Ecology of Freshwater Fish 2010: 19: 520–536
Printed in Malaysia · All rights reserved

ECOLOGY OF
FRESHWATER FISH

Influence of river conditions during seaward migration and ocean conditions on survival rates of Snake River Chinook salmon and steelhead

Petrosky CE, Schaller HA. Influence of river conditions during seaward migration and ocean conditions on survival rates of Snake River Chinook salmon and steelhead.
Ecology of Freshwater Fish 2010: 19: 520–536. © 2010 John Wiley & Sons A/S

C. E. Petrosky[1], **H. A. Schaller**[2]

[1]Idaho Department of Fish and Game, Boise, ID, USA, [2]Columbia River Fisheries Program Office, US Fish and Wildlife Service, Vancouver, WA, USA

Abstract – Improved understanding of the relative influence of ocean and freshwater factors on survival of at-risk anadromous fish populations is critical to success of conservation and recovery efforts. Abundance and smolt to adult survival rates of Snake River Chinook salmon and steelhead decreased dramatically coincident with construction of hydropower dams in the 1970s. However, separating the influence of ocean and freshwater conditions is difficult because of possible confounding factors. We used long time-series of smolt to adult survival rates for Chinook salmon and steelhead to estimate first year ocean survival rates. We constructed multiple regression models that explained the survival rate patterns using environmental indices for ocean conditions and in-river conditions experienced during seaward migration. Survival rates during the smolt to adult and first year ocean life stages for both species were associated with both ocean and river conditions. Best-fit, simplest models indicate that lower survival rates for Chinook salmon are associated with warmer ocean conditions, reduced upwelling in the spring, and with slower river velocity during the smolt migration or multiple passages through powerhouses at dams. Similarly, lower survival rates for steelhead are associated with warmer ocean conditions, reduced upwelling in the spring, and with slower river velocity and warmer river temperatures. Given projections for warming ocean conditions, a precautionary management approach should focus on improving in-river migration conditions by increasing water velocity, relying on increased spill, or other actions that reduce delay of smolts through the river corridor during their seaward migration.

Key words: seaward migration; hydropower dams; ocean conditions; Chinook salmon; steelhead; marine survival

Charles E. Petrosky, Idaho Department of Fish and Game, 600 S. Walnut Avenue, PO Box 25, Boise, ID 83707, USA; e-mail: charlie.petrosky@idfg.idaho.gov

Accepted for publication March 16, 2010

Introduction

Pacific salmon (*Oncorhynchus* sp.) exhibit complex life histories and variable levels of spawning abundance due to survival rates related to conditions in freshwater and ocean environments. These freshwater and ocean conditions can vary along time scales ranging from a few months to decades (Mantua et al. 1997; Peterson et al. 2006). Lawson (1993) provided a conceptual model illustrating the combined effects of declining habitat quality, cyclic changes in ocean productivity and harvest management on the abundance of Oregon coastal coho salmon (*Oncorhynchus kisutch*). While this concept is generally accepted among fisheries scientists and managers, the relative influences of freshwater and oceanic factors on salmon survival are seldom quantified. Separating the influence of ocean and freshwater factors on salmon survival is difficult, because of possible confounding factors. In addition, long time-series of life-stage-specific demographic data, which would allow such investigation, are lacking for many salmon populations. Increased understanding of these relative influences is important to management, conservation and

doi: 10.1111/j.1600-0633.2010.00425.x

recovery planning for many at-risk anadromous salmon populations along the Pacific coast.

Snake River spring/summer Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) populations declined dramatically in the 1970s coinciding with development and operation of the Federal Columbia River Power System (FCRPS) (Raymond 1988; Schaller et al. 1999). Both species have been listed as threatened under the Endangered Species Act (ESA; spring/summer Chinook in 1992 and steelhead in 1998). One effect of the FCRPS development was to alter drastically the migration habitat, survival and migration timing of juvenile salmon and steelhead (Williams et al. 2001; Budy et al. 2002; Schaller et al. 2007). Mainstem dam construction began in 1938 on the Columbia River with construction of Bonneville Dam. By 1964 four FCRPS dams were in place, with an additional four being added between 1968 and 1975 (Fig. 1). Snake River spring/summer Chinook salmon (hereafter, Chinook) and steelhead (hereafter, steelhead) evolved to migrate seaward in April through early June with the spring freshet (ISG 1999). Juvenile salmon and steelhead migrating to and from Snake River spawning streams must now pass eight large hydroelectric dams and 522 km of slack water. One effect of increased impoundment has been to slow the velocity of water and thus slow the outmigration of smolts to the estuary (Raymond 1979, 1988; Berggren & Filardo 1993; Schaller et al. 1999, 2007). Slowed outmigration may increase exposure to predation and higher temperatures during migration, increasing energetic costs, and result in poorly timed estuary entry relative to a smolt's physiological state and to the environmental conditions during early ocean residence, which affect mortality during the smolt migration and probably influence mortality in subsequent life stages (Budy et al. 2002; Muir et al. 2006).

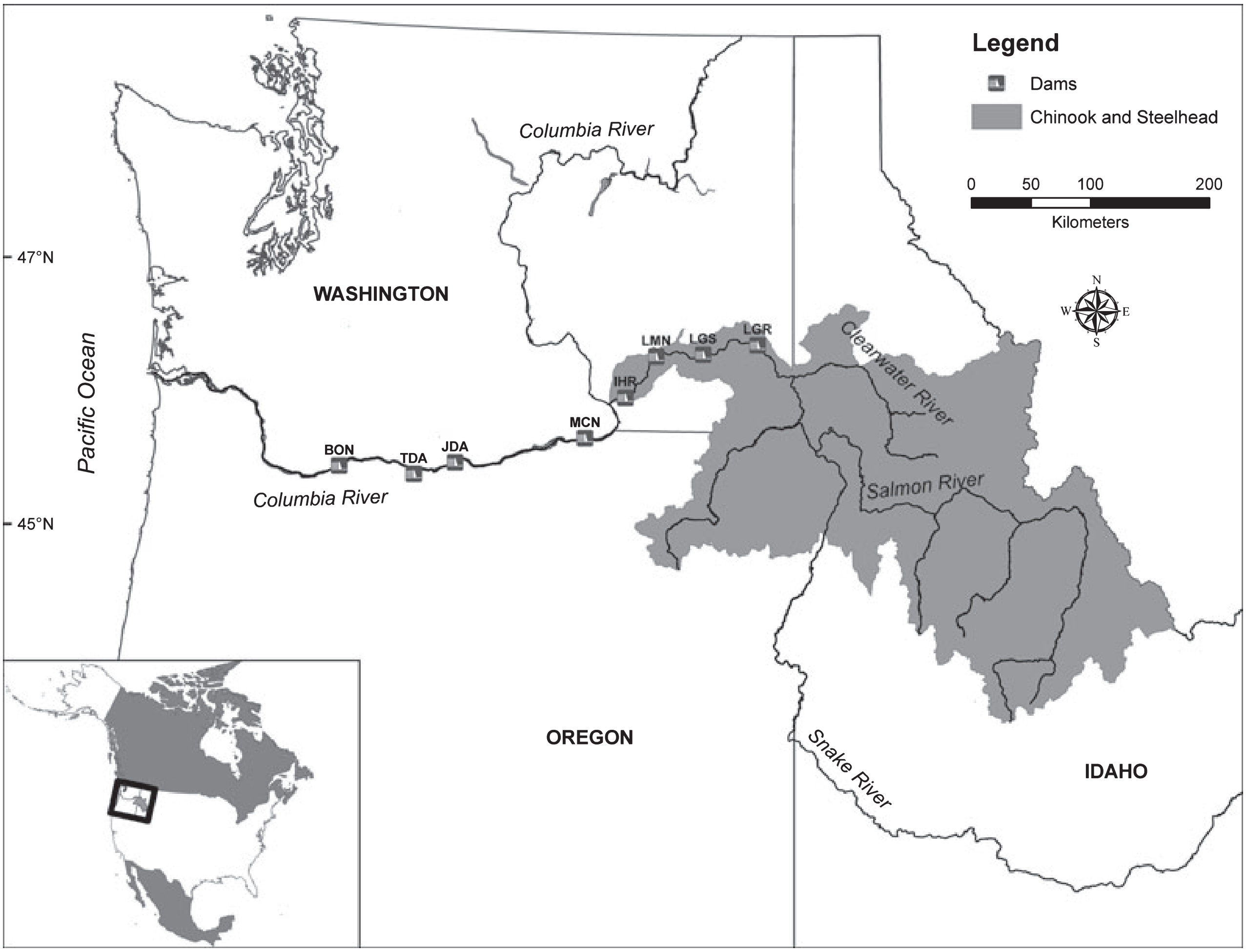

Fig. 1. Map of Columbia River Basin showing the area currently accessible to Snake River spring/summer Chinook and steelhead (shaded). The eight hydropower dams on the mainstem Snake and Columbia Rivers and dates of their completion are as follows: Lower Granite (LGR 1975). Little Goose (LGS 1970), Lower Monumental (LMN 1969), Ice Harbor (IHR 1961), McNary (MCN 1953), John Day (JDA 1968), The Dalles (TDD 1957) and Bonneville (BON 1938). Smolt collection and transportation facilities are LGR, LGS, LMN and MCN.

Juveniles have four possible routes past a dam: (i) over a spillway, avoiding the powerhouse; (ii) being diverted by submersible travelling screens into the powerhouse collection system and bypassed back to the river; (iii) being collected in the powerhouse for transportation in barges or trucks; or (iv) through the turbines. Several problems may occur through the powerhouse routes, including delay of smolts in the forebay, increased exposure to predation by birds and fish, large pressure changes, and mechanical injury (Budy et al. (2002). Passing a dam via spill has been hypothesised to be less stressful with less delay in the forebay and lower mortality than passing through turbines (Schaller et al. 2007). Past operations forced a higher proportion of the water and fish through the turbines for power production in low flow years. In higher flow years, and with recent hydropower system management, more water has passed over spillways, which combined with development of surface spillway weirs, results in a reduction of powerhouse passage (NMFS 2008). Turbine passage generally results in lower survival rates than other passage routes (Marmorek et al. 1998). To counteract this mortality, major fish screening efforts occurred in the 1980s and 1990s to exclude fish from turbine intakes, routing them to collection/bypass systems at the dams. Snake River salmon and steelhead smolts have been collected and transported around portions of the hydropower system since the 1970s to mitigate for mortality within the FCRPS. Mass transportation began in 1977 (Raymond 1988), and was institutionalised in 1981 as an operational program by the U.S. Army Corps of Engineers (Schaller et al. 2007). Spring migrating smolts are now collected and transported primarily by barge from the three uppermost Snake River dams. Transported smolts avoid most of the direct mortality of in-river migrants, but experience the stresses of collection systems at the transport dam, crowding and exposure to pathogens in holding raceways and barges, and altered estuary arrival timing (Budy et al. 2002).

