Chapter 9
Evaluation of Productivity and Survival Rate Trends in the Freshwater Spawning and Rearing Life Stage for Snake River Spring and Summer Chinook

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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 advice on alternatives to manage the hydropower system to recover the listed populations. A process was initiated in 1995 to clarify the nature of differences between the models. This paper examines evidence for, and tests whether, a net decrease in survival rate in freshwater spawning and rearing (FSR) life stage has occurred since completion of the hydropower system that could explain the decline in adult recruitment and productivity of Snake River spring and summer chinook. Numbers of wild spring and summer chinook spawners and smolts were indexed at the uppermost dam from available data sets for the following brood years: 1962-1973, 1962-1982, and 1990-1993. Regression models showed a significant density-dependence between ln(smolts/spawner) and spawner, when a wide range of spawning escapements was examined. Estimates of ln(smolts/spawner) versus spawner were generally consistent among the data sets, and recent estimates were well within the bounds of the historic estimates. While numbers of spawners declined significantly since completion of the hydropower system, smolts/spawner and ln(smolts/spawner) increased, consistent with density dependent production functions. Based on a means test of the residuals, the index of FSR survival rate showed no significant decline since completion of the hydropower system for four combinations of spawner and juvenile indices. Analysis of covariance of the same data sets indicated a significant decline in FSR productivity for one of the four combinations. But when drought years were dropped from the analysis, the index of FSR productivity again showed no significant decline. In essence, this evaluation does not rule out comparatively small decreases in FSR productivity and survival rate in recent years, but provides no empirical support for a hypothesis that spawner-to-smolt survival was the primary life stage responsible for the decline of Snake River spring and summer chinook following completion of the hydrosystem. However, this analysis does not address whether there was a significant decline in FSR survival prior to the completion of the hydrosystem.

9.1 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 and survival rates also declined and became more variable following the completion of the hydropower system (Petrosky and Schaller 1992; Schaller et al. 1996). 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 distribution of survival over the salmon life cycle, that result in disparate management advise.

The NMFS' 1995-1998 Biological Opinion on operation of the FCRPS 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 comparison of spawner and smolt patterns from the aggregate run of naturally spawning Snake River spring and summer chinook for available brood years, 1962-1993. Spawner (parent) and smolt indices (progeny) are used to evaluate the following question:

> *Has there been a net decrease in productivity and survival rate during the freshwater spawning and rearing stage for Snake River spring and summer chinook since completion of the FCRPS that could explain the corresponding decline in adult recruitment, productivity and survival rate?.*

We define productivity, for a specified time period, as the natural log of the ratio of smolts per spawner, in the absence of density dependent mortality, similar to the definition in Schaller et al. (1996). Productivity is measured here as the intercept of the regression of ln(smolts/spawner) versus spawner. Survival rate indices provide a time series of density independent mortality estimates through deviations of observed smolts/spawner ratios from those predicted by the fitted recruitment function (predicted smolts/spawner) for a specified time period.

Analysis of stock-recruit patterns indicated that productivity and survival rate of Snake River index populations decreased dramatically with completion and operation of the hydropower system (Schaller et al. 1996). A broad mix of land use influence, from relatively pristine to management for irrigated agriculture, livestock grazing, logging and mining, existed throughout the time series (Fulton 1968; Beamesderfer 1996). However, a majority of the land use impacts, in many Snake River drainages, occurred prior to time period of lower Snake River dam construction and completion (Fulton, 1968; Gebhards, 1959; Thompson and Haas, 1960; and Gildemeister, 1992). Potential mechanisms for a hypothesized net decrease in freshwater spawning and rearing (FSR) productivity and survival rate since completion of the FCRPS (post-1974 brood year) may include: overall decreases in Snake River Basin habitat quality in tributary spawning/rearing and over-wintering areas (e.g., sedimentation, loss of pools or instream cover, increased temperatures); or environmental fluctuation and cycles (e.g., drought, warming cycle, severe winter conditions). A decrease in FSR productivity and survival rate after brood year 1974 might be considered evidence for an overall decrease in habitat quality, or simply the occurrence of unfavorable environmental conditions. Increased hatchery releases in the basin (to mitigate for hydropower effects) might also decrease productivity and survival rates from spawner to smolt, if hatchery fish produced less viable offspring in the wild, or through competition. Evidence of decreased FSR productivity and survival rate could also be attributed to depensatory survival mechanisms (BRWG 1994), which are possible at the low spawning escapements experienced recently by most Snake River populations.

Data sources investigated were tributary production studies, counts and estimates of wild adult spring and summer chinook at the uppermost Snake River dam, and estimates or indices of wild smolts arriving at the uppermost Snake River dam.

Tributary production studies to *directly* address this question are scant in terms of number of years and streams. FSR life stage survival rate estimates are available for a limited number of streams and years. Available estimates include egg-to-migrant survival rates for the Lemhi River (1965-1973 brood years; Bjornn 1978) and Lookingglass Creek (1965-1969 brood years; Burke 1993); and egg-to-parr and parr-to-smolt survival rates for the upper Salmon River (1987-1991; Kiefer and Lockhart 1994). Research and monitoring were also initiated recently under the Fish and Wildlife Program and Lower Snake River Compensation Plan to estimate life stage survival rates in a number of other Snake River production areas, through supplementation evaluation and wild production studies.

