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Redistribution of salmon populations in the northeast Pacific ocean in response to climate

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Abstract

Species that migrate long distances or between distinct habitats— for example, anadromous or catadromous fish—experience the consequences of climate change in each habitat and are therefore particularly at risk in a changing world. Studies of anadromous species often focus on freshwater despite the ocean's disproportionate influence on survival and growth. To understand a prominent anadromous species' response to ocean climate, we use a new spatio-temporal model jointly estimating the ocean distribution of all major fall-run Chinook salmon (*Oncorhynchus tshawytscha*, Salmonidae) stocks from California to British Columbia over 40 years. We model hundreds of millions of tagged individuals, finding that different stocks have fundamentally different ocean distributions, distinct associations with sea surface temperature (SST), and contrasting distributional responses to historical ocean SST variation. We show species-level estimates of ocean distribution that ignore among-stock variation will lead to errant predictions of spatial distribution. Using future (2030–2090) SST projections to model focal stocks of fisheries importance we predict substantial ocean redistribution in response to SST change. Predicted aggregate distributional changes do not follow a simple, poleward shift. Instead, we predict net movement into some ocean regions (British Columbia, central California) but net movement out of others (northern California, Washington). Distribution shifts have implications for both major fisheries and marine mammal predators of Chinook salmon. We focus on the consequences of spatial changes in ocean distribution, but our approach provides a general structure to link marine and freshwater components of anadromous species under climate change.

KEYWORDS

climate change, distribution models, *Oncorhynchus*, spatio-temporal models, species range shifts, state-space models

1 | INTRODUCTION

Global changes to environmental conditions have caused extensive changes in the distribution and abundance of species worldwide (Poloczanska et al., 2016). Shifts of individual species can have cascading effects throughout ecosystems (Gilman et al., 2010), affecting important processes from predator–prey interactions (Gilg et al., 2009) to plant–pollinator networks (Aguirre-Gutiérrez et al., 2016; Bartomeus et al., 2011). Because humans derive value from many species—either directly via harvest or indirectly via the ecosystem services they provide—shifting abundances have the potential to affect the availability of resources among groups as access to resources are reduced for some and expanded for others (Hunsicker et al., 2013; Perry et al., 2005; Selden et al., 2018). In marine systems, there is a general expectation that a warming climate will drive species distributions towards the poles (Cheung et al., 2010; Perry et al., 2005), though detailed analyses have shown substantial among-species variation in practice (Pinsky et al., 2013).

Anadromous fish species may be sensitive to climatic changes as their bipartite life-history forces them to respond to climatic changes in both the freshwater and marine environments (Piou & Prévost, 2013). To date, investigations of the consequences of climate change have predominantly focused on the freshwater component of their life-history. Important responses of anadromous species to a changing climate include physiological shifts anticipated under warming temperatures (Muñoz et al., 2015) and low pH (Ou et al., 2015) in freshwater, phenological shifts in migration timing of both outmigrating juveniles (Cline et al., 2019; Otero et al., 2014; Scheuerell et al., 2009) and returning adults preparing to spawn (Finstad & Hein, 2012; Jonsson & Jonsson, 2009), and responses of populations to changing riverine hydrological regimes (Crozier et al., 2008; Jones et al., 2020; Sturrock et al., 2020). However, oceanic environments comprise the majority of many anadromous species' lifespans and favourable ocean conditions are an important determinant of growth and survival (Beamish & Mahnken, 2001; Duffy & Beauchamp, 2011); up to 90% of mass can be derived from ocean growth (Quinn, 2005). Oceanographic models suggest substantial changes to ocean temperatures and productivity will occur in the near future (Hu et al., 2017; Oliver et al., 2019). Links between broad oceanographic indices, abundance, and productivity have been extensively investigated (Cunningham et al., 2018; Friedland et al., 2000; Kilduff et al., 2015; Mantua & Hare, 2002) as have the effects of nearshore marine conditions during the transition from freshwater to the marine environment (e.g., Sharma et al., 2013; Su et al., 2004). However, the effects of a changing climate on the spatial distribution of anadromous fish in the ocean are poorly understood despite the fact that such shifts may have substantial consequences for both ecological communities and human economies. Many anadromous fish return to their rivers of origin and so their oceanic habitat is anchored, in part, by the location of river mouths. Thus anadromous species cannot simply shift their marine habitat in response to ocean conditions and therefore they may be particularly susceptible to climatic changes (Lassalle & Rochard, 2009).

Pacific salmon (*Oncorhynchus* spp., Salmonidae) are well known for their long-distance migrations from their rivers of origin to ocean feeding grounds. Chinook salmon (*O. tshawytscha*) in particular swim thousands of kilometres in the ocean during their lives, crossing oceanographic and political boundaries, and supporting important commercial and recreational fisheries throughout their range (Healey, 1991; Quinn, 2005). These long-distance migrations and broad distributions—they spawn in rivers from California to northern Alaska to Japan (Quinn, 2005)—make independent surveys to assess abundance and distribution particularly difficult. To our knowledge, no systematic survey spans the entire oceanic range of any salmon species. The absence of fishery-independent surveys can greatly complicate the estimation of distributional shifts (Thorson et al., 2016). Existing rigorous descriptions of ocean distribution are dependent upon recoveries of tagged fish captured in fisheries (e.g., Chinook Technical Committee [CTC], 2019; Shelton et al., 2019; Weitkamp, 2010). Other estimates of ocean distribution for salmon occur at the species level and rely on the spatial patterns of aggregate fisheries catch (i.e., not population- or stock-specific catches; for example, Cheung & Frölicher, 2020) or surveys from a portion of the species range. Analyses conducted at the species level will therefore confound changes in ocean distribution with both the covariation in abundance among component salmon stocks (e.g., Kilduff et al., 2015) and shifts in the spatial distribution of fisheries effort.

Fisheries have varied substantially in space and time in the northeast Pacific ocean over the past 50 years (CTC, 2019; Shelton et al., 2019), complicating the process of identifying shifts in ocean distribution. Specifically, any shifts in the patterns of tag recoveries could be caused by either a true shift in ocean distribution or changes to the location and intensity of fisheries. Historical shifts in fisheries effort have largely been driven by changes in Chinook salmon availability—either as a result of changes to the conservation status of some populations or shifts in hatchery practices for some regions. Fisheries for Chinook salmon predominantly target a subset of stocks from particular river systems and so aggregate measures of Chinook salmon catch are not reliable indicators of coast-wide abundance or distribution (CTC, 2019). Previous studies have indicated a lack of annual variation in broad-scale Chinook salmon ocean distributions (Norris et al., 2000; Weitkamp, 2010), suggesting little potential for distributions to shift in response to future climate change (Weitkamp, 2010). However, estimates of ocean habitat based on thermal tolerance have suggested strong changes to suitable ocean habitat in a warming ocean across the north Pacific Ocean (Abdul-Aziz et al., 2011) and a study of a single stock distributed along the California and Oregon coasts showed a relationship between fishery contact rates and water temperature (Satterthwaite et al., 2013). Because salmon home faithfully to their natal regions and management is applied at the level of individual stocks (Pacific Fisheries Management Council [PFMC], 2019), it is important to understand stock-specific responses to climate conditions as well as the response at the species level when aggregated across stocks.

