

Evaluating habitat effects on population status: influence of habitat restoration on spring-run Chinook salmon

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SUMMARY

1. A key element of conservation planning is the extremely challenging task of estimating the likely effect of restoration actions on population status. To compare the relative benefits of typical habitat restoration actions on Pacific salmon (*Oncorhynchus* spp.), we modelled the response of an endangered Columbia River Chinook salmon (*O. tshawytscha*) population to changes in habitat characteristics either targeted for restoration or with the potential to be degraded.
2. We applied a spatially explicit, multiple life stage, Beverton-Holt model to evaluate how a set of habitat variables with an empirical influence on spring-run Chinook salmon survivorship influenced fish population abundance, productivity, spatial structure and diversity. Using habitat condition scenarios – historical conditions and future conditions with restoration, no restoration, and degradation – we asked the following questions: (i) how is population status affected by alternative scenarios of habitat change, (ii) which individual habitat characteristics have the potential to substantially influence population status and (iii) which life stages have the largest impact on population status?
3. The difference in population abundance and productivities resulting from changes in modelled habitat variables from the ‘historical’ to ‘current’ scenarios suggests that there is substantial potential for improving population status. Planned restoration actions directed toward modelled variables, however, produced only modest improvements.
4. The model predicted that population status could be improved by additional restoration efforts directed toward further reductions in the percentage of fine sediments in the streambed, a factor that has a large influence on egg survival. Actions reducing fines were predicted to be especially effective outside the national forest that covers most of the basin. Scenarios that increased capacity by opening access to habitat in good condition also had a positive but smaller effect on spawner numbers.
5. Degradation in habitat quality, particularly in percent fine sediments, within stream reaches located in the national forest had great potential to further reduce this population’s viability. This finding supports current forest planning efforts to minimise road density and clear-cut harvests and to return forest stand structure in dry regions to the historical condition that promoted frequent low-intensity fires rather than catastrophic stand-replacing fires, as these landscape factors have been shown to influence percent fine sediment in streams.

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6. Together, these results suggest that planning focusing on protecting currently good habitat, reducing fine sediments to promote egg survival and increasing spawner capacity will be beneficial to endangered spring-run Chinook population status.

Keywords: Columbia River, life cycle, modelling, *Oncorhynchus tshawytscha*, Shiraz

Introduction

Predicting the response of populations to changing habitat is a challenging but necessary step toward optimally allocating limited resources in restoration efforts (Brooks *et al.*, 2006). However, such predictions are made difficult by a lack of monitoring data to describe habitat condition and variability as well as by a limited understanding of how key habitat characteristics are influencing a species' population status (Bernhardt *et al.*, 2005; Katz *et al.*, 2007). These challenges are exacerbated when species use more than one ecosystem as they progress through their life-history stages (Rich, 1939; Abell, 2002).

Pacific salmon (*Oncorhynchus* spp.) are an exemplary case in point. A dramatic decline in wild salmon populations in the U.S. Pacific Northwest followed pervasive human impacts during the 19th and 20th centuries (Nehlsen, Williams & Lichatowich, 1991; National Research Council, 1996; McClure *et al.*, 2003). Obvious among these impacts are habitat degradation and loss. Freshwater habitat for salmon spawning and rearing has been altered by floodplain and upland development, past forest management policies and dam construction for irrigation, flood-control, navigation and hydropower. Habitat restoration is therefore a major component of recovery plans for salmonid populations listed as threatened or endangered under the U.S. Endangered Species Act (e.g. Williams *et al.*, 1999; Shared Strategy for Puget Sound, 2005; Upper Columbia Salmon Recovery Board, 2007) with hundreds of millions of dollars thus far spent in the U.S.A. to restore habitat for Pacific salmon (Pacific Coastal Salmon Recovery Fund, 2007). The economic and cultural importance of this resource, as well as the high cost of recovery, increase the need for tools to direct recovery efforts where they will be most effective.

Our objective was to model and evaluate the effects on spring-run Chinook salmon (*O. tshawytscha* Walbaum) of stream habitat change resulting from

either further degradation or a suite of proposed restoration actions targeting Chinook spawning and rearing habitat in the Wenatchee River and its tributaries in the interior Columbia River basin. Wenatchee spring-run Chinook salmon are one of three extant independent populations (ICTRT, 2003) that make up the upper Columbia spring-run Chinook salmon Evolutionarily Significant Unit (ESU) which is listed as endangered under the ESA (National Marine Fisheries Service, 1999a,b). The quality and quantity of spring-run Chinook salmon habitat in the Wenatchee River basin have been degraded by the influences of roads, agricultural and residential development, reduced connectivity of off-channel floodplain habitat in the lower reaches due to berm construction and channelisation, decreased density and recruitment of large wood and water withdrawal during summer low flow periods (Andonaegui, 2001). Several local conservation plans have recently been developed to address these threats (Northwest Power and Conservation Council, 2005; Upper Columbia Salmon Recovery Board, 2007; Upper Columbia Regional Technical Team, 2008). These plans propose habitat restoration in the more heavily impacted lower catchment and conservation of habitat in the upper catchment which remains relatively intact.

To investigate the response of wild spring-run Chinook to habitat change resulting from restoration or degradation, we adapted a spatially explicit, life stage specific, population dynamics model, Shiraz (Scheuerell *et al.*, 2006; Battin *et al.*, 2007), to address the following questions for the Wenatchee basin population:

- How does population status change in response to alternative scenarios of habitat change?
- Which individual habitat characteristics have the potential to substantially influence population status, through either improvement or degradation?
- Do life stage specific habitat influences determine which life stage has the largest effect on population status?

Application of this population dynamics model involved developing new relationships between habitat characteristics and population vital rates (survivorship or carrying capacity) specific to this region. The model included direct effects of harvest, survival through the series of seven dams on the Columbia River, competition with hatchery fish, removal of wild fish for hatchery broodstock and climate effects on ocean survivorship in order to assess the extent to which freshwater habitat is a key factor limiting the abundance, productivity and distribution of spring-run Chinook salmon in the Wenatchee River basin. We used this model to compare the relative influences of important habitat characteristics on population status and to describe where in the basin those habitat characteristics may be altered by restoration actions and other landscape changes.