For both species, smolt to adult survival rates (SARs) also decreased coincident with development and operation of the FCRPS (Raymond 1988; Marmorek et al. 1998; Petrosky et al. 2001). Additionally, this period experienced generally warmer ocean/climatic conditions less favourable to salmon survival (Mantua et al. 1997; Marmorek et al. 1998; Petrosky et al. 2001). The Northwest Power and Conservation Council (NPCC 2003, 2009) adopted a goal of achieving SARs in the 2–6% range (minimum 2%; average 4%) for listed Snake River and upper Columbia River salmon and steelhead. The NPCC (2009) also adopted a strategy to identify the effects of ocean conditions on anadromous fish survival and use this information to evaluate and adjust inland management actions. The NPCC noted that while we cannot control the ocean, we can monitor ocean conditions and related salmon survival and take actions to improve the likelihood that Columbia River Basin salmon can survive varying ocean conditions. A better understanding of the ocean conditions that influence salmon survival should provide insight as to which management actions taken inland will provide the greatest restoration benefit.

Recruitment success in the ocean environment is generally believed to occur largely during the first critical months at sea (Ricker 1976; Nickelson 1986; Pearcy 1992; Mueter et al. 2002, 2005; Pyper et al. 2005; Peterson et al. 2006). As many scientists and salmon managers have noted, variations in marine survival of both coho and Chinook salmon correspond with periods of alternating cold and warm ocean conditions (Peterson et al. 2006). Peterson et al. (2006) evaluated local or nearshore physical indicators of conditions for salmon survival using: sea surface temperature (SST), upwelling, spring transition dates, and deep water temperature and salinity. Peterson's evaluation was for a shorter time-series, and only some of these variables are available for the longer time-series of survival rates that we evaluated. Upwelling indices have also been linked to ocean survival for Columbia River stream-type Chinook salmon (Scheuerell & Williams 2005) and Oregon coastal coho salmon (Nickelson 1986). The relative amount of coastal upwelling in the spring appears to be correlated with salmon production. Peterson et al.'s (2006) caution that the influence of the upwelling index should be interpreted in light of the type of source water that upwells in the northern California Current. Logerwell et al. (2003) also found that the timing of the spring transition from winter downwelling to spring/summer upwelling was linked to coho salmon survival. This date identifies the beginning of the upwelling season and can occur at any time between March and June. The earlier in the year that upwelling starts, in general, the greater the ecosystem productivity will be in that year (Peterson et al. 2006). The Pacific Decadal Oscillation (PDO) is a climate index based upon patterns of variation in SST of the North Pacific from 1900 to the present (Mantua et al. 1997). Mantua et al. (1997) identified that cool PDO years (1947–1976) coincided with high returns of Chinook and coho salmon and that during the warm PDO cycle that followed (1977–1998) salmon numbers steadily declined. Mueter et al. (2005) found that regional monthly averages of SST appeared to be better predictors of survival rates for a number of populations of salmon across a wide geographic range than the large scale measures of SST variability such as the PDO.

Smolt to adult survival rates reflect the combined influence of seaward migration through the FCRPS and ocean factors. Ocean fisheries have negligible affects on this investigation because these populations are rarely caught in the ocean (PFMC 2003). First year ocean survival reflects the influence of near shore and broad scale environmental conditions, but may also be influenced by the condition of fish when they reach saltwater due to experiences in an earlier life stage (Budy et al. 2002). Previous comparative analyses of spawner-recruit data from the Snake River and Columbia River Chinook populations have identified a component of mortality associated in time and space with FCRPS development and operation (Schaller et al. 1999; Deriso et al. 2001; Schaller & Petrosky 2007). Due to the cumulative impacts to juvenile fish that migrate through the hydropower system and their condition when they enter salt water, this component of mortality is hypothesised to occur in the early ocean environment, and, by inference, has been termed delayed hydropower system mortality based on its spatial/temporal association with FCRPS development, literature reviews and other evidence (Budy et al. 2002; Marmorek et al. 2004; Schaller & Petrosky 2007).

Our primary objective is to advance understanding of the role of river conditions during seaward migration and ocean conditions on survival rates of Snake River Chinook and steelhead, and to guide river management actions. In this study, we first investigated the association of Chinook and steelhead SARs with several juvenile migration corridor management and environmental variables and ocean variables. This survival evaluation was over a long time span (4 decades) and employed multiple regression methods to determine which set of variables best explains the variation in survival rates. We then partitioned first year ocean survival rates from the SAR time-series and investigated the association of first year ocean survival rates of Chinook and steelhead with the same river and ocean variables that we applied in the analysis of SARs. Our analysis uses independent data sets and a different approach from those of the spatial/temporal contrasts described above. Finally, we contrast results of relationships for the different life stages to provide a tool that improves understanding of the role of the hydropower system management on overall survival in the face of variable ocean and climate conditions.

Materials and methods

Study area and population description

Four evolutionarily significant units (ESUs) of salmon and three distinct population segments (DPSs) of steelhead are listed as endangered or threatened under the ESA in the Interior Columbia Basin (Fig. 1). Our study focuses on the Snake River spring/summer Chinook ESU and the Snake River steelhead DPS that were exposed to full impacts of development of the federal hydropower system (Fig. 1). All Chinook populations in the analysis are wild stream-type Chinook salmon (Healy 1991), producing yearling smolts that migrate seaward in the spring. Steelhead have a more complex life history than stream-type Chinook salmon, exhibiting multiple smolt ages and a freshwater overwintering period prior to spawning. Chinook and steelhead adults return predominately after spending 1–3 years in the ocean.

Survival rate indices

In the analysis, we focused on two survival rate indices that spanned different lengths of the life cycle for the populations of interest. These indices were chosen to assess the relative role of the Columbia River hydropower system on overall survival while accounting for the influence of variable ocean conditions on patterns in survival rates. The first index we analysed was smolt to adult survival rate (SAR), which provides a measure of overall survival from the outmigrating smolt stage to the returning adult recruit stage. The second index was first year of estuary/ocean survival rate (S3), which was estimated to provide a measure during a highly critical life stage for anadromous salmonids. For Chinook and steelhead we calculated SARs and S3 using all available data. In our multiple regression analysis we transformed the SAR and S3 survival rates into mortality rates by taking the negative natural log of these estimates. This transformation is appropriate due to the multiplicative nature of survival rates over differing life stages (Peterman 1981; Deriso et al. 2001).

SAR methods

Smolt to adult survival rates were estimated by dividing the number of smolts at the uppermost dam into the number of adults returning to the Columbia River mouth from that migration year. We used published smolt estimates for wild Chinook for 1964–1984 (Raymond 1988) and 1992–1993 (Petrosky et al. 2001). No wild Chinook smolt estimates were available for 1985–1991 due to insufficient marking at Snake River hatcheries (Petrosky et al. 2001). For the years 1994–2006, we used the Comparative Survival Study (CSS) estimates of Passive Integrated Transponder (PIT) tagged wild Chinook from Schaller et al. (2007). We used published smolt estimates for wild steelhead for 1964–1984 (Raymond 1988) and 1985–1996 (Marmorek et al. 1998). For the years 1997–2005, we used CSS estimates of PIT-tagged wild steelhead from Schaller et al. (2007).

We assigned adult recruits to smolt migration years using age structured wild adult counts at the upper dam in the Snake River. For wild Chinook, we used the method of Petrosky et al. (2001) for smolt migration years 1964–1984 and 1992–1993. For smolt migration years 1994–2006, we used the wild PIT-tag returns from Schaller et al. (2007). For steelhead, we used the methods of Marmorek et al. (1998) for smolt migration years 1964–1996. For smolt migration years 1997–2005, we used the wild PIT-tag returns from Schaller et al. (2007).

We expanded the adult returns to the uppermost dam by annual harvest rates and by survival rates of adults migrating through the FCRPS to account for a wide variation in annual harvest rates in Columbia River fisheries and upstream passage survival rates during 1964–2008. We used harvest rates from Petrosky et al. (2001) for Chinook smolt migration years 1964–1993 and wild Chinook harvest rates from U.S. versus Oregon Technical Advisory Committee (TAC 2008) for smolt migration years 1994–2006. We used the harvest rate estimates contained in Marmorek et al. (1998) for steelhead smolt migration years 1964–1996 and wild steelhead harvest rates from TAC (2008) for smolt migration years 1997–2006.

To estimate Chinook upstream passage survival rates through the FCRPS, we used a long time-series (1965–2003) of upstream migration survival rate estimates based on dam counts (TAC 2008) and PIT tag-derived survival estimates for 1999–2008 (Schaller et al. 2007). For the years of overlap (1999–2003), upstream passage survival rates averaged 0.88 based on PIT tags and 0.66 based on TAC estimates. We considered the PIT tag-derived estimates to be more accurate for the recent period, but they were limited to a time after major adult passage improvements (e.g., spill pattern management, attraction flows) had been implemented. Therefore, we assumed the TAC (2008) estimates captured the temporal pattern of the time-series and adjusted the TAC (2008) values by the ratio (1.32). For steelhead, we lacked a long time-series of upstream migration survival rate estimates. We had upstream passage survival rate estimates from Bonneville Dam to Lower Granite Dam from PIT-tagged Snake River steelhead for the years 2000–2005. These survival rates averaged 0.77 (range 0.68–0.82) for 2000–2005. The average upstream survival rate was assumed for the pre-2000 return years.

