ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE
Freshwater Ecology

How does habitat restoration influence resilience of salmon populations to climate change?

Timothy J. Beechie[1] ● | **Caleb Fogel**[2] | **Colin Nicol**[2] | **Jeff Jorgensen**[1] |
Britta Timpane-Padgham[3] | **Peter Kiffney**[1] ●

[1]Fish Ecology Division, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, Washington, USA

[2]Ocean Associates, Inc., Seattle, Washington, USA

[3]A.I.S., Inc., Seattle, Washington, USA

Correspondence
Timothy J. Beechie
Email: tim.beechie@noaa.gov

Present address
Caleb Fogel, University of Colorado, Boulder, Colorado 80309, USA.

Colin Nicol, PACE Engineers, Inc., Kirkland, Washington 98033, USA.

Abstract

A pressing question for managing recovery of depressed or declining species is: Can habitat restoration increase resilience to climate change? We addressed this question for salmon populations with varying life histories, where resilience is defined as maintaining or increasing population size despite climate change effects. Previous studies indicate that several interrelated mechanisms may influence salmon resilience to climate change, including improving either habitat capacity or productivity, and ameliorating climate change effects on flood flow, low flow, or stream temperature. Using the Habitat Assessment and Restoration Planning (HARP) model, we first examined the relative importance of each mechanism for increasing salmon population resilience by comparing projected salmon spawner abundance for seven individual restoration action types under current and projected mid- and late-century climates. We found that restoring habitats with the greatest restoration potential most increased resilience for all species, but the most beneficial restoration actions varied among species. Increasing habitat capacity and productivity both contributed to resilience, and ameliorating climate change effects was important in a few subbasins where the restoration opportunity was widespread. Cool-water climate refuges contributed to resilience of some subpopulations by reducing late-century declines in spawner abundance even without restoration. We also modeled more complex habitat restoration strategies comprised of several restoration action types at varying restoration intensities and found that the restoration action types and level of restoration effort needed to increase resilience varied among species. Less vulnerable species such as coho salmon responded well to four restoration actions (floodplain reconnection, wood augmentation, increased shade, and increased beaver ponds) applied at low restoration intensity and over a large area. More vulnerable species such as spring Chinook responded to fewer action types (floodplain reconnection, wood augmentation, and increased shade), but at much higher intensity and over a much smaller area. The analysis also identified important locations for each

restoration action type for each species, which helps focus habitat restoration effort on areas that are likely to provide the largest increases in resilience.

INTRODUCTION

Resilience has been defined as the ability of a system to absorb disturbance and reorganize in ways that retain essentially the same functions, structures, identities, and feedbacks (Holling, 1973; Walker et al., 2004), and more than 40 attributes of ecosystems or species that confer resilience to climate change have been identified (Timpane-Padgham et al., 2017). These attributes confer resilience via one of two primary mechanisms: resistance, or the ability of a system or species to persist through a disturbance, and recovery, or the rate at which a system or species returns to its previous state after a disturbance (Holling, 1973; Timpane-Padgham et al., 2017; Walker et al., 2004). Both mechanisms are likely to contribute to resilience of species to climate change, but mechanisms vary among species and depend on the type of environmental change to which species are exposed (Timpane-Padgham et al., 2017).

An important question for management of species in the face of climate change is: Can habitat restoration increase resilience of species to climate change? Several recent papers suggest general strategies for increasing species resilience, including increasing connectivity between habitats and populations, broadening the spatial distribution of subpopulations, increasing genetic or life history diversity, and reducing climate change effects on habitats (Beechie et al., 2013; Davies, 2010; Dunwiddie et al., 2009; Waldman et al., 2016). There is also evidence that restoring habitat capacity (e.g., increasing habitat area) may be more important for recovery of some species (Kautz et al., 2006; Kerr & Deguise, 2004; Walters, Copeland, & Venditti, 2013), whereas increasing productivity (reproductive success) may be more important for others (Grier, 1982; Watts et al., 2008). While each of these strategies has been considered individually, there have been few attempts to compare the likely effectiveness of different strategies for increasing resilience of species to climate change, nor of the mechanisms that may increase resilience (Battin et al., 2007; Justice et al., 2017).

In this paper, we compare the potential effectiveness of these strategies for three species of Pacific salmonids with four different life histories in the Chehalis River basin of the Pacific Northwest, USA. We use the Habitat Assessment and Restoration Planning (HARP) model (Beechie et al., 2021; Jorgensen et al., 2021), which was designed to evaluate the effects of alternative habitat restoration actions and climate change on salmonid populations (Fogel et al., 2022; Jorgensen et al., 2021; Nicol et al., 2022). The HARP model quantifies degradation and potential improvement in habitat conditions, translates environmental or habitat conditions into life stage parameters for each species, and uses salmon life cycle models to evaluate change in population size as a function of modeled habitat changes (Beechie et al., 2021). Previously we used the HARP model to identify restoration action types with the greatest potential to increase salmonid abundance under current climate conditions (Beechie et al., 2021; Jorgensen et al., 2021), and to model the individual effects of future increases in flood flow and stream temperature (Fogel et al., 2022; Nicol et al., 2022). In this paper, we add a novel set of analyses that compares the potential for individual habitat restoration action types and combinations of actions to increase resilience of the four salmonid species/runs to the combined climate change effects of increasing flood flow, decreasing low flow, and increasing stream temperature. We use the model output of median spawner abundance as the metric of resilience, where smaller decreases in abundance with climate change alone (no restoration) indicate greater intrinsic resilience, and larger increases in abundance with climate change and restoration indicate greater potential for restoration to increase resilience.

We identified five potential habitat restoration strategies that might increase resilience to climate change (i.e., increase spawner abundance despite climate change effects) and that we could potentially "test" using the HARP model. Three of the strategies focus on reducing existing habitat degradation, and two focus on ameliorating anticipated climate change effects. We tested these strategies by running individual restoration scenarios for each strategy, comparing their effects on spawner abundance currently and under future climate conditions, and running a sensitivity analysis to determine which life stage parameters most influenced spawner abundance. We also modeled scenarios that included combinations of restoration actions at varying levels of effort to estimate how much restoration might be needed for each species to be resilient to climate change.

METHODS

Study area and prior model results

The Chehalis River basin drains over 6800 km² from the Olympic Mountains, Cascade Foothills, and Willapa Hills, flowing generally westward into Grays Harbor and the Pacific Ocean (Figure 1). Headwater elevations are typically less than 600 m in the Willapa Hills, and over 1000 m in small portions of the Olympic Mountains and Cascade Foothills. Precipitation ranges from about 125 cm/year in the lowlands to over 450 cm/year in the Olympic Mountains (PRISM Climate Group, 2019).

Natural land cover was primarily conifer forest on the hillslopes, mixed conifer and deciduous forest on the floodplains, and substantial areas of wetland in wide, low-elevation valleys filled with glacial outwash deposits (Beechie et al., 2021; Franklin & Dyrness, 1973). Conifer species were predominantly Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), Sitka spruce

FIGURE 1 Study area map indicating key geographic features and locations mentioned in text.

(*Picea sitchensis*), and western red cedar (*Thuja plicata*). Deciduous species were primarily found in riparian and wetland areas, with the dominant species being black cottonwood (*Populus trichocarpa*) and red alder (*Alnus rubra*) (Franklin & Dyrness, 1973). Current land cover is commercial or publicly owned conifer forest in the uplands, with agriculture, rural residential, and developed areas concentrated in the valley bottoms and on low-elevation terraces (Beechie et al., 2021).

The dominant anadromous salmonid species in the basin include Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), chum salmon (*Oncorhynchus keta*), and steelhead (*Oncorhynchus mykiss*). Chinook salmon have two run timings, spring run and fall run. In this paper, we model four of the five species/runs: spring- and fall-run Chinook salmon, coho salmon, and steelhead. Each of these runs is at very low abundance relative to historical levels, although none of the populations are currently listed as threatened or endangered (Aquatic Species Restoration Plan Steering Committee, 2019). Spring-run Chinook are especially vulnerable as there are less than 1000 spawners returning in some years (Washington Department of Fish and Wildlife, unpublished data). Additional life history details for each species/run are described later in the life cycle model description.

In previous HARP model analyses in the Chehalis River basin, we quantified habitat change from historical to current conditions (Beechie et al., 2021), modeled potential changes in equilibrium spawner abundance for seven individual restoration action types (Jorgensen et al., 2021), and modeled two individual effects of climate change (increasing flood flow and increasing stream temperature) (Fogel et al., 2022; Nicol et al., 2022). We estimated changes in habitat conditions for seven specific impacts to salmon habitat: migration barriers, increased fine sediment, reduced wood abundance, decreased stream shade, channel straightening and bank armor, beaver removal, and disconnection of floodplain habitats (Beechie et al., 2021). We estimated that the Chehalis basin has lost ~90% of floodplain and beaver pond habitats but only 5% of main channel length. Seven percent of large river bank habitats are armored. Spawning gravel area has decreased between 23% and 68% among subbasins due to wood loss. Migration barriers and significant loss of shade affected less than 25% of salmon stream length but effects varied by species. For example, spring-run Chinook salmon have no migration barriers within their range, but 22% of coho habitat is partially or fully blocked by migration barriers. Basin-averaged modeled percent fine sediment has increased from 14% to 18%.

Previous life cycle model results indicated that habitat restoration actions with the greatest restoration potential varied among species, reflecting their life histories and habitat preferences (Jorgensen et al., 2021). For coho salmon, the greatest restoration potential was for actions that improve winter rearing capacity and productivity (floodplain reconnection, beaver pond restoration, and wood augmentation), and to a lesser extent shade restoration to improve summer rearing survival (Table 1). For spring-run Chinook salmon, actions that improve adult prespawn survival by reducing summer stream temperature (increased shade and floodplain connectivity) were most important, and wood augmentation had a similar potential to improve overall abundance. Fall-run Chinook and steelhead were less responsive to modeled restoration actions. Projected climate-related increases in flood flow reduced modeled median spawner abundance by −4% for steelhead and −15% for spring-run Chinook by late century, with intermediate reductions for coho

TABLE 1 Summary of results (percentage increases or decreases in spawners from current habitat and climate conditions) from prior Habitat Assessment and Restoration Planning model studies in the Chehalis River basin, including restoration potentials for the five most influential habitat restoration actions, and effects of projected increased flood flow and temperature in late century.

Modeled effect	Coho salmon	Spring-run Chinook	Fall-run Chinook	Steelhead
Restoration action, no climate change				
Floodplain reconnection	+54	+49	+14	+16
Increase beaver pond area	+76	0	+2	0
Wood augmentation	+36	+48	+29	+37
Increase shade	+13	+46	+3	+7
Fine sediment reduction	+22	+74	+32	+12
Climate change effect				
Flood flow increase (late century)	−9	−15	−9	−4
Temperature increase (late century)	−23	−87	−12	−20

Note: Data from Jorgensen et al. (2021), Nicol et al. (2022), and Fogel et al. (2022).

and fall-run Chinook (Table 1) (Nicol et al., 2022). Increasing temperature generally had larger effects on each species/run by late century, ranging from −12% for fall-run Chinook salmon to −87% for spring-run Chinook salmon (Table 1) (Fogel et al., 2022).

The extent of salmon habitat restoration in the Chehalis River basin to date has been relatively small compared with the scope of habitat loss and degradation, but restoration effort has been increasing due to a new focus on habitat restoration in the basin under the Chehalis Basin Strategy, initiated in 2017. Until recently, restoration actions tended to focus on relatively small projects such as removal of migration barriers and small-scale riparian restoration, but the recently developed Aquatic Species Restoration Plan relied heavily on the results of this model (Beechie et al., 2021; Jorgensen et al., 2021) and the Ecosystem Diagnosis and Treatment model (Lichatowich et al., 1995) to develop a new restoration strategy that aims to shift restoration effort toward larger projects that reconnect floodplain habitats, restore beaver pond habitat, and increase wood abundance (Aquatic Species Restoration Plan Steering Committee, 2019).

The HARP model

In the HARP model, drivers of habitat change alter habitat conditions, which alter the life stage capacities and productivities that are the inputs to the life cycle models (Figure 2). Life cycle models then calculate equilibrium spawner abundance for each species and habitat scenario modeled. The drivers include seven potential restoration actions, as well as external drivers such as climate change effects on stream flow and temperature. The HARP model has four main components: (1) a geospatial analysis that quantifies current and historical habitat conditions for each 200-m reach in the basin; (2) a set of sub-models that link changes in drivers to changes in habitat area or quality; (3) a suite of functions that translate habitat areas and qualities into life stage parameters for the life cycle models; and (4) the salmon life cycle models.

