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Climate Change Shrinks and Fragments Salmon Habitats in a Snow-Dependent Region

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Key Points:

- Warming from climate change accelerates runoff and decreases streamflow during low flow periods in many snow dependent regions
- Extended summer low flows reduce and fragment the capacity of freshwater habitats to support historical salmon abundances
- Climate adaptation actions for salmon should consider hydrologic changes and floodplain connectivity besides increasing water temperatures

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract Climate change threatens biodiversity through global alteration of habitats, but efficient conservation responses are often hindered by imprecise downscaling of impacts. Besides thermal effects, warming also drives important ancillary environmental changes, such as when river hydrology evolves in response to climate forcing. Earlier snowmelt runoff and summer flow declines are broadly manifested in snow-dependent regions and relevant to socioeconomically important cold-water fishes. Here, we mechanistically quantify how climate-induced summer flow declines during historical and future periods cause complex local changes in Chinook salmon (*Oncorhynchus tshawytscha*) habitats for juveniles and spawning adults. Changes consisted of large reductions in useable habitat area and connectivity between the main channel and adjacent off-channel habitats. These reductions decrease the capacity of freshwater habitats to support historical salmon abundances and could pose risks to population persistence in some areas.

Plain Language Summary The large majority of climate change research for aquatic organisms has focused on stream water temperature and discounted the importance of flow changes associated with evolving precipitation regimes. Using a high-resolution stream topographic map that supported a series of linked flow and fish habitat quality models, our research describes how observed historical flow reductions and projected future reductions affect local habitat quality, distributions, and connectivity for a salmon population. We demonstrated that as climate change continues to change flow regimes in snow-dependent regions, it will cause fragmentation and reduce the overall volume of available habitats in headwater streams where salmon and other cold-water fish species spawn and grow during early life stages.

1. Introduction

A changing climate pervasively affects life on Earth (Parmesan & Yohe, 2003) and is projected to drive to extinction many local populations and some taxa this century (Urban, 2015) and threaten the habitat of many cold-water fish such as salmonids (Isaak et al., 2018; Young et al., 2018). It leads to changes in temperature and hydrology with biological consequences that are complicated by complex interactions with local habitats and physical conditions (Wenger et al., 2011). Despite progress in recent decades, we still lack the ability to represent local climatic conditions at the resolutions needed for greatest relevance in ecological risk assessments and strategic application of conservation resources (Potter et al., 2013). Challenges are magnified in stream and river environments that are disproportionately biodiverse (Dudgeon et al., 2006), but difficult to study given their dynamic physical properties and problems associated with making measurements in flowing water. Emergence of new remote sensing (McKean et al., 2009) and hydrodynamic modeling technologies (Nelson et al., 2016), however, have enabled bathymetric surveys and analyses of lotic environments to progress rapidly in recent years and applications are proliferating (Carbonneau et al., 2012).

In the Columbia River Basin of the northwestern U.S., rivers provide habitats for world-renowned salmon populations and fisheries but the abundance of most species has declined precipitously due to habitat degradation, fragmentation, and overharvest (Nehlsen et al., 1991). This has prompted extensive restoration efforts in hundreds of rivers and streams and cost billions of US$ in previous decades (Lewis et al., 2015; Rieman et al., 2015). Hydrologic regimes within the region are snow-dependent and climate-sensitive, similar to most areas inhabited by salmon throughout North America and Eurasia because of salmon species' requirement for cold riverine environments. Increasing air temperatures throughout the northwest in recent decades are linked to reductions in winter

10.1029/2022GL098552

snow accumulations, earlier spring snowmelt runoff, and declining summer flows (Isaak et al., 2018; Kormos et al., 2016). The summer low flow period is an important bottleneck for most salmon populations that are territorial during juvenile and adult life stages (Quinn, 2005) because reductions in water volume enhance resource competition and translate to decreased habitat capacity and population abundance (Ohlberger et al., 2018). If decreases in habitat extent are accompanied by reductions in flow velocities or even stagnant backwater areas with no flow, remaining habitats are also likely to become less productive for juvenile salmon, which feed on passively drifting insects that are delivered at rates commensurate with flow velocities (Naman et al., 2016).

