


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

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## Abstract

Anadromous fishes, such as Pacific salmon, spend portions of their life cycle in freshwater and marine systems, thus rendering them susceptible to a variety of natural and anthropogenic stressors. These stressors operate at different spatiotemporal scales, whereby freshwater conditions are more likely to impact single populations or subpopulations, while marine conditions are more likely to act on entire evolutionarily significant units (ESUs). Coherence in population parameters like survival and productivity can therefore serve as an indicator of relative influence. The goal of this study was to elucidate scale-dependent shifts in Oregon Coast coho salmon productivity. We used a multivariate state-space approach to analyze almost 60 years of stock-recruitment data for the Oregon Coast ESU. Analyses were conducted separately for time periods prior to and after 1990 to account for improvements in abundance estimation methods and significant changes in conservation and management strategies. Prior to 1990, productivity declined for most Oregon Coast populations, especially through the 1980s. From 1990–onward, coherence increased, and trends tracked closely with the North Pacific Gyre Oscillation (NPGO). The latter period is associated with reductions in harvest rates and hatchery production such that the relative influence of the marine environment may have grown more apparent following the removal of these stressors. Furthermore, the link between productivity and NPGO is consistent with trends observed for several other Pacific salmon ESUs. If Oregon Coast coho salmon populations become more synchronous, managers can expect to face new challenges driven by reductions in the population portfolio effect and increasingly variable marine conditions due to climate change.

## KEYWORDS

climate indices, coho salmon, dynamic factor analysis, multivariate state-space models, population dynamics, productivity, time series

## 1 | INTRODUCTION

Over the past century, aquatic species in freshwater and marine ecosystems have been increasingly influenced by a multitude of stressors

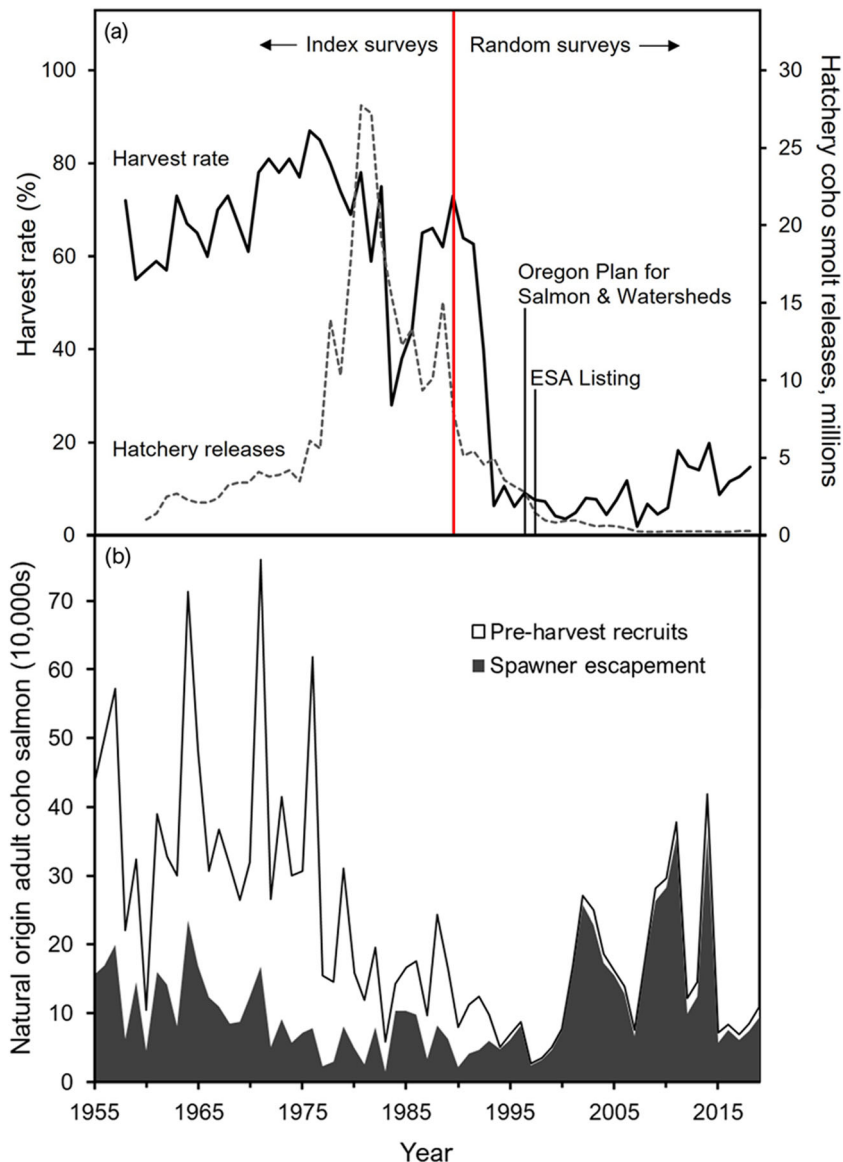
including climate change, overharvesting, and human encroachment on historical habitat (Arthington et al., 2016; Brander, 2010; Johnson & Welch, 2009; Pratchett et al., 2011; Wilberg et al., 2011). Anadromous species, such as Pacific salmon (*Oncorhynchus* spp.), are

likely to experience these stressors more acutely because they spend large portions of their life cycle in both freshwater and marine habitats (Crozier et al., 2021; Cunningham et al., 2018; Quinn, 2005). As an invaluable ecological, economic, and cultural resource, managers throughout the Pacific Coast of North America have recognized the importance of promoting healthy and stable salmon populations through sustainable harvest quotas, responsibly managed hatcheries, and habitat conservation and restoration actions. Nevertheless, many Pacific salmon populations have continued to decline despite an unprecedented level of investment in species and habitat conservation (Peterman & Dorner, 2012; Ward et al., 2015; Wilson et al., 2022).

Conservation of anadromous species is inherently difficult because stressors operate across multiple spatial and temporal scales (Crozier et al., 2008, 2021; Ohlberger et al., 2016; Schindler et al., 2008). For Pacific salmon, populations are sensitive to watershed-specific environmental stressors such as water temperature, salinity, stream flow, and hydrological connectivity during

freshwater and early marine rearing (Mueter et al., 2002, 2005; Pypers et al., 2005). When populations are more sensitive to these local-scale environmental drivers, strong spatial patterns emerge whereby survival, productivity, and other metrics of population health tend to have little spatial autocorrelation. Conversely, when ocean-scale drivers dominate, they favor high synchrony and high spatial autocorrelation in population metrics. Thus, the degree of coherence and spatial autocorrelation among populations is indicative of the scale at which stressors impact their survival and productivity (Dorner et al., 2018; Ohlberger et al., 2016; Ruff et al., 2017). This has implications for management because conservation and policy efforts tend to operate at local or regional scales (e.g., streams and watersheds), while climate-mediated shifts in ocean conditions are nearly impossible to manage (Schindler et al., 2008).

Managers and policymakers have enacted numerous conservation strategies to bolster survival and productivity. In the conterminous United States, more than 30 Pacific salmon stocks (or Evolutionarily Significant Units; ESUs) are listed as threatened or endangered under



**FIGURE 1** (a) Conservation and management of the Oregon Coast coho salmon evolutionarily significant unit (ESU) has shifted through time, including substantial reductions in harvest rates (solid line) and hatchery production (dashed line) through the 1990s. Several policy actions have influenced how these populations are managed as well. In 1997, the Oregon Plan for Salmon and Watersheds was established by the Oregon State Legislature to restore native fish and their aquatic habitats. Soon after, in 1998, the Oregon Coast coho salmon ESU was listed as threatened under the Endangered Species Act (ESA; 16 U.S.C. §§ 1531–1544). These conservation efforts occurred concurrently with a change in survey methodology from index site sampling to a randomized survey design (vertical red line). (b) High rates of harvest prior to the 1990s substantially reduced escapement, resulting in a period of low abundance of natural origin Oregon Coast coho salmon spawners and some of the lowest abundance estimates on record. Since the 1990s, natural origin spawner abundance has generally increased.

