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Research article

Forest restoration can bolster salmon population persistence under climate change

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ABSTRACT

As climate change alters freshwater, estuarine, and marine habitats, Pacific salmon need increasing levels of conservation action to maintain population health. In the Pacific Northwest, USA, coastal forests and estuarine ecosystems have experienced extensive anthropogenic change since the early 20th century, and significant investments in restoration and conservation are currently underway. Restoration is increasingly implemented within the broad-scale context of changing ocean conditions, but we lack an understanding of the relative extent to which land-based actions can contribute to the resilience of salmon populations under climate change. We addressed this challenge using an integrated population model of chum salmon (*Oncorhynchus keta*) in the Willapa basin (southwest Washington, USA). We first conducted a retrospective analysis, evaluating how chum population dynamics have varied with watershed-scale forest management, estuarine invasive species control efforts, and changing ocean conditions from 1984 to 2022. Forest management and estuarine restoration both had measurable effects on population dynamics, as did nearshore ocean conditions. Using this model, we projected chum population dynamics under a range of future climate and forest management scenarios. Our results suggest the viability of our focal populations may decline with ocean warming, but that maintaining and promoting watershed-scale forest structural complexity can decrease the risk of population collapse compared to a scenario in which forests are intensively harvested. Overall, our findings illustrate the capacity for multiple conservation actions to contribute to salmon population health and suggest that watershed-scale forest management has the potential to bolster the persistence of salmon populations under climate change.

1. Introduction

Pacific salmon (*Oncorhynchus* spp.) are integral to the cultures, economies, and ecosystems of western North America (Helfield and Naiman, 2006; Criddle and Shimizu, 2014; Carothers et al., 2021), and many populations are currently in dire need of restorative action. Since the early 20th century, many Pacific salmon populations have declined sharply due to habitat loss and degradation, barriers to fish passage, and detrimental fisheries practices, among other factors (National Research Council, 1996; Ruckelshaus et al., 2002). In response to these declines, efforts to recover salmon populations through improved fisheries management, improved hatchery genetics programs, removal of fish passage barriers, pollution reduction, and restoration of floodplains, estuaries, marine nearshore, and in-stream habitats have expanded throughout the region (Bennett et al., 2016; Silva et al., 2018; Tian et al., 2021; Toft et al., 2023; Bilby et al., 2024; Howe et al., 2024). Increasingly, however, climate change is posing additional challenges and further threatening Pacific salmon population health and long-term survival.

Climate-induced changes in ocean conditions, including warming temperatures, acidification, and decreased productivity, are altering salmon life histories and marine habitat suitability at broad scales (Abdul-Aziz et al., 2011; Cline et al., 2019; Crozier et al., 2019). Sea surface temperature and coastal upwelling are two key facets of the marine environment linked to ocean productivity and Pacific salmon population health (Williams et al., 2014; Daly and Brodeur, 2015; Henderson et al., 2019). Warming temperatures can decrease salmon

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recruitment indirectly through effects on trophic processes (Mueter et al., 2002; Fukuwaka et al., 2011), while coastal upwelling directly modulates nearshore ocean productivity via the transport of deep, nutrient-rich waters to the surface. Upwelling is projected to increase in some regions and decrease in others (Pozo Buil et al., 2021; Jacox et al., 2024) and could therefore offset or exacerbate the negative effects of warming temperatures, depending on the salmon species, region, and degree to which phenological mismatches between timing of ocean entry and ocean productivity occur (Crozier et al., 2021; Wilson et al., 2023). Simultaneously, climate-induced changes to freshwater systems, including warming stream temperatures and shifting hydrologic regimes, are impacting aquatic habitats across western North America (Vano et al., 2015; Ward et al., 2015; Jones et al., 2020). The effects of climate change are expected to persist for decades even under the most ambitious emissions reductions scenarios (IPCC, 2023). Thus, identifying near-term management strategies and restoration actions that can increase the resilience of Pacific salmon to climate change will be critical for their conservation and recovery (Crozier et al., 2021; Beechie et al., 2023).

Understanding the effects of climate change, along with the capacity of land management strategies to mitigate those effects, requires considering the full life cycle of anadromous salmon and accounting for changes occurring across multiple ecosystems simultaneously (Cunningham et al., 2018; Crozier et al., 2021). Pacific salmon life histories are complex and vary within and across species, with the general pattern of juveniles rearing in freshwater and estuarine environments, maturing at sea, and subsequently returning to their natal streams to spawn. Access to a well-connected mosaic of quality habitat across a range of freshwater, estuarine, and marine ecosystems is therefore necessary for anadromous salmon to complete their life cycles. Given the complexity of salmon life histories and the growing evidence that climate change will affect multiple life stages of salmon (Crozier et al., 2021), considering changes to any one of these habitat domains in isolation may fail to capture the cumulative effect of multiple simultaneous environmental stressors at the population level (Beechie et al., 2023; Cordoleani et al., 2024).

In the Pacific Northwest, USA, forest management is a key facet of land management affecting Pacific salmon populations. Freshwater habitats in this region are embedded within one of the most productive, biomass-rich forest ecosystems in the world (Waring and Franklin, 1979; Spies et al., 2018). After a century of intensive management largely focused on timber production, however, these forests are now characterized by younger, simpler structure and more homogenous species composition than they were prior to European colonization (DeMeo et al., 2018). The departure of temperate coastal forests from their historical condition has prompted calls to restore their structural complexity, with the goals of enhancing old-growth characteristics, carbon storage potential, and resilience to climate change (DeMeo et al., 2018; Case et al., 2023). Although forest management practices aimed at protecting salmon habitat (e.g., protecting riparian buffers) have been enacted in the Pacific Northwest for decades (Richardson et al., 2012), we lack an understanding of the relative extent to which forest management actions aimed at restoring forest structural complexity can improve the health of Pacific salmon populations. As salmon populations and forests each face increasing threats from climate change (Schindler et al., 2008; Halofsky et al., 2020), and as investments in salmon habitat and forest restoration increase (Katz et al., 2007; Haugo et al., 2015; NOAA, 2024), gaining a synthetic understanding of how salmon populations may respond to forest management within the context of climate change is critical.

Along the west coast of the contiguous United States, estuarine ecosystems have also experienced extensive anthropogenic change since the turn of the 20th century. Approximately 85% of vegetated tidal wetlands in this region have been lost to agriculture, industry, diking, and dredging (Brophy et al., 2019). Estuaries have been further degraded by declining water quality, altered hydrology, and the spread of invasive species, each of which can alter the structure and function of food webs or the ecosystem processes sustaining the estuarine mosaic of habitats (Ruiz et al., 1997; Grosholz et al., 2009). Significant investments in estuarine restoration and conservation are underway, with an eye towards supporting Pacific salmon recovery and resilience. The relative impact of these efforts in the context of climate change, or other synergistic upstream recovery actions, are still uncertain, although recent efforts to quantify the cumulative effects of conservation actions indicate that implementing multiple recovery actions is likely beneficial (Beechie et al., 2023).

Here, we evaluate the relative effects of climate- and management-induced ecosystem changes using an integrated population model for three index populations of chum salmon (*Oncorhynchus keta*) spawning in the Willapa basin, southwest Washington state, USA (Fig. 1). We first conduct a retrospective analysis, asking: *(1) How do concurrent land-based restoration strategies affect salmon populations within the context of climate change?* Using this model, we quantify how chum population productivity has changed with ocean conditions, estuarine invasive species control efforts, and management-induced changes to forest structure between 1984 and 2022. We then apply this model to project chum population dynamics and assess population viability under a range of future climate and forest management scenarios, asking: *(2) What is the potential for forest management practices to increase the probability of salmon population persistence under climate change?* Given the broad-scale changes in ocean conditions that will likely affect salmon into the future, our goal is to evaluate the extent to which restoration strategies deployed on land can benefit salmon populations under climate change.