S3 (first year of estuary/ocean survival rate) methods

We back-calculated first year ocean survival rates (S3) from SAR estimates for Chinook and steelhead taking into account year-to-year variability in hydropower system juvenile survival rates, and age composition of returning adults to the Columbia River mouth. This method was similar to approaches used by Wilson (2003) and Zabel et al. (2006) to estimate early ocean survival rates.

Specifically, we based this S3 estimate on smolt estimates at the uppermost dam in smolt year t and age-specific adult estimates at years $t + 1$, $t + 2$ and $t + 3$ at the Columbia River mouth (from that smolt year). We note that:

$$\mathrm{S3}_{(t)} = n3_{(t+1)}/n2_{(t)}, \tag{1}$$

where $ni_{(t)}$ is the number of individuals of age i at time t.

The $n2_{(t)}$ term is derived as follows:

$$n_{2(t)} = \mathrm{sd}_{(t)} \cdot \mathrm{smolts}_{(t)}, \text{ and} \tag{2}$$

$$\mathrm{sd}_{(t)} = \mathrm{pT}_{(t)} \cdot \mathrm{sT} + (1 - \mathrm{pT}_{(t)}) \cdot \mathrm{si}_{(t)}, \tag{3}$$

where $\mathrm{sd}_{(t)}$ is survival rate of downstream migrants through the hydropower system, $\mathrm{pT}_{(t)}$ is the portion of fish arriving at the uppermost dam that were transported, sT is the survival rate of transported fish and $\mathrm{si}_{(t)}$ is the survival rate of in-river migrants (Williams et al. 2001; Schaller et al. 2007). For Chinook, the estimates for proportion transported were from Marmorek et al. (1998) for 1971–1993 and Schaller et al. (2007) for 1994–2006. For steelhead, recent annual estimates of proportion of wild steelhead smolts transported from Snake River dams were from Schaller et al. (2007); for years prior to 1994, these proportions were based on Fish Transportation Oversight Team reports for migration years 1985–1992 (Ceballos et al. 1993) and Park (1985) for pre-1985 migration years. Transported smolts were in Lower Granite equivalents, which required expanding the numbers transported from lower dams by the in-river survival rate between Lower Granite and the lower collection dams. S3 was not estimated for either species for migration years 1985–1992 due to lack of $\mathrm{si}_{(t)}$ estimates (Williams et al. 2001).

The sT parameter includes a 'delayed differential mortality' of transported fish termed D (Schaller et al. 2007), accounting for the fact that transported fish generally return as adults at lower rates than fish that migrated in-river. Although this delayed mortality is most probably expressed during the early ocean life stage, we applied it to the downstream migration stage because it simplifies calculation of the early ocean survival rate and is consistent with previous analyses (Wilson 2003; Zabel et al. 2006). Annual D-values of wild Chinook for migration years 1994–2005 were obtained from the CSS (Schaller et al. 2007). The geometric mean of D-values was 0.53 (range 0.32–1.07), excluding the major drought year of 2001 when D equalled 2.16. For the pre-1993 migration years, we used the geometric mean D-value for all years except for major drought years (1973 and 1977) where we assumed the 2001 *D*-estimate applied. For steelhead calculations, we used the geometric mean *D*-value from CSS (1.03, range 0.11–2.69) for 1997–2005 (Schaller et al. 2007) for all years, similar to Zabel et al. (2006).

We back-calculated $n3_{(t+1)}$ from the number of adults returning in year $t + 1$ [designated $nA_{(t+1)}$], the number returning in year $t + 2$ [designated $nA_{(t+2)}$] and the number returning in year $t + 3$ [designated $nA_{(t+3)}$]. These counts were then adjusted for annual ocean survival rates. We estimated $n3_{(t+1)}$ as:

$$n3_{(t+1)} = (nA_{(t+1)}) + (nA_{(t+2)})/(\mathrm{so}) + (nA_{(t+3)})/(\mathrm{so}^2), \qquad (4)$$

where we assumed that sub-adult ocean survival rate, so = 0.8 (Ricker 1976) and applied it according to the number of years spent in the ocean. This assumption is consistent with previous cohort-based Chinook modelling studies (Pacific Salmon Commission 1988, Zabel et al. 2006), and assigns all ocean survival rate variability to the S3 life stage.

Independent variables

To assess the influence of broad scale oceanic conditions, near shore ocean conditions, and conditions in the Snake and Columbia rivers on Chinook and steelhead survival rates, we evaluated a number of independent variables.

River variables

We incorporated five river variables associated with the juvenile seaward migration in the analysis: water travel time (WTT), expected number of turbine passages, expected number of powerhouse passages, mean maximum daily temperature of the Snake River above the FCRPS, and the proportion of juvenile fish arriving at the upper most dam that were transported around dams. All variables were expressed as annual estimates for the spring migration period (April 16–May 31).

The effects of water velocity are generally expressed as the average time (in days) it takes a water particle to travel through a river reach (WTT). WTT is a function of reservoir volume and inflow. WTT affects fish travel time (FTT) through the reach (Schaller et al. 2007). This river reach is defined from the head of Lower Granite Reservoir on the Snake River at the mouth of the Clearwater River to Bonneville Dam (Fig. 1). We obtained historic annual estimates of WTT from the Fish Passage Center (Portland, OR) for the spring migration period. Prior to Bonneville Dam construction, WTT consistently averaged about 2 days through this reach. WTT increased to about 4.8 days by the late 1950s with three dams in place, and now averages about 19 days, ranging from 10 to 40 days depending on inflow (Fig. 2a).

Juvenile migrants that are not spilled over the dam go into the powerhouse through the turbines or through collection/bypass systems. The proportion of water spilled affects FTT, and has been found to be influential in Columbia River juvenile survival rate studies (e.g., Schaller et al. 2007). Because the number of dams changed during the 1964–2006 time period, we expressed the effects of spill in terms of number of powerhouse passages (N_Powerhouse). N_Powerhouse represents the most likely number of powerhouses passed through by a fish migrating in-river through the FCPRS, and is a function of the number of dams, the proportion spill at each dam, and spill passage efficiency (SPE). We obtained daily flow and spill volume data from the Fish Passage Center (Portland, OR) and calculated annual average spill proportion for each of the eight dams for the spring migration period. We assumed that the proportion of fish passing a dam by spill was equivalent to the proportion of spill volume to total flow volume (SPE = 1.0) and estimated annual N_Powerhouse as:

$$\mathrm{N\_Power\,House}(i) = \mathrm{Ndams}(i) - \sum_{j=1}^{\mathrm{Ndams}(i)} \mathrm{Prop\_spill}(i,j), \qquad (5)$$

where Ndams is number of dams completed in year *i* and Prop_spill is the spill proportion at dam *j* in year *i*. With all FCRPS dams in place and SPE = 1.0, N_Powerhouse has a correlation coefficient of −1.0 with the average spill proportion. Advantages of the N_Powerhouse variable include providing a retrospective description of effects of changes in number of dams and spill proportions; and, with appropriate fine-scale studies in the future, it may better describe efficacy of surface passage technology in combination with spill. Number of powerhouse passages ranged from 1.3 to 3.0 in the mid-1960s, increasing to 4.5–7.9 with FCRPS completion (Fig. 2b).

Juvenile migrants that enter the powerhouse pass through turbines or through collection/bypass systems. We estimated the expected number of turbines passed through by fish migrating in-river through the FCPRS (N_Turbine). N_Turbine is a function of the number of dams, the proportion spill at each dam, SPE and fish guidance efficiency (FGE) at the turbine intake screens. We used FGE estimates from Marmorek et al. (1998) and P. Wilson, (USFWS, unpublished data). We assumed SPE = 1.0 because there was no direct information to assume otherwise, therefore SPE dropped out of our calculation.

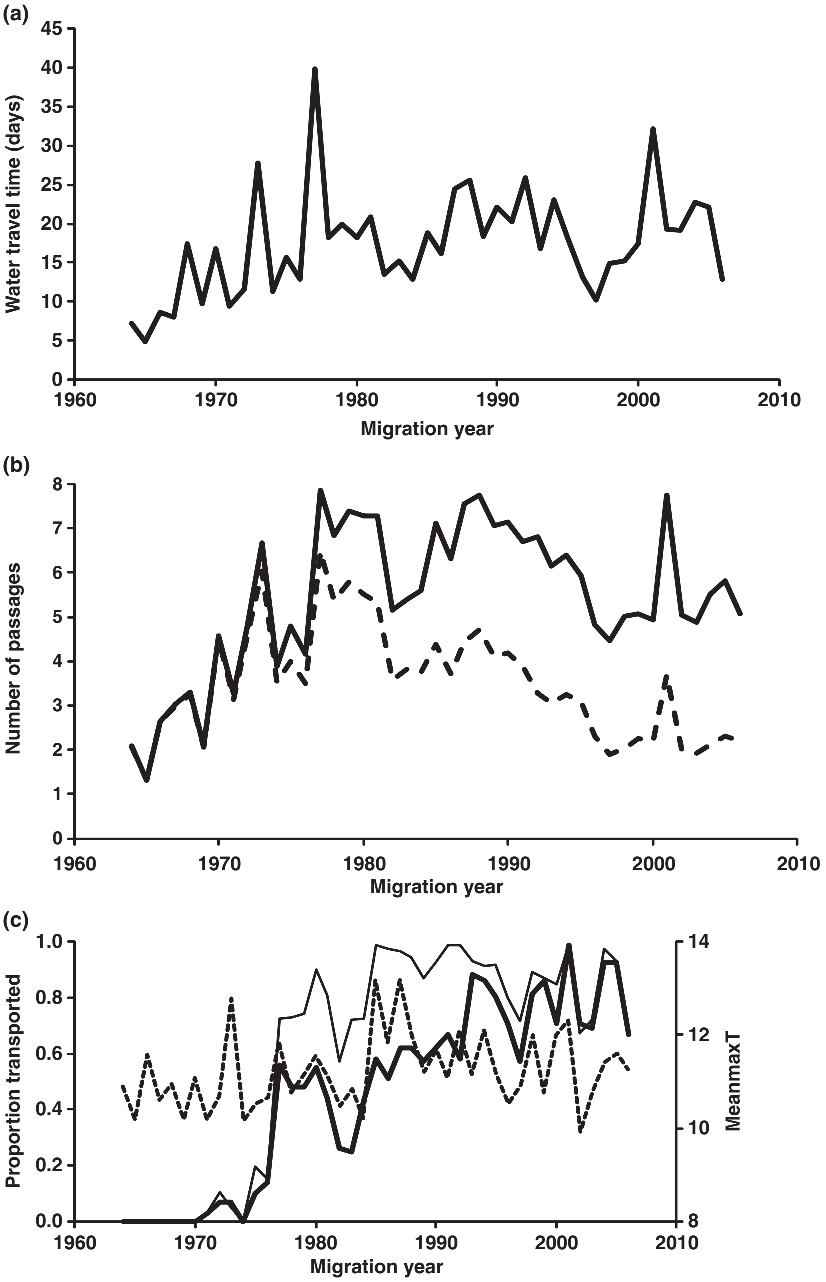

Fig. 2. River variables: (a) water travel time; (b) expected number of powerhouse passages (solid line) and turbine passages (dashed line); and (c) proportion of smolts transported (heavy solid line – Chinook, light solid line – steelhead) and mean maximum water temperature (dashed line), 1964–2006.

