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

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Abstract:

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. 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. 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. We suggest that management and conservation actions that reduce spatial synchrony can enhance short-term ecosystem resilience by promoting the

57 stabilizing effect multiple stocks have on aggregate Chinook salmon populations and overall
58 resource availability.

59

60 **Key Words:** Ecological patterns and processes, Spatial ecology, *Oncorhynchus*, Spatial portfolio
61 effect, Age-structured population model, Predator-prey, Fisheries

62 **Introduction:**

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

72 Increases in synchrony can, in turn, weaken the portfolio effect in a metapopulation - the
73 stabilizing effect of subpopulations on the variability of an aggregate population (Figge, 2004;
74 Markowitz, 1952; Schindler et al., 2010) – and amplify aggregate population variability. The
75 impacts of climate change and associated environmental variability are often interrogated at the
76 population level, but are pervasive across multiple levels of biological organization (Beamish et
77 al., 2012; Gilman et al., 2010). For example, systematic shocks, such as heat waves, may increase
78 temporal and spatial variability among prey species, with negative consequences that scale up to
79 dependent predators or human users (Jones et al., 2018; Smale et al., 2019; Wernberg et al.,
80 2013). While resource managers have recognized that portfolio effects are important in
81 maintaining population and ecosystem resilience, understanding portfolio effects in prey
82 metapopulations can provide insight into the ecosystem-wide implications of predation and
83 harvest (DuFour et al., 2015; Nesbitt & Moore, 2016; Oken et al., 2021).

84 Climate processes have become more spatially coherent over the last 100 years and
85 contribute to greater marine and terrestrial synchrony across North America (Black et al., 2018;

86 Koenig & Liebhold, 2016). This increased coherence is especially relevant for anadromous
87 salmon that spend the earliest and latest stages of their life cycles in freshwater ecosystems but
88 migrate to estuarine and then marine ecosystems for the middle portion. This life history
89 strategy makes salmon susceptible to synchronizing events in multiple ecosystems. While
90 portfolio effects act to stabilize anadromous Atlantic and Pacific salmon stocks (individual
91 subpopulations that return to natal rivers to reproduce) through multiple life stages (Olmos et
92 al., 2020; Schindler et al., 2010), relatively little consideration has been given to how factors
93 affecting ocean-stage population variability propagate throughout the life cycle.

94 Spatial covariance in Pacific salmon demographic rates and abundances during different life
95 stages have increased over the last 30-40 years (Kilduff et al., 2015; Moore et al., 2010; Sharma
96 et al., 2013), but it is unclear what is driving the increase in covariance and what the implications
97 are for dependent fisheries and marine predators. One potential explanation lies with early
98 marine survival (immediately following the migration of juvenile salmon from freshwater to the
99 ocean), which is linked with climate variability and is an important predictor of cohort strength
100 (Duffy & Beauchamp, 2011; Sharma et al., 2013; Crozier et al., 2021). Mechanisms that
101 synchronize early marine survival across stocks have been identified in freshwater and marine
102 ecosystems. For example, warm dry winters in the Central Valley of California abbreviate the
103 time juvenile Chinook salmon spend in estuaries before migrating to the open ocean, resulting in
104 smaller fish leaving for the ocean (Munsch et al., 2019). Importantly, juvenile salmon tend to
105 grow larger as they spend more time in estuaries before migrating to the open ocean, this larger
106 size correlates with a greater likelihood of early marine survival (Duffy & Beauchamp, 2011).
107 Periods of warm water and low productivity can adversely impact early marine survival by
108 decreasing prey availability or nutritional value and increasing competition for prey (Beamish &
109 Mahnken, 2001; Duffy & Beauchamp, 2011; Kilduff et al., 2014; Sabal et al., 2020). In the
110 California Current ecosystem, these conditions have led to low Chinook salmon survival rates,
111 occasionally resulting in fishery closures (Di Lorenzo et al., 2013; Richerson & Holland, 2017;
112 Sabal et al., 2020; Sydeman et al., 2013).

113 The causes and consequences of variable marine survival in Chinook salmon (*Oncorhynchus*
114 *tshawytscha*) are of particular research and management concern, as Chinook salmon contribute

115 to valuable ocean fisheries and are the prey of many marine mammals, including the
116 endangered Southern Resident killer whales (SRKWs; *Orcinus orca*) (Hanson et al., 2021). Due to
117 their long-distance transboundary ocean migrations and shifting phenologies, there is strong
118 geographic variability in the individual Chinook salmon stocks available for to fisheries and
119 dependent predators (Weitkamp 2010; Chinook Technical Committee 2019; Shelton *et al.* 2019,
120 2021). Chinook salmon ocean distribution estimates suggest considerable among-stock variation
121 in distribution (Weitkamp 2010; Shelton *et al.* 2019, 2021). Yet there is a lack of comprehensive
122 understanding in how ocean distributions interact with variability in stock abundances to affect
123 Chinook salmon predictability and availability for ocean harvest and predator populations (Jarillo
124 et al., 2020). Portfolio theory has been applied to understand Pacific salmon temporal variability
125 in freshwater regions, however the spatial variability of this migratory species indicates strong
126 patterns in spatial ocean portfolio's that have not been examined. Until recently this was not
127 possible, as estimates of stock-specific ocean distributions that account for fishing effort or
128 seasonal distribution did not exist (Shelton *et al.* 2019, 2021). Moreover, changes in the
129 population dynamics and spatial synchrony of individual Chinook salmon stocks due to
130 environmental forcing may change how a portfolio effect manifests across ocean regions (Engen
131 et al., 2002; Kilduff et al., 2015).

132 In this study, we develop a spatial and stochastic age-structured model to evaluate how
133 changes to the spatial coherence of early ocean salmon survival affect aggregate ocean
134 abundance and variability on the West Coast of North America (Alaska to California; 24,577km of
135 coastline, Fig. 1 and Fig. S1.1). We compare how ocean synchrony and portfolio effect strength
136 vary across regions for both oceanic fisheries and predators. Here, we focus on Fall Chinook
137 salmon ocean distributions because these life histories are currently the most abundant on the
138 West Coast and ocean distributions have been estimated for this life history type, however other
139 run-types can be incorporated as they become available (Shelton et al., 2020; Weitkamp, 2010).
140 Our study is the first to examine Chinook salmon spatial ocean portfolios at the spatial and
141 temporal scales relevant for both the large, mixed-stock Chinook salmon fisheries and marine
142 predators.

