

1 **Coherence among Oregon Coast coho salmon populations highlights increasing relative**  
2 **importance of marine conditions for productivity**

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4 RH: Oregon Coast coho salmon productivity

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18  
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35  
36 **Data Sharing:** As of publication, raw data are available from the ODFW Salmon Recovery  
37 Tracker (<http://odfwrecoverytracker.org/>) for the post-1990 time period. The full, quality-  
38 controlled data set is available from the corresponding author upon reasonable request.

39  
40 **Abstract**

41 Anadromous fishes, such as Pacific salmon, spend portions of their life cycle in freshwater and  
42 marine systems, thus rendering them susceptible to a variety of natural and anthropogenic  
43 stressors. These stressors operate at different spatiotemporal scales, whereby freshwater

44 conditions are more likely to impact single populations or sub-populations, while marine  
45 conditions are more likely to act on entire Evolutionarily Significant Units (ESUs). Coherence in  
46 population parameters like survival and productivity can therefore serve as an indicator of  
47 relative influence. The goal of this study was to elucidate scale-dependent shifts in Oregon Coast  
48 coho salmon productivity. We used a multivariate state-space approach to analyze almost sixty  
49 years of stock-recruitment data for the Oregon Coast ESU. Analyses were conducted separately  
50 for time periods prior to and after 1990 to account for improvements in abundance estimation  
51 methods and significant changes in conservation and management strategies. Prior to 1990,  
52 productivity declined for most Oregon Coast populations, especially through the 1980s. From  
53 1990-on, coherence increased and trends tracked closely with the North Pacific Gyre Oscillation  
54 (NPGO). The latter period is associated with reductions in harvest rates and hatchery production  
55 such that the relative influence of the marine environment may have grown more apparent  
56 following the removal of these stressors. Furthermore, the link between productivity and NPGO  
57 is consistent with trends observed for several other Pacific salmon ESUs. If Oregon Coast coho  
58 salmon populations become more synchronous, managers can expect to face new challenges  
59 driven by reductions in the population portfolio effect and increasingly variable marine  
60 conditions due to climate change.

61

62 **Keywords:** climate indices, coho salmon, dynamic factor analysis, multivariate state-space  
63 models, population dynamics, productivity, time series

64 **1. Introduction**

65 Over the past century, aquatic species in freshwater and marine ecosystems have been  
66 increasingly influenced by a multitude of stressors including climate change, overharvesting, and  
67 human encroachment on historical habitat (Johnson and Welch 2009, Brander 2010, Pratchett et  
68 al. 2011, Wilberg et al. 2011, Arthington et al. 2016). Anadromous species, such as Pacific  
69 salmon (*Oncorhynchus* spp.), are likely to experience these stressors more acutely because they  
70 spend large portions of their life cycle in both freshwater and marine habitats (Quinn 2005,  
71 Cunningham et al. 2018, Crozier et al. 2021). As an invaluable ecological, economic, and  
72 cultural resource, managers throughout the Pacific Coast of North America have recognized the  
73 importance of promoting healthy and stable salmon populations through sustainable harvest  
74 quotas, responsibly managed hatcheries, and habitat conservation and restoration actions.  
75 Nevertheless, many Pacific salmon populations have continued to decline despite an  
76 unprecedented level of investment in species and habitat conservation (Peterman and Dorner  
77 2012, Ward et al. 2015, Wilson et al. 2022).

78 Conservation of anadromous species is inherently difficult because stressors operate  
79 across multiple spatial and temporal scales (Crozier et al. 2008, Schindler et al. 2008, Ohlberger  
80 et al. 2016, Crozier et al. 2021). For Pacific salmon, populations are sensitive to watershed-  
81 specific environmental stressors such as water temperature, salinity, stream flow, and  
82 hydrological connectivity during freshwater and early marine rearing (Mueter et al. 2002, Mueter  
83 et al. 2005, Pyper et al. 2005). When populations are more sensitive to these local-scale  
84 environmental drivers, strong spatial patterns emerge whereby survival, productivity, and other  
85 metrics of population health tend to have little spatial autocorrelation. Conversely, when ocean-  
86 scale drivers dominate, they favor high synchrony and high spatial autocorrelation in population  
87 metrics. Thus, the degree of coherence and spatial autocorrelation among populations is  
88 indicative of the scale at which stressors impact their survival and productivity (Ohlberger et al.  
89 2016, Ruff et al. 2017, Dorner et al. 2018). This has implications for management because  
90 conservation and policy efforts tend to operate at local or regional scales (e.g., streams,  
91 watersheds), while climate-mediated shifts in ocean conditions are nearly impossible to manage  
92 (Schindler et al. 2008).

93 Managers and policymakers have enacted numerous conservation strategies to bolster  
94 survival and productivity. In the conterminous United States, more than 30 Pacific salmon stocks

95 (or Evolutionarily Significant Units; ESUs) are listed as threatened or endangered under the U.S.  
96 Endangered Species Act (ESA; 16 U.S.C. §§ 1531–1544), ranging in geographic scope from  
97 Southern California to Puget Sound, Washington. Under ESA-listing, commercial, recreational,  
98 and tribal harvest is limited. To compensate for reductions in wild salmon harvest, some  
99 managers have bolstered hatchery production to support sustainable fisheries, while others have  
100 reduced hatchery operations in hopes of promoting a recovered wild salmon stock (these  
101 strategies are not always used exclusively; Kostow 2009, Flagg 2015). Regardless, the ecological  
102 and genetic risks associated with hatchery programs are widely recognized (Waples 1991,  
103 Nickelson 2003, Myers et al 2004, Buhle et al. 2009).

104 The Oregon Coast coho salmon (*O. kisutch*) is one example of an ESU where hatchery  
105 production was sharply curtailed concurrently with ESA-listing and reductions in maximum  
106 allowable harvest rates (Fig. 1). Peak releases of over 27 million hatchery smolts occurred in  
107 1981. Since the ESU was declared threatened in 1998, smolt production has been further reduced  
108 from roughly 2.1 million to about 260,000 hatchery smolts, and hatchery-origin spawners have  
109 declined accordingly from a maximum of 31,530 individuals in 1986 to a minimum of 662  
110 individuals in 2015 (Falcu and Suring 2018). In addition, hundreds of millions of dollars (USD)  
111 of investments in freshwater habitat restoration were carried out through much of the 1990s and  
112 the beginning of the 21<sup>st</sup> century largely for the benefit of salmon (Nicholas et al. 2005, OWEB  
113 2017). This distinct shift in management strategies for Oregon Coast coho salmon poses a unique  
114 opportunity to evaluate the relative impacts of local-scale conservation actions and ocean-scale  
115 processes driving productivity trends.

116 To date, robust evaluations of scale-dependent factors have been challenging because  
117 changes in Oregon Coast coho salmon conservation and management occurred concurrently with  
118 a recognized regime shift in the North Pacific Ocean. In 1977 and 1989, distinct change points  
119 were observed for ocean indicators such as sea surface temperature and the Pacific Decadal  
120 Oscillation (PDO), with implications for numerous commercial fisheries (Hare and Mantua  
121 2000). PDO is a measure of Pacific climate variability that exhibits periodicity on a scale of 15–  
122 25 and 50–75 years, and has historically been aligned with salmon survival (Mantua and Hare  
123 2002); however, following the regime shift in 1989, the North Pacific Gyre Oscillation (NPGO)  
124 began to display a stronger relationship to salmon survival than PDO (Kilduff et al. 2015, Litzow  
125 et al. 2018). This shift was also accompanied by a general breakdown in the correlation between

126 salmon abundance (i.e., run strength) and traditional ocean indicators. The drivers and  
127 implications of these regime shifts and their influence on salmon population health are a topic of  
128 ongoing research and discussion.

129 In order to disentangle scale-dependent shifts in Oregon Coast coho salmon population  
130 dynamics, we evaluated spatial and temporal trends in population productivity using historical  
131 survey data. We addressed the following questions: 1) How have productivity trends changed  
132 following the implementation of conservation efforts and a concurrent oceanic regime shift in the  
133 mid-1990s? 2) How similar are productivity trends among populations, and has synchrony in  
134 productivity changed through time? 3) Is productivity influenced by freshwater and/or marine  
135 rearing conditions? To answer these questions, we used a multivariate state-space approach to  
136 quantify coherence in productivity through space and time and to relate productivity to several  
137 environmental covariates. Multivariate state-space models are particularly useful for analyzing  
138 ecological time series data due to their ability to partition process and observation error and  
139 handle missing data (Zuur et al. 2003, Dennis et al. 2006, Ward et al. 2010). Results from this  
140 approach will provide important information on how ESA-listed Oregon Coast coho salmon  
141 population dynamics have shifted through time, and how conservation efforts and changing  
142 marine conditions may be influencing population trends.

143

## 144 **2. Methods**

### 145 ***2.1 Population structure***

146 The Oregon Coast coho salmon ESU is comprised of 56 historical populations that are  
147 reproductively and behaviorally distinct from other coho salmon populations in the Pacific  
148 Northwest, USA (Lawson et al. 2007). The ESU's geographical range spans most of the Oregon  
149 Coast and is bounded by the Necanicum River to the north and the Sixes River to the south. For  
150 this analysis, we focused on 21 independent populations (i.e., those populations with a high  
151 likelihood of persisting in isolation from neighboring populations; Chilcote et al. 2005) and  
152 omitted dependent populations (i.e., populations that were most likely to rely on periodic  
153 immigration from other populations to maintain their abundance). Independent populations were  
154 grouped into five biogeographic strata with distinct genetic and geographic structure: North  
155 Coast, Mid-Coast, Lakes, Umpqua River, and Mid-South Coast (Lawson et al. 2007; Fig. 2,  
156 Table 1).

157

## 158 **2.2 Stock-recruitment and productivity data**

159 Oregon Department of Fish and Wildlife (ODFW) has consistently monitored spawning  
160 populations of Oregon Coast coho salmon since the mid-1950s. We used 59 years (1958–2016)  
161 of stock-recruitment time series data to evaluate productivity trends for the entire ESU and for  
162 each biogeographic stratum (Chilcote et al. 2005). We calculated productivity as the natural  
163 logarithm of the number of adult recruits per spawner,  $\log_e(R_{t+3}/S_t)$ , where  $S_t$  is the estimated  
164 total number of natural and hatchery origin fish on the spawning grounds in year  $t$ , and  $R_{t+3}$  is the  
165 number of pre-harvest, natural origin adult recruits returning three years later. Hatchery origin  
166 fish are included in  $S_t$  because adult strays may produce natural progeny, but they are excluded  
167 from  $R_{t+3}$  because they are not the progeny of naturally spawning fish themselves. Nearly all  
168 coho salmon mature and return to spawn as three-year-olds (Pearcy 1992). Precocious returns  
169 (“jacks”) were omitted from the analysis. To facilitate comparisons among populations,  
170 productivity data were standardized ( $z$ -transformed) by subtracting the mean from each value and  
171 dividing by the standard deviation.

