



# Interactive Effects of Water Diversion and Climate Change for Juvenile Chinook Salmon in the Lemhi River Basin (U.S.A.)

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**Abstract:** *The combined effects of water diversion and climate change are a major conservation challenge for freshwater ecosystems. In the Lemhi Basin, Idaho (U.S.A.), water diversion causes changes in streamflow, and climate change will further affect streamflow and temperature. Shifts in streamflow and temperature regimes can affect juvenile salmon growth, movement, and survival. We examined the potential effects of water diversion and climate change on juvenile Chinook salmon (*Oncorhynchus tshawytscha*), a species listed as threatened under the U.S. Endangered Species Act (ESA). To examine the effects for juvenile survival, we created a model relating 19 years of juvenile survival data to streamflow and temperature and found spring streamflow and summer temperature were good predictors of juvenile survival. We used these models to project juvenile survival for 15 diversion and climate-change scenarios. Projected survival was 42–58% lower when streamflows were diverted than when streamflows were undiverted. For diverted streamflows, 2040 climate-change scenarios (ECHO-G and CGCM3.1 T47) resulted in an additional 11–39% decrease in survival. We also created models relating habitat carrying capacity to streamflow and made projections for diversion and climate-change scenarios. Habitat carrying capacity estimated for diverted streamflows was 17–58% lower than for undiverted streamflows. Climate-change scenarios resulted in additional decreases in carrying capacity for the dry (ECHO-G) climate model. Our results indicate climate change will likely pose an additional stressor that should be considered when evaluating the effects of anthropogenic actions on salmon population status. Thus, this type of analysis will be especially important for evaluating effects of specific actions on a particular species.*

**Keywords:** carrying capacity, ESA, juvenile survival, *Oncorhynchus tshawytscha*, streamflow

Efectos Interactivos de la Desviación del Agua y el Cambio Climático en Individuos Juveniles de Salmón Chinook en la Cuenca del Río Lemhi (E.U.A.)

**Resumen:** *Los efectos combinados de la desviación del agua y el cambio climático son un gran obstáculo para la conservación de los ecosistemas de aguas continentales. En la cuenca del río Lemhi, Idaho (E.U.A.), la desviación del agua causa cambios en el caudal, y el cambio climático afectará más al caudal y a la temperatura. Los cambios en el caudal y en los regímenes de la temperatura pueden afectar al crecimiento, al movimiento y a la supervivencia de salmónes juveniles. Examinamos los efectos potenciales de la desviación del agua y el cambio climático sobre salmónes Chinook juveniles (*Oncorhynchus tshawytscha*), una especie enlistada como amenazada bajo el Acta Estadunidense de Especies en Peligro (ESA, en inglés). Para examinar los efectos para la supervivencia de juveniles, creamos un modelo relacionando 19 años de información de*

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Paper submitted June 25, 2012; revised manuscript accepted May 4, 2013.

supervivencia con el caudal y la temperatura y encontramos que el caudal en primavera y la temperatura en verano son buenos indicadores de la supervivencia juvenil. Usamos estos modelos para proyectar la supervivencia de los juveniles para 15 desviaciones y escenarios de cambio climático. La supervivencia estimada estuvo entre 42-58% más baja cuando los caudales fueron desviados que cuando permanecieron sin desvíos. Para los caudales desviados, 2040 escenarios de cambio climático (ECHO-G y CGCM3.1 T47) resultaron en una disminución adicional de 11-39% en la supervivencia. También creamos modelos relacionando la capacidad de carga de los hábitats con el caudal e hicimos proyecciones para la desviación y escenarios de cambio climático. La capacidad de carga de los hábitats estimada para caudales desviados fue de 17-58% más baja que para los caudales sin desvíos. Los escenarios de cambio climático resultaron en una disminución adicional en la capacidad de carga para el modelo de clima seco (ECHO-G). Nuestros resultados indican que el cambio climático probablemente será un estresante adicional que debería considerarse cuando se evalúen los efectos de las acciones antropogénicas sobre el estado poblacional de los salmones. Por esto, este tipo de análisis será realmente importante para evaluar los efectos de acciones específicas sobre especies particulares.

**Palabras Clave:** capacidad de carga, caudal, ESA, *Oncorhynchus tshawytscha*, supervivencia juvenil

## Introduction

Maintaining the ecological functioning of freshwater ecosystems given escalating human water use is a major challenge for the 21st century. Dam construction and irrigation are already strongly affecting freshwater ecosystems (Dudgeon et al. 2006), and conflicts between water use and conservation concerns are projected to increase. Humans currently appropriate 50% of the world's accessible surface water; by 2025 this figure is projected to reach 70% (Postel et al. 1996). Much of this surface water is obtained through diversions from streams and rivers.

Water diversion for irrigation constitutes the largest use of fresh water in the United States (Hutson et al. 2004). Human population growth, especially in the arid west, will increase demands for irrigation, placing further stress on freshwater resources (Sabo et al. 2010). Diversion alters the natural streamflow regime to which freshwater organisms have adapted (Poff et al. 1997). For fish, water diversion can lead to declines in abundance (Poff & Zimmerman 2010), shifts in community composition (Freeman & Marcinek 2006), and reductions in size structure (Walters & Post 2008).

Climate change also alters streamflow and temperature regimes. For fresh water, warmer future air temperatures will likely cause higher stream temperatures, earlier snowmelt, increased streamflow during winter, and decreased streamflow during late summer and early fall (Hamlet & Lettenmaier 1999; Mote & Salathe 2010). Collectively, these changes can degrade freshwater conditions and increase the extinction risk for fishes (Mantua et al. 2010).

