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Environmental Drivers of the Spatiotemporal Distribution of Dwarf Hake (*Merluccius productus*) Along the Pacific Coast of Baja California, Mexico

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The western coast of Baja California Sur lies within a transitional oceanographic zone influenced by distinct water masses and the California Current, creating a highly productive ecosystem that supports a population of *Merluccius productus* (Dwarf hake), a species of ecological and potential economic importance. Despite its relevance, information on its distribution and abundance remains limited. This study analyzed data from eight fishery-oceanographic surveys that combined midwater trawl sampling with conductivity, temperature, and depth measurements to evaluate biological and environmental variables. The objectives were to characterize the size structure and spatial distribution of Dwarf hake and to identify the oceanographic variables influencing its presence and catch per unit of effort. A delta generalized additive mixed modeling approach was used to analyze both presence or absence and catch per unit of effort based on environmental and geographic predictors. This framework included a binomial model for occurrence and a gamma model for catch rates conditional on presence. Model selection and validation were conducted using the Akaike Information Criterion. The binomial model explained 27.3 percent of the deviance, whereas the gamma model explained 79.8 percent. Temperature, distance to the edge of the continental shelf, longitude, and survey (temporal factor) were significant predictors of species presence. Once present, fishing haul depth, salinity, and distance to the continental shelf edge influenced catch rates. Individuals of Dwarf hake ranged from 3.5 to 40 (sd = 6.6) centimeters in total length and were captured between 19.5- and 321.5-meters depth, with shallower distributions observed at night. Highest abundance occurred during summer in the Gulf of Ulloa. This study provides the first comprehensive assessment along the Baja California Peninsula and identifies previously unreported areas of high density.

Keywords: Pacific hake, Environmental variables, CPUE, New fishery, Oceanography, Temperature

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BACKGROUND

The genus *Merluccius* comprises approximately 13 species distributed across the Atlantic, Pacific, and Mediterranean, representing some of the most commercially important marine fish worldwide (Lloris et al. 2003). Pacific hake (*M. productus*) sustains one of the largest trawl fisheries in the northeastern Pacific, with joint US–Canadian landings regularly exceeding 200,000 tonnes annually (Berger et al. 2019). In the southeastern Pacific, Peruvian hake (*M. gayi peruanus*) supports a major industrial fishery along the Humboldt Current, where trawl and acoustic surveys have documented strong associations between hake abundance and bottom-water temperature and oxygen conditions (IMARPE 2013). These contrasting examples from major eastern boundary current systems highlight that *Merluccius* populations are consistently structured by large-scale oceanographic forcing, yet the population inhabiting the western coast of Baja California remains poorly characterized. Pacific hake (*M. productus*) is closely associated with the California Current System (CCS), a highly productive eastern boundary current characterized by wind-driven upwelling that sustains high biological diversity and supports commercially important fisheries along the Pacific coast of North America (Checkley and Barth 2009; Weber et al. 2021).

Within this system, the continental shelf edge functions as a structurally important habitat feature across *Merluccius* species. Druon et al. (2015) demonstrated that the shelf break serves as a recurrent nursery ground for European hake (*M. merluccius*) in the Mediterranean, and similar shelf-edge associations have been documented for Pacific hake along the US coast (Cooke et al. 2006). Together, these findings suggest that affinity for the shelf break is a conserved ecological trait within the genus. Along the Pacific coast of the United States, *M. productus* is extensively exploited and forms the target of one of the largest single-species fisheries in the northeastern Pacific (Berger et al. 2019). Its southern range extends to Bahía Magdalena on the western coast of Baja California, Mexico, where a morphologically distinct form — Dwarf hake (*M. productus* var. *Dwarf*) — has been proposed as a separate population (Vrooman and Paloma 1977). The boundary between the northern migratory stock and the Dwarf form is considered to lie near the 28°N parallel; maximum total length for the Dwarf form is 30.5 cm, compared with approximately 60–91 cm for the northern stock (Lloris et al. 2003). The Dwarf hake reproduces between 25° and 28°N in the Gulf of Ulloa, at 10–20 nautical miles from the coast, with spawning occurring between April and February (Balart and Castro-Aguirre 1995).

Diet varies with life stage: larvae and juveniles feed primarily on copepods and euphausiids, while adults prey on euphausiids, fish, and the pelagic red crab (Grimothea *planipes*); cannibalism has been observed in larger individuals (Balart and Castro-Aguirre 1995, Lloris et al. 2003). Like other *Merluccius* species, Dwarf hake performs diel vertical migration, ascending to epipelagic depths at night to exploit surface prey aggregations and retreating to deeper, cooler waters during daylight hours (Álvarez-Colombo et al. 2014). This behavioral pattern has important implications for catchability and survey design, as trawling depth and time of day strongly influence the fraction of the population that is sampled. Malick et al. (2020) found that environmental conditions, particularly thermal conditions, significantly influence the distribution of hake, suggesting that ocean temperatures can serve as a useful predictor for hake distribution in the north. They further identified shelf-break distance as a strong predictor of historical hake occurrence.

In Mexican waters, scientific interest in Dwarf hake has grown substantially over the past decade. The first acoustic biomass estimate for the species in the Gulf of Ulloa was conducted by Godínez-Pérez (2013), providing an early baseline for abundance in the southern portion of the California Current. Population dynamics studies near Bahía Magdalena estimated the length at first maturity at 11.4 cm SL (Salinas-Mayoral 2018), while recent work has characterized age and growth patterns (Mora-Zamacona et al. 2024) and proposed frameworks for sustainable exploitation (Mora-Zamacona et al. 2023). Environmental investigations in the northern Gulf of California identified temperature as the dominant predictor of hake abundance, explaining 20.6% of the observed variability (Álvarez-Trasviña et al. 2022), and recent acoustic surveys have confirmed the presence of demersal hake aggregations in that region (Godínez-Pérez et al. 2025). Along the continental shelf of Baja California Sur, Rubio-Rodríguez et al. (2026) demonstrated that the seasonal dynamics of regional water masses — particularly the interaction between Subarctic Water and Equatorial Subsurface Water — structure the distribution of Dwarf hake at depth (100–250 m), with anomalous El Niño conditions reducing hake presence south of Bahía Magdalena through habitat redistribution rather than population decline. Despite these advances, no comprehensive, peninsula-wide assessment integrating spatiotemporal distribution with oceanographic drivers had been conducted along the entire western coast of Baja California (WCBC) prior to this study, leaving a critical gap in the scientific basis required to support fisheries management.

In Mexico, biomass is periodically assessed and catch quotas are estimated; however, a formal management system based on explicit harvest control rules is still lacking. In 2018, a regulatory framework for the hake fishery in the Gulf of California was incorporated into the National Fishing Chart. This framework defined specific fishing polygons within the Gulf of California, as well as an additional area off Bahía Magdalena along the western coast of the Baja California Peninsula, but it does not yet constitute a fully implemented quota-based management system (Álvarez-Trasviña et al. 2020). One legal instrument available to regulate hake harvesting in federal Pacific and Gulf of California waters is the draft Mexican Official Standard NOM-020-SAG/PESC-2019 (DOF 2019), currently pending approval. In contrast, no hake fishery currently operates along the western coast of the Baja California Peninsula (WCBC), although Dwarf hake has been proposed as a potential candidate for future exploitation. To support evaluation of its fishery potential and inform future management decisions, comprehensive information on its spatial distribution, abundance, population structure, and environmental drivers is required. Since 2019, the Mexican Institute for Sustainable Fisheries and Aquaculture Research (IMIPAS) has conducted multi-year research surveys in the northwestern region of Mexico as part of a broader national strategy aimed at supporting food sovereignty and food security by generating scientific knowledge on marine resources, identifying new potential fisheries, and promoting their sustainable use.

