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Key Points:
- Changing relationships between primary climate variables and the PDO index indicate the presence of a novel climate in the Gulf of Alaska
- This novel climate had a surprising ecosystem impact, indicated by a change in sign of PDO-salmon correlations
- Tracking changing relationships between primary climate variables and climate indices may be broadly useful for measuring climate novelty

Supporting Information:
- Supporting Information S1

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Quantifying a Novel Climate Through Changes in PDO-Climate and PDO-Salmon Relationships

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Abstract We used changing relationships between primary climate variables and the Pacific Decadal Oscillation (PDO) index to quantify novel climate conditions during rapid warming of the Gulf of Alaska in 2014–2019. Using Bayesian regression, we show that the PDO had a weaker relationship with North Pacific sea-level pressure than in previous decades and was associated with warmer regional temperatures, reduced wind mixing, and weaker alongshore transport. Climate conditions mapping onto the PDO during 2014–2019 appear to be unique in the historical record. The potential for surprising ecological responses to novel climates is highlighted by a switch to unique, negative correlations between the PDO and salmon production, contrasting with positive or neutral correlations during previous decades. Novel climates are emerging globally, and tracking changing associations between primary variables and climate indices may be a useful approach for quantifying both the degree of climate novelty and the potential for surprising ecological responses.

Plain Language Summary Novel climates, or combinations of climate conditions that have not been previously observed in a particular place, can cause surprising outcomes for ecosystem services like fisheries production. We found that during an extreme Gulf of Alaska warming event in 2014–2019, correlations changed between the Pacific Decadal Oscillation index and a variety of climate variables. Compared with previous decades, the Pacific Decadal Oscillation was associated with a weaker Aleutian Low, warmer ocean temperatures, weaker wind-driven mixing of the ocean, and weaker large-scale ocean currents. These individual atmosphere and ocean variables are all important to salmon survival, but this particular combination of those variables had never previously been observed. We also found that the Pacific Decadal Oscillation took on a novel, negative correlation with salmon fisheries production, which is markedly different from the neutral or positive correlations seen in earlier decades. Tracking changing relationships between a climate index, primary climate variables, and salmon catches allowed us to measure the degree of novelty in Gulf of Alaska climate and to summarize the impact of novel conditions on an important ecosystem service. This same general approach may be applicable to the problem of understanding novel climates in other ecosystems.

1. Introduction

Novel climates, or combinations of environmental conditions without a counterpart in the observed record, are a central issue in paleoecology and climate change ecology because of their propensity for producing ecological surprises (Williams & Jackson, 2007). The more that environmental conditions differ from the present, the more poorly that existing ecological understanding will constrain the range of possible ecological outcomes (Maguire et al., 2015; Williams et al., 2007). As anthropogenic climates emerge from the envelope of historical observations, rates of change differ among climate variables, raising the possibility of emerging climate conditions that are novel when compared with the very recent past (Henson et al., 2017; Radeloff et al., 2015). Novel climates present ecologists with two pressing and related questions (Radeloff et al., 2015; Williams & Jackson, 2007): (1) how do we measure the degree of novelty in a climate and (2) how do we understand an ecosystem state that we have never seen before?

Here we advance one approach for addressing these questions in the contemporary Gulf of Alaska (GOA) ecosystem, using probabilistic assessments of changes in the physical and ecological conditions mapping onto the Pacific Decadal Oscillation climate index (hereafter PDO). The PDO is the leading statistical mode in detrended North Pacific sea surface temperature (SST) anomalies calculated for a set reference period (1900–1993; Mantua et al., 1997). During 2014–2019, the GOA experienced unprecedented warm anomalies which climate model experiments indicate would have been impossible absent anthropogenic radiative forcing (Walsh et al., 2018). This GOA warming was part of a northeast Pacific warming event that was also characterized by extreme positive sea-level pressure (SLP) anomalies (SLPAs) that produced unprecedented anomalies in wind mixing, Ekman transport, and sensible and latent heat fluxes (Bond et al., 2015). The simultaneous occurrence of unprecedented conditions in both ocean temperature and atmosphere-ocean interactions suggests that this event represents a novel set of climate conditions, both in terms of extreme values for individual climate variables and combinations of atmosphere and ocean variables that were previously unobserved in the historical record (Litzow, Hunsicker, Ward, et al., 2020).

