

Geophysical Research Letters®



RESEARCH LETTER

10.1029/2024GL113431

Key Points:

- The springtime North Pacific High has been smaller, weaker, and less variable among years over the past decade compared to the long-term average
- Physical and biological conditions have time-varying relationships with basin-scale climate indices
- Short-term ecological trends do not track climate indices, contributing to time-varying relationships

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

M. L. Feddern,
megan.feddern@noaa.gov

Citation:

Feddern, M. L., Ward, E. J., Litzow, M. A., Hunsicker, M. E., Jacox, M. G., Schroeder, I. D., et al. (2025). Quantifying time-dependent climate and ecosystem relationships in the California Current System. *Geophysical Research Letters*, 52, e2024GL113431. <https://doi.org/10.1029/2024GL113431>

Received 21 NOV 2024

Accepted 15 APR 2025

Quantifying Time-Dependent Climate and Ecosystem Relationships in the California Current System

Megan L. Feddern^{1,2} , Eric J. Ward³ , Michael A. Litzow⁴ , Mary E. Hunsicker⁵, Michael G. Jacox^{6,7,8} , Isaac D. Schroeder^{6,8}, William H. Satterthwaite⁹ , Curry J. Cunningham¹, Nicholas A. Bond¹⁰ , Michael J. Malick¹¹ , and Brian J. Burke⁵ 

¹University of Alaska Fairbanks, College of Fisheries and Ocean Sciences, Juneau, AK, USA, ²Fishery Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA, USA, ³Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA, USA, ⁴Alaska Fisheries Science Center, National Marine Fisheries Service, Kodiak, AK, USA, ⁵Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Newport, OR, USA, ⁶Ecosystem Science Division, Southwest Fisheries Science Center, National Oceanic and Atmospheric Administration, Monterey, CA, USA, ⁷Physical Sciences Laboratory, National Oceanic and Atmospheric Administration, Boulder, CO, USA, ⁸Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, CA, USA, ⁹Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Santa Cruz, CA, USA, ¹⁰Climate Impacts Group, University of Washington, Seattle, WA, USA, ¹¹Environmental and Fisheries Sciences Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Port Orchard, WA, USA

Abstract Non-stationarity (time-varying mean or variance) in climate conditions can alter relationships between basin-scale climate indices and the ecological conditions that map onto them. We consider evidence of time-varying climate conditions in the California Current System (CCS) based on sea level pressure dynamics that characterize the North Pacific High (NPH), and evaluate the temporal stability of regional relationships between climate indices and physical and biological conditions across the CCS. We find relationships between climate indices and ecological conditions are relatively stable through time, but do not capture short-term ecological trends. These results show that popular basin-scale climate indices are insufficient in characterizing the North Pacific climate system, especially from ecosystem perspectives. Applications of associations between climate and ecological variables should consider proximate physical forcing mechanisms and the stability of relationships through time.

Plain Language Summary The northeast Pacific has recently experienced abnormal climate conditions, characterized by frequent and severe marine heatwaves, making it difficult to know how species will respond to the environment. We examined how relationships between marine fauna and environmental conditions have changed over the past decade compared to earlier time periods over the past 50+ years. We found that an important atmospheric system, known as the North Pacific High, has been weaker and located further north during the spring upwelling season from 2013 to 2023, when ocean temperatures have been exceptionally warm. This shift impacts weather patterns and ocean currents, which in turn affect marine life and ecosystems. Our research shows that indicators of basin-scale climate conditions do not track short-term trends in upwelling and marine fauna. This means that the relationships between large-scale climate and regional marine ecosystems are complex, making it difficult to predict how marine life will respond to current and future climate conditions without clearer mechanistic understanding.

1. Introduction

Climate indices distill spatially complex or multivariate times series of internal climate variability into single variables (Stenseth et al., 2003) and are widely used in ecology to understand climate-ecosystem interactions. Applications of climate indices often assume temporally consistent (stationary) associations between indices, the environmental forcing mechanisms they represent, and the proximate physical conditions that directly influence ecological responses. However, physical and biological variables can have non-stationary (time-varying) means and variances, and the leading patterns of physical variability summarized by climate indices may themselves be non-stationary (Deser et al., 2010; Williams & Jackson, 2007). These characteristics may lead to environmental

© 2025 The Author(s).

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

and ecological relationships decaying or changing through time (Myers, 1998) and make it challenging to interpret short-term ecological trends from basin-scale dynamics. Moreover, climate indices are constructed over finite intervals due to limits in historical records, which can lead to uncertainties in their robustness. In other words, these indices may not represent true modes of climate variability. Interest in developing forecasts and projections based on climate-biology relationships is growing among ecologists and fisheries scientists, but biological responses are difficult to predict when relationships between covariates change through time or space (Dormann et al., 2013).

Evidence for new interpretations of climate indices in the northeast Pacific is growing, which means the ability of climate indices to describe variability in local physical and biological conditions may be time-dependent. For example, the ecological conditions mapping onto the Pacific Decadal Oscillation (PDO) and North Pacific Gyre Oscillation (NPGO) changed over multidecadal timescales starting in 1989 due to an apparent change in the leading modes of atmosphere-ocean variability. This change was marked by northeast Pacific warming, declining variance of the intensity of the Aleutian Low (AL), and increasing correlation between the PDO and NPGO (Litzow, Hunsicker, et al., 2020; Sydeman et al., 2013; Trenberth & Hurrell, 1994). Most prior evidence of changes in the relationships associated with North Pacific climate indices is based on physical and ecological conditions in the Gulf of Alaska. By way of comparison, relatively stable relationships between the PDO/NPGO and sea surface height, temperature, bifurcation index, and sea level pressure (SLP) fields were observed in the CCS (Litzow, Hunsicker, et al., 2020). On the other hand, local manifestation of El Niño/La Niña has been temporally variable in the CCS due to (a) different tropical expressions of El Niño-Southern Oscillation (ENSO), for example, with Eastern Pacific El Niño events more common prior to 1990 and Central Pacific events predominant from 1990 to 2009 (Yu et al., 2017) and (b) internal variability unrelated to ENSO, which can produce diverse North Pacific responses to similar tropical temperatures (Deser et al., 2018).

Fluctuations in the AL and the North Pacific High (NPH) influence northeast Pacific climate such that the AL intensifies in response to strong ENSO events typically resulting in a positive PDO pattern with warmer than usual northeastern Pacific SST (Giamalaki et al., 2021). In the northeast Pacific, strongly positive temperature anomalies arose during the 2013–2014 winter (Bond et al., 2015) and a second event in 2019, followed by a multi-year period of MHW conditions (2014–2016), causing widespread changes to the food web at all trophic levels (Brodeur et al., 2019; Gomes et al., 2024; Nielsen et al., 2021; Peña et al., 2019). Simultaneously, a strong El Niño event (2015/2016) was associated with increased upwelling-favorable winds in the southern CCS, counter to climatological patterns of past El Niño events of similar magnitude (Jacox et al., 2016). Some studies (Di Lorenzo & Mantua, 2016; Holbrook et al., 2019, 2020) have highlighted connections between Northeast Pacific MHWs and patterns of Pacific climate variability, in particular El Niño conditions in the tropical Pacific (Capotondi et al., 2023) and the role of persistent local atmospheric forcing (Amaya et al., 2021; Bond et al., 2015). These unusual climate conditions, apparent ecological forcing by marine heatwaves, and previous evidence of distinct relationships between PDO/NPGO and environmental conditions in the northeast Pacific since 2013 (Litzow, Hunsicker, et al., 2020), motivate further investigation into the stability of climate-ecological relationships in the CCS particularly over the past decade.