Methods

Study area and species life history

The Wenatchee River catchment drains approximately 3400 km² in a southeasterly direction east of the crest of the Cascade Range in central Washington State (Fig. 1). While approximately 80% of the area of the catchment is in federal ownership (95% of which is managed by the USDA Forest Service), mostly in the upper catchment, a disproportionate amount (*c.* 33%) of the riparian zones of stream reaches currently accessible to anadromous salmonids is in private ownership (Northwest Power and Conservation Council, 2005). [Jorgensen *et al.* \(2009\)](#) provide a more detailed description of the basin.

Wenatchee River spring-run Chinook salmon are 'stream-type' Chinook (Healey, 1991): after juveniles emerge from gravels in spring, they rear in freshwater for approximately a year before outmigrating ('Ocean-type' fish migrate shortly after hatching). A varying percentage (15–60%) move downstream through the first summer or autumn and over-winter in the mainstem Wenatchee (Don Chapman Consultants Inc., 1989; Washington Department of Fish and Wildlife, WDFW, unpubl. data), before out-migrating to the ocean in the second spring along with those that over-wintered in the tributaries. To reach the ocean, juveniles must swim 754 km down the Columbia River and pass through seven public and private dams of the Columbia River hydropower system: Rock Island, Wanapum, Priest Rapids, McNary, John Day, The Dalles and Bonneville. Adults begin their return to the Wenatchee after 1–4 years at sea, most after 2 years, re-entering the Columbia from late March to early April (Washington State Department of Fisheries, 1993). After making their way upstream past the dams, adults remain in deeper reaches of the Wenatchee system from early May to late June before moving to the upper Wenatchee mainstem and upstream tributaries to spawn from August to mid-September, with the peak in mid- to late August ([Mullan *et al.*, 1992](#); [Chapman *et al.*, 1995](#)). Between 1960 and 1993, the average return of wild spring-run Chinook salmon to the Wenatchee basin was 2356 spawners; however between 1994 and 2003, the average return was only 423 wild fish (Fig. 2; West Coast Salmon Biological Review Team, 2003; ICTRT, 2007a).

We focused our study on the Wenatchee River basin because this subbasin of the Columbia River provided

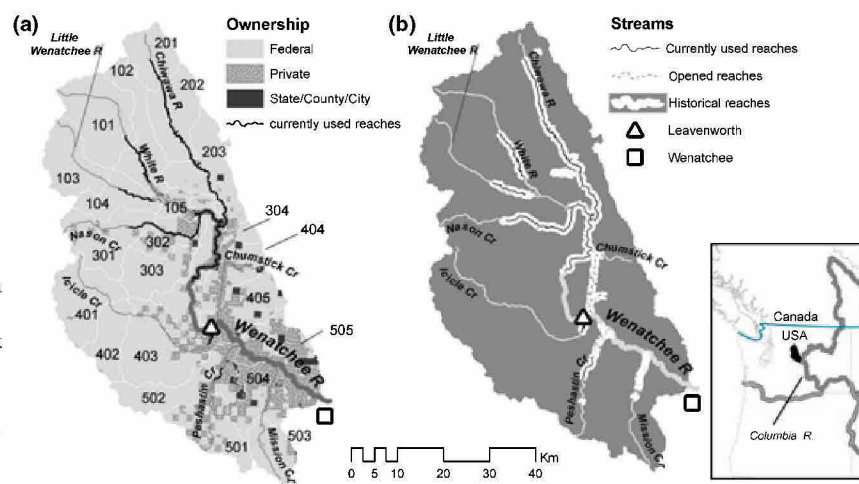


Fig. 1 Maps of the Wenatchee River basin showing (a) HUC6 model areas, current ownership and use by spring-run Chinook and (b) estimated extent of stream network occupied by Chinook historically, currently (same under no restoration and degradation scenarios), and under restoration.

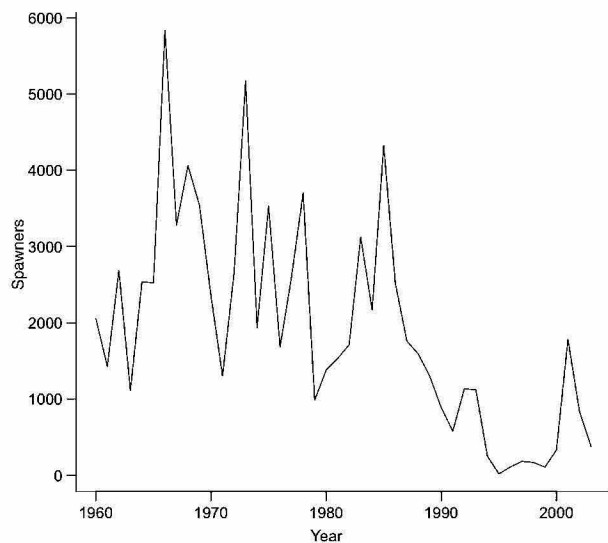


Fig. 2 The number of spring-run Chinook salmon spawners observed in the Wenatchee basin, 1960–2003.

a number of opportunities. It is included in the Intensively Monitored Watershed Project, a multi-agency effort in Washington State to determine the influence of habitat factors on salmon populations. Therefore, substantially more habitat and fish population data are available for the Wenatchee River basin than for others in the region. The diversity of impacts on spring-run Chinook salmon in the basin allowed us to produce a model that may be characteristic of populations in other subbasins of the Interior Columbia River basin; the active recovery community provided a forum for developing scenarios of restoration actions. These findings will inform future projects and monitoring efforts in the basin.

Population-habitat modelling

Population structure For modelling purposes, we separated Wenatchee basin spring-run Chinook salmon into four distinct and interacting groups, one wild and three hatchery, due to observed life stage dependent variations in spatial distributions and differences in fish response to habitat condition detailed below. The three hatchery groups were (i) the Leavenworth National Fish Hatchery (LNFH) group, produced to support a recreational and tribal fishery of spring-run Chinook salmon in Icicle Creek and to supplement harvest in the Columbia River; (ii) a Chiwawa hatchery group produced in an 'integrated recovery program' at the Rock Island Fish

Hatchery Complex and intended to increase the production of wild spring-run Chinook salmon in the Chiwawa River; and (iii) a White River Hatchery group, produced in a captive broodstock program established to support the recovery of spring-run Chinook salmon in the White River (Grant PUD, WDFW & Yakama Nation, 2007).