Anadromous Pacific salmonids (*Oncorhynchus* spp.) are susceptible to altered streamflow and temperature regimes. Some Pacific salmon populations have declined dramatically. Twenty-eight of the 52 identified evolutionarily significant units along the west coast of the contiguous United States are listed as threatened or endangered under the U.S. Endangered Species Act (ESA)

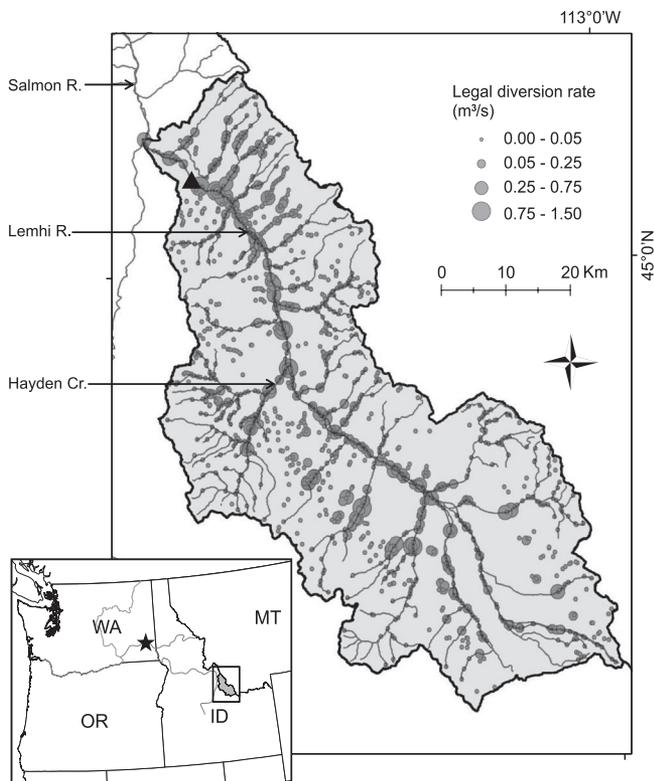
(NMFS 2011). The declines have been attributed to a combination of factors, including degradation of their freshwater habitat. Freshwater habitat conditions, especially streamflow and temperature, are critical drivers of juvenile salmonid growth, movement, survival, and reproduction (Arthaud et al. 2010; Crozier et al. 2010).

We explored 2 pressures that degrade freshwater habitat of salmonids by altering streamflow and temperature: water diversion and climate change. We sought to quantify the effects of these individual and simultaneous pressures on juvenile Chinook salmon (*Oncorhynchus tshawytscha*) survival and habitat carrying capacity. Survival and carrying capacity are important attributes for the recovery of threatened salmon populations (Kareiva et al. 2000; Zabel et al. 2006). We modeled survival and carrying capacity under alternative diversion and climate scenarios, including a specific proposed diversion action subject to ESA consultation, as a case study for incorporating climate change in such actions.

## Methods

### Study System

The Lemhi River is a high-elevation tributary to the Salmon River in Idaho (U.S.A.) (Fig. 1). Its basin encompasses approximately 3300 km<sup>2</sup> of forest, rangeland, and irrigated land and over 250 diversions, mostly for irrigation (IDWR 2006). As a result, streamflow is severely depleted and most tributaries are disconnected from the mainstem during the irrigation season (April–September) (NMFS 2009; Tyre et al. 2011). In 1992, the Chinook salmon population in the basin was listed as threatened as part of the Snake River spring-summer Chinook salmon evolutionarily significant unit (NMFS 1992). The population remains at high risk of extinction due to low abundance and productivity and lack of access to historic habitat. Adults migrate from the ocean in the spring and spawn in the fall, primarily in the upper mainstem



**Figure 1.** Map of the Lemhi Basin, Idaho (U.S.A.), where the Lemhi Chinook salmon population spawns and rears. Points of diversion with their legal diversion rates ( $\text{m}^3/\text{s}$ ) are shown, as are the locations of U.S. Geological Survey gauge 13305310 (triangle) and Lower Granite Dam (star).

and in Hayden Creek (Fig. 1). Juveniles emerge from the gravel the following March, and most out-migrate from the spawning grounds in the fall or the following spring (Healy 1991).

### Diversion and Climate Scenarios

To quantify the effects of water diversion and climate change on survival and capacity, we examined 15 alternative scenarios of diversion and climate conditions (Table 1 & Supporting Information). For diversion, we considered streamflow with current water diversion, streamflow if 16 diversions were removed, and streamflow with no water diversion. The diverted 16 scenario corresponds to an ongoing ESA Section 7 consultation covering 16 existing water diversions operated by the U.S. Forest Service. These diversions are on tributary streams and encompass approximately 6% of water diverted in the basin (NMFS 2009).

We also considered 5 climate scenarios: current climate and future projections for 2 climate models (ECHO-G and CGCM3.1 T47) and 2 time horizons (2040 and 2080) under the A1B emissions scenario (IPCC 2007).

**Table 1.** The 15 stream diversion and climate scenarios used in the Chinook salmon survival and carrying capacity analyses.

Diversion scenario	Climate scenario <sup>a</sup>				
	current	dry (ECHO-G)		wet (CGCM3.1 T47)	
		2040	2080	2040	2080
Diverted <sup>b</sup>	1 <sup>b</sup>	4	7	10	13
Diverted 16	2	5	8	11	14
Undiverted	3	6	9	12	15

<sup>a</sup>IPCC 2007. Values are scenario numbers used in the text.