The objective of this study was to conduct the first comprehensive, peninsula-wide assessment of the spatial and temporal distribution of Dwarf hake (*Merluccius productus*) along the WCBC. Specifically, we aimed to: describe the size structure and seasonal spatial patterns of occurrence; evaluate the effect of key environmental variables—particularly temperature, dissolved oxygen, and trawl depth—together with spatial predictors (longitude and latitude) and habitat-related metrics such as proximity to the continental shelf break, using delta generalized additive mixed models (GAMMs) to explain presence/absence and CPUE; and identify areas of increased occurrence that could inform future monitoring and support the development of a sustainable fishery for this understudied resource.

MATERIALS AND METHODS

Study area and field sampling

The study area extended from the northwestern boundary of Mexico's marine territory to the southern tip of the West Coast Baja California Peninsula (WCBC), off the coast of Los Cabos, Mexico. Within this region, eight research cruises were conducted using hydroacoustic equipment on board the R/V *Dr. Jorge Carranza Fraser* (*JCF*, offshore sampling) and the *BIP Inapesca I* (*INPI*, coastal sampling) during different seasons between 2019 and 2024 (Table 1). Survey routes were defined using a systematic grid of transects oriented perpendicular to the coastline, spaced approximately 10–15 nautical miles apart, with variable lengths depending on time constraints and available funding. This sampling design is part of an ongoing monitoring program primarily focused on small pelagic species (*e.g.*, sardines and anchovies), assessed through hydroacoustic methods complemented by biological sampling (*e.g.*, midwater trawls and oceanographic measurements). Although the surveys were not specifically designed to target other taxa, the multidisciplinary sampling approach allowed for the collection of additional biological information. Consequently, occurrences of species such as Pacific hake (*Merluccius productus*) correspond to opportunistic records derived from trawl samples conducted for acoustic ground-truthing, rather than from a species-specific survey design. These transects were navigated at a constant speed (~8 knots) (Fig. 1).

Oceanographic sampling was conducted at pre-established stations distributed along the survey area. At each station, vertical profiles were obtained using a CTD profiler (Conductivity, Temperature, and Depth; Idronaut model 320 Plus), allowing the characterization of the water column in terms of its physical properties.

Table 1. Information on the eight research surveys undertaken off the west coast of the Baja California between 2019 and 2024 aboard the R/V Dr. Jorge Carranza Fraser (JCF) and Inapesca I (INPI)

Survey (YYMM)	Survey period	Ship	Season	Hauls	Hauls with Dwarf hake	CTD sampling stations
1906	18/06/2019 - 21/08/2019	JCF	summer	55	17	110
2009	21/09/2020 - 23/10/2020	JCF	autumn	26	3	52
2111	25/11/2021 - 06/12/2021	JCF	autumn	8	3	38
2207	26/07/2022 - 13/09/2022	JCF	summer	55	8	47
2306	13/06/2023 - 17/07/2023	JCF	summer	54	28	61
2307	10/06/2023 – 04/07/2023	INPI	summer	29	4	-
2405	20/05/2024 – 19/06/2024	JCF	spring	49	22	78
2407	03/07/2024 – 23/07/2024	INPI	summer	27	3	50

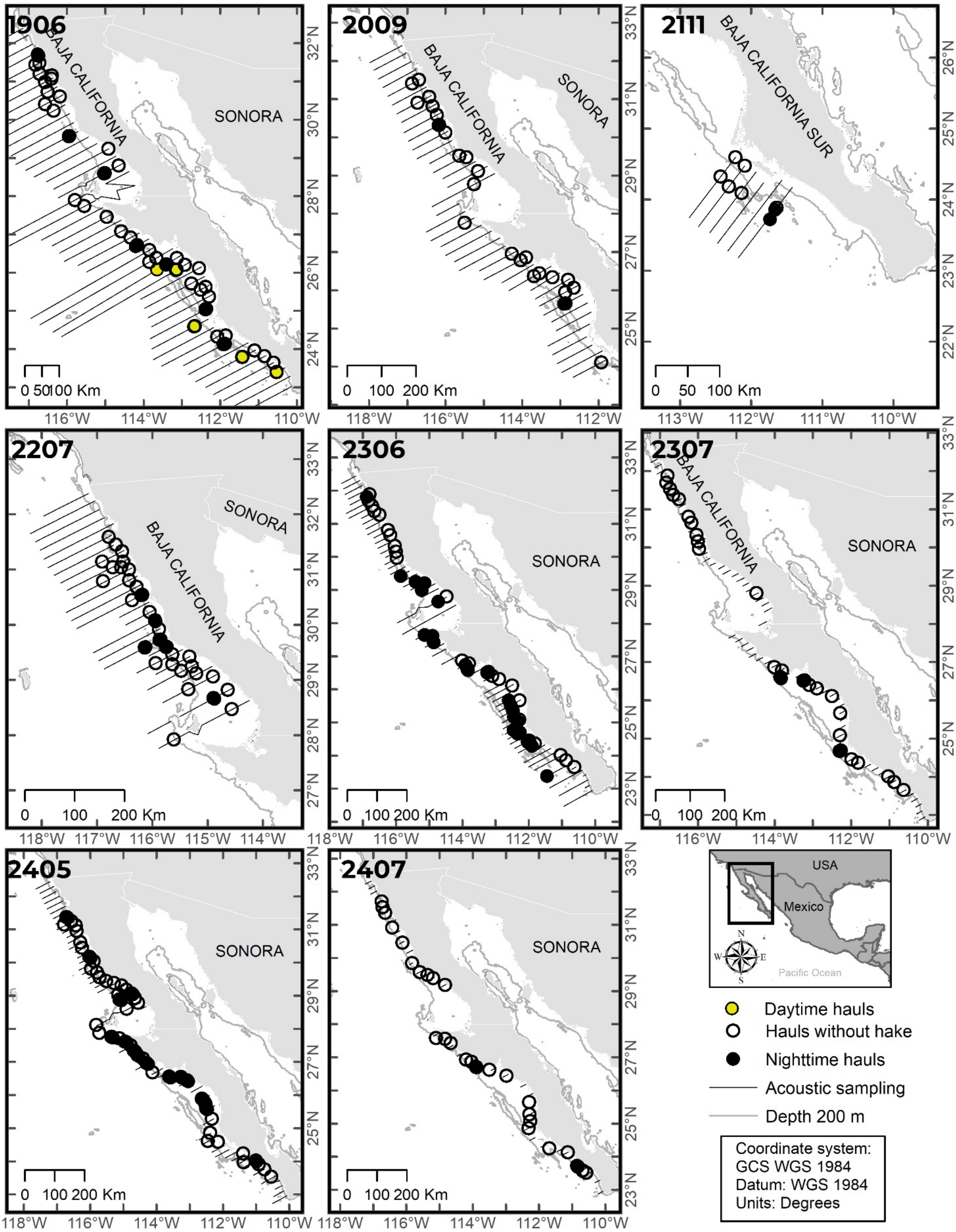

Fig. 1. Navigation routes during research cruises along the western coast of the WCBC. The numbers in the upper left corner indicate the cruise identification code by date (YYMM). The gray line marks the edge of the continental shelf (200 m).