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

The Oregon Coast coho salmon (*O. kisutch*) is one example of an ESU where hatchery production was sharply curtailed concurrently with ESA-listing and reductions in maximum allowable harvest rates (Figure 1a). Peak releases of over 27 million hatchery smolts occurred in 1981. Since the ESU was declared threatened in 1998, smolt production has been further reduced from roughly 2.1 million to about 260,000 hatchery smolts, and hatchery-origin spawners have declined accordingly from a maximum of 31,530 individuals in 1986 to a minimum of 662 individuals in 2015 (Falcy & Suring, 2018). In addition, hundreds of millions of dollars (USD) of investments in freshwater habitat restoration were carried out through much of the 1990s and the beginning of the 21st century largely for the benefit of salmon (Nicholas et al., 2005; OWEB, 2017). Before these conservation measures, high rates of harvest compounded declining productivity to result in a protracted period of low escapement, including several exceptionally poor years. Since the 1990s, improving spawner abundances have included some of the highest natural origin spawner returns in decades (Figure 1b). The distinct shift in management strategies for Oregon Coast coho salmon poses a unique opportunity to evaluate the relative impacts of local-scale conservation actions and ocean-scale processes driving productivity trends.

To date, robust evaluations of scale-dependent factors have been challenging because changes in Oregon Coast coho salmon conservation and management occurred concurrently with a recognized regime shift in the North Pacific Ocean. In 1977 and 1989, distinct change points were observed for ocean indicators such as sea surface temperature and the Pacific Decadal Oscillation (PDO), with implications for numerous commercial fisheries (Hare & Mantua, 2000). PDO is a measure of Pacific climate variability that exhibits periodicity on a scale of 15–25 and 50–75 years and has historically been aligned with salmon survival (Mantua & Hare, 2002); however, following the regime shift in 1989, the North Pacific Gyre Oscillation (NPGO) began to display a stronger relationship to salmon survival than PDO (Kilduff et al., 2015; Litzow et al., 2018). This shift was also accompanied by a general breakdown in the correlation between salmon abundance (i.e., run strength) and traditional ocean indicators. The drivers and implications of these regime shifts and their influence on salmon population health are a topic of ongoing research and discussion.

In order to disentangle scale-dependent shifts in Oregon Coast coho salmon population dynamics, we evaluated spatial and temporal trends in population productivity using historical survey data. We addressed the following questions: (1) How have productivity trends

changed following the implementation of conservation efforts and a concurrent oceanic regime shift in the mid-1990s? (2) How similar are productivity trends among populations, and has synchrony in productivity changed through time? (3) Is productivity influenced by freshwater and/or marine rearing conditions? To answer these questions, we used a multivariate time series approach to quantify coherence in productivity through space and time and to relate productivity to several environmental covariates. Multivariate state-space models are particularly useful for analyzing ecological time series data due to their ability to partition process and observation error and handle missing data, as well as incorporate non-stationary trends over time (Dennis et al., 2006; Ward et al., 2010; Zuur et al., 2003). Results from this approach will provide important information on how ESA-listed Oregon Coast coho salmon population dynamics have shifted through time, and how conservation efforts and changing marine conditions may be influencing population trends.

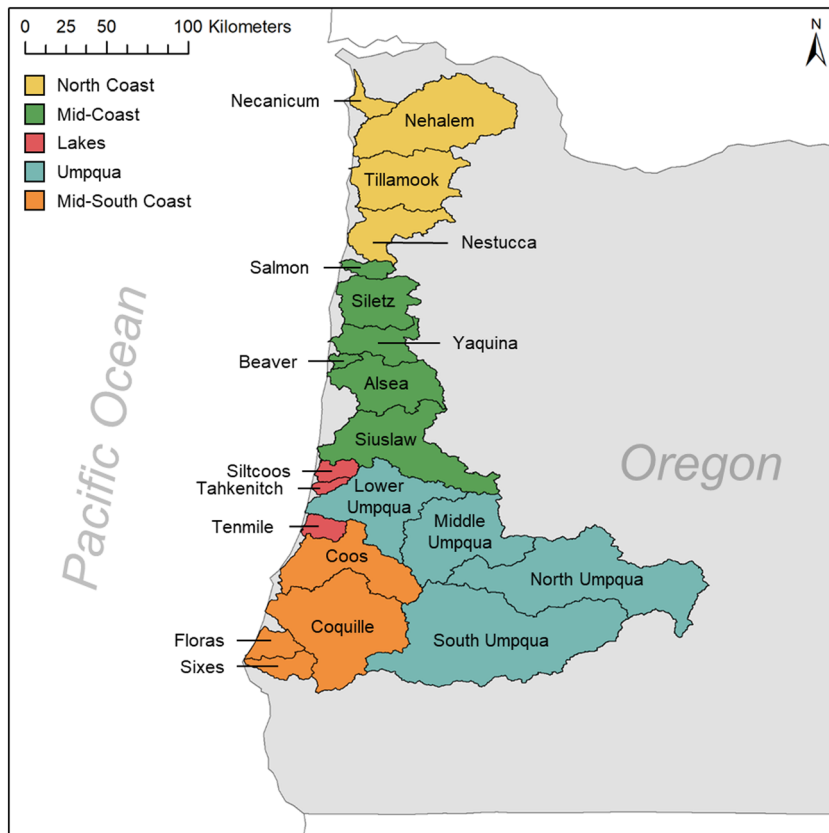
## 2 | METHODS

### 2.1 | Population structure

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

### 2.2 | Stock-recruitment and productivity data

Oregon Department of Fish and Wildlife (ODFW) has consistently monitored spawning populations of Oregon Coast coho salmon since the mid-1950s. We used 59 years (1958–2016) of stock-recruitment time series data to evaluate productivity trends for the entire ESU and for each biogeographic stratum (Chilcote et al., 2005). We calculated productivity as the natural logarithm of the number of adult recruits per spawner,  $\log_e(R_{t+3}/S_t)$ , where  $S_t$  is the estimated total number of natural and hatchery origin fish on the spawning grounds in year  $t$ , and  $R_{t+3}$  is the number of pre-harvest, natural origin adult recruits returning 3 years later (nearly all coho salmon mature and return to spawn as 3-year-olds; Pearcy, 1992). Hatchery origin fish are included in  $S_t$  because adult strays may produce natural progeny, but they are excluded from  $R_{t+3}$  because they are not the progeny of naturally



**FIGURE 2** Map of independent populations of the Oregon Coast coho salmon evolutionarily significant unit (ESU) and biogeographical strata.

spawning fish themselves. Precocious returns (“jacks”) were omitted from the analysis. To facilitate comparisons among populations, productivity data were standardized (z-transformed) by subtracting the mean from each value and dividing by the standard deviation.

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

Model-based estimation of time-varying observation errors can be difficult; however, conducting separate analyses allowed us to

account for these “change points” in methodology and management practices that were likely to affect observation error structure and productivity through time. It also allowed us to directly address our first study question regarding shifts in productivity trends following the implementation of conservation efforts and a concurrent oceanic regime shift in the mid-1990s. Pre-1990 analyses were not conducted for the Salmon, Floras, or Sixes populations due to missing data.

