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Quantifying thermal exposure for migratory riverine species: Phenology of Chinook salmon populations predicts thermal stress

Alyssa M. FitzGerald[1,2] | **Sara N. John**[1,2] | **Travis M. Apgar**[3] | **Nathan J. Mantua**[2] | **Benjamin T. Martin**[4]

[1]Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, CA, USA

[2]Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Santa Cruz, CA, USA

[3]Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA, USA

[4]Department of Theoretical and Computational Ecology, University of Amsterdam, Amsterdam, The Netherlands

Correspondence
Alyssa M. FitzGerald, Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 McAllister Way, Santa Cruz, CA, USA.
Email: alyssa.fitzgerald@noaa.gov

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Abstract

Migratory species are particularly vulnerable to climate change because habitat throughout their entire migration cycle must be suitable for the species to persist. For migratory species in rivers, predicting climate change impacts is especially difficult because there is a lack of spatially continuous and seasonally varying stream temperature data, habitat conditions can vary for an individual throughout its life cycle, and vulnerability can vary by life stage and season. To predict thermal impacts on migratory riverine populations, we first expanded a spatial stream network model to predict mean monthly temperature for 465,775 river km in the western U.S., and then applied simple yet plausible future stream temperature change scenarios. We then joined stream temperature predictions to 44,396 spatial observations and life-stage-specific phenology (timing) for 26 ecotypes (i.e., geographically distinct population groups expressing one of the four distinct seasonal migration patterns) of Chinook salmon (*Oncorhynchus tshawytscha*), a phenotypically diverse anadromous salmonid that is ecologically and economically important but declining throughout its range. Thermal stress, assessed for each life stage and ecotype based on federal criteria, was influenced by migration timing rather than latitude, elevation, or migration distance such that sympatric ecotypes often showed differential thermal exposure. Early-migration phenotypes were especially vulnerable due to prolonged residency in inland streams during the summer. We evaluated the thermal suitability of 31,699 stream km which are currently blocked by dams to explore reintroduction above dams as an option to mitigate the negative effects of our warmer stream temperature scenarios. Our results showed that negative impacts of stream temperature warming can be offset for almost all ecotypes if formerly occupied habitat above dams is made available. Our approach of combining spatial distribution and phenology data with spatially explicit and temporally explicit temperature predictions enables researchers to examine thermal exposure of migrating populations that use seasonally varying habitats.

KEYWORDS
Chinook salmon, climate change, migratory cycle, phenology, riverine habitats, spatial distribution, stream temperature modeling, thermal exposure

1 | INTRODUCTION

One of the most pressing problems in applied ecology is identifying species that are likely to be severely impacted by climate change and defining conservation actions to mitigate negative impacts (Bottrill et al., 2008). Migratory species are thought to be particularly susceptible to shifting climate regimes because they use a variety of different habitats throughout their lifespan, and each of these habitats (e.g., breeding grounds, migratory corridors, non-breeding grounds) needs to provide suitable conditions for these species to persist (e.g., Reynolds et al., 2017; Robinson et al., 2009; Runge et al., 2014; Seebacher & Post, 2015). The use of multiple habitats not only makes migratory species potentially more vulnerable to climate change but also makes predicting how they will respond to climate change more challenging, as vulnerability not only depends on conditions within a single habitat but also on how populations move among multiple habitats in space and time. Existing frameworks for predicting how populations will respond to climate change (e.g., climate envelope models) are not well suited for the complexities of migratory populations because they assume that the whole life cycle can be completed in one area or focus on a single life stage (Allen & Singh, 2016; Pearson & Dawson, 2003). Thus, predicting how migratory species will respond to climate change requires new approaches that account for the life stages that occur over multiple habitats (Allen & Singh, 2016; Fausch et al., 2002; Runge et al., 2014).

Perhaps nowhere is the need for such approaches more pressing than in riverine habitats. Unlike terrestrial or marine migratory species, which may have the capability to mitigate the impacts of climate change through gradual shifts in distribution (e.g., Davis & Shaw, 2001; Hiddink et al., 2015; Pinsky et al., 2013; Tingley et al., 2009), riverine species are largely constrained to a fixed habitat network. This means that thermal conditions within the network must be suitable for movement to occur (Comte & Grenouillet, 2013; Fagan, 2002; Fausch et al., 2002; Troia et al., 2019). Additionally, even estimating current thermal exposure is difficult for riverine species due to the lack of spatially continuous and seasonally varying stream temperature data at appropriate spatial resolutions (Johnson et al., 2019). In contrast, air and surface temperatures are available at fine temporal and spatial resolutions across large geographic regions (e.g., PRISM Climate Group, WorldClim). Standard spatial statistical methods that estimate temperatures in areas without temperature measurements are inappropriate for river systems due to the unique patterns of autocorrelation that emerge from directed flow and connectivity within river networks (Isaak et al., 2014; Peterson et al., 2013; Wenger et al., 2010; Wenger et al., 2010). However, over the last decade, the development of spatial statistical network models that account for the unique features of river networks has allowed for accurate predictions of water temperatures throughout a river network (Isaak, Wenger, Peterson, et al., 2017; Peterson & Ver Hoef, 2010; Rushworth et al., 2015). These models have recently been used to predict summer stream temperatures for the entire western U.S. at a 1 km spatial resolution (https://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html), allowing for estimates of current and future thermal impacts on riverine species during the warmest time of the year (Isaak et al., 2016, 2017, 2018).

However, summer may not always be the most relevant time of the year for migratory species as the movement of these species through river networks may allow them to avoid exposure to peak summer temperatures. Moreover, because migratory species complete different stages of the life cycle in different habitats, and different life stages can vary drastically in their thermal tolerances (Dahlke et al., 2020), the warmest month of the year is not necessarily the most thermally stressful (Crozier et al., 2008). Thus, quantifying thermal stress for migratory species requires estimates of water temperatures in river networks in both time and space, knowledge of how migratory species move through this river network to complete their life cycle, and how thermal exposure compares to thermal tolerances for each life stage.

Here, we develop a general approach to estimate thermal exposure for migratory species in riverine networks. To do this, we first extend an existing spatial steam network model to predict water temperature in rivers in the western U.S. for every month of the year. We then link these temperature predictions with data on the distribution and phenology of a migratory species to estimate thermal exposure. By comparing thermal exposure to life-stage-specific thermal tolerances, we assess thermal stress for each life stage based on nearness to upper thermal limits. We illustrate our approach on several freshwater life stages of an anadromous species with a migratory life history, but this approach can readily be applied to riverine, non-riverine, or non-migratory species as well.

1.1 | Study species: Chinook salmon

The anadromous Chinook salmon (*Oncorhynchus tshawytscha*) is an ecologically and economically important species but is declining in abundance throughout its range (National Marine Fisheries Service [NMFS], 2016; National Research Council [NRC], 1996; Waples, 1991). Across their multi-year migration, these cool-water fish hatch in freshwater, migrate to use the ocean as their primary growth habitat, and return as adults to their natal streams to spawn (Quinn, 2018). Populations are defined by their natal streams as well as the seasonal "run" timing of adult freshwater entry and migration to spawning grounds (Quinn, 2018). Run timing influences other phenological events and life stages, such as timing of adult maturation, spawn timing, incubation duration, and growth rate of juveniles (Quinn, 2018). The different run types likely evolved to avoid exposing sensitive life stages to unsuitable conditions, particularly low stream flows and warm temperatures that retard physiological functions, such as metabolism (e.g., Brannon et al., 2004; Healey et al., 1991; Quinn et al., 2016).

Because of their distinctive phenologies, sympatric runs are typically exposed to different environmental conditions. For example, a peak migration timing in the spring subjects adult fish to extended holding during the hot summer months prior to spawning. Fall migrants, on the other hand, do not hold for extended periods over the summer prior to spawning, but may migrate through warmer migration corridors than fish in the spring. Likewise, run timing is typically associated with habitat use, with early arrival populations (spring-run, winter-run, and some summer-run) typically spawning and rearing in higher elevation reaches that are farther upstream than populations with later arrivals (fall-run) (e.g., Beechie et al., 2006). Because runs are exposed to different environmental conditions and habitats, climate change may impact different runs in different ways.

Many salmon populations are already exposed to warmer temperatures than those they historically experienced due to the construction of large dams that block populations from their historical spawning and rearing grounds (McClure et al., 2008). Dams have eliminated higher elevation, cooler habitat throughout the continental U.S., effectively forcing fish into lower elevation waters, which may be too warm and potentially unsuitable in the summer, and will become warmer with climate change (e.g., Beechie et al., 2006; Lindley et al., 2004; McClure et al., 2008; Moyle et al., 2017; Myers et al., 1998). Early arrival runs historically occupied these higher elevation habitats, and these runs have been disproportionately extirpated and are declining more rapidly than fall-runs (Beechie et al., 2006; Gustafson et al., 2007; McClure et al., 2008). A proposed conservation strategy to mitigate the effects of climate change on salmon populations is the reintroduction of populations to their historical habitats above dams (Beechie et al., 2013; Herbold et al., 2018; NMFS, 2014), but a continental-scale assessment of thermal suitability above dams throughout the Chinook salmon freshwater life cycle has not been completed.

1.2 | Study objectives

This study evaluates thermal exposure and thermal stress (calculated based on thermal thresholds specific to each life stage) of four freshwater life stages for 26 different ecotypes of Chinook salmon. Here, an ecotype represents a geographically isolated population exhibiting one of the four seasonal adult spawning migration run types: winter-run, spring-run, summer-run, or fall-run. We evaluated thermal exposure and stress of these ecotypes to historical stream temperatures and future stream temperatures under two simple, yet informative, climate change scenarios. Thermal exposure and stress evaluations were done for both currently accessible and currently blocked (yet previously accessible) habitats that are under consideration for salmon reintroductions. We explored latitude, elevation, migration distance, and run timing as predictors for historical levels of thermal stress for each life stage across all ecotypes.