<sup>b</sup>Current diversion conditions.

Both ECHO-G and CGCM3.1 T47 project temperature changes that are close to the average projections (of 10 climate models) for the Columbia River Basin (Brekke et al. 2010). However, the ECHO-G model projects drier conditions and the CGCM3.1 T47 model projects wetter conditions than the average precipitation projections for the basin, bracketing the range of projected precipitation.

Our 15 climate and diversion scenarios covered a range of current and potential future conditions (Fig. 2 & Supporting Information). Scenario 1 represented current diverted streamflow, while Scenario 2 removed 16 diversions, and Scenario 3 removed all diversions (i.e., approximating historical streamflow). Streamflow during the irrigation season increased substantially for the undiverted scenario and slightly for the diverted 16 scenario (Fig. 2). In the dry (ECHO-G) climate scenarios (4–9), summer/fall streamflow decreased slightly (Fig. 2), while winter/spring streamflow remained similar to Scenario 1. In the wet (CGCM3.1 T47) scenarios (10–15), winter/spring streamflow showed the largest increases (Fig. 2). In all climate-change scenarios (4–15), air temperature increased by 1–2 °C for 2040 (Fig. 2) and 2–3 °C for 2080 (Supporting Information), relative to current temperatures.

### Juvenile Survival

Lemhi Chinook salmon data for brood years (i.e., year of spawning) 1991–2009 were supplied by the Idaho Department of Fish and Game (IDFG) and included yearly counts of salmon nests (redds) and juveniles past Lower Granite Dam (LGD) (Fig. 1). The IDFG estimated out-migrant numbers for each life-history strategy with rotary screw traps located on the Lemhi River and tagged a subset of the out-migrants with passive integrated transponder tags to estimate their survival to LGD (Venditti et al. 2010). We focused on the dominant life-history strategies (out-migrating from the spawning grounds in the fall [fall parr] or following spring [age-1 smolts] and passing LGD 1 year after emergence) and ignored the small percentage of juveniles that out-migrate the first spring and pass LGD

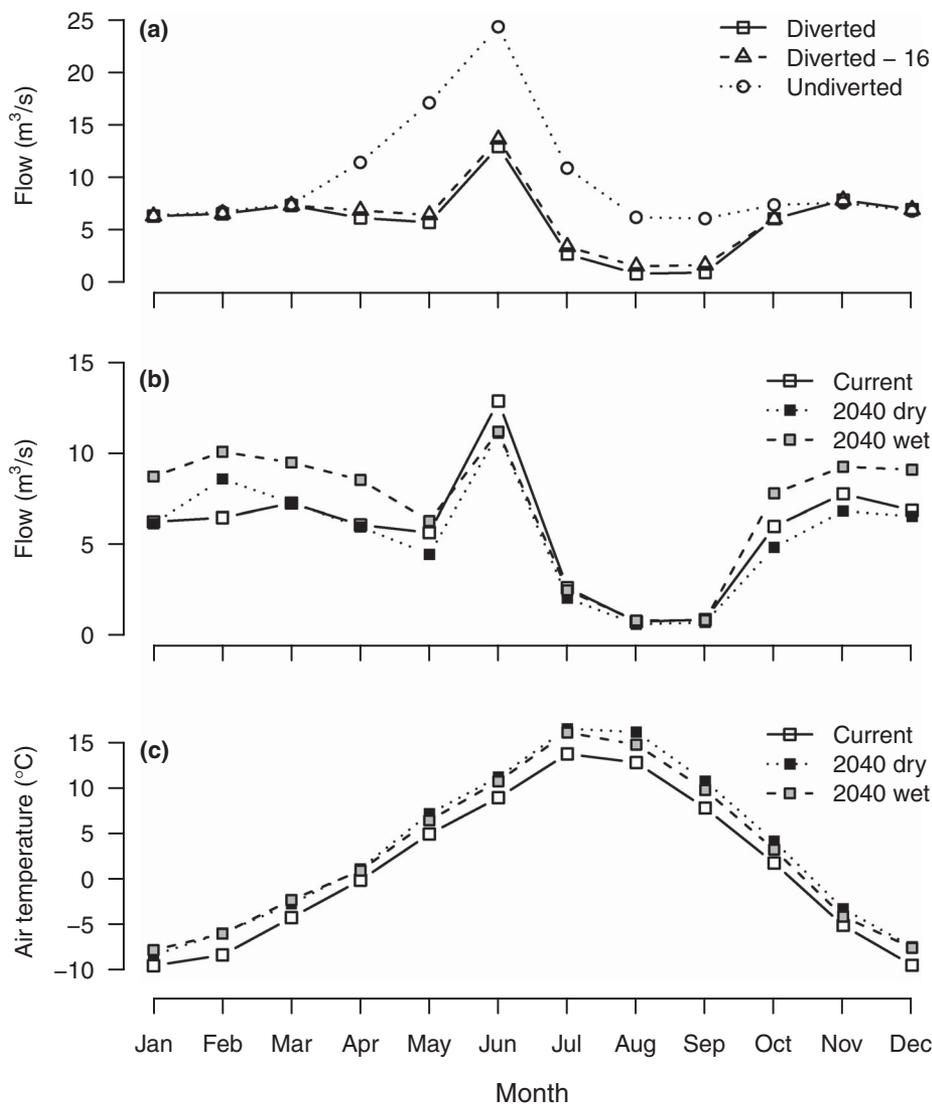


Figure 2. Streamflow and air temperature data used in analyses of juvenile Chinook salmon survival (see Supporting Information for description of calculations and tables of values). The 3 diversion scenarios (diverted, diverted 16, undiverted) are summarized as median monthly discharge at U.S. Geological Survey gauge 13305310, under (a) current climate. Climate scenarios for (b) diverted streamflow and (c) air temperature include current (1992–2008) average conditions and projected future conditions in 2040 for dry (ECHO-G) and wet (CGCM3.1 T47) climate models (IPCC 2007).

the same year they hatch. The number of juveniles past LGD was calculated as the number of outmigrants for each life-history strategy times their estimated survival.