Here, we provide a large-scale, integrated estimate of how Chinook salmon ocean distributions of individual stocks respond to a variation in ocean conditions. We construct a population dynamics model that includes all of the major fall-run Chinook salmon in the northeastern Pacific Ocean—fall-run Chinook salmon are the numerically dominant runs of salmon along the coasts of California, Oregon, Washington, and British Columbia—and provide stock- and year-specific estimates of ocean distribution. Our model extends and improves an ocean distribution model based on recoveries of tagged Chinook salmon (Shelton et al., 2019) by adding 20 years of recovery data, accommodating annual variation in distribution, and linking ocean distributions to observed sea surface temperatures (SST). We then use future projections of the ocean temperature to generate predictions of ocean distribution for six of the largest fall-run Chinook salmon stocks, and provide estimates of each stock's association with SST. Finally, we examine the relationship between climate scenarios and abundance to project abundance estimates and understand how aggregate Chinook salmon availability is projected to change among ocean regions.

2 | METHODS

2.1 | Population dynamics model

We present an overview of the model and data here with an emphasis on the specific methods relevant for estimating spatial distributions. Full descriptions of the statistical model and data sources are presented in Appendices S1 and S2.

We constructed a Bayesian state-space model to track the spatio-temporal population dynamics of 1,400 tagged groups of Chinook salmon representing fish from 16 distinct origins between 1979 and 2015 (Appendix S2: Table S2.1). State-space models separate the biological processes of populations (e.g., mortality, spatial distribution, maturation; the process model) from the observation of the population (e.g., fisheries catches; the observation models). This framework enables explicit accounting for varying levels of uncertainty in the data and missing data. We use data on the recapture of coded wire tagged (CWT) Chinook salmon from multiple fisheries (including both fisheries that target Chinook salmon and those where Chinook salmon are captured as by-catch) from California to Alaska (Figure 1) to estimate the parameters of the model (tag data maintained by the Regional Mark Processing Center; www.rmpc.org). Specifically, the model uses the rate at which groups of CWT fish are recaptured in each fishery and then uses information from all fisheries jointly to infer the abundance and distribution of each group. CWT recoveries are a function of four components (within a single ocean region and season): the abundance of the CWT group, the ocean distribution of the CWT group, the amount of fishery effort for each fishery, and the rate at which each fishery is sampled for CWTs. Thus changes in any of these four processes can affect CWT recoveries and our model accounts for all of these processes simultaneously for all ocean regions and seasons (see Appendix S1 for details).

Each released group is comprised of Chinook salmon arising from CWT individuals spawned and reared at a single hatchery in a single year and released (predominantly as fingerlings [salmon released within a few months of hatching], though some yearling release groups are also included). These 1,400 hatchery-stage-year groups (hereafter release groups) can include more than one CWT tag code and represent a total of 353 million Chinook salmon released between 1978 and 2010 (brood years 1977–2009; Appendix S2: Tables S2.2 and S2.3) and recovered in the ocean between 1979 and 2015 (an estimated 1.3 million recovered tags). As Chinook salmon originating from different rivers are known to have distinct ocean distributions (e.g., Healey, 1991; Shelton et al., 2019; Weitkamp, 2010), each release group was assigned to one of 16 origin regions ranging from California's Central Valley to southern British Columbia (Appendix S2: Table S2.2; fall-run Chinook salmon do not spawn in rivers north of southern British Columbia).

Our model uses the ocean region, season, and fishery where recovery occurred as well as information about the fisheries effort and catch sampling for CWT to infer four main biological processes: (a) the mortality of juvenile fish prior to spring of age 2; (b) fishing mortality by age and ocean region from each fleet; (c) the spatial distribution of fish in the ocean and relationship between SST and ocean distribution; and (d) the age-specific loss of fish from the ocean due to maturation (salmon leaving the ocean and returning to their streams of origin to spawn). We track the abundance of fish from the spring of age 2 (defined as calendar year minus brood year) to fall of age 6, encompassing 19 seasonal time steps and 17 ocean regions (Figure 1). We provide a table describing the fall-run Chinook salmon age classification used here in Appendix S1: Table S1.1. As the majority of both fishing effort and tag recoveries occur during the summer, we focus on the distribution of fish during the summer season (June–July).

While our model provides estimates of biological parameters for fish from all 16 origin regions (hereafter "stocks"), included in the model across all years, we focus on six stocks with the largest number of tagged fish in our dataset that contribute disproportionately to the major Chinook salmon fisheries along the west coast of North America (CTC, 2019; PFMC, 2019). We detail results for fall-run Chinook salmon from California's Central Valley (hereafter "SFB"), the Klamath basin in northern California ("NCA"), the lower Columbia River fall-run Chinook ("LCOL"; also known as "tules"), the bright run from the middle Columbia River ("MCOL"), the upriver bright run from the Columbia River ("URB"),