The objective of this analysis is to describe time-dependent climate-ecosystem relationships on regional scales in the CCS. Time-varying relationships between basin-scale climate and ecological responses can manifest through underlying non-stationarity in atmospheric and oceanographic processes coinciding with fundamental changes in regional physical conditions such as wind stress, SSH, and SLP gradients (*sensu* Litzow et al., 2018). Alternatively, time-varying climate-ecosystem relationships can occur when the variability in physical conditions that directly drive ecological trends are not fully represented by basin scale climate indices, especially at the regional scale or over short time periods. We expand previous lines of inquiry by including additional indices relevant to the CCS (Oceanic Niño Index [ONI], North Pacific High [NPH]) and additional years of observational data through 2022. We also evaluate the NPH for evidence of non-stationarity and we expect changes congruent to those observed in the AL. Further, we evaluate how time-varying relationships propagate through the foodweb by comparing climate-biology relationships in addition to regional upwelling-biology relationships which represent more direct forcing mechanisms. Given the importance of upwelling in driving biological production in the CCS, we focus on the upwelling season April–June (García-Reyes & Largier, 2012) and consider regionally-specific relationships across the system.

2. Data and Methods

For each component of this analysis, we were interested in climatological, biological, and environmental conditions during the months of April through June, that is, the early (and key) portion of the primary upwelling season in the CCS. We compared climate and ecological conditions across the three time periods of interest: from 1967 to the change in Aleutian Low variability in 1988 identified in Litzow, Hunsicker, et al. (2020); 1989–2012 which marked increased correlation between PDO and NPGO and 2013 until 2022 when northeast Pacific MHWs increased in frequency and amplitude and the PDO had an apparent change in its relationships with primary climate variables in the Gulf of Alaska (sea surface height, wind stress, sea surface temperature; Litzow, Malick, et al., 2020). See Text S1 in Supporting Information S1 for a complete description of each data set.

2.1. Climate Indices

Climate indices are designed to represent large-scale environmental patterns and often explain a higher proportion of ecological variance than a single local predictor (Hallett et al., 2004). In the CCS, four indices are frequently employed to understand climate forcing as it relates to ecosystem dynamics: PDO, NPGO, NPH, and ONI. The PDO is the dominant year-round pattern of North Pacific sea surface temperature (SST) variability, calculated as the leading EOF/PC of North Pacific monthly SST anomalies poleward of 20°N (Mantua & Hare, 2002). The PDO is a statistical pattern that integrates multiple physical processes, including heat fluxes and wind driven transport related to the AL (Newman et al., 2016), and is commonly related to inverse production regimes of Pacific salmon (*Oncorhynchus spp.*) in the Gulf of Alaska and CCS. Similar to the PDO, the NPGO is a statistical pattern, defined as the second mode of sea surface height variability in the Northeast Pacific, which captures variability in North Pacific gyre strength. The NPGO is associated with regional and basin-scale variations in wind-driven upwelling and horizontal advection, which control salinity and nutrient concentrations important for phytoplankton fluctuations in the CCS (Di Lorenzo et al., 2008).

Unlike the PDO and NPGO, which represent leading spatial modes, the NPH and ONI are derived from mean SLP and SST, respectively, averaged over specific regions of the Pacific. ONI is the primary measure for monitoring the ocean component of ENSO and is calculated as the 3-month running average of SST anomalies in the Niño 3.4 region, which spans from 120°–170°W to 5°S–5°N. ENSO is an important factor modulating upwelling in the CCS, with El Niño conditions tending to be associated with anomalously weak upwelling and warm, shallow source waters (Jacox et al., 2015). The NPH index is the area (km²) bounded by the 1,020 hPa isobar, which is typically located between 0°–50°N and 160°E–110°W although the location, expansion, and contraction of the system varies annually (Kenyon et al., 1999; Schroeder et al., 2013).

Regional atmospheric forcing driven by the position, strength, and timing of the NPH is associated with springtime upwelling (Schwing et al., 2006). Given evidence of time-varying mean and variance of the AL and the relationship between these two systems, we evaluated time-varying means and variance of atmospheric conditions that characterize the NPH by applying methods from Schroeder et al. (2013). Briefly, we used a monthly time series of position and amplitude of the NPH from monthly SLP fields over the domain 0°–50°N, 160°E–110°W. In addition to evaluating the areal extent of the NPH, we consider two additional indices to capture the location and strength of the NPH: (a) position was defined as the center of the area bounded by the 1,020 hPa isobar, and (b) intensity as the maximum SLP value contained within the 1,020 hPa contour while accounting for anisotropic pressure distributions (Schroeder et al., 2013). For all linear models the NPH index is characterized as areal extent.

2.2. Physical and Biological Conditions

We compared the relationship between climate indices and upwelling phenology across time periods to identify how consistently upwelling conditions relate to climate indices through time. We used three phenological indices (Bograd et al., 2009) based on the National Oceanic and Atmospheric Administration's upwelling indices (Bakun, 1973; Schwing et al., 1996) to evaluate relationships to the timing and magnitude of upwelling: total upwelling magnitude index (TUMI), spring transition index (STI), and length of upwelling season index (LUSI). Data sets were compiled for six locations in the California Current (Figure 1), which were assigned to one of three regions, northern (NCC), central (CCC), and southern (SCC) (Figure 1), based on biological and physical transitions and correlations across locations (Figures S3 in Supporting Information S1). Standardized anomalies

