Ecological Modelling 397 (2019) 95–106

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

On the variable effects of climate change on Pacific salmon

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ARTICLE INFO

Keywords:
Climate change
Salmon
Stream temperature
Water management

ABSTRACT

Water temperature has manifold effects on the biology of Pacific salmon. Thermal optima enable Pacific salmon to maximize growth while temperatures above thermal optima can induce stress and lead to mortality. This study investigated the impacts of climatic changes and water management practices on Chinook and Steelhead smolts in the Columbia River Basin using an integrated earth system model and a multiple regression model that incorporated nonlinear survival responses to water temperature. Results revealed that the effects would vary significantly with the species, location, and climate change scenario. Mean survival rates may increase by more than 10% in Upper Columbia River, while reduce by 1˜13% and 2˜35% for Chinook and Steelhead smolts respectively, in the Lower Columbia River by 2080s. This study highlights the importance of integrating the nonlinear response of survival rate to river temperature and water management effects in climate change vulnerability analysis for salmonid stocks.

1. Introduction

Pacific salmon are among the most iconic wild animals on the planet, known for their remarkable anadromous lifestyle that takes them from spawning grounds to the high seas and back again to complete their life cycle (Groot and Margolis, 1991). In the past several decades, many salmon species and populations have experienced dramatic declines and localized extirpations across their ranges as a result of natural and anthropogenic changes (Mote et al., 2003) causing scholars to ponder their future in the Anthropocene (Mote et al., 2003; Morrongiello et al., 2012; Ward et al., 2015). The fact that Pacific salmon span so many environments (from inland rivers, to estuaries, to coastal habitats, to the high seas) during their life cycle exposes them to diverse stressors and challenges that are amplified by human activities. The mortality of salmon (and other fish) depends on both intrinsic and extrinsic factors (Morrongiello et al., 2012), with the latter most directly related to environmental conditions. Water temperature is regarded as the “master factor” (Brett, 1971) - water temperature affects growth, feeding rates, metabolism, risk of diseases, availability of food, travel time, stress and other aspects of salmonids’ lifecycle and biology (EPA, 2001; Carter, 2005).

Between 1895 and 2011, the annual air temperature in the Pacific Northwest has warmed by about 0.7 °C (Crozier, 2014). Warmer air temperatures affect stream temperature, induce earlier snowmelt, and reduce flow during summer (Walters et al., 2013), resulting in a series of changes and uncertainties to the living conditions of Pacific salmon. Climate change is expected to further increase water temperature and alter flow regime throughout Columbia River Basin (CRB) (Mantua et al., 2010). Meanwhile, water demands are projected to rise with population growth and socio-economic development (Hejazi et al., 2015), which may require stronger water regulation and increased hydropower generation (Sternberg, 2010). These changes have the potential to generate considerable challenges for the salmon stocks in CRB and contribute further uncertainty regarding their future.

CRB is characterized by heavy regulation and management due to dam construction, hydropower generation and irrigation water withdrawal (Rechisky et al., 2013). Although previous studies have investigated the relationship between hydrosystem function, reservoirs and salmon (Keefer et al., 2004; Welch et al., 2008; Schaller and Petrosky, 2007), coupling such vulnerability analysis with consideration of climate change has been rare. Several studies of climate change impacts on survival of salmon in CRB suggest different outcomes although most project declining trends in survival rate (Mantua et al., 2010; Benjamin et al., 2013; van Vliet et al., 2013; Wade et al., 2013; Walters et al., 2013; Ward et al., 2015; DeBano et al., 2016). However, it remains unclear how climate change will affect salmon survival in the

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https://doi.org/10.1016/j.ecolmodel.2019.02.002
Received 10 September 2018; Received in revised form 6 February 2019; Accepted 8 February 2019
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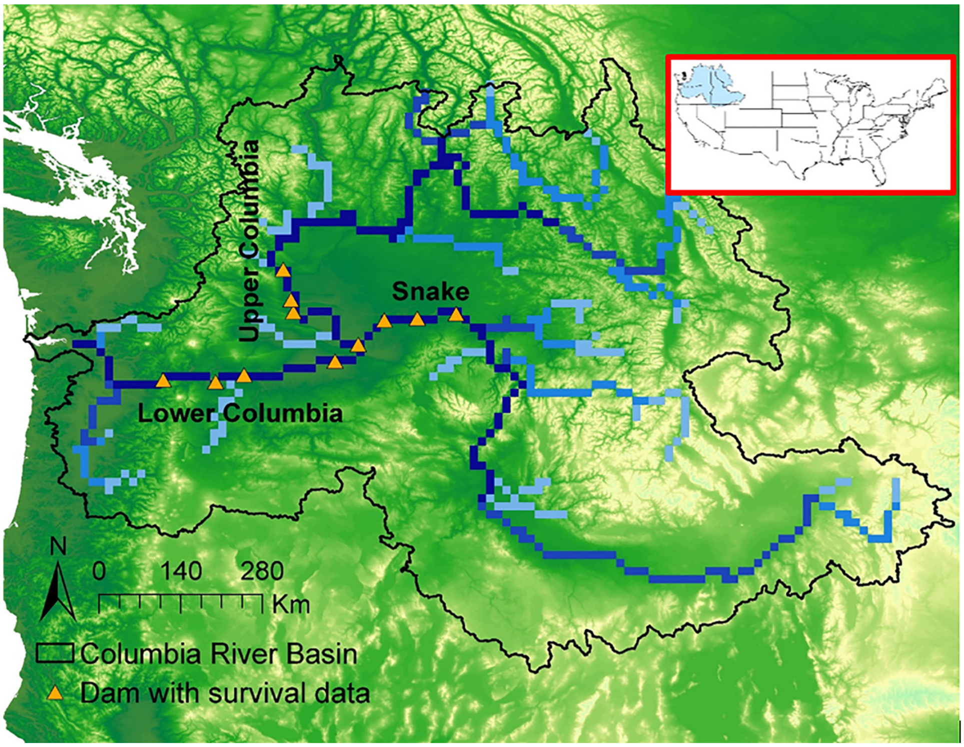

Fig. 1. Orange triangles represent data locations with survival data, background color shows vegetation coverage in terms of leaf area index extracted from Llaverie et al. (2014) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

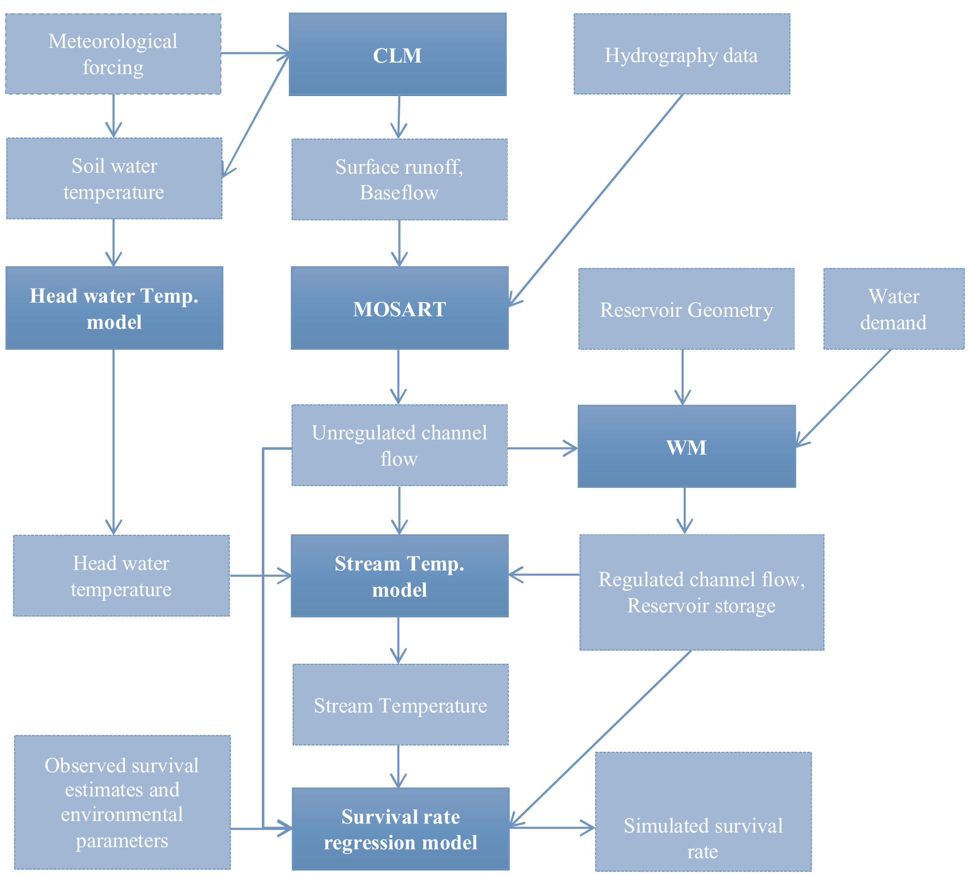

Fig. 2. Conceptual framework of MOSART and regression model (blocks with solid outline represent models, and blocks with dash outline represent data).

Table 1
A list of the CMIP5 models used in this study (Gao et al., 2014).