Biological sampling

Fishing hauls were carried out following the prior detection of fish aggregations using a Simrad EK60 scientific echosounder (Kongsberg), equipped with five split-beam transducers (18, 38, 70, 120, and 200 kHz). Each haul lasted an average of 45 minutes at a speed of 3.5 knots (6.48 km/h). On board the JCF, a midwater trawl net was deployed from the stern, featuring a mesh size gradient ranging from 1600 mm in the mouth to 50 mm toward the codend, constructed of multifilament nylon netting. The codend was internally lined with knotless nylon mesh of 17 mm to retain small-sized individuals. On board the INPI, an experimental trawl net adapted for both bottom and midwater operation was used. This net is characterized by a relatively fine mesh size throughout the body, with a codend mesh size of 38.1 mm, designed to maximize the capture of a broad size spectrum, including juvenile and small-sized individuals. Such configuration allows for a more representative sampling of the population structure by reducing size selectivity and improving the retention of multiple length classes.

Once the net was retrieved and the catch brought on deck, specimens were sorted by taxonomic group (crustaceans, fish, etc.), then the species were identified following the identification guides by Fisher et al. (1995), Fricke et al. (2025), Froese and Pauly (2025) and Robertson et al. (2024). Lengths were measured in total length (TL) and standard length (SL) by using a vernier caliper with a precision of 1 cm. Most of the fishing hauls were conducted at night in shallow waters (95%), with surface-oriented trawls designed to target species exhibiting vertical migratory behavior, such as small pelagic. Thus, given the vertical migratory behavior of hake, specimens feeding near the surface were predominantly captured using a midwater trawl. However, during summer (2019), five hauls were conducted at greater depths during daytime hours (5%) in Baja California Sur using midwater trawl too. Given the absence of maturity data in the present study to estimate L50, the value reported by Salinas-Mayoral (2018) was used for illustrative purposes. The L50 reported by Salinas-Mayoral corresponds to standard length (SL). Therefore, for comparative purposes, it was converted to total length (TL) using a linear regression derived from the present dataset ($y = 1.05x + 1.14$, $\alpha = 0.05$, $R^2 = 0.93$). This relationship showed a strong fit, supporting its use for length conversion, resulting in an estimated value of 11.4 cm SL ≈ 13.11 cm TL.

Thus, given the vertical migratory behavior of hake, specimens feeding near the surface were predominantly captured (midwater trawl). However, during summer (1906), five hauls were conducted at greater depths during the daytime (5%) in Baja California Sur (Fig. 1). Seasons were defined at the haul level based on collection date: spring (March 1–June 15), summer (June 16–September 30), and autumn (October 1–December 31), following the phenological cycle of the California Current System transitional zone off Baja California (Durazo 2015). This haul-level assignment was preferred over survey-level grouping to minimize misclassification in surveys spanning multiple months.

Multimodal size analysis

Given the lack of monthly representativeness of the surveys, the data were grouped by season to observe the cohorts. Multimodal size analysis was conducted by determining the size range using formulas compiled by Salgado Ugarte (2002) through the “bandw” routine. Density estimation was performed using the Weighted Averaging of Rounded Points (WARP) method approach (Härdle and Scott 1988), a generalized approach based on the Averaged Shifted Histograms (ASH) technique method (Scott 1985). This ASH-WARP procedure was applied to approximate kernel density estimators (KDEs), employing a Gaussian weight function via the “bandw.R” program in the R language (Saito-Quezada et al. 2020).

The smoothing parameter was assigned a fixed amplitude bandwidth, and its optimal value was calculated using the following equation: (Silverman 1986; Fox 1990; Saito-Quezada et al. 2020):

$$\hat{h} = 0.9A\, n^{-1/5}$$

Where $\hat{h}$ is Silverma’s optimal bandwidth value, A denote the smaller of two estimates of the dispersion parameter for the Gaussian distribution: the sample standard deviation ($\hat{\sigma}$) and the F-pseudosigma (*i.e.*, the interquartile range divided by 1.349). This choice ensures an estimator that is directly comparable to the standard deviation. These estimates were calculated using the R routines developed by Salgado-Ugarte and Saito-Quezada (2020) (Iglewics 1983; Hoaglin 1988; Fox 1990; Salgado Ugarte 2002).

$$A = min(\hat{\sigma}, \frac{IQR}{1.349})$$

Subsequently, the Bhattacharya (1967) method was applied to characterize Gaussian components within the multimodal size distributions of Pacific hake, using the R functions bhataplt.R and bhatgauc.R provided by Salgado-Ugarte and Saito-Quezada (2020). Finally, correlation analyses were conducted to evaluate the goodness-of-fit between the summed Gaussian components (SCG) and the original mixed frequency distribution (Salgado-Ugarte et al. 2005).

Catch per unit effort (CPUE)

Catch per unit effort (CPUE, kg/h) was calculated by dividing the catch (kg) by the effective trawl time (h) (Sparre and Venema 1997).

Environmental modeling

Delta generalized additive mixed models (GAMM; Wood 2017) were implemented to understand which variables, or interactions among them, explain CPUE and the presence–absence of Dwarf hake in the water column along the western coast of the Baja California Peninsula. Midwater fishing hauls were conducted at different depths in the water column depending on the targets observed on the EK60 echosounder. Values of environmental variables such as temperature (°C), salinity, and dissolved oxygen (µmol/kg) were obtained at the depth of each fishing haul. Geographic predictor variables included distance to the edge of the continental shelf (200 m), slope (°), bathymetry (m), latitude, and longitude. Random-effect variables included cruise ID codes, vessel type (JCF and INPI, to assess the influence of net type), and period (night or day), whereas season was included as a fixed effect, using spring as the reference because the coldest waters were reported during the study period (Durazo et al. 2005).
The general form of the generalized additive mixed models is as follows (Hastie and Tibshirani 1986):

$$g(\mu_i) = \beta_0 + \sum_{j=1}^{p} f_j\left(x_{ij}\right) + \sum_{k=1}^{q} Z_{ik}\, b_k$$

where μ is the response variable, g is the link function, β_0 is the intercept, $f_j\left(x_{ij}\right)$ smooth functions of the predictor variables and $Z_{ik}b_k$ random effects (Wood 2017).

To implement the delta approach, GAMM presence/absence models were first fitted (23% and 77%). Presence/absence was modeled with a binomial distribution and a logit link function. Positive hauls were coded as 1, whereas negative hauls were coded as 0. Models were trained with 70% of the data and evaluated on the 30% held out. The best model was selected using Akaike's information criterion (Yu et al. 2013) and the area under the ROC curve (AUC) on the test set (Bradley 1997). Subsequently, from all fishing hauls only the positive CPUE values (23%, n = 63) were retained and used as the response variable (kg/h). To choose the CPUE distribution (Tweedie, Gamma, and Gaussian with a logarithmic link), the Akaike Information Criterion (AIC) was used, and model selection was performed using AIC. Given the low number of positive observations, the data were not partitioned (70/30%). In the end, one model for presence/absence and another for

CPUE are presented, corresponding to the lowest AIC value (Burnham et al. 2010). The delta model was developed for explanatory rather than predictive purposes. Explanatory variables for both models were those described above, and models were built using the mgcv package (Wood 2017) in the R environment (R Core Team 2025).