The objectives of this study are to assess the degree of novelty in combinations of climate variables thought to affect marine survival in GOA salmon (*Oncorhynchus* spp.) and to assess the impact of novel climate combinations on salmon production. Correlations between climate variables and fisheries production in this system are nonstationary, or time dependent, over multidecadal time scales (Litzow et al., 2018; Litzow, Hunsicker, Bond, et al., 2020; Puerta et al., 2019). This prior history of time-dependent relationships appears to be related to changing combinations of atmosphere and ocean climate variables after a 1988/1989 North Pacific Ocean climate shift (Hare & Mantua, 2000). Before that shift, high interannual variance in the Aleutian Low was associated with strong, correlated responses in a number of regional climate variables that are thought to affect salmon survival, including regional SST, SLP gradients, coastal freshwater discharge, coastal salinity, wind mixing, coastal sea surface height anomalies (SSHAs), and gyre-scale advection. Prior to 1988/1989, correlations among these climate variables were strong, the PDO was also strongly correlated with the leading mode of variability in regional climate, and SST and the PDO were skillful predictors of salmon production (Mantua et al., 1997). Interannual variance in the Aleutian Low declined abruptly around 1988/1989, and regional climate variables apparently lost their strong signal of shared atmospheric forcing. Correlations among regional climate variables decayed towards zero, both regional SST and the PDO lost predictive skill for the leading mode of regional climate variability, and correlations between SST/PDO variability and salmon production also decayed towards zero (Litzow et al., 2018; Litzow, Ciannelli, Puerta, et al., 2019). The late 1980s decline in Aleutian Low variance may be part of a transition to novel patterns of extratropical atmospheric variability associated with the increased incidence of Central Pacific El Niño events (Di Lorenzo et al., 2010; Yeh et al., 2009). Declining Aleutian Low variance was centered on the late 1980s, generally supporting the hypothesized link to decaying SST/PDO correlations with salmon (Litzow et al., 2018; Litzow, Hunsicker, Bond, et al., 2020), but difficulty in determining the exact timing of changing interannual variance suggests caution in interpreting a single causative change point.

Anomalous Aleutian Low conditions during 2014–2019 (positive SLPA values) motivate us to ask if relationships between the PDO, GOA climate variables, and salmon production have again changed, beyond the 1988/1989 changes outlined above. Using Bayesian regression to resolve time-dependent relationships, we pursue two specific goals in this study: (1) determine the degree to which GOA climate patterns related to the PDO are novel during 2014–2019 and (2) evaluate the effects of these novel climate combinations on Alaskan salmon production.

2. Materials and Methods

As the measure of fisheries production for this study, we used commercial catch data from 1965–2019 for pink, sockeye, and coho salmon (*O. gorbuscha*, *O. nerka*, and *O. kisutch*, respectively). Justification for using fisheries production (catch) instead of population productivity (recruits produced per spawner) is presented in the supporting information. Production for genetically isolated odd and even year pink salmon populations has diverged over recent years (supporting information), and we analyzed these lineages separately.

