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Status Review
for
Snake River Fall Chinook Salmon

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STATUS REVIEW FOR SNAKE RIVER FALL CHINOOK SALMON

by

Robin S. Waples[1]
Robert P. Jones, Jr.[2]
Brian R. Beckman[1]
and George A. Swan[1]

[1]National Marine Fisheries Service
Northwest Fisheries Center
Coastal Zone and Estuarine Studies Division
2725 Montlake Boulevard East
Seattle, WA 98112

and

[2]National Marine Fisheries Service
Environmental and Technical Services Division
911 N.E. 11th Avenue Room 620
Portland, OR 97232

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SUMMARY

This report summarizes biological information gathered in conjunction with an Endangered Species Act (ESA) status review for Snake River fall chinook salmon (*Oncorhynchus tshawytscha*). As amended in 1978, the ESA allows listing of "distinct population segments" of vertebrates as well as named species and subspecies. National Marine Fisheries Service (NMFS) policy 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. The ESA evaluation of Snake River fall chinook salmon is complicated by the presence of spring- and summer-run chinook salmon in the Snake River. According to NMFS policy, those groups that are reproductively isolated from groups with other run-times should be considered separately for ESA purposes; fish of different run-times for which reproductive isolation cannot be established should be considered as a unit. Because of compelling evidence that fall chinook salmon are reproductively isolated from spring- and summer-run fish in the Snake River, this status review is confined to Snake River fall chinook salmon [see Matthews and Waples (1991) for the status review for Snake River spring and summer chinook salmon].

Prior to 1900, fall chinook salmon were widely distributed in the Snake River and supported important commercial and tribal fisheries. In this century, construction of 12 dams on the main-stem Snake River has reduced spawning habitat to a fraction of its former extent. With completion of the Hells Canyon Dam and Lower Snake River dam complexes between 1958 and 1975, the most productive areas were inaccessible or inundated, and only about 165 kilometers of habitat in the main-stem Snake River remains. Since 1975, the estimated number of wild fall

chinook salmon passing Lower Granite Dam on the Snake River has been less than 1,000 per year, and in 1990 the estimate was less than 100.

A brood-stock program designed to preserve the genetic integrity and enhance production of Snake River fall chinook salmon was initiated in the late 1970s. This program has been operated from Lyons Ferry Hatchery since its completion in 1984. Brood stock is composed of fish which have returned to the hatchery and hatchery and wild adults taken at Ice Harbor Dam.

Available evidence indicates that, at least through the early 1980s, Snake River fall chinook salmon met both of the requirements to be considered an ESU (Waples 1991)--reproductive isolation and ecological/genetic distinctness. Several lines of evidence indicate that the population with the closest affinity to Snake River fall chinook salmon is fall-run fish in the upper Columbia River. Tagging data suggest that the rate of natural straying of upper Columbia River fall chinook salmon into the Snake River is very low. Consistent genetic differences between upper Columbia and Snake River fish, documented over several years in the late 1970s and early 1980s, also indicate significant, long-term reproductive isolation of the two groups.

The main-stem upper Columbia and Snake Rivers differ ecologically in a number of ways, including water temperature, turbidity, total alkalinity, and pH. High summer water temperatures may prevent rearing of juvenile fall chinook salmon after July in many areas of the main-stem Snake River. Significant differences in average size have been reported between adults from the two areas, and tagging data indicate that Snake River fall chinook salmon have a more southerly ocean distribution than fish of similar run-timing from the upper Columbia River. In conjunction with the genetic data, these results suggest that, historically, fall chinook salmon in the Snake River contributed substantially to ecological/genetic diversity of the biological species. Utter et al. (1982) reached a similar conclusion in an earlier ESA evaluation of Snake River fall chinook salmon.

Information that has only recently become available casts doubt on the present status of the Snake River population. In recent years, strays from hatcheries producing upper Columbia River fall chinook salmon have appeared in the Snake River in increasing numbers; it is estimated that in 1989, such strays constituted almost 40% of the adults used for brood stock at Lyons Ferry Hatchery. A high percentage of adults taken at Lower Granite Dam and on spawning grounds in 1990 were estimated to be of hatchery origin, including strays from hatcheries using upper Columbia River fall chinook salmon. Protein electrophoretic data confirm that introgression of upper Columbia River genes into Lyons Ferry Hatchery brood stock has occurred, but there is no direct information about the genetic effects of hatchery strays on the wild Snake River population.

Although the NMFS Northwest Region Biological Review Team (BRT) concluded that, historically, Snake River fall chinook salmon were an ESU, it is not so clear whether this is still the case. One viewpoint is that introgression from Columbia River hatchery strays has caused the Snake River population to lose the qualities that made it "distinct" for ESA purposes. Evidence in support of this viewpoint includes genetic and tagging data documenting effects of straying on Lyons Ferry Hatchery brood stock, estimates that in 1990 a high proportion of fish passing Lower Granite Dam and found on nearby spawning grounds were hatchery strays, and the lack of any positive information documenting the continued existence of "pure" wild fish. However, given that 1) an ESU was present until at least the early 1980s, 2) substantial straying of upper Columbia River hatchery fish has occurred only within the last generation, and 3) no direct evidence exists for genetic change to wild fall chinook salmon in the Snake River, the BRT felt it would be premature to conclude that the ESU no longer exists.

In addition, the BRT concluded that Snake River fall chinook salmon face a substantial risk of extinction if factors affecting the population remain unchanged. This conclusion was based on the following considerations: 1) substantial reductions in habitat for fall chinook salmon in the Snake River have occurred in this century; 2) the present abundance of wild fish is a small fraction of the historical abundance, and estimates for 1990 are the lowest on record; 3) application of a simple stochastic model to recent abundance data indicates extinction is likely if present conditions continue; and 4) current hatchery operations pose clear and immediate threats to the genetic integrity of Snake River fall chinook salmon.

ACKNOWLEDGMENTS

This status review was conducted by the NMFS Northwest Region Biological Review Team. The extensive public record developed pursuant to this petition and discussions of that record by the ESA Technical Committee formed the basis for the review. Members of the BRT for fall chinook salmon were Brian Beckman, David Damkaer, Thomas Flagg, Elizabeth Garr, Lee Harrell, Orlay Johnson, Robert Jones, Conrad Mahnken, Gene Matthews, Desmond Maynard, Gerald Monan, Ben Sandford, Michael Schiewe, George Swan, Grant Thompson, Merritt Tuttle, Robin Waples, John Williams, Gary Winans, and Waldo Zaugg.

INTRODUCTION

Chinook salmon (*Oncorhynchus tshawytscha*) are native to the Snake River, the largest tributary of the Columbia River. In the Snake River Basin, three races (spring-, summer-, and fall-run fish) are recognized based on time of entry of adults into fresh water. Historically, chinook salmon were abundant throughout most of the large, complex Snake River drainage. From the latter 1800s until the present, a variety of factors have led to the current depressed status of these populations. This situation prompted Oregon Trout, Oregon Natural Resources Council, Northwest Environmental Defense Center, American Rivers, and the Idaho and Oregon Chapters of the American Fisheries Society to petition the National Marine Fisheries Service (NMFS) to list each of the races of Snake River chinook salmon as threatened or endangered "species" under the U.S. Endangered Species Act (ESA) of 1973 as amended (U.S.C. 1531 *et seq.*). This report summarizes a review of the status of Snake River fall chinook salmon conducted by the NMFS Northwest Region Biological Review Team (BRT). The status of spring and summer chinook salmon from the Snake River is reviewed elsewhere (Matthews and Waples 1991).

KEY QUESTIONS IN ESA EVALUATIONS

Two key questions must be addressed in determining whether a listing under the ESA is warranted:

1) Is the entity in question a "species" as defined by the ESA?
2) If so, is the "species" threatened or endangered?

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 Act provides no guidance for determining what constitutes a distinct population, and the resulting ambiguity has led to use of a variety of criteria in listing decisions over the past decade. To clarify the issue for Pacific salmon, NMFS published an interim policy describing how the agency will apply the definition of "species" in the Act to anadromous salmonid species (Federal Register Docket No. 910248-1048; 13 March 1991). A more detailed description of this topic appears in the NMFS "Definition of Species" paper (Waples 1991).

The NMFS policy stipulates that a salmon population (or group of populations) will be considered "distinct" for purposes of the Act if it represents an evolutionarily significant unit (ESU) of the biological species. An ESU is defined as a population that (a) is reproductively isolated from conspecific populations and (b) represents an important component in the evolutionary legacy of the species. Types of information that can be useful in determining the degree of reproductive isolation include incidence of straying, rates of recolonization, degree of genetic differentiation, and the existence of barriers to migration. Insight into evolutionary significance can be provided by data on phenotypic and protein or DNA characters, life-history characteristics, habitat differences, and the effects of stock transfers or supplementation efforts.

For ESA evaluations of Snake River chinook salmon, we also must consider races of fish that have traditionally been differentiated on the basis of run-timing. Following the framework of the "Definition of Species" paper, we must first determine whether spring-, summer-, and fall-run chinook salmon in the Snake

River are separate, reproductively isolated groups. Those groups that are reproductively isolated from groups with other run-times should be considered separately for ESA purposes; fish of different run-times for which reproductive isolation cannot be established should be considered as a unit.

Thresholds for Threatened or Endangered Status

Neither the National Marine Fisheries Service nor the U.S. Fish and Wildlife Service (USFWS), which share authority for administering the ESA, has an official policy regarding thresholds for considering ESA "species" as threatened or endangered. The Northwest Region of NMFS has recently published a paper on this topic (Thompson 1991). Written comments received by NMFS and extensive discussions in ESA Technical Committee meetings stressed the importance of incorporating the concepts of Population Viability Analysis (PVA) into threshold considerations. However, the field is rapidly evolving and a definitive policy position on this issue is not expected in the near future. Furthermore, most of the PVA models developed to date require substantial life-history information that often will not be available for Pacific salmon populations.

Therefore, instead of using a single, numerical threshold value, we used a variety of information in evaluating the level of risk faced by an ESU. Important factors considered included 1) absolute numbers of fish and their spatial and temporal distribution; 2) current abundance in relation to historical abundance and current carrying capacity of the habitat; 3) trends in abundance, based on indices such as dam or redd counts or on estimates of spawner-recruit ratios; 4) natural and human-influenced factors that cause variability in survival and abundance; 5) possible threats to genetic integrity (e.g., from strays or outplants from hatchery programs); and 6) recent events (e.g., a drought or improvements in main-stem passage) that have predictable short-term consequences for abundance of the ESU. In addition, until a more comprehensive PVA model becomes available for Pacific salmon, we used the stochastic extinction model of Dennis et al. (1991) to provide some idea of the likely status of the population in the future. This model is useful for identifying outcomes that are likely if no protective measures are taken because it assumes that future fluctuations in population abundance are determined by parameters of the population measured in the recent past.

Hatchery Fish and Wild Fish

Because most of the effort in the last decade directed toward restoring Snake River fall chinook salmon focused on brood-stock development at Lyons Ferry Hatchery (Fig. 1), the role of hatchery fish also needs to be addressed in this status review. NMFS policy stipulates that in determining whether a population is "distinct" for purposes of the ESA, attention should focus on "wild" fish, which are defined as progeny of naturally-spawning fish (Waples 1991).[1] This approach directs attention to fish that spend their entire life cycle in natural habitat and is consistent with the mandate of the Act 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.

The decision to focus on wild fish is based entirely on ecosystem considerations; the question of the relative merits of hatchery vs. wild fish is a separate issue. Fish are not excluded from ESA consideration simply because some

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[1] The term "wild" has been used in a variety of ways in the literature on Pacific salmon. Often, "wild" is used to indicate fish that meet two criteria: they must be 1) progeny of naturally spawning parents and 2) indigenous to the area, with little or no influence from stock transfers, hatchery straying, or other aspects of artificial propagation. In the present document, the term "wild" is used to identify fish that meet the first criterion; evaluation of the ancestry of naturally-spawning fish is a separate issue.