Model	Institution	Resolution (Lon × Lat)
1. ACCESS1.0	Commonwealth Scientific and Industrial Research Organisation (CSIRO), Australia and Bureau of Meteorology (BOM),	1.875 × 1.25
2. ACCESS1.3	Australia	1.875 × 1.25
3. BCC_CSM1.1	Beijing Climate Center, China Meteorological Administration	2.81 × 2.81
4. CanESM2	Canadian Centre for Climate Modelling and Analysis, Canada	2.81 × 2.81
5. CCSM4	National Center for Atmospheric Research, USA	1.25 × 0.9375
6. CESM1-BGC	University Corporation for Atmospheric Research	1.25 × 0.9375
7. CESM1-CAM5		1.25 × 0.9375
8. CMCC-CM	Euro-Mediterraneo sui Cambiamenti Climatici, Italy	0.75 × 0.75
9. CMCC-CMS		1.875 × 1.875
10. CNRM-CM5	Centre National de Recherches Meteorologiques, Meteo-France, France	1.41 × 1.40
11. CSIRO Mk3.6.0	Commonwealth Scientific and Industrial Research Organisation (CSIRO), Australia	1.875 × 1.875
12. EC_EARTH	Royal Netherlands Meteorological Institute	1.125 × 1.125
13. GFDL-ESM2M	NOAA/Geophysical Fluid Dynamics Laboratory, USA	2.5 × 2.0
14. GFDL-ESM2G		2.5 × 2.0
15. HadGEM2-CC	Met Office Hadley Centre, UK	1.875 × 1.25
16. HadGEM2-ES		1.875 × 1.24
17. INM-CM4.0	Institute of Numerical Mathematics, Russia	2.0 × 1.5
18. IPSL-CM5A-LR	L'Institut Pierre-Simon Laplace, France	3.75 × 1.875
19. IPSL-CM5A-MR		2.5 × 1.25
20. IPSL-CM5B-LR		3.75 × 1.875
21. MIROC-ESM	Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies and Japan	2.81 × 2.81
22. MIROC-ESM-CHEM	Agency for Marine-Earth Science and Technology	2.81 × 2.81
23. MIROC5		1.41 × 1.41
24. MPI-ESM-LR	Max Planck Institute for Meteorology, Germany	1.875 × 1.875
25. MPI-ESM-MR		1.875 × 1.875
26. MRI-CGCM3	Meteorological Research Institute, Japan	1.125 × 1.125
27. NorESM1-M	Norwegian Climate Centre	2.5 × 1.875

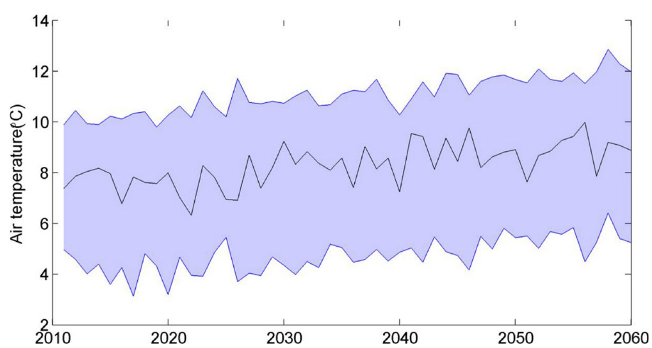

Fig. 3. Annual average air temperature of Columbia River Basin from the regional climate simulation used in this study (black line) compared to the range projected by 27 GCMs (Table 1) in CMIP5 (shaded area).

presence of complex water management.

It is also worth noting that many studies use the maximum temperature tolerance or upper thermal tolerance thresholds of salmon to quantify climate change influences (Mantua et al., 2010; van Vliet et al., 2013; Wade et al., 2013). In these studies, if water temperature exceeds the predefined threshold in one location, the local salmon population is assumed to be under threat. This approach ignores the fact that salmon respond nonlinearly to stream temperature with an optimum temperature range for growth (EPA, 2001; Carter, 2005; Elliott and Elliott, 2010). An optimum temperature range enhances growth and performance of salmon stocks, and survival chances are higher because of sufficient food availability, lower vulnerability to diseases, more optimal physiological performance and so forth. Temperature rises below their population-specific optimum temperature are generally beneficial for salmonid stocks, while further increase beyond the range results in stress for salmonid stocks and affects their behavior (Carter, 2005; Elliott and Elliott, 2010), cardiorespiratory and swimming performance (Farrell et al., 2008; Eliason et al., 2011) and even survival (Farrell, 2009). Estimating climate change impacts based on upper tolerable temperature alone tends to overestimate the negative influences from temperature warming, as it neglects the benefit of temperature rises from below to within the optimum range to growth, particularly during periods such as early life stages where rapid growth is critical. Such discussions are particularly salient if there is hope that current actions to stem carbon emissions (see IPCC, 2007; Buob and Stephan, 2011) could be successful such that water temperatures will not increase perpetually.

This study incorporates the nonlinear response of salmon to ambient water temperature and quantifies the changes in survival under climate change with effects of water management explicitly considered. Here we focus on juvenile Chinook salmon (*Oncorhynchus tschawytscha*) and Steelhead (*Oncorhynchus mykiss*) in the mainstream of Columbia and Snake River due to data availability (Fig. 1). These species start their life cycle start in freshwater, migrate to the ocean as juveniles and return home as adults to spawn. Details of the data and methodology are explained in Section 2. Section 3 illustrates climate change and water management induced changes on stream temperature and discharge, and presents potential impacts on survival rates of smolt Chinook and Steelhead. A summary of key findings and discussion of limitations and future work are provided in Section 4

2. Materials and methods

2.1. Earth system model

This study adopts a physically-based stream temperature model, Model for Scale Adaptive River Transport (MOSART) (Li et al., 2013, 2015) that is coupled with the Community Land Model (CLM, version 4.0). MOSART also includes a water management module (Voisin et al., 2013; Li et al., 2015) (Fig. 2). CLM (Lawrence et al., 2011) is the land component of the Community Earth System Model (CESM). Surface runoff and subsurface runoff simulated by CLM are routed separately into streams and through river networks using MOSART. Then the riverine heat balance is coupled to the river water dynamics, including the advective heat fluxes (from hillslopes laterally into rivers and from upstream to downstream rivers) and energy exchanges between water and air. Simulated stream temperatures have been validated against

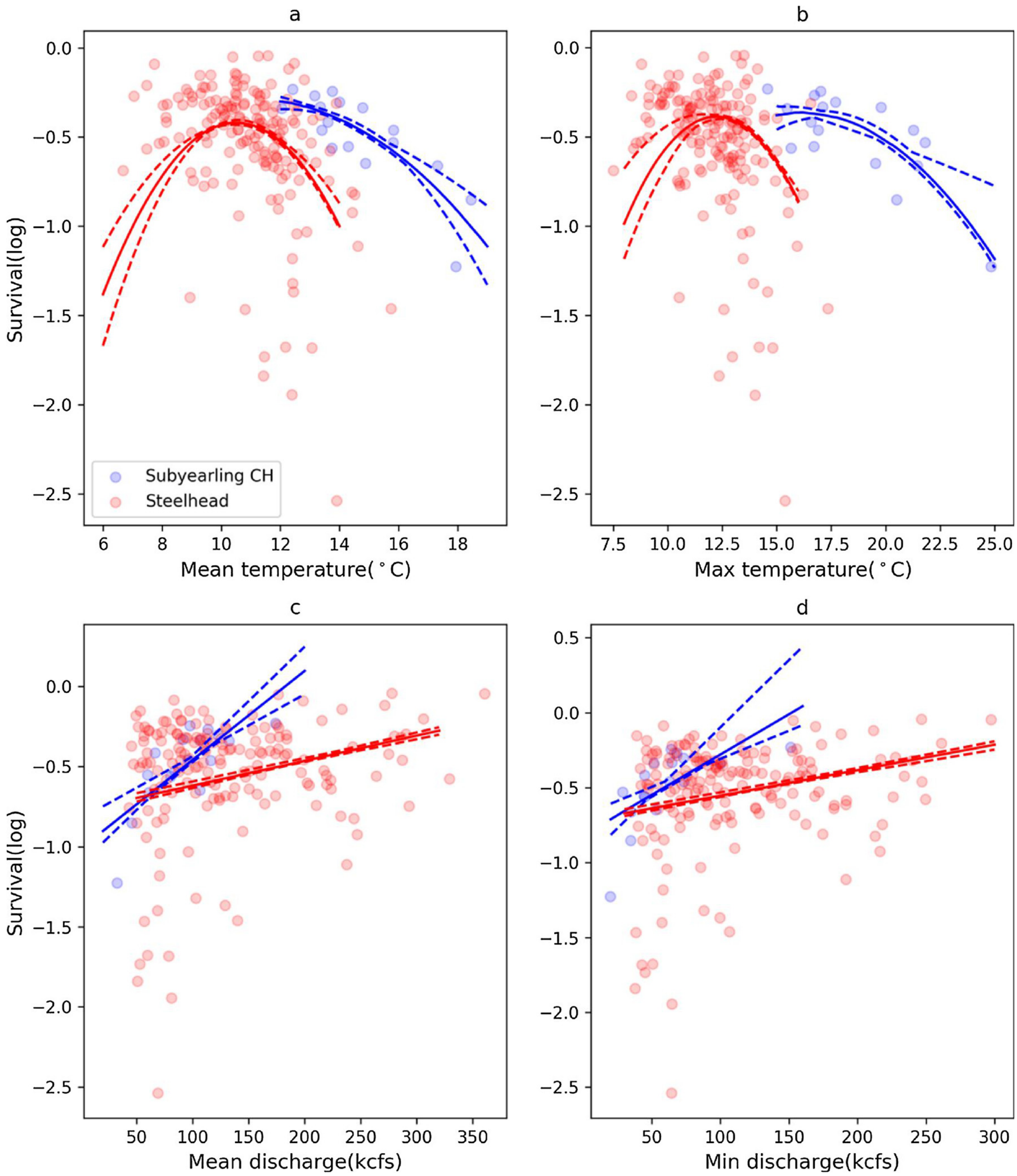

Fig. 4. Regression between logarithm of observed annual average juvenile survival rate and individual environmental parameter (mean temperature (a), max temperature (b), mean discharge (c) and min discharge over migration season (d)) for subyearling Chinook (blue, Snake River Species) and Steelhead (red) using quadratic functions for stream temperature and linear for discharge, dashed lines show 95% bootstrap confidence interval and solid lines represent median fitted values (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 2
Fitted coefficients in the nonlinear regression model of log(survival rate) with water temperature and discharge.