$$\mathrm{N\_Turbine}(i) = \mathrm{Ndams}(i) - \sum_{j=1}^{\mathrm{Ndams}(i)} \mathrm{N\_NonTurbine}(i,j), \quad (6)$$

where Ndams is number of dams completed in year *i*, and

$$\mathrm{N\_Nonturbine}_{(i,j)} = (\mathrm{Prop\_spill}_{(i,j)} + (1 - \mathrm{Prop\_spill}_{(i,j)}{}^{*}\mathrm{FGE}_{(i,j)})), \quad (7)$$

where Prop_spill is the spill proportion at dam *j* in year *i* and FGE is the fish guidance efficiency at dam *j* in year *i*. Number of turbine passages ranged from 1.3 to 3.0 in the mid-1960s, increasing to a range of 3.7–6.5 with FCRPS completion in the late 1970s–1980s, and decreasing with screening and spill programs to a range of 1.9–3.7 since the late 1990s (Fig. 2b).

Water temperature upstream of the FCRPS during the smolt migration is a function of the annual weather pattern and water management in the upstream Snake River and Clearwater River reservoirs. The mean maximum daily temperature (MeanMaxT, °C) of the Snake River entering the FCRPS during the spring migration period was calculated from data at the USGS Anatone gauge station on the Snake River and Spaulding gauge station on the Clearwater River (http://waterdata.usgs.gov/id/nwis/inventory/

?site_no=13334300&amp and http://waterdata.usgs.gov/id/nwis/inventory/?site_no=13342500&, respectively). Daily maximum temperature of the Snake River entering Lower Granite Reservoir was calculated by weighting the temperature at the two gauges by daily river flow; MeanMaxT was calculated by averaging the daily values across the 46-day period. River flow data at the two gauges were generally complete, but maximum temperature data gaps existed at both stations. We estimated annual MeanMaxT when data were missing using the following criteria. If at least 80% ($n > 36$) of daily observations were available per year, an annual mean was calculated from the available observations. The Anatone gauge missed the 80% criterion in 3 years (1969, 1985 and 1992), but the Spaulding gauge met the 80% criterion in each of these years. For these 3 years, we estimated the Anatone mean maximum temperatures from those at Spaulding which provided a complete data set for Anatone. Finally, we predicted Snake River MeanMaxT for the remaining 12 years using the regression (for years with complete data) between the Anatone mean maximum temperature and Snake River MeanMaxT. Snake River MeanMaxT ranged from 9.9 to 13.2 °C during the 1964–2006 smolt migrations (Fig. 2c).

In recent years, the majority of Chinook and steelhead smolts entering the powerhouse collection systems of Lower Granite, Little Goose or Lower Monumental dams on the Snake River have been transported. The proportion of these smolts arriving at the uppermost dam that are transported (pT) varies with spill and indirectly with WTT and is a function of probability of powerhouse passage, FGE and annual management operations. The information used for $pT_{(t)}$ is described in the methods for calculating S3 (above). pT for both species varied from 0.0 in the 1960s to 0.99 in 2001 (Fig. 2c; Schaller et al. 2007).

Ocean variables

We identified a number of long-term indices to evaluate whether variation in near shore and broad scale oceanic conditions influenced survival rate patterns of the Snake River Chinook and steelhead populations. We explored the relationship between survival rate indices of Snake River Chinook and steelhead with the following suite of long-term indices of nearshore and broad scale oceanic conditions:

We used monthly SST averages at 45°N latitude to capture the influence of nearshore temperature on survival (Fig. 3). SST values were obtained from the University Corporation for Atmospheric Research (UCAR) website, http://dss.ucar.edu/datasets/ds540.1/data/msga.form.html, managed on behalf of the National Science Foundation and the university community.

We used monthly upwelling indices (units are $m^3 \cdot s^{-1} \cdot 100\ m^{-1}$ of coastline) at 45°N latitude to capture the influence of strength of upwelling of nutrient rich water in the spring or downwelling in the fall (Fig. 3). Upwelling indices were obtained from NOAA Pacific Fisheries Environmental Laboratory website: http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html.

We used Logerwell et al.'s (2003) index of spring transition date, which is based on the first day when the value of the 10-day running average for upwelling is positive and the 10-day running average for sea level is negative.

The PDO data were from updated standardised values of the PDO index derived as the leading principal component of monthly SST anomalies in the North Pacific Ocean (Mantua et al. 1997). PDO indices were obtained from the University of Washington website: http://jisao.washington.edu/pdo/PDO.latest.

Modelling approach overview

We implemented analytical and statistical tools to make inferences about the effects of broad scale ocean, near shore ocean, and river conditions on wild Snake River Chinook salmon and steelhead survival rates. Specifically, our approach was to: (i) estimate SARs for Chinook and steelhead; (ii) estimate early ocean survival rates (S3) for Chinook and steelhead; (iii) use correlation and regression techniques to evaluate statistically candidate parameters which best explain the variation in survival rates for Chinook and steelhead; (iv) evaluate statistically various combinations of the parameters using multivariate regression techniques to produce a multivariate model with a high level of fit to the survival rate data series; and (v) use our best-fit models to isolate the influence of ocean and in-river conditions on overall survival rates.

Variable selection

We explored a number of potential broad scale ocean, near shore, and river condition indicators for predicting SARs and S3 survival rates. The analyses that follow used SAR and S3 for outmigration years: 1964–1984 and 1993–2006 for wild Chinook; and 1964–1984 and 1993–2005 for wild steelhead. These time-series were used to be consistent across survival rate indices and species. We evaluated the strength of the associations between 42 candidate predictor variables and survival rates in univariate analyses using correlation coefficients of at least $|0.4|$ as a preliminary screen. We adjusted the significance of the correlations (one-tailed t-test) by adjusting degrees of freedom to account for autocorrelation in the time-series using the methods of Pyper & Peterman (1998). We used

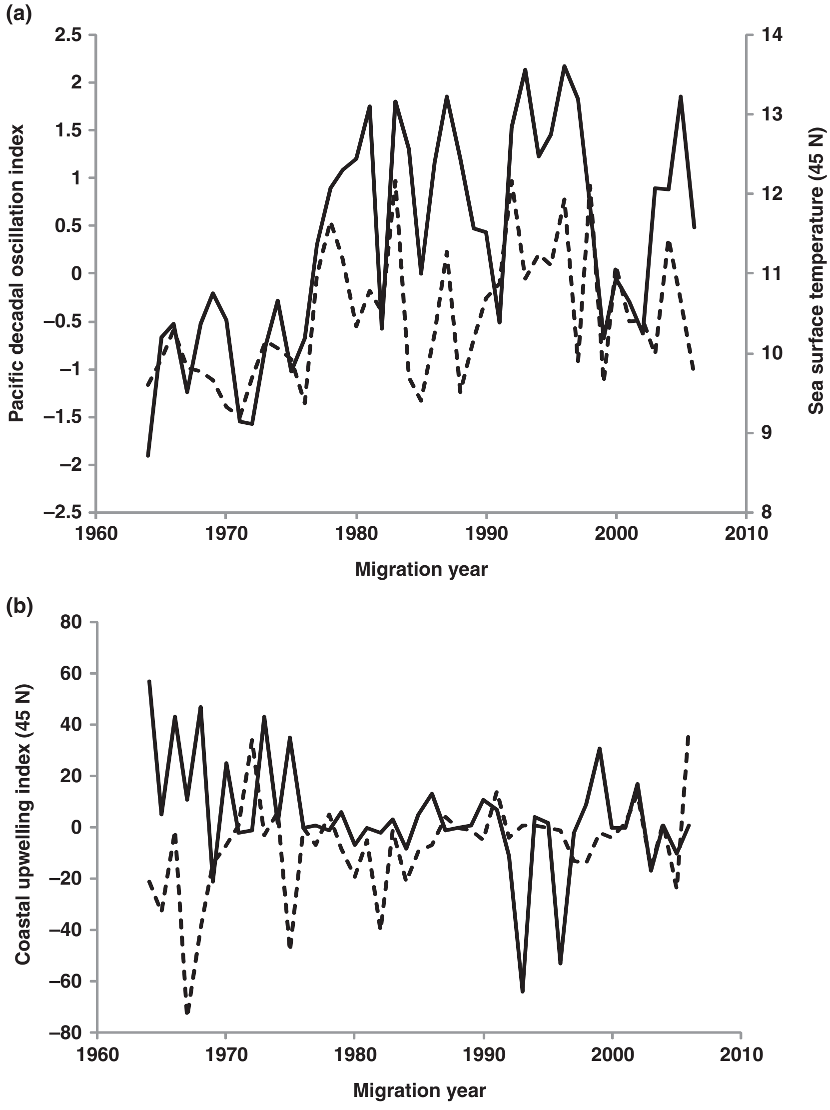

Fig. 3. Selected ocean and near shore environmental variables: (a) May Pacific Decadal Oscillation index (solid line) and April sea surface temperature at 45°N (dashed line); and (b) April (solid line) and October (dashed line) coastal upwelling indices at 45°N.

biological plausibility and correlation criteria ($r \geq |0.4|$, $P \leq 0.05$) to define the candidate predictor variables to use in our multiple regression analysis of survival rates for wild Chinook and steelhead.

