Chapter 3
Contrasts in Stock-Recruitment Patterns of Snake and Columbia River Spring and Summer Chinook Populations

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Abstract

Snake River spring and summer chinook populations have declined dramatically since completion of the Federal Columbia River Power System. They were listed as threatened under the Endangered Species Act in 1992, and reclassified as endangered in August 1994 on an emergency basis. Population dynamics models of salmon have evolved with different hypotheses regarding the distribution of survival rates at different stages of the life cycle, and regarding natural and anthropogenic causes. The different hypotheses yield different management advice on potential effectiveness of hydropower management options. A process was initiated in 1995 to clarify the nature of the differences between the models to assist long-term hydropower management decisions by 1999. This paper examines evidence related to three hypotheses: (1) whether productivity declined more and became more variable for stocks most affected by hydropower (Snake and upper Columbia rivers) than for similar stocks below fewer dams (lower Columbia River); (2) whether survival rates declined more and became more variable for stocks most affected by hydropower than for similar stocks below fewer dams; and (3) whether the interior Columbia River stocks have been in long-term decline, or the decline corresponded with completion of the hydropower system. Spawner (S) and recruit (R) data were developed for seven Snake River, three upper Columbia River and six lower Columbia River (above Bonneville Dam) spring and summer chinook stocks, and for an aggregate run of wild spring chinook (from above Bonneville Dam), which included all spring chinook index stocks. Hypothesis (1) was addressed by comparing Ricker production parameters and fits for the index stocks between time periods and region, and by analysis of covariance (ANCOVA) for effect of time period. Hypothesis (2) was addressed by comparing survival rate indices, ln[(observed R/S)/(predicted (R/S)], from fitted Ricker functions between regions and time period, using analysis of variance and multiple comparison procedures. Hypothesis (3) was addressed by ANCOVA tests for effect of time period for five decades of spawner recruit data for the aggregate upriver run, and by examination of plots of residuals (survival rate indices). Temporal patterns of productivity and survival from lower river index stocks indicate recent declines that might be attributed to poorer oceanic or environmental conditions. However, the spatial and temporal comparisons indicate that upriver stocks have fared much worse. Empirical evidence best supported the

hypotheses that the productivity and survival rate of spring and summer chinook stocks that were most affected by hydropower development (Snake and upper Columbia regions) declined more and became more variable over time than those of the lower river stocks. Evidence from the aggregate run best supported the hypothesis that productivity and survival rate declines over the last 50 years were quite abrupt and corresponded with construction and completion of the hydropower system.

3.1 Introduction

Snake River spring and summer chinook populations have declined dramatically since completion of the Federal Columbia River Power System (FCRPS). They were listed as threatened under the Endangered Species Act (ESA) in 1992, and reclassified as endangered in August 1994 on an emergency basis. Stock productivity also declined and became more variable following the completion of the hydropower system (Petrosky and Schaller 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.

For the past several years the Bonneville Power Administration, the Northwest Power Planning Council, the NMFS, and various state and tribal resource agencies have been attempting to work together to compare and enhance the models used by all of the agencies to evaluate management actions intended to recover depleted Columbia River Basin salmon stocks. Results from previous model comparison and peer-review efforts indicated that the models operate with different interpretations or hypotheses regarding the survival rates at different stages of the salmon life cycle, and result in disparate management advice.

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 PATH process was designed to clarify the nature of the differences among the models and point the way towards helping to resolve them (Marmorek and Parnell 1995). 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 which have significant management implications.

This paper presents a temporal and spatial comparison of spawner (parent) and recruit (progeny) patterns from Snake and Columbia River populations of spring and summer chinook to evaluate hypotheses regarding changes in productivity and survival rates relative to completion of the FCRPS. This paper focuses only on stream type chinook (Healy 1991) which outmigrate as yearling smolts. Productivity for a specified time period is defined as the natural log of the ratio of recruits to spawners, in the absence of density dependent mortality (Neave 1953). Productivity is measured here as the intercept, or “a” value, from Ricker (1975; equation 11.15). The measure of density independent productivity is relevant when assessing density independent mortality imposed by the development and operation of the FCRPS. Survival rate indices provide a time series of density independent mortality estimates through deviations of observed recruit per spawner ratios from those predicted by the fitted stock recruitment function (predicted R/S) for a specified time period.

Before Snake River dam development was completed in 1975, Snake River spring and summer chinook populations were productive, and supported substantial main stem and tributary harvest in commercial, sport and tribal fisheries (ODFW and WDFW 1995). A major decline in productivity occurred for Snake River populations during and after the period of major development of the Snake River dams (post-1970) compared to that in the 1950s and 1960s (Petrosky and Schaller 1992). The recent productivity of a down-river stock, which was less affected by hydropower development, remained fairly stable and closely matched that of pre-development Snake River populations (Petrosky and Schaller 1992). They noted that the building of the dams dramatically increased the cross-sectional area of the Snake and Columbia rivers, increasing the mean and the variability of water travel time. In addition to migration delay for smolts (Sims and Ossiander 1981; Berggren and Filardo 1993), hydroelectric projects caused site-specific mortalities and delays (Raymond 1979, 1988). Different flow levels in the presence of dams also resulted in variable exposure of smolts to turbine passage, due to a higher proportion of juveniles passing over spillways when flow levels were high. For recent brood years (1975-1986), water travel time, flow and fish travel time were significantly related to the annual survival rate patterns of Snake River stocks (Petrosky and Schaller 1992).

The stock performance comparison approach is being expanded through PATH to more completely describe the observed productivity and survival rate patterns of Snake River spring and summer chinook stocks over time, and to contrast these with those patterns for spring chinook stocks which migrate through fewer dams and reservoirs (lower Columbia River) or experience different juvenile migration conditions through the hydropower system (upper Columbia River). Within the Columbia River, Junge and Oakley (1966) identified spatial differences in production rates (recruits/spawner) between upriver and downriver spring chinook. A similar approach was applied by Bradford (1994) when he tested the hypothesis that proportionally smaller, regulated flows from the upper Nechako River, B.C. have had a greater impact on chinook productivity compared with further downstream stocks, where the discharge regime was closer to the historical hydrograph. His method relied on the assumption that variation in mortality after residence in the natal stream will be similar for both the Nechako chinook and the aggregate of stocks from unregulated streams, so that any differences in population trends will be due to effects specific to the Nechako River.

The focus of this analysis is on spawner-recruitment information rather on than simple escapement trends. Limitations of escapement data include: 1) a lack of accounting for density dependence; 2) exclusion of harvest and adult passage mortality, both of which have varied considerably through time and across stocks; and 3) a general lack of accounting of hatchery spawner contributions, or of direct effects of hatchery operations (natural brood stock removal or adult outplants). Historical reconstruction of numbers of spawners and recruits by brood year (Beamesderfer et al. 1996) avoids these general limitations of simple escapement data.

This paper examines the information developed to date to evaluate the following sets of alternative hypotheses for stream-type chinook.

> *H1a: Productivity (Ricker "a" from ln(R/S) versus S) has shown similar responses over time between upriver stocks and lower river stocks.*
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> *H1b: Productivity declined more and become more variable over time for upriver stocks, which were most affected by hydropower development, than for lower river stocks.*

and

> *H2a: Survival rate indices (ln[(observed R/S) / (predicted R/S)]) have shown similar responses over time between upriver stocks and lower river stocks.*
>
> *H2b: Survival rate indices declined more and become more variable for upriver stocks, which were most affected by hydropower development, than for lower river stocks.*

and

> *H3a: 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).*

H3b: Declines in productivity and survival rate of upriver runs of Columbia River wild spring chinook in the past 50 years corresponded with construction and completion of the FCRPS (post-1970 brood years).

3.2 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 upstream 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 and September. All stocks are stream-type chinook, producing yearling smolts which migrate seaward in the spring (primarily April and May). More detailed information on stock history, production and habitat conditions are in Beamesderfer et al. (1996).

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. 1996). The mainstem harvest rates were cut back dramatically as runs declined in the mid-1970s for spring chinook, and in the late 1960s for summer chinook. 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. 1996). Ocean harvest rates are less than 1% for stream-type chinook originating above Bonneville Dam (Berkson 1991).

