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Exploring the Relationship Between Zooplankton and Climate in the California Current System

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ABSTRACT

Describing zooplankton distributions in the California Current System is important to understanding its complex ecological dynamics as well as making policy and economic decisions. Zooplankton concentrations are known to vary seasonally, but less is known about how they are affected by long-term climate variability. Using krill concentrations from a coupled biological-physical model, we investigate the relationship between zooplankton hotspots and three modes of climate variability, the El Niño Southern Oscillation, the Pacific Decadal Oscillation, and the North Pacific Gyre Oscillation. We identify three major hotspots within a 300 km coastal band where there appears to be a significant association between krill concentration and these climate indices, also considering the effects of local physical factors. More work is needed to accurately quantify these relationships.

INTRODUCTION

Zooplankton are an important biological component of the California Current System (CCS). As primary consumers, they feed on phytoplankton blooms in the photic zone and are in turn preyed upon by a host of secondary consumers, including, fish, squid, seabirds, and whales. Surface current patterns tend to concentrate nutrients and plankton in certain locations at certain times, forming "hotspots" that attract consumers from great distances. Monitoring these hotspots is of great interest to marine scientists, fisheries managers, and regulatory agencies, as being able to reliably predict hotspot occurrence can aid in the design of marine protected areas and inform assessments of fish populations. Accurately describing zooplankton populations based on *in situ* measurements alone is difficult due to the scale of the CCS, which spans roughly 3000 km from British Colombia, Canada to Baja California, Mexico. However, researchers can also use known ecological relationships and satellite-derived measurements of primary productivity and physical oceanographic parameters to construct models with much larger spatial domains, with the caveat that these models must still be validated by *in situ* measurements.

One such model developed by Messié and Chavez (2017) uses a growth-advection method which accounts for the ecological dynamics of the plankton community as well as the advection of water masses by surface currents. While the model accounts for primary productivity and surface flows as drivers of zooplankton hotspot formation, there are several other physical parameters that could potentially affect the timing and location of hotspots, including regional climate patterns. Seasonal fluctuations represent the primary mode of variability in the California Current ecosystem, but interannual- to decadal-scale variability has been shown to play a significant role in modulating ecosystem dynamics as well (Chavez et al. 2002, Mantua et al. 1997, Di Lorenzo et al 2008). A 100-year EOF analysis of global sea surface temperature (SST) carried out by Messié and Chavez (2011) revealed three modes of long-term climate variability in the Pacific, designated M1, M3, and M4, which are related to established patterns. M1 is the El Niño Southern Oscillation (ENSO); the Pacific Decadal Oscillation (PDO) can be represented by a combination of M1 and M3, and M4 includes the North Pacific Gyre Oscillation (NPGO). The ENSO is an interannual phenomenon, while the PDO and NPGO both occur on decadal timescales. The ENSO and PDO tend to be associated with changes in SST and the NPGO with changes in salinity, nutrients, and chlorophyll, the latter being a proxy for primary productivity (Di Lorenzo et al 2008). Here, we examine the correlations between these climate indices and zooplankton concentrations in the CCS and construct a set of simple linear models relating krill, climate, and several other physical parameters.

MATERIALS AND METHODS

DATA

Monthly 1/8th degree resolution zooplankton concentrations (mmolC m^{-3}) are available as the output of a coupled physical-biological model from April 1993 to May 2021 in the region bounded by 134°W to 114°W and 28°N to 48°N (Messié et al in prep). Zooplankton outputs are grouped by size (small or large); we focus on the large zooplankton, which are analogous to krill. The data were filtered using a 13-term moving average to remove the seasonal signal driven by conditions that favor large-scale phytoplankton blooms from April to August (i.e., upwelled waters that are colder and richer in nutrients and dissolved oxygen relative to surface waters) and whose absence during the winter months is associated with a decrease in primary productivity (see Messié and Chavez 2015, Figure 4). Figure 1 compares "smoothed" and raw krill concentrations, as well as the ENSO, aPDO, and NPGO. The indices used to represent the ENSO [intensity approximated by the multivariate ENSO index (MEI)], PDO, and NPGO are defined by Wolter and Timlin (1993), Mantua et al (1997), and Di Lorenzo et al (2008), respectively. The other parameters considered in this analysis are satellite measurements of chlorophyll (chl), SST, sea level anomaly (SLA), and coastal upwelling. All datasets are summarized in Table 1.

