Projected impacts of climate change on salmon habitat restoration

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Throughout the world, efforts are under way to restore watersheds, but restoration planning rarely accounts for future climate change. Using a series of linked models of climate, land cover, hydrology, and salmon population dynamics, we investigated the impacts of climate change on the effectiveness of proposed habitat restoration efforts designed to recover depleted Chinook salmon populations in a Pacific Northwest river basin. Model results indicate a large negative impact of climate change on freshwater salmon habitat. Habitat restoration and protection can help to mitigate these effects and may allow populations to increase in the face of climate change. The habitat deterioration associated with climate change will, however, make salmon recovery targets much more difficult to attain. Because the negative impacts of climate change in this basin are projected to be most pronounced in relatively pristine, high-elevation streams where little restoration is possible, climate change and habitat restoration together are likely to cause a spatial shift in salmon abundance. River basins that span the current snow line appear especially vulnerable to climate change, and salmon recovery plans that enhance lower-elevation habitats are likely to be more successful over the next 50 years than those that target the higher-elevation basins likely to experience the greatest snow–rain transition.

Chinook salmon | hydrologic model | population model | Snohomish River | stream flow

Over the past decade, billions of dollars have been spent on the restoration of aquatic habitats throughout the United States (1). In the northwestern U.S., aquatic habitat restoration has been driven largely by the Endangered Species Act, under which several species of Pacific salmon have been listed. The listings have led to the development of salmon recovery plans for watersheds throughout the region. Long-term freshwater habitat protection and restoration projects are central to all plans. Planners rely heavily on fish habitat models to evaluate the potential effectiveness of proposed restoration strategies, and numerous models have been developed to predict restoration effects. In almost all cases, these models assume stationary future climate conditions when assessing how restoration will affect fish abundance and productivity. Given the increasing certainty that climate change is accelerating, models that ignore the potential effects of future climate may generate misleading predictions of the relative benefits of different recovery strategies.

The northwestern U.S. has warmed by between 0.7 and 0.9°C during the 20th century. Since 1950, average annual air temperatures at the majority of meteorological stations in the region have risen by ≈0.25°C/decade (2), and climate models predict another 1.5–3.2°C increase by the middle of the 21st century (3). Higher air temperatures are likely to increase water temperatures, which could be harmful to salmon during the spawning, incubation, and rearing stages of their life cycle (4). Warmer temperatures also lead to earlier snowmelt and to a lower proportion of precipitation falling as snow. In watersheds that receive a significant proportion of winter precipitation in the form of both rain and snow, the increased proportion of precipitation falling as rain can lead to elevated winter peak flows, which scour the streambed and destroy salmon eggs (5). Less snowpack results in lower flows in summer and fall, reducing the amount of available spawning habitat and further increasing water temperatures (3). Climate change also may alter rainfall patterns, but the historical record and model predictions are much more variable for rainfall than for air temperature (2, 3).

To investigate possible interactions between the impacts of climate change and habitat restoration, we modeled Chinook salmon (*Oncorhynchus tshawytscha*) population dynamics in the Snohomish River basin in western Washington State (Fig. 1) under a variety of future climate and habitat conditions. The Snohomish basin, which drains an area of ≈4,780 km^2, has been the subject of a collaborative planning effort involving local, state, tribal, citizen, and federal entities working together to develop a basin-wide salmonid recovery plan. The plan adopted for the basin is an ambitious combination of coarse-scale actions intended to protect and restore watershed hydrologic function (e.g., reforestation, reduction of impervious surface cover) and finer-scale actions designed to improve in-stream habitat conditions (e.g., reconnection of side channels, removal of dikes and culverts, restoration of natural bank conditions). We investigated the implications for Chinook salmon of the projections of two global climate models (GCMs), the Geophysical Fluid Dynamics Laboratory's GFDL R30 model (6) and the Hadley Center's HadCM3 model (7), at two future time periods: the decades centered on 2025 and 2050. The two models, both of which employed the A2 emissions scenario (8), were selected from seven GCMs on the basis of their ability to reproduce 20th century hydrologic conditions in the Puget Sound region (9). We examined the interaction between climate and restoration effects for three future (i.e., 2025) land-use scenarios: a scenario representing no change from current (2001) conditions ("current"), a scenario based on a linear future projection of current land-use change and population trends that includes the completion of current restoration projects but no further restoration ("moderate restoration"), and a scenario in which all restoration targets in the restoration plan are met ("full restoration").