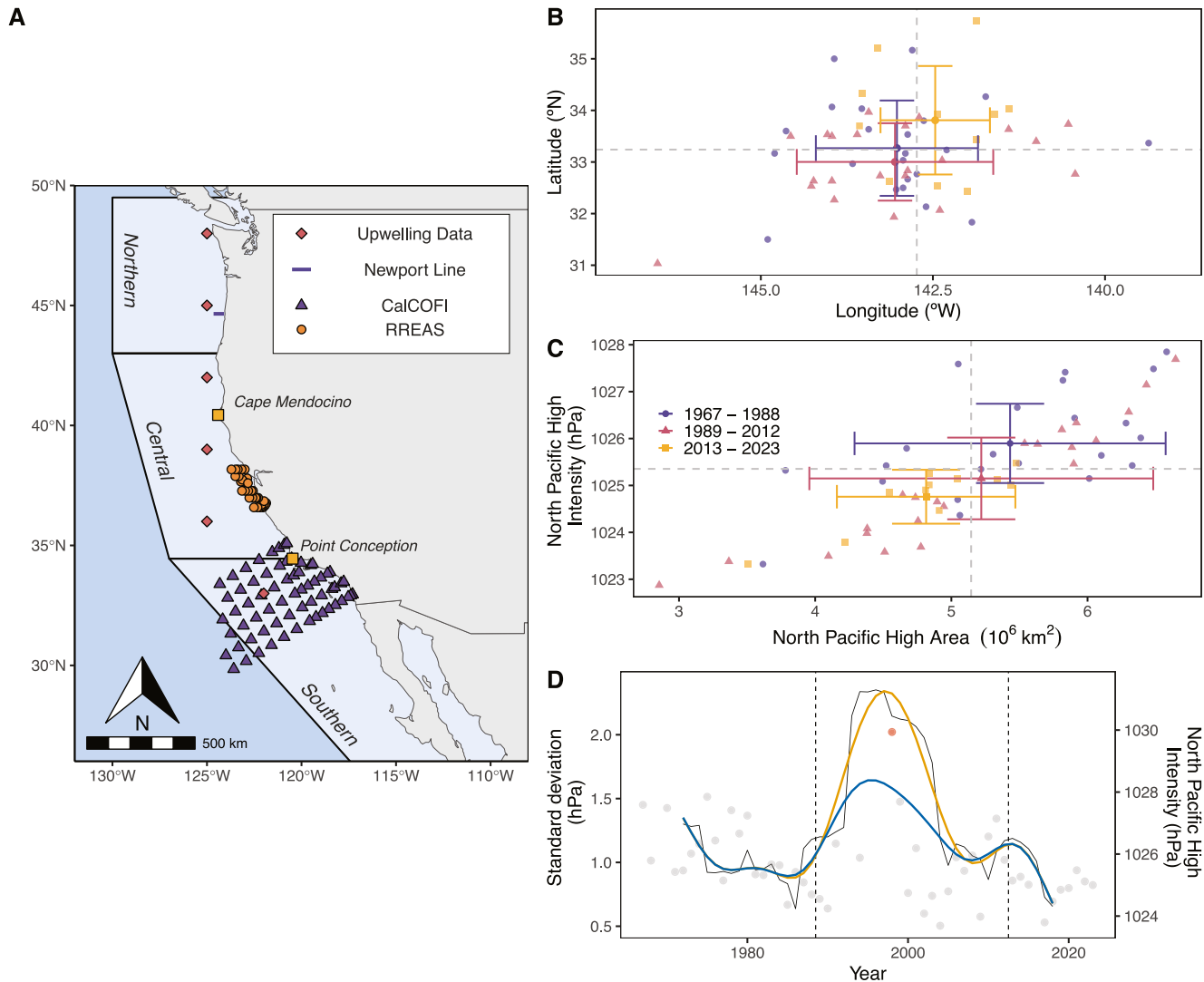


Figure 1. (a) Locations of biological sampling and upwelling indices in the California Current System included in this study. Three California Current regions are delineated (black boxes) at Point Conception and north of Cape Mendocino based on known physical and ecological differences and spatial correlations (Text S3, Figures S2, and S3 in Supporting Information S1). (b) Location, (c) intensity (hPa) and area (10^6 km^2), and (d) temporal variance (SD over 11-year rolling windows) of mean springtime (April–June) conditions of the North Pacific High-pressure system (black line) with trend lines (nonparametric linear regressions) illustrating the inclusion of an outlier in 1998 (orange) and exclusion of 1998 (blue). Points (b–d) are annual observations and period-specific means (1967–1988, purple; 1989–2012, red; 2013–2023, yellow) with tails denoting 1 SD. Dashed lines show (b) the 1967–2023 mean location, (c) 1967–2023 mean intensity and area, and (d) the breaks between 1988/1989 and 2012/2013 periods.

for each upwelling data set were calculated by taking the mean value across sites for each region, removing the long-term (1967–2022) mean for each region, and dividing by the standard deviation.

We summarized community abundance indicators for each region by identifying taxa we expected to respond to environmental change over 0–1 year. To characterize biological conditions in the NCC, we used monthly biomass anomalies for northern and southern copepods along the Newport Hydrographic Line (Fisher et al., 2015). Copepod abundance anomalies are related to El Niño/La Niña conditions and upwelling in the NCC and are expected to respond to changes in climate indices in 3–6 months. Using monthly copepod biomass anomalies (1996–2022) (Fisher et al., 2015) we compared the mean copepod abundance anomaly in summer (July–August) to climate index conditions in the springtime (April–June) to account for the expected temporally lagged response.

To characterize biological conditions in the CCC and SCC, we used data from the Rockfish Recruitment and Ecosystem Assessment Survey (RREAS, Field et al., 2021; Santora et al., 2021), which occurs during late spring, and the California Cooperative Oceanic Fisheries Investigations (CalCOFI), which occurs during spring and summer (Figure 1). We used a dynamic factor analysis (DFA) to summarize biological conditions in the CCC from RREAS (1984–2022) and SCC from CalCOFI (1968–2022) surveys following the methods in Hunsicker et al. (2022) to generate a community abundance indicator (latent trend) for each survey (Text S3 in Supporting Information S1). Data sets were updated through 2022 and a separate DFA was fit to each survey (Figure S5 in Supporting Information S1). We compared each community abundance indicator to the springtime climate indices and also considered the relationship with winter climate indices (Figures S11 and S12 in Supporting Information S1) and with a 1-year lag (Figures S13 and S14 in Supporting Information S1) to account for changes in biological conditions that may exhibit more delayed responses. We also evaluated the sensitivity of our results to extreme observations by comparing model parameters with and without potential leverage years (Figures S15 and S16 in Supporting Information S1). Finally, we compared the relationship between community abundance indicators and upwelling. We expected the biology-climate relationships to be more variable through time than biology-upwelling relationships due to the indirect nature of climate-foodweb forcing and the different spatial and temporal scales at which food webs respond to regional physical drivers relative to basin-scale climate.

2.3. Bayesian Linear Regression Models

To compare relationships between time periods we used Bayesian linear regressions to quantify the relationships between individual climate indices, and regional upwelling conditions and community abundance indices following the methods of Litzow, Hunsicker, et al. (2020). We modeled each of the physical and biological variables as a linear function of the climate indices with period- and region-specific slopes and intercepts. The posterior densities of regression intercepts provide an estimate of period- and region-specific mean expected values of physical and biological conditions. In contrast, the slope parameter represents the strength and direction of the ecosystem-climate index correlations among periods and regions. To quantify similarity in the relationships between time periods, the degree of overlap among period-specific posterior distributions was calculated (Pastore & Calcagni, 2019). Overlap coefficients provide a continuous estimate of the degree of similarity between two probability density functions and are not subject to categorical thresholds of frequentist approaches, thus providing a nuanced comparison of similarities, which motivated our use of Bayesian statistics. Posterior overlaps can be interpreted as the probability two time periods have the same relationship; we consider posterior overlaps of <0.05 (less than 5% probability of being the same) to be substantially different from one another to be considered distinct relationships.