Here, we investigate the effects of climate-induced summer flow reductions on salmon spawning and rearing habitats in both in-channel and off-channel habitats (OCH). To address our goal, we surveyed a typical Chinook salmon spawning stream and adjacent floodplain, at Bear Valley Creek (Idaho, US, Figure 1a), using an aircraft-mounted, water penetrating green LiDAR system (McKean et al., 2009). A detailed 1 m^2 resolution bathymetry (Figure 1b) was developed from the survey data and used to define channel boundary conditions for hydrodynamic models that quantified local flow velocity (Figure 1c) and habitat characteristics (Figures 1d and 1e) associated with historical and future summer discharge levels along a 7.4 km reach (Study site hydrology, Figure S1 in Supporting Information S1).

2. Study Site

Bear Valley Creek is a tributary to the Middle Fork of the Salmon River (Idaho, USA; Figure 1a). It is typical of many headwater streams used by salmon for adult spawning and juvenile rearing throughout the Pacific Northwest, USA. It is a small (bankfull width of 15 m), meandering (1.5 sinuosity index), low-gradient (0.0035 m/m), gravel bed (median grain size, d_{50}, of 0.052 m) stream that flows in a broad, gentle valley formed in glacial outwash deposits (McKean et al., 2008; McKean and Tonina, 2013; Schmidt & Mackin, 1970). The stream is largely unconfined in the study reach with small discontinuous terrace remnants breaking up the valley surface that is also marked with numerous abandoned and semi-abandoned channel fragments, sloughs, and shallow closed depressions that constitute the off-channel habitat when they are flooded (McKean et al., 2008). Near-channel vegetation is primarily grasses and willows with occasional conifer trees and there is very little in-stream wood. Base flows after snowmelt runoff are usually reached in late July in Bear Valley Creek and average approximately 1 m^3/s. Snowmelt bankfull flows in the spring average approximately 7 m^3/s.

3. Methods

We mapped the channel and floodplain topography in the study reach using the airborne aquatic-terrestrial Experimental Advanced Airborne Research Lidar (EAARL; McKean et al., 2009). The EAARL is a low power, narrow-beam, full-waveform instrument with a scanning and rapidly pulsing green laser that can take measurements subaerially and through water (Bonisteel et al., 2009; Nagle & Wright, 2016). Each laser pulse measures the location and elevation of a circular ground footprint 15–20 cm in diameter and the spacing of these measurements was 1–2 m. We then interpolated this LiDAR data point cloud of 500,000 elevation measurements to define a DEM with a 1 m pixel resolution and mapped the channel and floodplain features in that DEM (SI). The uncertainty associated with the LiDAR's vertical elevation measurements has a standard deviation of 0.1 m, which has a limited impact on flow hydraulic predictions for ecohydraulics applications, for example, 0.06 standard deviation of cell suitability index and less than 0.01 m error on water surface elevations (Tonina et al., 2020).

Trends in flow for the study reach were described for the 60-year period of 1957–2016 based on correlations with historic flow records measured at eight gauges in nearby streams. These gauges had incomplete records (average number of years with data was 44) and missing years were imputed to complete the time series using an iterative Principle Components Analysis (PCA) with the MissMDA package (Missing Values with Multivariate Data Analysis; Josse & Husson, 2016) in the R statistical program (version 3.2) (R Core Team, 2019). Because there was no permanent stream gauge in the study reach, a temporary staff gauge was operated there during 2008 to define the relationship between local discharge and water surface elevation in the channel (Stage-discharge relationship, Figure S2b in Supporting Information S1).

