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Declining Marine Survival of Steelhead Trout Linked to Climate and Ecosystem Change

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ABSTRACT

Species with complex life cycles, such as anadromous fish that perform spawning migrations between freshwater and the ocean, may be particularly sensitive to global change because freshwater and marine habitats experience distinct shifts in climate and ecosystem dynamics. Abundances of wild steelhead trout (*Oncorhynchus mykiss*) have declined across most of their range over the past 40–50 years. We examined whether declines in steelhead survival can be linked to changing climate conditions and species interactions. A novel hierarchical integrated population model that accounts for the species' complex life history was fitted to data from multiple wild steelhead populations on the Washington coast, U.S.A. The model estimates recruitment residuals and kelt survival rates as time-varying processes, which reflect annual variation in survival before and after first maturation. We found that survival rates of immature steelhead (recruits) and adult steelhead (kelts) have declined over time and that survival trends across populations were strongly associated with climate and ecosystem change, specifically summer sea surface temperature and pink salmon abundance in the North Pacific Ocean, the NPGO index and river flows. Including these drivers in the model reduced unexplained annual variation in shared recruitment and kelt survival anomalies and largely accounted for their negative long-term trends. Our findings provide evidence that rising temperatures and increased interspecific competition at sea have contributed to declines in steelhead survival over the last five decades. Considering projected warming and high pink salmon abundances in the ocean, steelhead will likely continue to experience low marine survival rates.

1 | Introduction

Species with complex life cycles such as anadromous fishes may be particularly sensitive to global change because freshwater and marine habitats differ in the magnitude and pace of climatic and ecosystem change (Burrows et al. 2011; IPCC 2023), and because life stages differ in their resource use and sensitivity to environmental factors, including temperature (Groot and Margolis 1991; Pörtner and Farrell 2008; Comte and Olden 2017; Crozier et al. 2021). In addition, changes in ecological conditions such as altered food availability or competitive interactions amongst species can have large effects on individual growth and survival and may alleviate or exacerbate climate-related impacts (Cline, Ohlberger, and Schindler 2019; Connors et al. 2020).

Life history complexity, such as diversity in age structure, habitat use and migration timing, is an essential component of the biocomplexity of populations, especially in anadromous salmonids

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(Hilborn et al. 2003; Schindler et al. 2010). Diverse life histories reduce the risk of cohort failure and stabilise population abundance in the face of a variable and uncertain environment (Wilbur and Rudolf 2006; Moore et al. 2014). Evidence suggests that shifts in life history traits, such as changes in the age structure of mature fish due to altered maturation schedules, survival rates or other factors, can affect population productivity and population responses to environmental change (Ohlberger et al. 2020; Rouyer et al. 2012). In iteroparous species, such as steelhead, the proportion of repeat spawners has important implications for lifetime reproductive success and population resilience (Moore et al. 2014; Christie et al. 2018).

Steelhead trout (*Oncorhynchus mykiss*) are a prime example of an anadromous, iteroparous fish species with a complex life cycle that are exposed to numerous environmental stressors. They start their life in freshwater and migrate to the ocean to grow and mature before returning to their natal streams to spawn. Being iteroparous, they can undergo multiple spawning migrations between the North Pacific Ocean and freshwater streams. Abundances of wild steelhead populations have declined across much of their range over the past 40–50 years, including in Washington (WA) State (Cram et al. 2018; Losee, Kendall, and Dufault 2019; Ford 2022). It has been hypothesized that changes in abundance and life history characteristics are linked to habitat destruction and changing ocean conditions, in particular climate change (Busby et al. 1996; Crozier et al. 2019). Declines in abundance and life history diversity have led to the listing of several Distinct Populations Segments (DPSs) of steelhead in WA under the U.S. Endangered Species Act (ESA). The exceptions are steelhead populations on the WA coast that belong to the Olympic Peninsula and Southwest Washington DPSs, which are not currently listed under the ESA, although their abundances have declined since at least the 1980s (Kendall, Marston, and Klungle 2017; Cram et al. 2018; McMillan et al. 2022).

Poor marine survival may contribute to declines in steelhead abundance. Multiple stressors in the marine environment including ocean warming, changing predator abundances, competition between salmonids and other broad ecosystem changes (Welch et al. 2000; Kendall, Marston, and Klungle 2017; Sobocinski et al. 2020; Moore et al. 2021) affect steelhead survival rates, which vary greatly over time (Moore et al. 2021; Kendall, Marston, and Klungle 2017; Wilson et al. 2021). Similar stressors in the marine environment influence distinct steelhead populations because they have overlapping marine distributions, especially once they leave coastal areas and migrate to common feeding grounds in the Gulf of Alaska and the North Pacific Ocean (Sutherland 1973; Light, Harris, and Burgner 1989; Welch et al. 1998; Courtney et al. 2022). Freshwater conditions such as increasing temperatures, changing flow regimes and habitat alteration can also impact the survival of salmonids during freshwater residence, in addition to changing ecological and climate conditions in the marine environment (Quinn 2005; Boughton et al. 2007; Crozier et al. 2010; Ward et al. 2015).

The North Pacific typically experiences strong interannual and interdecadal variation in ocean conditions, as reflected in climate patterns such as the Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO, Di Lorenzo et al. 2008) and upwelling dynamics (Mantua et al. 1997; Litzow et al. 2020). In addition, the North Pacific has experienced directional changes in ecological and environmental conditions over the past few decades. These changes include the recovery of pinniped populations such as harbour seals that feed on juvenile and adult salmonids (Thomas et al. 2017), increased temperatures due to climate warming (Burrows et al. 2011; Hu et al. 2024), shifting salmon distributions (Shelton et al. 2021) and altered production dynamics of both wild and hatchery salmonids (Ruggerone and Irvine 2018).

The abundance of anadromous salmonids in the North Pacific Ocean has increased steadily over the past few decades, due in part to increased hatchery production (Ruggerone and Irvine 2018). Pink salmon are the most abundant species and their numbers have more than doubled since the 1970s, whilst chum salmon are the most dominant species in terms of total biomass (Ruggerone et al. 2023). Pink salmon have far-reaching impacts on the marine ecosystem, including top-down and bottom-up trophic cascades and reduced growth and survival of other Pacific salmon (Ruggerone and Nielsen 2004; Springer and van Vliet 2014; Ruggerone and Connors 2015; Batten, Ruggerone, and Ortiz 2018), likely due to overlapping diets and ocean distributions (Myers et al. 1996; Kaeriyama et al. 2004; Johnson and Schindler 2008). Pink salmon and steelhead are known to compete for resources in the marine environment such as squid (Atcheson et al. 2012a) and there is some evidence suggesting that pink salmon may adversely affect the marine survival of steelhead (Ruggerone et al. 2023).

Here, we examined whether changing survival rates in freshwater and in the ocean have contributed to abundance trends in WA coastal steelhead and whether changes in survival are associated with altered ecological conditions, in particular shifts in climate, predation and competition. We fit a hierarchical integrated population model (IPM; Schaub and Abadi 2011; Maunder and Punt 2013; Zipkin and Saunders 2018) to data on multiple populations of wild winter steelhead on the WA coast (Figure 1), including populations in the Chehalis, Hoh, Humptulips, Queets, Quillayute and Quinault Rivers. By estimating time-varying processes that capture changes in survival to first maturation (recruitment) and after maturation (kelt survival) in addition to accounting for potential covariate effects on these processes, we can link changes in steelhead survival to shifts in environmental conditions and species interactions. In doing so, we demonstrate the utility of this analytical approach that can be applied to a variety of species with a range of life histories to answer important questions about what environmental pressures are shaping abundance and survival trends.