Multiple regression model selection

Following the univariate analyses, we evaluated the predictive capability of combinations of covariates on survival rates with multivariate regression. Given the research that has been conducted to date on environmental variables that have been associated with wild Chinook and steelhead survival rates, we held an *a priori* belief that a combination of broad scale ocean, near shore and river condition indicators were all likely important for predicting SAR and S3 survival rates. We were interested in evaluating models that contained variables from each of these three variable classes of indices. We used multiple regression techniques that initially selected combinations of covariates (from these three classes of variables) for alternative models based on adjusted R^2-values. We measured the degree of model fit using both Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) scores (Burnham & Anderson 2002) using the linear regression procedure of SAS (2002). We then used these best-fit models for evaluating the proportion of variation that each model explained of the various survival rates for wild Chinook and steelhead. For example, our multiple regression models for Chinook S3 and variables of multiple ocean and river environmental factors would take the form:

$$\begin{aligned} -\ln[\mathrm{S3}_{(t)}] = \beta 0 &+ \beta_{\mathrm{WTT}} \cdot \mathrm{WTT}_{(t)} \\ &+ \beta_{\mathrm{MayPDO}} \cdot \mathrm{PDOMay}_{(t)} \\ &+ \beta_{\mathrm{AprUP45N}} \cdot \mathrm{AprUP45N}_{(t)} \\ &+ \varepsilon_{(t)}, \end{aligned} \tag{8}$$

where t is the smolt year, $\beta 0$ is the intercept, β is the coefficient for each environmental variable (ocean and river variables described above) and $\varepsilon_{(t)}$ is the normally distributed residual. We also tested to detect the presence of autocorrelation in the residuals of our multiple regression analysis by applying a Durbin–Watson test to our analysis (Draper & Smith1998). Generally, a Durbin–Watson statistic (D-W) < 1.0 indicates strong positive autocorrelation of regression residuals.

Sensitivity analyses

We evaluated the sensitivity of the multiple regression model variable selection to alternative values of SAR and S3, to account for the possibility that SARs based on PIT tags may be an underestimate due to tagging effects (e.g., Schaller et al. 2007; Knudsen et al. 2009). Alternative SARs were obtained by multiplying the PIT-tag SARs (migration years 1994–2006 for Chinook and migration years 1997–2005 for steelhead) by 1.19, the geometric mean difference observed between run reconstruction and PIT-tag SARs (Schaller et al. 2007). We used these alternative SAR estimates for Chinook and steelhead to also calculate alternative S3 values for the sensitivity analysis.

Results

Life-stage survival rate estimates

Chinook SARs declined sharply from an average 6.0% in the 1960s (range, 4.8–8.6%) to an average 1.9% during 1970–1984, and 1.5% during 1992–2006 (Fig. 4a). Steelhead SARs showed a similar, though less dramatic decline through this period. Steelhead SARs averaged 7.3% in the 1960s, 3.5% during the 1970s and 1980s and 2.3% during 1990–2005 (Fig. 4a).

Estimates of first year ocean survival (S3) showed similar patterns of decline for both Chinook and steelhead (Fig. 4b). Estimated S3 for Chinook averaged 14.1% in the 1960s, decreasing to 7.8% during 1970–1984 and 2.9% during 1992–2006. Estimated S3 for steelhead averaged 21.1% in the 1960s, 11.0% during 1970–1984 and 2.7% during 1990–2005.

Variable selection

Chinook mortality rate during the smolt to adult life stage, $-\ln(\text{SAR})$, was correlated at a level of at least $|0.4|$ and significance of $P \leq 0.05$ with 11 variables (Table 1). For multiple regression analyses, we selected the following six variables: MayPDO, AprUP45n, MarSST45n, WTT, N_Powerhouse and pT. We rejected for model analysis MarPDO, AprPDO and AugPDO because they were highly correlated with MayPDO. We rejected MayUP45n, because of its high correlation with AprUP45n. We also rejected OctUP45n because of its inconsistent correlation pattern with mortality across life stages and species. The six variables resulted in 63 alternative regression

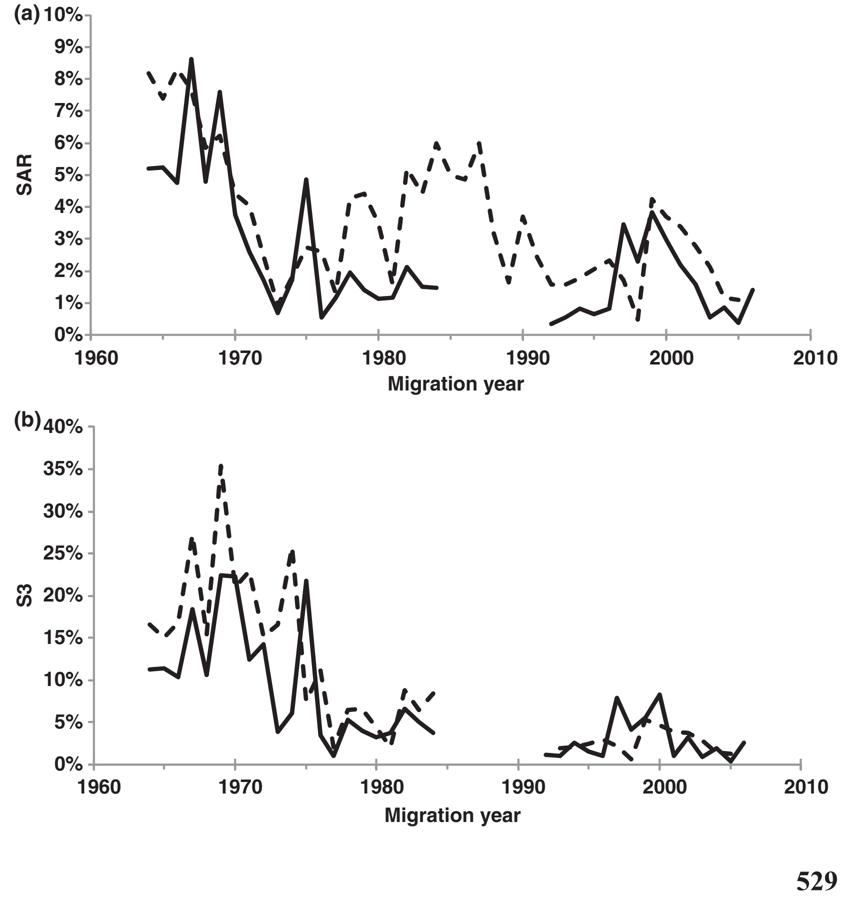

Fig. 4. Estimates of (a) smolt to adult survival rates (SAR) and (b) first year ocean survival rates (S3) for spring/summer Chinook (solid line) and steelhead (dashed lines), 1964–2006.

Table 1. Correlations of variables with −ln(SAR) and −ln(S3) for spring/summer Chinook and steelhead, 1964–2006. Significance levels, adjusted for autocorrelation, are identified for $*P < 0.05$ and $**P < 0.01$. Variables incorporated in multiple regressions are underlined.

	Chinook		Steelhead	
Variable	−ln(SAR)	−ln(S3)	−ln(SAR)	−ln(S3)
JanPDO	0.380*	0.579**	0.304	0.573**
FebPDO	0.310	0.497*	0.282	0.622**
MarPDO	0.400*	0.515*	0.337	0.658**
AprPDO	0.439*	0.522*	0.264	0.630**
MayPDO	0.588**	0.641**	0.421*	0.696**
JunPDO	0.346	0.433*	0.295	0.522**
JulPDO	0.387*	0.351*	0.221	0.404**
AugPDO	0.429**	0.370*	0.276	0.387**
SepPDO	0.324*	0.171	0.052	0.110
OctPDO	0.260	0.083	−0.074	−0.020
NovPDO	0.204	0.078	−0.031	0.047
DecPDO	0.271	0.206	0.051	0.150
JanUP45n	−0.183	−0.216	−0.203	−0.326**
FebUP45n	0.116	0.106	−0.001	−0.116
MarUP45n	−0.058	−0.042	0.122	0.052
AprUP45n	−0.482**	−0.494**	−0.259	−0.370**
MayUP45n	−0.405*	−0.358*	−0.546**	−0.457**
JunUP45n	−0.312*	−0.226	−0.120	−0.212
JulUP45n	−0.137	0.136	−0.175	0.029
AugUP45n	0.070	0.091	0.174	−0.006
SepUP45n	−0.058	0.151	0.108	0.232
OctUP45n	0.415*	0.277	0.326*	0.185
NovUP45n	0.221	0.114	0.092	−0.097
DecUP45n	−0.176	−0.265	−0.016	−0.078
Spring Transition	0.243	0.193	0.173	0.186
JanSST45n	0.104	0.201	0.189	0.457**
FebSST45n	0.226	0.371*	0.387*	0.577**
MarSST45n	0.493**	0.454**	0.440**	0.519**
AprSST45n	0.384*	0.464*	0.427*	0.661**
MaySST45n	0.259	0.179	0.330	0.378**
JunSST45n	0.064	0.198	0.097	0.255
JulSST45n	0.129	0.270	0.228	0.403
AugSST45n	−0.020	0.188	0.082	0.286
SepSST45n	0.166	0.234	0.088	0.305
OctSST45n	0.369*	0.468**	0.192	0.355**
NovSST45n	0.061	0.153	0.161	0.247
DecSST45n	0.054	0.151	0.098	0.311
MeanMaxT	0.307*	0.385*	0.477**	0.426**
WTT	0.493**	0.610**	0.515**	0.496**
N_Powerhouse	0.622**	0.620**	0.506*	0.591**
N_Turbine	0.223	0.029	0.117	−0.096
pT	0.558*	0.779**	0.461	0.878**

models with all combinations of river and ocean variables.

