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Salish Sea Chinook salmon exhibit weaker coherence in early marine survival trends than coastal populations

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28 **Running title:** Marine survival variability in Chinook salmon

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30

31 **Abstract**

32 Identifying factors that influence anadromous Pacific salmon (*Oncorhynchus* spp.) population

33 dynamics is complicated by their diverse life histories and large geographic range. Over the last

34 several decades, Chinook salmon (*O. tshawytscha*) populations from coastal areas and the Salish

35 Sea have exhibited substantial variability in abundance. In some cases, populations within the

36 Salish Sea have experienced persistent declines that have not rebounded. We analyzed time

37 series of early marine survival from 36 hatchery Chinook salmon populations spanning ocean

38 entry years 1980 – 2008 to quantify spatial and temporal coherence in survival. Overall, we

39 observed higher inter-population variability in survival for Salish Sea populations than non-

40 Salish Sea populations. Annual survival patterns of Salish Sea populations covaried over smaller

41 spatial scales and exhibited less synchrony among proximate populations relative to non-Salish

42 Sea populations. These results were supported by multivariate autoregressive state space

43 (MARSS) models which predominantly identified region-scale differences in survival trends

44 between northern coastal, southern coastal, Strait of Georgia and Puget Sound population

45 groupings. Furthermore, Dynamic Factor Analysis (DFA) of regional survival trends showed that

46 survival of southern coastal populations was associated with the North Pacific Gyre Oscillation,

47 a large-scale ocean circulation pattern, whereas survival of Salish Sea populations was not. In

48 summary, this study demonstrates that survival patterns in Chinook salmon are likely determined

49 by a complex hierarchy of processes operating across a broad range in spatial and temporal

50 scales, presenting challenges to management of mixed-stock fisheries.

51 **Key words:** Chinook salmon, Salish Sea, marine survival, spatio-temporal variability, resource

52 management, time series, MARSS models

53 **Introduction**

54   Sound management and conservation of exploited organisms requires an understanding

55 of the predominant spatial and temporal scales of variability governing both short- and long-term

56 population dynamics. Identifying the sources of this variability remains a critical challenge to

57 managers tasked with developing, modifying, and implementing resource management strategies

58   (Ludwig et al., 1993). Population dynamics of Pacific salmon (*Oncorhynchus* spp.), specifically

59   life-stage-specific survival or abundance, are particularly difficult to accurately project because

60   their life cycle encompasses both freshwater and marine environments (Quinn, 2011), subjecting

61   them to a large suite of factors that influence the overall viability of populations. Correlation in

62   survival and recruitment rates for populations separated by hundreds of kilometers indicate that

63   marine conditions common to a region influence population dynamics similarly (Dorner et al.,

64   2008; Malick & Cox, 2016; Sharma et al., 2013). This relationship occurs at a variety of spatial

65   scales, ranging from those as large as the Northeast Pacific Ocean (Kilduff et al., 2015) to as

66   small as local conditions encountered at the point of marine entry (Greene et al., 2005; Sharma et

67   al., 2013).

68   Here, we examine spatial and temporal complexity in marine survival of Chinook salmon

69   (*O. tshawytscha*) populations in the Northeast Pacific, focusing on the Salish Sea and develop

70   testable hypotheses about the spatial and temporal scales at which specific environmental and

71   biological drivers may influence smolt survival patterns. The Salish Sea is a unique inland

72   marine ecosystem encompassing the interconnected waters of the Strait of Georgia and Puget

73   Sound (Fig. 1) and connected to the Pacific Ocean via the Strait of Juan de Fuca and Johnstone

74   Strait. Glaciation of the region carved a network of basins and inlets with spatially-explicit

75   oceanographic properties such as salinity, temperature and vertical stratification (Moore et al.,

76   2008b). Chinook salmon are native throughout the Salish Sea and have experienced large

77   fluctuations in abundance throughout the last several decades (Good et al., 2005; Preikshot et al.,

78   2013; Peterman & Pyper, 2000). These fluctuations may be linked to a combination of human-

79   caused stressors (e.g. habitat loss, overharvest, and hatchery propagation) and natural

80   environmental drivers in both freshwater and marine environments (Lawson, 1993; Peterson &

81   Schwing, 2003; Ruckelshaus et al., 2002; Ward et al., 2015). Declines in abundance have led to

82   conservation measures such as protection under the U.S. Endangered Species Act for Puget

83   Sound populations (Ford et al., 2011; Ruckelshaus et al., 2006) and efforts to assess and

84   implement recovery measures for Strait of Georgia populations. Declines in the marine survival

85   of Puget Sound coho salmon (Zimmerman et al., 2015) and Steelhead trout (Kendall et al., *in*

86   *prep*), Strait of Georgia Chinook and coho salmon (Preikshot et al., 2013), and concurrent

87   changes in pelagic community structure (Greene et al., 2015) raise the possibility that

88   environmental change unique to the Salish Sea ecosystem has contributed to salmon declines.

89 Accordingly, one might expect that marine survival of Salish Sea salmon populations is lower
90 than, and potentially asynchronous with, marine survival of populations outside of the Salish
91 Sea.

92   Why might Salish Sea populations exhibit greater variation in smolt survival than non-
93 Salish Sea populations? As a semi-enclosed body of water, the Salish Sea may be subject to
94 more rapid changes in oceanographic properties than the open Pacific Ocean into which coastal
95 rivers drain. For example, annual variation in river discharge and local air temperature have a
96 large basin-scale influence on the Puget Sound ecosystem, and correlate more strongly with
97 Puget Sound oceanographic properties than larger scale climate indices such as PDO, ENSO and
98 the Aleutian Low (Moore et al., 2008b). Furthermore, within Puget Sound, environmental
99 variability tends to increase along a gradient from its outer, more oceanic waters (i.e., Admiralty
100 Inlet) to its more distal bays and inlets (Moore et al 2008). If the California Current off the coast
101 of North America is more strongly moderated by continental scale climatic processes than Puget
102 Sound, and these climate processes fluctuate on longer time frames than Puget Sound air
103 temperature and river discharge, Puget Sound Chinook salmon may encounter a more variable
104 environment than coastal populations during early marine rearing.

105   The broad geographic scales across which Chinook salmon co-mingle in the marine
106 environment make many populations susceptible to marine fisheries that occur well outside their
107 region of origin (Weitkamp, 2010). The failure of pre-season forecast models to accurately
108 predict early marine survival, which is critical to overall survival of populations (Beamish &
109 Mahnken, 2001; Beamish et al., 2004), can lead to significant errors in population-specific
110 abundance forecasts (see Scheuerell & Williams, 2005). Forecast error can lead to over- or
111 under- projections of total allowable mortality in marine fisheries contributing to either
112 unnecessary limitations on fisheries or overexploitation (PSC, 2015). Furthermore, the spatial
113 scale at which forecast abundance indices are calculated may not accurately reflect the spatial
114 scale of variability in early marine survival. This discrepancy can lead to disproportionate fishery
115 impacts on weaker populations. Therefore, a better understanding of the predominant spatial
116 scales across which populations co-vary in survival will help to inform appropriate spatial scales
117 of management and assessment for Chinook salmon.

118   In this study, we quantified spatial and temporal coherence in hatchery origin Chinook
119 salmon smolt survival. Smolt survival is defined as the period from hatchery release to the end of

120   the first year of ocean residence. We placed an emphasis on populations originating from within

121   the Salish Sea due not only to their cultural and economic importance to local communities, but

122   also their contribution to Northeast Pacific mixed-stock commercial troll and sport fisheries.