Bayesian regression models used Stan 2.19.1, R 3.6.0, and the rstan package (Carpenter et al., 2017; R Core Team, 2023). Models were fit to data, with three chains run for 10,000 iterations; the initial 1,000 iterations were discarded as a burn-in period. We examined chain convergence and model fits using the potential scale reduction factor ($R < 1.05$), and effective sample sizes ($ESS > 1,000$; Gabry et al., 2019) and found no issues with convergence.

3. Results

Our results show a northward shift of the springtime NPH during the 2013–2023 period (Figure 1b), a general weakening of the NPH (Figure 1c), an increase in variability of intensity occurring between 1988 and 2005 (Figure 1d). For most years since 2013, the location of the NPH is within the prior historical range, however its mean location has shifted nearly one degree, or approximately one standard deviation, farther north during the 2013–2023 period compared to the 1989–2012 period (Figure 1b). For most years during the 2013–2023 period, the NPH was smaller and weaker than the long-term average (Figure 1c). The observed increase in variability between 1988 and 2005 was partially driven by the exceptionally high intensity of 1998 ($lz\text{-score} > 3$, Figure 1d, orange point and line) although the variability in intensity did still increase with this potential outlier omitted (Figure 1d, blue line). Notably, 1998 was one of the strongest El Niño events on record with a quick transition to a strong La Niña during the summer. The changes in variability, intensity, and latitude of the North Pacific High and its associated impact on surface winds suggest that upwelling-climate relationships may be time-varying in the CCS (Schroeder et al., 2013). However, we find relationships between upwelling indices and climate indices were generally consistent through time, particularly in the NCC (Figures 2a and 3a), although there was a moderate increase in the intercept value of TUMI from 2012 to 2023 for the CCC and SCC compared to the earlier time

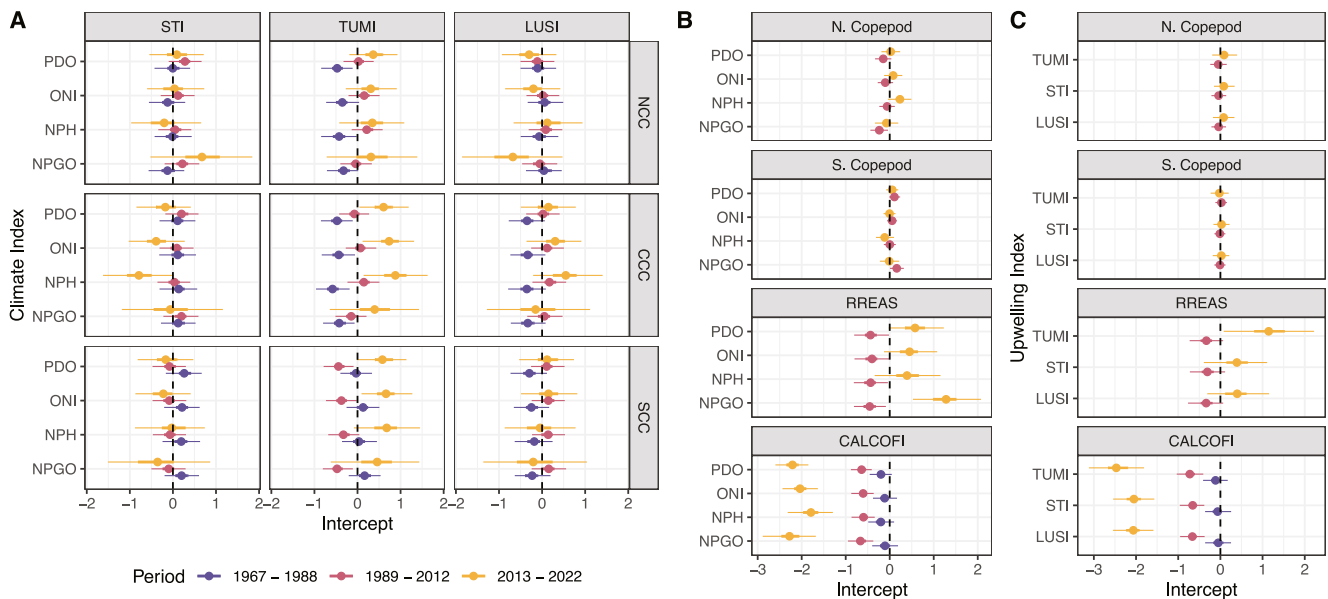


Figure 2. Posterior summaries of the intercepts from Bayesian linear regression models between (a) climate indices and proximate physical conditions described by upwelling indices, (b) climate indices and biological conditions, and (c) upwelling indices and biological conditions. RREAS and copepod data were not available for first period, and thus are not shown on (b) and (c). For all plots points denote the posterior median, thick lines show the 50% highest posterior density credible interval and thin lines show the 95% highest posterior density credible interval for 1967–1988 (purple, period 1), 1989–2012 (red, period 2) and 2013–2022 (yellow, period 3). See Figures S5–S11 in Supporting Information S1 for fits to data. Bayesian credible intervals can be interpreted as the probability a parameter falls within a given range, distributions that do not overlap can be considered time periods with distinct relationships.

periods. TUMI in the SCC and CCC was characterized by an increasing trend from 1980 to 2022 (Figure S2 in Supporting Information S1), and no climate index was able to resolve this trend, resulting in an increasingly positive intercept across time periods for all climate indices.

Biological conditions in the CCC and SCC exhibited trends through time that did not track climate indices, resulting in time-varying intercepts. For CalCOFI, the intercepts were substantially different (<0.01 overlap) for all indices across all time periods with the exception of NPH between 1967–1988 and 1989–2012. Similarly,