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Climate data included the PDO and mean GOA SST from ERSSTv5 (Huang et al., 2017). Winter (November-March [NDJFM]) mean values were used for each, matching the season of low-frequency variability. We used winter (NDFJM) values of the North Pacific Index (NPI, area-weighted SLP over 30°–65°N, 160°E–140°W) as a measure of the strength of the Aleutian Low (Trenberth & Hurrell, 1994). To measure regional manifestations of large-scale climate patterns, we selected climate variables previously associated with marine survival in GOA salmon that were available at relevant time scales (beginning no later than the early 1970s through 2019). No regional ocean model available over this time scale accounts for variable coastal freshwater discharge, a critical process in GOA oceanography (Weingartner et al., 2005). Accordingly, we used a mix of one observational time series (20-m salinity at the GAK1 site), variables from global data assimilation models (first principal component [PC1] of GOA SSHA, total GOA wind stress), and one model-derived metric of gyre-scale advection (the Papa advection index) as our measures of regional climate variability. Because global data assimilation models do not account for coastal processes, we used GOA-wide outputs from these models rather than trying to isolate finer-scale dynamics. These climate variables track regional processes that respond to Aleutian Low/PDO variability: alongshore transport in the Alaskan Stream (offshore SSHA gradients captured by PC1), water column mixing, orographic precipitation, and freshwater discharge (wind stress; Henson, 2007); gyre-scale advection and bifurcation in the West Wind Drift (Papa index; Malick et al., 2016); and baroclinic transport and water column stratification (coastal salinity; Henson, 2007; Weingartner et al., 2005). These variables showed strong statistical relationships with salmon productivity prior to 1988/1989 (Litzow et al., 2018), supporting hypothesized mechanistic relationships (Gargett, 1997; Malick, Cox, Mueter, & Peterman, 2015; Malick et al., 2016; Mueter et al., 2002). However, collinearity among the individual processes precludes an assessment of which are the most important drivers of survival (Dormann et al., 2013; Malick, Cox, Peterman, et al., 2015; Satterthwaite et al., 2020). The Papa advection index reflects winter patterns (December-February), and we used winter-spring (February-April [FMA]) values of SSHA PC1, wind stress, and salinity, corresponding to the onset of stratification that sets up the spring bloom (Henson, 2007; Malick, Cox, Mueter, & Peterman, 2015).

We divided data into three eras for analysis: catch years 1965–1988, 1989–2013, and 2014–2019. While different break points could be used, our objective was to test the a priori hypothesis that variables mapping onto the PDO during the 2014–2019 warming event differed from those during the eras of high variance (1965–1988) and low variance (1989–2013) in the Aleutian Low. Catch data were lagged by 1 (pink and coho) or 2 years (sockeye) to match the lag between catch and ocean entry, when survival is sensitive to ocean conditions (Beamish & Mahnken, 2001). Salmon catches are most strongly correlated with climate over a 3-year time period, reflecting conditions the year before, year of, and year after ocean entry (supporting information; Litzow et al., 2018). Accordingly, SST and PDO values were smoothed with a 3-year running mean prior to analysis. This smoothing is consistent with climate effects across multiple life history stages in salmon (Crozier et al., 2008; Malick, Cox, Peterman, et al., 2015; Satterthwaite et al., 2020). We assess the robustness of all presented results to this smoothing.

We began our analysis by using maps of correlations between salmon catches and North Pacific SST to identify large-scale climate patterns associated with salmon production in each era (Kilduff et al., 2015). We then used Bayesian regression to quantify the degree of novelty in relationships between individual climate variables and the PDO. We modeled each of the primary climate variables as a linear function of the PDO with era-specific slopes and intercepts. The posterior densities for regression intercepts provide probabilistic estimates for era-specific expected values of the primary climate variable when the PDO is at its mean value, while era-specific slopes quantify differences in climate-PDO correlations among eras. The degree of novelty in climate conditions mapping onto the PDO was quantified both as a standardized difference in the posterior means between eras, akin in concept to effect size, and in the degree of overlap among era-specific posterior distributions, which can be thought of as a measure of confidence that the distribution has changed (Pastore & Calcagni, 2019).

To quantify the impact to salmon fisheries of novel climate conditions mapping onto the PDO, we used Bayesian regression with salmon catch as the response variable and the PDO as the explanatory variable. This model estimated era-specific intercepts and slopes hierarchically, with global estimates as well as species-specific deviations from the mean effect. Details on data sources and analysis are presented in the supporting information.