123   Because Salish Sea Chinook salmon are harvested extensively in marine mixed-stock fisheries,

124   we used coded wire tag (CWT) data to estimate stock-specific harvest and escapement and

125   calculate smolt survival for 36 hatchery Chinook salmon populations distributed across a broad

126   geographic range, extending from coastal Southeast Alaska to Oregon and within the Salish Sea

127   (Fig. 1). However, the quality of smolt survival estimates derived from CWT recovery data can

128   vary substantially by population and year due to poor fishery and escapement sampling coverage

129   (PSCCWTWG, 2008). To address this challenge, we utilize multivariate state space models to

130   assess data support for hypotheses regarding the predominant spatial and temporal scales

131   governing variability in Chinook salmon smolt survival rates (see Table 1 for spatial scale

132   definitions). Recently, these models have received considerable attention regarding their

133   usefulness to evaluate noisy ecological time series (Ohlberger et al., 2016; Ward et al.,

134   2010; Zuur et al., 2003), particularly because of their ability to address problems with missing

135   data (Holmes et al., 2014) and effectively partition the total variance present in a data time series

136   into signal and noise components (Dennis et al., 2006), with the latter being important for

137   reducing bias in estimates of survival trends.

138   This study addresses the following questions: (1) Is smolt survival of Chinook salmon

139   populations within the Salish Sea similar to smolt survival of populations outside the Salish Sea

140   (i.e., region scale, Table 1)? (2) Do the two basins within the Salish Sea (Strait of Georgia and

141   Puget Sound) exhibit similar trends in survival? Results from this study will be used to inform

142   the appropriate spatial scales for future work to identify ecosystem indicators for improving the

143   accuracy and precision of stock assessment and forecasting methods necessary for effective

144   management and conservation of Salish Sea Chinook salmon.

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147   **Methods**

148   *Study area and CWT dataset*

149   Total releases and recoveries of CWT Chinook salmon were compiled from three

150   geographic areas: Northern Coastal (Southeast Alaska (SEAK) and Northern British Columbia

151 (NBC)), Salish Sea (Strait of Georgia (SOG), Puget Sound (PS), and Strait of Juan de Fuca

152 (JDF)), and Southern Coastal (West Coast Vancouver Island, Washington and Oregon Coast).

153 At least some oceanographic properties in the Strait of Juan de Fuca are transitional between the

154 Salish Sea and Pacific Ocean (Johannessen et al., 2006; Masson & Peña, 2009), so we tested this

155 area as both within and separate from the Salish Sea with MARSS models. Populations were

156 selected for inclusion in analyses based on data quality, time series length (minimum 20 years),

157 and geographic coverage within and outside the Salish Sea, resulting in a list of 36 populations

158 with survival data over ocean entry years (OEY) 1980-2008 (Table 2, Fig. 1). This dataset

159 represented the dominant life history types locally observed in wild Chinook salmon populations:

160 ocean entry ages mimicked by two release strategies (subyearling, yearling) and two run timing

161 groups (spring, summer-fall). CWT recovery data were downloaded from the coast-wide

162 Regional Mark Information System database (http://www.rmpc.org, accessed 6 June 2015).

163 *Calculation of smolt to age-2 or 3 survival of Chinook salmon*

164 Release and recovery data from CWT fish were used to estimate population- and brood-

165 specific smolt survival of Chinook salmon using backwards cohort reconstruction. The survival

166 metric encompasses all sources of post-release mortality of CWT fish to age-2 for Chinook

167 salmon released as subyearlings and to age-3 for Chinook salmon released as yearlings. Smolt

168 survival was calculated as follows:

169 $$\hat{S}_{i,BY,a'} = \frac{\hat{N}_{i,BY,a'}}{R_{i,BY}} \tag{1}$$

170 where $\hat{N}_{i,BY,a}$ is the estimated cohort size of population i, age a' $(a' = 2$ and 3 for subyearling and

171 yearling releases, respectively), and $R_{i,BY}$ is the number of fish released from population i, brood

172 year BY. Cohort sizes were computed using virtual population analysis (Coronado & Hilborn,

173 1998) by reconstructing specific cohorts recursively from the oldest age (age-5 for subyearling

174 releases and age-6 for yearling releases) to the youngest age (i.e., a') based on the estimated

175 numbers of CWT fish recovered from population $i,$ brood year $BY,$ at age a in pre-terminal (i.e.,

176 ocean) fisheries ($\hat{P}_{i,BY,a}$), terminal (i.e., freshwater) fisheries ($\hat{T}_{i,BY,a}$), and escapement ($\hat{E}_{i,BY,a}$):

177 $$\hat{N}_{i,BY,a} = \frac{\hat{P}_{i,BY,a} + \hat{T}_{i,BY,a} + \hat{E}_{i,BY,a} + \hat{N}_{i,BY,a+1}}{1 - M_a} \tag{2}$$

178 where M_a is the natural mortality occurring on each age prior to fishing mortality, assumed to be

179 40% for age-2, 30% for age-3, 20% for age-4, and 10% for age-5 and older Chinook salmon

180 (PSC, 2015; Sharma et al., 2013).

182   We used multiple analytical methods to examine the spatial and temporal coherence in

183 salmon smolt survival patterns both with and without prior assumptions of survival pattern

184 groupings according to geography, life history type, and release strategy. Because the focus of

185 this study was to determine the degree of similarity among trends rather than absolute

186 magnitudes, survival time series were logit-transformed and centered to a mean of 0 prior to

187 model fitting.

188   To examine the relationship between geographic proximity and correlation in survival

189 between Chinook salmon populations, we fit an exponential decay model of the form:

190    $\rho_d = \rho_0 e^{-d/v}$ (3)

191 where ρ_d is the Pearson correlation coefficient between smolt survival for each pair of

192 populations and d is the pairwise distance between each pair of populations at the point of marine

193 entry. The parameter v is the e-folding scale, or distance at which correlations are expected to

194 decrease by 37% (e^{-1}), and ρ_0 is the expected correlation for populations with $d = 0$. The e-

195 folding scale, although an arbitrary measure, has been used by other researchers, and thus

196 provides a direct comparison of the scale of spatial coherence among species and studies (Kilduff

197 et al., 2014; Pyper et al., 2002; Zimmerman et al., 2015). Distances between population pairs

198 were measured in a geographic information system (GIS) as the shortest distance within

199 saltwater between points of marine entry. Model parameters were estimated for Salish Sea and

200 non-Salish Sea population pairs separately using non-linear least squares, with pairwise

201 observations weighted per the number of years of available survival data. Only pairwise

202 correlations between populations with a 15-year minimum temporal overlap in survival time

203 series were included.

204   To further examine spatial coherence in survival patterns, we conducted a cluster analysis

205 based on the estimated Euclidean distance between annual estimates of population specific smolt

206 survival using Ward's hierarchical clustering algorithm (Legendre & Legendre, 2012). We used

207 the R package *pvclust* (Suzuki & Shimodaira, 2011) to provide the approximately unbiased

208 support for each node in the dendrogram, expressed as the proportion of bootstrapped

209 dendrograms (N = 1000) containing each node. Nodes with approximately unbiased P- values

210 greater than 0.95 were considered strongly supported.

211   We evaluated ten potential survival groupings among the Chinook salmon populations

212   included in our study based on geographic location (e.g., Salish Sea versus outside the Salish

213   Sea), hatchery release strategy (subyearling versus yearling), and run timing (spring versus

214   summer-fall) by fitting the general form of the MARSS model that allows for evaluating specific

215   informed hypotheses about the predominant spatial structure governing variability in survival.

