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Productivity and survival rate trends in the freshwater spawning and rearing stage of Snake River chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract: Stream-type chinook salmon (*Oncorhynchus tshawytscha*) populations in the Snake River (northwest United States) have declined dramatically since completion of the federal hydrosystem. Identifying the life stage that is limiting the survival of these stocks is crucial for evaluating the potential of management actions to recover these stocks. We tested the hypothesis that a decrease in productivity and survival rate in the freshwater spawning and rearing (FSR) life stage since completion of the hydropower system could explain the decline observed over the life cycle. The decline of chinook populations following completion of the hydrosystem was not accompanied by major survival changes in the FSR life stage. FSR productivity showed no significant decline, and the FSR survival rate decline was small relative to the overall decline. However, significant survival declines did occur in the smolt-to-adult stage coincident primarily with hydrosystem completion, combined with poorer climate conditions and possibly hatchery effects. Potential improvements in survival that occur only at the FSR life stage are unlikely to offset these impacts and increase survival to a level that ensures the recovery of Snake River stream-type chinook.

Résumé : Les populations du Saumon quinnat (*Oncorhynchus tshawytscha*) de type riverain de la rivière Snake du nord-ouest des États-Unis ont décliné de façon spectaculaire depuis l'achèvement de l'hydrosystème fédéral. L'identification du stade du cycle biologique qui limite la survie de ces stocks est une étape cruciale dans l'évaluation du potentiel des aménagements nécessaires pour la récupération de ces populations. Nous posons en hypothèse que la diminution de la productivité et du taux de survie dans la partie du cycle relié à la fraye et au développement en eau douce (stade FSR), depuis l'achèvement du système hydroélectrique, peuvent expliquer le déclin observé dans tout le cycle biologique. Le déclin des populations de Saumons quinnat après le parachèvement de l'hydrosystème n'a pas été marqué par des changements majeurs de la survie durant le stade FSR; la productivité durant ce stade n'a pas baissé de façon significative et la réduction des taux de survie a été faible par comparaison au déclin total. Cependant, des réductions significatives de la survie se sont manifestées durant le passage du stage saumonneau au stade adulte qui ont coïncidé particulièrement avec l'achèvement de l'hydrosystème, mais aussi avec des conditions climatiques défavorables et peut-être aussi avec des effets de pisciculture. Des améliorations potentielles de la survie au seul stade FSR sont donc peu susceptibles de compenser les impacts et d'augmenter la survie à un niveau qui assure la récupération des stocks de Saumons quinnat de type riverain de la rivière Snake.

[Traduit par la Rédaction]

Introduction

The Columbia River Basin once contained extremely abundant runs of chinook salmon (*Oncorhynchus tshawytscha*) that supported a substantial freshwater harvest (Chapman 1986). Over the last century, however, these stocks, in addition to sockeye (*Oncorhynchus nerka*) and steelhead (*Oncorhynchus mykiss*), have declined dramatically in response to a combination of factors including extensive hydroelectric development, harvest, habitat degradation, and emphasis on mitigating anthropogenic losses with hatchery releases. Snake River spring and summer chinook populations, once the predominant run of stream-type chinook in the Columbia River Basin, have declined dramatically since completion of the Federal Columbia River Power System (hereafter referred to as the hydrosystem). They have been listed as threatened under the Endangered Species Act since 1992. To address this population decline, the National Marine Fisheries Service's 1995–1998 biological opinion on operation of the hydrosystem created a process called PATH (Plan for Analyzing and Testing Hypotheses) (Marmorek et al. 1998). The PATH process evaluated hypotheses about the distribution of mortality over the life cycle and strengths and weaknesses of supporting evidence and tested those alternative hypotheses that had significant management implications (Marmorek et al. 1998).

The PATH modeling forum was a critical component of the evaluation of the effects of breaching four large hydroelectric dams on the lower Snake River for salmon recovery,

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and several important conclusions regarding the survival of chinook evolved from the PATH retrospective analyses that will help decision makers better evaluate options for recovery. Schaller et al. (1999) demonstrated that productivity and survival rates of Snake River stream-type chinook declined and also became more variable following the completion of the hydrosystem. Declines in survival rates for Snake River stocks were also greater than for similar stocks, which migrate past fewer dams (Schaller et al. 1999; Deriso 2001). Both of these analyses were based on spawner (parent) and recruit (progeny) data, which provide information about the overall survival of a salmon stock. However, in addition to considering the overall patterns, it is important to consider survival through specific life stages in order to identify which life stages are limiting the survival and recovery of a threatened population. For the Snake River, the National Marine Fisheries Service recently suggested that hydrosystem impacts might be mitigated through habitat improvements in combination with other nonhydro changes (i.e., offsite mitigation) (National Marine Fisheries Service 2000). These potential habitat improvements would hypothetically increase productivity and survival rates during the freshwater life stage occurring between spawning and the beginning of smolt migration to the ocean. However, if the proposed management actions do not address limiting factors, the populations will continue to face high extinction risk and will have a low chance of recovery.

If the pattern of decline for Snake River spring and summer chinook is largely due to the degradation of habitat conditions, we would expect to see a decrease in productivity and survival rate at the freshwater life stage. The parent–progeny approach used here (i.e., analysis of spawner and smolt patterns) evaluates whether productivity and survival rates changed in the freshwater stage for the aggregate Snake River spring and summer chinook population since the 1960s. In addition, we then evaluated whether the effects of habitat degradation or other influences early in the life cycle (e.g., hatchery effects) since the 1960s could explain a change in productivity and survival at the freshwater life stage. A broad mix of land use influence, from minor (wilderness) to management for irrigated agriculture, livestock grazing, logging, and mining, existed throughout the time series (Fulton 1968; Beamesderfer et al. 1997). However, a majority of the land use impacts in many Snake River drainages occurred prior to the time period of lower Snake River dam construction and completion (Thompson and Haas 1960; Fulton 1968). A decrease in freshwater spawning and rearing (FSR) productivity and survival rate after completion of the hydrosystem might be considered evidence for an overall decrease in habitat quality, or simply the occurrence of unfavorable environmental conditions (e.g., drought) during this life stage, negative effects of hatchery fish (e.g., competition), or depensatory survival mechanisms (Dennis 1989) expected at the low observed spawner levels.

In this paper, we present a temporal comparison of FSR productivity and survival rate patterns from the aggregate run of naturally spawning Snake River spring and summer chinook, brood years 1962–1997. Spawner (parent) and smolt (progeny) estimates are used to evaluate whether there has been a net decrease in FSR productivity and survival rate during the FSR stage for Snake River spring and summer chinook. We also evaluate whether a decrease, if detected, could be associated with a temporal change in habitat conditions across the landscape of stocks. Finally, we attempt to determine if a change in freshwater productivity and survival rates could explain the corresponding decline in adult productivity and survival rates (over the life cycle) observed since completion of the hydrosystem.