	R^2	*p*-value	Fitted coefficient					
			β_1	β_2	β_3	β_4	β_5	β_6
Chinook	0.877	< 0.01	0.0816	−0.0048	0.4440	−0.0117	0.0019	0.0011
Steelhead	0.514	< 0.01	0.8259	−0.0369	0.5122	−0.0225	0.0025	−0.0004

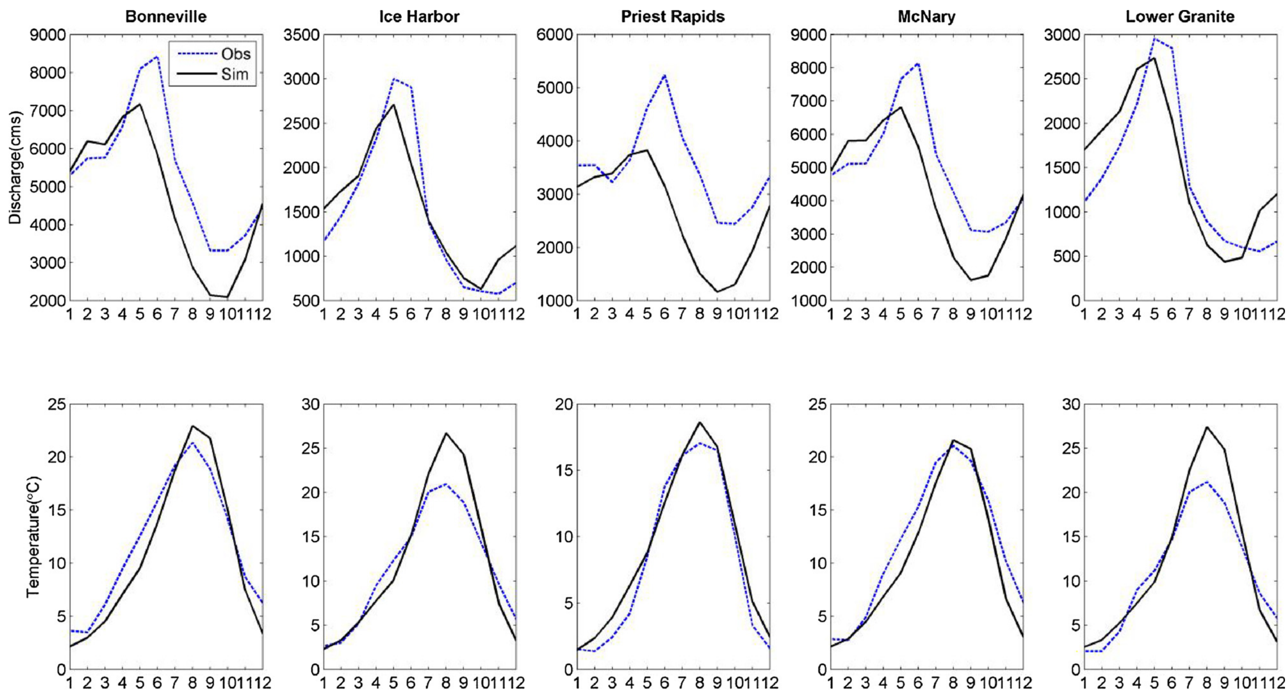

Fig. 5. Comparison of simulated mean monthly discharge and temperature from MOSART-WM with observed values from Columbia Basin Research at five dam locations in main stream of Columbia and Snake River.

observations from over 320 USGS gauge stations in the US (Li et al., 2015).

A water management module (WM) is integrated within MOSART to represent the impacts of anthropogenic activities including local water extraction and reservoir operation (Voisin et al., 2013; Li et al., 2015). Local extraction is performed for each grid cell and water is extracted first from the grid's surface and subsurface runoff and then from the river channel storage to satisfy the local water demand. The reservoir module regulates the reservoir storage based on generic operating rules for three categories: flood control, irrigation water supply and a combination of both (Voisin et al., 2013) to provide supply to grid cells where water demand is unmet by local extraction. A total of 1839 reservoirs are retrieved from the GRanD database in the conterminous US (Lehner et al., 2011). MOSART seamlessly integrates river routing, stream temperature, and water management in an earth system modeling framework, enabling it to represent the advective heat flux along the river network in a physically consistent manner. More details of MOSART stream temperature model are provided in Li et al. (2015).

The atmospheric forcing used to drive CLM-MOSART is derived from a Regional Earth System Model (RESM) (Gao et al., 2014) following the Representative Concentration Pathways (RCP) 4.5 and 8.5 scenarios (Riahi et al., 2011; Van Vuuren et al., 2011). The water demand data used by the WM module are derived from the Global Change Assessment Model (GCAM) (Edmonds and Reilly, 1983), which tracks water withdrawals and consumption for six water-demand sectors: irrigation, livestock, municipal, electricity generation, primary energy, and manufacturing water demands (Hejazi et al., 2015). In this study, the historical and projected water demand time series are provided at a monthly scale, and applied uniformly within each month since MOSART runs at an hourly time step. The impacts of two RCP emissions and land use and land cover scenarios are compared: RCP8.5 is a business-as-usual scenario that stabilizes the global radiative forcing at 8.5 W/m^2 by 2100 and RCP4.5 is a mitigation scenario capping the global radiative forcing at 4.5 W/m^2 by end of 21[st] century. The mean temperature of CRB projected by the Regional Earth System Model driven by the Community CESM4 falls well within the range and close to the average of 27 Global Climate Models (Table 1) in the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Fig. 3). The regional climate simulations used in model evaluation were bias-corrected to reproduce the mean and variance of the observed surface temperature and precipitation.

2.2. Regression model

Four parameters with data availability were used to represent the hydrological and environmental conditions for juvenile Chinook and Steelhead: mean daily stream temperature, maximum daily stream temperature in migration season, mean daily discharge and minimum daily discharge. Survival rate estimates during 1998–2014 were obtained based on observations from Fish Passage Center (Fish Passage Center (FPC), 2017) for three reaches: Snake River (Lower Granite Dam to McNary Dam), Lower Columbia (McNary Dam to Bonneville Dam) and Upper Columbia (Rock Island Dam to McNary Dam). After data screening (statistical model performance and bootstrap robustness), subyearling Chinook at Snake River is used in this study. Fig. 1 shows the main reaches and the locations of the observation sites within CRB. The observation period for smolt survival estimates is May 20-June 30 for subyearling Chinook and April 17-May 28 for Steelhead.

Observed data of environmental parameters during the same period were obtained from Columbia Basin Research (Columbia Research Center (COLUMBIA RIVER BASIN), 2017) for 11 dam locations within the three reaches (Lower Granite Dam, Little Goose Dam, Lower Monumental Dam, Ice Harbor Dam, McNary Dam, John Day Dam, the Dalles Dam, Bonneville Dam, Rock Island Dam, Priest Rapids Dam, Wanapum Dam), and then averaged by the river reach. The weekly/biweekly survival rate data and daily environmental parameters were aggregated over the observed period to represent inter-year variations.

A log-linear multiple regression analysis is performed to relate the observed annual smolt survival rate to water temperature and discharge as predictor variables. A log-transformation of the estimates of survival probabilities is used to stabilize the variance and model a multiplicative effect. The relationship between survival rate and stream temperature has a clear nonlinear pattern, in agreement with Carter (2005). Temperature related parameters are fit as a quadratic function. An optimal