143

144 **Methods**

145 *Overview of the simulation model*

146 We developed an age-structured population simulation model with parameters for major
147 fall-run Chinook salmon stocks in the Eastern Pacific Ocean to simulate the spatial variability in
148 Chinook salmon ocean portfolios (see Fig. 2 for a conceptual diagram of the model structure).
149 The relationships of interest in these simulations focus on how the scale of spatial covariance in
150 early marine survival affects 1) spatial and temporal population variability, measured by the
151 mean-variance portfolio effect (described in detail below), and 2) frequency of consecutive low
152 abundance years. We examine these variables across three spatial scales, 1) individual ocean
153 regions, 2) ocean regions aggregated into ocean areas used by commercial troll fishing fleets,
154 and 3) ocean areas used by resident killer whales. These three spatial frames enable
155 quantification of salmon variability at increasing spatial scales from the perspective of two
156 important resource users.

157 We included 16 stock groups of natural and hatchery origin fish that distribute to 17 ocean
158 regions (Fig. 1, Table S1.1). We parameterized the baseline model to values consistent with the
159 period 1979–2015 and ran the simulation for 200 years with 100 replicates. We run the
160 simulation model using five different survival covariance scenarios. Each scenario is defined by a
161 “critical distance”, which refers to the distance between each river entry point where correlation
162 in early marine survival falls below 0.50 (Fig. S1.2). We test an independent scenario, here critical
163 distance is 0km and early marine survival among river mouths fluctuate independently, in
164 addition to 150, 350, 706 and 1400km (Fig. 3, Table S1.2). We assume many parameters to be
165 temporally invariant (such as natural or fishery mortality and probability of spawning at age), in
166 order to focus comparisons across variation in survival covariance without random variation
167 from other parameters. Assumptions about reproduction and survival are described in detail
168 below and in the Supplement; additional information about ocean distribution estimates and
169 estimation methods can be found in Shelton et al. (2021).

170 *Reproduction*

171 Anadromous fish have complex lifecycles that begin in freshwater and include a marine-
172 adult phase before they return to natal rivers to spawn. Chinook salmon reproduction is

173 complicated by the presence of salmon hatcheries which produce and release large numbers of
 174 young salmon into rivers or the nearshore that join those that are naturally-spawned (hereafter,
 175 ‘natural origin’) prior to entering the ocean stage. We include both natural and hatchery origin
 176 fish in our model, however only natural origin fish reproduce. Intensive interrogation of hatchery
 177 practices on salmon ocean distribution dynamics are beyond the scope of this study but an
 178 important area of future research.

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

184 We model hatchery fish by simulating hatchery smolt releases for each stock group at
 185 age-0. Relative differences in hatchery release abundances are proportional to patterns of mean
 186 releases from 2008 -2017 (see Supplement 1 and Fig. S1.3). Releases were summarized using tag
 187 data from the Regional Mark Information System (RMIS;
 188 http://www.rmis.org/rmis_login.php?action=Login&system=cwt). We assume total coastwide
 189 hatchery releases vary through time, but the relative proportion of hatchery releases arising
 190 from each stock is constant (Fig. S1.3).

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

196 *Ocean distribution and mortality*

197 Once fish enter the ocean, they are lost to natural mortality $M_{a,f}$, which varies by season-age
 198 a and fish type (hatchery or natural origin) f , and harvest mortality $F_{a,l}$, which varies by season-
 199 age a and ocean region l (Fig. S1.5, Table S1.3 & S1.4). Fish age 3, 4 and 5 are susceptible to
 200 harvest; however harvest rate for age-3 fish is 40% lower than older fish (Shelton *et al.* 2021, see
 201 Shelton *et al.* Fig. S5.12). Both $M_{a,f}$ and $F_{a,l}$ are assumed constant across time. We vary fishing

202 mortality by ocean region based on relative mean recreational and commercial catch differences
 203 over the last decade to capture the relative influence of spatially variable salmon ocean fisheries
 204 (see Supplement 1 for further details and sensitivity testing results, Table S1.5, Fig. S1.6-S1.7).

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

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

219

220 Early Marine Survival

221 Generally, research suggests differences in early marine survival of hatchery and natural
 222 origin fish, though there is a need for a spatially coherent analysis of these patterns (Beamish *et al.*
 223 *et al.*, 2012; Woodson *et al.*, 2013). Based on existing evidence, we assume early marine survival is
 224 5% greater for ocean age-0 natural origin fish than for hatchery fish (Beamish *et al.*, 2012;
 225 Woodson *et al.*, 2013). We model covariance in natural- and hatchery-origin smolt survival using
 226 a stationary lag-1 multivariate autoregressive process, MAR(1) (Fig. 3, see Fig. S1.9 for sensitivity
 227 testing results). Past work has indicated that juvenile salmon survival rates have an AR-1
 228 structure (Kilduff *et al.*, 2015; Sharma *et al.*, 2013). Let $\pi_{t,a=0,f}$ be a vector of log age-0 survival
 229 rates of length r representing each stock group at year t for either hatchery or natural origin fish
 230 f . Survival of age-0 fish $\pi_{t,a=0,f}$, is the sum of A_f , a constant scalar, \mathbf{B} , a diagonal $r \times r$ matrix

231 whose elements ϕ_r , determine the autocorrelation structure for each stock group, and \mathbf{E}_t , the
 232 process error at year t .

$$233 \quad \boldsymbol{\pi}_{t,0,f} = \mathbf{A}_f + \mathbf{B}\boldsymbol{\pi}_{t-1,0,r,f} + \mathbf{E}_{t,r} \quad Eq(1)$$

$$234 \quad \mathbf{E}_t \sim MVN[0, \boldsymbol{\Sigma}]$$

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

244 The mean and variance of early marine survival do not vary among scenarios, allowing us
 245 to examine interactions between spatial covariance in early marine survival and Chinook salmon
 246 spatial portfolios without confounding the interpretation with changes to early marine survival
 247 mean and variance. We base the mean and variance of $\boldsymbol{\pi}_{t,0,f}$ on estimates from Shelton et al
 248 2021.

249 We use an exponential covariance function to simulate covariance among stocks given
 250 the critical distance w between rivers associated with each stock group. Kilduff et al. 2015
 251 suggest that Chinook salmon ocean survival shows a correlation of 0.50 at a distance of 706km,
 252 including a 95% confidence interval that reaches 1437km. To understand how changing the scale
 253 of correlation affects ocean portfolios and facilitate comparisons with previous studies, we
 254 simulate a range of scenarios that vary the distances at which the correlation among river
 255 mouths falls below 0.50. We test an independent scenario, here critical distance is 0km and early
 256 marine survival among stock groups fluctuate independently, in addition to 150, 350, 706 and
 257 1400km (Fig. 3).