Methods

Estimates of FSR survival were based on counts of returning spawners and smolts at the uppermost dam (Fig. 1). Counts and estimates of freshwater survival were for the aggregate of naturally spawning Snake River spring and summer chinook including stocks from streams in Idaho and Oregon, upriver from Lower Granite Dam. Spawning takes place primarily in August through September. The eggs are deposited and fertilized by spawning adults, the embryos incubate within the gravel substrate and then hatch, and the fry emerge into the freshwater habitat. The juvenile fish rear in headwater streams (stream-type chinook), producing yearling smolts, which migrate seaward in the spring (primarily April and May) nearly 2 years after egg deposition.

Returning adult spawners migrate through the eight hydroelectric dams on the lower Columbia River and Snake River and are counted at each dam during passage at ladders. Counts at the uppermost dam (Lower Granite Dam since 1975) provide estimates of the number of adults returning to spawn in the Snake River each year. Similarly, smolts are counted at Lower Granite Dam during their downstream migration. The number of smolts from each parent brood of spawners that survives to Lower Granite Dam provides a measure of survival and productivity in upstream spawning and rearing areas (smolts per spawner) (Fig. 1). The aggregate population of spring and summer chinook counted at Lower Granite Dam includes stocks that spawn in streams from a broad mix of habitat conditions ranging from wilderness areas (Minam River, Oregon, and Sulphur Creek, Idaho) to heavily impacted areas (Poverty Flat and Bear Valley Creek, Idaho) (Fulton 1968; Quigley et al. 1999; Schaller et al. 1999).

Freshwater spawning and rearing life stage

We define FSR productivity, for a specified time period, as the natural log of the ratio of smolts per spawner at very low abundance of spawners (i.e., in the absence of density-dependent mortality) (Schaller et al. 1999). In addition, survival rate indices for the FSR stage provide a time series of density-independent survival estimates through deviations of observed ln(smolts/spawner) at a spawner level from that predicted by the fitted parent–progeny (Ricker spawner–recruitment) function for a specified time period (Schaller et al. 1999).

Wild spawner (parent) estimates

In this evaluation, spawners were defined as adult spring and summer chinook counted at the uppermost Snake River dam. Spawners included wild- and hatchery-origin fish spawning in tributaries. The uppermost dam changed during this era as new projects were added: Ice Harbor in 1961, Lower Monumental in 1969, Little Goose in 1970, and Lower Granite in 1975 (Fig. 1).

Dam counts used to derive spawner (S) estimates included data for brood years 1962–1997. The dam counts are total numbers of adult (ages 4–5) spring and summer chinook for wild- and hatchery-origin adults combined. The wild component of S (S_w) was estimated by subtracting tributary harvest of wild fish and the total hatchery run size from the combined wild and hatchery dam count:

$$(1) \qquad S_w = U_{count} - W_{har} - \frac{R_{rtn} + H_{har}}{S_{ps}}$$

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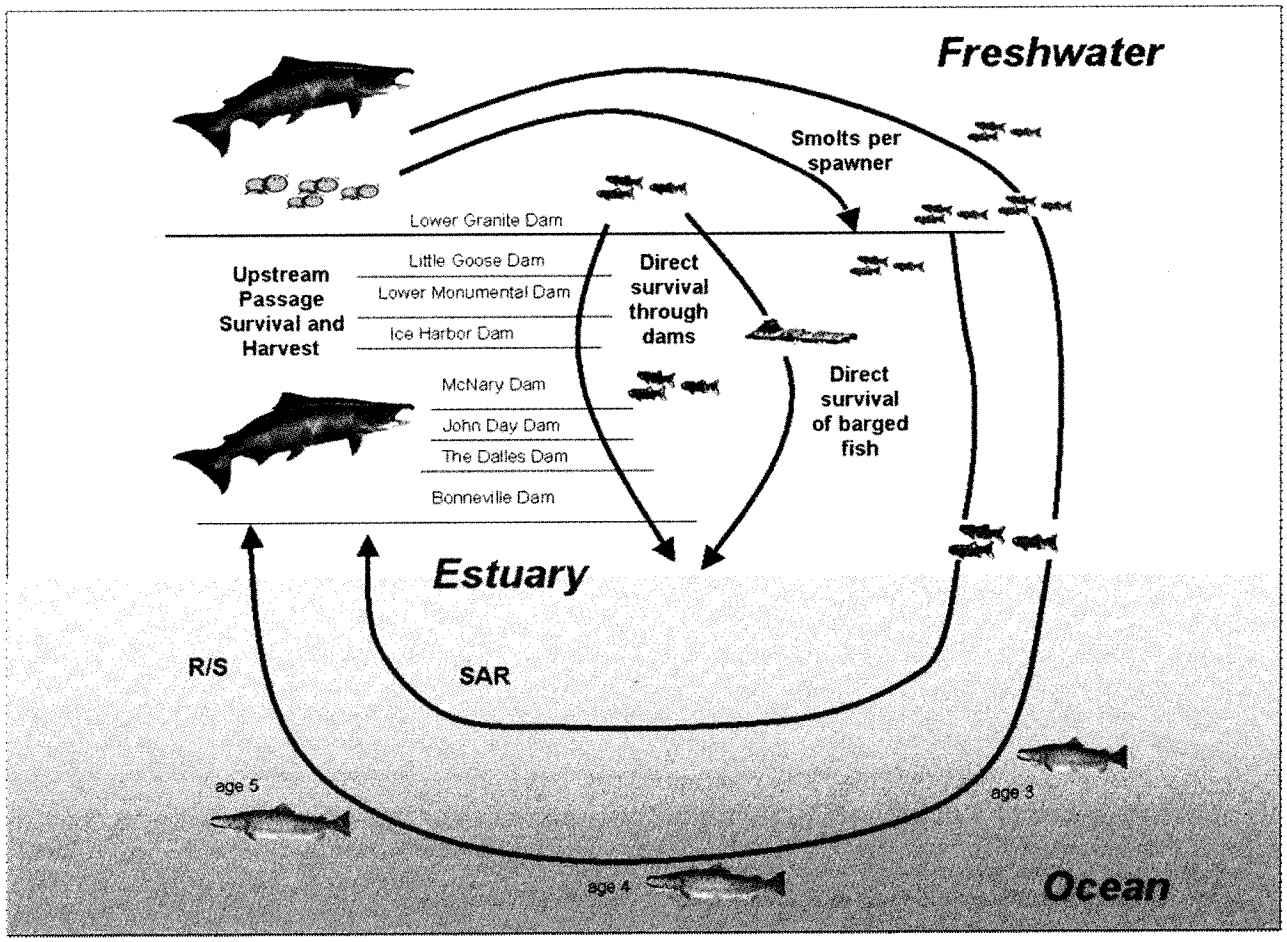
Fig. 1. Schematic life cycle diagram for Snake River salmon and steelhead showing passage past the dams and the different indices of survival across different life stages. Smolts per spawner provides an estimate of FSR survival, SAR is the survival rate of smolts to returning adults (smolt-to-adult), measured at the Columbia River mouth, and *R/S* is recruits per spawner, measured by back-calculating recruits (progeny) from spawners (parents) based on redd counts, age structure, and harvest.



where U_{count} is the total (wild and hatchery) adult spring and summer chinook count at the uppermost dam in the Snake River, R_{rtn} is the adult hatchery fish return to hatcheries for spring and summer chinook above the uppermost dam in the Snake River, W_{har} is harvest of adult wild spring and summer chinook above the uppermost dam in the Snake River, H_{har} is harvest of adult hatchery spring and summer chinook above the uppermost dam in the Snake River, and S_{ps} is prespawning survival rate (=0.8).

