**ORIGINAL ARTICLE**

# The influence of temperature on Pacific hake co-occurrence with euphausiids in the California Current Ecosystem

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**Abstract**

Understanding the influence of ocean conditions on predator–prey relationships can provide insight for ecosystem-based fisheries management. Pacific hake (*Merluccius productus*) are abundant and commercially important groundfish in the California Current Ecosystem (CCE) that consume euphausiids (krill) as a major prey item. We used data from the biennial joint U.S.-Canada Integrated Ecosystem & Acoustic Trawl Survey for Pacific hake (2007–2019, $n = 8$ surveys) to quantify co-occurrence of age 2+ hake with krill in relation to bottom depth, continental shelf break location, surface chlorophyll-a, and 100-m temperature. Vertical distributions of hake varied among years and were not correlated to krill depth. Hake hotspots occurred primarily off the Oregon coast and near Cape Mendocino, while most krill hotspots occurred in the northern CCE. The probability of co-occurrence was greatest during cool ocean conditions (100-m temperature 1°C below average), averaging 41.0% and extending throughout most of the CCE. During warm ocean conditions (100-m temperature 1°C above average), predicted co-occurrence averaged 17.0% and was concentrated near Cape Mendocino. These results indicate that hake-krill co-occurrence is a function of predator and prey spatial distributions and overall krill abundance. Furthermore, temperature influences hake-krill co-occurrence and may explain some of the variation in hake growth and recruitment to the fishery.

**KEYWORDS**

acoustic trawl survey, climate change, *Euphausia pacifica*, fisheries management, *Merluccius productus*, predator–prey interactions, *Thysanoessa spinifera*

## 1 | INTRODUCTION

Fisheries management can gain insights on short and long-term sustainability by incorporating information about ecosystem components into management decisions (Marshall et al., 2019; Townsend et al., 2019). Commercially important marine fish populations are influenced by dynamic ocean conditions that alter the abundance and distribution of prey populations, which can negatively impact growth

and recruitment to the fishery (Benson et al., 2002; Hunsicker et al., 2013; Wells et al., 2016). For example, increases in temperature are predicted to result in declines in eastern Bering Sea groundfish populations due in part to reduced availability of prey (Holsman et al., 2020). Quantifying relevant environmental factors that influence prey populations, and potential effects on commercially fished species, could help inform ecosystem-based fisheries management efforts, especially given predictions of increasingly variable and warmer future ocean temperatures due to climate change (Brander, 2010; Holsman et al., 2016; Punt et al., 2014).

Pacific hake (*Merluccius productus*; hereafter "hake") are abundant predators along the west coast of the United States and Canada and comprise one of the largest volume single species fisheries in the California Current Ecosystem (CCE) (Ressler et al., 2007). The CCE is a productive coastal ecosystem that extends along the west coast of the United States and Canada (Figure 1). Seasonal upwelling of nutrient-rich cold water supports a diverse food web that includes hake as well as other commercially important fish such as salmon, in addition to substantial populations of seabirds and marine mammals. Hake are generally thought to migrate north from offshore waters in southern California during spring, and form feeding aggregations throughout the CCE during summer, consuming euphausiids, or krill, as a key prey item (Methot & Dorn, 1995; Tanasichuk et al., 1991). While a number of krill species exist in the CCE, *Euphausia pacifica* and *Thysanoessa spinifera* dominate the community (Brinton, 1962, 1967; Brinton & Townsend, 2003) and are the primary species consumed by hake (Tanasichuk et al., 1991). Despite the importance of krill in hake diets, little is known about how shifts in krill abundance may affect hake distribution, growth, and recruitment.

The abundance of both *E. pacifica* and *T. spinifera* is typically enhanced during periods of increased upwelling and primary production in the CCE (Brinton, 1976; Brinton & Townsend, 2003; Cimino et al., 2020). Complex bathymetry along the west coast of the United States and Canada, including a narrow continental shelf with numerous shelf-incising submarine canyons in the southern and central portions of the CCE, and a wider shelf with shallow basins in the northern CCE, interacts with upwelled water to generate strong currents near the shelf and slope. These strong currents can enhance zooplankton density due to the swarming response of krill into dense layers against the currents (Mauchline, 1980; Santora et al., 2011; Siegel, 2000). Large krill aggregations often occur in areas with steeply sloping bathymetry, increasing their availability to hake (Mackas
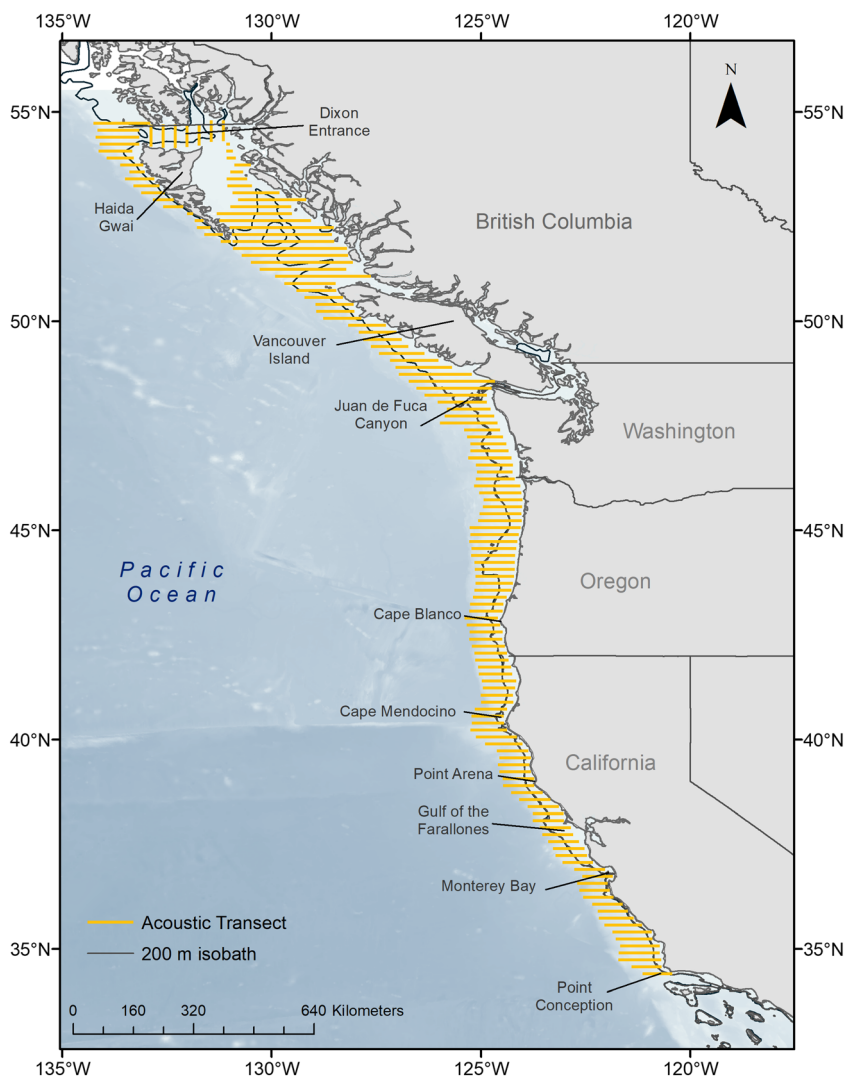


**FIGURE 1** Study area in the California Current Ecosystem, including locations of acoustic transects conducted during biennial joint U.S.-Canada Integrated Ecosystem & Acoustic Trawl surveys for Pacific hake between 2007 and 2019. Geographic points of interest mentioned in the text are labeled.