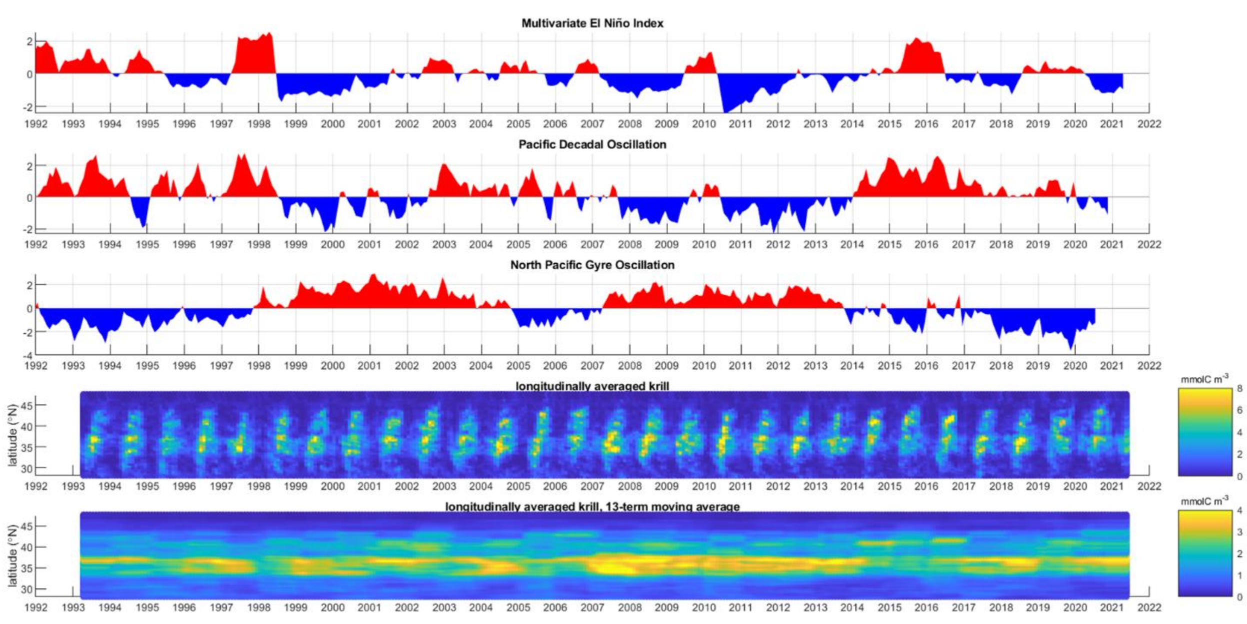

Figure 1. A comparison of the MEI, PDO, and NPGO indices to longitudinally-averaged krill concentrations.

Table 1. Summary of parameters included in the analysis.

Parameter	Abbreviation	Units	Dataset
Zooplankton/krill	-	mmolC m^{-3}	Messié et al (in prep)
Chlorophyll	chl	mg m^{-3}	MODIS
Sea surface temperature	SST	°C	MODIS
Sea level anomaly	SLA	m	AVISO
Coastal Upwelling	-	m^2/s	CCMP vector winds
El Niño Southern Oscillation	ENSO/MEI	-	Wolter and Timlin (1993)
Pacific Decadal Oscillation	PDO	-	Mantua et al (1997)
North Pacific Gyre Oscillation	NPGO	-	Di Lorenzo et al (2008)

CORRELATIONS AND LINEAR MODELS

All parameters were longitudinally averaged within a 300 km coastal band to simplify further computations, with the exception of upwelling (already longitudinally averaged) and the climate indices (time series at a single point). Correlations between krill concentration and each of the predictor variables were then computed every 1/8th degree of latitude (Figure 2). To investigate the combined effect of the variables on krill concentrations, linear models with krill concentration as the response variable were generated using the *fitlm* and *stepwiselm* functions in Matlab. These linear models relate a response variable (krill concentration) to one or more predictor variables in the form of a linear equation, $y = 1 + \beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n$, where y is the response variable, x_i are the predictor variables with coefficients β_i, and n is the number of predictor variables. The stepwise regression procedure begins with an initial model equation and adds or subtracts terms iteratively based on whether doing so generates a model that is significantly different than the previous iteration. The regression conditions were determined to be satisfied based on examination of residual plots. Models were initially fit to data averaged in ½ degree latitudinal increments to determine regions of high predictive power. Subsequent models used data averaged within these regions. The MEI was omitted from the set of predictors due to the fact that much of its variability is also captured by the PDO (Chhak et al 2009). SLA was omitted from the initial iterations of the stepwise regression models due to its similarity to SST (Figure 2) but permitted in subsequent iterations where it improved the amount of variation explained by the model.

