Contrasting patterns of productivity and survival rates for stream-type chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers

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Abstract: The effects of increasing hydropower development and operation appear extremely important in the decline and near extripation of stream-type chinook salmon (*Oncorhynchus tshawytscha*) stocks of the upper Columbia and Snake rivers. We evaluated temporal and spatial patterns of productivity and survival rates (for index stocks from the Snake, upper Columbia, and lower Columbia regions) to determine the cause of dramatic declines of the upriver stocks. This evaluation tested hypotheses about nonstationarity (changes over time in average productivity) in the Ricker recruitment function caused by changes in the physical environment. Individual stocks showed recent declines in indicators of productivity and survival rate; however, the comparisons indicate that upriver stocks showed greater declines coincident with the development and operation of the hydropower system. Evidence from the aggregate run indicates that declines over the last 50 years were quite abrupt and corresponded to construction and completion of the hydropower system.

Résumé : L'accroissement du développement et de l'exploitation de l'hydro-électricité semble jouer un rôle très important dans le déclin et la disparition presque complète des stocks de quinnat (*Oncorhynchus tshawytscha*) de type dulcicole dans le cours supérieur du Columbia et la Snake. Nous avons évalué les profils temporels et spatiaux de la productivité et du taux de survie (pour des stocks indicateurs des régions de la Snake, du haut Columbia et du bas Columbia) pour déterminer la cause des déclins marqués des stocks d'amont. Pour cette évaluation, on a testé des hypothèses concernant la non-stationnarité (changements temporels dans la productivité moyenne) dans la fonction de recrutement de Ricker causée par les changements dans le milieu physique. Les stocks individuels ont connu des déclins récents selon les indicateurs de la productivité et du taux de survie, mais les comparaisons montrent que les stocks d'amont ont connu des déclins plus importants par suite du développement et de l'exploitation du réseau hydro-électrique. Les données sur la remonte totale montrent que les déclins des 50 dernières années ont été assez abrupts et ont suivi la construction et la finalisation du réseau hydro-électrique.

[Traduit par la Rédaction]

Introduction

Snake River spring and summer (stream-type) chinook salmon (*Oncorhynchus tshawytscha*) populations have declined dramatically with the completion of the Federal Columbia River Power System (FCRPS). They have been listed as threatened under the Endangered Species Act (ESA) since 1992. Under the ESA, the National Marine Fisheries Service (NMFS) is charged with developing and implementing management plans to ensure survival and recovery of the listed salmon populations. The NMFS 1995–1998 Biological Opinion on operation of the FCRPS (NMFS 1995) created a process called PATH (plan for analyzing and testing hypotheses). The first phase of PATH is retrospective and involves explicitly stating hypotheses about the distribution of mortality over the life cycle, evaluating strengths and weaknesses of supporting evidence, and testing those alternative hypotheses that have significant management implications.

We describe a quantitative approach to test for nonstationarity (change over time in average productivity) in recruitment functions due to physical change in the environment. We applied this approach to spawner (parents) and recruit (progeny) information from populations of spring and summer chinook of the Columbia River basin. We provided spatial contrast by using replicate index stocks from three different regions of the basin (which presently experience very different conditions during their juvenile migrations through the FCRPS) for spatial contrast. Our work is based on a unique spatial and temporal contrast of stock performance, which evaluates hypotheses about causes of decline for Snake River populations.

The focus of this analysis is on spawner and recruitment information rather than on simple escapement trends. The productivity and survival rate indices are more robust mea-

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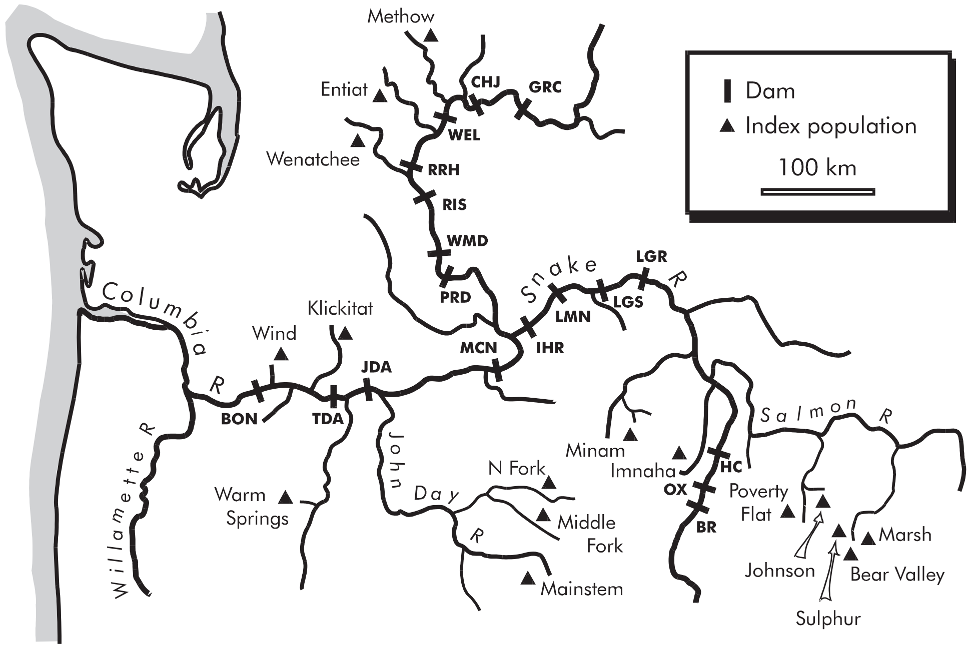
Fig. 1. Distribution of index stocks of spring and summer chinook. Mainstem dams: Bonneville (BON), The Dalles (TDA), John Day (JDA), and McNary (MCN) on the lower Columbia River, Ice Harbor (IHR), Lower Monumental (LMN), Little Goose (LGS), Lower Granite (LGR), Hells Canyon (HC), Oxbow (OX), and Brownlee (BR) on the Snake River, and Priest Rapids (PRD), Wanupum (WMD), Rock Island (RIS), Rocky Reach (RRH), Wells (WEL), Chief Joseph (CHJ), and Grand Coulee (GRC) on the upper Columbia River.



sures of stock performance because they account directly for several factors that may confound simple escapement measures. The productivity and survival rate indices account for hatchery fish, age composition of returns, variable harvest mortality rates and adult passage survival rates, and density dependence.

We evaluated the following sets of alternative hypotheses for stream-type chinook.

Hypothesis 1*a*: Productivity (Ricker *a* from ln(*R*/*S*) versus *S*) has shown similar responses over time between upriver stocks and downriver stocks. **Hypothesis 1*b***: Productivity declined more over time for upriver stocks, which were most affected by hydropower development, than for downriver stocks.

Hypothesis 2*a*: Survival rate indices (ln[(observed *R*/*S*)/(predicted *R*/*S*)]) have shown similar responses over time between upriver stocks and downriver stocks. **Hypothesis 2*b***: Survival rate indices declined more and become more variable for upriver stocks, which were most affected by hydropower development, than for downriver stocks.

Hypothesis 3*a*: Productivity and survival rate of the upriver run of Columbia River wild spring chinook have been in a long-term decline since escapements were first measured (1939). **Hypothesis 3*b***: Declines in productivity and survival rate of upriver runs of Columbia River wild spring chinook over the past 50 years corresponded to construction and completion of the FCRPS.

Methods

Index stocks

Four groups of naturally reproducing stocks are used in this analysis: Snake River spring and summer chinook, upper Columbia River spring chinook, lower Columbia River spring chinook, and the aggregate upriver run of spring chinook.

Index stocks were grouped geographically to reflect similar potential impacts from hydropower development and operation. All stocks in the analysis are classified as upriver runs (ODFW and WDFW 1995) because they originate from upriver of Bonneville Dam (Fig. 1), east of the Cascade Mountain Range. Upriver spring chinook adults enter the mouth of the Columbia River in March through May, and summer chinook adults enter the river in June and July (ODFW and WDFW 1995). Spawning takes place primarily in August through September. All stocks are stream-type chinook (Healy 1991), producing yearling smolts that migrate seaward in the spring (primarily April and May).

The aggregate upriver run of wild spring chinook consists of all wild spring chinook that originate upriver of Bonneville Dam, including all spring chinook stocks in this analysis. This aggregate run provides indices of productivity and survival rates over a much longer time series than is possible for the individual index stocks.

Spawning and rearing habitat factors would be expected to contribute to productivity and survival rate variability within regions. A broad mix of habitat condition exists within each of the three regions (Table 1), and significant effects of habitat degradation predate most of the time series (Fulton 1968; Beamesderfer et al. 1997).