Separating hatchery groups allowed us to (i) account for the multiple locations of broodstock collection and fry release, (ii) set hatchery-specific fractions of the wild return to be collected for broodstock each year, and (iii) have the influence of habitat condition on survivorship be group-specific. Group-specific survivorship may result when hatchery fish differ phenotypically and genetically from local wild fish. Such differentiation may occur when the original broodstock were taken from another basin, as is the case with the LNFH group (Columbia River Basin Hatchery Review Team, 2006; Murdoch *et al.*, 2006), and when selection pressures differ between hatchery and natural habitats (Busack & Currens, 1995; Knudsen *et al.*, 2006; McClure *et al.*, 2008a). Each of the hatchery groups also had a hatchery facility-specific survivorship between the life stage collected for broodstock and the stage released.

We included the hatchery groups in the model because of the potential for substantial influence on the wild population; however, our interest is in the status of the wild population in response to changes in habitat condition. Therefore all model output (e.g. productivity, mean number of smolts or spawners) is expressed in terms of wild fish.

Life history We modelled the wild fish through the following life-history stages: egg, fry, overwinter, smolt, ocean adult, upstream adult and spawner (Fig. 3). Spawners that mature without going to sea, predominantly male and termed 'mini-jacks', were not included because mini-jacks are not commonly observed among Wenatchee wild spring-run Chinook spawners (Murdoch *et al.*, 2006). Hatchery groups progressed through the same life stages after release as smolts until captured as spawning adults for broodstock. At hatchery broodstock collection, we removed an additional 3000 spawners from the LNFH group to account for those donated to tribes and other groups (Cooper, 2006). Hatchery fish that were not removed for broodstock or donation were modelled to

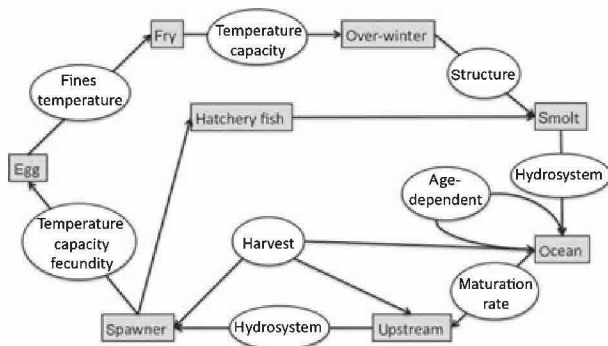


Fig. 3 Model life cycle with stages (shaded rectangles) and factors influencing stage transitions (ovals).

spawn naturally (WDFW, 2005; Columbia River Basin Hatchery Review Team, 2006) and the resulting progeny were added to the wild fish.

Harvest Harvest inflicts both direct mortality and has the potential to influence fish response to freshwater habitat changes (Scheuerell *et al.*, 2006), particularly when survival between life stages is density-dependent. The catch of interior Columbia River spring-run Chinook salmon is heavily regulated due to its importance to tribal fisheries, and the potential impacts of harvest on the recovery of these depleted populations. The harvest rates for the wild group were taken from the Spring Management Period Chinook Harvest Rate Schedule (Parties to U.S. v. Oregon, 2005). Run-size categories given on the schedule were scaled to the Wenatchee wild group based on the estimated proportion of wild fish from the Wenatchee basin among the total observed at Bonneville Dam, 1979–2001. The proportion of wild Wenatchee fish at Bonneville was back-calculated from the number and proportions of wild and hatchery spawners observed in the Wenatchee and the number of spring-run Chinook salmon counted at Bonneville Dam. A fishery for the wild group was modelled to take place only in the mainstem Columbia, reflecting current management policy (Parties to U.S. v. Oregon, 2005).

Sport and ceremonial tribal fisheries of hatchery fish (but aimed at LNFH fish) occur on Icicle Creek and in the mainstem below the hatchery facility. The harvest rates in these fisheries for the LNFH group were based on fishery-specific catches for 1999–2005 (Cooper, 2006). Ocean catch, including by-catch, took *c.*

0.2% of the return of the LNFH group and was combined with the fishery occurring in the Columbia River mainstem for simplicity. The other hatchery groups, for which we had no group-specific harvest data, were modelled at the same harvest rate as the LNFH group below Icicle Creek, because individuals in these groups have their adipose fins clipped to indicate hatchery origin and so are indistinguishable by fishers at the point of harvest. None were modelled to be harvested above Icicle Creek where there is no spring-run Chinook salmon fishery (WDFW, 2008).

Habitat-associated survival We modified a spatially explicit population dynamics model, Shiraz (Scheuerell *et al.*, 2006; Battin *et al.*, 2007), to investigate habitat influences on the status of Wenatchee basin spring-run Chinook salmon. In the model, fish were classified according to population group, life history stage, natal location and current location. Each class progressed through the life history stages and we modelled successive generations over 100 years. This sequence was repeated 500 times for each scenario of habitat conditions described below. A multi-stage, Beverton-Holt spawner-recruit function (Moussalli & Hilborn, 1986) was applied to each class at each life stage transition to determine the number of fish surviving to the next life stage:

$$N_{\text{stage}+1} = \frac{N_{\text{stage}}}{\frac{1}{p_{\text{stage}}} + \frac{1}{c_{\text{stage}}}} \quad (1)$$

where N_{stage} and $N_{\text{stage}+1}$ are the number in the current and next life stages, respectively, p_{stage} is the productivity or survivorship through residence in the current location and $c_{\text{stage}+1}$ is the capacity of the next location to which the group moves (more about movement below). Survivorship depended on fish location as a consequence of the relationship described below between habitat parameters (e.g. fine sediment, water temperature, habitat structure) and fish survivorship. The capacity parameter was used to cause a density-dependent response of population size at the fry and spawner life stages. To determine the density-dependent response at each location, the numbers of all wild and hatchery groups of the same life stage at that location were included in the calculation.