2. Methods

2.1. Study area

The Willapa basin drains a 2400 km^2 area in southwest Washington (USA) (Fig. 1). Most of this area drains into Willapa Bay, a large (380 km^2 or 93,000 acre), shallow estuary characterized by extensive tidal flats. This region has a maritime, temperate climate, with most precipitation falling as rainfall during the winter (i.e., between October and April) (PRISM Climate Group, 2024). The primary vegetation zones in the Willapa basin are the moist Sitka spruce (*Picea sitchensis*) and Douglas-fir/western hemlock zones, the latter of which is dominated by Douglas-fir (*Pseudotsuga menziesii*) successional to western hemlock (*Tsuga heterophylla*) (Reilly et al., 2021). The most common species of Pacific salmon found in this region are Chinook (*O. tshawytscha*), coho (*O. kisutch*), and chum (*O. keta*).

Within the Willapa basin, the Washington Department of Fish and Wildlife (WDFW) monitors index populations of salmon spawning in three watersheds (Fig. 1): Lower Salmon Creek (10,800 acres, elevation ranging from 2 to 300 m), Canon River (10,400 acres, elevation ranging from 3 to 370 m), and Ellsworth Creek (5000 acres, elevation ranging from 3 to 470 m). The Lower Salmon Creek and Canon River watersheds are primarily owned and managed by private industrial timber companies. The Ellsworth Creek watershed is owned by one private landowner, The Nature Conservancy, who acquired it in the early 2000s with the goal of restoring old-growth forests and enhancing wildlife habitat (Case et al., 2023). The forests within the Ellsworth Creek watershed were previously managed for timber production and generally range in age from 20 to 80 years old. Today, forest management consists mostly of restoration treatments focused on either pre-commercial thinning for young stands or commercial thinning for older stands. Commercial thinning treatments generally follow a variable density thinning with “skips and gaps” silvicultural design, focused on promoting structural heterogeneity and species diversity (Harrington, 2009; Churchill et al., 2013).

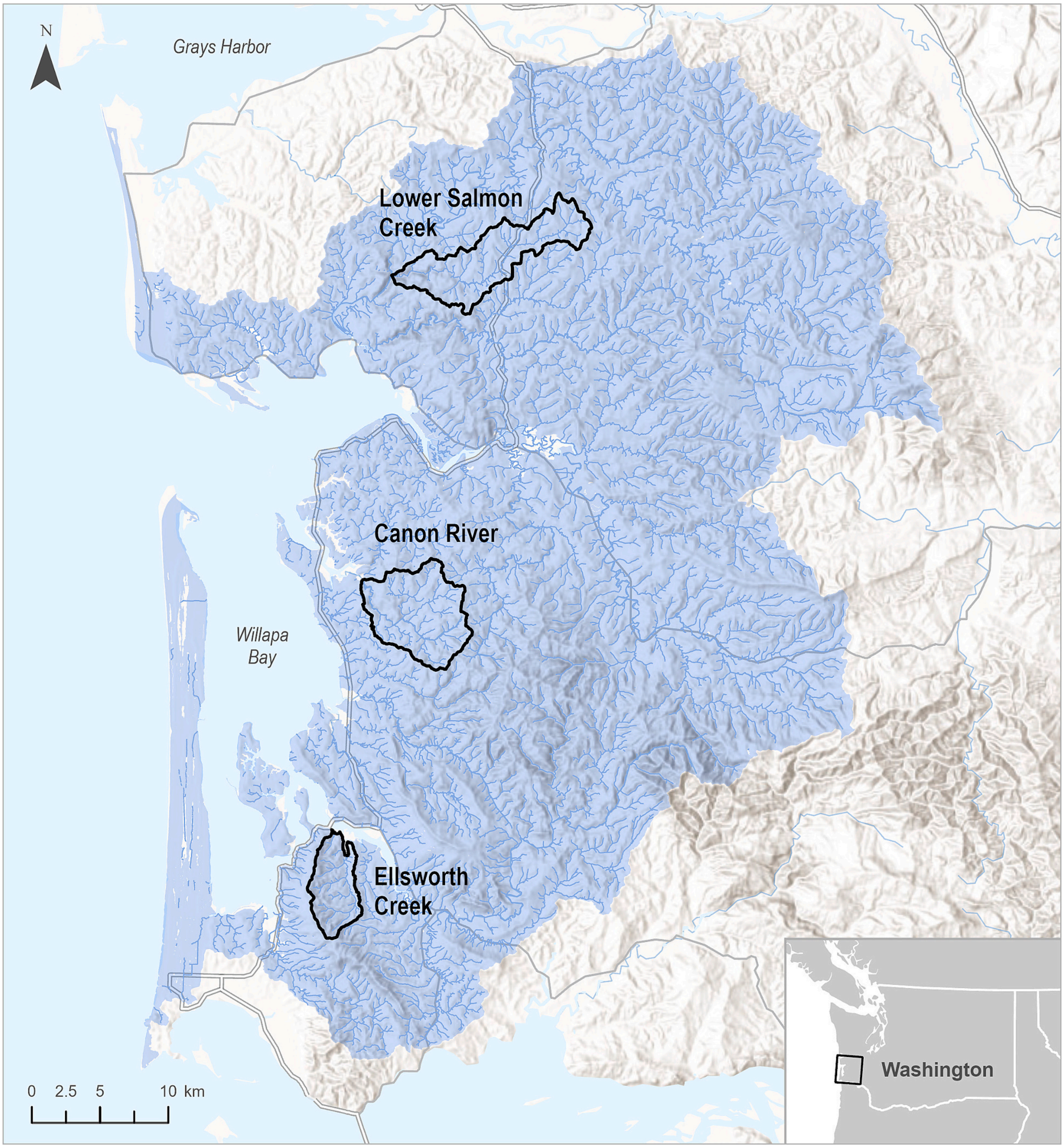

Fig. 1. Willapa basin (blue shading), located in southwestern Washington, with index reach watersheds (black outlines) highlighted. Forest management within the Canon River and Lower Salmon Creek watersheds is focused primarily on timber production, whereas management in the Ellsworth Creek watershed is focused on restoring old-growth structural characteristics and improving wildlife habitat. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Study species

Chum salmon are the most abundant species of Pacific salmon in the Willapa basin and are integral to local ecosystems (Coast Salmon Partnership, 2015). Beyond their economic importance to commercial fisheries (Criddle and Shimizu, 2014), chum provide numerous ecosystem benefits via transportation of biomass and nutrients from marine to freshwater and estuarine ecosystems, as well as bioturbation of stream substrates (Gende et al., 2004; Darimont et al., 2010). Chum are semelparous, meaning that they die after spawning. The increase in nutrients and availability of invertebrate prey associated with spawning chum benefit many other organisms, including other species of Pacific salmon (Minakawa and Gara, 1999; Nelson and Reynolds, 2015).

In the Willapa basin, chum freshwater life stages occur between October (beginning of spawning) and May (end of estuary entry) (Johnson et al., 1997). Juvenile chum emigrate from freshwater to estuaries quickly after emergence, with estuarine residence times ranging from 4 to 32 days prior to ocean entry (Simenstad et al., 1982). Chum are especially sensitive to estuary and early marine conditions, which strongly shape their growth and survival (Johnson et al., 1997; Beechie et al., 2021). After a period of growth and maturation in the ocean, chum typically return to their natal streams to spawn at ages of 3 to 5 years old.

WDFW conducts standardized index reach surveys annually in

Ellsworth Creek, Canon River, and Lower Salmon Creek. WDFW derives annual index reach-specific estimates of spawner abundance using an area-under-the-curve approach (English et al., 1992); these estimates reflect the surveyed reaches (Fig. 2a) and are not expanded to account for available spawning habitat not surveyed. As part of their index reach surveys, WDFW conducts fork length and scale-based age sampling, providing estimates of the size and age composition of spawning adults each year. Finally, WDFW also tracks commercial chum landings in Willapa Bay each fall, which are used to estimate basin-wide chum mortality rates due to fishery harvest. For more detail regarding the salmon data used in our analysis, see Appendix S1.

2.3. *Potential predictors of adult recruitment*

To evaluate land management effects on chum adult recruitment within the context of climate change, we accounted for habitat conditions experienced by chum during the freshwater, estuarine, and marine phases of their life cycle, along with basin-wide hatchery releases, as covariates in our modeling (Fig. 3, Appendix S1, Table S1).