To describe the historical summer discharge trend in the study reach, we calculated annual July–September mean monthly flow for 1957–2016 and fit a trend to the data time-series to smooth the annual variability (Stage-discharge

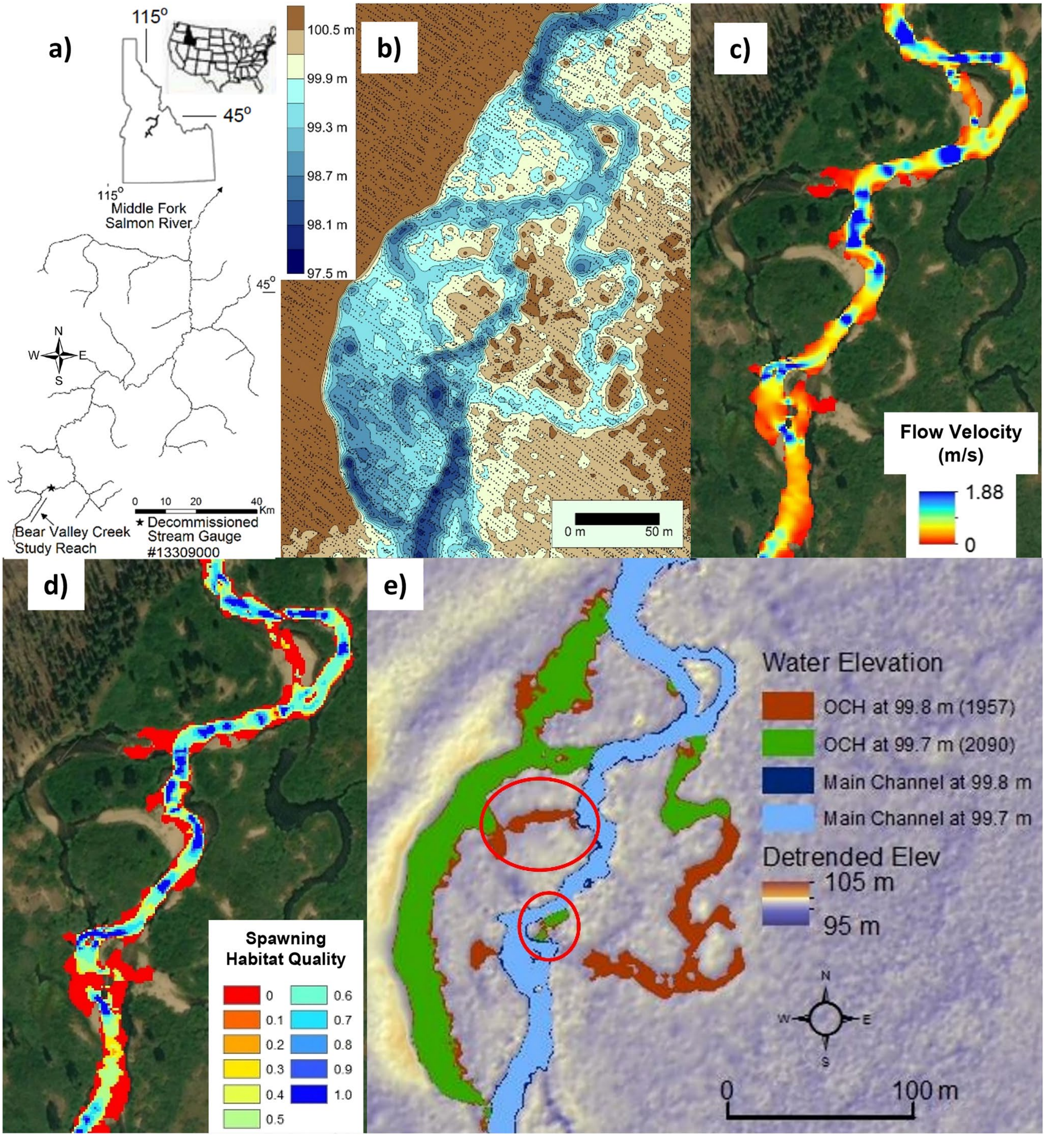

Figure 1. (a) Location of the study site in the northwestern U.S. (b) Floodplain topography and channel bathymetry mapped by the Experimental Advanced Airborne Research Lidar instrument. Black dots are individual LiDAR elevation measurement points. (c) Spatial pattern of flow velocity in the mainstem channel during a discharge of 1 m^3/s. (d) Distribution of Chinook salmon spawning habitat quality during a discharge of 1 m^3/s. See equation 3 in Supporting Information S1 for calculation of habitat quality. (e) Off-channel rearing habitat (OCH) as a function of water stages in 1957 and 2090. The two circled areas illustrate examples where water flows freely through the OCH at the higher stage (1957 conditions), but the habitat becomes fragmented and characterized by standing water at the lower stage (2090 conditions).

