rogers, J. S. 1972. Measures of genetic similarity and genetic distance. Studies in Genetics VII, Univ. Texas Publ. 7213:145-153.

Rogers, J. S. 1991. A comparison of the suitability of the Rogers, modified Rogers, Manhattan, and Cavalli-Sforza and Edwards distances for inferring phylogenetic trees from allele frequencies. Syst. Zool. 40:63-73.

Rohlf, F. J. 1993. NTSYS-pc. Numerical taxonomy and multivariate analysis system. Exeter Software, Setauket, New York.

Roppel, P. 1982. Alaska's salmon hatcheries 1891-1959. Alaska Hist. Comm. Stud. Hist. No. 20, 299 p.

Rounsefell, G. A. 1938. Pink salmon. *In* Rounsefell, G. A., and G. B. Kelez, The salmon and salmon fisheries of Swiftsure Bank, Puget Sound, and the Fraser River, p. 804-813. U.S. Bur. Fish. Bull. 27.

Royce, W. F. 1962. Pink salmon fluctuations in Alaska. *In* N. J. Wilimovsky (editor), Symposium on pink salmon, p. 15-33. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

Salmenkova, E. A., V. T. Omel'chenko, T. V. Malinina, K. I. Afans'ev, and Yu. P. Altukhov. 1981. Population genetic differences between closely related generations of pink salmon reproducing in rivers on the Asian coast of the North Pacific. *In* Genetics and reproduction of marine animals, p. 95-104. Far East Science Center, Akad. Nauk SSSR, Vladivostok. (In Russian, cited in Ivankov 1986.)

Scofield, N. B. 1916. The humpback and dog salmon taken in San Lorenzo River. Calif. Fish Game 2(1):41.

Scudder, G. G. E. 1989. The adaptive significance of marginal populations: A general perspective. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson (editors), Proceedings of the national workshop on effects of habitat alteration on salmonid stocks, p. 180-185. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Shaklee, J. B., J. Ames, and D. Hendrick. 1995. Genetic diversity units and major ancestral lineages for pink salmon in Washington. *In* C. Busack and J. B. Shaklee (editors), Genetic diversity units and major ancestral lineages of salmonid fishes in Washington. Wash. Dep. Fish Wildl. Tech. Rep. RAD 95-02, p. B1-B37. (Available from Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501.)

Shaklee, J. B., D. C. Klaybor, S. Young, and B. A. White. 1991. Genetic stock structure of odd-year pink salmon, *Oncorhynchus gorbuscha* (Walbaum), from Washington and British Columbia and potential mixed-stock fisheries applications. J. Fish Biol. 39(Suppl. A):21-34.

Shaklee, J. B., and N. V. Varnavskaya. 1994. Electrophoretic characterization of odd-year pink salmon (*Oncorhynchus gorbuscha*) populations from the Pacific Coast of Russia, and comparison with selected North American populations. Can. J. Fish. Aquat. Sci. 51(Suppl. 1):158-171.

Sharp, D., S. Sharr, and C. Peckham. 1994. Homing and straying patterns of coded wire tagged pink salmon in Prince William Sound. *In* Proceedings 16th Northeast Pacific pink and chum salmon workshop, p. 77-82. Alaska Sea Grant Coll. Progr. Rep. 94-02.

Shepard, M. P., C. D. Shepard, and A. W. Argue. 1985. Historic statistics of salmon production around the Pacific rim. Can. Manuscr. Rep. Fish. Aquat. Sci. 1819, 297 p.

Sheridan, W. L. 1962. Relation of stream temperatures to timing of pink salmon escapements in southeast Alaska. *In* N. J. Wilimovsky (editor), Symposium on pink salmon. H. R. MacMillan lectures in fisheries, p. 87-102. Univ. British Columbia, Vancouver.

Simon, R. C., J. D. McIntyre, and A. R. Hemmingsen. 1986. Family size and effective population size in a hatchery stock of coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 43:2434-2442.

