

## RESEARCH ARTICLE

# Synchrony erodes spatial portfolios of an anadromous fish and alters availability for resource users

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## Abstract

1. Environmental forces can create spatially synchronous dynamics among nearby populations. However, increased climate variability, driven by anthropogenic climate change, will likely enhance synchrony among spatially disparate populations. Population synchrony may lead to greater fluctuations in abundance, but the consequences of population synchrony across multiple scales of biological organization, including impacts to putative competitors, dependent predators or human communities, are rarely considered in this context.
2. Chinook salmon *Oncorhynchus tshawytscha* stocks distribute across the Northeast Pacific, creating spatially variable portfolios that support large ocean fisheries and marine mammal predators, such as killer whales *Orcinus orca*. We rely on a multi-population model that simulates Chinook salmon ocean distribution and abundance to understand spatial portfolios, or variability in abundance within and among ocean distribution regions, of Chinook salmon stocks across 17 ocean regions from Southeast Alaska to California.
3. We found the expected positive correlation between the number of stocks in an ocean region and spatial portfolio strength; however, increased demographic synchrony eroded Chinook salmon spatial portfolios in the ocean. Moreover, we observed decreased resource availability within ocean fishery management jurisdictions but not within killer whale summer habitat. We found a strong portfolio effect across both Southern Resident and Northern Resident killer whale habitats that was relatively unaffected by increased demographic synchrony, likely a result of the large spatial area included in these habitats. However, within the areas of smaller fishing management jurisdictions we found a weakening of Chinook salmon portfolios and increased but inconsistent likelihood of low abundance years as demographic synchrony increased.
4. We suggest that management and conservation actions that reduce spatial synchrony can enhance short-term ecosystem resilience by promoting the stabilizing effect multiple stocks have on aggregate Chinook salmon populations and overall resource availability.

## KEYWORDS

age-structured population model, ecological patterns and processes, Fisheries, *Oncorhynchus*, predator-prey, spatial ecology, spatial portfolio effect

## 1 | INTRODUCTION

Climate patterns can synchronize population dynamics through space and time (Allstadt et al., 2015; Black et al., 2018; Kilduff et al., 2015; Koenig & Liebhold, 2016; Moran, 1953). For example, synchrony among North American migrating bird populations is related to increased temperature covariance across the continent (Koenig & Liebhold, 2016). Furthermore, blue oak trees on the West Coast of North America and butterflies in Finland have each demonstrated increased covariance in population growth rates related to synchrony in climate patterns (Black et al., 2018; Kahilainen et al., 2018). Large-scale spatial synchrony in climate patterns and the frequency of anomalous events associated with anthropogenic climate change will likely increase synchrony among spatially disparate populations (Black et al., 2018; Hansen et al., 2020).

Increases in synchrony can, in turn, weaken the portfolio effect in a metapopulation—the stabilizing effect of subpopulations on the variability of an aggregate population (Figge, 2004; Markowitz, 1952; Schindler et al., 2010)—and amplify aggregate population variability. The impacts of climate change and associated environmental variability are often interrogated at the population level, but are pervasive across multiple levels of biological organization (Beamish et al., 2012; Gilman et al., 2010). For example, systematic shocks, such as heat waves, may increase temporal and spatial variability among prey species, with negative consequences that scale up to dependent predators or human users (Jones et al., 2018; Smale et al., 2019; Wernberg et al., 2013). While resource managers have recognized that portfolio effects are important in maintaining population and ecosystem resilience, understanding portfolio effects in prey metapopulations can provide insight into the ecosystem-wide implications of predation and harvest (DuFour et al., 2015; Nesbitt & Moore, 2016; Oken et al., 2021).

Climate processes have become more spatially coherent over the last 100 years and contribute to greater marine and terrestrial synchrony across North America (Black et al., 2018; Koenig & Liebhold, 2016). This increased coherence is especially relevant for anadromous salmon that spend the earliest and latest stages of their life cycles in freshwater ecosystems but migrate to estuarine and then marine ecosystems for the middle portion. This life-history strategy makes salmon susceptible to synchronizing events in multiple ecosystems. While portfolio effects act to stabilize anadromous Atlantic and Pacific salmon stocks (individual subpopulations that return to natal rivers to reproduce) through multiple life stages (Olmos et al., 2020; Schindler et al., 2010), relatively little consideration has been given to how factors affecting ocean-stage population variability propagate throughout the life cycle.

Spatial covariance in Pacific salmon demographic rates and abundances during different life stages have increased over the last 30–40 years (Kilduff et al., 2015; Moore et al., 2010; Sharma et al., 2013), but it is unclear what is driving the increase in covariance and what the implications are for dependent fisheries

and marine predators. One potential explanation lies with early marine survival (immediately following the migration of juvenile salmon from freshwater to the ocean), which is linked with climate variability and is an important predictor of cohort strength (Crozier et al., 2021; Duffy & Beauchamp, 2011; Sharma et al., 2013). Mechanisms that synchronize early marine survival across stocks have been identified in freshwater and marine ecosystems. For example, warm dry winters in the Central Valley of California abbreviate the time juvenile Chinook salmon spend in estuaries before migrating to the open ocean, resulting in smaller fish leaving for the ocean (Munsch et al., 2019). Importantly, juvenile salmon tend to grow larger as they spend more time in estuaries before migrating to the open ocean, this larger size correlates with a greater likelihood of early marine survival (Duffy & Beauchamp, 2011). Periods of warm water and low productivity can adversely impact early marine survival by decreasing prey availability or nutritional value and increasing competition for prey (Beamish & Mahnken, 2001; Duffy & Beauchamp, 2011; Kilduff et al., 2014; Sabal et al., 2020). In the California Current ecosystem, these conditions have led to low Chinook salmon survival rates, occasionally resulting in fishery closures (Di Lorenzo et al., 2013; Richerson & Holland, 2017; Sabal et al., 2020; Sydeman et al., 2013).