Snake River

The Snake River Region in this analysis includes streams in Idaho and Oregon, upstream of Lower Granite Dam (Figure 3-1). Spawner and recruit data were developed for seven Snake River spring and summer chinook stocks: Minam River (Grande Ronde Subbasin, Oregon), Imnaha River (Imnaha Subbasin, Oregon), Bear Valley/Elk, Marsh and Sulphur creeks (Middle Fork Salmon Subbasin, Idaho), and Johnson Creek and Poverty Flat (South Fork Salmon Subbasin, Idaho). The Grande Ronde River and Middle Fork Salmon River stocks in this analysis are spring chinook, and the South Fork Salmon River stocks are summer chinook. The Imnaha River stock has an adult run timing intermediate to spring and summer chinook. Spawner and recruit data extend from 1957 to 1990 brood years for all stocks, except Imnaha River (1949-1950, 1952-1990) and Minam River (1954-1990).

The seven stocks occupy a wide range of habitat condition. In general, the better habitats include: Minam River and Sulphur Creek, both in wilderness; Imnaha River; and Marsh Creek, which has had moderate degradation in portions of the drainage. Johnson Creek has experienced elevated sedimentation, but to a lesser degree than either the Bear Valley/Elk Creek drainage or Poverty Flat on the South Fork Salmon River. The latter spawning area was subjected to extreme sedimentation during the mid-1960s, however, conditions gradually improved during the 1970s and 1980s.

The Middle Fork Salmon River contains wild, native populations (Bear Valley/Elk, Marsh, Sulphur) with no history of hatchery production releases. The South Fork Salmon River (SFSR) index populations have been influenced indirectly by hatchery operations since 1981 when the McCall Hatchery operations began. McCall Hatchery stock was developed initially from trapping of the summer run at the Snake River dams, and is maintained by trapping SFSR returns; neither natural index area receives direct outplants, and hatchery straying appears to be slight. The Imnaha River has been managed for natural and hatchery populations since 1982; the Imnaha Hatchery population was developed from native broodstock. The Minam River has not been directly stocked with hatchery fish, but stray, non-native Lookingglass Hatchery adults have been recovered on the spawning grounds since the mid-1980s. Hatchery spawners are accounted for in the run reconstructions for both the Minam and Imnaha rivers.

Snake River populations now must migrate past eight dams on the Snake and Columbia rivers (Figure 3-1). The sequence of mainstem dam construction for Snake River stocks has been: 1938--Bonneville (BON); 1953--McNary (MCN); 1957--The Dalles (TDA); 1961--Ice Harbor (IHR); 1968--John Day (JDA); 1969--Lower Monumental (LMN); 1970--Little Goose (LGS); and 1975--Lower Granite (LGR). Since 1977, most Snake River juveniles arriving at the dams have been collected at either Lower Granite or Little Goose, and transported by barge or truck for release below Bonneville Dam (Mundy et al. 1994). The exception has been in high flow years with uncontrolled spill and management guidelines, when a higher proportion of juveniles pass over the spillways, avoiding turbine passage and collection. In addition a portion of Snake and upper Columbia River juveniles are transported from McNary Dam.

Upper Columbia River

The upper Columbia Region was defined as the Columbia River upstream of the confluence with the Snake River (Figure 3-1). Spawner and recruit data were developed for three upper Columbia River spring chinook stocks: Methow, Entiat and Wenatchee rivers in Washington (Beamesderfer et al. 1996). Spawner and recruit data extend from 1960 to 1990 brood years for the Methow, from 1955 to 1990 for the Entiat, and from 1958 to 1990 for the Wenatchee stocks.

All three rivers' headwaters are primarily forested, while their lower migratory corridors pass through orchards and grazing lands. Habitat conditions in this region were reviewed by Mullan et al. (1992). They concluded that despite some abuse from recent activities of humans, there appeared to be little or no net loss of the functional features of the tributaries. The turn-of-the-century sawmill, hydroelectric, and unscreened irrigation diversion dams that devastated the spring chinook salmon have long been corrected in the index areas. Chapman et al. (1996), in reference to Mullan et al., noted that water withdrawal in the Methow River is a serious local concern, especially during drought years. The upper reaches are subjected to natural dewatering, and the lower tributaries are often dewatered by property owners. Another qualification comes from the recent review of habitat conditions for the PATH retrospective analysis. While co-author Langness and WDFW Biologist Larrie LaVoy assigned moderate to good habitat rankings to all three index streams, the Entiat received a poor ranking for its overwintering habitat.

In 1939, the U. S. Fish and Wildlife Service (USFWS) implemented the Grand Coulee Fish Maintenance Project (GCFMP) The project intercepted all adult salmon and steelhead at Rock Island Dam between 1939 and 1943 and relocated them to the Wenatchee, Entiat, Methow and Okanogan river drainages. According to Fish and Hanavan (1948) spring chinook were only transplanted in Nason Creek (tributary of the upper Wenatchee River). Artificial propagation associated with the GCFMP was centralized on a hatchery facility located on Icicle Creek (another tributary of the Wenatchee River) with a portion of the eggs transferred to substations located on the Entiat and Methow rivers. By the 1950s, all of the spring chinook hatchery production went into the Methow River. By the 1960s, essentially no spring chinook releases were being made. Beginning in the mid-1970s, USFWS made spring chinook production a priority for the Leavenworth National Fish Hatchery (NFH) Complex. For the next decade most of the brood stock came from the hatcheries in the lower Columbia Region (Carson NFH on the Wind River, the Little White Salmon NHF, and the Cowlitz WDFW hatchery). Since 1984 the Leavenworth Complex hatcheries have used their own returns (or returns from within the Complex) for brood stock.

As part of the Federal Energy Regulatory Commission (FERC) relicensing for Rock Island and Wells Dams, Chelan and Douglas County Public Utility Districts (PUDs) reached settlement agreements that implemented natural supplementation projects in the Wenatchee and Methow rivers, respectively. Collection of Wenatchee River natural spawners for the Rock Island Fish Hatchery Complex was first made near the Chiwawa River acclimation pond in 1989. Collection of Methow River natural spawners for the Methow Fish Hatchery Complex was first made in 1992 at the Twisp River acclimation pond and at Fulton Dam on the Chewack River. Natural spawners were first collected in the upper Methow River at the Foghorn Diversion Dam in 1993. In both programs, progeny are returned for acclimation and release from ponds constructed at or near the site where their parents were collected.

Upper Columbia River populations must now migrate past seven (Wenatchee), eight (Entiat), or nine (Methow) dams on the Columbia Rivers (Figure 3-1). The sequence of main stem dam construction for upper Columbia River stocks has been: 1933--Rock Island (RIS); 1938--Bonneville (BON); 1953--McNary (MCN); 1957--The Dalles (TDA); 1959--Priest Rapids (PRD); 1961--Rocky Reach (RRH); 1963--Wanapum (WMD); 1967--Wells (WEL); and 1968--John Day (JDA). A fraction of juveniles arriving at McNary Dam have been transported since 1979 (Mundy et al. 1994).

Lower Columbia River

The lower Columbia Region was defined in this analysis as the Columbia River downstream of the Snake River confluence to Bonneville Dam (Figure 3-1). These populations are classified as upriver spring chinook (ODFW and WDFW 1995). Run reconstructions of six spring chinook stocks from the lower Columbia River were completed for this analysis: the mainstem John Day River, Middle Fork John Day River, North Fork John Day River/Granite Creek, and Warm Springs River, Oregon, and the Klickitat and Wind rivers, Washington (Beamesderfer et al. 1996). Spawner and recruit data were also developed for a pooled John Day River stock. Time series of spawner and recruit data range from 1959-1990 brood years for John Day, 1969-1990 for Warm Springs, 1966-1990 for Klickitat, and 1970-1990 for Wind River spring chinook.