Skud, B. E. 1973. Factors regulating the production of pink salmon. *In* B. B. Parrish (editor), Fish stocks and recruitment, p. 106-112. Rapports et Procès-Verbaux des Réunions, Vol. 164. Conseil International pour l'Exploration de la Mer, Charlottenlund Slot, Denmark.

Smedley, S. C. 1952. Pink salmon in Prairie Creek, California. Calif. Fish Game 38(2):275.

Smith, R. L. 1983. Physical features of coastal upwelling systems. Wash. Sea Grant Tech. Rep. WSG 83-2. Washington Sea Grant, Seattle, 34 p.

Smoker, W. W. 1984. Genetic effect on the dynamics of a model of pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon. Can. J. Fish. Aquat. Sci. 41:1446-1453.

Smoker, W. W., A. J. Gharrett, and M. S. Stekoll. In press. Genetic variation in timing of anadromous migration within a spawning season in a population of pink salmon. Can. Spec. Publ. Fish. Aquat. Sci.

Smoker, W. W., A. J. Gharrett, M. S. Stekoll, and J. E. Joyce. 1994. Genetic analysis of size in an anadromous population of pink salmon. Can. J. Fish. Aquat. Sci. 51(Suppl. 1):9-15.

Sneath, P. H. A., and R. R. Sokal. 1973. Numerical taxonomy. W. H. Freeman, San Francisco, CA.

Snyder, J. O. 1931. Salmon of the Klamath River, California. I. The salmon and the fishery of Klamath River. II. A report on the 1930 catch of king salmon in Klamath River. Calif. Fish Game, Fish Bull. 34, 130 p.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry: The principles and practice of statistics in biological research, 2nd ed. W. H. Freeman and Co., New York, 859 p.

Stefanson, A. P., L. Hop Wo, and A. P. Gould. 1991. The 1988 return of even year pink salmon stocks to the Johnstone Strait study area. Can. Manuscr. Rep. Fish. Aquat. Sci. 2112, 39 p.

Stefanson, A. P., L. Hop Wo, and A. P. Gould. 1993. The 1985 return of even year pink salmon stocks to the Johnstone Strait study area. Can. Manuscr. Rep. Fish. Aquat. Sci. 2195, 34 p.

Stefanson, A. P., L. Hop Wo, A. P. Gould, and A. Y. Federenko. 1989. The 1986 return of even year pink salmon to the Johnstone Strait study area. Can. Manuscr. Rep. Fish. Aquat. Sci. 2024, 42 p.

Taft, A. C. 1938. Pink salmon in California. Calif. Fish Game 24(2):197-198.

Takagi, K., K. V. Aro, A. C. Hartt, and M. B. Dell. 1981. Distribution and origin of pink salmon (Oncorhynchus gorbuscha) in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 40, 195 p.

Taylor, S. G. 1980. Marine survival of pink salmon fry from early and late spawners. Trans. Am. Fish. Soc. 109:79-82.

Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185-207.

Thompson, G. G. 1991. Determining minimum viable populations under the Endangered Species Act. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-198, 78 p.

Thompson, R. E. 1981. Oceanography of the British Columbia coast. Can. Spec. Publ. Fish. Aquat. Sci. 56, 291 p.

Thorpe, J. P. 1982. The molecular clock hypothesis: Biochemical evolution, genetic differentiation, and systematics. Annu. Rev. Ecol. Syst. 13:139-168.

Turner, C. E., and H. T. Bilton. 1968. Another pink salmon (*Oncorhynchus gorbuscha*) in its third year. J. Fish. Res. Board Can. 25(9):1993-1996.

U.S. Army Corps of Engineers. 1994. Annual fish passage report, Columbia and Snake Rivers for salmon, steelhead and shad. North Pacific Division, Portland, OR, and Walla Walla, WA.

U.S. Department of Commerce. 1968. (Natl. Oceanic Atmos. Admin. reprint 1983.) Climate atlas of the United States. Natl. Climatic Data Center, Asheville, NC, 80 p.