### 2.3 | Environmental covariates

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

**TABLE 1** Population characteristics for the 21 independent populations of Oregon Coast coho salmon used in the dynamic factor analysis (DFA) including average recruitment (pre-harvest adult returns,  $R$ ), average total escapement (natural and hatchery produced fish,  $S$ ), and average percent of spawners that were hatchery fish ( $H$ ).

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	2518	1310	38.00	1559	1537	15.70
Nehalem	NOR	1958–2016	2215	28,251	11,338	15.63	12,680	12,664	20.37
Tillamook	NOR	1958–2016	1455	12,743	5229	30.81	6054	5612	16.48
Nestucca	NOR	1958–2016	826	11,359	4639	17.00	3385	2833	5.56
Salmon	MID	1990–2016	193	-	-	-	696	1237	58.63
Siletz	MID	1958–2016	955	3821	1908	36.94	7379	6656	15.96
Yaquina	MID	1958–2016	650	16,936	6696	16.87	7252	6419	6.70
Beaver	MID	1958–1971, 1980–2016	87	2638	1255	18.11	2060	1877	3.52
Alsea	MID	1958–2016	1222	6850	3350	37.56	7843	7193	15.56
Siuslaw	MID	1960–2016	2008	29,250	9246	2.47	15,068	13,832	10.04
Siltcoos	LAK	1960–2016	197	8373	2896	2.00	4592	4055	0.70
Tahkenitch	LAK	1960–2016	94	4789	1579	1.00	3222	2885	0.44
Tenmile	LAK	1958–2016	233	21,491	7228	1.00	8333	7564	0.26
Lower Umpqua	UMP	1958–2016	1838	16,489	5262	1.25	11,711	9824	3.04
Middle Umpqua	UMP	1958–2016	2082	6796	1939	1.20	6584	6346	4.15
North Umpqua	UMP	1958–2016	3558	2041	1410	23.69	3083	5820	48.70
South Umpqua	UMP	1958–2016	4666	5523	1714	3.00	9940	9912	13.30
Coos	MSO	1958–2016	1556	24,256	6861	3.44	15,597	14,119	2.15
Coquille	MSO	1958–2016	2739	25,335	8225	8.38	15,776	13,937	1.74
Floras	MSO	1994–2016	330	-	-	-	2682	2712	3.83
Sixes	MSO	1990–2016	348	-	-	-	214	201	8.30

Note: A “-” indicates missing data.

**TABLE 2** Environmental covariates used in the dynamic factor analysis (DFA), time relative to brood year each variable was expected to impact coho salmon, and source from which the data 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>

## 2.4 | Correlations among populations

To evaluate spatial and temporal coherence in productivity, we calculated pairwise Pearson's correlation coefficients ( $r$ ) for each

independent population of coho salmon. Correlation coefficients were calculated separately for the pre- and post-1990 time periods. We then estimated mean and standard deviation correlation within and among strata.

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

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

where  $\rho$  is Pearson's correlation coefficient for each pairwise comparison of productivity between independent populations and  $\delta$  is the distance between populations at the point of marine entry (Kilduff et al., 2014; Pyper et al., 2002; Zimmerman et al., 2015). The parameter  $\nu$  is the  $e$ -folding scale (the distance at which correlation is expected to decrease by  $e^{-1}$  or 37%) and the parameter  $\rho_0$  is the intercept (expected correlation at  $\delta = 0$ ). The exponential decay function was fit separately for pre- and post-1990 data using nonlinear least squares in R (R Development Team, 2022). Distances among points of marine entry were estimated using ArgGIS 10.8.1 software (ESRI, West Redlands, California, USA) as the Euclidean distance between two entry points. For both time periods, we compared the fit

of the exponential decay model to a null model ( $\rho_\delta = m$ , where  $m$  represents the mean correlation among all pairwise comparisons) using the Akaike Information Criterion adjusted for small sample sizes (AICc). A  $\Delta\text{AICc}$  value  $>2$  indicated modest support for the exponential decay model over the null model (Burnham & Anderson, 2002).

## 2.5 | Dynamic factor analysis

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

$$y_t = Zx_t + a + Dd_t + v_t$$

where

$$v_t \sim \text{MVN}(0, R)$$

The loadings matrix ( $Z$ ) relates the observations ( $y_t$ ) to the hidden trends ( $x_t$ ) and assumes observation error ( $v_t$ ) is multivariate normally distributed (MVN) with a mean of zero and a variance-covariance matrix  $R$ . When covariates ( $d_t$ ) are included, the model can estimate the regression coefficients for each of the covariate effects (matrix  $D$ ). Our productivity data were z-scored, so the offset value ( $a$ ) was set to zero.

The true but unobserved trends ( $x_t$ ) are modeled as a random walk with process noise ( $w_t$ ):

$$x_t = x_{t-1} + w_t$$

where

$$w_t \sim \text{MVN}(0, I)$$

In the process equation, noise is also assumed to be normally distributed with a mean of zero; however, for identifiability reasons, the variance-covariance matrix is fixed as an identity matrix  $I$  (Holmes et al., 2012).

We conducted the DFA procedure separately for the pre- and post-1990 time periods. First, we ran the analysis for the entire Oregon Coast using all 21 populations (coast-wide). Then, to parse out regionally specific trends, we ran analyses separately for each stratum (regional). For the coast-wide analysis, we tested models with up to three hidden trends and for regional analyses we tested models with one or two hidden trends depending on the number of populations in each stratum ( $H = 1$  for  $N \leq 3$ ). We evaluated models with

various observation error structures (variance-covariance matrix  $R$ ): shared variance and no covariance ("diagonal and equal"), different variances and no covariance ("diagonal and unequal"), or shared variance and covariance ("equal variance and covariance"). We used the MARSS package in R (Holmes et al., 2012) to estimate parameter values and states for all model iterations. The best-fit model was selected using AICc, where a  $\Delta\text{AICc}$  value  $>2$  indicated modest support for one model over others (Burnham & Anderson, 2002).