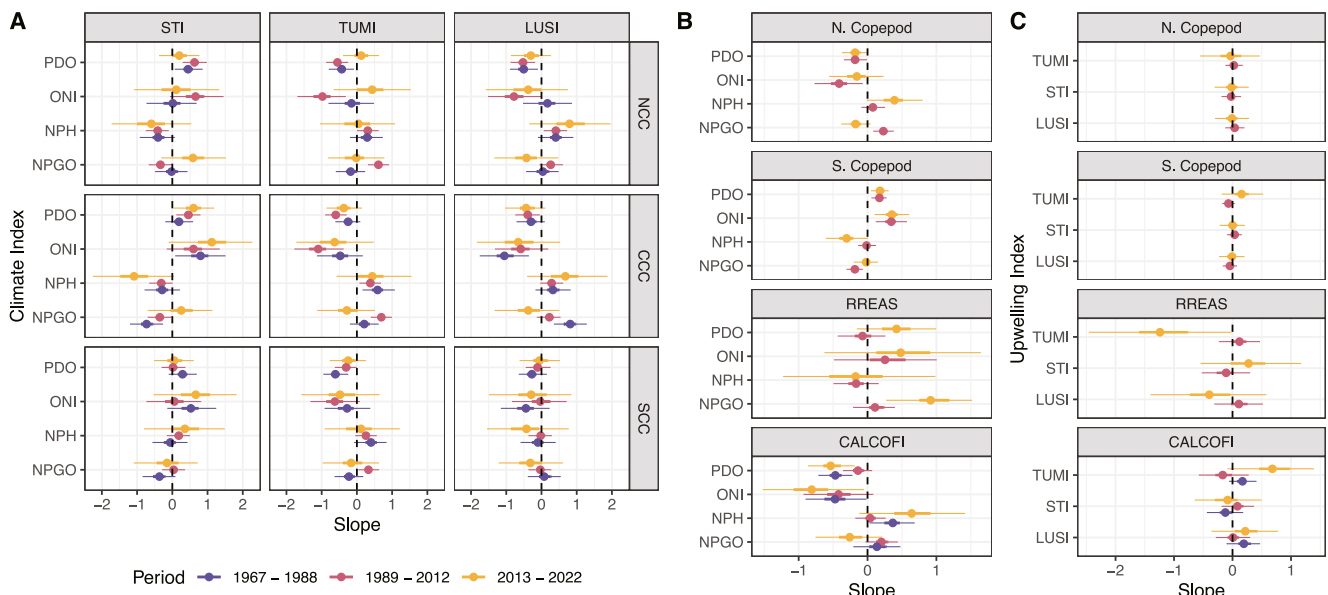


Figure 3. Posterior summaries of the slopes from Bayesian linear regression models. Interpretation is the same as Figure 2.

RREAS had substantial differences in the intercept of the relationship for all climate indices (overlap <0.02) when comparing the most recent two time periods (Figure 2b). We did not observe any substantial differences in the intercepts when comparing climate indices to S. copepod and N. copepod abundance, indicating no changes through time. In addition, there were no differences in the estimates of the slope parameters for any index in relation to biological conditions (Figure 3b). However, we did find the median of the slope estimate for relationships between biological conditions and both upwelling and climate indices was more sensitive to season, inclusion of leverage years, and temporal lag compared to the intercept, but posteriors for each comparison substantially overlapped for most comparisons (Figures S11–S16 in Supporting Information S1). One exception to this was the relationship between S. copepod abundance and climate indices where the estimated slope was highly sensitive to the inclusion of leverage years (Figure S16b in Supporting Information S1).

Despite the expected stability in relationships between upwelling and food web responses, the regional trends in the biology-upwelling relationships (Figure 2c) were similar to those of the biology-climate relationships (Figure 2b). This result indicates that (a) the upwelling indices used here do not fully capture the relevant upwelling dynamics and/or (b) environmental conditions not captured by upwelling are driving patterns in biological conditions through time. Climate indices and upwelling indices both perform inconsistently as correlates of short-term trends in biological conditions in the CCC and SCC.

We find these results are generally robust to temporal lags between biological conditions and climate index, seasonal characterization of climate indices (wintertime versus springtime), removal of leverage years (Appendix S5 in Supporting Information S1). Regardless of the methods applied, we find similar temporal patterns describing climate-ecosystem relationships that impact how climate conditions are interpreted to anticipate ecological conditions.

4. Discussion

The temporal stability of ecological responses to climate indices varies regionally and by response variable in the CCS and relationships between proximate physical conditions and biological responses can be equally susceptible to temporal instability. Previous work found the relationship between PDO/NPGO and proximate physical conditions, specifically SSH, SLP gradients, and temperature, were relatively stable through time in the CCS (Litzow, Hunsicker, et al., 2020) despite strong evidence of time-varying relationships in the Gulf of Alaska between PDO/NPGE and the same physical conditions. The time-varying climate-ecosystem relationships we identified are primarily driven by recent short-term trends in ecological conditions that are not reflected in climate indices. Increasing trends in TUMI in the CCC were documented by climate models and verified by satellite products showing a 25% increase in upwelling winds and associated Ekman transport from 1996 to 2018 (Quilfen et al., 2021) in agreement with our finding of changing intercepts of TUMI in the CCC and SCC. These trends may be associated with the observed northward shift in the NPH over the same time period and its associated relationship with upwelling winds at similar latitudes in early spring (Quilfen et al., 2021; Rykaczewski et al., 2015; Schroeder et al., 2013). In contrast, increasing upwelling trends in the SCC were not documented in other studies (Quilfen et al., 2021) and our findings may be attributed to an inability of Bakun indices to properly represent upwelling, especially in the SCC (Bakun, 1973; Jacox et al., 2018). We note other metrics used to describe NPH conditions such as the location or strength of subsidence (Ding et al., 2023) may be more ecologically relevant than the commonly used index representing the areal extent of the pressure system. Alternative characterizations of NPH dynamics may provide a more temporally robust representation of climate driven ecosystem dynamics in the future, potentially capable of capturing short-term trends.

The oceanographic conditions influencing nutrient availability and primary production in the CCS are complex and driven by dynamics operating across multiple spatial and temporal scales. Upwelling indices are expected to provide more temporally robust relationships with biological conditions given their mechanistic link to regional food web dynamics via nutrient availability. Here, we evaluated upwelling phenology indices (Bograd et al., 2009) representing Ekman transport which is one predictor of nutrient availability to food webs. However, these indices are not able to fully discern atmospheric pressure gradients in SCC in the summer (Bakun, 1973). This limitation may contribute to the observed time-varying relationship between CalCOFI and TUMI and may explain the stable association between the timing of upwelling (LUSI and STI) for the same response variable. Primary production is also regulated via other mechanisms that govern nutrient flux, including stratification and source water properties. For example, Hunsicker et al. (2022) found nitrate flux through the base of the mixed

layer exhibited the strongest relationship with species and community-level responses in the CCC and SCC. Upwelling indices that represent nitrate flux and geostrophic transport (Jacox et al., 2018; Jorgensen et al., 2024) or environmental indices that directly characterize regional transport and source waters (Schroeder et al., 2019) may provide better tools to capture short-term ecological trends, although these data sets come with the analytical costs of limited spatial and temporal extent.

Using climate indices to predict ecological conditions or interpret how environmental conditions impact ecosystems has tradeoffs. Climate indices provide analytical simplicity and consistency across a wide range of research by distilling multiple ecologically relevant conditions into a small number of basinwide, accessible, time series. Nevertheless, it has been shown that ecological relationships with climate indices are not always temporally, regionally, or taxonomically robust (Gosselin et al., 2021; Jacox et al., 2016; Schroeder et al., 2019). Our results show that the consistency of climate index performance through time is specific to the biological and environmental responses of interest. Disparate responses highlight a need for regional, ecologically relevant, metrics to understand their effects across the CCS (Jacox et al., 2016). Region-specific indices with mechanistic links to physical and biological conditions may be more useful for predicting ecological responses to the environment than the magnitude or phase of basinwide climate conditions. When basin-scale climate indices are used to interpret ecological conditions, statistical approaches that account for time-varying relationships (e.g., dynamic linear models, hidden Markov models) should be applied or the implications of assuming time-invariant relationships should be explicitly addressed.

