Mechanistic Simulations Suggest Riparian Restoration Can Partly Counteract Climate Impacts to Juvenile Salmon

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Research Impact Statement: Coupling a hydroclimatic and a fish model enabled us to mechanistically evaluate when and where riparian restoration was most likely to benefit a threatened salmon population in a future climate.

ABSTRACT: Climate change is reducing summertime water availability and elevating water temperature, placing human consumptive needs in competition with needs of coldwater fishes. We worked with natural resource managers in the Snoqualmie River (Washington, USA) to develop riparian management scenarios, and used a process-based modeling system to examine how a threatened population of Chinook salmon (*Oncorhynchus tschawytscha*) may respond to climate change and whether riparian restoration could reduce climate effects. Linking models of global climate, regional hydrology, water temperature, and fish, we projected that streams would become warmer year-round and drier during summer, further stressing salmon. Climate change accelerated egg emergence, increased juvenile growth and survival, and accelerated outmigration of sub-yearling migrants. Growth was depressed for salmon remaining instream during summer (potential yearling migrants). Riparian restoration counteracted ~10% of summer increases in water temperature, and affected salmon similarly regardless of whether riparian buffers were partially or fully restored, whereas riparian degradation further warmed streams. Riparian restoration fully mitigated climate change effects on potential yearling migrant size, but only minimally affected sub-yearling migrants (assessment metrics changed <2%). Our results will be useful for watershed managers in aligning priorities for fish and humans and our framework can be applied elsewhere.

(KEYWORDS: water temperature; flow; Pacific salmon; climate change; riparian management; mechanistic model.)*Citation:*

INTRODUCTION

Climate change has altered freshwater thermal regimes worldwide (van Vliet et al. 2011; Orr et al. 2015; Isaak et al. 2018). In the Pacific Northwest (PNW) USA, a warmer winter climate is expected to cause snow to accumulate less and to melt earlier, resulting in decreased water availability in summer (Jefferson 2011; Tohver et al. 2014). Lower summer flows may exacerbate warming in rivers where water temperatures have already increased (Kaushal et

al. 2010; Isaak et al. 2012; Orr et al. 2015). Lower summer flows and warmer water temperatures will challenge water resource managers tasked with ensuring an adequate supply of high-quality water for both humans (e.g., irrigation, drinking water) and aquatic species like coldwater fishes.

In a warmer future, fish populations are predicted to experience range reductions (Isaak and Rieman 2013; Radinger et al. 2017), phenology shifts (Otero et al. 2014; Peer and Miller 2014), changes in food webs (Albouy et al. 2014; Rosenblatt and Schmitz 2016), and altered physiological processes, growth, and survival (Lynch et al. 2016; Whitney et al. 2016). In the PNW, concern exists that economically, culturally, and ecologically valued Pacific salmon and steelhead (*Oncorhynchus* spp.) will be increasingly stressed by climate change in addition to existing stressors such as habitat loss and degradation, commercial harvest, hydropower, and hatchery practices that led to the listing of many populations under the United States Endangered Species Act (USESA; Ford et al. 2015). Fisheries managers are particularly interested in understanding natural spatiotemporal patterns of habitat, how human activities have modified these patterns, how climate-induced changes may impact fish populations, and what conservation strategies are most likely to maintain robust fish populations into the future. Despite the effectiveness of restoring riparian vegetation in modulating water temperature (Chen et al. 1998; Sun et al. 2015; Cao et al. 2016; Fabris et al. 2018; Seixas et al. 2018), previous efforts to revegetate riparian areas for improving instream conditions for salmon have been challenged by farmers concerned with losing productive land, and by local organizations and policy makers tasked with preserving and increasing local agriculture. Some of the most productive salmon habitat occurs in lowland tributaries, side channels, and floodplains that often abut or encompass productive agricultural lands (Jeffres et al. 2008; Lusardi et al. 2020). Hence, a collaborative, science-based approach and a transparent decision-making process is required for effective watershed management.

To that end, we present a case study in which we worked with natural resource managers to develop a set of riparian management scenarios, and used a process-based modeling system to examine how one threatened Pacific salmon population may respond to riparian management along with climate change. This study focused on Chinook salmon (*Oncorhynchus tschawytscha*) in the Snoqualmie River watershed (Washington State, USA; Figure 1). Our riparian management scenarios included one that represented the upper limit of what restored conditions could aspire to be if not constrained by land use, and two plausible scenarios—one scenario that included active restoration of riparian buffers in areas where it would be feasible to do so, and one scenario that only
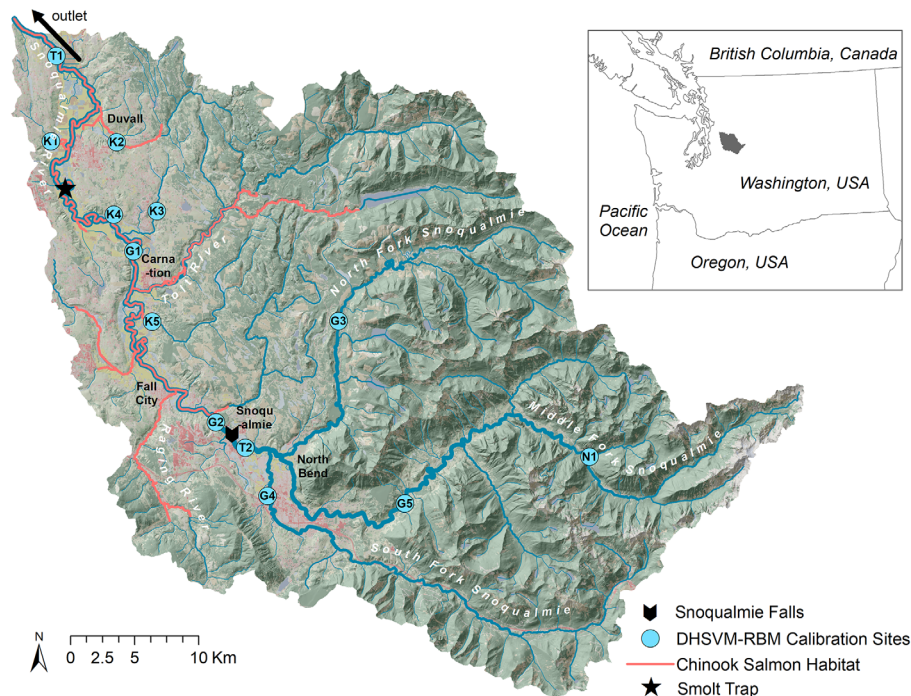

FIGURE 1. Map of the Snoqualmie River watershed and its location in Washington state USA. The base map is land use and land cover from 2019 (mrlc.gov). DHSVM-RBM, Distributed Hydrology Soil Vegetation Model-River Basin Model.

protected buffers coincident with existing legal limits (including degradation of intact areas to widths allowed by current regulations) with no active riparian restoration.

We adapted and linked an existing physically based hydrology and water temperature model (Wigmosta et al. 2002; Yearsley 2009; Sun et al. 2015) and an existing individual-based fish model (IBM; Fullerton et al. 2017; Hawkins et al. 2020). Both the physical model, DHSVM-RBM (distributed hydrology soil vegetation model—river basin model), and the fish IBM were previously and independently applied in the Snoqualmie watershed. Using DHSVM-RBM, Lee et al. (2020) predicted large increases in water temperature and decreases in summer flow due to a reduced future snowpack. However, their model did not account for the direct effects of snowmelt on water temperature. Hawkins et al. (2020) used spatiotemporally explicit water temperatures predicted from empirical data and a spatial stream network model (Steel et al. 2019) as inputs into the fish IBM. Their results indicated that Chinook salmon could be stressed by both warmer water temperatures and a non-native warmwater predator. Although survival (Beamer and Pess 1999; Greene et al. 2005; Ward et al. 2015) and migration rates of salmon (Aarestrup et al. 2002; Notch et al. 2020) have shown strong association with flow, data were unavailable at sufficient resolution for incorporation into the Hawkins et al. model.

For this study, we used the version of DHSVM-RBM updated by Yan et al. (2021), which accounts for the snowmelt cooling effect on water temperature, to predict spatiotemporally explicit water temperatures and flows needed as inputs to the fish IBM. We adapted the fish IBM to use these data, which allowed us to project into the future; this was not possible with the previous IBM where the temporal scope was limited by the availability of empirical water temperature data. We also developed fish-flow relationships for this version that allowed us to explicitly consider effects of flow on incubating eggs and outmigrating juveniles. Moreover, by dynamically linking DHSVM-RBM with the fish IBM, we were able to capture climate–river–fish dynamics that are sensitive to changing climate conditions. Our specific objectives were to (1) examine potential effects of future flows and temperatures on juvenile Chinook salmon and (2) consider the extent to which riparian restoration in the Snoqualmie watershed could offset potential climate impacts to juveniles during freshwater residence. Our predictions of possible outcomes for salmon can be used by managers to weigh the tradeoffs of potential management activities benefitting different water users.

METHODS

Study Area

The Snoqualmie River drains over 1,800 km^2 on the west side of the Cascade Range, Washington, USA (Figure 1). Its three main forks (North, Middle, and South) run through mostly forested public land before converging near the city of North Bend to form the mainstem Snoqualmie River which then flows over Snoqualmie Falls, an anadromous fish barrier. The Middle Fork (the upper mainstem) provides the majority of the Snoqualmie's flow in the summer. Below the falls, major tributaries include the Tolt and Raging Rivers and several smaller creeks used by salmon. The Tolt River is impounded and protected to provide drinking water for the City of Seattle, and the Raging River is a relatively warm tributary. Below the study area, the Snoqualmie River joins the Skykomish River to form the Snohomish River near the city of Monroe and enters Puget Sound shortly downstream. Streamflow peaks in winter from rain and again in spring from snowmelt. Snowmelt cools spring and early summer water temperatures.