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et al., 1997; Swartzman & Hickey, 2003; Ware & McFarlane, 1995). This has been demonstrated along the west coast of Vancouver Island, where krill and hake are co-located near basin and submarine canyon edges (Mackas et al., 1997; Swartzman, 2001; Tanasichuk, 1999).

Periods of warmer ocean conditions related to El Niño Southern Oscillation (ENSO) events, delayed upwelling, and marine heatwaves often lead to negative ecosystem impacts for predators and prey, including hake and krill. For example, anomalously warm water and increased poleward transport of surface and subsurface currents during ENSO events in 1983 and 1998 led to shifts in the species composition of zooplankton in the central CCE to lower energy density species (Brodeur, 1986; Marinovic et al., 2002), which negatively influenced juvenile hake growth rates (Grover et al., 2002). Unusually low primary production due to delayed upwelling in 2005 had substantial impacts on zooplankton in the CCE, leading to recruitment failure of multiple fish species and reproductive failure of seabirds in both California and British Columbia (Peterson et al., 2006; Sydeman et al., 2006). During an unprecedented marine heatwave between 2014 and 2016 (Bond et al., 2015; Cavole et al., 2016; Leising et al., 2015), warm water anomalies in surface waters of the CCE were linked to shifts in zooplankton community composition and declines in overall abundance, which negatively impacted the food web (Jones et al., 2018; Peterson et al., 2017; Sakuma et al., 2016). Ocean conditions including ENSO events also influence the extent of hake migrations, with more fish occurring further north when water temperatures are warmer than average and poleward transport is greater (Agostini et al., 2006; Dorn, 1995; Ware & McFarlane, 1995). Northerly movements of hake may relate to improved foraging opportunities in Canada, which can affect their growth and recruitment. For example, a regime shift in 1989 caused above average temperatures and greater relative krill abundances in the northern portion of the CCE, resulting in greater growth rates of juvenile hake in Canadian waters (Benson et al., 2002). Shifts in the abundance of krill may explain variation in the coast-wide distribution of hake, but a lack of data on krill availability throughout the full range of hake distribution in the CCE has precluded direct analyses of hake-krill dynamics.

Surveys that collect simultaneous data on predator and prey populations offer opportunities to evaluate distribution patterns in relation to concurrently observed environmental conditions. In this study, we evaluated the co-occurrence of hake and krill observed simultaneously during biennial joint U.S.-Canada Integrated Ecosystem & Acoustic Trawl Surveys for Pacific hake between 2007 and 2019. We assessed the influence of bathymetry (seafloor depth, location of the continental shelf break), primary productivity (near-surface chlorophyll-a concentrations), and temperature (100-m temperature anomaly) on the occurrence of hake and krill, and predicted how shifts in temperature may influence spatial co-occurrence. Our goal was to produce estimates of hake-krill co-occurrence during different ocean conditions, to inform species distribution models of hake, as well as predictions of hake growth and recruitment to the fishery.

## 2 | MATERIALS AND METHODS

### 2.1 | Survey area and study design

Data for this study were obtained from the National Oceanic and Atmospheric Administration Fisheries Northwest Fisheries Science Center (hereafter, NOAA) and Fisheries and Oceans Canada (hereafter, DFO), which have conducted joint U.S.-Canada Integrated Ecosystem & Acoustic Trawl Surveys for Pacific hake along the west coasts of the United States and Canada since 2003. The biennial surveys were conducted during the summer months (June–September) when hake occurred in feeding aggregations near the continental shelf. All surveys began in the south near Point Conception, California, U.S.A. (34.5°N) and moved north through British Columbia, Canada to Dixon Entrance, Alaska, U.S.A. (54.4°N) (Figure 1). Transects were spaced approximately 16 or 32 km (10 or 20 nmi) apart, and the southern and northern extents, and to a lesser degree offshore extent, were determined by observed hake distribution (Fleischer et al., 2008). We used data collected on surveys during 2007 to 2019 (odd years inclusive, plus 2012) that extended throughout the full study area.

### 2.2 | Predator and prey data

All surveys used downward-facing Simrad EK60 narrow-band, split-beam echosounders to collect synoptic acoustic data at multiple frequencies including 18, 38, 70, 120, and/or 200 kHz. Hake aggregations were detected acoustically and sampled using midwater trawls to verify species composition and assign size and age (Fleischer et al., 2008; Grandin et al., 2020; see Malick et al., 2020, for full details). A target strength-to-length relationship was used to convert hake composite length-frequency distributions to the expected backscattering cross-section ($\sigma_{bs}$) based on sizes sampled by the trawl (Traynor, 1996). Acoustic data were processed using Echoview 9.0 (Echoview Pty Ltd, Hobart, Australia), and acoustic backscatter in each hake aggregation was integrated in 0.5 nmi horizontal by 10 m vertical bins along each transect. Georeferenced mean volume backscattering strength ($S_v$ or MVBS, dB re 1 m$^{-1}$) and integrated area backscatter (nautical-area-backscattering coefficient, $s_A$ or NASC, m$^2$ nmi$^{-2}$) were reported (MacLennan, 2002). Hake length was converted to age using length-at-age calculations derived from otolith analysis (Grandin et al., 2020). Because krill consumption may vary with hake age (Buckley & Livingston, 1997; Livingston & Bailey, 1985), we initially grouped hake into three age groups based on ontogenetic life history stages. Age-2 hake represent immature fish (<50% mature); age-3–4 hake represent a transitional stage between immature and fully mature fish (50% > mature < 100%); and age-5+ hake represent fully mature fish (100% mature; Grandin et al., 2020). However, after visual examination of the spatial distribution of overlap (Figures S1, S2, and S3) and comparisons of the percentage of 25 km$^2$ cells where both hake and krill occurred, there was no clear pattern of differential co-occurrence of hake with krill based on age class (Figure S4), so we grouped all hake ages 2+ together for further analyses.