2.3.1. *Watershed-scale forest structure*

Forest management practices, particularly intensive harvesting, can affect the quality of salmon habitat via alterations to stream flow, temperature, and sedimentation (Picchio et al., 2021; Naman et al., 2024). Forest management practices vary widely across the Willapa basin; within the Canon River and Lower Salmon Creek watersheds, management is focused primarily on timber production, whereas management in the Ellsworth Creek watershed is focused on the development of old-growth structural characteristics and improving wildlife habitat (Case et al., 2023).

We quantified forest structure within the three index population watersheds using gradient nearest neighbor (GNN) data from the Landscape Ecology, Modeling, Mapping and Analysis (LEMMA) research group at Oregon State University (Bell et al., 2023). GNN forest structure maps are derived from field-based forest inventory data and Landsat satellite imagery; the data are available at a 30-m resolution and on an annual basis from 1986 to 2021. To characterize changes in forest structural complexity over time, we used the GNN old-growth structural index, which reflects the abundance of large live trees, snags and down wood, and diversity of tree sizes. The index, which ranges from 0 to 100, is unitless and thus not directly interpretable, but thresholds of ≥ 20 and ≥ 50 have been used to classify mature and late-successional forest structure, respectively, in our study region (Davis et al., 2022). We derived annual estimates of forest structural complexity by calculating the arithmetic mean index value mapped across the full extent of each watershed (Fig. 3a). To evaluate the potential importance of proximity to the stream network, we also conducted a sensitivity analysis using average index values within 250-m, 100-m, and 50-m buffers around potentially fish-bearing streams within the watersheds (streams classified type “S” or “F” by the Washington Department of Natural Resources) as covariates in our modeling (Appendix S2, Fig. S1). Because we hypothesize that forest structure in a given year will affect spawning and incubation conditions, we indexed forest structure to brood year (i.e., we did not apply any temporal lag to the forest structure covariate).

2.3.2. *Estuarine habitat conditions*

During our study period, estuarine habitat in Willapa Bay was altered substantially by the introduction and spread of *Spartina alterniflora*, an invasive species of cordgrass. *Spartina* was introduced to Willapa in the early 20th century and expanded rapidly through the early part of our study period. Acreage peaked around 2003, at which point *Spartina* was estimated to occupy 8500 solid acres throughout the estuary, the largest infestation on the West Coast (Civille et al., 2005; WSDA, 2018). We expect that the rapid spread and establishment of *Spartina* throughout the estuary could have affected chum by altering sedimentation and crowding out native eelgrass habitats (Feist, 1999), which juveniles rely on for foraging and predator avoidance (Simenstad et al., 2008; Kennedy et al., 2018). Efforts to eradicate and control *Spartina* in the early 2000s

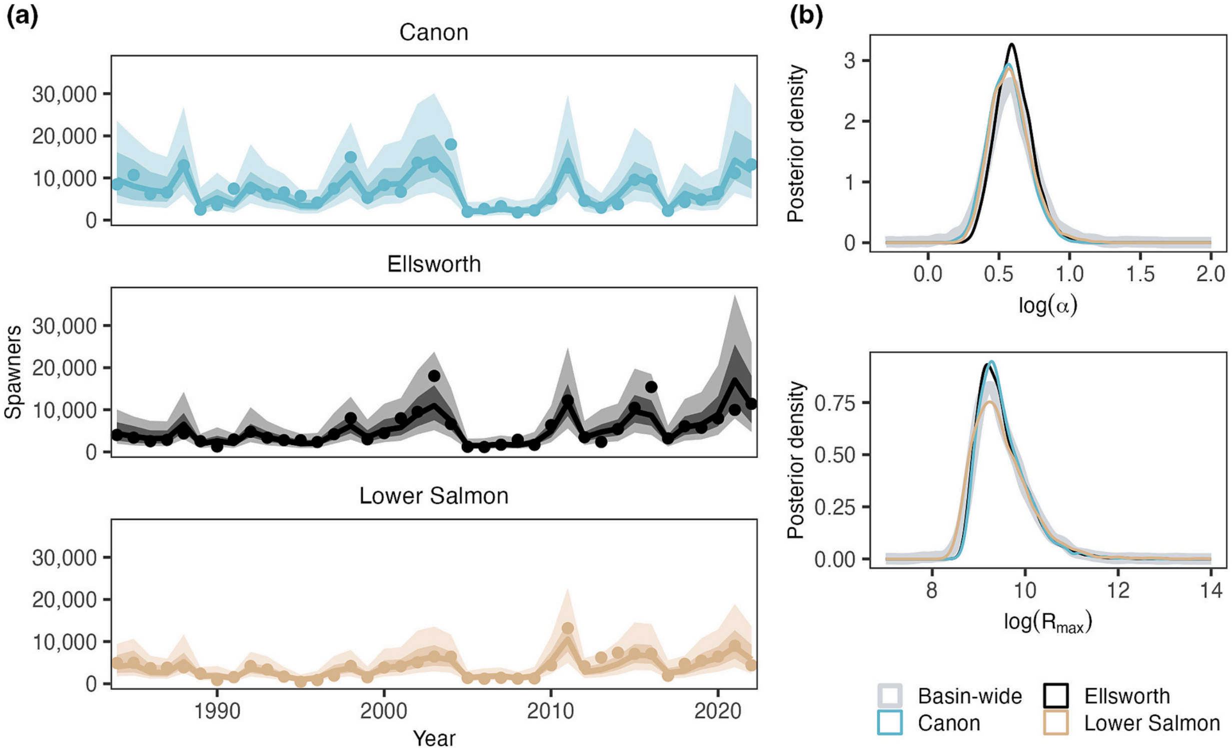

Fig. 2. (a) Observed and model-estimated spawner abundance within survey reaches. Points represent observed data, lines represent posterior medians of the model-estimated true states, and shaded intervals represent 90% credible intervals of the states (dark shading) and posterior predictive distribution of the observations (light shading). (b) Posterior densities for log intrinsic productivity (α) and log maximum recruitment ($R_{\max}$).