The headwaters are owned predominantly by the United States (U.S.) Forest Service and the Washington Department of Natural Resources. However, nearly a quarter of the watershed is held in private industrial timber production. Logging peaked during the early 20th Century, largely eliminating old-growth trees. Due to continued logging outside of a designated wilderness area, most of the current forest is third- or fourth-generation regrowth. The watershed provides traditional natural and cultural resources for the Snoqualmie, Tulalip, and Muckleshoot Indian Tribes, and over 16 km^2 of land in the watershed is protected for agricultural uses. Agriculture, residential, and commercial land use are prevalent near the convergence of the three forks and downstream in the Snoqualmie Valley.

The lower watershed below Snoqualmie Falls supports wild populations of several anadromous salmonids including Chinook (*O. tschawytscha*), chum (*O. keta*), coho (*O. kisutch*), and pink salmon (*O. gorbuscha*), and steelhead/rainbow trout (*O. mykiss*) and cutthroat trout (*O. clarkii*). Bull trout (*Salvelinus confluentus*) or Dolly Varden (*S. malma*) may have been present historically, but they have not been observed recently (Thompson et al. 2011). The Chinook salmon population is considered ocean type, with a mix of sub-yearling and yearling migrant life histories. The yearling life-history type is slightly more prevalent in the Snoqualmie River population than in other Puget Sound populations, with 25%–30% of returning adults

comprised of yearling migrants (King County 2017), although the proportion of yearling migrants in many Puget Sound populations was higher in the past (Beechie et al. 2006). Puget Sound Chinook Salmon, Puget Sound Steelhead, and bull trout are listed as threatened under the USESA. Local salmon populations have been in rapid decline, and are increasingly stressed by warm, low-flow conditions during summer, as well as by extreme events such as those observed during 2015 when a low snowpack led to record low summer flows and high water temperatures (King County 2016a; Steel et al. 2019). The habitats used by anadromous salmon (i.e., below the falls) are where the vast majority of residential and agricultural land uses occur.

Analytical Framework

We used a sequence of models to evaluate how Chinook salmon may respond to climate change and riparian management scenarios (Figure 2).

Specifically, we used outputs from 10 global circulation models (GCM), downscaled to produce regional projections of air temperature and precipitation (see "Climate Models"). We used these outputs to force DHSVM-RBM, which predicted flow and water temperature for each stream reach every 3 h (see "Physics-Based Hydrology and Water Temperature Model"). Finally, we used flows and water temperatures in the fish model (see "Individual-Based Fish Model") that predicted phenology, growth, and survival of juvenile Chinook salmon. Both the physical model and the fish model were calibrated for a period of years for which empirical data were available (2001–2013). Once calibrated, we simulated fish responses to flow and temperature for historical (1995–2005) and future (2089–2099) periods for which global climate model inputs were available. We ran all models through a set of four scenarios (see "Riparian Vegetation Scenarios") to examine the extent to which riparian restoration could offset expected impacts to salmon caused by climate change during freshwater residency.
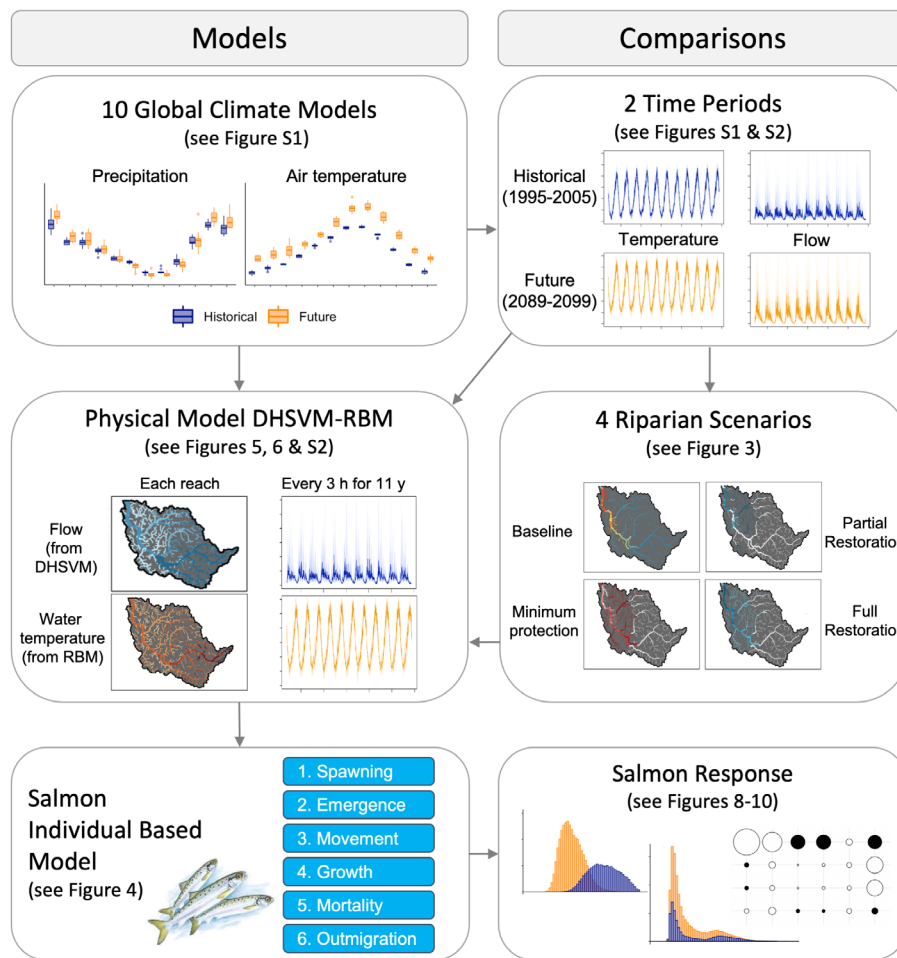

FIGURE 2. Models used and comparisons explored for examining how Chinook salmon may respond to climate change and riparian restoration.

Climate Models

To envision how salmon may respond to potential future streamflow and water temperature changes, we forced the hydrology and water temperature model with climate projections (Figure S1) from 10 GCMs produced under the representative concentration pathway (RCP) 8.5, which is a high warming future scenario associated with no climate action and high greenhouse gas emissions (van Vuuren et al. 2011). We used 10 GCMs from the Coupled Model Intercomparison Project Phase 5 (Taylor et al. 2012) that are known to perform well in reproducing historical climate variability in the PNW (Rupp et al. 2013): bcc-csm1-1-m, CanESM2, CCSM4, CNRM-CM5, CSIRO-Mk3-6-0, HadGEM2-CC365, HadGEM2-ES365, IPSL-CM5A-MR, MIROC5, and NorESM1-M. The GCM data were statistically downscaled to 1/16th degree resolution using the Multivariate Adaptive Constructed Analogs (MACA) method (Abatzoglou and Brown 2012), which bias corrects GCM outputs to the statistics of meteorological observations and downscales the outputs to a finer resolution by using a pattern matching constructed analogues algorithm. The MACA training data used for bias correction were the long-term (1950–2013) gridded surface meteorological dataset at a spatial resolution of 1/16 degree (Livneh et al. 2013), which were developed largely based on observations from National Climatic Data Center Cooperative Observer stations across the conterminous U.S.

Riparian Vegetation Scenarios

We evaluated four riparian vegetation scenarios: (1) *Baseline*: existing landscape conditions, (2) *Minimum protection*: conservation of riparian areas according to existing regulations, conserving existing intact riparian areas and further degrading other areas, (3) *Partial restoration*: conservation of existing intact riparian areas and partial restoration of lower quality riparian areas in congruence with existing and planned land uses, and (4) *Full restoration*: full restoration of all riparian areas (Figure 3). The first scenario captures current conditions and serves as a baseline to compare to future climate scenarios and other riparian management scenarios. The other scenarios reflect issues that natural resource managers grapple with and were designed to assist them in their decision-making process. For the minimum protection scenario, we protected riparian buffers in reaches that already had wide buffers that were unlikely to be altered due to existing forest protections (100–150 m), but we reduced riparian buffer widths in other reaches to 5–10 m to match existing regulations in particular land use categories and to reflect ongoing and increasing human influences. In
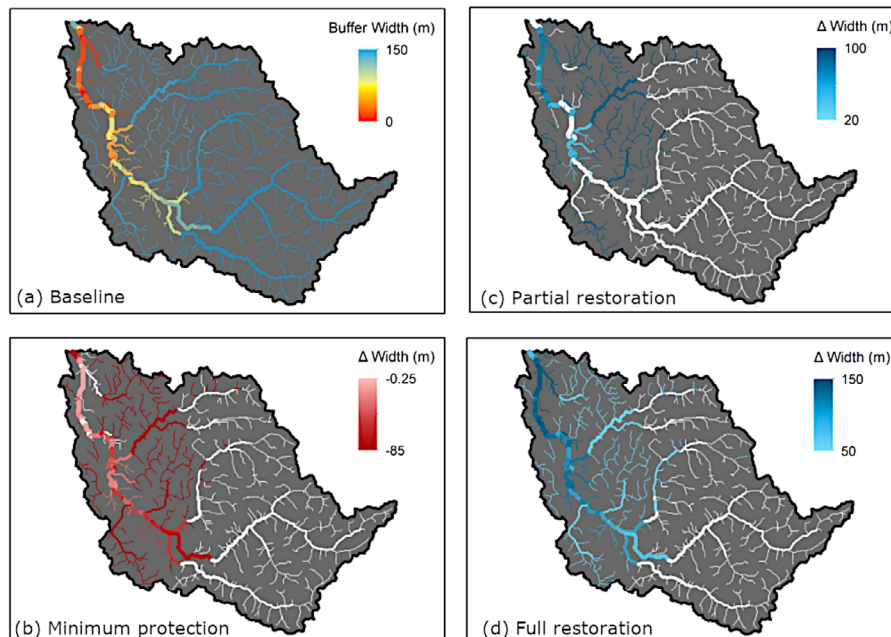
FIGURE 3. Riparian buffer widths (a) or change in buffer widths (b–d) associated with four riparian vegetation scenarios: (a) Baseline: existing riparian conditions; (b) Minimum protection: protect existing ≥150-m riparian areas and reduce all others to 5–10 m; (c) Partial restoration: protect existing ≥150-m riparian areas, increase existing 40- to 100-m buffers in forested areas to 150 m, and increase buffers along the mainstem to 20–40 m; and (d) Full restoration: all riparian areas become ≥150 m. Note that each panel has a unique color scale range.

the partial restoration scenario, we protected existing wide buffers as above, but we restored buffers in Forest Production-zoned areas to a width of 100–150 m, restored buffers within agricultural or residential areas to a width of 40–100 m, and restored riparian buffers in the lower basin below Snoqualmie Falls to a width of 20–40 m. The full restoration scenario represents a best-case scenario illustrating what might have been possible historically. In this scenario, we assumed riparian buffers were 100–150 m wide on both banks for all river reaches.