Geospatial analysis

The geospatial analysis focuses on estimating habitat area and quality for both current and natural potential
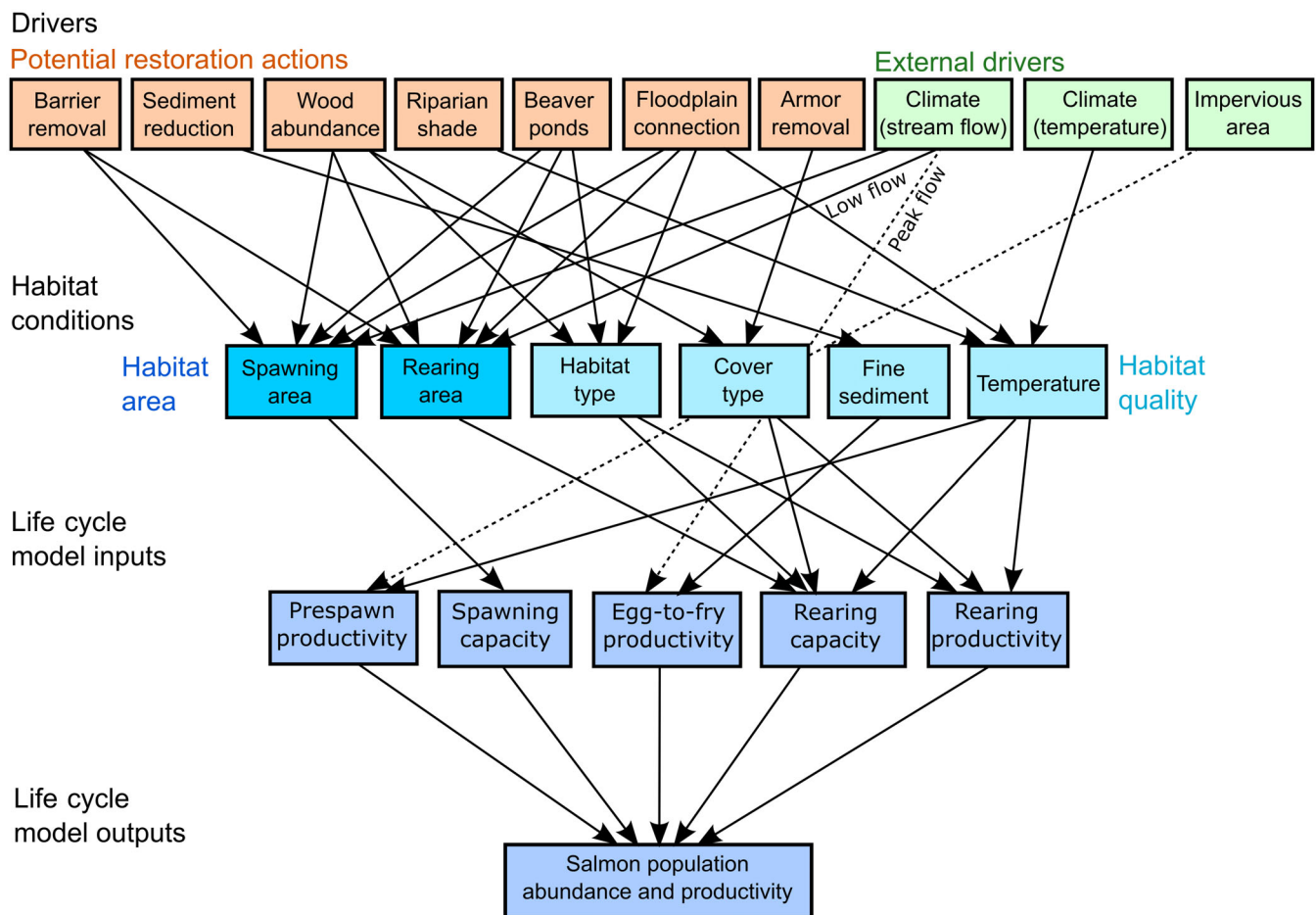

FIGURE 2 Diagram of the main process linkages in the Habitat Assessment and Restoration Planning model. Modified from Fogel et al. (2022).

conditions, and the difference between the two is the "restoration potential." Current conditions are estimated from recent empirical data for habitat area or quality for each 200-m-long reach in the stream network (Table 2) (Beechie et al., 2021). For the Chehalis River basin, some data sets have extensive coverage with reach-level resolution (e.g., shade, floodplain habitat), and confidence in reach-level values is relatively high. Other data sets are extrapolated from a subsample of reaches (e.g., habitat surveys, stream temperature, fine sediment), and for those attributes reach-level confidence is lower. Natural potential conditions are estimated from historical data, contemporary reference sites, or models (Beechie et al., 2021). As with current conditions, reach-level confidence is higher for those attributes with extensive coverage and lower for attributes that are extrapolated from a subsample of sites.

Linking drivers to habitat change

The model translates drivers (restoration actions, climate change, and land cover) into habitat changes via a series of process functions indicated by arrows linking the top two rows in Figure 2. We briefly summarize these process functions here (details in Beechie et al., 2021 and Jorgensen et al., 2021). Migration barriers influence habitat capacity and prespawn productivity via passage ratings, where 0 represents a full blockage, 1.0 represents a structure that is fully passable, and 0.33 and 0.67 are intermediate values indicating partial passage at a site (Beechie et al., 2021; Washington Department of Fish and Wildlife, 2019). Changes in forest road density alter percent fine sediment (<0.85 mm) in spawning gravels. Percent fine sediment is predicted by a two-stage model in which reaches with low shear stress index (reach slope × bankfull width ≤0.05) have consistently high fine sediment, and reaches with high shear stress index (>0.05) have fine sediment level predicted by changes in forest road density (Beechie et al., 2021).

Mainstem restoration actions include channel remeandering and bank armor removal. Remeandering increases channel length, which increases the area of large river habitats. Armor removal does not alter habitat area in the model, but changes habitat quality and increases density of rearing juveniles in edge habitats (Jorgensen et al., 2021). Wood augmentation can increase both habitat area and quality. In small streams (≤20-m bankfull width), areas of spawning gravel and rearing pools increase as wood abundance increases, using a linear scaling between current conditions (low wood abundance) and historical conditions (high wood abundance) (Beechie et al., 2021). In large rivers (>20-m bankfull width), wood augmentation increases spawning gravel area and rearing habitat quality in edge habitats.

TABLE 2 Brief description of methods used to calculate habitat areas and conditions for each 200-m reach (summarized from Beechie et al., 2021).

Assessment component	Methods description
Small-stream spawning habitat (channels ≤20-m bankfull width)	Estimated from data relating wood abundance to spawning gravel area (Beechie et al., 2021)
Small-stream rearing habitat	Extrapolated from 339 reach surveys, stratified by channel slope and adjacent land cover (Beechie et al., 2021)
Beaver ponds	Current pond area estimated from recent surveys; historical pond area modeled based on stream power (Pollock et al., 2004)
Large river spawning habitat (channels >20-m bankfull width)	Digitized from aerial imagery; modified by wood abundance for historical condition (Beechie et al., 2021)
Large river rearing habitat	Digitized from aerial imagery; modified by wood abundance and bank armor removal for historical condition (Beechie et al., 2021)
Floodplain habitat	Current condition from National Hydrography Dataset Plus (NHD+); historical condition from General Land Office surveys in the late 1800s and reference site data (side channels) (Beechie et al., 2021)
Migration barriers	Modified from Washington Department of Fish and Wildlife barrier database (Beechie et al., 2021)
Bank armor	Digitized from aerial imagery; armor removed for historical condition (Beechie et al., 2021)
Riparian shade	Calculated from lidar and aerial imagery inventory of riparian tree heights (Fogel et al., 2022; Seixas et al., 2018)
Stream temperature	Modeled from stream temperature loggers distributed across the basin; modified by shade and floodplain connectivity (Fogel et al., 2022)
Fine sediment	Modeled based on shear stress index and forest road density (Beechie et al., 2021)

Increasing abundance of beaver dams increases pond area in small streams, and also reduces the area of pools and riffles where beaver ponds inundate free-flowing stream reaches.

Floodplain reconnection increases the area of floodplain ponds, marshes, and side channels and decreases stream temperature via hyporheic exchange. To model a decrease in stream temperature via hyporheic exchange, we used a maximum potential decrease of −2°C based on a study in the Willamette River (Seedang et al., 2008) and scaled the magnitude of temperature decrease with the width of the connected floodplain corridor (Fogel et al., 2022; Seedang et al., 2008). The width of the restored floodplain corridor was a function of channel width: floodplain width of 61 m for channels <10-m bankfull width, 152 m for channels 10–20 m wide, 213 m for channels 20–30 m wide, and 305 m for channels >30 m wide (Aquatic Species Restoration Plan Steering Committee, 2019). Corresponding temperature reductions for those floodplain widths were −0.29, −0.72, −1.0, and −1.43°C, respectively (Fogel et al., 2022).

Potential temperature decrease due to increasing shade was estimated using a tree growth model combined with a shade-temperature model (Fogel et al., 2022; Seixas et al., 2018). The tree growth model is an empirical stand height model in which the height growth rate decreases as trees age (Beechie et al., 2000; Seixas et al., 2018). Shade is represented by the canopy opening angle, which is calculated from the channel width and tree height on each bank (Seixas et al., 2018). The change in stream temperature for each reach was related to a change in canopy opening angle by the function

$$\Delta T = 0.035 \times \Delta\theta, \qquad (1)$$

where ΔT is the change in temperature in degrees Celsius and $\Delta\theta$ is the change in canopy opening angle (Beechie et al., 2021). We used two different metrics for T in the model, the 7-day average daily maximum temperature (7-DADM), which affects juvenile summer rearing and spring-run Chinook adult holding, and the June 1–21 average daily maximum (Jun1–21 ADM), which affects the late portion of the juvenile Chinook outmigration (Jorgensen et al., 2021).

Translating habitat change into capacity and productivity change

The habitat model translates habitat area or quality into input parameters for the life cycle models, in which survival of eggs or fish through each life stage is a function of habitat capacity and productivity in a Beverton–Holt

function (Moussalli & Hilborn, 1986). Capacity is the maximum number of eggs or fish that can be produced through a life stage, and productivity is the density-independent survival rate of eggs or fish through a life stage when the population is near zero (Moussalli & Hilborn, 1986). Current densities for each species, life stage, and habitat type were based on empirical densities from prior studies (Beamer & Henderson, 1998; Bisson et al., 1988; Nickelson, 1998), and current productivities were based on typical observed productivities under current habitat conditions (Johnson et al., 1993; Jorgensen et al., 2021; Nickelson, 1998).

The habitat model uses empirical functional relationships to relate changes in habitat area or quality to changes in life stage parameters (arrows linking the second and third rows in Figure 2) (Table 3). Some habitat

TABLE 3 Summary of modeled effects of habitat change on life stage parameters (summarized from Jorgensen et al., 2021).

Habitat change	Capacity or productivity effect
Restoration effects	
Increased spawning gravel area	Increases spawning capacity
Increased rearing habitat area (pools, ponds, marshes, and side channels)	Increases rearing capacity; increases sub-population rearing productivity when restored habitats have higher productivity (e.g., marshes, ponds)
Increased wood cover	Increases rearing capacity and productivity
Bank armor removal	Increases rearing capacity
Decreased fine sediment in spawning gravels	Increases incubation productivity
Decreased stream temperature	Increases rearing capacity and productivity, increases prespawn survival for summer-run Chinook
Climate change effects	
Increased flood flow	Decreases incubation survival via egg scour
Decreased summer low flow	Decreases summer rearing capacity
Increased stream temperature	Decreases rearing capacity and productivity, decreases prespawn survival for summer-run Chinook
Development effect	
Increased impervious surface area and road area	Decreases prespawn survival for coho salmon

changes primarily affect capacity (e.g., removing migration barriers to access more habitat), whereas others primarily affect productivity (e.g., decreasing fine sediment increases survival of incubating eggs) (Jensen et al., 2009; Jorgensen et al., 2021) (Table 3). However, some habitat changes affect both capacity and productivity (e.g., stream temperature affects juvenile rearing capacity and productivity) (Jorgensen et al., 2021).

Salmon life cycle models

The salmon life cycle models are habitat-based, matrix-type population models (Honea et al., 2009; Jorgensen et al., 2021; Nickelson & Lawson, 1998) that track the abundance of eggs or fish through time in an array where columns represent subpopulations and rows represent annual time steps (Jorgensen et al., 2021). Each annual time step includes one or more life stages, and stochasticity in habitat conditions can be included in the model as a time series of events. Life stages can be density dependent or density independent. Density-dependent life stages were modeled with a Beverton–Holt function:

$$N_{stage+1} = \frac{p \times N_{stage}}{1 + \left(\frac{p}{c}\right) \times N_{stage}}, \qquad (2)$$

where N_{stage} is abundance of eggs or fish at the beginning of the stage, p is productivity, c is capacity, and $N_{stage+1}$ is abundance of eggs or fish at the end of the stage (Moussalli & Hilborn, 1986). Density-independent life stages were modeled with a linear survival function with no capacity limit (Greene & Beechie, 2004).

$$N_{stage+1} = p \times N_{stage}. \qquad (3)$$

The number and characteristics of life stages, and degree of overlap among life stages and climate change effects varied among species (Figure 3). Spring-run Chinook return to the river in spring, occupy holding areas through summer, and spawn in early fall (Jorgensen et al., 2021). Fall-run Chinook return to the river in late summer and early fall, and spawn shortly after reaching their spawning grounds. Chinook salmon juveniles rear in freshwater for 3 months or less and spend up to 5 years in the ocean before returning to spawn. Spring-run Chinook salmon are the only species with an extended adult holding period through summer, and hence they are the only species/run affected by increasing stream temperature in the adult stage. Chinook salmon eggs are sensitive to the effects of increasing flood flow because the incubation period overlaps the flood season. Most Chinook salmon juveniles

leave the river prior to summer high temperatures and the lowest flows, so both Chinook run types are less affected by climate change in the juvenile stage than either coho or steelhead. Coho salmon enter the river in early fall and spawn in fall and winter, juveniles rear in freshwater for one year, and adults spend two years in the ocean. Coho salmon eggs are sensitive to the effects of increasing flood flow, and juveniles are sensitive to decreasing low flows and increasing summer stream temperature. Steelhead enter the river in late winter and spawn in the spring, rear freshwater for one to three years, and spend up to five years in the ocean. Steelhead is the only species with repeat spawners. The steelhead incubation period has the least overlap with winter flood flows of the four species/runs, but their extended freshwater rearing period exposes juveniles to increasing stream temperature and decreasing low flows in multiple years. Species' ranges vary, with coho salmon occupying almost all tributaries in the basin, and spring-run Chinook salmon occupying only four tributaries (Appendix S1: Figure S1). Steelhead and fall-run Chinook salmon ranges are intermediate between those of coho and spring-run Chinook salmon. Additional details of the species' life histories are described in Jorgensen et al. (2021).

The spatial resolution of the life cycle model is the subbasin (equivalent to a subpopulation), so the habitat model aggregates all reach-level habitat attributes to the subbasin level to determine input parameters for the life cycle models (Jorgensen et al., 2021). The 63 subbasins are independent tributaries of the main stem Chehalis River or segments of the mainstem floodplain, ranging in area from ~15 to 750 km^2. Reaches are 200 m in length. Reach-level life stage capacities are calculated from areas of each habitat type in each reach multiplied by their respective densities of eggs or fish, and reach-level capacities are summed for each life stage in each subbasin to calculate the total capacity of each life stage for each subbasin (modeled as a subpopulation, with no straying of adults between subbasins). Life stage productivities are calculated as the weighted average of reach-level productivities for each subpopulation, where the weights are the life stage capacities for each reach.