The Snake River region in this analysis includes streams in Idaho and Oregon, upriver of Lower Granite Dam (Fig. 1). The seven Snake River stocks are from four subbasins and occupy a wide range of tributary habitat condition (Table 1) from wilderness (Minam and Sulphur) to heavily impacted (Poverty Flat and Bear Valley).

The upper Columbia region was defined as the Columbia River upriver of the confluence with the Snake River (Fig. 1). The three upper Columbia stocks represent three subbasins and occupy tributaries that have sustained moderate habitat impacts (Table 1).

The lower Columbia region was defined in this analysis as the Columbia River downriver of the Snake River confluence to

Table 1. Summary of years of data and attributes of index populations of wild spring and summer chinook.

Region, subbasin, population	Run	Years of data	Dams passed	Completion of last dam	Habitat quality	Hatchery influence	Year of first hatchery program
Snake							
Middle Fork Salmon							
Bear Valley	Spring	1957–1995	8	1975	Poor	Low	na
Marsh	Spring	1957–1995	8	1975	Good	Low	na
Sulphur	Spring	1957–1995	8	1975	Good	Low	na
South Fork Salmon							
Poverty Flat	Summer	1957–1995	8	1975	Poor	Moderate	1980
Johnson	Summer	1957–1995	8	1975	Fair	Moderate	1980
Grande Ronde							
Minam	Spring	1954–1995	8	1975	Good	Moderate	1986
Imnaha							
Mainstem	Spring/summer	1949–1995	8	1975	Good	Moderate	1982
Upper Columbia							
Methow							
Mainstem	Spring	1960–1995	9	1968	Fair	Moderate	1941
Entiat							
Mainstem	Spring	1955–1995	8	1968	Fair	Moderate	1942
Wenatchee							
Mainstem	Spring	1958–1995	7	1968	Fair	Moderate	1899
Lower Columbia							
John Day							
Mainstem	Spring	1959–1995	3	1968	Fair	Low	na
Middle Fork	Spring	1959–1995	3	1968	Poor	Low	na
North Fork	Spring	1959–1995	3	1968	Good	Low	na
Deschutes							
Warm Springs	Spring	1969–1995	2	1957	Fair	Moderate	1958
Klickitat							
Mainstem	Spring	1966–1995	1	1938	Fair	Moderate	1950
Wind							
Mainstem	Spring	1970–1995	1	1938	Good	High	1938
Upriver aggregate	Spring	1939–1995	Variable	Variable	Variable	Variable	Variable

Note: Imnaha data are for 1949–1950 and 1952–1995.

Bonneville Dam (Fig. 1). The six lower Columbia stocks are from four subbasins and occupy a wide range of tributary habitat condition (Table 1) from wilderness (North Fork John Day) to significantly impacted (Middle Fork John Day). Note that only the three John Day River stocks had sufficient pre-1970 spawner–recruit data to use in the productivity and survival rate analyses. Data from the other three stocks were incorporated in escapement comparisons.

Hatchery factors would also be expected to contribute to productivity and survival rate variability within regions. In the early years, wild fish predominated the aggregate Columbia River spring chinook run (Fig. 2*a*), with most of the production from the Snake and upper Columbia regions (Fulton 1968). The proportion of hatchery fish in the total run has increased with time, primarily from programs to compensate for loss of fish production due to hydropower development. The potential influence of hatchery programs ranges widely between stocks within each region (Table 1). Stocks with no anadromous fish hatchery programs within their subbasin are the three Middle Fork Salmon River stocks (Snake region) and the three John Day River stocks (lower Columbia region).

The estimates of recruits used in hypothesis testing explicitly take into account the tributary and mainstem Columbia River harvest rates. Historically, upriver spring and summer chinook supported substantial commercial and sport fisheries and Tribal commercial, ceremonial, and subsistence fisheries in the mainstem Columbia River (ODFW and WDFW 1995) and sport and Tribal fisheries in the tributaries (Beamesderfer et al. 1997). The mainstem harvest rates were cut back dramatically as runs declined in the mid-1970's for spring chinook and in the late 1960's for summer chinook (Fig. 2*b*). These harvest rates have remained at low levels. Snake River wild stocks last supported tributary harvest in 1978. In contrast, the index stocks below the Snake River confluence (lower Columbia River stocks) in this analysis (Wind, Klickitat, Warm Springs, and John Day rivers) have continued to support tributary sport and Tribal fisheries (Beamesderfer et al. 1997).

Ocean harvest rates are very small for stream-type chinook originating above Bonneville Dam, estimated at less than 1% based on a near absence of coded-wire tag (CWT) recoveries from ocean fishery mark recovery programs (Berkson 1991). For instance, only 62 marked stream-type chinook were recovered in ocean fisheries out of 2.1 million CWT marks released from Snake and lower Columbia region hatcheries in release years 1983–1990 (Pacific States Marine Fisheries Commission data). This is in stark contrast with much higher ocean recoveries and harvest rates for Columbia

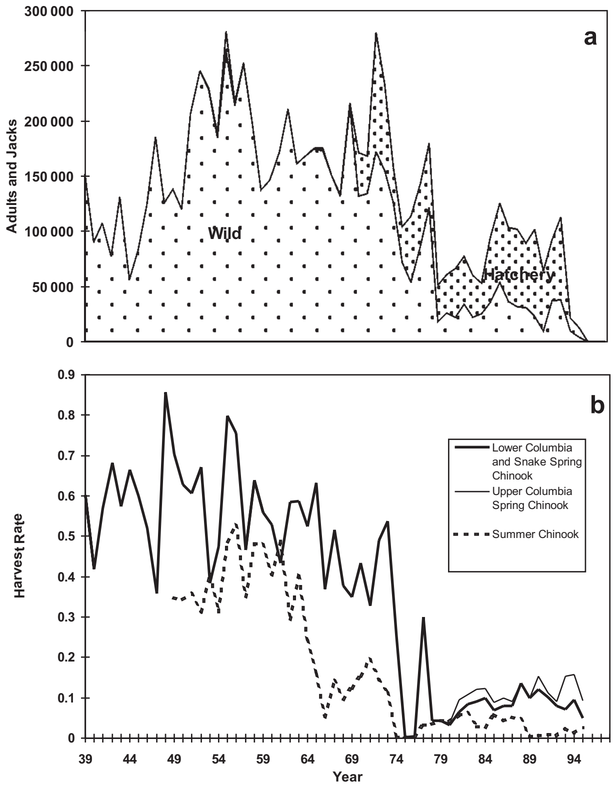


Fig. 2. (*a*) Run size of upriver aggregate spring chinook (wild and hatchery components) to the Columbia River mouth and (*b*) mainstem harvest rates (combined commercial, tribal, and sport) for Columbia River and Snake River spring and summer chinook index stocks, 1939–1995.

River basin ocean-type (fall) chinook. Both stream-type and ocean-type chinook are sampled by the same ocean recovery program.

The stocks from the three regions have experienced different juvenile migration conditions, due to mainstem hydropower development and operations. The maximum number of dams that Snake River and upper Columbia River chinook salmon encounter during migration has increased to eight and nine dams, respectively (Fig. 3*a*; Table 1). In contrast, the most dams encountered by lower Columbia River stocks are three. The completion dates for the final dam faced by stocks from the three regions are 1975 for Snake, 1968 for upper Columbia, and 1968 for lower Columbia (Table 1). Survival rates of smolts decreased as dams and reservoirs were built (Raymond 1988). To circumvent mortality of juveniles, most Snake River juveniles arriving at the dams have been collected at either Lower Granite Dam or Little Goose Dam since 1977 and transported by barge or truck for release below Bonneville Dam (Mundy et al. 1994). A fraction of juveniles arriving at McNary Dam from both the upper Columbia and Snake regions have been transported since 1979. None of the lower Columbia stocks are collected and transported.