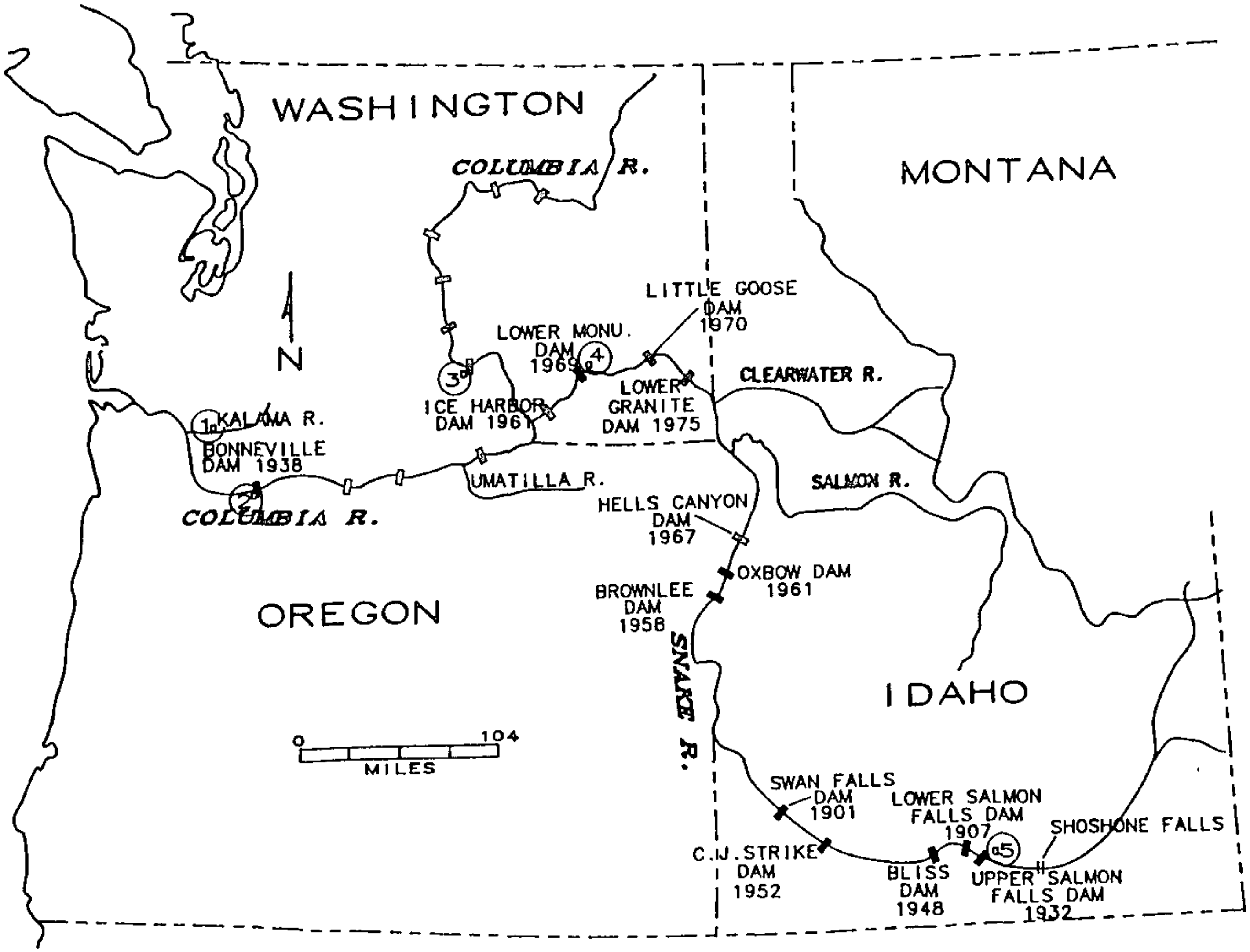

Figure 1.--Map showing location of Snake River dams (with first date of operation), rivers, and hatcheries described in the text. 1 = Kalama Falls Hatchery; 2 = Bonneville Hatchery; 3 = Priest Rapids Hatchery; 4 = Lyons Ferry Hatchery; 5 = Hagerman Hatchery. Locations for Bonneville Dam and other Columbia River dams are also indicated.

of their direct ancestors may have spent time in a fish hatchery, nor does identifying a group of fish as "wild" as defined here automatically mean that they are part of an ESU.

Once the wild component of a population has been identified, the next step is to determine whether this population component is "distinct" for purposes of the ESA. In making this determination, we used guidelines in the NMFS "Definition of Species" paper (Waples 1991). We considered factors outlined in Section IIIC (Effects of supplementation and other human activities) to determine the extent to which artificial propagation may have affected the wild fish, through either direct supplementation or straying of hatchery fish. Thus, fish meeting the definition of "wild" adopted here may subsequently be excluded from ESA considerations for other reasons.

Threshold determinations also will focus on wild fish, on the premise that an ESU is not healthy unless a viable population exists in the natural habitat. In developing recovery plans for "species" listed as threatened or endangered, the use of artificial propagation may be considered. If an existing hatchery is associated with the listed "species," an important question to address in formulating a recovery plan is whether the hatchery population is similar enough to the wild population that it can be considered part of the ESU. Factors to consider in this regard include origin of donor stock(s), brood-stock practices, evidence for domestication or artificial selection, population size, and the number of generations the stock has been cultured. In general, hatchery populations that have been substantially changed as a result of these factors should not be considered part of the ESU.

SUMMARY OF BIOLOGICAL AND ENVIRONMENTAL INFORMATION

Life History Characteristics

Chinook salmon have a diversity of juvenile and adult life history strategies that have been used to characterize and categorize different populations. One approach, commonly used in Alaska and Canada, is to differentiate between populations with "ocean" or "stream" juvenile life history patterns (Healey 1983; Taylor 1989). "Ocean" type fish migrate to sea as subyearlings, whereas "stream" type fish spend an additional year (occasionally more) in fresh water before outmigration. "Stream" type chinook salmon predominate in colder latitudes (Alaska and northern British Columbia) and higher elevations (e.g., the upper Fraser River and in some Columbia River tributaries), and "ocean" type fish are more common in warmer areas (coastal areas from Vancouver Island south, the Lower Fraser River, and the Klamath and Sacramento Rivers). In most other areas, there is a strong tendency for one or the other of the life history strategies to predominate; the Columbia River Basin is notable in that each life history strategy is represented by numerous runs.

In the United States, chinook salmon are typically characterized as "spring-", "summer-", or "fall-run" according to the time adults enter fresh water to begin the spawning migration (a "winter" run is also recognized in the Sacramento River). In general, "spring" chinook salmon are "stream" type fish and "fall" (and "winter") chinook salmon are "ocean" type fish. Populations identified as "summer" chinook salmon have "ocean" type life history patterns in some areas and "stream" type life histories in others.

In the Columbia River Basin, adult chinook salmon migrating upstream past Bonneville Dam (Fig. 1) from March-May, June-July, and August-October are categorized as spring-, summer-, and fall-run fish, respectively (Burner 1951). Spring chinook salmon occur in tributaries of the lower, mid-, and upper Columbia River[2] and in the upper Snake River Basin, and summer chinook salmon are found in the upper Columbia and Snake Rivers.

Fall chinook salmon in the Columbia River Basin can be divided into two physiologically distinct types: "tules" and "upriver brights." Tules, which are confined to the lower river tributaries (generally, those below Bonneville Dam), are sexually mature when they enter fresh water as adults, as indicated by their dark coloration. In contrast, fall-run fish destined to spawn in upriver areas are known as "brights" because they mature more slowly (having a greater distance to travel upriver before spawning) and therefore retain their silvery oceanic coloration well into their freshwater migration. Upriver brights are highly prized in river fisheries because their flesh is of high quality. Bright runs are found in the upper Columbia and Snake Rivers and in the Deschutes River in Oregon (Fig. 1). The most abundant remaining naturally-spawning bright runs are found in the Hanford Reach of the Columbia River (an 84-km stretch from near Richland, Washington, to Priest Rapids Dam), the last free-flowing stretch of the river between Bonneville Dam and the Canadian border (Swan 1989).

In the Snake River, habitat utilized by fall chinook salmon for spawning and early juvenile rearing is very different from that utilized by spring- and summer-run fish (Chapman et al. 1991). The latter two forms spawn and rear in small, high elevation streams, whereas fall chinook salmon use main-stem areas or the lower parts of major tributaries (Fig. 2). Juvenile behavior also distinguishes Snake River

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[2] In this document, the terms lower, mid-, and upper Columbia River refer, respectively, to areas below Bonneville Dam, between Bonneville Dam and the confluence with the Snake River, and above the confluence with the Snake River. Some other authors use the term "mid-Columbia" to include the area between the confluence with the Snake River and Grand Coulee Dam.

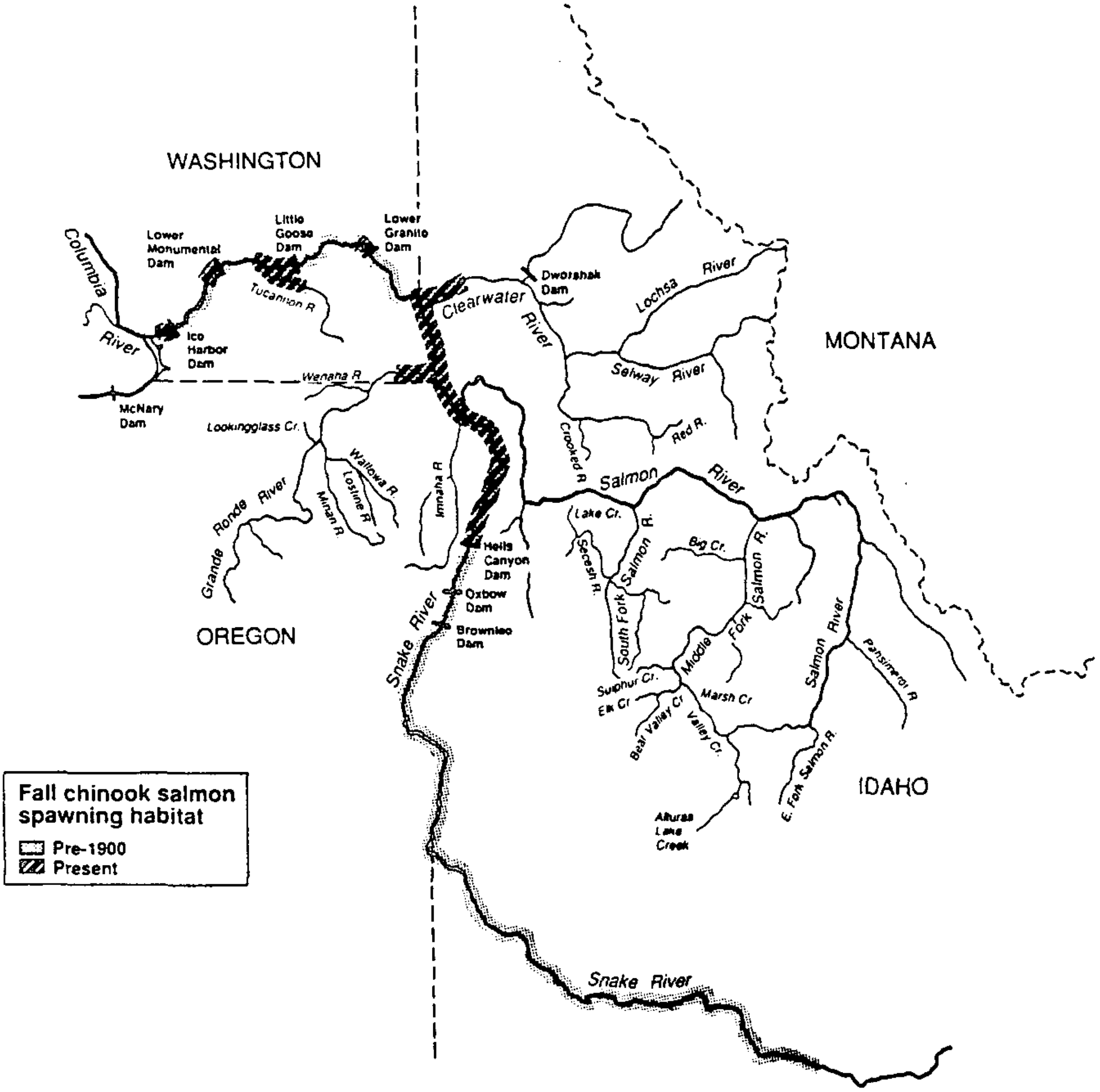

Figure 2.--Historical spawning habitat for spring-, summer-, and fall-run chinook salmon in the Snake River Basin.

fall chinook salmon (which move seaward slowly as subyearlings) from spring- and summer-run fish (which migrate swiftly to sea as yearling smolts) (Schreck et al. 1986; Chapman et al. 1991).

Adult Snake River fall chinook salmon enter the Columbia River in July and August and reach the mouth of the Snake River from the middle of August through October. Spawning occurs in the main stem and in the lower reaches of large tributaries in October and November (NWPPC 1989; Bugert et al. 1990). Based on what is known of upper Columbia River fall chinook salmon, juveniles in the Snake River presumably emerge from the gravel in March and April, and downstream migration usually begins within several weeks of emergence (Chapman et al. 1991). Trapping studies conducted in 1954 and 1955 showed that juveniles moving through the lower Snake River in March and April were less than 50 mm in length, whereas those migrating in May and June were 60 to 80 mm (Chapman et al. 1991). Bell (1959, 1961) found that peak fry migration in the Brownlee-Oxbow Dam reach of the Snake River occurred from April through the middle of May.