Additionally, a sensitivity analysis was performed using a Bayesian Zero-Inflated Negative Binomial (ZINB) model (Zhang and Yi 2022; Fagbamigbe et al. 2023) for the density of individuals per square kilometer (number/km^2); results are provided in the Supplementary Material.
The inverse distance weighting (IDW) interpolation method or spline interpolation (Hancock and Hutchinson 2006) was applied to environmental variables (temperature, salinity, and dissolved oxygen) obtained at oceanographic sampling stations, according to cross-validation (Lu and Wong 2008). This was done to obtain information on environmental factors at the depth where fishing hauls were conducted. In addition, to describe the spatial distribution of CPUE by season, the IDW interpolation method was used according to cross-validation (Lu and Wong 2008). The IDW method, when applied to the distribution of fishery resource density, is recommended over other spatial interpolation techniques due to the random factors affecting catches (Chen et al. 2016). The IDW formula is:

$$Z(x_0) = \frac{\sum_{i=1}^{n} w_i \cdot Z(x_i)}{\sum_{i=1}^{n} w_i}$$

Where the weights w_i are given by:

$$w_i = \frac{1}{d(x_0, x_i)^p}$$

Where $Z(x_0)$ is the estimated value at the interpolation point, $Z(x_i)$ is the observed value at location x_i, $d(x_0, x_i)$ represents the distance between x_0 and x_i, p, is the power parameter (typically $p = 2$), and n is the number of known data points used for interpolation (Lu and Wong 2008). The IDW interpolation was performed using the *gstat* package (Pebesma 2004) and the plots were generated using ggplot2 (Wickham 2016).

RESULTS

Multimodal size analysis

Between 2019 and 2024, biological sampling was conducted on 629 Pacific hake specimens. The average total length was 15.2 cm (sd = 6.6 cm), with a maximum of 40 cm and a minimum of 3 cm. A progressive development of hake cohorts was observed throughout the year. In spring, two modal size classes were recorded at 9.5 cm and 21.5 cm. During summer, similar modes were observed (11.9 cm and 21.6 cm), along with an additional mode representing larger individuals (34.3 cm). In autumn, the smallest specimens were recorded, with modal lengths of 4.1 cm and 14.1 cm (Table 2, Fig. 2).

Table 2. Multimodal analysis of Dwarf hake (*M. productus*) pattern length on the west coast of Baja California by season obtained from specimens collected between 2019 and 2024. The bandwidth, standard deviation (sd) and the coefficient of determination (r^2) are presented. The values of the Modes in italics represent the main mode

Season	Bandwidth (cm)	n	Mode (cm)	sd	r^2
Spring	2.3	148	9.5	3.3	0.97
			21.5	3.6	0.99
Summer	1.7	445	11.9	2.5	0.97
			21.6	3.5	0.99
			34.3	2.1	0.99
Autumn	2.3	27	4.1	2.4	0.99
			14.1	2.6	0.99

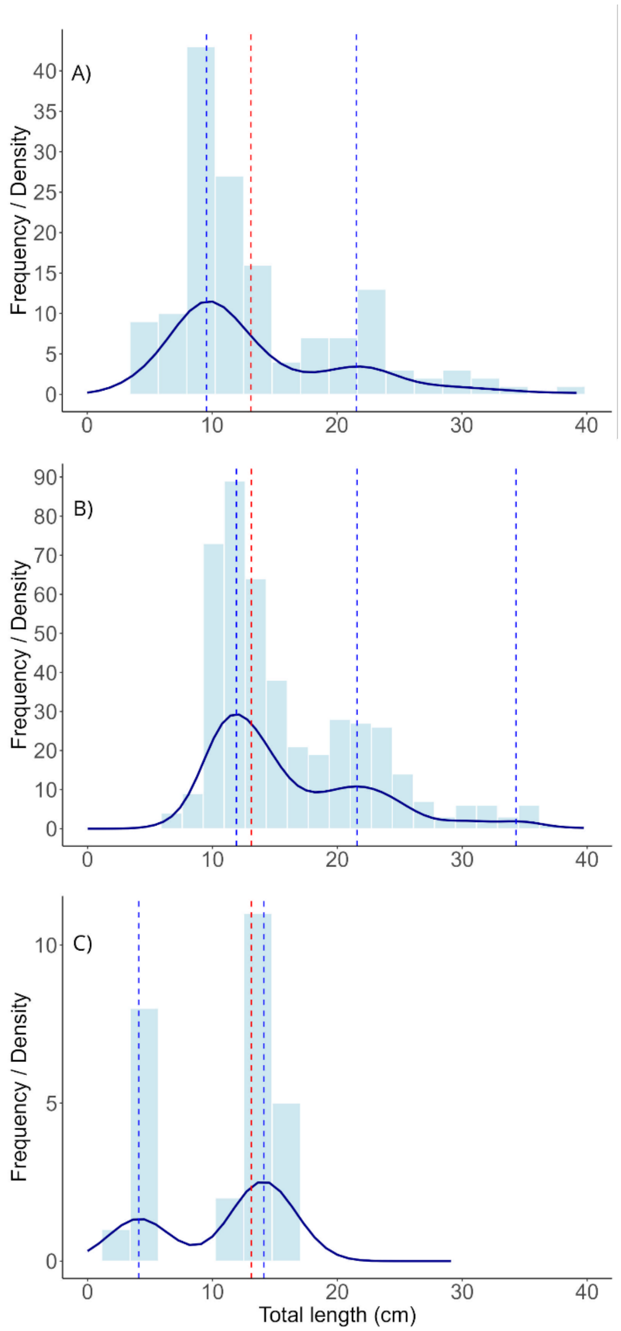

Fig. 2. Gaussian kernel density plots of Dwarf hake lengths observed during spring (A), summer (B), and autumn (C). The red line represents the length at first maturity (L50), estimated at 11.4 cm SL (13.11 cm TL), as reported by Salinas-Mayoral (2018).

The highest number of large specimens (~30 cm) was found in the Gulf of Ulloa (Punta Abreojos) during summer, although individuals exceeding 25 cm in length were also observed between Punta Baja and Puerto Canoas, Baja California. During spring, most specimens were captured in the Gulf of Ulloa and Bahía Magdalena, Baja California Sur, where the majority measured less than 20 cm in total length. In autumn very few individuals were captured, primarily in the central region of Baja California (Fig. 3).