Chinook mortality rate during the first year in the ocean, −ln(S3), met selection criteria ($r \geq |0.4|$, $P \leq 0.05$) for 13 variables (Table 1). For multiple regression analyses, we selected the following five variables: MayPDO, AprUP45n, MarSST45n, WTT and N_Powerhouse. We rejected for model analysis five PDO indices for January–April and June because they were highly correlated with MayPDO. We rejected AprSST45n, because of its high correlation with MarSST45n. We rejected OctSST45n because of its inconsistent correlation pattern across life stages and species. We also rejected pT, which was highly correlated with −ln(S3), because of the lack of biological plausibility. That is, the method we used to partition S3 from SAR placed the effects of differential delayed transport mortality (*D*; assuming recent estimates can be applied back to the late 1970s) into the downstream passage portion of the life cycle (Wilson 2003; Zabel et al. 2006). The five variables resulted in 31 alternative regression models with all combinations of river and ocean variables.

Steelhead mortality rate during the smolt to adult life stage, −ln(SAR), met selection criteria for seven variables (Table 1). For multiple regression analyses, we selected the following seven variables: MayPDO, MayUP45n, MarSST45n, MeanMaxT, WTT, N_Powerhouse and pT. We rejected for analysis AprSST45n because of its high correlation with MarSST45n. We also included pT in the multiple regression analysis because of its high correlation with −ln(SAR), although the significance ($P = 0.053$) for this variable after accounting for autocorrelation fell just short of the criterion. The seven variables resulted in 127 alternative regression models with all combinations of river and ocean variables.

Steelhead mortality rate during the first year in the ocean, −ln(S3), met selection criteria for 16 variables (Table 1). For multiple regression analyses, we selected the following six variables: MayPDO, MayUP45n, MarSST45n, MeanMaxT, WTT and N_Powerhouse. We rejected for model analysis six PDO indices for January–April and June–July because they were highly correlated with MayPDO. We rejected JanSST45n, FebSST45n and AprSST45n, because of their high correlation with MarSST45n. We also rejected pT, for the same biological plausibility reasons as for Chinook. The six variables resulted in 63 alternative regression models with all combinations of river and ocean variables.

Multiple regression analyses

Chinook

Best-fit, simplest models for mortality rate during the smolt to adult stage, −ln(SAR), and during the first year in the ocean, −ln(S3), included both river and ocean variables (Fig. 5a,b). There was little statistical support for ocean variables alone or river variables alone, implying that both river migration and ocean conditions are important to SARs and S3 of Chinook.

The best AIC and BIC model for Chinook SARs included one ocean variable and N_Powerhouse (Table 2). The highest adjusted R^2 model included two ocean variables and N_Powerhouse (Table 2). Although less parsimonious, the best four-variable model included two ocean and two river variables. Coefficients from the top models indicate that

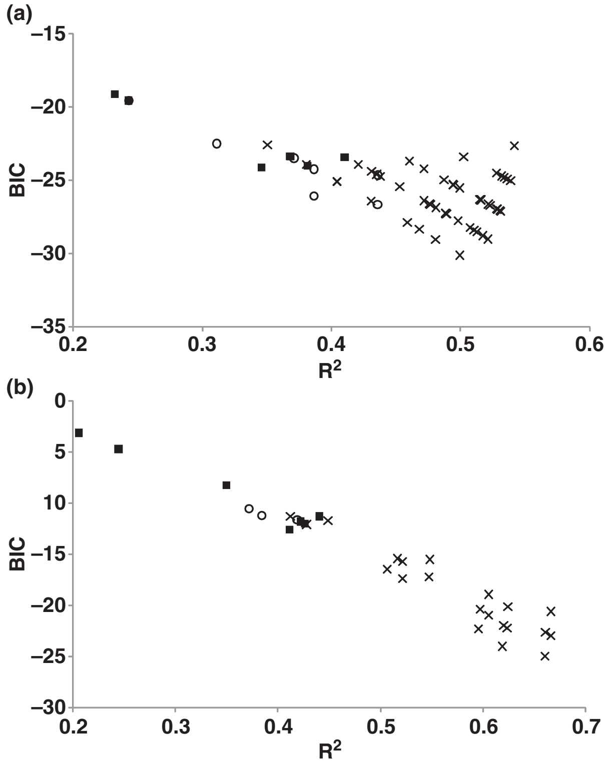

Fig. 5. Multiple regression fits (R^2 and BIC) to ocean and river (X), river only (open circle) and ocean only (closed square) classes of independent variables for (a) mortality rate during smolt to adult life stage [−ln(SAR)] and (b) mortality rate during first year ocean life stage [−ln(S3)] of Snake River wild spring/summer Chinook, 1964–2006.

decreased survival rate is associated with reduced upwelling in the spring, warmer ocean conditions and multiple powerhouse passages during the smolt migration.

The highest adjusted R^2, and best AIC and BIC model for Chinook S3 included two ocean variables and WTT (Table 2). The best four-variable model included two ocean and two river variables. Coefficients from the top models indicate that decreased survival rate is associated with warmer ocean conditions, reduced upwelling in the spring, and slower water velocity during the smolt migration.

There was evidence of slight positive serial correlation of residuals of the Chinook multiple regression models presented in Table 2 based on the D-W statistic. Autocorrelation of residuals did not appear extreme for either Chinook SAR or S3 models (D-W range, 1.512–1.539 and 1.403–1.685, respectively).

Steelhead

Best-fit, simplest models for steelhead mortality rate during the smolt to adult stage, −ln(SAR), and during the first year in the ocean, −ln(S3), also included both river and ocean variables (Fig. 6a,b). There was little statistical support for ocean variables alone or river variables alone, indicating that both river migration and ocean conditions are important to SARs and S3 of steelhead.

The best BIC model for steelhead SAR consisted of one ocean variable and MeanMaxT (Table 3). The highest adjusted R^2 and best AIC model included two ocean variables and MeanMaxT. The best four-variable model included two ocean and two river variables. Coefficients from the top models support that decreased survival rates during this life stage are associated with warmer ocean conditions, reduced spring upwelling and warmer river temperatures during the smolt migration.

The best AIC and BIC model for steelhead S3 included one ocean variable and WTT (Table 3). The highest adjusted R^2 model included one ocean variable, MeanMaxT and WTT. The best four-variable model included three ocean and one river variables. Coefficients from the top models support that decreased survival rates are associated with warmer ocean conditions, reduced spring upwelling and slower water velocity and warmer river temperatures during the smolt migration.

There was evidence of slight positive serial correlation of residuals of the steelhead multiple regression models presented in Table 3. Autocorrelation of residuals did not appear extreme for either steelhead SAR or S3 models (D-W range, 1.090–1.254 and 1.064–1.145, respectively).

Discussion

Survival rates for both Snake River Chinook and steelhead have declined dramatically since the 1960s. These populations remain listed as threatened under the ESA. Identifying a suite of effective inland restoration measures is a challenge due to the high variability of ocean conditions and their influence on survival of these populations.

Numerous researchers and management entities have stressed the importance of identifying the effects of ocean conditions on anadromous fish survival with the goal of more thoroughly evaluating and adjusting inland restoration actions (Lawson 1993; Nickelson & Lawson 1998; Francis & Mantua 2003; Wissmar & Bisson 2003; NPCC 2009). Separating the influence of ocean and freshwater factors is difficult, because of possible confounding factors and a general lack of long-term demographic data. However, a long time-series of life-stage survival rates does exist for Snake River Chinook and steelhead, which we were able to use to examine the influence of ocean and river conditions on survival rates. This approach provides a tool to investigate the potential benefits of various inland restoration options while directly considering

Table 2. Regression model results (selected) for (a) smolt to adult life-stage mortality rate, −ln(SAR), and (b) first year ocean mortality rate, −ln(S3), of Snake River spring/summer Chinook versus ocean and river environmental variables, smolt migration years 1964–2006.

Number of variables	Adjusted R^2	R^2	AIC	BIC	Variable	Estimate	SE	Pr > [*t*]	Selection criteria
(a)									
2	0.4682	0.4995	−32.9303	−30.1048	Intercept	2.7313	0.3452	<0.0001	Best AIC, BIC
					AprUP45n	−0.0119	0.0044	0.0113	
					N_Powerhouse	0.2662	0.0644	0.0002	
3	0.4750	0.5213	−32.4915	−28.9949	Intercept	1.3508	1.2105	0.2730	Best adjusted R^2
					AprUP45n	−0.0108	0.0045	0.0216	
					MarSST45n	0.1600	0.1346	0.2434	
					N_Powerhouse	0.2268	0.0721	0.0036	
4	0.4687	0.5312	−31.2193	−27.0989	Intercept	1.4215	1.2210	0.2535	Best 4 variable model
					AprUP45n	−0.0094	0.0048	0.0603	
					MarSST45n	0.1567	0.1354	0.2563	
					N_Powerhouse	0.1911	0.0853	0.0327	
					pT	0.3164	0.3986	0.4335	
(b)									
2	0.5951	0.6189	−26.3739	−24.0362	Intercept	1.8619	0.2907	<0.0001	Best 2 variable model
					MayPDO	0.4572	0.1004	<0.0001	
					WTT	0.0694	0.0166	0.0002	
3	0.6273	0.6602	−28.3852	−24.9680	Intercept	1.8600	0.2789	<0.0001	Best adjusted R^2, AIC, BIC
					MayPDO	0.3035	0.1247	0.0209	
					AprUP45n	−0.0113	0.0058	0.0615	
					WTT	0.0747	0.0162	<0.0001	
4	0.6214	0.6659	−26.9804	−23.0042	Intercept	2.0673	0.4032	<0.0001	Best 4 variable model
					MayPDO	0.3465	0.1392	0.0186	
					AprUP45n	−0.0115	0.0059	0.0599	
					WTT	0.0909	0.0279	0.0027	
					N_Powerhouse	−0.0961	0.1339	0.4787	

the variability in ocean conditions on anadromous fish survival.

We took advantage of a long time-series of life-stage survival rate information and environmental indices for ocean and in-river conditions to construct models that best explained the patterns of survival rates. The model selection process identified the combination of ocean and river conditions that were most effective in explaining the variation in survival rate patterns. We believe that this approach begins to address the confounding influences of ocean and inland conditions, on searching for inland restoration measures.