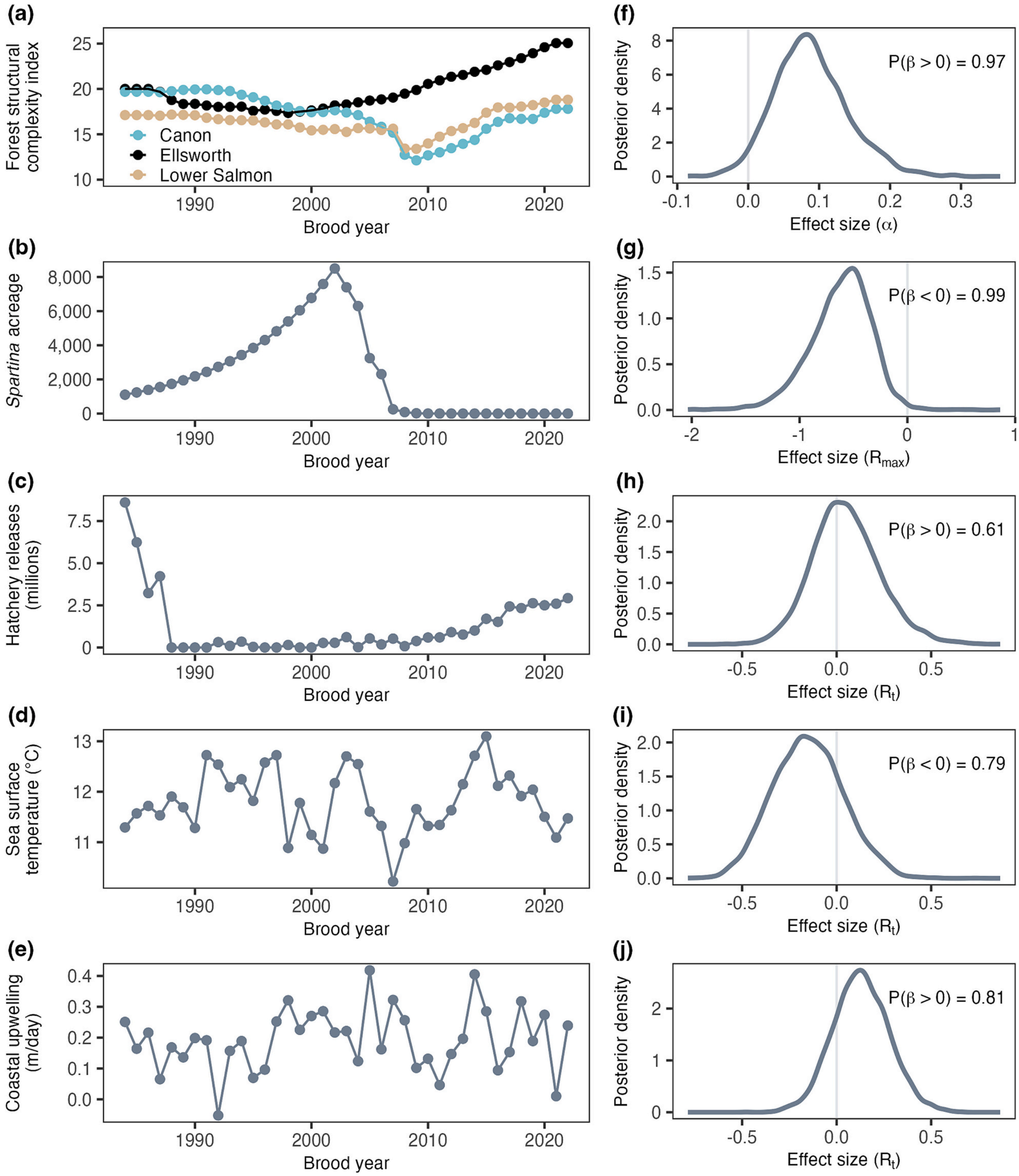

Fig. 3. Model covariates (a – e) and posterior densities of standardized effect sizes (f – j). Effects are per one standard deviation for each covariate and are linked to either intrinsic productivity (α), maximum recruitment (R_{max}), or annual recruit abundance (R_t). Posterior probability that the regression coefficient (β) for each covariate was positive or negative, whichever was more probable, is noted in each posterior density plot. Note that effect sizes can only be compared for covariates affecting the same parameter (i.e., those affecting annual recruitment anomalies, R_t, panels h – j).

led to a sharp reduction in acreage from 2003 to 2010, with acreage currently near-zero.

We obtained annual estimates of *Spartina* acreage in Willapa Bay over the period 2003–2022 from the Washington State Department of Agriculture (Fig. 3b) (WSDA, 2018; Phillips, C. personal communication Nov. 30, 2023). We derived pre-2003 acreages assuming a 12% annual encroachment rate within the estuary (Civille et al., 2005). We indexed *Spartina* acreage to outmigration year to reflect the conditions experienced by juvenile chum when they enter the estuary in the spring following spawning.

2.3.3. *Hatchery releases*

Three hatcheries (Forks Creek, Naselle, and Nemah) release unmarked hatchery-reared juvenile chum in the Willapa basin. Hatchery-origin chum have the potential to compete with natural-origin chum for resources and therefore may negatively affect natural recruit abundance (Cooney and Brodeur, 1998). Conversely, natural-area spawner abundance estimates may also be inflated by an unknown number of hatchery-origin strays (Josephson et al., 2021). To account for a potential effect of hatchery releases on natural recruitment, we included basin-wide hatchery releases reported by WDFW (Fig. 3c) as a covariate in our modeling. We indexed hatchery releases to outmigration year because we hypothesize that natural recruitment is most strongly affected by hatchery-origin chum entering the estuary in the same year as their natural-origin counterparts.

2.3.4. *Ocean conditions*

Ocean conditions experienced by chum during the early marine phase of their life cycle are expected to be strongly linked to their growth and survival (Beamish and Mahnken, 2001; Ottersen et al., 2010). Sea surface temperature (SST) and coastal upwelling are two potentially important facets of the marine environment experienced by chum during their first year at sea. We obtained annual average SST and coastal upwelling occurring in late spring (April–June) along the Washington coast (45–49°N, 123–127°W) (Fig. 3d,e). We indexed SST and upwelling to outmigration year to reflect the conditions experienced by juvenile chum when they enter the ocean the year following spawning. SST data were obtained from NOAA's Extended Reconstructed Sea Surface Temperature (ERSST) dataset (Huang et al., 2017). Upwelling data, specifically the Coastal Upwelling Transport Index (CUTI), were obtained from NOAA's Southwest Fisheries Science Center (Jacox et al., 2018; Jacox, 2023).

2.4. *Future climate and management scenarios*

To evaluate the sensitivity of Willapa chum to future climate, we used projected ocean conditions derived from global climate models (GCMs) (Fig. 4). We obtained SST projections from the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Earth System Grid Federation, 2023) under the Representative Concentration Pathway (RCP) 8.5 scenario. We selected four GCMs for SST (CanESM2, CCSM4, NorESM1-M, and GISS-E2-H), which vary in both the extent to which SST is projected to increase as well as the interannual variability of projections. We bias-corrected projected SST relative to historical SST using the quantile delta mapping approach (Cannon et al., 2015), implemented using the `MBC` package in R (Cannon, 2023). We obtained upwelling projections derived from three downscaled and bias-corrected GCMs from Jacox et al. (2024); since these projections largely do not differ in terms of the magnitude of potential changes in upwelling along the Washington coast, we used only one upwelling projection (derived from the HadGEM2-ES GCM) in our salmon forecasting. Thus, we consider four climate scenarios represented by the four GCM-projected estimates for SST.

To evaluate the potential for forest management practices to increase the probability of salmon population persistence under climate change, we developed two hypothetical future land management scenarios for the Ellsworth Creek watershed (Fig. 4). In the “industrial timber harvest” scenario, we assume that intensive harvesting occurs within the watershed beginning in 2035, resulting in a sharp decline in watershed-scale forest structural complexity over a five-year period. Following harvest, we then assume that forest structural complexity recovers to present-day levels following the trajectory observed within the watershed between 1998 and 2021. In the “ecological forest management” scenario, we assume that management within the watershed continues to prioritize the retention and development of old-growth structural characteristics and wildlife habitat. While we expect that forest structural complexity will continue to increase with ecological forest management practices within the watershed, for simplicity we assume that forest structural complexity in this scenario remains at the present-day, maximum observed levels. We note that The Nature Conservancy does not plan to conduct intensive timber harvesting within the Ellsworth Creek watershed; we construct these scenarios as hypothetical bookends to quantify the extent to which choosing ecological forest management practices over industrial timber harvesting might increase the viability of salmon populations under climate change.