216   Here, the vector of observed marine survival at time t ($\mathbf{y}_t$) is modeled such that

217    $$\mathbf{y}_t = \mathbf{Z}\mathbf{x}_t + \mathbf{v}_t \text{ where } \mathbf{v}_t \sim \mathrm{MVN}(\mathbf{0}, \mathbf{R}),\qquad\qquad(4)$$

218   where $\mathbf{Z}$ is an $n \times m$ matrix containing 1s and 0s to indicate whether or not a particular time

219   series is an observation of a latent trend ($\mathbf{x}_t$) and $\mathbf{v}_t$ is a vector of observation errors distributed as

220   a multivariate normal with mean $\mathbf{0}$ and a diagonal, unequal variance-covariance matrix $\mathbf{R}$ (i.e.,

221   each time series is distributed independently, but not identically). Hypotheses regarding spatial

222   groupings were evaluated by changing the elements in $\mathbf{Z}$ (0 or 1), with the columns representing

223   groupings and the rows representing populations.

224   The latent trends are assumed to follow an autoregressive process, such that

225    $$\mathbf{x}_t = \mathbf{B}\mathbf{x}_{t-1} + \mathbf{C}\mathbf{c}_t + \mathbf{w}_t \text{ where } \mathbf{w}_t \sim \mathrm{MVN}(\mathbf{0}, \mathbf{Q}),\qquad\qquad(5)$$

226   where $\mathbf{x}_t$ is a vector containing the values of the m latent smolt survival trends at time t, $\mathbf{B}$ is a

227   matrix wherein the values along the diagonal reflect the degree of mean reversion (i.e., how fast

228   the state reverts to the mean following some perturbation), $\mathbf{C}$ contains the estimated effects of

229   user specified covariates at time t ($\mathbf{c}_t$) described in more detail below, and $\mathbf{Q}$ is the variance-

230   covariance matrix of the process errors. $\mathbf{Q}$ was specified with different values on the diagonal

231   and 0's on the off diagonals to model the assumption of independent process errors and different

232   variances for each subpopulation or group being tested. When testing a priori grouping

233   hypotheses, we initially did not include any covariates, thereby setting matrix $\mathbf{C}$ to 0, which

234   removed the term from the equation.

235   To further evaluate regional survival trends, we implemented dynamic factor analysis

236   which is an alternative form of the MARSS model (Zuur et al., 2003). DFA is a dimension

237   reduction technique similar to principal component analysis (PCA), but it is designed specifically

238   for time series data. The general idea is to model n time series as a function of m latent

239   (unobserved) temporal trends, where $m << n$. Thus, instead of the vector of observed marine

240   survival at time t ($\mathbf{y}_t$) from equation 4 being a function of a constrained form of $\mathbf{Z}$, specific to a

241   grouping hypothesis, it is modeled as a linear combination of latent trends ($\mathbf{x}_t$) that are

242   represented by an unconstrained form of **Z**. This form of MARSS also assumes that the latent

243   trends in survival follow a random walk process, thereby modifying equation (5) above by

244   setting both the **B** matrix and variance-covariance matrix of the process errors (**Q**) equal to the

245   identity matrix (a diagonal matrix with 1s on the diagonal). Based on the predominant groupings

246   in survival identified in the prior MARSS analysis (see results for details), we fit separate models

247   to survival time series of populations originating from 4 geographic areas including Northern

248   (Alaska and Northern B.C.), Southern (Coastal and Strait of Juan De Fuca), and the two sub-

249   basins within the Salish Sea including Strait of Georgia, and Puget Sound. To test whether Salish

250   Sea populations may respond differently to continental scale environmental forcing than their

251   coastal counterparts, we included as a covariate to the model the annual seasonal average North

252   Pacific Gyre Oscillation (NPGO), a large-scale ocean circulation pattern that has recently been

253   linked to annual variability in survival of west coast Chinook and coho salmon populations

254   (Kilduff et al., 2015). We evaluated the data support for a maximum of 2 trends, both with and

255   without annual NPGO included as a covariate, resulting in a total of 4 candidate models

256   evaluated for each region.

257   Data support for all MARSS models was evaluated using the Akaike Information

258   Criterion corrected for finite sample sizes (AICc). In each case, the model with the lowest AICc

259   (ΔAICc = 0) was selected as the best explanatory model although models with a ΔAICc less than

260   2 were considered to be similarly competitive explanatory models (Burnham & Anderson, 2004).

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267   **Results**

268   Salish Sea Chinook salmon populations exhibited higher inter-population variability in

269   smolt survival (coefficient of variation across entire, untransformed dataset = 1.45) than non-

270   Salish Sea populations (CV = 1.21). Overall, Salish Sea populations exhibited weaker spatial

271   coherence in survival than coastal populations. Specifically, we observed a greater rate of decline

272   and a reduction in pairwise correlation in survival across increasing distances for Salish Sea

273 relative to coastal populations (Fig. 2, Table 3). Closer inspection revealed a higher frequency of

274 relatively strong correlations (r > 0.5) among Southern Coastal populations relative to among

275 Salish Sea populations (Fig. 2E, F).

276 Cluster analysis results provided some evidence for regional scale differences in survival

277 between Salish Sea and non-Salish Sea populations, but exceptions to the general pattern

278 confirmed high variability, particularly for Strait of Georgia populations. Two basal clusters

279 were identified, one consisting of predominantly Salish Sea populations (hereafter "Salish Sea

280 cluster"), and the other consisting of predominantly coastal populations (hereafter "coastal

281 cluster"). Each cluster contained populations from multiple geographic regions, and populations

282 from a single geographic region were distributed amongst multiple clusters (Fig. 3). Five Strait

283 of Georgia populations were grouped together in the Salish Sea cluster, and four Strait of

284 Georgia populations were widely dispersed throughout the coastal cluster. All but one Puget

285 Sound population was confined within the Salish Sea cluster. Of the fifteen Strait of Juan de

286 Fuca and Southern Coastal populations, and the five Northern Coastal populations, all but three

287 populations (all Southern Coastal) grouped with the coastal cluster. No association between

288 release strategy and survival trend was observed as yearling populations were broadly distributed

289 amongst several different clusters rather than grouped together.

290 Direct testing of *a priori* grouping hypotheses produced a best explanatory model based

291 on geographic regions (Table 4, Fig. 4). Groupings based on release strategy or run timing were

292 poorly supported. The best model supported three or four regional groupings in survival with

293 Strait of Georgia populations grouping with Southern Coastal and Strait of Juan de Fuca in the

294 three group model, and grouping separately in the four group model. For the four group model,

295 the following geographic groupings were identified including Northern Coastal (n = 5), Southern

296 Coastal + Juan de Fuca (n = 15), Strait of Georgia (n = 9), and Puget Sound (n = 7). Regionally-

297 grouped models were more strongly supported than models representing a geographically-

298 invariant (i.e., single grouping) hypothesis (Table 4).

299 The four regions identified by the MARSS models shared a general declining trend from

300 1980 to the early 1990s (Figs 4, S1). This trend was most pronounced in the Strait of Georgia

301 and least pronounced in Puget Sound, where it appeared to be caused by a few low survival years

302 during ocean entry years 1988-1990 (Fig 4). Following the early 1990s, populations in the

303 Southern Coastal + Juan de Fuca grouping exhibited more cyclical variability and increased

304 synchrony in survival. By contrast, populations in the Northern Coastal grouping exhibited a
305 largely flat trend from the early 1990s to present; Puget Sound and Strait of Georgia populations
306 gradually rebounded from the low survival in the early 1990s (Figure 4). In terms of the raw
307 untransformed estimates, Puget Sound survival remained consistently low across the entire time
308 series (rarely exceeding 5%), whereas some populations within each of the other four regions
309 experienced periods of higher survival (Fig S1).