One effect of increased impoundment has been to decrease water velocity and thus slow outmigration of fish from upriver areas (Raymond 1979, 1988; Berggren and Filardo 1993). Water velocity is generally expressed as the average time that it takes a water particle to travel through a river reach (water travel time). Average historic water travel times (in days and by region) for the juvenile mainstem migration period (April 16 – May 31) are depicted in Fig. 3*b*. The river reaches representing the three regions are the head of Lower Granite Reservoir to Bonneville Dam for the Snake region, the mouth of the Methow River to Bonneville Dam for the upper Columbia region, and the mouth of the John Day River to Bonneville Dam for the lower Columbia region. These data were provided by the Columbia River Inter-Tribal Fish Commission (E. Weber, Columbia River Inter-Tribal Fish Commission, personal communication (e-mail: webe@critfc.org)). Prior to Bonneville Dam completion in 1938, water travel time consistently averaged less than 3 days for the Snake and upper Columbia regions. Prior to 1968 when John Day Dam was completed, water travel time for these upriver regions generally averaged less than 10 days, with the earlier years averaging less than 5 days. Since completion of the final dams, average water travel times have been highly variable and have generally exceeded 2 weeks. In contrast, average water travel times for the lower Columbia region, while somewhat elevated, have remained under 5 days. The annual survival rates of Snake River stocks for brood years 1975–1986 were correlated with water travel times (Petrosky and Schaller 1992).

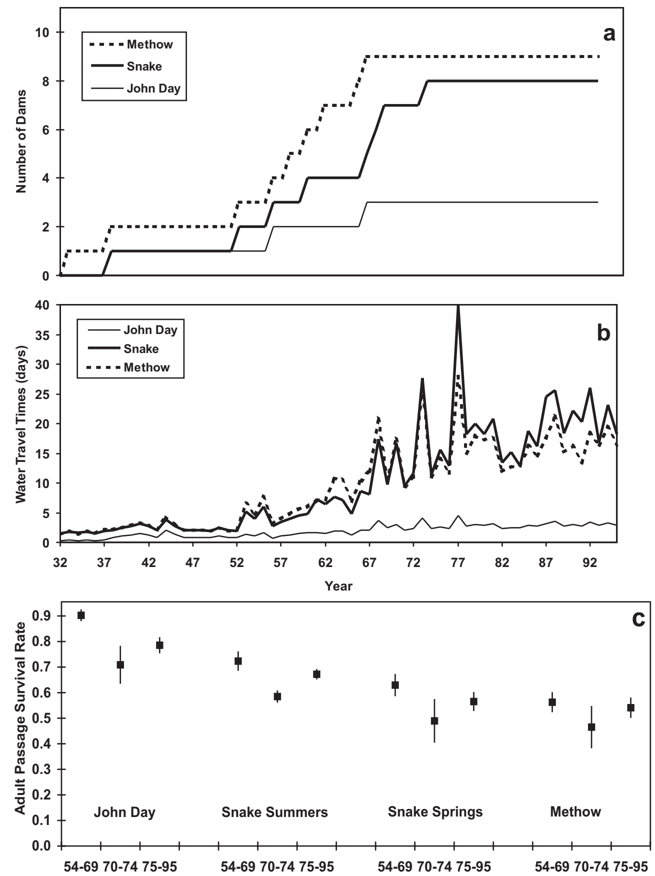


Fig. 3. (*a*) Maximum number of hydroelectric dams and (*b*) average annual water travel time experienced by spring and summer chinook yearling outmigrants from stocks representing the three regions of the interior Columbia River basin, 1932–1995 (E. Weber, Columbia River Inter-Tribal Fish Commission, personal communication (e-mail: webe@critfc.org)), and (*c*) upriver passage survival rates (average ± SE) of adult spring and summer chinook salmon from stocks representing the three regions of the interior Columbia River basin, 1954–1969, 1970–1974, and 1975–1995 (Beamesderfer et al. 1997).

Hydropower development in the basin has also reduced the survival of mature fish returning to spawn. Adult passage survival rates (Beamesderfer et al. 1997) were generally similar during the pre-1970 and post-1974 periods, with a notable decline during the transition period (Fig. 3*c*). The estimates of recruits used in hypothesis testing explicitly take into account the adult passage survival rates.

Spawning escapement trends

Time trends of spawning escapement were compared graphically among and within the geographic stock groups, and limitations of these comparisons were identified. These spawning escapement measures include both natural origin fish and, where applicable, hatchery fish spawning in the wild. All years of escapement data were standardized by dividing each year's value by the average escapement computed from all available years through 1995. Caution is needed when comparing escapement trends because of the following limitations: (*i*) a lack of accounting for density dependence, (*ii*) exclusion of harvest and adult passage mortality, both of which have varied considerably through time and across stocks, and (*iii*) a general lack of accounting of hatchery spawner contributions or of direct effects of hatchery operations (natural brood stock removal or adult outplants).

Spawners and recruits

We developed estimates of spawners and recruits for each of the index stocks; the data sources, run reconstruction methods, and results are documented in Beamesderfer et al. (1997). Spawners (returning fish with greater than 1 year of ocean residence) were independently estimated for each index area based on expanded ground and aerial redd counts or live fish and carcass counts. Recruits were measured to the mouth of the Columbia River and included jacks (precocious males that return after 1 year of ocean residence). We expanded age-structured spawners into recruitment by accounting for prespawning survival, tributary harvest, mainstem harvest, and adult passage losses at the dams. Computation of the recruits for different stocks relied on both unique and shared survival rates. In streams where hatchery fish spawned with natural fish, the hatchery contribution was estimated and subtracted from total recruits. Any natural-origin fish taken as brood stock were counted as natural recruits. Estimated numbers of spawners for index stocks included any hatchery strays or outplants. That is, the spawner estimates included all fish spawning in the wild, and recruits counted only those of natural origin. The numbers of age-structured wild spring chinook in the upriver aggregate run were estimated at Bonneville Dam by expanding hatchery rack returns for adult passage survival, harvest, and prespawning mortality rates back to Bonneville Dam and subtracting the expanded hatchery estimate from the total Bonneville count (Beamesderfer et al. 1997). The run reconstruction methods for the aggregate upriver spring chinook run expand numbers of wild spring chinook recruits to the Columbia River mouth for mainstem harvest rates of upriver spring chinook below Bonneville Dam (ODFW and WDFW 1995).

Time periods

For each index stock, spawner and recruit data were classified into two primary time periods (and a transition period), defined by FCRPS development and operations affecting the threatened Snake River index stocks. The first period, pre-1970 brood years, was prior to completion of the last two Snake River dams. All mainstem dams in the upper Columbia River migration corridor were completed and fully operational by 1969. The second primary period, post-1974 brood years, was marked by the initiation of mass transportation of smolts around the Snake River dams and gradual passage improvements. Upper Columbia River stocks were also influenced by incremental system improvements in this period and by transportation from McNary Dam since 1979. The transition period, 1970–1974 brood years, was a period of construction and changing operations in the Snake River that caused extremely high levels of atmospheric gas supersaturation in high-flow years (Raymond 1979).

Productivity and survival rates

Productivity and survival rate indices were estimated for different periods and stocks throughout the Columbia River Basin. Productivity is defined as the natural log of the ratio of recruits to spawners in the absence of density-dependent mortality (Neave 1953). Spawner (S) and recruit (R) data can be fit to the Ricker (1975) recruitment function:

$$(1) \qquad R = e^{a} S e^{-\beta S}.$$

The a and β parameters are typically estimated by the log transformation of eq. 1. Productivity is typically measured as the intercept, or Ricker a. The Ricker recruitment function exhibited a better fit to our first period data than a Beverton–Holt function.

Survival rate indices provide a time series of density-independent mortality estimates through deviations of observed R/S from those predicted by the fitted stock–recruitment function for a specified time period. Survival rate indices were expressed as the natural log of the ratio of observed R/S to the predicted R/S. The natural log of these ratios transforms the differences, such that they tend to be normally distributed (Peterman 1981).

Spawner–recruitment analysis normally assumes that the average spawner–recruitment relationship does not change over time. Often the spawner–recruitment curve will indeed change (nonstationarity) due to physical change in the environment or change in stock structure (Walters 1987; Hilborn and Walters 1992).

We tested for evidence of nonstationarity in the recruitment functions caused by physical change in the migratory habitat (due to hydroelectric development). Large changes in density-independent mortality (caused by change in the physical environment) within a time series of spawner–recruitment data would cause nonstationary behavior in the recruitment function. We used two methods, suggested by Walters (1987), to detect if a systematic change in the spawner–recruitment relationships took place associated with this dramatic change in the physical environment: (*i*) covariance analysis of data in time blocks associated with the physical change and (*ii*) evaluation of time series of recruitment model deviations.

We relied primarily on the analysis of multiple index stocks to address potential nonstationarity due to changes over time in the aggregate stock structure. Using an aggregation of stocks in spawner–recruitment analysis has the potential to overestimate productivity if stock structure changes. This nonstationarity in spawner–recruitment relationships could occur if the less productive stocks made a smaller contribution to the aggregate over time, due to an increasing level of density-independent mortality (e.g., dam passage mortality, incidental fishing mortality). Common patterns in productivity and survival rates between index stocks and an aggregate run would suggest that nonstationary behavior in the aggregate recruitment function was not primarily due to changes in aggregate stock structure.