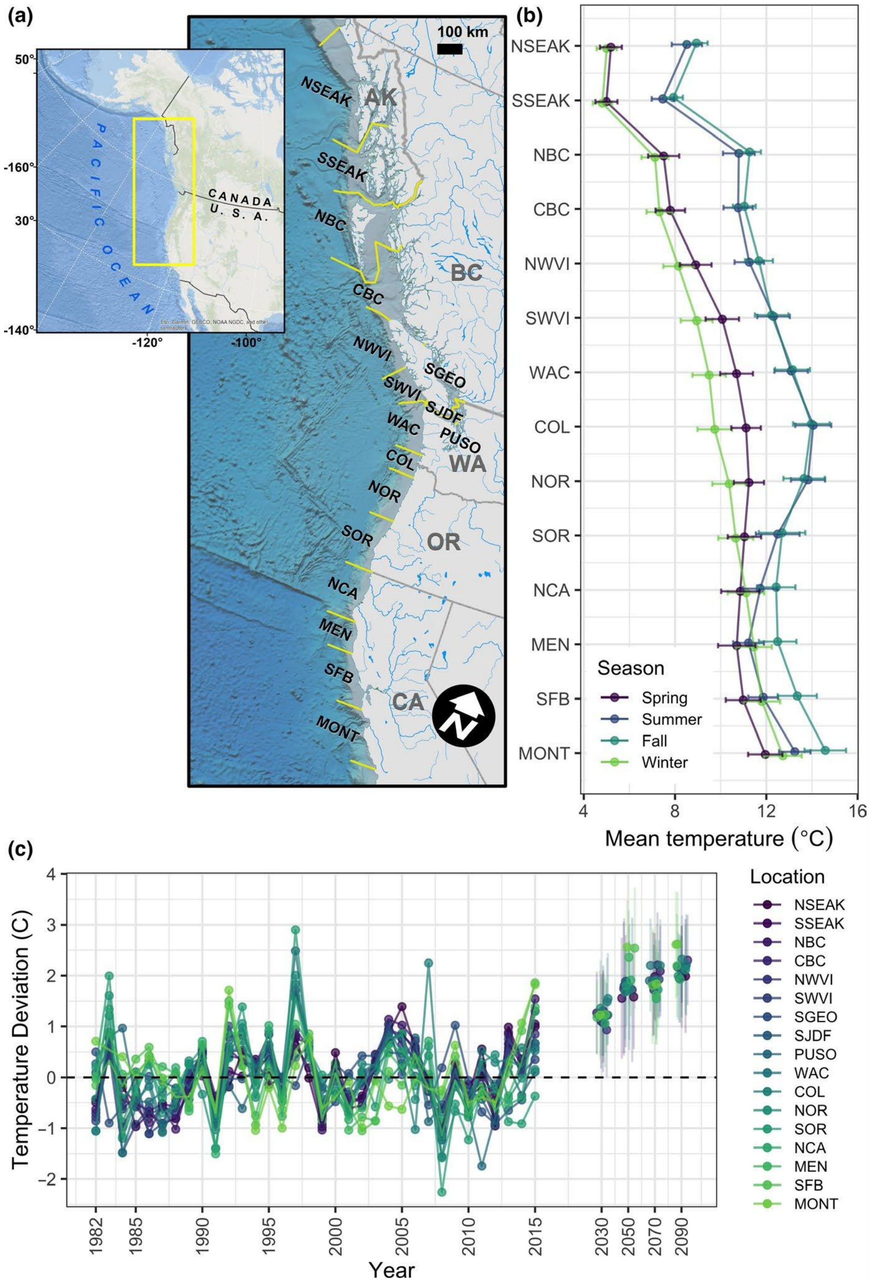

FIGURE 1 (a) Map of the study area with ocean region borders and region labels. Dots designate the location of hatcheries producing Chinook salmon used in the study estimation. (b) Mean among-year temperatures ±1 *SD* for each season and 14 ocean regions along the coast between California and Alaska (excluding the three Salish Sea regions: SJDF, PUSO, SGEO). (c) Summer SST anomalies for each ocean region from 1982 to 2015 derived from OISST and projected mean ± 1 *SD* anomalies for ten-year period centred on 2030, 2050, 2070, and 2090 from the MPI45 global circulation model

and the fall-run Chinook salmon from the Snake River ("SNAK"; the largest tributary of the Columbia River). Together, these stocks comprise approximately 71% (250.9 million) of the CWT releases used in the model and include multiple release groups in each year, providing sufficient information to allow for robust inference about year-to-year patterns in ocean distribution and abundance. Additionally, these stocks are rarely found in the Salish Sea (Shelton et al., 2019), an inland sea poorly described by large-scale oceanographic models used for future SST projections. We defer discussion of stocks that use the Salish Sea extensively to future work. Finally, these six focal stocks all have estimates of total population size over recent decades (see Appendix S4), allowing us to connect distributional changes to changes in both stock- and aggregate-level abundance.

We conduct all of our data analysis in R (v3.6.1) and implement the statistical models in Stan (Carpenter et al., 2017; Gelman et al., 2015) as implemented in the R statistical language (*rstan* v2.19.3; R Core Team, 2019; Stan Development Team, 2019).

2.1.1 | Ocean distribution models

Chinook salmon distributions vary by season. We let $\overline{\theta}_{r,l,s}$ be the mean proportion of fish from stock *r*, present in ocean region *l*, at the beginning of season *s*. Across ocean regions, the proportions must sum to one because these represent the entire ocean extent: $\sum_l \overline{\theta}_{r,l,s}$. Fisheries activity and therefore where tag recoveries occur are spatio-temporally patchy (Appendix S2) and vary in their spatial precision. We divide the coastal ocean into 17 ocean regions (Figure 1) defined largely by fishing regulation and political boundaries and assigned each CWT recovery to an ocean region. As in Shelton et al. (2019), within an ocean region, occurrence of Chinook salmon is assumed to be uniform. Among these ocean regions however, ocean distributions of Chinook salmon are assumed to be smooth—adjacent regions are more similar in abundance than distant regions, on average. Therefore we introduce a parameter for each stock, ocean region, and season, $\xi_{r,l,s}$ that defines the proportional occurrence in an average year,

$$\bar{\theta}_{r,l,s} = \frac{\exp\left(\xi_{r,l,s}\right)}{\sum_{l} \exp\left(\xi_{r,l,s}\right)} \tag{1}$$

We use a dimension reduction technique known as predictive process modelling (Banerjee et al., 2008; Finley et al., 2012; Shelton et al., 2019) to impose a smoothness constraint on $\xi_{r,l,s}$—adjacent spatial areas more correlated than distant areas (see Appendix S1 for details). We view the Salish Sea (ocean regions SGEO, PUSO, and SJDF) as distinct from the smooth distribution and treat these three regions separately.

We then allowed the ocean distribution for each stock to deviate from this average distribution as a function of regional ocean SST. Specifically, we used the Optimum Interpolation Sea Surface Temperature (OISST) dataset to derive season specific temperature series for each ocean region from 1982 to 2015 (Banzon et al., 2016; Reynolds et al., 2007). OISST did not provide reasonable temperature estimates for the Salish Sea, so we supplemented our data with direct observations of SST in those ocean regions (see Appendix S3). We calculated an anomaly for each ocean region-season combination by subtracting the among-year mean so that each ocean region(*l*)-season(*s*)-calendar year(*c*) combination, $T_{l,s,c}$, had a time-series average of zero (Figure 1). We estimated a coefficient for each stock ocean region-season, $\psi_{r,l,s}$, and therefore made proportional occurrence in ocean regions vary with SST,

$$\theta_{r,l,s,c} = \frac{\exp\left(\xi_{r,l,s} + \psi_{r,l,s} T_{l,s,c}\right)}{\sum_{l} \exp\left(\xi_{r,l,s} + \psi_{r,l,s} T_{l,s,c}\right)} \tag{2}$$

The anomalies, $T_{l,s,c}$, are the deviation from average SST and therefore $\psi_{r,l,s} T_{l,s,c}$ determined the effect of this deviation on ocean distribution. This form is very flexible. Even though it is linear in terms, it allows many possible relationships between proportional distribution and SST.

2.2 | Stock-specific temperature associations

To characterize the SST associated with each stock in each year, we calculated a weighted mean SST from the OISST data and our estimates of distribution. We use our estimates of proportional distribution as weights and then summarize this weighted mean SST to describe the temperature association for each stock among years (1982–2015) during the summer season. This allows us to compare the SST association among stocks.

2.3 | Ocean distributions in future ocean conditions

We used a global circulation model (GCM)—the medium resolution Max Planck Institute Earth System Model (Giorgetta et al., 2013; Jungclaus et al., 2013)—to provide predicted temperatures for SST for each season and ocean region. We used predictions from the RCP45 scenario (hereafter MPI45; see IPCC, 2014) and mapped predictions to our 14 ocean regions outside the Salish Sea (see Appendix S3). We chose Representative Concentration Pathway (RCP) 4.5 over two other available MPI-ESM-MR GCM scenarios, RCP2.6 and 8.5, because it represents a likely future of global carbon emissions (Thomson et al., 2011). Of the three alternative climate scenarios, RCP2.6 is the most optimistic, assuming CO_2 emissions decline starting in 2020, and 8.5 is the most pessimistic, assuming CO_2 emissions continue increasing until at least 2100. We felt RCP4.5 represented the most likely scenario of the three, given current circumstances and the fact that CO_2 emissions are still rising (see also Appendix S3).