Analyses

We extracted equilibrium spawner abundance estimates for each subpopulation of each species for each scenario to compare population responses across scenarios. There are three types of scenarios the HARP model can run: (1) diagnostic scenarios, (2) climate change scenarios, and (3) complex scenarios that include any combination
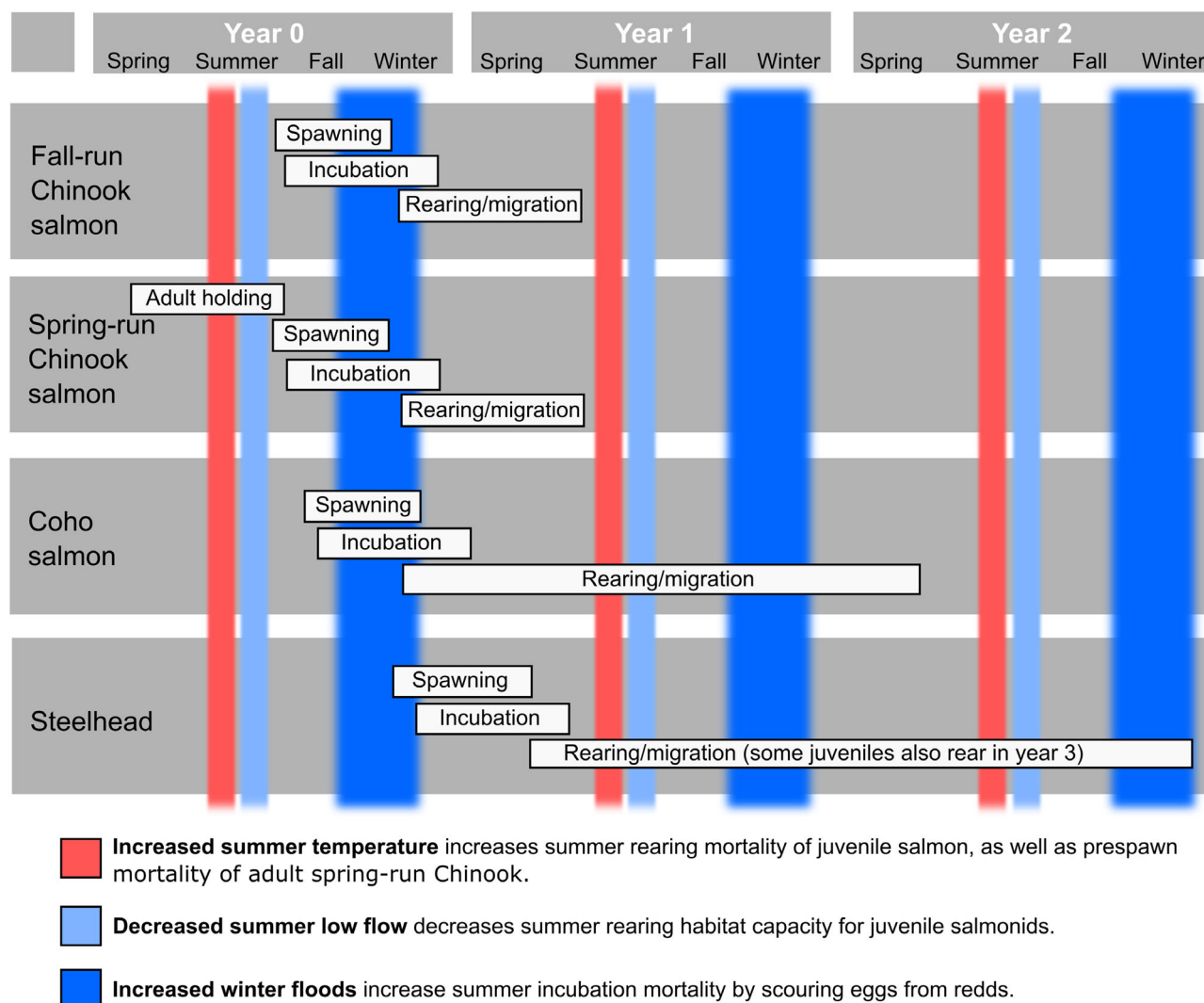
FIGURE 3 Overlap of key life stages and climate change effects for each species/run modeled. Modified from Beechie et al. (2013).

of restoration actions and climate change effects. The diagnostic scenarios compare restoration potentials (the difference between modeled current spawner abundance and modeled natural potential spawner abundance) among the seven potential restoration action types (migration barrier removal, fine sediment reduction, wood augmentation, increased shade, remeandering and bank armor removal, beaver pond restoration, and floodplain reconnection), as well as how restoration potential varies among subbasins. The climate change scenarios project how increasing stream temperature, increasing flood flows, and decreasing low flows will affect equilibrium spawner abundance of each species and subbasin in the future. The complex scenarios compare resilience potentials (the difference between current equilibrium spawner abundance and mid- or late-century equilibrium spawner abundance) among scenarios. For each of these scenarios, we specified the types and intensity of restoration to occur in each

subbasin, generated scenario-specific life cycle model inputs, and modeled each restoration strategy under current climate, mid-century climate, and late-century climate conditions.

In addition to the modeled scenarios, we conducted a one-at-a-time sensitivity analysis to evaluate which life stage capacities or survivals individually had more influence on abundance for each species. We varied the current capacity or density-independent productivity for each life stage independently in 1% increments from its current value to its natural potential value and plotted the population response against the proportional change in the parameter. Steeper slopes indicate greater sensitivity per 1% increment of change, and greater total magnitude of change indicates greater restoration potential. Model uncertainties are briefly discussed in Appendix S2, and additional details on uncertainties are in prior HARP model publications (Beechie et al., 2021; Fogel et al., 2022; Jorgensen et al., 2021; Nicol et al., 2022).

Modeled climate change effects

The most accurate local stream temperature model was based on extensive local temperature data processed with a statistical spatial network model (Fogel et al., 2022; Winkowski & Zimmerman, 2018), and future projections using that model were based on the ensemble average of 10 global climate models for the A1B (moderate emissions) scenario (IPCC, 2007; Isaak et al., 2017). Those studies projected an increase of +1.15°C in August average daily average (ADA) temperature across the basin by mid-century (2030–2059) and +3°C by late century (2070–2099) (Table 4). We added those values to the current stream temperature of all reaches to estimate reach-specific mid-century and late-century temperatures. In the HARP model, stream temperature affects prespawn productivity of spring-run Chinook salmon, out-migrant survival of spring- and fall-run Chinook salmon, and summer rearing survival of steelhead and coho salmon (Jorgensen et al., 2021).

Available stream flow projections (Mauger et al., 2016) were based on Representative Concentration Pathway (RCP) 4.5 (low emissions) and RCP 8.5 (high emissions) scenarios (Taylor et al., 2012). Stream flow projections for RCP 6.5 (moderate emissions) were not available. Both flood flow and low flow changes in the Chehalis River basin were similar between RCP 4.5 and 8.5 in both mid- and late century (Mauger et al., 2016), so we chose to use RCP 8.5. For future flood flows, we generated estimates of percent change in discharge across a range of flood flows at the US Geological Survey (USGS) stream gage at Porter (number 12031000). We used the average bias-corrected projections from two hydrologic models (Mauger et al., 2016) to construct regressions for mid- and late century under the RCP 8.5 emissions scenarios (Nicol et al., 2022). Examples of the modeled percent change in flood flows at varying return intervals are shown in Table 4. Flood flows scour eggs from the gravel,

and the impact on incubation survival is calculated as a function of flood recurrence interval (Nicol et al., 2022; Zimmerman et al., 2015).

For future low flows, we used projected changes in the 10-year 7-day average low flow (7Q10) at eight stations in rainfall-dominated parts of the basin (Mauger et al., 2016) and averaged percent changes in low flow across all stations and both models. The average projected change in the 7Q10 for both mid-century and late century for rain-dominated portions of the basin was −10% under RCP 8.5 (Table 4). To translate low flow changes into changes in wetted width, we used equations for confined channels ($Q = 0.0018 \times w^{2.299}$) and unconfined channels ($Q = 0.0138 \times w^{1.767}$), where Q is discharge in cubic meters per second and w is wetted width in meters (Laura McMullen, ICF International, personal communication, 2019). We rearranged both equations to estimate the change in width as a function of change in discharge ($w = (Q/0.0018)^{0.435}$, and $w = (Q/0.0138)^{0.567}$).

Because the modeled percent change in discharge is constant across all channel sizes (−10%), the rearranged equations can be reduced to $w_{future}/w_{current} = (0.9)^{0.435} = 0.96$ and $w_{future}/w_{current} = (0.9)^{0.567} = 0.94$. That is, a −10% change in discharge produces a wetted width change of −4% for confined channels and −6% for unconfined channels. Because we did not have data on locations of confined versus unconfined channels and the estimated changes are similar between the channel types, we estimated the change in wetted width as −5% for all reaches.

To simulate the stochastic effects of annual variation in flood flow, low flow, and stream temperature in the life cycle models, we generated a time series of those parameters from empirical data. We acquired coincident time series of flood flow and low flow from the USGS stream gage at Porter and air temperature from a weather station near the town of Chehalis (National Climate Data Center, station ID USC00451276). We then fit a multivariate auto-regressive state-space (MARSS) model to a current-condition time series of the three values that retain their empirical correlation structure (Holmes et al., 2012, 2020). We used air temperature instead of stream temperature because the period of record for stream temperature (22 years) was much shorter than the flow record used for the MARSS model fitting. Using the fitted MARSS model, we generated 10 time series of flood flow, low flow, and air temperature, spanning 100 years each. Details of the MARSS analysis are in Appendix S3.

We converted each annual air temperature to stream temperature based on a regression of annual 7-DADM stream temperature against annual maximum air temperature ($T\mathrm{max}_{air}$) for each simulation year. From the 22 years of stream temperature data, we removed years

TABLE 4 Summary of climate change effects modeled for mid- and late-century time periods.

Parameter	Mid-century	Late century
Water temperature	+1.15°C	+3°C
Flood flow (%; 2-year flood)	+11%	+12%
Flood flow (%; 10-year flood)	+29%	+27%
Flood flow (%; 50-year flood)	+48%	+42%
Low flow (%; average decrease)	−10%	−10%

Note: Flood flow changes are examples for three recurrence intervals to illustrate the range of modeled changes using the flood flow regression of Nicol et al. (2022).

with incomplete data during the warmest part of the summer (1 year) or apparent errors (2 years), leaving 19 years of data for the regression. The regression result was

$$7\text{DADM} = 5.64 + 0.49(T\text{max}_{\text{air}})$$
$$\left(\text{adjusted } r^2 = 0.57, \, p < 0.001\right). \tag{4}$$

Using this equation, we calculated stream temperature at the gage site for each year of the time series based on air temperature in each year. We assumed that interannual variation in temperature in other reaches in the basin was similar to that at the gage site and applied the same temperature difference in each year to all reaches. To generate time series of mid-century and late-century stream flow and temperature conditions, we applied each of the mid-century and late-century change estimates for stream flow and stream temperature to each year in the time series for current stream flows and air temperatures.

Restoration scenarios

We modeled five potential restoration strategies that might increase resilience to climate change (Table 5). The first strategy was to address the habitat impairments with the greatest potential to improve population performance under current conditions (Strategy 1). In this strategy, restoration actions addressed the most important habitat constraints for each species, under the

assumption that increases in climate change resilience are proportional to restoration potential. This strategy essentially assumes that large increases in abundance can increase resilience to climate change (Timpane-Padgham et al., 2017), regardless of whether those actions ameliorate a climate change effect.

The second and third strategies focused on whether actions that increase habitat capacity (Strategy 2) are more important than actions that increase productivity (Strategy 3). A number of studies have assumed that salmon populations are currently at such low abundance that capacity does not limit population size, and therefore that management actions should focus on increasing productivity in juvenile life stages (Kareiva et al., 2000). However, other studies suggest that at least some populations are near capacity (i.e., capacity is much reduced from historical levels), and that increasing productivity will not decrease extinction risk unless capacity is also increased (Bal et al., 2018; Hinrichsen & Paulsen, 2020; Walters, Copeland, & Venditti, 2013; Zabel et al., 2006). We examined the effect of these strategies by modeling the effect of restoration actions that increase productivity or capacity (fine sediment in spawning gravels and migration barriers, respectively) without directly ameliorating a climate change effect.

The remaining strategies focused on habitat restoration actions that may help ameliorate climate change effects on salmonid populations (Beechie et al., 2013) (Strategies 4 and 5). We first examined whether restoration actions that ameliorate the increase in summer high stream temperature increase resilience to climate change (Strategy 4). If this strategy increases resilience to climate

TABLE 5 Summary of potential strategies, restoration actions modeled to test each hypothesis, and modeled effects on life stage capacity and/or productivity.

Strategy	Restoration actions	Effect on life stage parameters
Strategy 1. Restoring habitats with the most potential for population improvements	Species specific (e.g., restore beaver pond and floodplain habitat for coho salmon, reduce stream temperature for spring-run Chinook)	Increased capacity and productivity; varies by subbasin
Strategy 2. Increasing life cycle productivity	Reduce fine sediment in spawning gravel	Increased incubation productivity (all species); does not address a climate change effect directly
Strategy 3. Increasing habitat capacity	Remove migration barriers	Increased spawning and rearing habitat capacity (all species); does not address a climate change effect directly
Strategy 4. Reducing summer stream temperature	Restore riparian shade to mitigate increasing stream temperature	Increased juvenile rearing capacity and productivity for all species; increased prespawn survival for spring-run Chinook salmon
Strategy 5. Mitigating effect of increasing flood flow (or its effect)	Reconnect floodplain habitats to increase juvenile survival during winter flood season	Increased winter rearing productivity (varies among species)

change more than other strategies, the effectiveness of this action in mid-century and late-century climate scenarios will be noticeably larger than that of other restoration actions. We also examined whether mitigating the effect of increasing flood flow (i.e., reducing flood flows or increasing fish survival during flood flows) can increase resilience to climate change (Strategy 5). We did not have sufficient data to model a scenario for mitigating the effects of decreasing low flow, although we did model the effects of climate change on low flows and their effects on salmon populations.