Results

We used a sequence of linked models to translate broad-scale patterns of climate and land-use change into projections of habitat condition and salmon abundance (Fig. 2). To model the

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Abbreviations: DHSVM, Distributed Hydrology Soil Vegetation Model; GCM, global climate model.

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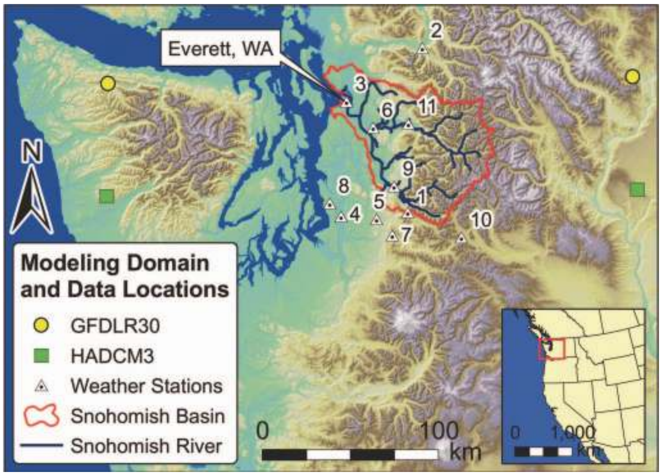

Fig. 1. Modeling domain and climate data locations. Numbers show the meteorological observation stations used to generate input data for the hydrologic model.

effects of climate and land-use change on water temperature and flow, we used a physically based hydrologic model that used spatially explicit land-cover data (the three land-use scenarios) and downscaled meteorological outputs from the two climate models as inputs. We then used the temperature and flow outputs from the hydrologic model, in conjunction with outputs from models of in-stream habitat capacity for salmon spawning and rearing, as inputs to a spatially explicit salmon life-cycle model.

Climate. We downscaled the predictions of each climate model to 11 locations in and surrounding the Snohomish basin. The two models exhibited similar increases in annual mean air temperature of 0.7 and 1.0°C for 2025 and 1.3 and 1.5°C for 2050 (Table 1). Projected changes in precipitation differed more between models, especially for 2050. The models also differed somewhat in the timing of temperature and precipitation changes [supporting information (SI) Figs. 6–9]. Because changes in precipitation frequency and intensity remain areas of great uncertainty in global climate modeling (10), the use of different precipitation scenarios provides insight into the extent to which uncertainty associated with climate modeling affected our results.

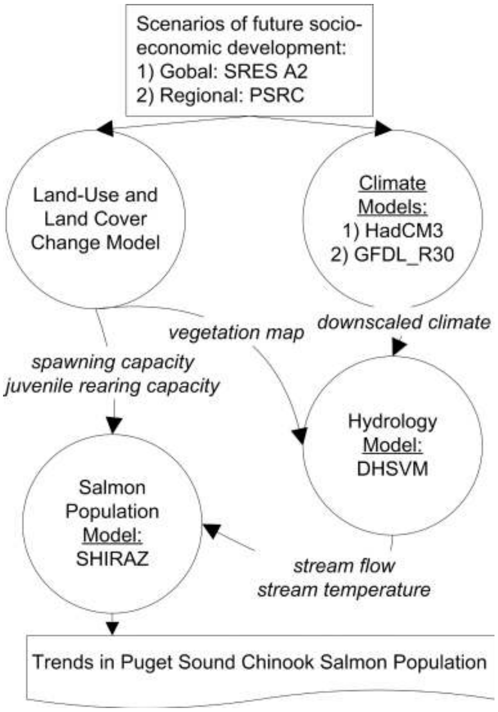

Fig. 2. Model linkage scheme.