Little information is available to determine the extent to which fall chinook salmon rear for extended periods in the Snake River. Juveniles have been found at Lower Granite Dam and in the reservoir behind the dam through June (Raymond and Sims 1980; Bennett et al. 1990). However, elevated water temperatures are thought to preclude rearing of fall chinook salmon in the Snake River after early to mid-July (Van Hyning 1968; Chapman et al. 1991; Mundy 1991). The preferred temperature range for chinook salmon has been variously described as 54-57°F (12.2-13.9°C; Brett 1952), 50-60°F (10-15.6°C; Burrows 1963), or 13-18°C (Theurer et al. 1985). Summer temperatures in the Snake River substantially exceed the upper limits of this range (see Environmental Features section, below).

Rich (1922) studied the downstream migration of chinook salmon in the lower Columbia River and concluded that fry were present from June to October. Fall chinook salmon fry were found to be abundant in May and June (Reimers 1964). Van Hyning (1968) reported that chinook salmon fry tend to linger in the lower Columbia River and may spend a considerable portion of their first year in the estuary.

Adults return to the Snake River at ages 2-5, with age 4 the most common age at spawning (Chapman et al. 1991).

Past and Present Distribution and Abundance

Historically, the Columbia River Basin produced more chinook salmon than any other river system in the world (Van Hyning 1973). Fall chinook salmon were widely distributed throughout the Snake River and many of its major tributaries, from its confluence with the Columbia River upstream 990 km to Shoshone Falls, Idaho (Columbia Basin Interagency Committee 1957; Haas 1965; Fulton 1968; Van Hyning 1968; Lavier 1976; see Fig. 2). Evermann (1896) reported that "we were not able to learn that salmon reached the foot of Shoshone Falls although it is very probable that they do so."

Limited information is available from which to estimate the abundance of Snake River fall chinook salmon during the 1800s and early 1900s. Craig and Hacker (1950) estimated that prior to the arrival of white settlers, 50,000 native Americans from the Columbia River tribes may have harvested an average of 18 million pounds of Pacific salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss*) annually. A large proportion of the catch was thought to be fall chinook salmon because these fish were present during low flow conditions that favored harvest. Evermann (1896) reported that the spawning grounds of chinook salmon in the

Snake River between Huntington [River Kilometer (RKm) 527] and Auger Falls (RKm 977) were the most important in Idaho, and that more salmon fishing for commercial purposes occurred there than in any other area in the state. According to one account cited in Evermann (1896), "salmon are most abundant about October 10, and are ripe when they first come. The smallest weigh about 5 pounds and the largest probably 60 pounds. Last year I caught about 6 tons, which I sold at 3 cents a pound." Prior to the 1960s, the Snake River was considered the most important drainage in the Columbia River system for the production of anadromous fishes. Approximately half of the fish returning to areas above McNary Dam were destined for the Snake River Basin (Bureau of Commercial Fisheries and Bureau of Sport Fisheries and Wildlife 1964).

The construction of 12 dams on the main-stem Snake River (Fig. 1) substantially reduced the distribution and abundance of Snake River fall chinook salmon (Irving and Bjornn 1981a). Fish passage facilities proved unsuccessful at several projects, and spawning habitats, particularly areas most frequently utilized by fall chinook salmon, were eliminated with the formation of reservoirs.

The construction of Swan Falls Dam (1901; RKm 734) obstructed passage of adults and rendered 256 km of main-stem habitat inaccessible to fall chinook salmon (Parkhurst 1950). During the early 1900s, the Fish Commission of Oregon placed a weir in the Snake River downstream from Swan Falls Dam near Ontario, Oregon (RKm 599), to collect fall chinook salmon brood stock for hatchery production. Although only a portion of the fall chinook salmon run was intercepted, more than 20 million eggs (a minimum of 4,000 females) were taken in a single year (Parkhurst 1950). This provides some indication of the distribution and large number of fall chinook salmon migrating into the upper reaches of the Snake River during this period.

Snake River fall chinook salmon remained relatively stable in abundance through the first part of this century, but declined substantially thereafter. Following the decline of Columbia River spring and summer chinook salmon during the late 1800s, fall chinook salmon constituted the major commercial fisheries, with annual catches ranging from 3 million to nearly 9 million kg (Table 1). Irving and Bjornn (1981b) estimated that the mean number of fall chinook salmon returning to the Snake River declined from 72,000 in the period 1938-49 to 29,000 during the 1950s. Fall chinook salmon escapement reflected in spawning ground surveys also declined during this period. In spite of this significant decline in abundance, the Snake River remained the most important natural production area for fall chinook salmon in the Columbia River Basin through the 1950s (Fulton 1968).

The upper reaches of the main-stem Snake River were the primary areas utilized by fall chinook salmon (Fig. 2), with only limited spawning activity reported downstream from RKm 439. The construction of Brownlee Dam (1958; RKm 459), Oxbow Dam (1961; RKm 439), and Hells Canyon Dam (1967; RKm 397) eliminated the primary production areas of Snake River fall chinook salmon. Habitat was further reduced with the construction of four additional dams on the lower Snake River: Ice Harbor Dam (1961; RKm 16), Lower Monumental Dam (1969; RKm 67), Little Goose Dam (1970; RKm 113), and Lower Granite Dam (1975; RKm 173). Apart from the possibility of deep-water spawning (discussed below) in lower areas of the river, the main-stem Snake River from the upper limit of the Lower Granite Dam reservoir to Hells Canyon Dam (approximately 165 km) and the lower reaches of the Imnaha, Grande Ronde, Clearwater, and Tucannon Rivers are the only remaining areas available to fall chinook salmon in the Snake River Basin.

Table 1.--Catch of chinook salmon (in thousands of kilograms) in the Columbia River by season, 1928-60 (from Fulton 1968).

	Run-timing		
Year	Spring	Summer	Fall
1928	1,000	2,318	4,140
1929	1,166	2,272	3,012
1930	1,324	1,900	4,118
1931	1,362	2,506	5,666
1932	1,164	2,510	3,509
1933	731	3,044	4,514
1934	743	2,264	5,344
1935	1,157	2,224	3,494
1936	958	1,661	4,595
1937	1,551	1,328	5,572
1938	815	992	3,857
1939	740	1,544	3,849
1940	360	847	4,924
1941	665	883	8,977
1942	503	660	7,307
1943	604	404	4,188
1944	490	528	5,367
1945	710	233	4,959
1946	559	207	5,710
1947	556	449	6,882
1948	902	289	6,699
1949	774	137	3,984
1950	595	196	3,936
1951	903	286	3,365
1952	1,322	319	1,658
1953	808	321	2,025
1954	660	269	1,515
1955	1,583	504	1,823
1956	1,158	776	1,794
1957	879	606	1,264
1958	1,066	658	1,243
1959	628	577	982
1960	451	366	998

Returns of adult fall chinook salmon to the Snake River have declined to very small numbers in recent years. Yearly adult counts at the uppermost Snake River main-stem project affording fish passage averaged 12,720 from 1964 through 1968, 3,416 from 1969 through 1974, and 610 from 1975 through 1980 (Table 2). Counts through 1980 presumably represent wild fish. The first hatchery-reared Snake River fall chinook salmon returned to the Snake River in 1981 (Busack 1991b), and since then, counts of adults at lower Snake River dams reflect a mixture of hatchery and natural production. Estimates of the abundance of naturally-produced Snake River fall chinook salmon over the last decade are discussed in the section on artificial propagation (below).

Straying

Salmon and steelhead that return to spawn in areas other than their natal stream are considered strays. Tagging data suggest that the natural rate of straying of fall chinook salmon into the Snake River is very low. In 1981, over 200,000 juvenile fall chinook salmon from the upper Columbia River were fitted with coded-wire tags (CWTs), and over the next 4 years adult returns were monitored in all Columbia River Basin hatcheries as well as on fall chinook salmon spawning grounds (McIsaac and Quinn 1988). All of the several hundred recoveries of tagged upper Columbia River fish occurred on the natal spawning grounds, upstream from the spawning grounds, or in gill-net fisheries that intercept fish migrating up the Columbia River. This result is consistent with the very low incidence of tagged upper Columbia River fall chinook salmon appearing in Lyons Ferry Hatchery brood stock; since the hatchery (situated near the upstream end of Lower Monumental Dam reservoir, 79 km from Ice Harbor Dam) opened in 1984, only three such tags have been recovered from fish that were collected at Ice Harbor Dam or swam

Table 2.--Adult fall chinook salmon counted at lower Snake River dams [from COE[a] and ODFW and WDF (1990)].

Year	Ice Harbor Dam	Lower Monumental Dam	Little Goose Dam	Lower Granite Dam
1964	8,100	-	-	-
1965	8,200	-	-	-
1966	12,800	-	-	-
1967	14,000	-	-	-
1968	19,500	-	-	-
1969	13,600	6,200	-	-
1970	9,000	5,300	4,500	-
1971	9,300	7,800	4,700	-
1972	7,500	4,100	1,800	-
1973	6,700	3,800	2,400	-
1974	2,400	2,200	900	-
1975	1,900	1,800	900	1,000
1976	1,100	1,100	430	470
1977	1,200	870	420	600
1978	1,100	500	490	640
1979	1,200	620	550	500
1980	1,200	570	500	450
1981	770	490	420	340
1982	1,600	930	-	720
1983	1,800	800	-	540
1984	1,700	620	-	640
1985	2,046	982	-	691
1986	3,104	1,741	-	784
1987	6,788	3,327	-	951
1988	3,847	1,647	-	627
1989	4,638	2,018	-	706
1990	3,477	-	-	385

[a] U.S. Army Corps of Engineers, Projected daily fish passage report for 1990, unpublished data, U.S. Army Engineer District, Portland, OR.

voluntarily into the hatchery (Busack 1991b). There is growing evidence, however, that hatchery fish of Columbia River origin have strayed into the Snake River in the past few years . This topic is discussed in the next section.

Artificial Propagation

Available information indicates that the few attempts at artificial propagation of fall chinook salmon in the Snake River prior to 1976 were of short duration and had little effect. As noted above, fall chinook salmon eggs were collected during the early 1900s in the upper Snake River near Ontario, Oregon, for hatchery production. The destination of resulting progeny and the duration of this effort are uncertain.

In the early 1960s, attempts were made to maintain natural production of fall chinook salmon in habitats above Oxbow Dam on the main-stem Snake River. A stream channel and facilities for incubating up to 5 million eggs annually were first used at Oxbow Dam in 1961 (Welsh et al. 1965). Fall chinook salmon were trapped on site and eyed eggs deposited in the stream channel or transferred to other locations. In 1961, 1,839 adult fall chinook salmon were collected, but only 701 survived to spawning. Although efforts were made to maintain fall chinook salmon production in the upper Snake River, fish passage facilities at these projects proved to be inadequate (Van Hyning 1968). Fall chinook salmon escapement declined dramatically (Table 3), and further attempts to maintain this population were discontinued. Fall chinook salmon were not transported above Oxbow Dam after 1962.

The Clearwater River was the focus of the other major artificial propagation effort involving Snake River fall chinook salmon prior to the 1970s. Native fall chinook salmon in the Clearwater River were virtually or totally eliminated following the construction of Lewiston Dam in 1929 (Columbia Basin Interagency

Table 3.--Adult and jack (age 2) Snake River fall chinook salmon counted past Brownlee Dam site (1957), past Oxbow Dam site (1958), transported past Oxbow Dam (1959-62), trapped and held at Oxbow Hatchery (1963-66), and trapped at Hells Canyon Dam and held at Oxbow Hatchery (1967-79) (from Irving and Bjornn 1981a).

Year	Number of fish
1957	15,160
1958	14,078
1959	11,830
1960	4,911[a]
1961	4,616[b]
1962	1,585[c]
1963	945
1964	1,503
1965	1,584
1966	3,612
1967	1,249
1968	412
1969	50
1970	12
1971	4
1972	2
1973	1
1974	15
1975	13
1976	0
1977	4
1978	1
1979	2

[a] 220 additional fish taken for eggs.
[b] 2,025 additional fish taken for eggs.
[c] 819 additional fish taken for eggs.

Committee 1957). The Clearwater was again accessible to fall chinook salmon in 1939 when the original fishway was remodeled and two new fishways constructed. Transfers of eyed eggs by the Idaho Department of Fish and Game from 1948 through 1955 represent the first efforts to reestablish fall chinook salmon in this drainage (Bureau of Commercial Fisheries and Bureau of Sport Fisheries and Wildlife 1964). The origin and extent of these early transfers are uncertain. Egg transfers from 1960 through 1967 ranged from 400,000 to nearly 1.6 million annually and originated primarily from adult fall chinook salmon trapped at Oxbow Dam. Approximately 250,000 of the 1.46 million eyed eggs collected at Oxbow in 1961 were transferred to the Clearwater River; in 1962, 424 females produced 1.9 million eggs that survived to the eyed stage, and 400,000 of these were transferred to the Clearwater River. Egg transfers to the Clearwater River were terminated in 1968, and adult returns thereafter declined to just a few individuals (Irving and Bjornn 1980). Approximately 500,000 eggs from Spring Creek National Fish Hatchery (NFH) (on the lower Columbia River) were planted in the Clearwater River in 1960. This instance, and a single transfer of juvenile fall chinook salmon from Spring Creek NFH to below Hells Canyon Dam in 1970, represent the only recorded introductions of nonindigenous fall chinook salmon into the Snake River Basin.