relationship, Figure S2a in Supporting Information S1). The estimated trend was −0.05 m^3/s/decade, or about −3%/decade relative to the summer average monthly flow average in 1957. To derive future late summer flow values, we forced the Variable Infiltration Capacity (VIC) hydrologic model with global climate model (GCM) projections, which were biased corrected (Maurer, 2007; Wood et al., 2002) (SI: Climate-change scenarios), of air temperature and precipitation changes associated with the A1B, B1 and ensemble mean, EM, emissions scenarios during the 2050s (2030–2059) and 2090s (2070–2099; Elsner et al., 2013). Comparisons between predicted monthly VIC discharges and those measured at Bear Valley Creek showed discrepancies around 24% of the historical values (1922–1957) and less than 10% in daily discharge collected between 2006 and 2008 (VIC model validation, Figure S3 in Supporting Information S1). The three emission scenarios provided similar future results, so we selected the EM predictions for further analysis (Reeder et al., 2021) because EM predictions weight the effect of all GSMs scenarios (Climate-change scenarios comparison: Figure S5 in Supporting Information S1).

To delineate off-channel habitats important for juvenile salmon rearing, we mapped the spatial patterns of inundated floodplain topography that were connected to the mainstem channel of Bear Valley Creek during water stages corresponding to the mean trend discharges in 1957, 2040 and 2090. Mapped polygons were georeferenced by their downstream connection point to the main channel. The surface area, volume, and mean depth of each off-channel habitat polygon were calculated at discrete water discharges, using their respective water stages and the high-resolution LiDAR-derived stream bathymetry.

We used the 2D hydrodynamic Flow and Sediment Transport with Morphological Evolution of Channels (FaSTMECH; Nelson et al., 2016) model that was calibrated and validated to the study reach to quantify flow hydraulics, for example, local depth, velocity and shear stress (Carnie et al., 2015). Comparison of predicted and measured water surface elevations and velocity at low discharge (1.6 m^3/s) showed good agreement with root mean square errors of 0.054 m and 0.06 m/s, respectively, which were within the error expected in the literature (Pasternack et al., 2006). We numerically computed in-channel flow characteristics at discharges between 1 and 7 m^3/s at 1 m^3/s increments. This covered the range in discharge values from low flows in late autumn-winter to spring snowmelt flood flows that fill the channel to the top of the streambanks. The model predicted water depth, flow velocity and shear stress near the channel bed with a 1 m^2 spatial resolution at each analyzed discharge (e.g., Figures S6 and S7 in Supporting Information S1). Mean velocity for the full study reach was computed from the mapped velocity distributions.

To predict in-channel spawning and rearing habitats for Chinook salmon, we coupled the results of the hydraulic model predictions with published habitat suitability curves from the Washington Department of Fish and Wildlife (Carnie et al., 2015; WDFW, 2004) that expressed the observed preferences of this species for ranges of flow depth, flow velocity, substrate grain size and percent sand. The quality of local spawning habitat, expressed as cell suitability index, CSI, was calculated at the cell scale, by using the geometric mean of the suitability index of each variable (Ecohydraulic modeling, Equation 3, Figure S8 in Supporting Information S1). We quantified the weighted useable area, WUA (SI: Ecohydraulic modeling, Equation 4), to provide a reach scale index of habitat availability (Reeder et al., 2021). The substrate grain size and sand concentrations were mapped in field surveys during 2011. Similar calculations with rearing suitability curves (WDFW, 2004) for flow depth, flow velocity and grain size distribution were made for local in-channel salmon rearing habitat quality (SI: Ecohydraulic modeling).