Utter, F. M., D. Campton, S. Grant, G. Milner, J. Seeb, and L. Wishard. 1980. Population structures of indigenous salmonid species of the Pacific Northwest. I. A within and between species examination of natural populations based on genetic variation of proteins. *In* W. J. McNeil and D. C. Himsworth (editors), Proceedings of the symposium on salmonid ecosystems of the North Pacific, p. 285-304. Sea Grant College Program, Oregon State Univ., Corvallis.

Valentine, J. W. 1966. Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. Limnol. Oceanogr. 11:198-211.

Van Hyning, J. M. 1959. Marked pink salmon. Oreg. Fish. Comm. Res. Briefs 7(1):82.

Varnavskaya, N. V., and T. D. Beacham. 1992. Biochemical genetic variation in odd-year pink salmon (*Oncorhynchus gorbuscha*). Can. J. Zool. 70:2115-2120.

Vernon, E. H. 1962. Pink salmon populations of the Fraser River system. *In* N. J. Wilimovsky (editor), Symposium on pink salmon, p. 121-230. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

Vernon, E. H. 1966. Enumeration of migrant pink salmon fry in the Fraser River estuary. Int. Pac. Salmon Fish. Comm. Bull. 19, 83 p.

Vernon, E. H., A. S. Hourston, and G. A. Holland. 1964. The migration and exploitation of pink salmon runs in and adjacent to the Fraser River Convention Area in 1959. Int. Pac. Salmon Fish. Comm. Bull. 15, 296 p.

Waples, R. S. 1991a. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. Mar. Fish. Rev. 53(3):11-22.

Waples, R. S. 1991b. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. Can. J. Fish. Aquat. Sci. 48 (Suppl. 1):124-133.

Waples, R. S., O. W. Johnson, P. B. Aebersold, C. K. Shiflett, D. M. VanDoornik, D. J. Teel, and A. E. Cook. 1993. A genetic monitoring and evaluation program for supplemented populations of salmon and steelhead in the Snake River Basin. Report to the U.S. Department of Energy, Bonneville Power Administration, Division of Fish and Wildlife, contract DE-A179-89BP00911. (Available from Bonneville Power Administration, P.O. Box 3621, Portland, OR 97208.)

Waples, R. S., and D. J. Teel. 1990. Conservation genetics of Pacific salmon. I. Temporal changes in allele frequency. Conserv. Biol. 4:144-156.

Ward, F. J. 1959. Character of the migration of pink salmon to Fraser River spawning grounds in 1957. Int. Pac. Salmon Fish. Comm. Bull. 10, 70 p.

Washington Department of Fisheries (WDF; formerly Washington Department of Fisheries and Game - Fisheries Division). 1916-64. Annual reports. Wash. Dep. Fish., Olympia, WA.

Washington Department of Fisheries (WDF). 1959. Pink salmon. In Fisheries, vol. 2. Contributions of western states, Alaska, and British Columbia to salmon fisheries of the North American Pacific Ocean, p. 37-39. Wash. Dep. Fish., Olympia, WA.

Washington Department of Fisheries (WDF), Washington Department of Wildlife (WDW), and Western Washington Treaty Indian Tribes (WWTIT). 1993. 1992 Washington State salmon and steelhead stock inventory (SASSI). Wash. Dep. Fish Wildl., Olympia, 212 p. + 5 regional vols. (Available from Washington Department of Fish and Wildlife, P.O. Box 43151, Olympia, WA 98501.)

Weitkamp, L. A., T. C. Wainwright, G. J. Bryant, G. B. Milner, D. J. Teel, R. G. Kope, and R. S. Waples. 1995. Status review of coho salmon from Washington, Oregon, and California. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-NWFSC-24, 258 p.

White, B. A., and J. B. Shaklee. 1991. Need for replicated electrophoretic analyses in multiagency genetic stock identification (GSI) programs: Examples from a pink salmon (*Oncorhynchus gorbuscha*) GSI fisheries study. Can. J. Fish. Aquat. Sci. 48:1396-1407.

Wickett, W. P. 1958. Review of certain environmental factors affecting the production of pink and chum salmon. J. Fish. Res. Board Can. 15:1103-1126.