Krill aggregations were also detected acoustically and identified using methods that are fully described in Phillips et al. (2022). Briefly, to classify krill from acoustic backscatter, we used frequency differencing methods that differentiate the frequency response of krill from other acoustic targets using MVBS at 38 and 120 kHz (De Robertis et al., 2010). The algorithm used a $\Delta MVBS_{120-38}$ range of 10.0–16.3 dB (Phillips et al., 2022). After files were reviewed for misclassifications (e.g., bottom intrusion), georeferenced volumetric (MVBS) and area-integrated (NASC) backscatter attributed to krill was exported in 0.5 nmi horizontal by 10 m vertical bins. We limited our analyses to data collected between 50 and 300 m of the water column, which encompasses the described distribution of adult krill during the day (~100–250 m; Mackas et al., 1997). All acoustic backscatter classified as krill was treated as non-differentiated *E. pacifica* and *T. spinifera* because the frequency response of these two species overlap (Phillips et al., 2022).

## 2.3 | Environmental data

To examine broad-scale biophysical drivers of hake and krill presence in our study area, which covers approximately 221,000 km² along the west coasts of the United States and Canada, we obtained environmental data that was available throughout the survey's full extent. This included *in situ* data collected from oceanographic instruments and satellite observations. A composite bathymetric grid was used to extract bottom depth (m) at the center of each 0.5 nmi cell along each transect and to measure the distance to the 200 m isobath (i.e., continental shelf break). Chlorophyll-a data (mg m⁻³) was obtained from the Aqua MODIS satellite (NASA/GSFC OBPG, 2020) using the R packages "rerddap" and "rerddapXtracto" (Chamberlain, 2019; Mendelssohn, 2020; Simons, 2019). We matched monthly chlorophyll-a composite grid values at 4 km resolution to the month of survey sampling to account for variation in primary production as the survey moved from south to north in the CCE, and extracted chlorophyll-a values to each 0.5 nmi cell along each transect, and used log-transformed values in our analysis. To remove the effect of latitude on temperature, gridded 100-m temperature anomalies were derived from *in situ* observations collected during the surveys (see Malick et al., 2020, for details). A single 100-m temperature anomaly value based on the shortest distance between the center of each 0.5 nmi cell and the kriged temperature surface was used for analyses.

## 2.4 | Data analysis

To facilitate analyses at the same spatial extent across all years, we limited data to transects that fell within the common latitudinal range of all surveys (35.8–54.7°N). We examined vertical distributions of hake and krill in the water column by calculating mean NASC in each 10 m vertical bin across all years. We also calculated the weighted mean depth of NASC attributed to hake and krill for each survey year

and tested for a relationship between depth distributions using Pearson's correlation (Zar, 1999).

To facilitate analyses of hake, krill, and physical datasets on a standardized spatial scale, we summed hake and krill NASC in each 10 m vertical bin for each 0.5 nmi horizontal cell and aggregated data into 25 km² grid cells. The choice of 25 km² grid cell sizes was twofold: We were interested in broad scale patterns across hundreds of kilometers, rather than fine-scale spatial patterns, and we sought to reduce spatial autocorrelation in the datasets following Malick et al. (2020). We calculated the mean NASC of hake and krill within each 25 km² cell, as well as the mean bottom depth, distance to the shelf break, chlorophyll-a concentration, and 100-m temperature anomaly. We also limited our analyses to grid cells that had 10 or more data points, and three or more years of observations, which resulted in the removal of 7% of observations.

To visualize areas of persistently high hake and krill abundance in grid cells across all survey years, we used kernel density estimation (KDE) and classified hotspots of hake and krill as kernel density estimates that fell in the upper 95th percentile (*sensu* Santora et al., 2011). KDE is a simple nonparametric statistical technique that estimates a real-valued function as the weighted average of neighboring observed data (Worton, 1989). The weight is defined by the kernel, such that closer points are given greater weights, and smoothness is set by the kernel bandwidth, which is the distance over which the data are smoothed. For this study we used a bandwidth of 50 km and 2000 cells to create the grid. We then estimated the area encompassed by each hotspot, and examined their location along the coast.

The effects of bathymetry and environmental conditions on hake and krill were quantified with generalized additive models (GAMs) using the mgcv package in R (R Core Team, 2016; Wood, 2011, 2017). We used binomial GAMs with a logit link to quantify hake or krill presence as a function of bottom depth, distance to the continental shelf break, chlorophyll-a concentration, and 100-m temperature anomaly. We used univariate thin plate regression splines as smoothing functions for bottom depth, shelf distance, and chlorophyll-a. Because previous work has shown spatially variable effects of temperature on hake distribution (Malick et al., 2020), we allowed the temperature effect to be nonstationary across space by combining the temperature covariate and a bivariate smooth of latitude and longitude. We also included a separate bivariate smooth of latitude and longitude to account for spatial autocorrelation. Spline shrinkage was used to perform automatic smoothness selection of covariates (Wood, 2006). We compared the full model with models that iteratively removed individual covariates to determine the best fit model. Model performance was evaluated by examining deviance explained, changes in Akaike information criterion (AIC), and Akaike weights ($\omega_i$). Normalized residuals were plotted to check for violations of model assumptions.

We then used the final GAM models to separately predict the probability of krill and hake presence in each 25 km² grid cell across the study area, and multiplied the separate spatially explicit predictions to estimate co-occurrence. Using the range of measured temperature anomalies in our dataset (minimum: −0.99°C, maximum: +1.93°C) as a guide, we developed three scenarios to examine