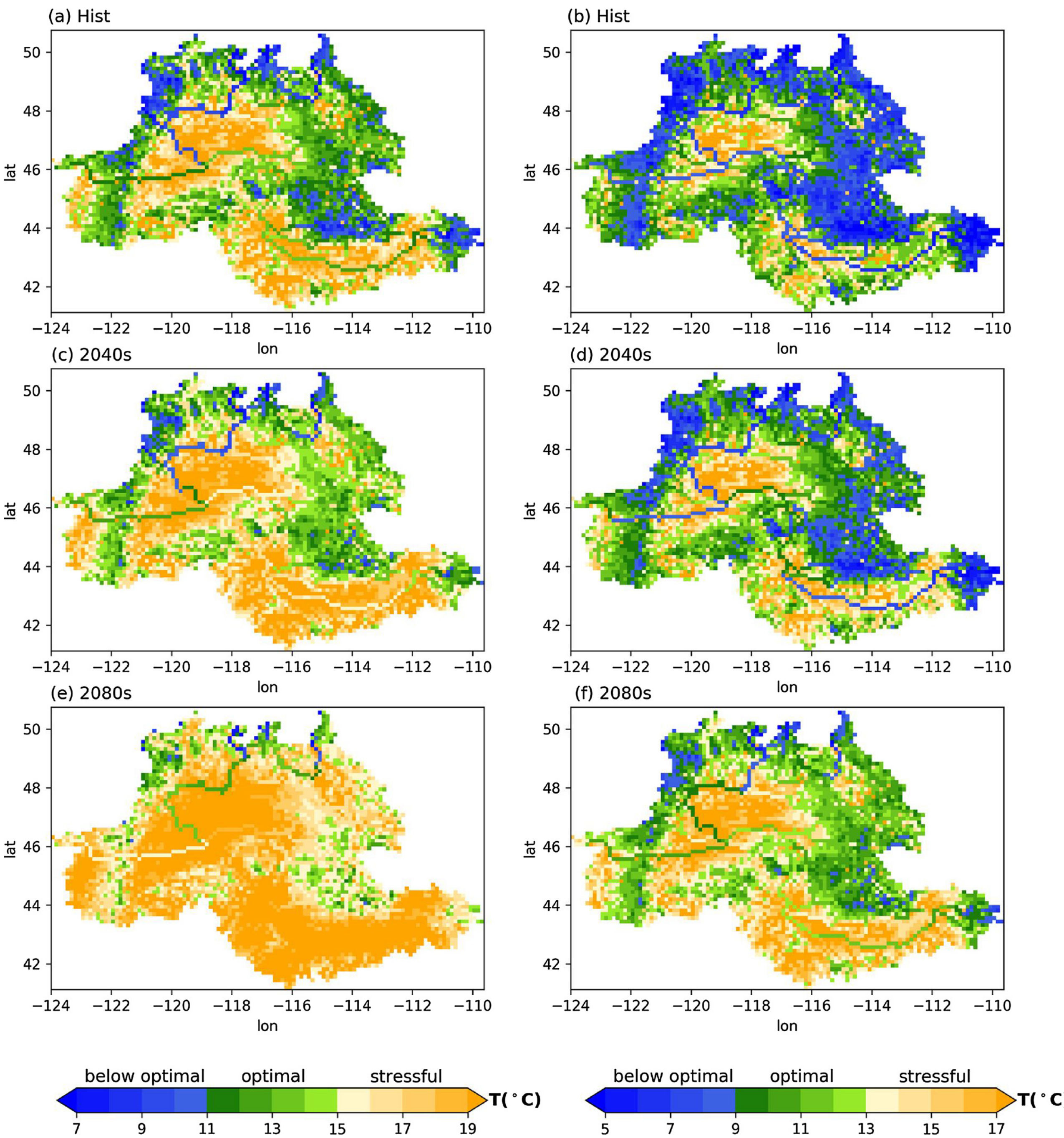

Fig. 6. Mean stream temperature of historical (a, b) and projected 2040s, RCP4.5 (c, d) as well as 2080s, RCP8.5 (e, f) in Columbia River Basin during migration season of juvenile Chinook (5/20˜6/30: left column) and juvenile Steelhead (4/17˜5/28: right column) with color representing temperature classification (blue colors: below optimal, green cFolors: optimum range, yellow colors: stressful for smolt) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

range around 11–15 °C for Chinook and 9–13 °C for Steelhead is found, with survival rate increasing and decreasing with water temperature below and above the optimal range (Fig. 4). The optimal temperature ranges are determined based on three criteria: 1) observed survival estimates are relatively high in this range, with obvious increase with temperature before this range and decline after this range; 2) regression from bootstrap resampling shows relative consistency which implies this range is stable and not significantly affected by sample size; 3) a comparison across literature (EPA, 2001; Carter, 2005; Wade et al., 2013; Mantua, 2015) confirms the selected ranges are reasonable representation for smolt survival in CRB. Generally, Steelhead is more sensitive to stream temperature rise compared to Chinook. The Steelhead survival rate decreases rapidly above 13 °C and is less than 0.4 above 15 °C. Smolt survival rate generally increases with discharge.

Quadratic function is chosen to represent the nonlinearity inherent in the relationship between estimated survival rate ($\hat{S}$) and mean stream temperature t_{ave} as well as maximum stream temperature t_{max} without increasing the regression complexity significantly. Linear function is used for streamflow-related parameters mean discharge (q_{ave}) and min discharge ($qmin$) in this case. This combination of functions has been used in Comprehensive Passage Model (COMPASS) and shown reasonable explanatory power (Zabel et al., 2008).

The model equation used in the regression analysis was

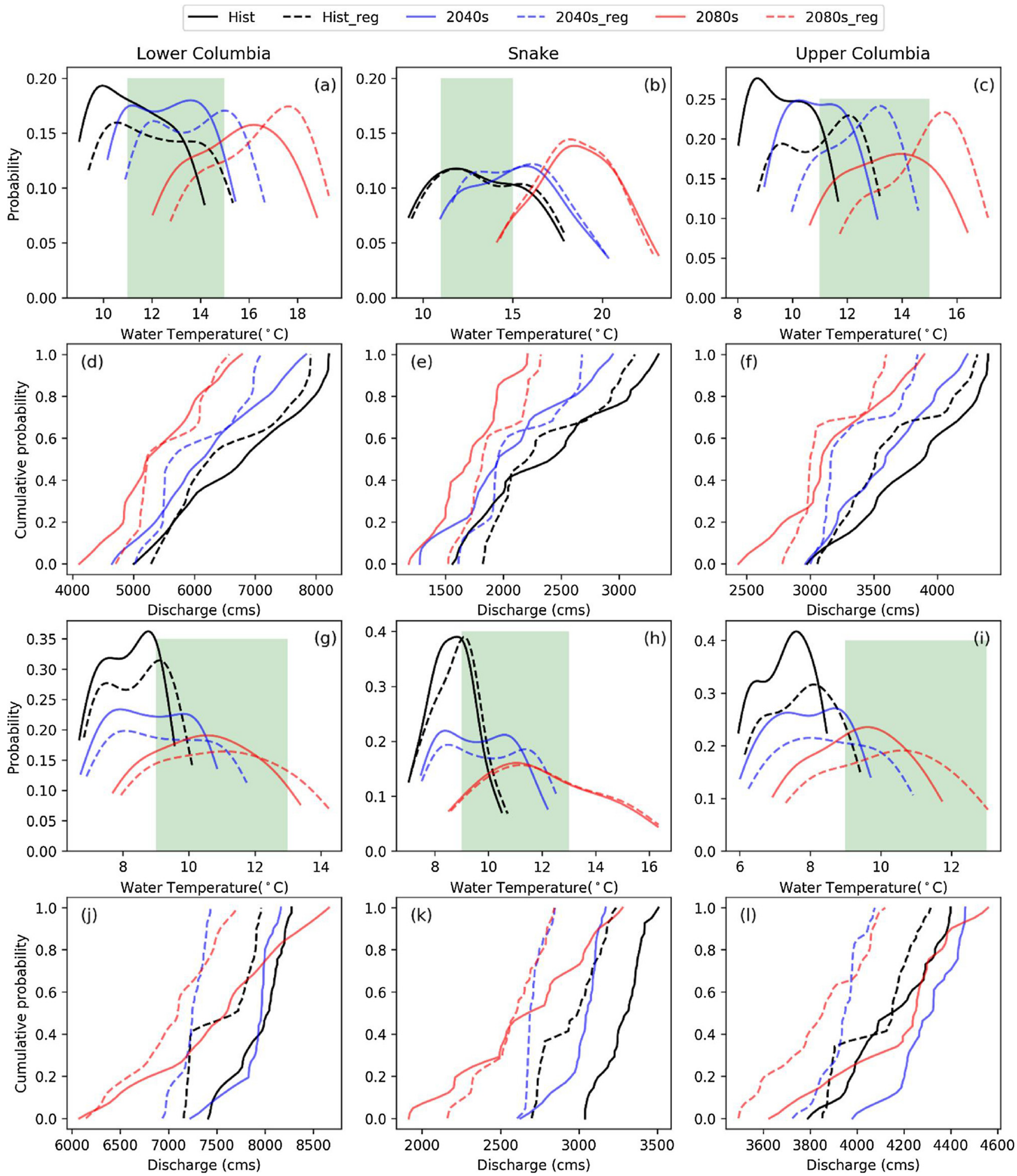

Fig. 7. Probability distribution of daily water temperature (a, b, c, g, h, i) (green shade represents the optimum temperature range) and cumulative distribution of daily discharge (d, e, f, j, k, l) during the migration season of juvenile Chinook (top two rows) and Steelhead (bottom two rows) in historical (black lines) and future periods (2040s: blue lines, 2080s: red lines) with free flowing flow (solid lines) and regulated flow (dashed lines) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

$$Log(\hat{S}) = \alpha + \beta_1 \bullet t_{ave} + \beta_2 \bullet t_{ave}{}^2 + \beta_3 \bullet t_{max} + \beta_4 \bullet t_{max}{}^2 + \beta_5 \bullet q_{ave} + \beta_6 \bullet q_{min} \tag{1}$$

with intercept (α) and partial regression coefficients (β_i; $i = 1, \cdots, 4$). Parameters were estimated using ordinary least squares. The R-square of regression of Chinook survival rate with the four parameters is 0.87. The corresponding R-square for Steelhead is 0.51. The *p*-value for the regression model is less than 0.001 (Table 2).