Hydrology. Three of the hydrologic variables included in our modeling framework had meaningful effects on salmon population dynamics: peak flow during the egg incubation period (October 15–February 15), stream temperature during the prespawning period (August 15–September 15), and minimum flow during the spawning period (September 15–November 15). A fourth variable, temperature during the incubation period, did not affect survival. To isolate the effects of climate change on these hydrologic variables, we first applied the hydrologic model to the current land use scenario (i.e., land cover held constant) with climate model outputs for 2000, 2025, and 2050. Simulations based on both climate models projected basin-wide increases in incubation peak flows and prespawning temperatures and decreases in spawning flows (Table 2), all of which resulted largely from increased air temperatures causing more winter precipitation to fall as rain rather than snow. Differences between climate models in predicted precipitation and seasonal climate patterns caused large differences in resulting projections of water temperature and flow variables. Simulations based on the GFDL climate model resulted in larger projected changes in incubation peak flow but smaller changes in prespawning temperature and spawning flow than did the equivalent simulations based on the HadCM3 model. Modeled climate effects on both stream flow variables were greatest in the more easterly, higher-elevation subbasins, where the effects of warmer winter temperatures on snow accumulation are expected to be most pronounced (Fig. 3).

In contrast to the effects of climate, land-use change had little effect on basin-wide average values of any of the three important hydrologic variables (Table 2). With climate held constant at 2025 levels, neither incubation peak flow nor spawning low flow deviated by >4% from the current land use scenario under either alternative scenario, and prespawning water temperature differed by no more than 0.16°C among scenarios. Holding climate constant at 2050 levels produced similar results. The moderate restoration scenario resulted in slightly higher minimum spawning flows and incubation peak flows but lower prespawning temperatures than the current scenario. The full restoration scenario resulted in somewhat lower incubation peak flows, with little change in prespawning temperatures. Spawning flows decreased slightly under the full restoration scenario because of increased evapotranspiration from the increased forest cover. Projected effects of restoration and land-use change were concentrated in the middle and lower watershed, because the upper potions of the basin consist primarily of federally protected lands where there is little potential for habitat restoration or degradation.

Salmon. To assess the effects of climate change and habitat restoration on Chinook salmon, we drove the salmon population model with the water temperature and flow variables derived from the hydrologic model in conjunction with habitat capacity estimates for juvenile and adult fish for each land-use scenario (11). Under current climate and land-use conditions, the model projected a mean basin-wide total of 6,096 (GFDL) to 6,174 (HadCM3) spawning adults, higher than the average for the last 20 years but lower than some recently recorded returns (11, 12). Holding land use constant to isolate the effects of climate, our models projected a strong negative effect of climate change on salmon. For 2050, the model based on the GFDL climate scenario projected a 40% average decline in basin-wide spawning populations (Fig. 4*A*), and the HadCM3 model projected a 20% decline (Fig. 4*B*). Although

Table 1. Mean change in climate from two climate models downscaled to the Snohomish River basin

	2025		2050	
Climate model	Temperature, °C	Precipitation, %	Temperature, °C	Precipitation, %
GFDL R30 A2	+1.0 ± 0.2	+1.5 ± 0.4	+1.5 ± 0.4	−0.2 ± 1.8
HadCM3 A2	+0.7 ± 0.2	+1.1 ± 1.3	+1.3 ± 0.4	−5.1 ± 1.3

Values represent the average difference between each model projection and that model's simulated 2000 climate. The plus-or-minus term indicates the magnitude of the range of values among 11 stations.

changes in flow and temperature from restoration were projected to be small (Table 2), large increases in juvenile rearing capacity associated with habitat restoration resulted in large population increases. All simulations based on the GFDL climate model for 2050 produced declines in salmon populations (Fig. 4*A*), although the full restoration scenario limited declines to 5%. In contrast, the scenarios based on the HadCM3 model for 2050 projected an increase in mean salmon abundance of 19% under full restoration (Fig. 4*B*), despite the negative impacts of climate change. Under both climate models, moderate restoration failed to balance the effects of climate change by 2050.