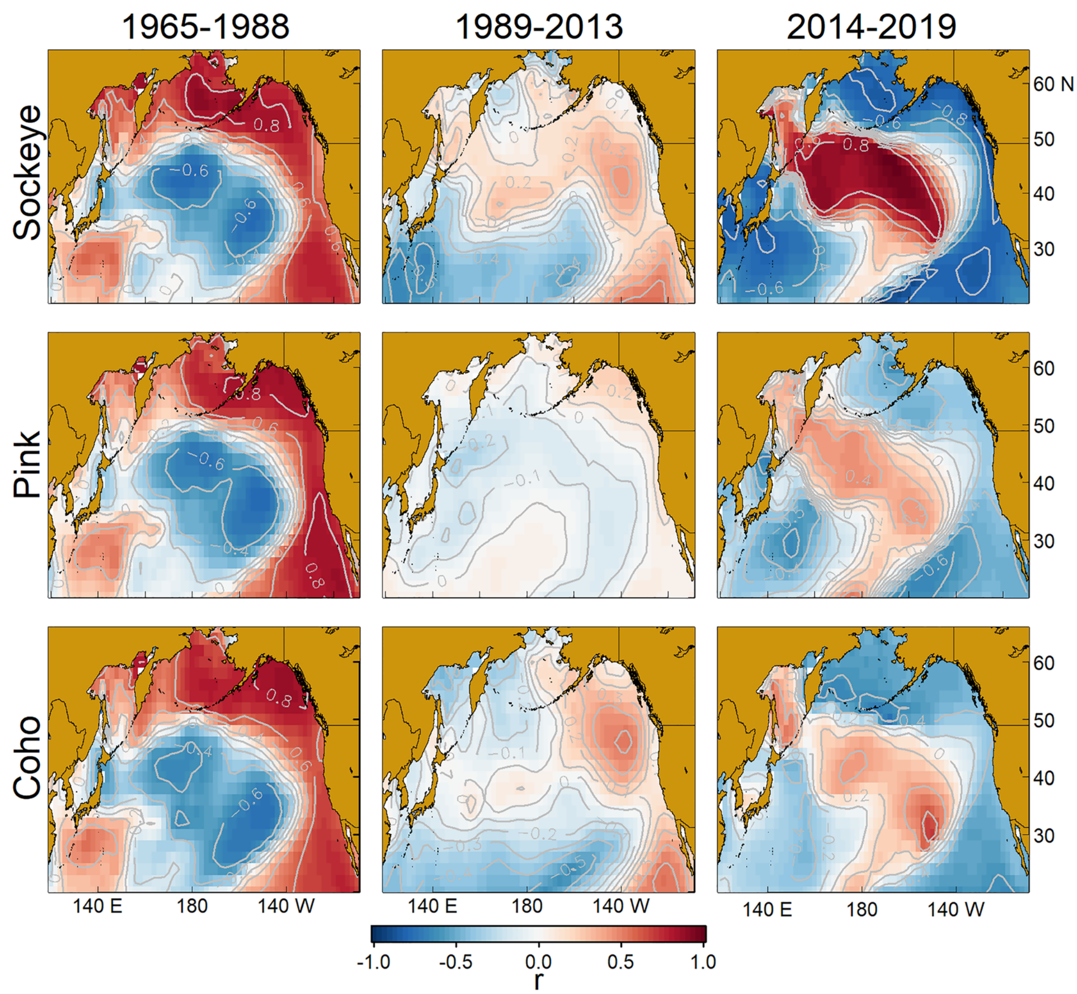

Figure 1. Correlations between Gulf of Alaska salmon catches (lagged to ocean entry) and winter (NDJFM) North Pacific sea surface temperature (smoothed with 3-year running mean) for each species-era combination. Note patterns resembling PDO-positive state prior to 1988/1989, neutral relationship during 1989–2013, and PDO-negative state during 2014–2019.