how changing ocean temperatures may influence hake-krill co-occurrence. The scenarios were as follows: "Neutral," where all temperature values corresponded to the average temperature anomaly observed in each cell during the study period; "Cool," where each temperature value was 1°C below the average in each cell; and "Warm," where each temperature value was 1°C above the average in each cell. We then predicted co-occurrence in each temperature scenario and calculated area overlap, defined as the percentage of 25 km$^2$ cells where the binary occurrence of both krill and hake was 1 (Carroll et al., 2019; Saraux et al., 2014). Finally, we mapped predictions to examine spatial variation in the probability of co-occurrence.
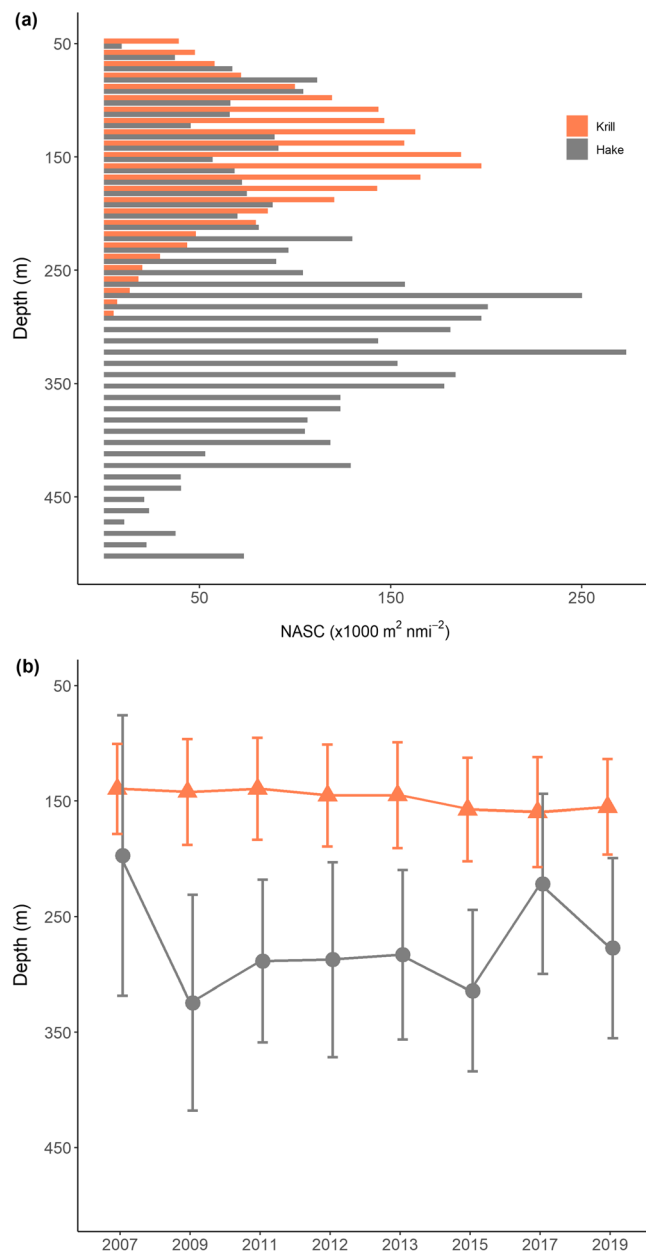


**FIGURE 2** Depth distribution of krill and hake abundance (NASC) in (a) 10-m depth bins during acoustic-trawl surveys between 2007 and 2019, and (b) weighted mean depth (± SD) in each year

## 3 | RESULTS

Hake and krill were vertically segregated in the water column, with most krill occurring between 150 and 200 m depth, while most hake occupied deeper waters between 250 and 350 m depth (Figure 2a). The weighted mean depth of krill averaged 147.9 ± 8.1 m and was stable across years, whereas hake annual weighted mean depths were more variable (Figure 2b). The average weighted mean depth of hake was 274.2 ± 43.6 m, although hake were approximately 100 m deeper in 2009–2015 compared with other years. There was no correlation between hake and krill annual weighted mean depths ($r = -0.015$, $p = 0.972$).

Hake hotspots (95th percentile of kernel density estimate) were found in multiple locations along the coast (Figure 3a), with the largest hotspot in Oregon waters encompassing a broad north–south area of 6285 km$^2$ near the 200 m isobath. Other hake hotspots were located offshore of the Gulf of the Farallones in an area of 3399 km$^2$, and near Cape Mendocino (1905 km$^2$). Two small hake hotspots (1906 and 1028 km$^2$) were detected in Washington and British Columbia waters. Krill hotspots were also in multiple locations (Figure 3b). The largest krill hotspot was located near the Juan de Fuca eddy system, encompassing an area of 5573 km$^2$. Another krill hotspot occurred in northern British Columbia near Dixon Entrance (2321 km$^2$) and in waters west of Haida Gwaii (1192 km$^2$). A relatively large krill hotspot was located in central Oregon waters (1928 km$^2$), and a number of smaller krill hotspots were present near Cape Mendocino in northern California (480 and 1012 km$^2$), Cape Blanco in southern Oregon (372 and 872 km$^2$), and Point Arena in northern California (372 km$^2$).

Final models of hake and krill presence indicated that all covariates included in the full models were significant (Table 1). Plots of partial effects indicated similar influences of bottom depth, distance to the continental shelf break, and chlorophyll-a on hake and krill occurrence. Hake occurrence was greatest in waters between 250 and 750 m water depth, within 20 km of the shelf break, and with intermediate values of chlorophyll-a (~1.0 mg m$^{-3}$; log scale; Figure 4). There was another peak in hake occurrence in deep waters (~2800 m) that was not observed for krill. Krill occurrence was greatest in waters between 250 and 750 m water depth, approximately 10 km offshore of the shelf break, and with intermediate chlorophyll-a concentrations (~1.0 mg m$^{-3}$; log scale; Figure 5). Plots of the 2-dimensional partial effects of 100-m temperature anomalies indicated a differential effect on the occurrence of hake and krill (Figure 6). We found a spatially variable influence of temperature on hake, with occurrence positively correlated with cooler temperatures in the southern part of the CCE, warmer temperatures in the central CCE and offshore of Vancouver Island, British Columbia, and cooler temperatures in the northern part of the study area (Figure 6a). In contrast, krill occurrence was positively correlated with cooler temperatures throughout most of the CCE, except in the northernmost part of our survey area, near Haida Gwaii, where there appeared to be a weak relationship to warmer waters (Figure 6b).