310 The prevalence of regional- and basin-scale asynchrony in Chinook salmon smolt
311 survival was further supported by DFA. A single common trend was identified for the Northern
312 Coastal, Southern Coastal, and Puget Sound areas, and two were identified for the Strait of
313 Georgia (Fig. 5, Table S1). The DFA trends for each region roughly matched the four survival
314 trends estimated from these same regions produced by the MARSS models (Strait of Georgia:
315 trend 1 only). Most populations exhibited positive loadings on each of the identified trends,
316 indicating synchrony in the survival dynamics within each grouping, although two of the five
317 populations within Northern Coastal Grouping and two of the seven populations within the Puget
318 Sound grouping showed negative loadings. Of the four geographic groupings, only the top model
319 for the Southern coastal grouping retained annual average NPGO as a driver of survival that
320 accounted for additional unexplained variability (Table S1). The survival rates of populations
321 within the Southern Coastal grouping were positively correlated with the annual NPGO index
322 (Fig. S2).

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343   **Discussion**

344   We used multiple analytical approaches to investigate spatial and temporal coherence in

345   smolt survival of 36 Chinook salmon populations. Each approach provided evidence for greater

346   spatial coherence in smolt survival among populations at the region/basin scale than at the

347   continental scale. Importantly, the degree of spatial coherence was substantially weaker for

348   Salish Sea populations compared to non-Salish Sea populations. This effect was due to the high

349   degree of inter-population variability in survival observed among Salish Sea Chinook salmon

350   (Figs 2 and 3). MARSS models testing different hypotheses on the predominant explanatory

351   scale of variability in smolt survival provided evidence for spatial coherence at the regional/basin

352   scale (Table 4, Fig. 4). Regional differences in shared trends identified from DFA models

353   suggest that coherence in annual survival rates is lower among regions. In general, estimated

354   trends show that survival of Chinook salmon declined from 1980 through the early 1990's and

355   increased moderately though 2008 (Figs 4 and 5). For the duration of this period, only in a single

356   year (1987) did average Puget Sound survival approach 5%, whereas populations in the other

357   three geographic areas frequently approached or exceeded 5 % (Fig S1). Furthermore, we found

358   regional differences in the effect of the NPGO index on annual survival rates, with strong

359   support for a positive association between the NPGO index and the survival dynamics of

360   Southern Coastal populations only, suggesting that local factors may be more important at

361   regulating survival of populations within the Salish Sea and Northern areas (Table S1, Fig S2).

362   Although we sought to identify the overarching spatial scale across which Chinook salmon

363   populations exhibit covariation in survival, our analysis provided evidence that sub-basin, basin,

364   and regional scales must be considered simultaneously; Kilduff et al. (2015) concluded that

365   continental scale processes also influence survival.

366   Research evaluating spatial and temporal scales of survival covariation in other salmon
367 species provides informative comparisons to our results. In general, our analysis of Chinook
368 salmon provided considerably less evidence for fine-scale spatial coherence in smolt survival
369 than a parallel investigation of Salish Sea coho salmon reporting stronger geographic association
370 in survival (Zimmerman et al. 2015). Specifically, Zimmerman et al. (2015) reported a much
371 higher correlation among proximate populations in the distance-decay model ($\rho_0 = 0.84$ across
372 entire time series) than our analysis of Chinook salmon (Salish Sea = 0.28, Coastal = 0.40). In
373 contrast, Pyper et al. (2002) identified a degree of synchrony among individual chum salmon
374 populations ($\rho_0 = 0.44$) similar to what we estimated for Chinook salmon.

375   Differences among species may be due in part to differences in the degree of life history
376 diversity exhibited by each species (Quinn, 2011). Coho salmon primarily enter the marine
377 environment at age-1 in this region, and mature predominantly at age three after spending only
378 18 months in the ocean. In contrast, Chinook and Chum salmon enter the marine environment at
379 age-0 (excepting the few yearling Chinook salmon stocks we analyzed), and exhibit multiple
380 ages at maturity and variable ocean rearing lengths. Furthermore, coho salmon spend less time
381 rearing in estuarine or nearshore environments compared to subyearling Chinook and chum
382 salmon. Perhaps the younger age, and therefore smaller size, at which Chinook and chum salmon
383 enter marine waters, combined with their greater use of nearshore and estuarine habitats, subject
384 them to a greater degree of local influence on smolt survival compared to coho salmon.

385   In our study, temporal covariation in early ocean survival for Chinook salmon was much
386 more strongly influenced by geographic region or basin than by release strategy or run timing.
387 Although uncertainty about the total number of geographic groupings remains, a geographically-
388 invariant survival trend was poorly supported compared to models tested with region and basin
389 scale groupings, suggesting that Salish Sea populations respond to basin-scale environmental
390 variability. Several different hypotheses could explain this finding. Notably, many Chinook
391 salmon populations reside within 100 – 200 km of their source river systems until their second
392 year at sea (Orsi & Jaenicke, 1996; Trudel et al., 2009; Tucker et al., 2011; Tucker et al., 2012),
393 so common rearing habitat may persist for a year or more. Therefore, populations from the same
394 basin likely share common rearing habitat within the first few months of marine entry and may
395 be affected by more localized environmental factors (Ohlberger et al., 2016; Hertz et al., 2016b).

396 Regional specificity in foraging ecology of juvenile Chinook salmon support this hypothesis
397 (Hertz et al., 2015).

398   Our results suggest that population scale processes are likely more pronounced for Salish
399 Sea origin populations compared to coastal populations. Although we did not directly evaluate
400 the influence of more localized environmental drivers in our study, only survival rates for
401 Southern Coastal populations (and not Salish Sea populations) were linked to the continental-
402 scale NPGO. Interestingly, Kilduff et al. (2015) identified a strong positive correlation between
403 the NPGO and survival of hatchery Chinook salmon populations from the eastern Pacific Rim
404 from central California to southeast Alaska, including Salish Sea populations. One possible
405 explanation for this discrepancy is that Kilduff et al. (2015) utilized regional average annual
406 survival rates for their analyses whereas we included survival rates for individual populations.
407 Although region- and basin-scale marine conditions such as sea surface temperature can be
408 driven by larger climatic processes occurring at the scale of the North Pacific Ocean (Moore et
409 al., 2008a), which in turn can affect the survival rates of Chinook salmon (Hertz et al.,
410 2016a; Sharma et al., 2013), their effects may be dampened by localized environmental drivers
411 within the Salish Sea.

412   We speculate that the synergistic effects of habitat loss (Good et al., 2005), long term
413 increases in predator abundance (Chasco et al., 2017), and poor water quality (Meador, 2013)
414 contributed to the lack of covariation in survival among Salish Sea Chinook salmon populations.
415 Magnusson and Hilborn (2003) observed higher early marine survival of coastal Oregon
416 hatchery Chinook salmon in more pristine estuaries. Due to greater human population density
417 and patterns in land use (e.g. agriculture and nearshore armoring), the quantity and quality of
418 Salish Sea estuarine habitats and their marine subsidies (material recruitment, production of
419 nearshore prey) are likely more variable than coastal systems outside the Salish Sea, which may
420 contribute to higher inter-population variability in survival (see Fig. 2). For example, within
421 Puget Sound, the estuary of the Green/Duwamish River Basin is wholly within the urbanized
422 boundary of Seattle while the estuary of the Skagit River, although modified from its historic
423 condition, is considerably more intact (NMFS, 2006). Furthermore, pelagic ecosystem changes
424 within Puget Sound have been associated with high levels of human development pressures not
425 present in many coastal systems included in our study (Greene et al., 2015).