Model results suggest that, because climate impacts on hydrology are greatest in the highest-elevation basins, and restoration impacts are concentrated at lower elevations, the combined effect of climate change and restoration will be to shift salmon distributions to lower elevations. The eastern-most subbasins, which drain high-elevation areas in the Cascade Mountains, exhibited the largest projected declines in salmon numbers by 2050, often in excess of 50%, regardless of the land-use scenario (Fig. 5). A similar pattern was seen in simulations for 2025. In contrast, salmon abundance in lower-elevation sites was projected to show relatively modest declines or even to increase, especially under full restoration. The largest single driver of climate-induced population declines was the impact of increased peak flows on egg survival.

To examine the probability of severe salmon population declines under each combination of future climate and land-use conditions, we used a low abundance threshold identified in the Snohomish River Basin Salmon Conservation Plan (13). For each scenario, we recorded the proportion of 500 salmon population model runs, each 100 years long, in which the 4-year moving average of spawner numbers fell below 2,800 fish. The percentage of runs falling below the abundance threshold showed a similar pattern to mean spawner numbers, with 91% and 26% of runs falling below the threshold for the GFDL and HadCM3 scenarios in 2050, respectively, when land use was held constant (SI Fig. 10). Full restoration reduced the percentage of runs falling below the threshold in 2050 to 25% for GFDL and 2% for HadCM3. For all future scenarios other than HadCM3 climate with full restoration, the projected proportion of runs falling below the abundance threshold was greater than that in 2001.

Discussion

Despite uncertainty in climate-change predictions, modeled impacts on freshwater salmon habitat and productivity were consistently negative. Two climate models that project similar levels of warming and differ only modestly in their projections of future precipitation and seasonal climate variation projected very different magnitudes of change in freshwater habitat conditions for salmon. Because the models were selected for this study largely because of their success in matching recent climate in the region, projections from other models may diverge even more. The direction and spatial pattern of the projected effects, however, was consistent between models, the impacts differing only in magnitude.

Higher water temperatures, lower spawning flows, and, most importantly, increased magnitude of winter peak flows are all likely to increase salmon mortality in the Snohomish River Basin and in hydrologically similar watersheds throughout the region. The resulting stress on salmon populations is liable to make recovery targets more difficult to achieve. Even if climate change conforms to the relatively benign projections of the HadCM3 climate model, our results suggest that, in the absence of habitat restoration, Snohomish Chinook salmon populations would decline by 20% by 2050. Climate effects on Chinook productivity are likely to be greatest in high-elevation areas because of the spatial distribution of stream-flow changes during the spawning and incubation periods. Projected temperature effects show less spatial pattern, but temperatures only reached levels detrimental to salmon in the lower watershed.

Our projections of Chinook salmon population declines may be conservative. We did not model climate effects such as rising sea levels and ocean warming that are likely to decrease survival in this region (14) but for which reliable regional projections have not been developed (15). We also considered only the dominant Chinook salmon life-history type in this system: subyearling outmigrant (or "ocean-type") fish, which rear in fresh water in the late winter and spring, migrating to sea by June. Subyearling outmigrants are likely to be more resilient to the effects of climate change than are yearling migrants, which rear in fresh water for a year, potentially exposing them to high temperatures and low flows during the summer. Also,

Table 2. Basin-wide average hydrologic impacts from climate and land-use scenarios

Impact	Scenario	Year	Climate model	Incubation peak flow, %	Minimum spawning flow, %	Prespawning temperature, ° C
Climate	Current land use	2025	GFDL R30 A2	13.0	−2.9	0.74
			HadCM3 A2	5.1	−9.5	0.69
		2050	GFDL R30 A2	27.5	−15.1	1.16
			HadCM3 A2	7.3	−21.5	1.34
Land use	Full restoration	2025	GFDL R30 A2	−1.1	−0.7	−0.16
			HadCM3 A2	−1.1	−0.3	−0.13
	Moderate restoration		GFDL R30 A2	1.2	3.2	0.04
			HadCM3 A2	1.5	3.8	0.03

Climate changes are relative to the year 2000 climate with current land use. Land-use changes are relative to current land use with the 2025 climate.