Our riparian scenarios were informed by recommendations for riparian buffer widths produced by a task force of co-managers (including one of us: MJB) that reflected the principles of balancing different land uses, and which differed across classes of stream type and land use (King County 2020). We shared our approach and early results with other resource managers and their stakeholders to solicit feedback for refining scenarios, and to illustrate the potential benefits and tradeoffs for fish. We worked with multiple local advisory groups, including the Snohomish Basin Salmon Recovery Technical Committee, the Snoqualmie Watershed Forum, and the Snoqualmie Fish, Farm & Flood Advisory Committee. These groups have membership from a broad swath of resource managers (tribal, local, county, state, federal, and nongovernmental organizations and universities). We did not receive any suggestions for refining riparian scenarios, likely because our scenarios were developed in alignment with ongoing riparian planning processes. We did not suggest a "best" course of action, but instead provided plausible generic options (to protect privacy of individual landowners) for consideration alongside other socioeconomic and political issues that could lead to a strategy that balances the needs of user groups. Our goal was to provide information about how the scenarios affected salmon so that the information could be incorporated into guidance that flexibly accommodates local knowledge and stakeholder values.

Physics-Based Hydrology and Water Temperature Model

We used DHSVM-RBM to explore the effect of riparian management scenarios and climate change on streamflow and water temperature under historical and future climates. DHSVM-RBM couples a physics-based hydrologic model (distributed hydrology soil vegetation model, DHSVM) and a vector-based semi-Lagrangian water temperature model (river basin model, RBM) to produce spatially distributed simulations of streamflow and water temperature at a time step of 3 h over the stream networks composed of river

segments ranging in length from 100 to 1,000 s of meters (Sun et al. 2015). The river network was generated using the Python-based pre-processing tool that determines stream topology and extracts vector stream lines from the watershed digital elevation model (Perkins et al. 2019). Wigmosta et al. (1994) and Wigmosta et al. (2002) outline the DHSVM model physics and structure, Yearsley (2009) describes RBM physics and structure, and Sun et al. (2015) describes the coupling scheme of DHSVM and RBM as well as the model representation of riparian shading. For a wide range of climate and physiographic conditions, DHSVM parameter sensitivity, model performance, and sources of uncertainties with respect to parameterization, model structure, and input data are well documented by a large body of literature, for example, Cuo et al. (2009), Cristea et al. (2014), Du et al. (2014), Perkins et al. (2019), Sun et al. (2016, 2019), and Thyer et al. (2004).

Essentially, segment-by-segment output of water fluxes (i.e., inflows and outflows) from DHSVM and radiation fluxes (i.e., downward shortwave and longwave radiations modified by topography and riparian vegetation) are passed to RBM for temperature modeling by solving the thermal energy budget using a semi-Lagrangian particle-tracking scheme in the stream network. The riparian shading effect on radiation fluxes incident on water surfaces is simulated as a function of segment-specific riparian characteristics (including canopy height, buffer width, leaf area index, and canopy-to-bank distance) and geometries of stream segments (including segment length, width, and orientation). The riparian vegetation parameters were estimated based on tree species, literature values, and forest surveys (Wharton et al. 2004; Yearsley et al. 2019). See Appendix S1 for a fuller description.

DHSVM-RBM does not include process representation of confined aquifers or hyporheic exchange on hydrology and temperature modeling. Such processes likely exist in the Snoqualmie watershed (McGill et al. 2021), and if present, may diminish variability and extremes in water temperature. Groundwater is known to produce temporally stable but spatially variable thermal habitats that can provide refuge to fish during thermally stressful periods (Torgersen et al. 1999; Snyder et al. 2015). We also did not adjust above-stream meteorology inputs (air temperature, wind speed) according to riparian scenarios due to a lack of data and because previous research suggests that net radiation is the dominant component of heat gain/loss in rivers (Caissie 2006).

For this study, we used a version of DHSVM-RBM (Yan et al. 2021) that explicitly accounts for snowmelt-induced sensible heat on the simulation of river temperature. The timing and sources of snowmelt are informed by DHSVM-simulated snowmelt

across the whole watershed. For streams and rivers that receive a substantial portion of their flow from melting snow in the headwaters, predictions of water temperature by the modified model can differ substantially from the prior model version that did not explicitly consider the melt effect. Under the current climate, vegetation, and riparian conditions, DHSVM-simulated snow water equivalent (SWE), streamflows, and water temperature agreed plausibly well with observations distributed across the watershed. In Tables S1 and S2, we summarize the findings of Yan et al. (2021) about the model performance based on a variety of metrics such as Nash-Sutcliffe Efficiency, Kling–Gupta Efficiency, Pearson correlation coefficient, and mean absolute error.

Individual-Based Fish Model

We used an individual-based model (IBM) to evaluate the individual and simultaneous effects of climate change and riparian management scenarios on threatened Chinook salmon in the Snoqualmie watershed (Figure 4). We summarized simulated behavior, growth, and survival of individuals to assess population-level responses including phenology of egg emergence from spawning gravels and smolt outmigration, body sizes of sub-yearling and yearling migrants, and life stage-specific survival rates. We refer readers to Fullerton et al. (2017) and Hawkins et al. (2020) for details on model parameterization, calibration and validation, and a global sensitivity analysis to evaluate assumptions. To take advantage of the spatiotemporally explicit flows produced by DHSVM, we developed and implemented two fish-flow relationships not present in the Hawkins et al. model. Specifically, we can now evaluate the effects of altered hydrology on egg survival and juvenile salmon outmigration (see "Flow Effects on Egg Survival and Juvenile Outmigration").

IBM Overview. The simulations begin on September 1 and end on August 31 of each year, and update

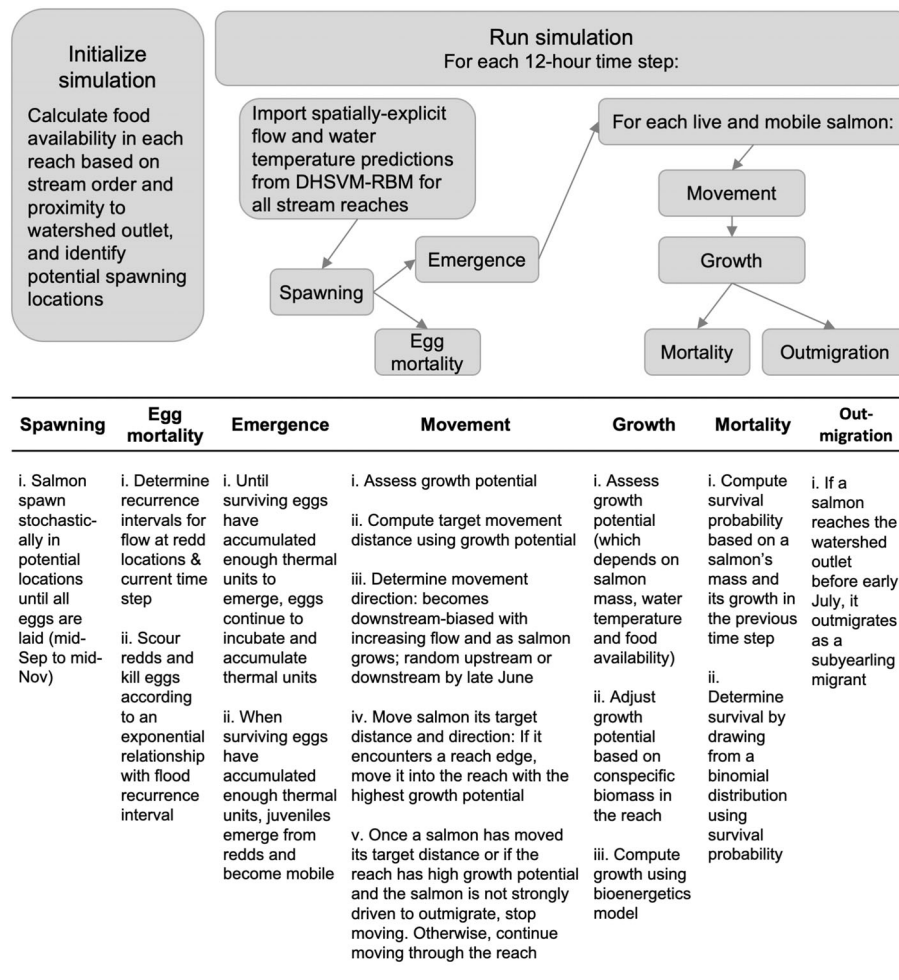| Spawning	Egg mortality	Emergence	Movement	Growth	Mortality	Out-migration
i. Salmon spawn stochastically in potential locations until all eggs are laid (mid-Sep to mid-Nov)	i. Determine recurrence intervals for flow at redd locations & current time step ii. Scour redds and kill eggs according to an exponential relationship with flood recurrence interval	i. Until surviving eggs have accumulated enough thermal units to emerge, eggs continue to incubate and accumulate thermal units ii. When surviving eggs have accumulated enough thermal units, juveniles emerge from redds and become mobile	i. Assess growth potential ii. Compute target movement distance using growth potential iii. Determine movement direction: becomes downstream-biased with increasing flow and as salmon grows; random upstream or downstream by late June iv. Move salmon its target distance and direction: If it encounters a reach edge, move it into the reach with the highest growth potential v. Once a salmon has moved its target distance or if the reach has high growth potential and the salmon is not strongly driven to outmigrate, stop moving. Otherwise, continue moving through the reach	i. Assess growth potential (which depends on salmon mass, water temperature and food availability) ii. Adjust growth potential based on conspecific biomass in the reach iii. Compute growth using bioenergetics model	i. Compute survival probability based on a salmon's mass and its growth in the previous time step ii. Determine survival by drawing from a binomial distribution using survival probability	i. If a salmon reaches the watershed outlet before early July, it outmigrates as a subyearling migrant

FIGURE 4. Schematic describing the sequencing of events during each individual-based model simulation. Egg mortality and the effect of flow on movement were new to this version.

twice daily at 06:00 and 18:00. During simulations, fish eggs are deposited stochastically on dates and at locations where spawning has been observed over the last decade (WDFW 2018). Egg development is based on accumulated thermal exposure (Steel et al. 2012), and egg survival is influenced by peak flows large enough to scour redds (Beamer and Pess 1999; Kinsel et al. 2008). After juveniles emerge (hatch and become free-swimming alevins), movements are driven by stochastic "decisions" by fish about where they would grow best. Movement behaviors reflect reach-specific conditions of water temperature, flow, and food availability. For instance, crowded conditions and suboptimal habitat cause higher movement. After a fish moves, its growth is calculated using a bioenergetics framework. Survival of juveniles is influenced by stochastic processes; larger fish and those that grew well in the previous time step have a better chance of surviving to the next time step. Outmigration (i.e. downstream-biased movement) is governed by body size, date, and environmental conditions including flow and temperature; fish are considered sub-yearling migrants when they reach the river mouth, and are removed from further simulation. Fish remaining instream after July 10 are considered potential yearlings, which remain in streams and if they survive winter, would become outmigrating smolts the following spring.