2 | MATERIALS AND METHODS

2.1 | Overview of approach

To quantify thermal exposure for the freshwater life stages of an anadromous species, we combined a spatiotemporal model of river temperatures with data on phenology and spatial distribution. Specifically, we extended an existing spatial stream network (SSN) model (Isaak et al., 2017) to predict mean stream temperature for every month of the year for 465,775 stream kilometers (km) in the western U.S. To account for complex spatiotemporal life-history patterns, we defined the spatial distribution and phenology for each distinct life stage of 26 Chinook salmon ecotypes. Then, we joined each spatiotemporal point to its associated stream temperature in space and time; each point therefore defines the temperature experienced by a specific life stage at that geographic location and time of year. For each life stage of each ecotype, we quantified thermal exposure and stress in the context of thermal criteria (thresholds) specific to each life stage (U.S. Environmental Protection Agency [U.S. EPA], 2003). Finally, we explored if thermal stress levels were influenced by geography, distance traveled, or phenotype. We discuss each of these datasets and our analyses in detail below.

2.2 | Datasets

2.2.1 | Monthly stream temperature

Seasonal stream temperature is essential for modeling differential vulnerability of contrasting ecotypes. We expanded a pre-existing SSN model (Isaak, Wenger, Peterson, et al., 2017), currently only available for summer months, to all months of the year to have a full picture of year-round thermal habitat. Following Isaak, Wenger, Peterson, et al. (2017), our SSN models included three autocovariance functions: tail-down, tail-up, and Euclidean distance. Tail-down autocovariance functions are moving average functions in the downstream direction that allow for correlation between sites that are flow-connected and sites that are flow-unconnected (Ver Hoef & Peterson, 2010). Tail-up autocovariance functions are moving average functions in the upstream direction, allowing for correlation between sites that are flow-connected and using spatial weighting to partition the moving average function at tributary confluences (Ver Hoef & Peterson, 2010). An autocovariance function based on Euclidian distance accounts for sources of autocorrelation not attributable to the network structure of rivers. Research has shown advantages in using a mixed model approach which combines multiple autocovariance functions (Peterson & Ver Hoef, 2010).

SSN models require a stream network, observed water temperatures at discrete locations, and spatially and/or temporally explicit covariates (Isaak, Wenger, Peterson, et al., 2017). This model uses the National Stream Internet (NSI) network, which was derived from the NHDPlus dataset and prepared for use with SSNs (Nagel et al., 2015). We queried the NorWeST database for observed water temperature data; the NorWeST database consists of temperature logger data collected by numerous agencies and groups and contains over 220,000,000 observations at greater than 22,700 sites throughout the western U.S. (Isaak, Wenger, Peterson, et al., 2017). As in Isaak, Wenger, Peterson, et al. (2017), we included all observed temperatures from 1993 on, with the end year varying by region

(2011–2015). Within each month, we averaged observed temperatures for sites that had multiple observations within a day and observations on at least 90% of days; we then used this monthly mean for the model. Mean monthly temperature was modeled as a function of 10 spatial and two temporal covariates. The spatial covariates are elevation (m), canopy (%), slope (m/m), annual precipitation (mm), cumulative drainage area (km^2), North American Albers northing coordinate (m), upstream watershed area that is lake or reservoir (%), the amount of flow that is base flow (%), upstream watershed area that is glacier (%), and tailwater (binary—0, 1). Each covariate was spatially linked with the stream network at a 1 km interval. The majority of these covariates are from NHDPlus, with the exception of baseflow index (developed by Wolock, 2003) and northing coordinate, glacier, and tailwater (determined by Isaak et al., 2017). The temporal covariates are historical air temperature (°C) and flow (m^3/s). We obtained historical air temperature from the National Center for Environmental Prediction Regional Climate Model version 3 (NCEP RegCM3) reanalysis in the form of 15 km gridded data (Hostetler et al., 2011) for the spatial extent of the study region. Monthly mean air temperatures were linked to the corresponding water temperature observations by year. We queried hydrographs from the USGS National Water Information System for gages within the spatial extent of the study region. We filled in gaps in the time series using an iterative PCA approach (Josse & Husson, 2016), then calculated monthly means and linked values to water temperature observations by year. Mean monthly temperature was modeled by fitting the SSN linear mixed model for each month in each of eight sub-regional watersheds, spanning most of California, Oregon, and Washington; the SSN model form can be found in Isaak, Wenger, Peterson, et al. (2017).

To validate each monthly model for each sub-regional watershed, we randomly split the water temperature data into a training dataset and a testing dataset based on spatial location such that approximately 80% of the data were used for model fitting and 20% of the data were used for model validation. When a site had data in multiple years, we assigned all data for that site to either the training or testing dataset rather than being split between them so that our out-of-sample metrics would be an estimate of how the model performed in areas where we had no data. We performed leave-one-out cross validation on the training dataset and calculated three performance metrics on each training dataset and testing dataset: the square of the correlation coefficient between observations and predictions (r^2), the root mean square prediction error (RMSPE), and the mean absolute prediction error (MAPE). We then used the model to predict water temperature at 1 km resolution for the period 2002–2011. Predictions used the universal kriging equation which accounts for both the model predictors and spatial autocorrelation (Cressie, 1993). The years 2002–2011 (Scenario 2 sensu Isaak et al., 2017) represent the most recent time period when most temperature records were collected, referred hereafter as "historical" temperatures. Finally, we removed reaches representing man-made lakes and reservoirs (Isaak et al., 2017).

Warming surface temperatures in the western U.S. are among the most robust features of future climate scenarios for the mid to late 21st century (U.S. Global Change Research Program [USGCRP], 2018). Isaak et al. (2017) incorporated projected air temperatures and flows for August from the A1B emissions scenario (IPCC, 2007) to simulate future stream temperatures in 2040 and 2080 using the SSN model. Based on these conditions, streams in our study region are predicted to warm by approximately 1°C by 2040 and 2°C by 2080 (Isaak, Wenger, Peterson, et al., 2017). We applied these increases to our 2002–2011 mean monthly temperature predictions for every river km to evaluate Chinook salmon thermal exposure under these two simple, yet informative, future stream temperature scenarios.

2.2.2 | Spatial distribution datasets

We defined the spatial distributions of freshwater life stages for each Chinook salmon ecotype. Chinook salmon consist of federally recognized Evolutionarily Significant Units (ESU sensu Waples, 1991) based on geography and genetic relatedness at neutral markers, but an ESU can contain multiple run types, the trait that specifies the peak seasonal timing (i.e., spring, summer, fall, winter) of adult migration into freshwater and is used most frequently to define populations (Myers et al., 1998; Waples et al., 2004). Therefore, if a recognized ESU contains multiple runs, we treated each run as a distinct ecotype. For example, the Puget Sound ESU contains three ecotypes: Puget Sound fall-run, Puget Sound spring-run, and Puget Sound summer-run); an ecotype in this study is therefore akin to a metapopulation. For brevity, we use ecotype abbreviations throughout this document, following the general format Q_R, where Q is the ESU group and R is the run type (F = fall, Sp = spring, Su = summer, W = winter); full names can be found in Table S1.1.

Chinook salmon observations were extracted from eight field-observational and distributional data sources (1. Aquatic Species Observation Database, obtained via California Dept. of Fish and Wildlife; 2. http://www.calfish.org/DataandMaps/CalFishDataExplorer.aspx; 3. www.gbif.org; 4. www.iobis.org; 5. https://www.streamnet.org/; 6. https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys;7.https://aquatic.biodata.usgs.gov; 8. http://vertnet.org) from August 2017 to January 2018. We divided linear distribution datasets (StreamNet and CalFish) into points separated by 1 km and then added the points to the observational dataset. Observations have a georeferenced accuracy to 500 m, and each observation was linked with the appropriate ecotype, life stage, and month. We removed fish of unknown ecotype, unknown life stage, or known hatchery origin. To match the temporal limit of the stream temperature modeling project, we removed observations prior to 1993. We specified the ecotype and/or ESU (if not specified) by spatially merging observation locations with ESU distribution shapefiles (http://www.westcoast.fisheries.noaa.gov/maps_data/Species_Maps_Data.html). Due to low numbers and ambiguity of other life stages (e.g., "juvenile" could indicate rearing or outmigration), we focused our efforts on observations listing spawning location, such as those based on redd counts or spawner surveys. We supplemented our dataset with additional spawning and redd observations from the upriver bright fall-run ecotype in the ~90 km Hanford Reach of the Columbia River, digitized from several references (Dauble & Geist, 2000; Dauble & Watson, 1997; Geist, 2000). We removed duplicate observations from the entire spatial distribution dataset using R. Finally, we removed observations that georeferenced >500 m from a stream. Ecotypes with fewer than 50 observations were not examined. This filtering resulted in a total of 44,396 spawning site observations (Figure 1; Table S1.1).

We defined pre-spawn holding habitat from spawning and redd locations (see *Phenology database* for a description of life stages). Early migrating salmonids will hold prior to spawning in suitable cool-water pools, often on or near the spawning grounds (Quinn, 2018; Yoshiyama et al., 2001), but little spatial distribution information exists on holding habitat for Chinook salmon on the broad geographic scale of this analysis. We also assumed that emergence occurs at redd locations and that newly emerged fry rear near natal grounds for at least 1 month (see *Phenology database*). Chinook salmon fry may move downstream every night, but most dispersals are a few meters at most (Bradford & Taylor, 1997). Our spatial resolution (1 km) will not be accurate for emergent fry dispersing >16 m a day for 60 days, but we find little to no information to support this degree of dispersal for Chinook salmon fry.

Adults entering freshwater in the summer may be exposed to particularly high stream temperatures, especially for inland ecotypes that have to swim hundreds or thousands of km to reach their spawning grounds. To reach spawning grounds, inland ecotypes are funneled through four major migration corridors: the Columbia River, Klamath River, Sacramento River, and San Joaquin River. For each ecotype, we extracted the migration route from the point of freshwater entry to the start of the spawning grounds. If an ecotype has multiple spawning grounds, we extracted the migration route to the point where migration diverges. For CV_F, the only inland ecotype that uses two major migration corridors, we analyzed both migration routes. We did not calculate migration routes for coastal ecotypes because coastal ecotypes are comprised of populations that have separate freshwater entry points and short migration routes.