We calculated season-ocean region means of SST from the 1982 to 2005 period from the MPI45 and then differenced that mean from the future projections in the MPI45 model (years 2025–2100) to produce temperature anomalies for each season-ocean region. These projected temperature anomalies are analogous to the OISST-derived values used in the estimation model (*T* in Equation 2) but *T* was derived from the years 1982 to 2005 rather than 1982–2015. To account for this difference in time-frame, we calculated the average temperature using OISST from 1982 to 2005, derived an offset between this value and the average for 1982–2015, and included this offset to ensure that MPI45 and *T* had identical reference levels. We then summarized predicted average temperature anomalies for each season-ocean region in ten-year blocks centred on 2030, 2050, 2070, and 2090 and used these projected anomalies to generate predicted spatial distributions for each of our focal stocks. We lacked predictions from the MPI45 model for the ocean regions in the Salish Sea. After examining the predictions for the non-Salish Sea ocean regions, we elected to use the average predicted offset from these 14 regions as the offset for each of the three Salish Sea regions (Appendix S3).

2.4 | Population size estimates

To understand how changes in SST may shift the abundance of Chinook salmon among ocean regions, we needed to combine our estimates of distributions (the proportion of the total ocean population of each stock in each ocean region) with estimates of stock-specific abundance. We estimated stock-specific abundances based on annual estimates of abundance for spawning or in-river returns for each of the focal stocks (see Appendix S4). We used information from the Pacific Fisheries Management Council (PFMC; SFB and NCA stocks; PFMC, 2019) or from the Pacific Salmon Commission's Chinook Technical Committee (CTC; LCOL, MCOL, URB, SNAK stocks; CTC, 2019). The models used by these management entities make different assumptions from our model and each other but they provide the best available abundance estimates, and are considered sufficiently reliable for use in management. They should adequately serve our purpose of approximating abundances for the focal stocks. They also provide total stock abundance (both hatchery and non-hatchery produced fish) whereas our model focuses on tagged fish exclusively. Total run (hatchery plus natural) abundance is a more appropriate metric of these runs than abundances that can be derived from our model estimates of juvenile survival (see also Appendices S4 and S5). To marry output from these fisheries management models to our distribution estimates, we first extracted estimates of total in-river population size—the abundance of fish that escaped ocean fisheries and either reached their spawning location or were captured by river fisheries. We then used estimates of annual ocean exploitation rates to expand in-river population size to the beginning of the summer season (June 1) to match our ocean distribution model (see Appendix S4). Importantly, this estimate includes multiple age-classes and represents only the fish that would mature, not the entire ocean population which includes individuals who will mature and spawn in later years. While the fraction of the ocean population represented by this maturing adult population will vary year-to-year due to varying cohort strength and other factors, on average the maturing adults should be a proportional representation of the ocean abundance.

To estimate ocean region-specific abundances, we first drew abundances from each stock from a joint distribution of abundances across stocks, to account for the observed covariation in abundance among stocks (Appendix S4). We then apportioned each stock's total abundance among the different ocean regions using the estimated proportional distribution (the θs) corresponding to the current average ($T = 0$) and future SST for 2030, 2050, and 2070. We drew 1,000 samples from the posterior distribution of $\boldsymbol{\theta}$ and 1,000 draws from the abundance distribution to propagate the uncertainty in distribution and abundance for each stock. We summarized both the proportional change in abundance for each stock and the overall change in predicted aggregate abundance. While we apportioned salmon into the 17 ocean regions, we summed across these regions to describe the total abundances into a smaller number of areas corresponding to major fishing or geographic regulatory areas (central California [regions MONT and SFB], northern California [MEND and NCA], Oregon [SOR and NOR], Salish Sea [SJDF, PUSO and SGEO], Washington [COL and WAC], southern British Columbia [SWVI and NWVI], northern British Columbia [CBC and NBC], and Alaska [SSEAK and NSEAK]; Figure 1).

3 | RESULTS

3.1 | Oceanography

We illustrate latitudinal patterns in ocean temperature by season from OISST data for our 14 ocean regions (1982–2015; excluding the three Salish Sea regions: SJDF, PUSO, SGEO; Figure 1). Of particular interest is that while the winter and spring seasons show the expected spatial trend—declining SST from south to north—the summer and fall patterns exhibit a notable trough in SST in the southern portion of the range along the coast of northern California (regions MEN, NCA).

Additionally, we plot the summer temperature deviations from 1982 to 2015 for each ocean region and the projected temperatures for the ten-year average deviation (±1 *SD*) for 2030, 2050, 2070, and 2090 derived from MPI45. As SSTs are driven in part by basin-scale oceanographic processes, historical temperature deviations are spatially synchronous with a coast-wide median pairwise correlations of 0.47 and some adjacent ocean regions having correlations of >0.90 (Appendix S3: Figure S3.4). While projected temperatures uniformly increase for all four future years, no future average temperature is beyond the range of observed temperature deviations between 1982 and 2015 (Figure 1c). Future average ocean conditions during the summer are generally comparable to extreme *ElNi ño* events observed since 1982 (e.g., 1983, 1997; see NOAA, 2020), though by 2070 most average temperature anomalies are expected to exceed SST observed since 1982 especially in the northern portion of the range (Figure 1). In future scenarios (including and beyond 2070), individual years are expected to significantly exceed the range of historically observed SST anomalies.

3.2 | Population dynamics model

The estimation model converged and mixed well ($\hat{R}$ convergence diagnostics: $\hat{R} < 1.01$ for all parameters; Gelman & Rubin, 1992; Vehtari et al., 2020). This is a large model, incorporating over 756,000 observations of presence/absence and 47,000 of positive CWT recoveries. Additional descriptions of model fit and diagnostics are presented in Appendix S5.

3.3 | Ocean distribution

The six focal stocks exhibited substantial differences in average ocean distribution and the model estimated some distributional variation as a function of SST (Figure 2). For clarity of plotting, we excluded the three Salish Sea ocean regions in all distributional plots and focused on the ocean regions outside the Salish Sea. All six stocks had individual ocean regions for which the proportion varied by more than 5% among years. However, in no case did the distribution radically shift in response to SST; the six stocks broadly followed their average distribution with a constrained amount of variability. In general, the California Central Valley (SFB) and Klamath (NCA) stocks were centred near the coastal location of their river of origin