Columbia River management agencies provided estimates of W_{har}, R_{rtn}, and H_{har} each year since 1979 and assumed that S_{ps} was 0.8 for hatchery fish (Washington Department of Fish and Wildlife and Oregon Department of Fish and Wildlife 1999). We estimated S_w for the earlier brood years, 1962–1978, using similar methods. Snake River sport harvest estimates for the earlier brood years were based on Beamesderfer et al. (1997).

The number of wild smolts estimated at the uppermost dam included progeny of tributary-spawning hatchery adults and, in some years, unmarked hatchery presmolts released into tributaries. Therefore, total spawner estimates (S) included the total number of hatchery adults released for natural spawning and the hatchery adults that contributed to the unmarked presmolt releases:

$$(2) \qquad S = S_w + \frac{(H_a + H_p)}{S_{ps}}$$

where H_a is the number of hatchery adults released into streams to spawn naturally, H_p is the number of hatchery adults contributing to the unmarked presmolt release, and S_{ps} is prespawning survival rate (=0.8).

Numbers of hatchery adults contributing to the unmarked presmolt releases (H_p) were estimated based on hatchery-specific average fecundity, a 1:1 sex ratio at spawning, and 0.9 survival rate from egg to presmolt release (Kiefer et al. 1991; Olsen et al. 1991; D. Cannamela, Idaho Department of Fish and Game, Boise, Idaho, personal communication). Unmarked hatchery-origin smolts contributed a small proportion (<10%) to the wild smolt estimate before brood year 1990. In recent brood years, 1990–1997, H_p was zero because the released presmolts were marked (or otherwise identified) and counted in the hatchery smolt estimate rather than in the wild smolt estimate. The survival rate of released hatchery chinook fry to the parr stage was comparable with that of wild chinook (15%) for selected Idaho streams (Scully et al. 1990); the H_p estimate is based on an assumption that parr-to-smolt survival is also comparable between hatchery and wild fish. Numbers of hatchery adults (H_a) and adults contributing to unmarked presmolt releases (H_p) are shown in Table 1.

Wild smolt (progeny) estimates

Numbers of wild spring and summer chinook smolts are also estimated at the uppermost dam (Fig. 1). However, in contrast with the adult spawner time series, there is not one continuous time series of estimates for wild smolt numbers. Therefore, we relied on

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two sets of smolt data that encompass different segments of time. Estimates of wild smolts were available for smolt years 1964–1984 (brood year + 2) from marking studies described in Raymond (1979, 1988). There was no way to estimate wild smolts for smolt years 1985–1991, and consequently, those years could not be included in this analysis. Estimates of wild smolts for smolt years 1992–1999 were available based on fish passage indices from the Fish Passage Center (1999).

Raymond (1979, 1988) estimated numbers of wild stream-type chinook smolts arriving at the uppermost dam, 1964–1984, using marked groups and estimates of collection efficiency at the dam. Raymond (1979) derived the proportions of wild and hatchery smolts from survival rate calculations on wild fish marked and released in the Salmon River, Idaho, and hatchery fish marked and released from Rapid River Hatchery on the Salmon River (the only hatchery releasing substantial numbers in these years). Raymond (1988) updated his earlier published estimates of numbers of wild and hatchery stream-type chinook smolts arriving at Lower Granite Dam using the same methods as in the 1979 paper. The number of hatchery smolts each year was derived from the total numbers released and their 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 smolts each year. For most years, Raymond (1988) concluded that sufficient numbers of marked hatchery smolts were recovered for survival rate calculations. 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, Idaho Department of Fish and Game, Boise, Idaho, personal communication) indicated no marking at this facility in smolt migration years 1976, 1978, and 1981.

Recent year (1992–1999) estimates of wild stream-type chinook smolts were derived from fish passage indices, which were calculated from smolt sampling programs at the uppermost dam (Fish Passage Center 1999). Wild smolts were identified at Lower Granite Dam by examination of fin clips in 1993–1999 (all hatchery fish were marked with adipose clips, ventral clips, and (or) tags) 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 at the dam by the proportion of flow passing through the sampled unit or powerhouse relative to river flow (Fish Passage Center 1999). There are four possible routes past the dams: (1) through turbines, (2) over the spillway, (3) guided by screens from turbine intakes, collected, and bypassed back to the river, or (4) guided, collected, and then transported in barges or trucks. Sampling programs enumerate smolts passing by routes 3 and 4. However, estimates of total smolts require estimates of the proportion of smolts guided away from the turbines (fish guidance efficiency (FGE)) and proportion of smolts passing via spill in relation to the proportion of river flow being spilled (spill efficiency). The daily passage indices account for daily changes in spill proportion under the assumption that the proportion of fish passing through spill will be close to the proportion of water being spilled (Fish Passage Center 1999) and do not account for the proportion of fish passing through turbines. We accounted for the total number of smolts passing through the dam by dividing the daily fish passage indices by an estimated FGE of 0.55 (Marmorek et al. 1998).

Annual productivity (ln(smolts/spawner))

The annual estimates for wild smolts and wild spawners were used to compute an annual freshwater productivity, expressed as ln(smolts/spawner). This is an annual productivity measured at the FSR life stage for the observed spawner numbers. We investigated evidence for density dependence in the relationship of ln(smolts/spawner) versus spawner by linear regression for the full time series of data and by analysis of covariance (ANCOVA) with spawner as the covariate and time period as the treatment (see below).

Smolt-to-adult return rates

Smolt-to-adult return rate (SAR) provides a measure of overall survival from the outmigrating smolt stage (after the FSR stage) to the returning adult recruit stage (Fig. 1). SARs were estimated for the aggregate population of Snake River wild spring and summer chinook, brood years 1962–1994. SAR was calculated as the total number of recruits (age 3 jacks, which are precocious males, and age 4–5 adults) returning to the Columbia River mouth by brood year divided by number of smolts from that brood arriving at the uppermost dam on the Snake River (Lower Granite Dam since 1975). We estimated SAR to the Columbia River mouth because that measure is consistent with the definition from the data set for adult survival rate indices (SRI-1; Schaller et al. 1999). We also updated the adult survival rate indices for brood years 1991–1994.

We estimated the number of wild adult recruits at the Columbia River mouth (Fig. 1) in order to have a consistent measure that accounts for variable harvest rates and adult upstream passage survival rates (Appendix). First, using the wild component of the uppermost dam count for return years 1962–1999 ($S_w + W_{har}$ from eq. 1 above), we partitioned the total counts by age (Beamesderfer et al. 1997; C.E. Petrosky, unpublished data). Because recruits should include all fish (ages 3–5) and adult returns from dam counts represented age 4–5 fish only, we increased the adult returns to include the age 3 fish (jacks). In the next step, we calculated returns by age to the Columbia River mouth by dividing the age-structured return to the upper dam by the annual upstream passage survival rate and then dividing by the annual survival rate through the main stem fisheries (Beamesderfer et al. 1997). In the final step, we allocated the age-structured returns to the Columbia River mouth to the appropriate smolt year (brood year + 2). We used the natural log transformation of SAR in analyses (Peterman 1981).