The uncertainty in the regression model due to the limited historical sample is estimated by bootstrap resampling of the historical data (100 bootstrap samples). Dashed lines in Fig. 4 show 95% confidence intervals from bootstrap resampling. The fitted patterns and trends remain consistent, which suggests the statistical relationships between survival rate and the four environmental parameters for subyearling

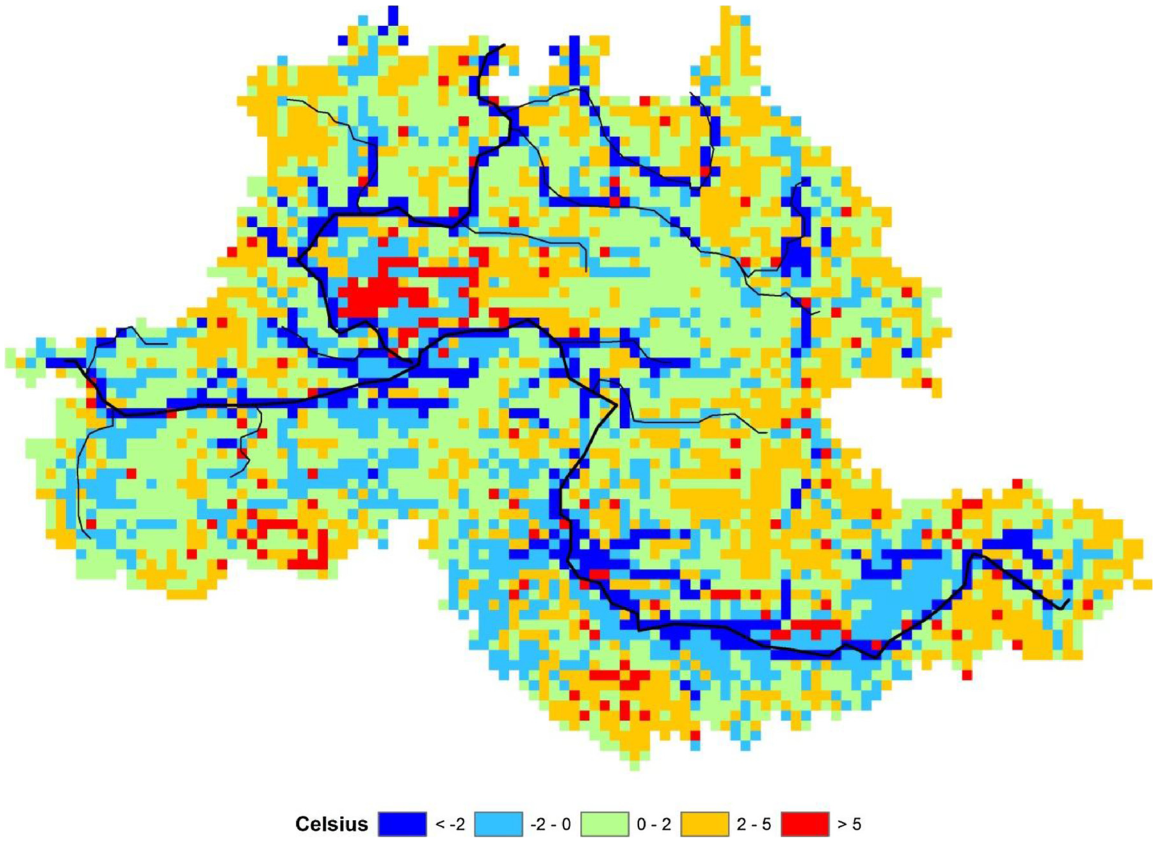

Fig. 8. Difference between average stream temperature and air temperature during April-June under RCP4.5 in the 2040s (blue color represents stream is cooler than air, other colors represent stream is warmer than air) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Chinook and smolt Steelhead hold solid.

Model evaluation is performed by feeding the regression models with simulated reanalysis historical streamflow and stream temperature of 1998–2012 that has been bias corrected to reproduce the mean and variance of the observed surface temperature and precipitation (*Experiment sim*). Another experiment is designed by feeding observed climate data to the regression model (*Experiment reg*) to delineate bias from the regression model and earth system model. Mean bias between survival rate from experiment *sim* and observed values is about 19% for smolt Chinook and 22% for juvenile Steelhead, and that between experiment *reg* and observation is 0.3% for Chinook and 12% for Steelhead. Results suggest the regression models produce satisfactory smolt survival rate with accurate environmental parameters. Although the earth system framework (MOSART) has been validated across the contiguous US and widely used in many studies, it focuses on large scale studies and needs to be further calibrated for regional studies. A comparison of the simulated streamflow and temperature (Fig. 5) at five dam locations in CRB shows that MOSART tends to underestimate water temperature in the main channel during migration season of juvenile Steelhead (April-May), which would lead to an underestimate of survival rate for Steelhead in historical period.

3. Results

3.1. Climate warming induced temperature change

Stream temperature is projected to warm throughout CRB in the 2040s and 2080s under both climate scenarios (RCP4.5 and 8.5). Fig. 6 illustrates the spatial distribution of water temperature in CRB for Chinook (left column) and Steelhead (right column) of historical and future periods with climate change effects alone. Colors represent the temperature zone for the two species respectively: water temperature of lower than 11 °C is below optimal for Chinook (blue colors), 11–15 °C is the optimum zone (green colors) and higher than 15 °C (yellow colors) is stressful for Chinook; temperature lower than 9 °C is sub-optimal for Steelhead, the optimum range is 9–13 °C and temperature rising above 13 °C is stressful for Steelhead. The optimum temperatures for juvenile Chinook and Steelhead are derived based on the correlation between observed survival estimates and migration season mean stream temperature on mainstreams of Columbia and Snake River (Fig. 4). The difference between the optimum temperature of Chinook and Steelhead results not only from the different sensitivity of each species to water temperature, but also variations in the migration season: juvenile Chinook migrate around May 20˜June 30 while juvenile Steelhead migrate around April 17˜May 28 based on the data from the Fish Passage Center (Fish Passage Center (FPC), 2017).

Results show that water temperature in the main stream of Lower Columbia River, which is downstream of CRB, is within the optimum range for juvenile Chinook in the historical period but is shifted to be stressful by the 2080s. Stream temperature in Lower Columbia is currently below optimum for Steelhead but rises to the optimal range for juvenile Steelhead due to climate warming by the 2080s. Stream temperature of Upper Columbia River is below the optimum range in the historical period for smolt Chinook and Steelhead, but it will shift to the optimal zone for both species by the 2080s. Current temperature in Snake River is within the optimum range for juvenile Chinook; it shifts to stressful in the 2040s even with a mitigation climate scenario (RCP4.5) and is likely to be lethal for smolt Chinook by the 2080s. In contrast, Steelhead may benefit from temperature increase in Snake River with temperature shifting from below optimum to optimum by the 2080s.