172 We analyzed pre-1990 and post-1990 data separately to account for potential  
173 discrepancies in monitoring methodology, management practices, and the reliability of  
174 population estimates. Sampling methods have shifted throughout the previous few decades and  
175 have generally become more reliable through time. Population estimates prior to 1990 were  
176 derived from index site sampling, whereby abundance estimates were based on calibrations of  
177 peak counts from non-random index surveys that tended to favor the reliable presence of fish.  
178 For analytical purposes, these peak counts were calibrated against abundance estimates derived  
179 from randomly selected spawning surveys during a period when the two methods were employed  
180 concurrently (1990–2003). ODFW switched from index site sampling to stratified random  
181 sampling in 1990 and then to generalized random tessellation sampling (a spatially balanced  
182 sampling design) in 1998 (Jacobs and Nickelson 1998, Rupp et al. 2012a, Falcy and Suring  
183 2018). Additionally, as mentioned above, major management shifts occurred in the 1990s. ESA-  
184 listing of Oregon Coast coho in 1998 resulted in an almost 90% reduction in ocean and  
185 freshwater harvest rates, while hatchery production also declined substantially through the 1990s  
186 after peaking in the late-1980s (Fig. 1; Melcher 2005, Falcy and Suring 2018).

187 Model-based estimation of time-varying observation errors can be difficult; however,  
188 conducting separate analyses allowed us to account for these “change points” in methodology  
189 and management practices that were likely to affect observation error structure and productivity  
190 through time. It also allowed us to directly address our first study question regarding shifts in  
191 productivity trends following the implementation of conservation efforts and a concurrent  
192 oceanic regime shift in the mid-1990s. Pre-1990 analyses were not conducted for the Salmon,  
193 Floras, or Sixes populations due to missing data.

194

### 195 ***2.3 Environmental covariates***

196 To examine the relative importance of freshwater and marine rearing conditions for Oregon  
197 Coast coho salmon productivity, we fit models with environmental covariates that were expected  
198 to affect salmon in their first or second year of life (Table 2). Covariates that were expected to  
199 affect coho salmon during freshwater rearing (Year 1) included average summer air temperature  
200 over land (a reliable proxy for aquatic thermal conditions and streamflow in rain-fed systems)  
201 and average winter precipitation. Covariates that were expected to affect coho salmon during  
202 early marine residence (Year 2) included the average annual Pacific Decadal Oscillation (PDO)  
203 and North Pacific Gyre Oscillation (NPGO), both of which have been linked to the survival of  
204 Pacific salmon populations and are correlated with other marine drivers such as sea-surface  
205 temperature, salinity, nutrient availability, and productivity (Di Lorenzo et al. 2008, Kilduff et al.  
206 2015). All environmental variables were  $z$ -transformed prior to analysis to allow comparison of  
207 the magnitude of estimated effects.

208

### 209 ***2.4 Correlations among populations***

210 To evaluate spatial and temporal coherence in productivity, we calculated pairwise Pearson’s  
211 correlation coefficients ( $r$ ) for each independent population of coho salmon. Correlation  
212 coefficients were calculated separately for the pre- and post-1990 time periods. We then  
213 estimated mean and standard deviation correlation within and among strata.

214 To determine whether the degree of covariation decreased with increasing distance (i.e.,  
215 to quantify spatial coherence), we fit an exponential decay function:

216

$$\rho_{\delta} = \rho_0 e^{-\delta/v}$$

217 where  $\rho$  is Pearson's correlation coefficient for each pairwise comparison of productivity  
 218 between independent populations and  $\delta$  is the distance between populations at the point of  
 219 marine entry (Pyper et al. 2002, Kilduff et al. 2014, Zimmerman et al. 2015). The parameter  $\nu$  is  
 220 the  $e$ -folding scale (the distance at which correlation is expected to decrease by  $e^{-1}$  or 37%) and  
 221 the parameter  $\rho_0$  is the intercept (expected correlation at  $\delta = 0$ ). The exponential decay function  
 222 was fit separately for pre- and post-1990 data using non-linear least squares in R (R  
 223 Development Team 2020). Distances among points of marine entry were estimated using  
 224 ArgGIS 10.8.1 software (ESRI, West Redlands, California, USA) as the Euclidean distance  
 225 between two entry points. For both time periods, we compared the fit of the exponential decay  
 226 model to a null model ( $\rho_\delta = m$ , where  $m$  represents the mean correlation among all pairwise  
 227 comparisons) using the Akaike Information Criterion adjusted for small sample sizes (AICc). A  
 228  $\Delta\text{AICc}$  value  $> 2$  indicated modest support for the exponential decay model over the null model  
 229 (Burnham and Anderson 2002).

230

### 231 **2.5 Dynamic factor analysis**

232 To evaluate trends in productivity through time, we used dynamic factor analysis. Dynamic  
 233 factor analysis (DFA) is a dimension reduction technique with state-space time series models that  
 234 aims to explain temporal variation in multiple time series using a linear combination of shared  
 235 unobservable trends (Zuur et al. 2003). The model uses a multivariate, autoregressive state-space  
 236 approach with the following structure:

$$237 \quad \mathbf{y}_t = \mathbf{Z}\mathbf{x}_t + \mathbf{a} + \mathbf{D}\mathbf{d}_t + \mathbf{v}_t$$

$$238 \quad \text{where } \mathbf{v}_t \sim \text{MVN}(0, \mathbf{R})$$

239 It estimates the loadings (matrix  $\mathbf{Z}$ ) on each of the hidden trends and assumes observation error  
 240 ( $\mathbf{v}$ ) is multivariate normally distributed (MVN) with a mean of zero and a variance-covariance  
 241 matrix  $\mathbf{R}$ . When covariates ( $\mathbf{d}_t$ ) are included, the model can estimate the regression coefficients  
 242 for each of the covariate effects (matrix  $\mathbf{D}$ ). Our productivity data were z-scored, so the offset  
 243 value ( $\mathbf{a}$ ) was set to zero.

244 The true but unobserved trends ( $\mathbf{x}_t$ ) are modeled as a random walk with process noise  
 245 ( $\mathbf{w}_t$ ):

$$246 \quad \mathbf{x}_t = \mathbf{x}_{t-1} + \mathbf{w}_t$$

$$247 \quad \text{where } \mathbf{w}_t \sim \text{MVN}(0, \mathbf{I})$$



248 In the process equation, noise is also assumed to be normally distributed with a mean of zero;  
249 however, for identifiability reasons the variance-covariance matrix is fixed as an identity matrix  
250 **I**.

251 We conducted the DFA procedure separately for the pre- and post-1990 time periods.  
252 First, we ran the analysis for the entire Oregon Coast using all 21 populations (coast-wide).  
253 Then, to parse out regionally specific trends, we ran analyses separately for each stratum  
254 (regional). For the coast-wide analysis, we tested models with up to three hidden trends and for  
255 regional analyses we tested models with one or two hidden trends depending on the number of  
256 populations in each stratum ( $H = 1$  for  $N \leq 3$ ). We evaluated models with various observation  
257 error structures: shared variance and no covariance (“diagonal and equal”), different variances  
258 and no covariance (“diagonal and unequal”), or shared variance and covariance (“equal variance  
259 and covariance”). We used the MARSS package in R (Holmes et al. 2012) to estimate parameter  
260 values and states for all model iterations. The best-fit model was selected using AICc, where a  
261  $\Delta AICc$  value  $> 2$  indicated modest support for one model over others (Burnham and Anderson  
262 2002).

263 We evaluated the relationship between environmental covariates (PDO, NPGO,  
264 temperature, precipitation) and predicted productivity trends from the coast-wide and regional  
265 analyses. Covariates can be directly integrated in the DFA via the  $d_t$  term in the model; however,  
266 these covariate effects (**D**) are included in the observation rather than the process model. Our  
267 interest is in the latter, so we also calculated correlation coefficients for the trends derived from  
268 the best-fit DFA models and each environmental covariate, and used a simple, linear model to  
269 evaluate whether trends were significantly correlated ( $P < 0.05$ ) with freshwater and marine  
270 conditions.

271

### 272 **3. Results**

#### 273 **3.1 Correlation among populations**

274 The degree of correlation in coho salmon productivity as measured by Pearson’s correlation  
275 coefficient ( $r$ ) trended positive and non-zero for most pairs and was greater within than among  
276 strata (Fig. 3, Table 3). Overall, the degree of correlation nearly doubled from the pre-1990 to  
277 post-1990 period and increases occurred both within and among strata. Prior to 1990, within-  
278 stratum correlation was strongest ( $r > 0.5$ ) for the North Coast and Umpqua strata and was

279 weakest for the Mid-South Coast stratum. This trend was also true for productivity data collected  
280 in 1990 and afterward. Lower cohesion for the Mid-South Coast stratum was likely driven by the  
281 Sixes River population, whose productivity trends did not appear to coincide with those of other  
282 Oregon Coast coho populations. In terms of among-stratum comparisons, the Lakes and Mid-  
283 South Coast strata appeared to have productivity trends that were most different from other strata  
284 and each-other, and this trend was more consistent during the post-1990 time period.

285         Within-stratum correlation was greater than among-stratum correlation in year-to-year  
286 productivity prior to 1990, yet the degree of correlation among population productivity trends did  
287 not decrease with increasing distance (Fig. 4). The AICc value for the null model was lower than  
288 the AICc value for the exponential decay model ( $\Delta\text{AICc} = 2.02$ ) and the parameters for the  
289 exponential decay model converged in such a way that the  $e$ -folding scale ( $v = 1,501$  km) was  
290 much larger than the extent of the Oregon Coast. From 1990-on, spatial autocorrelation was  
291 detectable but was still weak ( $v = 1,323$  km). There was marginal evidence that the fit of the  
292 exponential decay function was better than the fit of the null model ( $\Delta\text{AICc} = 1.82$ ).