Habitat conditions vary among and within the spawning and rearing areas for the lower Columbia River. Habitat quality within the John Day River Subbasin varies from heavily degraded by agriculture, grazing and forestry activities in the mainstem and Middle Fork to high quality wilderness in much of the North Fork and Granite Creek; streamside fencing has gradually improved riparian conditions in the Middle Fork since the 1970s. Riparian areas in the Warm Springs River had been degraded by various uses in the past 100 years, but riparian fencing and habitat improvement in the drainage have recently allowed vegetation to increase and stream banks to stabilize. Much of the Wind River Subbasin is within National Forest lands, and degradation of the habitat has been moderate. The Klickitat River subbasin spawning and rearing areas fall within the Yakama Indian Reservation. Habitat degradation has also been moderate. Both the Klickitat and Wind rivers had significant portions of upper reaches opened to natural production by the laddering of waterfalls during the late 1950s and early 1960s.

Stock origin and hatchery background vary widely among the lower Columbia River index stocks. John Day River spring chinook are a wild, native stock, with no history of hatchery production releases. Warm

Springs River spring chinook are a wild stock, with relatively minor hatchery influence. Warm Springs Hatchery has released only marked hatchery fish since 1980; some hatchery fish have spawned below the weir and, prior to 1987, small numbers of hatchery fish were released above the weir to spawn. Klickitat River natural spring chinook are a remnant run, and have been influenced by Klickitat Hatchery releases since the early 1950s. Primary emphasis in the Klickitat Subbasin is on hatchery production; hatchery stock originated from local and non-local (Carson, Willamette and Cowlitz) sources. Wind River natural spring chinook, are a non-native, introduced run which originated from Carson Hatchery and wild upriver spring chinook collected at Bonneville Dam. Primary emphasis in the Wind Subbasin is on hatchery production for Carson National Fish Hatchery.

The lower Columbia River stocks in this analysis now migrate past either one dam (Wind, Klickitat rivers), two dams(Warm Springs River), or three dams (John Day River; Figure 3-1). Bonneville and The Dalles Dams have been operating since before the spawner-recruit time series began for these stocks. John Day Dam, completed in 1968, likely subjected the John Day River stock to a higher smolt passage mortality relative to other stocks (Lindsay et al. 1986). Prior to 1985, spill was provided at John Day Dam for in-river juvenile migrants to minimize turbine passage. However, in these years most John Day River juveniles were subjected to turbine passage because of the proximity of the river mouth to the powerhouse side of the dam. John Day Dam passage improved in 1985 with installation of a bypass and screening system to help juvenile migrants avoid turbine intakes. None of the lower Columbia River populations have smolt collection and transportation programs around the dams (Mundy et al. 1994).

Aggregate Upriver Spring Chinook

Spawner and recruit data for the aggregate upriver run of Columbia River wild spring chinook for the period 1939-1990 were developed by Beamesderfer et al. (1996), using methods similar to those of Junge (1980). This aggregate run provides indices of productivity and survival rates over a much longer time period than is possible for the individual index stocks. The aggregate upriver run consists of all wild spring chinook that originate upstream of Bonneville Dam, including all spring chinook index stocks in this analysis. Because a majority of the upriver spring chinook escapement was from the Snake and upper Columbia rivers (Fulton 1968), performance of the aggregate productivity and survival rate indices will help address questions of long-term decline or decadal cycles in ocean survival for these stocks. Since the 1970s, the proportional contribution to the aggregate run from Snake River and upper Columbia River stocks has decreased, and accounting for the increased hatchery production (from mitigation programs) has become more complex.

3.3 Methods

Spawning Escapement Trends

Time trends of spawning escapement were compared graphically, among and within the geographic stock groups. These spawning escapement measures include both natural origin fish and, where applicable, hatchery fish spawning in the wild. All years of escapement data were normalized using the average escapement computed from all available brood years through 1990. These direct measurements of stock abundance are presented for the purpose of characterizing the abundance trends of the four index stock groups. Presently, escapement measures are used to evaluate the success of regional recovery and rebuilding programs. Caution is needed when comparing escapement trends because of the data limitations noted in the introduction.

ln(R/S) versus S Trends

Numbers of spawners and recruits for each of the index stocks were estimated using the run reconstruction methods documented in Beamesderfer et al. (1996). Recruits (R) were measured to the mouth of Columbia River, and include jacks. Spawners (S) were indexed as adults. In drainages 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 run reconstruction methods for all index stocks expand age-structured spawners into recruitment by accounting for prespawning survival, tributary harvest, mainstem harvest and upstream passage losses at the dams (Beamesderfer et al. 1996). The spawners are independently estimated for each index area based on ground and aerial redd counts, or live fish and carcass counts. Computation of the recruits for different stocks relied on both unique and shared survival rates. Recruits to the spawning grounds by brood year were obtained from estimates of spawners by run year and age composition which were unique to either the stock or subbasin. Estimates of brood year recruits to spawning grounds were then expanded for prespawning mortality and by annual tributary harvest rates estimated for each subbasin (or stock). The recruits to the subbasins were next expanded by mainstem harvest rates and upstream conversion rates (passage survival rates past the dams) to yield recruits to the Columbia River mouth. Mainstem harvest rates are independently estimated for spring and summer chinook runs based on run type, catch data, and Bonneville Dam counts (ODFW and WDFW 1995). These mainstem harvest rates are estimated based on data which are independent of index stock spawner numbers (derived from redd and fish surveys). Mainstem harvest rates used for the Imnaha River stock were obtained by averaging the annual spring and summer mainstem harvest rates, because the adult run timing is intermediate to spring and summer chinook. Upstream conversion rates were shared among stocks in the same geographic location and run timing; thus, the 16 index stocks in the analysis required nine different rates of upstream passage conversions. Upriver spring and stream-type summer chinook experience very low ocean harvest rates (< 1%; Berkson 1991); for this analysis, ocean harvest rates were not used in the computation of recruits.

The number of age-structured wild spring chinook in the upriver aggregate run were estimated at Bonneville Dam by expanding hatchery rack returns back to Bonneville Dam, and subtracting the expanded hatchery estimate from the total Bonneville count (TAC 1996; Beamesderfer et al. 1996). 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), similar to a previous analysis by Junge (1980). The aggregate upriver run includes all the spring chinook index stocks from the three regions.

Spawner and recruit data for each stock were summarized and plotted by decade for the entire time series. For the analysis, spawner and recruit data were classified into three primary time periods, defined by FCRPS development and operations affecting the endangered 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 period 1970-1974 brood years was a transitional period of construction and operations in the Snake River, marked by extremely high levels of atmospheric gas supersaturation in high flow years before installation of turbines and spill deflectors (Raymond 1979). The period post-1974 brood years was marked by relatively lower spill proportion, reduced gas, the initiation of mass transportation of smolts around the Snake River dams, and gradual improvements with turbine screens, and collection/bypass systems. Upper Columbia River stocks were also influenced by incremental system improvements in this period, and by transportation from McNary Dam since 1979.

Productivity and survival rate indices were estimated for different periods and stocks throughout the Columbia River Basin. Productivity, for a specified time period, is defined as the natural log of the ratio of recruits to spawners in the absence of density dependent mortality (Neave 1953). Productivity is measured here as the intercept, or "a" value, from Ricker (1975).

$$R = e^{a} S e^{-bS} \qquad \text{Eq..3-1}$$

where R is recruits and S is Spawners.

The a and beta parameters were estimated by the log transformation of Equation 3-1:

$$\ln(R / S) = a - bS \qquad \text{Eq. 3-2}$$

Survival rate indices provide a time series of density independent mortality estimates through deviations of observed recruit per spawner ratios from those predicted by the fitted stock recruitment function (predicted R/S) for a specified time period. Survival rates indices were expressed as the natural log of the ratio of observed R/S to the predicted R/S. The natural log form transforms the ratio such that these differences are normally distributed.

To assess changes in productivity and survival rate, spawner and recruit data for all stocks, ideally, would extend at least a decade before major hydropower development (pre-1970 brood year for the Snake River stocks), and include a wide range of escapements. However, spawner and recruit data were lacking for three of the lower river stocks in this period. The times series for Warm Springs, Klickitat and Wind rivers began in 1969, 1966 and 1970, respectively. To incorporate these three stocks into the analysis, it was necessary to also fit spawner-recruit data to a more recent period, post-1974 brood years, and to all years of available data. Spawner-recruit data are available for all stocks for the recent period, but the fitted production functions were hampered for some stocks by small spawner numbers. Hence, the residuals for larger escapements from earlier years would be from predicted values outside the fitted range of data. All statistical tests were performed at an alpha level of 0.05.

