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Population Structures
of Fall Chinook Salmon,
Oncorhynchus tshawytscha,
of the
Mid-Columbia and Snake Rivers

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POPULATION STRUCTURES OF FALL
CHINOOK SALMON, ONCORHYNCHUS TSHAWYTSCHA,
OF THE MID-COLUMBIA AND SNAKE RIVERS

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ABSTRACT

The possibility of genetic divergence between the fall chinook salmon runs returning to the Snake River and the Columbia River above its confluence with the Snake River was examined. Factors considered included geological history, timing and geographic location, displacement and transplantation, morphology, habitat and biochemical genetic data. Significant differences in mean length could not be unambiguously attributed to genetic divergence because of the distinct stream environments. However, biochemical genetic data from 12 variable genetic systems that were collected over a 4-year period indicated a substantial genetic divergence between the two groups. The magnitude of these differences precluded a recent divergence reflecting displacement of a common stock following dam impoundments. The authors believe that these groups are distinct, separate, and identifiable populations.

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INTRODUCTION

Under the Endangered Species Act of 1973, species which may be considered for protection through listing are defined as:

any subspecies of fish or wildlife or plants
and any distinct population segment of any species which
interbreeds when mature.

Utter (1981) sets forth a logical sequence of information required to decide whether a particular salmon stock is distinct or discrete, and a species under the Act. The National Marine Fisheries Service/Fish and Wildlife Service (NMFS/FWS) Policy Position Paper^{1/}, on the question of species definition, indicates which elements of information outlined in the Utter paper are sufficient for initial determinations of salmon species under the Act, and which are necessary to confirm this decision through a final positive determination.

This paper represents the authors' conclusions with regard to available data concerning populations of fall chinook salmon in the mid-Columbia (i.e., from above the confluence of the Snake River to confluence of the Okanogan River) and Snake Rivers in view of the definition of a species under the Act. The authors alone accept responsibility for the paper and it is not an official policy statement concerning the Act.

REVIEW OF AVAILABLE DATA

Geological History

The geological history of both the mid-Columbia and Snake Rivers is very recent. Both the fall chinook salmon stocks of the mid-Columbia and

^{1/}Pending approval of involved agencies.

the Snake Rivers have most likely arisen from common ancestry well within the last 10,000 yr following the last glacial recession (McKee 1972).

Timing and Geographic Location

The precision of homing and timing of natural runs of anadromous salmonids has resulted in temporal and geographic fragmentations within species, and varying degrees of genetic divergence among fragments. Consequently, it has often been possible to identify discrete breeding units within species on the basis of consistently distinct timings and locations of spawning groups. Thus timing has been important in distinguishing discrete segments of chinook salmon returning to various tributaries of the Columbia River. The major temporal components of Columbia River chinook salmon runs have been somewhat arbitrarily segregated into three groups--spring, summer, and fall runs of adult fish. The distinctness of each of these groups has been confirmed both by their returning to the same areas at the same time over many generations (Fulton 1968) and by the measurements of genetic differences among them (Milner et al. 1982). Representative runs of all three groups return to the mid- and upper Columbia and the Snake Rivers. The variable of timing has been reduced, however, to a single segment--the fall run--in this paper and our attention therefore shifts to considerations of location as criteria for confirming the existence of a species of fall run chinook salmon of the mid-Columbia and Snake Rivers.

The variable of location concerns two broad and adjacent regions. The distinctness of these regions might be sufficient to warrant designation of at least two species under the Act if: 1) data accumulated over many years indicated a consistent use of the same locations within regions, and 2) it could be demonstrated that progeny of numerous successive generations