Temporal changes in the way that the PDO and NPGO indices describe Pacific Ocean climate variability (Sydeman et al., 2013; Yeh et al., 2011) and alter the coupling between basin-scale climate and biological processes are well documented, particularly in relation to Pacific salmon (Litzow, Hunsicker, et al., 2020; Malick, 2020; Wainright, 2021). We show evidence of time-varying relationships across additional climate indices (ONI, NPH) as well as regional proximate physical conditions (i.e., TUMI) similar to other studies (Gosselin et al., 2021; Myers, 1998). Time-varying relationships can manifest from underlying non-stationary climate, shifting relative importance of environmental influence on biological indicators, and spatial heterogeneity in pathways linking climate and species abundance, all of which result in temporal patterns in variability or trends that are unresolvable at the basin-scale. Mechanistic modeling approaches and analyses capable of distinguishing stationary data with long-term persistence from a non-stationary process with a deterministic trend (Lins & Cohn, 2011) would advance our understanding on non-stationary climate indices in the northeast Pacific. In any case, the lack of temporal reliability in many physical-biological associations underscores the importance of using mechanistic links to taxon-specific life history strategies to interpret or predict ecological conditions based on physical covariates when possible (e.g., Schroeder et al., 2019).

Overall, coastwide climate indices are insufficient for characterizing the North Pacific climate system from regional ecosystem perspectives but are more stable through time in the CCS compared to the Gulf of Alaska. Determining whether processes are stationary or non-stationary can be difficult with short time series (an unavoidable component of most ecological data sets) as it is common to find both upward and downward trends within a stationary time series (Lins & Cohn, 2011; Myers, 1998). Therefore, associations between physical indices and response variables are highly sensitive to the temporal domain of ecological data sets (Gosselin et al., 2021; Lins & Cohn, 2011; Myers, 1998). We caution against assuming physical-ecological associations are static through space and time especially when using short-term (less than 100 years) data sets. For this reason, we do not recommend applying the associations we identified during the 2013–2022 period to be used to interpret recent or future ecological conditions in the CCS. Re-evaluating ecological relationships with physical conditions as new and longer data sets become available (Myers, 1998) will be important for understanding ecosystem dynamics as global climate change influences atmospheric processes that drive northeast Pacific ecosystems.

Data Availability Statement

Reproducible R scripts and data files to replicate analyses are available in GitHub (https://github.com/mfeddern/Nonstationary_ClimateIndices) and archived with Zenodo (Feddern, 2024). All primary data are from publicly available sources. Monthly climate index data were accessed through publicly available and frequently updated sources: the Pacific Decadal Oscillation and the North Pacific Gyre Oscillation indices available at NOAA National Center for Environmental Information (<https://www.ncei.noaa.gov/pub/data/cmb/ersst/v5/index/ersst>).

v5.pdo.dat), the Ocean Niño Index available at NOAA National Weather Service Climate Prediction Center (https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php), and the NPH Index Data provided by the Climate Analysis, NCAR, Boulder, USA, Trenberth and Hurrell (1994). Updated Regularly. Accessed 08 August 2023 (<https://climatedataguide.ucar.edu/climate-data/north-pacific-np-index-trenberth-and-hurrell-monthly-and-winter>). All upwelling time series and time series collected through the CalCOFI, RREAS, and Newport Hydrographic Line surveys are available through the ERDDAP data server (<https://coastwatch.pfeg.noaa.gov/erddap/index.html>).

Acknowledgments

We extend our gratitude to Aaron Berger, Owen Hamel, Chris Harvey, Brendan Connors, Sean Anderson, Jameal Samhour, John Field, Jennifer Fisher, and Samatha Zeman for helpful feedback, discussions, and support. We thank two anonymous reviewers whose feedback greatly improved the clarity and interpretation of this work. This research was funded by the Northwest Fisheries Science Center Internal Grant Program and partially funded by the Cooperative Institute for Climate, Ocean, & Ecosystem Studies (CICOES) under NOAA Cooperative Agreement NA20OAR4320271, Contribution No. 2024-1375.