Productivity and survival rate analysis

We compared spawners, smolts, ln(smolts/spawner), and ln(SAR) before and after the completion of the hydrosystem using analysis of variance (ANOVA). Periods were defined as brood years 1962–1974 for Period 1 and brood years 1975–1997 for Period 2, where data were available.

Productivity and survival rate indices at the FSR life stage were estimated for the two periods for the Snake River spring and summer chinook aggregate population. Productivity is defined here as the natural log of the ratio of progeny (smolts) to parents (spawners) in the absence of density-dependent mortality. Spawner and smolt data, at the FSR life stage, can be fit to the Ricker (1975) parent–progeny function

$$(3) \qquad R_{\text{smolts}} = e^{a} S e^{-\beta S}$$

where R_{smolts} is smolts measured at the uppermost dam and S is spawners. The a and β parameters are estimated by the log transformation of eq. 1, and productivity is measured as the intercept, or Ricker a.

Parent–progeny analysis normally assumes that the average parent–progeny relationship does not change over time. Often the parent–progeny curve will indeed change (nonstationarity) due to physical change in the environment or change in stock structure (Walters 1987; Hilborn and Walters 1992). We tested for evidence of nonstationarity in the parent–progeny functions caused by physical change in the FSR habitat or other influence early in the life cycle. Large changes in density-independent mortality (caused by change in the FSR stage physical environment) within a time series would cause nonstationary behavior in the parent–progeny function. We used two methods, suggested by Walters (1987), to detect

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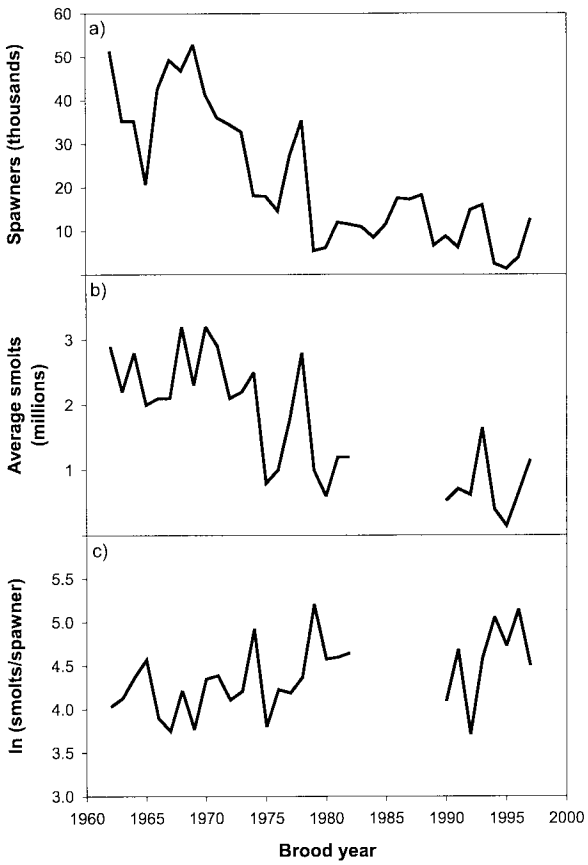
Fig. 2. (*a*) Spawners, (*b*) average smolts, and (*c*) annual FSR productivity (ln(smolts/spawner)) for brood years 1962–1997.



if a systematic change in the parent–progeny relationships took place associated with a change in the physical environment: (*i*) covariance analysis of data in time blocks associated with the physical change and (*ii*) evaluation of time series of parent–progeny model deviations.

We evaluated whether productivity declined for the aggregate Snake River population from Period 1 to Period 2 at the FSR life stage. We used ANCOVA to examine differences between the two periods for the intercept (Ricker a value) of the relationship of $\ln(R_{\text{smolts}}/S)$ versus S. Then, we contrasted change in FSR productivity with productivity change estimated over the entire life cycle (adult recruits/spawner) (Schaller et al. 1999) to determine if the change at the FSR life stage could explain the overall productivity change:

$$(4) \qquad \ln(R_{\text{smolts}_{i,j}}/S_{i,j}) = \tau_i + a - \beta(S_{i,j} - \bar{S}_{..}) + \varepsilon_{i,j}$$

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

The assumption of homogeneity of slopes was first tested based on significant interaction between treatment (period) and the covariate (spawners). Then ANCOVA was run to estimate the period effect on $\ln(R_{\text{smolts}}/S)$, taking into account spawning level (covariate). The measure of productivity by period was estimated using $\tau_i + a$ from the ANCOVA results (eq. 4). This is equivalent to the Ricker a parameter by period assuming a common slope (β) over periods. The ANCOVA also tests for density dependence as indicated by a significant negative slope for the relationship between smolts per spawner and spawners. Tests were conducted at the $\alpha = 0.05$ level.

Survival rate indices provide a time series of density-independent survival estimates through deviations of observed $R_{\text{progeny}}/S_{\text{parent}}$ from those predicted by the fitted parent–progeny function for a specified time period. The deviations, or survival rate indices at the FSR life stage, were expressed as ln[(observed R_{smolts}/S)/(predicted R_{smolts}/S)], where predicted values were based on fits to data from different time periods. The natural log of these ratios transform the differences, such that they tend to be normally distributed (Peterman 1981). This approach, using the residuals as an index of FSR survival rate, was used to be consistent with the method used by Schaller et al. (1999) for measuring survival over the entire life cycle and is similar to the approaches in Hilborn and Walters (1992, fig. 7.2.1), Myers et al. (1997), and Peterman et al. (1998). The FSR survival rate index represented the deviation of the Period 2 observations from Period 1 predicted values based on the ANCOVA fit of eq. 4. We evaluated if there was a change in FSR survival rate index between Period 1 and Period 2 using ANOVA and contrasted the time series of survival rates at the FSR stage with those for the entire life cycle.

We investigated the power and effect sizes for the ANCOVA tests of significance for the period effect on FSR productivity. Peterman (1990) noted that in fisheries applications, a large cost could be associated with falsely assuming that there is no effect (type II error) and argued the need to use information on power and minimum detectable differences. It is possible that a real difference in FSR productivity may exist, but no significant difference would be found because of large variability or small sample size. From a management perspective, our interest was threefold. First, how likely were we to detect a true difference in the FSR productivity at the magnitude estimated from the smolt/spawner analysis? Second, what magnitude of change in the FSR productivity would have been necessary in order to have sufficient power to measure the change, given the data? Finally, if we observed a change in FSR productivity similar to the change of the magnitude exhibited over the entire life cycle (Schaller et al. 1999), would there be sufficient power to be confident that we detected a true change at the FSR stage?