A long time series of direct survival rate estimates, dating to before completion of the FCRPS, would be desirable to rigorously evaluate hypotheses about decreased FSR survival. The following indirect method was used to index survival rates in the FSR life stage, and to test the hypothesis that FSR survival rate has declined since brood year 1974. FSR productivity and survival rate were indexed by estimating the aggregate Snake River escapements of wild spring and summer chinook and the subsequent aggregate smolt population size from those brood years. Observations of ln(smolts/spawner) versus spawner, and other statistics associated with this measurement, were then compared over time. Available data and estimates include life stages in addition to the FSR, specifically the prespawning and early smolt migration stages through free-flowing river, as well as passage through the first reservoir.

9.2 Methods

9.2.1 Spawner and Smolt Estimates

In this evaluation, one index of spawners was defined as wild adult spring and summer chinook, potentially available for spawning, indexed at the uppermost Snake River dam. This statistic is calculated by adjusting the total dam count by the hatchery rack returns and wild fish harvest rate in Snake River tributaries. A second index of potential spawners adjusted the first index for hatchery releases of adults and hatchery juveniles, in adult equivalent numbers, into Snake River tributaries. The adjustment of spawners from juveniles outplanted into Snake River tributaries was necessary because these juveniles were unmarked until recent years, and would have been counted as wild smolts in the subsequent outmigration year. Numbers of wild spring and summer chinook smolts are also indexed at the uppermost dam. Smolt estimates come from three sources: Raymond (1979) for brood years 1962-1973; Raymond (1988) for brood years 1962-1982; and Fish Passage Center smolt passage indices for recent brood years, 1990-1993.

9.2.3 Wild Spawner Estimates

The first index of wild spring and summer chinook escapements (SP1) for brood years 1979-1995 was represented by TAC (1996) estimates of wild run size at Lower Granite Dam. TAC derived these estimates by “backing out” hatchery run size based on rack returns and harvest (ODFW and WDFW 1995), assuming

80% prespawning survival of hatchery fish. No adjustment for Snake Basin harvest of wild chinook was necessary because the wild run harvest rate was essentially zero for these years.

SP1 escapements for the earlier brood years, 1962-1978, were estimated using methods similar to those of TAC (1996), with prespawning survival of hatchery fish assumed to be 80%. Snake River sport harvest estimates for this period are reported in Beamesderfer et al. (1996). A summary of calculations is provided in Table 9-1.

Hatchery releases of adults and juveniles outplanted into tributaries contributed to the wild smolts indexed at the uppermost dam in different proportions throughout the time series. Therefore a second index of potential spawners (SP2) was calculated to adjust SP1 for the total number of hatchery adults released (passed upstream of weirs or released for natural spawning) and the adult equivalents from fry and parr releases:

$$SP2 = SP1 + (AdW + AdR + AdE)/Sps \qquad \text{Eq. 9-1}$$

where AdW = hatchery adults released upstream of hatchery weirs
AdR = hatchery adults released into streams to spawn naturally
AdE = adult equivalents
= hatchery adults required to produce the juvenile release
Sps = prespawning survival = 0.8 (TAC 1996)

Adult equivalents were estimated based on hatchery-specific average fecundity (Kiefer et al. 1991; Olsen et al. 1991), a 1:1 sex ratio at spawning, and 0.9 survival rate from egg to juvenile release (D. Cannamela, IDFG, pers. comm.). In recent brood years, 1990-1993, AdE was zero because the released juveniles contributed to the hatchery smolt index, rather than wild smolt index (see Methods - Recent Smolt Estimates). The survival rate to parr stage of outplanted hatchery chinook fry was comparable to that of wild chinook for selected Idaho streams (Scully et al. 1990). Numbers of hatchery adults and fry/parr released are shown in Table 9-2.

The SP1 and SP2 indices bracket a range of potential spawners at the uppermost dam, and have slightly different implications in the analysis. If hatchery spawners and juvenile releases were completely ineffective producers of smolts, the index SP1 might be preferable for inferences regarding FSR trends in the Snake River Basin. Conversely, if hatchery fish were equally viable as wild fish, the SP2 index might be more representative.

Raymond (1979) Smolt Estimates

Raymond (1979) estimated numbers of wild stream-type (yearling outmigrant juvenile spring and summer chinook) smolts arriving at the uppermost dam, 1964-1975, using marked groups and estimates of collection efficiency at the dam. The uppermost dam changed during this era as new projects were added: Ice Harbor --1961; Lower Monumental--1969; Little Goose--1970; Lower Granite--1975. Raymond (1979) derived the proportions of wild and hatchery smolts from survival rate calculations on wild fish marked and released in the Salmon River and hatchery fish marked and released from Rapid River Hatchery (the only hatchery releasing substantial numbers in these years). This data set represents a period of relatively high escapements, predominated by wild fish (Tables 9-1 and 9- 2).