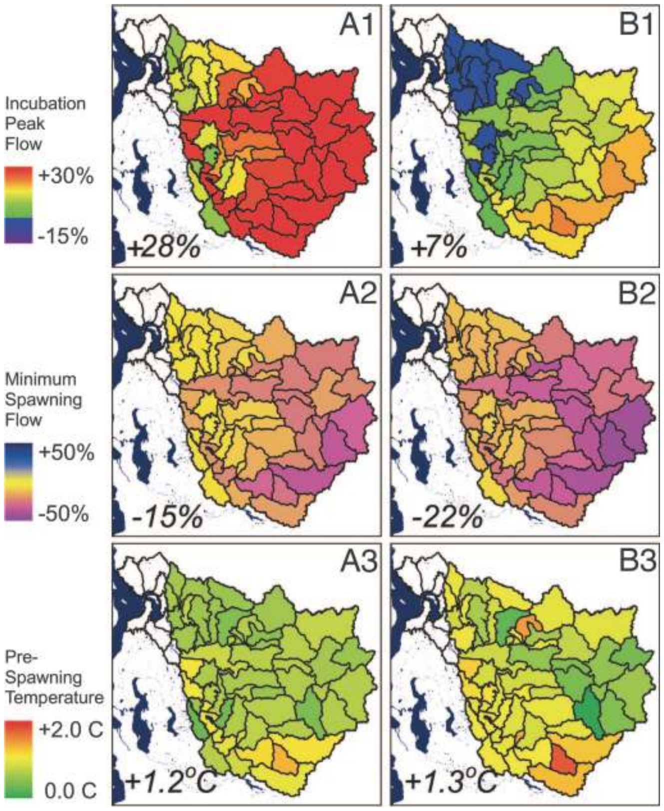

Fig. 3. Climate impacts on three hydrologic variables. (*A1–A3*) The results of the GFDL R30 climate model. (*B1–B3*) The results of the HadCM3 model. (*Top*) Percent change in incubation peak flow. (*Middle*) Percent change in minimum spawning flow. (*Bottom*) Change in prespawning temperature in degrees Celsius. The basin-wide average change is shown in the lower left corner of each figure. Black lines delineate subbasin boundaries. All simulations used the ''current'' land use scenario.

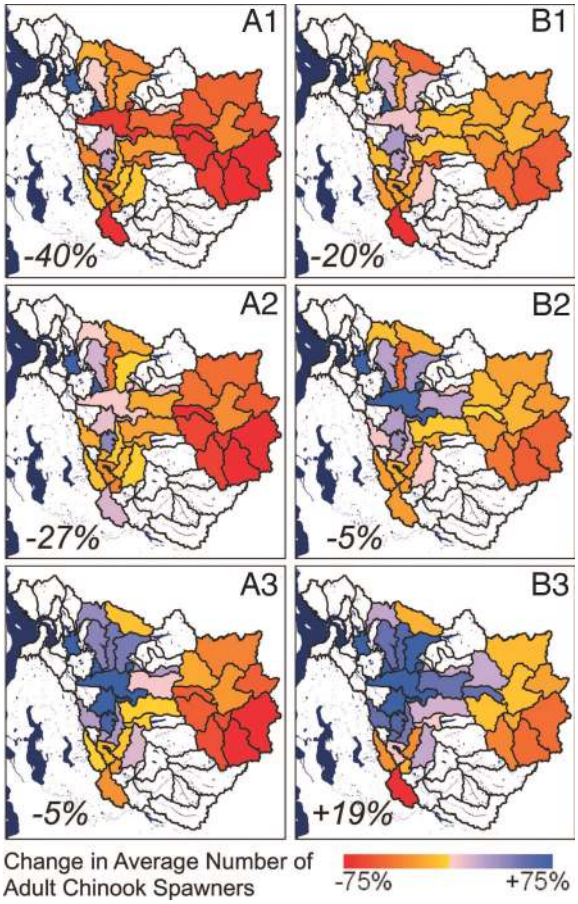

Fig. 5. Change in spawning Chinook salmon abundance between 2000 and 2050 under three future land-use scenarios. (*A1–A3*) The results of the GFDL R30 climate model. (*B1–B3*) The results of the HadCM3 model. (*Top*) Current land-use scenario. (*Middle*) Moderate restoration scenario. (*Bottom*) Full restoration scenario. The basin-wide total change appears in the lower left corner of each figure.

yearling migrants primarily spawn in the upper watershed (16), where climate impacts are projected to be greatest.