258 *Ocean Synchrony and Spatial Portfolios*

259 To understand the degree to which stock group abundances have concurrent temporal
 260 variation in the ocean, we calculate synchrony (Eq(2)) within ocean regions using a synchrony
 261 index between 0 and 1; where 1 indicates perfect synchrony and 0 indicates no synchrony
 262 (Loreau & de Mazancourt, 2008).

$$263 \quad \rho_j = \frac{\sigma_j^2}{(\sum_i \sigma_{i,j})^2}, \text{ Eq(2)}$$

264 Here, synchrony for each ocean-region ρ_j , is the variance of the aggregate ocean-region
 265 observed in the simulation, σ_j^2 , divided by the sum of the variance for each individual stock,
 266 $(\sum_i \sigma_{i,j})^2$.

267 We use portfolio effect strength as a metric for temporal variability in each ocean region
 268 for aggregate populations. We quantify the portfolio effect using the mean-variance relationship
 269 (MV), defined as the ratio between expected variance if each ocean region were composed of
 270 one homogenous stock, $\log(\hat{\sigma}_j^2)$ and the realized variance of multiple stocks within one ocean
 271 region, $\log(\sigma_{i,j}^2)$. In ecological populations, the relationship between mean sub-population
 272 abundance, $\mu_{i,j}$, and variance may increase non-linearly (Anderson et al., 2013). We use the MV
 273 relationship, rather than the coefficient of variation, to derive an empirical relationship for z , the
 274 slope of the linear regression of $\log(\sigma_{i,j}^2)$ and $\log(\mu_{i,j})$, among sub-populations (Anderson et al.,
 275 2013). Here, Eq(3) estimates z , the slope of the linear regression of $\log(\sigma_{i,j}^2)$ and $\log(\mu_{i,j})$,

$$276 \quad \log(\sigma_{i,j}^2) = \beta_0 + z \log(\mu_{i,j}) + \varepsilon_{i,j} \quad \text{Eq(3)}$$

278 where $\varepsilon_{i,j}$ is the residual error with a mean zero and an estimated variance that follows a normal
 279 distribution. We use Equation 3 to calculate the expected variance $\log(\hat{\sigma}_j^2)$ for a single
 280 population with the mean abundance set to the mean abundance across sub-populations. This
 281 metric describes temporal variability by quantifying the degree to which diversity in stock
 282 structure decreases variability in aggregate Chinook salmon ocean abundances. A portfolio
 283 strength of 1 indicates that aggregate stocks are acting as a homogenous population, whereas,
 284 for example, a portfolio strength of 1.5 means that the population within an ocean region is 1.5
 285

286 times more stable than it would be if the ocean region were composed of a single homogenous
287 stock (Anderson et al., 2013). We used the *synchrony()* and *pe_mv()* function within the R
288 Ecofolio package to calculate synchrony and mean-variance portfolio effect (Anderson et al.,
289 2013).

290 *Spatial Portfolios and Abundance Variability for Resource Users*

291 We use portfolio effect strength to understand relative changes in temporal and spatial
292 variability within and among ocean regions, with a focus on salmon population variability.
293 However, the mean-variance portfolio calculation does not inform changes in absolute
294 abundance. Change in abundance, in addition to the mean-variance relationship, can affect
295 abundance of oceanic predators and ocean fisheries that target Chinook salmon. To investigate
296 how synchrony may impact ocean abundance patterns, we tracked how often ocean age-4 and -
297 5 fish abundance fell below average for three years or more in killer whale habitat and in ocean
298 fishing management zones. We track consecutive low-abundance years of Chinook salmon
299 abundance because multiple years of low abundance could have higher consequences for
300 predators and fisheries than a single low abundance year (Ward et al., 2009). We select only age-
301 4 and age-5 fish because fisheries and predators generally prefer older, larger, fish due to
302 increased revenue and caloric value, respectively (Ford et al., 2010). We used established
303 summer habitat for the Northern and Southern killer whales (NRKW, SRKW respectively)
304 summarized by Chasco *et al.* 2017. To designate fishing regions, we used fishery management
305 zones defined by the Pacific Salmon Commission and the Pacific Fisheries Management Council,
306 for specific spatial designations refer to Table S1.6.

307

308 **Results**

309 We found that increased demographic synchrony eroded Chinook salmon spatial portfolios
310 in the ocean, and decreased resource availability within ocean fishery zones but not within killer
311 whale summer habitat. We present results in two sections that focus on 1) the interaction
312 between demographic synchrony in the ocean and spatial portfolios within ocean regions and 2)
313 the impact of demographic synchrony on spatial portfolios and likelihood of low abundance
314 within ocean fishery regions and killer whale summer habitat.

315 *Ocean Synchrony and Spatial Portfolios*

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

323 Ocean synchrony and portfolio effect strength were negatively correlated. We observed high
324 ocean synchrony and weak portfolios in ocean regions with low stock richness. Moreover, the
325 magnitude of change in ocean synchrony and portfolio effect strength among scenarios varied
326 by ocean region (Fig. 4). For example, ocean synchrony in Monterey (MONT) was high (0km:
327 0.94[0.02], Mean[SD]; 1400km: 0.97[0.01]) while the portfolio was weak (0km: 0.92[0.07]
328 (Mean[SD]); 1400km: 0.90[0.05])) across all spatial covariance scenarios (Fig. 4). The portfolio
329 effect within MONT was below 1 regardless of spatial covariance (Fig. 4b) indicating that the
330 aggregate population in this ocean region behaves as a single homogenous population. In
331 contrast, Southern Southeast Alaska (SSEAK) and Southwest Vancouver Island (SWVI)
332 demonstrated relatively low ocean synchrony (SSEAK 0km: (0.29)[0.05]; 1400km: (0.36)[0.04],
333 SWVI 0km: (0.29)[0.05]; 1400km: (0.36)[0.04]) (Fig. 4a) and strong ocean portfolios (SSEAK 0km:
334 (1.9)[0.18]; 1400km: (1.55)[0.2], SWVI 0km: (2.88)[0.5]; 1400km: (2.1)[0.25]).

335 *Spatial Portfolios and Abundance Variability for Resource Users*

336 Chinook salmon variability within fishing regions increased as the spatial extent of covariance
337 in early marine survival increased (Fig. 5a). Similar patterns occur for all fish ages, but the
338 magnitude of difference between 0km and 1400km increased when we considered older fish,
339 which are a target for fisheries and killer whales. The Alaska and Washington ocean troll fishing
340 regions had an overall greater portfolio effect than the California and Oregon ocean troll fishery
341 regions (Fig. 5a). When we set early-survival spatial covariance to 1400km, the portfolio strength
342 in Alaska and Washington decreased by 17% and 19%, while Oregon and California decreased by
343 16% and 9% respectively (Fig. 5a). Our model indicated that spatial covariance in early marine

344 survival increased the likelihood that aggregate ocean abundances in fishing regions will fall
345 below-average three or more consecutive years (Fig. 5b). This finding is relatively consistent
346 among fishing regions. We found that low abundance streaks are on average 1.8 times more
347 likely when critical covariance distance is 1400km compared to 0km critical. In contrast, we
348 found a strong portfolio effect across both Southern Resident and Northern Resident killer whale
349 summer habitat that did not change under increased covariance scenarios (Fig. 5). There was a
350 16% and 21% increase in the likelihood that fish abundance will be below average for 3 or more
351 years in NRKW and SRKW summer habitat, respectively. Thus, in comparison to ocean fishing
352 regions Chinook salmon variability within killer whale summer habitat was relatively robust to
353 increases in spatial covariance in early marine survival covariance.