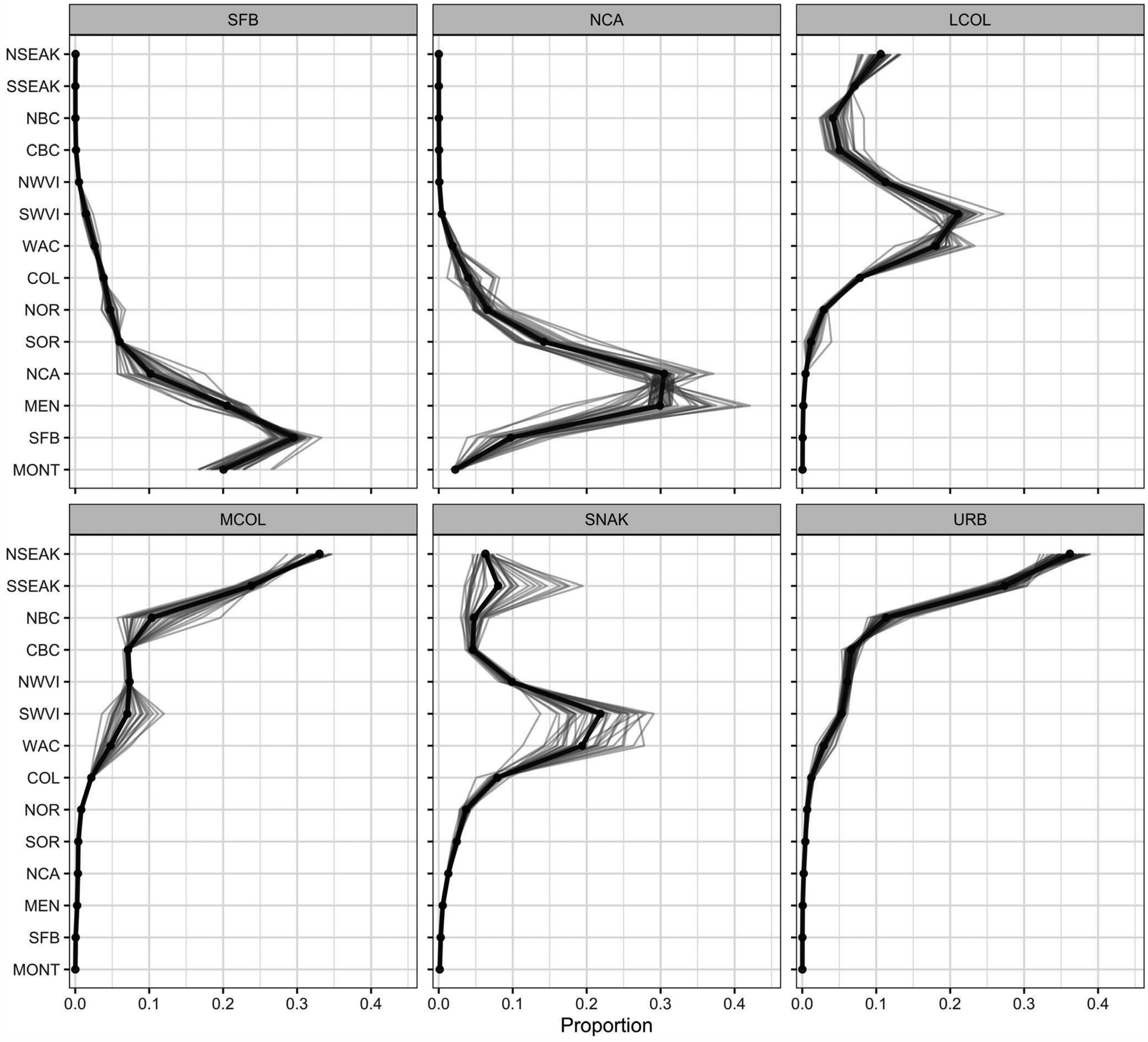

FIGURE 2 Estimated summer ocean distribution for six focal stock (SFB: California Central Valley fall-run; NCA: Klamath River fall-run; LCOL: Lower Columbia tules; MCOL: Middle Columbia brights; SNAK: Snake River fall brights; URB: Columbia River upriver brights). Black line and ribbon shows estimated among-year average proportional distribution (90% CI) (ribbon may be smaller than the line). Point estimates for distribution in individual years are shown in thin lines

(ocean regions SFB and NCA, respectively; Figure 2). The Columbia river stocks were estimated to be distributed substantially north from their river of origin (COL; Figure 2). The URB stock showed the smallest distribution shifts in response to SST.

There were differences in summer ocean distribution between cool (e.g., 2008) and warm (e.g., 1997) years (Figure 3). For the Klamath (NCA), and four Columbia river stocks (LCOL, MCOL, SNAK, URB), ocean distributions shifted north in a warm year (1997) relative to a cool year (2008; see also Figure 1). In general the difference between a cool and a warm year amounted to the ocean region with the largest proportion of fish shifting one ocean region north (a shift on the order of 100–200 km). In contrast, SFB shifted to become more concentrated in the southernmost ocean regions (MONT and SFB), with accompanying declines in the northern California regions of MEN and NCA, and slightly increasing in the northern edges of its range (Washington state (WAC) and southern British Columbia (SWVI; Figure 1).

3.4 | Stock-specific temperature associations

We show substantial variation in weighted mean summer SST experienced by individual fish, based on their distribution across ocean regions with different water temperatures both among stocks and within stocks. Among stocks, the median weighted mean SST ranged nearly 2.7°C from 9.5°C for the URB stock to 12.2°C for SFB (Figure 4). Within a given stock, the weighted mean SST among years varied