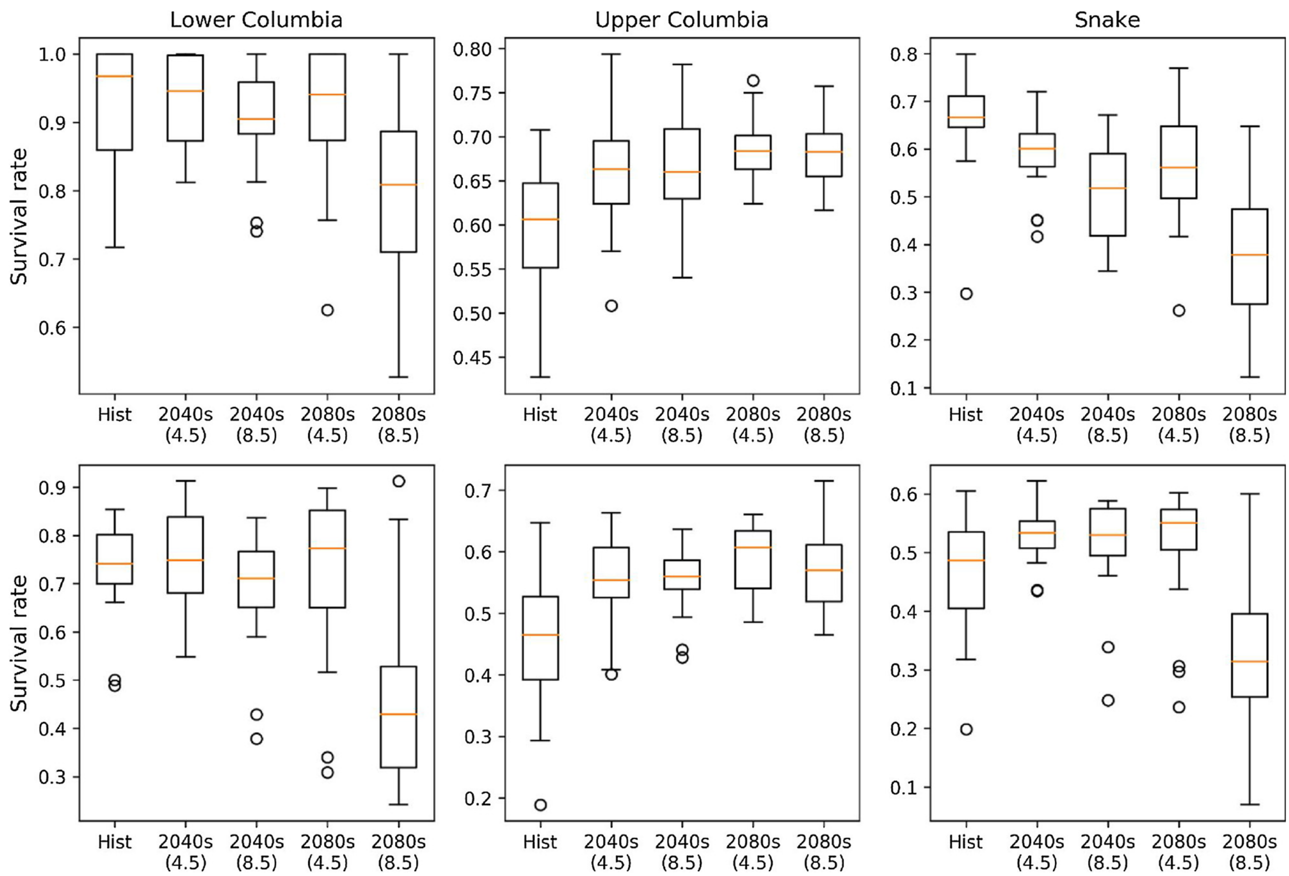

Fig. 9. Survival rate of juvenile Chinook (top row) and Steelhead (bottom row) during historical (1985–2004) and projected periods (2040s and 2080s) under two climate scenarios (RCP4.5 and RCP8.5) in Lower, Upper Columbia and Snake River.

3.2. *Water management impacts*

River regulation has significant influences on stream flow (Arheimer et al., 2017). Here we compare water management (including regulation and water withdrawal) effects on daily discharge during the migration period of smolt Chinook and Steelhead. Fig. 7 illustrates the historical and future cumulative distribution of discharge in Upper Columbia, Lower Columbia and Snake River. Climate change (solid lines) results in consistent flow decline in Columbia and Snake River during the migration season of Chinook smolts (5/20 ˜ 6/30) (Fig. 7, d–f). In contrast, it leads to more flow in Upper Columbia during the migration season of Steelhead smolts (Fig. 7, l). The effects of water management on streamflow depend on whether upstream reservoirs release or store water and how much water is withdrawn from the channels. Water management (dashed lines) in general reduces flow in Upper Columbia (Fig. 7, f and l) and has a mixed effect on streamflow in Snake River (Fig. 7, e and k). If water releases in June can offset water withdrawals, channel flow in the Snake River is predicted to increase. Lower Columbia is downstream of Upper Columbia and Snake, so its flow is affected by the accumulated effects from upstream regulation as well as regulation and withdrawal within its own segment.

Fig. 7 also presents the probability distribution of stream temperature during the migration season, and how it relates to the optimum temperature. Climate change (solid lines) leads to uniform shifts of temperature to higher values. Interestingly, water management (dashed lines) also results in a noticeable shift to the right for Upper and Lower Columbia River. As flow is reduced by regulation, the heat exchange between the warmer air and the reduced volume of water likely increases and elevates water temperature since stream temperature in the main channels is generally cooler than the overlying air during April-June (Fig. 8). Water management has minor effects on stream temperature in Snake River, which can be attributed to the negligible changes in streamflow.

3.3. *Changes of juvenile survival*

The stream temperature and discharge at the main stems of Columbia and Snake River simulated by the integrated human-nature system model (Li et al., 2015) are used as inputs to the regression model to quantify smolt survival at three main reaches (Upper Columbia, Lower Columbia and Snake) in CRB. Results show that juvenile Chinook and Steelhead inhabiting the Upper Columbia may benefit with warmer climate (Fig. 9). Projected mean survival rates are likely to increase by more than 10% for both species largely because the water temperature shifts to the optimum range with climate change (Fig. 7). In contrast, survival rates of juvenile Chinook and Steelhead in Lower Columbia may decline by the 2080s and even by the 2040s under the more aggressive climate scenario RCP8.5. This results from the combined effects of temperature stress and decreased streamflow. Smolt Chinook in Snake River tends to decline by 12 ˜23% till the 2040s and 15˜ 43% by the end of this century, caused by stressful temperature warming and less flow in the river channels. Juvenile Steelhead, on the contrary, may expect more than 10% increase in survival rate by the 2040s due to the preferable water temperature.

There is no significant change in inter-year variability of survival rates for most scenarios except in the 2080s under RCP8.5. This abrupt increase is mainly attributed to the larger variability in maximum temperature (Fig. 10). Extreme hot temperatures projected in this business-as-usual scenario are lethal for salmonid stocks and result in low survival rate.

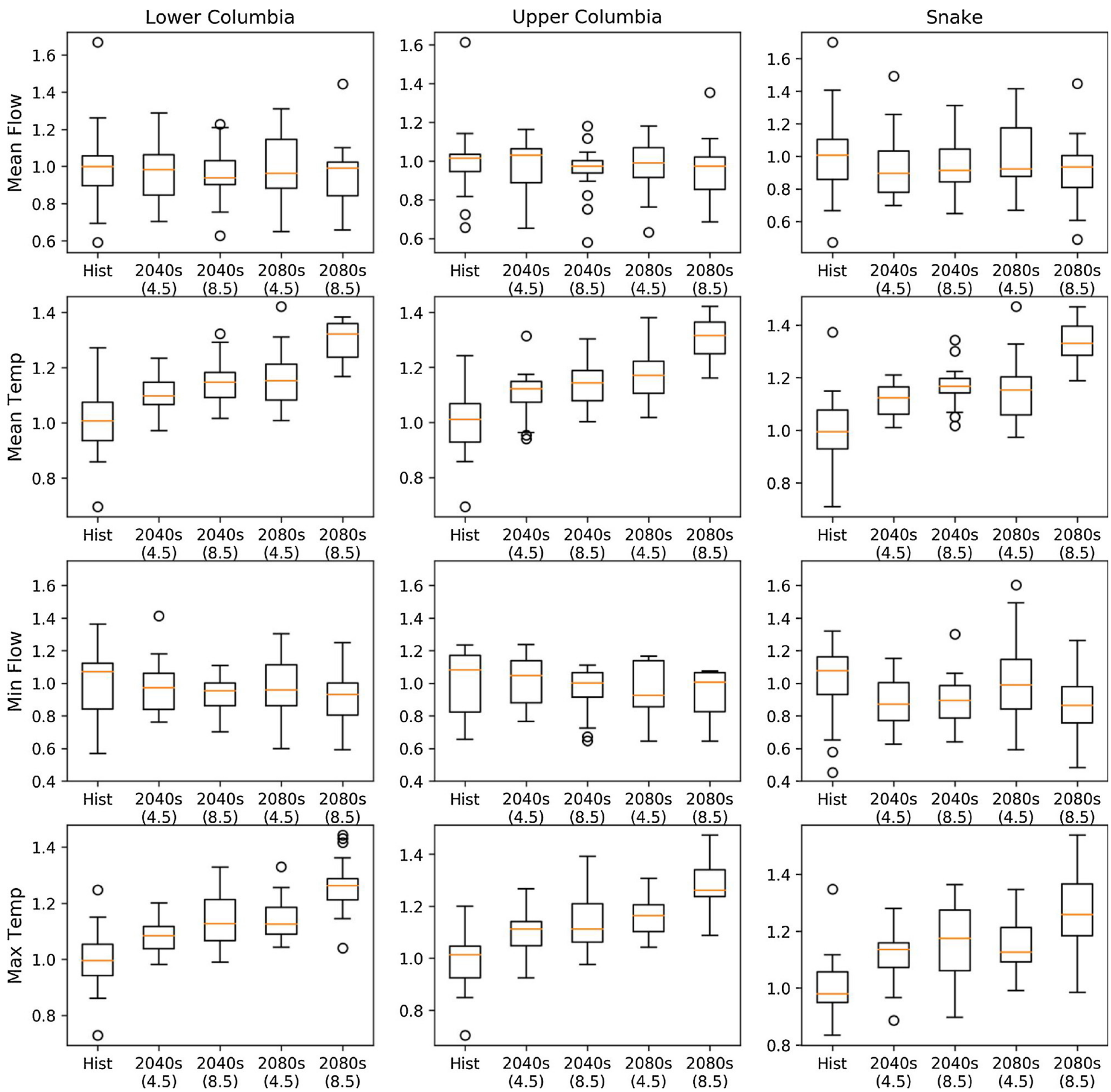

Fig. 10. Normalized mean flow, mean temperature, min flow and max temperature of April-June by historical 20-year average of each at Upper Columbia, Lower Columbia and Snake River for historical (1985–2004) and future scenarios (2031–2050 and 2071–2090), each data point is seasonal statistics of one year.

4. Discussion and conclusions

Instead of using a tipping point to classify water temperature into suitable and lethal, this study acknowledges the fact that the biological response of salmon to water temperature is continuous and nonlinear, and incorporates the nonlinear response into climate change impact analysis. Our results suggest that whether climate warming brings detrimental or beneficial effects on juvenile salmon depends on its relation with the optimum temperature range. If warming results in temperature closer to or within the optimum range, then it enhances smolt growth. If temperature rises beyond the preferred temperature range, then it becomes stressful for salmonids and may reduce survival rate. We recognize that there can be population-specific thermal optima, at scales more refined than what we used in this paper. As such, further efforts to characterize population-specific thermal performance (e.g., like Eliason et al., 2011) would be particularly important for future model refinement.