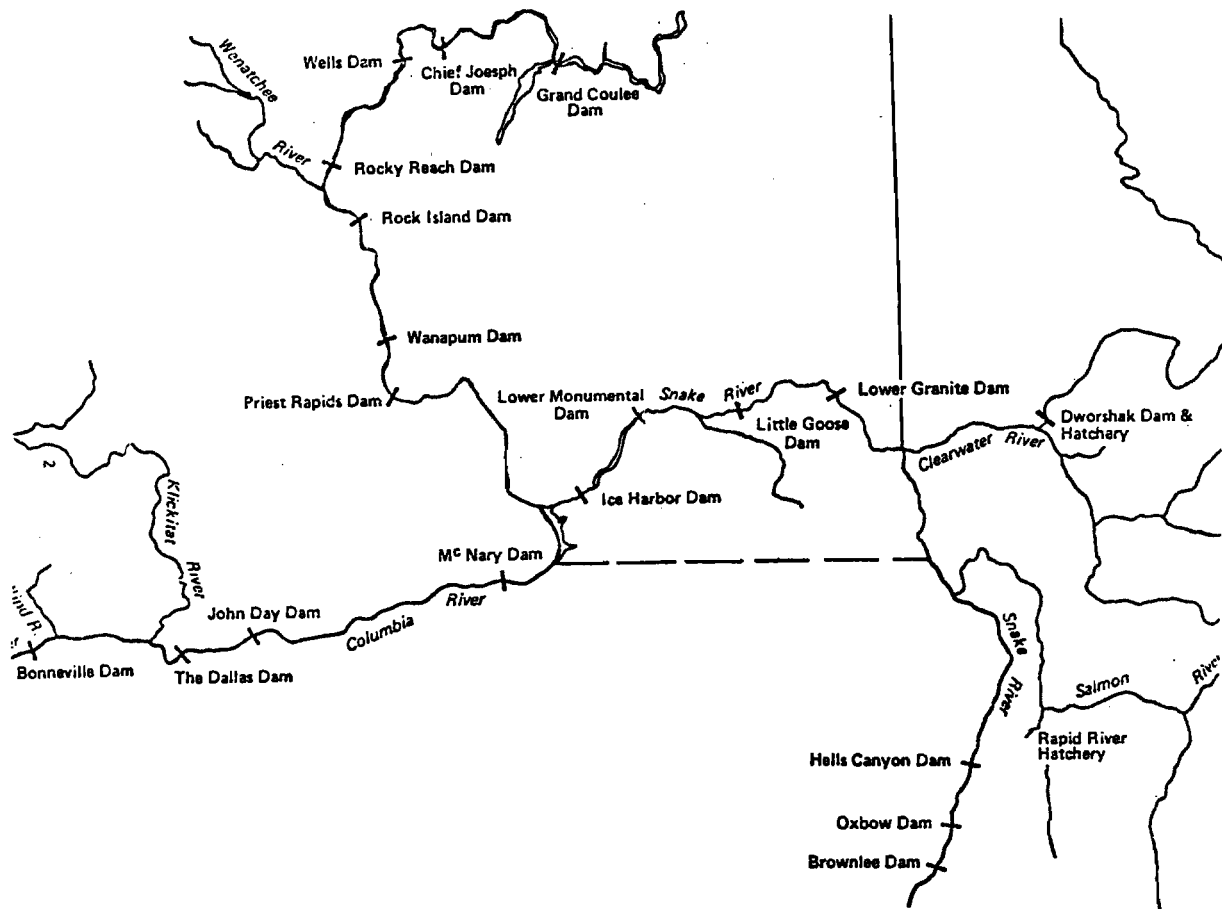
returned to the same locations for spawning. Specific data do not exist to satisfy these requirements, but it is well documented that established runs of most anadromous salmonids including chinook salmon return faithfully to their precise areas of origin with little, if any, straying (Banks 1969). Geographic distinctness of the magnitude under consideration here has therefore often resulted in measurable genetic distinctions among localities in anadromous salmonid species (Ricker 1972; Allendorf and Utter 1979). It will be seen in the following section, however, that the two geographic segments under consideration might have had a recent common ancestry and therefore would not warrant designation as species in spite of their geographic distinctness because of recent changes in the populations caused by dam construction.

Displacement and Transplantation

A distinct trend has been recorded in the counts of fall chinook salmon passing McNary Dam (Figure 1) since data collection began in 1954. Counts averaged about 12,000 fish during the first 3 yr; however, subsequent counts have been consistently much higher, averaging about 50,000 fish (Van Hyning 1973; Anon. 1979). Van Hyning (1973) postulated that this increase was a reflection of the cessation of the extensive annual harvest at Celilo Falls which followed the impoundment of the Columbia River in the area by The Dalles Dam in 1957. Alternatively, the increased count at McNary Dam may be a result of upstream displacement of fish formerly spawning in the impounded areas behind The Dalles and John Day Dams (Mathews and Paulik 1967; C. O. Junge^{2/}).