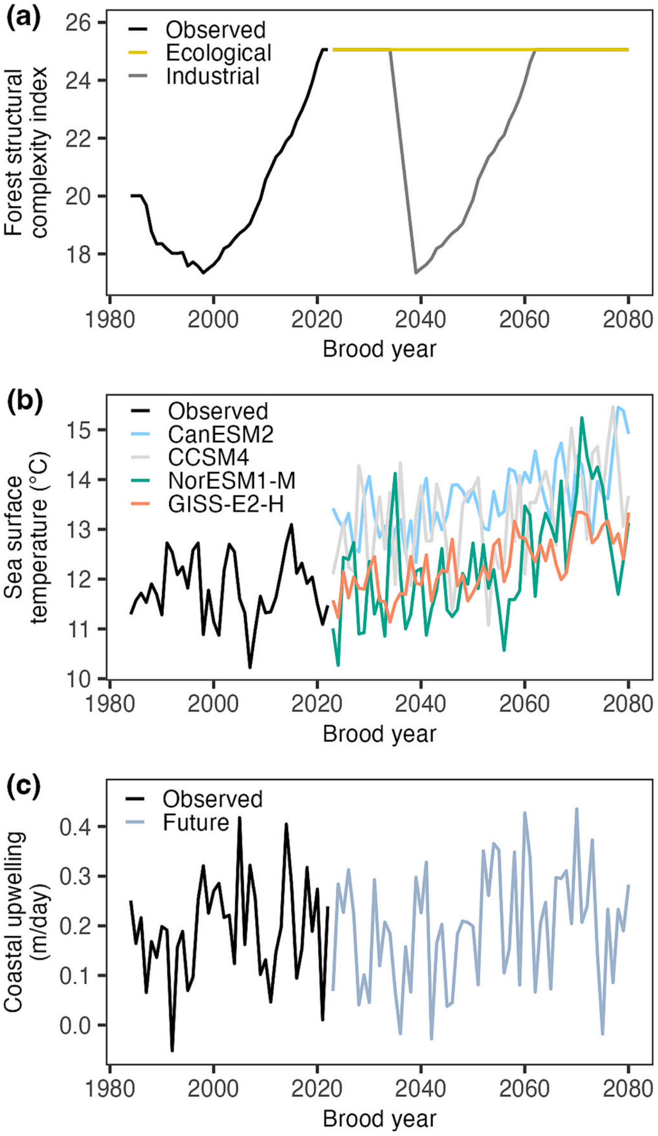

Fig. 4. Covariates under different future climate and forest management scenarios. Forest management scenarios include ecological forest management and industrial timber harvest, denoted “Ecological” and “Industrial” respectively in panel (a). Climate scenarios include the four GCM-derived projections for sea surface temperature shown in panel (b). Covariates included in forecasting but not shown include *Spartina* acreage (assumed to stay near zero) and hatchery releases (assumed to stay near basin-wide goal of 2.5 million fry).

For all future years, we assumed *Spartina* acreages will remain at the near-zero levels observed in 2022 (0.02 acres) with continued control efforts. We assumed that hatchery releases will remain at the current basin-wide goal of 2.5 million released chum fry.

2.5. *Integrated population model*

We use an integrated population model (IPM) for anadromous Pacific salmonids developed by Buhle et al. (2018) to make inferences regarding the three index populations of Willapa basin chum. An IPM is a form of state-space model, partitioning sources of uncertainty into a process model that describes the unknown true population dynamics and an observation model that describes the noisy sampling of the true population state (de Valpine and Hilborn, 2005). In addition, an IPM synthesizes the full information about the dynamics contained in multiple data types (e.g., abundance and age composition) by constructing a joint observation likelihood from the corresponding component likelihoods (Schaub et al., 2007; Maunder and Punt, 2013; Zipkin et al., 2019). Bayesian inference then approximates the joint posterior distribution of all model parameters and latent states, which captures the uncertainty and correlations among them. The IPM of Buhle et al. (2018) includes hierarchical structure across multiple populations whose dynamics are governed by parameters that are themselves modeled by hyper-distributions. This allows information-sharing among related populations experiencing a common environment, such that inferences for populations with relatively sparse data may borrow strength from more data-rich ones (Punt et al., 2011).

2.5.1. Process model

The process model begins with a density-dependent spawner-recruit function. The expected number of recruits, or offspring in population j produced in brood year t that survive to adulthood ($\widehat{R_{jt}}$) is a function of the true number of adult spawners (S_{jt}) given parameters $\boldsymbol{\theta}_j$:

$$\widehat{R_{jt}} = f(S_{jt}|\boldsymbol{\theta}_j). \tag{1}$$

Specifically, we use a Ricker model with parameters α_j (intrinsic productivity, or maximum recruits per spawner at low density) and $R_{max,j}$ (maximum recruitment). $R_{max,j}$ is expressed as a density (fish per unit stream length), which is converted to an abundance by A_j (length of the index reach surveyed for population j),

$$f(S_{jt}|\boldsymbol{\theta}_j) = \alpha_j S_{jt} exp\left(-\frac{\alpha_j S_{jt}}{eA_j R_{max,j}}\right), \tag{2}$$

where e is Euler's constant. We find this reparameterization of the Ricker function is better identified by data than the more familiar parameterization based on per capita density dependence.

The spawner-recruit parameters are modeled with a bivariate lognormal hyperdistribution that allows correlation across populations,

$$[\log\alpha_j, \log R_{max,j}] \sim N([\mu_\alpha, \mu_{R_{max}}], \boldsymbol{\Sigma}_{\alpha R_{max}}), \tag{3}$$

where the covariance matrix is parameterized by the log-SDs $[\sigma_\alpha, \sigma_{R_{max}}]$ and the correlation $\rho_{\alpha R_{max}}$.

The realized number of adult recruits (the unknown true state R_{jt}) incorporates two hierarchical levels of lognormal process error, representing unexplained environmental stochasticity occurring after density-dependent reproduction. The first level is a shared annual anomaly η_{Rt}, which corresponds to regional environmental factors and is modeled as a first-order autoregressive process with autocorrelation ρ_R and innovation SD σ_R^{year}. The second level represents independent population- and year-specific stochasticity with SD σ_R:

$$\log R_{jt} \sim N(\log\widehat{R_{jt}} + \eta_{Rt}, \sigma_R)$$

$$\eta_{Rt} \sim N(\rho_R \eta_{R,t-1}, \sigma_R^{year}). \tag{4}$$

The conditional adult age distribution of recruits from population j and brood year t, given that they survive and return to spawn, is specified by the simplex $\mathbf{p}_{jt}$. For Willapa basin chum, which mature at ages 3–5, $\mathbf{p}_{jt} = [p_{3jt}, p_{4jt}, p_{5jt}]$. These age distributions are modeled with a hierarchical multivariate logistic normal hyperdistribution (i.e., a normal distribution on the vector of additive log ratios; Aitchison, 2003):

$$\text{alr}(\mathbf{p}_{jt}) = \left[\log\left(\frac{p_{3jt}}{p_{5jt}}\right), \log\left(\frac{p_{4jt}}{p_{5jt}}\right)\right]. \tag{5}$$

This hyperdistribution includes among-population heterogeneity and interannual within-population fluctuations around the hyper-mean $\boldsymbol{\mu}_\mathbf{p}$,

$$\text{alr}(\mathbf{p}_{jt}) \sim N(\text{alr}(\boldsymbol{\mu}_\mathbf{p}) + \boldsymbol{\eta}_{\mathbf{p}j}, \boldsymbol{\Sigma}_\mathbf{p})$$

$$\boldsymbol{\eta}_{\mathbf{p}j} \sim N(\mathbf{0}, \boldsymbol{\Sigma}_\mathbf{p}^{pop}), \tag{6}$$

where the within- and among-population covariance matrices $\boldsymbol{\Sigma}_\mathbf{p}$ and $\boldsymbol{\Sigma}_\mathbf{p}^{pop}$, respectively, are parameterized by SD vectors $\boldsymbol{\sigma}_\mathbf{p}$ and $\boldsymbol{\sigma}_\mathbf{p}^{pop}$ and correlation matrices $\mathbf{R}_\mathbf{p}$ and $\mathbf{R}_\mathbf{p}^{pop}$.

Finally, the unknown true number of spawners in year t (the state S_{jt}) is the product of the total recruits from brood year $t-a$ and the proportion that returned to spawn at age a, summed over age classes and adjusted by the fishery mortality rate F_{jt}:

$$S_{jt} = (1 - F_{jt}) \sum_{a=3}^{5} R_{j,t-a} p_{a,j,t-a}. \tag{7}$$

The spawner age distribution, given by the simplex $\mathbf{q}_{jt} = [q_{3jt}, q_{4jt}, q_{5jt}]$, is found by normalizing the summands in Eq. 7.

2.5.2. Incorporating covariates

Covariates are incorporated into the process model and are linked to intrinsic productivity (α_j), maximum recruitment ($R_{max,j}$), and annual recruit abundance (R_{jt}) as described below. Covariate effects are shared among populations (i.e., it is assumed the coefficients do not differ), and covariates are lagged by an appropriate time to reflect the life stage that the covariate is expected to affect most strongly.