Raymond (1988) Smolt Estimates

Raymond (1988) updated his earlier published estimates of numbers of wild and hatchery stream-type chinook smolts arriving at Lower Granite Dam for 1964-1984 using the same methods as the 1979 paper.

The number of hatchery smolts each year was derived from the total numbers released and their relative survival rate to the first dam; this number, when subtracted from the total population estimate calculated at the first dam, provided an estimate of wild fish each year. For most years, Raymond concluded that sufficient numbers of marked hatchery fish were recovered for calculations of relative survival. For the few years in which there was no marking at hatcheries, or recoveries were insufficient for the analysis, he used the average survival rate for years bracketing the missing data. Raymond (1988) did not specify the years to which he applied average survival rates, however, a review of Rapid River Hatchery annual reports (T. Elms-Cockrum, IDFG, pers. comm.) indicated no marking at this facility for NMFS survival studies in smolt migration years 1976, 1978 and 1981. Note that some of the annual estimates in this paper differed from those in the 1962-1973 brood year data set. The data set for 1962-1982 brood years represents a broader range of escapements, with wild fish declining and hatchery fish becoming more numerous later in the time series (Tables 9-1 and 9-2).

Recent Smolt Estimates

Recent year (1992-1995) estimates of wild stream-type chinook smolts were derived from Fish Passage Center (FPC) passage indices (FPC 1993, 1994, 1995a). Wild stream-type abundance was indexed by examination of fin clips in 1993-1995 (all hatchery fish were marked with adipose and/or ventral clips), and by scale pattern analysis in 1992 (Borgeson and Bowden 1994). The passage indices represent a relative indicator of population abundance, computed by dividing the daily fish collection estimate by the proportion of flow passing through the sampled unit or powerhouse relative to river flow (FPC 1994). This adjustment compensated for different daily project operations (e.g., spill and unit loading) assuming fish passed through spill and powerhouse units in numbers proportional to the flow through these passage routes. The FPC did not further divide the passage index by any estimate of the fish guidance efficiency (FGE), because FGE estimates vary within and between years. The FPC (1994) indicates that annual passage indices can be compared among years for a particular species and site, provided they are not considered in isolation of other information.

This analysis bounds wild smolt abundance estimates for recent years, using a range of reported FGEs. The first estimate of wild smolt abundance used the weighted average value of 0.56 FGE at Lower Granite Dam from the 1995-1998 Biological Opinion modeling (Toole 1995). This represents a direct estimate, based on NMFS fyke net studies (Swan et al. 1990). A higher estimate of smolt abundance is obtained if FGE is interpreted to be lower than the direct estimates indicate. A lower FGE (as low as 0.40) is implied from the recent NMFS/UW survival studies (Iwamoto, et al. 1994; Muir, et al. 1995), assuming the detection probability and survival rate estimates are not biased by violation of the homogeneity assumption (FPC 1995b). The range of FGE estimates used in the analysis contained the point estimates for detection probabilities estimated in 1995 at Lower Granite Dam for periods before spill occurred (April 9-25 releases; Muir, et al. 1996). Based on estimates of median migration rate and 20th and 80th percentiles, release groups after April 25 would have encountered spill at Lower Granite Dam (Figure 9 and Tables 12, 14 of Muir et al. 1996).

9.2.3 Comparison of Recent and Historical Smolts/Spawner

Comparisons were made between recent (1990-1993 brood years) estimates of smolts/spawner, and those predicted from the Raymond 1979 and 1988 data sets (1962-1973 and 1962-1982 brood years). Predicted values were based on the regression:

$$\ln(Sm / Sp) = a + bSp \qquad \text{Eq. 9-2}$$

where Sm = smolts and Sp = spawners (SP1 or SP2). This form is analogous to a Ricker recruitment curve (Ricker 1975; equation 11.15), where recruits are represented by smolts. Comparison methods consisted of updating regressions for historic data (brood years 1962-1973 and 1962-1982) with the recent data sets (1990-1993).

Potential data limitations include discontinuity in the wild smolt indices between the historic periods and 1990, and changes in smolt estimation methods. Also, because spawning escapements have decreased precipitously since completion of the FCRPS, recent observed spawning escapements and predicted values of smolts/spawner fall outside the Raymond (1979) data range for the 1962-1973 period. This was not a limitation for the 1962-1982 data set (Raymond 1988). Changes in smolt estimation methods were addressed here by applying a range of FGE assumptions to the recent smolt indices.

9.2.4 Pre- vs. Post-FCRPS Completion

Hypothesis testing, involving the difference between two population means (Daniel 1978), was used to compare parameter estimates, 1962-1974 and 1975-1993 brood years for the full time series (Raymond 1988 and recent data sets). Tests included: 1) numbers of wild spawners; 2) Sm/Sp; 3) ln(Sm/Sp) and 4) a residual expressed as ln[(observed Sm/Sp) / (predicted Sm/Sp)]. This approach uses the residuals as an index of survival rate, similar to approaches in Hilborn and Walters (1992; Figure 7.2.1), Peterman (1981) and Cushing (1973). Tests 2), 3) and 4) used alternative assumptions for FGE (0.56 or 0.40) to estimate wild smolt abundance for the recent brood years. Calculated t values were corrected for positive autocorrelation according to Bence (1995; equation 6). Two-tailed t-tests were used to examine whether parameter estimates *differed* between the two periods. One-tailed t-tests examined hypotheses that parameter estimates *declined* from the first to the second period. Tests were performed at 0.01, 0.05 and 0.10 levels of significance.