3. Results

Catch-SST correlations suggest three distinct relationships between GOA salmon production and basin-scale climate during the three eras we examined. Correlations during catch year 1965–1988 are similar to the PDO-positive state for all three species (Figure 1), consistent with the 20th century paradigm of increased Alaskan salmon production during positive PDO phases (Mantua et al., 1997). During 1989–2013, correlation maps indicate a weaker relationship with SST, consistent with declining SST-production and PDO-production relationships with reduced Aleutian Low variance (Litzow et al., 2018; Litzow, Ciannelli, Puerta, et al., 2019; Litzow, Hunsicker, Bond, et al., 2020). For 2014–2019, correlation maps begin to resemble a PDO-negative state, with catch being negatively (positively) correlated with alongshore (central North Pacific) SST anomalies (Figure 1). This result suggests the potential for a transition to novel, negative PDO-salmon relationships during the 2014–2019 warming event.

To better understand this apparent change in the relationship between salmon production and large-scale climate patterns, we tested for novel relationships between the PDO and individual climate variables during 2014–2019. Scatter plots suggest that relationships with four primary climate variables changed during this time (NPI, SST, SSHA PC1, and wind stress; Figure 2e). The largest differences involved changing intercepts in the relationship, rather than the slope (Table 1). Compared with previous observations, in 2014–2019, the