Chinook salmon exhibit remarkable plasticity in many life-history traits and may be able to respond evolutionarily or behaviorally to climate change in ways not captured in our models. Our findings do not support the notion that fish will react to climate change by moving to higher elevations (17), but they may be able to mitigate temperature effects by sheltering in thermal refugia when temperatures become too high (18). Although their need to lay eggs in areas of high subgravel flows (19) makes it unlikely that Chinook could alter redd placement to avoid the effects of higher peak flows, changes in the timing of migration, egg laying, and other life stages may allow fish to prosper in altered habitats. More southerly populations of Chinook, which migrate and spawn later in the year, may provide a model for how Puget Sound populations will respond to warming, but climate change also may produce conditions unlike anything currently experienced by salmon. Little is known about the capacity of salmon to adjust to climate change, and the potential for evolutionary or behavioral responses is one of the most important avenues for future research.

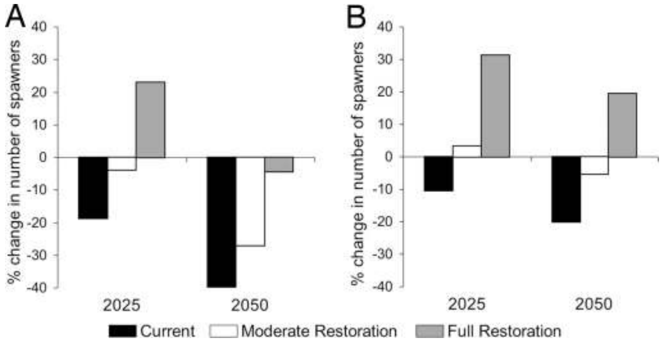

Fig. 4. Basin-wide percent change from 2000 in numbers of spawning Chinook under different combinations of climate change and habitat restoration for the GFDL R30 (*A*) and HadCM3 (*B*) climate models.

Habitat restoration can play an important role in offsetting the effects of climate change, although our results suggest that most expected climate impacts cannot be mitigated entirely. In relatively narrow streams, reforestation may decrease water temperatures by increasing shading, but in wide, main-stem reaches where most Chinook salmon spawn, riparian vegetation has a minor effect on water temperature. New reservoirs and flood-control structures could mitigate flow impacts, but because these effects are likely to be most severe in headwater streams, it is unlikely that such actions would be feasible or desirable. As in many river basins, the highest-elevation portions of the Snohomish watershed, where projected climate impacts are greatest, are largely protected and pristine, with little potential for further restoration. Although direct mitigation of the hydrologic impacts of climate change may not be possible, habitat restoration, particularly the restoration of juvenile rearing capacity, may benefit salmon populations threatened by climate change. Such benefits would likely accrue by boosting lower-elevation sub-populations to compensate for declines at higher elevations. Allowing streams and side channels to flow across a greater proportion of their historical floodplain and reconnect with freshwater and estuarine wetland habitats can improve low flows and lessen the negative impacts of peak flows (20). Other positive impacts of restoration not captured in this analysis, such as a decrease in fine sediment load (11), may provide additional benefits. Although our results suggest landscape-scale restoration of hydrologic processes may provide little direct mitigation of climate effects, it may still be essential to the overall success of habitat restoration (20). At the least, restoration may buy valuable time for further measures to curb climate impacts.

Explicit consideration of future climate conditions may improve the long-term effectiveness of restoration planning for salmon throughout their range. A regional assessment of the impact of climate change to 2050 projected large increases in winter peak flows and decreases in summer flows for the entire Georgia Basin/Puget Sound region (21). It is thus likely that climate-change impacts on fish habitat in most river basins in this region will resemble those seen in the Snohomish, although the magnitude and timing of effects will depend on elevation, snowpack, landscape context, and current temperature and flow conditions. Projects that rely on the preservation of relatively undisturbed high-elevation streams that derive a significant proportion of their flow from snowmelt (areas that may currently appear to be excellent salmon habitat) may be especially vulnerable to climate change, and the intuitively appealing idea that high-elevation watersheds should be the top priority for restoration and preservation in the face of climate change (22) may prove to be incorrect in this region. However, watersheds at elevations and latitudes higher than those considered here may continue to receive most of their winter precipitation as snow and thus respond differently to climate change.