During cool conditions, when temperature anomalies were 1°C below average, hake-krill co-occurrence overlap was predicted to be 41.0% and the probability of co-occurrence was high throughout most of California waters, and in shelf and slope waters offshore of Oregon,
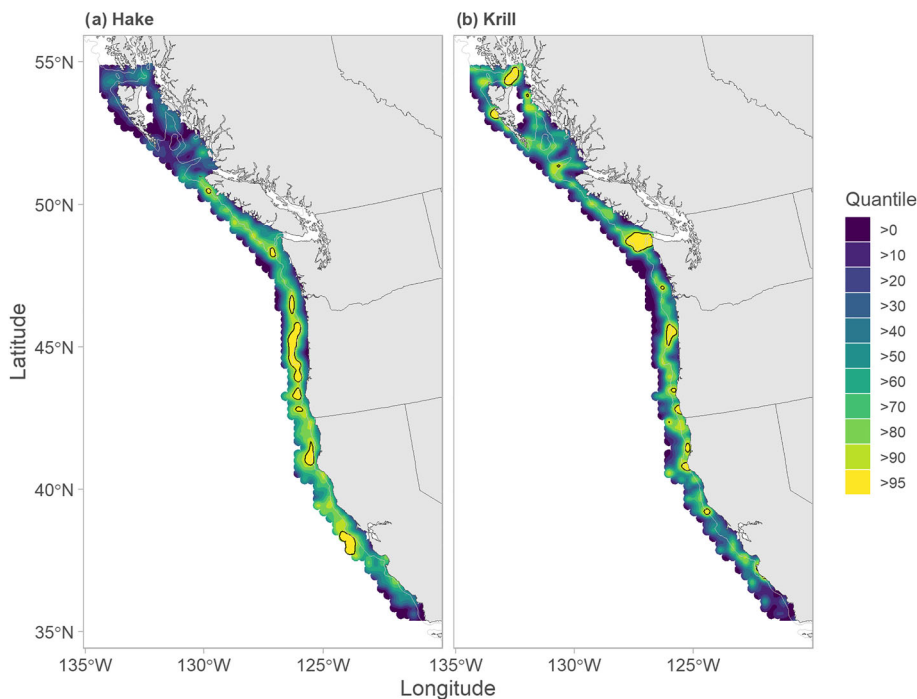
**FIGURE 3** Plots of hotspots (95th percentile of kernel density estimate) of (a) hake and (b) krill abundance observed during 2007–2019. Hotspots are colored yellow and outlined with black lines.

**TABLE 1** Description of generalized additive models developed to quantify hake and krill presence in the study area. Models of hake and krill presence both used the same formulations, and were evaluated based on deviance explained, Akaike information criterion (AIC) and differences (ΔAIC), and Akaike weights ($\omega_i$). Selected final models are in bold.

| | Model construction | Formulation | Edf | Deviance explained | AIC | ΔAIC | $\omega_i$ |
|---|---|---|---|---|---|---|---|
| Hake | **Full model** | **Hake ~ s (Lat, Lon) + s (bottom depth) + s (Lat, Lon, by temperature) + s (chlorophyll) + s (distance to shelf)** | **34.7** | **29.6** | **2000.7** | **0.00** | **1.00** |
| | Drop shelf distance | Hake ~ s (Lat, Lon) + s (bottom depth) + s (Lat, Lon, by temperature) + s (chlorophyll) | 29.9 | 24.4 | 2134.8 | 134.09 | 0.00 |
| | Drop chlorophyll | Hake ~ s (Lat, Lon) + s (bottom depth) + s (Lat, Lon, by temperature) | 28.1 | 23.3 | 2162.3 | 161.55 | 0.00 |
| | Drop bottom depth | Hake ~ s (Lat, Lon) + s (Lat, Lon, by temperature) | 14.7 | 6.9 | 2587.8 | 587.08 | 0.00 |
| | Drop spatial-temp interaction | Hake ~ s (Lat, Lon) | 20.4 | 7.6 | 3543.1 | 1542.34 | 0.00 |
| Krill | **Full model** | **Krill ~ s (Lat, Lon) + s (bottom depth) + s (Lat, Lon, by temperature) + s (chlorophyll) + s (distance to shelf)** | **32.0** | **17.7** | **1587.9** | **0.00** | **0.984** |
| | Drop shelf distance | Krill ~ s (Lat, Lon) + s (bottom depth) + s (Lat, Lon, by temperature) + s (chlorophyll) | 29.0 | 16.9 | 1596.2 | 8.30 | 0.016 |
| | Drop chlorophyll | Krill ~ s (Lat, Lon) + s (bottom depth) + s (Lat, Lon, by temperature) | 26.3 | 15.4 | 1625.5 | 37.50 | 0.000 |
| | Drop bottom depth | Krill ~ s (Lat, Lon) + s (Lat, Lon, by temperature) | 20.2 | 8.7 | 1737.0 | 149.50 | 0.000 |
| | Drop spatial-temp interaction | Krill ~ s (Lat, Lon) | 21.3 | 5.5 | 2532.9 | 944.90 | 0.00 |

Washington, and northern British Columbia, near Haida Gwaii (Figure 7a). During neutral ocean conditions, when temperature anomalies were kept at the average across the time series, area overlap estimates were 25.8% and the probability of hake and krill co-occurrence was greatest near Cape Mendocino, and along the shelf break between Oregon and Vancouver Island (Figure 7b). During warm conditions, when temperature anomalies were 1°C above average, area overlap was 17.0%, and co-occurrence was concentrated

primarily near Cape Mendocino, with lower co-occurrence estimates in Oregon, Washington, and British Columbia (Figure 7c).

## 4 | DISCUSSION

We demonstrated that variation in temperature influences hake-krill co-occurrence in the CCE, suggesting that predator–prey interactions