References

- Amaya, D. J., Alexander, M. A., Capotondi, A., Deser, C., Karnauskas, K. B., Miller, A. J., & Mantua, N. J. (2021). Are long-term changes in mixed layer depth influencing North Pacific marine heatwaves? *Bulletin of the American Meteorological Society*, 102(1), S59–S66. <https://doi.org/10.1175/BAMS-D-20-0144.1>
- Bakun, A. (1973). *Coastal upwelling indices, west coast of North America, 1946–1971*, NOAA technical report NMFS SSRF-671 (p. 103) U.S. Department of Commerce.
- Bograd, S. J., Schroeder, I., Sarkar, N., Qiu, X., Sydeman, W. J., & Schwing, F. B. (2009). Phenology of coastal upwelling in the California Current. *Geophysical Research Letters*, 36(1), L01602. <https://doi.org/10.1029/2008gl035933>
- Bond, N. A., Cronin, M. F., Freeland, H., & Mantua, N. (2015). Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophysical Research Letters*, 42(9), 3414–3420. <https://doi.org/10.3389/fmars.2019.00212>
- Brodeur, R. D., Auth, T. D., & Phillips, A. J. (2019). Major shifts in pelagic micronekton and macrozooplankton community structure in an upwelling ecosystem related to an unprecedented marine heatwave. *Frontiers in Marine Science*, 6, 212. <https://doi.org/10.3389/fmars.2019.00212>
- Capotondi, A., McGregor, S., McPhaden, M. J., Cravatte, S., Holbrook, N. J., Imada, Y., et al. (2023). Mechanisms of tropical Pacific decadal variability. *Nature Reviews Earth and Environment*, 4(11), 754–769. <https://doi.org/10.1038/s43017-023-00486-x>
- Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., et al. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, 76(1), 1–32. <https://doi.org/10.18637/jss.v076.i01>
- Deser, C., Alexander, M. A., Xie, S. P., & Phillips, A. S. (2010). Sea surface temperature variability: Patterns and mechanisms. *Annual Review of Marine Science*, 2(1), 115–143. <https://doi.org/10.1146/annurev-marine-120408-151453>
- Deser, C., Simpson, I. R., Phillips, A. S., & McKinnon, K. A. (2018). How well do we know ENSO's climate impacts over North America, and how do we evaluate models accordingly? *Journal of Climate*, 31(13), 4991–5014. <https://doi.org/10.1175/JCLI-D-17-0783.1>
- Di Lorenzo, E., & Mantua, N. (2016). Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nature Climate Change*, 6(11), 1042–1047. <https://doi.org/10.1038/nclimate3082>
- Di Lorenzo, E., Schneider, N., Cobb, K. M., Franks, P. J. S., Chhak, K., Miller, A. J., et al. (2008). North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters*, 35(8), L08607. <https://doi.org/10.1029/2007GL032838>
- Ding, H., Alexander, M. A., & Ting, M. (2023). Revisiting the relationship between the North Pacific high and upwelling winds along the west coast of North America in the present and future climate. *Journal of Climate*, 36(23), 8211–8224. <https://doi.org/10.1175/JCLI-D-23-0238.1>
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., et al. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Feddern, M. (2024). mfeddern/Nonstationary_ClimateIndices: Journal submission (version v2) [Dataset]. *Zenodo*. <https://doi.org/10.5281/zenodo.15178048>
- Field, J. C., Miller, R. R., Santora, J. A., Tolimieri, N., Haltuch, M. A., Brodeur, R. D., et al. (2021). Spatiotemporal patterns of variability in the abundance and distribution of winter-spawned pelagic juvenile rockfish in the California Current. *PLoS One*, 16(5), e0251638. <https://doi.org/10.1371/journal.pone.0251638>
- Fisher, J. L., Peterson, W. T., & Rykaczewski, R. R. (2015). The impact of El Niño events on the pelagic food chain in the northern California Current. *Global Change Biology*, 21(12), 4401–4414. <https://doi.org/10.1111/gcb.13054>
- Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., & Gelman, A. (2019). Visualization in Bayesian workflow. *Journal of the Royal Statistical Society - Series A: Statistics in Society*, 182(2), 389–402. <https://doi.org/10.1111/rssa.12378>
- García-Reyes, M., & Largier, J. L. (2012). Seasonality of coastal upwelling off central and northern California: New insights, including temporal and spatial variability. *Journal of Geophysical Research*, 117(C3), C03028. <https://doi.org/10.1029/2011jc007629>
- Giamalaki, K., Beaulieu, C., Henson, S. A., Martin, A. P., Kassem, H., & Faranda, D. (2021). Future intensification of extreme Aleutian low events and their climate impacts. *Scientific Reports*, 11(1), 18395. <https://doi.org/10.1038/s41598-021-97615-7>
- Gomes, D. G., Ruzicka, J. J., Crozier, L. G., Huff, D. D., Brodeur, R. D., & Stewart, J. D. (2024). Marine heatwaves disrupt ecosystem structure and function via altered food webs and energy flux. *Nature Communications*, 15(1), 1988. <https://doi.org/10.1038/s41467-024-46263-2>
- Gosselin, J. L., Crozier, L. G., & Burke, B. J. (2021). Shifting signals: Correlations among freshwater, marine and climatic indices often investigated in Pacific salmon studies. *Ecological Indicators*, 121, 107167. <https://doi.org/10.1016/j.ecolind.2020.107167>
- Hallett, T. B., Coulson, T., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M., & Grenfell, B. T. (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature*, 430(6995), 71–75. <https://doi.org/10.1038/nature02708>
- Holbrook, N. J., Scannell, H. A., Sen Gupta, A., Benthuyzen, J. A., Feng, M., Oliver, E. C., et al. (2019). A global assessment of marine heatwaves and their drivers. *Nature Communications*, 10(1), 2624. <https://doi.org/10.1038/s41467-019-10206-z>
- Holbrook, N. J., Sen Gupta, A., Oliver, E. C., Hobday, A. J., Benthuyzen, J. A., Scannell, H. A., et al. (2020). Keeping pace with marine heatwaves. *Nature Reviews Earth and Environment*, 1(9), 482–493. <https://doi.org/10.1038/s43017-020-0068-4>
- Hunsicker, M. E., Ward, E. J., Litzow, M. A., Anderson, S. C., Harvey, C. J., Field, J. C., et al. (2022). Tracking and forecasting community responses to climate perturbations in the California Current Ecosystem. *PLOS Climate*, 1(3), e0000014. <https://doi.org/10.1371/journal.pclm.0000014>
- Jacox, M. G., Edwards, C. A., Hazen, E. L., & Bograd, S. J. (2018). Coastal upwelling revisited: Ekman, Bakun, and improved upwelling indices for the US West Coast. *Journal of Geophysical Research: Oceans*, 123(10), 7332–7350. <https://doi.org/10.1029/2018jc014187>
- Jacox, M. G., Fiechter, J., Moore, A. M., & Edwards, C. A. (2015). ENSO and the California Current coastal upwelling response. *Journal of Geophysical Research: Oceans*, 120(3), 1691–1702. <https://doi.org/10.1002/2014JC010650>