A lack of contrast in spawner abundance could give a distorted picture of average recruitment rates, with productivity being overestimated at low stock sizes (Walters 1990). To provide a large contrast in spawner abundance, we fit spawner and recruit data for the longest available time series (with a period effect).

The hypothesis testing of productivity in this paper was primarily concerned with estimating the relative change in spawner–recruitment functions between time periods and among geographic regions of the interior Columbia River basin. In hypothesis testing of survival rates, the deviation from the average spawner–recruitment relationship was of primary importance to the analyses, and estimation of average parameter values was secondary, consistent with the approach of Hilborn and Walters (1992). All statistical tests were performed at an α level of 0.05.

Hypothesis 1. Productivity changes

We evaluated whether productivity declined more for upriver stocks (which were most affected by the hydrosystem) in the post-

1974 period than for downriver stocks. We would expect a temporal change in the density-independent mortality, such as that imposed by hydroelectric development and operation, to be reflected primarily in the intercept (Ricker *a*) rather than in the slope (β) of the regressions. Therefore, hypothesis 1 was tested with analysis of covariance (ANCOVA) using the SAS (1993) general linear model (GLM) procedure to examine differences between the two periods for the intercept (Ricker *a* value) of the relationship of ln(*R*/*S*) versus *S*:

$$(2) \qquad \ln(R_{i,j}/S_{i,j}) = \tau_i + a - \beta(S_{i,j} - \bar{S}..) + \varepsilon_{i,j}$$

where τ_i is the class effect (period), a is the overall intercept, β is the overall slope, $\varepsilon_{i,j}$ is the normally distributed residual, i is the class (period), j is the observation

First, the assumption of homogeneity of slopes was tested for significant interaction between treatment (period) and the covariate (spawners). Then, ANCOVA was run to estimate the period effect on the ln(*R*/*S*), taking into account spawning level. The measure of productivity by period was estimated using $\tau_i + a$ from the ANCOVA results (eq. 2). This is equivalent to the Ricker *a* parameter by period assuming a common slope (β) over periods.

Hypothesis 2. Survival rate changes

We tested whether survival rates declined more and became more variable for upriver stocks (which were most affected by the hydrosystem) in the post-1974 period than for downriver stocks. Survival rate indices provide a time series of density-independent mortality estimates through deviations of observed *R*/*S* from those predicted by the fitted stock–recruitment function for a specified time period. The deviations, or survival rate indices, were expressed as ln[(observed *R*/*S*)/(predicted *R*/*S*)], where predicted values were based on fits to data from different time periods. This approach, using the deviations as an index of survival rate, is similar to approaches in Hilborn and Walters (1992, fig. 7.2.1), Peterman (1981), and Peterman et al. (1998).

We tested for changes in survival rates between regions using two indices. Survival rate index 1 (SRI-1) represented the deviation of post-1974 observations from pre-1970 predicted values based on the ANCOVA fit of eq. 2, and SRI-2 represented the deviation of pre-1970 observations from the post-1974 predicted values from the same ANCOVA fit. Attributes of SRI-1 and SRI-2 include the assumption of a common β between periods (i.e., temporal changes are explained by density-independent factors, τ_i and a) and use of the three John Day River stocks to represent the lower Columbia region. The use of SRI-1 and SRI-2 was consistent with our expectation that effects of hydropower development and operation would impose additional density-independent mortality on upriver stocks.

Period differences in survival rate indices (SRI-1 and SRI-2) were tested between stock groups from different regions with one-way classification analysis of variance (ANOVA) under the GLM procedure of SAS (1993). The GLM procedure was used because of unequal sample sizes between categories (regions). Differences in survival rate indices among the Snake, upper Columbia, and lower Columbia regions were then compared using Bonferroni's multicomparison test (SAS 1993), fixed to a prescribed experimentwise error rate of $\alpha = 0.05$. Bonferroni's pairwise procedure is the most appropriate test when making only a small number of comparisons (Milliken and Johnson 1984).

The hypothesis that survival rates became more variable for upriver stocks in the recent period was examined using *F* tests of survival rate variance of the two periods. The survival rate variance for the pre-1970 period was calculated using the SRI-1 for that period. The survival rate variance for the post-1974 period was calculated using the SRI-2 for that period.

Hypothesis 3. Long-term changes in aggregate upriver run

We evaluated whether the aggregate upriver spring chinook run has been in long-term decline since escapements were first measured (1939) or whether declines in productivity and survival rates were more associated with completion of the FCRPS during the 1970's. Data were categorized for these hypotheses by decade: 1939–1949, 1950–1959, 1960–1969, 1970–1979, and 1980–1990. The ANCOVA was run using the SAS GLM procedure to examine differences between the five periods in the relationship of ln(*R*/*S*) versus *S*. The covariance model for this test is also represented by eq. 2. The assumption of homogeneity of slopes was first tested for significant interaction between treatment (period) and the covariate (spawners). Then, ANCOVA was run to estimate the effect of period on ln(*R*/*S*), taking into account spawning level. The least squares means test was used in the ANCOVA (with homogenous slopes) to compare the period effect on productivity (Freund et al. 1986).

In addition, ANCOVA was run for the pre-1970 and post-1974 periods to parallel the individual index stocks analysis. The assumption of homogeneity of slopes was tested as described above.

For the aggregate upriver spring chinook run, SRI-1 represented the deviation of post-1974 observations from pre-1970 predicted values based on the ANCOVA fit of eq. 2, and SRI-2 represented the deviation of pre-1970 observations from the post-1974 predicted values from the same ANCOVA fit. SRI-1 and SRI-2 for the aggregate upriver spring chinook run were plotted and compared for the brood years 1939–1990.

Results

Spawning escapement trends

Patterns of standardized escapements for Snake River stocks exhibited a similar trend of decline, which was particularly noticeable by the mid-1970's (Fig. 4*a*). Before 1970, Snake River stock escapements ranged from 33 to 541% of their average escapement level. After 1974, escapements ranged from 0 to 184%. All Snake River stocks experienced severely depressed returns in 1994 and 1995.

Standardized escapements for upper Columbia River stocks exhibited a similar trend of decline, beginning in the late 1960's (Fig. 4*b*). Before 1970, escapements ranged from 32 to 337% of their average escapement level. After 1974, escapements ranged from 1 to 161%. Like the Snake River stocks, the upper Columbia River stocks experienced severely depressed returns in 1994 and 1995.

Standardized escapements for the lower Columbia River stocks were quite variable and appeared to show no trend during the past three decades (Fig. 4*c*). Before 1970, escapements ranged from 5 to 234% of their average escapement level. After 1974, escapements in the lower Columbia River index stocks ranged from 9 to 506%.

Escapements for the upriver aggregate run showed a weak upward trend up through the mid-1970's, at which time a major decline was evident (Fig. 2). Before 1970, escapements ranged from 29 to 227% of their average escapement level. After 1974, escapements ranged from 6 to 189%. The upriver run experienced severely depressed returns in 1994 and 1995.

Hypothesis 1. Productivity changes

The majority of index stocks exhibited a decrease in productivity from the pre-1970 period to the post-1974 period;

Fig. 4. Spawner escapements of spring and summer chinook index stocks, standardized to their average escapements (computed for all available brood years through 1990) and plotted on a natural logarithm scale, for the (*a*) Snake, (*b*) upper Columbia, and (*c*) lower Columbia regions. MIN, Minam; IMN, Imnaha; BVE, Bear Valley; MAR, Marsh; SUL, Sulphur; POV, Poverty Flat; JON, Johnson; WEN, Wenatchee; ENT, Entiat; MET, Methow; WIN, Wind; KLI, Klickitat; WS, Warm Springs; JDMA, mainstem John Day; JDMI, Middle Fork John Day; JDNG, North Fork John Day. ln(0) values plotted as 0.01.