The power of the ANCOVA was estimated using the SAS power macro (Latour 2000) as

$$(5) \qquad \text{Power} = 1 - F\{F_{\text{crit}}, \text{df}_{\text{hyp}}, n - \text{df}_{\text{mod}} - 1, \lambda\}$$

and delta, the effect size, is

$$(6) \qquad \delta^2 = \frac{\text{SS}_{\text{hyp}}}{n}$$

where

$$(7) \qquad \lambda = \frac{n\delta^2}{\sigma^2} = \frac{\text{SS}_{\text{hyp}}}{\sigma^2} \approx \frac{\text{SS}_{\text{hyp}}}{\text{MSE}}.$$

We first estimated the power of the period effect for ANCOVA for FSR productivity and used that data set, with its associated variance and sample size, to generate a relationship between power and the difference in period effects between Period 1 and Period 2 ($\tau_1 - \tau_2$) for FSR productivity. The $\tau_1 - \tau_2$ can then be converted directly to the change in productivity for smolts per spawner ($=1 - e^{-(\tau_1 - \tau_2)}$). We then compared the change in overall productivity estimated from the adult recruits/spawner versus spawner in Schaller et al. (1999) with the change in FSR productivity from this data set. This comparison allowed us to determine how much power we would have had for detecting the difference in overall productivity between periods (e.g., before and after the hydrosystem). The sensitivity of the productivity analyses to alternative estimates for smolts (using the PATH set of parameter val-

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Table 1. Snake River spring and summer chinook dam counts (U_{count}), hatchery returns (R_{rtn}), wild and hatchery harvest, wild spawners (S_w), hatchery adults released for spawning (H_a), hatchery adults used in presmolt releases (H_p), and total spawners (S).

Brood year	Upper dam U_{count}	R_{rtn}	Upper dam wild	Proportion wild in harvest	Harvest wild plus hatchery	S_w	H_a	H_p	S
1962	64 252		64 252	1.00	12 816	51 436			51 436
1963	47 653		47 653	1.00	12 390	35 263			35 263
1964	44 700	763	43 746	1.00	8 465	35 281			35 281
1965	21 900	649	21 089	1.00	414	20 675			20 675
1966	54 500	1 789	52 264	1.00	9 744	42 520			42 520
1967	57 700	1 083	56 143	0.98	7 057	49 249			49 249
1968	63 000	4 390	57 125	0.97	10 599	46 836			46 836
1969	68 300	2 817	64 089	0.95	12 198	52 443	324	12	52 863
1970	54 400	6 476	45 734	0.92	5 803	40 388	358	438	41 383
1971	43 200	3 357	38 308	0.85	3 657	35 208	119	533	36 023
1972	57 100	12 310	38 073	0.56	6 667	34 318	152		34 508
1973	63 700	17 099	38 788	0.71	9 859	31 760	369	428	32 756
1974	23 100	3 494	18 344	0.79	1 500	17 155	67	721	18 140
1975	23 700	4 739	17 776	0.00		17 776		167	17 985
1976	22 900	6 734	14 483	0.00		14 483		106	14 615
1977	43 900	10 460	29 128	0.61	3 500	26 986	24	238	27 313
1978	52 300	7 735	40 978	0.81	7 000	35 301		124	35 455
1979	9 551	3 438	5 253	0.00		5 253	32	153	5 484
1980	8 148	1 612	6 133	0.00		6 133	33		6 174
1981	16 441	4 162	11 238	1.00	49	11 189	661		12 016
1982	16 577	4 228	11 292	1.00	26	11 266	144	53	11 512
1983	13 402	2 749	9 965	1.00	31	9 934	271	544	10 953
1984	11 921	3 413	7 654	0.00		7 654	568	105	8 495
1985	30 269	12 942	8 822	0.00	4 216	8 822	1 104	1032	11 492
1986	37 876	17 985	11 288	0.00	3 287	11 286	4 319	689	17 546
1987	34 726	15 909	10 969	0.01	3 132	10 933	3 610	1450	17 258
1988	35 640	14 676	11 540	0.01	4 638	11 506	3 575	1832	18 264
1989	16 124	7 513	5 548	0.02	964	5 532	917	21	6 704
1990	22 408	9 812	6 926	0.01	2 591	6 909	1 475	31	8 791
1991	10 432	4 018	5 407	0.33	3	5 406	598	59	6 227
1992	24 405	8 927	11 465	0.02	1 458	11 432	2 452	274	14 839
1993	28 924	13 110	10 824	0.07	1 468	10 726	3 414	757	15 940
1994	3 915	1 749	1 721	0.25	8	1 719	595		2 463
1995	1 799	510	1 162	1.00	2	1 160	113		1 301
1996	6 823	2 685	3 474	0.00	40	3 474	367		3 932
1997	44 563	22 710	7 559	0.00	7 049	7 551	4 255		12 870
1998	14 242	3 566	8 337	0.05	1 263	8 269			8 269
1999	6 743	2 623	3 432	0.00	133	3 432			3 432
Average	31 611	6 375	22 315	0.47	3 738	19 649	787	257	20 954
Minimum	1 799		1 162	0.00		1 160			1 301
Maximum	68 300	22 710	64 252	1.00	12 816	52 443	4 319	1832	52 863

ues for FGE and spill efficiency) and adults (using wild-origin spawners, S_w) was evaluated.

Results

Wild spawner estimates

The estimated number of spring and summer chinook spawners (S) averaged 20 954 (range 1301 – 52 863) for brood years 1962–1999 (Fig. 2*a*; Table 1). Wild-origin adults (S_w) made up from 59 to 100% of the spawners. Spawner numbers dropped steadily in the early 1970s and remained at low levels through the most recent years (Fig. 2*a*). Spawners in Period 2, after the completion of the hydrosystem, were significantly lower than those in Period 1, before the completion of the hydrosystem (F = 67.53, P = 0.0001).

Wild smolt estimates

Wild smolt estimates at the upper dam averaged 1 680 000 for the time series with a range of 147 000 – 3 200 000 (Table 2; Fig. 2*b*). Smolt numbers demonstrated a period of high variability in the 1970s followed by very low numbers in the early 1980s and recent years. Similar to spawner estimates, smolt numbers were significantly lower in the period after the development of the hydrosystem was completed

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Table 2. Estimated number of wild chinook smolts passing the uppermost dam, smolts per spawner, and ln(smolts/spawner).

Brood year	Smolt year	Wild smolts	Smolts per spawner	ln(smolts/spawner)
1962	1964	2 900 000	56	4.03
1963	1965	2 200 000	62	4.13
1964	1966	2 800 000	79	4.37
1965	1967	2 000 000	97	4.57
1966	1968	2 100 000	49	3.90
1967	1969	2 100 000	43	3.75
1968	1970	3 200 000	68	4.22
1969	1971	2 300 000	44	3.77
1970	1972	3 200 000	77	4.35
1971	1973	2 900 000	81	4.39
1972	1974	2 100 000	61	4.11
1973	1975	2 200 000	67	4.21
1974	1976	2 500 000	138	4.93
1975	1977	800 000	44	3.80
1976	1978	1 000 000	68	4.23
1977	1979	1 800 000	66	4.19
1978	1980	2 800 000	79	4.37
1979	1981	1 000 000	182	5.21
1980	1982	600 000	97	4.58
1981	1983	1 200 000	100	4.60
1982	1984	1 200 000	104	4.65
1983	1985	na	na	na
1984	1986	na	na	na
1985	1987	na	na	na
1986	1988	na	na	na
1987	1989	na	na	na
1988	1990	na	na	na
1989	1991	na	na	na
1990	1992	527 424	60	4.09
1991	1993	680 793	109	4.69
1992	1994	604 313	41	3.71
1993	1995	1 577 215	99	4.59
1994	1996	389 376	158	5.06
1995	1997	146 873	113	4.73
1996	1998	680 989	173	5.15
1997	1999	1 156 931	90	4.50
Average		1 678 066	86	4.38
Range		146 873 – 3 020 000	41–182	(3.71–5.21)

(F = 23.44, P = 0.0001), although no data were available for a few years in Period 2.