2 | Materials and Methods

The IPM described below is a statistical population dynamics model that integrates information on adult return abundances (estimates of harvest and escapement) and demographic structure (age composition) into a combined run-reconstruction and spawner-recruit model for multiple populations. It provides population-level estimates of parameters such as productivity and capacity, as well as time-varying recruitment residuals and covariate effects on each of these parameters or states. The

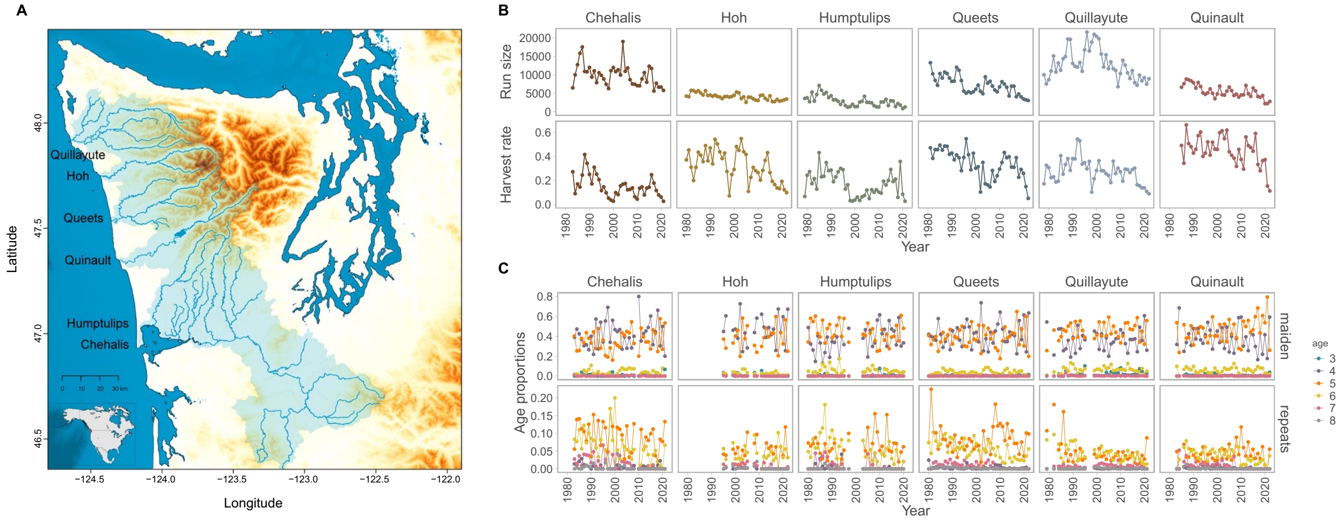

FIGURE 1 | Map of study region with observational data for examined steelhead populations. The main map shows the study region and major river systems with their main tributaries (A). Light blue areas indicate the full extent of the watersheds and river names indicate the modelled steelhead populations. The inset map of North America indicates the geographical extent of the main map (small red box). Data for each population are presented as annual observations of total run size and harvest rates (B) and age proportions for maiden and repeat spawners based on scale samples in tribal fisheries (C).

model further accounts for iteroparity by distinguishing maiden steelhead from repeat spawners and estimates changes in kelt survival rates that reflect variation in survival after first maturation. We first discuss the data types used to fit the IPM and then detail the model structure.

2.1 | Steelhead Life History

Steelhead reproduce, hatch and rear in freshwater streams and rivers. Juveniles migrate to the ocean after 1–7 years in freshwater and spend up to 5 years at sea (Scott and Gill 2008). Once in salt water, steelhead migrate thousands of kilometres across the open ocean to feeding grounds in the North Pacific Ocean, including the Gulf of Alaska, the southern Bering Sea and the east coast of Asia (Burgner et al. 1992; Light, Harris, and Burgner 1989; Welch et al. 1998; Courtney et al. 2022). Based on their run timing and sexual maturity, steelhead are typically categorised into summer and winter runs. Whilst our focus is on wild winter-run steelhead that typically return to freshwater as mature adults between November and April, several of the examined rivers have smaller populations of summer-run steelhead that typically return between May and October in a state of sexual immaturity and continue to develop in fresh water for several months prior to spawning. Steelhead in WA coastal rivers have a spawning period from January through June with peak spawning from March through May. The vast majority of coastal winter steelhead migrate to sea in late spring at age 2, spend 2–3 summers in the ocean and return in the fall as total age of 4 or 5 fish. First-time or *maiden* spawners can be distinguished (using a fish's scales) from *repeat* spawners that have previously spawned (becoming *kelts*) and then returned to marine waters. Female winter steelhead and younger age classes of maiden spawners often survive to repeat spawn at higher rates than older and male spawners (Withler 1966; Ward and Slaney 1988; Seamons and Quinn 2010). Additionally, steelhead co-occur with rainbow trout, the resident form of *O. mykiss* that completes the entire life cycle in freshwater and is often male-biased due to sex-specific tradeoffs in the benefits of anadromy (Jonsson and Jonsson 1993). The anadromous and resident forms can interbreed to produce offspring that may adopt either life history strategy, depending on a combination of genetic and environmental factors (Kendall et al. 2015; Berejikian, Campbell, and Moore 2013).

2.2 | Population Data

Steelhead on the WA coast have provided an important food and cultural resource for indigenous communities (henceforth referred to as Tribes) in the Pacific Northwest for millennia, and as Washington State's gamefish they are a keystone of sport fisheries. However, consistent monitoring of spawner abundance did not begin until the late 1970s (Cooper and Johnson 1992; Johnson et al. 1997). Since then, extensive surveys of redds (gravel depressions that females dig to deposit eggs) have been performed by state, tribal and federal fisheries managers. Redd counts are used to produce annual estimates of spawner abundance in the wild. We gathered spawner abundance estimates for the period 1978–2022, although these estimates were not available for all years in all populations (Figure 1). Spawner abundance estimates are based on spawning ground surveys conducted after March 15th each year to exclude early run hatchery steelhead that may spawn naturally in rivers (Cram et al. 2018). This cut-off date may negatively bias estimates of wild spawner abundance because a small proportion of wild winter steelhead spawn prior to March 15th whilst the proportion of hatchery fish spawning after that date is negligible.

We also assembled data on fishing mortality that have been curated by the Tribes (Hoh Tribe, Quileute Tribe and Quinault Indian Nation) and Washington Department of Fish and Wildlife. Harvest impacts include tribal commercial, subsistence and ceremonial harvest and non-tribal sport catch.

Release of wild steelhead has been required year-round since 2016. Our harvest mortality estimates do not include non-retention mortality such as incidental hooking mortality in the sport catch and release fishery or net drop-out in the tribal net fisheries because these are not consistently available. Whilst our harvest rates may be underestimated due to a lack of information on non-retention mortality, we believe that the magnitude of potential bias is low. For example, assuming that the proportion of the run encountered by a sport fishery ranges between 50% and 150% (Bentley 2017) and the catch-and-release mortality rate is between 1.4% and 5.8% (Nelson, Rosenau, and Johnston 2005), we would estimate a non-retention mortality rate of roughly 0.7%–8.7%. We therefore evaluated the sensitivity of our results by fitting a model that assumed harvest rate (F) estimates were biased low by 5% in each year and river (i.e., bias-corrected $F=$ estimated $F+5\%$).

We used information on the age structure of returning fish as a complementary dataset to the abundance data to reconstruct cohort recruitment from the adult return data (Figure 1). Scale samples have been taken from steelhead captured in tribal gillnet fisheries and aged since the 1970s, providing information on freshwater age, saltwater age and number of repeat spawning events for each sampled fish. The age and iteroparity estimates generated from scales are used for fishery management and conservation of wild steelhead from coastal Washington (Busby et al. 1996; Scott and Gill 2008). Age estimates are made by visual interpretation of alternating zones of tightly and widely spaced scale circuli, termed annuli, to describe the total age and the number of winter annuli (i.e., years) formed in freshwater and at sea (Shapovalov and Taft 1954). Iteroparity can be identified because scales resorb during previous spawning migrations and then regrow, leaving a scar that is identifiable (Copeland et al. 2018; Seamons et al. 2009). Whilst scales are the preferred structure for age determination in steelhead, a study comparing scale age with genetic analysis for age assignment found that age was misclassified 13% of the time and repeat spawners were misclassified as maiden spawners 6.5% of the time (Seamons et al. 2009). The scale analysis used in this study was completed by the Quinault Indian Nation Department of Fisheries and the Fish Ageing Laboratory of the Washington Department of Fish and Wildlife which use comparable ageing methodology (Scott and Gill 2008). Average age proportions of maiden spawners across years and populations in our data were 1.0% (age 3), 45.8% (age 4), 47.6% (age 5), 5.4% (age 6) and 0.2% (age 7).