426   In the Salish Sea, outmigrant subyearling Chinook smolts encountering poor habitat
427 conditions may move offshore prior to achieving the body size or growth trajectory that
428 maximizes survival potential. Duffy and Beauchamp (2011) demonstrated that the body size of
429 juvenile Chinook salmon captured offshore in Puget Sound during July was a strong predictor of
430 total marine survival, emphasizing the importance of early marine growth. Fish experiencing
431 poor growth conditions in the estuary or nearshore may become more vulnerable to predation
432 because of increased time and energy spent foraging. Abundance of harbor seals within Puget
433 Sound increased substantially in recent decades, resulting in a corresponding increase in total
434 annual consumption of Chinook salmon smolts, from 1.0 million in 1970 to 8.5 million in 2015
435 (Chasco et al., 2017). Due to variation in the quality and quantity of estuarine habitat as well as
436 patchy predator distributions, the effects of seal predation on long term survival may not be
437 uniform throughout the Salish Sea, further contributing to asynchrony in survival between
438 geographically proximate populations within the Salish Sea.

439   Migratory pathways and residency times influence early marine survival patterns (Furey
440 et al., 2015; Melnychuk et al., 2010). Melynchuk et al. (2010) described significant variation
441 among populations in early marine migration patterns, so any differences in migratory behavior
442 between coastal and Salish Sea populations might be a source for regional-scale survival
443 variation. Notably, of the 14 southern coastal Chinook salmon populations included in our study,
444 9 populations were from the Columbia River basin (Table 2). Despite having the same point of
445 marine entry, some of these populations exhibited differing temporal patterns of survival (Fig. 3),
446 suggesting that additional factors may affect overall survival of individual populations such as
447 in-river survival or variation in ocean migratory pathways (see Jorgensen et al., 2016).

448   Other factors we did not address in our analyses may also impact smolt survival. For
449 example, genetic factors may influence performance of salmon populations (Unwin et al.,
450 2003; Braun et al., 2016). Unfortunately, our study and similar studies (Kilduff et al.,
451 2014; Kilduff et al., 2015; Sharma et al., 2013) were unable to effectively account for the effects
452 of hatchery breeding, rearing, and release practices, which are known to influence smolt survival
453 (Satterthwaite et al., 2014). Furthermore, significant reductions in domestic fisheries targeting
454 both Puget Sound and Strait of Georgia populations throughout the same time period in our
455 analysis may have affected the accuracy of smolt survival estimates of these populations.
456 Specifically, in cases where the catch component of CWT recoveries has been significantly

reduced, estimates of population specific smolt survival relies on large expansions of adult escapement from a small sub-sample of CWT recoveries. This issue is most pronounced in low abundance populations. For Puget Sound populations, high observation errors associated with the coded wire tag derived survival estimates may have contributed to our inability to detect any signal of covariation with other populations throughout the Salish Sea. Of the four geographic regions, survival rates for Puget Sound populations contained the highest average observation error estimated by the MARSS model (0.90 versus 0.76 for South coastal + JDF, 0.65 for SOG, and 0.39 for Northern populations).

The high degree of inter-population variability in smolt survival of Chinook salmon, particularly among Salish Sea populations, presents challenges to fisheries managers. Harvest regulations in mixed-stock fisheries aim to minimize impacts on weaker populations, while maintaining harvestable opportunity targeting more robust populations. Salish Sea populations make far-reaching northward ocean migrations, and are vulnerable in mixed-stock commercial net, troll, and sport fisheries occurring from the West Coast of Vancouver Island to Southeast Alaska (PSC, 2015; Weitkamp, 2010). This underscores the importance of developing a cohesive monitoring framework that identifies physical and biological indicators of survival acting across multiple spatial and temporal scales relevant to the early rearing and marine life history of Chinook salmon. Such information will help inform robust management strategies aimed at protecting weak or threatened populations (e.g., Schindler & Hilborn, 2015). If managers focus on physical environmental or biological factors that affect survival at a single spatial scale, they will likely ignore variability caused by localized factors (Ohlberger et al., 2016). This would result in inaccurate abundance forecasts, thereby increasing the risk of either overexploitation of a population, or foregone opportunity in specific fisheries.

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494 **Supporting Information**

495 **Table S1.** Model selection results for the regional DFA models fit with a maximum of 2 trends

496 and with and without average annual NPGO as a covariate.

497 **Fig. S1.** Untransformed estimates of smolt survival aggregated by each region included in the

498 study.

499 **Fig. S2.** Maximum likelihood estimates bounded by 95% confidence intervals for the effect of

500 annual average NPGO on survival of populations originating from the southern coastal region.

501 **Fig. S3.** Fitted values obtained by the regional dynamic factor models fit separately to each

502 geographic region including Northern Coastal (SEAK and NBC), Southern Coastal (WA, OR,

503 and WCVI) and Strait of Juan de Fuca (JDF), Strait of Georgia (SOG), and Puget Sound (PS)

504 population.

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517 **Acknowledgements**

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693

694 **Tables**

695 **Table 1.** Description of spatial scale terminology used to describe geographic coherence in
696 Chinook salmon smolt survival.

Scale	Description
Continental	Entire west coast of North America
Region	Broad regions of western North America: Northern Coastal, Salish Sea, Southern Coastal
Basin	Basins within the Salish Sea: Puget Sound, Strait of Georgia, and Strait of Juan de Fuca
	States or provinces within the northern region: Southeast Alaska, British Columbia
	Southern region: Columbia River or coastal
Sub-basin	Areas within Puget Sound (Whidbey, Central, South, Hood Canal) and the Strait of Georgia (Northern, Central, Southern) defined by shared oceanographic attributes
Population	Individual populations in the analysis

697

698 **Table 2.** List of all Chinook salmon populations included in the study. A time series of smolt survival was generated using coded-wire

699 tag recovery data for each population, with a minimum time series length of 20 years. Populations are divided by region (SS: Salish

700 Sea, Northern, Southern) and basin (SOG: Strait of Georgia, PS: Puget Sound, JDF: Strait of Juan de Fuca, SEAK: Southeast Alaska,

701 NBC: Northern British Columbia, ColR: Columbia River). Population numbers align with map in Fig 1. Time series are reported in

702 terms of ocean entry year (OEY) with the total number of years represented by each time series in parentheses. Run timing (spring,

703 summer-fall) and release strategy (Y: yearling, SY: subyearling) are noted.