4. Results and Discussion

During a recent historical period of 1957–2016, average flows in the study reach declined by 19% (−3%/decade) during the summer months of July, August, and September (Figure 2a), a decrease that was consistent, although smaller, with declines observed at the majority of gauges on unregulated streams in the region during this period (Figure S4 in Supporting Information S1, Isaak et al., 2018). This flow decrease affected physical conditions within the main channel used by adults for spawning and in adjacent off-channel areas used for rearing by juvenile salmon. The overall wetted dimensions of the main channel decreased by a small amount (−2% to −3%; Figure 2b), but the average flow velocity through the channel dropped more substantially (−17%; Figure 2a). The surface area of off-channel rearing sites also declined over the same time (−6%; Figure 2c). Importantly, the spatial distribution of these changes was not uniform. For example, the largest drops in velocity occurred within an approximately 1000 m^2 area composed of riffle channel habitats where adult spawning is usually concentrated.

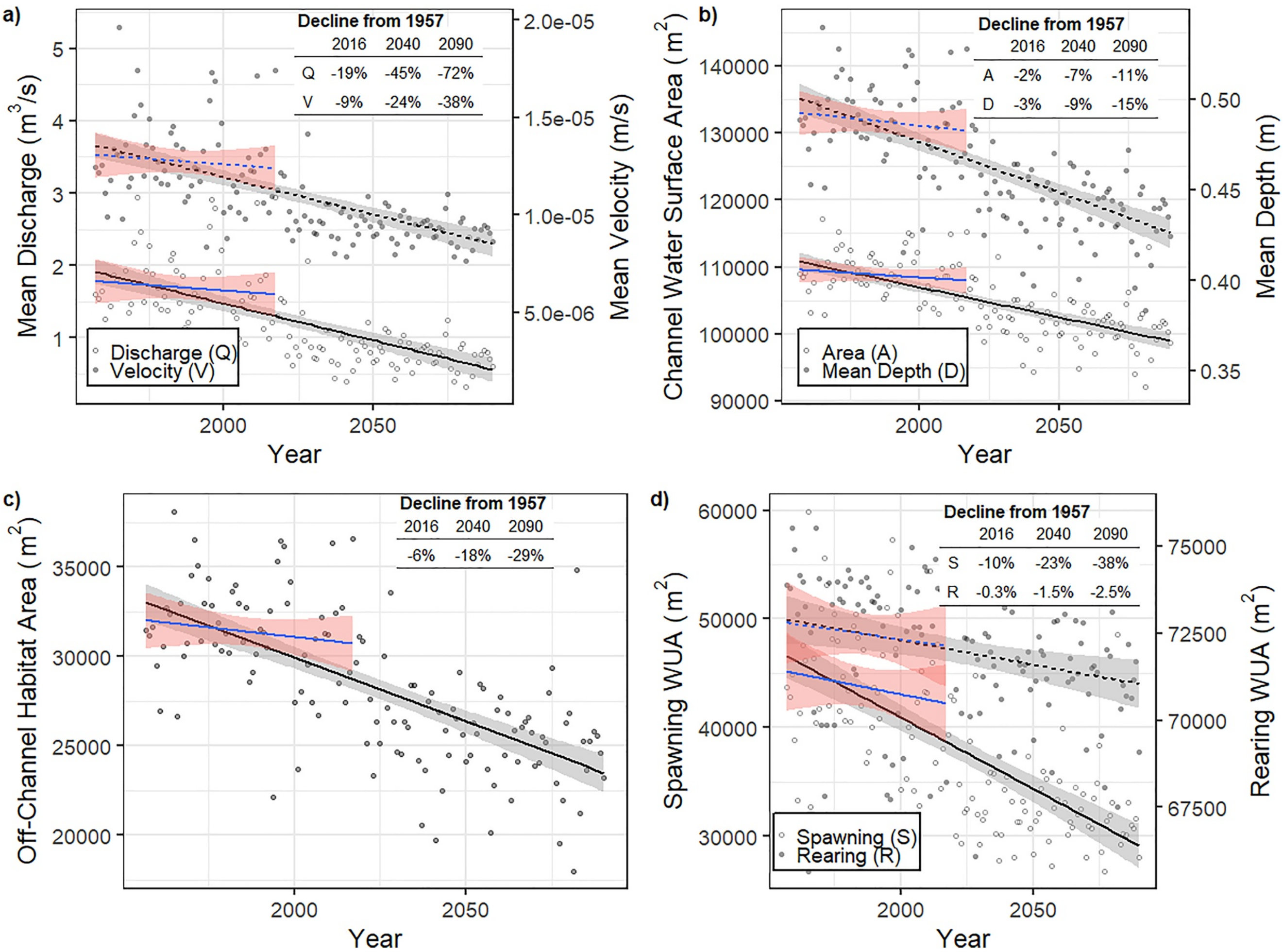

Figure 2. Trends estimated from linear regressions for the historic period (1957–2021, blue lines with pink fill for standard error) and over the full study extent (1957–2090, black lines with gray fill for standard error) in yearly values of average summer reach conditions for Bear Valley Creek under the ensemble mean warming scenario. Reach characteristics are: (a) Discharge and flow velocity, (b) wetted area and depth, (c) off-channel habitat area, and (d) weighted useable area for adult spawning and juvenile rearing. Trends over the full study extent are statistically significant ($p < 0.001$), $Q = -0.01$ year + 21.74, $V = -0.001$ year + 2.37, $A = -88.91$ year + 284,539, $D = -0.00055$ year + 1.58, $OCH = 71.5$ year + 172,771.7, $S = -130.78$ year + 302,129, and $R = -13.45$ year + 99122.3 (year expressed as calendar year, e.g., 1957), whereas those for the historic period are not statistically significant. Shaded areas around the linear trends identify the 95% confidence level intervals.