To assess thermal exposure in historically accessible reaches above dams and the potential of restored access as a recovery management option under future thermal conditions, we first had to define historical spatial distributions above dams. First, we extracted all stream reaches in our network that fell within the “historical watershed: anthropogenically blocked” boundary for each ecotype (http://www.westcoast.fisheries.noaa.gov/maps_data/Species_Maps_Data.html). In general, these reaches represent those now blocked by dams, and hereafter we refer to these reaches as “above dams” for clarity. The “above dams” layer includes all reaches within the watershed (*n* = 80,768 km), but some reaches were likely never inhabited by Chinook due to unsuitable conditions. We next wanted to eliminate reaches above dams that are unsuitable to Chinook salmon due to factors other than temperature. To do this, we first joined our stream temperature dataset with physical stream characteristics from the NHDPlus flowline dataset (https://nhdplus.com/NHDPlus/NHDPlusV2_data.php) and a flow metric dataset (http://www.fs.fed.us/rm/boise/AWAE/projects/modeled_stream_flow_metrics.shtml). We then removed reaches with >5% channel gradient (Agrawal et al., 2005; Quinn, 2018), mean annual discharge <30 cfs (cubic feet per second; Bjornn & Reiser, 1991), and streams that are intermittent (FCODE = “46003”; Isaak et al., 2017) because these are unsuitable conditions for Chinook salmon. Next, we removed reaches upstream of natural, impassable barriers without fish passageways (e.g., waterfalls, debris jams) by comparing our potential Chinook salmon “above dams” network to the barrier dataset maintained by StreamNet, a database that compiles fish passage barrier datasets from state agencies (https://www.streamnet.org/data/interactive-maps-and-gis-data/). Although fishways or trap-and-hauls could provide fish passage across these impassable barriers, Chinook salmon were likely not historically present upstream of these natural barriers. In total, we explored potential thermal exposure for 31,699 km in this currently inaccessible yet suitable Chinook salmon habitat (Figure 2); the amount of potential habitat varied by ecotype, ranging from 96 to 7,556 km (Figure 2 inset). Stream temperature modeling in eastern Oregon, eastern Washington, and Idaho is still ongoing, so we do not have the full scope of available or blocked habitat for ecotypes in those regions (e.g., SnakeR_F). Other ecotypes did not have a substantial amount of habitat blocked by dams (ORCoast_F,

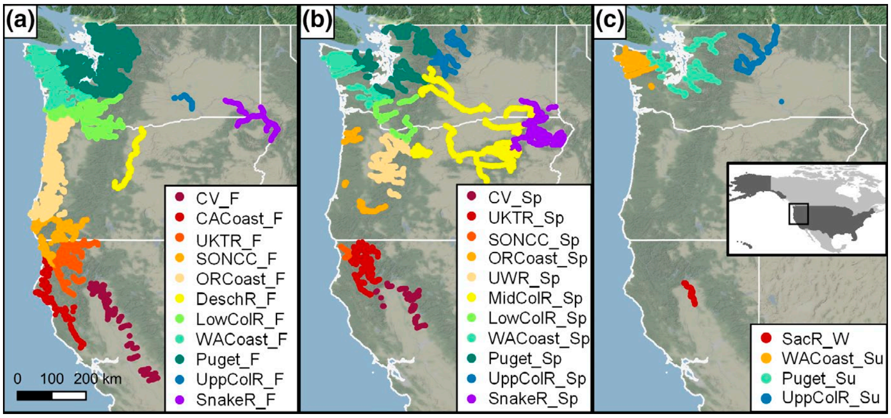

FIGURE 1 Final set of spawning site observations (i.e., spatial distribution) for each defined ecotype for (a) fall-runs, (b) spring-runs, and (c) summer-runs and the lone winter-run. The number of observations for each ecotype is listed in Table S1.1. Note that we do not have observations for all ecotypes because some spatial distributions are not well-studied, or we did not have predicted stream temperatures in those sub-regions (e.g., all of Idaho)

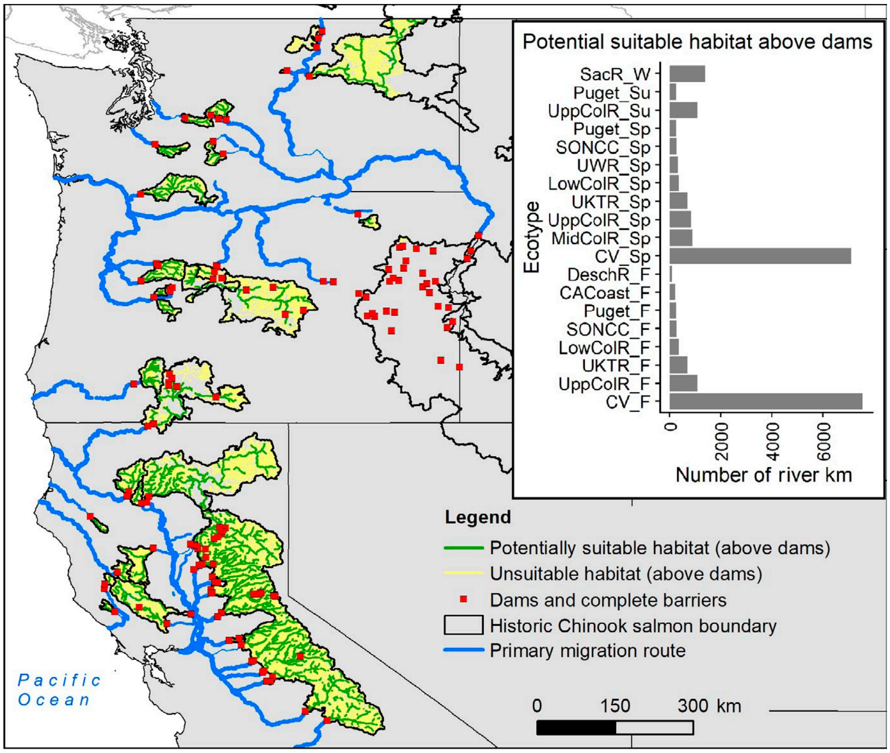

FIGURE 2 Potential habitat above dams. In the study area, 80,768 river km are currently inaccessible to Chinook salmon (green and yellow) due to damming. Of these inaccessible reaches, 31,699 river km are potentially habitable for the Chinook salmon ecotypes in this study (green), and ~61% of river km are currently inaccessible and are likely unsuitable (yellow). Inset: The potential amount of suitable habitat above dams for each ecotype. We removed ecotypes for which we did not have empirical distribution data below dams

ORCoast_Sp, WACoast_F, WACoast_Sp, or WACoast_Su). For these ecotypes without substantial habitat above dams, we assessed below dams thermal exposure only.

2.2.3 | Phenology database

We developed a modern phenology database for each life-history stage for 31 ecotypes in the continental U.S.; note that some ecotypes do not have spatial distribution datasets (Table S2.1, List S2.1). Our database is on a monthly time-step to match the temporal resolution of the stream temperature dataset. The peak month (or median if peak was unknown) and core (i.e., duration and timing for the majority of individuals) were defined from the completed phenology database for the following life stages: adult migration, holding, incubation, and early rearing. Adult migration extends from freshwater entry to arrival at spawning grounds, but we examined thermal exposure during the peak month of migration. Core holding was defined as the months from peak adult return to natal streams through peak spawning. If an ecotype does not hold for extended periods of time (e.g., many fall-run ecotypes hold for only a few days or weeks before spawning), we defined "core" holding as the month of peak spawning. Core incubation was designated as occurring between peak spawning and peak emergence, the point when fry emerge from the gravel where they were spawned and are self-sufficient. Early rearing was defined as the month of peak emergence and the following month. If peak emergence occurs across two months for an ecotype, we included both peak months and the following month. Chinook juveniles may remain in freshwater for a week to many months prior to outmigration, with the decision to outmigrate influenced by photoperiod, fish size, fish density, flow, predation, and temperature (Moyle et al., 2017). However, we assumed that most individuals rear near emergence locations for up to 2 months before moving downstream or to other rearing areas.

2.3 | Analyses

To assess which life stages and ecotypes were thermally stressed, we quantified thermal exposure and stress in the context of thermal criteria (thresholds) specific to each life stage (U.S. EPA, 2003). In brief, the EPA thermal criteria were developed to be protective of salmonids while they are in freshwater. For this study, thermal stress was defined by thermal exceedance of these thresholds. Specifically, thermal stress was defined as follows: adult migration exceeding 20°C, adults holding prior to spawning exceeding 16°C, spawning, incubation, or emergence exceeding 13°C, and rearing exceeding 16°C. The EPA thermal criteria are based on the 7DADM (7-day average daily maximum) temperature, whereas the SSN model predicts mean monthly stream temperature. However, if our analyses based on mean monthly averages reveal that exposure exceeds thermal criteria based on the 7DADM, it is likely that populations are exposed to even higher temperatures and more stressful conditions than we predict.

First, we quantified mean monthly thermal exposure throughout the freshwater residency (i.e., from core holding through incubation to early rearing, defined by the phenology database) at the spawning grounds for each ecotype. This first analysis gives a broad overview of the thermal exposure of each ecotype and shows how thermal exposure changes throughout the year. Because salmonids can experience mortality from exposures to high temperatures (U.S. EPA, 2003) and a single life stage can be found in freshwater for multiple months, we next analyzed the warmest month (based on mean monthly temperature) experienced during the peak (migration) or core (holding, incubation, early rearing) period of each life stage. We calculated the proportion of the spatial distribution of each ecotype exhibiting thermal stress during the warmest month of exposure. Then, we compared the proportion of stress for each ecotype to latitude, elevation, migration distance, and run type to determine whether thermal stress was influenced by geography, distance traveled, or phenotype.

For each analysis, we evaluated thermal exposure and thermal stress (a) for current distributions under historical climate conditions, (b) for historical distributions above dams under historical climate conditions, and (c) under future +1°C and +2°C stream temperature change scenarios both below and above currently impassable dams. For ecotypes with historical distributions above dams, we assumed that each ecotype would exhibit the same phenology above dams as below dams. We then determined how thermal exposure and thermal stress during migration would change under our stream temperature change scenarios.