Hypothesis 1 -- Productivity Changes

Hypotheses 1a and 1b related to whether productivity declined more and became more variable for upriver stocks (in the post 1974 period), which were most affected by the hydrosystem, than for downriver stocks. These were addressed by fitting Ricker production functions to different time periods and comparing the parameter estimates between time periods, and within and among stocks from different regions of the Columbia River Basin. Equation 3-2 was fit to three time periods: pre-1970 brood years (pre lower Snake River dam completion); post-1974 brood years (post lower Snake River dam completion); and the full time series of available data (all years). To evaluate relative productivity change and the change in variation among regions and between time periods, graphic comparisons of the Ricker “a” values and their standard error were made.

Other parameter estimates of the Ricker function were compared to characterize index stock size and spawning capacity among stocks and between regions. These parameter estimates were slope (beta), estimated numbers of spawners at maximum sustained production (MSP; -1/beta), and equilibrium replacement (-a/beta) for pre-1970, post-1974, and all available brood years.

Analysis of covariance (ANCOVA) was run 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 ln(R/S) versus S. 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 the ln(R/S), taking into account spawning level.

Hypothesis 2 -- Survival Rate Changes

Hypotheses 2a and 2b related to whether survival rates declined more and became more variable for upriver stocks (in the post 1974 period), which were most affected by the hydrosystem, than for downriver stocks. Survival rate indices provide a time series of density independent mortality estimates through deviations of observed recruit per spawner ratios from those predicted by the fitted stock recruitment function (predicted R/S) for a specified time period. The residuals, or survival rate indices, were expressed as ln[(observed R/S)/(predicted R/S)], where predicted values were based on fits to three time periods. Survival rate index 1 represented residuals from production functions fit to pre-1970 brood years, survival rate index 2 used the post-1974 brood years, and survival rate index 3 used all spawner-recruit data. This approach, using the residuals as an index of survival rate, is similar to approaches in Hilborn and Walters (1992; fig. 7.2.1), Peterman (1981) and Cushing (1973). The reason for developing survival rate index 1 and 2 is because a number of the lower Columbia stocks have little or no spawner and recruit data in the pre-1970 period. The survival rate index 2 allows us to contrast the survival rate patterns of these lower Columbia stocks with the other lower Columbia stocks and the Snake and upper Columbia stocks with longer time series of data.

A correlation matrix of the two survival rate indices was calculated for all stocks for the brood years pre-1970 and post-1974. From the correlation matrices, the frequency of correlations between stocks for survival rate indices 1 and 2 were summarized within and between geographic regions (Snake, upper Columbia and lower Columbia) for the two time periods. Survival rate indices for the John Day pooled stock were excluded from the correlation summary because the pooled stock was a composite of the individual John Day stocks, and not an independent measure. In addition, the survival rate indices (residuals) based on the two time periods were grouped by region and plotted for available years of data. Survival rate indices were compared graphically within and among regions.

Period differences in survival rate indices were tested between stock groups from different regions with one way classification analysis of variance 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 between Snake, upper Columbia, and lower Columbia regions were then compared using Bonferroni’s and Tukey’s HSD tests (SAS 1993), which is fixed to a prescribed experiment-wise error rate of alpha = 0.05. The Bonferroni’s pairwise procedure will be more powerful for a small number of categories (Wilkinson 1990), it performs particularly well when making only a small number of comparisons (Millekin and Johnson 1984). Survival rate index 1, fit to pre-1970 data, was compared between region for brood years 1975-1990. Survival rate index 2, fit to post-1974 data was compared between region for pre-1970 brood years. Survival rate indices for the pooled John Day River stock were used only in the graphical comparisons and not in the analysis of variance because the pooled stock was not independent of the individual John Day stocks.

Hypothesis 3 -- Long-Term Changes in Aggregate Upriver Run

Hypotheses 3a and 3b relate to 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 were more associated with completion of the FCRPS (post-1970 brood years).

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 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 intercepts among the five periods (Freund et al. 1986). The survival rate indices 1, 2 and 3 for the aggregate upriver spring chinook run, were plotted and compared for the brood years 1939 through 1990.

3.4 Results

Spawning Escapement Trends

Escapements, normalized to average escapement levels for all available brood years through 1990, for the seven Snake River spring and summer chinook index populations are shown in Figure 3-2. Escapements for all Snake River stocks exhibited a similar trend of decline which was particularly noticeable by the mid-1970s. 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.

Escapements, normalized to average escapement levels for all available brood years through 1990, for the three upper Columbia River spring chinook index populations are shown in Figure 3-3. Escapements for all upper Columbia River stocks exhibited a similar trend of decline beginning in the late-1960s. 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.

Escapements, normalized to average escapement levels for all available brood years through 1990, for the six lower Columbia River spring chinook index populations are shown in Figure 3-4. Escapement levels, in all six stocks, were quite variable and appeared to show no trend during the past three decades. Before 1970, escapements ranged from 5% to 234% of their average escapement level. Wind River escapements in 1971 and 1972 were unusually high, followed by unusually low escapements in 1975 and 1976. Wind River spawner estimates for the 1970s were taken from summary documents, rather than raw data; it was not clear whether hatchery practices may have resulted in these abnormal escapement numbers, or if spawner accounting methods differed from current methods. After 1974, escapements in the lower Columbia River index stocks ranged from 9% to 506%.

Escapements, normalized to average escapement levels for all available brood years through 1990, for the aggregate upriver run of wild spring chinook are shown in Figure 3-5. The aggregate run showed a weak upward trend up through the mid 1970s, at which time a major decline was evident. 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.

Different trends were apparent between upper and lower river index stocks. Escapement comparisons alone do not isolate two accountable sources of mortality: harvest and upstream adult passage conversions. In the early years, wild fish predominated the aggregate run, with most of the production from the Snake and upper Columbia regions (Figure 3-6a). 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. Mainstem harvest rates decreased dramatically (Figure 3-6b) and numbers of dams have increased (Figure 3-6c) over the time series. Water particle travel time in the lower Snake River was relatively low and stable in the pre-1970 period, during the post- 1974 period it increased and became highly variable (Figure 3-6d).

ln(R/S) versus S Trends

Plots of Snake River stocks (Marsh Creek, Bear Valley/Elk Creek, Sulphur Creek, Johnson Creek, Poverty Flat, Imnaha River, and Minam River) exhibited similar patterns in ln(R/S) versus S with time (Figures 3-7 to 3-13). However, Poverty Flat, appeared to be somewhat of an outlier because the ln(R/S) versus S did not appear linear for the pre-1970 period. The stocks exhibited higher ln(R/S) at S in the 1950s and 1960s than for the 1970-1990 brood years, when escapement levels were fairly similar. The pre-1970 relationships of ln(R/S) versus S appeared relatively linear for all stocks except Poverty Flat. These other six stocks, during the pre-1970 brood years, maintained productive levels during a period of substantial harvest rates (Figure 3-6b). Historic productivity of Poverty Flat summer chinook, which suffered severe habitat degradation in the 1960s, appeared lower than for other Snake River spring and summer chinook stocks. All the stocks, during 1970-1990, showed a decline in ln(R/S) versus S and increases in variability in ln(R/S) for a narrow escapement range (Figures 3-7 to 3-13). Spawner numbers declined, even with large reductions in harvest rates.

The plots of Upper Columbia River stocks (Methow River, Entiat River, and Wenatchee River) exhibited similar patterns in the relationship of ln(R/S) versus S over time as those of Snake River stocks (Figures 3-14 to 3-16 and 3-7 to 3-13) for the pre-1970 period. The Upper Columbia River stocks exhibited higher ln(R/S) at S for the pre-1970 brood years than for the 1970-1990 brood years when escapement levels were fairly similar. The pre-1970 relationships of ln(R/S) versus S appeared relatively linear. These stocks, during the pre-1970 brood years, maintained productive levels during a period of substantial harvest rates (Figure 3-6b). The stocks, during 1970-1990, showed a decline in the relationships of ln(R/S) versus S and increases in the variability of ln(R/S) for a narrow escapement range. Spawner numbers declined, even with large reductions in harvest rates.