293

### 294 ***3.2 Dynamic factor analysis***

#### 295 *3.2.1 Coast-wide*

296 The coast-wide DFA using the pre- and post-1990 data sets identified several different Oregon  
297 Coast coho salmon productivity trends and indicated greater coherence in population  
298 productivity from 1990-on. Prior to 1990, the best-fit model estimated three trends with  
299 independent and unique observation variances for each population (Table S1). Trends 1 and 2  
300 were characterized by stochastic, year-to-year fluctuations in productivity between 1958 and  
301 1990, with a slight dip for Trend 2 in the mid-1980s (Fig. 5). Populations in the Mid-Coast  
302 stratum had the greatest loadings on Trend 2, while populations in the Umpqua River had strong  
303 positive loadings on Trend 1. Trend 3 was characterized by a slight increase in productivity  
304 through the mid-1980s, followed by a very sharp increase; however, loadings on this trend were  
305 widespread and negative, indicating that most Oregon Coast coho salmon populations actually  
306 experienced a productivity crash in the mid-to-late 1980s. The unique error structure implied that  
307 there may have been among-population variation in the accuracy of abundance estimates, which  
308 is consistent with what we know about calibration and estimation methods through the 1990s.  
309 Observation error ( $R$ ) ranged from a low of 0.16 for the North Umpqua population to a high of

310 0.85 for the Tahkenitch Lake population. R was generally low ( $\leq 0.2$ ) for the Middle, North, and  
311 South Umpqua populations and high ( $\geq 0.6$ ) for the Lakes and Mid-South Coast strata, but was  
312 variable among North- and Mid-Coast populations (Table S2).

313 From 1990-on, the best-fit model supported a single observation error ( $R = 0.82$ ) and  
314 shared covariances ( $R = 0.39$ ) and identified a single productivity trend. Despite the change in  
315 survey methodology and expected increase in precision for post-1990 surveys, the observation  
316 error variance for this era was higher than for all but two populations pre-1990 (Table S2). The  
317 estimated trend appeared to be cyclical and increasing with peaks in the late 1990s, mid-2000s,  
318 and mid-2010s. Productivity correlated significantly with NPGO ( $r = 0.59$ ,  $R^2 = 0.33$ ,  $P = 0.002$ ;  
319 Fig. S1), indicating that marine processes have had a notable impact on Oregon Coast coho  
320 productivity since the 1990s (Trends 1–3 from the pre-1990 DFA did not correlate significantly  
321 with NPGO or PDO). Loadings were greatest for populations in the North- and Mid-Coast strata  
322 and negative for the Lakes stratum and Sixes River population (Fig. 5). Drivers other than  
323 marine conditions may have limited the productivity of populations with weak or negative  
324 loadings.

325

### 326 3.2.2 Regional

327 Regional DFAs identified trends that were specific to individual strata. Prior to 1990, among-  
328 stratum trends were highly variable (Fig. 6, Table S3). For instance, the best-fit models for the  
329 North Coast and Lakes strata were characterized by an observation error structure with a single  
330 variance and covariance (North Coast  $R_{\text{var}} = 0.69$ ,  $R_{\text{cov}} = 0.20$ ; Lakes  $R_{\text{var}} = 0.71$ ,  $R_{\text{cov}} = 0.33$ ),  
331 and showed widespread declines in productivity through the 1980s. Loadings were generally  
332 consistent among populations. For the Mid-Coast stratum, the best-fit model included two hidden  
333 trends with independent and unique observation error variances ( $R = 0.02$ – $0.78$ ). Trend 1  
334 demonstrated a gradual increase in productivity, with the greatest loadings from the Siletz and  
335 Alsea populations. Trend 2 showed a gradual decrease in productivity and a very sharp decline  
336 through the mid-1980s, with the greatest loadings from the Yaquina and Siuslaw populations.  
337 For the Umpqua stratum, the best-fit model had two hidden trends with independent and unique  
338 observation error variances ( $R = 0.01$ – $0.88$ ). Trend 1 exhibited a steady-but-slight decline  
339 through the late 1970s with a sharp decline thereafter. Trend 2 showed productivity was  
340 generally steady or increasing, and was the predominant trend for the Middle, North, and South

341 Umpqua populations. The Lower Umpqua population had weak loadings on both trends,  
342 indicating that productivity may have followed a separate trajectory for this population during  
343 the pre-1990 time period. For the Mid-South Coast stratum, data were only available for the  
344 Coos and Coquille populations. The best-fit model had a single observation error variance ( $R =$   
345  $0.87$ ) and demonstrated a declining trend that was similar to those observed for the North Coast  
346 and Lakes strata.

347 From 1990-onward, productivity trends became much more cohesive (Fig. 7, Table S3).  
348 Most predicted trends were similar to what was observed for the coast-wide DFA, with peaks in  
349 the late 1990s, mid-2000s, and mid-2010s. This pattern was exhibited by the North Coast (single  
350 observation error variance,  $R = 0.28$ ), Mid-Coast (Trends 1 and 2; unique observation error  
351 variances,  $R = 0.08$ – $0.67$ ), and Umpqua populations (Trend 1; unique observation error  
352 variances,  $R = 0.03$ – $0.40$ ). The best-fit model for the Mid-South Coast stratum was slightly  
353 distinct in that it showed sharp peaks in productivity in the late-1990s and mid-2000s, with a  
354 single observation error variance and covariance ( $R_{\text{var}} = 0.77$ ,  $R_{\text{cov}} = 0.33$ ). The DFA procedure  
355 for the Mid-Coast stratum identified two best-fit models; one with two trends and unique  
356 observation error variances and one with two trends and a single variance and covariance. From  
357 here on, we report on the output for the model with unique observation error variances, which  
358 had a lower root-mean-square error. Both trends for the Mid-Coast stratum were highly similar,  
359 with divergence in the early 1990s. Loadings on Trend 1 were strongest for the Salmon and  
360 Yaquina populations, while loadings for Trend 2 were strongest for the Siletz and Alsea  
361 populations. The best-fit model for the Umpqua stratum had two trends; however, loadings were  
362 very weak for Trend 2, which demonstrated a sharp increase in productivity after the year 2000.  
363 The Lakes stratum was the only one with a distinct, declining trajectory, and had a single  
364 observation error variance and covariance ( $R_{\text{var}} = 0.87$ ,  $R_{\text{cov}} = 0.53$ ).

365 Including environmental covariates in the DFA as observation error covariates did not  
366 improve model fit for any of the coast-wide or regional analyses (Table S4); however, when  
367 predicted trends were directly correlated with covariates, some strong relationships emerged  
368 (Fig. S2–S6, Table S5). Prior to 1990, productivity for the Lakes, Umpqua (Trend 1), and Mid-  
369 South Coast strata was negatively correlated with PDO, while productivity for the Mid-Coast  
370 stratum was marginally correlated with summer temperature, although this relationship appeared  
371 to be biologically insignificant. From 1990-onward, NPGO emerged as an important

372 environmental driver and exhibited a significantly high degree of overlap with productivity  
373 trends for the North Coast ( $r = 0.53$ ), Mid-Coast (Trend 2;  $r = 0.68$ ), and Mid-South Coast strata  
374 ( $r = 0.57$ ; Fig. 8). PDO was also negatively correlated with productivity for the Mid-Coast  
375 (Trend 2;  $r = -0.46$ ), Umpqua ( $r = -0.44$ ), and Mid-South Coast ( $r = -0.45$ ) strata. Mid-Coast  
376 Trend 2 was positively correlated with winter precipitation ( $r = 0.41$ ). For Lakes populations,  
377 productivity was negatively correlated with summer air temperature ( $r = -0.95$ ), but not with any  
378 of the marine drivers.

379

#### 380 **4. Discussion**

381 We used a quantitative approach to evaluate scale-dependent shifts in productivity for 21  
382 independent populations of Oregon Coast coho salmon. Our analyses supported a clear change  
383 point in the 1990s whereby coast-wide declines in productivity transitioned to a more cyclical  
384 pattern and regional trends became more coherent both within and among biogeographical strata.  
385 There are several possible explanations for this change point and they are not necessarily  
386 mutually exclusive: 1) less reliable survey methods and uncertainty in population-specific  
387 harvest rates and the proportion of hatchery spawners introduced more variability and obscured  
388 potential relationships with environmental drivers, and 2) a mechanistic change point in  
389 productivity occurred sometime in the 1990s following a coast-wide population crash for Oregon  
390 Coast coho salmon and concurrent with conservation efforts and an oceanic regime shift (Hare  
391 and Mantua 2000, Falcay and Suring 2018). Our findings and the existing literature lend support  
392 for the second explanation. Between 1990 and 2010, coho salmon productivity appears to have  
393 tracked closely with marine conditions, especially NPGO, which is an indicator of ocean current  
394 and circulation patterns and is closely linked to phytoplankton concentrations (Di Lorenzo et al.  
395 2008, Kilduff et al. 2015). Increased dependence on marine conditions in the first ocean year of  
396 life (as opposed to freshwater conditions, which can be highly variable among watersheds) and  
397 among-population coherence demonstrate a shift from local- to broad-scale drivers of  
398 productivity (Ohlberger et al. 2016, Ruff et al. 2017, Dorner et al. 2018). Furthermore,  
399 reductions in hatchery production and limited harvest concurrent with ESA-listing appear to have  
400 slowed declines in productivity for the Oregon Coast coho salmon ESU, even if the number of  
401 recruits per spawner has not improved (Falcay and Suring 2018). We provide a more in-depth  
402 discussion of these trends below.

403

#### 404 **4.1 Temporal productivity trends**

405 Prior to 1990, coho salmon productivity was best described by three trends according to the  
406 DFA, and loadings on these trends varied by population. For most populations, loadings were  
407 moderately-to-strongly positive for Trend 2, which indicated that productivity fluctuated until  
408 about 1980, when it began to gradually decline. Trend 3, for which most loadings were weak and  
409 negative, pointed to a gradual decrease in productivity from about 1958 to 1984 and a steep  
410 decrease in productivity through the rest of the 1980s. When considered in tandem, these trends  
411 suggest that the 1980s were a period of starkly declining productivity for the Oregon Coast coho  
412 salmon ESU, especially for populations from the North Coast, Mid-Coast (with the exception of  
413 the Siletz and Alsea), Lakes, and Mid-South Coast strata (Fig. S7). Regional trends corroborated  
414 steep declines in productivity through the 1980s for the North Coast, Lakes, Mid-South Coast,  
415 and some of the Mid-Coast (Trend 2) strata, along with the Lower Umpqua population (Trend 1).  
416 Ocean survival through the 1980s and/or 1990s was poor for many Pacific Northwest salmon  
417 populations, including coho and Chinook salmon (*O. tshawytscha*; Loggerwell et al. 2003, Rupp  
418 et al. 2012b, Sharma et al. 2013, Falcu and Suring 2018), and steelhead trout (*O. mykiss*, which  
419 have continued to exhibit low survival rates; Kendall et al. 2017).