3 | RESULTS

3.1 | Stream temperature predictions

We predicted mean monthly stream temperature for 465,775 river km across eight sub-regional watersheds in the western U.S. (Figure 3); note that these results include all stream segments in our study area, not just those with relevance to salmonids. When grouping all sub-regions and months, predicted error was fairly low for the out-of-sample testing dataset (mean RMSE = 1.351°C; mean MAPE = 0.915°C; Table S3.1; Figure 4a), and similar to that of Isaak, Wenger, Peterson, et al. (2017) for the month of August (RMSE = 1.10°C, MAPE = 0.72°C). The overall r^2 was 0.928 for the testing dataset (Figure 4a). Of the eight sub-region, Coastal California had the highest error (RMSE = 1.856°C, MAPE = 1.384°C, Table S3.1). Within a sub-region-month, datasets that resulted in low r^2 consisted of fewer than 125 observations (Table S3.1). In general, r^2 plateaued around 0.8 when the number of observations exceeded ~300 for a given sub-regional watershed (Figure 4b).

3.2 | Thermal exposure and thermal stress of Chinook salmon life stages and ecotypes

Thermal exposure on the spawning grounds varied considerably by life stage and ecotype, but ecotypes with analogous run timing displayed similar overall patterns of exposure (Figure 5a–c; Table S1.1). Stream temperature peaked in the summer months, when most spring-runs and some summer-runs are holding, and several ecotypes exceeded thermal thresholds during this time. Monthly thermal exposure under our +1°C and +2°C scenarios was still, on average, below EPA thermal criteria for all fall-runs except Upper Klamath-Trinity River fall-run (UKTR_F), Central Valley fall-run (CV_F), and Upper Columbia River fall-run (UppColR_F; Figure 5a). Some ecotypes arriving to spawning grounds in late spring and

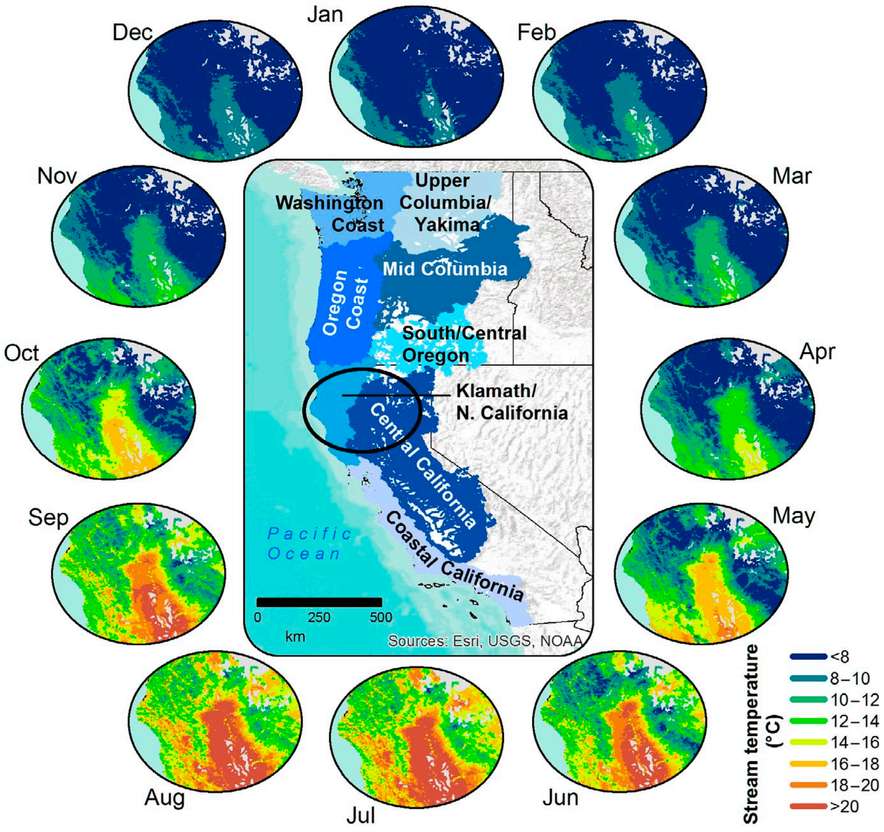

FIGURE 3 Predicted monthly mean stream temperatures (outer figures) for 465,775 river km in eight sub-regional watersheds in the western U.S. (central figure). The outer figures highlight how historical thermal regimes (average of 2002–2011) shifted throughout the year in a section of northern California spanning two sub-regions (area circled in central figure). Note that sub-region names do not correspond to Chinook salmon ecotype or ESU names

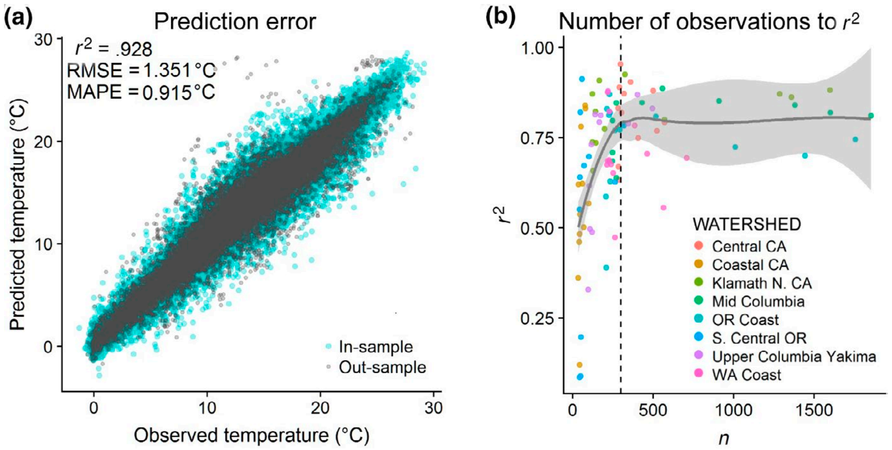

FIGURE 4 Performance of the stream temperature model for all sub-regional watersheds for all months. (a) Observed stream temperatures vs. predictions. The in-sample dataset (gray) was used to fit the model with 135,698 temperature observations, and the out-of-sample dataset (blue) tested the prediction capability of the model using 33,998 temperature observations. The statistical summary metrics were calculated from the out-of-sample testing dataset. (b) Relationship of the number of temperature observations to r^2 for the testing (out-of-sample) dataset. The dashed line at n = 300 shows where r^2 begins to plateau

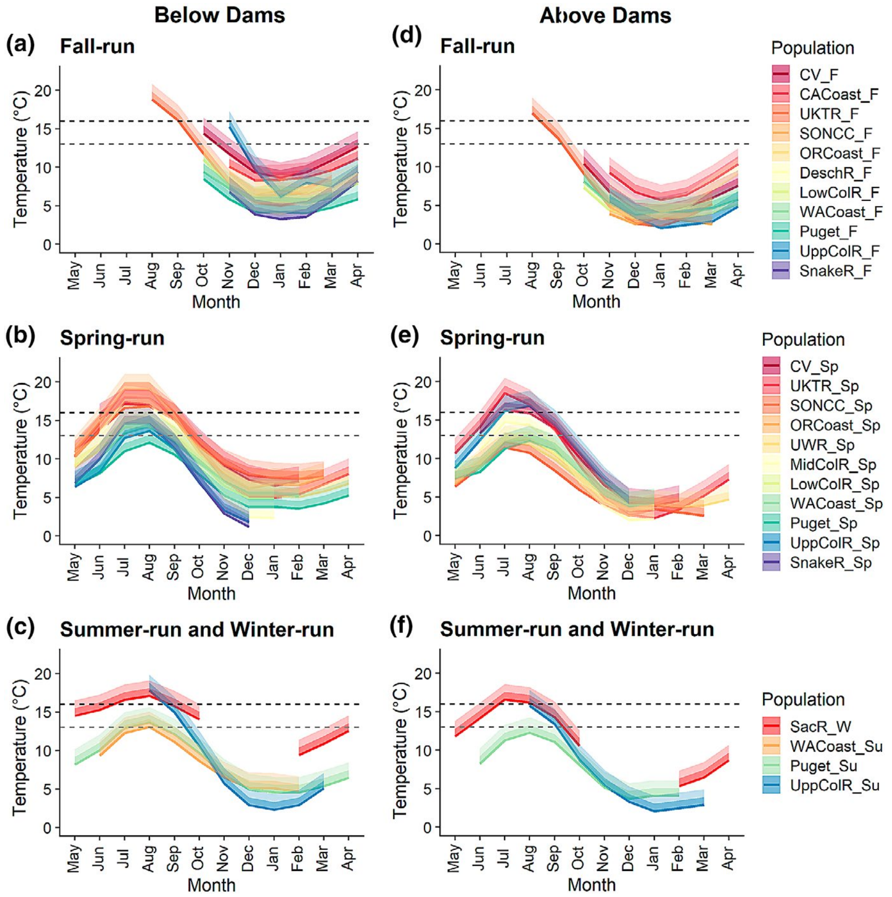

FIGURE 5 Historical and projected future thermal exposures of Chinook salmon ecotypes throughout their freshwater residency, from peak holding throughout early rearing (i.e., the month after peak emergence), at empirical observations below dams and above dams. (a–c) shows actual thermal exposure below dams, and (d–f) shows potential thermal exposure above dams. Mean temperature exposure (historical: dark line; +1°C scenario: medium shading; +2°C scenario: light shading) are shown for each ecotype. EPA salmonid thermal criteria are shown for spawning, incubation, and emergence (black dotted line; 13°C) and core juvenile rearing and adults holding (gray dotted line; 16°C). Peak holding begins approximately October for fall-runs, May for spring-runs, June for summer-runs, and February for the lone winter-run; see Table S2.1 for ecotype-specific phenology. Note that several ecotypes do not have predicted thermal exposure above dams (d–f) because they are not blocked by dams or we do not have temperature predictions in their blocked ranges

early summer experience longer periods above EPA criteria below dams under our stream warming scenarios (Figure 5b,c). Sacramento River winter-run (SacR_W) would experience too-warm mean temperatures for all life stages by 2040, and mean temperatures are predicted to be well above thermal criteria during incubation, emergence, and early rearing (Figure 5c). Above dams, all ecotypes would experience mean temperatures cooler than below dams (Figure 5d–f). Furthermore, average thermal exposure above dams would generally be cooler than EPA criteria. An exception is SacR_W, which would still experience too-warm spawning and incubation temperatures in the summer, even above dams (Figure 5f). Even with stream temperature increases of 2°C, mean thermal exposure above dams would likely not exceed thresholds for almost all ecotypes (Figure 5d–f).