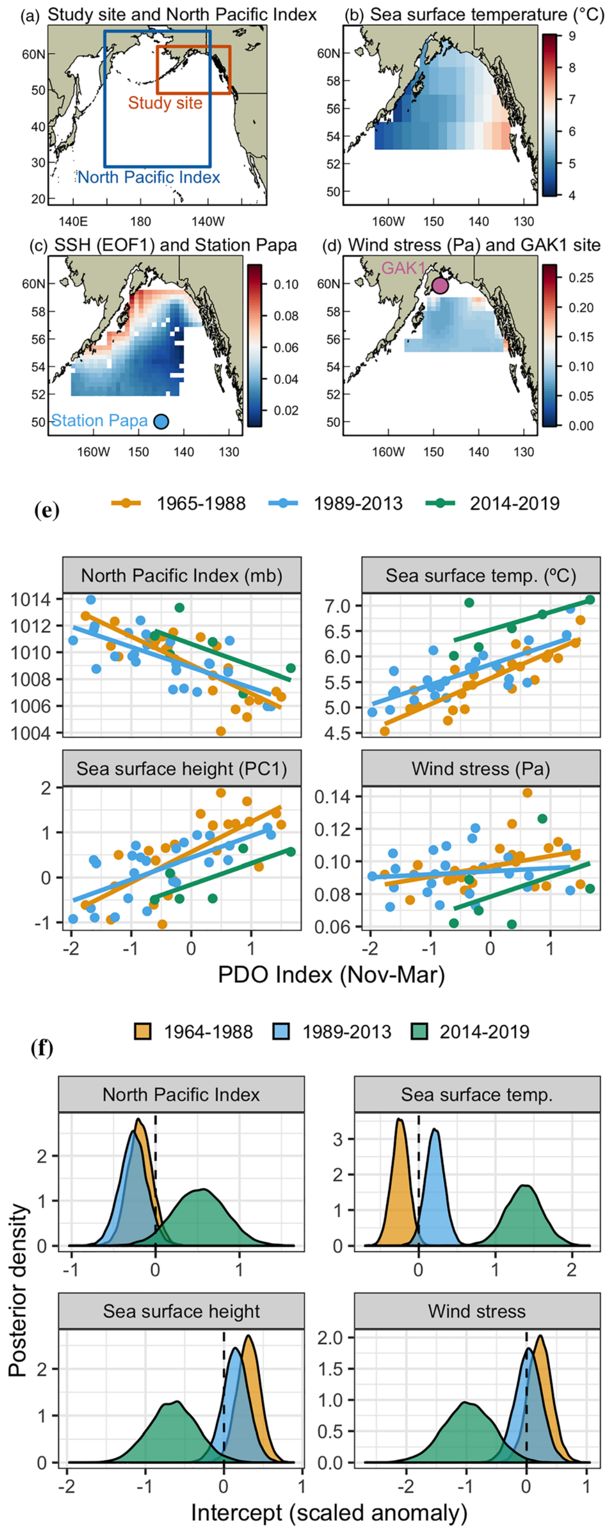

Figure 2. Nonstationary relationships between the PDO index and primary climate variables. Spatial extent of climate data: (a) study site and NPI area; (b) SST (NDJFM mean); (c) SSH EOF1 (FMA) and Ocean Station Papa; (d) total wind stress (FMA mean) and GAK1 site. (e) Scatter plots showing best linear relationship to PDO for each era; (f) era-specific intercepts as estimated by Bayesian regression models. For GAK1 salinity and Papa advection results, see supporting information.

PDO predicted weaker atmospheric forcing associated with the Aleutian Low (NPI), warmer GOA SST, weaker alongshore transport (lower SSHA PC1 values), and reduced wind mixing (Figure 2f). Overlap between posterior distributions for intercepts during 2014–2019 and other years was ≤7.9% for all four variables, indicating meaningful changes in the relationship to the PDO (Table 1). Similar era changes were not seen in regression slopes of relationships for these four variables, or for the slope or intercept of coastal salinity and the Papa advection index (supporting information).

Finally, we evaluated the impacts of novel climate conditions on salmon production by testing for era-specific relationships with the PDO. Scatter plots of these relationships support the hypothesis of a change in slope between eras suggested by the correlation maps (positive slope in 1965–1988, neutral in 1989–2013, negative slope in 2014–2019; Figure 3a). Bayesian regression results provide strong evidence for a change in the sign of slope: from a 100% chance of a positive slope in 1965–1988, to a 68% (32%) chance of positive (negative) slope in 1989–2013, to a 98.6% chance of a negative slope in 2014–2019 (Figure 3b). Differences among species-specific slopes within an era were negligible (i.e., we observed strong shrinkage towards the mean effect), indicating coherent era changes in responses to the PDO across species. All results were robust to smoothing of SST/PDO values (supporting information).

4. Discussion

The short observation period for the 2014–2019 warming event suggests caution when evaluating our results. However, downscaled global climate model outputs indicate that the GOA has embarked on a period of rapid anthropogenic warming (Walsh et al., 2018), presenting the need to evaluate fisheries impacts from transient, novel climate states. Catch-SST correlations (Figure 1) and PDO-salmon relationships (Figure 3) were similar across species groups, and this coherence across species improves our confidence in findings derived from very short observations. The Bayesian methods we employed provide a rigorous assessment that climate-PDO and salmon-PDO relationships were materially different during the 2014–2019 warming event. More broadly, these results speak to the inadequacy of assuming stationary relationships in the GOA climate-salmon system during anthropogenic change (Wolkovich et al., 2014).

For much of the 20th century, GOA salmon production showed low-frequency anomalies that were out of phase with production in more southern areas (Hare et al., 1999). But after 1988/1989, these inverse production patterns weakened (Litzow, Ciannelli, Cunningham, et al., 2019), and GOA salmon production fluctuated near historical highs regardless of variability in coastal SST and the PDO (Litzow et al., 2018). Our results indicate that the post-1988/1989 hiatus in ocean climate effects apparently came to an end during the 2014–2019 warming event. Salmon production again showed a measurable response to PDO values during this time, and the PDO-salmon relationship took on a novel, negative sign (Figure 3). An extensive literature attempted to develop mechanistic explanations for positive PDO-salmon correlations during the 20th century

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Table 1
Comparison of Time-Dependent Regression Parameters for Relationships of Climate Variables and Salmon Production to the PDO: Overlap Between Era-Specific Posterior Distributions and Standardized Difference (i.e., Difference in Posterior Means, Units of SD)