Flow Effects on Egg Survival and Juvenile Outmigration.   In this version of the IBM, we included the potential for flow to (1) scour salmon eggs from redds during high winter flow events and (2) enhance downstream movement and outmigration by sub-yearling migrants. Specific model adaptations, equations, and parameters are detailed in Appendix S2.

Survival of salmon has been shown to strongly decrease when incubating eggs are exposed to flows high enough to scour redds (Beamer and Pess 1999; Greene et al. 2005; Kinsel et al. 2008; Ward et al. 2015). We related egg survival to high flow events by (a) using established flood recurrence interval (FRI) curves derived from 9 gages in the watershed (King County 2016b) and their relationship to bankfull flow to estimate spatiotemporally explicit FRI from DHSVM-predicted flows and (b) applying the egg survival-FRI relationship from Beamer and Pess (1999), calibrated for twice-daily events affecting individuals instead of annual events affecting the whole population. We assume that this adaptation is reasonable but we note that the published relationship in Beamer and Pess (1999) represented spatially averaged peak flows and outmigrant survival measured at a single gage and not a flow–survival relationship at individual sites. A potential bias of our assumption that every flow event contributes proportionally to mortality is that in reality the relationship may be nonlinear with a threshold

above which flows kill eggs but below which eggs remain unscathed.

Salmon are known to move downstream and outmigrate at higher rates during high flow pulses (Aarestrup et al. 2002; Kubo et al. 2013; Notch et al. 2020; but see Kelson and Carlson 2019). Fish movement in the IBM is implemented as a four-step process that estimates how far a fish could move, its innate downstream drive (i.e., a downstream bias that increases as fish grow and then tapers off as summer progresses), selection of which reach the fish enters at confluences, and whether the fish stops early if it encounters high-quality habitat (Hawkins et al. 2020). Because the propensity of fish to stop early may be counteracted during high flows, we adapted the IBM such that high flows diminish the probability that an outmigrating fish will stop early. We also assumed that larger fish could swim farther.

IBM Calibration.   Predictions of salmon mass, survival, and timing of smolt outmigration were calibrated by iteratively adjusting parameters such that outcome metrics matched distributions of data from smolt traps operated by the Tulalip Tribes from 2001 to 2019 (Kubo et al. 2013; Tulalip Tribes 2019). We began with the parameter set from Hawkins et al. (2020) and performed additional calibration due to the new potential for flow to affect two life stages, and because in many reaches DHSVM-RBM predicted more extreme water temperatures (i.e., cooler during winter and warmer during summer) compared to the stream temperature data used in Hawkins et al. (2020). All parameters were the same as reported in Hawkins et al. (2020) except for the 11 parameters in Table S3, which were tuned during this study. A comparison of salmon outcome metrics to empirical distributions is presented in Table S4.

RESULTS

DHSVM-RBM Flow and Water Temperature Projections

The overall magnitude of DHSVM-predicted flow at the river outlet was not projected to change very much in the future (grand median across GCMs of −16 mm/s, range of −701 and 999 mm/s); although there was uncertainty across GCMs, there was a small increase during winter due to increased peak flows and a slight decrease during summer (Figure 5; Figure S2). Variability was greatest across the 10 GCMs during winter and least during summer. In other words, flow may or may not increase during winter, but the models are in agreement that it will
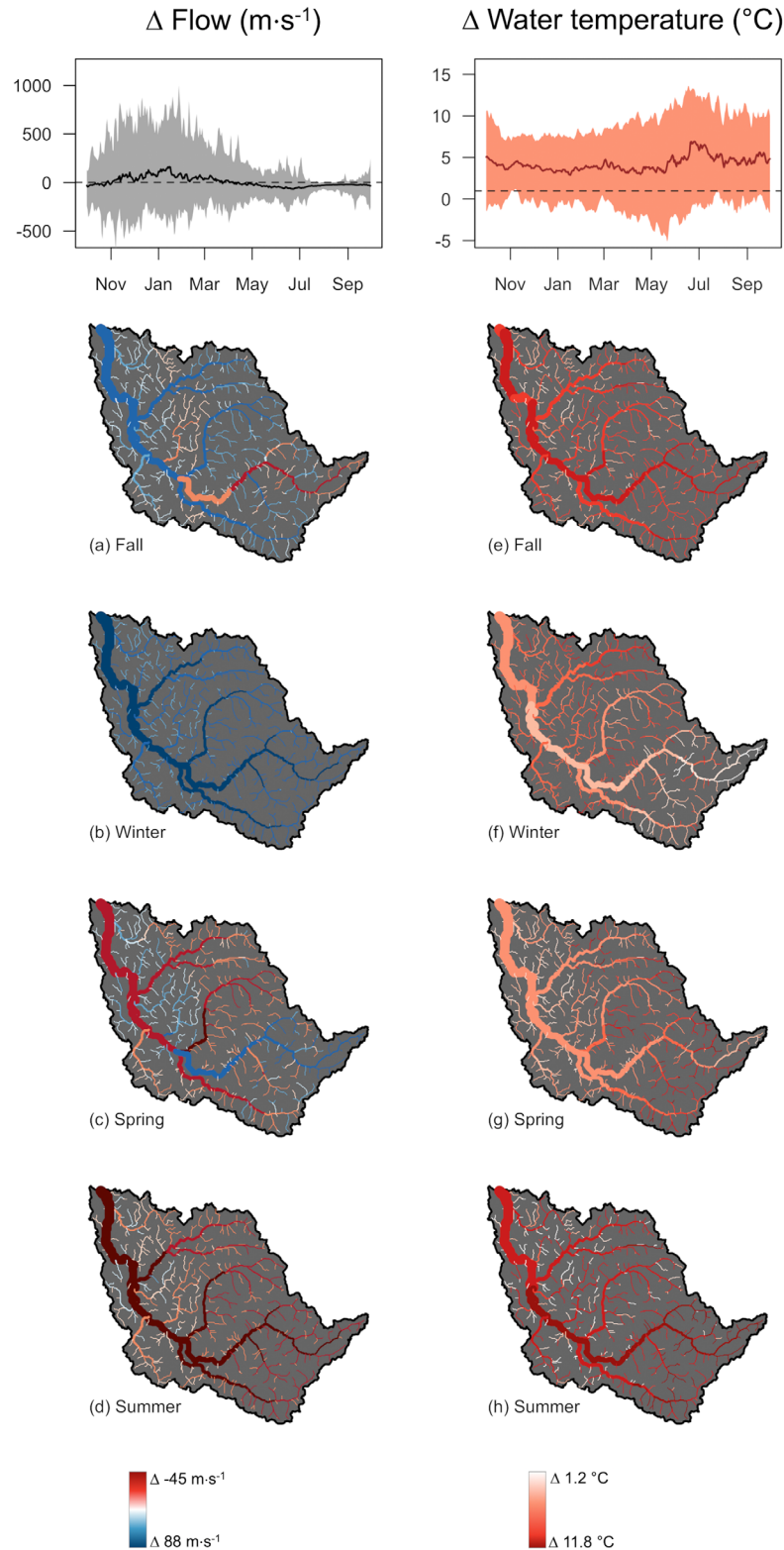
FIGURE 5. Changes in DHSVM-RBM-predicted flow (left) and water temperature (right) resulting from climate change. Data are the difference between mean future (2089–2099) and historical (1995–2005) predictions across 10 global climate models and 11 years. Time-series panels (top) show annual patterns in median daily change (dark line) and 5th and 95th percentiles (shading) at the river outlet. Maps show mean seasonal changes in flow during (a) fall (September–November), (b) winter (December–February), (c) spring (March–May), and (d) summer (June–August), and seasonal changes in water temperature (e–h). Map color ramps were binned as quantiles with probabilities of 0, 0.05, 0.15, 0.3, 0.45, 0.6, 0.75, 0.95, and 1.

remain the same or be slightly lower during summer. Future flows were projected to increase the most during winter (everywhere), fall (lower mainstem), and spring (headwater reaches), and to decrease the most during summer (especially in the mainstem) (Figure 5a–5d). Low elevation tributaries were projected to experience the least hydrological change across seasons.