Minimum detectable differences were calculated for the tests of residuals that failed to reject the null hypothesis. Peterman (1989, 1990) noted that in fisheries applications, a large cost can be associated with falsely assuming there is no effect (type II error), and argued the need to use information on b, power and minimum detectable difference. Minimum detectable differences were calculated at an alpha level of 0.10 and power of 0.80 based on the formula (Zar 1985; Equation 9.25):

$$d \geq \sqrt{\frac{2 s_p^2}{n}} \left(t_{a,n} + t_{b(1),n} \right) \qquad \text{Eq. 9-3}$$

where n is the harmonic mean of sample sizes and v represents degrees of freedom. Differences between variances of the two periods were examined using two-tailed F tests at an alpha level of 0.10 (Daniel 1978).

Analysis of covariance (ANCOVA; Wilkinson 1990) was used as an alternative to the means test of residuals to examine differences in productivity between the two periods in the relationship of ln(Sm/Sp) versus S. The assumption of homogeneity of slopes was first tested for significant interaction (alpha = 0.10) between treatment (period) and the covariate (spawner index). Given homogeneity of slope, ANCOVA was run to estimate the effect of period on ln(Sm/Sp), taking into account spawning level.

9.3 Results

9.3.1 Spawner and Smolt Estimates

Raymond (1979)

The estimated number of wild origin spring and summer chinook adults available for spawning (SP1) averaged 39,600 (range, 20,700 - 52,300) for brood years 1962-1973 (Tables 9-1 and 9-3). Wild origin adults made up from 66% to 100% of the run. Adjusted for hatchery releases, the potential number of spawners (SP2) averaged slightly higher (39,900; Table 9-3).

Raymond (1979) estimated that the number of wild stream-type chinook smolts arriving at the upper Snake River Dam averaged 2.33 million (range, 1.00 - 3.08) during migration years 1964-1975 (brood years 1962-1973; Tables 9-3 and 9-4). Wild fish made up from 25% to 100% of the total smolts during this period.

For the SP1 index, an average of 61 wild smolts/spawner was estimated for the period (range, 28 - 105; Tables 9-3 and 9-5). For the SP2 index, an average 61 smolts/spawner was also estimated for the 1962-1973 brood years.

Raymond (1988)

The estimated number of wild origin spring and summer chinook adults available for spawning (SP1) averaged 30,200 (range, 5,300 - 52,300) for brood years 1962-1982 (Tables 9-1 and 9-3). Wild origin adults made up from 55% to 100% of the run. Adjusted for hatchery releases, the potential number of spawners (SP2) averaged slightly higher (30,500; Table 9-3).

Raymond (1988) estimates of the number of wild stream-type chinook smolts arriving at the upper Snake River Dam averaged 2.04 million (range, 0.60- 3.20) during migration years 1964-1984 (brood years 1962-1982; Tables 9-3 and 9-6). Wild fish made up from 22% to 100% of the total smolts during this period.

For the SP1 index, an average of 80 wild smolts/spawner was estimated for the period (range, 42 - 189; Tables 9-3 and 9-7). For the SP2 index, an average 78 smolts/spawner (range, 42-181) was produced by the 1962-1982 brood years.

Recent Period

The estimated number of wild origin spring and summer chinook adults available for spawning (SP1) in brood years 1990-1993 averaged 8,500 (range, 5,020 - 12,400; Tables 9-1 and 9-3), about one-fifth of that in the Raymond (1979) data set. Wild origin adults made up from 29% to 51% of the run for the recent period. Adjusted for hatchery releases, the potential number of spawners (SP2) averaged 11,000, or 28% higher than SP1 (Table 9-3).

The wild stream-type chinook passage index at Lower Granite Dam for brood years 1990-1993 ranged from about 290,000 to 866,500 (e.g., FPC 1993). Wild fish made up from 12% to 21% of the total passage index during this recent period (Tables 9-3 and 9-8). Based on an FGE of 0.56, the estimated wild run averaged 0.83 million (range, 0.52 - 1.55). Based on an FGE of 0.40, the estimated wild run averaged 1.16 million (range, 0.72 to 2.17).

Estimated numbers of wild smolts/spawner averaged 104 (range, 48 - 155) for the recent period, based on the SP1 index and 0.56 FGE (Tables 9-3 and 9-9). Based on SP1 and 0.40 FGE, an average of 145 wild smolts per spawner were produced (range, 67 - 217). For the SP2 index, the recent period averaged 81 smolts/spawner (range, 38 - 116) for 0.56 FGE, and 114 smolts/spawner (range, 54 - 162) for 0.40 FGE.