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

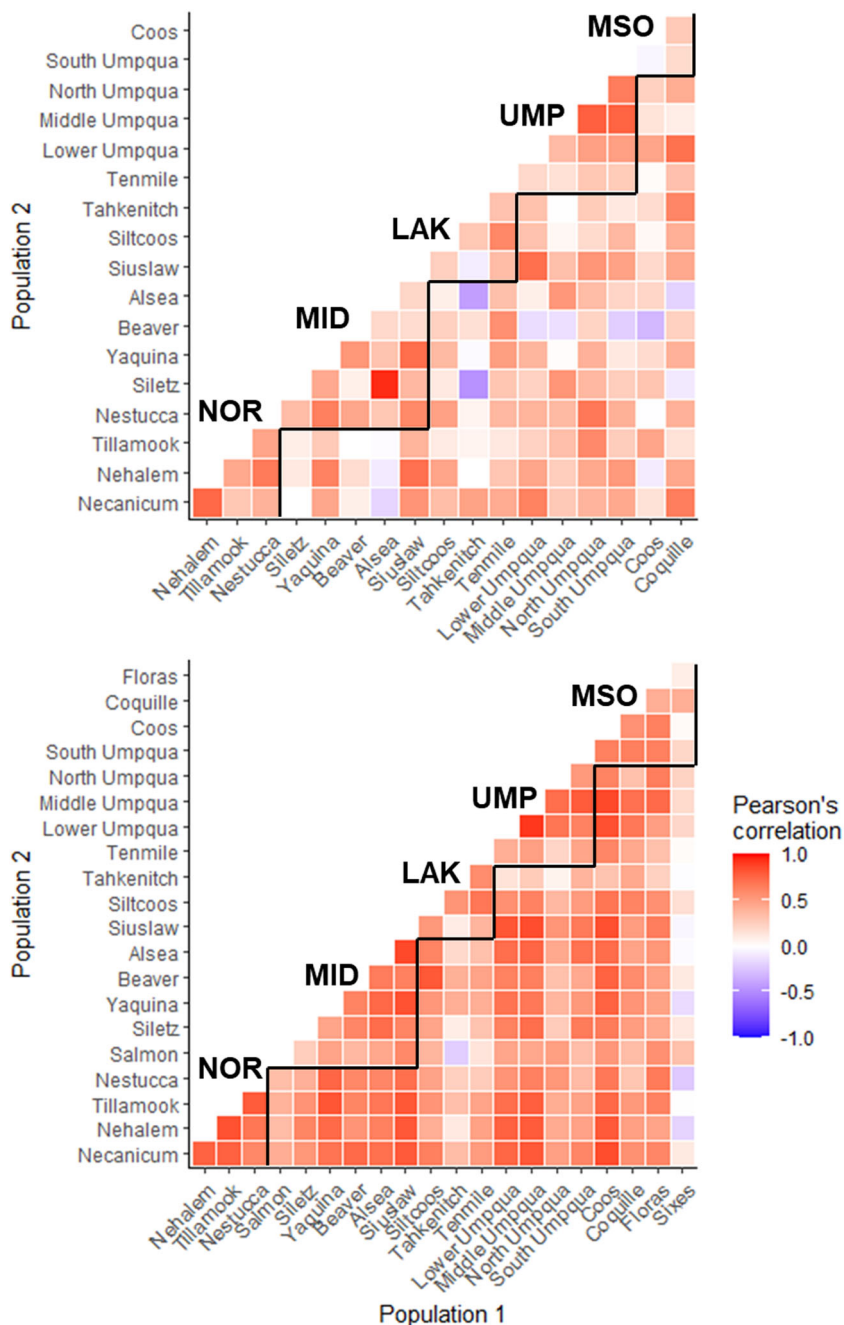
## 3 | RESULTS

### 3.1 | Correlation among populations

The degree of correlation in coho salmon productivity as measured by Pearson's correlation coefficient ( $r$ ) trended positive and non-zero for most pairs and was greater within than among strata (Figure 3 and Table 3). Overall, the degree of correlation nearly doubled from the pre-1990 to post-1990 period and increases occurred both within and among strata. Prior to 1990, within-stratum correlation was strongest ( $r > 0.5$ ) for the North Coast and Umpqua strata and was weakest for the Mid-South Coast stratum. This trend was also true for productivity data collected in 1990 and afterward. Lower cohesion for the Mid-South Coast stratum was likely driven by the Sixes River population, whose productivity trends did not appear to coincide with those of other Oregon Coast coho populations. In terms of among-stratum comparisons, the Lakes and Mid-South Coast strata appeared to have productivity trends that were most different from other strata and each-other, and this trend was more consistent during the post-1990 time period.

Within-stratum correlation was greater than among-stratum correlation in year-to-year productivity prior to 1990, yet the degree of correlation among population productivity trends did not decrease with increasing distance (Figure 4). The AICc value for the null model was lower than the AICc value for the exponential decay model ( $\Delta\text{AICc} = 2.02$ ) and the parameters for the exponential decay model converged in such a way that the  $e$ -folding scale ( $v = 1501$  km) was much larger than the extent of the Oregon Coast. From 1990-onward, spatial autocorrelation was detectable but was still weak ( $v = 1323$  km). There was marginal evidence that the fit of the exponential decay function was better than the fit of the null model ( $\Delta\text{AICc} = 1.82$ ).

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



### 3.2 | Dynamic factor analysis

#### 3.2.1 | Coast-wide

The coast-wide DFA using the pre- and post-1990 data sets identified several different Oregon Coast coho salmon productivity trends and indicated greater coherence in population productivity from 1990–onward. Prior to 1990, the best-fit model estimated three trends with independent and unique observation variances for each population (Table S1). Trends 1 and 2 were characterized by stochastic, year-to-year fluctuations in productivity between 1958 and 1990, with a slight dip for Trend 2 in the mid-1980s (Figure 5). Populations in the Mid-Coast stratum had the greatest loadings on Trend 2, while

populations in the Umpqua River had strong positive loadings on Trend 1. Trend 3 was characterized by a slight increase in productivity through the mid-1980s, followed by a very sharp increase; however, loadings on this trend were widespread and negative, indicating that most Oregon Coast coho salmon populations actually experienced a productivity crash in the mid-to-late 1980s. The unique error structure implied that there may have been among-population variation in the accuracy of abundance estimates, which is consistent with what we know about calibration and estimation methods through the 1990s. Observation error variance ( $R$ ) ranged from a low of 0.16 for the North Umpqua population to a high of 0.85 for the Tahkenitch Lake population. Observation error variance was generally low ( $\leq 0.2$ ) for the Middle, North, and South Umpqua populations and high ( $\geq 0.6$ )

for the Lakes and Mid-South Coast strata, but was variable among North- and Mid-Coast populations (Table S2).

From 1990–onward, the best-fit model supported a single observation error variance ( $R = 0.82$ ) and shared covariances ( $R = 0.39$ ) and identified a single productivity trend. Despite the change in survey methodology and expected increase in precision for post-1990 surveys, the observation error variance for this era was higher than for all but two populations pre-1990 (Table S2). The estimated trend appeared to be cyclical and increasing with peaks in the late 1990s, mid-2000s, and mid-2010s. Productivity correlated significantly with

NPGO ( $r = 0.59$ ,  $R^2 = 0.33$ ,  $P = 0.002$ ; Figure S1), indicating that marine processes have had a notable impact on Oregon Coast coho productivity since the 1990s (Trends 1–3 from the pre-1990 DFA did not correlate significantly with NPGO or PDO). Loadings were greatest for populations in the North- and Mid-Coast strata and negative for the Lakes stratum and Sixes River population (Figure 5). Drivers other than marine conditions may have limited the productivity of populations with weak or negative loadings.

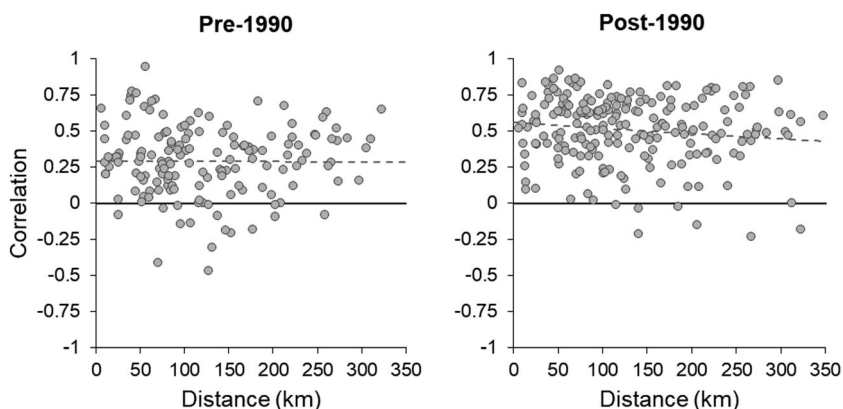
### 3.2.2 | Regional

**TABLE 3** Mean and standard deviation (SD) Pearson's correlation coefficients ( $r$ ) calculated for pre- and post-1990 time periods and within- and among-regional strata for Oregon Coast coho salmon.

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>

Abbreviations: LAK, Lakes; MID, Mid-Coast; MSO, Mid-South Coast; NOR, North Coast; UMP, Umpqua River.