We incorporated all habitat variables with empirical links to spring-run Chinook salmon survivorship and for which data were available in the Wenatchee basin.

Some habitat–survival relationships were identified from the literature while others were developed from data collected in the basin, as detailed below. Where functional relationships linking habitat parameters to survivorship through a life stage were not available, survivorship through that stage was given a fixed value from the literature or based on data available from the basin as described below.

Spawner stage: Survivorship of spring-run Chinook spawners is influenced by water temperature (see reviews by McCullough, 1999; and Richter & Kolmes, 2005). We used a water temperature-dependent survivorship function developed by Scheuerell *et al.* (2006) from observations by Cramer (2001) of wild spring-run Chinook:

$$p_{1,Tw} = \begin{cases} 1 & \text{if } T_{pre} < 16 \\ 1 - 0.15(T_{pre} - 16) & \text{if } 16 \leq T_{pre} < 22.6 \\ 0.01 & \text{if } T_{pre} \geq 22.6 \end{cases} \quad (2)$$

where T_{pre} is the mean of daily maximum temperature (°C) August–September. We developed a separate function for hatchery spring-run Chinook survival based on Cramer's (2001) observations of reduced survivorship of hatchery fish in the same conditions:

$$p_{1,Th} = \begin{cases} 1 & \text{if } T_{pre} < 16 \\ 5.43 - 0.28 * T_{pre} & \text{if } 16 \leq T_{pre} < 19 \\ 0.01 & \text{if } T_{pre} \geq 19 \end{cases} \quad (3)$$

Fecundities of age-three, -four, -five and -six females from LNFH were derived from the mean fecundity of grouped ages and mean age distribution 1994–2005 reported by Cooper (2006) (Table 1). The fecundities for age-four wild and Chiwawa hatchery females were taken from Murdoch *et al.* (2006). For age-three and -five spawners of the wild and Chiwawa hatchery groups, we selected the values used in another modelling effort (Cooney *et al.*, 2002) that incorporated age-specific fecundities for upper Columbia River spring-run Chinook which were derived from data in Chapman *et al.* (1995). The White River hatchery spawner fecundities were assumed to be the same as those of adults from the Chiwawa hatchery. The fecundity of age-six females of each group was assumed to be the same as that of age-five fish from the respective groups, except for the LNFH group for which data were available for age-six females (Cooper, 2006).

Table 1 Fecundity per spawner

Spawner age	Wild	LNFH	Chiwawa and White hatcheries
3	1000	500	1000
4	2417	2100	2338
5	2700	2500	2700
6	2700	2500	2700

We estimated spawner capacity using the intrinsic potential analysis of the Interior Columbia Technical Recovery Team (ICTRT, 2007b) which predicts historical fish numbers based on stream gradient, width and valley confinement – applied to available spawning area. We also considered actual spawner and redd counts conducted by the Chelan County Public Utility District and the WDFW from 1958 to 2003 (C. Baldwin, WDFW, W.A. Wenatchee, pers. comm.). When the maximum number of spawners observed in an area was greater than the number estimated based on the intrinsic potential analysis, we used the observed values.

Egg stage: Water temperature influences egg-to-fry survivorship in a nonlinear fashion with decreased survival above and below an optimal range (Fowler, 1972; Murray & McPhail, 1988). We used the same survivorship function employed in Scheuerell *et al.* (2006):

$$p_{2,T} = \begin{cases} 0.273T_{inc} - 0.342 & \text{if } 1.3 \leq T_{inc} < 4.7 \\ 0.94 & \text{if } 4.7 \leq T_{inc} < 14.3 \\ -0.245T_{inc} + 4.44 & \text{if } 14.3 \leq T_{inc} < 18.1 \\ 0.01 & \text{if } T_{inc} \geq 18.1 \end{cases} \quad (4)$$

based on the findings of Velsen (1987) and Beacham & Murray (1989), where T_{inc} is the mean of 24 h daily means of water temperature (°C) during the incubation period (August–May).

The percentage of fine sediments in the streambed also has a strong negative effect on egg-to-fry survivorship (Tappel & Bjornn, 1983; Wood & Armitage, 1997). We used data from Tappel & Bjornn (1983) to develop a relationship for fines:

$$p_{2,f} = \begin{cases} 0.93 & \text{if } f < 11.6 \\ -5.21 + 1.54 & \text{if } 11.6 \leq f < 28.3 \\ 0.06 & \text{if } f \geq 28.3 \end{cases} \quad (5)$$

where f is % fines < 1.7 mm.

Fry stage: Survivorship through the fry stage to the overwintering stage is influenced by summer water

temperatures (see reviews by McCullough, 1999; Richter & Kolmes, 2005). We used the survivorship function developed by McHugh, Budy & Schaller (2004) based on data from Brett (1952), McCormick, Hokanson & Jones (1972), and Coutant (1973):

$$p_{3,T} = \begin{cases} \exp\left\{-\left[\left(\frac{T_{\text{sum}}}{27.0271}\right)^{10.74}\right]\right\} & \text{if } T_{\text{sum}} > 17.8^\circ\text{C} \\ 1 & \text{if } T_{\text{sum}} \leq 17.8^\circ\text{C} \end{cases} \quad (6)$$

where T_{sum} is mean daily temperature ($^\circ\text{C}$) August–September.

We estimated fry capacity using the intrinsic potential analysis of the ICTRT (2007b), which predicts historical fish numbers based on a relationship they developed between maximum fry densities observed in relatively pristine reaches of Salmon River drainage (Idaho) tributaries (Petrosky & Holubetz, 1988), and stream gradient, width and valley confinement.