Management approaches that emphasize flexibility and adaptation (in management systems, landscapes, and the fish themselves) may have the greatest potential to meet the challenges posed by climate change. The uncertainty associated with predictions of future climate change makes the development of effective monitoring programs imperative (23). Monitoring permits managers to assess the pace and magnitude of change and adapt accordingly. Although it is still unclear how salmon might adapt to climate change, preserving remaining genetic and life history diversity in threatened populations is likely to increase their resilience.

Methods

Land-Use and Restoration Modeling. We used land-use targets developed by Snohomish Basin planners as the basis for our two restoration scenarios (11, 13). Because the development of these land-use targets relied on proprietary land cover maps not available to us, we first replicated the planners' method for producing land-use projections (24), substituting data from the 2001 National Land Cover Database (NLCD) map (25) for the original base map. This produced a set of land-use targets similar to those in the restoration plan for the year 2025 for each land use scenario (current, moderate restoration, and full restoration) for habitat variables that affect habitat capacity and salmon survival (SI Table 3).

Because the land cover targets in the restoration plan were specified for 11 subbasin groups (11), but the hydrologic model required spatially explicit maps as input, we developed a land-cover allocation model to translate the targets for each restoration scenario into land-cover maps. The model had two components: an urban-growth model and a forest-conversion model. In ArcGIS Spatial Analyst (ESRI, Redlands, CA), we developed raster-based cost-distance models, which calculated land conversion probability for each grid cell by weighting its distance from a source by its conversion cost, for urban growth and forest conversion. For the urban growth model, conversion costs for each land-cover type were calculated from the proportion of that type converted to urban areas between 1995 and 2001, as calculated from NLCD maps (SI Table 4). Costs were further weighted by slope, with steeper slopes less likely to be converted. For the forest-conversion model, conversion costs were calculated from slope and distance from a source. Current urban areas were used as the source for urban growth and clear-cuts for forest conversion. Protected areas and wetlands were masked out of all analyses, leaving land cover in these areas unchanged. We first ran the urban-growth model until urban-cover targets (SI Table 3) were met. We then ran the forest-cover model, masking the new urban areas, and merged the results of the two models.

We used a habitat capacity model, described in ref. 11, to estimate the effects of changes in riparian forest cover, off-channel habitat, stream-edge habitat, and in-stream barrier removal on habitat capacity for juvenile salmon rearing. Adult spawning capacity calculations relied on a similar model based on stream width, gradient, and riparian condition and did not vary among scenarios other than being modified by spawning period stream discharge (described below).

Climate Data. Future global climate projections were taken from two GCMs: GFDL R30 and HadCM3, both with the SRES A2 emissions scenario (8). Because of the long lag between CO_2 emissions and climate effects, differences in climate projections among models based on different emissions scenarios for 2025 and 2050 are modest; we chose the A2 scenario because it was plausible and widely modeled. The GCM data were extracted, downscaled, and converted into future climate scenarios by the method of Wiley (9). The downscaling approach was based on the quantile mapping method (26), which assumes shifts in climate variables manifest with different magnitudes at different points in the variable's distribution. The method reproduces local phenomena while preserving the statistics associated with the GCM. Each resulting climate scenario is a time series of weather data for a point location corresponding to the regional or global time series produced by a climate model, yet also contains features unique to the station location and the full range of observed natural variability. These local features are defined by using the observed record at each station location.

The downscaling process maps the monthly temperature and precipitation distributions from 21 years of GCM data to the historic, local-scale distribution of each variable, expanding the GCM projections into a 72-year time series of daily temperature and precipitation at 11 weather station locations (Fig. 1). A different 72-year climate time series of temperature and precipitation distributions was developed for each period of investigation (i.e., the 21-year periods centered on 2000, 2025, and 2050). The downscaling process is described in more detail in ref. 27.