Our metric of juvenile survival was egg-to-juvenile-at-LGD survival because it was an integrative metric of survival from emergence to outmigration. We estimated it from the number of eggs produced in a given brood year (4000 eggs/redd) (Healy 1991) and the number of juveniles that passed LGD in the corresponding year. Juvenile survival varied between 0.005 and 0.101 for the 19 years of data.

We used daily mean streamflow data from U.S. Geological Survey gauge 13305310 and daily air temperature data from SNOTEL's (snow telemetry) Moonshine site (Fig. 1 & Supporting Information). Limited Lemhi River water temperature data were available (U.S. Geological Survey gauge 13305000 for summers 1998, 2001, and 2005) and climate models project air temperature, so we used air temperature in our models. Daily mean air temperatures were highly correlated

with the Lemhi River water temperature data ( $p = 0.90$ ) and the more extensive hourly water temperature data from the Sawtooth Hatchery (<https://www.webapps.nwfsc.noaa.gov/WaterQuality>, NOAA Fisheries Service) in the upper Salmon River ( $p = 0.91$ ).

To assess the effect of climate on juvenile survival, we created a model relating 19 years of survival to climate data. No data were available for other variables that also may affect survival, such as food availability and the presence of competitors or predators. In all models, we compared juvenile survival ( $\ln[\text{egg-to-juvenile-at-LGD survival}]$ ) to density ( $\ln[\text{redd count}]$ ), streamflow for the previous 15 months, and temperature for the previous 15 months in linear models with terms entered additively. The 15-month period spanned juvenile emergence (March, brood year +1) to juvenile passage of LGD (May, brood year +2). We considered seasonal indices that were averages of 3 monthly values: spring1 (March–May, brood year +1), summer (June–August), fall (September–November), winter (December–February, brood year

+2), and spring2 (March–May). These were chosen to integrate conditions across periods of potential sensitivity to changes in streamflow and temperature (emergence, summer and fall rearing, overwinter survival, and out-migration). We combined all seasonal indices with a correlation  $>0.8$ , which resulted in summer, fall, and winter streamflow being combined.

We took a model-selection approach and considered all combinations of the variables (density, streamflow, and temperature) up to a maximum of 4 parameters (excluding the intercept). The choice to limit it to 4 parameters was somewhat arbitrary, but none of the 10 models with the lowest Akaike's information criterion corrected for small sample sizes ( $AIC_c$ ) scores had more than 3 parameters (Supporting Information), which suggests 4 was appropriate. To rank models we calculated  $R^2$  and  $AIC_c$  for each model (Burnham & Anderson 2002).

We performed a series of model diagnostic and validation exercises for the top 10 models. First, we computed the variance inflation factor of each model to test for multicollinearity. Second, we examined the partial autocorrelation function plot of the model residuals to check for temporal autocorrelation. Third, we calculated Cook's distance to assess whether there were any influential outliers that could be leading to spurious correlations. Because we did not include interactions in our models, we also explored whether the inclusion of interactions in our models improved  $R^2$  values. Last, we examined the predictive performance of the models by conducting a leave-one-out cross-validation in which we sequentially removed 1 year of data, refit the top 10 models, and used model averaging to project survival for the missing year.

We used the suite of 10 best models to make projections; these included all models with individual Akaike weights  $>0.025$  with a combined weight of 0.53. We reweighted these models so the Akaike weights totaled 1.00 and projected juvenile survival under each of the 15 diversion and climate-change scenarios (Table 1 & Supporting Information). We used the Akaike weights of each model to weight the response variable (juvenile survival) and its standard error. All analyses were carried out in R (R Development Core Team 2011).

We assumed the relation between streamflow or temperature and survival was static and used linear extrapolation when streamflow and temperature values for a scenario were outside values recorded in the last 19 years. This occurred primarily for the 2080 climate-change scenarios. Projected summer air temperatures for the 2080 climate scenarios were  $3.8\text{ }^\circ\text{C}$  higher, and projected spring streamflows for the undiverted wet 2080 climate scenarios were  $3.79\text{ m}^3/\text{s}$  higher than historical values.

### Habitat Carrying Capacity

To quantify the effects of water diversion and climate change on the number of juvenile Chinook salmon the

Lemhi Basin can support, we adapted a model developed in 1989 to estimate carrying capacity in 31 sub-basins of the Columbia River Basin, including the Lemhi (NPPC 1989). Capacity was defined for this model as the maximum natural production of juveniles in a particular area, assuming habitat area was limiting. It was calculated for a given sub-basin ( $s$ ) with a simple 3-term equation that incorporated the area of a stream segment or reach ( $r$ ), the proportion of the area used by age-zero juveniles, and the density of juveniles in the area. We further simplified this equation to

$$\text{capacity}_s = \sum (\text{area}_r \times \text{density}_r) \quad (1)$$

by including only reaches with usable area. Therefore, our capacity estimates essentially involved quantifying the amount of usable area and the density of juvenile Chinook in that area at the reach scale. Reaches were defined by a geographic information system data set for Chinook salmon in the Columbia River Basin (ICBTRT 2007) that divided the Lemhi Basin stream network into 5144 different 200-m-long reaches attributed with physical characteristics, including drainage area, channel gradient, bankfull width, and wetted width.