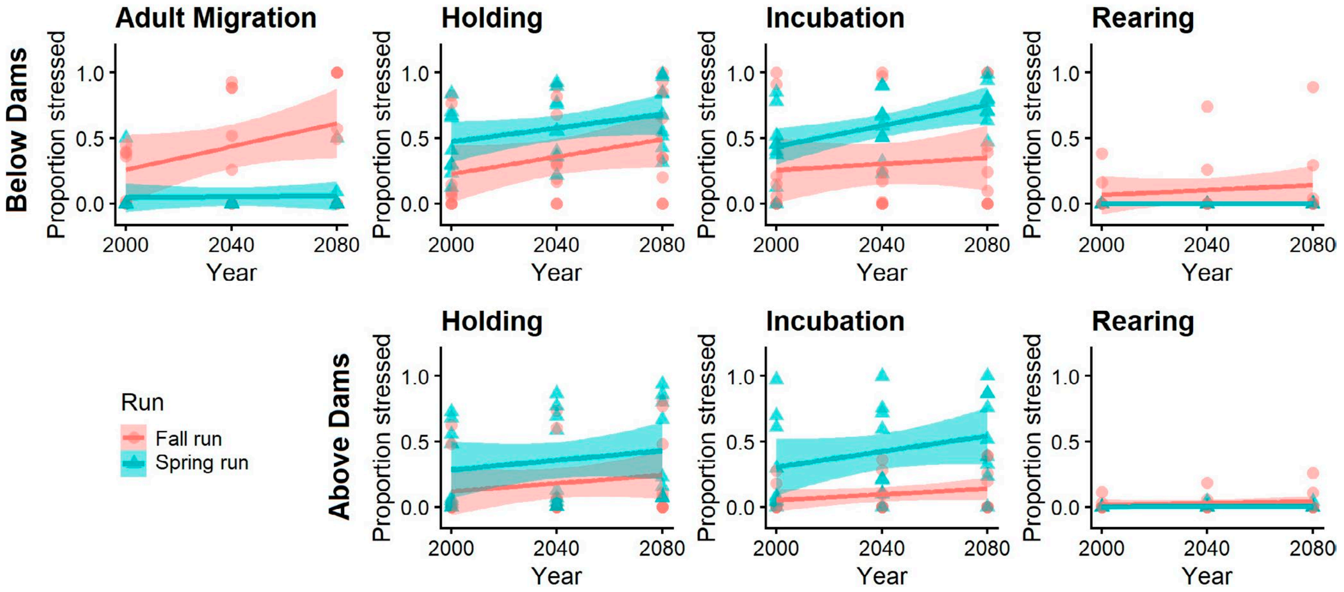

FIGURE 6 Proportion of historical and future thermal stress below dams (top panel) and above dams (bottom panel) for fall- (pink, circles) and spring-run (teal, triangles) spatial distributions, shown with standard error (shading). Future stream temperatures (2040, 2080) are represented by stream temperature warming scenarios of +1°C and +2°C, respectively. Holding, incubation, and rearing show the warmest month of exposure during the core of that life stage for each ecotype, and adult migration shows the exposure during the peak month of adult migration. For this analysis, summer-runs were re-classified as spring-run like (Puget_Su, WACoast_Su) or fall-run like (UppColR_Su) based on phenology

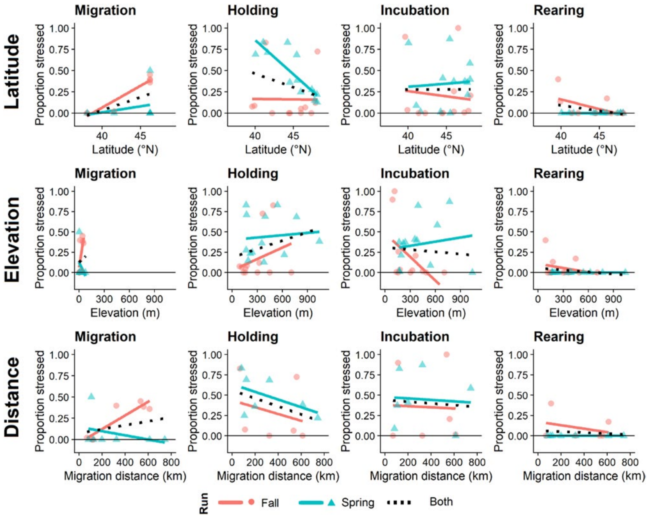

FIGURE 7 Patterns in proportion of thermal stress for fall- (pink, circles) and spring-run (teal, triangles) ecotypes based on latitude, elevation, and migration distance. The dotted black line shows the best fit line for all run types. Note that thermal stress for migration distance measures the minimum distance to spawning grounds and only includes interior ecotypes. For this analysis, summer-runs were re-classified as spring-run like (Puget_Su, WACoast_Su) or fall-run like (UppColR_Su) based on phenology

During the warmest month of exposure for each life stage, almost all ecotypes were exposed to some proportion (i.e., non-zero) of thermal stress below dams for at least one freshwater life stage (Figure 6 top panel). Spring-runs showed higher levels of thermal stress than fall-runs during adult holding and egg incubation, whereas fall-runs showed higher levels of thermal stress during adult migration. Neither run type was thermally stressed during early juvenile rearing, even when using the EPA's 13°C emergence threshold rather than the 16°C core rearing threshold. During holding and incubation, thermal stress under the +1°C scenario was predicted for more than 50% of spring-run ecotypes and about 25% of fall-run ecotypes. Still, thermal stress of all fall-run ecotypes was predicted to exceed 25% under the +1°C scenario during both holding (or month of peak spawning) and incubation. Above dams, although levels of thermal stress would be reduced relative to the current distributions for almost all ecotypes, some ecotypes may still be exposed to some amount of thermal stress (Figure 6 bottom panel). Still, the amount of thermal stress and the rate of increase of thermal stress are predicted to be lower above dams than below them.

The proportion of thermal stress explained by latitude, elevation, or distance varied by ecotype (i.e., spring-run vs. fall-run) and life stage (Figure 7). In other words, run types and life stages often showed opposing relationships (i.e., opposite slopes) or different slope magnitudes. Run type in combination with latitude, elevation, or distance was generally a better predictor of thermal stress for each life stage than latitude, elevation, or distance alone.

4 | DISCUSSION

4.1 | Adult migration timing largely determines thermal exposure for West Coast Chinook salmon

Here, we combined stream temperature modeling, spatiotemporal distributions for each life stage of each population, and thermal criteria specific to each life stage to predict thermal exposure and thermal stress for the freshwater life stages of an anadromous species. We expected that the proportion of thermal stress would decline with increasing latitude, increasing elevation, and decreasing migration distance. However, we found that the thermal exposure of salmon populations depended more strongly on migration phenology than geography such that sympatric ecotypes with divergent phenology are predicted to respond differently to climate change. Ecotypes with early migration phenology (i.e., winter-run, spring-run, and some summer-run) had higher proportions of thermal stress on spawning grounds than fall-run, and the winter-run was consistently stressed across all scenarios. This prediction is consistent with other studies (e.g., Crozier et al., 2019; Moyle et al., 2017). However, we also found that later migration phenology (i.e., some summer-run and fall-run) exhibited thermal stress during adult migration. Our results highlight the fact that migratory species with variable phenology typically require population-specific management approaches to mitigate the negative effects of climate change, and geography is not always the best predictor of responses.

Spring-run ecotypes have declined precipitously relative to fall-run in recent decades (Gustafson et al., 2007; Moyle et al., 2017) due to a disproportionate loss of historic habitat from fish passage barriers (Beechie et al., 2006; NRC, 1996). Our results showed that spring-run ecotypes were more thermally stressed than fall-run ecotypes on the spawning grounds, particularly during pre-spawn holding. Thermally stressed adults may die during pre-spawn holding (Bowerman et al., 2017), produce fry with developmental abnormalities (Berman, 1990), or produce smaller eggs and fry (Berman, 1990; Bouck et al., 1975; Kinnison et al., 2001); the smaller fish are then more vulnerable to predation (Lorenzen, 1996; Peterson & Wroblewski, 1984). Furthermore, spring-run embryos, which typically emerge earlier in the winter or spring than fall-run embryos, are exposed to cooler temperatures and thus slower growth rates (Perry et al., 2015) that may expose spring-run embryos to higher rates of size-dependent predation (Lorenzen, 1996; Peterson & Wroblewski, 1984). Together, the above observations and our estimates of thermal exposure suggest that the spring-run ecotypes evaluated in this work are at much higher risk of extirpation on the spawning grounds than fall-run ecotypes.

Thermally stressed ecotypes may be able to mitigate the effects of a warming climate by a shift in phenology that avoids exposing sensitive life stages to excessively high temperatures (Crozier & Hutchings, 2014; Mantua et al., 2015). For example, Chinook salmon fall-runs could migrate a few weeks later in the fall to avoid high levels of thermal stress. Although arrival timing is likely partially genetically controlled (Narum et al., 2018; Prince et al., 2017; Quinn, 2018; Thompson et al., 2019), there is some evidence of phenotypic plasticity in Chinook salmon and other salmonid species (e.g., Crozier & Hutchings, 2014; Quinn et al., 2001), indicating that Chinook salmon may be able to shift their migration dates to avoid thermal stress. On the other hand, phenological shifts in one part of the salmon life cycle must work in concert with viable phenological changes in the rest of the life cycle, and such changes in response to rising temperatures must be limited (Muñoz et al., 2015).