RBM-predicted water temperature was projected to increase year-round at the river outlet (grand median across GCMs of 4.0°C, range of −5.1°C and 13.6°C), with slightly greater increases during summer, although there was uncertainty across GCMs (Figure 5; Figure S2). Water temperature in the mainstem was projected to increase the most during summer and the least during winter. Future water
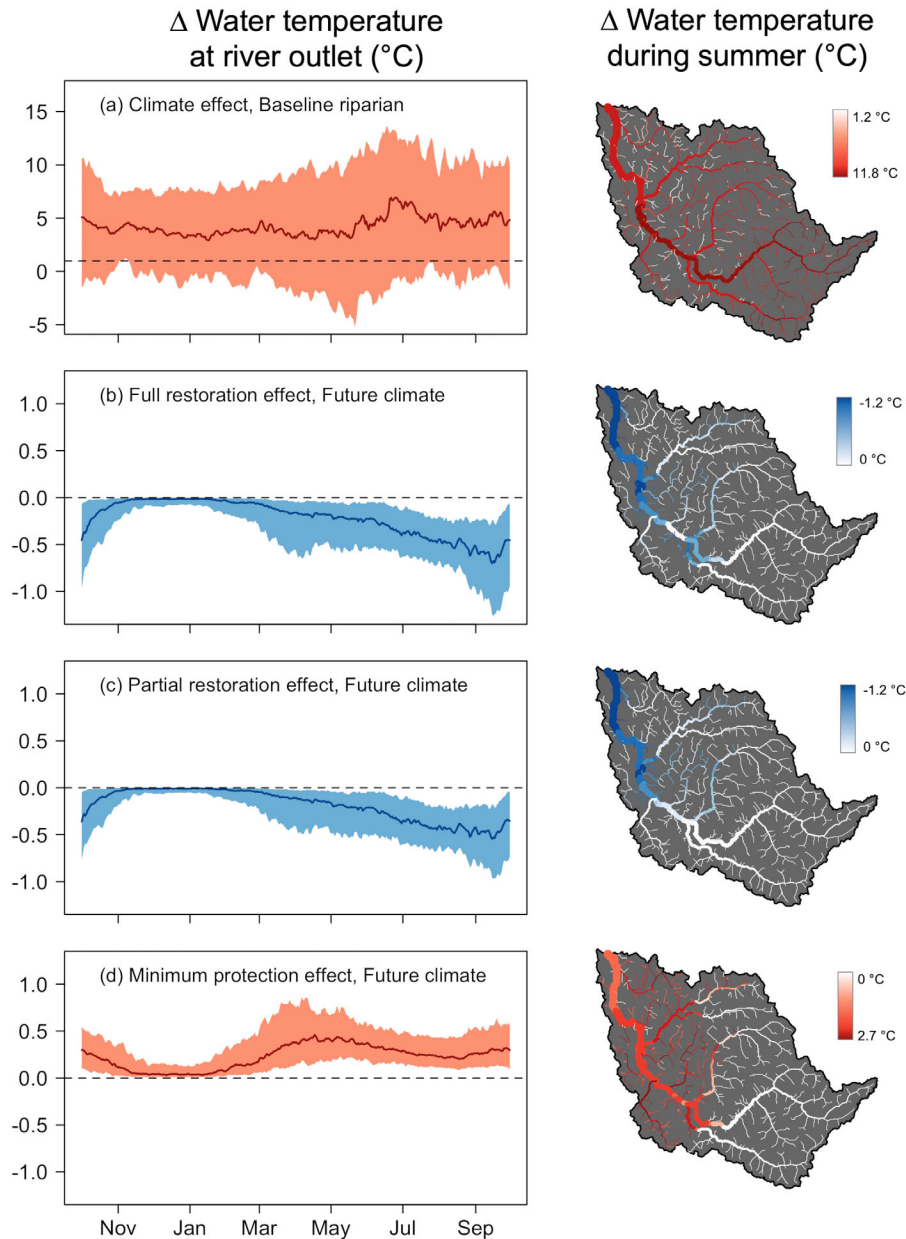

FIGURE 6. Changes in DHSVM-RBM-predicted water temperature resulting from climate change and riparian scenarios. Time-series panels (left) show annual patterns of water temperature at the river outlet in median daily change (dark line) and 5th and 95th percentiles (shading). Maps show mean seasonal changes during summer (June–August); color ramps were binned as quantiles as in Figure 5. (a) Changes in water temperature under baseline riparian conditions attributable to climate change. Changes in water temperature relative to baseline riparian conditions in a future climate attributable to (b) full riparian restoration, (c) partial riparian restoration, and (d) minimum protection riparian management. Data for all scenarios are ensemble means for 10 global climate models over 11 years. Panels (b–d) depict riparian scenario effects alone so that performance of various riparian actions can be compared, given a common future climate; note difference in y-axes from panel (a). The net effect of climate and riparian scenarios on future temperature is the sum of panel (a) and one of panels (b–d).

temperature warming was greatest in the historically snow-influenced upper Middle Fork and mainstem Snoqualmie River during summer and fall, high elevation tributaries during spring, and in lowland tributaries during winter (Figure 5e–5h).

The riparian restoration scenarios decreased the climate signal, whereas the minimum protection scenario amplified the climate signal. The full restoration scenario decreased temperatures at the river outlet by a grand median across GCMs of 0.2°C (range 0–1.3), the partial restoration scenario by 0.1°C (0–1.0), and the minimum protection scenario increased temperatures by 0.1°C (0.2–0.9). However, changes associated with riparian scenarios were modest relative to the ~4°C increases associated with climate change (Figure 6). The two riparian restoration scenarios (full and partial) produced similar decreases in future water temperature during spring, summer, and fall but had no effect during winter due to low radiation inputs (Figure 6b, 6c). The minimum protection riparian scenario produced the opposite effect, warming temperatures during spring, summer, and fall (Figure 6d). Notable differences in water temperature between the full and partial restoration scenarios occurred near the convergence zone of the North, Middle, and South Forks. The minimum protection scenario increased temperatures in the Raging River and other lowland tributaries.

Chinook Salmon Response to Flow

Scour of eggs incubating in redds accounted for 79% of salmon mortalities in the baseline riparian scenario and historical climate, and occurred during late fall and early winter when eggs were still in the gravel and flows were annually highest (Figure S3a). The stochastic mortality events affecting mobile juveniles predominantly affected smaller fish <1 g (Figure S3b).

The timing of Chinook salmon outmigration ranged from late December into July, peaking in April and May (Figure 7b, "Historical"), which matched well with empirical observations at smolt traps. Outmigration distributions for individual years were often bimodal and consisted of an early wave of fry migrants that were pushed downstream by higher flows, and a later and smaller wave of larger parr migrants (Figure 8a). Bimodal peaks are commonly observed in the smolt trap data (Kubo et al. 2013).

Chinook Salmon Response to Climate Change

Our model predicted that survival of sub-yearling and potential yearling Chinook salmon would increase by 86% and 46%, respectively, by the end of the century under current baseline riparian conditions (Table 1; Figure S4). Stochastic mortality of juveniles increased by 68% (median of 401,000 fish) in the future, presumably due to decreased growth (Figure S3). However, this increase was counteracted by a 47% decrease (median of 715,000 fish) in the number of eggs that were scoured. Alevins emerged from redds nearly three months earlier in the future climate (Figure 7a), allowing many to avoid the effects of high winter flows (scour affected eggs but not alevins in our model), and giving them a head start on the growing season. With warmer spring rearing conditions, fish attained sizes necessary for outmigrating nearly three months earlier (Figure 7b). Growth of fish that remained in streams over summer (i.e., potential yearling migrants) decreased during summer months but remained largely positive during the historical climate (Figure 9a). However, in a warmer future climate, growth of potential yearlings during summer became negative causing fish to lose weight (Figure 9b).

The size distribution for both sub-yearlings and potential yearlings remained similar (Figure 8), but became skewed toward smaller sizes on average, especially for potential yearlings (Table 1). This change could be explained by the effect of higher survival leading to higher conspecific density, which has a negative effect on salmon growth due to increased intraspecific competition. The bimodal distribution of fry and parr outmigrants was preserved (Figure 8a). The fraction of potential yearlings to all survivors (i.e., sub-yearling migrants and potential yearlings remaining alive at the end of the simulation) decreased from about 12% to about 8% on average.

Chinook Salmon Response to Riparian Scenarios

The riparian management scenarios influenced salmon performance, but most changes were small relative to climate impacts (Figure 10). The largest effects of riparian scenarios in a future climate were increases in the mass of potential yearling migrants in the full (31%) and partial (29%) restoration scenarios. The magnitude of change was similar for these two scenarios and both were large enough to counteract the 21% decrease in mass of potential yearling migrants expected as a result of climate change. Potential yearling growth was higher during winter relative to the historical climate but was less negative than the baseline scenario during summer in the future climate (Figure 9c). Effects on sub-yearlings were small and in the expected directions, with marginally higher sub-yearling migrant mass (~1%), lower survival (1%–1.5%), and later outmigration (one day) (Table 1). The fraction of potential
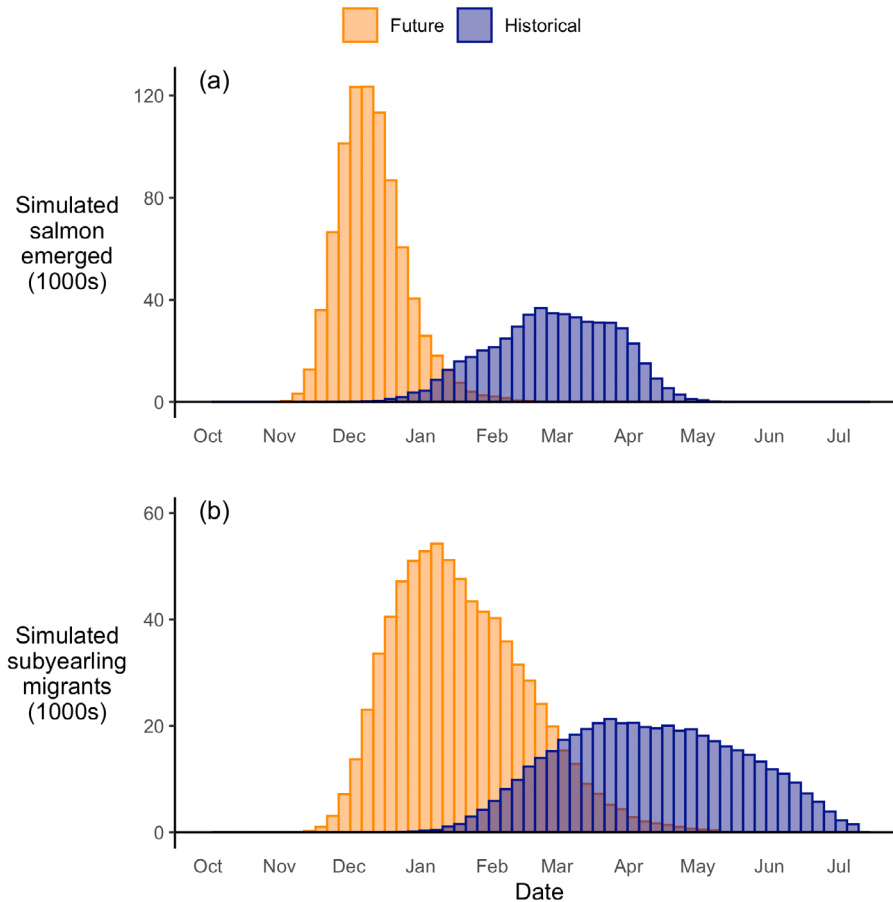
FIGURE 7. Phenology of Chinook salmon emergence (a) and sub-yearling outmigration (b) under baseline riparian conditions for historical (1995–2005; blue) and future (2089–2099; orange) climates. Histograms depict the thousands of simulated salmon (y-axis) that emerged or outmigrated over time (x-axis); bar height is the median of simulated fish responses to 10 global climate models. Data are only plotted for surviving salmon, which differ by life-history strategy and scenario.

yearlings to all survivors increased by about 1.5%. The minimum protection riparian scenario had the opposite effect on survival (1% increase) and outmigration (one day earlier), but no effect on mass.