We also modeled combination scenarios that included several restoration action types at varying restoration intensities. We selected the actions for each combination scenario based on the prior modeling results, showing which action types are likely to provide the greatest benefit to the four species (Table 1) (Beechie et al., 2021; Jorgensen et al., 2021). The combination strategies included (1) the four most responsive actions with relatively high model confidence (wood loss, shade loss, beaver pond loss, and floodplain disconnection), and (2) those four actions plus reducing fine sediment (low model confidence). We modeled each group at restoration intensities of 25%, 50%, and 75% (labeled Top4 25%, Top4 50%, Top4 75%, and Top5 25%, Top5 50%, Top5 75%). Restoration intensity is the percentage of restoration potential targeted in each subbasin (i.e., an intensity of 25% means that we modeled restoring 25% of the restoration potential for an action type in each subbasin). With these scenarios, the restoration benefit in each subbasin is a function of the restoration potential for each action type in that subbasin, so the scenario implicitly targets those actions that are likely to be most beneficial in each subbasin. For example, in a subbasin with good riparian conditions but severely reduced floodplain connectivity, the difference in shade between current and historical conditions will be near zero, and modeling 50% intensity will produce a very small change in habitat conditions and spawner abundance, reflecting low riparian restoration potential and low restoration effort. In contrast, the difference in floodplain habitat availability between current and historical conditions is large, and modeling 50% intensity represents a larger restoration effort, resulting in substantial modeled increases in floodplain habitat availability and spawner abundance.

RESULTS

We first present results for basin-scale population changes, and then results at the subbasin scale. Restoration potentials are the gap between current spawner abundance and natural potential spawner abundance, and resilience potentials are the gap between current spawner abundance and mid- or late-century spawner abundance.

Basin-scale model results

At the basin scale, the effectiveness of each restoration action type at maintaining salmon spawner abundance in late century essentially mirrored the restoration potential of each action type under current conditions (Strategy 1), as the actions with the most restoration potential under current conditions also have the largest effect on future abundance relative to a no-action alternative (Figure 4). The results also suggest that restoration actions that increase survival (Strategy 2) may have greater influence on resilience than actions to increase capacity (Strategy 3). For example, increasing incubation productivity by reducing fine sediment (Strategy 2) has relatively high potential to increase resilience of fall-run Chinook salmon to climate change, whereas barrier removal and large river restoration (Strategy 3) have relatively low potential to increase resilience for any species. Restoration actions to ameliorate increased temperature (Strategy 4) or increased flood flow (Strategy 5) do not produce resilience responses that noticeably exceed their restoration potentials under current climate conditions at the Chehalis basin scale.

The sensitivity analysis supports the abundance results, as all species are generally more sensitive to life stage productivities at small percent changes (steeper slope of the line near the origin) (Figure 5). However, many of the productivity parameters have little total potential to increase abundance (indicated by their maximum value on the y-axis), suggesting that the current habitat condition influencing that parameter is not substantially degraded from its potential (e.g., prespawn survival for coho salmon). Hence, for some species such as coho salmon, increasing habitat capacity has greater potential to increase resilience than increasing productivity (Figure 5). Notably, spawner abundance is very sensitive to prespawn productivity for all species, but only spring-run Chinook have significant restoration potential for that life stage.

The combination restoration scenarios indicate that coho salmon and fall-run Chinook may require less restoration effort to increase resilience, whereas spring-run Chinook and steelhead require greater restoration effort. Restoring 25% of four important drivers—wood, shade, floodplain habitat, and beaver ponds—(Top4 25%) produces a modeled late-century abundance near current abundance for coho and fall Chinook, but spring-run Chinook and steelhead still show substantial declines by
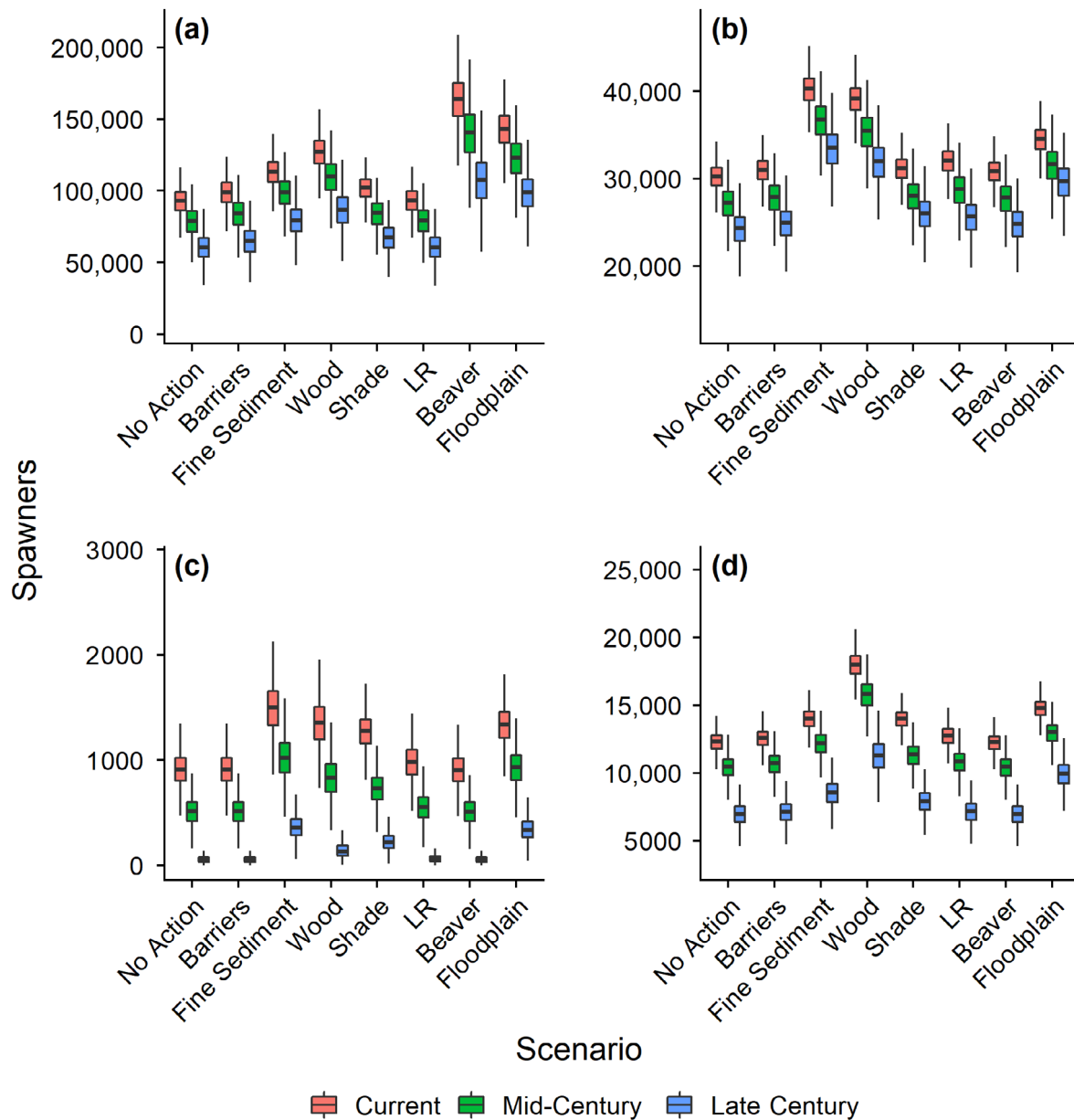
FIGURE 4   Effect of modeled restoration actions and scenarios on spawner abundance for (a) coho salmon, (b) fall-run Chinook salmon, (c) spring-run Chinook salmon, and (d) steelhead under current climate, projected mid-century climate, and projected late-century climate. Note different *y*-axis scales for each species. LR is large river restoration (bank armor removal).

late century (Figure 6). Restoring 25% of the top five drivers (Top5 25%) produces larger responses, especially for spring-run Chinook. However, modeled late-century abundances for spring-run Chinook and steelhead do not exceed current abundance until the Top5 75% scenario, which restores 75% of the restoration potential for each of the top five actions.

Subbasin-scale model results

At the subbasin scale, the potential for each restoration action type to increase resilience reflects the subbasin-scale

restoration potentials (Strategy 1), which can differ significantly from the basin-scale restoration potential (Figure 7). For example, coho salmon have significant capacity constraints in some subbasins, and the restoration potential for barrier removal (Strategy 2) can be relatively large (Figure 7a). However, these are typically small subbasins with low spawner abundance for all species/runs, and there is little potential to increase the basin-wide population (Figure 8). For coho salmon in most other subbasins, actions that increase both capacities and productivities (Strategies 2 and 3 combined), such as restoring beaver pond habitat or floodplain reconnection, tend to produce larger benefits and in more subbasins than actions that
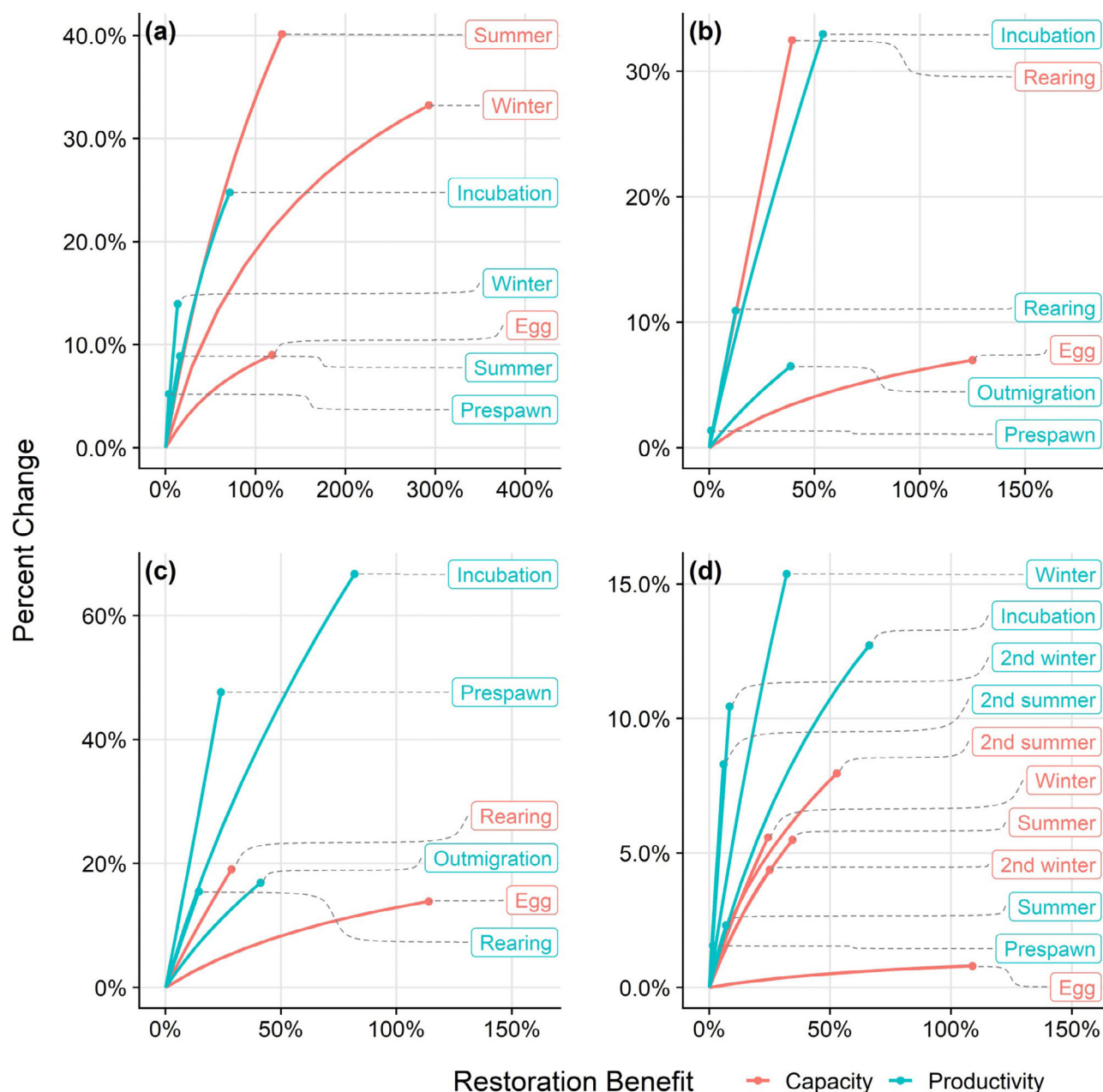
FIGURE 5 Sensitivity analysis of life stage parameters for (a) coho salmon, (b) fall-run Chinook salmon, (c) spring-run Chinook salmon, and (d) steelhead. Baseline is the modeled spawner abundance using current habitat conditions for each parameter (0% on the x-axis). The x-axis is percent increase in a capacity or productivity parameter from the baseline value up to the maximum value of the parameter under historical conditions, indicating restoration intensity. The y-axis is percent change in spawner abundance corresponding to the change in a capacity or productivity parameter (note different y-axis scales). Blue lines are productivity parameters and orange lines are capacity parameters.

affect only one or the other (Figures 7b,d). This general result holds true for all species/runs, as the most important actions at the basin scale are also the most important actions in most subbasins, and those actions tend to affect both capacities and productivities of various life stages (Appendix S4: Figures S1–S4).