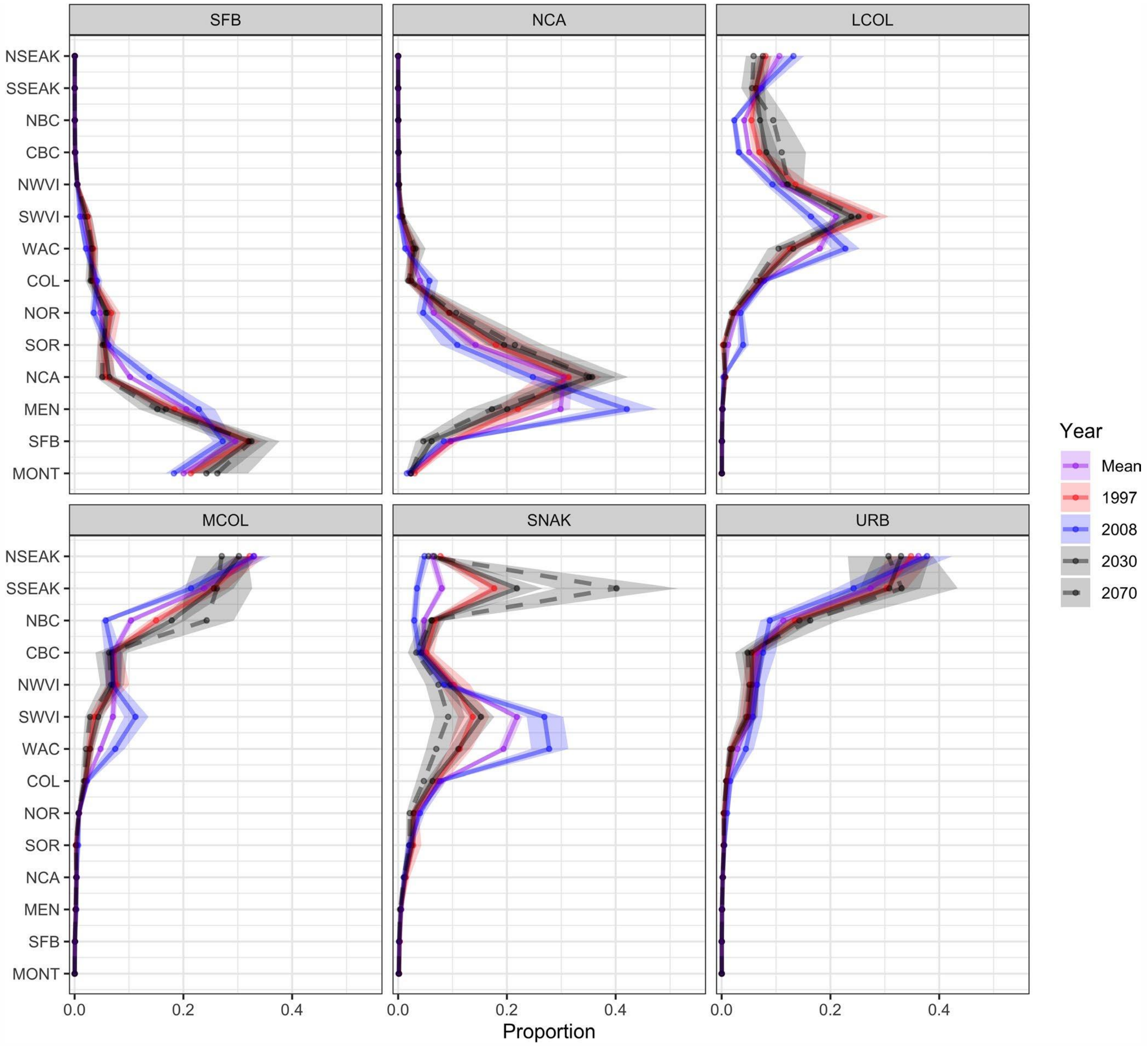

FIGURE 3 Estimated summer ocean distribution for six focal stocks under the average climatology for 1982–2015 (mean), a warm summer (1997), a cool summer (2008), and projected distribution under average projected summer SST conditions for 2030 and 2070. Mean and 90% CI shown

from 1.7°C (SNAK; maximum weighted SST minus minimum weighted SST) up to 3.1°C (NCA) among years, indicating both among-stock and among-year variability in the association between SST and ocean distribution. For reference, the simple average SST (all ocean regions weighted equally) was 11.9°C with a range of 2.2°C (Figure 4).

3.5 | Future ocean distribution and abundance

For all stocks, future predicted average summer ocean distribution for 2030 and 2070 appear generally similar to the distribution of a strong *El Niño* year (1997; Figure 3). In most cases, estimates of stock-specific ocean distributions for both 2030 and 2070 diverged substantially from cool years (e.g., 2008) and the distribution for a year with the average climatology from 1982 to 2015 ("Mean" in Figure 3). Predictions for 2070, when SST are predicted to mostly exceed the observed range of temperatures from 1982 to 2015, are more uncertain than the predictions for 2030 which fall clearly in the range of observed SST deviations (Figure 1).

We combined historical abundance estimates of spawning Chinook salmon with predicted changes in ocean distribution to understand how aggregate abundance across these six focal stocks may shift in response to projected oceanic conditions. On average these stocks contribute about 1.2 million maturing adults a year (*SD* = 0.52 million; range 0.50–2.33 million). We show ocean regions have

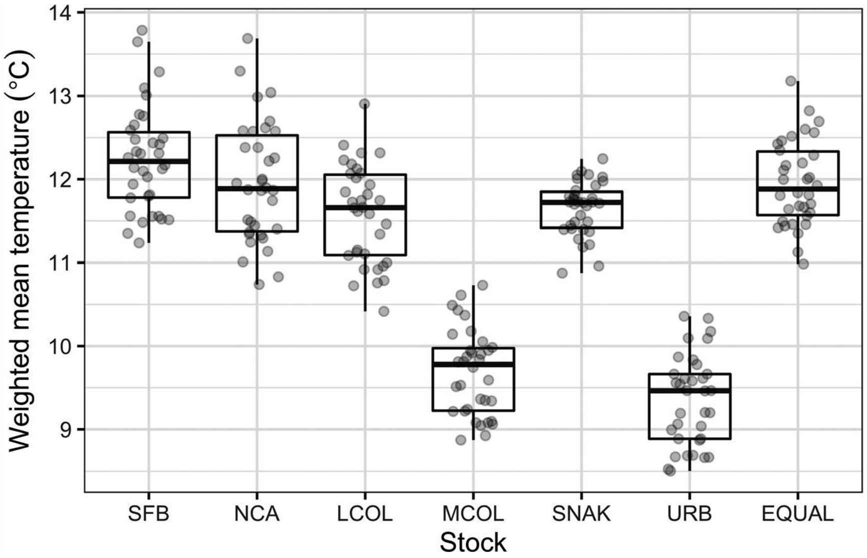

FIGURE 4 Weighted mean SST for the six focal stocks during the summer season. The "EQUAL" category is the weighted mean SST using equal weights for all of the 17 ocean regions. Points represent weighted mean temperature for individual years, boxplots show median, interquartile range, and 95% whiskers among years

stock-specific patterns of loss and gain in their ocean distribution (as measured by the difference between the summer distribution under average temperatures from 1982 to 2015 and projected average temperatures in 2050; Figure 5a). Ocean regions that have decreased abundance for one stock generally show an increase for one or more other stocks (see Appendix S5: Table S5.1 for uncertainty bounds for results from Figure 5a). Notable exceptions are northern British Columbia, which are predicted to remain stable or increase for all stocks, and northern California which is predicted to decrease. In terms of aggregate abundance across stocks, this does not mean that shifts in ocean distribution simply balance out because the focal stocks do not provide equivalent numbers of maturing adults. The annual number of maturing adults ranged from a high of 426 thousand on average from the SFB stock to 33 thousand for the SNAK stock (Figure 5a; Appendix S4). Maturing adult abundances were mostly positively correlated among stocks (pairwise Pearson correlation range from −0.2 to 0.8 but only one of 15 pairwise correlations was negative; Appendix S4: Figure S4.2) indicating that a high abundance year in one stock generally corresponded to a year of high abundance in other stocks. The large uncertainty bounds in Figure 5c for both current and future ocean conditions primarily reflect the substantial year-to-year variation in abundance of maturing fish.

After accounting for differences in relative abundances as well as the covariation among stocks in maturing adult abundance (see Appendix S4), we predict in 2050 aggregate abundance for these six stocks will increase or remain largely unchanged in northern British Columbia and Alaska (changes of 33 [23, 49], and −6 [−14, 0.5] thousand fish, respectively, median [interquartile range]). This is a median change of 16% and −2% over current conditions, respectively; Figure 5c). At the far southern extent of the area, there are substantial changes, with predicted increases in central California (44 [24, 74] thousand, +21%) and declines in northern California (−62 [−95, −40] thousand, −33%). These changes occur primarily because of the southerly distributional shift of the abundant SFB stock. While Oregon and southern British Columbia are predicted to be largely unchanged (both change less than 10%), Washington is predicted to decline substantially (−26 [−36, −19] thousand, −24%), though this change declines slightly to −16% if we account for the few thousand fish from LCOL and SNAK stocks estimated to be present in the Strait of Juan de Fuca (Appendix S5). Qualitatively, projections for 2030 and 2070 show the same patterns of change but differ in magnitude (Appendix S5: Figures S5.16 and S5.17).