DISCUSSION

This study indicated how a warmer climate may affect a threatened coldwater fish population and to what extent riparian restoration could counteract some of the projected freshwater impacts. Our projections about flow, water temperature, and Chinook salmon in the Snoqualmie River can be used by local watershed managers in conjunction with socioeconomic priorities to consider tradeoffs that meet the needs of multiple water users. Our analytical framework, modeling tools, and general insights can be adapted and applied to similar problems in other watersheds.

Chinook Salmon Response to Flow

Including the effect of flow (i.e., on egg survival and sub-yearling outmigration) overcame a shortcoming of earlier model versions and improved realism by better representing known mechanisms (Greene et al. 2005; Ward et al. 2015). Experiments examining the relationship between scour and egg survival have occurred in nearby watersheds, but we do not have local data to validate simulated egg survival rates. However, incorporating these fish-flow relationships into the model produced a better match to distributions of sub-yearling migrant size and timing observed at the smolt trap in the lower Snoqualmie River (Table S4; trap location depicted in Figure 1). Moreover, we reproduced the observed bimodal outmigration distribution, including the early peak of fry migrants.

There are other potential fish-flow relationships that may be useful to explore in future modeling. For instance, the response by alevins to scouring flows may be an important but unaccounted-for influence on early juvenile survival. Additionally, it is likely that flow affects
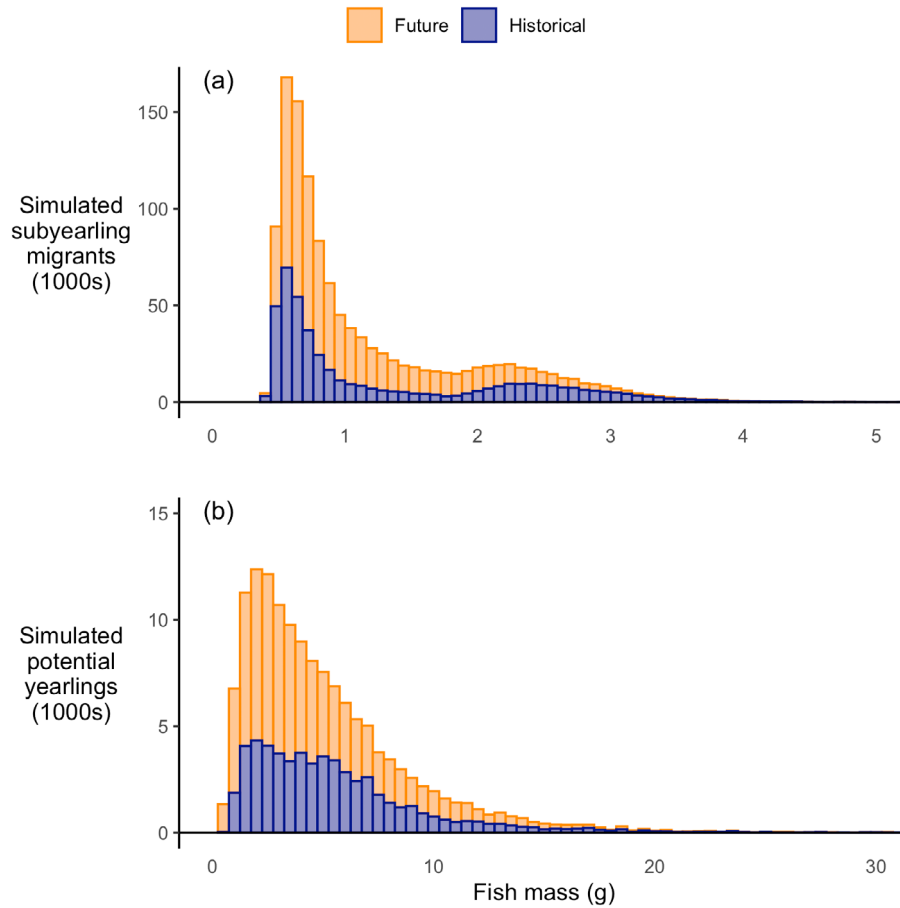
FIGURE 8. Final mass of Chinook salmon sub-yearling migrants (a) and potential yearlings (b) under baseline riparian conditions for historical (1995–2005; blue) and future (2089–2099; orange) climates. Histograms depict the thousands of simulated salmon (y-axis) reaching a given mass by the end of the simulation (x-axis) that outmigrated as sub-yearlings or remained in the watershed as fish that may become yearling migrants the following year; bar height is the median of simulated fish responses to 10 global climate models. Data are only plotted for surviving salmon, which differ by life-history strategy and scenario.

TABLE 1. Summary metrics for Chinook salmon that were alive at the end of one-year simulations in each scenario. Survival, dates, and mass of sub-yearling and potential yearling migrants are medians (5th and 95th percentiles) for surviving fish in each scenario, pooled across 10 global climate models and 11 years. Dates are formatted as month/day.

| Riparian scenario	Sub-yearling survival	Potential yearling survival	Date emerged	Date outmigrated	Mass of sub-yearlings	Mass of potential yearlings
Historical climate (1995–2005)						
Baseline	0.105 (0.04, 0.28)	0.013 (0.01, 0.03)	2/27 (1/12, 4/7)	4/8 (2/7, 6/12)	0.81 (0.48, 3.13)	4.73 (1.37, 13.53)
Full restoration	0.104 (0.04, 0.27)	0.013 (0.00, 0.03)	2/28 (1/12, 4/8)	4/11 (2/9, 6/13)	0.85 (0.49, 3.14)	5.44 (1.75, 14.44)
Partial restoration	0.106 (0.04, 0.28)	0.011 (0.00, 0.03)	2/27 (1/12, 4/7)	4/11 (2/8, 6/13)	0.84 (0.49, 3.15)	5.31 (1.77, 14.21)
Minimum protection	0.112 (0.05, 0.29)	0.012 (0.01, 0.03)	2/21 (1/6, 4/2)	4/3 (2/2, 6/8)	0.82 (0.48, 3.10)	4.31 (1.46, 12.05)
Future climate (2089–2099)						
Baseline	0.195 (0.12, 0.48)	0.019 (0.01, 0.10)	12/9 (11/19, 1/6)	1/14 (12/9, 3/10)	0.84 (0.52, 2.47)	3.75 (1.10, 11.91)
Full restoration	0.192 (0.12, 0.48)	0.019 (0.01, 0.09)	12/9 (11/20, 1/7)	1/15 (12/9, 3/11)	0.85 (0.52, 2.49)	4.91 (1.65, 13.82)
Partial restoration	0.193 (0.12, 0.48)	0.019 (0.01, 0.10)	12/9 (11/20, 1/7)	1/15 (12/9, 3/11)	0.85 (0.52, 2.49)	4.84 (1.65, 13.94)
Minimum protection	0.197 (0.12, 0.48)	0.020 (0.01, 0.10)	12/7 (11/18, 1/5)	1/13 (12/7, 3/8)	0.85 (0.52, 2.48)	3.65 (1.10, 10.45)
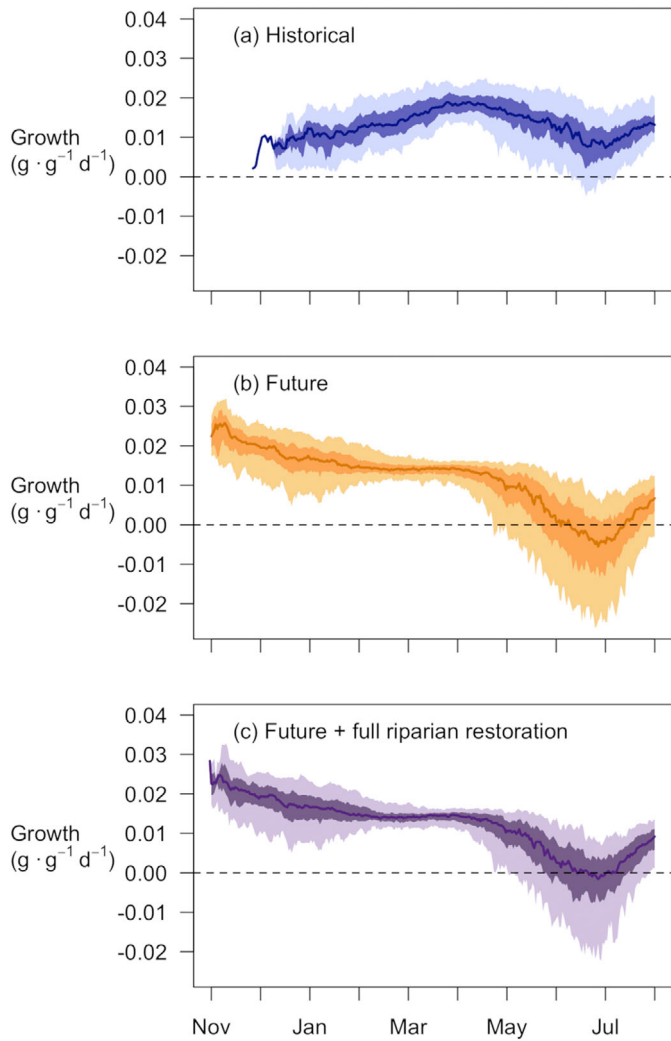
FIGURE 9. Daily per capita growth rates for potential yearling Chinook salmon over time for (a) historical (1995–2005; blue) and (b) future (2089–2099; orange) climates, and for (c) the future climate plus full riparian restoration (2089–2099; purple). Plots depict the mean growth rates across all potential yearlings in each simulation. Variance across 10 global climate models and 11 years is shown as medians (dark lines), the interquartile range (dark shading), and the 5th and 95th percentiles (light shading).

habitat area available to rearing juvenile salmonids, and that increased floodplain access may increase growth and delay outmigration due to increased foraging opportunities in productive floodplain habitats (Jeffres et al. 2008). Flow also affects invertebrate drift rate that could alter food availability to salmon (Imbert and Perry 2000), and may influence energy expenditure by juveniles holding against currents (Enders et al. 2003).