		2014–2019 vs. 1989–2013		2014–2019 vs. 1965–1988	
Variable	Parameter	Overlap (%)	Standardized difference	Overlap (%)	Standardized difference
NPI	Intercept	5.6	1.16	3.5	1.30
SST	Intercept	2.3	0.93	0.5	1.18
SSHA PC1	Intercept	7.9	−1.03	2.4	−1.41
Wind stress	Intercept	4.5	−1.54	2.5	−1.75
Salmon	Slope	9.9	−0.30	0.0	−1.03

(e.g., Gargett, 1997; Malick, Cox, Peterman, et al., 2015; Mueter et al., 2002). The change in sign of the PDO-salmon relationship provides an intuitive way to grasp the fact that novel climate conditions during 2014–2019 may make preceding mechanistic understanding of climate-salmon relationships outmoded: the sets of climate conditions mapping onto the PDO have changed in a way that apparently changes the ecological "meaning" of the PDO for salmon production.

The PDO is a statistical summary that is driven by a variety of quasi-independent climate processes, so that identical values of the PDO can be created by different combinations of physical conditions (Newman et al., 2016). A variety of relevant changes appears to have occurred in the northeast Pacific atmosphere-ocean climate system in 2014. The PDO is calculated from detrended SST data, so the nonstationary PDO-SST relationships we observed are expected as the North Pacific warms. However, changes in other variables mapping onto the PDO also accompanied the warming event. Perhaps most fundamentally, 2014 marked a step-like increase in the NPI relationship to the PDO. The years of 2014 through 2019 included the usual negative NPI-PDO correspondence (Newman et al., 2016), but the overall increase in SLP—a weakening of the Aleutian Low—has resulted in the new functional relationship illustrated in Figure 3e. This transition was accompanied by concomitant shifts towards reductions in wind stress and alongshore transport, as indicated by SSHA PC1.

We are of the opinion that these changes in climate-PDO relationships are meaningful and merit consideration. Importantly, these changes are of a different nature than those that occurred around 1988/1989. Previous analysis showed a change in slope between the PDO and the leading statistical mode of GOA climate after 1988/1989 (Litzow et al., 2018; Litzow, Ciannelli, Puerta, et al., 2019). In 2014–2019, changing relationships between individual climate variables and the PDO were expressed as a change in the intercept and not the slope, which we relate to the change in Aleutian Low mean state (i.e., extremely positive SLPA; Bond et al., 2015) rather than variance. It bears noting that these results were not consistent across all

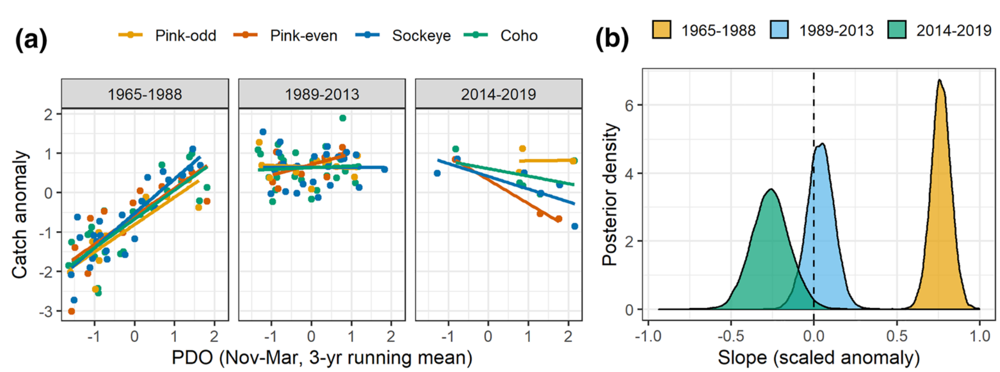

Figure 3. Nonstationary PDO-salmon relationships: (a) scatter plots and best linear fits to salmon catch (lagged to ocean entry) and the PDO index; (b) era-specific slopes of salmon catches on PDO values, as estimated by hierarchical Bayesian regression.

variables examined. Minimal changes were found with respect to the Papa advection and GAK1 salinity. We are unsure of the implications of these results, but they may provide some hints for future research.