Subbasin responses to increasing stream temperature depend on current temperature conditions, and shade

restoration can partly ameliorate the climate change temperature increase in some subbasins for all species (Strategy 4) (Appendix S4: Figures S1–S4). For example, larger abundance declines for coho salmon in the no-action scenarios are in subbasins with streams that are currently warm and the predicted 2080s temperatures are above species tolerances (Figure 7a,b). These small, vulnerable subpopulations may be extirpated by
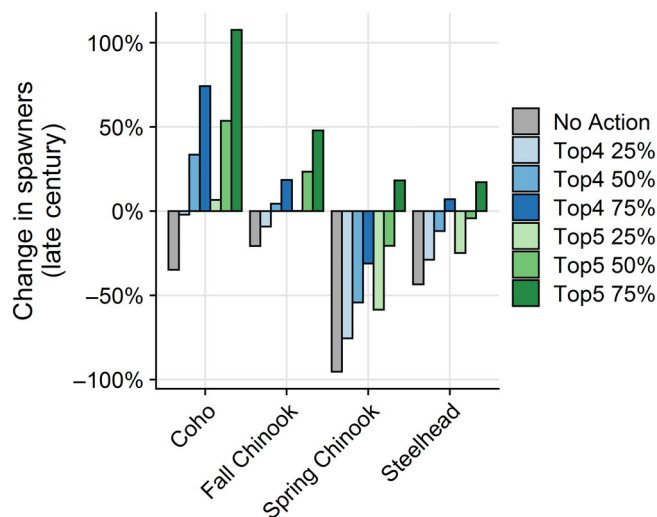
FIGURE 6 Modeled response of salmon populations to alternative restoration scenarios under the projected late-century climate. Top4 includes floodplain reconnection, shade restoration, wood augmentation, and beaver pond restoration; Top5 includes those four actions plus fine sediment reduction. Intensity values of 25%, 50%, and 75% indicate percent of restoration potential (the maximum potential increase in spawner abundance for a restoration action type) modeled for each action. The *y*-axis is percent change from current spawner abundance for each restoration scenario.

the 2080s without habitat restoration. However, ameliorating the climate change effect through shade restoration can substantially reduce the future decline in spawner abundance relative to other actions (Figure 7b), but only in a few subbasins (Appendix S4: Figure S1). Smaller declines in the no-action scenarios are in subbasins with cooler current and future temperatures (Figure 7c,d). These cooler subbasins (or portions of them) may function as climate refuges because they have high-elevation cool-water reaches or reaches fed by cool groundwater.

One action that has the potential to ameliorate combined near-term climate change effects for multiple species is floodplain restoration (Figure 8). This action ameliorates at least two of the climate change effects (temperature and flood flow, Strategies 4 and 5), and modeling the full restoration potential produces stable or increasing populations for all species in many subbasins by the 2040s. However, by the 2080s, even the full floodplain restoration potential does not prevent spawner abundance declines in roughly half the subbasins for coho and fall Chinook, and all subbasins are declining for spring-run Chinook and steelhead. Nonetheless, floodplain restoration (Strategies 4 and 5) may be an important contributor to increasing salmon resilience in a number of subbasins, especially for coho salmon.

The combination scenarios that broadly represent Strategy 1 produce relatively strong increases in resilience for all species/runs, although the restoration intensity required to increase resilience varies among subbasins for each species/run. For example, the scenario that addresses 25% of the restoration potential for the five actions with the greatest restoration potential (Top5 25%) is sufficient to produce a modeled 2080s abundance that is higher than the current abundance in most subbasins for coho salmon, but spring-run Chinook require 75% intensity (Top5 75%) to increase 2080s abundance above current abundance in only a few subbasins (Figure 9). Fall-run Chinook and steelhead show a similar contrast, with fall-run Chinook requiring less restoration effort to increase resilience and steelhead requiring greater restoration effort (Appendix S4: Figure S5).

DISCUSSION

A general conclusion from our analysis is that habitat restoration actions that are most likely to increase resilience of each Chehalis basin salmon species/run are tightly linked to the habitat losses that most constrain each population (Strategy 1). The climate change effects we examined reduced either capacity or productivity for each species by varying degrees (Fogel et al., 2022; Nicol et al., 2022), and actions that created the largest increases in either productivity or capacity (Strategies 2, 3) appeared to generate greater resilience to climate change. For example, restoration actions that reduce fine sediment in spawning gravel substantially increase egg incubation survival for spring- and fall-run Chinook salmon (Strategy 2), which partially counters productivity losses due to other climate-related mortality mechanisms in other life stages.

Restoration actions that directly ameliorate a climate change effect (Strategies 4–5) do not appear to disproportionately increase resilience relative to other actions at the basin scale, but ameliorating climate change effects at the subbasin scale may increase resilience where the opportunity to ameliorate the climate change effect is widespread. For example, restoring riparian forests in subbasins with uniformly poor shade conditions can increase resilience of those subpopulations, but in our study, there were only a few small subbasins with widespread shade loss. Therefore, ameliorating the climate change effect increased abundance for only a few small subpopulations, and those increases did not have much influence on the total Chehalis basin population.

Our analysis also illustrates that effective restoration strategies to increase resilience will vary among species and locations. At the basin scale, substantially increasing resilience of coho salmon could require a focus on four
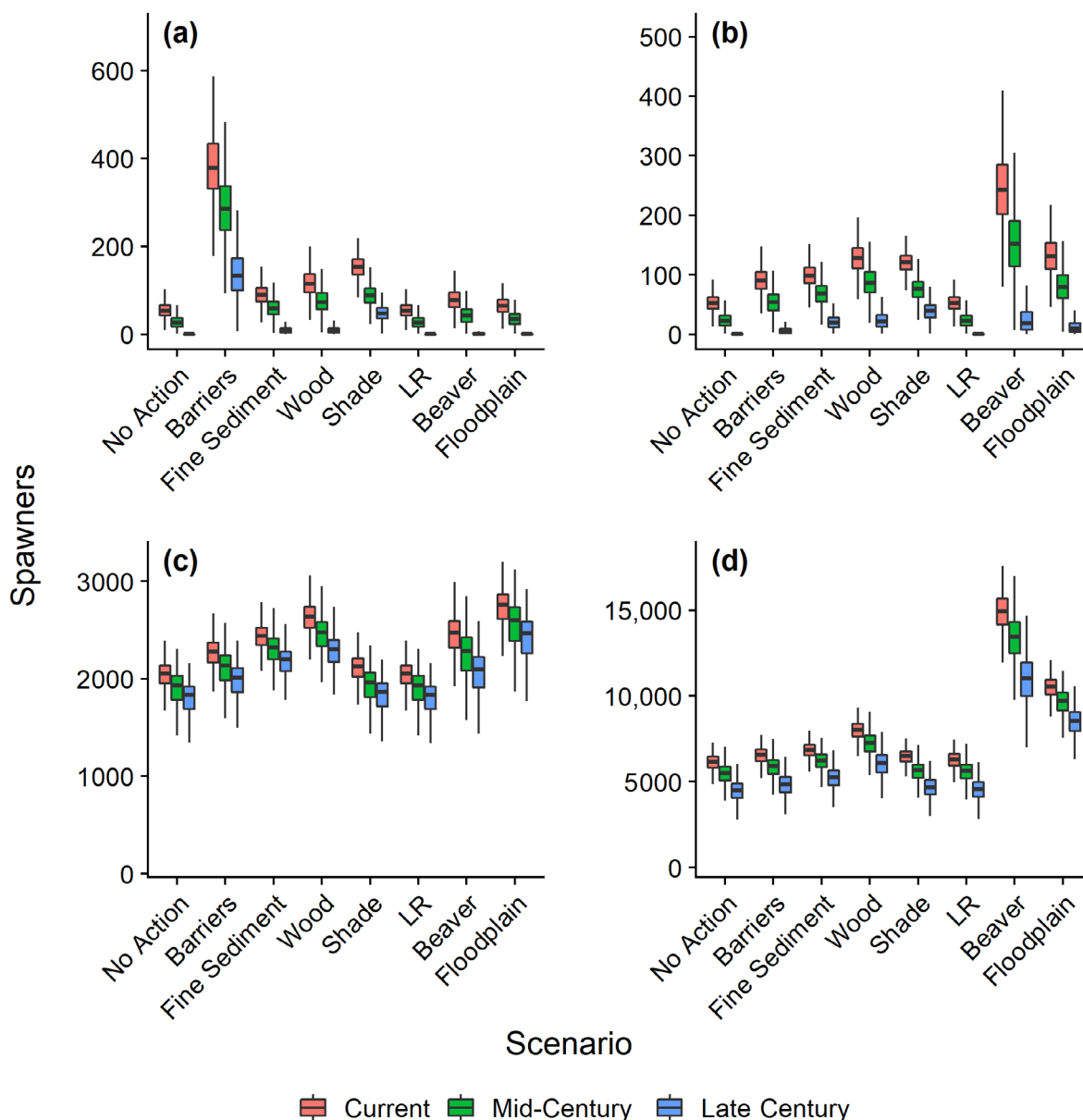
FIGURE 7 Effect of modeled restoration actions and scenarios on spawner abundance for coho salmon in four example subbasins under current climate, projected mid-century climate, and projected late-century climate. Subbasins are (a) Dillenbaugh Creek, (b) Salzer Creek, (c) Mox Chehalis Creek, and (d) Wynoochee River. LR is large river restoration (bank armor removal). Note different *y*-axis scales for each subbasin.

important action types (wood augmentation, shade restoration, floodplain reconnection, and beaver pond restoration) over a large area but at a relatively lower intensity than for other species (Table 6). By contrast, spring-run Chinook may require a focus on fewer action types but at the highest intensity and over the smallest spatial extent. Fall-run Chinook and steelhead are responsive to the fewest action types over moderate to large spatial extents and with intermediate intensity compared with coho and spring-run Chinook.

Restoration potential for each action type also varies by subbasin, so some restoration actions that are less

important at the whole basin scale may have a large influence on resilience in some subbasins (e.g., barrier removal). Moreover, some of the most important action types at the basin scale will be less important in some subbasins because restoration potential is not uniformly high among subbasins (e.g., shade and floodplain habitat reconnection) (Beechie et al., 2021; Jorgensen et al., 2021). We also note that while the analysis suggests that reducing fine sediment to increase incubation survival may be important to each species, there is uncertainty in the fine sediment analysis that precludes identification of specific locations and causes of high fine sediment. Additional
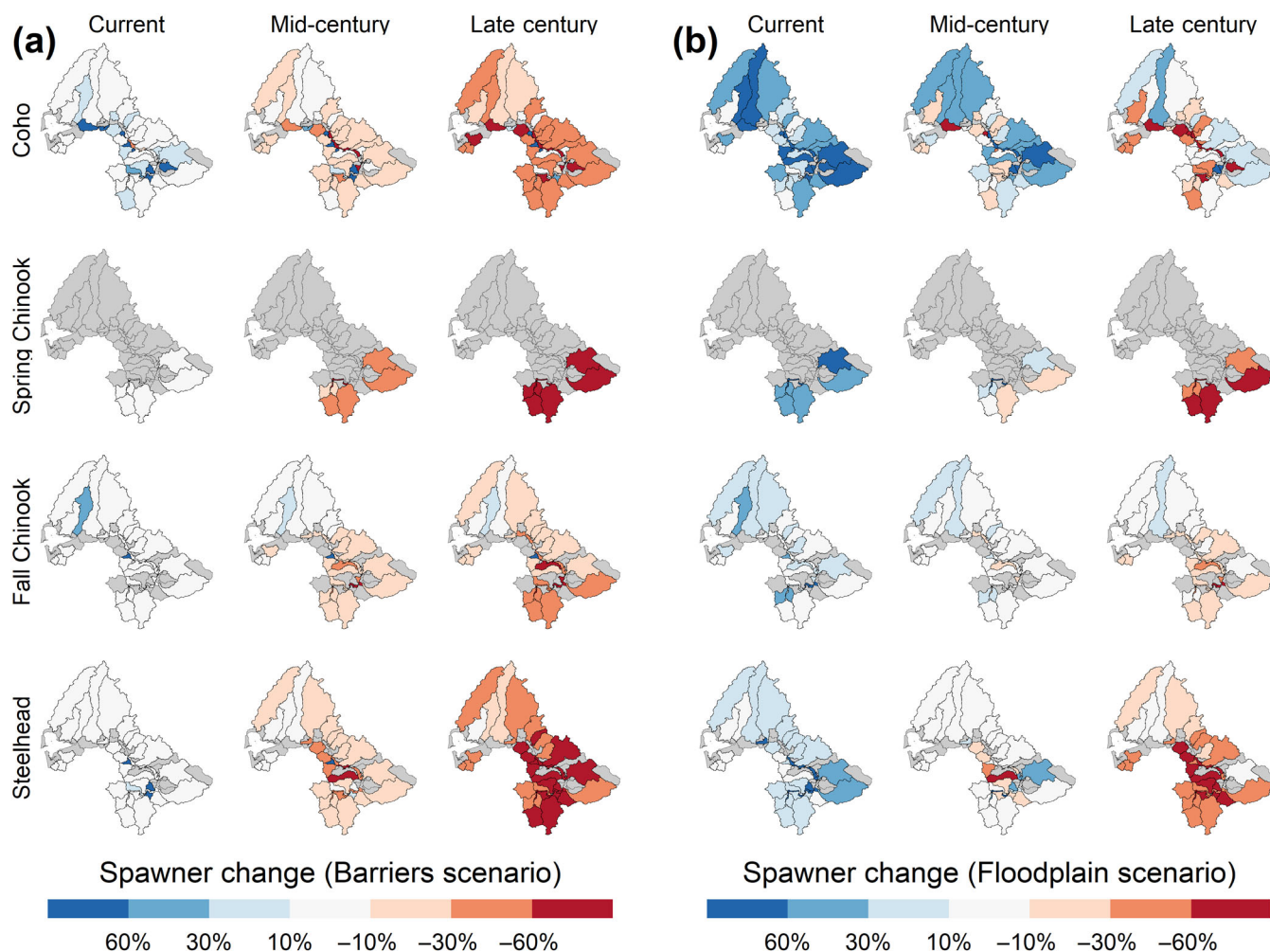
FIGURE 8 Restoration potential (first column) and resilience potentials (second and third columns) for (a) barrier removal and (b) floodplain reconnection for each species/run and time period. In each map, spawner change is percent difference between spawner abundance with restoration and current spawner abundance (no restoration, current climate). Increases indicate more spawners than at present, and declines indicate fewer spawners than at present. Gray subbasins indicate species not present.

inventory of fine sediment levels and sources is needed before we can confirm the degree of impairment or propose a restoration strategy (Beechie et al., 2021; Jorgensen et al., 2021).