Overwinter stage: Structures in pools have a strong influence on survivorship through the overwintering stage (Hillman, Chapman & Griffith, 1989a,b). To model the influence of structure we used a function developed by Cramer (2001) based on work by Raleigh, Miller & Nelson (1986):

$$p_{4,\text{str}} = \begin{cases} \left(20 + 80 * \frac{\% \text{structure}}{15}\right) / 100 & \text{if } \% \text{structure} < 15 \\ 1 & \text{if } \% \text{structure} \geq 15 \end{cases} \quad (7)$$

where $\% \text{structure}$ is the percent of pool area covered by cobbles and boulders. We assumed that fish numbers were not limited by capacity during this stage, given the combination of downstream movement and capacity limits during the previous fry stage in summer when there was less habitat area due to lower discharge.

Smolt and ocean stages: We used literature values for survival through the Columbia River mainstem (Grant PUD, 2003; Skalski *et al.*, 2005). From Rock Island dam (rkm 729.7), downstream of the mouth of the Wenatchee River (rkm 753.8), to Bonneville dam (rkm 235.1), upstream of the Columbia River Estuary, survivorship was set at 0.441. We assumed that capacity was unlimited during the smolt stage.

Survival rate for the first ocean year included survival through the estuary as well, following McClure *et al.* (2008b) (Table 2). The wild fish group was assigned a rate of 0.0643 ± 0.05 (SD), reflecting mean survivorship through this stage as estimated by

Table 2 Survival rates for ocean stages

Ocean stage	Wild	LNFH	Chiwawa and White hatcheries
First year	0.064 (0.05)	0.032 (0.05)	0.048 (0.05)
Second year	0.80	0.80	0.80
Third year	0.90	0.90	0.90
Fourth year	0.90	0.90	0.90

Values in parentheses are SD.

McClure *et al.* (2008b) for the entire period of record (1966–2001). The survival rates of hatchery groups were set at 50% (LNFH group) and 75% (all other hatchery groups) of that of the wild group (Cooney *et al.*, 2002). Survival rates for subsequent ages of ocean fish were taken from an upper Columbia River spring-run Chinook salmon model (Cooney *et al.*, 2002) which used values from the Pacific Salmon Commission (2001) for simulating harvest management scenarios. Capacity during all ocean ages was assumed to be unlimited.

Maturation and Columbia mainstem survivorship: Age-specific maturation rates, i.e. the probability that ocean fish will return upstream to spawn (Table 3), were derived from the age distribution of all spawners and age-specific sex ratios (Chapman *et al.*, 1995; Cooper, 2006; Murdoch *et al.*, 2006). For wild and Chiwawa hatchery fish, the sex ratio of age-five spawners was not available, so we used the same sex ratio as for age-four fish. The maturation rates for White River hatchery fish were assumed to be the same as those from the Chiwawa hatchery. The maturation rates were based on females because they produce the eggs for the next generation.

The survival rate for maturing adults returning upstream through the Columbia mainstem was set at 0.794 based on the analysis by McClure *et al.* (2008b) of recent PIT-tag data. Capacity was assumed to be unlimited for adults in the mainstem Columbia River.

Table 3 Rates at which ocean stages mature to upstream stages

Ocean stage	Wild	LNFH	Chiwawa and White hatcheries
First year	0	0.051	0.485
Second year	0.650	0.723	0.986
Third year	0.999	0.987	1
Fourth year	1	1	1

Juvenile movement and spawner distribution With sixth-field hydrologic unit codes (HUC6; Seaber, Kapinos & Knapp, 1987) as our unit of scale, we allowed fish to redistribute themselves at the beginning of the fry stage by either remaining in their natal location or moving one HUC6 upstream or downstream, within observed upstream limits (NMFS unpublished GIS layer). Within these limits, fry distributed themselves in an ideal-free manner by moving to the HUC6 with habitat variable values that resulted in the greatest survivorship as constrained by capacity for each area.

We developed another movement function to address observations that a variable percentage of fry move downstream in late summer to overwintering habitat in the Wenatchee mainstem (Don Chapman Consultants Inc, 1989). To identify predictors for the number of early emigrants observed from the Chiwawa River 1992–2003 (Andrew Murdoch, WDFW, Wenatchee, WA, pers. comm), we used multiple linear regression to investigate various predictors related to discharge and fish density. The model with the lowest AIC ($P < 0.001$, adjusted $R^2 = 0.872$, AIC = 189.2886) was

$$mvmt_{4,Q} = -17040 + 102.9Q_{8low} + 0.03221 \text{ egg} \quad (8)$$

where $mvmt_{4,Q}$ is the number of fish in a tributary moving downstream to overwinter in the mainstem Wenatchee, Q_{8low} is minimum August discharge (cfs) at the tributary mouth and egg is the total number eggs deposited in the tributary. We excluded water temperature as a predictor because we had only 3 years of data from the Chiwawa River. Minimum August discharge at the mouth of each tributary was estimated based on a relationship between yearly minimum August discharge and drainage area at each of 14 USGS stations for which data were available in the Wenatchee basin (1907–2005, with the range of years of data varying with stations; USGS, 2006; Raymond R. Smith, USGS, Spokane, WA, pers. comm). This movement function was applied following summer survivorship of the fry stage, when fry transitioned to the overwintering stage.

We used the distribution of model output spawners among the four Level IV Ecoregions (Omernik, 1987) present in the Wenatchee basin to characterise the diversity of Wenatchee spring-run Chinook salmon. In this way we used spatial distribution across

distinctly different habitats, ecoregions in this case, as a proxy for genetic diversity.

Scenarios of change in habitat variables We used the habitat–survivorship relationships described above to model spring-run Chinook salmon response to five scenarios of habitat quality and quantity: (i) current conditions, (ii) historical conditions, a depiction of what the basin might have been like before European settlement, (iii) no restoration, where current rates of change in natural and human activities were extended into the future, (iv) restored conditions resulting from implementation of restoration actions proposed in local conservation plans (Northwest Power and Conservation Council, 2005) (Upper Columbia Salmon Recovery Board, 2007) and (v) a prediction of future habitat degradation (described below). [Jorgensen et al. \(2009\)](#) describe the development of scenarios one to four.