The causes and consequences of variable marine survival in Chinook salmon (*Oncorhynchus tshawytscha*) are of particular research and management concern, as Chinook salmon contribute to valuable ocean fisheries and are the prey of many marine mammals, including the endangered Southern Resident killer whales (SRKWs; *Orcinus orca*) (Hanson et al., 2021). Due to their long-distance transboundary ocean migrations and shifting phenologies, there is strong geographic variability in the individual Chinook salmon stocks available for fisheries and dependent predators (Chinook Technical Committee, 2019; Shelton et al., 2019, 2021; Weitkamp, 2010). Chinook salmon ocean distribution estimates suggest considerable among-stock variation in distribution (Shelton et al., 2019, 2021; Weitkamp, 2010). Yet there is a lack of comprehensive understanding in how ocean distributions interact with variability in stock abundances to affect Chinook salmon predictability and availability for ocean harvest and predator populations (Jarillo et al., 2020). Portfolio theory has been applied to understand Pacific salmon temporal variability in freshwater regions, however, the spatial variability of this migratory species indicates strong patterns in spatial ocean portfolios that have not been examined. Until recently this was not possible, as estimates of stock-specific ocean distributions that account for fishing effort or seasonal distribution did not exist (Shelton et al., 2019, 2021). Moreover, changes in the population dynamics and spatial synchrony of individual Chinook salmon stocks due to environmental forcing may change how a portfolio effect manifests across ocean regions (Engen et al., 2002; Kilduff et al., 2015).

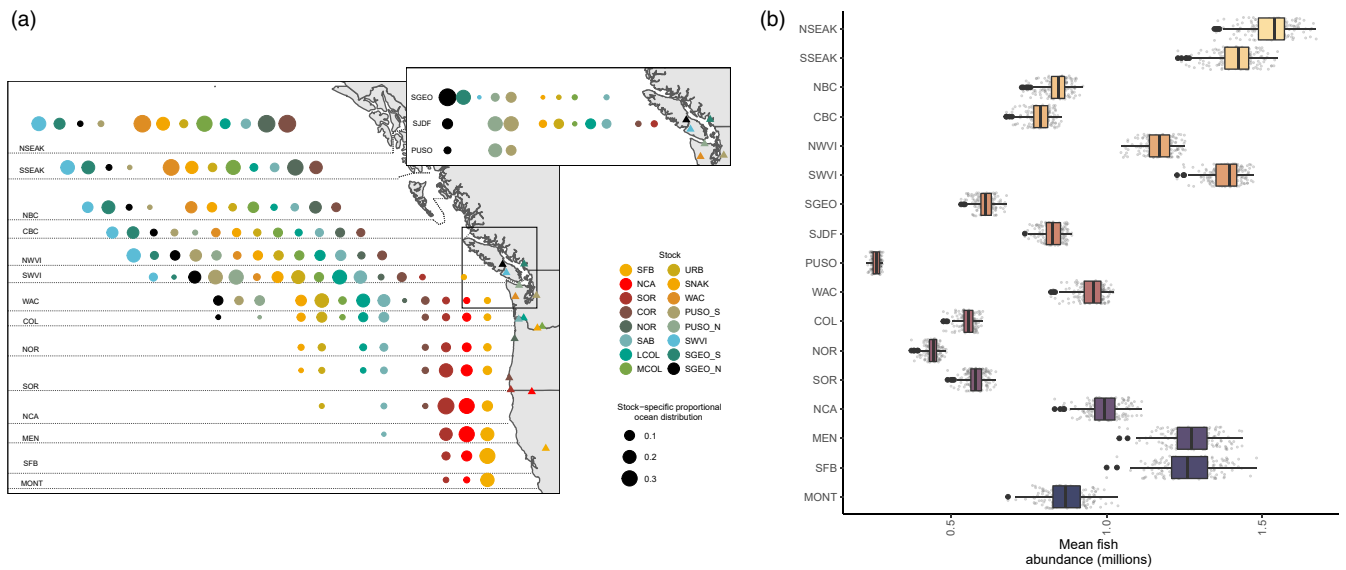
In this study, we develop a spatial and stochastic age-structured model to evaluate how changes to the spatial coherence of early

ocean salmon survival affect aggregate ocean abundance and variability on the West Coast of North America (Alaska to California; 24,577 km of coastline, Figure 1; Figure S1.1). We compare how ocean synchrony and portfolio effect strength vary across regions for both oceanic fisheries and predators. Here, we focus on fall Chinook salmon ocean distributions because these life histories are currently the most abundant on the West Coast and ocean distributions have been estimated for this life-history type, however, other run types can be incorporated as they become available (Shelton et al., 2021; Weitkamp, 2010). Our study is the first to examine Chinook salmon spatial ocean portfolios at the spatial and temporal scales relevant for both the large, mixed-stock Chinook salmon fisheries and marine predators.

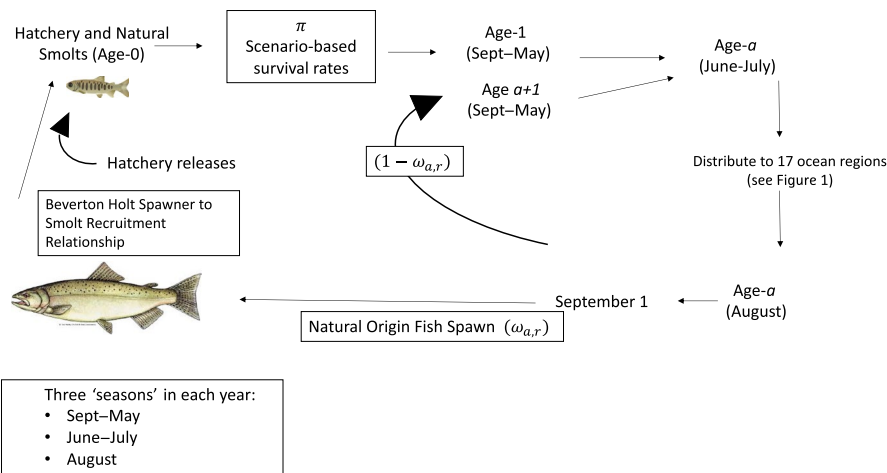
## 2 | MATERIALS AND METHODS

### 2.1 | Overview of the simulation model

We developed an age-structured population simulation model with parameters for major fall-run Chinook salmon stocks in the Eastern Pacific Ocean to simulate the spatial variability in Chinook salmon ocean portfolios (see Figure 2 for a conceptual diagram of the model structure). The relationships of interest in these simulations focus on how the scale of spatial covariance in early marine survival affects (a) spatial and temporal population variability, measured by the mean-variance portfolio effect (described in detail below), and (b) frequency of consecutive low