Finally, we calculated the amount of habitat accessible to steelhead in each river such that population capacity could be estimated per unit habitat. Accessible stream kilometres used in the model were 1965 km (Chehalis), 242 km (Hoh), 224 km (Humptulips), 332 km (Queets), 658 km (Quillayute) and 253 km (Quinault), and were derived from the WDFW SWIFD dataset (https://geo.wa.gov/datasets/wdfw::statewide-washington-integrated-fish-distribution/about).

2.3 | Covariate Data

Because the IPM allows the estimation of covariate effects on recruitment and kelt survival anomalies, we collected data on ecological or environmental factors that have been identified or hypothesized to effect steelhead survival, including ocean conditions such as indices of food availability or competition for resources, temperature, large-scale climate indices and pinniped abundances as proxies for predation (Busby et al. 1996; Crozier et al. 2021; Moore et al. 2021).

Thermal conditions in the ocean influence steelhead distribution and growth at sea (Sutherland 1973) and variation in sea surface temperature (SST) has been linked to variation in steelhead ocean growth (Atcheson 2010). As such, SST data for the North Pacific Ocean were obtained from NOAA's Extended Reconstructed Sea Surface Temperature Version 5 dataset (Huang et al. 2017, ncei.noaa.gov/pub/data/cmb/ersst/v5/netcdf/). We used ocean SSTs in the coastal region (46°–49° N ∣ 124°–127° W) during June–August to reflect conditions during ocean entry of steelhead (Figure S1). SST is representative of the thermal conditions experienced by steelhead at sea because steelhead are surface-oriented and remain in the upper 20 m with periodic dives to 40–60 m (Burgner et al. 1992). We used SSTs in the North Pacific to reflect thermal conditions experienced by steelhead in the ocean 2–4 years after recruits were spawned. Specifically, areas were defined by latitudes and longitudes 47°–55° N ∣ 149°–165° W, 45°–53° N ∣ 157°–173° W and 43°–51° N ∣ 167°–183° W for lags 2, 3 and 4, respectively (Figure S1). We further used the area defined by 43°–51° N ∣ 159°–175° W to reflect thermal conditions experienced by kelts. These areas were based on spatial correlation analyses where estimated recruitment or kelt survival anomalies from a model without covariates were correlated with a 2° × 2° grid of average ocean SSTs from June to August (independent for each grid cell). This analysis suggested that the highest correlations shifted slightly westward from the central to the western Gulf of Alaska and the North Pacific Ocean from ocean age-0 (lag-2) to ocean age-2 (lag-4). These areas and the spatial shift with age align well with known ocean distributions of steelhead in the North Pacific Ocean (Light, Harris, and Burgner 1989; Welch et al. 1998; Langan et al. 2024).

Pink salmon abundance has been shown to be associated with changes in growth and survival of salmon from regions along the west coast of North America, presumably due to broad-scale trophic impacts on the marine ecosystem of the North Pacific Ocean or due to direct competition for shared prey (Batten, Ruggerone, and Ortiz 2018; Cline, Ohlberger, and Schindler 2019; Kendall, Nelson, and Losee 2020; Ruggerone and Connors 2015; Ruggerone and Nielsen 2004; Springer and van Vliet 2014). We used the total abundance of pink salmon as well as the total abundance of chum salmon in the North Pacific Ocean as indices for competition at sea (Ruggerone and Irvine 2018; Ruggerone, Connors, and Irvine 2021).

River conditions are an important factor related to steelhead juvenile survival and growth (Grantham et al. 2012; Thompson and Beauchamp 2014) and migration to the marine environment (Sandstrom et al. 2020; Sobocinski et al. 2020). We used river discharge data as an index of conditions experienced in freshwater by juveniles and kelts. Discharge data were obtained from stream gages operated by the U.S. Geological Survey (waterdata.usgs.gov) for the Chehalis (12031000), Hoh (12041200), Humptulips (12039005), Queets (12040500), Quillayute (12043000) and Quinault (12039500) rivers. We calculated annual metrics of low flows and high flows based on average daily stream discharge expressed as ft^3/s. We used the period May–April to align with the steelhead life history, and tested conditions during the first and second year after spawning, that is, we calculated the minimum and maximum daily values in each period. Annual low and high flows were log-transformed, normalised to zero mean and unit SD within each river, and then averaged across rivers to produce mean standardised log-discharge metrics for the examined coastal rivers. Average pairwise Pearson correlations amongst the river-specific time series were 0.68 and 0.74 for minimum and maximum flows, respectively.

We also included the North Pacific Gyre Oscillation (NPGO) index, a dominant pattern of sea surface height variability (Di Lorenzo et al. 2008; http://www.o3d.org/npgo/npgo.php). We used the annual (calendar year) average index. The NPGO is a broad-scale climate index that has been linked to key biological variables in the North Pacific ecosystem (Litzow et al. 2020) and is positively associated with productivity in other steelhead populations (Scheuerell et al. 2021).

Pinniped abundance has increased in the North Pacific Ocean concurrently with declines in many steelhead populations (Myers 2018) and several studies have identified pinniped predation on juvenile and adult steelhead (Moore et al. 2021; Naughton et al. 2011). In this study, harbour seal abundance was used as a proxy for pinniped predation on steelhead juveniles or adults; however, California and Stellar sea lions also prey on steelhead at multiple life stages, and we did not include all pinniped predation effects due to a lack of time series data.

2.4 | Integrated Population Model

An IPM consists of a process model that describes the unknown true population dynamics and an observation model that describes the noisy observations given the true state of the population (de Valpine and Hilborn 2005; Schaub and Abadi 2011; Maunder and Punt 2013; Zipkin and Saunders 2018). This state-space model captures the full information and uncertainty in the abundance and age structure data by constructing a joint likelihood from the component observation likelihoods. Bayesian inference then estimates the joint posterior distribution of all model parameters and latent states, which represents the uncertainty and correlations amongst them. Our steelhead IPM builds on an IPM for Pacific salmon previously developed by Buhle et al. (2018), which is similar to the models of Fleischman et al. (2013) and Scheuerell et al. (2021), though it differs in some details of parameterization and priors. The main innovation in the present model is that it accounts for iteroparity by accommodating a complex age structure that includes maiden and repeat spawners and allows estimation of the kelt survival rate. In addition, the steelhead IPM is hierarchical in space as well as time, describing multiple populations whose dynamics are governed by parameters that are themselves modelled by hyperdistributions. This structure allows information sharing amongst related populations experiencing a common marine environment, such that inferences for populations with relatively sparse data may borrow strength from more data-rich ones (Barrowman et al. 2003; Punt, Smith, and Smith 2011; DeFilippo et al. 2021).