Annual productivity

Snake River spring and summer chinook produced an average of 86 smolts per spawner for the time series (Table 2). The ln(smolts/spawner) estimates averaged 4.38 (Table 2). Annual FSR productivity, ln(smolts/spawner), showed a weak (insignificant) increasing trend through the time series (Fig. 2*c*) (F = 4.18, P = 0.0508). The increasing trend in ln(smolts/spawner) combined with a decreasing trend in spawner numbers (Figs. 2*a* and 2*c*) is consistent with density dependence in the FSR life stage. Regression of ln(smolts/spawner) versus spawner for the entire time series (Fig. 3) had a significant negative slope (F = 20.62, P = 0.0001).

Smolt-to-adult return rates

SARs of Snake River wild spring and summer chinook declined sharply after the 1960s. Mean SARs were 5.2% in Period 1 and 1.2% in Period 2 (Fig. 4; Appendix). ln(SAR) values were significantly lower in Period 2 (posthydrosystem) compared with Period 1 (prehydrosystem completion) (F = 12.93, P = 0.0015). The SARs estimated here differ from those reported in Raymond (1988) because we recalculated and updated wild recruits and incorporated adult upstream passage survival (which was not incorporated in Raymond's (1988) SAR estimates; Fig. 1). The pattern of declining SARs after the completion of the hydrosystem, however, is the same for both estimates.

Survival of smolts entering the hydrosystem to adults returning to the Columbia River mouth (SAR) demonstrated a major decline (Fig. 4). This decline was not observed in the annual pattern of smolts per spawner through the FSR life stage. Whereas ln(SAR) declined from –3.5 to –4.5 from Period 1 to Period 2, ln(smolts/spawner) increased slightly from 4.2 to 4.5. The relationship between smolts and spawn-

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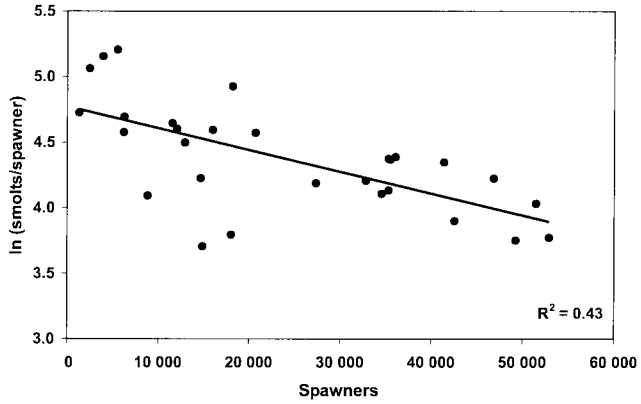
Fig. 3. Relationship between annual FSR productivity (ln(smolts/spawner)) and spawners (S) for the time series of brood years 1962–1997.



ers exhibited density dependence (Fig. 3). Hence, we would expect ln(smolts/spawner) to increase as spawner numbers decreased, if average FSR conditions had indeed remained stationary through the time series.

Productivity and survival rate analysis

The FSR productivity showed no significant decline since completion of the hydropower system. The period effect was not significant in the ANCOVA tests (P = 0.058); however, the point estimate for the period effect suggested a decrease in FSR productivity of –0.37 (insignificant). Results were also insensitive to alternative PATH parameter values of FGE and spill efficiency used for smolt estimates (Marmorek et al. 1998) and to the use of only wild-origin spawners (S_w) in the ANCOVA. Period effects were insignificant for all alternative assumptions (P range 0.059–0.154) in this sensitivity analysis.

The ANCOVA test demonstrated a strong pattern of density dependence (decreasing smolts per spawner at high spawner levels), as demonstrated by the slope parameter (β) in the ANCOVA. The slope was negative and highly significant (β = –0.000026, P = 0.0001). The assumption of a common slope between time periods (homogeneity of β) was plausible based on an insignificant test (P = 0.96) for interaction of period effect (treatment) and spawners (covariate).

We compared an overall survival rate index (updated SRI-1 from Schaller et al. 1999), which represents deviations in survival rate across the salmon life cycle, with the FSR survival rate index, which represents deviations in survival rate for the egg-to-smolt FSR stage alone. The overall survival rate index across the life cycle showed a steep decline that was significantly lower after the completion of the hydrosystem as compared with before the hydrosystem was completed (Fig. 5) (F = 9.87, P = 0.0042). The pattern of this overall survival rate index also indicated greater variability in Period 2 (Schaller et al. 1999). In contrast, the pattern from the FSR index showed less of a downward trend through time and was considerably less variable in Period 2 compared with the overall survival rate index (Fig. 5). However, there was a significant difference in the FSR survival rate index between the two periods, before and after the completion of the hydrosystem (F = 10.84, P = 0.0029). For the FSR index, three of the largest negative residuals (poor survival) occurred in Period 2 and were associated with major drought years during the year of smolt migration (1977, 1992, and 1994). Overall survival based on the survival rate index was also very low following smolt years 1977 and 1992.

The change in productivity measured by τ represents the average change in density-independent survival rates between periods. Power analysis indicates that most of the productivity decline, from period 1 to period 2, over the entire life cycle cannot be explained by decreases in FSR productivity but that comparatively small changes cannot be ruled out. The FSR productivity showed no significant decline since completion of the hydrosystem; however, the power to detect a true difference of this magnitude was moderately low (power = 0.47) (Fig. 6). This power estimate corresponds to a change in period effect ($\tau_1 - \tau_2$) of 0.37 or a drop in productivity of 31% ($1 - e^{-(\tau_1 - \tau_2)}$ = 0.31). However, for this data set, if we had observed a change in period effect of 0.7 or greater, or a drop in productivity of 50% or greater, we would have had >80% power to detect a change, given the observed variance and sample size in the FSR data set. In contrast with the FSR stage, overall productivity for adult recruits/spawner dropped by 86% averaged across the seven indicator stocks ($\tau_1 - \tau_2$ = 1.96; see Schaller et al. 1999). That magnitude of change would have resulted in almost 100% power to detect a change, or period effect, in the FSR data set (Fig. 6). This comparison indicates that if the FSR productivity had declined by 86%, as observed for adult recruit/spawner, we would have had very high power to detect that type of change in the FSR life stage.