We quantified the amount of area usable for rearing under each scenario in 3 steps. First, we estimated reach-scale streamflow under each scenario in May and August (Supporting Information). These months were selected because they occur during the irrigation season and because May streamflow may affect juvenile Chinook survival (Arthaud et al. 2010) and August streamflow tends to be the lowest of the year. Second, we estimated reach-scale streamflow thresholds of usability. Minimum streamflow thresholds have been generated for specific reaches in the Lemhi Basin (e.g., Sutton & Morris 2006). Because these thresholds did not encompass all reaches, we estimated minimum streamflows basin-wide by determining the relation between published thresholds for 59 reaches and the physical characteristics of those reaches (Supporting Information). We used the resulting equations to generate minimum streamflow thresholds for all reaches. Third, we applied various criteria to assess reach usability. We considered a reach usable if access was not blocked by barriers; channel gradient was  $<7.0\%$  and bankfull width was  $>6.6\text{ m}$  (values that support rearing [ICBTRT 2007]); estimated streamflow (from step 1) equaled or exceeded the minimum streamflow threshold (from step 2); and the same was true for reaches downstream. We then calculated the amount of usable area for each scenario, in both May and August, by multiplying the length and wetted width of reaches classified as usable in the basin and summing the resulting areas.

To estimate carrying capacity, we also quantified the density of juvenile Chinook salmon in a given reach (Eq. 1). We used data from surveys of juvenile salmon conducted at 10 reaches in the Lemhi Basin from 2000 to

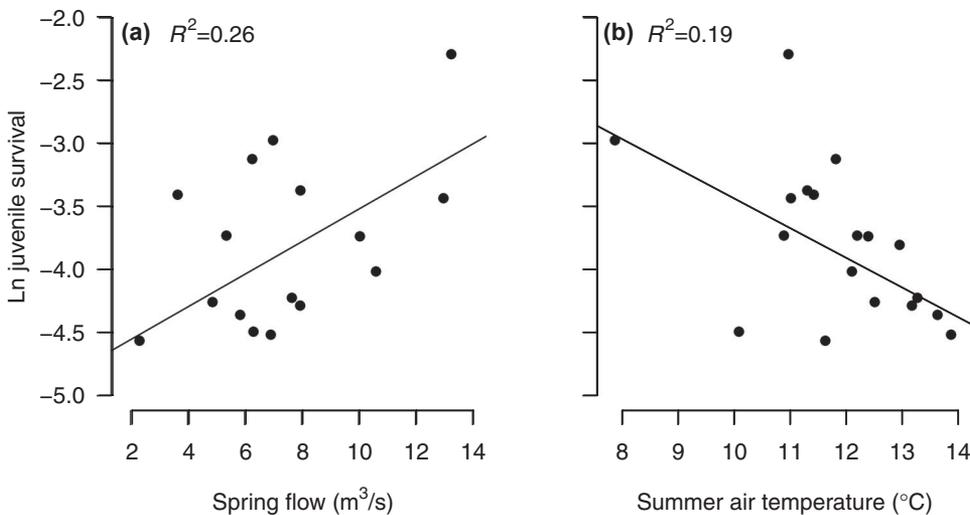


Figure 3. Relation between (a) spring streamflow and (b) summer air temperature and juvenile Chinook salmon survival.

2006 (Copeland et al. 2007) to calculate densities (age-zero Chinook salmon per square meter) from recorded catches for each reach and year surveyed. Unsurveyed reaches were assigned proxy densities from nearby surveyed reaches with similar drainage areas (Supporting Information). Therefore, densities varied by reach, but were static among scenarios in this analysis.

We used Monte Carlo simulations to generate distributions around the capacity estimates. In short, we estimated capacity 5000 times/scenario in R by randomly sampling the juvenile densities from different survey years and then multiplying the sampled densities by the appropriate usable areas for May and August (Eq. 1). We also compared capacity estimated under scenario 1 with capacity generated by fitting 2 stock-recruitment models (Beverton-Holt and Ricker) to empirical redd count and juvenile production data (Supporting Information) to ascertain whether use of densities of a threatened population to generate distributions would lead to unrealistically low median capacity values.

## Results

### Juvenile Survival

Spring streamflow (variable weight = 0.75) and summer temperature (variable weight = 0.57) affected survival the most on the basis of Akaike weights (Fig. 3). The model results also suggested summer to winter streamflow and density could affect survival (Supporting Information). The best model included spring streamflow and summer temperature and had an  $R^2$  of 0.42.

The model diagnostics did not raise any serious concerns about multicollinearity, autocorrelation, or influential outliers (Supporting Information). In the leave-one-out cross-validation, projected survival was correlated to projections that were based on the entire data set ( $\rho = 0.91$ ) and to the original data ( $\rho = 0.47$ ) (Supporting