Those changes in channel hydraulics also translated to effects on aquatic habitat conditions. For example, the WUA of good spawning habitat (CSI > 0.8) was reduced by about 10% (Figure 2d), That occurred while the habitat area for in-channel rearing of juveniles had a negligible decline (−0.1%). These differences in habitat response within the main channel reflect both a stronger dependence of good spawning sites on higher local water velocity and the larger declines in velocity at the spawning sites relative to the rearing areas. Overall, off-channel juvenile rearing habitats also declined strongly over time (−6%) as these rearing areas shrank or became disconnected at lower discharges and water stages. The off-channel habitat was also predicted to begin breaking up into smaller patches (<200 m^2) in the future as average water stages decreased and large patches disappear (Figure 3).

In addition to the loss of habitat area over time, other ecologically important changes also occur at lower stream discharges. For example, off-channel rearing habitats for juvenile salmon often consist of secondary channels with flows that return to the main channel at downstream connection points (Figure 1d). As flows decline, one end of these habitats may be severed from the main channel or they may separate in the middle, causing flows to stagnate and declines in habitat quality for salmon as water temperatures increase, dissolved oxygen levels decrease (Henning et al., 2006) and macroinvertebrate communities adjust in ways that alter the potential food supply (Paillex et al., 2006, 2009). Locations of connection points along the reach depend on subtleties in geomorphic

