

Where are the hake going? How age, environmental signals, and shelf habitat shape Pacific Hake (*Merluccius productus*) summer distribution

Rebecca E. Thomas¹, Julia Clemons¹, Stéphane Gauthier², Alicia Billings¹, Chelsea Stanley¹, Dezhang Chu^{1,3}, Elizabeth M. Phillips¹, John Pohl¹, Sabrina Beyer¹, Stephen de Blois¹

¹Fishery Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington, USA

²Fisheries and Oceans Canada, Institute of Ocean Sciences, Sidney, BC, Canada

³Retired

Corresponding author: Rebecca Thomas, Rebecca.Thomas@noaa.gov

Keywords: Pacific hake migration, environmental conditions, fisheries acoustics, acoustic-trawl survey, *Merluccius productus*

Abstract

Sustainably managing a multinational fishery on a transboundary, relatively long-lived and migratory fish stock is challenging, especially in a changing ocean environment. In a warming world, Pacific hake (*Merluccius productus*, Merlucciidae), jointly managed by the U.S. and Canada, have been hypothesized to move north. However, in recent years the proportion of Pacific hake in the northern part of their historical range has been declining. Because Pacific hake have a complex migration pattern depending on age and other factors, we developed models to relate the effects of fish age, length, biomass, El Niño conditions, and Pacific Decadal Oscillation (PDO) indices on interannual shifts in the latitudinal distribution of the Pacific hake stock, using fisheries-independent survey data spanning 30 years (1995-2025). We found that older Pacific hake and warmer PDO conditions significantly contributed to explaining the proportion of migration into the northern part of their range during summer months. Over the 30-year time series, Pacific hake exhibited a southward shift in their northern extent, along with a decrease in area occupied, suggesting a change in movement patterns and overall contraction of the stock. Distance from the continental shelf break positively correlated with age for fish up to 8 years old. We estimated that 95% of the Pacific hake biomass occurred within 31 nautical miles of the shelf break, and that the distribution of Pacific hake extends farther offshore as biomass increases. These results provide insight on interannual shifts in the distribution of Pacific hake that can inform predictions for future management strategies.

1 Introduction

Transboundary fish stocks require international collaboration to ensure that effective and reasonable management agreements are in place. Multinational fisheries are often jointly managed using stock assessments and management strategy evaluations to assess stock status (Melnychuk et al., 2020; Perryman et al., 2021), and frequently rely on fishery-independent data, which provides an estimation of a targeted fish stock's abundance, size and age structure, and geographic distribution (Hilborn et al., 1992; Cooper et al., 2006). For example, the stock of Pacific hake (*Merluccius productus*, Merlucciidae, hereafter “hake”) has been jointly assessed and managed by the United States (U.S.) and Canada under the Pacific Hake (Pacific Whiting) Treaty since 2003 (United States, 2003). Due to their transboundary movements, the hake stock is surveyed jointly by the U.S. and Canada during the Joint US-Canada Pacific Hake Integrated Ecosystem and Acoustic Trawl Survey, which produces fishery-independent data that facilitates the understanding of abundance and distribution of the stock and supports decisions on total allowable catch (TAC) limits on an annual basis. Although some international stock assessments account for environmental drivers (Pepin et al., 2022; Caserta et al., 2025), considerable numbers of stock assessments including hake, do not explicitly include drivers of environmental change when modeling the overall stock biomass and/or distribution. There is a general need for increased understanding of drivers of fish stock productivity and shifts in distribution to better inform management (Ferriss et al., 2026).

Fish population abundances and distributions change in relation to human pressures, such as exploitation rates and anthropogenically driven climate change (Denechaud et al., 2020), as well as to naturally occurring environmental variables (Mantua et al., 1997). Fish distributions also naturally vary based on stock size and age structure (MacCall, 1990; Marquez et al., 2021). However, there is a general lack of knowledge of the mechanisms that drive natural and climate-related changes in fish distribution, and how shifts in spatial distributions are linked to changes in the size and age structure of the population. This study sought to investigate some of the demographic and environmental factors associated with shifts in the spatial distribution of hake through time.

Hake is an abundant groundfish stock that occurs along the west coast of North America between southern California, U.S. and British Columbia, Canada, and at times as far north as Alaska, U.S. (Ressler et al., 2007; Hamel et al., 2015). Hake are thought to migrate north from offshore waters in southern California during spring, and form feeding aggregations along the continental shelf break (200 m isobath) during summer (Methot et al., 1995). Hake are typically located between 50-500 m below the sea surface during the day, although average depth distributions vary and are likely related to oceanographic conditions and prey availability (Ressler et al., 2007; Phillips et al., 2023).