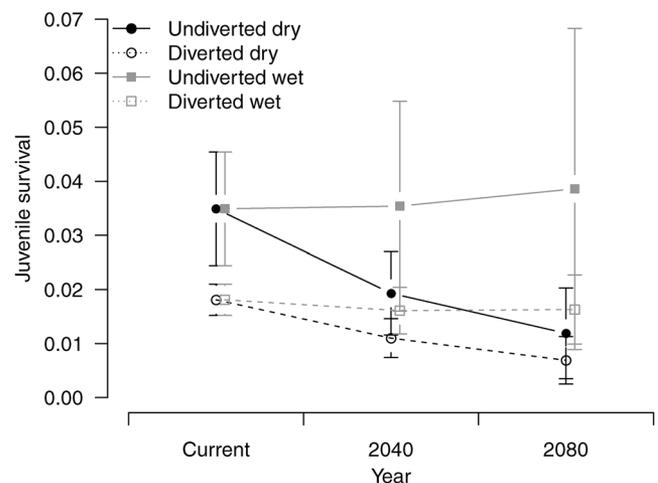


Figure 4. Juvenile survival ( $\pm 1$  SE) for Chinook salmon in the Lemhi Basin, Idaho, under diversion (diverted, undiverted) and climate (current, 2040, 2080) scenarios. Estimates are based on 2 climate models: dry (ECHO-G) and wet (CGCM3.1 T47) (IPCC 2007). See Supporting Information for survival under the diverted 16 scenario.

Information). The predicted points were significantly related to the original data (linear regression,  $p < 0.05$ ) and explained 17% of the variation in that data.

Survival was projected to be 93% higher under undiverted streamflows (Scenario 3) than under diverted streamflows (Scenario 1) (Fig. 4 & Supporting Information). The diverted 16 scenario (Scenario 2) had 6% higher survival than diverted streamflows (Scenario 1) (Supporting Information). We projected additional decreases in survival under all streamflows in the dry climate-change scenarios (Fig. 4), but the wet climate-change scenarios showed relatively constant survival (Fig. 4). The diverted 16 scenarios were not graphed; they closely tracked the trends for the diverted scenarios, but with a 5–8%

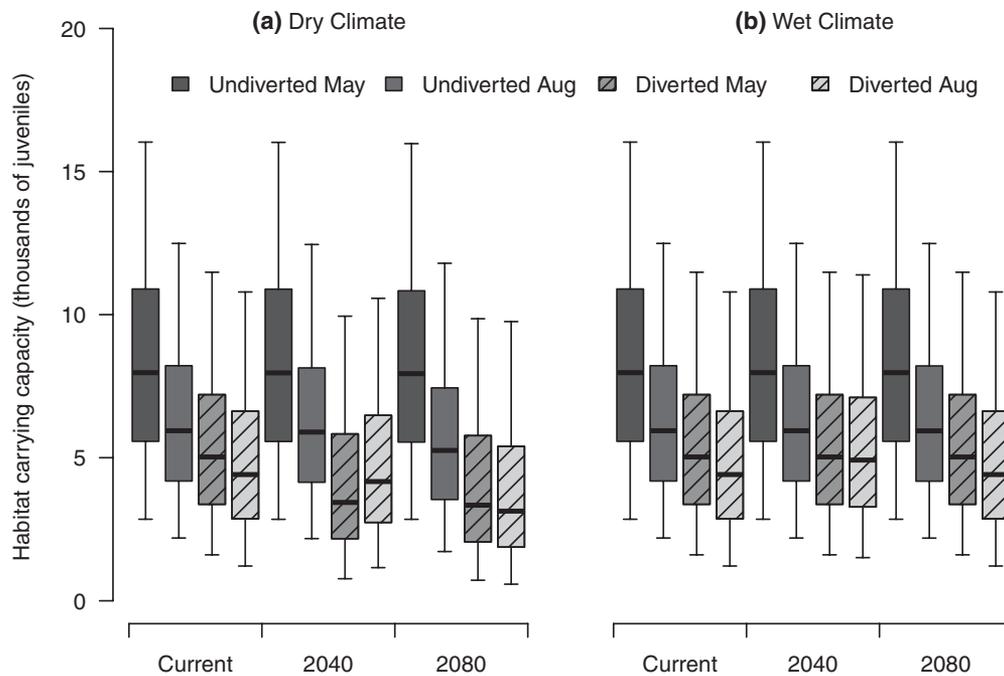


Figure 5. Carrying capacity for Chinook salmon in the Lemhi Basin, Idaho, under different diversion (diverted, undiverted) and climate (current, 2040, 2080) scenarios estimated for May and August for (a) dry (ECHO-G) and (b) wet (CGCM3.1 T47) climate models (IPCC 2007). See Supporting Information for carrying capacity under the diverted 16 scenario.

increase in survival (Supporting Information). Error bars were large in projections for the undiverted wet climate-change scenarios (Fig. 4). This is likely because both temperature and streamflow values for these scenarios were outside historical values.

### Habitat Carrying Capacity

The estimated amount of usable area, a key term in the capacity calculations (Eq. 1), ranged from 121.2 to 200.4 ha basin wide, depending on the scenario. It was smaller under diverted than undiverted streamflow by 15–38%; differences declined to 12–27% when the diverted 16 and undiverted scenarios were compared (Supporting Information). When the dry climate model results were examined for a given diversion scenario, the amount of usable area decreased over time. Conversely, under the wet climate model usable area was relatively stable over time for a given streamflow. Differences in usable area among scenarios were driven by projected reach-scale changes in streamflow (Supporting Information).

Capacity estimates, expressed as the median number of juveniles surviving to LGD, varied more than 2-fold among the scenarios (3133–7972 juveniles) (Fig. 5). Capacity was consistently lower under diverted than undiverted streamflows, with differences ranging from 17% to 58%, depending on the month and climate scenario (Fig. 5 & Supporting Information). Likewise, capacity was identical or lower (by as much as 32%) under diverted than diverted 16 scenario streamflows (Supporting In-

formation). Capacity estimates for the dry climate model decreased over time by as much as 34% (Fig. 5a), whereas estimates for the wet climate model were relatively constant (Fig. 5b). In general, habitat capacity was greater in undiverted relative to diverted scenarios, in current relative to future scenarios, and in May relative to August (but see Supporting Information). Independent measures of current capacity (from fitting stock-recruitment models) more closely matched the upper ends of the 95% CIs than the medians estimated under scenario 1 for May and August (Fig. 6), a result that suggests these upper bounds may be more appropriate for use in projections.