Plots of lower Columbia River stocks (John Day River Mainstem, Middle Fork, and North Fork/Granite Creek, John Day River pooled, Warm Springs River, Klickitat River, and Wind River) exhibited several patterns (Figures 3-17 to 3-23). The John Day stocks were the only lower river stocks with a pre and post time series of spawners and recruits, which were consistent with the time series for the Snake River stocks. The John Day stocks exhibited slightly higher ln(R/S) at S for the pre-1970 brood years than for the 1970-1990 brood years, when escapement levels were fairly similar. The pre-1970 relationship of ln(R/S) versus

S, for the John Day stocks, appeared relatively linear (Figures 3-17 to 3-20). These stocks, during the pre-1970 brood years, maintained productive levels during a period of substantial harvest rates (Figure 3-6b). The John Day stocks, 1970-1990 brood years, showed slight declines in the relationship of ln(R/S) versus S and a slight increases in variability of ln(R/S) for a wide range of escapements. The 1970-1990 brood years relationships of ln(R/S) versus S maintained relatively linear forms. The recent ln(R/S) at S pattern of the Warm Springs River stock (Figure 3-21) was similar to patterns for pre-1970 Snake River and upper Columbia River stocks (Figures 3-7 to 3-16). The Warm Springs stock had only one observation before 1970, but that single point appeared consistent with those of the recent period. The last two years of the time series showed a decrease in ln(R/S) at S relative to the general linear pattern (Figure 3-21). The Klickitat River stock had four years of spawner and recruit data before the 1970 brood year. Compared to these years, the Klickitat plot suggested a small reduction in ln(R/S) at S in the 1970-1990 brood years (Figure 3-22). Any productivity shift between time periods appeared to be less than that observed in the Snake River stocks. The Wind River had no pre-1970 observations. The Wind River values of ln(R/S) were very low for brood years 1971 and 1972, but at unusually high escapements. The Wind River stock exhibited low ln(R/S) at S (Figure 3-23), and no apparent shift since the time series began in 1970. Spawner numbers did not decline markedly for lower Columbia River stocks.

The aggregate upriver run of wild spring chinook exhibited a similar pattern in the relationship of ln(R/S) versus S over time compared to those of Snake River and upper Columbia River stocks (Figures 3-24 and 3-7 to 3-16) for the 1939-1969 period. The aggregate stock 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. 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 (Figure 3-6b). The ln(R/S) at S of the aggregate upriver run declined after 1969 (Figure 3-24). Spawner numbers decreased, even with large reductions in harvest rates.

Hypothesis 1 -- Productivity Changes

Fits to Ricker production functions for index stocks in the Snake, upper Columbia and lower Columbia regions revealed several temporal and spatial differences. Most Snake and upper Columbia stocks showed reasonably good fits (r^2 ranged from 0.22 - 0.82) for the pre-1970 brood years. The productivity values for these stocks, Ricker “a” fit to the pre-1970 brood years, were fairly high and ranged from 1.94 - 3.16 (Table 3-1). The exception was Poverty Flat summer chinook stock (r^2 0.07 and Ricker “a” 0.974).

In contrast to the pre-1970 brood years period, the Snake and upper Columbia stocks showed poorer fits to the Ricker function (r^2 ranged from 0.02 - 0.42) for the post-1974 brood years. Most of the Snake and upper Columbia stocks exhibited much lower productivity (Ricker “a” ranged from 0.66 - 1.34) for the post-1974 brood years (Table 3-2, Figures 3-25 and 3-26). The only stock in the Snake and upper Columbia regions which showed an improvement in fit and an increase in productivity, was Poverty Flat (Table 3-1 and 3-2, Figure 3-25). In this post 1974 period, the Ricker “a” estimate for Poverty Flat was within the range of the other upriver stocks. In addition, most Snake and Columbia stocks exhibited an increase in variability in productivity from the pre-1970 period to the post-1974 period (Figures 3-25 and 3-26).

The John Day River stocks were the only representatives for lower Columbia River for the pre-1970 period. The spawner-recruit time series began for index stocks from the Warm Springs, Klickitat and Wind rivers in 1969, 1966 and 1970, respectively. The John Day stocks showed reasonably good fits to the Ricker function (r^2 ranged from 0.38 - 0.86) for the pre-1970 brood years. The productivity values for these stocks, Ricker “a” fit to the pre-1970 brood years, were fairly good and ranged from 2.41-2.77 (Table 3-1). In contrast to the pre-1970 brood years period, these stocks showed a small decrease in fits to the Ricker function (r^2 ranged from 0.49 -0.55) for the post-1974 brood years. The John Day stocks exhibited lower productivity (Ricker "a" ranged from 1.25- 1.54) for the post-1974 brood years (Table 3-2, Figure 3-27). However, the John Day stocks maintained productive levels unlike the majority of Snake and upper Columbia stocks (Tables 3-1 and 3-2, Figures 3-25, 3-26, and 3-27).

The rest of the lower Columbia stocks showed mixed results. The Warm Springs stock, for the pre-1974 period, exhibited a fair fit to the Ricker production function (r^2 0.40). This stock was productive during this period, with a Ricker "a" value of 1.95. The Klickitat stock was less productive than the Warm Springs with a Ricker "a" value of 1.33 and the Wind River stock exhibited the poorest productivity of the lower Columbia stocks (Ricker "a" value of 0.71).

Ricker functions fit to the entire time series of available data differed considerably between region (Table 3-3). The Ricker "a" values were again substantially lower than for the pre-1970 brood years for most Snake River and upper Columbia River index stocks. The fit to a Ricker function was very poor for all Snake and upriver Columbia River stocks (r^2 range, <0.01 - 0.07). Again, the fit for lower Columbia River index stocks was better (r^2 range, 0.24 - 0.69). The John Day River and the Warm Springs River stocks showed higher productivity (Ricker "a") than upriver stocks, whereas Klickitat River and Wind River stocks showed a similar range of productivity.

For the Snake, upper and lower Columbia stocks during the pre-1970 period, in all but one case, we rejected the Ho that beta > 0 at the alpha of 0.05 (Table 3-1). However, during the post-1974 period, in the Snake and upper Columbia stocks, we rejected the Ho that beta > 0 at the alpha of 0.05 for 5 stocks. The estimated spawners at MSP decreased for all Snake and upper Columbia stocks from the pre-1970 to the post-1974 period (Tables 3-1 and 3-2). The estimated spawners at equilibrium decreased for most Snake and upper Columbia stocks from the pre-1970 to the post-1974 period (Tables 3-1 and 3-2). For the lower Columbia stocks during both periods, in all cases we rejected the Ho that beta > 0 at the alpha 0.05.

To test for productivity changes between periods, we first tested for homogeneity of slopes through the ANCOVA procedure. The probability values for the treatment (period) by covariate (spawners) interaction were significant for three of fourteen stocks tested (Table 3-4), so the assumption of homogeneity of slopes was plausible for the majority of stocks. Furthermore, the three stocks with significant interactions were from three different regions. Because there was no apparent regional pattern to the interactions, the ANCOVA was applied to all the stocks. The ANCOVA tests for differences between periods (pre-1970; post-1974), in the relationship of ln(R/S) versus S, were significant for 12 of the 14 stocks tested (Table 3-4). 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 1960s and 1970s. In all cases the productivity (intercept) dropped from the pre-1970 period to the post-1974 period (Table 3-4). Overall, productivity declined more (from pre-1970 period to post-1974 period) in the Snake River and the upper Columbia River stocks than in the lower Columbia River stocks (Table 3-4).

Hypothesis 2 -- Survival Rate Changes

The pattern of survival rate index 1 (fit to the pre-1970 brood years) for Snake River and upper Columbia River stocks exhibited a marked decline in the post-1974 brood years (Figures 3-28 and 3-29), except for Poverty Flat which had no apparent pattern. The pattern of survival rate index 1 for lower Columbia River stocks exhibited little to no decline (Figure 3-30).