We assume that forest structural complexity will affect freshwater habitat *quality* and therefore density-independent survival as represented by the intrinsic productivity parameter. We thus model time-varying intrinsic productivity (α_{jt}) as a function of the population-level mean (α_j) plus the effects of the covariate $x_{\alpha jt}$ with coefficient β_α on the log link scale:

$$\log\alpha_{jt} = \log\alpha_j + \beta_\alpha x_{\alpha jt}. \tag{8}$$

We assume that *Spartina* acreage in Willapa Bay will affect estuarine habitat *quantity* and therefore maximum recruitment. Thus time-varying maximum recruitment ($R_{max,jt}$) is a function of the overall mean ($R_{max,j}$) plus the covariate effect:

$$\log R_{max,jt} = \log R_{max,j} + \beta_{R_{max}} x_{R_{max},j,t+1}. \tag{9}$$

Finally, we assume hatchery releases and oceanographic covariates will affect annual recruit abundance R_{jt} via survival processes after intra-population density dependence. Thus we modify Eq. 1 to model expected recruitment including the effect of covariate row vector $\mathbf{x}_{Rjt}$ with coefficient vector $\boldsymbol{\beta}_R$:

$$\log\widehat{R_{jt}} = \log f(S_{jt}|\boldsymbol{\theta}_j) + \mathbf{x}_{R,j,t+1}\boldsymbol{\beta}_R. \tag{10}$$

2.5.3. Observation model

Data are incorporated via the observation model, which includes likelihood components for spawner abundance and age composition. We assume the observed spawner abundance estimates (S_{jt}^{obs}) are lognormally distributed about the true state with observation error SD τ:

$$\log S_{jt}^{obs} \sim N(\log S_{jt}, \tau). \tag{11}$$

We assume the observed spawner age frequencies, $\mathbf{n}_{jt}^{obs} = [n_{3jt}, n_{4jt}, n_{5jt}]$, follow a multinomial distribution with sample size equal to the total number of spawners aged in population j and year t:

$$\mathbf{n}_{jt}^{\text{obs}} \sim \text{Multinomial}\left(\mathbf{q}_{jt}\right). \tag{12}$$

Finally, for simplicity we assume the estimated mortality rate due to fisheries harvest (F_{jt}) is observed without error (Appendix S1, Fig. S3).

2.5.4. Priors

Hyperparameters in the IPM were given weakly informative default priors (Lemoine, 2019) designed to mildly regularize the posterior to rule out biologically implausible values and avoid numerical issues when sampling. We assessed prior influence by comparing prior and posterior distributions. See Appendix S2, Table S1 for a full list of hyperprior specifications.

Priors are also needed for the initial states (e.g., spawner abundance and age structure in years 1 – 5 of each time series that cannot be generated by previous spawning cohorts in the process model). The abundance of these "orphan" spawners was given a data-aware but weakly informative lognormal prior with log-mean equal to the marginal log-mean of S_{jt}^{obs} across the entire data set scaled by the proportion of orphan age classes in each year, and log-SD equal to the marginal log-SD of S_{jt}^{obs}. The age distribution of orphan age classes was simplex-uniform. Finally, the prior on the initial value of the autoregressive shared recruitment anomalies was the stationary distribution, $\eta_{R1} \sim N\left(0, \sigma_R^{\text{year}} / \sqrt{1-\rho_R^2}\right)$.

2.5.5. Model fitting and population projections

The IPM described here is among the models implemented in the R (R Development Core Team, 2024) package `salmonIPM` (Buhle and Scheuerell, 2024). Models are fitted in a Bayesian framework using the No-U-Turn Sampler (Monnahan et al., 2017) in Stan (Carpenter et al., 2017) via the `rstan` package (Stan Development Team, 2024). We simulated draws from the posterior distribution with four parallel chains of 2000 iterations. The first 1000 warmup iterations of each chain were discarded, resulting in 4000 samples from the joint posterior distribution. We assessed convergence through visual inspection of trace plots and verifying that the potential scale reduction factor (Gelman and Rubin, 1992) was ≤ 1.01 for all parameters. A small number ($< 0.4\%$) of divergent transitions occurred but decreased with stricter target Metropolis acceptance ratio and did not affect inferences, suggesting they were false positives.

To project future population dynamics, we augmented the dataset used for model-fitting by including future projected values for all covariates. We then re-fit the model, with the unknown future spawner and recruit abundances treated as missing data and estimated as additional parameters (Buhle et al., 2018). During this model refitting, we retained observed data for all three index populations and included unknown future values only for Ellsworth Creek, as we were primarily interested in evaluating future forest management scenarios within this watershed.

For each climate and management scenario, we projected population dynamics through the year 2080 (a 58-year or approximately 15-generation time horizon). From each scenario projection, we calculated the probability of quasi-extinction (PQE), defined as the probability that spawner abundance drops below a quasi-extinction threshold indicating the population may be at risk for severe decline (McElhany et al., 2000; ICTRT and Zabel, 2007; Crozier et al., 2021). Following McElhany et al. (2000), we used a quasi-extinction threshold of 50 spawners. We calculated PQE for each scenario as the proportion of posterior projection trajectories in which the four-year (approximately one generation) running mean number of spawners fell below the quasi-extinction threshold at least once. Because chum are integral to overall ecosystem health in the Willapa basin, and even a moderate decline in their populations could be of concern, we also calculated the proportion of posterior projection trajectories in which the four-year running mean spawner abundance fell below 1000 (the lowest annual spawner count observed in Ellsworth Creek during our study period) at least once.

3. Results

Trends in spawner abundance were highly synchronous across the three Willapa basin index populations from 1984 to 2022 (Fig. 2a). The multi-population IPM captured these trends well; median estimates of true spawner abundance closely agreed with the observed data and all observed values fell within the 95% credible intervals of the posterior predictive distribution.

Estimated spawner–recruit functions were comparable among populations (Fig. 2b). Population-specific estimates of intrinsic productivity (α, the slope of the spawner–recruit curve near the origin) and maximum recruitment ($R_{\max}$, the peak of the Ricker curve) clustered closely around the basin-wide means (μ_α and $\mu_{R_{\max}}$, respectively). The posterior median of μ_α was 1.8 recruits per spawner (95% credible interval = 1.2–2.7). The posterior median of $\mu_{R_{\max}}$ was approximately 12,000 adults per surveyed river mile (95% credible interval = 5500–52,600). Observation error in spawner abundance was smaller than recruitment process error, the latter of which was dominated by the autoregressive component shared among populations (posterior median of $\tau = 0.34$ versus $\sigma_R^{\text{year}} = 0.81$). The basin-wide mean age-at-return distribution ($\boldsymbol{\mu}_{\mathbf{p}}$) was dominated by age-4 spawners, followed by ages 3 and 5 (posterior median of $\boldsymbol{\mu}_{\mathbf{p}} = [0.22, 0.70, 0.08]$), with the observed data suggesting a trend towards a greater proportion of age 3 (i.e., younger) spawning adults in recent years (Appendix S1, Fig. S1).

Forest structural complexity was positively related to intrinsic productivity ($P[\beta_\alpha > 0] = 0.97$; Fig. 3f), suggesting that older, more complex forest structure may increase freshwater habitat quality for spawning and juvenile chum, and conversely that reductions in forest structural complexity due to intensive timber harvest may decrease habitat quality. A sensitivity analysis evaluating the spatial footprint captured by the forest structural complexity covariate (i.e., the entirety of each index population watershed versus 250-m, 100-m, or 50-m stream buffers) suggested that the effect of forest structure becomes slightly more pronounced with increasing proximity to the stream network (Appendix S2, Fig. S1).

Spartina acreage in the Willapa Bay estuary was negatively related to maximum recruitment ($P\left[\beta_{R_{\max}} < 0\right] = 0.99$; Fig. 3g). This suggests that the *Spartina* infestation may have reduced the amount of estuarine habitat available for juvenile chum, and conversely that the successful bay-wide *Spartina* eradication efforts benefited chum by restoring critical estuarine habitat.

The effect of basin-wide hatchery releases on annual recruit abundance (R_t) was essentially zero ($P[\beta_R > 0] = 0.61$; Fig. 3h), providing no evidence for competitive interaction between hatchery- and natural-origin juveniles. Willapa Bay hatchery fry production is much lower than natural fry production, and hatchery strays are therefore expected to introduce minimal bias into our population estimates. See Appendix S1 for additional details.