Discussion

Snake River stream-type chinook have declined dramatically since completion of the hydrosystem and have been listed as threatened under the Endangered Species Act since 1992. Declines in life cycle productivity and survival rates for Snake River stocks were greater than for similar stocks, which migrate past fewer dams (Schaller et al. 1999). In this paper, we tested the hypothesis that a decline in productivity and survival rate in the FSR stage since completion of the hydrosystem was at a magnitude that might explain the declines observed over the entire life cycle.

We found little to no empirical support for a marked decline in FSR productivity and survival rate since completion of the hydrosystem of the magnitude observed over the entire life cycle (Schaller et al. 1999). However, we cannot rule out comparatively minor decreases in FSR productivity and survival rate since the hydrosystem was completed. Estimated change in FSR productivity between pre- and post-hydrosystem completion was insignificant and small compared with the overall productivity decline. FSR productivity and survival rate change was insensitive to uncertainty in the smolt and spawner estimates. We found strong evidence for density dependence at the FSR stage consistent with observations of density dependence over the entire life cycle (Schaller et al. 1999).

Power was moderately low for detecting change of the estimated magnitude for FSR productivity but clearly would be sufficient to detect the magnitude of change observed over the entire life cycle, had the overall decline occurred

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Fig. 4. SAR (bars) and smolts per spawner (line) for those years in the time series where data were available. The SAR describes survival during mainstem downstream migration back to returning adults, whereas the number of smolts per spawner describes freshwater productivity in upstream FSR areas.

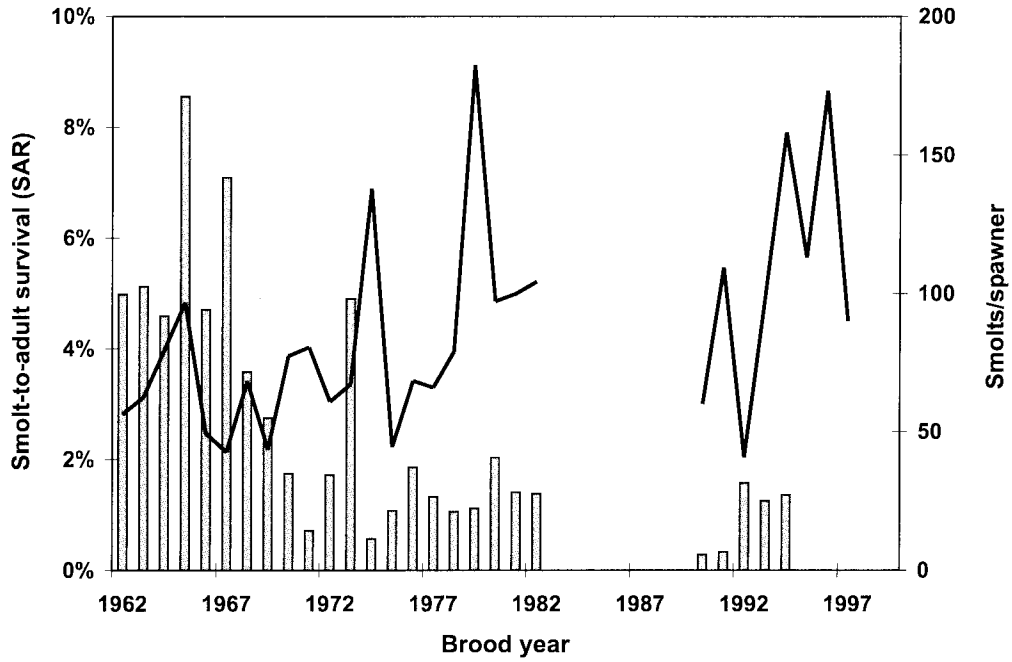
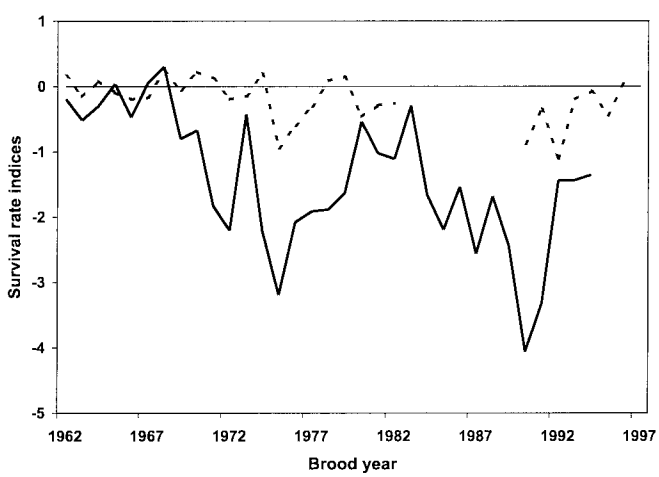


Fig. 5. Survival rate indices calculated over the entire life cycle from adult spawner and recruit data (solid line) and from the FSR stage (broken line). The overall survival rate index (updated SRI-1 from Schaller et al. 1999) represents deviations in survival rate across the salmon life cycle. The FSR survival rate index (ln(smolts/spawner)) represents deviations in survival rate for the egg-to-smolt FSR stage alone.



primarily in the FSR stage. In order to have a statistically significant result for change in FSR productivity between periods, we would have needed to observe a drop of 50% in smolts per spawner (at low spawner density). In comparison, productivity estimated from adult recruit/spawner information declined 86% over the same period. Although we could not rule out small changes in FSR productivity and observed small changes in FSR survival rates relative to the overall decline, this relatively small decrease is not trivial (approximately 30% in smolts per spawner and in survival rate). The decrease was presumably due to some combination of FSR habitat change, drought, or other climate condition, hatchery effect, or depensatory mechanism affecting the aggregate population.

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 minor (wilderness) to management for irrigated agriculture, livestock grazing, logging, and mining, existed throughout the time series (Fulton 1968; Beamesderfer et al. 1997). Negative trends in habitat condition (quality pools) are evident in several managed watersheds, whereas streams in 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 productivity and survival rate of individual populations would be expected to track with these localized trends, the aggregate data provide no evidence for a major shift in the FSR stage since completion of the hydrosystem. However, this analysis did not address whether there was a significant decline in FSR productivity and survival rate prior to the completion of the hydrosystem because the smolt and spawner data were not collected prior to the 1960s.

In contrast with the relative stationarity in FSR productivity and survival rates since hydrosystem completion, significant survival decreases were evident in the smolt-to-adult

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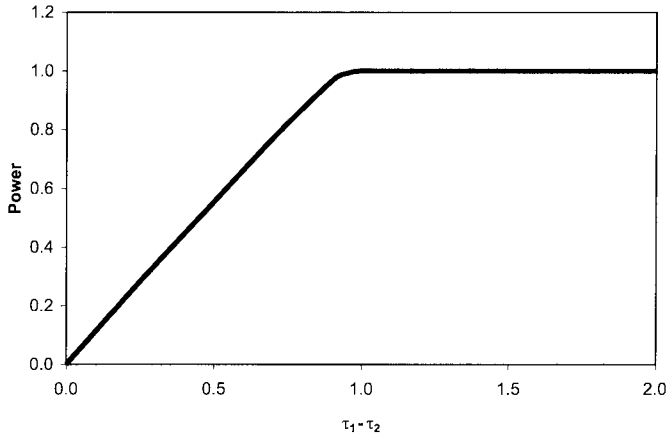
Fig. 6. Relationship between statistical power and the difference in productivity between periods for the ANCOVA ln(smolts/spawner) versus spawner with periods before and after the completion of the hydrosystem (Period 1, 1962–1974; Period 2, 1975–1997).



life stage. This life stage includes most of the life cycle except for the FSR stage, from the time shortly after smolts enter the hydrosystem to adults returning to the Columbia River mouth. The magnitude of change in ln(SAR) (–1.0, a 63% drop in survival rate) could explain most of the drop in productivity estimated for the entire life cycle (Schaller et al. 1999). Decreases in SAR are most likely due to factors outside the FSR life stage, such as degradation of migratory habitat through construction and operation of the hydrosystem, increased hatchery production, and changing estuary and ocean conditions.