2.4.1 | Process Model

The process model begins with the spawner-recruit function $f(S_{jt}|\boldsymbol{\theta}_j)$, where S_{jt} is the unknown true abundance of spawners in population j in year t. We use the Ricker model,

$$f(S_{jt}|\boldsymbol{\theta}_j) = \alpha_j S_{jt} \exp\left(-\frac{\alpha_j S_{jt}}{e A_j R_{\max,j}}\right), \tag{1}$$

whose population-specific parameters $\boldsymbol{\theta}_j$ include intrinsic productivity α_j (maximum recruits per spawner at low abundance) and maximum adult recruitment $R_{\max,j}$, the latter scaled by habitat size A_j such that its units are density (fish/km). Euler's constant is denoted e. In our experience, 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 follow a bivariate lognormal hyperdistribution across populations,

$$\left[\log \alpha_j, \log R_{\max,j}\right] \sim \mathrm{N}\left(\left[\mu_\alpha, \mu_{R_{\max}}\right], \boldsymbol{\Sigma}_{\alpha R_{\max}}\right), \tag{2}$$

where the diagonal elements of the covariance matrix $\boldsymbol{\Sigma}_{\alpha R_{\max}}$ are the variances $\left[\sigma_\alpha^2, \sigma_{R_{\max}}^2\right]$ and the off-diagonal elements are the product of the log-SDs $\left[\sigma_\alpha, \sigma_{R_{\max}}\right]$ and the correlation $\rho_{\alpha R_{\max}}$ between the two parameters. The number of eventual adult recruits R_{jt} produced by these spawners, which may return at a range of mature ages, is then lognormally distributed around the log-mean value, which incorporates the effects of covariates represented by row vector $\mathbf{x}_{Rjt}$ with coefficient vector $\boldsymbol{\beta}_R$,

$$\begin{gathered} \log R_{jt} \sim \mathrm{N}\left(\log f(S_{jt}|\boldsymbol{\theta}_j) + \mathbf{x}_{Rjt}\boldsymbol{\beta}_R + \eta_{Rt}, \sigma_R\right) \\ \eta_{Rt} \sim \mathrm{N}\left(\rho_R \eta_{R,t-1}, \ \sigma_R^{\text{year}}\right) \end{gathered}. \tag{3}$$

The recruitment process variability represents unexplained environmental stochasticity occurring after intra-population density dependence and consists of two hierarchical components. The first is a shared annual anomaly η_{Rt}, which corresponds to regional environmental conditions not captured by measured covariates and is modelled as a lag-1 autoregressive process with autocorrelation ρ_R and innovation SD σ_R^{year}. The second level of recruitment process error represents independent variation within population j at time t with SD σ_R.

Maiden recruits from cohort t return to spawn in subsequent years, with the true probability of surviving adults returning at each age given by the simplex $\mathbf{p}_{jt}$. Steelhead in our dataset first mature at age 3–8, so $\mathbf{p}_{jt} = \left[p_{3jt}, \ \ldots, p_{8jt}\right]$. Parameterizing the age distribution conditional on survival to adulthood avoids the need to estimate or assume annual survival and maturation rates during ocean residence, which are not identifiable from the available data. The conditional maiden age probabilities follow a hierarchical logistic normal model (Aitchison 2003) that includes among-population heterogeneity and interannual within-population fluctuations around the hyper-mean $\boldsymbol{\mu}_\mathbf{p}$,

$$\begin{gathered} \mathrm{alr}\left(\mathbf{p}_{jt}\right) \sim \mathrm{N}\left(\mathrm{alr}\left(\boldsymbol{\mu}_\mathbf{p}\right) + \boldsymbol{\eta}_{\mathbf{p}j}, \boldsymbol{\Sigma}_\mathbf{p}\right) \\ \boldsymbol{\eta}_{\mathbf{p}j} \sim \mathrm{N}\left(\mathbf{0}, \boldsymbol{\Sigma}_\mathbf{p}^{\text{pop}}\right) \end{gathered}, \tag{4}$$

where the additive log-ratio transformation is $\mathrm{alr}(\mathbf{p}_{jt}) = \left[\log(p_{3jt}/p_{8jt}), \ldots, \log(p_{7jt}/p_{8jt})\right]$. The within-population covariance matrix $\mathbf{\Sigma}_{\mathbf{p}}$ is parameterized by the SD vector $\boldsymbol{\sigma}_{\mathbf{p}}$ and correlation matrix $\mathbf{R}_{\mathbf{p}}$, and likewise for the among-population covariance matrix $\mathbf{\Sigma}_{\mathbf{p}}^{\mathrm{pop}}$.

Iteroparity is modelled by the spawner-to-spawner survival rate s_{jt}, parsimoniously assumed to be age- and sex-invariant and independent of the number of previous spawning migrations. Survival follows a logistic normal process model that, like maiden recruitment, includes covariate effects, shared autocorrelated annual anomalies and independent errors around a hyper-mean μ_s:

$$\begin{gathered}\mathrm{logit}(s_{jt}) \sim \mathrm{N}\left(\mathrm{logit}(\mu_s) + \mathbf{x}_{sjt}\boldsymbol{\beta}_s + \eta_{st}, \sigma_s\right) \\ \eta_{st} \sim \mathrm{N}\left(\rho_s \eta_{s,t-1},\ \sigma_s^{\mathrm{year}}\right)\end{gathered}. \tag{5}$$

The abundance of age-a maiden and repeat adults, denoted by M and K (for kelt) respectively, returning to population j to spawn in year t is then

$$\begin{gathered}\tilde{S}_{ajt}^{\mathrm{M}} = R_{j,t-a}\, p_{a,j,t-a} \\ \tilde{S}_{ajt}^{\mathrm{K}} = S_{a-1,j,t-1}\, s_{j,t-1}\end{gathered}. \tag{6}$$

The exception is the oldest age class, in this case 9+, which is a plus-group that includes recruits 9 years and older, so $\tilde{S}_{9jt}^{\mathrm{K}} = \left(S_{8,j,t-1} + S_{9,j,t-1}\right) s_{j,t-1}$. Our model assumes, as is typical for winter steelhead on the west coast, that adults do not skip years between spawning events. Returning adult recruits are subject to fishery mortality F_{jt}, parsimoniously assumed to be nonselective with respect to age because we do not have estimates of age-specific fishery selectivity. Total spawner abundance is thus the sum over age classes,

$$S_{jt} = \sum_{a=3}^{8} \left(\tilde{S}_{ajt}^{\mathrm{M}} + \tilde{S}_{a+1,j,t}^{\mathrm{K}}\right)\left(1 - F_{jt}\right) = \tilde{S}_{jt}\left(1 - F_{jt}\right). \tag{7}$$

The true age distribution of maiden and repeat adult recruits captured in the fishery is given by the age composition simplex $\mathbf{q}_{jt}$, where

$$\mathbf{q}_{jt} = \left[\tilde{S}_{3jt}^{\mathrm{M}}, \cdots, \tilde{S}_{8jt}^{\mathrm{M}}, \tilde{S}_{4jt}^{\mathrm{K}}, \cdots, \tilde{S}_{9jt}^{\mathrm{K}}\right] / \tilde{S}_{jt} = \left[q_{3jt}^{\mathrm{M}}, \cdots, q_{8jt}^{\mathrm{M}}, q_{4jt}^{\mathrm{K}}, \cdots, q_{9jt}^{\mathrm{K}}\right]. \tag{8}$$

2.4.2 | Observation Model

The observation model consists of two likelihood components: spawner abundance and age composition. Note that the IPM handles missing observations automatically, in the sense that they are ignored and do not contribute to the likelihood. Observed spawner abundance S_{jt}^{obs} is modelled as lognormal, given the true state and the observation error SD τ,

$$\log S_{jt}^{\mathrm{obs}} \sim \mathrm{N}\left(\log S_{jt}, \tau\right). \tag{9}$$

Observed age-frequencies of maiden and repeat adult recruits in the tribal fishery $\mathbf{n}_{jt}^{\mathrm{obs}}$ are modelled as multinomial, given the corresponding true distribution:

$$\mathbf{n}_{jt}^{\mathrm{obs}} \sim \mathrm{Multinomial}\left(\mathbf{q}_{jt}\right). \tag{10}$$

2.4.3 | Priors

Hyperparameters in the IPM were generally given weakly informative default priors (Lemoine 2019) intended to mildly regularise the posterior to rule out biologically implausible values and avoid numerical issues when sampling. The exceptions were μ_α, $\boldsymbol{\mu}_{\mathbf{p}}$ and μ_s, for which we used informative priors based on knowledge of other steelhead populations (Quinn 2005; Scott and Gill 2008; Scheuerell et al. 2021). We assessed prior influence by comparing prior and posterior distributions (e.g., Figure S2). See Table S1 for a full list of hyperprior specifications.