To offset losses of anadromous fish resulting from the construction and operation of Ice Harbor, Lower Monumental, Little Goose, and Lower Granite Dams, the Lower Snake River Compensation Plan (LSRCP) was authorized under the Water Resources Development Act of 1976 (Public Law 94-587). Federal and state resource agencies collaborated to estimate impacts on fish stocks and develop compensation measures. Hatchery facilities designed to produce 18,300 adult fall chinook salmon returning to the project area were determined necessary to compensate for downstream migrant passage mortality and loss of spawning habitat. The production potential of the remaining free-flowing reach of the Snake River was estimated to be more than 13,000 adults (Herrig 1990).

During the planning and design of LSRCP production facilities, substantial declines in fall chinook salmon returns prompted the initiation of an egg bank program to ensure that brood stock of Snake River origin would be available when these facilities became operational. The egg bank program utilized several facilities in the Columbia River Basin in a "spread the risk" philosophy. A primary objective of the egg bank program was to maintain the genetic integrity of the Snake River fall chinook salmon population (Bugert and Hopley 1989).

Adults for the egg bank program were first captured in 1976 at Little Goose Dam and raised at Bonneville Fish Hatchery. Resulting progeny, which had their ventral fin clipped so they could be identified if they returned as adults, were released in the Kalama River, a tributary of the lower Columbia River (Bugert and Hopley 1989). A release site in the lower river was selected so that juveniles and adults would not have to negotiate dams on the Columbia and Snake Rivers.

From 1977 to 1984, Snake River fall chinook salmon brood stock were trapped at Ice Harbor Dam (Table 4). Eggs were transferred to Kalama Falls Hatchery (Fig. 1) from 1977 through 1983, and adults returning to this hatchery from 1979 to 1986 contributed to the LSRCP egg bank program. In 1978, because of concerns that a single hatchery operation was vulnerable to disease outbreak, a parallel operation was initiated by USFWS at Hagerman NFH, near Twin Falls, Idaho, at RKm 944 on the Snake River (Fig. 1). The first releases of juvenile fall chinook salmon into the Snake River under the LSRCP were in 1979 (from the 1978 brood at Hagerman NFH). These releases continued through 1985 and ranged from

Table 4.--Sources of adult fall chinook salmon brood stock for Snake River egg bank program (from Busack 1991b).

Year	Ice Harbor Dam	Kalama Falls Hatchery	Lyons Ferry Hatchery
1976	162[a]	-	-
1976	395	-	-
1978	368	-	-
1979	439	-	-
1980	394	208	-
1981	407	561	-
1982	473	98	-
1983	619	86	-
1984	663	220	-
1985	589	952	6
1986	212	576	245
1987	1,613	-	1,654
1988	1,076	-	327
1989	1,179	-	704
1990	1,142[b]	-	586

[a] Collected at Little Goose Dam.
[b] Includes 50 adults taken at Lower Granite Dam.

approximately 45,000 to 475,000 fish (Herrig 1990). Adult returns to the Snake River from these releases began in 1981 and ranged from 0.01 to 0.24% (Bugert and Hopley 1989).

All brood-stock operations for Snake River fall chinook salmon were transferred to Lyons Ferry Hatchery following its completion in 1984. Annual releases of juveniles from Lyons Ferry Hatchery have fluctuated from approximately 380,000 to more that 4.5 million fish. The first adults from Lyons Ferry releases returned in 1987 (Herrig 1990).

Although available evidence indicates that efforts to maintain the genetic integrity of the Snake River fall chinook salmon population through the generation or so that fish were transferred to the lower Columbia River were successful (Seidel et al. 1988; Busack 1991b), the goal of enhancing natural production has been more elusive. Presumably at least in part as a result of the hatchery program, adult returns to Ice Harbor Dam have increased from low numbers observed in the late 1970s and early 1980s. However, a similar increase has not occurred in the count at Lower Granite Dam, which provides a better indication of the abundance of naturally-spawning fish. The total count has remained under 1,000 fish since 1975, and the count for 1990 was the lowest on record (Table 5).

Furthermore, in recent years, stray Columbia River fish of hatchery origin have appeared in alarming numbers in the Lyons Ferry Hatchery brood stock (Table 6). Most of the strays are part of the Bonneville egg bank program for upper Columbia River fall chinook salmon. Adults for brood stock are collected from fish that migrate over Bonneville Dam in the time period designated for fall-run fish (i.e., after 1 August). Releases occur at various sites in the Columbia River, including the Umatilla River. Seasonal dewatering of the Umatilla River for irrigation eradicated native chinook salmon runs, and releases of Bonneville stock

Table 5.--Estimated number of adult hatchery and wild chinook salmon at Lower Granite Dam, 1975-90 (from Busack 1991a). See text for discussion of estimation methods.

		Snake River hatcheries		Columbia River hatcheries				
Year	Total	Lyons Ferry	Hagerman	Umatilla[a]	Other	Wild	Percent hatchery[b]	Percent Columbia River
1975	1,000	-	-	-	-	1,000	-	-
1976	470	-	-	-	-	470	-	-
1977	600	-	-	-	-	600	-	-
1978	640	-	-	-	-	640	-	-
1979	500	-	-	-	-	500	-	-
1980	450	-	-	-	-	450	-	-
1981	340	-	-	-	-	340	-	-
1982	720	-	-	-	-	720	-	-
1983	540	-	112	-	-	428	21	-
1984	640	-	310	6	-	324	49	1
1985	691	-	241	12	-	438	37	2
1986	784	64	261	5	5	449	43	1
1987	951	575	69	43	11	253	73	6
1988	627	192	9	49	9	368	41	9
1989	706	206	-	158	47	295	58	29
1990	335[c]	174	-	77	6	78	77	25

[a] Originated from Bonneville egg bank program and released into the Umatilla River.

[b] Hatchery fish may have appeared at Lower Granite Dam prior to 1983, but there is no basis for estimating their numbers.

[c] Excluding 50 coded-wire tagged fish trapped and taken to Lyons Ferry Hatchery.

Table 6.--Origins of fall chinook salmon brood stock used in Lyons Ferry Hatchery, as estimated from analysis of coded-wire tag data (from Busack 1991a).

		Estimated contribution (%)		
Brood year	Total adults	Snake River[a]	Umatilla[b]	Other
1984	569	95	5	0
1985	549	89	10	1
1986	1,377	97	2	2
1987	3,530	96	3	1
1988	1,674	82	15	3
1989	2,205	61	34	5

[a] Fish not accounted for by expansion of tags for non-Snake River returns.
[b] Originated from Bonneville egg bank program and released into the Umatilla River.

fall chinook salmon which began in 1983 are intended to help reestablish a Umatilla run (Howell et al. 1985). Unfortunately, poor acclimation of juveniles prior to release and lack of sufficient water for spawning in the fall apparently contribute to an increased rate of straying in these fish (Chapman et al. 1991).

Based on analysis of CWT-fish spawned at Lyons Ferry Hatchery, Cooney (in Busack 1991a) estimated that strays from the Columbia River made up 4% of the adults in 1987, 18% in 1988, and 39% in 1989 (Table 6), and Bugert et al. (1990) estimated that strays made up approximately 25% of the adults at Lyons Ferry Hatchery in 1990. The majority of strays were from releases into the Umatilla River.

Progeny from brood years prior to 1989, which sustained straying rates of up to 18%, had already been released from Lyons Ferry Hatchery before the problem was realized. Only a portion of these fish were marked, so there is no way to identify all returning adults resulting from these broods. However, following the discovery of the magnitude of straying (Roler 1990), the Washington Department of Fisheries (WDF) initiated measures to reduce the effects of these strays on the genetic integrity of Lyons Ferry Hatchery brood stock (Busack 1991b). All juvenile progeny from adults spawned in 1989 were marked prior to release, so this entire year class can be prevented from making any future genetic contribution to the hatchery brood stock. In addition, gametes from adults returning in 1990 were not mixed until CWTs (if any) were read and the hatchery of origin determined. This resulted in segregation of three groups of adults for spawning: A--fish carrying CWTs indicating a Lyons Ferry Hatchery origin, B--fish carrying CWTs from other hatcheries (known strays), and C--untagged fish (a mixture of wild fish, untagged strays, and untagged Lyons Ferry Hatchery fish). Only progeny from Group A will be allowed to contribute to future generations in Lyons Ferry Hatchery (Busack 1991b). Thus, there is an opportunity to reduce or eliminate the effects of straying into Lyons Ferry Hatchery for the 2 years (1989, 1990) with the highest incidence of straying.

The discovery that upper Columbia River hatchery fish are straying into the Snake River in substantial numbers raised concern that some of these fish may also stray onto spawning grounds in the Snake River. To evaluate this possibility, biologists from WDF and the Oregon Department of Fish and Wildlife (ODFW) attempted to estimate the number of hatchery fish that passed Lower Granite Dam in 1990; the number of wild fish could then be estimated by subtraction from the total adult count. The method depends on screening CWT fish at the dam and determining the hatchery of origin. However, two factors complicate this process: 1) not all hatchery fish are marked, and the proportion of marked fish varies considerably among hatcheries [e.g., from an average of about 55% in Lyons Ferry Hatchery (Bugert et al. 1990) to generally less than 10% for the Umatilla program] and 2) CWT fish were not screened at Lower Granite Dam until 1990. The standard approach to the first problem is to "expand" the number of observed tag recoveries to account for untagged fish from the same locality. This amounts to estimating the total contribution from a hatchery by dividing the number of observed recoveries by the fraction tagged. There are intrinsic statistical difficulties in computing the standard errors for the resulting estimates, but the errors are generally thought to be large, particularly if the tagging rate is low. To address the second factor, ODFW (1991b) and WDF (Busack 1991a) estimated the number of hatchery fish at Lower Granite Dam in previous years by assuming that strays from each hatchery reached the dam in the same proportions they were represented in the brood stock at Lyons Ferry hatchery for that year. Clearly, there is an additional degree of uncertainty associated with this estimation procedure.

Estimates of hatchery and wild fish reaching Lower Granite Dam based on these methods are shown in Table 5 and Figure 3. Several points are worth noting. First, an appreciable fraction (about 20-80%) of the total fish reaching the dam each year since 1983 is estimated to have been of hatchery origin. Second, after subtracting the estimated number of hatchery fish from the total, the estimated number of wild fish shows a pronounced downward trend in the past decade. Third, the estimated percentage of hatchery fish at Lower Granite Dam in 1990 (77%) was the highest to date, and the estimated number of wild fish the lowest. In fact, the 78 estimated wild fish in 1990 are only 31% of the next lowest estimate (253 in 1987).

In addition to the natural spawning areas upstream from Lower Granite Dam, there are two additional locations in the Snake River where wild Snake River fall chinook salmon may spawn in limited numbers. The first area is in the lower Tucannon River, where fall-spawning fish have been found in recent years (Bugert 1991). The ancestry of these fish is uncertain. The second area is in the tailraces of the lower Snake River dams. Although there is no documented evidence of spawning near the dams, several lines of evidence suggest this may be the case. Fall chinook salmon are known to utilize deep-water spawning areas in the upper Columbia River (Swan 1989), and this may be true in the Snake River as well. A preliminary analysis indicates that about 75-80 km of habitat between the mouth of the Snake River and the mouth of the Clearwater River is potentially suitable for deep-water fall chinook salmon spawning (G. Swan[3]). Furthermore, a substantial

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[3] G. Swan, National Marine Fisheries Service, 2725 Montlake Blvd. E., Seattle, WA 98112. Pers. commun., March 1991.