420 From 1990-on, coast-wide productivity followed a single, cyclical trend for most  
421 populations, with distinct peaks occurring in the late-1990s, mid-2000s, and mid-2010s.  
422 Regional trends for the North, Mid-, Umpqua, and Mid-South strata again corroborated coast-  
423 wide trends; however, productivity in the Lakes stratum appeared to continue to decline. Lakes  
424 coho salmon are subject to different stressors and use different life history strategies due to the  
425 region's unique geography. Adult coho salmon spawn in the various tributaries that drain into the  
426 large, shallow lakes while juveniles rear in the tributary streams or in the highly-productive lakes  
427 and surrounding marshes. Historically, optimal rearing and spawning conditions have led to  
428 higher than average juvenile salmon growth rates, relative abundance, and smolt-to-adult  
429 survival (Zhou 2000, Nickelson 2001). As such, Lakes coho salmon were previously considered  
430 to be a benchmark for the Oregon Coast ESU. This stratum continued to have high persistence  
431 and sustainability scores in the most recent ESU status review (NMFS 2022), but recent declines  
432 in productivity have highlighted uncertainty in these populations' long-term resilience. The  
433 southernmost Sixes River population also diverged from post-1990 trends in productivity in that

434 they were generally more stochastic; however, the reasons for this are less clear. Cape Blanco is  
435 used as a geological dividing point between the Oregon Coast ESU and the Southern  
436 Oregon/Northern California Coast (SONCC) ESU, but more analysis is needed to determine  
437 whether the Sixes River population's productivity might track more closely with that of the Elk  
438 River and other SONCC coho salmon populations to the south. If that were the case, it would  
439 suggest this population's evolutionary history, life history characteristics, and/or behavior place  
440 it more in-line with SONCC populations or as its own population unit. Studies have indicated  
441 that the Sixes population is genetically distinct from other Oregon and Washington coho salmon  
442 populations (Ford et al. 2004).

443

#### 444 **4.2 Coherence among populations**

445 Pairwise comparisons of productivity using Pearson's correlation coefficient revealed strong  
446 spatiotemporal trends for Oregon Coast coho salmon (particularly within strata), although there  
447 was limited evidence for a decrease in covariation with increasing distance. Based on previous  
448 studies using similar methods, we expected baseline rates of correlation to be high due to the  
449 narrow spatial scope of our analysis, with some dampening in the decay signal (i.e., *e*-folding  
450 scale). For example, the 350 km maximum distance among Oregon Coast watersheds was  
451 roughly 1/6 of the maximum distance evaluated in Ruff et al. (2017), who analyzed population  
452 coherence in marine survival for Chinook salmon along most of the coast of Oregon,  
453 Washington, and British Columbia. Nevertheless, they did observe a measurable decay with  
454 distance both along the Pacific Coast and within the Salish Sea (*e*-folding scale of 517 and 292  
455 km, respectively compared to our estimates of 1,323–1,501 km). Zimmerman et al. (2015) also  
456 observed relatively low *e*-folding scale values in their analysis of coho salmon **smolt** survival  
457 (129–506 km depending on time period). Even considering differences in life history strategies  
458 among species and the external factors impacting productivity vs. marine survival (Quinn 2005),  
459 we would have expected a lower *e*-folding scale, especially considering that within-stratum  
460 correlation was considerably greater than among-stratum correlation.

461 Pairwise correlation in productivity was consistently higher within-strata than among-  
462 strata, and this was true for both the pre- and post-1990 time periods. The Umpqua River  
463 populations had the greatest within-stratum correlation overall, with several likely  
464 methodological and ecological explanations. Pre-1990 Middle, North, and South Umpqua

465 abundance estimates were all calibrated using counts at Winchester Dam, which explains why  
466 these populations had the greatest loadings on predicted trends while Lower Umpqua loadings  
467 were fairly weak. Ecologically, the four Umpqua populations out-migrate through the same river  
468 mouth and are more likely to experience analogous environmental conditions while doing so.  
469 This lends support to the theory that early marine conditions are critical drivers of salmon  
470 survival (Mortensen et al. 2000, Beamish and Mahnken 2001, Beamish et al. 2004). Within the  
471 Umpqua watershed, topography, climate, and anthropogenic influence are highly variable  
472 because the river flows through two mountain ranges (the Cascades and the Coast Range) and  
473 several urban areas. Based on this, one might expect to see more variability among the Umpqua  
474 populations, yet within-stratum correlation in productivity was high during both the pre- and  
475 post-1990 time periods. Conversely, the Mid-Coast, Mid-South Coast, and Lakes strata had the  
476 lowest degree of within-stratum correlation despite experiencing very similar freshwater  
477 conditions among their respective watersheds. Although the Mid-Coast and Lakes populations  
478 became more coherent with each-other and with other Oregon Coast populations from 1990-on,  
479 within- and among-stratum cohesion for the Mid-South Coast remained fairly low. As mentioned  
480 above, from 1990-on this was driven by the Sixes River population, which had productivity  
481 trends that differed from those of other populations throughout the Oregon Coast.

482         The degree of within- and among-stratum correlation among independent populations of  
483 coho salmon increased between the pre- to post-1990 period for all comparisons, in some cases  
484 more than doubling. Removal of stressors such as harvest and hatchery production likely  
485 decreased spatial variability in the freshwater component of productivity (Falcy and Suring  
486 2018). Indeed, the degree of hatchery production, which has been shown to negatively impact  
487 natural origin coho salmon populations (Nickelson 2003, Buhle et al. 2009), was highly variable  
488 among populations, ranging from 0–99% of spawning adults prior to 1990 (the coast-wide  
489 average was 10–27% depending on year). After roughly the year 2000, hatchery production  
490 declined precipitously to a coast-wide average of 1–16% of spawning adults, and the percentage  
491 of hatchery spawners was consistently lower than 5% for most populations. Harvest, which was a  
492 major source of pre-spawn mortality prior to ESA-listing, was estimated as a single value for the  
493 Oregon Coast. The percentage of adults lost to commercial and recreational harvest ranged from  
494 28–87% prior to 1990 (Lawson 1992). After ESA-listing in 1998, harvest rates were only 1–  
495 20%. Substantial investments in freshwater habitat restoration, conservation, and enhancement



496 were also carried out during this time period; however, direct linkages between restoration and  
497 salmon populations are challenging to detect. The extent and quality of restored habitat may not  
498 yet have reached a threshold where its effects on population parameters are detectable (Roni et  
499 al. 2010), and a considerable amount of variability in habitat conditions still exists among  
500 watersheds. Furthermore, the process and time scale over which complete restoration occurs is  
501 such that improvements in habitat quality may not transpire for decades, or even centuries, after  
502 restoration actions are enacted.

503 It is possible that improved survey methods may have also contributed to increased  
504 synchrony during the post-1990 time period. Surveys transitioned from the use of index sites to a  
505 less biased randomized sampling design in the 1990s (Jacobs and Nickelson 1998, Rupp et al.  
506 2012a, Faley and Suring 2018). Estimation of the proportion of hatchery spawners on the  
507 spawning grounds also improved through time with the widespread utilization of external  
508 markings. As mentioned above, a single annual harvest rate was used for all populations, which  
509 would have masked potential among-population differences in adult mortality, thus creating  
510 more uncertainty in estimated productivity values prior to ESA-listing during high-harvest years.  
511 When considered in tandem, these methodological factors could have certainly affected  
512 productivity estimates. One benefit of using a multivariate state-space approach such as DFA is  
513 that it can account for differences in observation error due to different surveying methods (Zuur  
514 et al. 2003, Dennis et al. 2006, Holmes et al. 2012), whereas correlation coefficients do not  
515 account for such error. In our analysis, differences in observation error pre- and post-1990 were  
516 highly variable among populations and between the coast-wide and regional DFAs. The coast-  
517 wide analysis did not detect a decline in observation error for all but two populations, but when  
518 the analysis was split by biogeographic strata, observation error did decline for many  
519 populations. Increased cohesion among population productivity was still clearly reflected in the  
520 coast-wide DFA, where the number of hidden trends was reduced from 3 to 1 between the pre-  
521 and post-1990 periods.

522

#### 523 ***4.3 Influence of freshwater and marine rearing conditions***

524 We tested the effects of environmental variables related to freshwater (summer temperature,  
525 winter precipitation) and marine conditions (average annual PDO and NPGO) by including them  
526 as covariates in the DFA models and by assessing whether they were correlated with best-fit

527 productivity trends. There was little support for covariates when they were included in the DFA,  
528 but when best-fit trends were directly compared to the standardized covariates, some significant  
529 correlations emerged.

530 Prior to 1990, PDO demonstrated a negative relationship with trends for the Lakes,  
531 Umpqua, and Mid-South Coast strata; however, this relationship was more noticeable prior to  
532 sharp regional declines in productivity through the 1980s. Aforementioned methodological  
533 considerations and declines in productivity may have masked the influence of marine drivers.  
534 From 1990-on, the relationship between productivity and environmental conditions became  
535 much clearer for some strata. Between 1990 and 2010, coast-wide, productivity appeared to be  
536 closely related to the NPGO index. This was also reflected in the regional analyses such that  
537 trends for the North-, Mid-, and Mid-South Coast populations tracked closely with each other  
538 and with NPGO. The NPGO index has been implicated as a driver of marine survival and  
539 productivity for several salmon species (Kilduff et al. 2014, 2015, Ohlberger et al. 2016, Ruff et  
540 al. 2017, Dorner et al. 2018). This is unsurprising as it is closely linked to coastal upwelling,  
541 nutrient cycling, and phytoplankton and krill concentrations (Di Lorenzo et al. 2008, Sydeman et  
542 al. 2013, Kilduff et al. 2014, 2015). From about 2010-on, the correlation between productivity  
543 and NPGO weakened. Variance in NPGO and other ocean indicators (including PDO, which has  
544 been negatively correlated with NPGO in recent years) has increased in recent decades, signaling  
545 that the stability of the marine environment may be declining (Di Lorenzo et al. 2010, Sydeman  
546 et al. 2013, Kilduff et al. 2014). Given the apparent relationship between salmon survival,  
547 productivity, and Pacific climate, more frequent and unpredictable periods of unfavorable ocean  
548 conditions may lead to destabilization of highly synchronous populations such as the Oregon  
549 Coast coho salmon (Kilduff et al. 2015, Mantua 2015).