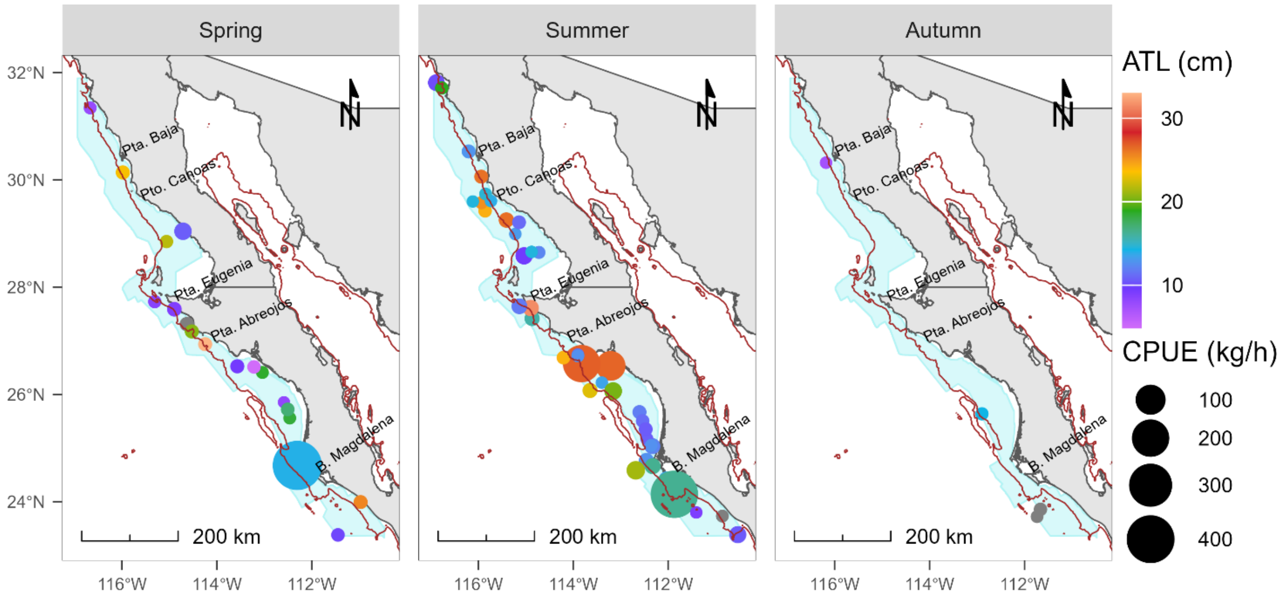

Fig. 3. Seasonal distribution and abundance (CPUE) per fishing haul, using a scaled representation (circle diameter) of *M. productus*, where colors indicate the average total length (ATL). The light blue polygon indicates the species' presence area during the study period. The brown line marks the edge of the continental shelf (200 m).

GAMM model of *Merluccius productus* presence/absence and environmental variables

Nine models were built in which hake presence was the response variable, using a binomial distribution with a logit link function. The models were trained with 70% of the data (n = 189) and evaluated on the withheld 30% (n = 82). The best model achieved an area under the ROC curve of 0.77 on the test set, indicating acceptable discriminatory ability. After validation, the final binomial model was refit using all data (n = 271) to obtain the final coefficients. The formula is as follows:

$$\log\left(\frac{p_i}{1-p_i}\right) = \beta_0 + \beta_{Season(i)} + \beta_1 temp_i + f_1(long_i) + f_2\left(\text{dist\_cs}_i\right) + b_{survey(i)}$$

where p_i is species presence, $season$ is the fixed effect, f_1 and f_2 represent nonparametric smooth terms for longitude (long) and distance to the continental shelf edge (dist_cs), whereas $survey$ represents the random effect. The model had an AIC of 241.1 and explained deviance of 27.3%.

The results of the binomial model (Table S2) showed that temperature had a negative and highly significant linear effect on the probability of hake presence (estimate = –0.525, $p < 0.001$). Longitude exhibited a significant non-linear effect (edf = 3.07, $p < 0.001$), with a higher probability of presence in certain areas (–114 to –111°) along the coast of Baja California Sur (Fig. 1). Distance to the continental shelf edge also had a negative effect (edf ≈ 1, p = 0.0029), indicating a higher probability of capture close to this geomorphological feature (Fig. 4). The cruise random effect was significant (p = 0.0024), explaining part of the variability among surveys. Season showed a marginal effect: autumn exhibited a slightly positive, non-significant trend ($p = 0.082$) relative to spring (reference category), whereas summer did not differ from it. The model explained 27.3% of the deviance and showed acceptable discriminatory power in cross-validation (AUC = 0.77 in the 30% test set). The effects of temperature and longitude were maintained in the complementary ZINB analysis (Table S1).

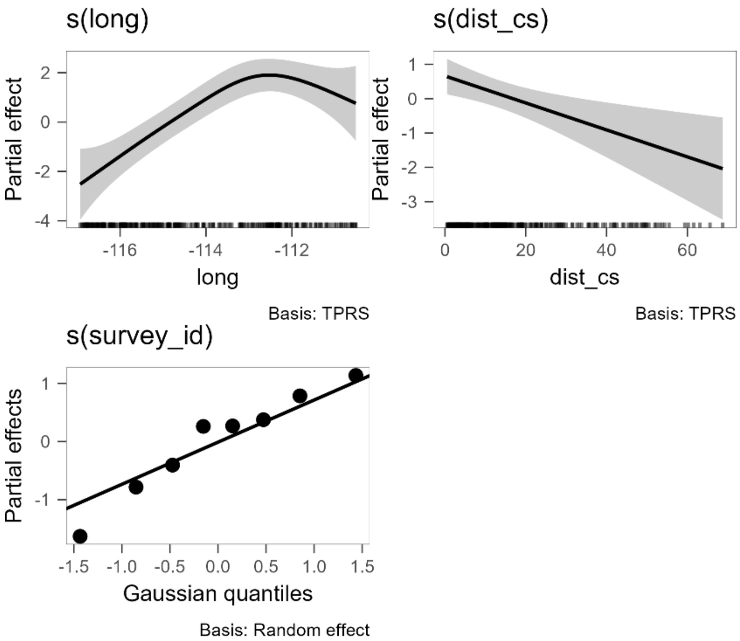

Fig. 4. Partial effects of the binomial presence/absence GAMM model (logit link function) showing the influence of longitude (long), distance of continental shelf (dist_cs) and survey (Random effect) for Dwarf hake along the western coast of the Baja California Peninsula. Shaded areas represent 95% confidence intervals.

Generalized additive mixed-effects model of *Merluccius productus* CPUE and environmental variables

Eighteen models were fitted, using CPUE (kg h^{-1}) as the response variable and assuming a Gamma distribution with a log link function. Based on the explained deviance and AIC values, the selected model was:

$$\log(\mathbb{E}[\mathrm{CPUE}]) = \beta_0 + \beta_{season(i)} + te\left(\mathrm{sal}_i, \mathrm{trawl\_depth}_i\right) + f\left(\mathrm{dist\_cs}_i\right)$$

where $\log(\mathbb{E}[\mathrm{CPUE}])$ is the response variable, $season$ is the fixed effect, te denotes a smooth tensor-product term that models the nonlinear interaction of salinity (sal) with fishing-haul depth (trawl_depth), and f is the nonparametric smooth term for distance to the edge of the continental shelf (dist_cs). The model had an AIC of 221.2 and explained 79.8% of the variability in *Merluccius productus* CPUE along the western coast of the Baja California Peninsula.

For hauls with positive catch ($n = 63$), the Gamma model of CPUE (Table S3) showed a significant interaction between salinity and trawl depth (te(sal, trawl_depth): F = 4.04, $p < 0.001$; edf = 15.7). CPUE increased at intermediate values of both variables (Fig. 6). Distance to the continental shelf edge (dist_cs) had a non-linear effect (edf = 2.73, $p = 0.0007$), with higher catches at shorter distances (Fig. 5). However, in offshore areas, substantial volumes could also be caught, as occurred near the coast southeast of Punta Abreojos. Overall, in areas less than 20 km from the continental shelf edge along the western coast of the Baja California Peninsula, high CPUE values of *M. productus* are more likely to be found. The autumn season showed a marginal negative trend ($p = 0.052$) compared with spring, whereas summer did not differ from the reference season (spring).

The highest CPUEs were detected at 8 m (430 kg/h; sd = 76.48) and 92 m depth (390.36 kg/h; sd = 76.48), at 11.99 and 5.86 km (sd = 13.65 m) from the continental shelf edge and at salinities of 34.3 and 34.73 (sd = 0.42), respectively. Along the western coast of the Baja California Peninsula, salinity progressively decreases southward because the California Current reaches its maximum intensity toward the south in spring (Fig. 6).