Priors were also specified for the initial states, that is, spawner abundance and age structure in the early years of each time series that cannot be generated by previous spawning cohorts in the process model. The abundance of these 'orphan' spawners in years 1–8 was given a data-aware but weakly informative lognormal prior with a log-mean equal to the marginal log-mean of S_{jt}^{obs} across the entire dataset 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 prior age distribution of maiden and repeat age classes in year 1, and orphan maiden age classes in years 2–8, was simplex uniform. Finally, the priors on the initial values of the AR(1) shared anomalies η_{R1} and η_{s1} were their respective stationary distributions $\eta_{k1} \sim \mathrm{N}\left(0, \sigma_k / \sqrt{1 - \rho_k^2}\right)$, where $k \in \{R, s\}$.

2.4.4 | Model Fitting

The steelhead IPM was developed in the new R (v. 4.2.1, R Core Team 2022) package `salmonIPM` (Buhle and Scheuerell 2024), which allows users to specify and fit a variety of IPMs representing a range of anadromous salmonid life histories and data structures. The models are fitted in a Bayesian framework using the No-U-Turn Sampler (Monnahan, Thorson, and Branch 2017; Hoffman and Gelman 2014) implemented in Stan (Carpenter 2017) via the `rstan` package (v. 2.32.2, Stan Development Team 2023). The code to reproduce the analysis presented in this paper is available on GitHub (https://github.com/janohlberger/IPM_steelhead_coastal_WA).

For inference, we simulated 2000 draws from the posterior distribution from three randomly initiated chains where the first 1000 iterations were discarded as warmup, for a total posterior sample of 3000 draws. We assessed convergence by visual inspection of trace plots, by verifying that the potential scale reduction factor $\hat{R} < 1.01$ for all parameters and states (Vehtari et al. 2021), and by confirming that divergent transitions were absent or false positives (Gabry et al. 2019). We evaluated model fit and adequacy by comparing hyperparameter estimates with biologically plausible values and by graphical posterior predictive checks (e.g., plotting observations along with posterior predictive distributions; see Figure 2).

2.4.5 | Covariate Selection

Covariates were lagged to account for the time difference between observed conditions and recruitment (relative to spawn year) or kelt outmigration, considering the most common life history types of winter steelhead on the WA coast. These steelhead typically spend 2 years in freshwater (~90% of those that return) and one or two full years and a partial year in the ocean before first maturation (Figure S3). To relate environmental drivers to recruitment by spawn year (i.e., brood year), we used lags of 0–1 years for freshwater flow conditions, 2 years for coastal SST, 3–4 years for open ocean SST and salmon abundance, 2–4 years for pinniped predation and 2–4 years for broad-scale climate indices (NPGO). No lags were used to relate environmental drivers to kelt survival by outmigration year. Abundance estimates for coastal harbour seals based on actual counts were only available for about half of the years considered (Jeffries et al. 2003; Pearson et al. 2024). Therefore, we only tested for predation effects in a model fitted to a subset of the steelhead population data. Seal abundances were not included in the selected covariate model. We therefore dropped this predictor from the model and tested the remaining covariates on the full dataset.

Because of the challenging nature of information-theoretic model selection for state-space models and the computational demands of fitting models with all possible subsets of covariates, we performed model selection by fitting a base IPM without covariates and then using multiple linear regression to model the estimated shared maiden recruitment (η_{Rt}) and kelt survival (η_{st}) anomalies as functions of covariates. For these regressions we used the shared process error anomalies as the response variable, corresponding to the shared annual values of the predictors. Each covariate time series was standardised to zero mean and unit SD, and recruitment or kelt survival anomalies were represented by posterior medians with posterior uncertainties used as weights (SD^{-2}).

We performed AIC$_c$-based model selection using the `dredge` function of the R package `MuMIn` (v. 1.46.0, Bartoń 2022) and chose the most parsimonious model out of all possible covariate combinations, that is, the one with the lowest AIC$_c$, unless a model with fewer parameters had an AIC$_c$ value within 2 of the lowest value, in which case that model was chosen (Burnham and Anderson 2002).

Once covariates were selected (Figure S4), we incorporated them into the IPM and re-fit the model to obtain estimates for the regression coefficients jointly with all other parameters and states. This two-step approach allows us to compare trends in maiden recruitment and kelt survival anomalies between the models with and without covariates to evaluate whether accounting for ecological and environmental factors in the IPM partially or fully removed any long-term trends in the anomalies that were apparent in the base model.

3 | Results

We examined wild winter steelhead populations on the WA coast (Figure 1). These populations have experienced considerable variation in abundance, that is, total run size (2- to 8-fold), since the early 1980s (Figure 1B). Harvest rates have varied considerably within populations, with maximum harvest rates between 42% and 66%, and decreasing rates in recent years.

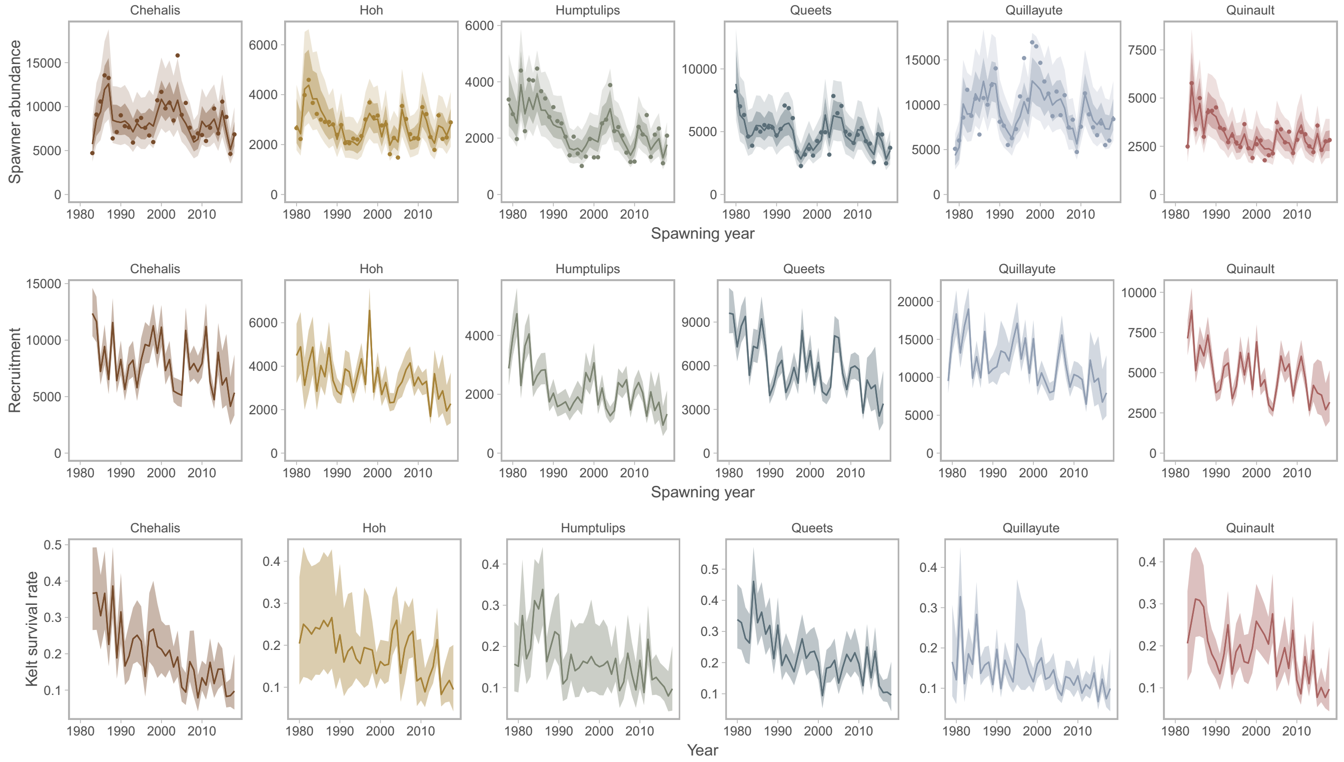

FIGURE 2 | Estimated spawner abundance, recruitment and kelt survival by population. Thick lines with dark bands indicate medians with 90% credible intervals of the state. Points in the top row indicate observed spawner abundances and light bands indicate the 90% range of the posterior predictive distribution of observed spawner abundances. Spawner abundance and recruitment are indexed by spawning year, and kelt survival rates are indexed by kelt outmigration year.