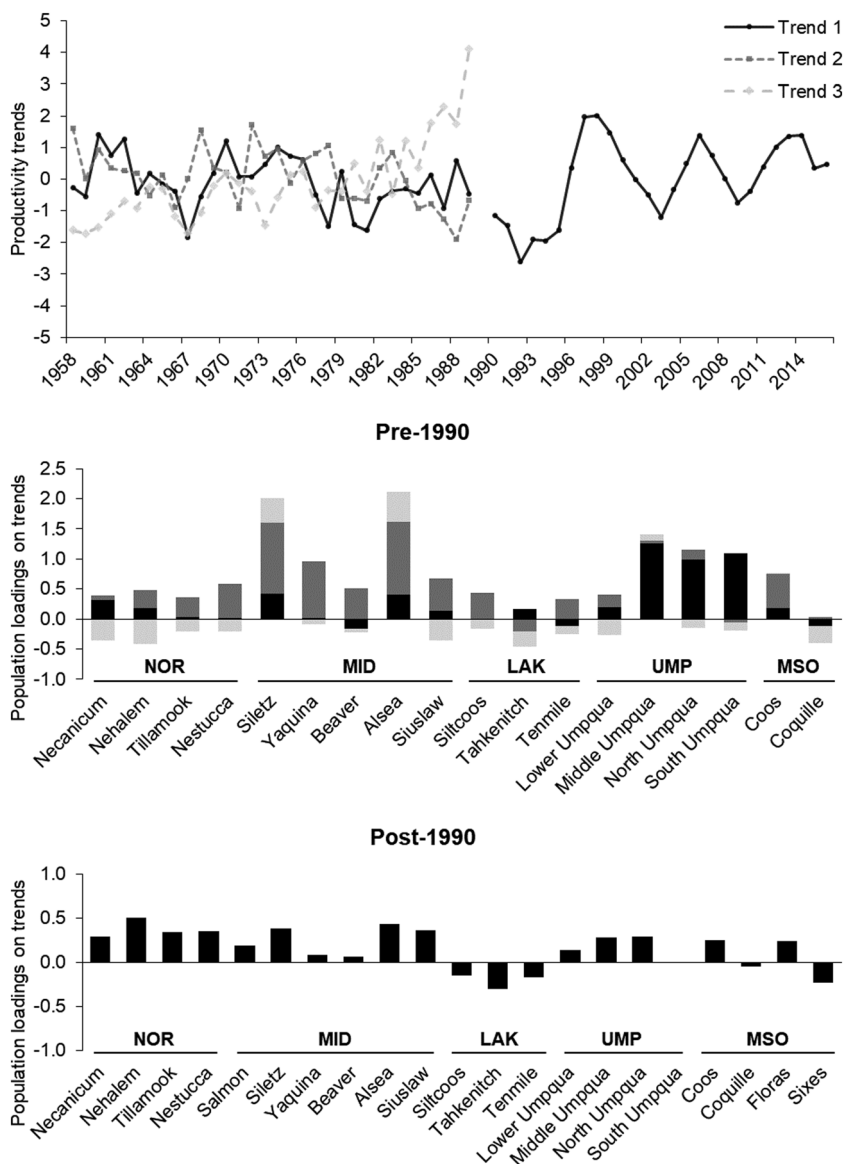
Regional DFAs identified trends that were specific to individual strata. Prior to 1990, among-stratum trends were highly variable (Figure 6 and Table S3). For instance, the best-fit models for the North Coast and Lakes strata were characterized by an observation error structure with a single variance and covariance (North Coast variance  $R_{var} = 0.69$ , covariance  $R_{cov} = 0.20$ ; Lakes variance  $R_{var} = 0.71$ , covariance  $R_{cov} = 0.33$ ) and showed widespread declines in productivity through the 1980s. Loadings were generally consistent among populations. For the Mid-Coast stratum, the best-fit model included two hidden trends with independent and unique observation error variances ( $R = 0.02$ – $0.78$ ). Trend 1 demonstrated a gradual increase in productivity, with the greatest loadings from the Siletz and Alsea populations. Trend 2 showed a gradual decrease in productivity and a very sharp decline through the mid-1980s, with the greatest loadings from the Yaquina and Siuslaw populations. For the Umpqua stratum, the best-fit model had two hidden trends with independent and unique observation error variances ( $R = 0.01$ – $0.88$ ). Trend 1 exhibited a steady-but-slight decline through the late 1970s with a sharp decline thereafter. Trend 2 showed productivity was generally steady or increasing, and was the predominant trend for the Middle, North, and South Umpqua populations. The Lower Umpqua population had weak loadings on both trends, indicating that productivity may have followed a separate trajectory for this population during the pre-1990 time period. For the Mid-South Coast stratum, data were only available for the Coos and Coquille populations. The best-fit model had a single observation error variance ( $R = 0.87$ ) and demonstrated a declining



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



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

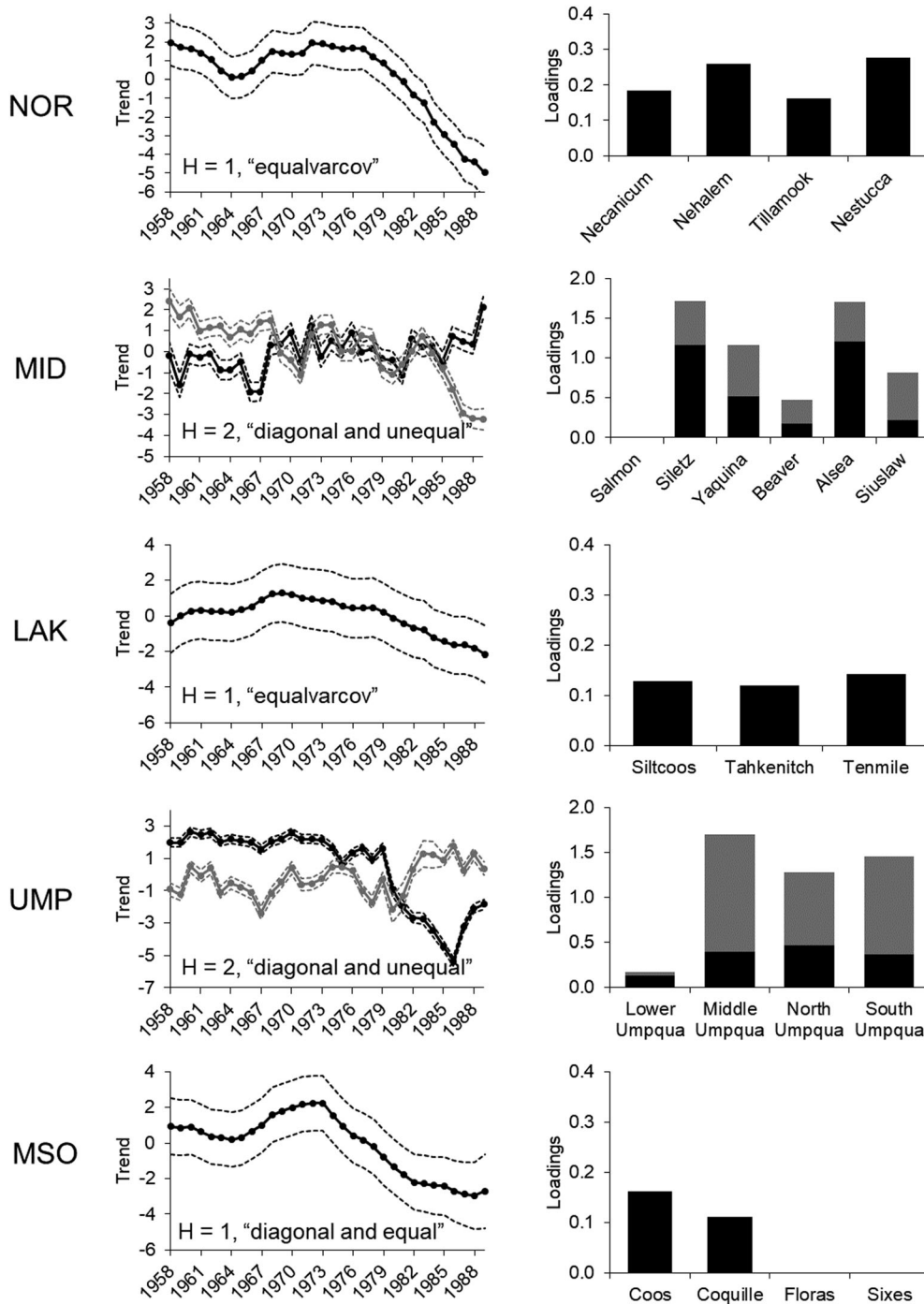


trend that was similar to those observed for the North Coast and Lakes strata.