Phenological shifts may also increase overlap between spring-run and fall-run ecotypes. In many rivers, phenology coupled with spatial separation is the major prezygotic barrier between fall- and spring-runs; in rivers with impassable dams, phenology may be the only prezygotic barrier such that shifts in phenology can increase overlap in spawn timing. Overlapping spawn timing without spatial separation can then result in hybridization between runs. For example, fall-run and spring-run ecotypes in the Rogue River have hybridized following completion of Lost River Dam in 1977 (Thompson et al., 2019). Arrival timing is strongly associated with a distinct genomic region on chromosome 28, and individuals heterozygous for these alleles tend to have an intermediate (summer-time) adult return timing (Narum et al., 2018; Prince et al., 2017; Thompson et al., 2019) that will likely be selected against in a warmer climate (Crozier et al., 2019). In rivers with little spatial separation where fall-run have much greater abundance, hybridization would likely result in the genetic swamping by fall-run, potentially resulting in a loss of the early arrival phenotype. This loss of Chinook salmon phenotypic and genetic diversity could ultimately lower the species' ability to withstand future perturbations (Anderson et al., 2020; Thompson et al., 2019).

A shift in spatial distribution without altering phenology could reduce too-warm thermal exposure, but most Chinook salmon ecotypes cannot shift spatially to cooler, higher elevation waters because this cooler habitat is currently blocked by impassable dams (e.g., Beechie et al., 2006; Crozier et al., 2019; Gustafson et al., 2007; Lindley et al., 2004; Mantua et al., 2015; McClure et al., 2008; Moyle et al., 2017). Dams have not only reduced the amount of habitat available to many spring-run ecotypes but have reduced or eliminated suitable cold water required for holding, spawning, incubation, and/or freshwater rearing. Dams have effectively increased thermal exposure for ecotypes that historically used these higher elevation, cooler waters, but are now confined to lower elevations (Beechie et al., 2006; Lindley et al., 2004; McClure et al., 2008; Myers et al., 1998). Some salmon conservation work focuses on making habitat above dams accessible to salmon by creating fish ladders or passageways, trucking fish around dams, or removing dams entirely. For this study, we assessed the historical and future thermal suitability of all potentially habitable reaches above impassable dams (31,699 river km in total) for each ecotype (96–7,556 km per ecotype). Above dams, almost all ecotypes—on average—would be exposed to temperatures below U.S. EPA (2003) thermal thresholds from holding through early rearing, even if streams warmed by 2°C. The difference in thermal exposure below dams versus above dams was most dramatic for ecotypes with prolonged holding times in the summer. In total, thousands of stream km currently blocked by dams are thermally suitable and likely habitable. Providing access to these habitats along thermally suitable migration corridors offers a potentially effective avenue for mitigating warming stream temperatures, particularly for thermally stressed spring-run Chinook salmon ecotypes.

4.2 | Stream temperature model

Riverine species, especially those that are migratory, are especially vulnerable to climate change, yet predicting current and expected levels of thermal stress for such species is limited by the availability of spatially continuous and seasonally varying stream temperature data. Here we made an important step forward in increasing the availability of such estimates, by extending an existing stream temperature model to predict stream temperatures for every month of the year at the kilometer scale in the western U.S. The stream temperature model results pave the way for landscape-scale modeling of annual thermal regimes in riverine habitats in the western U.S. The stream temperature predictions can be used to examine temperature exposure across populations, explore potentially suitable thermal habitat for species reintroductions into unoccupied habitats, or assess the likelihood of colonization of invasive species, making our work particularly important in the era of rapid anthropogenic change and human-mediated conservation. However, we urge caution when using this model or our results (a) if there are fewer than ~1,500 total stream temperature observations within a watershed per month (e.g., Coastal California for some winter months); (b) for bodies of water that are stagnant or slow-moving, deep, or with known hyporheic flow influence, for which the model may not predict well (Isaak, Wenger, Peterson, et al., 2017); or (3) in systems where any spatial covariate (e.g., canopy coverage) may have changed since our study time period.

4.3 | Limitations in our approach

Estimating thermal stress for 26 Chinook ecotypes for thousands of km of stream habitat required us to make several simplifying assumptions. First, our estimates of thermal stress are based on estimated stream temperatures, rather than measured stream temperatures. Our temperature predictions had a prediction error of ~1°C, suggesting some caution when interpreting results near survival thresholds. Moreover, the spatial resolution of our stream temperature model (1 km) may not resolve microreaches or small refugia with more suitable temperatures (Fullerton et al., 2018), and freshwater fish may behaviorally thermoregulate by moving to these suitable microhabitats within the stream (e.g., Bardach & Bjorklund, 1957; Berman & Quinn, 1991; Brett, 1971; Kaya et al., 1977). Second, we did not explicitly consider population-specific thermal tolerances. The thermal criteria applied in our study were based on extensive research, primarily on Pacific Northwest salmonids (U.S. EPA, 2003), and are protective of salmonids in general, but specific salmonid populations may have different thermal tolerances (Chen et al., 2013; Eliason et al., 2011; Martins et al., 2011; Stitt et al., 2014; Zillig et al., 2018). However, in cases where population-specific tolerances are known, these estimates can be easily incorporated in our framework to more accurately quantify thermal stress. Third, we represented the movement of salmon populations through stream habitats in a relatively coarse way, for example, by assuming holding and early rearing take place within known spawning distributions for specific populations. Thus, we did not explicitly account for more fine-scale movement within or among habitats that individuals may use to reduce exposure to unsuitable temperatures.

Finally, river temperatures will likely change in more complex ways than the simple climate scenarios we considered. We based the +1°C and +2°C increases on modeling work by Isaak, Wenger, Peterson, et al. (2017) for August, but applied these predicted stream temperature changes to all months of the year because a lack of seasonal flow projections prevented us from expanding stream temperature projections to other months. We also assumed that all streams would show the same increase, but regionally averaged air temperature warming is unlikely to represent actual stream temperature responses (Arismendi et al., 2014). Additionally, it is difficult to predict stream temperature responses for regulated rivers (i.e., below dams), although temperatures in the lakes and reservoirs above dams will increase with climate warming (e.g., Gooseff et al., 2005; Helfer et al., 2012; Williamson et al., 2009), indicating that downstream temperatures may similarly increase. Cooler streams may be less sensitive to increasing air temperature than warmer streams, and Isaak et al. (2017) calculated sensitivity parameters for each watershed. However, these sensitivities resulted in small differences; for example, the maximum sensitivity parameter (0.06, for Central California) would change future predicted temperatures of 11°C (from historical 10°C) and 21°C (from historical 20°C) to 10.4 and 21.1°C, respectively. For our study, these small sensitivities are likely negligible compared to the broad insights we have gained regarding which ecotypes, life stages, and regions are likely to be more or less sensitive to stream warming.

4.4 | Conclusions

Combining spatial distribution and phenology data with spatially explicit and temporally explicit temperature predictions enables researchers to examine temperature exposure for populations throughout the year. Our expansion of the stream temperature model to all months of the year allows assessment of historical and future thermal conditions for >460,000 stream km in the western U.S. Examining seasonal thermal exposure is particularly important for migratory taxa with multiple life stages that have different sensitivities to temperatures, as we illustrated with Chinook salmon. Our results highlight that populations of species with variable phenology and spatial distribution may respond differently to climate change, and responses may be more closely related to intraspecific variation in phenology (e.g., adult migration timing) than environmental constraints imposed by local geography. For Chinook salmon, ecotypes with early adult migration phenotypes and prolonged adult holding times in the summer (i.e., spring-run, winter-run, and some summer-run) will experience higher levels of thermal stress with climate change relative to ecotypes with later arrivals (i.e., fall-run). However, hope lies in the thousands of stream km currently blocked by dams, where thermal stress would be substantially reduced or even eliminated for most ecotypes, even if stream temperatures warm by 2°C.

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DATA AVAILABILITY STATEMENT

The stream temperature model results and the Chinook salmon spatial distribution data, including all linked temperature data needed to replicate our thermal exposure results, are openly available in DRYAD at https://doi.org/10.5061/dryad.n5tb2rbtq. The Chinook salmon phenology database developed in this study is available in the supplementary material of this article.

ORCID

Alyssa M. FitzGerald https://orcid.org/0000-0002-9850-2003

REFERENCES

Agrawal, A., Schick, R. S., Bjorkstedt, E. P., Szerlong, R. G., Goslin, M. N., Spence, B. C., Williams, T. H., & Burnett, K. M. (2005). Predicting the potential for historical coho, chinook and steelhead habitat in northern California. NOAA Technical Memorandum NMFS, NOAA-TM-NMFS-SWFSC-379.

Allen, A. M., & Singh, N. J. (2016). Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution*, *3*, 155.

Anderson, E. C., Ford, M. J., Garza, J. C., & Kiernan, J. D. (2020). *Upper Klamath and Trinity River Chinook Salmon ESU-configuration review-panel report*. Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration.

Arismendi, I., Safeeq, M., Dunham, J. B., & Johnson, S. L. (2014). Can air temperature be used to project influences of climate change on stream temperature? *Environmental Research Letters*, *9*(8), 084015.

Bardach, J. E., & Bjorklund, R. G. (1957). The temperature sensitivity of some American freshwater fishes. *The American Naturalist*, *91*(859), 233–251.

Beechie, T., Imaki, H., Greene, J., Wade, A., Wu, H., Pess, G., Roni, P., Kimball, J., Stanford, J., Kiffney, P., & Mantua, N. (2013). Restoring salmon habitat for a changing climate. *River Research and Applications*, *29*(8), 939–960.

Beechie, T. J., Ruckelshaus, M., Buhle, E., Fullerton, A., & Holsinger, L. (2006). Hydrologic regime and the conservation of salmon life history diversity. *Biological Conservation*, *130*, 560–572.

Berman, C. H. (1990). *The effect of elevated holding temperatures on adult spring Chinook salmon reproductive success*. Doctoral dissertation. University of Washington.