Another key finding of this study was that water mangement, including reserovir regulation and water withdrawl, is seamlessly coupled within the earth system model to provide a realistic representation of streamflow, water temperature and juvenile survival. Water management reduces flow in the channel and causes temperature rise in Columbia River during smolt migration season. This study provides survival projections of juvenile Chinook and Steelhead with spatial details as well as insight on how interactions between climate change and water management may affect smolts in CRB. Similar modeling exercises extending through to the adult spawning migration would be particularly informative in the future.

Previous literature found that climate change has negative impacts on juvenile survival rate (Mantua et al., 2010; Benjamin et al., 2013; van Vliet et al., 2013; Wade et al., 2013; Walters et al., 2013; Ward et al., 2015; DeBano et al., 2016). This study shows that the effects of climate change vary by location, climate change scenario and specie. There are two possible reasons for the differences. First, many studies

Table 3
Comparison of this study with similar studies.

	Van Vliet et al. (2013)	Wade et al. (2013)	Walters et al. (2013)	DeBano et al. (2016)	This study
Modeling framework	Temperature tolerance and flow change analysis	Compare climate exposure and sensitivity	Linear regression model	Stressor analysis	Linear regression model
Parameters	Water temperature and streamflow	Stream temperature and discharge	Air temperature and discharge	Riparian function, woody debris, embeddedness and find sediment, low flow, summer stream temperature	Mean stream temp. Max stream temp. Mean discharge Min discharge
Model resolution	Daily at 0.5 degree	Weekly at 1/16 degree	Daily at one USGS gauge	Daily at 1/8th degree	Daily at 1/8th degree
Study region	Global	Pacific Northwest (PNW)	Lemhi River Basin (tributary to Salmon River, Idaho)	Umatilla Subbasin (Oregon)	Columbia River Basin
Species	None	Steelhead	Chinook	None	Chinook (wide and hatchery), Steelhead
Projected period	2031-2060 and 2071-2100	2030-2059	2040 and 2080	2040 and 2080	2005-2090
GCMs	ECHAM5/MPIOM, CNCRM-CM3, IPSL-CM4	Ensemble of 20 GCMs	ECHO-G and CGCM3.1 T47	Ensemble of 10 GCMs	1 GCM: RESM
Emission scenarios	A2 and B1	A1B	A1B	A1B	RCP4.5 and RCP8.5
Human activities	None	None	Water diversion	Agricultural intensification	Local water extraction and reservoir regulation
Main results	Increase in frequency and magnitude of exceeded temperature tolerance	Exposure to temperature increase in the southern PNW and flow changes in northern and interior	Diverted flow causes 42-58% decrease in juvenile survival rate than undiverted; climate change results in additional 11-29% decrease	Agricultural intensification has negative impacts on water quality	Smolt survival is projected to increase in Upper Columbia and decrease in Lower Columbia for both Chinook and Steelhead
Major scientific merit	First global assessment	Vulnerability analysis; Spatial results	Water diversion	Agricultural intensification	Reservoir operation and water extraction; integration of nonlinear effects from water temperature

examined the frequency or time of reaching lethal threshold based on one or multiple metrics (Mantua et al., 2010; van Vliet et al., 2013; Ward et al., 2015; DeBano et al., 2016) or utilized linear relationship between survival and temperature (Walters et al., 2013), which do not capture the inherent nonlinearity of survival rate response to physical parameters. In particular, the effects of optimal stream temperature range are not considered. Second, effects of regulation on streamflow and stream temperature are not considered in these studies. A detailed comparison of this study and previous literature is described in Table 3. It is worth noting that changing river conditions could alter the predator community (e.g., more invasive species such as smallmouth bass) and the relative performance of the predators (e.g., increased food consumption, improved feeding efficiency) and this should be considered in future studies.

Estimates in this study focus on main stream of Columbia and Snake Rivers because of data availability and need of consistence in pursuit of accuracy. Extrapolation of the regression relationship to other areas in the basin or other basins should be adjusted based on local conditions. Survival results presented in this study do not consider factors such as climate variability including Pacific Decadal Oscillation and El Niños-Southern Oscillation, intra-annual hydrological variability, change in reservoir operation, harvesting, land use changes and restoration (Battin et al., 2007; Hilborn, 2013; Kilduff et al., 2015; Mantua, 2015), which affect growth and survival of salmonid stocks and should be investigated in future research. This study uses an integrated modeling framework consisting of a single model for each earth system and human component to predict changes in stream temperature and juvenile salmon survival. Although the models have been verified in previous studies particularly over the US to provide reasonable representation (Li et al., 2013, 2015; Hejazi et al., 2015; Voisin et al., 2013;Liu et al., 2017 Wan et al., 2017), a comparison across climate and earth system models is useful to quantify the uncertainty in simulation but beyond the scope of this study. Moreover, effects of reservoir stratification on stream temperature are not considered in the stream temperature model and need to be incorporated in future research. Hence our results should be interpreted with caution because of the large spatial variance in the survival rate change and uncertainty in migration path. On the other hand, Pacific salmon have evolved for thousands of years so neglecting the adaptation capacity (both in terms of plasticity and genetic changes) of salmon may result in an overestimate of the negative impacts from environmental change. Nevertheless, climatic extremes may reduce the adaptive potential (Kovach et al., 2015) and cause unprecendented losses in salmon populations. Many actions can be taken to tackle the hotspots with high risk such as restoring the connectivity of floodplains (*18*) or riparian restoration (Justice et al., 2017). Diverse and connected habitats through all life stages are particularly useful to buffer against changes such as warming (Crozier et al., 2008). Finer scale analysis with more details on all life-stages of salmon is necessary before it will be possible to determine which conservation actions are optimal for different species, populations, and locations within the habitats transited during their entire lives.

Acknowledgements

This research is supported by the U.S. Department of Energy Office of Science Biological and Environmental Research through the Regional and Global Climate Modeling programs. PNNL is operated for DOE by Battelle Memorial Institute under contract DE-AC05-76RL01830. The source code and input data used in this study can be freely downloaded at https://github.com/IMMM-SFA/mosart-heat. The authors declare no competing financial interests.

References

Arheimer, B., Donnelly, C., Lindström, G., 2017. Regulation of snow-fed rivers affects flow regimes more than climate change. Nat. Commun. 8 (1). https://doi.org/10.1038/s41467-017-00092-8. 62.

Battin, J., Wiley, M.W., Ruckelshaus, M.H., Palmer, R.N., Korb, E., Bartz, K.K., Imaki, H., 2007. Projected impacts of climate change on salmon habitat restoration. Proc. Natl. Acad. Sci. 104 (16), 6720–6725. https://doi.org/10.1073/pnas.0701685104.

Benjamin, J.R., Connolly, P.J., Romine, J.G., Perry, R.W., 2013. Potential effects of changes in temperature and food resources on life history trajectories of juvenile Oncorhynchus mykiss. Trans. Am. Fish. Soc. 142 (1), 208–220. https://doi.org/10.1080/00028487.2012.728162.

Brett, J.R., 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (Oncorhynchus nerkd). Am. Zool. 11 (1), 99–113.

Buob, S., Stephan, G., 2011. To mitigate or to adapt: how to confront global climate change. Eur. J. Polit. Econ. 27 (1), 1–16. https://doi.org/10.1016/j.ejpoleco.2010.05.001.

Carter, K., 2005. The Effects of Temperature on Steelhead Trout, Colo Salmon and Chinok Salmon Biology and Function by Life State. California Regional Water Quality Control Board.

Columbia Research Center (COLUMBIA RIVER BASIN), 2017. River Basin.washington.edu/dart/query/river_daily. http://www.Columbia.

Crozier, L., 2014. Impacts of Climate Change On Columbia River Salmon, Northwest Fisheries Science Center, National Marine Fisheries Service. NOAA.

Crozier, L.G., Zabel, R.W., Hamlett, A.F., 2008. Predicting differential effects of climate change at the population level with life-cycle models of spring Chinook salmon. Glob. Change Biol. 14, 236–249. https://doi.org/10.1111/j.1365-2486.2007.01497.x.

DeBano, S.J., Wooster, D.E., Walker, J.R., McMullen, L.E., Horneck, D.A., 2016. Interactive influences of climate change and agriculture on aquatic habitat in a Pacific Northwestern watershed. Ecosphere 7 (6). https://doi.org/10.1002/ecs2.1357. e01357.

Edmonds, J., Reilly, J., 1983. A long-term, global, energy-economic model of carbon dioxide release from fossil fuel use. Energy Econ. 5 (2), 74–88. https://doi.org/10.1016/0140-9883(83)90014-2.

Eliason, E.J., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., et al., 2011. Differences in thermal tolerance among sockeye salmon populations. Science 332 (6025), 109–112. https://doi.org/10.1126/science.1199158.

Elliott, J., Elliott, J.A., 2010. Temperature requirements of Atlantic salmon Salmo salar, brown trout Salmo trutta and Arctic charr Salvelinus alpinus: predicting the effects of climate change. J. Fish Biol. 77 (8), 1793–1817. https://doi.org/10.1111/j.10958649.2010.02762.x.

EPA, 2001. Salmonid Behavior and Water Temperature. United States Environmental Protection Agency.

Farrell, A.P., 2009. Environment, antecedents and climate change: lessons from the study of temperature physiology and river migration of salmonids. J. Exp. Biol. 212 (23), 3771–3780. https://doi.org/10.1242/jeb.023671.