The pattern of survival rate index 2 (fit to the recent brood years) for Snake River and upper Columbia River stocks exhibited much higher survival rate in the pre-1970 brood years (Figures 3-31 and 3-32). The pattern of survival rate index 2 for lower Columbia River stocks exhibited a slightly higher level in the pre-1970 brood years (Figure 3-33). Survival rate index 2 allowed us to incorporate three additional lower Columbia River stocks. For two stocks a few years of pre-1970 indices were available (Warm Springs-1969, Klickitat -1966-1969). Pre-1970 patterns for these two stocks were consistent with those of the John Day stocks (Figure 3-33).

The pattern of survival rate index 3 (fit to the all brood years) for Snake River and upper Columbia River stocks generally exhibited higher survival rate in the pre-1970 brood years (Figures 3-34 and 3-35). The pattern of survival rate index 3 for lower Columbia River stocks exhibited a slightly higher level in the pre-1970 brood years (Figure 3-36). Survival rate index 3 incorporated three additional lower Columbia River stocks (Warm Springs; Klickitat; and Wind). Patterns of survival rate index 3 for the other lower Columbia stocks were generally consistent with those of the John Day stocks (Figure 3-36).

Correlations of survival rate indices between stocks within the Snake River region, were higher in the post-1974 period than the pre-1970 period (Tables 5 and 6). Correlations of survival rate indices between stocks from the Snake and the upper Columbia regions were also higher in the post-1974 period than the pre-1970 period. The survival rate indices did not exhibit higher correlations between stocks from the Snake River and lower Columbia River regions in the post-1974 period than in the pre-1970 period (Tables 3-5 and 3-6). The results for upper Columbia River versus lower Columbia River regions were mixed.

The ANOVA results for survival rate index 1 (fit to pre-1970 data) exhibited significant differences among regions for brood years 1975 through 1990 (Table 3-7). The means for survival rate index 1 for Snake, upper Columbia and lower Columbia regions were -1.60, -1.72 and -0.17, respectively. For survival rate index 1, a larger negative value indicated a greater decline from the pre-1970 brood years. The results of the multiple comparison tests for survival rate index 1 indicated no significant difference between Snake and upper Columbia stocks at the alpha of 0.05. There were significant differences between Snake and lower Columbia stocks and between upper Columbia and lower Columbia river stocks at the alpha of 0.05. The Snake and upper Columbia survival rate indices declined, over time, more than lower Columbia indices as indicated by the negative difference between means (Table 3-8). Boneferroni and Tukey’s pairwise procedures yielded the same results.

The ANOVA results for survival rate index 2 (fit to post-1975 data) exhibited significant differences among regions for pre-1970 brood years (Table 3-7). The means for survival index 2 for Snake, upper Columbia and lower Columbia were 2.85, 1.67 and 0.80, respectively. In this case, a larger positive value indicated a greater decline from the pre- 1970 brood years. The results of the multiple comparison tests for survival rate index 2 indicated significant difference between Snake and upper Columbia stocks at an alpha of 0.05. There were also significant differences between Snake and lower Columbia stocks and between upper Columbia and lower Columbia stocks at an alpha of 0.05. The Snake survival rate indices declined, more over time, than lower Columbia indices as indicated by higher positive differences between means (Table 3-8). Also, Snake survival rate indices declined, more over time, than upper Columbia indices (Table 3-8). Boneferroni and Tukey’s pairwise procedures yielded the same results.

Hypothesis 3 -- Long-Term Changes in Aggregate Upriver Run

Again, we first tested for homogeneity of slopes through the ANCOVA procedure. The probability value for the treatment (period) by covariate (spawners) interaction was not significant (Table 3-9), so the assumption of homogeneity of slopes was plausible. The ANCOVA test for differences between periods (1939-1949, 1950-1959, 1960-1969, 1970-1979, and 1980-1990) in the relationship of ln(R/S) versus S (productivity) was significant (Table 3-9). The Ricker "a" values (intercepts) for the first three decades were 1.87, 1.98, and 1.80. The Ricker "a" values for 1970s and 1980s decades were 0.63 and 0.37, indicating a decline in productivity. The Least Squares Means (LSMEAN) test in the ANCOVA analysis indicated no significant differences among Ricker "a" values for the first three decades (Table 3-9). The LSMEAN results indicated a significant difference between the 1970s Ricker "a" and Ricker "a" values for each of the first three decades, and between the 1980s Ricker "a" and Ricker "a" values for each of the first three decades. The Ricker "a" values did not differ significantly between the 1970s and 1980s decades.

The pattern of survival rate index 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 (Figure 3-37); the post-1970 survival rate indices exhibited a declining pattern. The same pattern was evident for survival indices 2 and 3 (Figures 3-38 and 3-39).

3.5 Discussion

Hypotheses addressed in this paper relate primarily to the relative influence of hydropower system effects versus natural variability in estuary and ocean survival on the decline of Snake River wild spring and summer chinook. Spawner and recruit data from several Snake River, upper Columbia River and lower Columbia River wild spring and summer chinook index stocks, and the aggregate upriver run of wild spring chinook were compared over time to examine the level of empirical support for alternative hypotheses. Based on a comparison of the productivity and survival rate indices amongst 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 empirical evidence from spawner and recruit data most supported hypothesis 1b, that productivity declined and became more variable for those stocks most affected by hydropower development, while lower river stocks have remained more stable. All index stocks compared showed some decline in productivity between the periods pre-1970 and post-1974. However, productivity, as measured by Ricker "a" values, declined more in the Snake River and upper Columbia River than in the lower Columbia River. Ricker production functions for upriver stocks also had very poor fits to data from the post-1974 period, in contrast to fits for most lower river stocks. ANCOVA tests for period effects were significant in 12 of 14 stocks tested; declines in the Snake River and the upper Columbia River, were greater overall than those in the lower Columbia River. In the Snake River, the smallest decrease in productivity (insignificant in ANCOVA) was for the Poverty Flat stock. In this case, the "a" value in the first period was low, and fell within the range of other upriver stocks in the second period. This result was consistent with the observation of habitat disturbance in the 1960s, followed by partial habitat recovery through the recent period. A similar pattern occurred for the Middle Fork John Day River, which also experienced partial habitat recovery through the recent period. Estimates of the Ricker "a" were fairly low for the Wind River stock, compared to other lower river stocks in recent years. Wind River spring chinook were introduced from non-native hatchery and wild stocks, which may partially explain their observed low productivity.

Available spawner and recruit data from throughout the Columbia Basin also lent support to hypothesis 2b, that survival rate declined and became more variable for those stocks most affected by hydropower development, while lower river stocks have remained more stable. All index stocks compared showed some decline in survival rate indices between the periods pre-1970 and post-1974. However, survival rate, as measured by residuals from Ricker functions 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. Survival rate index 1 did not differ significantly between Snake and upper Columbia rivers; but survival index 2 indicated that survival rate declined most in the Snake River.

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 hypothesis 3b, that 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. Analysis of covariance and least square means tests found no differences in intercepts of Ricker functions (with common slope) between the periods 1939-1949, 1950-1959 and 1960-1969, indicating no detectable decrease in productivity over the first three decades of the time series. Intercepts from periods 1970-1979 and 1980-1990 were significantly less than any of the early periods, however, linking the productivity decline with these later periods. Plots of survival rate indices 1, 2, and 3 for the aggregate upriver run also indicated the major declines in survival rate began about 1970.

This study relies on the assumption that the estuary and early ocean conditions have a similar effect on survival for stream-type chinook stocks across regions of the interior Columbia River basin. This approach is similar to the studies for chinook stocks of Bradford (1994), Walters et al.(1989), Deriso et al. (1996), and Junge and Oakley (1966). Indices of ocean survival suggest both inter-annual and cyclic variability for coho (Lawson 1993) and pink, chum and sockeye salmon (Beamish and Boullion 1992). Relatively little information has been developed for chinook salmon, particularly for wild, spring or stream-type stocks. The temporal patterns of productivity and survival rate from lower Columbia River index stocks indicate recent declines in survival and productivity that might be attributed to poorer oceanic conditions. However, the spatial and temporal comparisons indicate that the upriver stocks have fared much worse. The observed patterns are analogous to Lawson’s (1993) conceptual model of effects of declining habitat quality (in this case, hydropower) combined with cyclical changes in ocean productivity. Based on spawner and smolt indices, there was no empirical support for a hypothesis that a decrease in freshwater spawning and rearing survival was primarily responsible for the decline of Snake River spring and summer chinook since the 1960s (Petrosky and Schaller 1996).