Schaller et al. (1999) concluded that factors other than hydropower development have not played a significant role in the differential decline in performance between upriver and downriver stocks. The Snake River stocks above eight dams survived one third as well as downriver stocks migrating through three dams (Schaller et al. 1999; Deriso 2001) for this time period, after taking into account factors common to both groups. The additional decline in productivity of upriver stocks relative to downriver stocks indicates that this portion of the mortality is related to factors unique to upriver stocks. Patterns of Pacific Decadal Oscillation and salmon production would indicate that poor ocean conditions existed for Columbia River salmon after the late 1970s (Hare et al. 1999). However, the natural fluctuations in ocean productivity affecting all Columbia River stocks, in combination with mortality as a result of the hydrosystem, appear to have caused the severe declines in productivity and survival rates for the Snake River stocks. Temporal and spatial patterns of hatchery release numbers did not coincide with the differential changes in survival rates between upriver and downriver stocks (Schaller et al. 1999). Harvest rates were drastically reduced, in the early 1970s, in response to declines in upriver stream-type chinook abundance. Given that FSR life stage survival rate changes cannot explain the decreases in SAR or overall survival rates for Snake River stocks, it appears that the altered migration corridor has had a strong influence on the mortality that causes these differences in stock performance.

The analysis discussed here has important management implications for the recovery of Snake River stocks in relation to the decision of whether or not to remove the four lower Snake River dams. Recently, federal agencies have indicated that hydrosystem impacts may be compensated through off-site mitigation measures, which might improve habitat or change hatchery practices (National Marine Fisheries Service 2000). Based on this premise, some federal agencies believe that dam removal will therefore be unnecessary. For off-site mitigation through habitat improvements to offset hydrosystem impacts, life cycle survival rates of these stocks would have to increase nearly threefold overall (Peters and Marmorek 2000). The absence of major declines in FSR productivity and survival rates, combined with significant declines in SAR after hydrosystem completion, indicates that it is unlikely that we will be able to increase overall survival to a level sufficient for recovery based on improvements to FSR habitat. In addition, overall productivity and survival rate declines were common to Snake River index stocks in wilderness areas (Sulphur Creek, Minam River) and those with varying degrees of habitat degradation (Schaller et al. 1999). Past attempts to mitigate for hydrosystem impacts through hatcheries have also failed to recover the natural populations (Lichatowich 1999).

These examples demonstrate the importance of identifying the factor that is limiting the population for management decisions regarding the recovery of an endangered species. For some stocks, improvements to habitat would likely improve survival in the spawning and rearing stage. However, the expected improvements in survival in that life stage are unlikely to offset the impacts of the hydrosystem and increase survival overall to a level that ensures the recovery of Snake River spring and summer chinook.

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Appendix

Table A1. Smolt-to-adult survival rates (SAR) and adult return data required to estimate SAR.

Return year	Age 3 returns	Age 4 returns	Age 5 returns	Upstream passage survival rate	Mainstem harvest rate	Brood year recruits (ages 3–5)	SAR (%)
1962	3969	29 436	34 816	0.61	0.44	144 385	4.98
1963	8704	17 401	30 252	0.62	0.49	112 629	5.12
1964	4246	26 427	17 319	0.59	0.38	128 510	4.59
1965	4320	12 044	9 044	0.43	0.40	171 030	8.55
1966	6789	28 006	24 258	0.63	0.21	98 776	4.70
1967	6543	23 339	32 804	0.68	0.33	148 902	7.09
1968	6296	30 574	26 551	0.73	0.24	114 482	3.58
1969	4790	41 965	22 123	0.49	0.24	63 224	2.75
1970	2836	24 017	21 717	0.65	0.29	55 819	1.74
1971	4500	26 116	12 192	0.50	0.26	20 730	0.71
1972	1519	15 646	22 427	0.46	0.32	36 075	1.72
1973	746	15 461	23 327	0.66	0.32	107 870	4.90
1974	562	9 566	8 778	0.43	0.13	14 277	0.57
1975	152	3 847	13 929	0.49	0.00	8 623	1.08
1976	1230	8 697	5 785	0.51	0.00	18 598	1.86
1977	899	19 082	10 046	0.65	0.17	23 882	1.33
1978	15	3 562	37 416	0.56	0.04	29 511	1.05
1979	401	2 025	3 228	0.57	0.04	11 144	1.11
1980	442	3 868	2 265	0.48	0.04	12 201	2.03
1981	606	6 169	5 070	0.57	0.06	16 946	1.41
1982	628	6 077	5 215	0.50	0.07	16 539	1.38
1983	253	1 965	8 000	0.56	0.06	28 100	na
1984	421	3 927	3 727	0.66	0.06	8 355	na
1985	298	5 046	3 776	0.75	0.06	9 918	na
1986	555	5 098	6 190	0.72	0.06	14 033	na
1987	184	5 715	5 254	0.65	0.07	10 421	na
1988	200	1 687	9 853	0.60	0.09	22 991	na
1989	371	2 786	2 762	0.58	0.05	4 633	na
1990	80	4 045	2 881	0.68	0.06	1 475	0.28
1991	286	1 517	3 890	0.59	0.05	2 276	0.33
1992	346	6 704	4 761	0.66	0.04	9 502	1.57
1993	109	1 696	9 128	0.81	0.05	19 787	1.25
1994	13	332	1 389	0.78	0.05	5 305	1.36
1995	109	621	541	0.64	0.04		
1996	215	2 784	689	0.58	0.04		
1997	136	4 957	2 602	0.63	0.04		
1998	198	1 295	7 042	0.65	0.04		
1999	398	1 866	1 566	0.53	0.03		
Average							2.58
Minimum							0.28
Maximum							8.55

Note: Upstream passage survival rates and mainstem harvest rates are from Beamesderfer et al. (1997).

Appendix reference

Beamesderfer, R.C.P., Schaller, H.A., Zimmerman, M.P., Petrosky, C.E., Langness, O.P., and LaVoy, L. 1997. Spawner–recruit data for spring and summer chinook salmon populations in Idaho, Oregon, and Washington. *In* PATH — Plan for Analyzing and Testing Hypotheses: report of retrospective analysis for fiscal year 1997. *Compiled and edited by* D.R. Marmorek and C. Peters. ESSA Technologies Ltd., Vancouver, B.C.

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