Survival rate patterns for both species were associated with indicators of both ocean and river conditions. Coefficients from best-fit, simplest models support findings from other investigations that lower survival rates for Chinook are associated with warmer ocean conditions and reduced upwelling in the spring (e.g., Mantua et al. 1997; Logerwell et al. 2003; Pyper et al. 2005; Scheuerell & Williams 2005; Peterson et al. 2006; Schaller & Petrosky 2007), and with slower water velocity or multiple powerhouse passages during the smolt migration (Berggren & Filardo 1993; Smith et al. 2002; Williams et al. 2005; Schaller et al. 2007). Similarly, lower survival rates for steelhead are associated with warmer ocean conditions, reduced upwelling in the spring, and with slower water velocity and warmer river temperatures. Overall, ocean and river variables in combination better explained the survival rate variability for Chinook than for steelhead. Generally, regression model results were similar for SAR and S3 indices. This result provides evidence that river conditions that influence survival rates during seaward migration are also influential after smolts reach the estuary/ocean. Spatial/temporal comparisons of spawner/recruit patterns (Schaller et al. 1999; Deriso et al. 2001; Schaller & Petrosky 2007), literature reviews and other evidence (Budy et al. 2002; Marmorek et al. 2004; Schaller et al. 2007; Scheuerell et al. 2009) have suggested substantial delayed mortality related to development and operation of the FCRPS. Our present investigation provides additional evidence of delayed hydropower system mortality. The best-fit, simplest model explaining Chinook first year ocean survival rate patterns (S3) included two ocean variables and WTT. WTT in the absence of dams was about 2 days. WTT experienced by Snake River Chinook increased from an average of about 4.8 days in the late 1950s with three FCRPS dams in place to 19.2 days after completion of the final dam, Lower Granite. In either case, the WTT model coefficient predicts a threefold or greater decrease in first year ocean survival rate from a WTT increase of this magnitude. The delayed mortality increase predicted by the regression model, from WTT changes, was similar to that estimated from

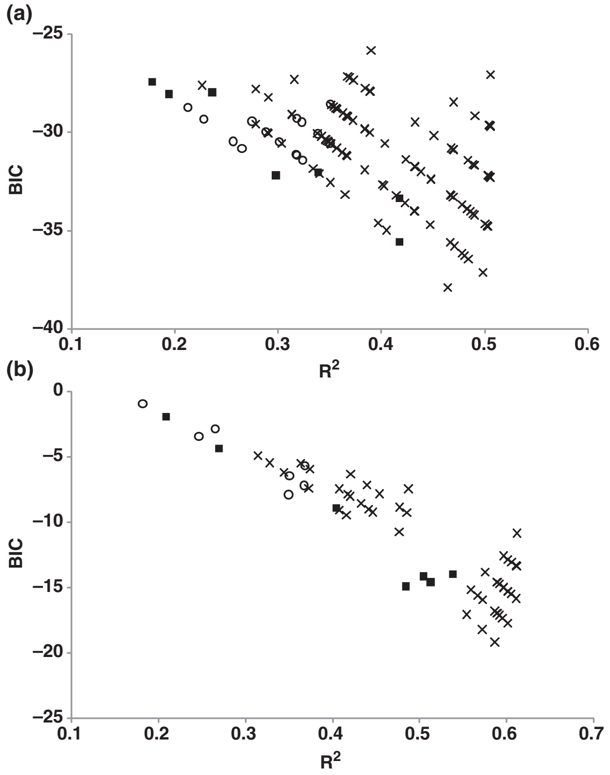

Fig. 6. Multiple regression fits (R^2 and BIC) to ocean and river (X), river only (open circle) and ocean only (closed square) classes of independent variables for (a) mortality rate during smolt to adult life stage [−ln(SAR)] and (b) mortality rate during first year ocean life stage [−ln(S3)] of Snake River wild steelhead, 1964–2005.

independent data sources and analytical methods by Schaller & Petrosky (2007) for Snake River Chinook.

The magnitude of delayed mortality for steelhead appears to be less than for Chinook based on our regression model results. The WTT model coefficient predicts about a twofold decrease in first year ocean survival rate for steelhead from a WTT increase from 4.8 to 19.2 days.

Some uncertainty in the SAR and S3 time-series exists due to a change in methods from run reconstruction to use of CSS PIT tags beginning in 1994 for Chinook and 1997 for steelhead (Schaller et al. 2007). Knudsen et al. (2009) estimated that SARs for Yakima River PIT-tagged hatchery spring Chinook were 25% lower than for untagged fish due to tag shedding and possible tagging mortality. Schaller et al. (2007) reported that SARs for Snake River wild PIT-tagged Chinook averaged 19% less than from run reconstruction methods. However, because run reconstruction methods contained many assumptions, Schaller et al. (2007) could not conclusively determine whether an actual bias existed in either method. For our present purposes, a 19% bias in PIT-tag SARs appears inconsequential. Multiple regression analyses were generally insensitive to using a correction factor of 1.19 for PIT-tag SARs for both Chinook and steelhead.

This study advanced the understanding of the role of river conditions during seaward migration and ocean conditions on SARs and marine survival rates of

Table 3. Regression model results (selected) for (a) smolt to adult life-stage mortality rate, −ln(SAR), and (b) first year ocean mortality rate, −ln(S3), of Snake River steelhead versus ocean and river environmental variables, smolt migration years 1964–2005.

Number of variables	Adjusted R^2	R^2	AIC	BIC	Variable	Estimate	SE	Pr > [*t*]	Selection criteria
(a)									
2	0.4293	0.4639	−41.0335	−37.8851	Intercept	−0.5883	1.4881	0.6953	Best BIC
					MayUP45n	−0.0127	0.0034	0.0008	
					MeanMaxT	0.4121	0.1329	0.0041	
3	0.4479	0.4981	−41.2720	−37.1372	Intercept	−1.1737	1.5200	0.4461	Best adjusted R^2, AIC
					MayUP45n	−0.0120	0.0034	0.1634	
					MarSST45n	0.1606	0.1124	0.0361	
					MeanMaxT	0.3198	0.1458		
4	0.4346	0.5032	−39.6168	−34.7912	Intercept	−0.9010	1.6179	0.5819	Best 4 variable model
					MayUP45n	−0.0113	0.0037	0.0051	
					MarSST45n	0.1386	0.1207	0.2605	
					MeanMaxT	0.3052	0.1500	0.0511	
					pT	0.1554	0.2858	0.5908	
(b)									
2	0.5599	0.5865	−22.1864	−19.1585	Intercept	1.8773	0.3093	<0.0001	Best AIC, BIC
					MayPDO	0.5337	0.1056	<0.0001	
					WTT	0.0486	0.0176	0.0094	
3	0.5616	0.6015	−21.4373	−17.7264	Intercept	−0.5318	2.2929	0.8182	Best adjusted R^2
					MayPDO	0.5306	0.1055	<0.0001	
					MeanMaxT	0.2411	0.2273	0.2975	
					WTT	0.0336	0.0225	0.1465	
4	0.5572	0.6109	−20.2503	−15.8177	Intercept	−0.6682	2.3101	0.7744	Best 4 variable model
					MayPDO	0.4934	0.1149	0.0002	
					MayUP45n	−0.0045	0.0054	0.4090	
					MeanMaxT	0.2787	0.2329	0.2410	
					WTT	0.0262	0.0243	0.2883	

Snake River Chinook and steelhead. This advanced understanding will be valuable to inform which actions taken inland will provide the greatest benefits for these at-risk populations. The large declines in these populations following FCRPS completion was not accompanied by major survival rate decreases in the spawner to smolt stage (Petrosky et al. 2001; Wilson 2003; Yuen & Sharma 2005; Budy & Schaller 2007). For both species, we found evidence that SARs and marine survival rates were impacted by conditions in the migratory corridor associated with FCRPS development and operation. Results of this study considerably contribute to improved understanding of how seaward migration conditions in the FCRPS have influenced SARs during varying ocean conditions.

Given this decrease in SARs, the NPCC (2009) emphasis on achieving SAR goals in the face of varying ocean conditions is critical for recovery. Our analysis suggests that it will be extremely difficult to achieve the NPCC goal of 2–6% SARs without modifying river conditions in the FCRPS. Given projections for degrading ocean conditions (i.e., global warming), our analysis suggests that a precautionary management approach would focus on improving in-river migration conditions by reducing WTT, relying on increased spill to reduce passage through powerhouse turbines and collection/bypass systems, or other actions that would increase water velocity, reduce delay at dams and substantially reduce FTT through the FCRPS.

Acknowledgements

We thank staff of the Fish Passage Center and Eric Tinus for environmental and management data sets and David Hines for creating the map. We greatly appreciate the reviews and comments of Christina Luzier, Tim Roth, Eric Tinus, Paul Wilson and two anonymous referees. Partial funding was provided by Bonneville Power Administration Contract 19960200. The findings and conclusions in this manuscript are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

References

Berggren, T.J. & Filardo, M.J. 1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River Basin. North American Journal of Fisheries Management 13: 48–63.

Budy, P. & Schaller, H. 2007. Evaluating tributary restoration potential for Pacific salmon recovery. Ecological Applications 17: 1068–1086.

Budy, P., Thiede, G.P., Bouwes, N., Petrosky, C.E. & Schaller, H. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. North American Journal of Fisheries Management 22: 35–51.

Burnham, K.P. & Anderson, D.R. 2002. Model selection and inference – a practical information-theoretic approach, 2nd edn. New York: Springer-Verlag.

Ceballos, J.R., Pettit, S.W., McKern, J.L., Boyce, R.R. & Hurson, D.F. 1993. Fish Transportation Oversight Team Annual Report – FY 1992. Transport Operations on the Snake and Columbia Rivers. NOAA Technical Memorandum NMFS F/NWR-32.

Deriso, R.B., Marmorek, D.R. & Parnell, I.J. 2001. Retrospective patterns of differential mortality and common year-effects experienced by spring and summer Chinook (*Oncorhynchus tshawytscha*) of the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 58: 2419–2430.

Draper, N.R. & Smith, H. 1998. Applied regression analysis, 3rd edn. New York: John Wiley & Sons, Inc.

Francis, R.C. & Mantua, N.J. 2003. Climatic influences on salmon populations in the Northeast Pacific. In: MacCall, A. & Wainwright, T., eds. Assessing extinction risk for West Coast Salmon. Proceedings of the Workshop, November 1996. National Marine Fisheries Service, NOAA Technical Memorandum NMFS-NWFSC-56 April 2003, pp. 37–76.