For the restoration scenarios involving increases in habitat, the locations of removed culverts and reconnected side channels were determined by actions currently proposed for the basin (Northwest Power and Conservation Council, 2005). Where descriptions were only generally given (e.g. 'Peshastin River below Ingalls Creek'), we placed side-channels in unconfined valleys (valley width > four times bankfull width) and estimated area as the length of the main channel by an arbitrary 0.25 of the width of the main channel. For the historical scenario, we removed all culverts that blocked Chinook passage and we used the same side-channel additions as in the restoration scenario due to the absence of data describing historical side-channel distribution. Table 4 shows the resulting scenario-specific fry and spawner capacities.

We also developed a scenario of future degradation of habitat to predict the impact on the wild population of a reasonable decline in habitat quality. We estimated habitat degradation in each HUC6 by increasing or decreasing habitat values from the no restoration future scenario by one standard deviation, derived from the posterior distributions of the habitat estimates ([Jorgensen et al., 2009](#)), depending on whether increasing or decreasing the value decreased fish survivorship. For example, the percent of fine sediment in spawning gravels was increased while percent cobble and boulders in pools was decreased. We did not have a distribution for the capacity estimates or a reliable means of estimating degradation of habitat quantity, so we used the current

Table 4 Fry and spawner capacities for each model scenario (separated by '/'). 'No restoration' and 'degradation' scenarios used the same values as the 'current' scenario

Area	Historical	Current	Restoration
101	13 837/92	13 837/92	13 837/92
102	229 144/1060	224 325/1038	224 325/1038
103	0/0	0/0	0/0
104	121 764/563	106 549/493	106 549/493
105	9059/41	6910/31	6910/31
201	20 976/97	17 778/95	17 778/95
202	239 042/1404	233 240/1404	233 240/1404
203	237 617/1100	209 937/971	209 937/971
301	66 746/283	51 715/245	57 159/245
302	219 471/929	197 201/912	219 471/929
303	5104/23	0/6	0/6
304	271 169/1255	270 778/1253	270 778/1253
401	0/0	0/0	0/0
402	0/0	0/0	0/0
403	48 118/539	35 242/539	35 242/539
404	49 712/192	0/0	49 712/192
405	86 185/395	0/5	26 377/118
501	281/25	0/25	0/25
502	67 597/354	23 675/354	28 103/354
503	0/0	0/0	0/0
504	41 198/190	0/0	0/0
505	0/1	0/1	0/1

capacity estimates with the degraded habitat characteristics in this scenario.

Sensitivity analysis We conducted sensitivity analyses to evaluate which specific habitat variables had the greatest influence on fish population dynamics, where those key habitat variables had the greatest potential to effect change in fish numbers, and which life stages were therefore the most sensitive to habitat changes likely to be influenced by restoration or degradation. For this sensitivity analysis, we changed one variable by ± 1 SD from its estimated value in either the historical scenario (for improvement) or the no restoration future scenario (for degradation) across all HUC6 areas while each of the other variables was held at its estimated current value. We then repeated the analysis for each habitat variable in turn, changing only one variable at a time. Because the SD used was a measure of the variation in posterior estimates of habitat condition under different scenarios (Jorgensen *et al.*, 2009), these values fell inside the range of current observed values and are therefore realistic values of improvement or degradation. To test the sensitivity of response to changes in capacity, we used estimates of historical capacity.

Results

Comparing predicted and observed population parameters

A comparison between estimates from field surveys and model results under the current habitat conditions showed a close correspondence in values for smolts, spawners and spawners-per-spawner, thus providing evidence for the validity of the model and its assumptions. The predicted mean number of wild spawners (1600, SD 800) was similar to that observed (1276, SD 1097) over the years 1980–2001 (ICTRT, 2007a). The mean number of smolts predicted by the model (338 800 SD 690 200) was greater than that estimated for brood-years for which smolt-trap data were available (1999–2002: 164 011, SD 122 094; Andrew Murdoch, WDFW, Wenatchee, WA, unpubl. data). However, there were few years with smolt observations and the model estimate fell within the range observed during that period.

Scenarios of habitat change

The restoration scenario had approximately the same abundance and productivity of wild spawners as the scenario with current habitat conditions, as did the scenario of no future restoration actions (Fig. 4). The scenario of future degradation had 51% fewer spawners and 40% lower productivity at its peak relative to the scenario with current conditions. The historical habitat condition scenario resulted in 54% more wild spawners than the estimated number of wild spawners in the scenario with current habitat conditions (excluding hatchery strays in counts under current conditions in all of these reported values). Productivity was greatest in the historical conditions scenario as well, with spawner-to-spawner survivorship greater than the replacement rate at abundances less than *c.* 3400 spawners.

The geographical distributions of spawners were similar among scenarios (Table 5). In all scenarios, more than 95% of spawners occurred in the same two Ecoregions: Chiwaukum Hills and Lowlands (49–54%) and Wenatchee/Chelan Highlands (42–48%). A small proportion of spawning was predicted to occur in the North Cascades Highland Forests in all scenarios. A fourth ecoregion, the Channeled Scablands, is located in the lower mainstem and the predicted historical spawning areas in this ecoregion are now

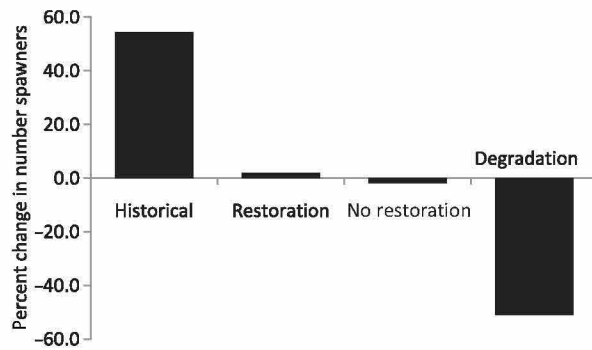


Fig. 4 Percent change in annual spawners, relative to the current scenario, for scenarios of habitat change.

encompassed by the city of Cashmere. No spawning was predicted in the other scenarios to occur in the now degraded reaches of this ecoregion.