From 1990-onward, productivity trends became much more cohesive (Figure 7 and Table S3). Most predicted trends were similar to what was observed for the coast-wide DFA, with peaks in the late 1990s, mid-2000s, and mid-2010s. This pattern was exhibited by the North Coast (single observation error variance,  $R = 0.28$ ), Mid-Coast (Trends 1 and 2; unique observation error variances,  $R = 0.08$ – $0.67$ ), and Umpqua populations (Trend 1; unique observation error variances,  $R = 0.03$ – $0.40$ ). The best-fit model for the Mid-South Coast stratum was slightly distinct in that it showed sharp peaks in productivity in the late-1990s and mid-2000s, with a single observation error variance and covariance (variance  $R_{\text{var}} = 0.77$ , covariance  $R_{\text{cov}} = 0.33$ ). The DFA procedure for the Mid-Coast stratum identified two best-fit models; one with two trends and unique observation error variances and one with two trends and a single variance and covariance. From here on, we report on the output for the model with unique observation error variances, which had a lower root-mean-

square error. Both trends for the Mid-Coast stratum were highly similar, with divergence in the early 1990s. Loadings on Trend 1 were strongest for the Salmon and Yaquina populations, while loadings for Trend 2 were strongest for the Siletz and Alsea populations. The best-fit model for the Umpqua stratum had two trends; however, loadings were very weak for Trend 2, which demonstrated a sharp increase in productivity after the year 2000. The Lakes stratum was the only one with a distinct, declining trajectory, and had a single observation error variance and covariance (variance  $R_{\text{var}} = 0.87$ , covariance  $R_{\text{cov}} = 0.53$ ).

Including environmental covariates in the DFA as observation error covariates did not improve model fit for any of the coast-wide or regional analyses (Table S4); however, when predicted trends were directly correlated with covariates, some strong relationships emerged (Figure S2–S6 and Table S5). Prior to 1990, productivity for the Lakes, Umpqua (Trend 1), and Mid-South Coast strata was negatively correlated with PDO, while productivity for the Mid-Coast stratum was marginally correlated with summer temperature, although this



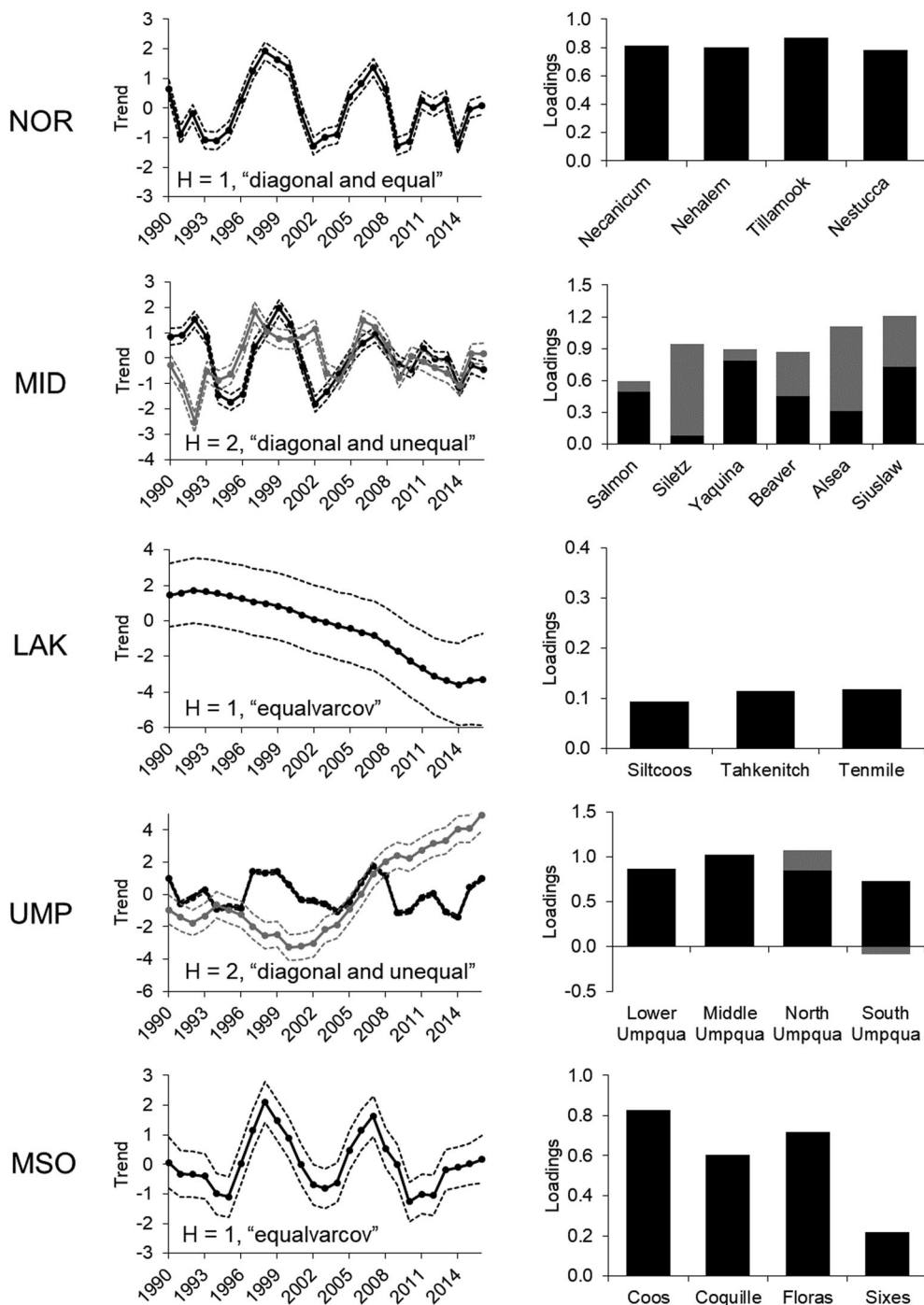
**FIGURE 6** Modeled productivity trends and population loadings for pre-1990 regional DFAs. Black bars correspond with Trend 1 and gray bars correspond with Trend 2.

relationship appeared to be biologically insignificant. From 1990 onward, NPGO emerged as an important environmental driver and exhibited a significantly high degree of overlap with productivity trends for the North Coast ( $r = 0.53$ ), Mid-Coast (Trend 2;  $r = 0.68$ ), and Mid-South Coast strata ( $r = 0.57$ ; Figure 8). PDO was also negatively correlated with productivity for the Mid-Coast (Trend 2;  $r = -0.46$ ), Umpqua ( $r = -0.44$ ), and Mid-South Coast ( $r = -0.45$ ) strata. Mid-Coast Trend 2 was positively correlated with winter precipitation ( $r = 0.41$ ). For Lakes populations, productivity was negatively correlated with summer air temperature ( $r = -0.95$ ), but not with any of the marine drivers.