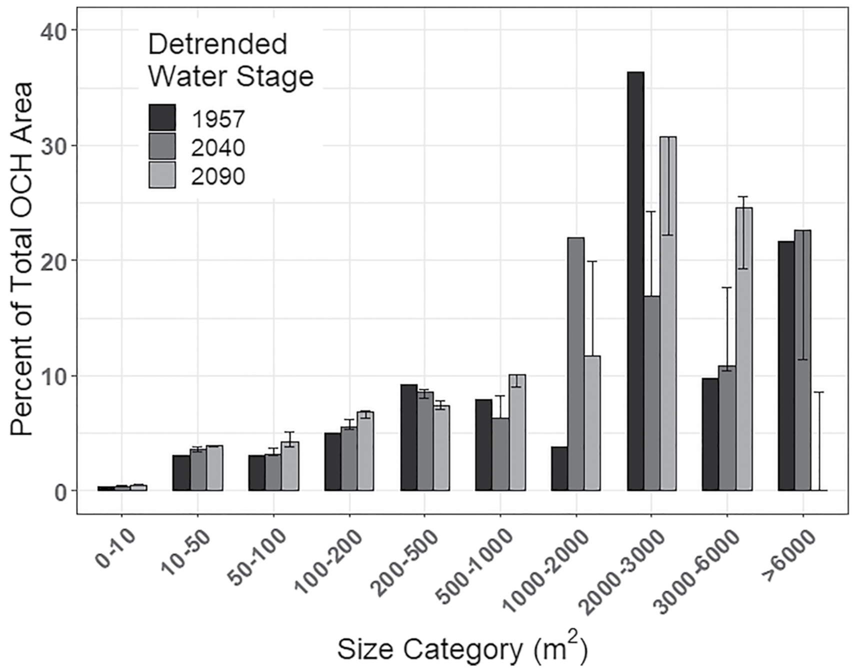

Figure 3. Change in summer off-channel rearing habitat, off-channel habitats (OCH), size frequency distributions between historical, 1957, and future, 2040 and 2090, periods when the mean water stage height is predicted to decline by 10 cm. Whiskers represents OCH variability due to 24% discharge uncertainty quantified for future predictions. The symmetrical uncertainty of the discharge results in unsymmetric whiskers around the expected OCH value because OCH extension is due to the interaction between discharge stage and off-channel topography.

floodplain characteristics but are often spatially clustered (McKean et al., 2008). Once critical low-flow thresholds are exceeded, some sub-reaches experience large local habitat losses and fragmentation of networks despite the total wetted surface area remaining relatively constant. Our estimates suggest about 20% of the off-channel rearing habitat with through-flowing water was lost between 1957 and 2016 (Figure 2d).

Observed decreasing historical trends in wetted channel dimensions and salmon habitats are predicted to continue and intensify later this century under the EM scenario, with mean summer flows estimated to decline by about 45% in 2040 and 72% in 2090 relative to the 1957 baseline. If these changes transpire, the amount of main-channel habitat for juveniles is again predicted to show relatively small changes compared to the decreases in spawning (−38%) and off-channel rearing habitats (−29%; Figures 2c and 2d). Besides shrinking, the reduction in mean summer discharge from nearly 2 m^3/s historically (1957) to 1 m^3/s around 2040 is predicted to decrease the size of habitat patches (average habitat size reduces by 46% from 84 to 46 m^2, respectively) (Table S1 in Supporting Information S1). The spawning habitat also became more fragmented as the number of habitat patches with less than the minimum patch size of 6 m^2 (corresponding to the average surface area of a salmon nest) increased by 95% compared to larger habitats of good and excellent quality (Table S1 in Supporting Information S1). About 30%–35% percent of the remaining off-channel habitat with flowing water would also be fragmented and reduced to areas of standing water. Uncertainty on OCH increases with OCH extension (low uncertainty for small OCH size) but it does not mask a systematic reduction and or disappearance of large contiguous OCH patches (Figure 3).

Summer flow reductions are common to many snow-dependent regions (Stewart, 2009) suggesting detrimental effects not only to the Chinook salmon considered here, but also to other species of salmon, trout and char that require cold water from snowmelt runoff and are regulated at multiple life stages by density-dependent growth, survival, and reproduction (Quinn, 2005). As rearing juveniles, the fish organize into spatial hierarchies where dominant individuals occupy bioenergetically profitable positions to maximize growth opportunities. Similar territorial mechanisms occur at the adult life stage when dominant females establish breeding territories in the best habitats to build nests and males compete aggressively for access to the females. Even at contemporary abundance levels that are reduced from historical numbers, these density-dependent processes often manifest strongly at local scales (Achord et al., 2003). Habitat reductions are especially problematic during the summer low-flow season when bioenergetic expenditures are greatest to take advantage of limited seasonal growth opportunities or to cope with physiological stresses in warm environments. Biological responses may take one of several forms, including direct mortality caused by increasing female superimposition of nests when spawning is confined to smaller useable habitat areas (von Biela et al., 2022), reduced juvenile growth rates, or altered juvenile emigration rates and timing (Holtby, 1988). Reductions in juvenile size-at-age may contribute to higher mortality rates (Quinn, 2005) and forced emigration is also usually disadvantageous. Whereas warmer water temperatures may sometimes increase growth because of high metabolic rates if sufficient food is also available; higher fish densities caused by a decrease in rearing habitat could negate the effect (Reeder et al., 2021).