4 | DISCUSSION

We integrated disparate data sources spanning over 25° of latitude and 40 years to provide estimates of stock-specific ocean distribution for Chinook salmon and how ocean distributions will shift with SST. Our results show that individual stocks vary substantially in their current distribution, have stock-specific relationships to SST, and respond meaningfully to observed historical SST variation. However, estimated responses to SST are not uniform in direction or magnitude, with one stock (SFB) estimated to shift distribution southward in response to SST warming while another (MCOL) shifted strongly northward and a third (URB) showed a minimal response to SST (Figures 3 and 5). Finally, we married stock-specific distributions with future temperature projections and estimates of abundance to predict distributional shifts in aggregate Chinook salmon abundance among ocean regions.

We predict that changes in the distribution of Chinook will result in differential availability of Chinook salmon to resource users in the future. Chinook salmon support major commercial, charter, and recreational fleets across their range as well as being a major prey item for marine mammal predators including harbour seals (*Phoca vitulina*, Phocidae), sea lions (*Zalophus californianus* and *Eumetopias jubatus*, Otariidae), and fish eating populations of killer whales (*Orcinus orca*, Delphinidae) including the endangered Southern Resident Killer Whale population (Ford & Ellis, 2006; Hilborn et al., 2012). We show that predicted shifts in abundance are not straightforward, with

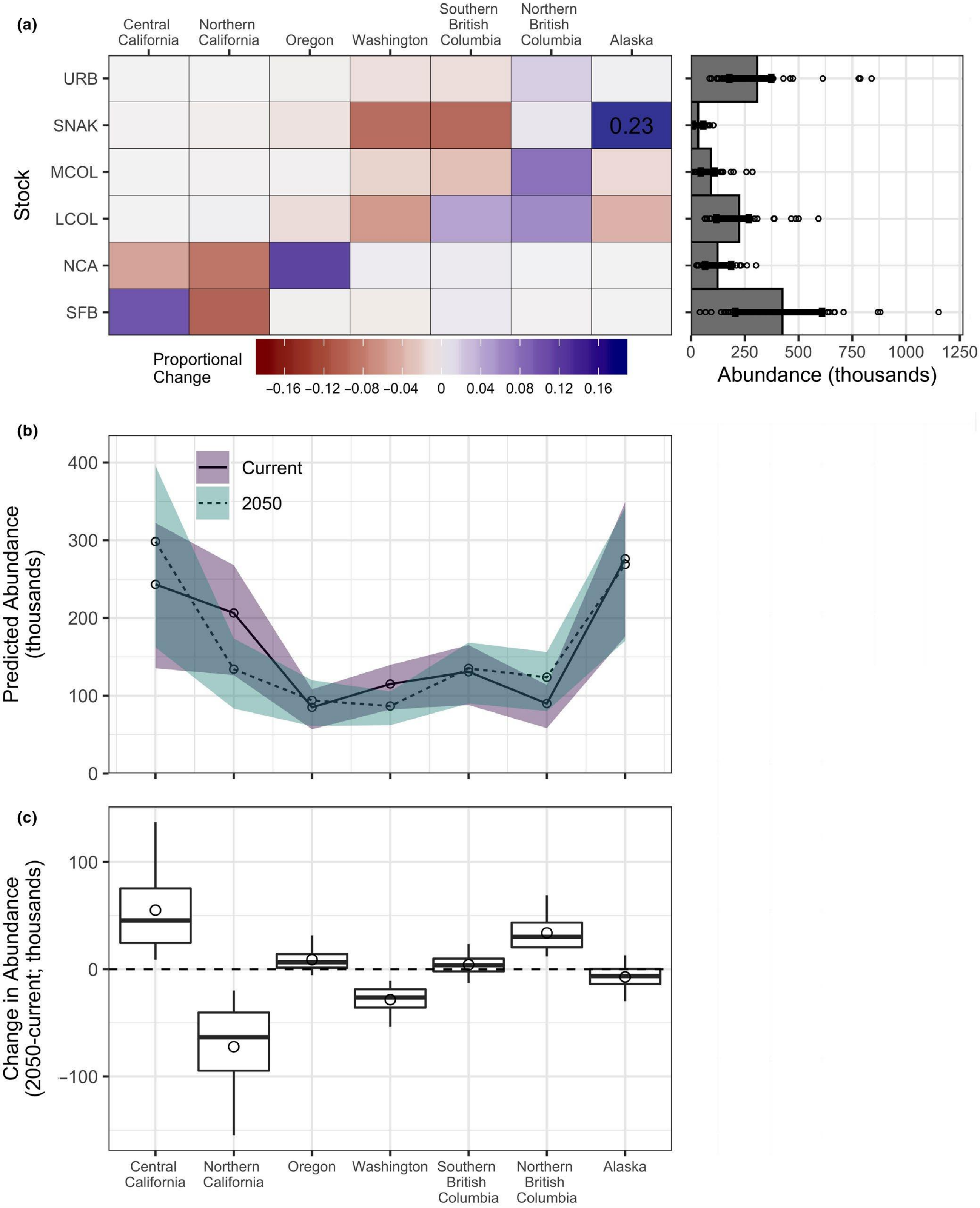

FIGURE 5 Estimated proportional change in summer ocean distribution for focal stock between current conditions and 2050 (top left). (a) Historical maturing adult Chinook salmon abundances (1983–2015) for focal stocks (mean, interquartile range, and individual years shown). (b) Cumulative abundance for focal stocks in ocean regions outside the Salish Sea under average (mean, interquartile range, and 90% interval). (c) Projected change in cumulative abundance across all six focal stocks in 2050 relative to average conditions (1982–2015) due to climactic driven distributional shifts. Points are means and boxplots show median, interquartile range, and 95% whiskers

both northern ocean regions (northern British Columbia) and southern ocean regions (central California) predicted to have increased abundance while in between there are ocean regions of predicted decline (northern California, Washington), and others with almost no change (Oregon, southern British Columbia, Alaska). Predicted changes in abundance can be substantial for an individual ocean region (in some cases an approximate 25% change over current abundances). The projected increase in central California abundance, driven primarily by a southern shift in the SFB stock, might seem unexpected, especially since this is already the southern extreme of the species range. However, an independent modelling effort also estimated southern shifts in SFB spatial distributions when conditions were warmer (Satterthwaite et al., 2013). The Central California ocean region contains multiple areas (e.g., Monterey Bay and the Gulf of the Farallones) where prevailing winds and coastal topography creates retention areas enriched by coastal upwelling (Hickey & Banas, 2018), and these hotspots of productivity may provide refuges in the face of generally declining productivity along the coast. We emphasize that our results are not inclusive of all Chinook salmon populations present in these waters and so are not a complete picture of all Chinook salmon in these waters, but they do represent a majority of individuals in many ocean fisheries (see below) and suggest that individual shifts in stock ocean distribution will translate to substantial shifts in aggregate abundance. Compiling information on additional Chinook salmon groups— for example, spring, summer, and winter run populations—to more fully understand aggregate distributional shifts is a major direction for future work.