### Discussion

Our results suggest that water diversion in the Lemhi Basin has decreased juvenile Chinook salmon survival and habitat carrying capacity and that this effect may be exacerbated by changes in climate. The greatest future climatic uncertainty centers around overall precipitation patterns. If this area becomes drier, as some models (e.g., ECHO-G) project, negative effects on this species are likely to be greater.

### Climate-Change Projections

Air-temperature projections among downscaled climate models are relatively consistent for the Columbia River Basin. However, water temperatures are likely to be

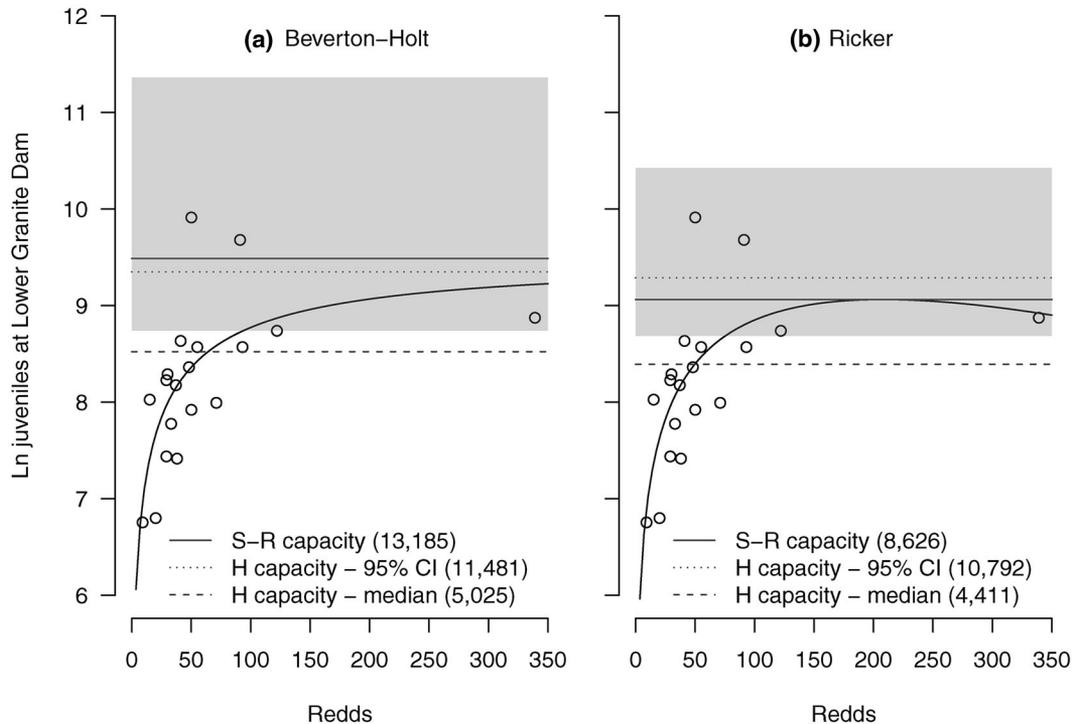


Figure 6. (a) Beverton-Holt and (b) Ricker stock-recruitment models fit to yearly counts of Chinook salmon nests versus juveniles for brood years 1991–2009. Carrying capacity on the basis of each stock-recruitment model (S-R capacity) is shown with the 95% CI (gray area). Also shown are the median and upper 95% CI habitat capacity estimates (H capacity) generated under scenario 1 (see Table 1) for (a) May and (b) August.

more variable due to the presence of groundwater inputs and small-scale cold-water refugia in the river (Torgersen et al. 1999). In addition, water diversion could affect water temperatures. Water diversion could moderate stream temperatures by increasing the proportion of groundwater inputs, but generally it is predicted it will increase stream temperatures (Poole & Berman 2001). If this is the case, our results would underestimate the effects of water diversion.

Precipitation projections show considerable variability. We chose one wet model and one dry model to bracket potential responses, but these models do not project uniformly wetter or drier conditions. For the wet model, streamflow increased during winter but decreased slightly during peak summer snowmelt because more winter precipitation falls as rain. The drier model only projected streamflow reductions during spring and summer, yet these are the seasons during which streamflow is important for juvenile salmonids.

Climate change could alter land-use and water-diversion practices as well as streamflow and temperature. For example, farmers may switch crops or modify irrigation practices in response to increased temperatures or water shortages. If farmers replace ditch with sprinkler or drip irrigation to increase water-use efficiency, return flow could be reduced, further lowering streamflow levels. Alternatively, the reduction in usage might increase

streamflow levels. These human responses to climate change make forecasting ultimate effects uncertain.

#### Juvenile Survival and Habitat Carrying Capacity

The climate variables that best explained juvenile survival were spring streamflow and summer temperature; higher streamflow and lower temperature increased survival. This effect of spring streamflow on juvenile survival is consistent with results of an earlier study on the Lemhi Basin (Arthaud et al. 2010) and suggests it is important to maintain sufficient streamflow during the low-flow period between the start of irrigation season and the snowmelt runoff peak. Although spring streamflow and summer temperature were clearly important there was considerable unexplained variation, which suggests there are also important nonclimate factors (e.g., resource availability) driving juvenile survival.