Steelhead typically return as first-time spawners at age 4 or 5, a pattern that has been remarkably consistent over time and across populations (Figure 1C). Most of the repeat spawners are of total ages 5–7 and their proportions have generally decreased over time, especially for the older age groups.

Recruitment of WA coastal steelhead populations has varied 2- to 4-fold over the past 40 years and has shown declining trends in all populations (Figure 2). Estimated spawner abundance values closely matched redd-based observations in most but not all years, due to observation error which had an estimated median SD of $\tau = 0.19$ (95% credible interval, 0.16–0.22). About 98% of the observations fell within the 95% credible interval of the posterior predictive distribution. Populations differed in their estimated intrinsic productivity, with posterior medians from 1.9 to 4.0 and a log hyper-mean of $\mu_\alpha = 1.1$ (0.79–1.50). Maximum recruitment per river km ranged from 4.2 to 21.4 based on median values, with a log hyper-mean of $\mu_{R_{\max}} = 2.62$ (2.03–3.25). Median productivity and capacity estimates with credible intervals for all rivers are presented in the supplement (Figure S5).

Shared recruitment anomalies, which reflect shared variation in survival to first maturation due to environmental impacts occurring after population-level density dependence, showed a clear negative trend over time when covariates were not included in the IPM, but no decline when the model accounted for covariate effects on recruitment (Figure 3). In the full model, based on the post hoc regression of shared recruitment anomalies from the IPM without covariates (Table S2; Figure S6), recruitment was modelled as a function of the North Pacific Gyre Oscillation (NPGO_{t+2}), summer sea surface temperature in the North Pacific Ocean ($\mathrm{SST}_{\mathrm{NP},t+4}$), and pink salmon abundance (Pinks_{t+4}), at lags of 2, 4, and 4 years after recruits were spawned, respectively. The covariates explained about 60% of the interannual variation in recruitment anomalies in the post hoc regression. The pairwise Pearson correlations amongst the covariate time series were −0.16, −0.09 and 0.30. When the selected environmental drivers were included in the IPM, posterior estimates of the coefficients indicated a positive effect of NPGO (posterior median = 0.09, $P[\beta > 0] = 0.99$), a negative effect of summer SST (−0.10, $P[\beta < 0] = 0.99$) and a negative effect of pink salmon abundance (−0.14, $P[\beta < 0] = 0.98$) on recruitment (Figure 3). The model with covariates did not show strong long-term trends in population-specific recruitment anomalies (Figure S7). The SD of the shared recruitment anomalies was higher than that of the unique recruitment process errors (Table S1).

Kelt survival rates have also varied considerably over time and showed declining trends in all populations, though to varying degrees (Figure 2). Whilst estimated kelt survival rates across populations during the mid- to late 1980s varied between 15% and 40%, they have been around 10% for the most recent five outmigration years across all populations examined. Kelt survival anomalies were modelled as a function of summer SST and pink salmon abundance in the North Pacific Ocean, as well as maximum river flows during the kelt outmigration year. In the post hoc regression, these covariates explained about 77% of the interannual variation in estimated kelt survival anomalies from the base IPM (Table S2; Figure S8). The pairwise Pearson correlations amongst the covariate time series were −0.12, 0.33 and 0.49. Including the selected covariates in the IPM largely removed the long-term trend in kelt survival anomalies, and the estimated regression coefficients indicated a negative effect of summer SST (posterior median = −0.12, $P[\beta < 0] = 0.99$), a negative effect of pink salmon (−0.17, $P[\beta < 0] = 0.99$) and a slight positive effect of river flow (0.08, $P[\beta > 0] = 0.88$) on kelt survival rates (Figure 3). The model with covariates did not show strong long-term trends in population-specific kelt survival anomalies (Figure S9), but the SD of the shared kelt survival anomalies was lower than that of the unique kelt survival process errors (Table S1), suggesting significant variation in kelt survival rates that is not shared amongst populations.

Our sensitivity analysis of a potential negative bias in harvest rates of 5% showed that estimated population productivities were slightly higher (up to 12%), as expected, and that the estimated covariate effects on recruitment and kelt survival were up to 8% stronger when assuming that harvest rate was consistently underestimated (Figure S10).

Finally, recruitment and kelt survival anomalies from a model without environmental drivers tended to be positive in years with low average SST and low pink salmon abundance, and vice versa (Figure 4). This pattern illustrates that a cold and low-competition ocean environment is favourable for steelhead survival at sea, whereas a warm and high-competition ocean environment is generally associated with low marine survival.

4 | Discussion

Our analysis suggests that declining trends in survival rates of steelhead populations on WA's Pacific coast are linked to changing ecological and environmental factors, in particular ocean conditions in the North Pacific. Steelhead recruitment was associated with summer SST, pink salmon abundance and the NPGO index. Kelt survival was associated with summer SST, pink salmon abundance and river flow. Including these environmental drivers in the model reduced the unexplained shared interannual variation in recruitment and kelt survival and largely removed their trends. Whilst other latent ocean variables that have not been observed or included may explain part of these trends, our finding that most of the variation and nearly all of the long-term trends in the survival of immature (recruit) and mature (kelt) steelhead can be explained by marine environmental indices implies that changing ocean conditions are a primary contributor to observed declines in these populations over the study period. Changes in ocean climate and ecological conditions may also drive survival and abundance trends of other North American steelhead populations because their ocean distributions largely overlap after their first year at sea (Light, Harris, and Burgner 1989; Welch et al. 1998). Modelling approaches similar to those applied here could be used to investigate links between changing ocean conditions and steelhead survival throughout their range.

Integrated population models have been used extensively in marine fisheries stock assessment for decades (Maunder and Punt 2013) and have been increasingly adopted in terrestrial wildlife ecology and conservation (Lee et al. 2015; Saunders, Cuthbert, and Zipkin 2018; Schaub et al. 2007), but their