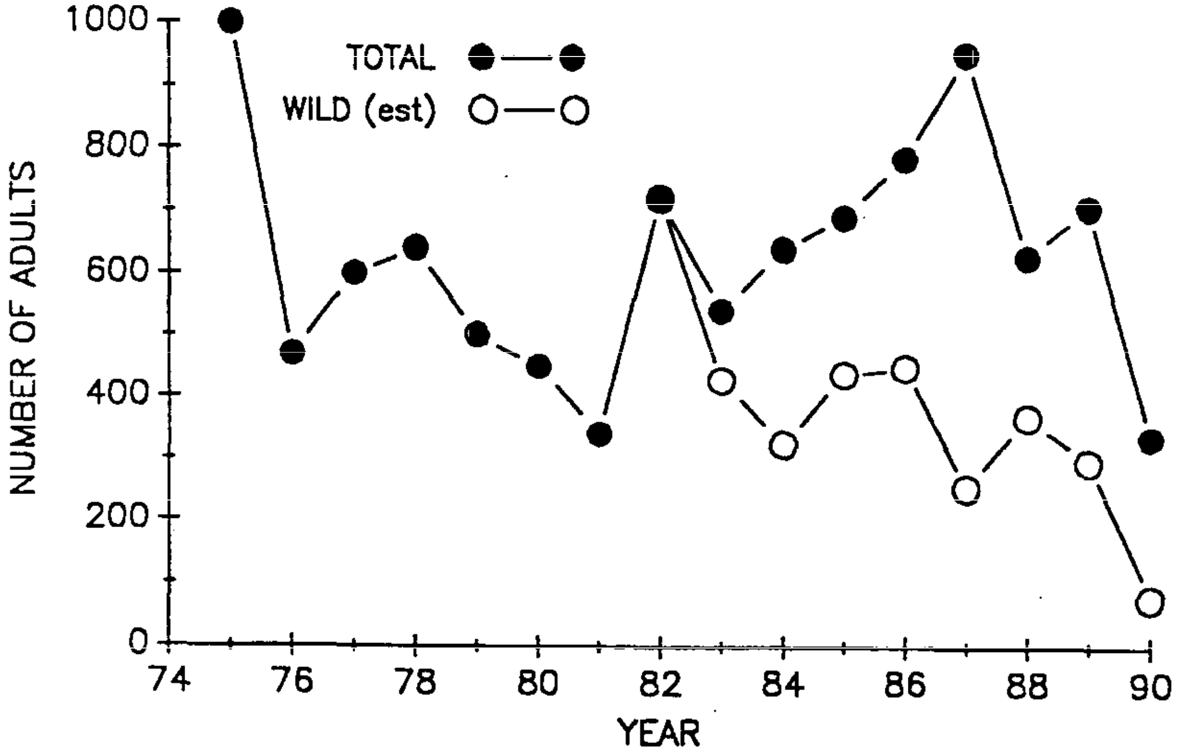

Figure 3.--Counts of adult fall chinook salmon at Lower Granite Dam since its completion in 1975. Estimates of the number of wild fish are obtained by subtracting estimated number of hatchery fish from the total. Based on data in Table 5; see text for discussion of estimation procedures.

fraction of fall chinook salmon counted at Ice Harbor Dam each year do not reach Lower Granite Dam (Table 2). Although other explanations cannot be ruled out, one hypothesis is that many of these unaccounted for fish spawn in the interdam areas. Whether the deep-water spawning, if it occurs, involves hatchery or wild fish (or a mixture of both) is unknown.

The high numbers of hatchery fish at Lower Granite Dam are a concern for several reasons. Every fish of hatchery origin represents one less wild fish in the total count, and discounting the hatchery contribution makes the status of the wild population appear more precarious than was thought to be the case only a year ago. There are also concerns that possible hybridization of hatchery strays may reduce fitness of native fish; this may occur if domestication selection has favored genotypes that are adapted to the hatchery environment but not to surviving in the wild. In the case of Snake River fall chinook salmon, however, artificial propagation has been a relatively recent enterprise, so cumulative genetic changes associated with artificial propagation may be limited. Wild fish are also incorporated into the brood stock each year, and this should reduce divergence from the wild population. Release of subyearling fish may also help to minimize the differences in mortality patterns between hatchery and wild populations that can lead to genetic change (Waples in press).

A greater concern for the status of the wild population than the numbers of stray hatchery fish is the origin of those strays. As shown in Table 5, 1987 and 1988 were the first years in which hatchery strays of upper Columbia River origin are thought to have appeared at Lower Granite Dam in any number (an estimated 6-9% of the total). In each of the last 2 years, about one-quarter of the fish passing

Lower Granite Dam are thought to have originated from hatcheries using upper Columbia River fall chinook salmon.

That hatchery fish appear at Lower Granite Dam does not prove they reach the spawning grounds upstream from the dam, nor does it indicate the degree of reproductive success of strays that do reach the spawning grounds. Unless the strays produce viable offspring that themselves survive to reproduce, they will have no permanent genetic impact on the native population. There is evidence from other studies of Pacific salmon and steelhead that suggests hatchery-reared fish may have less reproductive success in natural habitat than do wild fish (Reisenbichler and McIntyre 1977; Chilcote et al. 1986; Fleming and Gross 1989; Leider et al. 1990). This may be particularly true for hatchery fish (e.g., strays or transplants) that are not spawning in their native habitat. In a recent review, Hindar et al. (in press) cited salmonid studies showing that, in some cases, repeated hatchery releases over a period of years have had no detectable genetic effect on the resident population. However, other scenarios, involving hybridization with or replacement of the resident population with massive outplantings, have also been documented. This diversity of outcomes illustrates the principle that the genetic consequences of straying, supplementation, and stock transfers of Pacific salmon are largely unpredictable.

In an attempt to evaluate the extent to which genetic characteristics of wild Snake River fall chinook salmon may have been affected by upper Columbia River strays, WDF collected postspawning adults from the spawning grounds in 1990. Unfortunately, only 18 carcasses were recovered--too small a sample for meaningful analysis using protein electrophoresis. However, estimates based on CWT data and scale pattern analysis (which can identify fish that were released from hatcheries as yearlings, in contrast to the subyearling pattern typical of wild fish) indicate that at least three-quarters of the fish collected on spawning grounds were hatchery fish, including two carrying tags indicating releases from the Umatilla River (Bugert 1991).

The present status of the wild Snake River fall chinook salmon population is thus in some doubt. The appearance of a substantial fraction of hatchery strays on spawning grounds is alarming. However, the sample size was small, and all of the spawners collected in 1990 were taken from areas in the first 15 km of the 165 km of remaining spawning habitat (ODFW 1991a). The distribution of hatchery and wild fish at more remote spawning areas is unknown. Furthermore, the genetic effects strays may have had on the wild population have not been determined.

Ocean Distribution

No direct information is available regarding the ocean distribution of wild Snake River fall chinook salmon, and efforts to study wild upper Columbia River fish have only recently been initiated. However, CWTs have been used on hatchery fish from both rivers since the late 1970s, and catches of tagged fish in ocean and river fisheries provide some insight into migratory patterns. Complete data for year classes from 1978 to 1984 are available (Busack 1991c), and Figure 4 shows the proportion of adult recoveries from different geographic areas. To avoid possible biases from comparison of releases at different ages, only zero+ age (subyearling) releases were considered.

Although there are inherent difficulties in making statistical comparisons of CWT recoveries for different populations (Busack 1991c), a clear difference was evident in the ocean distribution of Snake and upper Columbia River fall chinook salmon, and the patterns were consistent over the duration of the study. In the years studied, Snake River fish had a more southerly distribution, with a significant

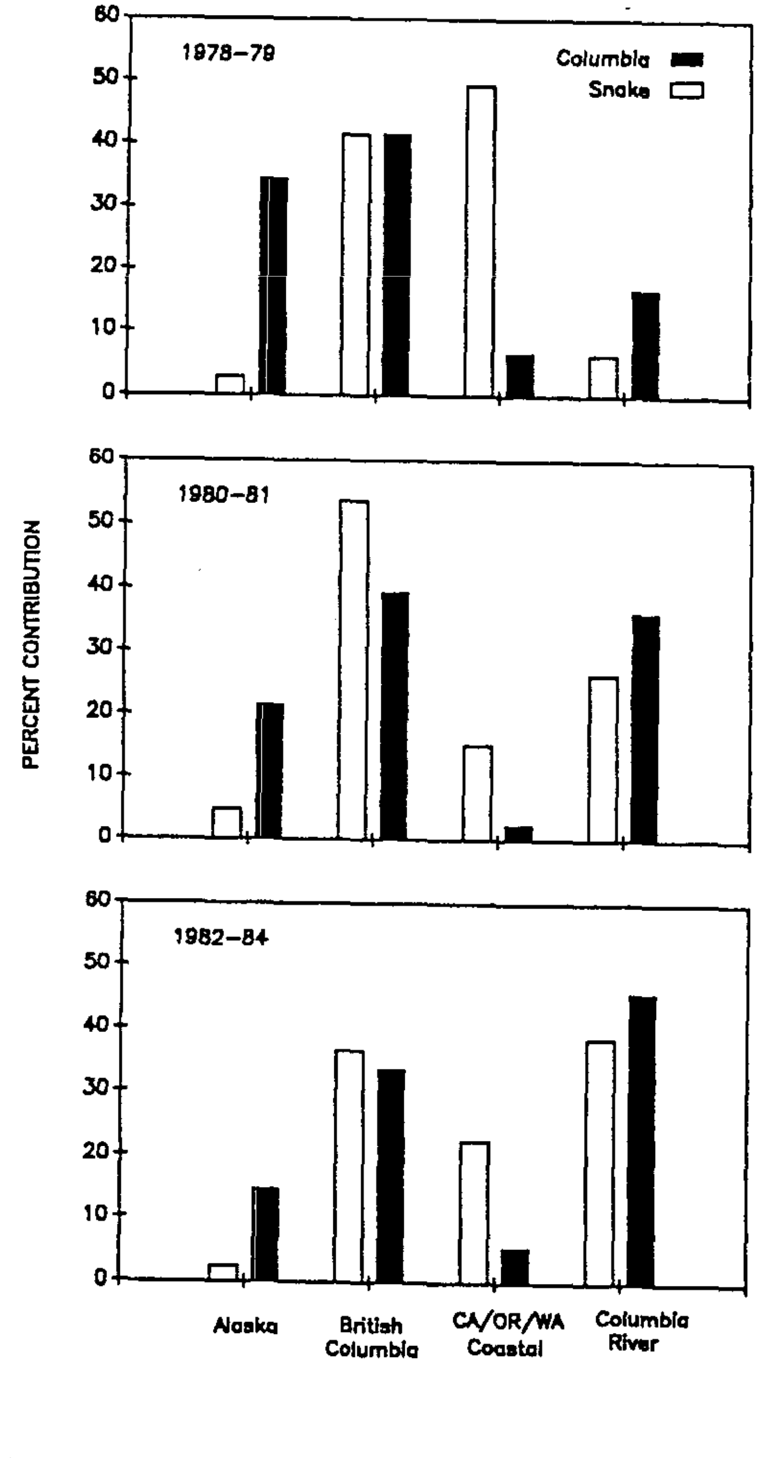

Figure 4.--Proportion of coded-wire-tag recoveries in different geographic areas for hatchery fall chinook salmon from the Snake River (Hagerman and Lyons Ferry Hatcheries) and the upper Columbia River (Priest Rapids Hatchery). Results are summarized by brood year, and all data are for zero-age (subyearling) releases (from Busack 1991c). See also Berkson (1991) and McNeil (1991) for additional treatments of these and other CWT data.

proportion (about 20-50%) of recoveries taken in Washington, Oregon, and California and very few (<5%) in Alaska. The converse was true of upper Columbia River fish; there were substantial catches in Alaska (20-35%) and few in southern areas (<10%). McNeil (1991) summarized the CWT data using a slightly different format and showed that for brood years 1978-85, the proportion of all CWT recoveries occurring in California and Oregon was much higher for Snake River fish (24.5%) than for upper Columbia River fish (6%). According to data presented by Howell et al. (1985), the proportion of CWT recoveries taken off California and Oregon is also very low for fall chinook salmon from the lower Columbia River (about 1-6% for wild fish from the Lewis and Willamette Rivers and hatchery fish from Bonneville pool and lower river facilities). Fall chinook salmon from the Sacramento River "migrate north along the California and Oregon coast with numbers decreasing rapidly along the Washington coast" (Van Hyning 1973, p. 73).

Phenotypic Characteristics

Utter et al. (1982) compared available data for adult fall chinook salmon females and found that fish from the upper Columbia River were significantly larger than those from the Snake River. Mean length in three collections (1977-79) of fish from the upper Columbia River ranged from 86 to 88.6 cm, compared to a range of 75.2 to 83.8 cm in seven collections (1957-79) from the Snake River. Caution should be used in interpreting these results because 1979 was the only year both populations were sampled; furthermore, Utter et al. provided no details on the method(s) used for measuring length. Nevertheless, Mains and Smith (1964) found a similar difference in juvenile size, with migrant chinook salmon fry in the Columbia River being larger than those in the Snake River. Because adults in both rivers spawn at about the same time, Utter et al. (1982) concluded that the differences in fry size reflect environmental differences between the upper Columbia and Snake Rivers and/or genetic differences between the two populations.

Environmental Features

Geological, topographical, and hydrological features of the Snake River Basin are unique in the Pacific Northwest (Chapman et al. 1991). The basin extends into five states (Idaho, Oregon, Washington, Wyoming, and Nevada); drains an area of approximately 267,000 km^2; and incorporates a range of vegetative life zones, climatic regions, and geological formations, including the deepest canyon (Hells Canyon) in North America.