**FIGURE 1** (a) Map of study area with ocean region borders and labels (for larger spatial context of the study area reference Figure S1.1). Triangles designate approximate hatchery locations, triangle and point colors correspond with each stock group (16) that were used for ocean distribution estimates in Shelton et al., 2021. Point size corresponds to the proportional distribution of each stock group to a corresponding ocean region (see Table S1.1 for specific values). (b) Mean annual summer fish abundances for each ocean region when spatial covariance is 0 km. Points represent mean summer fish abundance across simulated years for each replicate. See Table S1.1 for ocean region and stock group acronym definitions



**FIGURE 2** Conceptual model and timing of life history events in the simulation model. Adult natural mortality is applied within each seasonal time step

abundance years. We examine these variables across three spatial scales, (a) individual ocean regions, (b) ocean regions aggregated into ocean areas used by commercial troll fishing fleets and (c) ocean areas used by resident killer whales. These three spatial frames enable quantification of salmon variability at increasing spatial scales from the perspective of two important resource users.

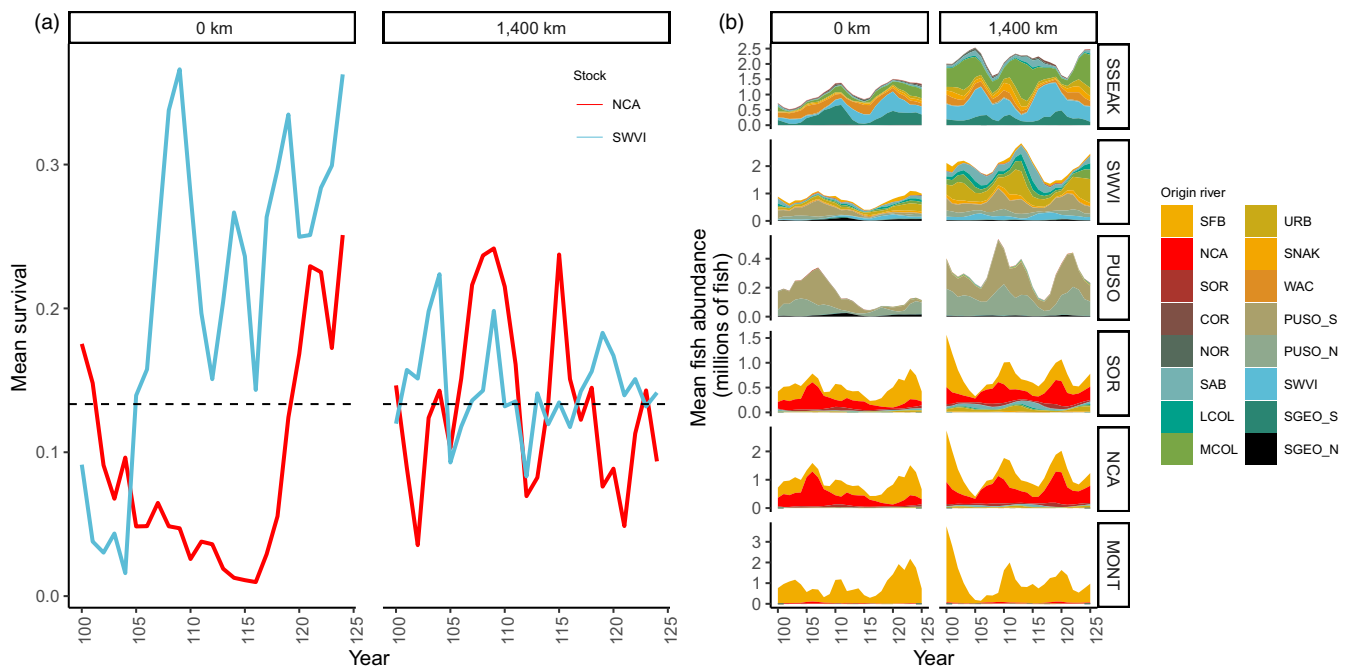
We included 16 stock groups of natural and hatchery origin fish that distribute to 17 ocean regions (Figure 1; Table S1.1). We parameterized the baseline model to values consistent with the period 1979–2015 and ran the simulation for 200 years with 100 replicates. We run the simulation model using five different survival covariance scenarios. Each scenario is defined by a 'critical distance', which refers to the distance between each river entry point where correlation in early marine survival falls below 0.50 (Figure S1.2). We test an independent scenario, here critical distance is 0 km and early marine survival among river mouths fluctuate independently, in addition to 150, 350, 706 and 1,400 km (Figure 3; Table S1.2). We assume many parameters to be temporally invariant (such as natural or fishery mortality and probability of spawning at age), in order to focus comparisons across variation in survival covariance without random variation from other parameters. Assumptions about reproduction and survival are described in detail below and in the Supplement; additional information about ocean distribution estimates and estimation methods can be found in Shelton et al. (2021).

## 2.2 | Reproduction

Anadromous fish have complex life cycles that begin in freshwater and include a marine-adult phase before they return to natal rivers to spawn. Chinook salmon reproduction is complicated by the presence of salmon hatcheries which produce and release large numbers of young salmon into rivers or the nearshore that join those that are naturally spawned (hereafter, 'natural origin') prior to entering the ocean stage. We include both natural and hatchery origin fish in our model, however, only natural origin fish reproduce. Intensive interrogation of hatchery practices on salmon ocean distribution dynamics is beyond the scope of this study but an important area of future research.