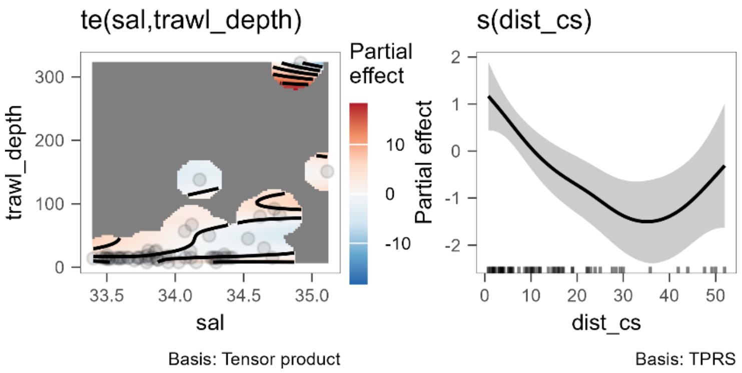

Fig. 5. Partial effects of the Generalized Additive Mixed Models (GAMM) showing the influence of trawl depth, salinity (sal) and distance of continental shelf (dist_cs) on Dwarf hake (*Meluccius productus*) CPUE (kg/km^2). Shaded areas represent 95% confidence intervals.

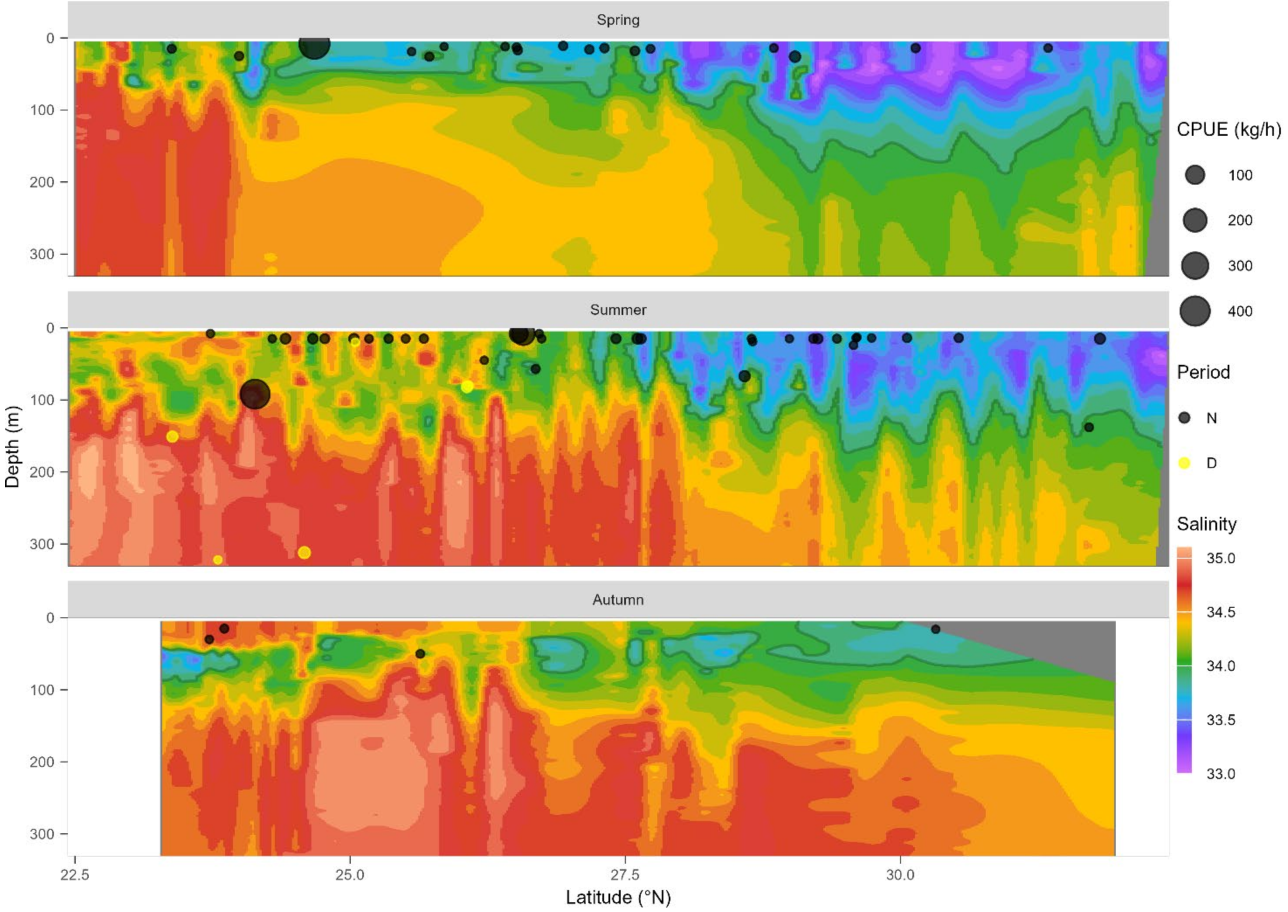

Fig. 6. Vertical distribution of salinity and scaled (circle diameter) CPUE (kg/h) of *M. productus* along the WCBC. Note the yellow dots on the summer panel, which correspond to the deepest daytime catches.

During spring, the core area of Dwarf hake abundance was located off Bahía Magdalena, while aggregations in the rest of the region were sparse. In summer, two distinct centers of *M. productus* abundance were identified: the first, with higher density, was observed southwest of Bahía Magdalena, and the second was located south of Punta Abreojos in the Gulf of Ulloa (Fig. 7).

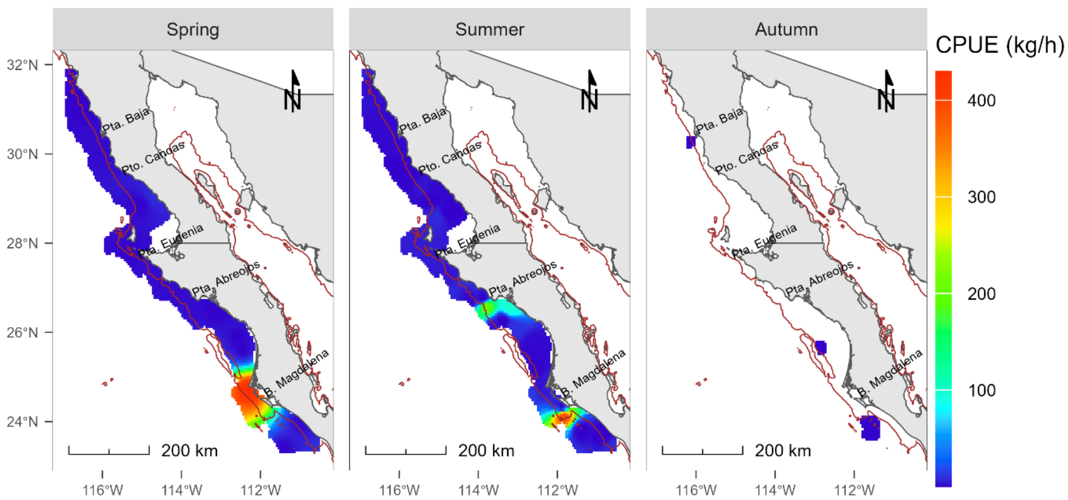

Fig. 7. Seasonal spatial distribution and abundance of Dwarf hake along the western coast of the Baja California Peninsula. The brown line indicates the edge of the continental shelf (200 m depth).