## 4 | DISCUSSION

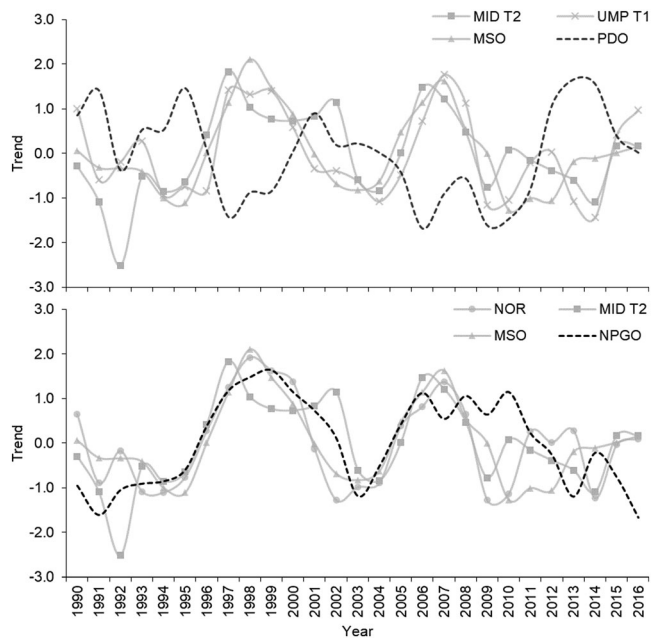
We used a quantitative approach to evaluate scale-dependent shifts in productivity for 21 independent populations of Oregon Coast coho salmon. Our analyses supported a clear change point in the 1990s whereby coast-wide declines in productivity transitioned to a more cyclical pattern and regional trends became more coherent both within and among biogeographical strata. There are several possible explanations for this change point and they are not necessarily mutually exclusive: (1) less reliable survey methods and uncertainty in population-specific harvest rates and the proportion of

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



hatchery spawners introduced more variability and obscured potential relationships with environmental drivers and (2) a mechanistic change point in productivity occurred sometime in the 1990s following a coast-wide population crash for Oregon Coast coho salmon and concurrent with conservation efforts and an oceanic regime shift (Falcu & Suring, 2018; Hare & Mantua, 2000). Our findings and the existing literature lend support for the second explanation. Between 1990 and 2010, coho salmon productivity appears to have tracked closely with marine conditions, especially NPGO, which is an indicator of ocean current and circulation patterns and is closely linked to phytoplankton concentrations (Di Lorenzo et al., 2008;

Kilduff et al., 2015). Increased dependence on marine conditions in the first ocean year of life (as opposed to freshwater conditions, which can be highly variable among watersheds) and among-population coherence demonstrate a shift from local- to broad-scale drivers of productivity (Dorner et al., 2018; Ohlberger et al., 2016; Ruff et al., 2017). Furthermore, reductions in hatchery production and limited harvest concurrent with ESA-listing appear to have slowed declines in productivity for the Oregon Coast coho salmon ESU, even if the number of recruits per spawner has not improved (Falcu & Suring, 2018). We provide a more in-depth discussion of these trends below.



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

#### 4.1 | Temporal productivity trends

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

From 1990–onward, coast-wide productivity followed a single, cyclical trend for most populations, with distinct peaks occurring in the late-1990s, mid-2000s, and mid-2010s. Regional trends for the North, Mid-, Umpqua, and Mid-South strata again corroborated coast-

wide trends; however, productivity in the Lakes stratum appeared to continue to decline. Lakes coho salmon are subject to different stressors and use different life history strategies due to the region's unique geography. Adult coho salmon spawn in the various tributaries that drain into the large, shallow lakes while juveniles rear in the tributary streams or in the highly-productive lakes and surrounding marshes. Historically, optimal rearing and spawning conditions have led to higher than average juvenile salmon growth rates, relative abundance, and smolt-to-adult survival (Nickelson, 2001; Zhou, 2000). As such, Lakes coho salmon were previously considered to be a benchmark for the Oregon Coast ESU. This stratum continued to have high persistence and sustainability scores in the most recent ESU status review (NMFS, 2022), but recent declines in productivity have highlighted uncertainty in these populations' long-term resilience. The southernmost Sixes River population also diverged from post-1990 trends in productivity in that they were generally more stochastic; however, the reasons for this are less clear. Cape Blanco is used as a geological dividing point between the Oregon Coast ESU and the Southern Oregon/Northern California Coast (SONCC) ESU, but more analysis is needed to determine whether the Sixes River population's productivity might track more closely with that of the Elk River and other SONCC coho salmon populations to the south. If that were the case, it would suggest this population's evolutionary history, life history characteristics, and/or behavior place it more in-line with SONCC populations or as its own population unit. Studies have indicated that the Sixes population is genetically distinct from other Oregon and Washington coho salmon populations (Ford et al., 2004).

#### 4.2 | Coherence among populations

Pairwise comparisons of productivity using Pearson's correlation coefficient revealed strong spatiotemporal trends for Oregon Coast coho salmon (particularly within strata), although there was limited evidence for a decrease in covariation with increasing distance. Based on previous studies using similar methods, we expected baseline rates of correlation to be high due to the narrow spatial scope of our analysis, with some dampening in the decay signal (i.e.,  $e$ -folding scale). For example, the 350 km maximum distance among Oregon Coast watersheds was roughly 1/6 of the maximum distance evaluated in Ruff et al. (2017), who analyzed population coherence in marine survival for Chinook salmon along most of the coast of Oregon, Washington, and British Columbia. Nevertheless, they did observe a measurable decay with distance both along the Pacific Coast and within the Salish Sea ( $e$ -folding scale of 517 and 292 km, respectively compared to our estimates of 1323–1501 km). Zimmerman et al. (2015) also observed relatively low  $e$ -folding scale values in their analysis of coho salmon smolt survival (129–506 km depending on time period). Even considering differences in life history strategies among species and the external factors impacting productivity vs. marine survival (Quinn, 2005), we would have expected a lower  $e$ -folding scale, especially considering that within-stratum correlation was considerably greater than among-stratum correlation.

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

The degree of within- and among-stratum correlation among independent populations of coho salmon increased between the pre- to post-1990 period for all comparisons, in some cases more than doubling. Removal of stressors such as harvest and hatchery production likely decreased spatial variability in the freshwater component of productivity (Falcy & Suring, 2018). Indeed, the degree of hatchery production, which has been shown to negatively impact natural origin coho salmon populations (Buhle et al., 2009; Nickelson, 2003), was highly variable among populations, ranging from 0% to 99% of spawning adults prior to 1990 (the coast-wide average was 10–27% depending on year). After roughly the year 2000, hatchery production declined precipitously to a coast-wide average of 1–16% of spawning adults, and the percentage of hatchery spawners was consistently lower than 5% for most populations. Harvest, which was a major source of pre-spawn mortality prior to ESA-listing, was estimated as a single value for the Oregon Coast. The percentage of adults lost to commercial and recreational harvest ranged from 28 to 87% prior to 1990 (Lawson, 1992). After ESA-listing in 1998, harvest rates were only 1–20%. Substantial investments in freshwater habitat restoration, conservation, and enhancement were also carried out during this time period; however, direct linkages between restoration and salmon populations are challenging to detect. The extent and quality of restored habitat may not yet have reached a threshold where its effects on population parameters are detectable (Roni et al., 2010),

and a considerable amount of variability in habitat conditions still exists among watersheds. Furthermore, the process and time scale over which complete restoration occurs is such that improvements in habitat quality may not transpire for decades, or even centuries, after restoration actions are enacted.