704

Region/Basin	Sub-basin	Population	OEY	Run timing	Release strategy
SS/SOG	Northern SOG	1. Quinsam Fall (QUI)	1975-2008 (34)	summer/fall	SY
SS/ SOG	Northern SOG	2. Puntledge Summer (PPS)	1976-2009 (33)	summer/fall	SY
SS/ SOG	Central SOG	3. Big Qualicum Fall (BQR)	1974-2009 (36)	summer/fall	SY
SS/ SOG	Central SOG	4. Cowichan Fall (COW)	1986-2009 (22)	summer/fall	SY
SS/ SOG	Central SOG (Fraser River)	5. Harrison Fall (HAR)	1982-2009 (27)	summer/fall	SY
SS/ SOG	Central SOG (Fraser River)	6. Chilliwack Fall (Harrison Stock) (CHI)	1982-2009 (28)	summer/fall	SY
SS/ SOG	Central SOG (Fraser River)	7. Nicola Spring (NIC)	1987-2010 (24)	spring	Y
SS/ SOG	Central SOG (Fraser River)	8. Lower Shuswap Summer (SHU)	1985-2009 (25)	summer/fall	SY
SS/ SOG	Southern SOG	9. Samish Fall Fingerling (SAM)	1975-2008 (26)	summer/fall	SY
SS/PS	Whidbey Basin	10. Skagit Spring Yearling (SKS)	1983-2009 (23)	spring	Y
SS/PS	Whidbey Basin	11. Stillaguamish Summer Fingerling (STL)	1981-2008 (23)	summer/fall	SY

SS/PS	Central Sound	12. Grovers Creek Fall Fingerling (GRO)	1982-2008 (27)	summer/fall	SY
SS/PS	Central Sound	13. Green River Fall Fingerling (GRN)	1972-2008 (32)	summer/fall	SY
SS/PS	South Sound	14. Nisqually Fall Fingerling (NIS)	1980-2008 (29)	summer/fall	SY
SS/PS	South Sound	15. South Puget Sound Fall Yearling (SPY)	1980-2009 (24)	summer/fall	Y
SS/PS	Hood Canal	16. George Adams Fall Fingerling (GAD)	1973-2008 (30)	summer/fall	SY
SS/JDF		17. Hoko Fall Fingerling (HOK)	1986-2007 (21)	summer/fall	SY
Southern/Coastal		18. Robertson Cr Fall (RBT)	1974-2009 (36)	summer/fall	SY
Southern/Coastal		19. Sooes Fall Fingerling (SOO)	1986-2007 (21)	summer/fall	SY
Southern/Coastal		20. Queets Fall Fingerling (QUE)	1978-2007 (29)	summer/fall	SY
Southern/ColR		21. Columbia Lower River H (LRH)	1977-2008 (32)	summer/fall	SY
Southern/ColR		22. Cowlitz Fall Tule (CWF)	1978-2008 (31)	summer/fall	SY
Southern/ColR		23. Lewis River Wild (LRW)	1978-2008 (28)	summer/fall	SY
Southern/ColR		24. Willamette Spring (WSH)	1977-2008 (32)	spring	Y
Southern/ColR		25. Spring Creek Tule (SPR)	1973-2008 (36)	summer/fall	SY
Southern/ColR		26. Lyons FerryYearling (LYY)	1986-2009 (21)	summer/fall	Y
Southern/ColR		27. Hanford Wild (HAN)	1987-2008 (22)	summer/fall	SY
Southern/ColR		28. Upriver Brights (URB)	1976-2008 (33)	summer/fall	SY
Southern/ColR		29. Columbia Summer (SUM)	1976-2008 (28)	summer/fall	SY
Southern/Coastal		30. Salmon River (SRH)	1977-2007 (30)	summer/fall	SY
Southern/Coastal		31. Elk River (ELK)	1978-2008 (31)	summer/fall	SY
Northern/NBC		32. Atnarko Summer (ATN)	1987-2008 (20)	summer/fall	SY
Northern/NBC		33. Kitsumkalum Summer (KLM)	1980-2008 (28)	summer/fall	SY
Northern/SEAK		34. Unuk Spring (UNU)	1984-2009 (21)	Spring	Y
Northern/SEAK		35. Alaska Central Inside (ACI)	1978-2009 (32)	Spring	Y

| Northern/SEAK | 36. Taku Spring (TAK) | 1977-2009 (24) | Spring | Y |

705 **Table 3.** Parameter estimates from pairwise distance decay model fit to the relationship between

706 Pearson pairwise correlation in survival versus distance for Salish Sea populations and non-

707 Salish Sea origin separately.

708

	v (*e*-folding scale)		ρ_0 (intercept)	
Period/Region	Estimate	95 % CI	Estimate	95% CI
Salish Sea	292 km	151 – 1916 km	0.28	0.16 – 0.41
Coastal	517 km	355 – 783 km	0.4	0.34 – 0.47

709

710 **Table 4.** Model selection results for MARSS models testing for one to five hypothesized

711 groupings (m = number groups) based on common trends of temporal variability in smolt

712 survival among 36 Chinook salmon populations from within and outside the Salish Sea ($t_{min} = 20$

713 years). Models are shown in order of increasing ΔAICc relative to the top ranked model (shown

714 in bold) and cumulative AICc weights.

Model	parameters	groups	ΔAICc	Cumulative AICc Weight
4 groups (SEAK & NBC-SOG-PS- Southern & JDF)	45	4	0.00	0.50
3 groups (SEAK & NBC-Southern & JDF & SOG-PS	43	3	0.12	0.97
3 groups (SEAK & NBC-SOG & PS-Southern & JDF)	43	3	6.53	0.99
4 groups (SEAK & NBC-SOG-PS & JDF-Southern)	45	4	7.79	1.00
2 groups (SEAK & NBC-Southern & JDF & SOG & PS	41	2	16.14	1.00
3 groups (SEAK & NBC-Southern & PS & JDF-SOG)	43	3	23.05	1.00

2 groups (spring-summer/fall)	41	2	26.14	1.00
2 groups (subyearling – yearling)	41	2	29.47	1.00
2 groups (PS & SOG – JDF & Southern & SEAK & NBC)	41	2	32.09	1.00
1 group	39	1	35.25	1.00

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716

Figures

Figure 1. Study area showing the geographic extent of Chinook salmon populations included in analyses with the Salish Sea shown in reference to the spatial extent of the study. Numbers correspond to population information provided in Table 2.

Figure 2. Regional covariation in survival for all 36 hatchery Chinook salmon populations for ocean entry years 1980 – 2008. A: exponential decay models were fit to coastal populations (solid line, open light grey circles), and Salish Sea populations only (dashed line, open dark grey triangles) separately. The *e*-folding scale (*v)* and the associated correlation predicted by each model are represented by the horizontal and vertical line segments. B: boxplots comparing pairwise correlations in smolt survival Salish Sea (dark gray) and non-Salish Sea (light gray) populations across increasing distance between the point of marine entry of each population in 100 km increments up to 400 km. Here the thick line is the median, the boxes are the interquartile range, and the remainder of the data are contained in the whiskers and outlier points. The maximum pairwise distance for Salish Sea populations is approximately 400 km. C: Pearson pairwise correlations for all hatchery Chinook salmon populations organized by region including Strait of Georgia (1- 9), Puget Sound (10 – 16), Strait of Juan de Fuca (17), Southern Coastal (18 – 31), and Northern Coastal (32 – 36). Number labels correspond to population information in Table 2 and geographic location in Figure 1. Survival data were logit-transformed and centered to mean = 0.

Figure 3. Dendrogram of temporal trends in smolt survival of 36 Chinook salmon populations. Survival data were logit-transformed and centered to mean = 0 prior to cluster analysis. On the vertical axis, line height represents the magnitude of difference between pairs of populations. Bootstrap support for each cluster is provided as an approximately unbiased P-value (significance at P ≥ 0.95).