Utter et al. (1982) presented data documenting substantial differences in water temperature between the upper Columbia and Snake Rivers. Over a 2-year period in the 1960s, mean monthly summer water temperature in the Snake River (Weiser, Idaho) was 6-8°C higher than at Rock Island Dam in the upper Columbia River (Fig. 5). The annual temperature range was also considerably greater in the Snake River. Sylvester (1959) and Chapman et al. (1991) present data indicating that a similar pattern has been found at other sites in the two rivers, both more recently and in the past. The high summer water temperatures apparently prevent juvenile fall chinook salmon from rearing in the main-stem Snake River after July. In contrast, in the upper Columbia River, some fall chinook salmon may rear in the river into August, reaching lengths of 110 to 130 mm before migrating to the ocean (Allen and Meekin 1973).

The two rivers also differ in other water characteristics. In a 4-year study, Sylvester (1959) found monthly means for pH and total alkalinity of 8.2 and 99 ppm, respectively, at the mouth of the Snake River, and 7.8 and 64 ppm in the Columbia River at Pasco, Washington, just upstream from the confluence with the

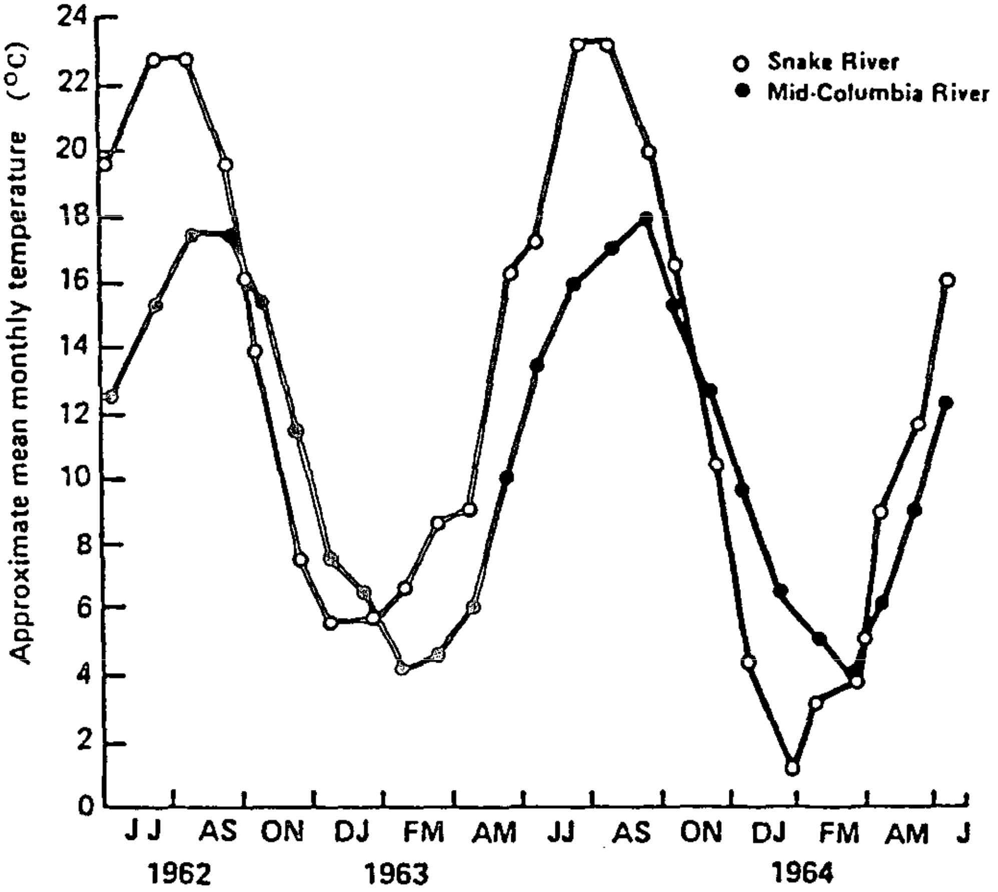

Figure 5.--Mean monthly water temperatures over a 2-year period for the Snake River (Weiser, Idaho) and at Rock Island Dam on the upper Columbia River (from Utter et al. 1982).

Snake River. In addition, the Snake River is typically much more turbid than the Columbia River.

Genetics

Recent reports (Utter et al. 1982; Schreck et al. 1986; Utter et al. 1989; Waples et al. 1991) summarizing electrophoretic information for Columbia River Basin chinook salmon establish the following genetic relationships:

1) On a broad scale [Nei's (1978) genetic distance[4] > 0.02], populations can be grouped into three clusters (Fig. 6): a) spring- and summer-run fish from the Snake River and spring-run fish from mid- to upper-Columbia River, b) spring chinook salmon from the Willamette River, and c) fall chinook salmon. The third cluster also includes some hatchery stocks of spring chinook salmon from the lower Columbia River and some upper Columbia River summer-run fish with life history patterns similar to fall-run fish.

2) Substantial genetic differences also exist between lower Columbia River ("tule") fall chinook salmon and "brights" from the upper Columbia and Snake Rivers (genetic distance > 0.01).

3) Upriver bright fall chinook salmon can be further divided into upper Columbia and Snake River components (separated by a genetic distance of about 0.005). The two forms differ by about 10-20% in frequencies of alleles at several gene loci, and these differences were relatively constant across several years of sampling in the late 1970s and early 1980s. An upriver bright run also occurs in the Deschutes River, a mid-Columbia River tributary, and samples from there were

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[4] Genetic distance values discussed here and shown in Figure 7 are based on polymorphic (variable) gene loci only. The distance values provide a means of comparing the relative degree of genetic differentiation among populations within a single dataset. Caution should be used, however, in comparing values reported here with values from other studies that used data for monomorphic (invariant) gene loci as well.

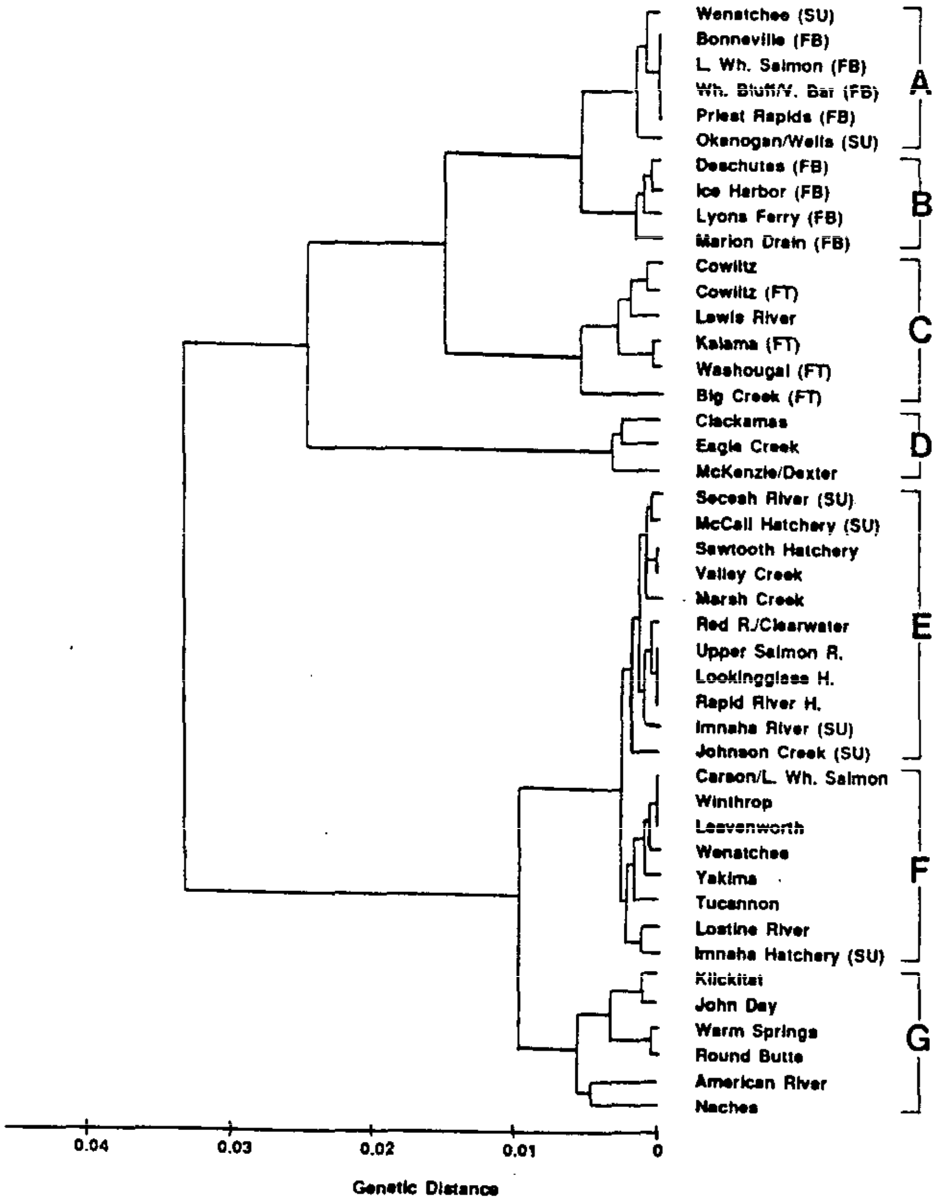

Figure 6.--Dendrogram showing clustering of pairwise genetic distance values (Nei 1978) computed for 21 polymorphic gene loci in chinook salmon from the Columbia River Basin. Modified from Waples et al. (1991), and based on published and unpublished data from NMFS and WDF. Run-time designations in parentheses are SU (summer), FB (fall "upriver bright"), and FT (fall "tule"); others are spring-run stocks. In general, clusters can be characterized by geography and run-timing: A--upper Columbia River summer- and fall-run; B--Snake River fall-run; C--lower Columbia River fall-run; D--Willamette River spring-run; E--Snake River spring- and summer-run; F--upper Columbia River spring-run; G--mid-Columbia River spring-run.

genetically more similar to Snake River than to upper Columbia River samples. An upriver bright sample from a small irrigation ditch (Marion Drain) in the Yakima River Basin also showed a greater genetic affinity to Snake River samples than to upper Columbia River samples from the Hanford Reach area.

4) More recent (1985-90) samples of Snake River fall chinook salmon from Lyons Ferry Hatchery suggest that some mixing with upper Columbia River fish has occurred. At several gene loci (sAH*, sIDHP-1,2*, PEP-LT*, and sSOD-1*), allele frequency differences between the two populations are currently much smaller than they were a decade ago (Fig. 7). This result is consistent with reports (see above) that, in recent years, a sizeable fraction of the Lyons Ferry brood stock has been stray hatchery fish of upper Columbia River stock.

Figure 7 also shows that measures taken to reduce the genetic impacts of straying into Lyons Ferry Hatchery can be effective. Two data points are shown for Snake River fall chinook salmon in 1990; the open circle represents a "random" sample from all untagged fish (Group C above), and the open triangle represents returning Lyons Ferry Hatchery adults identified by CWTs (Group A above). Allele frequencies for Group C have clearly converged toward profiles typical of upper Columbia River fish, whereas allele frequencies in Group A are more typical of pre-1980 Snake River wild fish. This latter result reflects the fact that tagged Lyons Ferry Hatchery adults returning in 1990 were primarily from the 1986 brood year, which predated the most extensive straying events.