354

355 Discussion

356 Climate variability can synchronize populations across large spatial scales (Hansen et al.,
357 2020; Moran, 1953). Understanding the extent populations may vary due to climate can improve
358 expectations of ecosystem-scale patterns across spatial scales, with direct repercussions for
359 species conservation and management. Here, we demonstrate that increased spatial synchrony
360 can lead to greater variability in Chinook salmon ocean abundances and a weakening of the
361 portfolio effect in individual ocean regions. Additionally, we found that geographically variable
362 portfolio effects emerge for ocean life stages, resulting in differences in portfolio strengths and
363 fish availability for resource users. These results broaden our understanding of ecological
364 portfolio theory for anadromous species, where much of the literature has focused on
365 freshwater life stages (eg. (Griffiths et al., 2014; Moore et al., 2010; Satterthwaite & Carlson,
366 2015)). Moreover, we observed a stronger portfolio effect as we broadened the spatial region.
367 This outcome is a facet of statistical averaging that manifests in real ecological situations, where
368 a larger spatial area increases the likelihood of including a subpopulation, or a salmon stock, in
369 the aggregate. That this phenomenon emerges in our simulations of Chinook salmon dynamics
370 has important implications for resource users. Mobile resource users that cover a larger area can
371 take advantage of decreased aggregate variability, while place-based resource users experience
372 increased resource fluctuations (Fisher et al., 2021; Okamoto et al., 2020; Stier et al., 2020).

373 Our study adds to a growing literature exploring the degree to which diversity can confer
374 population resilience to climate variability and the extent to which this buffering effect is
375 influenced by population synchrony (Valencia et al., 2020). Our model shows a positive
376 relationship between portfolio strength and salmon stock richness, where ocean regions with
377 more stocks have less variability, measured by the mean-variance portfolio effect, than ocean
378 regions with fewer stocks (Fig. 4c). This positive relationship is in part due to statistical averaging,
379 where increases in diversity in an aggregate population will concomitantly decrease variability
380 (Doak et al., 1998). We found that the ocean portfolio is two times stronger when stock richness
381 is twelve compared to three (Fig. 4c). In part, the spatial variation in stock richness is related to
382 biogeography, for example California lies at the edge of the Fall Chinook salmon range and
383 consequently not many stocks distribute to that area. Independent of biogeographical gradients,
384 we found that as spatial covariance in early survival increases, Chinook salmon abundances
385 became more variable, even in ocean regions with high stock richness. Our study and others like
386 it highlight that conserving diversity can partially but not completely mitigate impacts of climate
387 or anthropogenic disturbances (Holsman et al., 2020; Valencia et al., 2020).

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

402 (Aikens et al., 2017; Fisher et al., 2021; Middleton et al., 2018; Okamoto et al., 2020; Stier et al.,
403 2020).

404 Compared to northern resident killer whales, endangered Southern Resident killer whales
405 (SRKWs) have a moderate increase in likelihood of low abundance streaks as spatial covariance in
406 marine survival increases. Improving Chinook salmon availability and access for SRKWs is a
407 primary element of their recovery plan (National Marine Fisheries Service, 2008). Thus
408 conserving the inherent population diversity of Puget Sound salmon may buffer endangered
409 SRKWs against low abundance years and allow them to exploit inherent phenological diversity in
410 Chinook salmon stocks (Ettinger et al., In review). Investigating smaller scale whale-Chinook
411 salmon distributions and interactions will help evaluate the degree to which whales take
412 advantage of the full salmon portfolio across the habitat that we considered.

413 Chronic reductions in fish availability at the smaller spatial scales used by participants in the
414 ocean salmon fishery can result in low-revenue for fishermen and related industry, increased
415 likelihood of departure from the fishery, and in some cases, fishery closures (Richerson et al.,
416 2018; Richerson & Holland, 2017). The West Coast ocean salmon fishery in the California Current
417 has undergone multiple closures, often attributed to un-productive warm ocean conditions and
418 low fish survival. The 2008-2009 fishery closure ultimately led to fishers exiting the fishery and
419 dispersal of \$170 million USD for federal fishery disaster relief funding (Richerson & Holland,
420 2017). Based on our results, those fishery participants that are able to move between ocean
421 regions – usually those with larger vessels and presumably more capital (Fisher et al., 2021)-- are
422 more likely to mitigate any negative impacts of increased spatial synchrony on fish abundance
423 (Okamoto et al., 2020). Understanding how climate impacts spatial processes and fish variability
424 can help to enhance adaptive capacity among fisheries and management entities.

425 While our study examines how changes in Chinook salmon early marine survival coherence
426 affects abundance and variability from the perspective of alternative users of this critical
427 resource, we did not address how specific management actions can counteract or amplify the
428 extent of spatial coherence. One approach employed in many regions along the US West Coast
429 to reduce variability in Chinook salmon populations is hatchery supplementation. This practice
430 artificially augments salmon abundance by producing and releasing large numbers of young

431 salmon into rivers or estuaries; this has significant impacts to the Pacific Salmon ecosystem. For
432 example, research in Puget Sound, WA, indicates negative density dependence between
433 hatchery and natural origin fish in marine and freshwater life stages (Kendall et al., 2020).
434 However, research investigating hatchery and natural origin fish interactions is often conducted
435 on a local or regional scale and does not fit into the scope of our model (Kendall et al., 2020;
436 Nelson et al., 2019). Including hatchery and natural origin stock density dependence will be an
437 important avenue for future work, especially as some West Coast states propose to increase
438 hatchery production (WA State Orca Task Force).

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

449

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456

457 **Conflict of Interest Statement**

458 The authors have no conflict of interest to disclose.

459

460 Authors' Contributions

461 GS, AOS and JS conceived the ideas and designed methodology; GS and AOS wrote simulation
462 code; GS analyzed the data, created figures and led the writing of the manuscript. All authors
463 contributed critically to the drafts and gave final approval for publication.