550 Site specific changes in environmental conditions may have contributed to the Lakes  
551 populations' continual decline in productivity throughout the study period. For instance, in the  
552 1960s, dams were built on Siltcoos and Tahkenitch lakes to control the flow of water for nearby  
553 paper mills, and these dams can act as a partial barrier to upstream migration under some  
554 conditions. Other factors include reduced natural seasonal variation in lake levels, eutrophication  
555 due to increased nutrient inputs, harmful algal blooms, and the presence of nonnative species  
556 such as bluegill (*Leponis macrochirus*) and largemouth bass (*Micropterus salmoides*), which  
557 may consume juvenile salmon (Reimers 1989, Gray 2005, ODFW 2007). Productivity for these

558 populations was negatively correlated with PDO prior to 1990 and with temperature from 1990-  
559 on. It is not out of the question that fish rearing in a shallow lake and its adjacent marshes during  
560 their first year of life would be more sensitive to temperature than those rearing in a lotic  
561 environment with access to thermal refugia. Temperature plays a major role in dictating growth  
562 and metabolism for ectothermic organisms such as fish, and an extended period of exposure to  
563 elevated temperatures can be lethal (Brett 1952, Richter and Kolmes 2005, Beauchamp 2009). In  
564 general, the lakes are not suitable for juvenile coho salmon rearing in the summer due to water  
565 quality and predation risk. Rather, they benefit coho salmon by providing high quality  
566 overwintering habitat (NMFS 2016). The relationship between temperature and productivity in  
567 this stratum is consistent with limited summer rearing habitat upstream from the lakes, and a  
568 temperature-mediated risk of predation in the lakes themselves.

569

#### 570 ***4.4 Management implications***

571 Our analysis of spatiotemporal trends in Oregon Coast coho salmon productivity yielded  
572 information that will be useful for researchers and managers. The time series analysis was  
573 indicative of a change in both productivity trends and coherence in productivity among  
574 populations before and after 1990. These changes coincided with a major ocean regime shift,  
575 ESA-listing, and other conservation efforts through the 1990s such as decreased hatchery  
576 production, decreased harvest pressure, and increased investment in habitat conservation. We  
577 acknowledge that less reliable survey methods, uncertainty in population-specific harvest rates,  
578 and the relative influence of hatchery and harvest-related stressors prior to 1990 may have  
579 influenced our findings; however, results from our study and others are indicative of a  
580 mechanistic change point in productivity driven by conservation efforts and marine conditions.  
581 Both of these factors have had widespread and measurable effects on salmon (Buhle et al. 2009,  
582 Falcy and Suring 2018).

583         Spatial patterns of productivity became less variable during the post-1990 period and  
584 tracked more closely with marine conditions during the second year of life. Increased coherence  
585 in productivity generally signals that broad-scale (marine) drivers have a greater influence on  
586 survival and fitness (Zimmerman et al. 2015, Ohlberger et al. 2016, Ruff et al. 2017), and  
587 certainly productivity from 1990-on tracked closely with NPGO. This poses potential challenges  
588 to conservation. Managers have little, if any, control over the ocean conditions that salmon

589 experience during their first marine year, and these conditions are becoming more complex with  
590 climate change (Harley et al. 2006, Overland and Wang 2007, Di Lorenzo et al. 2010, Abdul-  
591 Aziz et al. 2011). ESU-wide coupling also leads to a reduction in the population “portfolio  
592 effect” such that marine conditions can be detrimental if temperature, prey availability, and other  
593 factors that impact survival deteriorate for several years at a time (Schindler et al. 2010, Kilduff  
594 et al. 2014, 2015). This was most recently observed with the high temperature “blob” off the  
595 Pacific Coast of North America (Bond et al. 2015, Di Lorenzo and Mantua 2016). Conversely, a  
596 direct relationship with environmental indicators such as NPGO may be helpful for managers if  
597 they can integrate that information along with existing stock-recruitment data to more accurately  
598 predict adult returns over the short-term (Rupp et al. 2012b, Burke et al. 2013, DeFilippo et al.  
599 2021). Such forecasting methods are error prone in instances where the relationship between  
600 productivity and the environment is inconsistent or decouples, as was the case for Oregon Coast  
601 coho salmon starting around 2010.

602 We did not observe a strong relationship between productivity and freshwater rearing  
603 conditions, but by no means are these conditions unimportant. For example, the Lakes  
604 populations of coho salmon have declined almost continuously since the 1960s and this is likely  
605 due to a variety of stressors in the lakes and their surrounding tributaries. Such stressors include  
606 climactic shifts in temperature and precipitation, which we tested using the DFA models, or they  
607 could be anthropogenic, like barriers to inland migration, eutrophication, and invasive species  
608 (Sheer and Steel 2006, Mantua et al. 2010, Wainwright and Weitkamp 2013, Rubenson and  
609 Olden 2020). These stressors are not unique to the Lakes stratum and may become more  
610 impactful for other Oregon Coast coho populations, especially if marine conditions deteriorate.  
611 Freshwater and estuarine habitat conditions are the lever by which managers influence  
612 population productivity and resilience, and they are central to state and federal salmon recovery  
613 plans (Lawson 1993, ODFW 2007, NMFS 2016). With respect to marine habitat conditions, the  
614 relationship between NPGO and productivity appears to have decoupled to some extent over the  
615 last decade. It is uncertain whether this is due to declining freshwater habitat quality for  
616 spawning and juvenile rearing, conditions in the nearshore environment, or other environmental  
617 variables that we did not measure. Within the Oregon Coast ESU, there are clearly opportunities  
618 for robust and diverse management strategies to maximize life history diversity among  
619 populations, taking advantage of the unique environmental attributes of coastal watersheds,

620 dendritic coastal lakes, and the Umpqua River basin. The greatest amount of benefit will occur  
621 when managers work across multiple spatial scales to bolster productivity and survival  
622 (Ohlberger et al. 2016, Ruff et al. 2017). Knowing if, and how, regional- and population-level  
623 processes differ, and how they respond to specific environmental factors during freshwater and  
624 marine rearing is an important step for managing salmon populations in rapidly changing  
625 ecosystems.

626

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965 **Tables**

966 **Table 1.** Population characteristics for the 21 independent populations of Oregon Coast coho  
 967 salmon used in the dynamic factor analysis (DFA) including average recruitment (pre-harvest  
 968 adult returns, *R*), average total escapement (natural and hatchery produced fish, *S*), and average  
 969 percent of spawners that were hatchery fish (*H*). A “-” indicates missing data.

Population	Stratum	Data years	Watershed area (km <sup>2</sup> )	Pre-1990			Post-1990		
				R	S	H (%)	R	S	H (%)
Necanicum	NOR	1958 – 2016	216	2,518	1,310	38.00	1,559	1,537	15.70
Nehalem	NOR	1958 – 2016	2,215	28,251	11,338	15.63	12,680	12,664	20.37
Tillamook	NOR	1958 – 2016	1,455	12,743	5,229	30.81	6,054	5,612	16.48
Nestucca	NOR	1958 – 2016	826	11,359	4,639	17.00	3,385	2,833	5.56
Salmon	MID	1990 – 2016	193	-	-	-	696	1,237	58.63
Siletz	MID	1958 – 2016	955	3,821	1,908	36.94	7,379	6,656	15.96
Yaquina	MID	1958 – 2016	650	16,936	6,696	16.87	7,252	6,419	6.70
Beaver	MID	1958 – 1971, 1980 – 2016	87	2,638	1,255	18.11	2,060	1,877	3.52
Alsea	MID	1958 – 2016	1,222	6,850	3,350	37.56	7,843	7,193	15.56
Siuslaw	MID	1960 – 2016	2,008	29,250	9,246	2.47	15,068	13,832	10.04
Siltcoos	LAK	1960 – 2016	197	8,373	2,896	2.00	4,592	4,055	0.70
Tahkenitch	LAK	1960 – 2016	94	4,789	1,579	1.00	3,222	2,885	0.44
Tenmile	LAK	1958 – 2016	233	21,491	7,228	1.00	8,333	7,564	0.26
Lower Umpqua	UMP	1958 – 2016	1,838	16,489	5,262	1.25	11,711	9,824	3.04
Middle Umpqua	UMP	1958 – 2016	2,082	6,796	1,939	1.20	6,584	6,346	4.15
North Umpqua	UMP	1958 – 2016	3,558	2,041	1,410	23.69	3,083	5,820	48.70
South Umpqua	UMP	1958 – 2016	4,666	5,523	1,714	3.00	9,940	9,912	13.30
Coos	MSO	1958 – 2016	1,556	24,256	6,861	3.44	15,597	14,119	2.15
Coquille	MSO	1958 – 2016	2,739	25,335	8,225	8.38	15,776	13,937	1.74
Floras	MSO	1994 – 2016	330	-	-	-	2,682	2,712	3.83
Sixes	MSO	1990 – 2016	348	-	-	-	214	201	8.30

971 **Table 2.** Environmental covariates used in the dynamic factor analysis (DFA), time relative to  
972 brood year each variable was expected to impact coho salmon, and source from which the data  
973 set was derived.

Variable	Year	Source
Average summer air temperature (TEMP)	1	<a href="https://www.ncei.noaa.gov/access/search/data-search/global-summary-of-the-month">https://www.ncei.noaa.gov/access/search/data-search/global-summary-of-the-month</a>
Average winter precipitation (PRECIP)	1	<a href="https://www.ncei.noaa.gov/access/search/data-search/global-summary-of-the-month">https://www.ncei.noaa.gov/access/search/data-search/global-summary-of-the-month</a>
Pacific Decadal Oscillation (PDO)	2	<a href="https://psl.noaa.gov/data/climateindices/list">https://psl.noaa.gov/data/climateindices/list</a>
North Pacific Gyre Oscillation (NPGO)	2	<a href="http://www.o3d.org/npgo/">http://www.o3d.org/npgo/</a>

974

975 **Table 3.** Mean and standard deviation (SD) Pearson's correlation coefficients (*r*) calculated for  
 976 pre- and post-1990 time periods and within- and among-regional strata for Oregon Coast coho  
 977 salmon. NOR = North Coast, MID = Mid-Coast, LAK = Lakes, UMP = Umpqua River, and  
 978 MSO = Mid-South Coast.