^{2/} Charles O. Junge, Oregon Department of Fish and Wildlife, Clackamas, OR 97015. Pers. commun.

Figure 1. Main stem dams in the Columbia River Basin.



It is important to determine which of these two possibilities is the more likely factor in this increase prior to any ESA action. If present runs are descended from historical runs returning to the same areas, it is likely that the Snake River and mid-Columbia River runs are distinct or discrete and may warrant coverage as a species under the Act. However, if fish of both the mid-Columbia and Snake Rivers are predominantly descended from displaced downstream river stocks, both groups should be genetically similar and each might not qualify for coverage as a species under the Act. To address the possibility of displacement, it is important to review and consider other indicators of similarity and differences between the mid-Columbia River and Snake River fall chinook salmon stocks.

Intentional transplantations of fall chinook salmon between the mid-Columbia and Snake Rivers have not been recorded (T. C. Bjorn^{3/}).

Morphology

Some comparative data are available which indicate morphological differences between Snake River and mid-Columbia River fall chinook salmon. Length frequency data from adults (Table 1) indicates that significant differences exist between the two groups, with the larger fish occurring in the Columbia River. These differences are consistent with larger migrant fry (presumably entirely progeny of fall-run fish) of the Columbia River observed in a study comparing migrant chinook salmon of the mid-Columbia and Snake Rivers (Mains and Smith 1964).

The size differences of fry could be a reflection of earlier emergence of the Columbia River fish. As noted above, however, spawning peaks of

^{3/} Ted C. Bjorn, Cooperative Fishery Unit, Univ. of Idaho, Moscow, ID 83843. Pers. commun.

Table 1.--Mean lengths of fall chinook salmon females from samples collected from the mid-Columbia River and the Snake River. Differences between areas are significant ($p = 0.016$; Wilcoxon rank sum test, Dixon & Massey 1969).

Area and year	Mean length (cm)	N
Mid-Columbia River		
1979 ^{1/}	88.6	300
1977(a) ^{2/}	87.3	194
1977(b) ^{2/}	86.0	59
Snake River ^{3/}		
1979 (Ice Harbor)	83.6 ^{4/}	24
1962 (Spawning grounds)	79.5	52
1961	84.3	327
1960	75.2	75
1959	83.8	98
1958	82.3	147
1957	79.2	253

^{1/} Data from records of Washington State Department of Fisheries.

^{2/} Data from Bauersfeld 1978.

^{3/} Data from records of Idaho Department of Fish and Game.

^{4/} Converted from mean lengths calculated to the nearest lower inch; 1 cm added for statistical analysis to each Snake River mean to compensate for bias in rounding off.

both groups occur near mid-November (Parametrix, Inc. et al. 1979; T. C. Bjorn^{3/}) so that the differences appear to reflect environmental or genetic variables other than different spawning times.

Habitat

Measurable temperature differences do exist between the mid-Columbia and Snake River drainages (Figure 2). The warmer average summer temperatures of the mid-Columbia River could be reflected in more rapid growth of these fish, although the fry migrants would not be affected by these differences. These temperature differences could result in differential adaptation of all chinook salmon populations where juveniles remained in the rearing areas during the summer months.

Differences in pH and total alkalinity also exist: 4-yr monthly means for these two variables during 1954-57 were 8.2 and 99 ppm, respectively, at the mouth of the Snake River and 7.8 and 64 ppm, respectively, in the Columbia River near Pasco, Washington (Sylvester 1959). Such differences usually affect numerous ecological variables that may, in turn, lead to differential adaptations of Columbia River and Snake River fall chinook salmon runs.