464

465 Data Availability Statement

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

470 Author please add the Zenodo citation to your reference list

471

472 Figure Captions:

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

481

482 **Figure 2:** Conceptual model and timing of life history events in simulation. Adult natural
483 mortality is applied within each seasonal time step.

484 **Figure 3: A)** Time series of simulated survival rates, $\pi_{t,0,f=w}$, for natural origin fish within
485 Northern California (NCA), which is characteristic of Klamath and Trinity hatcheries in California
486 and Southwest Vancouver Island (SWVI), which is characteristic of Vancouver Island, British
487 Columbia, Canada. Each panel represents the distance at which there is 50% covariance in early
488 marine survival. We plotted a single realization of survival and truncated the time series to years

489 100-125 to make the figure more interpretable. **B)** Truncated time series of stock abundance
 490 within six ocean regions for a single realization in scenarios for critical distances 0km and
 491 1400km.

492 **Figure 4: A)** Synchrony for six ocean regions in scenarios with a critical distance of 0km and
 493 1400km (Mean and ± 1 standard deviation are shown). **B)** Portfolio effect strengths for six ocean
 494 regions across all critical distance scenarios that we tested (Mean and ± 1 standard deviation
 495 are shown). **C)** The mean-variance portfolio effect as a function of stock richness (the number of
 496 stocks) in each ocean region using 0km and 1400km critical distance scenarios (Mean and ± 1
 497 standard deviation are shown).

498 **Figure 5: A)** Portfolio effect strengths for four fishing regions using 0km and 1400km critical
 499 distance scenarios (Mean and ± 1 standard deviation are shown). **B)** Probability that aggregate
 500 ocean fish abundance for age 4 and 5 Chinook salmon will be below the long term mean for at
 501 least 3 years within ocean fishing regions. We present results from the 0km and 1400km critical
 502 distance scenarios (Mean and ± 1 standard deviation are shown). **C)** Portfolio effect strengths
 503 for Northern Resident and Southern Resident (NRKW, SRKW, respectively) critical habitat for
 504 0km and 1400km critical distance scenarios (Mean and ± 1 standard deviation are shown). **D)**
 505 Probability that aggregate ocean fish abundance for age 4 and 5 Chinook salmon will be below
 506 the long term mean for at least 3 years within Southern Resident and Northern Resident killer
 507 whale critical habitat. We present results from the 0km and 1400km critical distance scenarios
 508 (Mean and ± 1 standard deviation are shown).