9.3.2 Comparison of Recent and Historic Smolts/Spawner

Raymond (1979)

For brood years 1962-1973, numbers of smolts per potential wild spawner (SP1) showed a weak pattern of density dependence (Table 9-10). For comparison purposes, we converted our estimated Ricker “a” values to the limiting rate of reproduction (alpha) by raising $e^{\text{"a"}}$. An alpha value of 100 means that at a very low level in stock abundance each spawner would produce, on average, one hundred smolts (Ricker 1975). The regression alpha value is 119 smolts per spawner at zero density, with a wide confidence interval (95% CI, 42 to 338). The 1962-1973 data range for spawners was very limited at the low end of escapements, which partially explains the wide CI. There was only one observation of fewer than 30,000 spawners, and no observations of fewer than 20,000 spawners.

The addition of recent, low escapement data (brood years 1990-1993) to the 1962-1973 data improved the fit of the regression for the SP1 index and 0.56 FGE assumption. The numbers of smolts per SP1, with the recent data added, showed significant density dependence for the 0.56 FGE (Table 9-10). Changes in the prediction line were slight when recent data for the 0.56 FGE assumption were added, with the alpha decreasing from 119 to 111 smolts per spawner.

The addition of recent data using 0.40 FGE increased the alpha value from 119 to 158 smolts per SP1 (Table 9-10). The numbers of smolts per SP1, with the recent data added, showed significant density dependence for the 0.40 FGE assumptions (Table 9-10).

With the spawner index adjusted for hatchery releases, numbers of smolts per SP2 again showed a weak pattern of density dependence for brood years 1962-1973 (Table 9-10). The regression alpha value was 122 smolts per SP2, with a wide confidence interval (95% CI, 42 to 351).

The addition of recent, low escapement data (brood years 1990-1993) to the 1962-1973 data slightly changed the fit of the regression for the SP2 index and 0.56 FGE assumption. The numbers of smolts per SP2, with the recent data added, showed weak density dependence for the 0.56 FGE (Table 9-10). The alpha value of the updated regression decreased from 121 to 90 smolts per SP2.

The addition of recent data using 0.40 FGE increased the alpha from 121 to 130 smolts per SP2 (Table 9-10). The numbers of smolts per SP2, with the recent data added, showed significant density dependence for the 0.40 FGE assumptions (Table 9-10).

The new intercepts, slopes and bounds, for both FGE assumptions, were well within the bounds of the 1962-1973 data set regression for both the SP1 and SP2 indices (Table 9-10).

Raymond (1988)

For brood years 1962-1982, numbers of smolts per SP1 showed significant density dependence (Table 9-10). The regression alpha value was 128 smolts per, similar to that (121) from the Raymond (1979) data set. Neither slope nor intercept changed significantly from the Raymond (1979) data set (Table 9-10), however, the confidence interval was narrower in comparison (95% CI, 96 to 170). This was in part due to a relatively broader range of SP1 escapements (5,300 - 52,300).

Figure 9-1 shows plots of ln(Sm/SP1) versus SP1 for recent brood years (1990-1993) assuming 0.56 FGE overlaid on brood year 1962-1982 data. Estimates using the 0.56 FGE assumption appear consistent with the historic values at lower escapements. The addition of recent, low escapement data to the historic period data reduced the fit of the regression slightly for the 0.56 FGE assumption. The numbers of smolts per SP1, with the recent data added, showed significant density dependence with 0.56 FGE (Table 9-10). Slight changes in the prediction line occurred when recent data using 0.56 FGE were added, with the alpha decreasing from 128 to 120 smolts per SP1.

Figure 9-2 shows plots of ln(Sm/SP1) versus SP1 for recent brood years assuming 0.40 FGE overlaid on brood year 1962-1982 data. Estimates using the 0.40 FGE assumption also appear consistent with the historic values at lower escapements. The addition of recent, low escapement data to the historic period data improved the fit of the regression slightly (Table 9-10). For the 0.40 FGE assumption, the addition of recent data increased the alpha value from 128 to 140 smolts per spawner.

With the spawner index adjusted for hatchery releases, numbers of smolts per SP2 also showed significant density dependence for brood years 1962-1982 (Table 9-10). The regression alpha value was 124 smolts per SP2, similar to that (121) from the Raymond (1979) data set. Neither slope nor intercept changed significantly from the Raymond (1979) data set (Table 9-10), however, the confidence interval was narrower in comparison (95% CI, 93 to 164). This was due, in part, to a broader range of SP2 escapements (5,500 - 52,700).

Figure 9-3 shows plots of ln(Sm/SP2) versus SP2 for recent brood years (1990-1993) assuming 0.56 FGE overlaid on brood year 1962-1982 data. Recent estimates using the 0.56 FGE assumption appear to be in the mid to low range of the historic values at lower escapements. The addition of recent, low escapement data to the historic period data reduced the fit of the regression slightly for the 0.56 FGE assumption. The numbers of smolts per SP2, with the recent data added, showed significant density dependence for the 0.56 FGE (Table 9-10). Changes in the prediction line were slight when recent data for the 0.56 FGE assumption were added, with the alpha value decreasing from 124 to 108 smolts per SP2.