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 (Lindsay et al. 1986, 1989; Raymond 1979; Hymer et al. 1992). Current hypotheses regarding ocean survival of Pacific salmon generally focus on the juveniles’ critical first months at sea (Pearcy 1988, 1992; Lichatowich 1993), where juveniles of these index stocks are most likely to overlap in time and space. Columbia River stream-type chinook from upstream of Bonneville Dam distribute as adults offshore from the ocean fisheries, based on a near absence of coded wire tag (CWT) recaptures in ocean harvest sampling programs (Berkson 1991). The near absence of Columbia River stream-type chinook CWT samples is in stark contrast to the large numbers of CWT recaptures of ocean-type Columbia River chinook (PSC 1994). 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 it appears that Columbia Basin stream-type chinook share a common estuary and nearshore ocean environment, and distribute offshore of the ocean fisheries, changes that may have occurred in the estuary and ocean are unlikely to account for the differential decline in productivity and survival rates between the upriver and downriver index stocks.

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). Also, development of the Canadian storage projects in the upper Columbia River, in the mid-1970s, and hydroregulation have reduced flows during the spring smolt migration for all stream-type chinook (Raymond 1988). Since Columbia 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-1970s are unlikely to account for the differential decline in productivity and survival rates between the upriver and downriver index stocks.

The escapement trend comparisons support the major conclusions of this paper, but the use of escapement indices alone are confounded by the accounting of hatchery fish, variable harvest mortality rates, and upstream passage conversion rates. The productivity estimates and survival rate indices are more robust measures of stock performance, because these estimates directly account for hatchery fish, variable harvest rates, brood year age structure, and variable upstream conversion rates.

A review of the literature, yielded three reports that addressed the productivity of Columbia River spring chinook (Table 3-10). To make a comparison we converted our estimated Ricker “a” values to the limiting rate of reproduction (alpha) by raising $e^{\text{"a"}}$. An alpha value of 3 means that at a very low level in stock abundance each spawner would produce, on average, three recruits (Ricker 1975). Our post-1974 estimates for alpha values matched Reisenbichler (1990) estimates for the Methow and Entiat index stocks, despite differences in the time series of spawner and recruit data. Our post 1974 alpha values for the Wenatchee stock differs from Reisenbichler’s estimates, perhaps due to his lack of accounting for hatchery fish in a basin which is heavily influenced by hatchery fish. For the Warm Springs stock, Reisenbichler’s reported value is lower than our estimate for alpha. This is probably due to the most recent brood years, with low recruit per spawner ratios at low spawner levels, being included in our estimates. Our 1939 through 1990 alpha value estimate for the upriver spring chinook aggregate was similar to Reisenbichler’s alpha value for the Snake River spring chinook aggregate estimate for the years 1964 through 1983. Our pre-1970 alpha value estimate for the upriver spring chinook aggregate was nearly identical to Chapman et al. (1982), but did differ from Barton (1979). Chapman’s data had 20 years of overlap, opposed to Barton having only 13 years. In conclusion, it would appear that our estimates of productivity are within the realm of estimates reported previously by other authors.

In the draft review of Chapter 3, C. Walters and J. Collie both expressed concern about possible severe bias in R/S, due to incorrect calculation of R (i.e., substantial R with little or no S). However, in this paper, estimates of R were not obtained by proportionally dividing total catch to subbasins, as described for the problems with the Fraser River sockeye salmon. Abundance and catch data were available by run type, and harvest rates for lower mainstem Columbia River fisheries were estimated separately for spring and summer chinook (ODFW and WDFW 1995). Spring and summer chinook stocks in the Snake River region showed similar R/S patterns with different time series of harvest rates. In addition, harvest rates were greatly reduced over time, and R/S ratios at spawning levels declined. Note that a number of the rates used to compute recruits in the various subbasins were obtained independently. In addition, the results from the frequency of correlations of survival rate indices (Tables 3-5 and 3-6) revealed that stocks within the Snake region were weakly correlated for the pre-1970 brood years when the harvest rates were high. In the post-1974 brood years, the correlations of survival rate indices strengthened when harvest rates were greatly reduced (Figure 3-6b). This temporal pattern of survival rate correlations between stocks would not be consistent with the recruitment bias concerns of the reviewers.

The PATH process was initiated under the 1995-1998 Biological Opinion to assist decision making by 1999 regarding the long-term management of the hydrosystem to ensure survival and recovery of Snake River chinook and sockeye salmon. Key to the decision is 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 endangered Snake River spring and summer chinook and depressed upper Columbia River spring chinook 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.

3.6 Recommendations

Certain concepts and approaches in this paper have applicability to an active adaptive management strategy and associated monitoring and evaluation program being considered under the ESA for Snake and Columbia River spring, summer, and fall chinook and steelhead. An active strategy could purposefully construct a range of alternative models that are consistent with historical stock performance, and use these to identify management strategies that provide balance between probing for information (directed experimentation) and caution about short-term conservation concerns for stock survival (Hilborn and Walters 1992). In contrast, status quo management (not perturbing the present system) would have two major problems: 1) the rate of learning would be extremely slow; and 2) it may be extremely risky given the dire conservation status of Snake River stocks. The construction of the alternative models, consistent with the historic stock performances presented in this paper, should be the focus of the prospective phase of the PATH project.

Criteria need to be established in terms important to stock survival and recovery. A basin-wide monitoring and evaluation program involving index population response needs to be established and tied to those criteria. The spawner and recruit information developed for this paper (Beamesderfer et al. 1996) 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, would allow managers to estimate the productivity of individual stocks and track changes in stock productivity and survival over time. The basic data set, 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.

For the hydropower management actions, the cumulative response should be in terms of smolt-to-adult (e.g., Raymond 1988) or adult-to-adult (e.g., BRWG 1994) survival rates 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. Therefore, the experimental design should attempt to control or account for the natural variability (e.g., Deriso et al. 1996).

The monitoring program for hydropower management actions should contain replicate treatment stock units and temporal and spatial control units. This experimental design should enable managers to: 1) test whether treatments produce repeatable effects in situations with similar conditions; 2) distinguish treatment effects from natural variation; 3) estimate the variance associated with various parameters; and 4) test significance (McAllister and Peterman 1992). Finally, this experimental design should provide the ability to distinguish amongst competing hypotheses for salmon population survival and recovery.

3.7 Acknowledgments

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3.8 Tables and Figures

Tables 3-1 to 3-10 and Figures 3-1 to-3-39 are on the following pages.

Table 3-1: Ricker stock-recruitment function fit to pre 1970 brood years for spring (SP) and summer (SU) chinook index populations in the upper and lower Columbia River, and the Snake River.

Table 3-2: Ricker stock-recruitment function fit to post 1974 brood years for spring (SP) and summer (SU) chinook index populations in the upper and lower Columbia River, and the Snake River.

Table 3-3: Ricker stock-recruitment function fit to all brood years for spring (SP) and summer (SU) chinook index populations in the upper and lower Columbia River, and the Snake River.

Table 3-4: Analysis of covariance results for Ricker production functions using period (treatment) and spawners (covariate) for spring/summer chinook index stocks from Snake, upper Columbia and lower Columbia rivers.

Table 3-5: Frequency of correlations for spring/summer chinook survival rate indices within and between regions, 1949-1969 brood years. Survival rate indices 1 and 2 were based on residuals from production functions fit to pre-1970, post 1974, respectively.

Table 3-6: Frequency of correlations for spring/summer chinook survival rate indices within and between regions, 1975-1990 brood years. Survival rate indices 1 and 2 were based on residuals from production functions fit to pre-1970, post 1974, respectively.

Table 3-7: Analysis of Variance (ANOVA) tests for significant region differences in mean survival rate indices [Ln((R/S)obs/(R/S)pred)].