Pre-1990			Post-1990		
Comp	Mean	SD	Comp	Mean	SD
<b>Within</b>	<b>0.46</b>	<b>0.22</b>	<b>Within</b>	<b>0.60</b>	<b>0.20</b>
NOR-NOR	0.50	0.17	NOR-NOR	0.74	0.08
MID-MID	0.40	0.27	MID-MID	0.60	0.17
LAK-LAK	0.40	0.18	LAK-LAK	0.60	0.07
UMP-UMP	0.59	0.17	UMP-UMP	0.71	0.14
MSO-MSO	0.28	-	MSO-MSO	0.36	0.25
<b>Among</b>	<b>0.26</b>	<b>0.24</b>	<b>Among</b>	<b>0.49</b>	<b>0.23</b>
MID-NOR	0.28	0.27	MID-NOR	0.62	0.15
LAK-NOR	0.27	0.19	LAK-NOR	0.40	0.15
LAK-MID	0.15	0.30	LAK-MID	0.35	0.23
UMP-NOR	0.42	0.13	UMP-NOR	0.60	0.15
UMP-MID	0.26	0.25	UMP-MID	0.58	0.16
UMP-LAK	0.21	0.11	UMP-LAK	0.38	0.17
MSO-NOR	0.27	0.26	MSO-NOR	0.44	0.34
MSO-MID	0.14	0.25	MSO-MID	0.45	0.27
MSO-LAK	0.27	0.23	MSO-LAK	0.37	0.23
MSO-UMP	0.28	0.24	MSO-UMP	0.54	0.23
<b>TOTAL</b>	<b>0.29</b>	<b>0.25</b>	<b>TOTAL</b>	<b>0.51</b>	<b>0.23</b>



980 **Figure Legends**

981

982 **Figure 1.** Conservation and management of the Oregon Coast coho salmon Evolutionarily  
983 Significant Unit (ESU) has shifted through time, including substantial reductions in harvest rates  
984 and hatchery production through the 1990s. Several policy actions have influenced how these  
985 populations are managed as well. In 1997, the Oregon Plan for Salmon and Watersheds was  
986 established by the Oregon State Legislature to restore native fish and their aquatic habitats. Soon  
987 after, in 1998 the Oregon Coast coho salmon ESU was listed as threatened under the Endangered  
988 Species Act (ESA; 16 U.S.C. §§ 1531–1544). These conservation efforts occurred concurrently  
989 with a change in survey methodology from index site sampling to a randomized survey design  
990 (vertical red line).

991

992 **Figure 2.** Map of independent populations of the Oregon Coast coho salmon Evolutionarily  
993 Significant Unit (ESU) and biogeographical strata.

994

995 **Figure 3.** Pearson's correlation coefficients ( $r$ ) calculated among pairwise populations prior to  
996 1990 (top) and from 1990-on (bottom) for Oregon Coast coho salmon. Black lines denote  
997 groupings within regional strata. NOR = North Coast, MID = Mid-Coast, LAK = Lakes, UMP =  
998 Umpqua River, and MSO = Mid-South Coast.

999

1000 **Figure 4.** Pearson's correlation coefficient by distance between marine entry points for all  
1001 pairwise comparisons of Oregon Coast coho salmon. Gray line indicates exponential decay trend,  
1002 which exhibited a poor fit for the pre-1990 data and a marginal fit for the post-1990 data.

1003

1004 **Figure 5.** Modeled productivity trends and population loadings for the coast-wide dynamic  
1005 factor analysis (DFA) of Oregon Coast coho salmon. NOR = North Coast, MID = Mid-Coast,  
1006 LAK = Lakes, UMP = Umpqua River, and MSO = Mid-South Coast.

1007

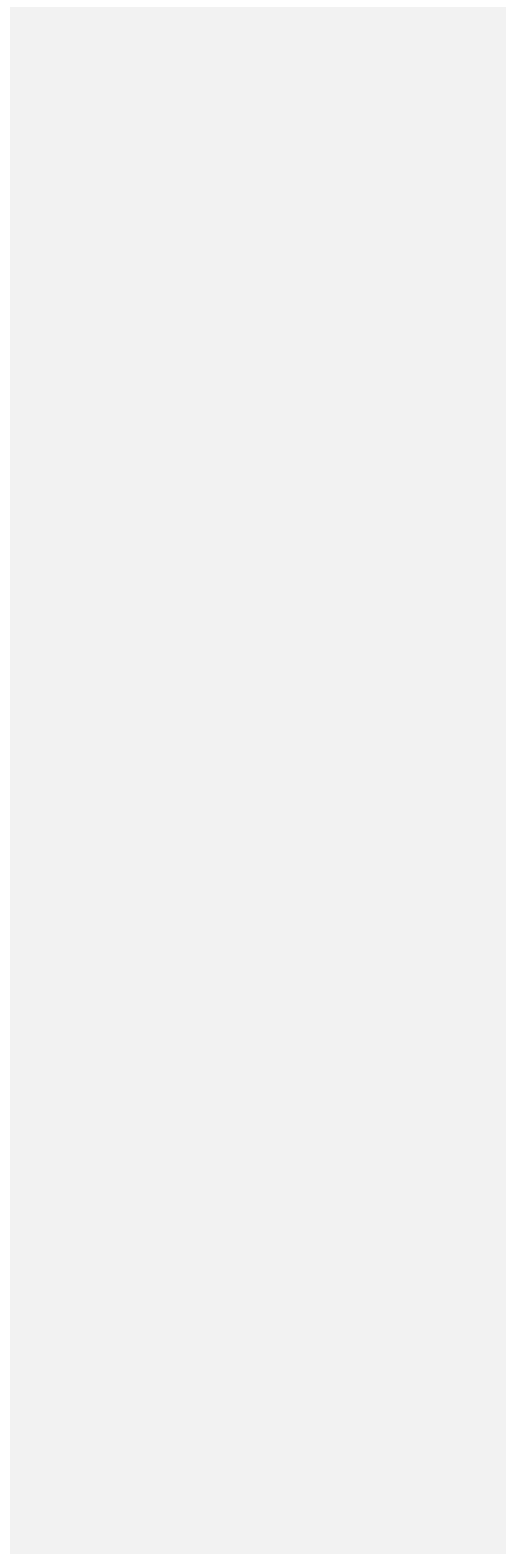
1008 **Figure 6.** Modeled productivity trends and population loadings for pre-1990 regional DFAs.  
1009 Black bars correspond with Trend 1 and gray bars correspond with Trend 2.

1010

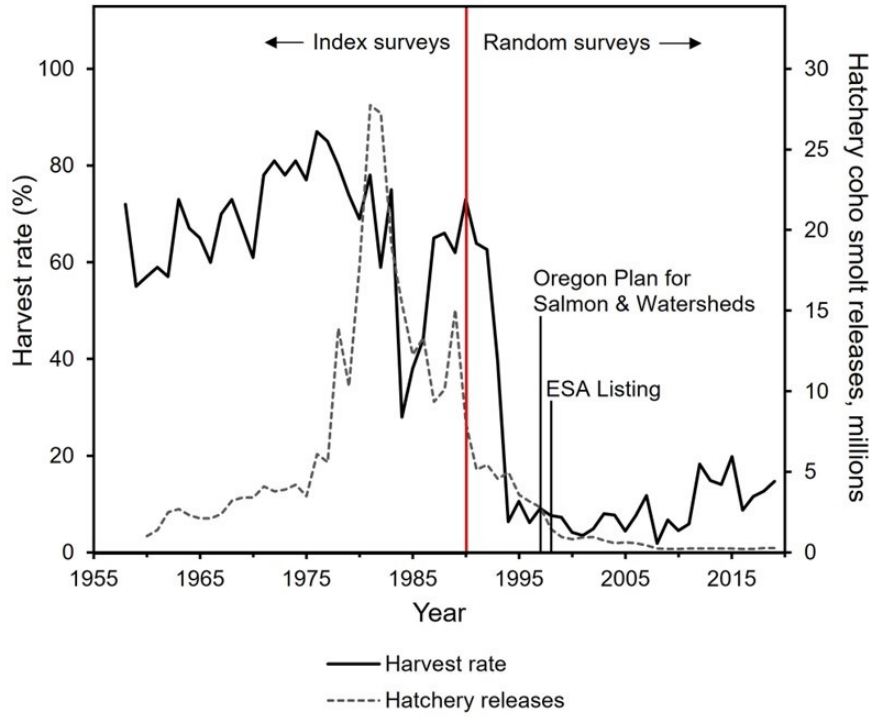
1011 **Figure 7.** Modeled productivity trends and population loadings for post-1990 regional dynamic  
1012 factor analyses (DFAs) of Oregon Coast coho salmon. Black bars correspond with Trend 1 and  
1013 gray bars correspond with Trend 2. Plotted values are means, dashed lines are 95% confidence  
1014 intervals. NOR = North Coast, MID = Mid-Coast, LAK = Lakes, UMP = Umpqua River, and  
1015 MSO = Mid-South Coast.

1016

1017 **Figure 8.** Predicted productivity trends for the North- (NOR), Mid- (MID), Umpqua (UMP;  
1018 Trend 1), and Mid-South Coast (MSO) strata of Oregon Coast coho salmon overlaid with *z*-  
1019 transformed Pacific Decadal Oscillation (PDO; top) and North Pacific Gyre Oscillation (NPGO;  
1020 bottom). These trends demonstrated a significant ( $P < 0.05$ ) correlation with marine drivers.