741   **Figure 4.** Fitted smolt survival values (black lines) with 95% confidence intervals (shaded area)

742   estimated by the best-fit MARSS model identifying four distinct groupings with a breakpoint in

743   survival trends among 36 hatchery Chinook salmon populations according to the following

744   geographic groupings: A) Northern Coastal (SEAK/NBC), B) Juan de Fuca & Southern Coastal

745   (WCVI/WA/OR Coast), C) Puget Sound, and D) Strait of Georgia. Solid (subyearling) and

746   dashed (yearling) grey lines are observed normalized survival values.

747   **Figure 5.** Estimated trends and factor loadings for individual DFA models fit to Northern

748   Coastal (n = 5), Southern Coastal – JDF (n = 14), Strait of Georgia (n = 9), and Puget Sound (n =
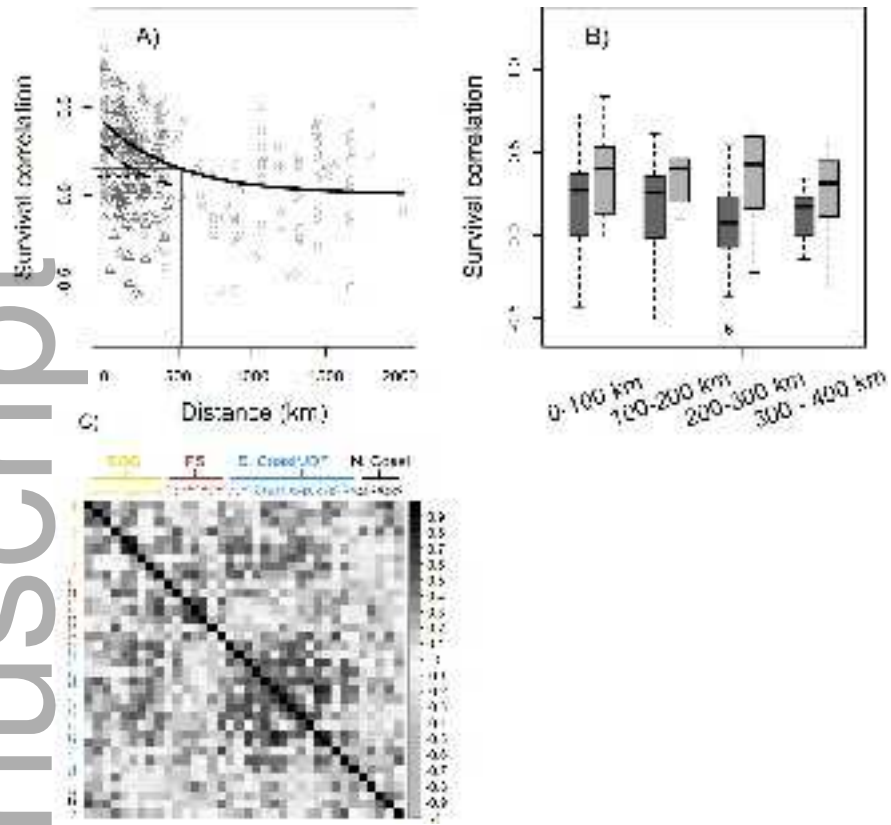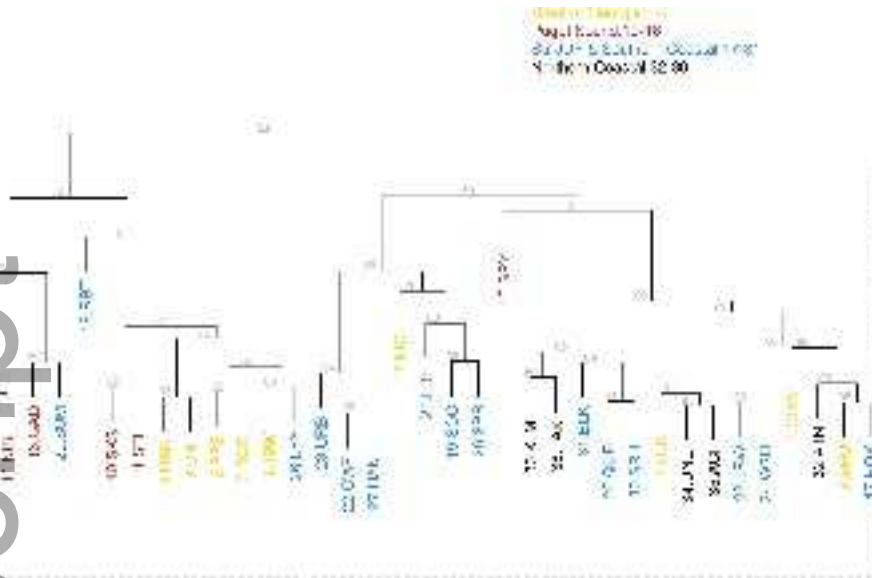
749   5) population groupings.
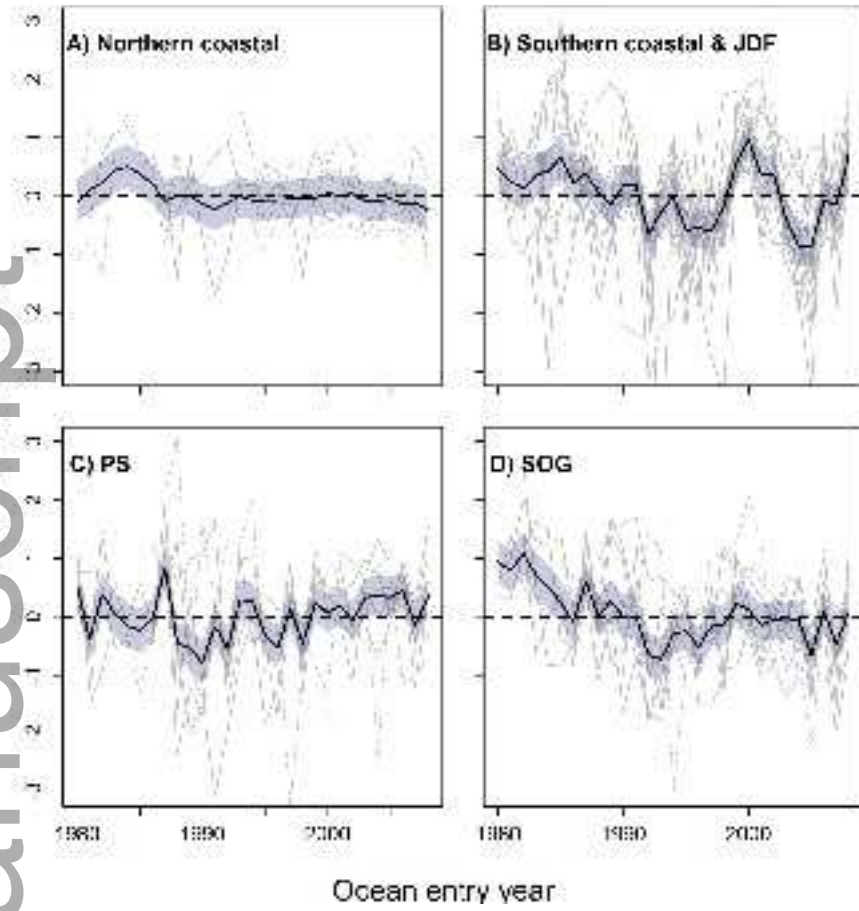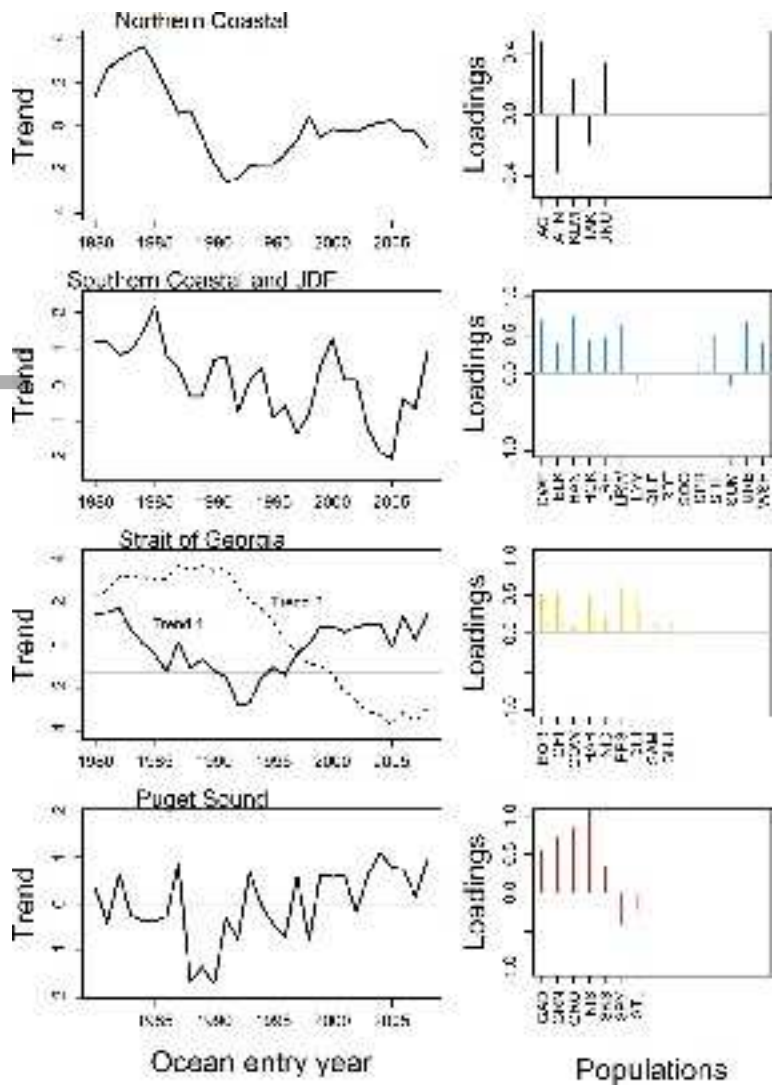
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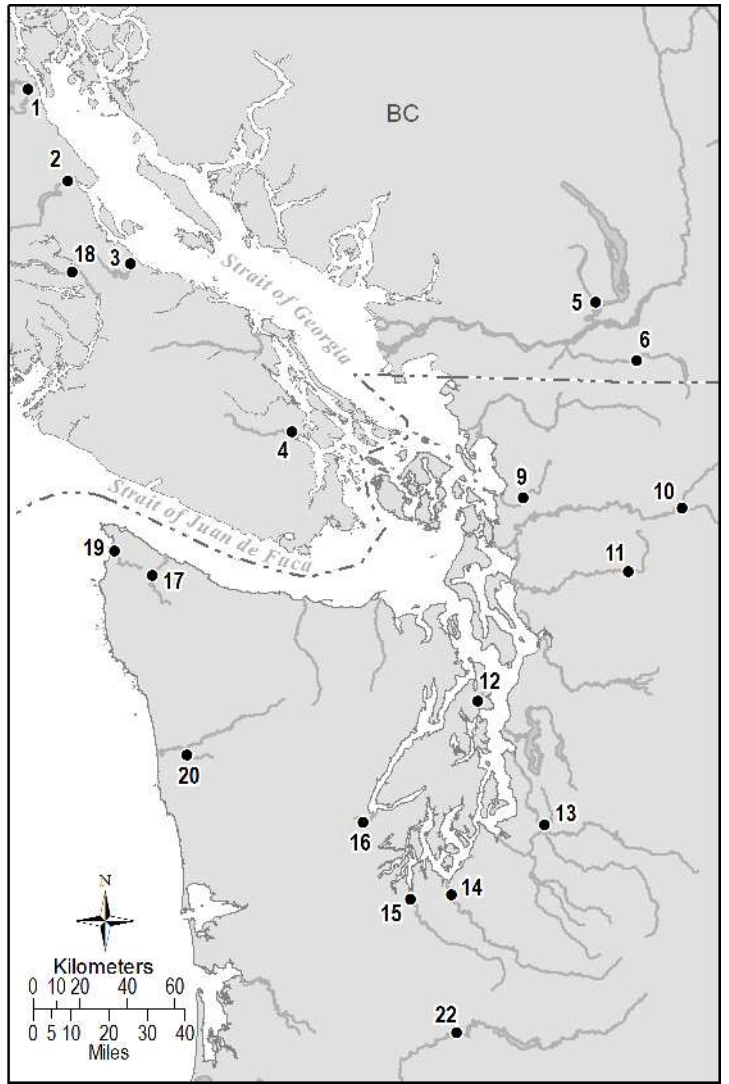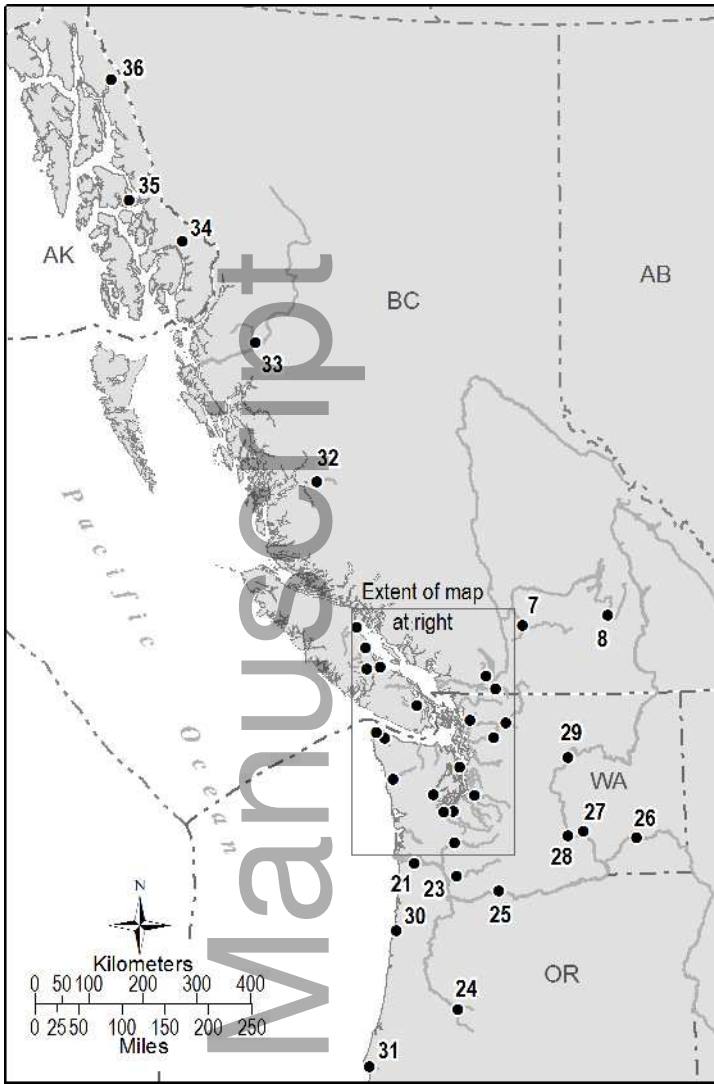
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