Sea surface temperature had a largely negative effect on annual recruit abundance ($P[\beta_R < 0] = 0.79$; Fig. 3i) and coastal upwelling had a largely positive effect ($P[\beta_R > 0] = 0.81$; Fig. 3j). This suggests that increasing sea surface temperatures may reduce chum growth and survival during the marine phase of their life cycle, whereas coastal upwelling (which drives nearshore ecosystem productivity) may increase chum growth and survival, leading to increased recruitment.

Projected spawner abundances for Ellsworth Creek were characterized by wide uncertainty intervals (Fig. 5a) resulting from variability in demographic processes and environmental stochasticity that compounds over time. Projections were sensitive to future climate conditions, with probability of quasi-extinction (PQE) ranging from ~3–11% in the climate scenarios characterized by greater increases in sea surface temperature (CanESM2 and CCSM4), versus <1% in the climate

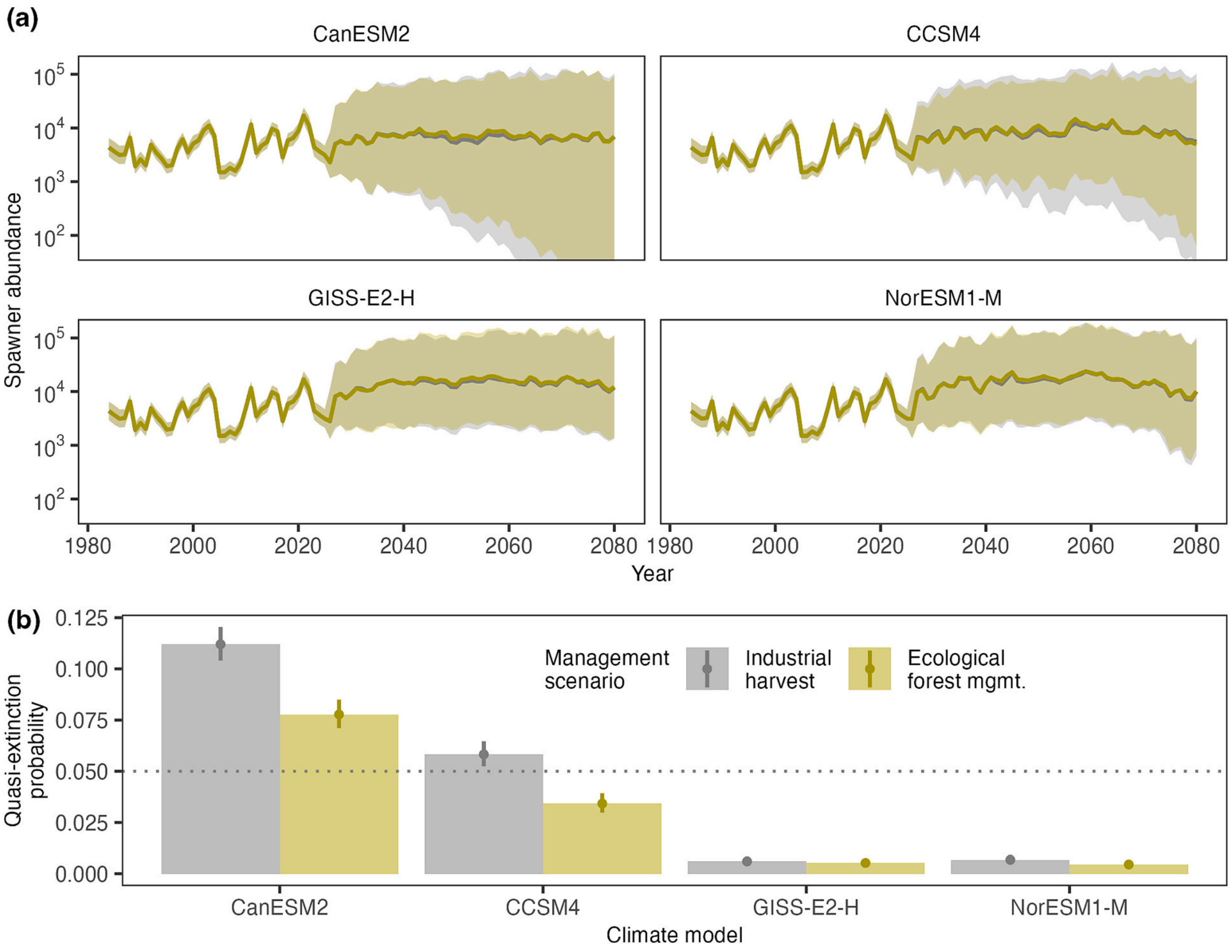

Fig. 5. (a) Spawner abundance projections under different climate and forest management scenarios. Solid lines represent posterior medians, and shaded intervals represent 90% credible intervals. (b) Corresponding probabilities of quasi-extinction under different climate and forest management scenarios. Vertical lines represent 90% binomial confidence intervals based on the $n = 4000$ posterior projection outcomes. Horizontal dotted line denotes the 5% quasi-extinction probability threshold below which NOAA guidance suggests populations are considered viable (McElhany et al., 2000).

scenarios with less pronounced warming (GISS-E2-H and NorESM1-M) (Fig. 5b). Similarly, the probability that four-year (approximately one generation) spawner abundances will decline below 1000 spawners (the lowest single-year observed level) ranged from ~20–33% in the CanESM2 and CCSM4 climate scenarios, versus ~6–10% in the GISS-E2-H and NorESM1-M climate scenarios (Appendix S2, Fig. S2).

Across climate scenarios, PQE was lower in the "ecological forest management" scenario relative to the "industrial timber harvest" scenario (Fig. 5b), suggesting forest management strategies that maintain forest structural complexity may increase the probability of chum population persistence under climate change. The potential benefit of ecological forest management was most apparent in the climate scenarios with more pronounced sea surface temperature warming (PQE reduced from 11% to 8% in the CanESM2 climate scenario and from 6% to 3% in the CCSM4 scenario). NOAA guidance suggests populations with <5% probability of extinction are considered viable (McElhany et al., 2000); thus, in the CCSM4 climate scenario, ecological forest management practices reduced the PQE to a level meeting the acceptable threshold for a viable population.

4. Discussion

4.1. Land-based restoration strategies can increase the probability of salmon population persistence under climate change

Our findings illustrate that watershed-scale forest management strategies have the capacity to bolster salmon population persistence under climate change. Across climate scenarios, our model projections suggest that Ellsworth Creek chum could face an increasing risk of potential population collapse by the late 21st century due to declining recruitment associated with rising sea surface temperatures. Across forest management scenarios, however, our projections suggest that continuing to maintain and promote forest structural complexity across the Ellsworth Creek watershed may meaningfully reduce the risk of chum population collapse, relative to a hypothetical future scenario in which the watershed is intensively harvested for timber. To the best of our knowledge, this is the first study using field-collected observations to quantify the extent to which watershed-scale forest management may help buffer the negative impacts of climate change for Pacific salmon. In the Pacific Northwest, USA, coastal temperate forests are broadly in need of restoration following more than a century of management predominantly focused on timber production (Haugo et al., 2015). Increasingly, land managers are implementing forest management strategies that seek to maintain or increase forest structural complexity for a variety of objectives, including climate resilience, carbon storage, and wildlife habitat (Case et al., 2023). Our findings suggest that improved long-term salmon population health can be seen as an additional benefit of ecological forest management practices that address these multiple objectives.

In addition to forest management, estuarine invasive species control efforts also had measurable effects on chum population dynamics, highlighting the benefits of multiple conservation efforts targeting the full mosaic of habitats that salmon require to complete their life cycle. Other habitat changes occurred within our study system during the 1984–2022 period, including climate-induced changes to freshwater and estuarine habitats, as well as in-stream habitat restoration efforts along the mainstem of Ellsworth Creek. Although we were not able to incorporate all these concurrent habitat changes into our analysis, our findings nevertheless illustrate the capacity for multiple types of conservation action stacked within a watershed to contribute to salmon population resilience (Beechie et al., 2023).