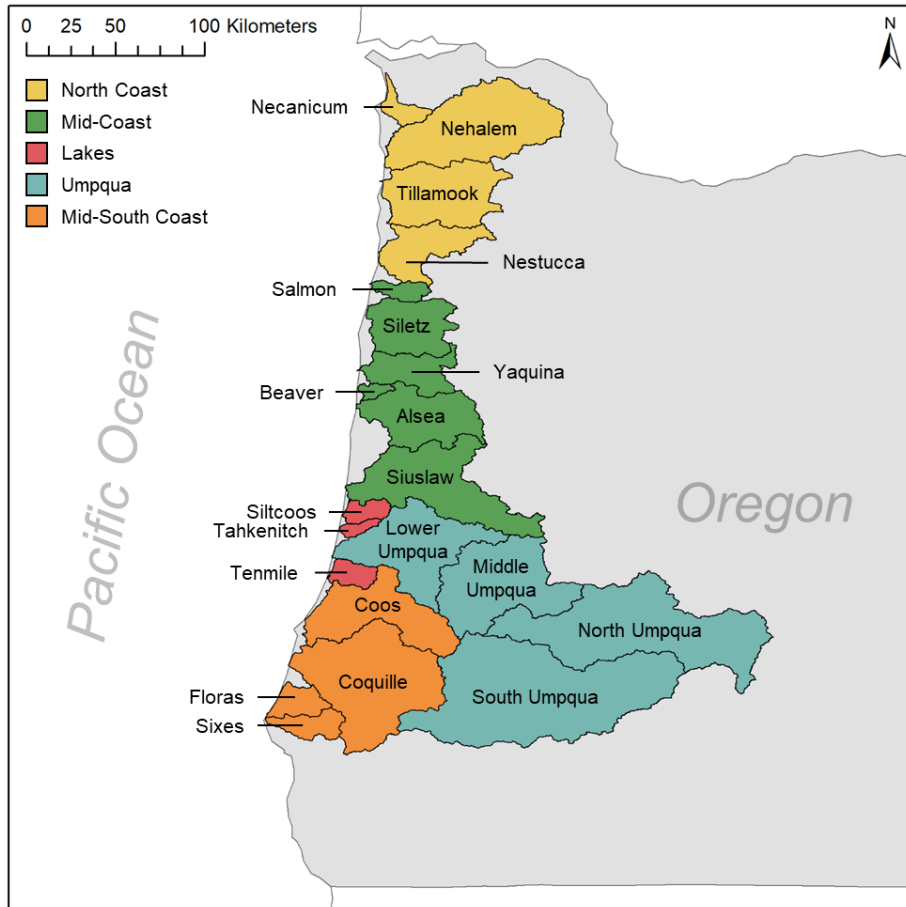


1021 **Figure 1**

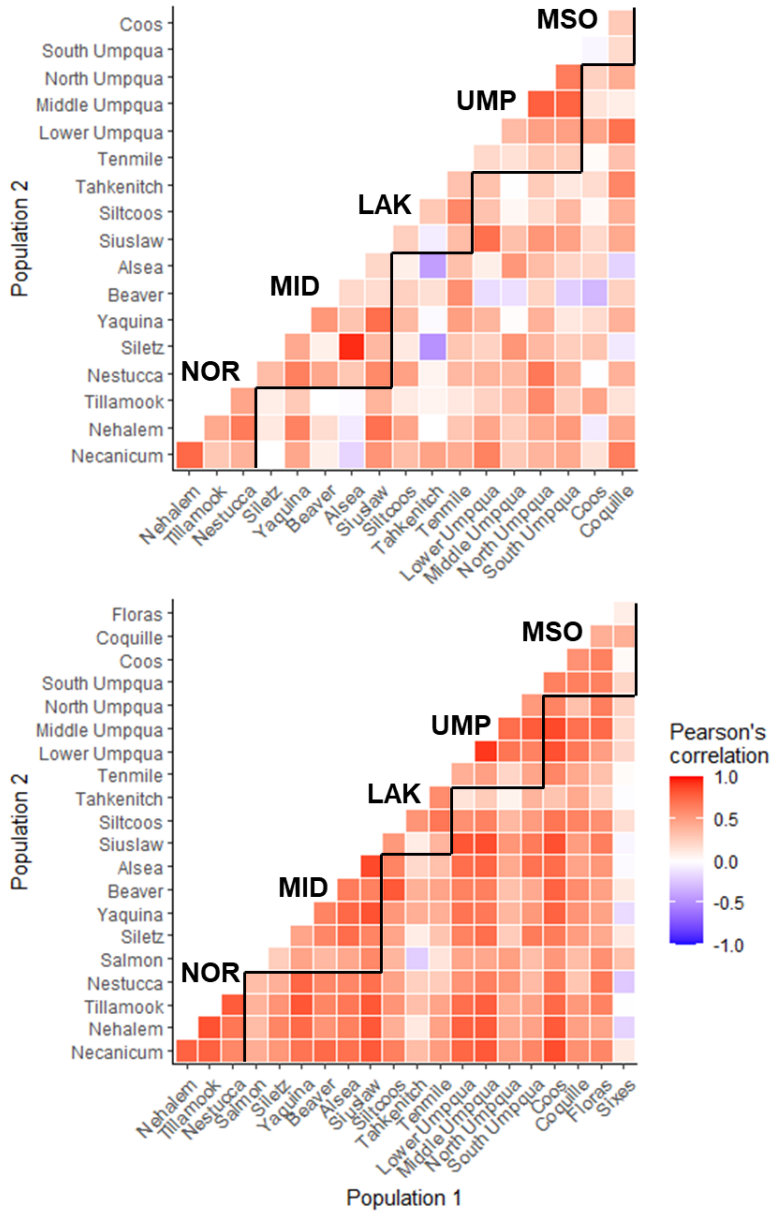


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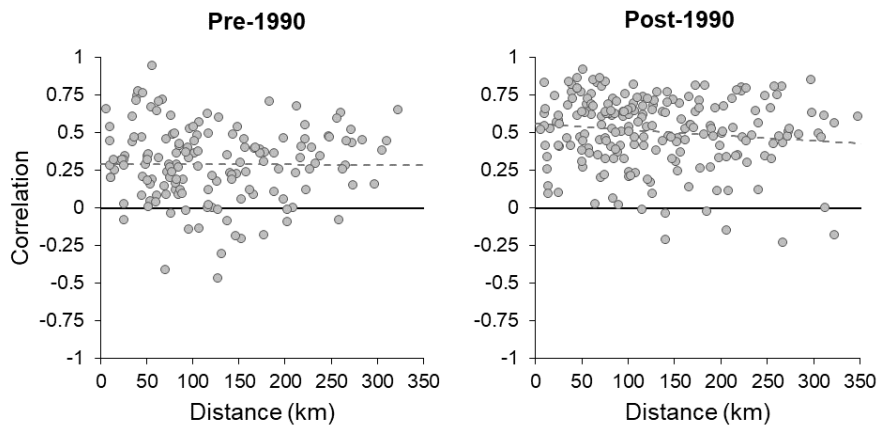
1023 **Figure 2**



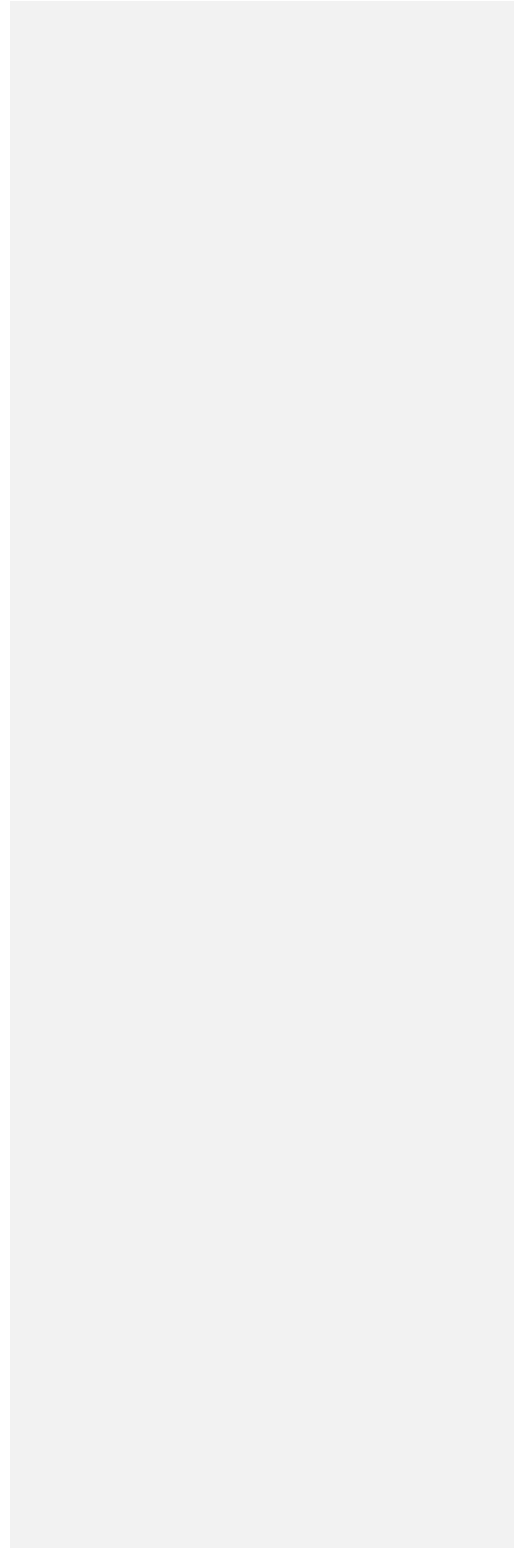
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1027 **Figure 4**



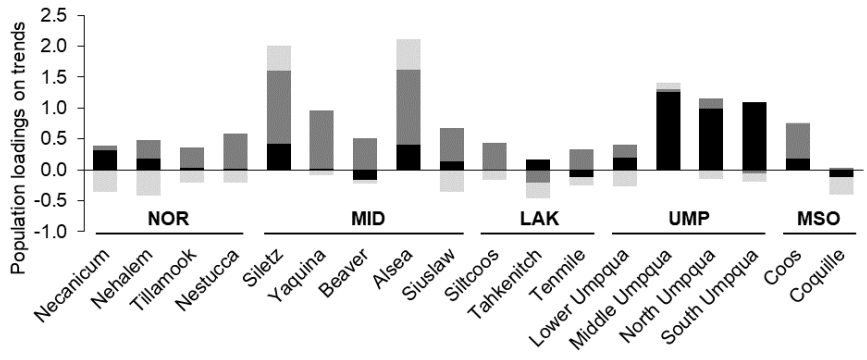
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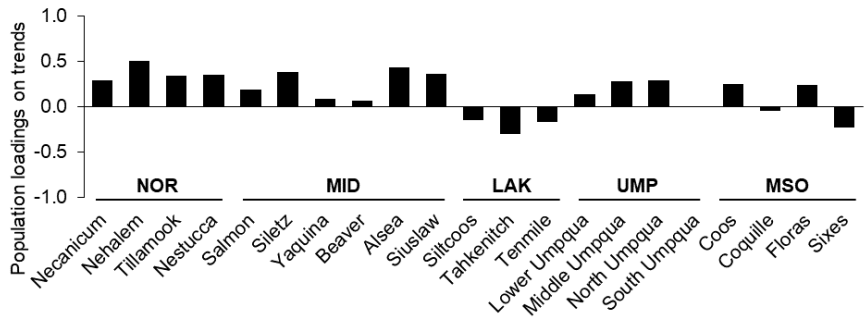
1029 **Figure 5**