Figure 9-4 shows plots of ln(Sm/SP2) versus SP2 for recent brood years assuming 0.40 FGE overlaid on brood year 1962-1982 data. Estimates using the 0.40 FGE assumption also appear consistent with the historic values at lower escapements. The addition of recent, low escapement data to the historic period data improved the fit of the regression slightly (Table 9-10). For the 0.40 FGE assumption, the addition of recent data increased the alpha value from 124 to 126 smolts per SP2.

The new intercepts and slopes, for both FGE assumptions and both SP1 and SP2, were well within the bounds of the 1962-1982 data set regressions, and the confidence intervals overlapped considerably (Table 9-10).

9.3.3 Pre- vs. Post-FCRPS Completion

Based on two-tailed means tests between brood year periods 1962-1974 and 1975-1993, spawner numbers declined significantly, while most smolt per spawner indices increased significantly (Tables 9-11 and 9-12). Only the spawner indices exhibited strong positive autocorrelation (0.79-0.81); adjusting for autocorrelation substantially decreased the t values for spawner numbers. There were no significant differences between periods for residual tests for either FGE assumption or spawner index. The minimum detectable difference for the test of survival rates ranged from 0.31 to 0.33 for the four combinations of spawner index and FGE assumptions, larger than the measured differences between the means (Tables 9-11 and 9-12). That is, if the true differences were 0.31 to 0.33 or greater, there would be a probability of 0.80 of getting a significant result at an alpha level of 0.10.

Based on one-tailed means tests, only the numbers of spawners (for both SP1 and SP2) was found to be significantly lower after brood year 1974 (Tables 9-11 and 9-12). Indices of smolts per spawner increased from the first to second period, hence one-tailed tests for declines were moot. The minimum detectable difference for the test of survival rates ranged from 0.26 to 0.28 for the four combinations of spawner index and FGE assumption, larger than the measured differences between the means (Tables 9-11 and 9-12). That is, if the true differences were at least a 0.26 to 0.28 *decline*, there would be a probability of 0.80 of getting a significant result at an alpha level of 0.10.

The pattern of survival rates from 1962 to 1993 brood years (Figure 9-5) indicate greater variability in the later period, and F-tests of the variances were significant ($p<0.05$) for all four combinations of spawner index and FGE assumption. It should be noted that three of the largest negative residuals from the means tests occurred in the second period (Figure 9-5), and were associated with major drought years during the year of smolt migration (1977, 1992 and 1994). The other major drought year in the time series (1973) did not have negative residuals. The influence of different spawner indices on the survival rate pattern predictably became more pronounced with time, because of increases in hatchery adult releases into Snake River tributaries. Different FGE assumptions affected the residual patterns to some extent, even prior to the recent brood years to which they were applied (1990-1993).

The probability values for the treatment by covariate interaction were not significant for any combination of spawner index and FGE assumption (range, 0.65 - 0.94), so the assumption of homogeneity of slopes was plausible. ANCOVA tests for differences in productivity between periods (1962-1974; post-1974 brood years) were significant only for the combination SP2 and 0.56 FGE (Table 9-13). A second analysis was run with a reduced data set that removed drought years (smolt years 1973, 1977, 1992 and 1994). Again, the probability values for the treatment by covariate interaction were not significant (range, 0.59 - 0.89), indicating homogeneity of slopes. With the drought years removed, ANCOVA indicated none of the combinations of spawner index and FGE assumption had a significant effect on productivity for period (Table 9-13).

9.4 Discussion

This paper addresses the hypothesis that there has been a net decrease in productivity and survival rate during the freshwater spawning and rearing stage for Snake River spring/summer chinook since completion of the Federal Columbia River Power System that could explain the decline in adult recruitment, productivity, and survival rate.

These analyses provide little to no empirical support for a marked decline in FSR productivity and survival rate since completion of the FCRPS of the magnitude observed by Schaller et al. (1996). The numbers of spawners declined significantly from the first to second period. Productivity as measured by smolts per spawner or ln(smolts/spawner) increased as the population declined following FCRPS development. This increase is consistent with density dependence as expressed in production functions (Ricker 1975). The recent year estimates for smolts per spawner versus spawner generally agree with those predicted from the two historic periods, regardless of the spawner index or FGE assumption.

The analyses do not rule out comparatively minor decreases in FSR productivity and survival rate since FCRPS completion. The index of density independent FSR survival rate, as measured by residual, showed no significant decline from the first to second period for four combinations of spawner index and FGE assumption (Tables 9-11 and 9-12). However, the residual pattern (Figure 9-5) and comparison of variance between the two periods indicate greater variability in the later period. In addition, ANCOVA showed a significant decrease in density independent productivity from the first to second period for one of the four combinations of spawner and juvenile indices (Table 9-13). Adverse environmental conditions, such as below average runoff, may have reduced FSR survival rate in some years. The Snake and Columbia River basins experienced prolonged drought from 1987 through 1994. When drought years were removed from the data set, ANCOVA showed no significant decrease in productivity from the first to second period for any of the four combinations (Table 9-13).