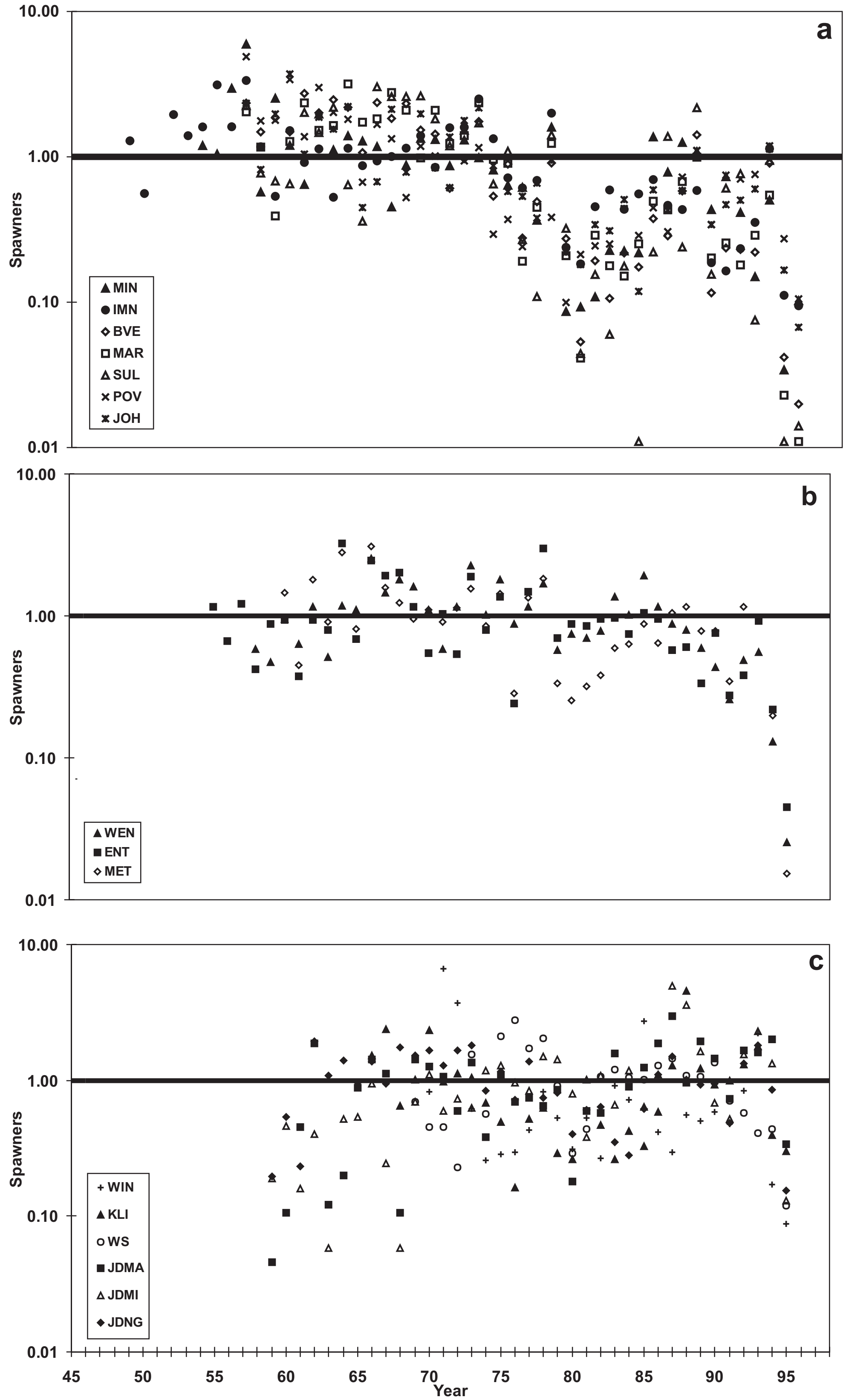


Table 2. ANCOVA results for Ricker recruitment functions using period (treatment) and spawners (covariate) for spring/summer chinook index stocks from the Snake, upper Columbia, and lower Columbia regions and upriver aggregate run.

Region, subbasin	Index stock	Intercept $\tau_1 + a$, pre-1970	Intercept $\tau_2 + a$, post-1974	$\tau_1 - \tau_2$	Intercept H_0: $\tau_1 = \tau_2$, p	SE (τ)	Slope β	Slope H_0: $\beta \leq 0$, p	R^2	Homogeneity of slope, p
Snake										
Middle Fork Salmon	Bear Valley	3.3707	0.7611	2.6096	0.0016	0.7397	0.001309	0.0214	0.36	0.2785
	Marsh	3.7245	0.7134	3.0110	0.0001	0.6464	0.002933	0.0047	0.46	0.1325
	Sulphur	3.3884	0.8709	2.5175	0.0002	0.5818	0.003535	0.0034	0.44	0.5176
South Fork Salmon	Poverty Flat	1.4731	0.7851	0.6880	0.1125	0.4189	0.000368	0.1503	0.10	0.1700
	Johnson	2.1315	0.6829	1.4486	0.0016	0.4123	0.001952	0.0239	0.32	0.5915
Imnaha	Mainstem	2.1318	0.6869	1.4450	0.0001	0.2394	0.000662	0.0002	0.53	0.8842
Grande Ronde	Minam	2.5967	0.6230	1.9737	0.0001	0.4011	0.001556	0.0004	0.49	0.0079
Upper Columbia										
Methow	Mainstem	3.3043	1.6028	1.7014	0.0001	0.3417	0.000725	0.0003	0.56	0.2099
Entiat	Mainstem	2.5445	1.0778	1.4667	0.0001	0.2603	0.002014	0.0009	0.58	0.2398
Wenatchee	Mainstem	2.3930	0.4544	1.9387	0.0001	0.3520	0.000208	0.1661	0.55	0.0684
Lower Columbia										
John Day	Mainstem	2.2200	1.6027	0.6174	0.0188	0.2451	0.003279	0.0001	0.66	0.3814
	Middle Fork	1.7562	1.3519	0.4043	0.2742	0.3613	0.001680	0.0010	0.52	0.0451
	North Fork	2.8774	1.4983	1.3792	0.0001	0.1926	0.000874	0.0001	0.75	0.6614
Upriver aggregate		2.0562	0.4085	1.6477	0.0001	0.1333	0.000016	0.0001	0.79	0.1651

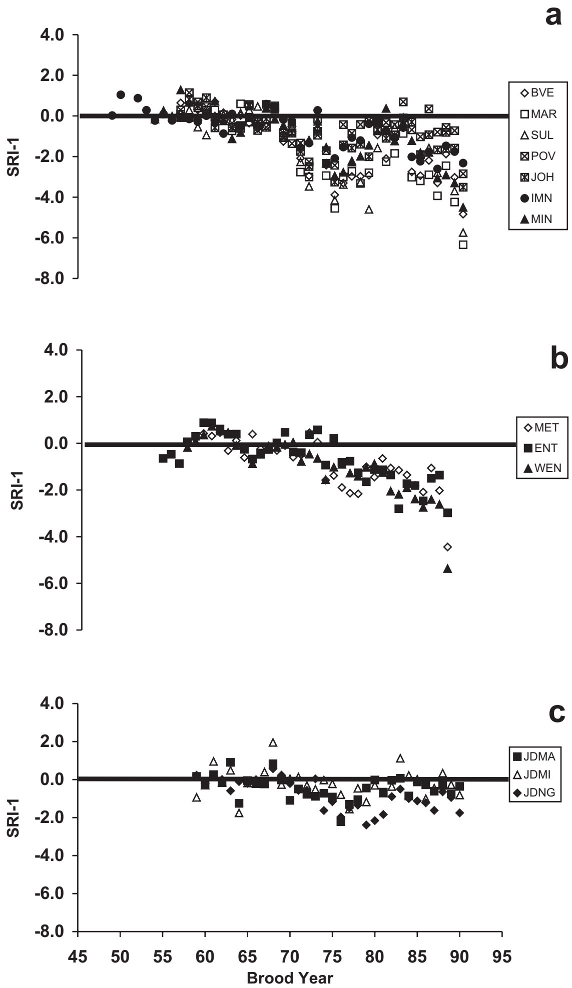
however, the upriver stocks showed greater declines. The ANCOVA tests for differences between periods (pre-1970 and post-1974), in the relationship of ln(R/S) versus S, were significant for 11 of the 13 stocks tested (Table 2). The two exceptions were Poverty Flat and Middle Fork John Day River. It should be noted that degraded spawning and rearing habitats for these two stocks had shown gradual improvements since the late 1960's and 1970's. In all cases the productivity ($\tau_i + a$) dropped from the pre-1970 period to the post-1974 period (Table 2). Overall, productivity declined more between periods in the Snake River and the upper Columbia River stocks than in the lower Columbia River stocks (Table 2). The average decline in productivity from the pre-1970 period to the post-1974 period was 1.96 in the Snake River stocks, 1.7 in the upper Columbia River stocks, and 0.8 in the lower Columbia River stocks. These reductions in productivity were approximately equal to a decrease in recruits per spawner (in the absence of density dependence) of seven for Snake River stocks, six for upper Columbia River stocks, and two for lower Columbia River stocks. The assumption of a common β between periods (homogeneity of slopes) was plausible for the majority of stocks, since the probability values for the treatment (period) by covariate (spawners) interaction were not significant for 11 of 13 stocks tested (Table 2). Furthermore, the two stocks with significant interactions (Minam and Middle Fork John Day) were from different regions. Because there was no apparent regional pattern to the interactions, the ANCOVA was applied to all the stocks.