Although the electrophoretic data are extensive both in space and time, they have a major limitation--little direct information is available regarding the genetic makeup of wild Snake River fall chinook salmon. All of the electrophoretic data for Snake River fall chinook salmon collected after 1981 are for fish taken at Lyons

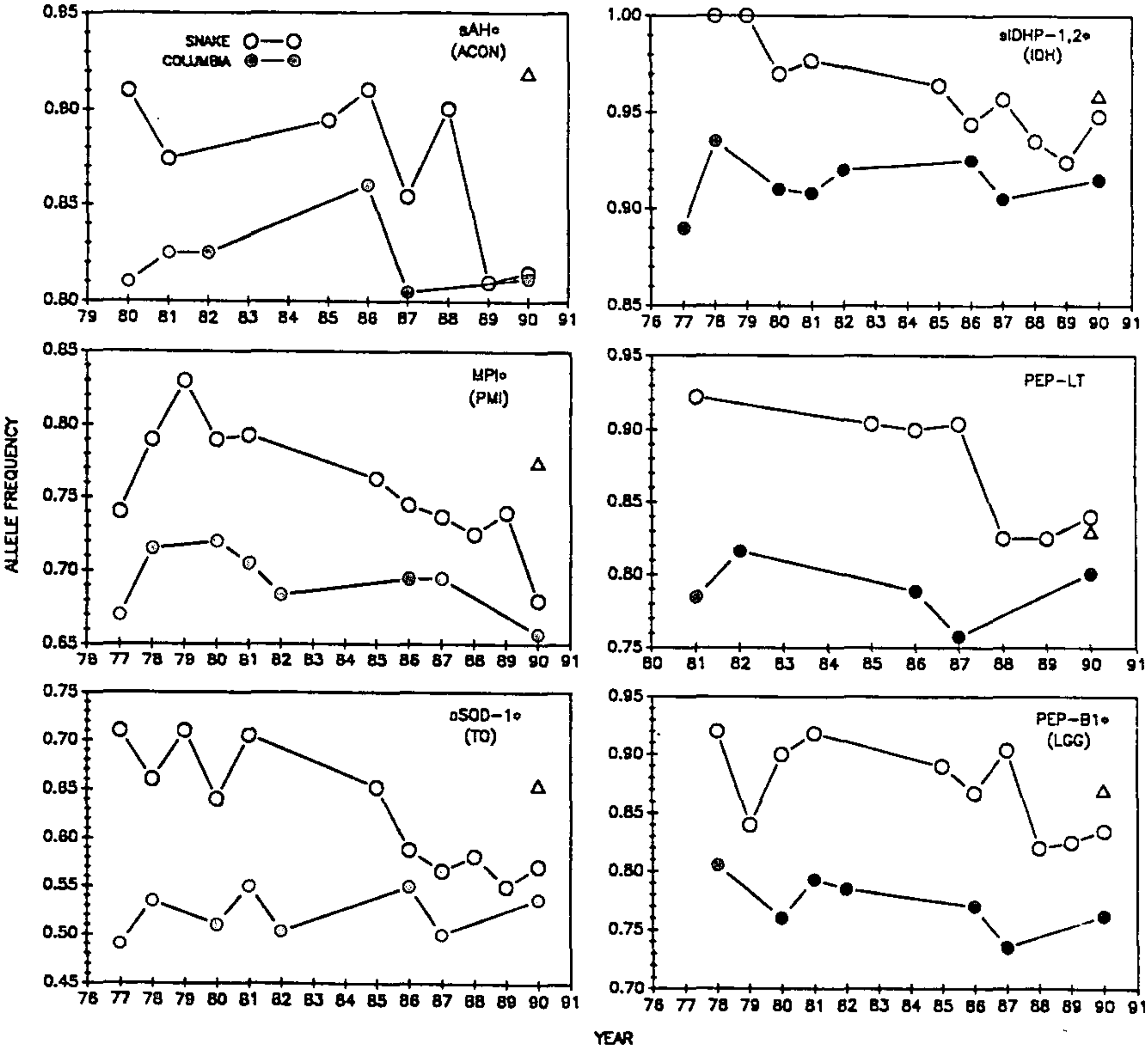

Figure 7.--Time series of allele frequency data at six gene loci for fall chinook salmon from the Snake and upper Columbia Rivers, based on NMFS and WDF data summarized by Busack (1991b, Table 10). Old locus names (as used by Utter et al. 1982) are shown in parentheses below current names. Upper Columbia River data points are for wild samples from the Hanford Reach area and samples from Priest Rapids Hatchery; unweighted averages were used in combining multiple samples from the same year. Pre-1985 samples for the Snake River are for presumably wild fish collected at Ice Harbor Dam; later samples are from Lyons Ferry Hatchery. Two Lyons Ferry samples were analyzed in 1990; the open circle represents a sample of all untagged fish, and the open triangle represents the sample of returning CWT Lyons Ferry fish (primarily from the 1986 brood).

Ferry Hatchery. An attempt in 1990 by WDF to collect a sample of wild fish for electrophoretic analysis was not successful. Early (1977-81) samples of adults trapped at Ice Harbor Dam presumably represent wild fish; however, the location of Ice Harbor Dam (on the lower Snake River just 15 km above the confluence with the Columbia River) raises some questions regarding samples collected there. First, if discrete populations of fall chinook salmon occurred historically in the Snake River [as suggested by ODFW (1991a)], the Ice Harbor Dam samples may have included mixtures of fish from different gene pools. Second, if some of the fish trapped at Ice Harbor Dam were actually upper Columbia River fish, the true differences between native Columbia River and Snake River fall chinook salmon may have been greater than indicated by the early Ice Harbor collections.

The latter concern is based on the observation that chinook salmon, as well as other Pacific salmon species, occasionally wander into nearby rivers before eventually making their way to their natal spawning area (Chapman et al. 1991); collecting adults prior to spawning (as occurs at Ice Harbor Dam) can "create" strays by preventing this behavior. However, the tagging study of McIsaac and Quinn (1988) and the CWT data for Lyons Ferry Hatchery suggest that homing of wild upper Columbia River fall chinook salmon is very precise, so this may not have been a substantial factor in the early Ice Harbor collections.

Concerns about a possible mixture of Snake River populations in the early Ice Harbor collections are difficult to evaluate. Data demonstrating the existence of multiple populations of Snake River fall chinook salmon are lacking. Smouse et al. (1990) reported allele frequency differences between two temporally-spaced samples taken in 1981 at Ice Harbor Dam, but the differences were relatively small and not statistically significant.

DISCUSSION AND CONCLUSIONS

Differences in Run-timing

Results reported by Schreck et al. (1986) and Utter et al. (1989) suggest that neither spring-, summer-, nor fall-run chinook salmon represent monophyletic lineages in the Pacific Northwest. Both authors found that, in general, geographic proximity was more important than run-timing in predicting similarities between stocks. Thus, fish with different run-times from the same area often were more similar than were fish from different areas with the same run-timing. This pattern suggests that run-time differences may have evolved independently a number of times following colonization of a new area by one form. Foote et al. (1989) concluded that a similar phenomenon--derivation of freshwater kokanee from anadromous sockeye salmon--occurred numerous times within the species *O. nerka.*

However, in spite of this general pattern, in some cases substantial differences are found between populations from the same geographic area having different run-times. Striking examples of this are the pronounced genetic and life history differences between fall chinook salmon and spring/summer chinook salmon in the Snake River. In that drainage, fall chinook salmon spawn in lower elevations, generally main-stem areas and migrate to sea as subyearlings, whereas spring and summer chinook salmon spawn in smaller, higher elevation tributaries and outmigrate as yearlings. Several studies have also shown large allele frequency differences between spring/summer- and fall-run fish in the Snake River. Therefore, because of compelling evidence that fall chinook salmon in the Snake River are reproductively isolated from spring and summer chinook salmon, Snake River fall chinook salmon are being considered separately from the other two forms in this

ESA evaluation (see also NMFS Status Review for Snake River Spring and Summer Chinook Salmon; Matthews and Waples 1991).

Distinct Population Segments

We next address the question whether Snake River fall chinook salmon constitute one or more ESUs. If they are not an ESU, then presumably they are part of a larger ESU that would have to be identified and defined. To be considered an ESU, and hence a "species" under the ESA, a population must satisfy two criteria: it must be reproductively isolated, and it must contribute substantially to the ecological/genetic diversity of the biological species.

Reproductive Isolation

Historically, the primary spawning areas for Snake River fall chinook salmon were geographically well separated from fall chinook salmon habitat in the upper Columbia River. Since about 1960, impassable dams in the Hells Canyon complex have restricted Snake River fall chinook salmon to the lower 397 km of the river, closer to upper Columbia River spawning grounds. However, four dams on the lower Snake River also flooded spawning habitat there, thus increasing possibilities for isolation of the remaining population from Columbia River populations (ODFW 1991a). In addition, tagging data suggest at most a low level of straying of upper Columbia River fish into the Snake River through the mid-1980s. Furthermore, protein electrophoretic data gathered over several years in the late 1970s and early 1980s showed consistent genetic differences between Snake River and upper Columbia River fall chinook salmon that would not be expected unless reproductive isolation between the two forms had been strong for a substantial time.

The reason for the genetic similarity of samples from the Deschutes River and Marion Drain to Snake River fall chinook salmon is not clear at this time. The Marion Drain is a channel that facilitates return to the Yakima River of water used for irrigation. It was dug earlier in this century and, for reasons that are not well understood, has attracted spawning populations of salmon and steelhead. Another sample from the nearby Yakima River is genetically more similar to other upper Columbia River fall chinook salmon than to the Marion Drain sample (Busack 1991b). It is possible that fish displaced by destruction of spawning habitat in the Snake River have colonized the drainage ditch in recent years. The Deschutes River appears to have sustained a native run of "fall" chinook salmon, although tagging studies have shown that fish spawning there in the fall cross Bonneville Dam during the June-July period designated for summer-run fish (Howell et al. 1985). WDF plans to take new samples for genetic analysis from the current fall run in the Deschutes River (C. Busack[5]), and results may help to better define the relationship between these fish and the Snake River population.

There is genetic and tagging evidence that, beginning in the mid-1980s, Columbia River fall chinook salmon of hatchery origin have strayed into the Snake River and have been used for brood stock at Lyons Ferry Hatchery. The effects of this straying are considered in the next section.

Ecological/Genetic Diversity

Genetic differences detected by protein electrophoresis between fall chinook salmon and spring/summer chinook salmon in the Snake River are quite substantial and clearly reflect independent evolutionary lineages. As a group, the "upriver

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[5] Craig Busack, Washington Department of Fisheries, 115 General Administration Bldg., Olympia, WA 98504. Pers. commun., May 1991.

bright" fall chinook salmon are also clearly distinguished genetically from lower Columbia River "tule" fall chinook salmon. Within the "upriver bright" group, consistent differences indicating reproductive isolation are also found between populations in the Snake and upper Columbia Rivers. These latter differences, however, are not large quantitatively. Thus, the genetic data are consistent with the existence of adaptive differences between the two "upriver bright" populations, but the data do not in themselves provide strong evidence for such adaptations. In evaluating the contribution of Snake River fall chinook salmon to ecological/genetic diversity of the species, therefore, attention should focus on other factors.

As the largest historic producer of chinook salmon in the world, the Columbia River Basin clearly plays an integral role in maintaining the long-term health and viability of the species. In turn, the Snake River, which is the largest tributary of the Columbia River, contributes substantially to the ecological diversity and productivity of the Basin. Prior to construction of the Hells Canyon complex of dams, the Snake River was the most important natural production area in the Basin for fall chinook salmon (Fulton 1968).

Among North American chinook salmon populations with the "ocean" type juvenile life history pattern, the fall run in the Snake River historically migrated the farthest from the ocean (over 1,500 km). Fall chinook salmon in the upper Columbia River also undergo a lengthy freshwater migration. In contrast, "ocean" type chinook salmon in other major North American river systems (Sacramento, Klamath, Fraser) migrate no more than a few hundred kilometers into fresh water. Although the Snake River population is currently restricted to habitat in the lower river, genes associated with the more lengthy migration may still reside in the population. In general, longer freshwater migrations in chinook salmon are associated with more extensive oceanic migrations (Healey 1983). Thus, maintaining populations occupying habitat well inland can be important in maintaining diversity in the marine ecosystem as well.

Habitat characteristics and adult ocean distribution provide the strongest evidence for adaptive differences between fall chinook salmon in the Snake and upper Columbia Rivers. The best-documented environmental difference between the Snake and upper Columbia Rivers is water temperature. In the summer months, water temperatures in the Snake River can exceed 25°C, and during this period average monthly temperatures are often 6-8°C higher than the upper Columbia River. These temperature regimes may exclude juvenile fall chinook salmon from rearing in the main-stem Snake River during this period, thus encouraging the evolution of behavioral mechanisms to avoid the warm water. Summer water temperatures in fall chinook salmon habitat in the lower Columbia River are also typically much lower than the Snake River (Van Hyning 1973).

The high summer water temperatures in the Snake River suggest that, if the present populations were lost, other chinook salmon might have difficulty successfully colonizing this area. Even if exogenous adults can move into the area (as has occurred recently with stray hatchery fish of upper Columbia River origin), their progeny may have poor survival in the new environment. Of course, this is difficult to demonstrate experimentally without placing the native population at risk. However, numerous other studies show that, in general, transfers of Pacific salmon within the historic range of the species have not been successful (e.g., Withler 1982). This is particularly true of attempts to establish lower river fish in upriver areas. Presumably, this failure reflects the importance of local adaptation and the inability of transplanted fish to home accurately.

Substantially higher pH, alkalinity, and turbidity (relative to the upper Columbia River) also characterize Snake River water. Although the effects of these factors on salmonids are not as well understood as are thermal effects, these environmental differences also may lead to local adaptations.

Tagging studies demonstrate substantial differences in ocean distribution between fish from the Snake and upper Columbia Rivers, and the patterns are consistent over several years. Snake River fish have a more southerly distribution, with a significant proportion (about 20-50%) of recoveries taken in southern Oregon and California and very few (<5%) in Alaska. The converse is true of upper Columbia River fish; substantial catches occur in Alaska (20-35%) and few in southern areas (<10%). These differences indicate that the two populations utilize the marine habitat in different ways. It is important to the long-term health of the species to maintain such interpopulation differences because 1) this diversity allows the species as a whole to more effectively utilize available habitat and 2) loss of this diversity would place the species at greater risk from unpredictable changes in the environment.