- Jacox, M. G., Hazen, E. L., Zaba, K. D., Rudnick, D. L., Edwards, C. A., Moore, A. M., & Bograd, S. J. (2016). Impacts of the 2015–2016 El Niño on the California Current System: Early assessment and comparison to past events. *Geophysical Research Letters*, 43(13), 7072–7080. <https://doi.org/10.1002/2016GL069716>
- Jorgensen, E. M., Hazen, E. L., Jacox, M. G., Pozo Buil, M., Schroeder, I., & Bograd, S. J. (2024). Physical and biogeochemical phenology of coastal upwelling in the California Current System. *Geophysical Research Letters*, 51(7), e2024GL108194. <https://doi.org/10.1029/2024gl108194>
- Kenyon, K. E. (1999). North pacific high: An hypothesis. *Atmospheric Research*, 51(1), 15–34. [https://doi.org/10.1016/S0169-8095\(98\)00110-0](https://doi.org/10.1016/S0169-8095(98)00110-0)
- Lins, H. F., & Cohn, T. A. (2011). Stationarity: Wanted dead or alive? *Journal of the American Water Resources Association*, 47(3), 475–480. <https://doi.org/10.1111/j.1752-1688.2011.00542.x>
- Litzow, M. A., Ciannelli, L., Puerta, P., Wettstein, J. J., Rykaczewski, R. R., & Opiekun, M. (2018). Non-stationary climate–salmon relationships in the Gulf of Alaska. *Proceedings of the Royal Society B*, 285(1890), 20181855. <https://doi.org/10.1098/rspb.2018.1855>
- Litzow, M. A., Hunsicker, M. E., Bond, N. A., Burke, B. J., Cunningham, C. J., Gosselin, J. L., et al. (2020). The changing physical and ecological meanings of North Pacific Ocean climate indices. *Proceedings of the National Academy of Sciences*, 117(14), 7665–7671. <https://doi.org/10.1073/pnas.1921266117>
- Litzow, M. A., Malick, M. J., Bond, N. A., Cunningham, C. J., Gosselin, J. L., & Ward, E. J. (2020). Quantifying a novel climate through changes in PDO-climate and PDO-salmon relationships. *Geophysical Research Letters*, 47(16), e2020GL087972. <https://doi.org/10.1029/2020GL087972>
- Malick, M. J. (2020). Time-varying relationships between ocean conditions and sockeye salmon productivity. *Fisheries Oceanography*, 29(3), 265–275. <https://doi.org/10.1111/fog.12469>
- Mantua, N. J., & Hare, S. R. (2002). The Pacific decadal oscillation. *Journal of Oceanography*, 58, 35–44.
- Myers, R. A. (1998). When do environment–recruitment correlations work? *Reviews in Fish Biology and Fisheries*, 8(3), 285–305. <https://doi.org/10.1023/a:1008828730759>
- Newman, M., Alexander, M. A., Ault, T. R., Cobb, K. M., Deser, C., Di Lorenzo, E., et al. (2016). The Pacific decadal oscillation, revisited. *Journal of Climate*, 29(12), 4399–4427. <https://doi.org/10.1175/JCLI-D-15-0508.1>
- Nielsen, J. M., Rogers, L. A., Brodeur, R. D., Thompson, A. R., Auth, T. D., Deary, A. L., et al. (2021). Responses of ichthyoplankton assemblages to the recent marine heatwave and previous climate fluctuations in several Northeast Pacific marine ecosystems. *Global Change Biology*, 27(3), 506–520. <https://doi.org/10.1111/gcb.15415>
- Pastore, M., & Calcagni, A. (2019). Measuring distribution similarities between samples: A distribution-free overlapping index. *Frontiers in Psychology*, 10, 1089. <https://doi.org/10.3389/fpsyg.2019.01089>
- Peña, M. A., Nemcek, N., & Robert, M. (2019). Phytoplankton responses to the 2014–2016 warming anomaly in the northeast subarctic Pacific Ocean. *Limnology & Oceanography*, 64(2), 515–525. <https://doi.org/10.1002/lno.11056>
- Quillen, Y., Shutler, J., Piolle, J. F., & Autret, E. (2021). Recent trends in the wind-driven California current upwelling system. *Remote Sensing of Environment*, 261, 112486. <https://doi.org/10.1016/j.rse.2021.112486>
- R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Rykaczewski, R. R., Dunne, J. P., Sydeman, W. J., García-Reyes, M., Black, B. A., & Bograd, S. J. (2015). Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. *Geophysical Research Letters*, 42(15), 6424–6431. <https://doi.org/10.1002/2015gl064694>
- Santora, J. A., Schroeder, I. D., Bograd, S. J., Chavez, F. P., Cimino, M. A., Fiechter, J., et al. (2021). Pelagic biodiversity, ecosystem function, and services. *Oceanography*, 34(2), 16–37. <https://doi.org/10.5670/oceanog.2021.212>
- Schroeder, I. D., Black, B. A., Sydeman, W. J., Bograd, S. J., Hazen, E. L., Santora, J. A., & Wells, B. K. (2013). The North Pacific High and wintertime pre-conditioning of California current productivity. *Geophysical Research Letters*, 40(3), 541–546. <https://doi.org/10.1002/grl.50100>
- Schroeder, I. D., Santora, J. A., Bograd, S. J., Hazen, E. L., Sakuma, K. M., Moore, A. M., et al. (2019). Source water variability as a driver of rockfish recruitment in the California current ecosystem: Implications for climate change and fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, 76(6), 950–960. <https://doi.org/10.1139/cjfas-2017-0480>
- Schwing, F. B., Bond, N. A., Bograd, S. J., Mitchell, T., Alexander, M. A., & Mantua, N. (2006). Delayed coastal upwelling along the US west coast in 2005: A historical perspective. *Geophysical Research Letters*, 33(22), L22S01. <https://doi.org/10.1029/2006gl026911>
- Schwing, F. B., O'Farrell, M., Steger, J. M., & Baltz, K. (1996). Coastal upwelling indices west coast of North America. *NOAA Technical Report, NMFS SWFSC NMFS SWFSC* (Vol. 231, p. 144).
- Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K. S., et al. (2003). Studying climate effects on ecology through the use of climate indices: The North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1529), 2087–2096. <https://doi.org/10.1098/rspb.2003.2415>
- Sydeman, W. J., Santora, J. A., Thompson, S. A., Marinovic, B., & Lorenzo, E. D. (2013). Increasing variance in North Pacific climate relates to unprecedented ecosystem variability off California. *Global Change Biology*, 19(6), 1662–1675. <https://doi.org/10.1111/gcb.12165>
- Trenberth, K. E., & Hurrell, J. W. (1994). Decadal atmosphere-ocean variations in the Pacific. *Climate Dynamics*, 9(6), 303–319. <https://doi.org/10.1007/bf00204745>
- Wainwright, T. C. (2021). Ephemeral relationships in salmon forecasting: A cautionary tale. *Progress in Oceanography*, 193, 102522. <https://doi.org/10.1016/j.pocean.2021.102522>
- Williams, J. W., & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, 5(9), 475–482. <https://doi.org/10.1890/070037>
- Yeh, S. W., Kang, Y. J., Noh, Y., & Miller, A. J. (2011). The North Pacific climate transitions of the winters of 1976/77 and 1988/89. *Journal of Climate*, 24(4), 1170–1183. <https://doi.org/10.1175/2010jcli3325.1>
- Yu, J. Y., Wang, X., Yang, S., Paek, H., & Chen, M. (2017). The changing El Niño–Southern Oscillation and associated climate extremes. *Climate Extremes: Patterns and Mechanisms*, 1–38.

References From the Supporting Information

- Jorgensen, J. C., Ward, E. J., Scheuerell, M. D., & Zabel, R. W. (2016). Assessing spatial covariance among time series of abundance. *Ecology and Evolution*, 6(8), 2472–2485. <https://doi.org/10.1002/ece3.2031>

- Ohlberger, J., Scheuerell, M. D., & Schindler, D. E. (2016). Population coherence and environmental impacts across spatial scales: A case study of Chinook salmon. *Ecosphere*, 7(4), e01333. <https://doi.org/10.1002/ecs2.1333>
- Stachura, M. M., Essington, T. E., Mantua, N. J., Hollowed, A. B., Haltuch, M. A., Spencer, P. D., et al. (2014). Linking Northeast Pacific recruitment synchrony to environmental variability. *Fisheries Oceanography*, 23(5), 389–408. <https://doi.org/10.1111/fog.12066>
- Ward, E. J., Anderson, S. C., Damiano, L. A., Malick, M. J., Hunsicker, M. E., Litzow, M. A., et al. (2024). bayesdfa: Bayesian dynamic factor analysis (DFA) with 'stan'. *R package version 1.3.3*. Retrieved from <https://fate-ewi.github.io/bayesdfa/>
- Zuur, A. F., Tuck, I. D., & Bailey, N. (2003). Dynamic factor analysis to estimate common trends in fisheries time series. *Canadian Journal of Fisheries and Aquatic Sciences*, 60(5), 542–552. <https://doi.org/10.1139/f03-030>