Hypothesis 2. Survival rate changes

The pattern of survival rates as measured by SRI-1 (ANCOVA estimate for the pre-1970 brood years) for Snake River and upper Columbia River stocks exhibited a marked decline in the post-1974 brood years (Figs. 5*a* and 5*b*), except for Poverty Flat, which had no apparent pattern. The pattern of SRI-1 for lower Columbia River stocks exhibited little to no decline (Fig. 5*c*). Patterns for SRI-2 were very similar to those for SRI-1, except for the change in scale of the survival rate index (not shown; see Fig. 7 for example).

The survival rate declines were significantly greater, over time, for upriver stocks than for downriver stocks. The means for SRI-1 for the Snake, upper Columbia, and lower Columbia regions were –1.95, –1.70, and –0.80, respectively. For SRI-1, a larger negative value indicated a greater decline from the pre-1970 brood years. The means for the SRI-2 are nearly identical to SRI-1 means except for having opposite signs (Table 3). There were significant regional differences in mean survival rates ($F = 17.03$ and $p < 0.0001$ for SRI-1; $F = 23.96$ and $p < 0.0001$ for SRI-2) (Table 3).

Fig. 5. Deviations of ln[(observed *R*/*S*)/(predicted *R*/*S*)] from ANCOVA fit to the pre-1970 period (SRI-1) for the (*a*) Snake, (*b*) upper Columbia, and (*c*) lower Columbia regions, brood years 1949–1990. Abbreviations as described in Fig. 4.



The multiple comparison tests for SRI-1 and SRI-2 indicated no significant difference between Snake and upper Columbia stocks (Table 3). There were significant differences between Snake and lower Columbia stocks and between upper Columbia and lower Columbia stocks (Table 3). The Snake and upper Columbia survival rates declined more over time than lower Columbia indices, as indicated by SRI-1 and SRI-2 (Table 3).

The survival rates of Snake and upper Columbia region stocks became more variable in the post-1974 period than in the pre-1970 period (Table 4). The variance of survival rate indices increased significantly in the post-1974 period for six of 10 Snake and upper Columbia region stocks (Table 4). For the lower Columbia region stocks, variance of survival rate indices increased significantly for one and decreased significantly for another.

Hypothesis 3. Long-term changes in aggregate upriver run

The aggregate upriver run of wild spring chinook for the pre-1970 brood years exhibited higher ln(*R*/*S*) at *S* than for the 1970–1990 brood years, when escapement levels were fairly similar (Fig. 6). The pre-1970 relationship of ln(*R*/*S*) versus *S* appeared relatively linear over a long time series (1939–1969). This aggregate wild run, during the pre-1970 brood years, maintained high levels of escapement during a period of substantial harvest rates (Fig. 2). The ln(*R*/*S*) at *S* of the aggregate upriver run declined after 1969 (Fig. 6). Spawner numbers decreased, even with large reductions in harvest rates. The same temporal pattern was also evident in ln(*R*/*S*) versus *S* plots for the individual index stocks in the Snake River and upper Columbia River regions (Schaller et al. 1996). These patterns of ln(*R*/*S*) versus *S* are indicative of a shift in density-independent mortality in the later period.

The productivity of the upriver aggregate run did not exhibit a significant decline until the post-1970 decades. The difference in productivity ($\tau_i + a$) among decades (1939–1949, 1950–1959, 1960–1969, 1970–1979, and 1980–1990) was significant (Table 5). The productivity estimates for the first three decades were 1.93, 2.04, and 1.86. The productivity estimates for the 1970's and 1980's decreased to 0.69 and 0.42. The analysis indicated no significant differences among productivity values for the first three decades (LSMEAN, Table 5). The results indicated a significant difference between the 1970's productivity and those for each of the first three decades and between the 1980's productivity and those for each of the first three decades. The productivity values did not differ significantly between the 1970's and 1980's. The probability value for the treatment (period) by covariate (spawners) interaction was not significant (Table 5), so the assumption of a common β among decades was plausible.

The productivity estimate of the upriver aggregate declined from 2.06 in the pre-1970 period to 0.41 in the post-1974 period (Table 2). The probability value for the treatment (period) by covariate (spawners) interaction was not significant (Table 2).

The survival rates of the upriver aggregate run exhibited a sharp reduction, beginning in the early 1970's. The pattern of SRI-1 (fit to the pre-1970 brood years) for the aggregate upriver run of wild spring chinook exhibited no apparent trend for the pre-1970 brood years (Fig. 7*a*); the post-1970 survival rate indices exhibited a declining pattern. The same pattern was evident for SRI-2 (Fig. 7*b*).

Discussion

We analyzed a wide range of Snake River, upper Columbia River, and lower Columbia River wild spring and summer chinook index stocks to evaluate hypotheses concerning change in productivity and survival rates. The differences in productivity and survival rates between upriver (Snake River and upper Columbia River regions) and downriver (lower Columbia River region) stream-type chinook stocks coincided in space and time with development and operation of the hydropower system. Based on these comparisons of the productivity and survival rate indices among stocks, the effects of increasing hydropower development and operation appear extremely important in the decline of upriver stocks and near extirpation of Snake River spring and summer chinook. The escapement trend comparisons, while less robust measures of stock performance, are consistent with this conclusion.

Table 3. Results of tests for regional differences in survival rate indices.

Parameter, attribute	SRI-1	SRI-2
Productivity estimated from brood years	1949–1969	1975–1990
Comparison brood years	1975–1990	1949–1969
Estimated change in survival rate indices by region		
Snake	–1.9511	1.9222
Upper Columbia	–1.7022	1.6832
Lower Columbia	–0.8003	0.8004
ANOVA, H_0: no region differences in mean survival rate indices		
F	17.03	23.96
p	<0.0001	<0.0001
Reject H_0	Yes	Yes
Pairwise difference		
Snake – upper Columbia	–0.2489	0.2390
Snake – lower Columbia	–1.1509	1.1218
Upper Columbia – lower Columbia	–0.9020	0.8829
Multicomparison test, reject H_0: no significant pairwise region differences		
Snake – upper Columbia	No	No
Snake – lower Columbia	Yes	Yes
Upper Columbia – lower Columbia	Yes	Yes

Table 4. Results of *F* tests for change in variance between periods based on SRI-1 and SRI-2.

Region, subbasin	Index stock	Variance of pre-1970 deviations	Variance of post-1974 deviations	*F*	df1, df2	*p* > *F*	Direction of change
Snake							
Middle Fork Salmon	Bear Valley	0.3015	4.5062	14.95	11, 14	0.000035	+
	Marsh	0.2162	8.2398	38.11	11, 14	0.000000	+
	Sulphur	0.1502	10.6512	70.93	11, 13	0.000000	+
South Fork Salmon	Poverty Flat	0.6414	0.8798	1.37	11, 14	0.302874	0
	Johnson	0.4481	1.0433	2.33	11, 14	0.082588	0
Imnaha	Mainstem	0.3669	0.8152	2.22	18, 14	0.067463	0
Grande Ronde	Minam	0.6393	7.5784	11.86	14, 14	0.000019	+
Upper Columbia							
Methow	Mainstem	0.1541	0.4919	3.19	8, 14	0.051982	0
Entiat	Mainstem	0.4334	1.4469	3.34	13, 14	0.018239	+
Wenatchee	Mainstem	0.2430	0.8537	3.51	10, 14	0.025912	+
Lower Columbia							
John Day	Mainstem	0.4396	0.2607	1.69	9, 14	0.183621	0
	Middle Fork	3.7356	1.0344	3.61	9, 14	0.015747	–
	North Fork	0.1049	0.3408	3.25	9, 14	0.040506	+

Note: Negative or positive direction of change based on significance at $\alpha = 0.05$.

The empirical evidence from spawner and recruit data supported the hypothesis that productivity declined more for those stocks most affected by hydropower development, while lower river stocks have remained relatively stable. All index stocks compared showed some decline in productivity between the pre-1970 and post-1974 periods (nonstationarity). However, productivity estimates declined more in the Snake River and upper Columbia River than in the lower Columbia River.