The VIC model forced by several GCMs and emissions scenarios predicted similar future hydrographs with mean summer discharges declining (−6%/decade) at faster rates than historic (−3%/decade) values within Bear Valley Creek but comparable to historic summer flow reductions in nearby unregulated streams that ranged between −4 and −6%/decade (VIC model validation, Figure S4 in Supporting Information S1). Residuals between VIC discharge predictions and values measured during the historic period are also constrained within 24% with a marginal error of 0.27 m^3/s, which is smaller than the change in flow prediction over several decades. An important assumption in our study is that we considered the streambed and floodplain morphologies fixed over time (Reid et al., 2020). Whereas previous research predicts limited streambed mobility in this stream over a range of flood sizes (McKean and Tonina, 2013), changes in hillslope processes with increased potential for wildfires and fine sediment delivered to the stream could increase the deposition of fine sediment (Sankey et al., 2017). This would negatively impact spawning habitat by clogging flow through nest sites, which may reduce embryo survival by decreasing oxygen delivery and waste removal (Zimmermann & Lapointe, 2005; Tonina & Buffington, 2009). Increased fine loading could also cause development of natural levees (Maturana et al., 2013) that inhibit connection with lateral channels and reduce the available OCH area. Consequently, our calculations of the impacts of climate change on future salmon habitat quality may be conservative.

Climate-induced reductions in the regional capacity of freshwater habitats to support salmon populations or traditional life histories pose unanticipated challenges for conservation strategies that assume reversals of past habitat degradation will be sufficient to ensure long-term population persistence (Kareiva et al., 2000). Toward that end, billions of US$ have been spent on habitat restoration and population conservation efforts in the northwestern U.S. while the biological benefits remain subject to debate (Rieman et al., 2015). Nonetheless, costly investments will continue this century, so efforts to improve investment strategies should be ongoing and can benefit from more precise, spatially explicit information about the biological consequences of habitat improvements and climate trends. To achieve better river analyses and management, we must also survey or model many biophysical aspects of stream systems. At a minimum, these include channel and floodplain topography, water depth, temperature and velocity, the grain size of sediment on the stream bed and the location of logs and other large woody debris that force small scale hydraulics as well as provide local habitat. Furthermore, stream biota conduct their daily activities in microhabitats with a scale of a few meters, but highly mobile species like anadromous fish also use thousands of kilometers of rivers during their migratory life stages. Thus, we need to accurately describe relevant biological phenomena such as distributions, growth, and productivity at high-resolution over a comparable range of spatial scales to facilitate strategic assessments of habitat use and means of restoration (Torgersen et al., 2021). This is difficult, but achievable by exploiting recent advances using new technologies such as bathymetric lidars and drone-based optical surveys and improved numerical models of channel hydrodynamics.

5. Conclusions

Climate change is not only impacting stream water temperature regimes in high elevation spawning and rearing meadow systems, like Bear Valley Creek, but is also affecting hydrological regimes. Expected future summer flows will be lower than historic (∼−72%), which will cause continued reductions in and fragmentation of spawning (∼−38%) and rearing (∼−2.5%) and off-channel (∼−29%) habitats by the end of the century. These predicted negative impacts on habitat extent and distribution will be potentially exacerbated by an increase of late summer water temperature and potentially by deposition of fine sediment, which may also further disconnect the main stem from off-channel habitats. This detailed analysis also demonstrates that new technologies, able to define and analyze continuous physical conditions of the stream and floodplain at the micro-habitat scale over long stream domains, can improve riverine ecosystem analyses and management.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

All data are available in the supporting material or stored in HydroShare repository (Tonina et al., 2020, HydroShare, http://www.hydroshare.org/resource/952304525d0a450b93842ce5068b2d11).

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