These general model results for each species are likely transferable to other river basins in the region because they are closely linked to the species' life histories. However, our subbasin-scale results illustrate that the relative importance of restoration action types will vary among watersheds depending on the geophysical template that determines habitat potential, and the degree and spatial distribution of habitat degradation (Beechie et al., 2010). For example, the glacial history of the Chehalis basin created many wide, low-gradient valleys that favored formation of numerous floodplain marshes, ponds, and side channels (Beechie et al., 2021). This created localized areas of high floodplain restoration potential, but floodplain restoration potential is lower in narrow mountain valleys of

the basin. Similar geological patterns exist at a larger spatial scale across the Pacific Northwest, USA, so other river basins may not have the same degree of floodplain restoration potential as the Chehalis basin. Moreover, development may preclude floodplain restoration in some areas. Nonetheless, most rivers in the region have substantial river length with wide floodplains (Bond et al., 2019; Stefankiv et al., 2019), and floodplain reconnection is likely to be an important restoration action in many river basins.

Projected climate change impacts also vary across the region, with the largest increases in flood flows and largest decreases in low flows expected in mountain areas where spring snowpack will disappear (Tohver et al., 2014). Most of the Chehalis basin is low elevation and does not have spring snowpack (Mauger et al., 2016), so changes in flood and low flows may be smaller than in other basins with more high-elevation habitat. By contrast, basins with more
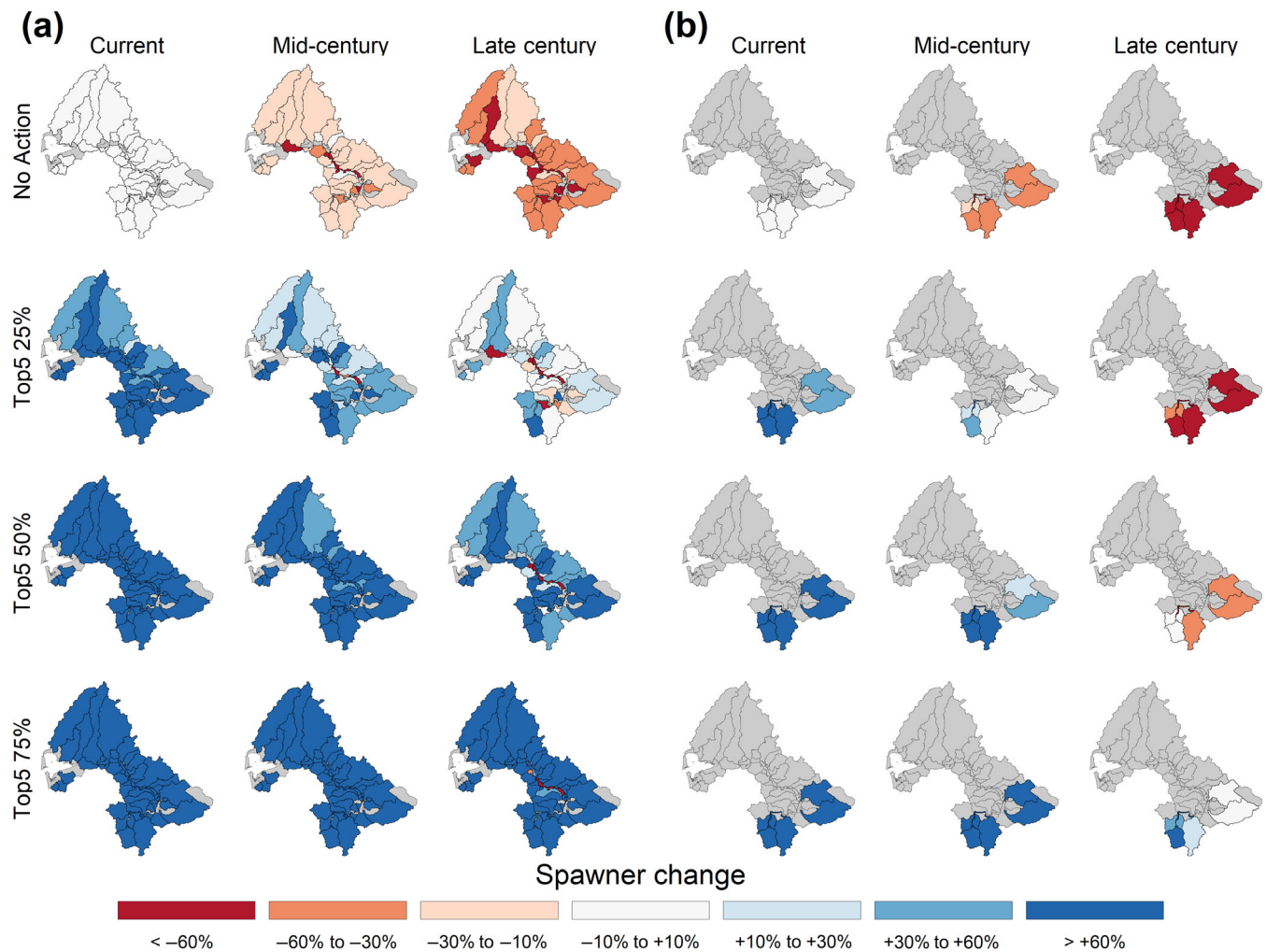
FIGURE 9 Resilience potential for varying levels of effort for the top five restoration actions for (a) coho salmon and (b) spring-run Chinook salmon in mid-century and late century. In each map, spawner change is percent difference in spawner abundance between each mid- or late-century restoration scenario and the no-action scenario under current climate conditions. Declines indicate that there are fewer mid- or late-century spawners than at present, and increases indicate more spawners than at present. Gray subbasins indicate species not present.

TABLE 6 Characteristics of restoration strategies that may help increase resilience for each species.

Species/run	Restoration actions	Spawning range	Relative intensity
Coho salmon	1. Wood augmentation 2. Shade restoration 3. Reconnect floodplain habitat 4. Restore beaver ponds	Large	Lowest
Spring-run Chinook	1. Wood augmentation 2. Shade restoration 3. Reconnect floodplain habitat	Small	Highest
Fall-run Chinook	1. Wood augmentation	Moderate	Lower
Steelhead	1. Wood augmentation	Large	Higher

high-elevation habitat have lower temperatures (Isaak et al., 2017), and salmonids will be less affected by temperature increases because temperatures are below critical

thresholds and may remain so into late century (Mantua et al., 2010; Wade et al., 2013). Therefore, other basins may have more intrinsic resilience to climate-related

temperature increases than the Chehalis basin, and restoration actions to reduce stream temperature may be less important.

Is it more important to increase capacity or productivity?

A question raised in the literature is whether increasing capacity or productivity is more likely to increase the abundance of salmon populations (Kareiva et al., 2000; Zabel et al., 2006) and therefore more likely to increase resilience to climate change (Timpane-Padgham et al., 2017). Not surprisingly, our analysis indicated that it depends on which life stages limit abundance for each species. We found that increasing habitat capacity to lessen density dependence is most important for coho salmon and to a lesser extent fall-run Chinook salmon. For coho salmon, both summer and winter rearing capacities have been substantially reduced, and increasing those capacities through restoration of wood, beaver ponds, and floodplain habitats may help improve resilience. For fall-run Chinook, increasing fry colonization capacity via wood augmentation increases population size by increasing the proportion of sub-yearling migrants, which have higher marine survival than fry migrants (Anderson & Topping, 2018; Jorgensen et al., 2021).

While our model identified only a few areas where a capacity-increasing action like barrier removal is most limiting, other studies in the Fraser River and Elwha River clearly show that a significant increase in capacity (Strategy 3) is necessary to substantially increase the abundance of salmon populations where a migration barrier blocks a significant amount of habitat (Pess et al., 2008, 2012, 2014). Numerous similar barriers exist in Puget Sound (Beechie et al., 2006), the Willamette Valley (Sheer & Steel, 2006), the Columbia River basin (Johnson et al., 2019), and the Central Valley (Herbold et al., 2018; McEwan, 2001). In these and other locations, barrier removal or passage modifications to increase capacity may be important to increasing salmon population resilience.

Other studies suggest that increasing productivity in some life stages is more important, particularly when the population is well below capacity (Kareiva et al., 2000). Our results suggest that this may be true for spring-run Chinook and steelhead, for which both the incremental change and maximum potential change tend to be highest for life stage productivities. However, this assumes that the carrying capacity of these populations has not also been reduced by loss of marine-derived nutrients (salmon eggs and carcasses) or by spawners using a reduced portion of their potential range, both of which can create a carrying capacity limitation even at population sizes far below historical levels (Achord et al., 2003; Atlas et al., 2015; Bal et al., 2018; Walters, Copeland, & Venditti, 2013).

Ultimately, identifying whether it is more important to increase productivity or capacity may only matter when an obvious constraint on a life stage capacity or survival can be identified, such as a migration barrier reducing habitat capacity. Moreover, many restoration actions affect capacity and survival for multiple life stages (Jorgensen et al., 2021) and disentangling the importance of capacity versus productivity may be academic. Rather, identifying the most effective action types is more important for restoration planning. This points to the importance of analyses across the full life cycle of species (Crozier et al., 2021; Radchuk et al., 2013) and the need to understand which habitat factors constrain abundance in order to effectively target restoration actions and increase climate change resilience (Battin et al., 2007; Honea et al., 2016; Scheuerell et al., 2006).

Restoration to ameliorate climate change effects

Ameliorating a climate change effect appeared to be an effective strategy only at smaller scales where the restoration opportunity to ameliorate an effect was widespread. We found this situation to be rare for subpopulations in the Chehalis River basin. However, when this situation occurs, there are two potential means of ameliorating a climate change effect: (1) reducing the habitat change itself, and (2) restoring habitat diversity and refuges that allow fish to avoid exposure to the climate change effect (Battin et al., 2007; Beechie et al., 2013; Ebersole et al., 2020; Moritz & Agudo, 2013; Waldman et al., 2016). Restoration actions that can reduce climate change effects include restoring riparian shade and floodplain connectivity to reduce stream temperature (Fogel et al., 2022; Justice et al., 2017; Seedang et al., 2008; Steel et al., 2017), floodplain reconnection to reduce flood flows (Sholtes & Doyle, 2011), and reducing water withdrawals or increasing irrigation efficiency to increase summer low flows (Poff et al., 2010; Walters, Bartz, & Mcclure, 2013). Restoration actions that allow fish to avoid climate change effects include actions such as creating off-channel habitats in which fish can avoid flood flows (Nicol et al., 2022; Waples et al., 2009), or creating thermal refuges that fish can occupy to escape high stream temperatures (Battin et al., 2007; Kurylyk et al., 2015; Torgersen et al., 2012).

Where shade conditions are currently poor and stream temperatures are high, restoring riparian shade

reduces stream temperature and temperature reduction may exceed anticipated climate change increases in some reaches (Battin et al., 2007; Fogel et al., 2022; Justice et al., 2017). This is especially true in small streams where even young trees can provide significant shade (Fogel et al., 2022; Seixas et al., 2018). Restoring floodplain connectivity can also reduce average summer stream temperatures (Arrigoni et al., 2008; Fogel et al., 2022; Seedang et al., 2008), although restoring connectivity also creates cool-water refuges in side channels or alcoves (Fernald et al., 2006). There is also evidence that using artificial beaver dams or wood jams to re-aggrade incised channels may increase subsurface water storage and ultimately reduce summer stream temperatures (Weber et al., 2017).

For flood flow increases, several studies show that restoring floodplain connectivity can increase flood water storage and reduce downstream flood peaks (Jacobson et al., 2015; Sholtes & Doyle, 2011). Studies for portions of the Chehalis basin also show that floodplain reconnection in the upper Chehalis and Newaukum Rivers might decrease flood peaks by 3%–16% depending on tributary and flood recurrence interval (Abbe et al., 2016, 2020), which is generally half or less of the projected climate change increase. Moreover, off-channel habitats such as alcoves and wetlands afford fish an escape from high-velocity flood flows (Bell et al., 2001; Waples et al., 2009), and such habitats also increase growth and survival throughout winter rearing for a variety of species (Nickelson et al., 1992; Ogston et al., 2015; Sommer et al., 2001). Low flow decreases can be mitigated where water withdrawals can be reduced, or where increased water storage via beaver dams or beaver dam analogs is possible (Kendy et al., 2018; Weber et al., 2017).

Importance of climate refuges

Cold-water refuges for salmon are important both for avoiding harmful temperatures and regulating metabolism (Armstrong & Schindler, 2013; Berman & Quinn, 1991; Brett, 1971). Where temperatures are high but not lethal, salmon metabolism increases and food consumption must increase to sustain positive growth rates (Brett, 1971; Wurtsbaugh & Davis, 1977). However, cool-water refuges may help sustain growth with lower food resources when fish can access cooler water when not feeding (Brett, 1971). Where temperatures are very cold, fish may increase growth by feeding on high-energy food in cold water and then moving to warmer water to increase the efficiency of digestion (Armstrong & Schindler, 2013). At the basin scale, maintaining or restoring longitudinal connectivity to cooler upper

reaches is also important for supporting species and life history diversity (Waples et al., 2009), and long (2.7–13 km) thermal refuges occurring in rivers throughout the west may help salmonids survive warmer summers (Fullerton et al., 2018). However, it is also important to recognize that warmer reaches also have conservation value, as reaches that are too warm in summer may provide significant growth opportunities during other seasons (Armstrong et al., 2021).