Wickett, W. P. 1962. Environmental variability and reproduction potentials of pink salmon in British Columbia. *In* N. J. Wilimovsky (editor), Symposium on pink salmon, p. 73-86. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.

Williams, R. W., R. M. Laramie, and J. J. Ames. 1975. A catalog of Washington streams and salmon utilization, vol. 1. Puget Sound region. Wash. Dep. Fish., Olympia, WA, 704 p. + Appendices.

Withler, R. E. 1988. Genetic consequences of fertilizing chinook salmon (*Oncorhynchus tshawytscha*) eggs with pooled milt. Aquaculture 68:15-25.

Wright, S. 1951. The genetical structure of populations. Ann. Eugenics 15:323-354.

Zhivotovsky, L. A., A. J. Gharrett, A. J. McGregor, M. K. Glubokovsky, and M. W. Feldman. 1994. Genetic differentiation in Pacific salmon (*Oncorhynchus* spp.): Facts and models with reference to pink salmon (*O. gorbuscha*). Can. J. Fish. Aquat. Sci. 51(Suppl. 1): 223-232.

Appendix

Glossary

GLOSSARY

allele

An **allele** is an alternate form of a **gene** (the basic unit of heredity passed from parent to offspring). By convention, the **"100 allele"** is the most common allele in a population and is the reference for the electrophoretic mobility of other alleles of the same gene. Other genetic terms used in this document include **allozymes** (alternate forms of an enzyme produced by different alleles and often detected by protein electrophoresis); **gene locus** (pl. **loci**; the site on a chromosome where a gene is found); **genetic distance (D)** (a quantitative measure of genetic differences between a pair of samples); and **introgression** (introduction of genes from one population or species into another). *See also* **DNA**, **electrophoresis**, **phenogram**, and **multidimensional scaling**.

artificial propagation

See **hatchery**.

Biological Review Team (BRT)

A team of scientists from National Marine Fisheries Service formed to conduct the status review.

broodline

The generation of pink salmon that reproduces every other year. Because of the lack of variable age structure in this species, **even-year pink salmon** are reproductively isolated from **odd-year pink salmon**.

coded-wire tag (CWT)

A small piece of wire, marked with a binary code, that is normally inserted into the nasal cartilage of juvenile fish. Because the tag is not externally visible, the adipose fin of coded wire-tagged fish is removed to indicate the presence of the tag. Groups of thousands to hundreds of thousands of fish are marked with the same code number to indicate stock, place of origin, or other distinguishing traits for production releases and experimental groups.

DNA (deoxyribonucleic acid)

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

electrophoresis

Electrophoresis refers to the movement of charged particles in an electric field. It has proven to be a very useful analytical tool for biochemical characters because molecules can be separated on the basis of differences in size or net charge. **Protein electrophoresis**, which measures differences in the amino acid composition of proteins from different individuals, has been used for over two decades to study natural populations, including all species of anadromous Pacific salmonids. Because the amino acid sequence of proteins is coded for by DNA, data provided by protein electrophoresis provide insight into levels of genetic variability within populations and the extent of genetic differentiation between them. Genetic techniques that focus directly on variation in DNA also routinely use electrophoresis to separate fragments formed by cutting DNA with special enzymes (**restriction endonucleases**). *See also* **allele** and **DNA**.

ESA

The U.S. Endangered Species Act.

escapement

The number of fish that survive to reach the spawning grounds or hatcheries. The escapement plus the number of fish removed by harvest form the **total run size**.

even-year pink salmon

Pink salmon that spawn in even-numbered years. The distribution of these fish is variable, but their abundance tends to increase at higher latitudes in both Asia and North America. Even-year pink salmon spawning regularly south of British Columbia are found only in the Snohomish River, Washington.

evolutionarily significant unit (ESU)

A "distinct" population of Pacific salmon, and hence a species, under the Endangered Species Act.