509

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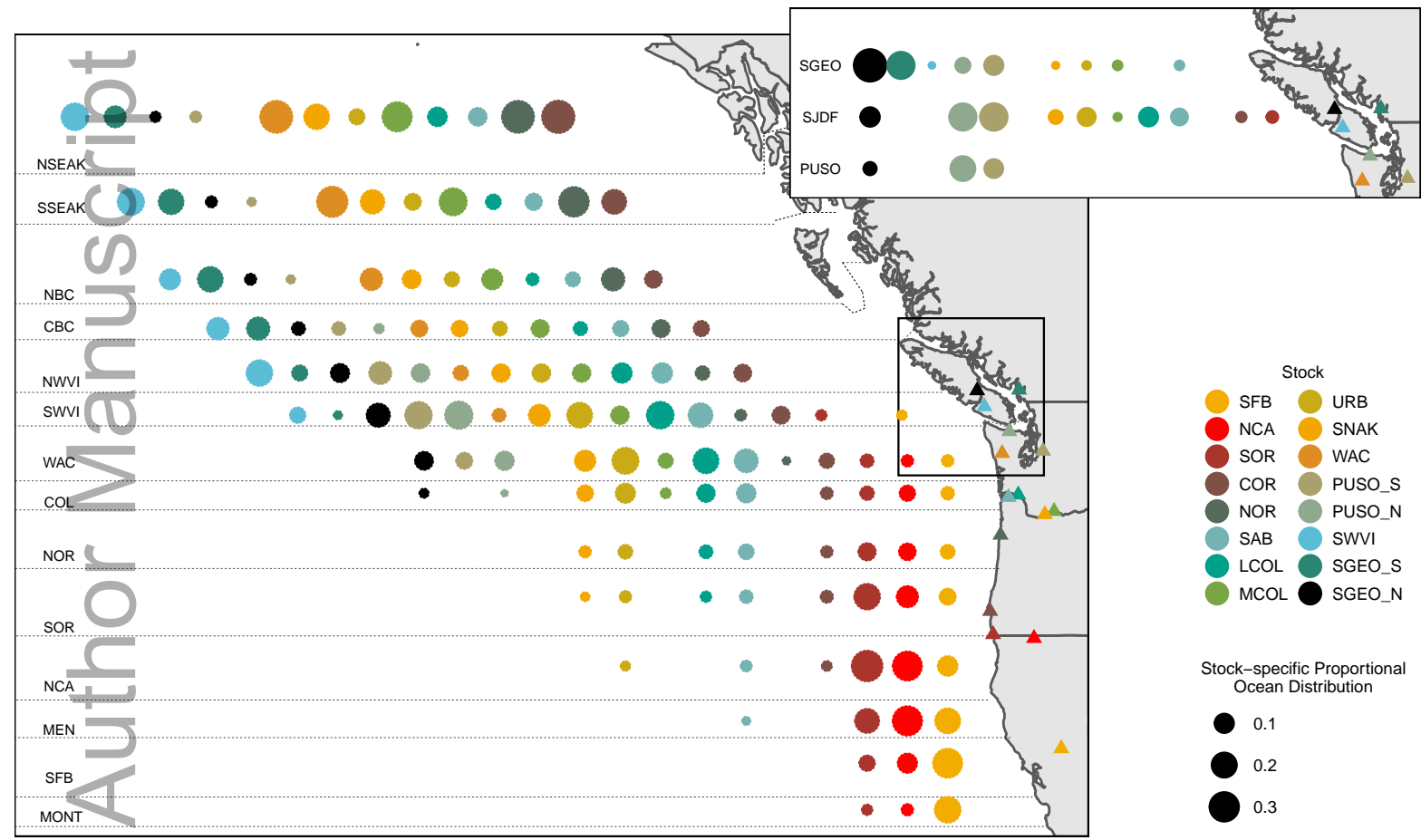
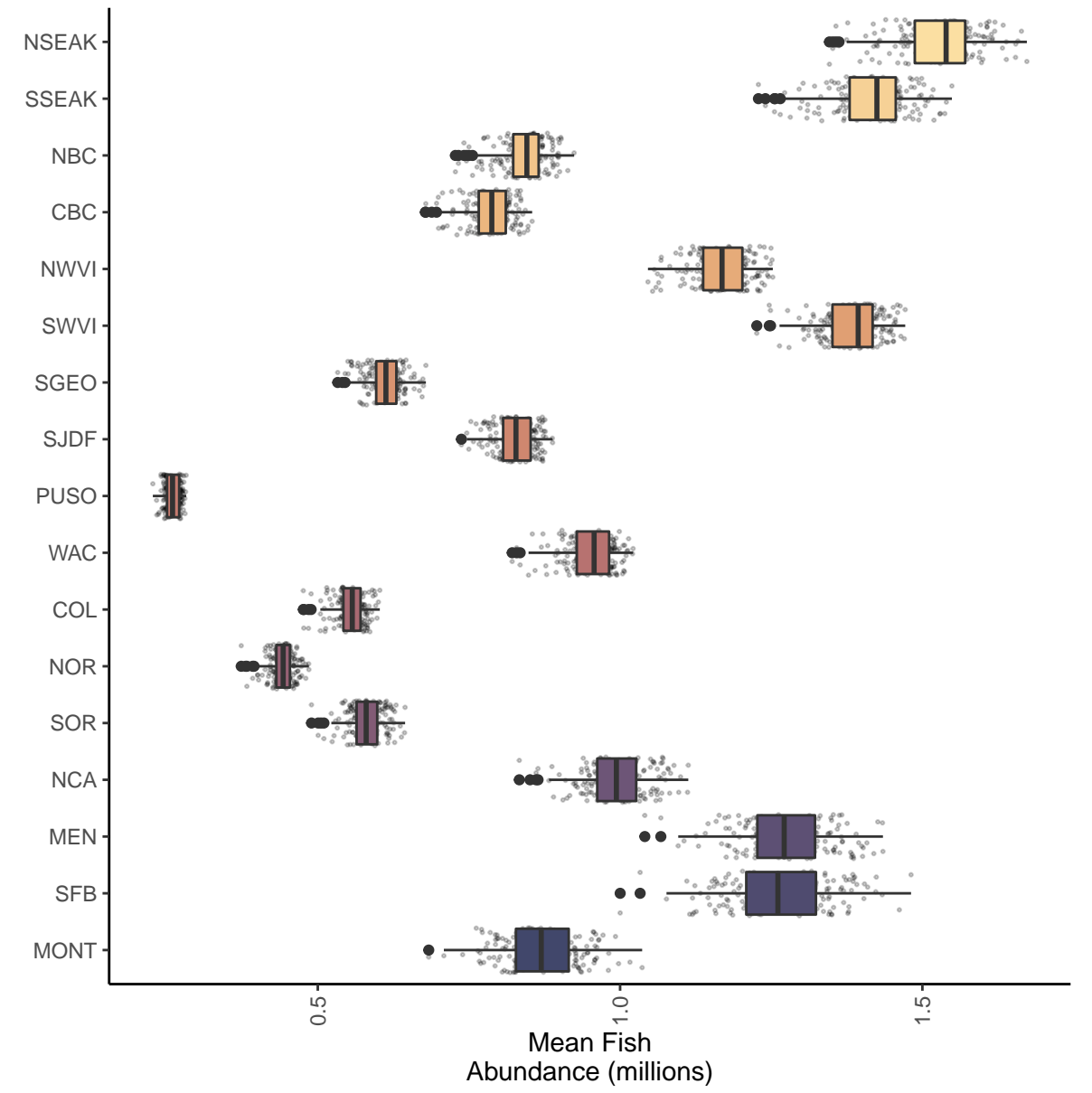
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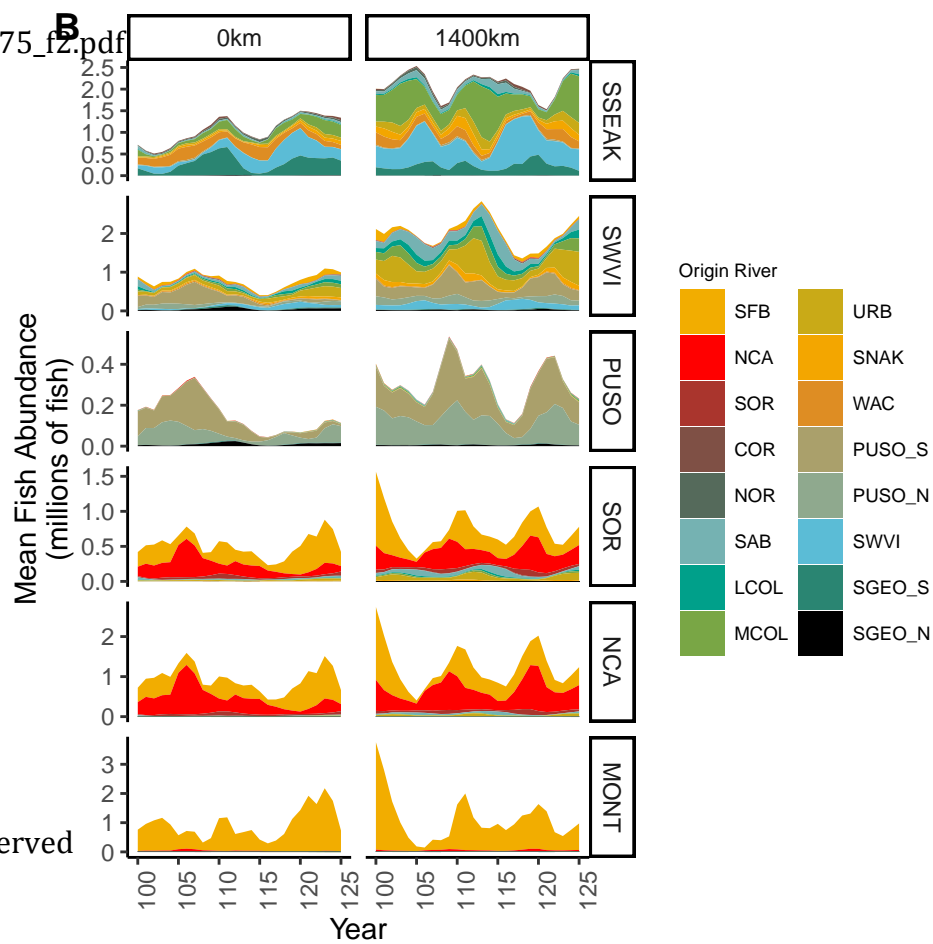
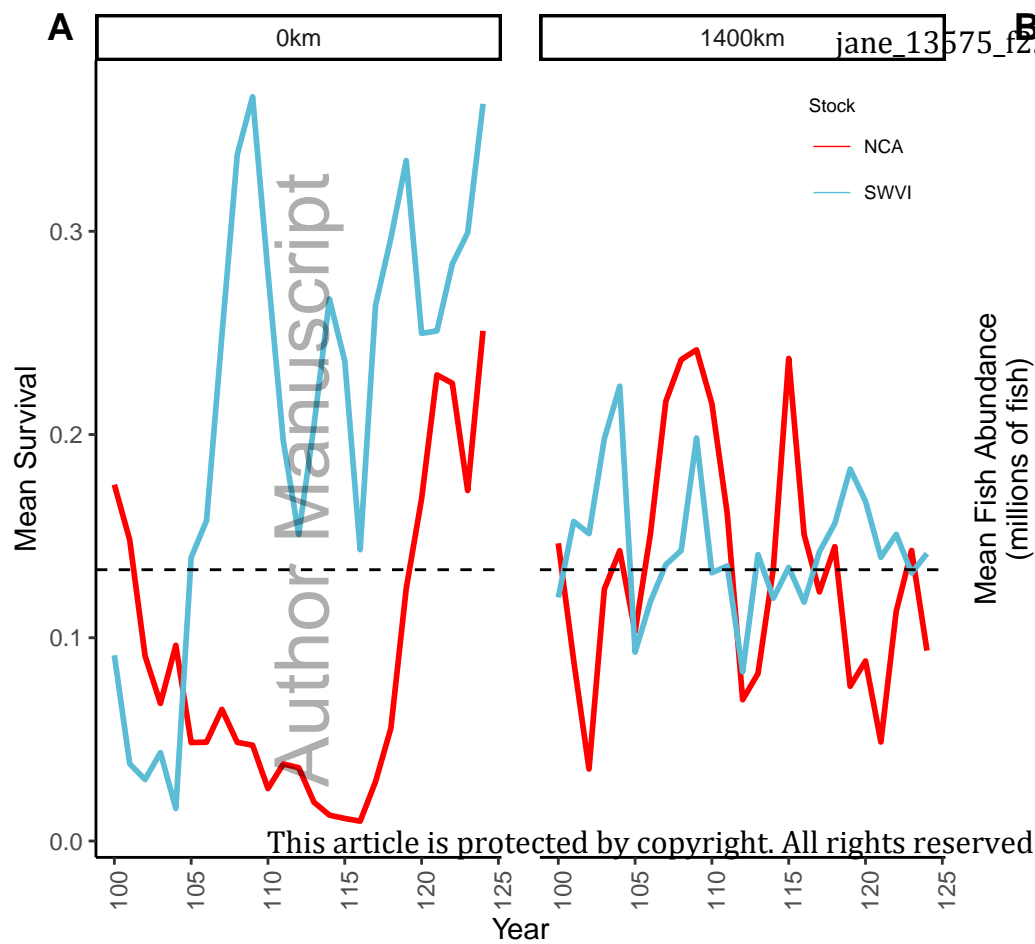