We assume the production of natural origin age-0 smolts follows a Beverton–Holt stock–recruitment relationship for each stock. As empirical estimates of Beverton–Holt parameters and stock productivity are not available for most Chinook salmon stocks, we use available spawner abundance information to generate reasonable parameters for the Beverton–Holt equation (for detailed estimation information see Supplement 2).

We model hatchery fish by simulating hatchery smolt releases for each stock group at age 0. Relative differences in hatchery release abundances are proportional to patterns of mean releases from 2008 to 2017 (see Supplement 1 and Figure S1.3). Releases were summarized using tag data from the Regional Mark Information System (RMIS; [http://www.rmiso.org/rmis\\_login.php?action=Login](http://www.rmiso.org/rmis_login.php?action=Login)



**FIGURE 3** (a) Time series of simulated survival rates,  $\pi_{t,0,f=w}$ , for natural origin fish within Northern California (NCA), which is characteristic of Klamath and Trinity hatcheries in California and Southwest Vancouver Island (SWVI), which is characteristic of Vancouver Island, British Columbia, Canada. Each panel represents the distance at which there is 50% covariance in early marine survival. We plotted a single realization of survival and truncated the time series to years 100–125 to make the figure more interpretable. (b) Truncated time series of stock abundance within six ocean regions for a single realization in scenarios for critical distances 0 km and 1,400 km

&system=cwt). We assume total coastwide hatchery releases vary through time, but the relative proportion of hatchery releases arising from each stock is constant (Figure S1.3).

The number of natural and hatchery origin fall Chinook salmon entering the ocean is a function of smolt abundance and smolt survival  $\pi_{t,a=0,r,f}$  (for year  $t$ , age group  $a$  where  $a = 0$  for smolts, stock group  $r$  and fish type  $f$ , hatchery or natural origin, see Figure S1.4 for sensitivity testing results). Our simulation focuses on generating a range of spatial and temporal covariance in smolt survival scenarios and so we discuss this covariance in detail below and in Supplement 1.

## 2.3 | Ocean distribution and mortality

Once fish enter the ocean, they are lost to natural mortality  $M_{a,f}$ , which varies by season-age  $a$  and fish type (hatchery or natural origin)  $f$ , and harvest mortality  $F_{a,l}$ , which varies by season-age  $a$  and ocean region  $l$  (Figure S1.5; Tables S1.3 and S1.4). Fish age 3, 4 and 5 are susceptible to harvest; however, harvest rate for age-3 fish is 40% lower than older fish (Shelton et al., 2021, see Shelton et al., 2021, Figure S5.12). Both  $M_{a,f}$  and  $F_{a,l}$  are assumed constant across time. We vary fishing mortality by ocean region based on relative mean recreational and commercial catch differences over the last decade to capture the relative influence of spatially variable salmon ocean fisheries (see Supplement 1 for further details and sensitivity testing results, Table S1.5; Figures S1.6–S1.7).

After initial ocean entry, fish distribute to discrete summer ocean regions, where  $\psi_{r,l}$  is the proportion of fish from stock group  $r$  that distribute to ocean location  $l$  (Figure 1; Table S1.1, Shelton et al., 2021). Available evidence suggests limited among-year variation in the ocean distribution of Chinook salmon populations (Shelton et al., 2021) and so we assume  $\psi_{r,l}$  is constant in our simulations. We focus on the summer ocean distribution here because data availability and fishing effort are greatest during the summer months. We consider stock richness for each ocean region as the count of stocks that distribute greater than 1% of their abundance to that area during summer.

We assume fish return to natal rivers to spawn on 1 September, however, there is intra- and inter-stock variation in the age at which Chinook salmon reach maturity. To address this variation, we use a scalar  $\omega_{a,r}$ , which determines the fraction of fish remaining in the ocean at age  $a$  and stock group  $r$  that spawn (Figure S1.8, Shelton et al., 2021). As with other parameters, because our focus is on spatial covariation in early marine survival and due to data limitations, we assume that  $\omega_{a,r}$  does not vary among years.

## 2.4 | Early marine survival

Generally, research suggests differences in early marine survival of hatchery and natural origin fish, although there is a need for a spatially coherent analysis of these patterns (Beamish et al., 2012; Woodson et al., 2013). Based on existing evidence, we assume early

marine survival is 5% greater for ocean age-0 natural origin fish than for hatchery fish (Beamish et al., 2012; Woodson et al., 2013). We model covariance in natural and hatchery origin smolt survival using a stationary lag-1 multivariate autoregressive process, MAR(1) (Figure 3, see Figure S1.9 for sensitivity testing results). Past work has indicated that juvenile salmon survival rates have an AR-1 structure (Kilduff et al., 2015; Sharma et al., 2013). Let  $\pi_{t,a=0,f}$  be a vector of log age-0 survival rates of length  $r$  representing each stock group at year  $t$  for either hatchery or natural origin fish  $f$ . Survival of age-0 fish  $\pi_{t,a=0,f}$  is the sum of  $A_f$ , a constant scalar,  $B$ , a diagonal  $rxr$  matrix whose elements  $\phi_r$  determine the autocorrelation structure for each stock group, and  $E_t$ , the process error at year  $t$ .

$$\pi_{t,0,f} = A_f + B\pi_{t-1,0,r,f} + E_{t,r}, \quad (1)$$

$$E_t \sim \text{MVN}[0, \Sigma].$$

We use a multivariate normal distribution to describe spatial covariance in log age-0 survival among stock groups. Elements of  $E_t$  are independent through time.  $\Sigma$  is a  $rxr$  variance-covariance matrix that is composed of the spatial covariance among stocks and a spatially independent nugget effect,  $\Sigma = R\delta^2 + I\tau^2$ , where  $R$  is a square matrix with element  $c_{ij}$  containing the correlation between stock  $i$  and stock  $j$  (see below),  $\delta^2$  is the variance in log age-0 survival and  $I$  is the identity matrix. We incorporated a nugget effect  $\tau^2$  to ensure that different stock groups originating from the same river, for example the Columbia River, do not have identical survival rates. We scale  $\tau^2$  to be 10% of  $\delta^2$  for all simulations (see Figure S1.10 for sensitivity testing results).