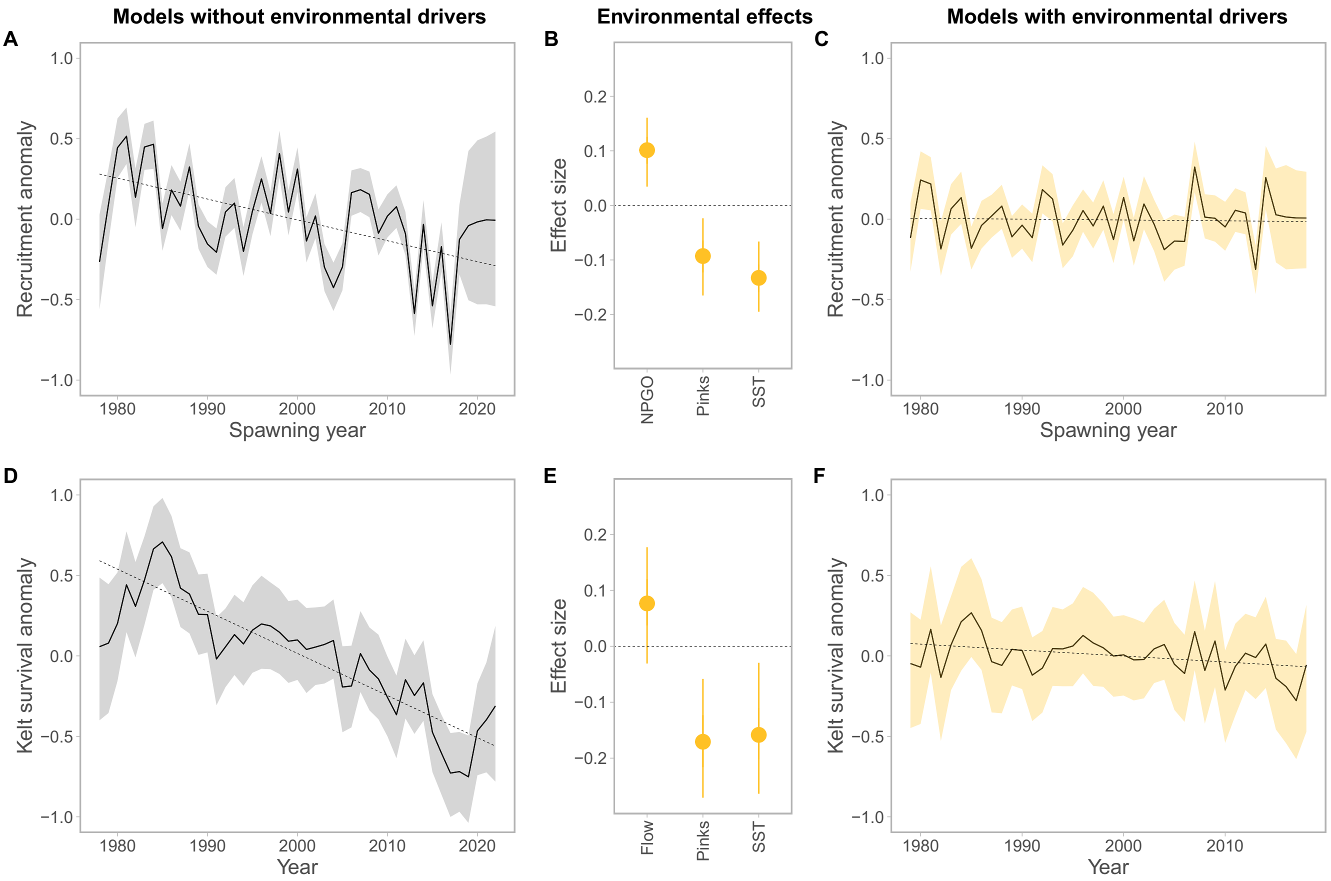

FIGURE 3 | Estimated covariate effects on recruitment and kelt survival anomalies. Shown are the shared recruitment and kelt survival anomalies from models without covariates (A, D), estimated regression coefficients for the environmental drivers (B, E) and recruitment and kelt survival anomalies from models with these covariates included (C, F). Environmental drivers are NPGO, pink salmon abundance, mean summer SST and river high flow. Covariate model output is shown in yellow. Thick lines with bands and circles with error bars indicate medians with 90% credible intervals, respectively. Dotted lines represent linear regressions of posterior median anomalies against year with weights based on posterior standard deviations (SD^{-2}), indicating stronger negative slopes in models without covariates compared to models with covariates: −0.98 (A) versus −0.04 (C) for recruitment anomalies and −2.11 (D) versus −0.68 (F) for kelt survival anomalies.

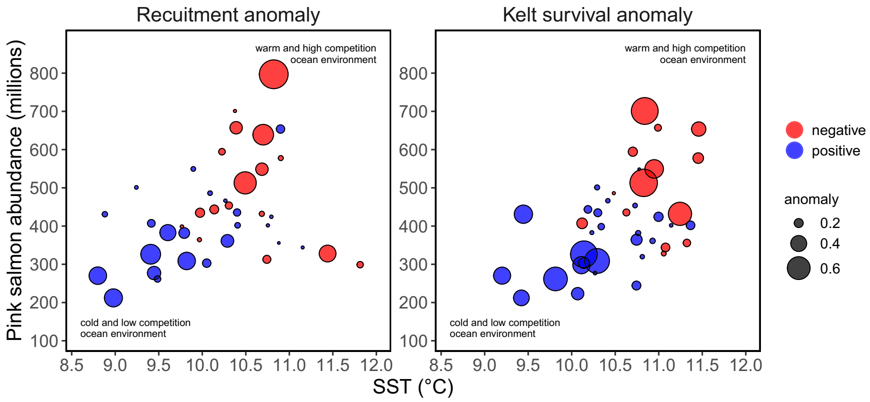

FIGURE 4 | Recruitment and kelt survival anomalies as functions of pink salmon abundance and summer SST. Shown are the shared recruitment (left) and kelt survival (right) anomalies from a model without environmental drivers as functions of pink salmon abundance (millions) and average summer SST (°C) in the North Pacific Ocean. Circle size indicates the percent deviation and circle colour indicates whether the anomaly was positive (blue) or negative (red). Environmental drivers of recruitment and kelt survival anomalies reflect conditions during the fourth year after recruits were spawned and during the kelt outmigration year, respectively.

application to anadromous salmonids is relatively recent and not yet widespread (Newman et al. 2006; Fleischman et al. 2013; Massiot-Granier et al. 2014; Winship, O'Farrell, and Mohr 2014; Buhle et al. 2018; Falcy and Suring 2018; DeFilippo et al. 2021; Scheuerell et al. 2021). Our study suggests that IPMs could be a powerful addition to the salmonid population ecologist's toolbox, offering a number of advantages over traditional run-reconstruction and regression approaches. These include the ability to separate process and observation error, extract information about demographic parameters and states contained jointly in abundance and composition data along with their uncertainties and trade-offs and seamlessly handle missing observations. It is also feasible to expand the model to include additional life cycle complexity and corresponding data types. For example, our spawner-recruit function is based on total spawner abundance and thus does not explicitly account for the effects of variation in age composition or size-at-age on reproductive output (Ohlberger et al. 2020). If age-specific fecundity data were available, the process model could incorporate age-weighted intrinsic productivity. Furthermore, like Buhle et al. (2018), Falcy and Suring (2018) and DeFilippo et al. (2021), we demonstrate the utility of modelling multiple biologically and geographically related populations hierarchically in an IPM. This allows information sharing between data-rich and data-poor populations (Barrowman et al. 2003; Punt, Smith, and Smith 2011) and provides estimates of unique and shared process error components, in particular the maiden and kelt recruitment anomalies that were the focus of our analysis of environmental factors driving the recent declines.

Shared recruitment anomalies represent regional variation in survival rates to first maturation occurring after intra-population density dependence. Population-level density effects can be strong during freshwater residence, thus stabilising recruitment to the smolt stage (Bailey et al. 2018; Scheuerell et al. 2021). Whilst annual variation in smolt abundance can be considerable, much of the observed variation in recruitment may be caused by environmental influences during the marine phase of the steelhead life cycle, where density-dependent compensatory mechanisms that stabilise populations are largely absent (Smith and Ward 2000). Declining trends over time in shared recruitment anomalies were largely explained by (i) summer SST during late ocean residence ($\text{SST}_{\text{NP},t+4}$), (ii) abundance of pink salmon in the ocean (Pinks_{t+4}), including Asian and North American populations and (iii) the NPGO index (NPGO_{t+2}), which has been linked to key biological variables in the North Pacific ecosystem (Di Lorenzo et al. 2008; Litzow et al. 2020). There is uncertainty around these specific lags of covariate effects on recruitment because steelhead show a highly diverse life history with variable freshwater and ocean ages such that identifying specific lags at which environmental conditions impact survival during their life cycle is challenging. For example, covariate lags are most likely to map onto the dominant return age if environmental impacts are most pronounced during late ocean residence. This is in line with our finding that recruitment anomalies are linked to ocean conditions 4 years after recruits were spawned, as the dominant age group amongst maiden spawners is a total age of 5 (Figure S3). On the other hand, fish that return at younger ages may not experience the same ocean conditions. In addition, the covariate time series show significant autocorrelation (autocorrelation coefficients of 0.51 at lag 1 for summer SST and 0.58 at lag 2 for pink salmon abundance). Using an IPM for steelhead in the Skagit River, Puget Sound, WA, Scheuerell et al. (2021) likewise found a positive effect of NPGO during the first year of ocean entry on recruitment anomalies (their model does not include iteroparity) but did not rule out later lags.