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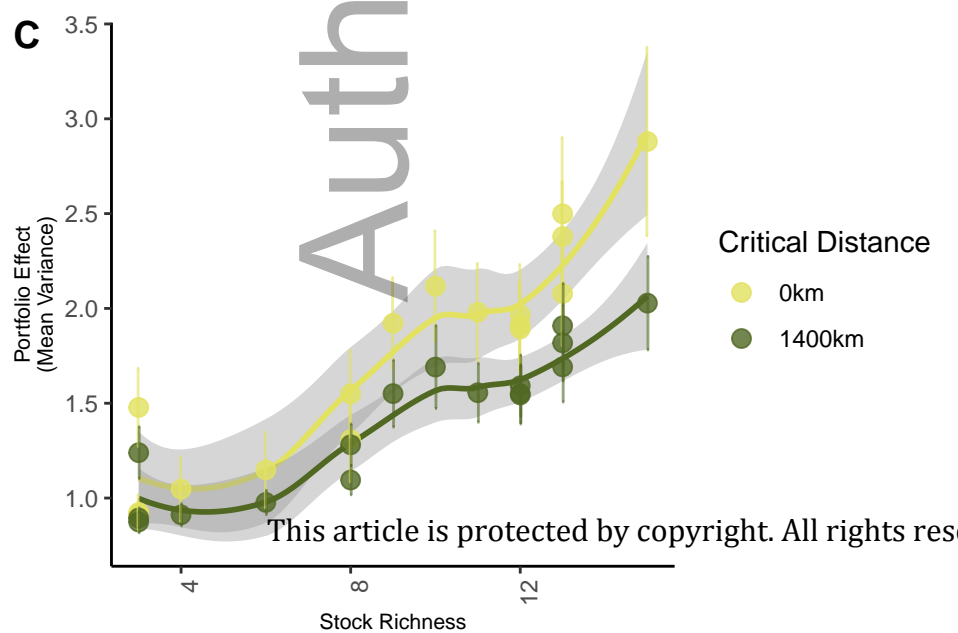
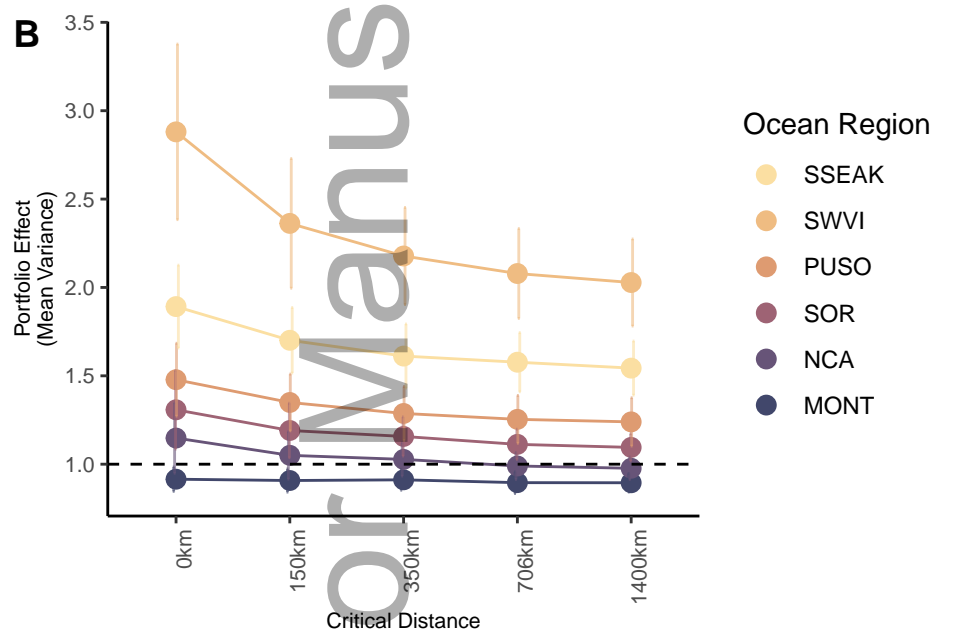
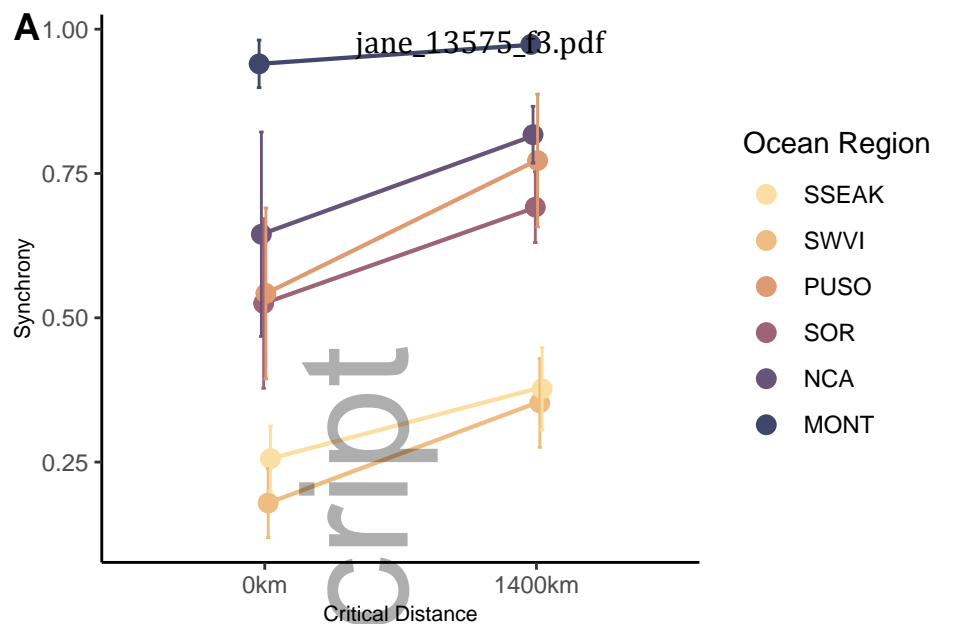
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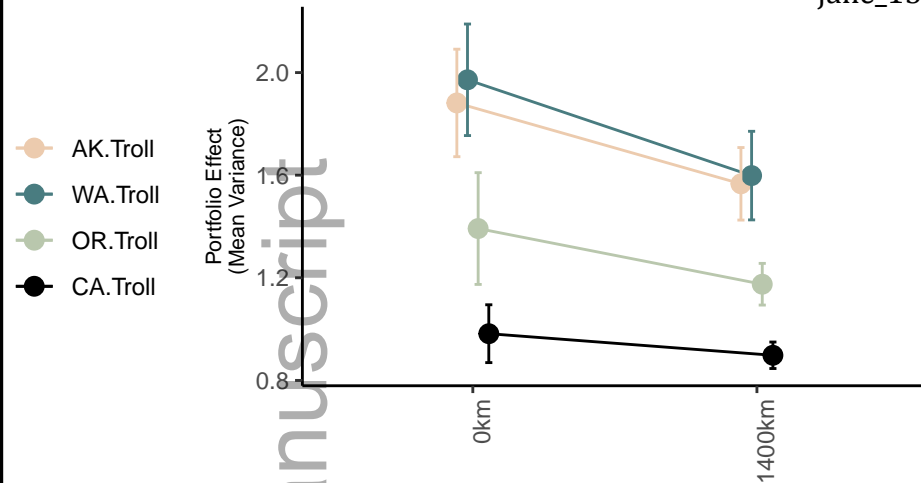
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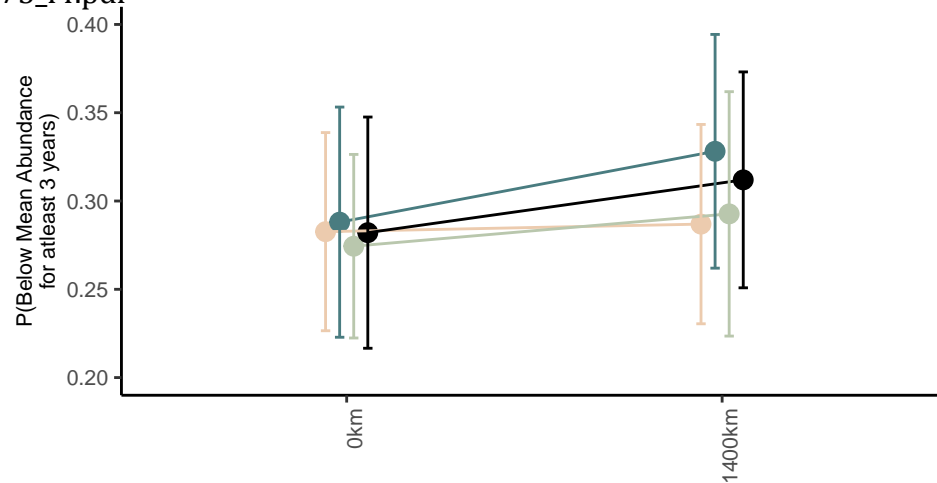