The mean and variance of early marine survival do not vary among scenarios, allowing us to examine interactions between spatial covariance in early marine survival and Chinook salmon spatial portfolios without confounding the interpretation with changes to early marine survival mean and variance. We base the mean and variance of  $\pi_{t,0,f}$  on estimates from Shelton et al. (2021).

We use an exponential covariance function to simulate covariance among stocks given the critical distance  $w$  between rivers associated with each stock group. Kilduff et al., 2015 suggest that Chinook salmon ocean survival shows a correlation of 0.50 at a distance of 706 km, including a 95% confidence interval that reaches 1,437 km. To understand how changing the scale of correlation affects ocean portfolios and facilitate comparisons with previous studies, we simulate a range of scenarios that vary the distances at which the correlation among river mouths falls below 0.50. We test an independent scenario, here critical distance is 0 km and early marine survival among stock groups fluctuate independently, in addition to 150, 350, 706 and 1,400 km (Figure 3).

## 2.5 | Ocean synchrony and spatial portfolios

To understand the degree to which stock group abundances have concurrent temporal variation in the ocean, we calculate synchrony (Eq(2)) within ocean regions using a synchrony index between 0 and

1; where 1 indicates perfect synchrony and 0 indicates no synchrony (Loreau & de Mazancourt, 2008).

$$\rho_j = \frac{\sigma_j^2}{(\sum_i \sigma_{ij})^2}, \quad (2)$$

Here, synchrony for each ocean region  $\rho_j$  is the variance of the aggregate ocean region observed in the simulation,  $\sigma_j^2$ , divided by the sum of the variance for each individual stock,  $(\sum_i \sigma_{ij})^2$ .

We use portfolio effect strength as a metric for temporal variability in each ocean region for aggregate populations. We quantify the portfolio effect using the mean–variance relationship (MV), defined as the ratio between expected variance if each ocean region was composed of one homogenous stock,  $\log(\hat{\sigma}_j^2)$  and the realized variance of multiple stocks within one ocean region,  $\log(\sigma_{ij}^2)$ . In ecological populations, the relationship between mean subpopulation abundance,  $\mu_{ij}$ , and variance may increase nonlinearly (Anderson et al., 2013). We use the MV relationship, rather than the coefficient of variation, to derive an empirical relationship for  $z$ , the slope of the linear regression of  $\log(\sigma_{ij}^2)$  and  $\log(\mu_{ij})$ , among subpopulations (Anderson et al., 2013). Here, Eq(3) estimates  $z$ , the slope of the linear regression of  $\log(\sigma_{ij}^2)$  and  $\log(\mu_{ij})$ .

$$\log(\sigma_{ij}^2) = \beta_0 + z \log(\mu_{ij}) + \varepsilon_{ij}, \quad (3)$$

where  $\varepsilon_{ij}$  is the residual error with a mean zero and an estimated variance that follows a normal distribution. We use Equation 3 to calculate the expected variance  $\log(\hat{\sigma}_j^2)$  for a single population with the mean abundance set to the mean abundance across subpopulations. This metric describes temporal variability by quantifying the degree to which diversity in stock structure decreases variability in aggregate Chinook salmon ocean abundances. A portfolio strength of 1 indicates that aggregate stocks are acting as a homogenous population, whereas, for example, a portfolio strength of 1.5 means that the population within an ocean region is 1.5 times more stable than it would be if the ocean region were composed of a single homogenous stock (Anderson et al., 2013). We used the *synchrony()* and *pe\_mv()* function within the R *Ecofolio* package to calculate synchrony and mean–variance portfolio effect (Anderson et al., 2013).

## 2.6 | Spatial portfolios and abundance variability for resource users

We use portfolio effect strength to understand relative changes in temporal and spatial variability within and among ocean regions, with a focus on salmon population variability. However, the mean–variance portfolio calculation does not inform changes in absolute abundance. Change in abundance, in addition to the mean–variance relationship, can affect abundance of oceanic predators and ocean fisheries that target Chinook salmon. To investigate how synchrony may impact ocean abundance patterns, we tracked how often ocean

age-4 and age-5 fish abundance fell below average for 3 years or more in killer whale habitat and in ocean fishing management zones. We track consecutive low abundance years of Chinook salmon abundance because multiple years of low abundance could have higher consequences for predators and fisheries than a single low abundance year (Ward et al., 2009). We select only age-4 and age-5 fish because fisheries and predators generally prefer older, larger, fish due to increased revenue and caloric value respectively (Ford et al., 2010). We used established summer habitat for the Northern and Southern killer whales (NRKW, SRKW respectively) summarized by Chasco et al., 2017. To designate fishing regions, we used fishery management zones defined by the Pacific Salmon Commission and the Pacific Fisheries Management Council, for specific spatial designations refer to Table S1.6.