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**FIGURE 4** Plots of the partial effects of bottom depth, distance to the shelf break (negative values on inshore of 200 m isobath, positive values are offshore of 200 m isobath), and chlorophyll-a on presence of hake during biennial joint U.S.-Canada Integrated Ecosystem & Acoustic Trawl surveys between 2007 and 2019. Gray shading around smooth fits represents 95% confidence intervals, and data availability is indicated by tick marks above x-axis.
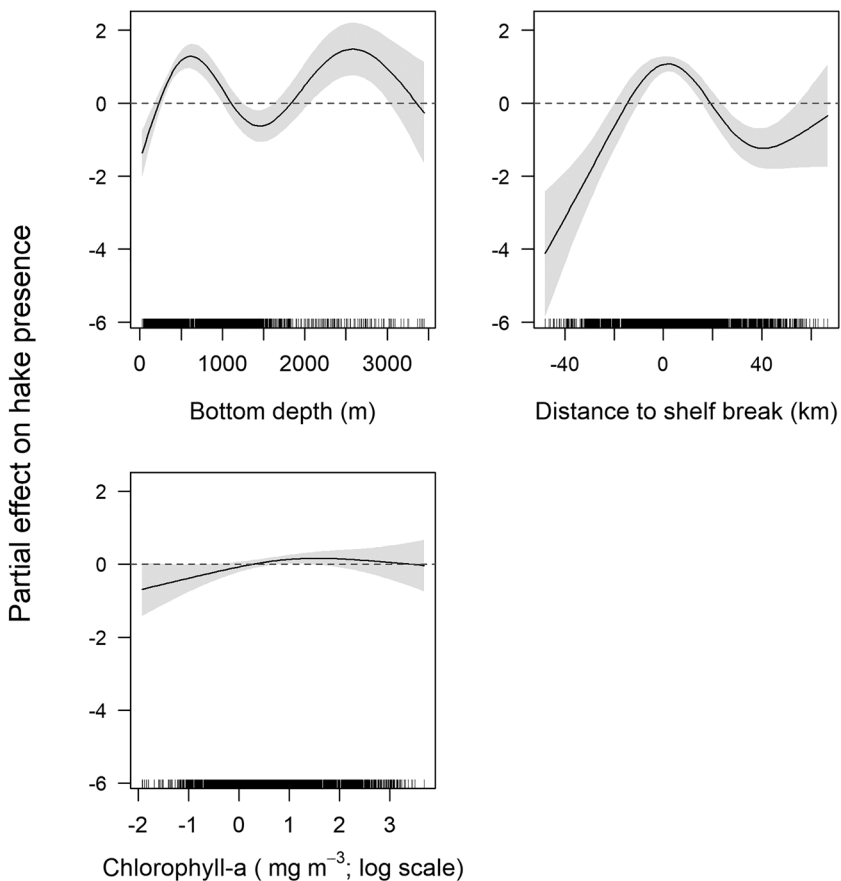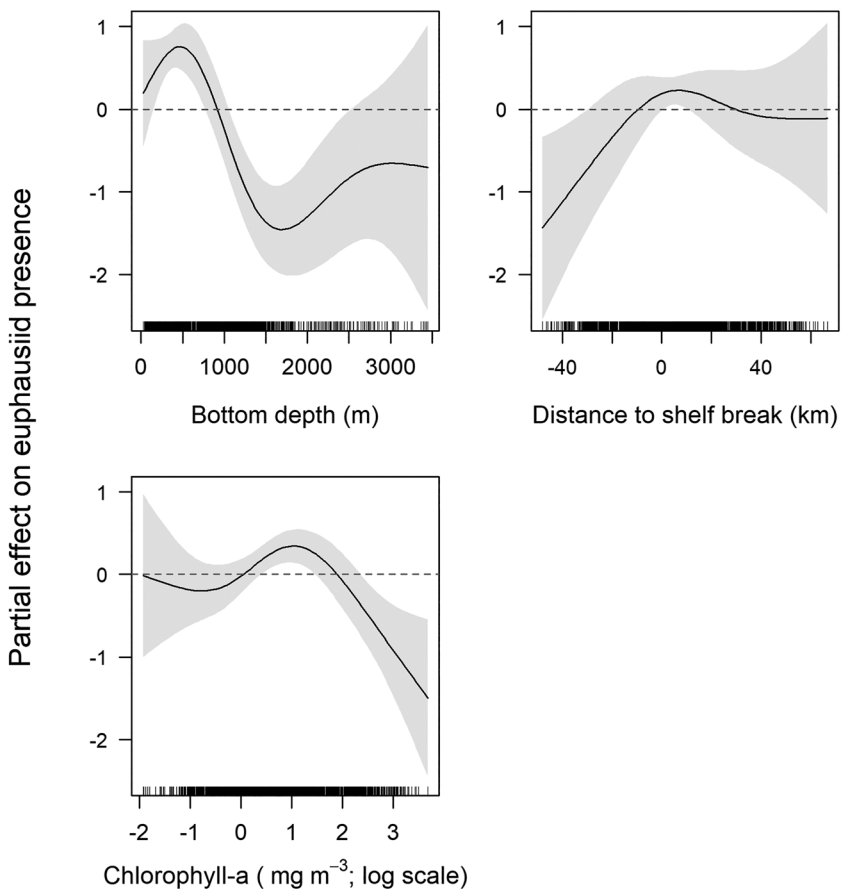


**FIGURE 5** Plots of the partial effects of bottom depth, distance to the shelf break (negative values represent locations inshore of the 200 m isobath, positive values represent values offshore of 200 m isobath), chlorophyll-a, and 100-m temperature anomaly on presence of euphausiids during biennial joint U.S.- Canada Integrated Ecosystem & Acoustic Trawl surveys between 2007 and 2019. Gray shading around smooth fits represents 95% confidence intervals, and data availability is indicated by tick marks above x-axis.
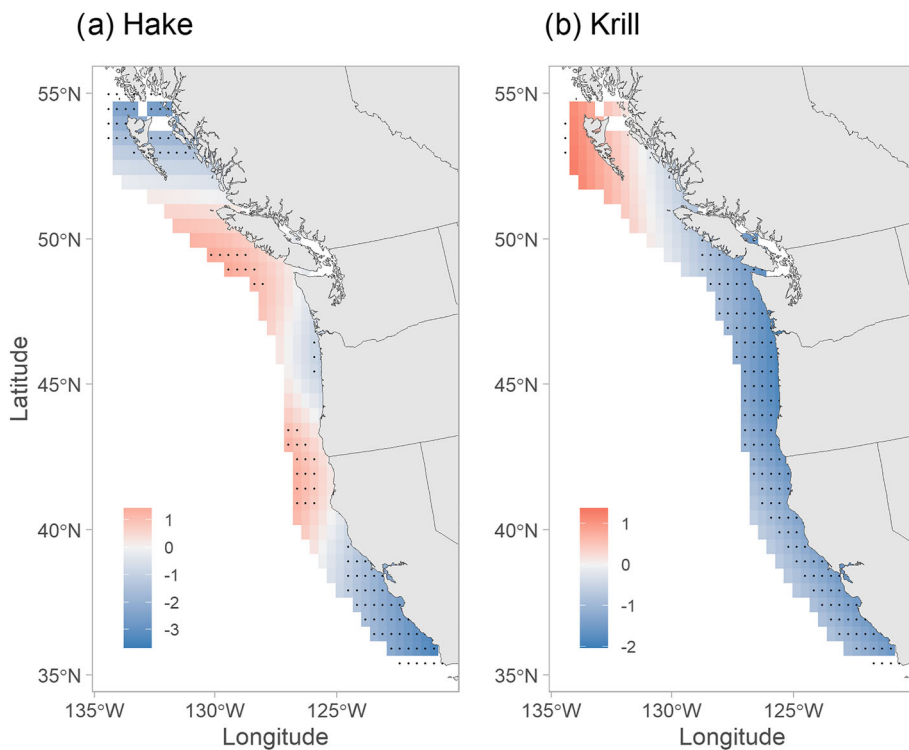
**FIGURE 6** Plots of the two-dimensional partial effects of 100 m temperature anomalies on hake and krill presence during biennial joint U.S.-Canada Integrated Ecosystem & Acoustic Trawl surveys between 2007 and 2019. Black dots indicate locations where the relationship was significant.
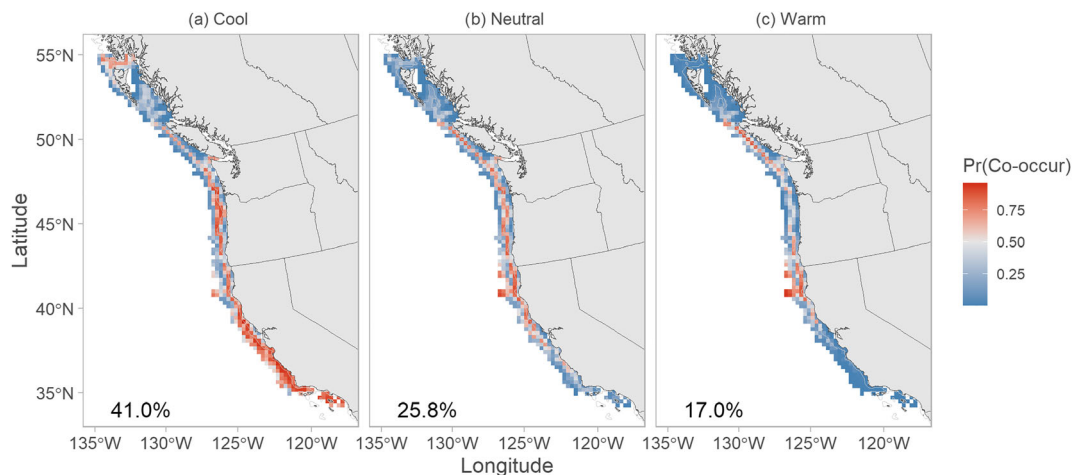
**FIGURE 7** Plots of the probability of co-occurrence hake and krill during (a) cool, (b) neutral, and (c) warm ocean conditions. Percentages are the percent of 25 km² cells where both hake and krill were predicted to co-occur.