Biochemical Genetic Data

Biochemical genetic data collected by electrophoretic methods measure purely genetic differences among populations through the evaluation of genetic variations in proteins. The purely genetic basis of these differences make these data the most powerful single method available for detecting and measuring population differences (Utter 1981; Hartl 1980). These methods may be used alone for determining population structures or as

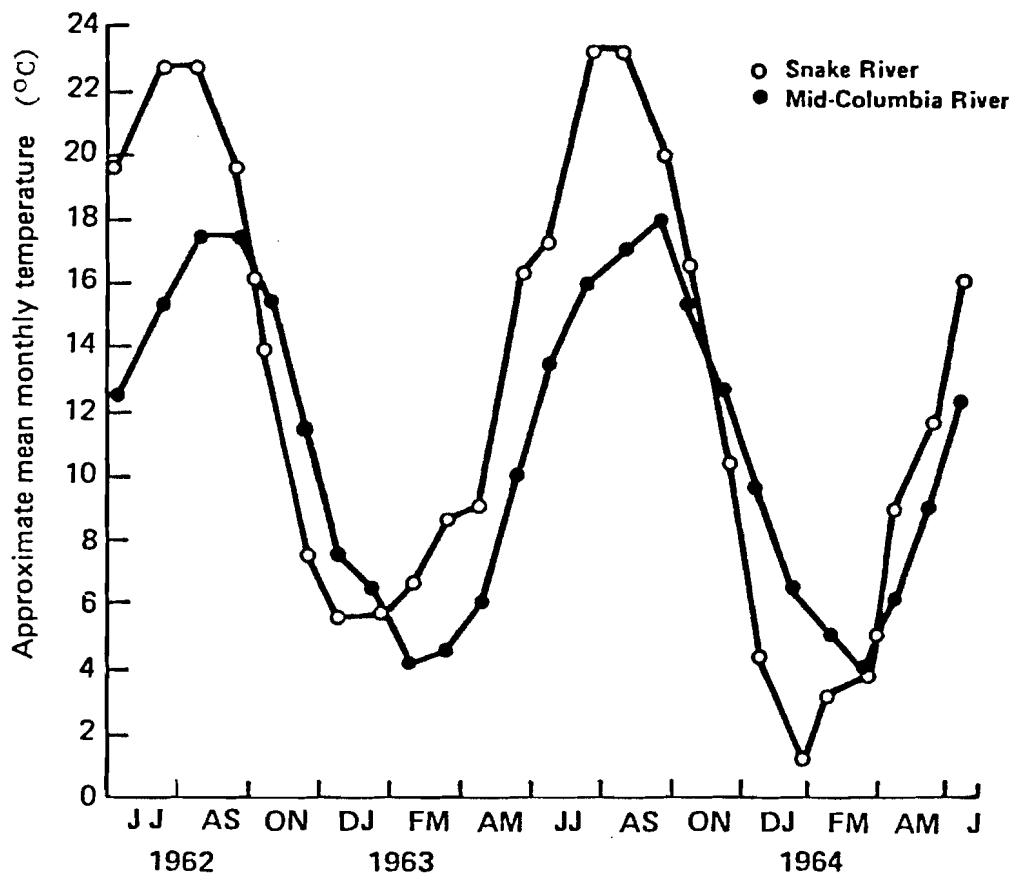


Figure 2.--Mean monthly temperatures for 2 yr on the Snake River (Weiser, Idaho) and the mid-Columbia River (Rock Island Dam). Snake River data from Ebel and Koski (1968); Columbia River data from records of U.S. Geological Survey, Northwest Water Resources Data Center, Portland, OR.

a means of corroborating structures determined by other methods. Because these electrophoretic data sample only a small fraction of the total genetic composition of a particular population, however, they can only identify differences; the absence of detectable genetic differences using the electrophoretic method does not preclude or negate determinations of population distinctness based upon other characteristics of the population in question.

Biochemical genetic data are available for comparing mid-Columbia River and Snake River fall chinook salmon populations. Sufficient data are presently available to look for genetic divergence of the Snake River and mid-Columbia River fall chinook salmon runs (Table 2). Collections of both adult and juvenile fish have been taken over four consecutive years at Ice Harbor and Priest Rapids Dams. Tissues of these fish have been electrophoretically analyzed for allelic frequencies at 12 polymorphic loci (Milner et al. 1980, 1982); the allelic frequencies at 7 loci are very similar with variant alleles occurring only at low frequencies and no distinct distributions between the two areas.