## 3 | RESULTS

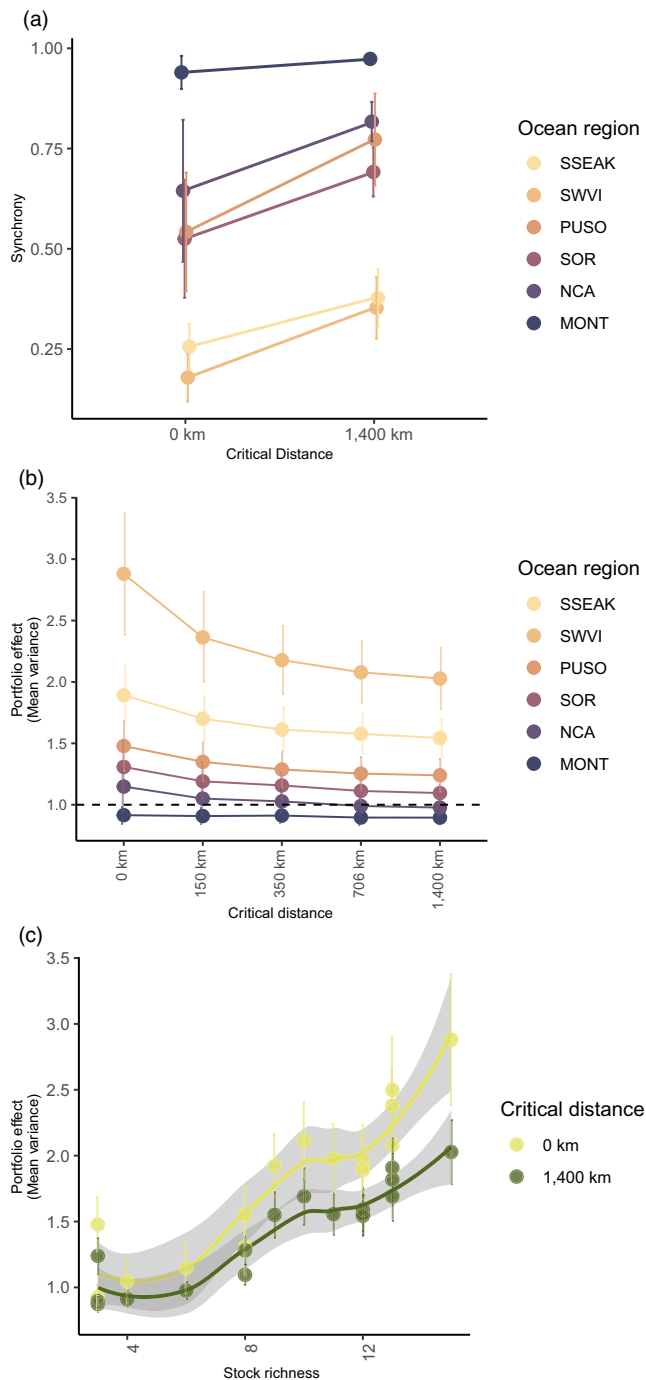
We found that increased demographic synchrony eroded Chinook salmon spatial portfolios in the ocean, and decreased resource availability within ocean fishery zones but not within killer whale summer habitat. We present results in two sections that focus on (a) the interaction between demographic synchrony in the ocean and spatial portfolios within ocean regions and (b) the impact of demographic synchrony on spatial portfolios and likelihood of low abundance within ocean fishery regions and killer whale summer habitat.

### 3.1 | Ocean synchrony and spatial portfolios

Spatial covariance in early-marine survival decreased the stabilizing effect multiple stocks have on aggregate ocean abundance (Figure 4) by causing higher temporal synchrony in aggregate ocean abundance for later life stages (Figure 4a; six representative ocean regions shown) and a decreased portfolio effect (Figure 4b). That is, spatial variation in synchrony and portfolio strength was driven both by the number of stocks and relative abundance of the stocks that contribute to each region (Figure 4). However, among ocean regions we observed substantial variation in both synchrony and portfolio effect strength.

Ocean synchrony and portfolio effect strength were negatively correlated. We observed high ocean synchrony and weak portfolios in ocean regions with low stock richness. Moreover, the magnitude of change in ocean synchrony and portfolio effect strength among scenarios varied by ocean region (Figure 4). For example, ocean synchrony in Monterey (MONT) was high (0 km: 0.94[0.02], Mean[SD]; 1,400 km: 0.97[0.01]) while the portfolio was weak (0 km: 0.92[0.07] (Mean[SD]); 1,400 km: 0.90[0.05]) across all spatial covariance scenarios (Figure 4). The portfolio effect within MONT was below 1 regardless of spatial covariance (Figure 4b) indicating that the aggregate population in this ocean region behaves as a single homogenous population. In contrast, Southern Southeast Alaska (SSEAK) and Southwest Vancouver Island (SWVI) demonstrated relatively





**FIGURE 4** (a) Synchrony for six ocean regions in scenarios with a critical distance of 0 km and 1,400 km (Mean and  $\pm 1$  SD are shown). (b) Portfolio effect strengths for six ocean regions across all critical distance scenarios that we tested (Mean and  $\pm 1$  SD are shown). (c) The mean-variance portfolio effect as a function of stock richness (the number of stocks) in each ocean region using 0 km and 1,400 km critical distance scenarios (Mean and  $\pm 1$  SD are shown)