F_{ST}

A measure of population structure that estimates the variance of **allele** frequencies among populations, standardized relative to the maximum value possible given the observed mean allele frequency.

gene diversity analysis

A hierarchical analysis of the genetic variation observed at polymorphic **loci** (*see* **allele**) in a set of samples that partitions this variation into several, typically geographic, components. Diversity analysis commonly estimates the proportions of observed variation expressed 1) among areas or regions, 2) among populations within areas, and 3) within populations. The total of these proportions equals 1.

hatchery

Salmon hatcheries typically spawn adults in captivity and raise the resulting progeny in fresh water for release into the natural environment. In some cases, fertilized eggs are outplanted (usually in "hatch-boxes"), but it is more common to release **fry** (young juveniles) or **smolts** (juveniles that are physiologically prepared to undergo the migration into salt water). Pink salmon are unusual among Pacific salmon in that they are "smolts" upon emergence from the gravel and do not require extensive freshwater rearing before migrating to the ocean.

The fish are released either at the hatchery (**on-station release**) or away from the hatchery (**off-station release**). Releases may also be classified as **within basin** (occurring within the river basin in which the hatchery is located or the stock originated from) or **out-of-basin** (occurring in a river basin other than that in which the hatchery is located or the stock originated from).

The broodstock of some hatcheries is based on adults that return to the hatchery each year; others rely on fish or eggs from other facilities, or capture adults in the wild each year.

island model of migration

An equilibrium model of gene flow and genetic drift that is applied under the assumption that a species (or **operational taxonomic unit** or **ESU**) is subdivided into populations of equal size, all of which exchange migrants at a constant rate, with migrants coming with equal probability from all other populations.

minimum spanning tree

A means of depicting nearest genetic neighbors. The tree is an undirected network of smallest genetic distances between genetic samples superimposed on **multidimensional scaling** graphs to reveal local distortion (pairs of points which look close together in one dimension, but which are far apart in other dimensions). *See also* **multidimensional scaling**.

multidimensional scaling

A nonmetric ordination technique used to visualize genetic relationships among populations in two or three dimensions. This technique requires that the distances between samples in two- or three-dimensional graphs have monotonic relationships to the original genetic distances between pairs of samples. *See also* **minimum spanning tree** and **phenogram**.

odd-year pink salmon

Pink salmon that spawn in odd-numbered years. The distribution of these fish is variable, but their abundance tends to increase at lower latitudes in both Asia and North America. Odd-year pink salmon are common in both southern British Columbia and Washington.

phenogram

A graphical means of depicting genetic relationships among populations in the form of a branching "tree" (also often referred to as a **dendrogram**). The phenogram is generated from summary statistics, such as genetic distances or similarities, and shows the results of clustering these populations based on these statistics. A clustering algorithm commonly used to generate phenograms from genetic distances or similarities is the **unweighted pair group method with averages (UPGMA)**. *See also* **multidimensional scaling.**

polymorphic

Having more than one form (e.g., polymorphic gene loci have more than one **allele**).

recruit-to-spawner ratio

Several measures are employed to estimate the productivity of salmon populations. The **recruit-to-spawner ratio** estimates the number of **recruits** (fish that are available for harvest in addition to those that escape the fishery to spawn) produced by the previous generation's spawners. The **spawner-to-spawner ratio** estimates the number of spawners (those fish that reproduced or were expected to reproduce) in one generation produced by the previous generation's spawners. A spawner-to-spawner ratio of 1.0 indicates that, on average, each spawner produced one offspring that survived to spawn; the size of such a population would remain unchanged over that generation.

river kilometer (RKm)

Distance, in kilometers, from the mouth of the indicated river. Usually used to identify the location of a physical feature, such as a confluence, dam, waterfall, or spawning area.

spawner surveys

Spawner surveys utilize counts of **redds** (nests dug by females in which they deposit their eggs) and fish carcasses to estimate spawner escapement and identify habitat being used by spawning fish. Annual surveys can be used to compare the relative magnitude of spawning activity between years. Surveys are conducted on a regular basis on **standard stream segments**, groups of which form a spawner **index**, and are occasionally conducted on **supplemental stream segments** (those that are not part of the standard surveying plan).