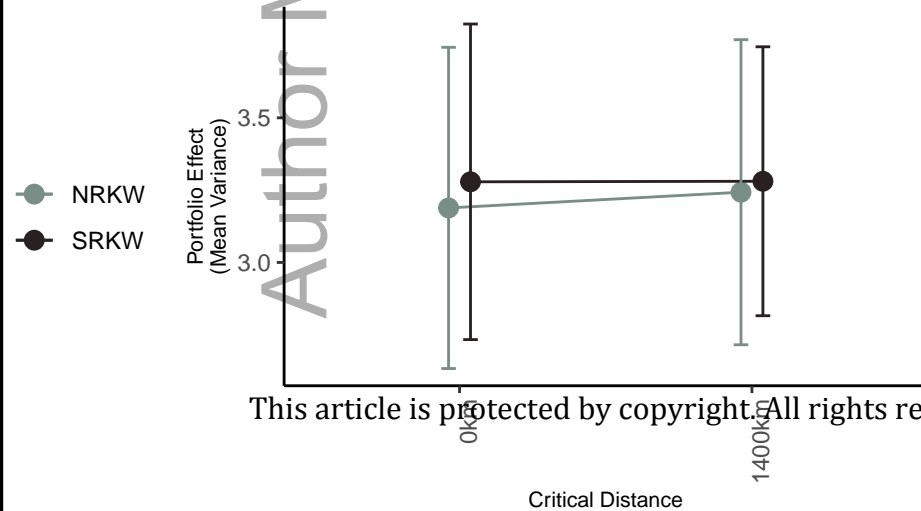
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