Hydrology Model. To project hydrologic conditions, we used the Distributed Hydrology Soil Vegetation Model (DHSVM), a watershed-scale hydrologic model that has been tested extensively for the mountainous, forested watersheds typical of the Pacific Northwest (28, 29). Previous versions of DHSVM have only modeled water flows on the surface and in the subsurface soil layer (30), which tends to underestimate summer base flows (31). To model summer low flows, we added a groundwater layer based on the model of Waichler *et al.* (32) but modified for use in less arid, more mountainous areas. The groundwater component of the model routes water flow according to methods developed for topographically driven saturated subsurface flow (33) but uses the groundwater table elevation rather than surface elevation to define the hydraulic gradient between cells.

To model the direct effects of shifts in climate on water temperature, we added a radiative and conductive heat balance routine on the basis of the methods described by Chapra (34). The stream temperature component tracks water temperature at all points in the channel network at every model time step.

We drove the hydrologic model with the 72-year down-scaled meteorological time series for each time period. The lowest elevation and most highly urbanized portions of the watershed were not modeled because of complications associated with storm water conveyance systems and tidal effects near the river mouth. Excluding these areas had little effect on salmon model outcomes, because modeled hydrologic impacts were limited to the spawner and egg life stages, and few Chinook salmon spawn in the excluded areas.

Salmon Population Model. To model the effects of changes in flow, temperature, and habitat capacity on Chinook salmon, we used the Shiraz population model (12, 35), a spatially explicit life-cycle model that simulates the effects of environmental change on salmon populations. The mathematical details of the model and parameter values specific to the Snohomish basin, including the values of stage-specific survival and fecundity parameters, the form of functional relationships linking environmental variables to salmon survival, movement algorithms, hatchery fish behavior, and harvest policy are described in ref. 12. We modified this model to allow it to function as a stochastic population model and to use time series from DHSVM as inputs.

The Shiraz model is based on a multistage Beverton–Holt model (36), in which two parameters, fish productivity and habitat capacity, determine the number of fish surviving from one life stage to the next. We modeled the life cycle of wild, subyearling migrant Chinook salmon in eight stages: spawning adults, eggs, fry, smolt outmigrants, and ocean fish aged 1–4 (some or all of which return to spawn, depending on age). We focused on the wild stock, but we also included hatchery fish because of potential competitive interactions (12). We modeled the basin as a network of 62 interconnected subbasins, with fry rearing downstream from their natal areas.

Environmental variables affected either capacity or survival for a given life stage. Three environmental variables affected productivity: High temperatures during the prespawning period caused mortality of returning adults, high temperatures during the egg incubation period caused egg mortality, and high flows during the incubation period caused egg mortality due to bed scour. We used the same functional relationships as in previous model versions (12), except that incubation peak flows were normalized to 1990–2002 mean peak flows rather than the 100-year recurrence flow. One environmental variable, minimum flow during the spawning period, affected spawning capacity. For spawning, Chinook generally require water at least 10-cm deep and enough subgravel flow to provide adequate oxygen to eggs (19). We assumed the change in spawning capacity was proportional to minimum discharge during the spawning period. Although this method is imprecise, the model is relatively insensitive to changes in spawning capacity (12), so this calculation had a relatively small effect on model results.

Two variables, harvest rate and ocean survival, were considered to be normally distributed random variables, with coefficients of variation of 2% and 10%, respectively. Ocean survival values for 2-, 3-, and 4-year olds were each lowered by 10 percentage points from those used in ref. 11 to reflect ocean survival rates for Puget Sound salmon populations over the last 20 years. Each DHSVM-generated 72-year time series of flows and temperatures was used as the basis for a Monte Carlo analysis. For each climate and land-use scenario, the Shiraz model was run 500 times, each run spanning 100 years. At each annual time step in each run, a year was randomly selected from the 72-year time series, and the appropriate functional relationships were applied to each temperature and flow value for that year. This approach maintained within-year correlations among variables while allowing us to explore the widest possible range of future climate time series.

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