Berman, C. H., & Quinn, T. P. (1991). Behavioural thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. *Journal of Fish Biology*, *39*(3), 301–312.

Bjornn, T. C., & Reiser, D. W. (1991). Habitat requirements of salmonids in streams. In W. R. Meehan (Ed.), *Influence of forest and rangeland management of salmonid fishes and their habitat* (pp. 83–138). American Fisheries Society, Special Publication 19.

Bottrill, M. C., Joseph, L. N., Carwardine, J., Bode, M., Cook, C., Game, E. T., Grantham, H., Kark, S., Linke, S., McDonald-Madden, E., Pressey, R. L., Walker, S., Wilson, K. A., & Possingham, H. P. (2008). Is conservation triage just smart decision making? *Trends in Ecology & Evolution*, *23*(12), 649–654.

Bouck, G. R., Chapman, G. A., Schneider, P. W., & Stevens, D. G. (1975). Effects of holding temperatures on reproductive development in adult sockeye salmon (*Oncorhynchus nerka*). In J. R. Donaldson (Ed.), *26th Annual northwest fish culture conference* (pp. 24–40). Otter Creek.

Bowerman, T., Roumasset, A., Keefer, M. L., Sharpe, C. S., & Caudill, C. C. (2017). Prespawn mortality of female Chinook Salmon increases with water temperature and percent hatchery origin. *Transactions of the American Fisheries Society*, *147*(1), 31–42.

Bradford, M. J., & Taylor, G. C. (1997). Individual variation in dispersal behaviour of newly emerged chinook salmon (Oncorhynchus tshawytscha) from the Upper Fraser River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(7), 1585–1592.

Brannon, E. L., Powell, M. S., Quinn, T. P., & Talbot, A. (2004). Population structure of Columbia River Basin Chinook salmon and steelhead trout. *Reviews in Fisheries Science*, *12*(2–3), 99–232.

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 nerka). *American Zoologist*, *11*(1), 99–113.

Chen, Z., Anttila, K., Wu, J., Whitney, C. K., Hinch, S. G., & Farrell, A. P. (2013). Optimum and maximum temperatures of sockeye salmon (*Oncorhynchus nerka*) populations hatched at different temperatures. *Canadian Journal of Zoology*, *91*(5), 265–274.

Comte, L., & Grenouillet, G. (2013). Do stream fish track climate change? Assessing distribution shifts in recent decades. *Ecography*, *36*(11), 1236–1246.

Cressie, N. (1993). *Statistics for spatial data*, (Rev ed.). John Wiley.

Crozier, L. G., Hendry, A. P., Lawson, P. W., Quinn, T. P., Mantua, N. J., Battin, J., Shaw, R. G., & Huey, R. B. (2008). Potential responses to climate change in organisms with complex life histories: Evolution and plasticity in Pacific salmon. *Evolutionary Applications*, *1*(2), 252–270.

Crozier, L. G., & Hutchings, J. A. (2014). Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications*, *7*(1), 68–87.

Crozier, L. G., McClure, M. M., Beechie, T., Bograd, S. J., Boughton, D. A., Carr, M., Cooney, T. D., Dunham, J. B., Greene, C. M., Haltuch, M. A., Hazen, E. L., Holzer, D. M., Huff, D. D., Johnson, R. C., Jordan, C. E., Kaplan, I. C., Lindley, S. T., Mantua, N. J., Moyle, P. B., ... Willis-Norton, E. (2019). Climate vulnerability assessment for Pacific salmon and steelhead in the California Current Large Marine Ecosystem. *PLoS One*, *14*(7).

Dahlke, F. T., Wohlrab, S., Butzin, M., & Pörtner, H. O. (2020). Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, *369*(6499), 65–70.

Dauble, D. D., & Geist, D. R. (2000). Comparison of mainstem spawning habitats for two populations of fall chinook salmon in the Columbia River basin. *Regulated Rivers: Research & Management*, *16*(4), 345–361.

Dauble, D. D., & Watson, D. G. (1997). Status of fall Chinook salmon populations in the mid-Columbia River, 1948–1992. *North American Journal of Fisheries Management*, *17*(2), 283–300.

Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, *292*(5517), 673–679.

Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jeffries, K. M., Gale, M. K., Patterson, D. A., Hinch, S. G., & Farrell, A. P. (2011). Differences in thermal tolerance among sockeye salmon populations. *Science*, *332*(6025), 109–112.

Fagan, W. F. (2002). Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology*, *83*(12), 3243–3249.

Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. (2002). Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience*, *52*(6), 483–498.

Fullerton, A. H., Torgersen, C. E., Lawler, J. J., Steel, E. A., Ebersole, J. L., & Lee, S. Y. (2018). Longitudinal thermal heterogeneity in rivers and refugia for coldwater species: effects of scale and climate change. *Aquatic Sciences*, *80*(1), 3.

Geist, D. R. (2000). Hyporheic discharge of river water into fall chinook salmon (*Oncorhynchus tshawytscha*) spawning areas in the Hanford Reach, Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(8), 1647–1656.

Gooseff, M. N., Strzepek, K., & Chapra, S. C. (2005). Modeling the potential effects of climate change on water temperature downstream of a shallow reservoir, Lower Madison River, MT. *Climatic Change*, *68*(3), 331–353.

Gustafson, R. G., Waples, R. S., Myers, J. M., Weitkamp, L. A., Bryant, G. J., Johnson, O. W., & Hard, J. J. (2007). Pacific salmon extinctions: quantifying lost and remaining diversity. *Conservation Biology*, *21*(4), 1009–1020.

Healey, M. C. (1991). Life history of Chinook salmon (*Oncorhynchus tshawytscha*). In P. S. L. Histories (Ed.), *Groot and margolis* (pp. 311–394). University of British Columbia Press.

Helfer, F., Lemckert, C., & Zhang, H. (2012). Impacts of climate change on temperature and evaporation from a large reservoir in Australia. *Journal of Hydrology*, *475*, 365–378.

Herbold, B., Carlson, S. M., Henery, R., Johnson, R. C., Mantua, N., McClure, M., Moyle, P. B., & Sommer, T. (2018). Managing for salmon resilience in California's variable and changing climate. *San Francisco Estuary and Watershed Science*, *16*(2).

Hiddink, J. G., Burrows, M. T., & García Molinos, J. (2015). Temperature tracking by North Sea benthic invertebrates in response to climate change. *Global Change Biology*, *21*(1), 117–129.

Hostetler, S. W., Alder, J. R., & Allan, A. M. (2011). *Dynamically downscaled climate simulations over North America: Methods, evaluation, and supporting documentation for users* (Open File Rep. 2011–1238) (pp. 1–64). U.S. Geological Survey.

Intergovernmental Panel on Climate Change [IPCC]. (2007). *Climate Change 2007: The physical science basis*. Cambridge University Press.

Isaak, D. J., Luce, C. H., Horan, D. L., Chandler, G. L., Wollrab, S. P., & Nagel, D. E. (2018). Global warming of salmon and trout rivers in the Northwestern US: Road to ruin or path through purgatory? *Transactions of the American Fisheries Society*, *147*(3), 566–587.

Isaak, D. J., Peterson, E. E., Ver Hoef, J. M., Wenger, S. J., Falke, J. A., Torgersen, C. E., Colin Sowder, E., Steel, A., Fortin, M.-J., Jordan, C. E., Ruesch, A. S., Som, N., & Ruesch, A. S. (2014). Applications of spatial statistical network models to stream data. *Wiley Interdisciplinary Reviews: Water*, *1*(3), 277–294.

Isaak, D. J., Wenger, S. J., Peterson, E. E., Ver Hoef, J. M., Nagel, D. E., Luce, C. H., Hostetler, S. W., Dunham, J. B., Roper, B. B., Wollrab, S. P., Chandler, G. L., Horan, D. L., & Chandler, G. L. (2017). The NorWeST summer stream temperature model and scenarios for the western US: A crowd-sourced database and new geospatial tools foster a user community and predict broad climate warming of rivers and streams. *Water Resources Research*, *53*(11), 9181–9205.

Isaak, D. J., Wenger, S. J., & Young, M. K. (2017). Big biology meets microclimatology: Defining thermal niches of ectotherms at landscape scales for conservation planning. *Ecological Applications*, *27*(3), 977–990.

Isaak, D. J., Young, M. K., Luce, C. H., Hostetler, S. W., Wenger, S. J., Peterson, E. E., Ver Hoef, J. M., Groce, M. C., Horan, D. L., & Nagel, D. E. (2016). Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences*, *113*(6), 4374–4379.

Johnson, Z. C., Torgersen, C., Fullerton, A., Mejia, F., Casola, J., Lee, S.-Y., Shirk, A. J., Rautu, R., & Ege, A. (2019). *Stream temperature handbook: A new primer on data and models*. Paper presented at American Fisheries Society annual meeting, Reno, NV.

Josse, J., & Husson, F. (2016). missMDA: A package for handling missing values in multivariate data analysis. *Journal of Statistical Software*, *70*(1), 1–31.

Kaya, C. M., Kaeding, L. R., & Burkhalter, D. E. (1977). Use of a cold-water refuge by rainbow and brown trout in a geothermally heated stream. *The Progressive Fish-Culturist*, *39*(1), 37–39.

Kinnison, M. T., Unwin, M. J., Hendry, A. P., & Quinn, T. P. (2001). Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. *Evolution*, *55*(8), 1656–1667.

Lindley, S. R., Schick, R., May, B. P., Anderson, J. J., Greene, S., Hanson, C., Low, A., McEwan, D., MacFarlane, R. B., Swanson, C., & Williams, J. G. (2004). Population structure of threatened and endangered Chinook salmon ESUs in California's Central Valley basin. NOAA Technical Memorandum, NOAA-TM-NMFS-SWFSC-360.

Lorenzen, K. (1996). The relationship between body weight and natural mortality in juvenile and adult fish: A comparison of natural ecosystems and aquaculture. *Journal of Fish Biology*, *49*(4), 627–642.