between hake and krill may be driven by thermal ocean conditions. These results have important implications for Pacific hake fisheries management as well as ecosystem-based fisheries management efforts (Holsman et al., 2020). By accounting for similar effects of bottom depth, proximity to the continental shelf break, and chlorophyll-a concentrations, we quantified a spatially variable effect of temperature on hake-krill co-occurrence. In particular, during warm ocean conditions, the average area overlap of hake and krill was only 17%, suggesting that hake may not have access to much krill, and could experience greater competition for prey, which may alter their growth and recruitment to the fishery. Warmer waters also increase metabolic demands of marine fishes (Deutsch et al., 2015; Neuheimer et al., 2011), and the lower predicted co-occurrence of hake with krill

may be compounded by increasing overall energetic demands of hake (Holsman et al., 2020). To meet their consumption needs, hake may switch to alternative prey, which could alter the abundance of other important forage fish species and in turn reduce prey resources for other predators and competitors in the CCE food web including Pacific salmon, seabirds, and marine mammals (Field et al., 2006).

The probability of hake-krill co-occurrence was consistently elevated near the continental shelf break along the west coast of the United States and Canada, highlighting the importance of this productive habitat for predator–prey interactions. The data used in this study were collected during surveys that occurred in late spring and summer, a typically productive period in the CCE due to increased upwelling of nutrient-rich waters near the continental shelf break and wind

relaxation events that allow phytoplankton blooms to proliferate. Because hake are mobile, they may be able to maintain a closer association with the productive shelf break region to maximize prey foraging opportunities, including feeding on krill (Mackas et al., 1997; Swartzman, 2001; Ware & McFarlane, 1995). Compared to hake, krill in this study were found in a wider range of bottom depths and distances to the shelf break, which may relate to the displacement of zooplankton away from areas with strong currents (Dorman et al., 2011), or species-specific differences in *E. pacifica* and *T. spinifera* distributions that we could not discern in the acoustic data. Interestingly, we detected an unexpected second peak in hake presence in deep waters (>2500 m). The distribution of hake in these deeper waters may relate to factors including alternative prey availability, discrepancies in age-class spatial distributions that were not evaluated in this study, or the sampling strategy to survey further offshore into deeper waters if hake were detected on the westernmost portion of a transect. Most of the hake detected in deep waters in this study were located between 36°N to 42°N, an area of northern California where the shelf break is very narrow, suggesting that the latter explanation is the most likely. However, further research on hake occurring in deep, offshore waters may reveal additional insights.

In cooler years, hake-krill co-occurrence was predicted to be high throughout the CCE but especially in waters in the southern and central California Current and near the shelf break in Oregon and Washington waters. This suggests that during cool ocean conditions, hake may have access to krill in many areas of the CCE, which could lead to increased consumption and greater growth rates of individual fish. In comparison, during neutral and warmer years, hake co-occurrence with krill declined substantially and shifted from southern and central California waters to near Cape Mendocino in northern California and along the shelf break from Oregon to the west coast of Vancouver Island. The probability of co-occurrence was particularly low during warm ocean conditions and focused in the waters north and west of Cape Mendocino. This suggests that hake-krill co-occurrence is driven by the availability of krill as well as the spatial distribution of hake. Recent research has shown that krill density declined in southern parts of the CCE during warm ocean conditions, particularly during the marine heatwave in 2015 (Phillips et al., 2022). Lower spatial overlap with krill in the southern part of the CCE during neutral and warm years suggests that hake migrated further north, consistent with previous research (Agostini et al., 2006; Dorn, 1995; Ware & McFarlane, 1995). The region between Cape Mendocino and Cape Blanco in the central CCE appears to be an important area for hake regardless of ocean conditions, because co-occurrence with krill was still high even during warm ocean conditions. Multiple small krill hotspots occurred along the section of the coast near Cape Mendocino, suggesting that enough krill may be present to sustain hake populations during poor ocean conditions. Krill densities are known to be elevated in this area of the CCE and may support numerous predator populations including hake (Phillips et al., 2022).

By using oceanographic measurements made *in situ* closer to the daytime depths of hake and krill, we expanded our understanding of the influence of temperature on predator–prey co-occurrence. The temperature anomalies that we observed at depth in this study were not as extreme as those observed near the surface during the recent marine heatwave (Bond et al., 2015; Cavole et al., 2016), indicating that even less extreme variations in temperature can have a significant impact on predator–prey co-occurrence. These results have important implications for potential temperature-induced shifts in hake feeding, growth, and recruitment. The diet of hake is predominantly composed of krill (Tanasichuk, 1999; Tanasichuk et al., 1991), but during warm ocean conditions, hake may switch to alternative prey to meet energetic demands if krill are not encountered, which could negatively impact growth (Grover et al., 2002). Conversely, in cool years, hake may consume more krill and experience greater growth and recruitment. Hake growth, measured by weight- and length-at-age in stock assessments (Johnson et al., 2021; Smith et al., 1990), fluctuates substantially through time (Ressler et al., 2007), and this study provides insight on the potential role that temperature and krill availability may play in some of this variation. Examination of hake stomach contents and relationships between krill consumption and availability will reveal whether growth is linked to prey availability. Furthermore, research on the links between temperature, prey abundance, and hake growth will inform the development of management strategy evaluations aimed at improving our understanding of variation in hake recruitment to the fishery, and how robust Pacific hake fisheries management is to environmental variability and climate change (Jacobsen et al., 2021).