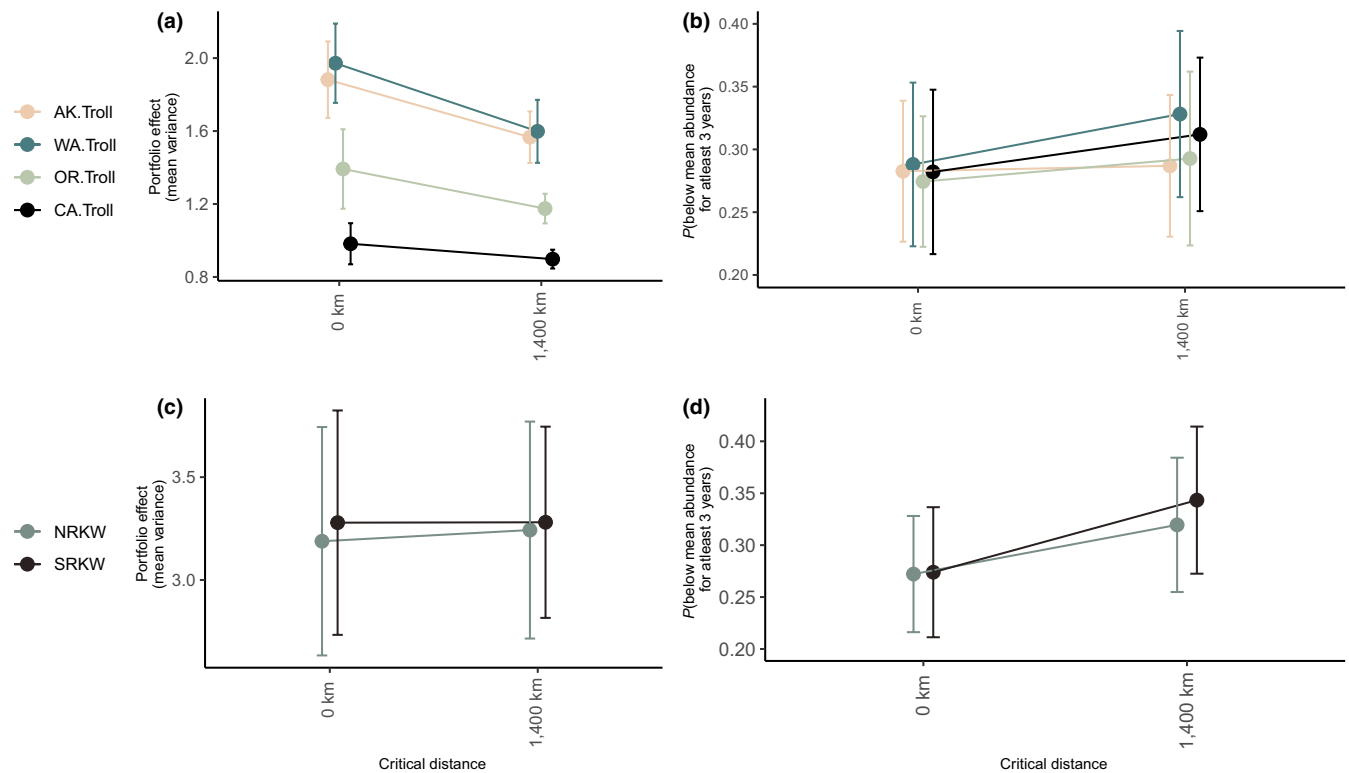
low ocean synchrony (SSEAK 0 km: (0.29)[0.05]; 1,400 km: (0.36)[0.04], SWVI 0 km: (0.29)[0.05]; 1,400 km: (0.36)[0.04]) (Figure 4a) and strong ocean portfolios (SSEAK 0 km: (1.9)[0.18]; 1,400 km: (1.55)[0.2], SWVI 0 km: (2.88)[0.5]; 1,400 km: (2.1)[0.25]).

### 3.2 | Spatial portfolios and abundance variability for resource users

Chinook salmon variability within fishing regions increased as the spatial extent of covariance in early marine survival increased (Figure 5a). Similar patterns occur for all fish ages, but the magnitude of difference between 0 km and 1,400 km increased when we considered older fish, which are a target for fisheries and killer whales. The Alaska and Washington ocean troll fishing regions had an overall greater portfolio effect than the California and Oregon ocean troll fishery regions (Figure 5a). When we set early-survival spatial covariance to 1,400 km, the portfolio strength in Alaska and Washington decreased by 17% and 19%, while Oregon and California decreased by 16% and 9% respectively (Figure 5a). Our model indicated that spatial covariance in early marine survival increased the likelihood that aggregate ocean abundances in fishing regions will fall below-average three or more consecutive years (Figure 5b). This finding is relatively consistent among fishing regions. We found that low abundance streaks are on average 1.8 times more likely when critical covariance distance is 1,400 km compared to 0 km critical. In contrast, we found a strong portfolio effect across both Southern Resident and Northern Resident killer whale summer habitat that did not change under increased covariance scenarios (Figure 5). There was a 16% and 21% increase in the likelihood that fish abundance will be below average for 3 or more years in NRKW and SRKW summer habitat respectively. Thus, in comparison to ocean fishing regions Chinook salmon variability within killer whale summer habitat was relatively robust to increases in spatial covariance in early marine survival covariance.

## 4 | DISCUSSION

Climate variability can synchronize populations across large spatial scales (Hansen et al., 2020; Moran, 1953). Understanding the extent populations may vary due to climate can improve expectations of ecosystem-scale patterns across spatial scales, with direct repercussions for species conservation and management. Here, we demonstrate that increased spatial synchrony can lead to greater variability in Chinook salmon ocean abundances and a weakening of the portfolio effect in individual ocean regions. Additionally, we found that geographically variable portfolio effects emerge for ocean life stages, resulting in differences in portfolio strengths and fish availability for resource users. These results broaden our understanding of ecological portfolio theory for anadromous species, where much of the literature has focused on freshwater life stages (e.g. Griffiths et al., 2014; Moore et al., 2010; Satterthwaite & Carlson, 2015)). Moreover, we observed a stronger portfolio effect as we broadened the spatial region. This outcome is a facet of statistical averaging that manifests in real ecological situations, where a larger spatial area increases the likelihood of including a subpopulation, or a salmon stock, in the aggregate. That this phenomenon emerges in our simulations of Chinook salmon dynamics has important implications for



**FIGURE 5** (a) Portfolio effect strengths for four fishing regions using 0 km and 1,400 km critical distance scenarios (Mean and  $\pm 1$  SD are shown). (b) Probability that aggregate ocean fish abundance for age-4 and age-5 Chinook salmon will be below the long-term mean for at least 3 years within ocean fishing regions. We present results from the 0 km and 1,400 km critical distance scenarios (Mean and  $\pm 1$  SD are shown). (c) Portfolio effect strengths for Northern Resident and Southern Resident (NRKW, SRKW respectively) critical habitat for 0 km and 1,400 km critical distance scenarios (Mean and  $\pm 1$  SD are shown). (d) Probability that aggregate ocean fish abundance for age-4 and age-5 Chinook salmon will be below the long-term mean for at least 3 years within Southern Resident and Northern Resident killer whale critical habitat. We present results from the 0 km and 1,400 km critical distance scenarios (Mean and  $\pm 1$  SD are shown)

resource users. Mobile resource users that cover a larger area can take advantage of decreased aggregate variability, while place-based resource users experience increased resource fluctuations (Fisher et al., 2021; Okamoto et al., 2020; Stier et al., 2020).