Important reach-scale thermal refuges in the Chehalis basin are at higher elevations where temperatures are relatively low in the summer, and projected increases in summer temperature of 2–3°C or more may have relatively little effect on capacity or survival of temperature-sensitive life stages. These higher elevation refuges are concentrated in the Olympic Mountains, and to a lesser degree in the Cascade Foothills and Willapa Hills (Winkowski & Zimmerman, 2018). Reach-scale groundwater-driven thermal refuges are found in the East Fork Satsop River and South Fork Newaukum River (Aquatic Species Restoration Plan Steering Committee, 2019; Winkowski & Zimmerman, 2018). Site-scale thermal refuges have been identified in portions of the mainstem by a variety of methods, including forward-looking infrared radar (FLIR) (Vonada, 2018), in situ temperature measurements (Liedtke et al., 2016, 2017), and radio tracking of spring-run Chinook salmon adults (Liedtke et al., 2016). Each of these refuge types can contribute to resilience of salmon populations under a future climate (Daigle et al., 2015; Fullerton et al., 2018), and actions to preserve or restore them may be important to salmon recovery and persistence (Kurylyk et al., 2015; Torgersen et al., 2012).

CONCLUSIONS

We found that identifying which types of restoration actions are most likely to help increase resilience of salmon populations to climate change depends primarily on the relative importance of restoration action types to each species' recovery. Moreover, vulnerability of each species to climate change influences the level of restoration effort needed to increase resilience. Not surprisingly, there is greater potential for habitat restoration to increase climate change resilience for species that are less vulnerable and in locations with more refuges (e.g., coho salmon), and more effort is required for more vulnerable species with fewer refuges (e.g., spring Chinook salmon).

Our analysis suggests that targeting action types with the greatest restoration potential for each species can increase resilience to climate change. For example, targeting four key actions that are important for coho salmon (shade, wood, beaver ponds, and floodplain

habitat) at relatively low intensity across the basin may be sufficient to maintain or increase abundance in the future. By contrast, a much higher intensity of restoration is required for spring-run Chinook, although there are fewer important action types (shade, wood, and flood-plain habitat) and the spring-run Chinook range is much smaller than the ranges of other species in the basin. Steelhead are widespread in the basin but respond to very few restoration action types, and a larger restoration effort on fewer action types may prove more advantageous.

These results are relevant to salmon habitat restoration planning in most watersheds in the region because the most important actions for each species depend on their life histories and habitat needs, which are similar from watershed to watershed. However, the relative rank of each restoration action type may vary across watersheds as a function of the geophysical template that determines natural habitat potential, as well as the spatial distribution of habitat impairments. A habitat-based model such as the HARP model is well suited to identifying the most important habitat actions in multiple watersheds because the model functions are transferable, and running the model in new locations primarily requires collection of watershed-specific habitat data.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Model code and supporting data (Beechie et al., 2022) are available from Zenodo: https://zenodo.org/record/7098248#.YypF-ezMJpQ. Additional supporting data and model application summaries are available at https://www.fisheries.noaa.gov/resource/tool-app/habitat-assessment-and-restoration-planning-harp-model.

ORCID

Timothy J. Beechie https://orcid.org/0000-0003-2029-0669

Peter Kiffney https://orcid.org/0000-0003-0863-0085

REFERENCES

Abbe, T. B., B. Anderson, C. Carlstad, D. L. Devier, K. L. Fetherston, S. Dickerson-Lange, L. Embertson, et al. 2016. *Preliminary Scientific and Technical Assessment of a Restorative Flood Protection Approach for the Upper Chehalis River Watershed*. Draft Report. Seattle, WA: Natural Systems Design.

Abbe, T. B., C. Carlstad, D. L. Devier, S. Dickerson-Lange, J. Jay, M. Nelson, L. Embertson, S. Higgins, B. Keller, and K. L. Fetherston. 2020. *Chehalis Basin Strategy Restorative Flood Protection Advanced Feasibility Evaluation for the North and South Forks of the Newaukum River, Washington*. Seattle, WA: Natural Systems Design.

Achord, S., P. S. Levin, and R. W. Zabel. 2003. "Density-Dependent Mortality in Pacific Salmon: The Ghost of Impacts Past?" *Ecology Letters* 6: 335–42.

Anderson, J. H., and P. C. Topping. 2018. "Juvenile Life History Diversity and Freshwater Productivity of Chinook Salmon in the Green River, Washington." *North American Journal of Fisheries Management* 38: 180–93.

Aquatic Species Restoration Plan Steering Committee. 2019. *Chehalis Basin Strategy: Aquatic Species Restoration Plan*. Publication #19-06-009. Olympia, WA: Office of the Chehalis Basin.

Armstrong, J. B., A. H. Fullerton, C. E. Jordan, J. L. Ebersole, J. R. Bellmore, I. Arismendi, B. E. Penaluna, and G. H. Reeves. 2021. "The Importance of Warm Habitat to the Growth Regime of Cold-Water Fishes." *Nature Climate Change* 11: 1–8.

Armstrong, J. B., and D. E. Schindler. 2013. "Going with the Flow: Spatial Distributions of Juvenile Coho Salmon Track an Annually Shifting Mosaic of Water Temperature." *Ecosystems* 16: 1429–41.

Arrigoni, A. S., G. C. Poole, L. A. K. Mertes, S. J. O'Daniel, W. W. Woessner, and S. A. Thomas. 2008. "Buffered, Lagged, or Cooled? Disentangling Hyporheic Influences on Temperature Cycles in Stream Channels." *Water Resources Research* 44: W0948.

Atlas, W. I., T. W. Buehrens, D. J. F. McCubbing, R. Bison, and J. W. Moore. 2015. "Implications of Spatial Contraction for Density Dependence and Conservation in a Depressed Population of Anadromous Fish." *Canadian Journal of Fisheries and Aquatic Sciences* 72: 1682–93.

Bal, G., M. D. Scheuerell, and E. J. Ward. 2018. "Characterizing the Strength of Density Dependence in at-Risk Species through Bayesian Model Averaging." *Ecological Modelling* 381: 1–9.

Battin, J., M. W. Wiley, M. H. Ruckelshaus, R. N. Palmer, E. Korb, K. K. Bartz, and H. Imaki. 2007. "Projected Impacts of Climate Change on Salmon Habitat Restoration." *Proceedings of the National Academy of Sciences* 104: 6720–5.

Beamer, E., and R. Henderson. 1998. *Juvenile Salmonid Use of Natural and Hydromodified Stream Bank Habitat in the Mainstem Skagit River, Northwest Washington.* La Conner, WA: Skagit River System Cooperative.

Beechie, T., E. Buhle, M. Ruckelshaus, A. Fullerton, and L. Holsinger. 2006. "Hydrologic Regime and the Conservation of Salmon Life History Diversity." *Biological Conservation* 130: 560–72.

Beechie, T., H. Imaki, J. Greene, A. Wade, H. Wu, G. Pess, P. Roni, et al. 2013. "Restoring Salmon Habitat for a Changing Climate." *River Research and Applications* 29: 939–60.

Beechie, T. J., C. Fogel, C. Nicol, J. Jorgensen, B. Timpane-Padgham, and P. Kiffney. 2022. "How Does Habitat Restoration Influence Resilience of Salmon Populations to Climate Change?" https://zenodo.org/record/7098248.

Beechie, T. J., C. Fogel, C. Nicol, and B. Timpane-Padgham. 2021. "A Process-Based Assessment of Landscape Change and Salmon Habitat Losses in the Chehalis River Basin, USA." *PLoS One* 16: e0258251.

Beechie, T. J., G. Pess, P. Kennard, R. E. Bilby, and S. Bolton. 2000. "Modeling Recovery Rates and Pathways for Woody Debris Recruitment in Northwestern Washington Streams." *North American Journal of Fisheries Management* 20: 436–52.

Beechie, T. J., D. A. Sear, J. D. Olden, G. R. Pess, J. M. Buffington, H. Moir, P. Roni, and M. M. Pollock. 2010. "Process-Based Principles for Restoring River Ecosystems." *BioScience* 60: 209–22.

Bell, E., W. G. Duffy, and T. D. Roelofs. 2001. "Fidelity and Survival of Juvenile Coho Salmon in Response to a Flood." *Transactions of the American Fisheries Society* 130: 450–8.

Berman, C. H., and T. P. Quinn. 1991. "Behavioural Thermoregulation and Homing by Spring Chinook Salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River." *Journal of Fish Biology* 39: 301–12.

Bisson, P. A., K. Sullivan, and J. L. Nielsen. 1988. "Channel Hydraulics, Habitat Use, and Body Form of Juvenile Coho Salmon, Steelhead, and Cutthroat Trout in Streams." *Transactions of the American Fisheries Society* 117: 262–73.

Bond, M. H., T. G. Nodine, T. J. Beechie, and R. W. Zabel. 2019. "Estimating the Benefits of Widespread Floodplain Reconnection for Columbia River Chinook Salmon." *Canadian Journal of Fisheries and Aquatic Sciences* 76: 1212–26.

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: 99–113.

Crozier, L. G., B. J. Burke, B. E. Chasco, D. L. Widener, and R. W. Zabel. 2021. "Climate Change Threatens Chinook Salmon Throughout Their Life Cycle." *Communications Biology* 4: 1–14.

Daigle, A., D. I. Jeong, and M. F. Lapointe. 2015. "Climate Change and Resilience of Tributary Thermal Refugia for Salmonids in Eastern Canadian Rivers." *Hydrological Sciences Journal* 60: 1044–63.

Davies, P. M. 2010. "Climate Change Implications for River Restoration in Global Biodiversity Hotspots." *Restoration Ecology* 18: 261–8.

Dunwiddie, P. W., S. A. Hall, M. W. Ingraham, J. D. Bakker, K. S. Nelson, R. Fuller, and E. Gray. 2009. "Rethinking Conservation Practice in Light of Climate Change." *Ecological Restoration* 27: 320–9.

Ebersole, J. L., R. M. Quiñones, S. Clements, and B. H. Letcher. 2020. "Managing Climate Refugia for Freshwater Fishes under an Expanding Human Footprint." *Frontiers in Ecology and the Environment* 18: 271–80.

Fernald, A. G., D. H. Landers, and P. J. Wigington. 2006. "Water Quality Changes in Hyporheic Flow Paths between a Large Gravel Bed River and Off-Channel Alcoves in Oregon, USA." *River Research and Applications* 22: 1111–24.

Fogel, C. B., C. L. Nicol, J. C. Jorgensen, T. J. Beechie, B. Timpane-Padgham, P. Kiffney, G. Seixas, and J. Winkowski. 2022. "How Riparian and Floodplain Restoration Modify the Effects of Increasing Temperature on Adult Salmon Spawner Abundance in the Chehalis River, WA." *PLoS One* 17: e0268813.

Franklin, J. F., and C. T. Dyrness. 1973. *Natural Vegetation of Oregon and Washington.* General Technical Report PNW-8. Portland, OR: U.S.D.A. Forest Service.

Fullerton, A. H., C. E. Torgersen, J. J. Lawler, E. A. Steel, J. L. Ebersole, and S. Y. Lee. 2018. "Longitudinal Thermal Heterogeneity in Rivers and Refugia for Coldwater Species: Effects of Scale and Climate Change." *Aquatic Sciences* 80: 1–15.

Greene, C. M., and T. J. Beechie. 2004. "Consequences of Potential Density-Dependent Mechanisms on Recovery of Ocean-Type Chinook Salmon (*Oncorhynchus tshawytscha*)." *Canadian Journal of Fisheries and Aquatic Sciences* 61: 590–602.

Grier, J. W. 1982. "Ban of DDT and Subsequent Recovery of Reproduction in Bald Eagles." *Science* 218: 1232–5.

Herbold, B., S. M. Carlson, R. Henery, R. C. Johnson, N. Mantua, M. McClure, P. B. Moyle, and T. Sommer. 2018. "Managing for Salmon Resilience in California's Variable and Changing Climate." *San Francisco Estuary and Watershed Science* 16: 3.

Hinrichsen, R. A., and C. M. Paulsen. 2020. "Low Carrying Capacity a Risk for Threatened Chinook Salmon." *Ecological Modelling* 432: 109223.

Holling, C. S. 1973. "Resilience and Stability of Ecological Systems." *Annual Review of Ecology and Systematics* 4: 1–23.

Holmes, E. E., E. J. Ward, and K. Wills. 2012. "MARSS: Multivariate Autoregressive State-Space Models for Analyzing Time-Series Data." *The R Journal* 4: 11–9. https://journal.r-project.org/articles/RJ-2012-002/.

Holmes, E. E., E. J. Ward, and K. Wills. 2020. "MARSS: Multivariate Autoregressive State-Space Modeling." R Package Version 3.11.1.

Honea, J. M., J. C. Jorgensen, M. M. McClure, T. D. Cooney, K. Engie, D. M. Holzer, and R. Hilborn. 2009. "Evaluating Habitat Effects on Population Status: Influence of Habitat Restoration on Spring-Run Chinook Salmon." *Freshwater Biology* 54: 1576–92.

Honea, J. M., M. M. McClure, J. C. Jorgensen, and M. D. Scheuerell. 2016. "Assessing Freshwater Life-Stage Vulnerability of an Endangered Chinook Salmon Population to Climate Change Influences on Stream Habitat." *Climate Research* 71: 127–37.

IPCC. 2007. *Climate Change 2007: Synthesis Report*. Geneva: IPCC.

Isaak, D. J., S. J. Wenger, E. E. Peterson, J. M. V. Hoef, D. E. Nagel, C. H. Luce, S. W. Hostetler, et al. 2017. "The NorWeST Summer Stream Temperature Model and Scenarios for the Western U.S.: 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: 9181–205.

Jacobson, R. B., G. Lindner, and C. Bitner. 2015. "The Role of Floodplain Restoration in Mitigating Flood Risk, Lower Missouri River, USA." In *Geomorphic Approaches to Integrated Floodplain Management of Lowland Fluvial Systems in North America and Europe*, edited by P. F. Hudson and H. Middelkoop, 203–43. New York, NY: Springer.

Jensen, D. W., E. A. Steel, A. H. Fullerton, and G. R. Pess. 2009. "Impact of Fine Sediment on Egg-to-Fry Survival of Pacific Salmon: A Meta-Analysis of Published Studies." *Reviews in Fisheries Science* 17: 348–59.