Sensitivity analyses

Across the variables we tested, the greatest increase in mean smolt and spawner numbers occurred with a decrease in percent fine sediments in the Middle and Lower Chiwawa, Lower Nason, Lower White and Upper Wenatchee mainstem (Table 6). Increasing spawner capacity also increased fish numbers, although not as much as fines. Spawner capacity increases resulted in small increases in spawner numbers in the Lower Chiwawa, Upper Nason and Lower Little Wenatchee Rivers. The variables with the greatest potential to contribute to reductions in both mean smolt and spawner numbers were percent fine sediments and incubation temperature. The negative effect of increasing percent fine sediments was greatest in the Lower Little Wenatchee, Middle Chiwawa and Upper Nason and White Rivers. Decreasing incubation temperature had the greatest effect in the

Table 5 Distribution of spawners among Level IV Ecoregions, as estimated under three scenarios. 'No restoration' and 'degradation' scenarios had the same values as the 'current' scenario

Ecoregions	Historical	Current	Restoration
Channeled Scablands	0.01	0	0
Chiwaukum Hills and Lowlands	0.54	0.49	0.51
North Cascades Highland Forests	0.03	0.03	0.03
Wenatchee/Chelan Highlands	0.42	0.48	0.46

Table 6 Change relative to current scenario in the number of smolts and spawners resulting from sensitivity analysis: improvement and degradation of individual habitat variables with other variables held at estimated current values

Habitat variable	Improved (%)		Degraded (%)	
	Smolts	Spawners	Smolts	Spawners
Fine sediment	161*	75*	-29*	-12*
Incubation water temperature	1	0	-17*	-10*
Spawner capacity	2	5*	-1	-1
Fry capacity	3	1	0	-1
Spawner water temperature	0	0	-2	-3
Fry water temperature	0	-1	-1	-1
Cobble and boulder in pools	0	0	-1	-1

*Significantly different from result of current scenario with *t*-tests, $\alpha = 0.05$ and Bonferroni adjustment for multiple comparisons.

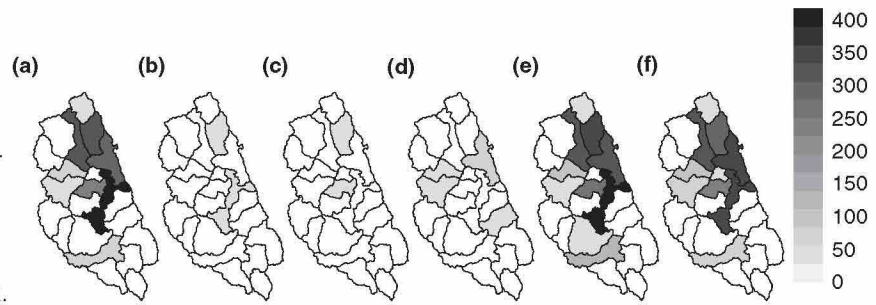
Middle and Lower Chiwawa and Upper Wenatchee mainstem.

Improving all variables for particular life stages showed that, among freshwater stages, survival through the egg stage is the most sensitive to restoration, a response driven primarily by the influence of fine sediment on survival (Fig. 5). The greatest potential increases in spawner abundance due to maximum habitat improvement occur in those areas where survival through the egg stage is limiting in the current scenario. We did not include first year ocean survival in the sensitivity analysis because we were unable to identify empirical influences of freshwater habitat change on survival through this life stage (although see McGurk, 1996). However because the value in the model for mean survival through this stage is quite low (0.0643), first year ocean survival also has a substantial influence on spawner numbers.

Discussion

Our modelling suggests that, historically, populations had substantially higher productivity and abundance. While the restoration actions that we were able to model are by themselves not predicted to meet restoration goals, the results of the degradation scenario indicate that these actions are critical to prevent substantial worsening of this population's status. Our measure of diversity, distribution of

Fig. 5 Change, relative to current scenario, in mean number of annual spawners and their distribution within the basin resulting from optimising: (a) habitat characteristics influencing egg-to-fry survivorship, (b) habitat characteristics influencing fry-to-overwintering stage survival, (c) fry capacity, (d) spawner capacity, (e) both a and c, (f) both a and d.



spawners among ecoregions, was little affected by scenarios of future habitat condition. However, in contrast to abundance and productivity, current diversity was not markedly different from the historical habitat scenario. This is consistent with the lack of spatial structure impairment identified by the ICTRT (2005).

The potential for increases in population abundance and productivity, as indicated by the difference between the current and historical conditions scenario, suggests that restoration efforts may need to be redirected or the level of actions increased in order to improve natural production of Wenatchee River spring-run Chinook salmon. Results from our sensitivity analysis indicated where additional and redirected restoration efforts may achieve a more positive fish response, as well as where habitat degradation posed the greatest risk. Of the habitat variables we modelled, percent fine sediment in the streambed had the greatest potential to either increase or decrease the spawner numbers and productivity of spring-run Chinook salmon. In fact the influence of fines was responsible for most of the decrease in numbers from the historical to current to degraded scenarios. The areas with the greatest potential for a reduction in fine sediment from estimated current values are the upper Wenatchee mainstem and the lower reaches of the major spawning tributaries, spawning areas where higher values of percent fines were correlated with less forest cover, more anthropogenic impervious surface area and higher road density (Jorgensen *et al.*, 2009). The areas with the greatest potential to be degraded by an increase in fines, from for example future development, are the upper White and Nason Rivers, the middle section of the Chiwawa River and the lower section of the Little Wenatchee. These important areas for Chinook production currently have relatively low fine sediment values and lie almost

entirely within the Wenatchee National Forest where high quality habitat is being protected. In fact, clear-cuts and roads, factors likely to contribute to increased fine sediment (Meehan, 1991; Jorgensen *et al.*, 2009), are to be further minimised according to the most recent draft Forest Plan (Hayman & Bond, 2006). By decommissioning roads, eliminating clear-cuts and returning forest structure to a state that promotes frequent low-intensity fires rather than catastrophic stand-replacing fires, the draft Forest Plan promises to maintain current conditions of fine sediments that are favourable to spring-run Chinook salmon production.