RESULTS

LATITUDINAL PROFILES

Statistically significant (p-value < 0.05) correlations exist between krill concentrations and each of the variables under consideration, though the strength of the correlation varies with both parameter and latitude. The correlations for the MEI and PDO are the most similar. Both exhibit a moderate (r ~ 0.4) negative correlation with krill concentration between 32°N and 38°N (Figure 2). The PDO also exhibits weak (r < 0.2), but significant, correlations between 40-43°N. As noted previously, these indices explain much of the same climate variability, so it is not surprising that their latitudinal correlation profiles are so alike. This finding supports the decision to omit the MEI when constructing linear models. Krill concentrations are also moderately correlated with the NPGO within roughly the same latitudinal band (32-41°N), but the correlation is positive rather than negative (Figure 2). The NPGO also displays a weak, negative correlation with krill concentration north of 42°N (r ~ -0.25).

Chlorophyll concentration shows a moderate, positive correlation with krill concentration from 32-45°N (Figure 2). The correlation is strongest (r ~ 0.5) from 32-34°N and north of 38°N. The drop between 34°N and 38°N coincides with peaks in the MEI and PDO correlations. The correlations for SLA and SST are very similar patterns (Figure 2). Both are moderate and negative (r ~ -0.5), and their strength decreases from south to north. Each also displays peaks at 36°N and 38°N where the correlation is slightly stronger (r ~ -0.6) and peak representing a weak, but still significant correlation at 43°N. The correlation between upwelling and krill concentration is the strongest of any of the parameters (r ~ 0.7), with peaks between 32-38°N, 41-43°N, and 44-46°N (Figure 2). The strength of this correlation is to be expected, since upwelling is one of the variables used in the biological-physical model of which krill concentrations are an output. Generally, this analysis reveals two latitude bands within which correlations with krill concentration are strongest, one spanning roughly 32-38°N where all parameters have some significance and the other from 42-48°N where only the NPGO, chlorophyll, and upwelling are significant.