Whilst these results suggest that trends in survival are largely attributable to changing ocean conditions, lower survival rates may also be caused by other environmental changes such as altered freshwater temperatures, increased predation in freshwater or the ocean (Chasco et al. 2017; Nelson et al. 2019; Losee et al. 2021) and reduced food availability due to changes in prey abundance (Daly et al. 2013) or phenology (Wilson et al. 2023). Freshwater variables may be more likely to have population-specific impacts and hence cause additional variation and trends in recruitment that are unique to each population and are therefore not captured by the shared anomalies (see Figures S7 and S9). Impacts on survival during early freshwater residence may further be masked by density dependence at the population level. Pinniped predation effects remain poorly quantified considering the limited species inclusion and short time series used here and should be further examined in future studies. The potential effects of freshwater predators such as birds were also not investigated due to a lack of time series data on their abundances.

Kelt survival anomalies, which reflect shared variation in survival after first maturation, showed declines over time that were largely explained by summer SST and pink salmon abundance in the year that kelts return to the ocean. Declines in kelt survival rates result in lower proportions of repeat spawners, which suggests that the degree of iteroparity in these populations has declined since the mid-1980s. This decline has likely resulted in lower lifetime reproductive success of spawners because repeat-spawning fish can produce 2–2.5 times as many progeny during their lifetimes as single-spawning fish (Seamons and Quinn 2010; Christie et al. 2018). A lower average reproductive success of steelhead spawners may reduce population productivity and stability (Moore et al. 2014). An important caveat is that our model assumes maiden and repeat spawners returning in a given year experience the same harvest rates, although an unquantified portion of the retained and non-retained catch is comprised of post-spawn kelts. An increase in this unaccounted-for kelt-specific mortality over time could contribute to observed changes in kelt survival.

The shared variation and trends in maiden recruitment and kelt survival provide evidence that these patterns are caused by broad-scale changes in ecological and environmental conditions in the North Pacific Ocean. This contrasts with earlier work on salmonids indicating that conditions during later ocean residence were less influential in determining marine survival (Mueter, Pyper, and Peterman 2005; Welch et al. 2011; Kendall, Marston, and Klungle 2017). Specifically, we found that the standard deviation of shared recruitment anomalies was of similar magnitude to that of the population-specific anomalies. This covariation of survival with ocean conditions suggests that coastal steelhead populations will respond similarly to future changes in the ocean, and that the amongst-population capacity to buffer risks due to ecosystem change may be relatively weak (i.e., a limited portfolio effect, Schindler et al. 2010).

Our findings suggested a negative effect of increasing pink salmon abundance on steelhead survival. This result is consistent with recent studies reporting that higher pink salmon abundance in the North Pacific Ocean reduces the growth and survival of Chinook, sockeye, coho and chum salmon (Ruggerone and Nielsen 2004; Ruggerone and Connors 2015; Cline, Ohlberger, and Schindler 2019; Connors et al. 2020; Sobocinski et al. 2021; Ohlberger et al. 2023; Ruggerone et al. 2023). Similarly, a recent study found that body lengths of steelhead returning to the Snake River Basin were negatively correlated with the abundance of pink salmon from North America and eastern Kamchatka and suggested that competition for limited resources at sea occurs during later stages of ocean residence (Vosbigian et al. 2024). Changes in steelhead survival due to increased competition with pink salmon have also been hypothesized (Atcheson et al. 2012b; Bowersox et al. 2019), however, negative associations between pink salmon abundances and steelhead survival across multiple populations have not previously been identified. Such associations could arise via direct competition for resources or complex linkages within the North Pacific food web.

We found a significant negative effect of summer SST on steelhead survival during late ocean residence. Similarly, previous work identified negative correlations between summer SST during the post-smolt year and the return rate of steelhead, but not their initial growth at sea (Friedland et al. 2014), although for that population (Keogh River, BC) the strongest correlations with SST in the North Pacific were found further to the south. Within the range of observed average North Pacific June–August temperatures of 9°C–12°C, higher SST was associated with lower steelhead survival. The estimated upper thermal limit to steelhead distributions in summer is 11°C–15°C (Welch et al. 1998), and steelhead are frequently observed in the ocean at spring-fall SST around 6°C–12.5°C with a median of 9.1°C (Abdul-Aziz, Mantua, and Myers 2001; Langan et al. 2024). A tagging study of steelhead kelts in southeast Alaska found that mean temperatures experienced by individual fish were 8.4°C–12.7°C (Seitz and Courtney 2021). A bioenergetic model estimated optimal growth temperatures of ~12°C for 2-lb ocean age-1 steelhead feeding at half maximum consumption rates (Atcheson et al. 2012b); however, optimal growth temperature declines with body size (Lindmark, Ohlberger, and Gårdmark 2022) and at lower feeding rates (Brett 1971), suggesting lower optima for larger steelhead experiencing food limitation. This also points to an interaction between warming and increased competition in the ocean. By lowering food availability and thus the scope for growth at a given temperature, intensified competition in the marine environment may further exacerbate the negative impacts of ocean warming on steelhead growth and survival. Such an interaction between temperature and density dependence is well documented, including in Pacific salmon (Crozier et al. 2010).

Our results showed a positive effect of maximum river flow on kelt survival, indicating that freshwater conditions impact kelt survival in addition to the marine environment. Along the WA coast, increased hydrologic variability and extreme flow events have been shown to negatively affect juvenile salmonid production (Ward et al. 2015; Ohlberger et al. 2018) and our results indicate that adult stages of steelhead are also affected by flow events and possibly temperatures. A recent study found that wild winter steelhead kelts in Forks Creek, WA, spent on average 30 days in freshwater reaches below the spawning grounds and that kelt mortality was greater in freshwater reaches versus nearshore marine habitats (Harbison et al. unpublished). This points to the importance of freshwater factors like flow and temperature to kelt conditions and survival that ultimately impact repeat spawning rates (Penney et al. 2016). In addition to higher water temperatures associated with altered climate dynamics in the North Pacific Ocean (Overland and Wang 2007), climate change is projected to result in higher freshwater temperatures and more extreme hydrological events, including river flow conditions (Mote and Salathé Jr 2010). On the other hand, climate change effects on freshwater production of steelhead and kelt survival in WA coastal watersheds may be less severe because water temperatures in summer are expected to largely remain within tolerable ranges (Winkowski 2023).

Climate change poses threats to anadromous species due to changing stressors in the ocean and in freshwater, including carryover effects of climate-induced changes in one life stage that influence the ecology and life history of other life stages (Cline, Ohlberger, and Schindler 2019; Crozier et al. 2021; Gosselin et al. 2021). Differences in the magnitude and pace of climate change in freshwater versus marine habitats could present additional challenges for behavioural and physiological adaptations to elevated temperature (Crozier and Hutchings 2014). Further, higher temperatures increase consumption rates needed to meet the metabolic demands of steelhead and competitors such as pink salmon, suggesting that a warming climate may cause intensified competition for limited resources. Our findings suggest that steelhead will be vulnerable to future climate change and may continue to experience ocean conditions that result in lower marine survival rates than in the recent past. These results have direct implications for fisheries managers responsible for rebuilding or maintaining steelhead populations.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Code and data are available at https://github.com/janohlberger/IPM_steelhead_WA_coast.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.