DISCUSSION

In the present study, Dwarf hake (*Merluccius productus*) was found to be distributed along the entire Baja California Peninsula, with larger individuals predominantly located in the northern region of the Gulf of Ulloa, showing seasonal variations. Based on size composition, the population included both juvenile and mature individuals, which is consistent with previous studies (Vrooman and Paloma 1977; Salinas-Mayoral 2018). Vrooman and Paloma (1977), in an early assessment of hake biology in the eastern Pacific, reported that Dwarf hake reach sexual maturity within their first year of life, highlighting their relatively fast life cycle. Similarly, Salinas-Mayoral (2018), in a study conducted off Bahía Magdalena, estimated the length at first maturity for the general population to be 13.11 cm TL (11.4 cm SL), providing a regional reference for reproductive parameters. Salinas-Mayoral (2018) reported that populations of Dwarf hake off Bahía Magdalena are dominated by small-sized individuals, typically below 20 cm TL, with a high proportion of organisms close to the length at first maturity. Similarly, Mora-Zamacona et al. (2024) described a population structure characterized by relatively small sizes and rapid growth, with most individuals concentrated in early age classes, consistent with a short-lived species. These patterns support the size distribution observed in the present study and reinforce the idea that Dwarf hake populations are composed mainly of small-bodied individuals with fast turnover rates.

The modal lengths observed during summer and autumn in the present study exceeded this threshold (Table 2), suggesting increased reproductive activity during these seasons. Adult-sized individuals were most frequently found in the northern Gulf of Ulloa (Punta Abreojos) and Bahía Magdalena, whereas smaller specimens (juveniles) were more commonly observed within the interior of the Gulf of Ulloa and Bahía El Vizcaíno. Nevertheless, both juveniles and adults were associated with the edge of the continental shelf (Fig. 3), where the highest abundances of the species were also recorded.

In this study, the delta approach was implemented to relate the presence/absence and CPUE of Dwarf hake per fishing haul to environmental variables using GAMM models along the WCBC. These models were developed to address the high frequency of zeros in the CPUE data. This approach is recommended for fisheries data (Maunder and Punt 2004; Zuur et al. 2009) because it allows the ecological processes that determine species presence to be separated from those that modulate CPUE once the species is present (Grüss et al. 2014).

Temperature emerged as the main negative predictor of presence, which agrees with previous studies indicating hake preferences for temperate or cold waters (Swartzman 1997, Sion et al. 2019). According to the GAMM presence/absence model along the WCBC, Dwarf hake shows some preference for the 11 to 17°C range. This thermal range coincides with what was reported by Rubio-Rodríguez et al. (2026) off Bahía Magdalena (12 to 15°C) and is similar to what was found by Álvarez-Trasviña et al. (2022) in the northern Gulf of California (13.2 to 14.0°C) and by Sion et al. (2019) in the Mediterranean Sea (14 to 18°C). The spatial effect (longitude) suggests a heterogeneous distribution, possibly related to the orientation of the Baja California Peninsula (northwest–southeast). The consistency of thermal and longitudinal effects between this model and the Bayesian ZINB indicates that these patterns are robust (Supplementary Material). The higher probability of presence near the continental shelf edge matches what has been found for the species in other regions (Ware and McFarlane 1995; Sion et al. 2019; Álvarez-Trasviña et al. 2022), in the Gulf of Ulloa (Godínez-Pérez 2013), and off Bahía Magdalena (Rubio-Rodríguez et al. 2026); the latter two areas are located along the western coast of Baja California Sur. The cruise random effect indicates that hake presence varies among years. This factor may be associated with each cruise having a slightly different study area, which could introduce bias (Fig. 1). The presence/absence model using the 70/30 split showed an AUC of 0.771, which is considered acceptable for species distribution models in marine ecology. The low deviance explained by the binomial model (27.3%) is common when there are many false negatives or when the species is rare, and it does not invalidate the predictive usefulness of a model (Pearce and Ferrier 2000; Grüss et al. 2014).

The salinity–depth interaction was the strongest predictor of positive CPUE, suggesting that once hake is present, its abundance responds to finer-scale oceanographic conditions. Intermediate values of salinity and depth produced the highest CPUEs, possibly associated with the transitional water mass (Rubio-Rodríguez et al. 2026). Trawl depth was also a significant variable explaining hake CPUE, because catches were found mainly within the upper 100 m of the water column where the subsurface flow of the California Current is located (Agostini et al. 2006). This depth range is relatively similar to that reported in other studies, although those works refer to bottom depth (Sion et al. 2019; Álvarez-Trasviña et al. 2022; Bahamon et al. 2022). Distance to the continental shelf edge was also an important variable, as the most notable CPUEs occurred near it and within 20 km of this threshold. This result is similar to that found by Ware and McFarlane (1995), Godínez-Pérez (2013), Druon et al. (2015), and Rubio-Rodríguez et al. (2026), who describe that the largest aggregations (kg/km-2, kg/haul) occur in the vicinity of the continental shelf edge (175–375 m). Druon et al. (2015) for instance, proposed that the continental shelf edge serves as a nursery ground for European hake. Cooke et al. (2006) noted that Pacific hake is distributed throughout the water column and is closely associated with the continental shelf break. In the Gulf of California, live specimens of Pacific hake have been documented in their natural habitat at depths ranging from 331 to 742 meters, associated with seamounts (Huidobro-Campos et al. 2023). In the present study, nighttime trawls occurred at depths ranging from 19.5 to 91.5 m, reflecting the species' diel vertical migration for feeding. This daily vertical migration is a common behavior in hake species (Álvarez-Colombo et al. 2014).

The red crab (*Pleuroncodes planipes*) was the species most frequently associated with Dwarf hake (*M. productus*) in the study area. Commonly inhabiting the edge of the continental shelf, *P. planipes* is not only highly abundant in the region but also constitutes a regular component of the hake's diet (Balart and Castro-Aguirre 1995, Balart 1996). Previous studies have identified both the northern Gulf of Ulloa and Bahía Magdalena as key distribution centers for *P. planipes*, hosting large aggregations of this species (Vallarta-Zárate et al. 2023). Consequently, the Gulf of Ulloa provides an optimal habitat for Dwarf hake, offering high prey availability and favorable environmental conditions, as further described below.

Our findings primarily reflect surface distributions during nocturnal foraging, rather than the full habitat range of *Merluccius productus.* with frequent captures occurring at depths shallower than 20 meters—within the subsurface flow zone described by Agostini et al. (2006) in the California Current system. Although the species (*M. productus*) is known to inhabit relatively cool subsurface waters at greater depths, often in environments influenced by low-oxygen conditions (Keller et al. 2017, Álvarez-Trasviña et al. 2022), the nighttime surface observations likely correspond to transient foraging behavior near the surface. Given that sampling occurred at ~15 m during nighttime (median = 15 m, maximum = 138 m, minimum = 11 m, and sd = 21.14 m), the data may represent juvenile or adult hake exploiting epipelagic prey fields. As previously noted, proximity to the continental shelf edge was another key variable in the model, with high abundances typically recorded within 20 km of the shelf break.

The negative autumn trend (marginal, *p*-value 0.052) relative to spring could indicate seasonal migrations. This negative trend in CPUE contrasts with the positive (marginal, *p*-value 0.082) trend in the presence/absence model. However, this may be due to the seasonal data being unbalanced. Although in both models the lack of statistical significance (p-value > 0.05) suggests caution in interpretation. While only two surveys were conducted during autumn (2009 and 2111), catches were low, like what was found during October to December by Rubio-Rodríguez et al. (2026) off Bahía Magdalena. The northward migration of hake (United States and Canada) during summer and its return southward in winter has been documented (Dorn 1995; Benson et al. 2002). This process could explain the negative CPUE trend in autumn; however, we are not sure due to the lack of additional cruises at that time of year.