Farrell, A.P., Hinch, S.G., Cooke, S.J., Patterson, D.A., Crossin, G.T., Lapointe, M., Mathes, M.T., 2008. Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. Physiol. Biochem. Zool. 81 (6), 697–708. https://doi.org/10.1086/592057.

Fish Passage Center (FPC), 2017. Oregon, Portland. www.fpc.org.

Gao, Y., Leung, L.R., Lu, J., Liu, Y., Huang, M., Qian, Y., 2014. Robust spring drying in the southwestern US and seasonal migration of wet/dry patterns in a warmer climate. Geophys. Res. Lett. 41 (5), 1745–1751. https://doi.org/10.1002/2014GL059562.

Groot, C., Margolis, L., 1991. Pacific Salmon Life Histories, Vancouver, BC. University of British Colombia Press.

Hejazi, M.I., Voisin, N., Liu, L., Bramer, L.M., Fortin, D.C., Hathaway, J.E., et al., 2015. 21st century United States emissions mitigation could increase water stress more than the climate change it is mitigating. Proc. Natl. Acad. Sci. 112 (34), 10635–10640. https://doi.org/10.1073/pnas.1421675112.

Hilborn, R., 2013. Ocean and dam influences on salmon survival. Proc. Natl. Acad. Sci. 110 (17), 6618–6619. https://doi.org/10.1073/pnas.1303653110.

IPCC, 2007. Climate Mitigation of climate change. Summary Policymak. 10 5.4.

Justice, C., White, S.M., McCullough, D.A., Graves, D.S., Blanchard, M.R., 2017. Can stream and riparian restoration offset climate change impacts to salmon populations? J. Environ. Manage. 188, 212–227. https://doi.org/10.1016/j.jenvman.2016.12.005.

Keefer, M.L., Peery, C.A., Bjornn, T.C., Jepson, M.A., Stuehrenberg, L.C., 2004. Hydrosystem, dam, and reservoir passage rates of adult Chinook salmon and steelhead in the Columbia and Snake rivers. Trans. Am. Fish. Soc. 133 (6), 1413–1439.

Kilduff, D.P., Di Lorenzo, E., Botsford, L.W., Teo, S.L., 2015. Changing central Pacific El Niños reduce stability of North American salmon survival rates. Proc. Natl. Acad. Sci. 112 (35), 10962–10966. https://doi.org/10.1577/T03-223.1.

Kovach, R.P., Muhlfeld, C.C., Wade, A.A., Hand, B.K., Whited, D.C., DeHaan, P.W., et al., 2015. Genetic diversity is related to climatic variation and vulnerability in threatened bull trout. Glob. Change Biol. 21 (7), 2510–2524. https://doi.org/10.1111/gcb.12850.

Lawrence, D.M., Oleson, K.W., Flanner, M.G., Thornton, P.E., Swenson, S.C., Lawrence, P.J., Bonan, G.B., 2011. Parameterization improvements and functional and structural advances in version 4 of the Community Land Model. J. Adv. Model. Earth Syst. 3 (1). https://doi.org/10.1029/2011MS00045. M03001.

Lehner, B., Liermann, C.R., Revenga, C., Vörösmarty, C., Fekete, B., Crouzet, P., Döll, P., Endejan, M., Frenken, K., Magome, J., Nilsson, C., Robertson, J.C., Rödel, R., Sindorf, N., Wisser, D., 2011. High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management. Front. Ecol. Environ. 9, 494–502. https://doi.org/10.1890/100125.

Li, H., Wigmosta, M.S., Wu, H., Huang, M., Ke, Y., Coleman, A.M., Leung, L.R., 2013. A physically based runoff routing model for land surface and earth system models. J. Hydrometeorol. 14 (3), 808–828 ttps://doi.org/10.1175/JHM-D-12-015.1.

Li, H.Y., Ruby Leung, L., Tesfa, T., Voisin, N., Hejazi, M., Liu, L., Yang, X., 2015. Modeling stream temperature in the Anthropocene: an earth system modeling approach. J. Adv. Model. Earth Syst. 7 (4), 1661–1679. https://doi.org/10.1002/2015MS000471.

Liu, L., Hejazi, M., Li, H., Forman, B., Zhang, X., 2017. Vulnerability of US thermoelectric power generation to climate change when incorporating state-level environmental regulations. Nat. Energy 2 (8), 17109. https://doi.org/10.1038/nenergy.2017.109.

Llaverie, Martin, Vermote, Eric, NOAA CDR Program, 2014. NOAA Climate Data Record (CDR) of Leaf Area Index (LAI) and Fraction of Absorbed Photosynthetically Active Radiation (FAPAR), Version 4.

Mantua, N.J., 2015. Shifting patterns in pacific climate, West Coast salmon survival rates, and increased volatility in ecosystem services. Proc. Natl. Acad. Sci. 112 (35), 10823–10824. https://doi.org/10.1073/pnas.1513511112.

Mantua, N., Tohver, I., Hamlet, A., 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Clim. Change 102 (1-2), 187–223. https://doi.org/10.1007/s10584-010-9845-2.

Morrongiello, J.R., Thresher, R.E., Smith, D.C., 2012. Aquatic biochronologies and climate change. Nat. Clim. Change 2 (12), 849. https://doi.org/10.1038/NCLIMATE1616.

Mote, P.W., Parson, E.A., Hamlet, A.F., Keeton, W.S., Lettenmaier, D., Mantua, N., Snover, A.K., 2003. Preparing for climatic change: the water, salmon, and forests of the Pacific Northwest. Clim. Change 61 (1-2), 45–88. https://doi.org/10.1023/A:1026302914358.

Rechisky, E.L., Welch, D.W., Porter, A.D., Jacobs-Scott, M.C., Winchell, P.M., 2013. Influence of multiple dam passage on survival of juvenile Chinook salmon in the Columbia river estuary and coastal ocean. Proc. Natl. Acad. Sci. 110 (17), 6883–6888. https://doi.org/10.1073/pnas.1219910110.

Riahi, K., Rao, S., Krey, V., Cho, C., Chirkov, V., Fischer, G., et al., 2011. RCP 8.5—a scenario of comparatively high greenhouse gas emissions. Clim. Change 109 (1-2), 33. https://doi.org/10.1007/s10584-011-0149-y.

Schaller, H.A., Petrosky, C.E., 2007. Assessing hydrosystem influence on delayed mortality of Snake River stream-type Chinook salmon. N. Am. J. Fish. Manag. 27 (3), 810–824. https://doi.org/10.1577/M06-083.1.

Sternberg, R., 2010. Hydropower's future, the environment, and global electricity systems. Renew. Sustain. Energy Rev. 14 (2), 713–723. https://doi.org/10.1016/j.rser.2009.08.016.

Van Vliet, M.T., Ludwig, F., Kabat, P., 2013. Global streamflow and thermal habitats of freshwater fishes under climate change. Clim. Change 121 (4), 739–754. https://doi.org/10.1007/s10584-013-0976-0.

Van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., et al., 2011. The representative concentration pathways: an overview. Clim. Change 109 (1-2), 5. https://doi.org/10.1007/s10584-011-0148-z.

Voisin, N., Li, H., Ward, D., Huang, M., Wigmosta, M., Leung, L.R., 2013. On an improved sub-regional water resources management representation for integration into earth system models. Hydrol. Earth Syst. Sci. 17 (9), 3605–3622. https://doi.org/10.5194/hess-17-3605-2013.

Wade, A.A., Beechie, T.J., Fleishman, E., Mantua, N.J., Wu, H., Kimball, J.S., et al., 2013. Steelhead vulnerability to climate change in the Pacific Northwest. J. Appl. Ecol. 50 (5), 1093–1104. https://doi.org/10.1111/1365-2664.12137.

Walters, A.W., Bartz, K.K., McClure, M.M., 2013. Interactive effects of water diversion and climate change for juvenile Chinook salmon in the Lemhi River Basin (USA). Conserv. Biol. 27 (6), 1179–1189. https://doi.org/10.1111/cobi.12170.

Wan, W., Zhao, J., Li, H.Y., Mishra, A., Ruby Leung, L., Hejazi, M., Wang, H., 2017. Hydrological drought in the Anthropocene: impacts of local water extraction and reservoir regulation in the US. J. Geophys. Res. Atmos. 122 (21). https://doi.org/10.1002/2017JD026899.

Ward, E.J., Anderson, J.H., Beechie, T.J., Pess, G.R., Ford, M.J., 2015. Increasing hydrologic variability threatens depleted anadromous fish populations. Glob. Change Biol. 21 (7), 2500–2509. https://doi.org/10.1111/gcb.12847.

Welch, D.W., Rechisky, E.L., Melnychuk, M.C., Porter, A.D., Walters, C.J., Clements, S., et al., 2008. Survival of migrating salmon smolts in large rivers with and without dams. PLoS Biol. 6 (10), e265. https://doi.org/10.1371/journal.pbio.0060265.

Zabel, R.W., Faulkner, J., Smith, S.G., Anderson, J.J., Van Holmes, C., Beer, N., Iltis, S., Krinke, J., Fredicks, G., Bellerud, B., Sweet, J., Giorgi, A., 2008. Comprehensive passage (COMPASS) model: a model of downstream migration and survival of juvenile salmonids through a hydropower system. Hydrobiologia 609 (1), 289–300. https://doi.org/10.1007/s10750-008-9407-z.