Species Determination

Available evidence indicates that historically, fall chinook salmon in the Snake River were substantially isolated from other chinook salmon populations. The importance of the Columbia River Basin to the long-term health of the biological species is clear. Among chinook salmon populations with "ocean" type life-history strategies, Snake River fall-run fish are exceptional in the length of their freshwater migration. High summer temperatures require special adaptations in juvenile behavior and reduce the possibility that other populations could rapidly colonize the habitat. Together with the distinctive ocean distribution of Snake River fall chinook salmon, these factors argue for the important role the Snake River population plays in contributing to the ecological/genetic diversity of the species. We therefore conclude that historically, Snake River fall chinook salmon were an ESU of the biological species *O. tshawytscha*. Although hydropower development has drastically reduced available habitat for this population, evidence indicates that it remained distinct at least through the early 1980s. This is the same conclusion reached by Utter et al. (1982), who reviewed evidence for distinct population segments of fall chinook salmon in conjunction with an ESA evaluation a decade ago. As noted above, further work is necessary to establish the relationship between the Snake River population and fall chinook salmon in the Deschutes River and the Marion Drain.

Evidence for the existence of multiple distinct populations of fall chinook salmon within the Snake River Basin is scant. Some population subdivision may occur (or may have in the past), but the inability to clearly identify and sample discrete spawning populations has precluded a more definitive study of this possibility.

Information that has become available only within the last year raises some questions regarding the present status of the Snake River population. In recent years, strays from hatcheries producing upper Columbia River fall chinook salmon have appeared in the Snake River in increasing numbers and have been incorporated into brood stock at Lyons Ferry Hatchery. According to data collected in 1990, a high percentage of adults taken at Lower Granite Dam and on fall chinook salmon spawning grounds are estimated to be of hatchery origin, including strays from the Columbia River. Protein electrophoretic data confirm that introgression of upper Columbia River genes into Lyons Ferry Hatchery brood stock has occurred, but there is no direct information about the genetic effects of hatchery strays on the wild Snake River population.

Although the NMFS Northwest Region Biological Review Team (BRT) concluded that, historically, Snake River fall chinook salmon were an ESU, it is not so clear whether this is still the case. One viewpoint is that introgression from Columbia River hatchery strays has caused the Snake River population to lose the qualities that made it "distinct" for ESA purposes. Evidence in support of this viewpoint includes genetic and tagging data documenting effects of straying on Lyons Ferry Hatchery brood stock, estimates that in 1990 a high proportion of fish passing Lower Granite Dam and found on nearby spawning grounds were hatchery strays, and the lack of any positive information documenting the continued existence of "pure" wild fish. However, given that 1) an ESU was present until at least the early 1980s, 2) substantial straying of upper Columbia River hatchery fish has occurred only within the last generation, and 3) no direct evidence exists for genetic change to wild fall chinook salmon in the Snake River, the BRT felt it would be premature to conclude that the ESU no longer exists.

Status of the ESU

The BRT evaluated a number of factors in considering the level of risk faced by Snake River fall chinook salmon. The current population occupies a fraction of its former range, the remaining (and, historically, the most productive) habitat having been inundated by reservoirs or blocked by dams. Although historical abundance of fall chinook salmon in the Snake River is difficult to estimate, adult returns have declined by about three orders of magnitude since the 1940s, and perhaps by another order of magnitude from pristine levels.

Relatively precise estimates of the number of fall chinook salmon entering the Snake River have been available only since the completion of Ice Harbor Dam. The estimated numbers of wild spawners in 1987, 1989, and 1990 are the second, fourth, and first lowest on record, respectively. In 1990, just 78 wild fish are estimated to have passed Lower Granite Dam, only 31% of the number in the next lowest year (1987).

We applied the model of Dennis et al. (1991) to time series of adult counts at Ice Harbor Dam (1960-present) and Lower Granite Dam (1980-present). Inputs for the model were 5-year running sums of the number of adults at the uppermost dam on the lower Snake River (this running sum is termed the "index"). For the more recent time series, estimated numbers of wild adults at Lower Granite Dam (Table 5) were used. Two time series were considered because predictions of the model can vary substantially depending on the time series chosen. In particular, a time series that spans a fundamental change in parameters affecting the population can give misleading results. The first time series provides information for the period following construction of the first of the four dams on the lower Snake River, and the second shows trends for the period following construction of the last dam (1980 is the first year for which almost all returning adults had to outmigrate through Lower Granite Dam as juveniles). Although the first series is longer (and, other things being equal, would be preferred), the second series may more accurately reflect the population's response to conditions during the past decade. A test described by Dennis et al. (1991) verified that a statistically significant change in growth rate parameters of the population occurred in 1980.

Based on the time series beginning in 1960, the Dennis model indicates that extinction of the ESU is a virtual certainty in the absence of any changes (probability of the index dropping below one fish within 100 years > 99.9%). Predictions are not quite so bleak for the more recent time series, but even so, the model estimated the probability of extinction within 100 years as 10.8%.

In light of the above factors, and further considering that a) drought conditions have likely adversely affected juvenile survival in several recent years, reducing the prospects for recovery in the near future as these year classes return as adults and b) there is clear evidence that stray hatchery fish of non-Snake River origin pose a serious threat to the genetic integrity of the wild population, the BRT concluded that Snake River fall chinook salmon face a substantial risk of extinction if present conditions continue.

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APPENDIX

Glossary

GLOSSARY

Ageing

A fish that is less than 1 year old (counted from time of spawning by its parents) is considered a **subyearling**, or **zero-age**. A **yearling** fish is more than 1 year and less than 2 years old. Adult ages are also reckoned from time of egg deposition and are typically based on counts of annual rings on scales or otoliths (a calcareous "earstone" found in the internal ear of fishes). The age of an adult is sometimes estimated by length.

Adult Fish Counts

A fish-viewing window is at the upstream end of most fish ladders. Observers count the number of fish, by species and size, passing the window for 50 minutes of every hour for 16 hours per day. Extrapolations are made for the hours and minutes not counted to provide an estimate of daily adult fish passage for each dam. In general, separate counts are made for adults and **jacks** (precocious males that can be identified by their smaller size).

Adult Fish Ladders

The main-stem hydroelectric dams on the Columbia and lower Snake Rivers have fish ladders that allow adults to pass the dams on their upstream spawning migration. Entrances for fish ladders are placed on shorelines. For fish attracted to turbine discharge flows, a collection channel built across the downstream face of the dams provides a conduit to move fish toward the fish ladders. Fish ladders that are in compliance with established performance guidelines effectively pass most fish that enter them; however, a small percentage of fish at each dam may not find the entrances to the ladders.

Bypass Systems

Juvenile salmonid bypass systems consist of moving screens lowered into turbine intakes to divert fish away from turbines at hydroelectric dams. Fish move into a channel that transports them safely around the dam. Bypassed fish are then typically returned directly to the river below the dam, although some Columbia River Basin dams have facilities to load bypassed fish into barges or trucks for transport to a release site downstream from all the dams.

PIT-tag detectors (see below) interrogate all PIT-tagged fish passing through the bypass system. In addition, the systems are equipped with subsampling capabilities that allow hands-on enumeration and examination of a portion of the collection for coded-wire tags (CWT), brands, species composition, injuries, etc. Recovery information at bypass systems is used to develop survival estimates, travel time estimates, and run timing; to identify problem areas within the bypass system; and as the basis for flow management decisions during the juvenile migrations.

Coded-Wire Tags

Coded-wire tags (CWT) are tiny pieces of wire which are implanted in the cartilage in snouts of juvenile salmon. Each tag is notched with a binary code that identifies the fish with a particular release group. CWTs are inserted into the snout using a tagging machine. A head mold, which is sized for the fish being tagged, ensures proper placement of the tag to avoid injury to the fish. Large groups of fish can be coded-wire tagged quickly and inexpensively without altering the behavior of the fish.

Fish that have been coded-wire tagged are identified by an external mark (generally, removal of the adipose fin). This enables fish samplers to later identify tagged fish for recovery of the tag. Coded-wire tags are usually retrieved from dead fish by using a core sampler and a magnetic detector; the code is then read under a microscope.

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 2 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. Utter et al. (1987) provide a review of the method using examples from Pacific salmon, and the laboratory manual of Aebersold et al. (1987) provides detailed descriptions of analytical procedures. Genetic techniques that focus directly on variation in DNA also routinely use electrophoresis to separate fragments of DNA of different lengths.

Other genetic terms used in this document include **allele** (an alternate form of a gene); **dendrogram** (a branching diagram, sometimes resembling a tree, that provides one way of visualizing similarities between different groups or samples); **gene** (the basic unit of heredity passed from parent to offspring); **gene locus** (pl. **loci**; the site on a chromosome where a gene is found); **genetic distance** (a quantitative measure of genetic differences between a pair of samples); and **introgression** (introduction of genes from one population or species into another).

Hatchery

Salmon hatcheries use artificial procedures to spawn adults and raise the resulting progeny in fresh water for release into the natural environment, either directly from the hatchery or by transfer into another area. In some cases, fertilized eggs are outplanted, but it is more common to release **fry** (young juveniles) or **smolts** (juveniles that are physiologically prepared to undergo the migration into salt water).

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

PIT Tags

Passive integrated transponder (PIT) tags have been developed to monitor the movements of anadromous salmonids primarily through juvenile bypass systems or adult fish ladders at dams. In contrast to radio tags, which have a battery that eventually will cease to function, PIT tags contain a small computer chip that transmits its code only when induced by an external energy source. Using current technology, the PIT tag can only be detected at a distance of up to 18 cm in water. Although this limits some applications of PIT tags, bypass facilities at hydroelectric dams provide excellent opportunities for monitoring movements of juvenile and adult fish.

Each PIT tag is 12.0 mm long by 2.1 mm in diameter and is coded with one of 34 billion unique codes. Tags are inserted into the body cavity with nearly 100% tag retention and high fish survival. The tag is interrogated at 400 kHz and transmits a return signal at 40 to 50 kHz. In specially designed facilities at hydroelectric dams, computerized systems automatically detect, decode, and record individual PIT tag codes, thereby providing time, date, and location of detection and eliminating the need to anesthetize, handle, or restrain fish during data retrieval. The information collected daily at each dam is automatically transferred from the monitor system to a central data base for storage and processing.

Although only developed in the mid-1980s by NMFS scientists, PIT tags have already provided a wealth of information about the distributions, migration timing, migration rates, and survival of juvenile salmonids.

Phenotype

The phenotype is the appearance of an organism resulting from the interaction of the genotype and the environment.

Population viability analysis (PVA)

PVA provides a means of quantifying future risks faced by a population due to demographic, environmental, and genetic factors. PVA methods can be used to identify the minimum viable population size (MVP)--that is, the smallest number of individuals that will allow the population to persist for a specified amount of time (t) with a specified degree of certainty (P). There is no purely scientific way of choosing optimal values for t and P, but combinations most commonly suggested in the literature are $t = 100$ years and $P = 95\%$ probability or, more conservatively, $t = 1{,}000$ years and $P = 99\%$ probability (Thompson 1991).

Some detailed PVA models have been described in the literature, but they generally require types of data [e.g., means and variances (over a number of years) of sex ratio, fecundity, and age-specific survival rates] not typically available for Pacific salmon. In the current ESA evaluations, the BRT used the stochastic extinction model of Dennis et al. (1991) to provide some idea of the likely status of the population in the future. A major advantage of the **Dennis model** is its simplicity, requiring as input only a time series of abundance data. Predictions are obtained by taking the current state of the population and projecting it into the future, based on the assumption that future fluctuations in population abundance are determined by parameters of the population measured in the recent past. However, the simplicity of the model also means that it may fail to capture some important aspects of population dynamics. In particular, it does not take density-dependent factors into consideration. Nevertheless, the model is useful for identifying outcomes that are likely *if no protective measures are taken.*

The Dennis model can be used to identify "extinction" and "threatened" thresholds to compare with the current abundance of a population. In this evaluation, the BRT identified an "endangered" threshold as the abundance at which the population was estimated to have a $P = 95\%$ chance of surviving for $t = 100$ years. Populations whose current abundance was above the "endangered" threshold were evaluated with respect to a "threatened" threshold, which was defined as the abundance at which the population was estimated to have a 50% chance of falling below the "endangered" threshold within 10 years (Thompson 1991).

Redd Counts

A spawning female salmon prepares a series of nests, called a redd, in suitable areas of streams by turning onto her side and beating her caudal fin up and down. Primary factors affecting suitability of spawning habitat include the size of rocks in the substrate and stream flow (high enough to provide adequate aeration for the eggs; low enough to prevent erosion of the nest). A completed redd is a shallow depression in the stream bottom with a rim extending to the downstream end. During spawning, the female continuously digs upstream, covering previously deposited eggs with gravel. Most redds occur in predictable areas and are easily identified by an experienced observer by their shape, size, and color (lighter than surrounding areas because silt has been cleaned away).

Redd counts are conducted annually in certain heavy use areas of streams called index streams, which are usually surveyed repeatedly through the spawning season. Colored flags are sometimes placed on nearby trees to identify redds so that they will not be counted repetitively. Annual redd counts are used to compare the relative magnitude of spawning activity between years.