The hake fishery, a major source of protein and revenue, is shared between the U.S. and Canada (Johnson et al., 2025). The hake fishery is the largest by volume single-species fishery on the west coast of the United States, with a 2023 total ex-vessel value of all hake caught (excluding catch from Tribal fisheries) of \$46.5 million (Steiner et al., 2025). The hake stock is typically fished by U.S. and Canadian vessels between May and December (Hamel et al., 2015), with trawl locations and greatest catch volumes varying based on fish distribution and availability to the fleet. The Agreement between the Government of the United States of America and the Government of Canada on Pacific Hake/Whiting, which was signed in November 2003 (United States, 2003), codified that 26.12% of the total allowable catch would be allocated to Canada each year, and the remaining 73.88% would go to the U.S. However, variability in

hake northern migrations can present an issue if either country consistently fails to catch its allocation due to lack of hake in each country's waters. It is critical that spatial distribution and influences on hake migration between the U.S. and Canada be well understood to ensure that the management principles of the Treaty can be met.

The spatial distribution of hake is complex and thought to be influenced by factors such as age and environmental conditions (Dorn, 1995; Ressler et al., 2007; Agostini et al., 2008; Vestfals et al., 2023) as well as by proximity to the shelf break (Dorn, 1995; Swartzman, 2001; Ressler et al., 2007; Malick et al., 2020). Variation in the extent of annual hake migrations is postulated to relate to variation in ocean conditions, including El Niño Southern Oscillation (ENSO) events, when more hake occur further north when water temperatures are warmer than average and poleward transport is greater (Dorn, 1995; Ware et al., 1995; Agostini et al., 2006). The Pacific Decadal Oscillation (PDO), historically the first empirical orthogonal function of Sea Surface Temperature (SST) anomalies in the North Pacific, has been linked to general changes in oceanic fish production (Mantua et al., 1997; Hare et al., 2000), with some species flourishing in cold regimes with more upwelling and increased number of cold-water zooplankton (e.g., anchovy, Chavez et al. 2003), other species flourishing in warm regimes (e.g., sardine, King et al. 2011), with other species responding in more complex ways (e.g., Chinook salmon, King et al. 2011); effects on hake production from changes in PDO regimes may include potential changes in hake recruitment (Vestfals et al., 2023) and/or spawning (King et al., 2011). In terms of cross-shelf distribution, hake are distributed around the shelf break, with larval and juvenile hake frequently found more inshore and adult aggregations typically extending offshore (Hamel et al., 2015). Hake thermal niches are projected to narrow with a changing climate (Ward et al., 2024), and hake have simultaneously been hypothesized to have a low probability of shifting range (McClure et al., 2023) as well as to shift further north with ocean warming from climate change (Beamish, 2008; King et al., 2011; Malick et al., 2020; Jacobsen et al., 2021). Current gaps exist in our understanding of the historic spatial distribution of hake, the effects of environmental variables, and how the distribution may have shifted in more recent years, limiting the ability to ensure that a well-managed fishery continues for all treaty parties.

In this study we investigated correlations in biological (age, length) and environmental (El Niño and PDO indices) factors with shifts in the latitudinal (north/south, [N/S]) and onshore/offshore (east-west, [E/W]) distribution of hake, and documented recent year trends in an apparent reduced abundance of hake in Canadian waters in recent years. Observed reductions in northward migration are confounded by variation in movement at age and require analyses that can account for variation in multiple variables such as the mean age of individuals in the population, biomass, and environmental conditions. From previous studies referenced above, we hypothesize that older, larger hake will be observed further north, especially in warm El Niño and PDO years, with the stock either maintaining its distribution or shifting northward over the past 3 decades as the ocean has warmed. In addition, we also expect to see juvenile fish closer to the shelf break, and adult fish extending further offshore.

2 Methods

2.1 Survey Data collection

The data used in this study were collected between 1995-2025 during the Joint U.S.-Canada Pacific Hake Integrated Ecosystem and Acoustic Trawl Survey. This acoustic-trawl survey utilizes fisheries echosounders to enumerate fish alongside targeted trawling to ground-truth fish aggregations and collect

biological samples (Fleischer et al., 2008). The survey provides crucial abundance estimates of adult hake for stock assessments. Following established management and biological conventions for this species, individuals aged 2 years and older (age-2+) were classified as adults, whereas age-0 and age-1 individuals were classified as juveniles (Edwards et al., 2026).

While earlier survey designs exist, the survey has been conducted every two or three years since 1995 (with the exception of an additional survey in 2012) as a joint effort between Fisheries and Oceans Canada and the National Oceanic and Atmospheric Administration (NOAA). The survey occurs from mid to early June through mid-September, spanning the continental slope and shelf from 50 to 1,500 m bottom depths along a series of E/W parallel transects (Fig. 1). The survey starts south of Monterey Bay, California (~35°N) and extends into northern British Columbia, Canada or southern Alaska (~55°N) with some interannual variation. The nominal transect spacing is 10 nautical miles (nmi), although due to logistical constraints, in some survey years and/or areas a transect spacing of 15 to 30 nmi has been used.