Chinook Salmon Response to Climate Change

We predicted that warmer stream temperatures would lead to accelerated egg emergence, higher winter, spring and fall growth rates, earlier sub-yearling outmigration, lower summer growth rates, and increased survival. These findings are consistent with Hawkins et al. (2020). Accelerated egg development may be caused by a combination of warmer winter incubation temperatures (Mundy and Evenson 2011), such as in our modeling, and shifts in adult spawn timing (Beer and Steel 2018; Austin et al. 2021), which we did not model. Higher salmonid growth has been attributed to warmer temperatures associated with climate change, riparian alteration and wildfire (Dunham et al. 2007; Beer and Anderson 2013; Rosenberger et al. 2015; Falke et al. 2019). The increased growth afforded by a warmer fall, winter and spring may provide sufficient energy stores for salmon to survive stressfully warm summers, provided that other aspects of seasonal habitats such as food and shelter availability remain intact (Armstrong et al. 2021). Data on food availability in the Snoqualmie watershed are scarce; thus, we cannot say how it would limit or enhance growth under altered fish densities and increased temperatures. However, given that salmon abundance is much lower than it was historically, fish are likely not food limited at currently observed densities. Climate-induced timing shifts in one life stage (e.g. spawning) constrain possible outcomes in others (e.g. emergence and outmigration) (Crozier et al. 2008). Because our model did not follow fish through the entire life cycle, we were unable to evaluate such effects.

An earlier, warmer, and longer growing period is known to accelerate outmigration (Otero et al. 2014; Peer and Miller 2014; Munsch et al. 2019). The consequences of earlier outmigration are unknown. Survival of Columbia River Chinook and steelhead to adulthood was higher when fish outmigrated earlier during spring (Scheuerell et al. 2009; Chasco et al. 2021). However, outmigration that is too early may be detrimental if the food supply for juvenile salmon in the marine environment is meager (Tomaro et al. 2012; Satterthwaite et al. 2014), if predators are more abundant (Miller et al. 2013; Weitkamp et al. 2015), or if ocean conditions are unfavorable for salmon when they arrive (Henderson et al. 2018; Crozier et al. 2021). Thus, a larger number of smaller salmon reaching marine waters early may not translate into survival to adulthood (Munsch et al. 2019).

In our simulations, sub-yearling migrant survival was much higher in the future. Whether instream survival of juveniles will increase or decrease in a warmer climate will be case specific and will depend on numerous factors including ecological interactions. Our findings could be partly explained by the reduced duration that eggs were exposed to scouring flows, that we did not model the effect of scouring flows on
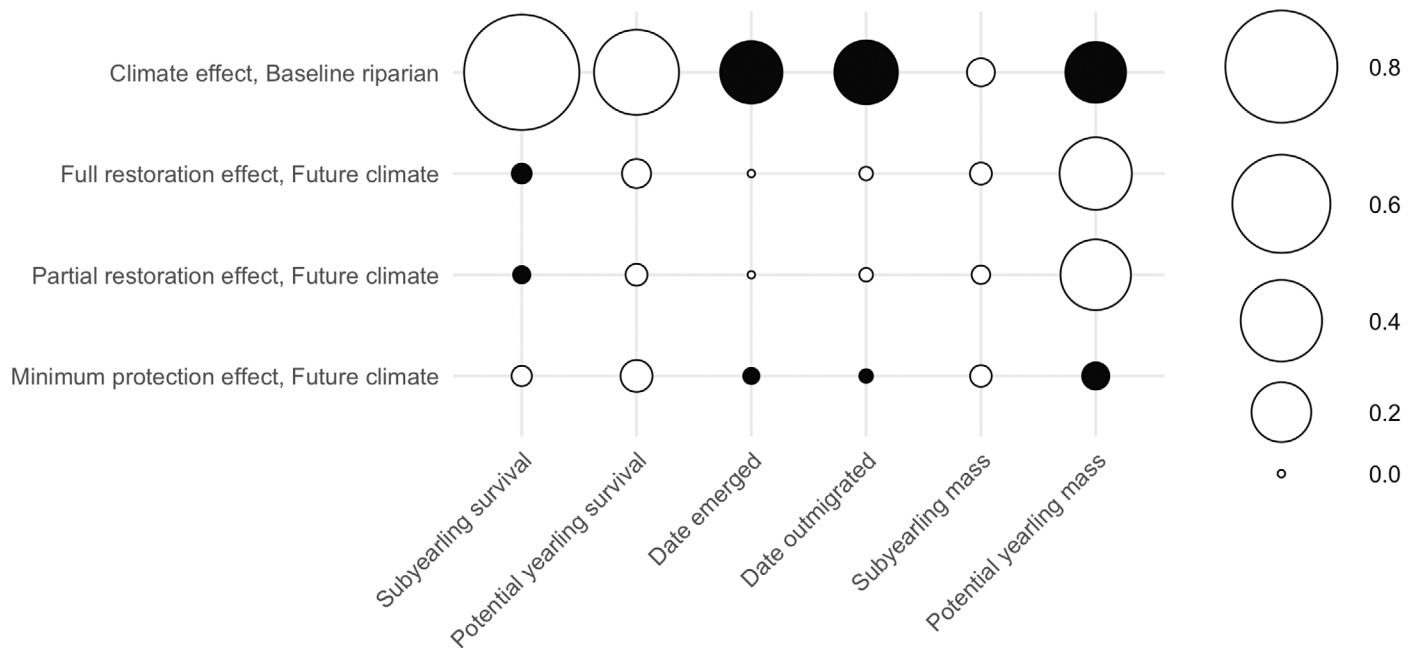
FIGURE 10. Change in simulated Chinook salmon outcomes (x-axis) across scenarios (y-axis). Circle size indicates proportional change and colors indicate whether metrics increased (white) or decreased (black). Climate effect, Baseline riparian (row 1): changes in outcomes attributable to climate change under baseline riparian conditions. Full restoration effect, Future climate (row 2): changes in outcomes attributable to full riparian restoration in the future relative to baseline riparian conditions in the future. Partial restoration effect, Future climate (row 3): changes in outcomes attributable to partial riparian restoration in the future relative to baseline riparian conditions in the future. Minimum protection riparian effect, Future climate (row 4): changes in outcomes attributable to the least protective riparian management in the future relative to baseline riparian conditions in the future. As in Figure 6, rows 2–4 depict riparian scenario effects in a future climate alone (i.e., without also including the climate change effect). See Table 1 for absolute values.

alevins, or that we did not model the effect of climate on spawn timing. Or it may be that enhanced growth during a warmer winter and spring allowed salmon to leave the system before the onset of stressfully high spring and summer temperatures. Ecological interactions may also be affected by climate change (Lynch et al. 2016). Salmon growth is highly sensitive to ration (Beauchamp 2009); if climate change alters prey abundance or composition, this could significantly alter future growth and survival (Lusardi et al. 2020). Warmer temperatures can increase exposure to pathogens, potentially reducing survival (McCullough et al. 2009), and warmwater nonnative predators may expand their range as the climate warms (Rubenson and Olden 2017).

We found that more potential yearling salmon survived until the end of summer (when our simulations terminated) but these survivors lost mass over summer. The decrease in mass likely resulted from increased metabolic demand during high summer temperatures and increased competition with a higher number of surviving conspecifics. A larger cohort of smaller fish at the start of winter may not convey higher survival until outmigration because overwinter survival is a known bottleneck for stream salmonids (Quinn and Peterson 1996; Ebersole et

al. 2006). Yearling Chinook salmon and other species that remain in streams for one or more years such as coho salmon and steelhead may be especially stressed by climate change (Myrvold and Kennedy 2015). Thermal refuges will be increasingly important habitats for these species during summer in the future (Torgersen et al. 1999; Fullerton et al. 2018) as long as refuges do not increase risk to predation or angling (Keefer et al. 2009).

Chinook Salmon Response to Riparian Scenarios

There is ample evidence that riparian vegetation has the potential to significantly reduce stream temperatures (Sun et al. 2015; Fabris et al. 2018; Seixas et al. 2018), but there is mixed support about whether riparian vegetation improvements can offset temperature increases and impacts to salmon expected from climate change (Justice et al. 2017; Trimmel et al. 2018; Ayllon et al. 2019; Wondzell et al. 2019; Yonce et al. 2020). This is unsurprising because the processes involved are highly watershed specific. In the Snoqualmie watershed, our riparian restoration scenarios were unable to completely counteract expected increases to water temperature

caused by climate change. However, our study demonstrated that riparian restoration has the potential to increase the mass and proportion of yearling migrants by the end of their first summer, relative to future conditions where riparian vegetation remains unchanged. This is salient because the yearling migrant life-history type has historically been an important component of the Snoqualmie population (Kubo et al. 2013; King County 2017, 2021) and contributes to the broader diversity of the Puget Sound Chinook Salmon Evolutionarily Significant Unit (Beechie et al. 2006). Habitat conservation and restoration activities that benefit this dwindling life-history type will be important for recovery of this population. Protecting intact thermal regimes would presumably also benefit other species with yearling life-history strategies (Quinn et al. 2019).