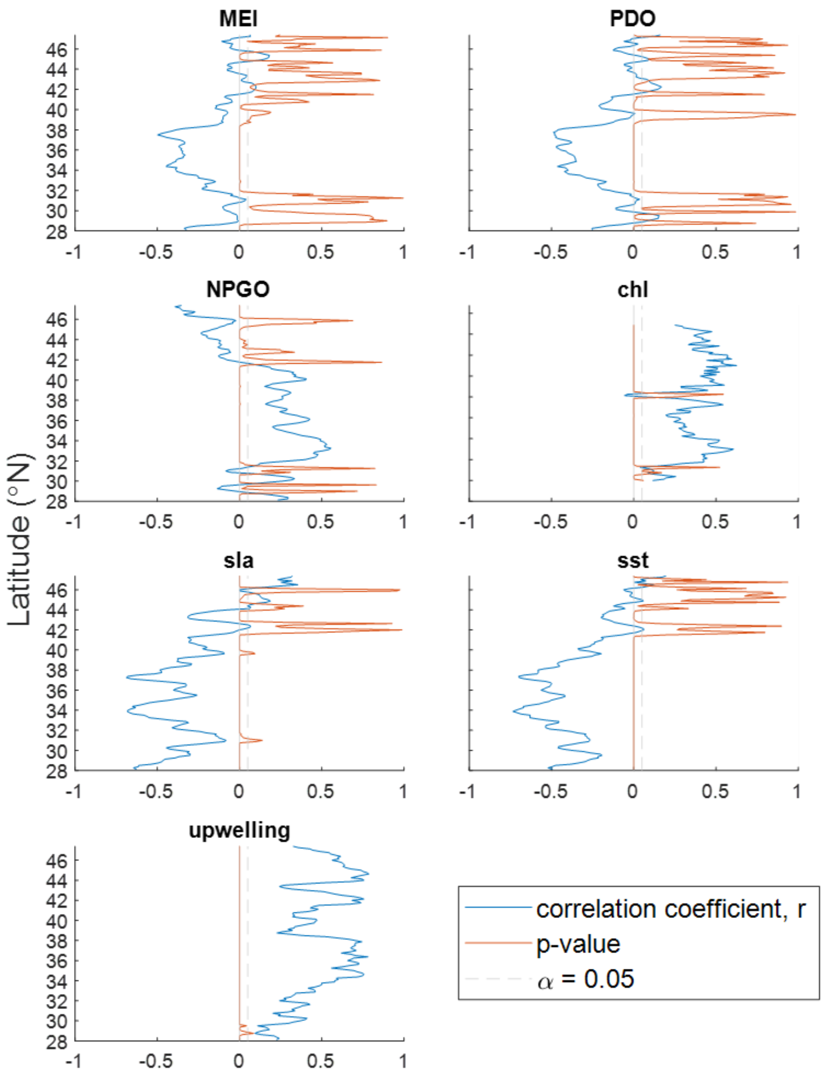

Figure 2. Latitudinal profiles of the correlations between krill concentration and the other variables in Table 1.

REGIONAL HOTSPOTS

Latitudinal incremental models reveal four distinct regions with high predictive power, which coincide with the locations of krill hotspots (Figure 3). The southernmost is not considered for further analysis due to concerns about the reliability of the krill model south of Pt. Conception (~34°N). The remaining three are designated the central (36-38°N), northern 40.5-42.5°N), and northernmost (43.5-44.5°N) hotspots (Figure 3). Regions of high krill concentration in the mean of the annual maximums from April 1993 – May 2021 align reasonably well with boundaries of these hotspots. A one-way ANOVA for the mean predicted krill concentration of the hotspots reveals that concentrations are highest in the central hotspot (3.0292 mmolC m^{-3}), followed by northern (1.8288 mmolC m^{-3}) and northernmost (1.0399 mmolC m^{-3}) hotspots (Figure 4). A follow-up multiple comparison test indicates that each mean is significantly different from the others. The amount of variation explained by the models also varies regionally; the central hotspot model has R^2 = 0.66, the northern hotspot R^2 = 0.59, and the northernmost hotspot R^2 = 0.60.

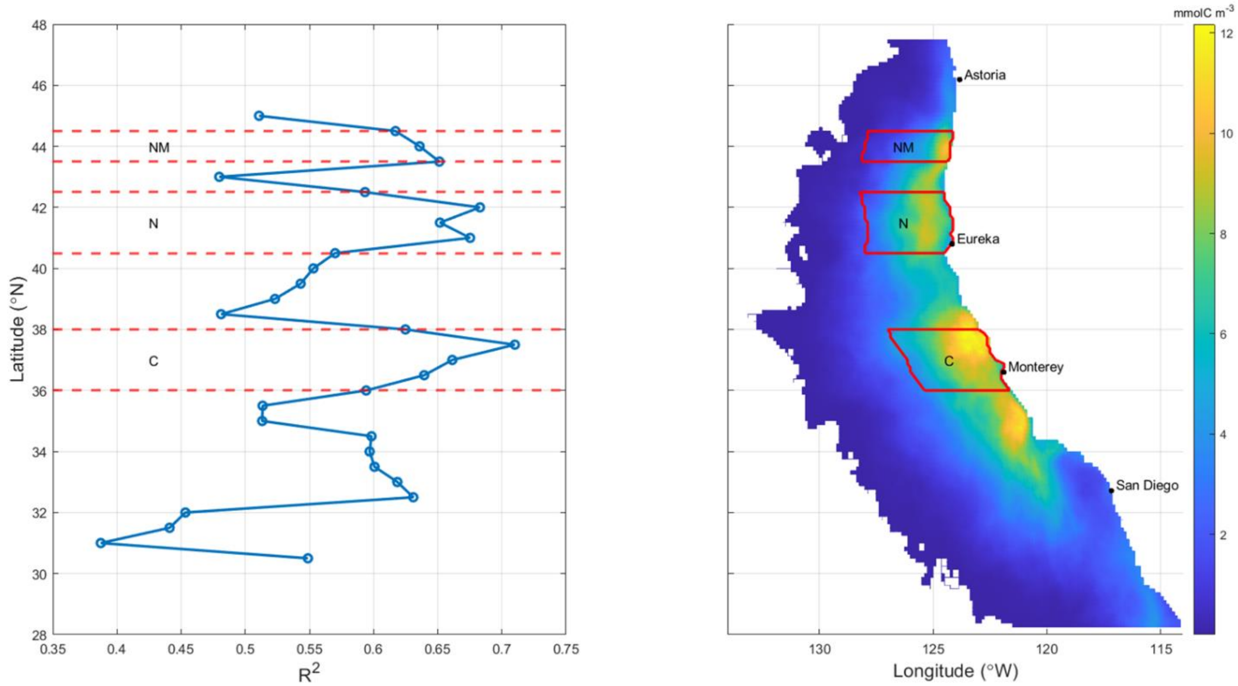

Figure 3. Map showing the central (C, 36-38°N), northern (N, 40.5-42.5°N), and northernmost (NM, 43.5-44.5°N) hotspots withing the 300-km coastal band. Krill concentrations shown are the mean of the annual maximums from April 1993 – May 2021. The R^2 of the incremental models is plotted against latitude for comparison.