These changes in atmospheric forcing associated with the PDO, and resulting changes in ocean variables mapping onto the PDO, provide a plausible mechanistic explanation for changing PDO-salmon relationships. Reductions in wind mixing and alongshore transport associated with PDO variability may have deleterious effects on higher trophic level species such as salmon due to bottom-up trophic processes (prey availability). Decreased wind mixing and reduced transport are associated with lower coastal nutrient supplies and may impact the onset of spring stratification and spring bloom timing or intensity (Henson, 2007; Stabeno et al., 2004). It bears noting that the increase in SLP in 2014 was greatest in the western and central GOA, where the net change has been reduced wind speeds from a more southeasterly mean direction (Bond et al., 2015). These novel wind conditions mapping onto the PDO conceivably disrupted the conditions that previously made a PDO-positive state favorable for GOA salmon. In addition, we cannot dismiss the role of direct temperature as a driver of reduced production. There are thermal limits on salmon distributions through direct mechanisms such as increased metabolic rates. However, SST values in the GOA did not exceed temperatures commonly observed for the high seas distribution of the species we consider (Abdul-Aziz et al., 2011; supporting information), suggesting a limited role of direct temperature effects in the GOA to date. Simultaneous bottom-up and top-down trophic effects may have severely depleted forage resources during the warming event (the "ectothermic vise"; Piatt et al., 2020). This effect would be felt by returning adult salmon, which justifies grouping catch years from 2014 (the first returning cohort to experience extreme warm anomalies) onwards. This results in cohorts exposed to only a single year of novel climate conditions being analyzed as a group with cohorts exposed at multiple life history stages, and reflects uncertainty in the exact pathway by which climate affects salmon (Crozier et al., 2008; Malick, Cox, Peterman, et al., 2015; Satterthwaite et al., 2020). We also cannot rule out the role of management changes, such as the cessation of international fisheries within the 200 nautical mile limit, which may have contributed to the statistical relationship between salmon production and the switch to PDO-positive conditions in the 1970s, the role of competition from hatchery-produced pink salmon on other salmon species (Connors et al., 2020; Ward et al., 2017), or other possible community interactions.

5. Conclusions

We used probabilistic statements concerning changing relationships with the PDO to quantify a contemporary novel climate. This method for defining a novel climate avoids subjective categorizations that have plagued similar efforts in ecology; it allows us to quantify different degrees of novelty; and by focusing on primary climate variables thought to affect salmon production, it allows us to focus on dimensions of novelty of interest to a specific ecosystem service (Radeloff et al., 2015). Reshuffling of climate variables makes the assumption of stationary relationships that traditionally informs climate indices obsolete (Litzow, Hunsicker, Bond, et al., 2020). Climate indices were originally advanced as a tool for reducing complex patterns of climate variability into a single variable (Stenseth et al., 2003). Our approach proposes that in a world increasingly defined by nonstationarity, climate indices can be used to track change in relationships among climate variables.

A 25-year period of neutral ocean climate effects on regional salmon production apparently came to an end in 2014–2019. Climate-salmon interactions took on a surprising form (negative correlation to the PDO) under this novel climate. These results have important and possibly urgent implications for stakeholders in GOA salmon fisheries. Current management practices, such as a high degree of reliance on hatchery salmon, have arisen during the post-1988/1989 period, when both hatchery and wild salmon were largely unaffected by ocean climate (Litzow et al., 2018; Malick, 2020). Past experience in the southern range of Pacific salmon indicates that unanticipated outcomes are possible when management approaches fail to respond to change in the sets of abiotic factors controlling fish production in the system (Schindler et al., 2008).

Conflict of Interest

The authors declare that they have no conflicts of interest.

Data Availability Statement

Data and code are available on Litzow et al. (2020) (https://doi.org/10.5281/zenodo.3722648).

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