Differences among areas in gene frequencies occur at 5 loci. The largest difference is at the T0 locus where there is no overlap of frequencies of alleles and an average difference of 16%. This difference is highly significant (Chi square - 27.8, 1 df; p less than 0.001), and is strong positive evidence by itself for regarding the two groups as genetically isolated subpopulations of chinook salmon. The distinctness of the T0 allelic distribution is supported by additional differences. Similarly distinct and highly significant frequency differences between areas are observed for the IDH and LGG loci, and the frequency of the PMI variants also suggests a different distribution

Table 2.--Allelic frequencies and approximate 95% confidence intervals of common alleles of 12 polymorphic loci of chinook salmon in collections of fall run fish from the Snake and mid-Columbia Rivers.

Allelic frequencies of polymorphic loci expressed as percentages (95 % confidence intervals)													
Location	N	PMI	TO	MDH-B	LGG	GL	IDH	LDH-4	LDH-5	TO-2	ADH	GL-2	ACON
Ice Harbor Dam													
Adult-1977	65	74(8)	71(8)	99 (2)	---	98(2)	---	100(2)	100(2)	100(2)	---	---	---
Adult-1978	100	79(6)	66(7)	98 (2)	92(4)	100(2)	100(2)	100(2)	99(2)	---	100(2)	100(2)	---
Juvenile - 1979 brood	185	83(4)	71(5)	97 (2)	84(4)	98(1)	100(1)	100(1)	100(1)	100(1)	97(2)	99(1)	---
Adult-1980	300	79(4)	64(5)	97 (2)	90(3)	98(2)	97(2)	100(1)	99(1)	100(1)	---	---	91(3)
Total	650												
Grand mean		79(3)	68(3)	98 (1)	91(2)	98(1)	99(1)	100(.3)	99(1)	100(.3)	98(1)	99(1)	91(3)
Priest Rapids Hatchery													
Juvenile - 1977 brood	120	67(6)	49(7)	98 (2)	---	100(2)	89(4)	100(1)	99(1)	100(1)	97(2)	---	---
Wild juvenile - 1978 brood	45	75(9)	57(10)	96 (4)	81(8)	98(3)	94(5)	100(3)	99(2)	100(3)	99(2)	100(3)	---
Hatchery juvenile - 1978 brood	98	68(7)	50(7)	94 (3)	80(6)	99(1)	93(4)	100(1)	100(1)	100(1)	98(2)	100(1)	---
Adult-1980	150	72(5)	51(5)	97 (2)	76(5)	99(1)	91(3)	100(1)	97(2)	100(1)	---	---	81(4)
Total	413												
Grand mean		70(3)	52(3)	96 (1)	79(3)	99(.8)	92(2)	100(.4)	99(1)	100(.4)	98(1)	100(1)	81(4)
Difference between allelic frequencies in fish from Ice Harbor Dam and Priest Rapids Hatchery													
		9	16	2	12	1	7	0	0	0	0	0	10

between the two areas. The ACON data, available only for the 1980 adult collections, also indicate a substantial difference between the two groups. These data cumulatively argue strongly against a recent common ancestry for mid-Columbia River and Snake River fall chinook salmon populations and support a divergence interval of many hundreds, perhaps thousands, of years.

CONCLUSIONS

We have reviewed various factors relating to the distinctness of the Snake River and mid-Columbia River fall chinook salmon runs as separate species under the Endangered Species Act of 1973. No conclusions can be drawn from data pertaining to the geological history of the two regions, and the timing of returns, by definition, is the same. The fact that the locations are distinct, however, is suggestive of differences which may warrant species distinction.

Habitat differences exist between the two regions, and morphological differences between the two populations were also indicated, but these could be due to either genetic divergence or to differential responses of a common gene pool to different environments. There is the possibility that both groups may have recently descended from common ancestors that were displaced by dam impoundment from a historical spawning area downstream. However, strong evidence of biochemical genetic differences between the two groups indicate a divergence time from common ancestry of a much longer duration than the few decades since dam impoundment. These differences reflect a sufficient passage of time since common ancestry for the occurrence of differential adaptations to the different habitats.

Based on our analysis of the available evidence, especially the strong genetic differences, we conclude that the mid-Columbia River and the Snake River fall chinook salmon runs are separate, distinct, and identifiable populations.

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