The most sensitive tests for between period change in FSR survival rate (one-tailed, alpha of 0.10, and power of 0.80), had minimum detectable differences in the range of -0.26 to -0.28. In contrast, the estimated change in adult-to-adult survival rate for Snake River index stocks following FCRPS completion was much greater, -1.60 (Schaller et al. 1996; survival index 1, Table 7). Therefore, the power of the smolt and spawner indices to detect change in FSR survival rates would be adequate to detect whether changes at this life stage explained much of the change in adult survival rates estimated for Snake River index stocks following completion of the FCRPS. However, a true FSR survival rate change of -0.28, while not explaining much of the recent decline of Snake River stocks, would not be trivial.

Because both spawners and smolts were indexed at the uppermost dam, spawner-to-smolt productivity and survival rate estimates include life stages in addition to the FSR, specifically the prespawning and early smolt migration stages through free-flowing river, and passage through the first reservoir. Throughout the time series, the spawner-to-smolt estimates consistently contained the effects of passage through one reservoir, which presumably had similar impacts on survival rate given a similar suite of runoff conditions (e.g., flow volume and timing, turbidity, temperature). Any comparison of smolt/spawner estimates reported here with those from other systems, or within the Snake River Basin, would need to take into account differences in the stage at which smolts and spawners are indexed (e.g., tributary smolt indices generally include migrating and rearing juveniles). Preliminary analyses for the PATH process found no evidence for a decreasing trend in prespawning survival rate indices of Snake River wild spring/summer chinook from 1953-1994 (Petrosky 1995).

The proportion of hatchery fish spawning and contributing to wild smolts increased during recent years (Table 9-2). If reproductive success was lower for hatchery fish spawning in streams than for wild spawners (e.g., Chilcote et al. 1986), then, in theory, aggregate FSR productivity and survival rate would exhibit an apparent decline. The two spawner indices in the analyses bracket a range of potential spawners at the uppermost dam. Use of the SP1 index implicitly assumes hatchery spawners are completely ineffective, while use of SP2 assumes hatchery spawners are equally effective as wild spawners. If SP1 were true, no significant decreases in FSR productivity and survival rate were detected. If SP2 were true, FSR productivity decreased significantly in a single case. If hatchery spawners were somewhat less effective than wild spawners, only weak or nonsignificant decreases might be expected from these results.

The trends and patterns in FSR productivity and survival rate observed for aggregate populations may not extend to individual populations within the Snake River Basin. Although poorly quantified, dynamics of individual spawning populations at the FSR life-stage can be expected to respond to habitat conditions at the local and basin scales. A broad mix of land use influences, from relatively pristine to management for irrigated agriculture, livestock grazing, logging and mining, existed throughout the time series (Fulton 1968; Beamesderfer et al. 1996). Negative trends in habitat condition (quality pools) are evident in several managed watersheds, whereas wilderness or unroaded watersheds have shown greater stability, over half-century time scales (McIntosh et al. 1994). Reductions in sediment deposition have also been documented in the heavily-degraded South Fork Salmon River since the mid-1960s (Platts et al. 1989), and major fish screening programs were completed by the late 1960s in the upper Salmon and Grand Ronde rivers. While FSR survival of individual populations would be expected to track with these localized trends, the aggregate data provide no evidence for a major shift in spawner-to-smolt productivity and survival rate that would explain much of the precipitous decline in productivity and survival rate of Snake River spring and summer chinook since completion of the FCRPS (Schaller et al. 1996). However, this analysis did not address whether there was a significant decline in FSR survival prior to the completion of the hydrosystem, because the smolt and spawner data were not collected prior to the 1960s.

Aggregate population data should be used with caution to infer the strength of depensatory mechanisms for Snake River spring and summer chinook. Stronger populations tend to dominate recruitment patterns within the aggregate (Ricker 1975); those populations most likely experiencing depensation would be underrepresented in the aggregate. As pointed out in BRWG (1994), classic production functions of the form used here, inevitably overestimate production at low escapements. This is because, in these functions, productivity increases to a maximum value at one spawner, well below levels postulated to be influenced by demographic (uneven sex ratio, Allee effects, etc.), genetic or environmental factors. A function, which diminishes productivity from that predicted by a Ricker function when escapement is below a minimum escapement threshold (Dennis 1989), would appear reasonable for individual spawning populations. Recently, most of the individual Snake River populations have experienced extremely low escapements. Aggregate escapements for brood years 1994 and 1995 were substantially lower (1,100-1,700) than those used in these analyses (5,000-52,700). Thus, it is reasonable to expect a drop in estimated productivity in upcoming smolt migration years (brood years 1994-1995) relative to Ricker functions fitted to the aggregate Snake River populations. Future estimates of smolts/spawner from these brood years may provide additional insight into the relative strength of depensatory mechanisms in Snake River spring and summer chinook. Ensuring survival and recovery of these populations will be more difficult, the more that productivity declines at low escapements.