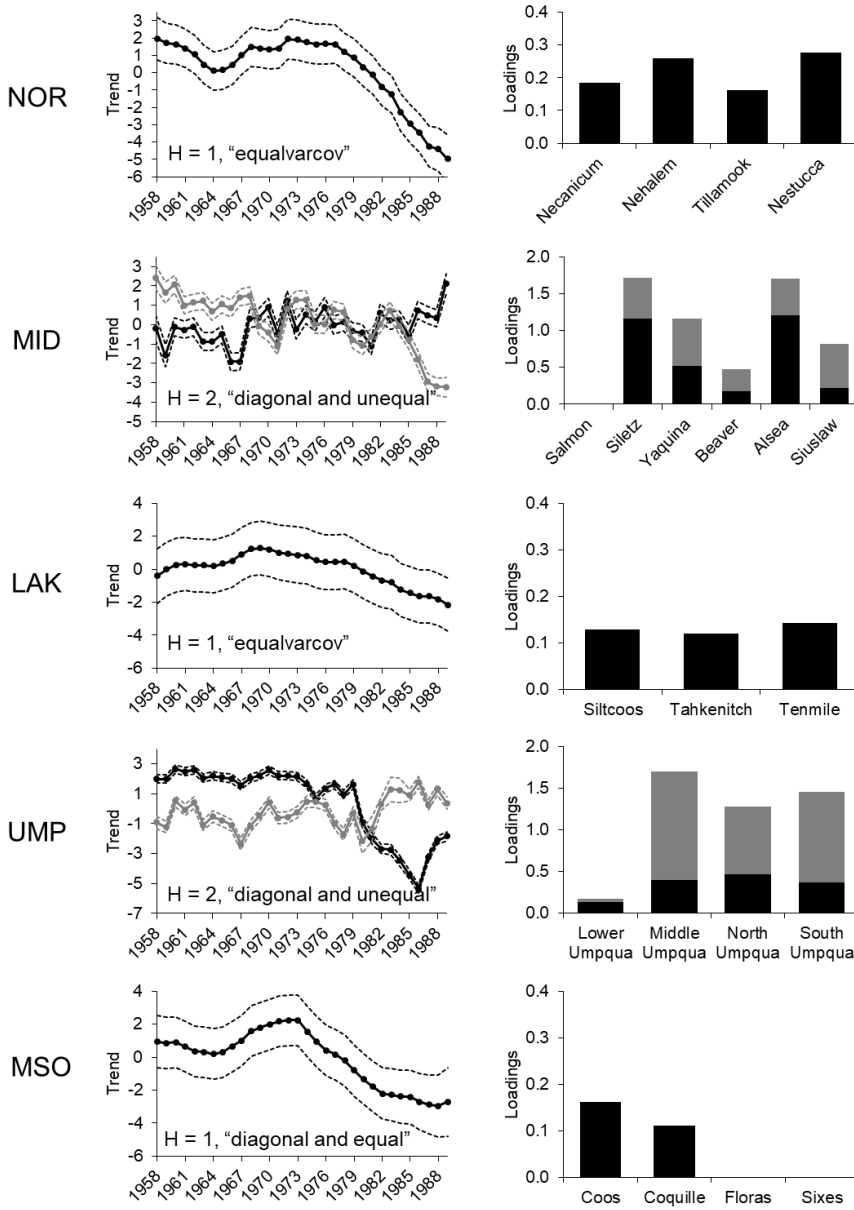
**Pre-1990**



**Post-1990**

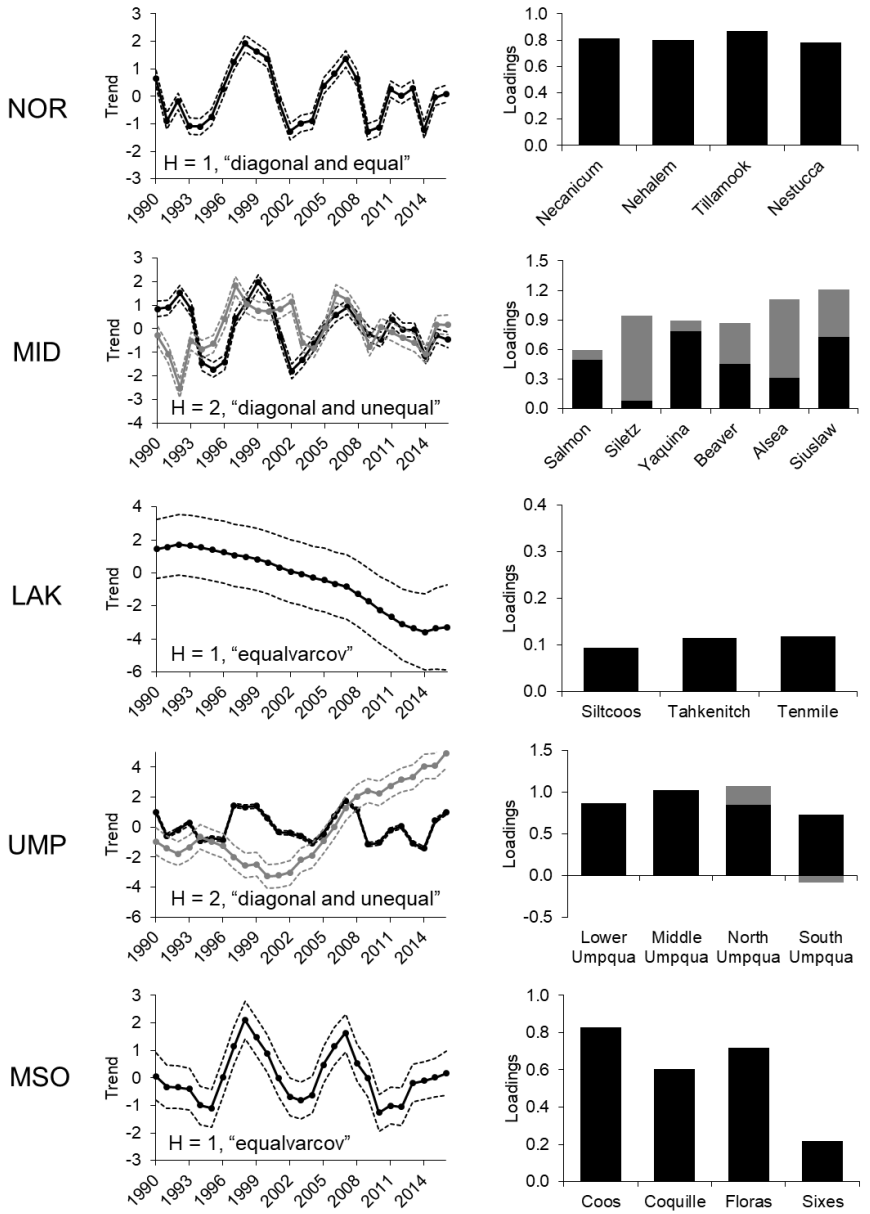


1031 **Figure 6**

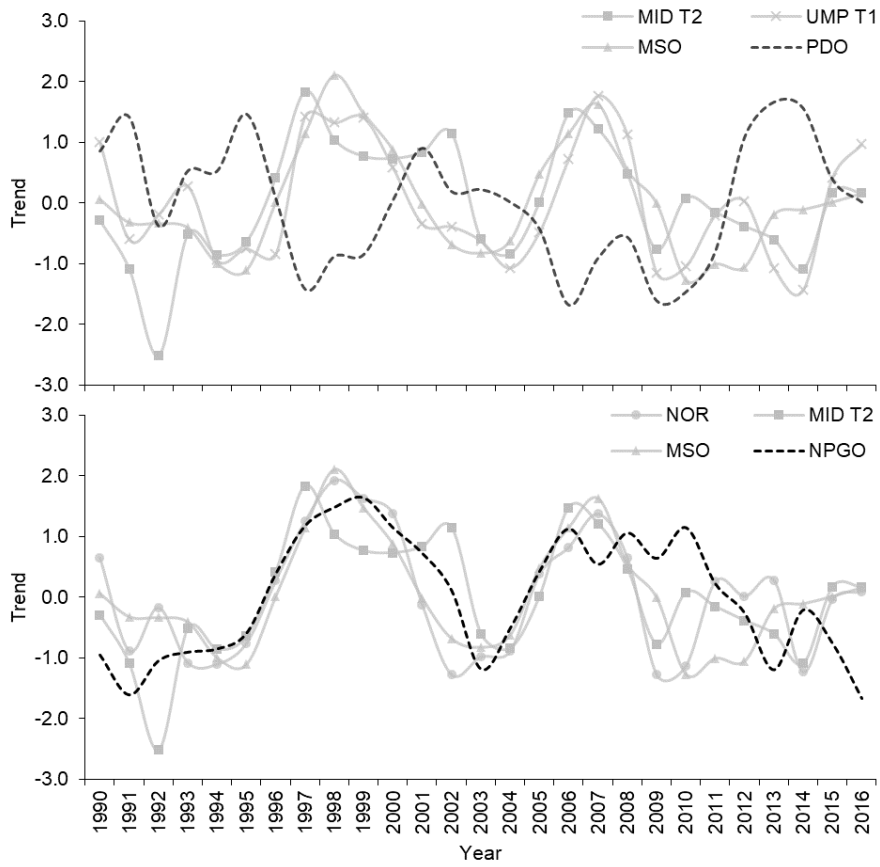




1033 **Figure 7**



1035 **Figure 8**



1036