Proposed mechanisms driving negative effects of lowered streamflow include habitat loss, increased density dependence, and decreased resource availability (Nislow et al. 2004; Harvey et al. 2006). Stream drying may also result in increased predation due to increased densities and loss of high-quality habitat along the sides of the stream that provide cover from predators (Hardy et al. 2006). These factors may directly lower survival or result in decreased growth, which can then lead to decreased

survival (Tipping 2011). Potential interactions between growth and survival may partially explain the effect of May streamflow on survival because spring is an important time for growth (Xu et al. 2010).

Salmonids are sensitive to temperature; water temperatures above approximately 14 °C cause increased juvenile mortality and temperatures of 24–25 °C are lethal (Myrick & Cech 2004). Even lower temperatures (10–14 °C) intensify density-dependent processes in juvenile Chinook salmon, possibly due to limited food availability (Crozier et al. 2010). Small fish are especially susceptible to warmer temperatures due to their already high metabolic demands (Jenkins & Keeley 2010). This suggests that the certainty of temperature increase will lead to some survival reduction, although the projected magnitudes are variable.

The carrying capacity of fish populations is often defined on the basis of the assumption that habitat limits population size. We used this assumption as a premise to estimate capacity through a simple analysis supported by a long precedent in the salmon literature (e.g., Burns 1971; NPPC 1989; Nickleson et al. 1992). We know of no other studies that have compared habitat-based capacity estimates with estimates derived from stock-recruitment analysis. Our results indicate that the upper bounds of the habitat-based distributions better approximate capacity than the medians.

Reductions in capacity—due to water diversion, climate change, or both—greatly affect long-term population size, and thus population viability, of threatened stream-rearing salmonids. These reductions are driven by loss of habitat and potentially by some of the same mechanisms that may affect survival, such as increased density dependence and predation and decreased resource availability and cover.

We focused on 2 important components of the juvenile freshwater-rearing stage (survival and capacity), but climate change and water diversion can also affect disease resistance, development rates, spawning and migration timing, and ocean survival (Crozier et al. 2011). Given these cumulative and interacting effects across the life cycle, our results almost certainly underestimate the total effect (Healy 2011).

### Implications for Evaluating Effects of Actions

We evaluated the likely effects of removing 16 diversions considered in an ongoing ESA section 7 consultation in the Lemhi Basin. The removal of diversions was projected to increase capacity under some but not all combinations of month and climate. Survival was consistently projected to increase with the removal of the 16 water diversions, but that increase in survival was lower under the dry climate-change scenarios. Overall, the survival estimates were within the standard error of projections for the diverted scenarios, but they pointed to a consistent di-

rection of effect. Having these projections in hand allows decision makers to determine whether effects are likely to be substantial under future scenarios that differ from and are more likely than present conditions. This will be important in determining the true level of risk that an action poses. If the action does have an appreciable effect, it provides managers with a sense of the magnitude of change that should be dealt with in mitigation actions under probable future conditions. It also shows that even what appear to be small effects (e.g., 16 diversions out of over 250 in the basin) can be non-negligible and can be exacerbated substantially by worsening environmental conditions.

Our study provides a strong example of how climate change can be integrated into a study of water-diversion effects. This type of analysis has applications beyond fish because insects, crayfish, birds, aquatic insects, and riparian vegetation can also be negatively affected by water diversion (Dewson et al. 2007; Stromberg et al. 2007). Integrating climate change is especially crucial for the conservation of populations such as the Lemhi River Chinook salmon, which is already estimated to reproduce at rates that do not replace adult spawner numbers and may be capacity limited (McClure et al. 2003). The inclusion of climate-change considerations highlights the precarious status of this population and the importance of continued conservation efforts for population recovery. Other ESA-listed and at-risk populations are likely to have similar population dynamics and are likely to benefit from the improvement that reducing nonclimate stressors can provide to cope with a changing climate.

Studies that incorporate potential future climate scenarios are important for all local conservation planning. Conservation efforts planned under a no-change scenario are unlikely to sufficiently address ongoing effects of human actions. In fact, conservation efforts will, in cases where climate change will likely worsen the status of species of concern, have to work harder just to maintain current (poor) status. This is likely to be particularly important in ESA section 7 consultations, where managers are seeking to evaluate effects of a particular action against an environmental baseline and propose a reasonable and prudent alternative to mitigate negative effects.

### Acknowledgments

We thank T. Copeland, D. Venditti, J. Morrow, D. Arthaud, A. LaMontagne, K. Troyer, D. Holzer, H. Imaki, and A. Rea for data, advice, and help with analyses. E. Seney, D. Boughton, J. Jorgensen, C. Toole, E. Schott, P. Levin, L. Crozier, N. Munn, and 2 anonymous reviewers provided helpful comments on the manuscript. A.W.W. was supported by a National Research Council postdoctoral research associateship. Any use of trade, firm, or

product names is for descriptive purposes only and does not constitute endorsement by the U.S. Government.

## Supporting Information

Streamflow and temperature estimates for scenarios in the survival and capacity analyses (Appendix S1), top-10 juvenile survival models, relative importance of regression variables, and model diagnostic results (Appendix S2), streamflow threshold models (Appendix S3), juvenile Chinook salmon densities and resulting capacity estimates (Appendix S4), and juvenile survival, usable area, and carrying capacity estimates for the Lemhi Basin (Appendix S5) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of material) should be directed to the corresponding author.

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