Johnson, B. M., M. S. Johnson, and G. H. Thorgaard. 2019. "Salmon Genetics and Management in the Columbia River Basin." *Northwest Science* 92: 346–63.

Johnson, S., J. D. Rodgers, and M. Solazzi. 1993. *Development and Evaluation of Techniques to Rehabilitate Oregon's Wild Salmonids*. Fish Research Project F-125-R-5, Annual Progress Report. Portland, OR: Oregon Department of Fish and Wildlife.

Jorgensen, J. C., C. Nicol, C. Fogel, and T. J. Beechie. 2021. "Identifying the Potential of Anadromous Salmonid Habitat Restoration with Life Cycle Models." *PLoS One* 16: e0256792.

Justice, C., S. M. White, D. A. McCullough, D. S. Graves, and M. R. Blanchard. 2017. "Can Stream and Riparian Restoration Offset Climate Change Impacts to Salmon Populations?" *Journal of Environmental Management* 188: 212–27.

Kareiva, P., M. Marvier, and M. McClure. 2000. "Recovery and Management Options for Spring/Summer Chinook Salmon in the Columbia River Basin." *Science* 290: 977–9.

Kautz, R., R. Kawula, T. Hoctor, J. Comiskey, D. Jansen, D. Jennings, J. Kasbohm, et al. 2006. "How Much Is Enough? Landscape-Scale Conservation for the Florida Panther." *Biological Conservation* 130: 118–33.

Kendy, E., B. Aylward, L. S. Ziemer, B. D. Richter, B. G. Colby, T. E. Grantham, L. Sanchez, et al. 2018. "Water Transactions for Streamflow Restoration, Water Supply Reliability, and Rural Economic Vitality in the Western United States." *JAWRA Journal of the American Water Resources Association* 54: 487–504.

Kerr, J. T., and I. Deguise. 2004. "Habitat Loss and the Limits to Endangered Species Recovery." *Ecology Letters* 7: 1163–9.

Kurylyk, B. L., K. T. B. MacQuarrie, T. Linnansaari, R. A. Cunjak, and R. A. Curry. 2015. "Preserving, Augmenting, and Creating Cold-Water Thermal Refugia in Rivers: Concepts Derived from Research on the Miramichi River, New Brunswick (Canada)." *Ecohydrology* 8: 1095–108.

Lichatowich, J., L. Mobrand, L. Lestelle, and T. Vogel. 1995. "An Approach to the Diagnosis and Treatment of Depleted Pacific Salmon Populations in Pacific Northwest Watersheds." *Fisheries* 20: 10–8.

Liedtke, T. L., W. R. Hurst, R. G. Tomka, T. J. Kock, and M. S. Zimmerman. 2017. *Preliminary Evaluation of the Behavior and Movements of Adult Spring Chinook Salmon in the Chehalis River, Southwestern Washington, 2014*. USGS Open-File Report 2017-1004. Reston, VA: U.S. Geological Survey.

Liedtke, T. L., M. S. Zimmerman, R. G. Tomka, C. Holt, and L. Jennings. 2016. *Behavior and Movements of Adult Spring Chinook Salmon (Oncorhynchus tshawytscha) in the Chehalis River Basin, Southwestern Washington, 2015*. USGS Open-File Report 2016-1158. Reston, VA: U.S. Geological Survey.

Mantua, N., I. Tohver, and A. Hamlet. 2010. "Climate Change Impacts on Streamflow Extremes and Summertime Stream Temperature and Their Possible Consequences for Freshwater Salmon Habitat in Washington State." *Climatic Change* 102: 187–223.

Mauger, G., S. Y. Lee, C. Bandaragoda, Y. Serra, and J. Won. 2016. *Effect of Climate Change on the Hydrology of the Chehalis Basin*. Seattle, WA: Climate Impacts Group, University of Washington.

McEwan, D. R. 2001. "Central Valley Steelhead." *Fish Bulletin* 179: 1–43.

Moritz, C., and R. Agudo. 2013. "The Future of Species under Climate Change: Resilience or Decline?" *Science* 341: 504–8.

Moussalli, E., and R. Hilborn. 1986. "Optimal Stock Size and Harvest Rate in Multistage Life History Models." *Canadian Journal of Fisheries and Aquatic Sciences* 43: 135–41.

Nickelson, T. E. 1998. *A Habitat-Based Assessment of Coho Salmon Production Potential and Spawner Escapement Needs for Oregon Coastal Streams*, 17 pp. Information Reports Number 98-4. Portland, OR: Oregon Department of Fish and Wildlife.

Nickelson, T. E., and P. W. Lawson. 1998. "Population Viability of Coho Salmon, *Oncorhynchus kisutch*, in Oregon Coastal Basins: Application of a Habitat-Based Life Cycle Model." *Canadian Journal of Fisheries and Aquatic Sciences* 55: 2383–92.

Nickelson, T. E., M. F. Solazzi, S. L. Johnson, and J. D. Rodgers. 1992. "Effectiveness of Selected Stream Improvement Techniques to Create Suitable Summer and Winter Rearing Habitat for Juvenile Coho Salmon (*Oncorhynchus kisutch*) in Oregon Coastal Streams." *Canadian Journal of Fisheries and Aquatic Sciences* 49: 790–4.

Nicol, C. L., J. C. Jorgensen, C. B. Fogel, B. Timpane-Padgham, and T. J. Beechie. 2022. "Spatially Overlapping Salmon Species Have Varied Population Response to Early Life History Mortality from Increased Peak Flows." *Canadian Journal of Fisheries and Aquatic Sciences* 79: 342–51.

Ogston, L., S. Gidora, M. Foy, and J. Rosenfeld. 2015. "Watershed-Scale Effectiveness of Floodplain Habitat Restoration for Juvenile Coho Salmon in the Chilliwack River, British Columbia." *Canadian Journal of Fisheries and Aquatic Sciences* 72: 479–90.

Pess, G. R., R. Hilborn, K. Kloehn, and T. P. Quinn. 2012. "The Influence of Population Dynamics and Environmental Conditions on Pink Salmon (*Oncorhynchus gorbuscha*) Recolonization after Barrier Removal in the Fraser River, British Columbia, Canada." *Canadian Journal of Fisheries and Aquatic Sciences* 69: 970–82.

Pess, G. R., M. L. McHenry, T. J. Beechie, and J. Davies. 2008. "Biological Impacts of the Elwha River Dams and Potential

Salmonid Responses to Dam Removal." *Northwest Science* 82: 72–90.

Pess, G. R., T. P. Quinn, S. R. Gephard, and R. Saunders. 2014. "Re-Colonization of Atlantic and Pacific Rivers by Anadromous Fishes: Linkages between Life History and the Benefits of Barrier Removal." *Reviews in Fish Biology and Fisheries* 24: 881–900.

Poff, N. L., B. D. Richter, A. H. Arthington, S. E. Bunn, R. J. Naiman, E. Kendy, M. Acreman, et al. 2010. "The Ecological Limits of Hydrologic Alteration (ELOHA): A New Framework for Developing Regional Environmental Flow Standards." *Freshwater Biology* 55: 147–70.

Pollock, M. M., G. R. Pess, T. J. Beechie, and D. R. Montgomery. 2004. "The Importance of Beaver Ponds to Coho Salmon Production in the Stillaguamish River Basin, Washington, USA." *North American Journal of Fisheries Management* 24: 749–60.

PRISM Climate Group. 2019. *PRISM Climate Data.* Corvallis, OR: Oregon State University.

Radchuk, V., C. Turlure, and N. Schtickzelle. 2013. "Each Life Stage Matters: The Importance of Assessing the Response to Climate Change over the Complete Life Cycle in Butterflies." *Journal of Animal Ecology* 82: 275–85.

Scheuerell, M. D., R. Hilborn, M. H. Ruckelshaus, K. K. Bartz, K. M. Lagueux, A. D. Haas, and K. Rawson. 2006. "The Shiraz Model: A Tool for Incorporating Anthropogenic Effects and Fish–Habitat Relationships in Conservation Planning." *Canadian Journal of Fisheries and Aquatic Sciences* 63: 1596–607.

Seedang, S., A. G. Fernald, R. M. Adams, and D. H. Landers. 2008. "Economic Analysis of Water Temperature Reduction Practices in a Large River Floodplain: An Exploratory Study of the Willamette River, Oregon." *River Research and Applications* 24: 941–59.

Seixas, G. B., T. J. Beechie, C. Fogel, and P. M. Kiffney. 2018. "Historical and Future Stream Temperature Change Predicted by a Lidar-Based Assessment of Riparian Condition and Channel Width." *Journal of the American Water Resources Association* 54: 974–91.

Sheer, M. B., and E. A. Steel. 2006. "Lost Watersheds: Barriers, Aquatic Habitat Connectivity, and Salmon Persistence in the Willamette and Lower Columbia River Basins." *Transactions of the American Fisheries Society* 135: 1654–69.

Sholtes, J. S., and M. W. Doyle. 2011. "Effect of Channel Restoration on Flood Wave Attenuation." *Journal of Hydraulic Engineering* 137: 196–208.

Sommer, T. R., M. L. Nobriga, W. C. Harrell, W. Batham, and W. J. Kimmerer. 2001. "Floodplain Rearing of Juvenile Chinook Salmon: Evidence of Enhanced Growth and Survival." *Canadian Journal of Fisheries and Aquatic Sciences* 58: 325–33.

Steel, E. A., T. J. Beechie, C. E. Torgersen, and A. H. Fullerton. 2017. "Envisioning, Quantifying, and Managing Thermal Regimes on River Networks." *BioScience* 67: 506–22.

Stefankiv, O., T. J. Beechie, J. E. Hall, G. R. Pess, and B. Timpane-Padgham. 2019. "Influences of Valley Form and Land Use on Large River and Floodplain Habitats in Puget Sound." *River Research and Applications* 35: 133–45.

Taylor, K. E., R. J. Stouffer, and G. A. Meehl. 2012. "An Overview of CMIP5 and the Experiment Design." *Bulletin of the American Meteorological Society* 93: 485–98.

Timpane-Padgham, B. L., T. Beechie, and T. Klinger. 2017. "A Systematic Review of Ecological Attributes That Confer Resilience to Climate Change in Environmental Restoration." *PLoS One* 12: e0173812.

Tohver, I. M., A. F. Hamlet, and S.-Y. Lee. 2014. "Impacts of 21st-Century Climate Change on Hydrologic Extremes in the Pacific Northwest Region of North America." *Journal of the American Water Resources Association* 50: 1461–76.

Torgersen, C. E., J. L. Ebersole, and D. M. Keenan. 2012. *Primer for Identifying Cold-Water Refuges to Protect and Restore Thermal Diversity in Riverine Landscapes.* EPA 910-C-12-001. Seattle, WA: U.S. Environmental Protection Agency.

Vonada, W. 2018. "Assessing Spatiotemporal Stream Temperature Trends and Drivers through Integrated Longitudinal Thermal Profiling and Stationary Data Logger Methodology on the Upper Chehalis River, WA." MS thesis, Portland State University.

Wade, A. A., T. J. Beechie, E. Fleishman, N. J. Mantua, H. Wu, J. S. Kimball, D. M. Stoms, and J. A. Stanford. 2013. "Steelhead Vulnerability to Climate Change in the Pacific Northwest." *Journal of Applied Ecology* 50: 1093–104.

Waldman, J., K. A. Wilson, M. Mather, and N. P. Snyder. 2016. "A Resilience Approach Can Improve Anadromous Fish Restoration." *Fisheries* 41: 116–26.

Walker, B., C. S. Holling, S. R. Carpenter, and A. Kinzig. 2004. "Resilience, Adaptability and Transformability in Social–Ecological Systems." *Ecology and Society* 9: 5.

Walters, A. W., K. K. Bartz, and M. M. Mcclure. 2013. "Interactive Effects of Water Diversion and Climate Change for Juvenile Chinook Salmon in the Lemhi River Basin (U.S.A.)." *Conservation Biology* 27: 1179–89.

Walters, A. W., T. Copeland, and D. A. Venditti. 2013. "The Density Dilemma: Limitations on Juvenile Production in Threatened Salmon Populations." *Ecology of Freshwater Fish* 22: 508–19.

Waples, R., T. Beechie, and G. Pess. 2009. "Evolutionary History, Habitat Disturbance Regimes, and Anthropogenic Changes: What Do These Mean for Resilience of Pacific Salmon Populations?" *Ecology and Society* 14: art3.

Washington Department of Fish and Wildlife. 2019. *Fish Passage Inventory, Assessment, and Prioritization Manual*, 284 pp. Olympia, WA: Washington Department of Fish and Wildlife.

Watts, B. D., G. D. Therres, and M. A. Byrd. 2008. "Recovery of the Chesapeake Bay Bald Eagle Nesting Population." *The Journal of Wildlife Management* 72: 152–8.

Weber, N., N. Bouwes, M. M. Pollock, C. Volk, J. M. Wheaton, G. Wathen, J. Wirtz, and C. E. Jordan. 2017. "Alteration of Stream Temperature by Natural and Artificial Beaver Dams." *PLoS One* 12: e0176313.

Winkowski, J., and M. Zimmerman. 2018. *Thermally Suitable Habitat for Juvenile Salmonids and Resident Trout under Current and Climate Change Scenarios in the Chehalis River, WA.* Final Report. Olympia, WA: Washington Department of Fish and Wildlife.

Wurtsbaugh, W. A., and G. E. Davis. 1977. "Effects of Temperature and Ration Level on the Growth and Food Conversion Efficiency of Salmo Gairdneri, Richardson." *Journal of Fish Biology* 11: 87–98.

Zabel, R. W., M. D. Scheuerell, M. M. McClure, and J. G. Williams. 2006. "The Interplay between Climate Variability and Density

Dependence in the Population Viability of Chinook Salmon." *Conservation Biology* 20: 190–200.

Zimmerman, M. S., C. Kinsel, E. Beamer, E. J. Connor, and D. E. Pflug. 2015. "Abundance, Survival, and Life History Strategies of Juvenile Chinook Salmon in the Skagit River, Washington." *Transactions of the American Fisheries Society* 144: 627–41.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.