Spawner numbers were also sensitive to changes in mean water temperature during the incubation period. Road density was most closely associated with water temperature during the incubation period (Jorgensen *et al.*, 2009). It seems unlikely that there is a causal connection between road density and water temperature; although Bartz *et al.* (2006) found a similar relationship using different methods. Perhaps road density is related to some causal process not explicitly accounted for, but somehow incorporated into the road density variable (Jorgensen *et al.*, 2009). At any rate, the current draft of the Wenatchee Forest Plan would prevent increased road density in most of the Chiwawa basin, one of the two areas with potential for reduced egg-to-fry survival due to degradation of water temperature during this period. In the other area, the upper section of the Wenatchee mainstem, a greater percentage of the area is in private ownership. Increased development and any associated increase in road density may degrade water temperature during the incubation period. In addition, the future increase in air temperature predicted for the region due to climate change (Mote *et al.*, 2003) also may have a significant impact on water temperature and thus egg-to-fry survivorship in the future.

Our model predicted that actions increasing spawning capacity beyond the amount estimated for the restoration scenario may also be effective, although not as much as reducing fine sediment (Fig. 5). When we modelled an increase in spawner capacity only, by removing culverts that are barriers to upstream passage, the mean number of spawners increased. Increases in spawner abundance only occurred where the newly accessible habitat was able to support spring-run Chinook salmon. Some of the culverts scheduled for removal or improvement opened stream reaches with a relatively high gradient, targeting steelhead (*O. mykiss*, Walbaum), but not suitable for spring-run Chinook salmon (Everest & Chapman, 1972; Petrosky & Holubetz, 1988). In other cases, newly accessible habitat was encompassed by urban or rural development and of poor quality due to extensive impervious area, high road density and limited forest cover. Sensitivity analyses highlighted reaches where additional barrier removal would increase adult abundance. For example, ICTRT (2007b) estimated that currently inaccessible portions of Big Meadow Creek, a tributary of the Chiwawa River, have high intrinsic potential to support fish. Removal of barriers to that habitat would likely further increase spring-run Chinook salmon population size. On the other hand, Mission Creek, another stream that includes some reaches with high intrinsic potential ICTRT (2007b), is currently degraded and additional barrier removal there was not predicted to significantly increase spawner success.

Areas for future exploration

This first step in developing a habitat model for the Wenatchee basin indicates some important areas for further work. For example, available data did not allow us to include some restoration actions planned for the Wenatchee basin, such as the placement of large wood in channels and salmon carcass additions for nutrient enhancement. With sufficient data to incorporate such relationships into the model, larger suites of recovery actions could be evaluated to determine their effects on the predicted number of spawners.

The influence on Chinook salmon population dynamics of such other types of restoration actions can be incorporated easily into the model via the Moussalli & Hilborn (1986) multi-stage Beverton-Holt

spawner-recruit function as data become available to link specific habitat changes to fish survivorship or capacity. For this reason, monitoring fish response to restoration actions and other habitat change is key to establishing and validating links between landscape change, habitat change and species response (McDonald *et al.*, 2007), thereby improving models. To be useful in this respect, monitoring must explicitly link fish survivorship between life stages to measurable habitat variables at those stages. Our model used habitat variable values based on data collected from the Wenatchee River basin; however the habitat-survivorship relationships were developed from observations of other spring-run Chinook salmon populations. Current monitoring efforts in the Wenatchee River basin, as part of the multi-agency Intensively Monitored Watershed Project, promise to result in habitat-survivorship relationships specific to this population. These can be readily incorporated into our model, thereby increasing confidence in its results. Models based on relationships so established will be invaluable in assessing the relative impacts and interactions of the multiple factors contributing to species recovery.

Another important area for additional work is exploring the impact of artificial propagation on this population. Hatchery fish can influence the viability of wild spring-run Chinook salmon primarily by competing for shared resources (Fresh, 1997) and by interbreeding with them (Gharrett & Smoker, 1993; Utter, 2001). The ambitious hatchery supplementation programs that have been initiated in the Wenatchee River have the potential to generate a substantial number of returns to natural spawning areas in the Wenatchee River, resulting in a significant number of hatchery fish competing with wild fish for spawning sites and opportunities to fertilise eggs. For example, stray returns from the Leavenworth hatchery program have contributed up to 35% of the naturally spawning Chinook salmon in extremely low natural return years. Any interbreeding between hatchery and wild fish may lead to reduced fitness of endangered wild fish (Taylor, 1991; Araki *et al.*, 2008). The Shiraz model framework is well suited to exploring how population responses to habitat restoration may be influenced by life stage specific survivorship decrements due to hatchery parentage when there is interbreeding between hatchery and wild fish.

This model may also be used to predict the influences of other factors on life stage specific survivorship and fecundity. These include climate change impacts on freshwater habitat characteristics such as water temperature and quantity (Battin *et al.*, 2007; Crozier, Zabel & Hamlet, 2008), toxic chemicals (e.g. Spromberg & Meador, 2005) and variability in predation (e.g. Good *et al.*, 2007). The flexibility to account for diverse impacts at each life stage in a spatially explicit manner makes this modelling framework ideal for informing the management of any species by directing the most appropriate actions toward the locations and life stages where they will be the most effective.

Our model of Wenatchee basin spring-run Chinook salmon population dynamics predicted that a subset of proposed restoration actions would not appreciably increase mean smolt or spawner numbers. However, increases were predicted with further improvements in modelled habitat variables, particularly the percentage of fine sediments in spawning gravels and to a lesser extent opening access to habitat in good condition. Furthermore, the model indicated strong potential for further deterioration of this population's status if habitat conditions worsen. Productive stream reaches with currently low fine sediment values, primarily in the Wenatchee National Forest, should therefore be a priority for preservation. The current draft of the Wenatchee Forest Plan, scheduled to be complete in 2009, addresses the key human-influenced landscape factors impacting percent fine sediments: roads and forest cover.

Using a spatially explicit model that integrates across life stages the known factors influencing fish population dynamics, we have shown that habitat restoration has the potential to increase spring-run Chinook salmon abundance and productivity and thereby contribute to their recovery. Equally importantly, our work strongly suggests that protecting and restoring freshwater habitat is important to prevent further declines. Such actions will also be necessary for increasing the resilience of endangered salmon populations to other threats, such as poor ocean conditions (McClure *et al.*, 2003; Scheuerell & Williams, 2005).

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