The stepwise regression procedure used results in regional models with unique combinations of predictor variables, with chlorophyll, SST, the PDO, NPGO, and the interaction between the NPGO and chlorophyll as common terms among all three models. Upwelling was a significant term in the central and northern hotspot models, while the northern and northernmost models both included terms for SLA, the interaction between chlorophyll and SST, and the interaction between the PDO and NPGO. The interaction terms for chlorophyll with SLA and the PDO are unique to the northernmost model; similarly, the interaction terms for SST with SLA, the PDO, and the NPGO are unique to the northern model. The central model has no unique terms. These findings are summarized in Table 2. To quantify the importance of the PDO and NPGO to the models, we ran the same stepwise regression procedure without these two variables. The variance explained by the models without the PDO and NPGO is noticeably less than the models that include them (central R^2 = 0.61, northern R^2 =0.45, northernmost R^2 =

0.35), and the terms of these models also differ from those that include the two climate indices (Table 3).

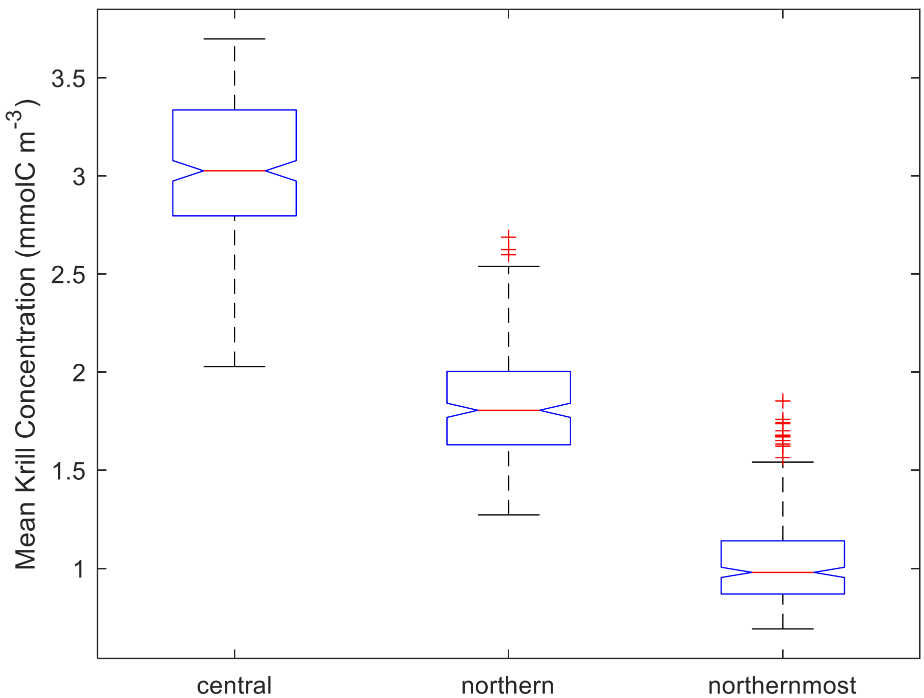

Figure 4. Differences in mean predicted krill concentrations between regions as determined by a one-way ANOVA.

Table 2. Summary of model predictive power and model terms in order of importance.

Region	R^2	R^2 (adj.)	Terms
Central	0.66	0.65	sst, NPGO, chl:NPGO, upwelling, chl, PDO
Northern	0.59	0.57	sst:PDO, PDO, sst:NPGO, NPGO, sst, chl:NPGO, PDO:NPGO, upwelling, sla:sst, chl, chl:sst, sla
Northernmost	0.60	0.59	chl:NPGO, chl, sst, chl:sst, NPGO, chl:PDO, PDO, sla, chl:sla, PDO:NPGO

Table 3. Summary of model predictive power and model terms in order of importance without the PDO and NPGO.