Healy, M. 1991. Life history of Chinook salmon. In: Groot, C. & Margolis, L., eds. Pacific salmon life histories. Vancouver, BC: University of British Columbia Press, pp. 313–391.

ISG (Independent Scientific Group) 1999. Return to the river: scientific issues in the restoration of salmonid fishes in the Columbia River. Fisheries 24: 10–19.

Knudsen, C.M., Johnson, M.V., Schroder, S.V., Bosch, W.J., Fast, D.E. & Strom, C.R. 2009. Effects of Passive Integrated Transponder tags on smolt to adult recruit survival, growth, and behavior of hatchery spring Chinook salmon. North American Journal of Fisheries Management 29: 658–669.

Lawson, P.W. 1993. Cycles in ocean productivity, trends in habitat quality, and the restoration of salmon runs in Oregon. Fisheries 18: 6–10.

Logerwell, E.A., Mantua, N.J., Lawson, P.W., Francis, R.C. & Agostini, V.N. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fisheries Oceanography 12: 554–568.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. & Francis, R.C. 1997. A Pacific decadal climate oscillation with impacts on salmon. Bulletin of the American Meteorological Society 78: 1069–1079.

Marmorek, D.R., Peters, C.N. & Parnell, I. (eds) 1998. PATH final report for fiscal year 1998. Compiled and edited by ESSA Technologies, Ltd., Vancouver, BC. Bonneville Power Administration, Portland, Oregon, 263 pp. Available at: http://www.essa.com/documents/1998_Final_Report.pdf. Accessed website on April 06, 2010.

Marmorek, D.R., Porter, M., Parnell, I.J. & Peters, C. (eds) 2004. Comparative Survival Study Workshop, February 11–13, 2004; Bonneville Hot Springs Resort. Report compiled and edited by ESSA Technologies Ltd., Vancouver, BC for Fish Passage Center, Portland, OR and the US Fish and Wildlife Service, Vancouver, WA, 137 pp.

Mueter, F.J., Peterman, R.M. & Pyper, B.P. 2002. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. Canadian Journal of Fisheries and Aquatic Sciences 59: 456–463.

Mueter, F.J., Pyper, B.J. & Peterman, R.M. 2005. Relationships between coastal ocean conditions and survival rates of Northeast Pacific salmon at multiple lags. Transactions of the American Fisheries Society 134: 105–119.

Muir, W.D., Marsh, D.M., Sanford, B.P., Smith, S.G. & Williams, J.G. 2006. Post-hydropower system delayed mortality of transported Snake River stream-type Chinook salmon: unraveling the mystery. Transactions of the American Fisheries Society 135: 1523–1534.

Nickelson, T.E. 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production Area. Canadian Journal of Fisheries and Aquatic Sciences 43: 527–535.

Nickelson, T.E. & Lawson, P.W. 1998. Population viability of coho salmon, *Oncorhynchus kisutch*, in Oregon coastal basins: application of a habitat-based life cycle model. Canadian Journal of Fisheries and Aquatic Sciences 55: 2383–2392.

NMFS (National Marine Fisheries Service) 2008. Operation of the Federal Columbia River Power System, 11 Bureau of Reclamation projects in the Columbia Basin and ESA Section 10(a)(1)(A) Permit for Juvenile Fish Transportation Program. (Revised and reissued pursuant to court order, NWF v. NMFS, Civ. No. CV-01-640-RE (D. Oregon)). Bonneville Power Administration, U.S. Department of Energy, U.S. Bureau of Reclamation, National Marine Fisheries Service, Portland, OR, USA. Available at: http://www.salmonrecovery.gov/BiologicalOpinions/FCRPS.aspx. Accessed website on April 06, 2010.

NPCC (Northwest Power and Conservation Council) 2003. Mainstem Amendments to the Columbia River Basin Fish and Wildlife Program. Council Document 2003-11. Available at: http://www.nwcouncil.org/library/2003/2003-11.htm.

NPCC (Northwest Power and Conservation Council) 2009. Columbia River Basin Fish and Wildlife Program. Council Document 2009-02. Available at: http://www.nwcouncil.org/library/2009/2009-02.htm.

Pacific Salmon Commission 1988. Chinook Technical Committee 1987 Annual Report (88-2), Appendix II: Exploitation rate analysis. Vancouver, BC: Pacific Salmon Commission.

Park, D.L. 1985. A review of smolt transportation to bypass dams on the Snake and Columbia rivers. NMFS Report, U.S. COE contract DACW68-84-H-0034.

Pearcy, W.G. 1992. Ocean ecology of North Pacific salmonids. Seattle, WA: University of Washington Press.

Peterman, R.M. 1981. Form of random variation in salmon smolt-to-adult relations and its influence on production estimates. Canadian Journal of Fisheries and Aquatic Sciences 38: 1113–1119.

Peterson, W.T., Hooff, R.C., Morgan, C.A., Hunter, K.L., Casillas, E. & Ferguson, J.W. 2006. Ocean conditions and salmon survival in the Northern California Current. Newport, OR: Northwest Fisheries Science Center, Newport Research Station. Available at: http://www.nwfsc.noaa.gov/research/divisions/fed/ecosysrep.pdf.

Petrosky, C.E., Schaller, H.A. & Budy, P. 2001. Productivity and survival rate trends in the freshwater spawning and rearing stage of Snake River chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 58: 1196–1207.

PFMC (Pacific Marine Fisheries Council) 2003. Pacific Coast Salmon Plan – Fishery Management Plan for commercial and recreational salmon fisheries off the coasts of Washington, Oregon and California as revised through amendment 14 (Adopted March 1999). PFMC, Portland, OR, USA.

Pyper, B.J. & Peterman, R.M. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. Canadian Journal of Fisheries and Aquatic Sciences 55: 2127–2140.

Pyper, B.J., Mueter, F.J. & Peterman, R.M. 2005. Across-species comparisons of spatial scales of environmental effects on survival rates of Northeast Pacific salmon. Transactions of the American Fisheries Society 134: 86–104.

Raymond, H.L. 1979. Effects of dams and impoundments on migrations of smolt chinook salmon and steelhead from the Snake River, 1966–1975. Transactions of the American Fisheries Society 90: 58–72.

Raymond, H.L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer Chinook salmon and steelhead in the Columbia River Basin. North American Journal of Fisheries Management 8: 1–24.

Ricker, W.E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. Journal of the Fisheries Research Board of Canada 33: 1483–1524.

SAS. 2002. SAS/STAT users guide, version 9.1. Cary, NC: SAS Institute.

Schaller, H.A. & Petrosky, C.E. 2007. Assessing hydrosystem influence on delayed mortality of Snake River stream-type Chinook salmon. North American Journal of Fisheries Management 27: 810–824.

Schaller, H.A., Petrosky, C.E. & Langness, O.P. 1999. Contrasting patterns of productivity and survival rates for stream-type Chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers. Canadian Journal of Fisheries and Aquatic Sciences 56: 1031–1045.

Schaller, H., Wilson, P., Haeseker, S., Berggren, T., Petrosky, C., Tinus, E., Dalton, T., Woodin, R., Weber, E., Bouwes, N., McCann, J., Rassk, S., Franzoni, H. & McHugh, P. 2007. Comparative Survival Study (CSS) of PIT-tagged spring/summer Chinook and steelhead of the Columbia River Basin: ten-year retrospective analyses report. BPA Contract # 19960200. Prepared by Fish Passage Center and Comparative Survival Study Oversight Committee representing the Columbia Basin Fish and Wildlife Agencies and Columbia Basin Tribes, 675 pp. Available at: http://www.fpc.org/documents/CSS/FINAL%20COMPLETE%2010%20YEAR%20CSS%20REPORT-8-31-07withfrontpage.pdf. Accessed website on April 6, 2010.

Scheuerell, M.D. & Williams, J.G. 2005. Forecasting climate-induced changes in the survival of Snake River spring/summer Chinook salmon. Fisheries Oceanography 14: 1–10.

Scheuerell, M.D., Zabel, R.W. & Sandford, B.P. 2009. Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus* spp.). Journal of Applied Ecology 46: 983–990.

Smith, S.G., Muir, W.D., Williams, J.G. & Skalski, J.R. 2002. Factors associated with travel time and survival of migrant yearling Chinook salmon and steelhead in the Lower Snake

River. North American Journal of Fisheries Management 22: 385–405.

TAC (U.S. versus Oregon Technical Advisory Committee) 2008. Biological Assessment of Incidental Impacts on Salmon Species listed under the Endangered Species Act in the 2008-2017 Non-Indian and Treaty Indian fisheries in the Columbia River Basin. April 21, 2008. National Marine Fisheries Service, Portland, OR, USA.

Williams, J.G., Smith, S.G. & Muir, W. 2001. Survival estimates for downstream migrant yearling juvenile salmonids through the Snake and Columbia rivers hydropower system, 1966-1980 and 1993-1999. North American Journal of Fisheries Management 21: 310–317.

Williams, J.G., Smith, S.G., Zabel, R.W., Muir, W.D., Scheuerell, M.D., Sandford, B.D., Marsh, D.M., McNatt, R.A. & Achord, S. 2005. Effects of the Federal Columbia River Power System on salmonid populations. NOAA Technical Memorandum NMFS-NWFSC-63. Available at: http://www.nwfsc.noaa.gov.

Wilson, P.H. 2003. Using population projection matrices to evaluate recovery strategies for Snake River spring and summer Chinook salmon. Conservation Biology 17: 782–794.

Wissmar, R.C. & Bisson, P.A. (eds) 2003. Strategies for restoring rivers: problems and opportunities. In: Strategies for restoring river ecosystems: sources of variability and uncertainty in natural and managed systems. Bethesda, MD: American Fisheries Society, pp. 248–262.

Yuen, H. & Sharma, R. 2005. Using simulation techniques to estimate management parameters on Snake River steelhead: declines in productivity make rebuilding difficult. North American Journal of Fisheries Management 25: 446–463.

Zabel, R.W., Scheuerell, M.D., McClure, M.M. & Williams, J.G. 2006. The interplay between climate variability and density dependence in the population viability of Chinook salmon. Conservation Biology 20: 190–200.