Patterns of hake-krill co-occurrence in the northern part of the California Current contrasted somewhat with results from the rest of the CCE. The probability of co-occurrence was elevated in the region north of Vancouver Island during cool ocean conditions compared to periods of neutral and warm conditions. The northern CCE is defined by the transition zone where the North Pacific Current (NPC) bifurcates to form the poleward flowing Alaska Current and the equatorward flowing California Current (Cummins & Freeland, 2007; Freeland, 2006). This area is also shallower than other parts of the CCE, and variation in horizontal transport due to north–south shifts in the NPC bifurcation can significantly impact the coastal ecosystem (Malick et al., 2016; Sydeman et al., 2011). Thus, a greater probability of hake-krill co-occurrence in the area north of Vancouver Island during cool ocean conditions may relate to local shifts in upwelling or transport, which could enable zooplankton to remain on the wider, productive shelf and become available to hake that occur in this area (Benson et al., 2002). A finer-scale study of hake and krill in the northernmost part of the California Current will enable a better understanding of the influence of variation in basin-scale and local transport and temperature on predator–prey interactions. Adult hake ages 5+ migrate further north than younger age classes (Ressler et al., 2007), suggesting that some of these results may also relate to differing distributions of hake age classes in the northernmost portion of our study area.

Aggregations of hake are regularly observed near the Juan de Fuca eddy system (Mackas et al., 1997; Ware & McFarlane, 1995), but increased hake-krill co-occurrence was not predicted in this area, despite the large krill hotspot that was identified. The Juan de Fuca eddy system is one of the most productive habitats in the Northeastern Pacific Ocean (Hickey & Banas, 2003, 2008; Ware & Thomson, 2005),

and many migratory predators including seabirds and marine mammals regularly forage in this area (Burger, 2003; Davis, 2015; Menza et al., 2016). The lack of predicted hake-krill co-occurrence in this area may be due to interannual variation in the northern extent of hake migration, or variation in hake distributions near the numerous submarine canyons and shallow banks in the area. There is evidence that hake preferentially consume *T. spinifera* over *E. pacifica* (Emmett & Krutzikowsky, 2008; Tanasichuk, 1999), and recent research suggests that *T. spinifera* hotspots are more often located in northern British Columbia while *E. pacifica* are more likely to form hotspots near the Juan de Fuca eddy system (Evans et al., 2021). Thus, the lower predicted hake-krill co-occurrence near the Juan de Fuca eddy system may relate to species-specific differences in krill aggregations. Additional analysis of hake diets from this area may illuminate the total amount of krill consumed by hake near the Juan de Fuca eddy system, and the extent that hake preferentially feed on *T. spinifera*. Despite the lack of predicted hake-krill co-occurrence in this study, the large krill hotspot near the Juan de Fuca eddy system could become an important area for hake to access zooplankton prey in the future, especially if hake distributions along the coast shift northward with climate change (Malick et al., 2020; Morley et al., 2018).

The use of fisheries acoustics allowed us to examine the fine-scale vertical distributions of hake and krill and illuminate the segregation of predator and prey during the daytime. Krill vertical distributions were consistently centered around ~150 m water depth and were generally 100–200 m shallower than hake. The daytime depths of hake were more variable, and while the average depth was always deeper than krill, there was no correlation between depth distributions of predator and prey, even during years with the greatest area overlap of hake and krill (2007, 2019). This suggests that separate physical or biological processes affect hake and krill distributions in the water column. Interestingly, temperature does not appear to be a significant factor. During the 2015 marine heatwave, average krill depth did not differ from other years of our study, and likewise hake occupied similar water depths in 2015 compared to periods of 'neutral' or 'cool' ocean conditions in 2009, 2011, 2012, and 2013. This suggests that daytime krill depth distributions may be driven by light or the behavioral response of krill to swim downward against vertical upwelling currents (Genin et al., 2005). Both krill and hake undergo diel vertical migrations and occupy surface waters at night to feed. During the day, however, predator and prey may occupy different parts of the water column to avoid predation. Hake may also move to deeper, colder waters to prolong digestion, while krill may occupy waters at shallower depths to reduce advection by currents and remain near productive areas (Mackas et al., 1997). The more variable depth distributions of hake may also relate to age-class specific differences in water column occupancy. For example, younger hake (age-2) are often located shallower than age-5+ hake (R. Thomas, pers. obs). Future research on the influence of oceanographic factors, including local upwelling and sub-surface current strength on age-specific vertical distributions of hake may expand our understanding of daytime depth distributions of hake and krill.

It is important to note that the results presented here represent a snapshot of synoptic daytime hake and krill distributions during the summer and may not capture dynamic predator–prey interactions. For example, low krill abundance in some areas may indicate depletion by hake during their migration north prior to our survey (Mackas et al., 1997; Tanasichuk, 1999; Tanasichuk et al., 1991). Similarly, high krill abundance in some areas may relate to environmentally driven variation in the seasonal phenology of zooplankton hotspot formation that is not influenced by hake presence (Evans et al., 2021; Fiechter et al., 2020). Also, our analyses focused on predictions of hake-krill co-occurrence based solely on temperature, but recent research indicates that surface chlorophyll concentrations are also likely to shift under climate change (Pozo Buil et al., 2021), suggesting that future projected areas of hake-krill co-occurrence may become more spatially variable in the future. Despite these limitations, this study provides evidence that hake-krill co-occurrence is influenced by temperature and indicates that warmer ocean conditions may alter predator–prey interactions in spatially complex ways. As climate change continues to disrupt marine ecosystems, including food web dynamics (Bartley et al., 2019; Sydeman et al., 2015), our study also suggests that some areas along the west coast, including waters off Cape Mendocino, may support predator–prey hotspots even as oceans continue to warm.

## AUTHOR CONTRIBUTIONS

EMP and MJM conceived of this work. EMP drafted the manuscript, and EMP, MJM, SG, MAM, MEM, SPS, and RET revised the manuscript. All authors approve of the submitted version.

## DATA AVAILABILITY STATEMENT

The raw acoustic data underlying this article are available from the National Centers for Environmental Information, https://www.ncei.noaa.gov/. Processed data will be made available through NOAA Fisheries, Northwest Fisheries Science Center, and are currently available by request to the corresponding author.

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