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

### 4.3 | Influence of freshwater and marine rearing conditions

We tested the effects of environmental variables related to freshwater (summer temperature, winter precipitation) and marine conditions (average annual PDO and NPGO) by including them as covariates in the DFA models and by assessing whether they were correlated with best-fit productivity trends. There was little support for covariates when they were included in the DFA, but when best-fit trends were directly compared to the standardized covariates, some significant correlations emerged.

Prior to 1990, PDO demonstrated a negative relationship with trends for the Lakes, Umpqua, and Mid-South Coast strata; however, this relationship was more noticeable prior to sharp regional declines in productivity through the 1980s. Aforementioned methodological considerations and declines in productivity may have masked the influence of marine drivers. From 1990–onward, the relationship between productivity and environmental conditions became much clearer for some strata. Between 1990 and 2010, coast-wide, productivity appeared to be closely related to the NPGO index. This was also

reflected in the regional analyses such that trends for the North-, Mid-, and Mid-South Coast populations tracked closely with each other and with NPGO. The NPGO index has been implicated as a driver of marine survival and productivity for several salmon species (Dorner et al., 2018; Kilduff et al., 2014, 2015; Ohlberger et al., 2016; Ruff et al., 2017). This is unsurprising as it is closely linked to coastal upwelling, nutrient cycling, and phytoplankton and krill concentrations (Di Lorenzo et al., 2008; Kilduff et al., 2014, 2015; Sydeman et al., 2013). From about 2010-on, the correlation between productivity and NPGO weakened. Variance in NPGO and other ocean indicators (including PDO, which has been negatively correlated with NPGO in recent years) has increased in recent decades, signaling that the stability of the marine environment may be declining (Di Lorenzo et al., 2010; Kilduff et al., 2014; Sydeman et al., 2013). Given the apparent relationship between salmon survival, productivity, and Pacific climate, more frequent and unpredictable periods of unfavorable ocean conditions may lead to destabilization of highly synchronous populations such as the Oregon Coast coho salmon (Kilduff et al., 2015; Mantua, 2015).

Site specific changes in environmental conditions may have contributed to the Lakes populations' continual decline in productivity throughout the study period. For instance, in the 1960s, dams were built on Siltcoos and Tahkenitch lakes to control the flow of water for nearby paper mills, and these dams can act as a partial barrier to upstream migration under some conditions. Other factors include reduced natural seasonal variation in lake levels, eutrophication due to increased nutrient inputs, harmful algal blooms, and the presence of nonnative species such as bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*), which may consume juvenile salmon (Gray, 2005; ODFW, 2007; Reimers 1989). Productivity for these populations was negatively correlated with PDO prior to 1990 and with temperature from 1990-onward. It is not out of the question that fish rearing in a shallow lake and its adjacent marshes during their first year of life would be more sensitive to temperature than those rearing in a lotic environment with access to thermal refugia. Temperature plays a major role in dictating growth and metabolism for ectothermic organisms such as fish, and an extended period of exposure to elevated temperatures can be lethal (Beauchamp, 2009; Brett, 1952; Richter & Kolmes, 2005). In general, the lakes are not suitable for juvenile coho salmon rearing in the summer due to water quality and predation risk. Rather, they benefit coho salmon by providing high quality overwintering habitat (NMFS, 2016). The relationship between temperature and productivity in this stratum is consistent with limited summer rearing habitat upstream from the lakes, and a temperature-mediated risk of predation in the lakes themselves.

#### 4.4 | Management implications

Our analysis of spatiotemporal trends in Oregon Coast coho salmon productivity yielded information that will be useful for researchers and managers. The time series analysis was indicative of a change in

both productivity trends and coherence in productivity among populations before and after 1990. These changes coincided with a major ocean regime shift, ESA-listing, and other conservation efforts through the 1990s such as decreased hatchery production, decreased harvest pressure, and increased investment in habitat conservation. We acknowledge that less reliable survey methods, uncertainty in population-specific harvest rates, and the relative influence of hatchery and harvest-related stressors prior to 1990 may have influenced our findings; however, results from our study and others are indicative of a mechanistic change point in productivity driven by conservation efforts and marine conditions. Both of these factors have had widespread and measurable effects on salmon (Buhle et al., 2009; Falcu & Suring, 2018).

Spatial patterns of productivity became less variable during the post-1990 period and tracked more closely with marine conditions during the second year of life. Increased coherence in productivity generally signals that broad-scale (marine) drivers have a greater influence on survival and fitness (Ohlberger et al., 2016; Ruff et al., 2017; Zimmerman et al., 2015), and certainly productivity from 1990-onward tracked closely with NPGO. This poses potential challenges to conservation. Managers have little, if any, control over the ocean conditions that salmon experience during their first marine year, and these conditions are becoming more complex with climate change (Abdul-Aziz et al., 2011; Di Lorenzo et al., 2010; Harley et al., 2006; Overland & Wang, 2007). ESU-wide coupling also leads to a reduction in the population “portfolio effect” such that marine conditions can be detrimental if temperature, prey availability, and other factors that impact survival deteriorate for several years at a time (Kilduff et al., 2014, 2015; Schindler et al., 2010). This was most recently observed with the high temperature “blob” off the Pacific Coast of North America (Bond et al., 2015; Di Lorenzo & Mantua, 2016). Conversely, a direct relationship with environmental indicators such as NPGO may be helpful for managers if they can integrate that information along with existing stock-recruitment data to more accurately predict adult returns over the short-term (Burke et al., 2013; DeFilippo et al., 2021; Rupp et al., 2012). Such forecasting methods are error prone in instances where the relationship between productivity and the environment is inconsistent or decouples, as was the case for Oregon Coast coho salmon starting around 2010.

We did not observe a strong relationship between productivity and freshwater rearing conditions, but by no means are these conditions unimportant. For example, the Lakes populations of coho salmon have declined almost continuously since the 1960s and this is likely due to a variety of stressors in the lakes and their surrounding tributaries. Such stressors include climactic shifts in temperature and precipitation, which we tested using the DFA models, or they could be anthropogenic, like barriers to inland migration, eutrophication, and invasive species (Mantua et al., 2010; Rubenson & Olden, 2020; Sheer & Steel, 2006; Wainwright & Weitkamp, 2013). These stressors are not unique to the Lakes stratum and may become more impactful for other Oregon Coast coho populations, especially if marine conditions deteriorate. Freshwater and estuarine

habitat conditions are the lever by which managers influence population productivity and resilience, and they are central to state and federal salmon recovery plans (Lawson, 1993; NMFS, 2016; ODFW, 2007). With respect to marine habitat conditions, the relationship between NPGO and productivity appears to have decoupled to some extent over the last decade. It is uncertain whether this is due to declining freshwater habitat quality for spawning and juvenile rearing, conditions in the nearshore environment, or other environmental variables that we did not measure. Within the Oregon Coast ESU, there are clearly opportunities for robust and diverse management strategies to maximize life history diversity among populations, taking advantage of the unique environmental attributes of coastal watersheds, dendritic coastal lakes, and the Umpqua River basin. The greatest amount of benefit will occur when managers work across multiple spatial scales to bolster productivity and survival (Ohlberger et al., 2016; Ruff et al., 2017). Knowing if, and how, regional- and population-level processes differ, and how they respond to specific environmental factors during freshwater and marine rearing is an important step for managing salmon populations in rapidly changing ecosystems.

#### AUTHOR CONTRIBUTIONS

Melanie J. Davis conceived the project, analyzed the data, and drafted the manuscript. James Anthony conceived the project, provided the data, assisted with data interpretation, and provided comments on the manuscript. Eric J. Ward assisted with analyses and provided comments on the manuscript. Julie Firman and Christopher Lorion provided the data, assisted with data interpretation, and provided comments on the manuscript.

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#### CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

#### DATA AVAILABILITY STATEMENT

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

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#### SUPPORTING INFORMATION

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