Available spawner and recruit data from throughout the interior Columbia River basin also supported the hypothesis that survival rate declined and became more variable for those stocks most affected by hydropower development, while lower river stocks have remained relatively stable. All index stocks compared showed some decline in survival rate indices between the pre-1970 and post-1974 periods. However, survival rate, as measured by deviations from recruitment function fit to pre-1970 and post-1974 brood year data, declined significantly more in the Snake and upper Columbia rivers than in the lower Columbia River. The lack of significant interaction between the Ricker β and the period effect implies that the survival rate declines were primarily due to increases in density-independent mortality, consistent with our expectation about the FCRPS. In addition, similar

Fig. 6. ln(*R*/*S*) versus *S* for upriver wild aggregate spring chinook, brood years 1939–1990.

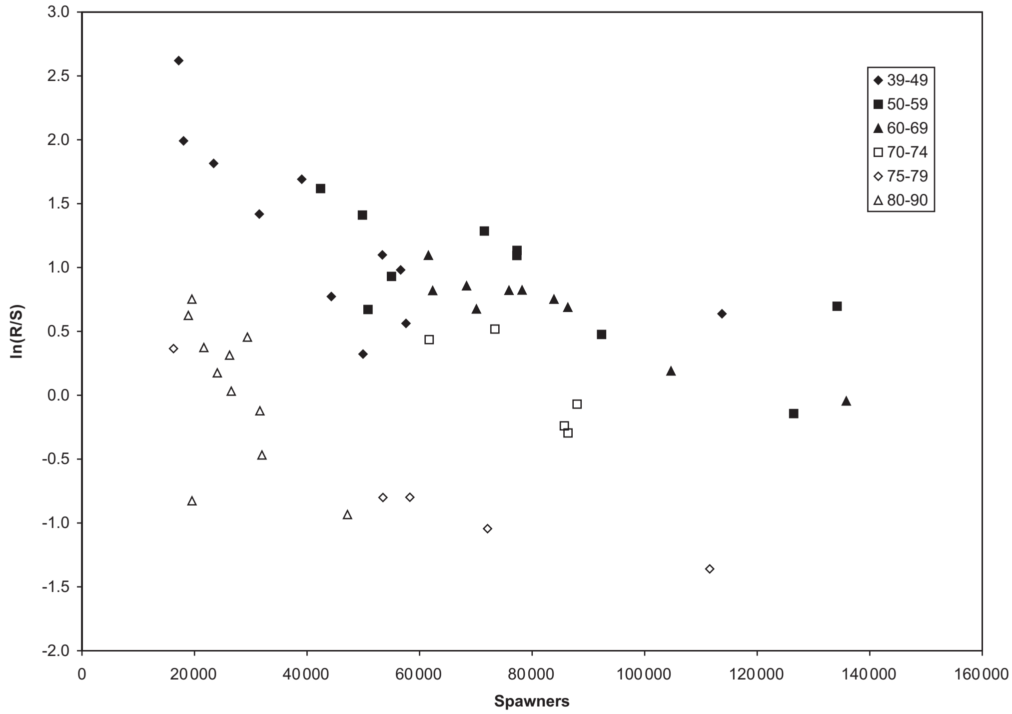


Table 5. ANCOVA for Ricker recruitment functions using period (treatment) and spawners (covariate) for the upriver aggregate wild spring chinook run, 1939–1990 brood years.

Period	Intercept $\tau_i + a$	SE	Intercept H_0: $\tau_i = \tau_j$, p	Slope β	Slope H_0: $\beta \le 0$, p	R^2	Homogeneity of slope, p
Overall	0.4231	0.1577	0.0001	0.000014	0.0001	0.71	0.4826
1939–1949	1.9263	0.2033					
1950–1959	2.0380	0.2455					
1960–1969	1.8601	0.2537					
1970–1979	0.6903	0.2349					
1980–1990	0.4231						

Results of least squares means tests for differences between periods: t for H_0: LSMEAN(i) = LSMEAN(j)/$p > t$

	1939–1949	1950–1959	1960–1969	1970–1979	1980–1990
1939–1949	1				
1950–1959	0.6138	1			
1960–1969	0.7705	0.3934	1		
1970–1979	0.0001	0.0001	0.0001	1	
1980–1990	0.0001	0.0001	0.0001	0.2612	1

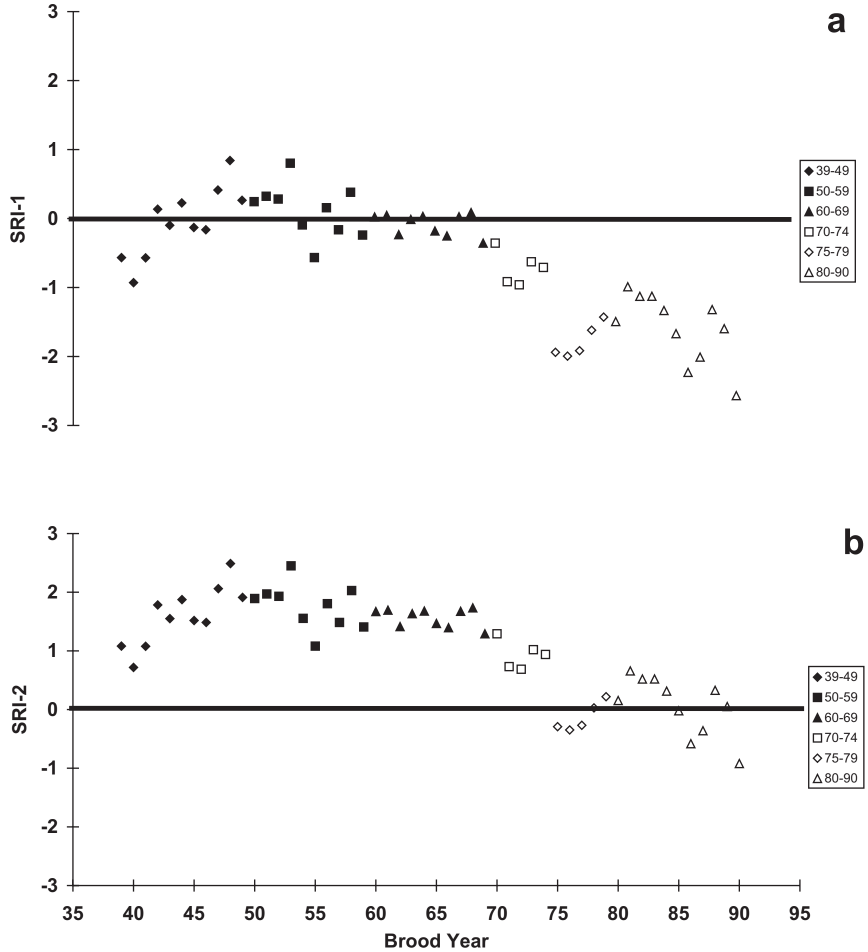
Note: Periods represented decades, with 1939 and 1990 brood years incorporated into the nearest decadal interval.

results were obtained when slopes were allowed to vary by period (i.e., tests of residuals based on log transformation of eq. 1; Schaller et al. 1996).

Spawner and recruit data of the aggregate upriver run of wild spring chinook for brood years 1939–1990 provided little or no evidence of a long-term, gradual decline in productivity and survival rate. Rather, the analyses provided support for the hypothesis that the productivity and survival rate of upriver spring chinook remained fairly stable from early hydropower development (1939) until the era of major hydropower development (about 1970), when major declines began. ANCOVA and least squares means tests found no differences in productivity estimates among the periods 1939–1949, 1950–1959, and 1960–1969. Productivity estimates from the periods 1970–1979 and 1980–1990 were significantly less than those from any of the early periods. This aggregate provides a longer time series of *R*/*S* data than any of the index stocks. The indices of climate change over the Pacific Ocean, which Beamish et al. (1997) linked to sockeye salmon (*Oncorhynchus nerka*) production, varied widely from 1939 to 1970. Interestingly, the productivity of the aggregate remained fairly stable through these decades and then decreased coincident with the period of major hydropower development and operation and similar to productivity changes of the upper basin index stocks. Plots of survival rate indices for the aggregate upriver run also indicated that the major declines in survival rate began about 1970.