Raymond (1988) stated that annual estimates of the smolt-to-adult return rates of salmon and steelhead would form the basis for assessing effects of hydroelectric development and enhancement measures taken to offset dam related mortalities. However, from the mid-1980s to the early 1990s, the advent of compensation hatchery programs in the Snake River Basin, and incomplete marking, thwarted efforts to estimate annual numbers of wild and hatchery smolts migrating through the system. Incomplete hatchery marking and limited sampling for age of returning adults also complicated assessment of adult return rates of wild and hatchery fish. These limitations have been eased since brood year 1991, when 100 percent marking (adipose and/or ventral fin clips) of all hatchery spring and summer chinook began in the Snake River Basin.

Future monitoring should include visual inspection of adults for marks at the uppermost Snake River dam to estimate hatchery/wild and age composition. Visual inspection should be augmented, as needed, by a sampling program with scale collection and inspection for marks. Similar programs should be implemented throughout the Columbia Basin to achieve meaningful temporal and spatial comparisons of productivity and survival rate patterns from adult-to-smolt and smolt-to-adult stages. In particular, these programs would be helpful if they were instituted for index populations in the lower river which are currently being used to monitor numbers of spawners and adult recruits (Beamesderfer et al. 1996; Schaller et al. 1996).

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Table 9-1: Estimated number of wild-origin spring/summer chinook adults available for spawning (SPI), brood years 1962-1995.

Table 9-2: Estimated number of spring/summer chinook adults available for spawning, adjusted for hatchery releases, brood years 1962-1995.

Table 9-3: Mean and standard deviation for numbers of wild spawners (SP1 and SP2), wild smolts, smolts/spawner, and ln(smolts/spawner), for various time periods and data sets used in analyses.

Table 9-4: Estimated number of wild- and hatchery chinook yearlings passing the uppermost dam, 1964-75 (Raymond 1979; Table 8). NS indicates no sampling in the Salmon River

Table 9-5: Smolts per spawner summaries, for potential wild spawners and wild smolts estimated at uppermost dam (Raymond 1979), brood years 1962-1973. NS indicates no sampling in Salmon River.

Table 9-6: Estimated number (millions) of wild and hatchery yearlings passing the uppermost dam, 1964-84 (Raymond 1988; Tables 2 and 4). 1/

Table 9-7: Smolt per spawner summaries, for potential wild spawners and wild smolts estimated at uppermost dam (Raymond 1988), brood years 1962-1982.

Table 9-8: Estimated number of wild chinook yearlings passing the uppermost dam, 1992-1995 (FPC data, adjusted for FGE). 1/.

Table 9-9: Smolt per spawner summaries, for spawner index SP1 and SP2 and wild smolts estimated at uppermost dam, brood years 1990-1993.

Table 9-10: Summary of ln(SM/Sp) vs. SP1 and SP2 regression statistics for brood years 1962 -1973 (Raymond 1979) and brood years 1962-1982 (Raymond 1988), updated for recent (1990 - 1993) brood years, assuming 0.56 and 0.40 FGE.

Table 9-11: Snake River spring/summer chinook hypothesis test results for differences in means between two brood year periods for spawner index SP1, Sm/SP1, ln(Sm/SP1) and ln(observed/expected), where u1 = mean for brood years 1962-1974, and u2 = mean for brood years 1975-1982, 1990-1993. t-tests are based on t adjusted for positive autocorrelation. 1/.

Table 9-12: Snake River spring/summer chinook hypothesis test results for differences in means between two brood year periods for spawner index SP2, Sm/SP2, ln(Sm/SP2) and ln(observed/expected), where u1 = mean for brood years 1962-1974, and u2 = mean for brood years 1975-1982, 1990-1993. t-tests are based on t adjusted for positive autocorrelation. 1/.

Table 9-13: Analysis of covariance results for ln(Sm/Sp) versus Sp using period (treatment) and spawner index (covariate), Snake River spring/summer chinook. Periods 1 and 2 were brood years 1962-1974 and 1975-1982, 1990-1993, respectively. Analyses included all years, and a reduced data set that removed drought years (smolt years 1973, 1977, 1992 and 1994).

Figure 9-1: Relationship of ln(smolts/spawner) versus spawner for wild Snake River spring/summer chinook assuming spawner index SP1 and 0.56 FGE, brood years 1962-1982, 1990-1993.

Figure 9-2: Relationship of ln(smolts/spawner) versus spawner for wild Snake River spring/summer chinook assuming spawner index SP1 and 0.40 FGE, brood years 1962-1982, 1990-1993.

Figure 9-3: Relationship of ln(smolts/spawner) versus spawner for wild Snake River spring/summer chinook assuming spawner index SP2 and 0.56 FGE, brood years 1962-1982, 1990-1993.

Figure 9-4: Relationship of ln(smolts/spawner) versus spawner for wild Snake River spring/summer chinook assuming spawner index SP2 and 0.40 FGE, brood years 1962-1982, 1990-1993.

Figure 9-5: Plot of residuals by brood year 1962-1982, 1990-1993 wild Snake River spring/summer chinook for four sets of assumptions: SP1 and 0.56 FGE, SP1 and 0.40 FGE, SP2 and 0.56 FGE, and SP2 and 0.40 FGE.