Interestingly, the partial and full riparian restoration scenarios had nearly the same magnitude of benefit for potential yearling migrants. Both scenarios reduced spring, summer, and fall temperatures similarly in the lower mainstem and neither scenario reduced temperatures in the Raging River or other lowland tributaries. The full restoration scenario decreased temperatures to a greater extent upstream of Snoqualmie Falls, suggesting that potential yearlings primarily using downstream habitats benefitted only minimally from changes in the reaches at and above the upper extent of their distribution. It is possible that the benefits of riparian shade in these reaches were too localized to affect the large body of water or very far downstream (Caissie 2006; Webb et al. 2008). Shade benefits provided by riparian vegetation will depend on the tree species (Dugdale et al. 2018), and the riparian community may shift in the future (Nilsson et al. 2013). Incorporation of these details into modeling could yield practical restoration planning insights.

In our study system, riparian restoration did not appear to influence sub-yearling migrants. Riparian restoration has the largest effect on stream temperature during summer when solar radiation is most direct and intense (Caissie 2006), whereas the sub-yearling migrants left the system during spring before temperatures got too warm. If other factors keep Chinook salmon in the watershed longer in the future such as if spawning is delayed due to high fall temperatures (Crozier et al. 2008), then riparian restoration would likely also benefit sub-yearling migrants that would be exposed to warm temperatures during late spring and early summer.

The minimum protection riparian scenario affected salmon similarly to climate change, but effects were smaller. Compared to climate change, the minimum protection riparian scenario elevated temperatures earlier in the season (maximum temperatures occurred in spring instead of summer), and increased temperatures to a greater extent in smaller low elevation tributaries. Because sub-yearling salmon outmigrated before summer, they were largely unaffected, whereas the mass of potential yearling salmon decreased. This scenario included both conservation of intact riparian areas and further degradation of already narrowed riparian buffers. The benefits of protecting the intact areas were not sufficient for counteracting the impacts of the degraded areas for potential yearling salmon, likely because fish spend less time in reaches with intact riparian buffers (i.e., lower-order reaches at higher elevations).

Our riparian restoration scenarios influenced only water temperature. It is likely that altered riparian vegetation would also influence flow pathways, bank stability, geomorphology, instream habitat, and supply of terrestrial invertebrates as a food source (Quinn et al. 2019). Increased wood supply could increase the abundance of cold deep pools. Our predictions of water temperature did not capture localized thermal refuges that can sustain fish in too-warm reaches (Corey et al. 2020; Sullivan et al. 2021). Moreover, our riparian scenarios assumed riparian buffers were immediately 100% functional. In reality, shade benefits will accrue gradually as trees mature (Quinn et al. 2019), and successful reestablishment and growth of riparian vegetation depends on site suitability, competition with nonnatives, and biological disruption by deer, beaver, and other riparian animals (Wondzell et al. 2019). Finally, riparian restoration is only one type of restoration action that can improve thermal habitats for salmon. Reconnecting streams to off-channel floodplain habitats (Bond et al. 2018), re-introducing beaver (Dittbrenner et al. 2018), and directly manipulating coldwater patches (Kurylyk et al. 2015) are also important.

Management Implications

Snoqualmie Watershed. The outcomes we predicted can be used by practitioners in the Snoqualmie River watershed to consider what kinds of management plans could be practically and effectively implemented to benefit USESA-listed salmon while also meeting the needs of other water users. Importantly, our study suggests that riparian restoration is worth the effort, especially as it benefits yearling Chinook salmon, which are an important life-history type for this population and for Puget Sound in general. That we did not observe an effect on sub-yearling migrants does not mean that they would not benefit from riparian restoration if other factors were considered such as shifted spawn timing and altered ecological interactions that cause juveniles to delay outmigration, or if other stressors increased.

Our finding that the full restoration scenario added little compared to the partial restoration scenario suggests that even some level of riparian restoration is beneficial. However, because we did not see as much benefit of protecting intact habitats if others are allowed to degrade, it also suggests that more refined studies are necessary to understand how much and particularly where riparian or other temperature-reducing restoration will be most useful. For example, given that riparian restoration did not affect temperatures in the Raging River, whereas this tributary was affected negatively by the minimum protection riparian scenario, this may be an important location to enact conservation measures to protect existing high-quality riparian habitats that can modulate future climate change. Field studies to better understand the seasonal habitats used by yearling migrant juveniles (e.g., King County 2017, 2021) will be essential for understanding where riparian restoration may best enhance thermal conditions for salmon at different life stages. Our model did not examine the effects of thermal stress on upstream migration and spawning by adults. This life stage is notoriously sensitive to high temperatures (Crozier et al. 2008; Bowerman et al. 2018; Keefer et al. 2018) and should also be assessed before conclusions about utility for salmon of different riparian restoration scenarios are made. Because spawning adult Chinook salmon typically use the mainstem and lower sections of the major tributaries for spawning, temperatures in these reaches could become limiting in a warmer climate.

Conservation planners in the Snoqualmie Basin are grappling with what kinds of riparian restoration to pursue (https://kingcounty.gov/services/environment/watersheds/snoqualmie-skykomish/fish-farms-flooding.aspx). Their difficult decisions about how to balance the needs for fish with other water uses (e.g., irrigation, municipal water, flood control) will ultimately include both ecological and socioeconomic factors. Our simple scenarios provide book ends (i.e., the full restoration and baseline scenarios) and two plausible yet somewhat generic scenarios (partial restoration and minimum protection) that can help planners envision possible responses by salmon. Our models and analytical framework can easily be used to examine more specific scenarios of riparian restoration in light of climate change, and could be adapted to consider other life stages, other species, other factors, and other potential management actions.

Broader Applicability. There may be an upper limit to what riparian restoration can do for salmon and other aquatic species, as suggested by our finding that the full and partial restoration scenarios produced similar results. This may be due in part to diminishing benefits as buffer width increases, or

because effects of restoration in upstream reaches are localized and do not translate downstream to fish-bearing reaches. Riparian shading can help cool stream temperatures when solar elevations are high and when trees have maximum leaf coverage, for example, at noon in summer (Caissie 2006). It is not an effective measure for reducing water temperatures during late fall through early spring when solar elevations are lower and trees lose foliage, or in streams that are already shaded topographically or that are too wide for riparian vegetation to provide shade (Caissie 2006; Dugdale et al. 2018). Riparian restoration will most benefit salmon and other aquatic life during summer, which may or may not coincide with times they experience thermal stress.

Water temperature is only one of many potential stressors influencing the viability of salmon and other aquatic species into the future. Managers will likely need to employ multifaceted strategies to conserve coldwater species. In addition to riparian restoration, actions in freshwater may include protecting/establishing coldwater refuges, restoring physical habitats, improving connectivity, increasing food supply, and controlling predator and competitor populations (Beechie et al. 2012; Kurylyk et al. 2015; Naman et al. 2018). Increasing exchange between surface water, hyporheic water, and groundwater may reduce diel variability and buffer fish from exposure to daily thermal extremes (Arrigoni et al. 2008). Practitioners would need to adapt the coupled modeling system we describe here to accommodate these additional sources of uncertainty.

Here, we have demonstrated potential implications for juveniles of one species in one watershed, but other life stages (adults) and species (coho, steelhead, bull trout, non-salmonids including warmwater species) may also be directly affected by altered flow and thermal regimes, especially in regions expected to experience substantial change. Our modeling framework could be applied with a life cycle approach (Crozier et al. 2021; Jorgensen et al. 2021) to examine what life stages may be most sensitive to climate-induced habitat changes, and whether riparian restoration or other actions could benefit populations long term. Managing for viable salmon populations will require a holistic strategy that extends beyond the watershed boundary and into the marine environment.

An analytical framework such as the one we presented here can be useful for exploring the effects of multiple freshwater actions simultaneously to see their cumulative effect on fish populations. The physically based DHSVM-RBM is ideal for investigating how changes to the landscape affect hydrology and water temperature, and the mechanistic fish IBM can provide insights about how fish may respond to these

changes. This coupled modeling system could be easily adapted for other watersheds where similar management questions exist, provided that sufficient empirical data are available for calibrating models. At a minimum, several flow and temperature sensors that capture the spatial breadth of conditions in a watershed are needed for parameterizing DHSVM-RBM (Cao et al. 2016; Yearsley et al. 2019; Yan et al. 2021). For basins with seasonal snowpack, measurements of snow depth or SWE from Snow Telemetry (SNOTEL) stations are also important for calibrating the snow submodel of DHSVM-RBM for proper representation of snow processes that are key to hydrological and thermal regimes (Sun et al. 2019; Yan et al. 2021). Basin-specific estimates of when and where fish spawn, spawner abundance, and when juveniles go to sea are key for parameterizing and calibrating the fish IBM (Hawkins et al. 2020; Table S3). Some important next steps will be to incorporate deep groundwater pathways into the physical model and to develop the fish model into a full life cycle model (e.g., Crozier et al. 2021; Jorgensen et al. 2021) and consider multispecies interactions (as in Hawkins et al. 2020) and additional management actions. Investments in such improvements should produce useful and practical management insights.

DATA AVAILABILITY STATEMENT

Data inputs and code for the salmon IBM are available at https://github.com/aimeefullerton/SnoIBM.

SUPPORTING INFORMATION

Additional supporting information may be found online under the Supporting Information tab for this article: **Appendix S1.** Brief summary of the physics-based hydrology and water temperature model, incorporating flow effects into the salmon IBM, and additional figures.

AUTHOR CONTRIBUTIONS

Aimee H. Fullerton: Conceptualization; formal analysis; funding acquisition; software; visualization; writing – original draft; writing – review and editing. Ning Sun: Conceptualization; formal analysis; supervision; writing – review and editing. Matthew J. Baerwalde: Conceptualization; funding acquisition; project administration; writing – review and editing. Brooke L. Hawkins: Formal analysis; software; writing – review and editing. Hongxiang Yan: Formal analysis; methodology; writing – review and editing.

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