We conclude that the dams had a major effect on the de-

Fig. 7. Deviations of ln[(observed *R*/*S*)/(predicted *R*/*S*)] from ANCOVA fit to (*a*) pre-1970 data (SRI-1) and (*b*) post-1974 data (SRI-2) for upriver aggregate spring chinook, brood years 1939–1990.



cline of upriver stocks. Our results provide evidence that productivity and survival rates declined more for upriver stocks than for downriver stocks. This differential decline coincided with the development and operation of the FCRPS. As discussed below, we see little evidence of an alternative systematic stressor that selected against upriver stocks, coincident with the declines and unrelated to the hydropower system. Estuary and early ocean conditions do not appear to exert a systematically different effect on survival of stream-type chinook stocks from upriver regions of the interior Columbia River basin. Climatic influences appear to affect populations on large geographic scales. The stocks contrasted in our analysis are similar in life history and overlap in time and space during their early ocean residence (and beyond). Finally, we see little evidence that hatchery, spawning, and rearing habitat or harvest factors could explain the spatial and temporal patterns of stock performance.

Evidence that oceanic influences on salmon populations operate on broad regional scales supports the stock comparison approach within the interior Columbia River basin. Deriso et al. (1996) found evidence of a common year effect for our index stocks of stream-type chinook from the Snake River and lower Columbia River regions. Such a common year effect is consistent with other literature. Beamish and Bouillon (1993) provided evidence that indices of climate over the North Pacific Ocean may play an important role in catch (an index of abundance) of different species of salmon originating over a wide geographic range. Bradford (1994) found common year-to-year trends in spawning escapements of stream-type chinook stocks from widely separated streams of the Fraser River, B.C. Adkison et al. (1996) found that productivity (*R*/*S*) covaried among sockeye stocks from the Bristol Bay region, Alaska. Peterman et al. (1998) presented evidence that large-scale environmental processes can strongly influence survival rates (residuals from spawner–recruitment relationships) of sockeye on broad regional scales (i.e., Bristol Bay and Fraser River). Their results suggested that, within each of these broad regions, common environmental processes influenced survival rates but that these processes were distinct for the stocks of each region. Furthermore, year of ocean entry appeared to determine variability in survival rate for Bristol Bay sockeye (Peterman et al. 1998).

There are several lines of evidence suggesting that the interior Columbia River basin stream-type chinook stocks are exposed to similar estuary and ocean conditions, particularly during the critical first year. Current hypotheses regarding ocean survival of Pacific salmon generally focus on the juveniles' critical first months at sea (Pearcy 1992), where juveniles of these index stocks are most likely to overlap in time and space. Of the lower Columbia River stocks in this analysis, at least the John Day River and Warm Springs River spring chinook smolt timing appears very similar to that of Snake River spring and summer chinook. Smolts of these lower Columbia River, Snake River, and upper Columbia River stocks migrate through the mainstem to the estuary primarily in late April and May (Mains and Smith 1964; Raymond 1979; Lindsay et al. 1986, 1989; Hymer et al. 1992). Year-class strength for these spring and summer chinook is apparently established, for the most part, within the first year in the ocean, as evidenced by the ability of fishery managers to predict subsequent adult escapements from jack counts (e.g., Fryer and Schwartzberg 1993).

Since Columbia River basin stream-type chinook share a common estuary and nearshore ocean environment through a critical life stage and have overlapping distributions in later ocean residence, it seems very unlikely that differential estuary and ocean conditions could explain systematic differences in stock survival. Such a factor seemingly would have to operate on later life stages, after juveniles have dispersed from near the Columbia River mouth. Ocean distributions of upriver and downriver stream-type chinook are not well known because ocean recoveries of CWT-marked stream-type chinook have been infrequent. However, the few recaptures (62 recoveries) of 2.1 million tagged smolts released over 8 years from hatchery stocks in both the Snake River (21 recoveries) and lower Columbia River (41 recoveries) were widely scattered from California to Alaska ocean fisheries (Pacific States Marine Fisheries Commission, unpublished data). Finally, the productivity and survival rates of the aggregate spring chinook run, which is weighted heavily by Snake and upper Columbia stocks (Fulton 1968), were relatively stable from 1939 until the era of major hydropower development. It is difficult to imagine an oceanic phenomenon that would have systematically depressed upriver stocks, coincident with, and unrelated to, development of the hydropower system.

It is noteworthy that even the lower Columbia stocks have been affected by hydropower and that a portion of their recent decline may be hydropower related, rather than environmental. John Day River stocks, in particular, were likely subjected to a higher smolt passage mortality at John Day Dam relative to other stocks passing the dam between 1968 and 1984 (Lindsay et al. 1986). Development of the Canadian storage projects in the upper Columbia River in the mid-1970's and hydrosystem regulation have reduced flows during the spring smolt migration for all stream-type chinook (Raymond 1988). Since Columbia River basin stream-type chinook share a common lower river migratory corridor and estuary, changes that may have occurred due to the development of storage projects in the mid-1970's are unlikely to account for the differential decline in productivity and survival rates between the upriver and downriver index stocks.

In order for hatchery, habitat, and harvest factors to have caused the temporal and spatial differences that we observed in stock performance, those factors would also have had to show temporal and spatial differences. Hatchery releases have increased in the post-1974 period for all regions. However, there was little indication that stock performance declined more in index areas directly influenced by hatchery releases. In fact, the Middle Fork Salmon River stocks, which had no direct hatchery releases, showed larger declines in productivity than the other Snake River stocks that had hatchery fish runs. Hatchery programs are for the most part mitigation for hydropower, and therefore, any influences are hard to separate from hydropower impacts. For most index stocks, habitat conditions have been relatively stable over the period of study. Where habitat conditions have changed over time (Poverty Flat and Middle Fork John Day River), we observed improving conditions, which would not induce declines in stock performance. A broad range of habitat conditions were represented in each region, so spatial differences in habitat factors are unlikely to account for differential stock performances. Petrosky and Schaller (1996) did not find decreases in productivity and survival rates (where recruits were measured as smolts entering the hydrosystem during 1964–1995) that could explain the overall decline in Snake River stream-type chinook. We can draw some inferences about harvest impacts by examining the harvest data that we used to adjust recruits. Harvest rates were drastically reduced in response to declines in upriver stream-type chinook abundance. Furthermore, given that the upriver spring chinook stocks share common fisheries (except for some additional tributary harvest in the lower Columbia River stocks), it seems unlikely that differential harvest rates could explain systematic differences in stock performance. We conclude that factors other than hydropower development have not played a significant role in differential decline in performance between upriver and downriver stocks.

Certain concepts and approaches in this paper have applicability to an adaptive management strategy and associated monitoring and evaluation program being considered under the ESA for Snake River and Columbia River spring, summer, and fall chinook and steelhead (*Oncorhynchus mykiss*). Criteria need to be established in terms important to stock survival and recovery. A basinwide monitoring and evaluation program involving index population response needs to be established and tied to those criteria. The spawner and recruit information that we developed for this paper (Beamesderfer et al. 1997) should be continued and augmented with population response data. A core set of information, such as the age, sex, and size composition of escapements and hatchery/wild accounting, coupled with estimates of catch in intercepting fisheries, allows managers to estimate the productivity of individual stocks and to track changes in stock productivity and survival rate over time. Such information, if available for stocks in different geographic areas, would allow managers to understand how healthy stocks perform under natural variations and to better interpret performance of damaged stocks, allowing the design of effective recovery plans.

Fish population responses to recovery actions should be assessed in terms of smolt-to-adult and adult-to-adult survival rates that are sufficiently high for short-term preservation and ultimate recovery and rebuilding. While use of survival rate criteria is key to sound resource decisions, natural variability of survival rates may confound interpretation of responses to management actions. An experimental design for management actions should enable managers to (*i*) test whether treatments produce repeatable effects in situations with similar conditions, (*ii*) distinguish treatment effects from natural variation, (*iii*) estimate the variance associated with various parameters, and (*iv*) test significance (McAllister and Peterman 1992). Finally, future management actions need to deviate substantially from status quo operations so that experimental designs could be able to distinguish among competing hypotheses for salmon population survival and recovery.

The PATH process was initiated to assist regional fish managers in making long-term hydrosystem management decisions, which need to ensure survival and recovery of Snake River chinook and sockeye. Key to salmon recovery and rebuilding plans will be a determination of whether adequate survival can be attained with existing measures, such as collection and transportation of smolts, or whether other actions will be necessary, including restoring portions of the natural migration corridor. These analyses indicate that mainstem measures to date, including smolt collection and transportation in the Snake River, have not mitigated adequately for hydropower impacts on these stocks. The threatened Snake River spring and summer chinook and depressed upper Columbia River spring chinook have exhibited considerably greater declines in productivity and survival rate in recent years (even with those mitigation measures) than stocks whose migration corridor has been impacted by considerably fewer dams and reservoirs.

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