Predicted shifts in ocean distributions will result in changing availability of Chinook salmon to ocean fisheries. Major commercial fisheries exist in each state and province and different permits are required to participate in fisheries in different states and provinces; fishers cannot easily relocate from, say, Washington to British Columbia or from California to Washington to track shifting Chinook salmon abundance. Even within a single management jurisdiction, shifting distributions may have significant consequences. For example, the predicted divergence between SFB and NCA may make it easier to target abundant SFB when NCA are rare, or vice versa. However, the predicted distributional shifts may create new problems as well. For example, a southward shift in SFB would increase its overlap with the endangered Sacramento River Winter Chinook salmon (Satterthwaite et al., 2013). Allocation among these fishing areas and between different fishing sectors (e.g., commercial or recreational) is determined by a complex web of management bodies and permits that include an international body (the Pacific Salmon Treaty), an inter-state body (the Pacific Fisheries Management Council), state- and province-specific managements groups (representing Alaska, Washington, Oregon, Idaho, California, and British Columbia), and Tribal Nations in the United States and First Nations in Canada who are co-managers of these resources. Avoidance of Chinook salmon by-catch is also an important consideration of pelagic trawl fisheries for Pacific hake (Holland & Martin, 2019) and walleye pollock (Ianelli & Stram, 2015). Such complexity emphasizes the broad importance of Chinook salmon culturally and economically in the northeast Pacific ocean. At present, no fisheries affecting salmon incorporate explicit ocean distribution models for Chinook salmon or include any oceanographic effects on distribution. Our work suggests that integrating ocean distribution information warrants consideration for future management scenarios in a warming ocean (Lewison et al., 2015).

An important caveat for our simulations is that we assume the abundance of the focal stocks is represented by the abundance in recent decades (1983 to present). While this assumption allows us to identify predicted shifts that stem solely from ocean climate, it is likely that future climate conditions will differentially affect the productivity of individual stocks through changes at various stages in the lifecycle (Crozier et al., 2008; Jones et al., 2020; Oke et al., 2020). Currently, stock-specific abundance projections are not available for all stocks, but a broad literature suggests climate change will affect the productivity and population dynamics for many salmon populations during freshwater life-stages (Battin et al., 2007; Crozier et al., 2008; Kovach et al., 2015; Morita et al., 2014). Future production of Chinook salmon from hatcheries may also change substantially from current levels; hatchery production has fluctuated over the past 50 years for many Chinook salmon populations (Huber & Carlson, 2015; Nelson et al., 2019). Our model provides a framework that can be used in the future to link changes in freshwater productivity and hatchery practices to ocean distribution and availability.

An additional caveat to our analysis is its dependence on data from hatchery-origin fish, which dominate CWT data, to make inferences about stocks consisting of a composite of hatchery- and natural-origin fish. Although Beacham et al. (2020) found fine-scale differences in the distributions of geographically proximate coho salmon (*O. kisutch*) populations, they noted that Weitkamp and Neely (2002) did not find differences between hatchery- and natural-origin coho salmon distributions at a resolution more comparable to our study. Similarly, generally minor differences have been found between the ocean distributions of natural- versus hatchery-origin Chinook salmon when such comparisons are possible (Satterthwaite et al., 2018; Sharma & Quinn, 2012; Weitkamp, 2010). Additionally, the SFB, LCOL, MCOL, and SNAK stocks are predominantly of hatchery-origin (see Appendix S3 of Shelton et al., 2019, noting that SNAK is classified within the UCOL stock there). Minimal differences have been documented in the distribution of hatchery- versus natural-origin URB fish (Sharma & Quinn, 2012), and distribution inferences for the genetically identified composite NCA stock were similar to distributions inferred from hatchery-origin CWT alone (Satterthwaite & O'Farrell, 2018).

Our results also have general implications for estimating suitable or optimal habitat based on observed relationships between SST and abundance and for projecting distributional change under oceanographic change. Many studies attempt to identify the relationship between SST and estimates of abundance which use this relationship to project distribution under future ocean conditions (e.g., Abdul-Aziz et al., 2011; Cheung & Frölicher, 2020; Cheung et al., 2010). SST is one of the main oceanographic covariates used in such analyses (e.g., Hazen et al., 2018; Rogers et al., 2019). We show that the weighted mean SST varied among stocks by 2.7°C, suggesting there is not a fundamental, physiologically driven SST that universally predicts Chinook salmon abundance and occurrence. Tagging data from a single stock of Atlantic salmon also suggest flexibility in their thermal habitat use (Strøm et al., 2020). Conducting a species-level analysis that ignores stock-specific differences in distribution (e.g., Abdul-Aziz et al., 2011; Cheung & Frölicher, 2020) would yield errant projections of future distribution. In the absence of information on the ocean distribution of all Chinook salmon stocks (see below for more detail), it is not possible to determine the magnitude or even the direction of error introduced by ignoring among-stock variation in ocean distribution. Similar phenomena seem likely to occur for other salmonids and we speculate this may be a more prevalent feature of anadromous species than strictly marine species. We do not suggest that Chinook salmon as a species do not track particular oceanographic conditions—potentially including temperature, salinity, and productivity—but rather that SST may not be a particularly good descriptor of the true environmental signal they are tracking. Ideally, we would know the identity of such oceanographic features and develop a distribution model using that set of variables. Unfortunately, there is a relatively limited set of historical ocean observations that are available to link to species distributions and SST comprises the longest and most complete historical time-series which is also is available from future ocean projections. Retrospective analyses of ocean biogeochemical models may be useful in expanding the suite of variables available to ocean distributions and environmental variables as they have in other ocean regions (e.g., Fernandes et al., 2020). We anticipate using alternative environmental covariates in or different mathematical forms for Equation (2) to improve estimates of Chinook salmon ocean distribution. Nevertheless, model diagnostics showed that the current formulation including SST deviations as covariates substantially improved model fit (Appendix S5: Table S5.2).

Our study for distribution for all fall-run Chinook salmon stocks that have a significant CWT program and makes projections for six focal stocks for which we have adequate tagging data as well as accessible abundance data. Genetic analyses suggest that the six stocks included here comprise 90% of commercial catch in central California (Satterthwaite et al., 2015), approximately 75% of fish in northern California and Oregon (Bellinger et al., 2015), approximately 50% of fish caught along the outer coast of Washington state (Moran et al., 2018), and at least 25% of Chinook caught in northern British Columbia (Winther & Rupert, 2016) and southeastern Alaska (Gilk-Baumer et al., 2013). Other fall-run stocks either are common in the Salish Sea (for which we have limited future oceanographic predictions), have limited or uncertain abundance estimates, or lack replicate CWT release and recovery data to derive reliable estimates of SST-distribution relationships. Future work should aim for a full accounting of all Chinook salmon stocks from California to Alaska. This will require gathering data from additional fishing fleets to extend ocean distribution estimates into the Gulf of Alaska (specifically information on trawl by-catch), collating CWT data on other run types such as spring- and summer-run Chinook which predominate in the rivers of British Columbia and Alaska, and incorporating genetic data from captured salmon to allow inclusion of stocks that entirely lack CWT or are only sparsely tagged.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data used in this paper are derived from publicly available sources. Distinct data sources for fisheries data, coded wire tag data, oceanographic data, and Chinook salmon abundance are described in detail in online Appendices S1–S4. Tables S1.4–S1.6 provide size limits for Chinook retention fisheries collected from grey literature sources. Table S2.4 provides a complete list of coded wire tag codes used to estimate the statistical model. Derived data products used in the estimation code and the estimation code are archived at Zenodo (https://zenodo.org/badge/latestdoi/314361767). These files and additional data products are also available from the corresponding author upon request.

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SUPPORTING INFORMATION

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

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