In the present study, gear type (associated with vessel type) and fishing period (night/day) were not significant, so they were excluded from the models. This is due to a strong sampling imbalance: hauls conducted with the JCF predominated (213) compared with the INPI (58), as did nighttime periods (238) compared with daytime (33). For positive CPUE, the imbalance was even greater: JCF (58) and INPI (5); in addition, only six daytime hauls yielded positive catches, whereas the rest occurred during the nighttime period (57).

The presence/absence model and the ZINB did not consider salinity and haul depth; this may be because some hauls captured small individuals, whereas others captured large individuals or a mixture of both, which causes variability in CPUE. An analysis of this variability is beyond the scope of this research and could be considered in future studies. The reduced sample size for positive CPUE (n = 63; 23% of the data) limited the inclusion of additional random or fixed effects (cruises, period, vessel type, or gear type were not significant) and may have reduced the power to detect other effects. Future studies should incorporate more surveys. In addition, one aspect that should be explored is a balanced sampling design across both vessels (gear type) and times of day. Cooke et al. (2006) investigated the geographic distribution of Pacific hake (*Merluccius productus*) along the U.S. coast through acoustic surveys conducted during summer months (June to September) between 1995 and 2005. Their findings indicated that hake distribution is closely linked to the flow of the California Current and areas of high primary productivity. During summer and autumn—the period of highest Dwarf hake abundance in the present study—the California Current contracts southward to the vicinity of Punta Eugenia. As a result, the Gulf of Ulloa functions as a transitional zone between warm and temperate marine currents (Durazo 2015), creating a habitat with distinct characteristics, predominantly warmer conditions, which are exploited by species such as hake and red crab. Although the National Fishing Charter, published as part of Mexican fisheries management legislation, recognizes hake fishing zones in Bahía Magdalena and the northern Gulf of California, it does not differentiate between the stocks of Dwarf hake and Pacific hake. However, differences in size distribution should lead to the identification of independent management measures. Furthermore, as previously mentioned, in addition to the abundance center of Dwarf hake in Bahía Magdalena, this study identified another seasonal abundance center of Dwarf hake located between Punta Abreojos and Laguna San Ignacio. It suggests that the species is associated with coastal lagoons and other ecosystems of high ecological importance, as demonstrated for estuarine stocks of Pacific hake in Canada (King and McFarlane 2006). The hauls were conducted near the surface, and due to the species' diel vertical migration behavior, captured individuals were likely engaged in nocturnal feeding near the surface. This behavioral trait is key to understanding catchability patterns and has implications for the design of future surveys and management strategies. Sex and maturity stage data were not recorded during sampling, as this was an opportunistic survey focused on abundance and environmental characterization of another species. This limitation restricts the interpretation of size structure and population composition, particularly for *Merluccius productus*, a species known to exhibit sexual dimorphism (Zamora-García et al.

2020). Nonetheless, the size analysis provides valuable insights into habitat associations and potential life stages present in surface waters.

The availability of Dwarf hake in northwestern Mexico represents a potentially valuable fishery resource for the region (Balart 1996). The global hake market is dominated by Europe, which serves as the primary importer of this resource (Ospina-Alvarez et al. 2024). Although Dwarf hake (*M. productus*) typically exhibits smaller sizes compared to Pacific hake found in North America and the Gulf of California, the Baja California fishing sector may still find promising opportunities to market this species in regions where such fish are valued.

It is essential to assess the existing biomass of this species, ideally through targeted research efforts that also enable spatiotemporal monitoring of the population. Hydroacoustic surveys combined with trawl sampling represent a viable approach (Balart 1996; Lluch-Cota et al. 2006; Godínez-Pérez et al. 2025), building upon previous initiatives conducted in the region, such as the scientific surveys presented in this study and those documented by Godínez-Pérez (2013).
Beyond the earlier biological studies, recent advances have yielded substantive contributions to fisheries management, particularly concerning the age and growth of Dwarf hake (*M. productus*) (Mora-Zamacona et al. 2024), as well as through specific proposals for fisheries exploitation (Mora-Zamacona et al. 2023). Therefore, it is equally important to promote the development of sustainable fishing technologies that translate scientific findings into efficient and responsible harvesting practices.

CONCLUSIONS

The Dwarf morphotype of Pacific hakes was found throughout the WCBC, but its highest abundances and largest individuals consistently occurred near the edge of the continental shelf, particularly in the northern Gulf of Ulloa and Bahía Magdalena. These results demonstrate that both juvenile and adult hake rely heavily on the shelf-break environment, a zone that also concentrates prey such as the pelagic red crab *Pleuroncodes planipes*.

Environmental modeling revealed that temperature, trawl depth, and distance to the continental shelf were the strongest predictors of hake abundance. Peak CPUE occurred within a relatively narrow temperature range (14–17°C) and at distances ≤ 20 km from the shelf edge, highlighting the ecological importance of transitional habitats shaped by the California Current System. The diel vertical migration of hake strongly influenced catchability, indicating that nighttime surface distributions represent transient foraging behavior rather than the species’ full depth range.

These findings expand current knowledge of Dwarf hake ecology and identify two seasonal centers of abundance—Bahía Magdalena and Punta Abreojos–Laguna San Ignacio—that should be considered priority zones for future monitoring. The presence of multiple cohorts and individuals exceeding previously reported maximum lengths for the Dwarf form suggests population structure and life-history patterns that merit further study.

Given the species' consistent availability, ecological significance, and association with productive coastal systems, Dwarf hake represents a promising candidate for the development of a small-scale, sustainably managed fishery. However, robust biomass assessments and stock-specific management strategies will be essential, particularly because Dwarf hake differs markedly from the northern Pacific hake stock. Our results provide a scientific baseline for such efforts and highlight the need for targeted acoustic surveys and continued spatiotemporal monitoring to support responsible exploitation and conservation of this regional resource.

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Supplementary materials

Supplementary material provides additional methodological details and complementary analyses to support the main results. Specifically, it includes a Bayesian zero-inflated negative binomial (ZINB) modeling approach used to evaluate Dwarf hake density, along with full model specifications, diagnostics, and parameter estimates. The section also presents supplementary tables and figures (Tables S1–S3, Figures S1–S4) illustrating model performance, residual analyses, and predicted effects of environmental variables, as well as further discussion of consistency and differences relative to the main modeling framework. (download)

Fig. S1. Diagnostics for the zero-inflated Bayesian (ZINB) model fitted with *brms*. Convergence and model-fit diagnostics. (download)

Fig. S2. Estimated conditional effects of the explanatory variables on the number of Dwarf hake individuals. Solid lines indicate the posterior mean and shaded bands the 95% credibility intervals. The plots show predicted marginal relationships: density declines rapidly as temperature increases; increases with longitude (eastward); and is higher in autumn than in spring or summer. The effect of distance to the continental shelf edge is relatively flat with wide uncertainty, consistent with the credibility interval crossing zero. (download)

Fig. S3. Vertical distribution of all fishing hauls, including zero CPUE, by season and time of day. Vertical temperature section, where the x-axis is latitude and the y-axis is depth. The magenta line is the 17.5°C isotherm. (download)

Fig. S4. Residuals of the CPUE GAMM model (gamma distribution) for Dwarf hake along the western coast of the Baja California Peninsula. (download)

Table S1. Summary of the Dwarf hake ZINB model for the western coast of the Baja California Peninsula. (download)

Table S2. Summary of the binomial presence/absence GAMM model (logit link function) for Dwarf hake along the western coast of the Baja California Peninsula. (download)

Table S3. Summary of the CPUE GAMM model (gamma distribution) for Dwarf hake along the western coast of the Baja California Peninsula. (download)