Region	R^2	R^2 (adj.)	Terms
Central	0.61	0.60	chl, chl:sst, chl:sla, sla, sst, upwelling
Northern	0.45	0.44	sla, sla:sst, chl, upwelling, chl:sst, sst
Northernmost	0.35	0.34	chl, sst, chl:sla, sla

DISCUSSION

SPATIAL VARIABILITY

The relative importance of the selected parameters in predicting krill concentrations varies with latitude. The region between 42-48°N, where only chlorophyll concentration, upwelling, and the NPGO show at least a moderate correlation with krill concentration, aligns with the northern and northernmost hotspots identified in the incremental latitudinal analysis. Terms for the NPGO, chlorophyll concentration, and their interaction appear in the model equations for both these hotspots, but northern model equation includes an upwelling term while the northernmost does not. SST is weakly correlated with krill concentration within the northern and northernmost hotspots but is still an important term in both model equations. Though it has a similar correlation profile to SST and also appears in the model equations, SLA is not as important a predictor of krill concentration. There is a term for the PDO in both the northern and northernmost model equations, but it is far more important in the northern model where it coincides with a spike in the correlation profile around 40-41°N.

All of the variables included in the analysis display at least a moderate correlation with krill concentration within the central hotspot, and its equation contains terms for all except SLA, plus a term for the interaction between the NPGO and chlorophyll concentration. The absence of an SLA term could be due to its similarity to SST within in the central hotspot, as the parameters track each other much more closely here than in the northern and northernmost hotspots. The high degree of correlation between SST and SLA could be due to mesoscale eddies in the central hotspot; cyclonic "cold-core" eddies are associated with negative SLA and anticyclonic "warm-core" eddies with positive SLA. Both types of eddies are known to occur throughout the CCS and have also been observed to have significant impacts on plankton distribution (Kurian et al 2011, Chenillat et al 2016). Some eddies are ephemeral features, while others persist for months, and further investigation of the SLA and SST datasets is necessary to determine whether signals associated with eddy features are preserved by the moving average filter and regional averaging techniques used in this analysis. Eddy effects notwithstanding, the parameters considered in this analysis predict krill concentrations in the central hotspot much better than in the northern or northernmost hotspots.

EFFECTS OF CLIMATE

The PDO and NPGO are important predictors of krill concentration in all three hotspots. When the climate indices are omitted from the stepwise linear models, the predictive power of the models is greatly diminished. This reduction is most notable in the northern and northernmost hotspots, where the R^2 decreases from 0.59 to 0.45 and 0.60 to 0.35, respectively. While it is tempting to conclude that the PDO and NPGO account for 14% of the variation in krill concentration in the northern hotspot and 25% in the northernmost hotspot, the stepwise regression process introduces new interaction terms between the non-climate predictors, invalidating this assumption. The same is true for the central hotspot, where the R^2 decreases from 0.66 to 0.60. To better quantify the relative importance of climate (and the other predictor variables) in predicting krill concentration, one should perform an ANOVA for each model to compute the sum of squares for each of the terms in the model equation; this can be accomplished using the *anova* function in MatLab. The ratio of the sum of squares of a term to the total sum of squares (SSTotal = SSRegression + SSError) is the amount of variation in krill concentration explained by that term. This analysis should be performed for each of the three models that include the PDO and NPGO as predictors.

CONCLUSION

Modeling the distribution of krill in the CCS is of interest to scientists, fisheries, and government agencies alike because of its ecological significance. Researchers have employed both *in situ* sampling techniques and remote sensing methods to develop a range of models of varying scope and scale. Here, we examine the outputs of a coupled biological-physical model in relation to modes of long-term climate variability in the Eastern Pacific (PDO, NPGO), as well as several local physical oceanographic parameters (SST, SLA, chlorophyll, upwelling). Computing latitudinal correlation profiles reveals that associations between krill concentration and environmental factors vary regionally and indicate that there are distinct northern and southern regions within the CCS. A series of linear models for averaged latitudinal increments further refines these regions into central, northern, and northernmost hotspots where the relationship between krill concentration and the predictor variables is strongest. Constructing linear models for each of these hotspots using stepwise regression reveals significant differences in krill concentration, the amount of variability explained by the model, and the terms of the model equation between the three regions. These results in and of themselves are intriguing, but further analysis is necessary to better quantify the effects of the PDO and NPGO on krill concentrations and assess how these findings fit into the existing body of literature on krill and climate in the CCS.

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