4.2. *Forest structure affects salmon at multiple scales*

Forest structure can affect salmon at multiple spatial scales within watersheds, and our findings highlight the importance of watershed-scale management that considers the structure of surrounding upland forests in addition to the riparian zone (Burnett et al., 2006; Andrew and Wulder, 2011; Stanfield and Kilgour, 2013). The productivity of our study populations increased with both watershed-wide and stream-buffer-scale forest structural complexity, likely through effects that forest structure can have on runoff, stream flow, sedimentation, shading, and woody inputs to streams (Andrew and Wulder, 2011; Anlauf et al., 2011; Steel et al., 2017). We estimated positive effects of forest structural complexity that were slightly more pronounced at the stream-buffer scale than at the watershed-wide scale (Appendix S2, Fig. S1). Nonetheless, the positive relationship that we observed between chum productivity and watershed-wide forest structural complexity illustrates the potential for the entire catchment, not just the riparian zone, to influence the quality of in-stream habitat for salmon.

Forest structure can also affect salmon at multiple temporal scales, particularly following stand-replacing disturbance (Martens et al., 2020). The relationship we quantify between chum productivity and forest structural complexity is likely driven by the pronounced effects of intensive timber harvest, which caused sharp declines in forest structural complexity within two of our focal watersheds in the mid-2000s. Removal of forest cover via intensive timber harvest can affect salmon habitat by altering channel morphology, stream temperature, and flow, among other factors (Hicks et al., 1991; Crampe et al., 2021; Naman et al., 2024). In the initial years following intensive harvest, forest re-establishment benefits salmon by facilitating soil stabilization and hydrologic recovery (Stednick, 2008; Kaylor et al., 2017). Over long time scales (i.e., many decades to centuries), the development of old-growth forest structure benefits salmon via inputs of large wood, which provide critical in-stream habitat complexity (Reeves and Bisson, 2009; Martens et al., 2020). Over intermediate time scales (i.e., the initial decades to century following forest re-establishment), the dense canopy shading and small tree sizes that typically characterize mid-seral forest stages have the potential to limit in-stream productivity and large wood recruitment (Martens et al., 2019, 2020), thus it is less clear whether the development of forests through these stages benefits salmon population health. By maintaining and accelerating the development of forests towards more complex structure, however, forest management strategies such as longer-term rotations and variable density thinning are likely to enhance the long-term health of salmon populations, thus increasing their ability to withstand broad-scale stressors introduced by climate change. Because restoration of old-growth forest structure is inherently a slow process (Case et al., 2023), coupling these strategies with in-stream restoration actions that can improve near-term habitat complexity or flow regimes (e.g., large wood additions) may help support salmon productivity through interim stages of forest development (Martens et al., 2019).

4.3. *Climate change is putting pressure on salmon populations*

Our findings add to the growing body of evidence that climate change threatens the health of many Pacific salmon populations (Abdul-Aziz et al., 2011; Crozier et al., 2019, 2021; Adams and Zimmerman, 2023). The chum populations that we evaluated are not currently listed as threatened or endangered under the United States Endangered Species Act, but our model projections suggest that the viability of these populations may drop below acceptable levels (i.e., $<$ 95% probability of persistence over a 100-year period; McElhany et al., 2000) with continued ocean warming. Because our study populations play a key role in the function of the local ecosystem (Coast Salmon Partnership, 2015), even moderate declines in spawner abundance could pose a concern for overall watershed health. These findings highlight that addressing global climate change is critical for protecting and restoring the health of Pacific salmon populations, even those not currently at risk of extinction. Given the relatively long timeframes over which climate change trajectories can potentially be mitigated (e.g., through emissions reductions), our findings also highlight the need for interim restoration and climate adaptation measures that can be taken now to strengthen the long-term resilience of salmon populations (Adams and Zimmerman, 2023; Beechie et al., 2023).

Although climate change can affect organisms in both positive and negative ways, the net effects of changing ocean conditions on our focal chum populations appear strongly negative. Projected increases in sea surface temperatures are likely to result in declining chum population viability by the end of the 21st century, due to the estimated negative effect of sea surface temperature on chum recruitment. Our results suggest chum recruitment may respond positively to increases in coastal upwelling, which has the potential to offset some of the negative effects of temperature on nearshore ocean productivity (Crozier et al., 2021). However, climate projections for our study region suggest upwelling may increase only slightly by the end of the century (Jacox et al., 2024). Thus, although it is possible that coastal upwelling may mitigate the negative effects of rising temperatures for some salmon populations, this is more likely to be the case in regions where upwelling is expected to increase more substantially with climate change.

Our study likely underestimates the negative effects of climate change on salmon populations, as we accounted for shifting ocean conditions but did not also account for climate-induced changes to freshwater or estuarine habitats. Warming stream temperatures, altered stream flows, and loss of estuarine habitats due to rising sea levels (Wainwright and Weitkamp, 2013; Adams and Zimmerman, 2023) are expected to put additional pressure on salmon populations and further exacerbate broad-scale ocean effects. Although our analysis likely underestimates climate pressures, it also does not account for the potential adaptive capacity of salmon to changing habitat conditions via phenological shifts (e.g., timing of ocean outmigration) and plasticity in other dimensions of their life histories (Crozier et al., 2008). Refining our understanding of the ways that climate change will affect salmon populations, along with the ways in which populations may adapt to changing conditions, will be critical to identifying the conservation actions most likely to support persistence of these populations into the future.

4.4. *Model strengths and uncertainties*

Integrated population models (IPMs) like the one described here offer numerous advantages over other life cycle modeling approaches. A key strength is their ability to account for the combined uncertainties in multiple data sources, thus reducing bias and leading to more precise estimates of demographic parameters (Zipkin et al., 2019; Scheuerell et al., 2021). We used an IPM developed specifically for Pacific salmon life histories and the structure of common salmon monitoring data (Buhle et al., 2018; Buhle and Scheuerell, 2024). Ohlberger et al. (2025) used a similar `salmonIPM` model, expanded to include iteroparity, to identify environmental factors in the decline of recruitment and repeat spawning rates in Washington coast steelhead populations. While that was a retrospective analysis, here we show how the IPM structure is easily used to evaluate both the relative effects of past management actions and also the extent to which future forest management practices might increase the persistence of our study populations under climate change. We considered a relatively long time horizon for future projections (2023–2080), recognizing that quantitative population-dynamic forecasts over long time horizons are characterized by large uncertainties, regardless of the model used (Fieberg and Ellner, 2000; Schindler and Hilborn, 2015). Our goal, however, was not to precisely forecast salmon abundances, but rather to conduct a comparative scenario assessment for climate and management processes that diverge over several decades.

5. Conclusion

As climate change continues to alter the quality and quantity of habitat for Pacific salmon, identifying land-based restoration strategies that can increase the resilience of salmon populations to climate change is becoming increasingly important (Beechie et al., 2023). We evaluated population-level responses to management- and climate-induced changes occurring simultaneously across freshwater, estuarine, and marine nearshore ecosystems, an approach that is needed to account for the compounding environmental stressors experienced by salmon throughout their life cycle (Gosselin et al., 2021). Our findings suggest that continued ocean warming through the end of the century will cause declines in the viability of chum populations in our focal watersheds, but that maintaining and promoting watershed-scale forest structural complexity can meaningfully decrease the risk of population collapse, relative to a baseline scenario in which forests are intensively managed for timber. Overall, our study highlights the capacity for multiple types of conservation action within a watershed to contribute to salmon population health, even within the broader-scale context of increasing pressures posed by climate change.

CRediT authorship contribution statement

Michele S. Buonanduci: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Eric R. Buhle:** Writing – review & editing, Software, Methodology. **Michael J. Case:** Writing – review & editing, Conceptualization. **Emily R. Howe:** Writing – review & editing, Conceptualization. **James C. Robertson:** Writing – review & editing, Data curation, Conceptualization. **Nicholas VanBuskirk:** Writing – review & editing, Investigation, Conceptualization. **Ailene K. Ettinger:** Writing – review & editing, Supervision, Project administration, Methodology, Conceptualization.

Declaration of competing interest

The authors have nothing to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111099.

Data availability

Data and code are available on Zenodo: https://doi.org/10.5281/zenodo.15041752.

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