Several methodologies have been used to estimate trends in spawner abundance based on the results of redd counts or spawner surveys. The **peak count (PC)** methodology simply uses the largest number of fish observed during the peak of spawning activity. The **area under the curve (AUC)** approach estimates the number of "fish days" (one "fish day" is equal to one fish (spawner) present on the spawning ground for one day) for a given stream segment; AUC is calculated from the total number of spawners observed over the course of the season, divided by the average residence time of spawners on the spawning ground. **Stratified random sampling (SRS)** provides an estimate of the number of spawners in a given area based on spawner counts in both standard and supplemental surveys.

Strait of Georgia

The body of water separating the southern portion of Vancouver Island and the British Columbia mainland. The strait extends from Cortes Island and Desolation Sound in the north to the San Juan Islands in the south.

Strait of Juan de Fuca

The body of water separating the southern portion of Vancouver Island and the Olympic Peninsula in Washington. The strait extends from the Pacific Ocean east to the San Juan and Whidbey Islands. The Dungeness and Elwha Rivers on the Olympic Peninsula drain into the Strait of Juan de Fuca.

west coast pink salmon

For the purposes of this document, west coast pink salmon are defined as pink salmon originating from fresh waters of southern British Columbia, Washington, Oregon, and California.

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24 WEITKAMP, L. A., T. C. WAINWRIGHT, G. J. BRYANT, G. B. MILNER, D. J. TEEL, R. G. KOPE, and R. S. WAPLES. 1995. Status review of coho salmon from Washington, Oregon, and California. NTIS No. PB96-106554.

23 HINTON, S. A., G. T. MCCABE, JR., and R. L. EMMETT. 1995. In-water restoration between Miller Sands and Pillar Rock Island, Columbia River: Environmental surveys, 1992-93, 47 p. NTIS No. PB95-274445.

22 WAKNITZ, F. W., G. M. MATTHEWS, T. WAINWRIGHT, and G. A. WINANS. 1995. Status review for mid-Columbia River summer chinook salmon, 80 p. NTIS No. PB95-260923.

21 REPPOND, K. D., and J. K. BABBITT. 1995. Frozen storage stability of fillets, mince, and mixed blocks prepared from unfrozen and previously frozen pink salmon *(Oncorhynchus gorbuscha),* 57 p. NTIS No. PB95-239828.

20 HINTON, S. A., and R. L. EMMETT. 1994. Juvenile salmonid stranding in the lower Columbia River, 1992 and 1993, 48 p. NTIS No. PB95-199352.

19 BUSBY, P. J., T. C. WAINWRIGHT, and R. S. WAPLES. 1994. Status review for Klamath Mountains Province steelhead, 130 p. NTIS No. PB95-179677.

18 GESSEL, M. H., B. P. SANDFORD, B. H. MONK, and D. A. BREGE. 1994. Population estimates of northern squawfish, *Ptychocheilus oregonensis,* at Bonneville Dam First Powerhouse, Columbia River, 21 p. NTIS No. PB95-198362.

17 PARK, L. K., P. MORAN, and R. S. WAPLES (editors). 1994. Application of DNA technology to the management of Pacific salmon: Proceedings of the workshop, 178 p. NTIS No. PB95-172755.

16 MEADOR, J. P., R. C. CLARK, JR., P. A. ROBISCH, D. W. ERNEST, J. T. LANDAHL, U. VARANASI, S-L. CHAN, and B. MCCAIN. 1994. National Status and Trends Program, National Benthic Surveillance Project: Pacific Coast. Analyses of elements in sediment and tissue, Cycles I to V (1984-88), 206 p. NTIS No. PB95-125027.

15 JOHNSON, O. W., R. S. WAPLES, T. C. WAINWRIGHT, K. G. NEELY, F. W. WAKNITZ, and L. T. PARKER. 1994. Status review for Oregon's Umpqua River sea-run cutthroat trout, 122 p. NTIS No. PB94-194115.

14 REICHERT, W. L., and B. FRENCH. 1994. The ^{32}P-Postlabeling protocols for assaying levels of hydrophobic DNA adducts in fish, 89 p. NTIS No. PB94-203122.