Table 3-8: Multi-comparison tests for significant pairwise region differences in mean survival rate indices given there was a significant region difference (see Table 3-7).

Table 3-9: Analysis of covariance for Ricker production functions using period (treatment) and spawners (covariate) for the upriver aggregate wild spring chinook run, 1939-1990 brood years. Periods represented decades, with 1939 and 1990 brood years incorporated into the nearest decadal interval.

Table 3-10: Comparison of limiting rate of reproduction ($a=e^a$), for selected spring chinook stocks in the Columbia Basin, with those reported by other authors.

Figure 3-1: Distribution of index stocks of spring and summer chinook salmon.

Figure 3-2: Snake River spring/summer chinook spawner escapements normalized to their average escapements computed from all available brood years through 1990.

Figure 3-3: Upper Columbia spring chinook spawner escapements normalized to their average escapements computed from all available brood years through 1990.

Figure 3-4: Lower Columbia River spring chinook spawner escapements normalized to their average escapements computed from all available brood years through 1990.

Figure 3-5: Columbia Basin upriver spring chinook aggregate spawner escapement normalized to its average escapement computed from all available brood years through 1990.

Figure 3-6a: Columbia Basin upriver spring chinook aggregate run to the Columbia River mouth, 1939-95.

Figure 3-6b: Mainstem combined (commercial, tribal, and sport) harvest rates for Columbia and Snake rivers spring/summer index stocks, 1939-95.

Figure 3-6c: Maximum hydroelectric dams encountered by spring/summer chinook yearling out-migrants from the three regions above Bonneville Dam.

Figure 3-6d: Lower Snake River flow and water particle travel time for the period April 15 through June 15 (Source: Idaho Department of Water Resources).

Figure 3-7: Natural log of recruits per spawner as it relates to the number of spawners for the Marsh Creek spring chinook index stock in the Middle Fork of the Salmon Subbasin (Snake Region), brood years 1957-90.

Figure 3-8: Natural log of recruits per spawner as it relates to the number of spawners for the Bear Valley / Elk Creek spring chinook index stock in the Middle Fork of the Salmon Subbasin (Snake Region), brood years 1957-1990.

Figure 3-9: Natural log of recruits per spawner as it relates to the number of spawners for the Sulphur Creek spring chinook index stock in the Middle Fork of the Salmon Subbasin (Snake Region), brood years 1957-90.

Figure 3-10: Natural log of recruits per spawner as it relates to the number of spawners for the Johnson Creek summer chinook index stock in the South Fork of the Salmon Subbasin (Snake Region), brood years 1957-90.

Figure 3-11: Natural log of recruits per spawner as it relates to the number of spawners for the Poverty Flat summer chinook index stock in the South Fork of the Salmon Subbasin (Snake Region), brood years 1957-90.

Figure 3-12: Natural log of recruits per spawner as it relates to the number of spawners for the Imnaha River spring/summer chinook index stock in the Imnaha Subbasin (Snake Region), brood years 1949-90..

Figure 3-13: Natural log of recruits per spawner as it relates to the number of spawners for the Minam River spring chinook index stock in the Grande Ronde Subbasin (Snake Region), brood years 1954-90.

Figure 3-14: Natural log of recruits per spawner as it relates to the number of spawners for the Methow River spring chinook index stock in the Methow Subbasin (Upper Columbia Region), brood years 1960-90.

Figure 3-15: Natural log of recruits per spawner as it relates to the number of spawners for the Entiat River spring chinook index stock in the Entiat Subbasin (Upper Columbia Region), brood years 1955-90.

Figure 3-16: Natural log of recruits per spawner as it relates to the number of spawners for the Wenatchee River spring chinook index stock in the Wenatchee Subbasin (Upper Columbia Region), brood years 1958-90.

Figure 3-17: Natural log of recruits per spawner as it relates to the number of spawners for the John Day River spring chinook (Mainstem) index stock in the John Day Subbasin (Lower Columbia Region), brood years 1959-90.

Figure 3-18: Natural log of recruits per spawner as it relates to the number of spawners for the John Day River spring chinook (Middle Fork) index stock in the John Day Subbasin (Lower Columbia Region), brood years 1959-90

Figure 3-19: Natural log of recruits per spawner as it relates to the number of spawners for the John Day River spring chinook (North Fork and Granite Creek) index stock in the John Day Subbasin (Lower Columbia Region), brood years 1959-90.

Figure 3-20: Natural log of recruits per spawner as it relates to the number of spawners for the John Day River spring chinook (Pooled) index stock in the John Day Subbasin (Lower Columbia Region), brood years 1959-90.

Figure 3-21: Natural log of recruits per spawner as it relates to the number of spawners for the Warm Springs River spring chinook index stock in the Deschutes Subbasin (Lower Columbia Region), brood years 1969-90.

Figure 3-22: Natural log of recruits per spawner as it relates to the number of spawner for the Klickitat River spring chinook index stock in the Klickitat Subbasin (Lower Columbia Region), brood years 1966-90.

Figure 3-23: Natural log of recruits per spawner as it relates to the number of spawners for the Wind River spring chinook index stock in the Wind Subbasin (Lower Columbia Region), brood years 1970-90.

Figure 3-24: Natural log of recruits per spawner as it relates to number of spawners for the upriver spring chinook aggregate, brood years 1939-90.

Figure 3-25: Comparison of Snake River stocks Ricker "a" value (and associated standard error) fitted to the pre-1970 period (P70) versus post-1974 period (P74).

Figure 3-26: Comparison of upper Columbia stocks Ricker "a" value (and associated standard error) fitted to the pre-1970 period (P70) versus post-1974 period (P74).

Figure 3-27: Comparison of lower Columbia stocks Ricker "a" value (and associated standard error) fitted to the pre-1970 period (P70) versus post-s1974 period (Pst74)

Figure 3-28: Deviations of observed recruits per spawner ratios (for Snake River index stocks) from those predicted by the stock recruitment functions fitted to the pre-1970 brood years (Survival Rate Index 1).

Figure 3-29: Deviations of observed recruits per spawner ratios (for Upper Columbia River index stocks) from those predicted by the stock recruitment functions fitted to the pre-1970 brood years (Survival Rate Index 1).

Figure 3-30: Deviations of observed recruits per spawner ratios (for Lower Columbia River index stocks) from those predicted by the stock recruitment functions fitted to the pre-1970 brood years (Survival Rate Index 1).

Figure 3-31: Deviations of observed recruits per spawner ratios (for Snake River index stocks) from those predicted by the stock recruitment functions fitted to the post-1974 brood years (Survival Rate Index 2).

Figure 3-32: Deviations of observed recruits per spawner ratios (for Upper Columbia River index stocks) from those predicted by the stock recruitment functions fitted to the post-1974 brood years (Survival Rate Index 2).

Figure 3-33: Deviations of observed recruits per spawner ratios (for Lower Columbia River index stocks) from those predicted by the stock recruitment functions fitted to the post-1974 brood years (Survival Rate Index 2).

Figure 3-34: Deviations of observed recruits per spawner ratios (for Snake River index stocks) from those predicted by the stock recruitment functions fitted to all brood years (Survival Rate Index 3).

Figure 3-35: Deviations of observed recruits per spawner ratios (for Upper Columbia River index stocks) from those predicted by the stock recruitment functions fitted to all brood years (Survival Rate Index 3).

Figure 3-36: Deviations of observed recruits per spawner ratios (for Lower Columbia River index stocks) from those predicted by the stock recruitment functions fitted to all brood years (Survival Rate Index 3).

Figure 3-37: Deviations of observed recruits per spawner ratios (for the upriver spring chinook aggregate) from those predicted by the stock recruitment functions fitted to the pre-1970 brood years (Survival Rate Index 1).

Figure 3-38: Deviations of observed recruits per spawner ratios (for the upriver spring chinook aggregate) from those predicted by the stock recruitment functions fitted to the post-1974 brood years (Survival Rate Index 2).

Figure 3-39: Deviations of observed recruits per spawner ratios (for the upriver spring chinook aggregate) from those predicted by the stock recruitment functions fitted to all brood years (Survival Rate Index 3).