Our study adds to a growing literature exploring the degree to which diversity can confer population resilience to climate variability and the extent to which this buffering effect is influenced by population synchrony (Valencia et al., 2020). Our model shows a positive relationship between portfolio strength and salmon stock richness, where ocean regions with more stocks have less variability, measured by the mean-variance portfolio effect, than ocean regions with fewer stocks (Figure 4c). This positive relationship is in part due to statistical averaging, where increases in diversity in an aggregate population will concomitantly decrease variability (Doak et al., 1998). We found that the ocean portfolio is two times stronger when stock richness is 12 compared to three (Figure 4c). In part, the spatial variation in stock richness is related to biogeography, for example California lies at the edge of the fall Chinook salmon range and consequently not many stocks distribute to that area. Independent of biogeographical gradients, we found that as spatial covariance in early survival increases, Chinook salmon abundances became more variable, even in ocean regions with high stock richness. Our study

and others like it highlight that conserving diversity can partially but not completely mitigate impacts of climate or anthropogenic disturbances (Holsman et al., 2020; Valencia et al., 2020).

Conserving spatial diversity in prey populations can also effectively buffer human and non-human users of these resources against low abundance years (Armstrong et al., 2016; Schindler et al., 2013). Mobile resource users can exploit spatial variation across a landscape, while less mobile or place-based resource users experience increased resource fluctuations (Armstrong et al., 2016; Fisher et al., 2021; Okamoto et al., 2020; Stier et al., 2020). The summer habitats of both Northern and Southern Resident killer whales span a large geographic area and aggregate across larger spatial areas than those occupied by Chinook salmon ocean fishing regions. As a result, we predict that the killer whales experience greater fish abundance, stock richness and portfolio strength in their summer habitat areas than fishery participants do in ocean fishing regions. For example, without imposing spatial covariance in survival, the portfolio effect for SRKW habitat was on average 3.4 compared to a mean-portfolio size of 2.4 for WA Troll and 2.2 for the WA ocean region, the smallest spatial resolution we use. This contrast is congruent with emerging literature showing that resource users that can exploit larger spatial areas can better mitigate increased variability and



reduced abundance of the species on which they are reliant (Aikens et al., 2017; Fisher et al., 2021; Middleton et al., 2018; Okamoto et al., 2020; Stier et al., 2020).

Compared to northern resident killer whales, endangered Southern Resident killer whales (SRKWs) have a moderate increase in likelihood of low abundance streaks as spatial covariance in marine survival increases. Improving Chinook salmon availability and access for SRKWs is a primary element of their recovery plan (National Marine Fisheries Service, 2008). Thus conserving the inherent population diversity of Puget Sound salmon may buffer endangered SRKWs against low abundance years and allow them to exploit inherent phenological diversity in Chinook salmon stocks (A. K. Ettinger, C. J. Harvey, J. F. Samhour, C. K. Emmons, M. B. Hanson, J. K. Olson, & E. J. Ward, pers. comms.). Investigating smaller scale whale-Chinook salmon distributions and interactions will help evaluate the degree to which whales take advantage of the full salmon portfolio across the habitat that we considered.

Chronic reductions in fish availability at the smaller spatial scales used by participants in the ocean salmon fishery can result in low revenue for fishermen and related industry, increased likelihood of departure from the fishery, and in some cases, fishery closures (Richerson & Holland, 2017; Richerson et al., 2018). The West Coast ocean salmon fishery in the California Current has undergone multiple closures, often attributed to un-productive warm ocean conditions and low fish survival. The 2008–2009 fishery closure ultimately led to fishers exiting the fishery and dispersal of \$170 million USD for federal fishery disaster relief funding (Richerson & Holland, 2017). Based on our results, those fishery participants that are able to move between ocean regions—usually those with larger vessels and presumably more capital (Fisher et al., 2021)—are more likely to mitigate any negative impacts of increased spatial synchrony on fish abundance (Okamoto et al., 2020). Understanding how climate impacts spatial processes and fish variability can help to enhance adaptive capacity among fisheries and management entities.

While our study examines how changes in Chinook salmon early marine survival coherence affects abundance and variability from the perspective of alternative users of this critical resource, we did not address how specific management actions can counteract or amplify the extent of spatial coherence. One approach employed in many regions along the US West Coast to reduce variability in Chinook salmon populations is hatchery supplementation. This practice artificially augments salmon abundance by producing and releasing large numbers of young salmon into rivers or estuaries; this has significant impacts to the Pacific Salmon ecosystem. For example, research in Puget Sound, WA, indicates negative density dependence between hatchery and natural origin fish in marine and freshwater life stages (Kendall et al., 2020). However, research investigating hatchery and natural origin fish interactions is often conducted on a local or regional scale and does not fit into the scope of our model (Kendall et al., 2020; Nelson et al., 2019). Including hatchery and natural origin stock density dependence will be an important

avenue for future work, especially as some West Coast states propose to increase hatchery production (WA State Orca Task Force).

Understanding how the environment drives population dynamics is a central tenant in ecology; a frontier in this realm focuses on how climate impacts influence spatially structured population dynamics. Increased population variability, especially for populations that use multiple ecosystems across their life cycles, can ripple across trophic levels or resource user groups. We demonstrate that demographic synchrony results in increased population variability for a spatially structured anadromous fish, and that diversity, in the form of stock richness, can partially mitigate populations and dependent resource users against population variability. While increases in climate variability and related spatial synchrony are pervasive (Black et al., 2018; Hansen et al., 2020), and occur across large spatial scales, management and conservation actions that disrupt synchrony can enhance short-term population and ecosystem resilience.

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## CONFLICT OF INTEREST

The authors have no conflict of interest to disclose.

## AUTHORS' CONTRIBUTIONS

G.H.S., A.O.S. and J.O.S. conceived the ideas and designed methodology; G.H.S. and A.O.S. wrote simulation code; G.H.S. analysed the data, created figures and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data used in this paper are derived from publicly available sources, and data products referenced from Shelton et al. (2021) are archived at Zenodo <https://zenodo.org/badge/latestdoi/314361767> (Shelton, 2021). Data sources for fisheries data, coded wire tag data are publicly available, these are described and referenced in the Supplemental Information.

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## SUPPORTING INFORMATION

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