Mantua, N. J., Crozier, L. G., Reed, T. E., Schindler, D. E., & Waples, R. (2015). Correspondence RE: Muñoz et al Adaptive potential of a Pacific salmon challenged by climate change. *Nature Climate Change*, *5*, 613–614.

Martins, E. G., Hinch, S. G., Patterson, D. A., Hague, M. J., Cooke, S. J., Miller, K. M., Lapointe, M. F., English, K. K., & Farrell, A. P. (2011). Effects of river temperature and climate warming on stock-specific survival of adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*). *Global Change Biology*, *17*(1), 99–114.

McClure, M. M., Carlson, S. M., Beechie, T. J., Pess, G. R., Jorgensen, J. C., Sogard, S. M., Sultan, S. E., Holzer, D. M., Travis, J., Sanderson, B. L., Power, M. E., & Carmichael, R. W. (2008). Evolutionary consequences of habitat loss for Pacific anadromous salmonids. *Evolutionary Applications*, *1*(2), 300–318.

Moyle, P., Lusardi, R., Samuel, P., & Katz, J. (2017). *State of the Salmonids: Status of California's emblematic fishes 2017*. Center for Watershed Sciences, University of California Davis, and California Trout.

Muñoz, N. J., Farrell, A. P., Heath, J. W., & Neff, B. D. (2015). Correspondence RE: Muñoz et al Adaptive potential of a Pacific salmon challenged by climate change. *Nature Climate Change*, *5*, 615.

Myers, J. M., Kope, R. G., Bryant, G. J., Teel, D., Lierheimer, L. J., Wainwright, T. C., & Waples, R. S. (1998). Status review of Chinook salmon from Washington, Idaho, Oregon, and California (pp. 443). NOAA Technical Memorandum NMFS-NWFSC-35.

Nagel, D., Peterson, E., Isaak, D., Ver Hoef, J., & Horan, D. (2015). National Stream Internet protocol and user guide. US Forest Service, Rocky Mountain Research Station Air, Water, and Aquatic Environments Program. http://www.fs.fed.us/rm/boise/awae/projects/NationalStreamInternet/downloads/NationalStreamInternetProtocolandUserGuide.pdf

Narum, S. R., Di Genova, A., Micheletti, S. J., & Maass, A. (2018). Genomic variation underlying complex life-history traits revealed by genome sequencing in Chinook salmon. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1883), 20180935.

National Marine Fisheries Service [NMFS]. (2014). *Recovery plan for the evolutionarily significant units of Sacramento river winter-run Chinook Salmon and Central Valley Spring-run Chinook Salmon and the distinct population segment of California central valley steelhead*. National Marine Fisheries Service, West Coast Region.

National Marine Fisheries Service [NMFS]. (2016). *Final coastal multispecies recovery plan*. National Marine Fisheries Service, West Coast Region.

National Research Council {NRC}. (1996). *Upstream: Salmon and society in the Pacific Northwest*. National Academies Press.

Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography*, *12*(5), 361–371.

Perry, R. W., Plumb, J. M., & Huntington, C. W. (2015). Using a laboratory-based growth model to estimate mass-and temperature-dependent growth parameters across populations of Juvenile Chinook Salmon. *Transactions of the American Fisheries Society*, *144*(2), 331–336.

Peterson, E. E., & Ver Hoef, J. M. (2010). A mixed-model moving-average approach to geostatistical modeling in stream networks. *Ecology*, *91*(3), 644–651.

Peterson, E. E., Ver Hoef, J. M., Isaak, D. J., Falke, J. A., Fortin, M.-J., Jordan, C. E., McNyset, K., Monestiez, P., Ruesch, A. S., Sengupta, A., Som, N., Steel, E. A., Theobald, D. M., Torgersen, C. E., & Wenger, S. J. (2013). Modelling dendritic ecological networks in space: An integrated network perspective. *Ecology Letters*, *16*(5), 707–719.

Peterson, I., & Wroblewski, J. S. (1984). Mortality rate of fishes in the pelagic ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences*, *41*(7), 1117–1120.

Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., & Levin, S. A. (2013). Marine taxa track local climate velocities. *Science*, *341*(6151), 1239–1242.

Prince, D. J., O'Rourke, S. M., Thompson, T. Q., Ali, O. A., Lyman, H. S., Saglam, I. K., Hotaling, T. J., Spidle, A. P., & Miller, M. R. (2017). The evolutionary basis of premature migration in Pacific salmon highlights the utility of genomics for informing conservation. *Science Advances*, *3*(8), e1603198.

Quinn, T. P. (2018). *The behavior and ecology of pacific Salmon & trout* (2nd ed.). University of Washington Press.

Quinn, T. P., Kinnison, M. T., & Unwin, M. J. (2001). Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica*, *112*(1), 493–513.

Quinn, T. P., McGinnity, P., & Reed, T. E. (2016). The paradox of "premature migration" by adult anadromous salmonid fishes: patterns and hypotheses. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(7), 1015–1030.

Reynolds, M. D., Sullivan, B. L., Hallstein, E., Matsumoto, S., Kelling, S., Merrifield, M., Fink, D., Johnston, A., Hochachka, W. M., Bruns, N. E., Reiter, M. E., Veloz, S., Hickey, C., Elliott, N., Martin, L., Fitzpatrick, J. W., Spraycar, P., Golet, G. H., McColl, C., & Morrison, S. A. (2017). Dynamic conservation for migratory species. *Science Advances*, *3*(8), e1700707.

Robinson, R. A., Crick, H., Learmonth, J. A., Maclean, I., Thomas, C. D., Bairlein, F., Forchhammer, M. C., Francis, C. M., Gill, J. A., Godley, B. J., Harwood, J., Hays, G. C., Huntley, B., Hutson, A. M., Pierce, G. J., Rehfisch, M. M., Sims, D. W., Santos, B. M., Sparks, T. H., ... Visser, M. E. (2009). Travelling through a warming world: Climate change and migratory species. *Endangered Species Research*, *7*(2), 87–99.

Runge, C. A., Martin, T. G., Possingham, H. P., Willis, S. G., & Fuller, R. A. (2014). Conserving mobile species. *Frontiers in Ecology and the Environment*, *12*(7), 395–402.

Rushworth, A. M., Peterson, E. E., Ver Hoef, J. M., & Bowman, A. W. (2015). Validation and comparison of geostatistical and spline models for spatial stream networks. *Environmetrics*, *26*(5), 327–338.

Seebacher, F., & Post, E. (2015). Climate change impacts on animal migration. *Climate Change Responses*, *2*(1), 5.

Stitt, B. C., Burness, G., Burgomaster, K. A., Currie, S., McDermid, J. L., & Wilson, C. C. (2014). Intraspecific variation in thermal tolerance and acclimation capacity in brook trout (*Salvelinus fontinalis*): physiological implications for climate change. *Physiological and Biochemical Zoology*, *87*(1), 15–29.

Thompson, T. Q., Bellinger, M. R., O'Rourke, S. M., Prince, D. J., Stevenson, A. E., Rodrigues, A. T., Sloat, M. R., Speller, C. F., Yang, D. Y., Butler, V. L., Banks, M. A., & Miller, M. R. (2019). Anthropogenic habitat alteration leads to rapid loss of adaptive variation and restoration potential in wild salmon populations. *Proceedings of the National Academy of Sciences*, *116*(1), 177–186.

Tingley, M. W., Monahan, W. B., Beissinger, S. R., & Moritz, C. (2009). Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(2), 19637–19643.

Troia, M. J., Kaz, A. L., Niemeyer, J. C., & Giam, X. (2019). Species traits and reduced habitat suitability limit efficacy of climate change refugia in streams. *Nature Ecology & Evolution*, *3*(9), 1321–1330.

U.S. Environmental Protection Agency [U.S. EPA]. (2003). *EPA region 10 guidance for pacific northwest state and tribal temperature water quality standards*. EPA 910-B-03-002. Region 10 Office of Water.

U.S. Global Change Research Program [USGCRP]. (2018). In D. R. Reidmiller, C. W. Avery, D. R. Easterling, K. E. Kunkel, K. L. M. Lewis, T. K. Maycock, & B. C. Stewart (Eds.), *Impacts, risks, and adaptation in the United States: Fourth national climate assessment* (Vol. *II*, pp. 1515). U.S. Global Change Research Program. https://doi.org/10.7930/NCA4.2018

Ver Hoef, J. M., & Peterson, E. E. (2010). A moving average approach for spatial statistical models of stream networks. *Journal of the American Statistical Association*, *105*(489), 6–18.

Waples, R. S. (1991). Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. *Marine Fisheries Review*, *53*(3), 11–22.

Waples, R. S., Teel, D. J., Myers, J. M., & Marshall, A. R. (2004). Life-history divergence in Chinook salmon: Historic contingency and parallel evolution. *Evolution*, *58*(2), 386–403.

Wenger, S., Isaak, D., & Luce, C. (2010). Comparison of hydrologic predictions from the Variable Infiltration Capacity (VIC) model and the MC1 model to observed gage data in the region around the Shoshone National Forest, Idaho. Trout Unlimited and U.S. Forest Service Rocky Mountain Research Station.

Wenger, S. J., Luce, C. H., Hamlet, A. F., Isaak, D. J., & Neville, H. M. (2010). Macroscale hydrologic modeling of ecologically relevant flow metrics. *Water Resources Research*, *46*(9), W09513.

Williamson, C. E., Saros, J. E., Vincent, W. F., & Smol, J. P. (2009). Lakes and reservoirs as sentinels, integrators, and regulators of climate change. *Limnology and Oceanography*, *54*(6part2), 2273–2282.

Wolock, D. M. (2003). *Base-flow index grid for the conterminous United States* (Open File Rep. 03-263). U.S. Geological Survey.

Yoshiyama, R. M., Gerstung, E. R., Fisher, F. W., & Moyle, P. B. (2001). Historical and present distribution of Chinook salmon in the Central Valley drainage of California. *Fish Bulletin*, *179*(1), 71–176.

Zillig, K. W., Lusardi, R. A., & Fangue, N. A. (2018). Variation in thermal eco-physiology among California salmonids: Implications for management. California Water Board, UC Davis Agreement # D16-15001.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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