Following standard acoustic-trawl survey methods (Simmonds et al., 2005), trawl locations and durations were not determined a priori, but rather were based on characteristics of the echosign to target a representative sample of the acoustically observed aggregation. The survey predominantly uses midwater trawls, with occasional bottom trawls used prior to 2012. Head-rope sensors (e.g., SIMRAD FS70) were deployed on the net to ensure the trawl caught the desired echosign as well as to record time, depth, and temperature in the water where the net sampled. The attributes of the nets and echosounders used across thirty years of the survey are shown in Table S1 and Table S2.

Acoustic data were collected as described in Thomas et al. (2024). In summary, acoustic backscatter were observed in real-time to identify potential hake aggregations, and trawls were performed opportunistically during each survey to obtain species identification and biological data. All acoustic analyses since 2003 have been carried out using Echoview software (Echoview Software Pty Ltd, Hobart, Australia); previous analyses were carried out in Simrad BI500 software. Within echograms, analysts manually drew acoustic regions around backscatter that were visually identified as hake using scattering data from multiple echosounder frequencies and as informed by the trawling information. Each region of hake backscatter was assigned biological information from a single trawl that had either fished on that particular sign, or from a nearby trawl fished on echosign with similar acoustic and depth characteristics.

Trawl catches were processed using standard sorting and counting methods (Hughes 1976; Weir and Station 1978). Catches under approximately 1,500 kilograms (kg) were sorted and weighed entirely, while larger catches were randomly subsampled. For hake, a random sample of 300-400 fish per trawl was taken to determine sex and length with a further subset of ~50 fish selected for individual weights, otolith collection (for age determination), visual maturity states and other biological sampling.

2.2 Post-survey data processing:

Trawl data were grouped into hake length-based strata by forming groupings of trawls with similar length-frequency distributions using Kolmogorov-Smirnov goodness-of-fit statistics on each pair of trawls as a guide (Simmonds et al., 2005). From 1995-2013, this grouping was done manually, and from 2015-2025 strata were calculated automatically using hierarchical cluster analysis. The acoustic backscatter data attributed to hake, in units of S_A , (also known as Nautical Area Scattering Coefficient

(NASC), m^2/nmi^2) were exported in 0.5 nmi sampling units along each transect within each acoustic region assigned to a hake trawl. Target strength (TS, dB re 1 m^2) of hake and σ_{bs} (m^2) from the associated stratum were used to estimate number density (numbers nmi^{-2}) and biomass density (kg nmi^{-2}) of hake within each acoustic region, where σ_{bs} is the acoustic backscattering cross-section calculated from the length of hake in each stratum (see Appendix). The backscatter along each transect was interpolated within the survey area using ordinary kriging and a uniform grid with 2.5×2.5 nautical mile cells to estimate total hake biomass and variance. Kriging is a geostatistical estimator used to interpolate spatially distributed data onto an unobserved location (Petitgas, 2001) and has been used in a number of acoustic-trawl surveys to estimate the abundance and variance of many fish stocks (Petitgas, 1993; Agostini et al., 2006; Rivoirard et al., 2008; Woillez et al., 2009). For the stock assessment of hake, the survey provides an age-2+ biomass estimate and age-1 abundance index. All biomass from hake strata associated with fish age-2 or greater were summed together to estimate total adult hake biomass, and hake strata associated with age-1 fish were treated separately. Both kriged and unkriged estimates were produced; details of the calculations are given in the appendix.

2.3 Biological data subsampling & aggregation:

To examine the effects of hake length and age on distribution, we subsampled and aggregated data from the opportunistic trawls used for ground-truthing. Subsampling or aggregation was necessary to ensure the robustness of the data use in the analyses and to minimize bias, as fish within the same trawl often correlate by length and age due to schooling behavior. We addressed these correlations in three different ways for different analyses: 1) subsampling specimen biological data (hake ages and lengths) via “inverse-catch”, “equal-age” and “equal-length” techniques, 2) aggregating biological data by trawl, and 3) aggregating biological data by trawl stratum. Respectively, these methods were applied to 1) minimize bias when analyzing data from single fish to evaluate the length and age distribution across the survey range, 2) to generate unique geographic locations of trawls by age group to characterize age-based latitudinal distributions, and to 3) minimize bias when analyzing broad-scale cross-shelf characteristics of hake distributions by age.

2.3.1 Subsampling trawl specimen data:

The first method of addressing correlation used three subsampling techniques to subsample the biological data across all trawls with no aggregation. (a) The first subsampling technique, termed “inverse-catch”, sampled the specimen data within a trawl inversely proportional to the number of fish in the trawl, so that fish in a large catch were less likely to be subsampled than fish in a smaller catch. This effectively made the subsampled data a random sample of what was caught in all trawls. Inverse-catch subsampled data were used in the GAM models of age and length vs. latitude and to generate sex-specific von Bertalanffy growth curves relating length to age using generalized non-linear least squares estimation (Kimura, 1979). (b) The second technique, termed “equal-age”, subsampled the data inversely proportional to the number of fish in each age bin (1-10+). The third technique, termed “equal-length”, subsampled the data inversely proportional to the number of fish in each length bin (5-80 cm). These latter two forms of subsampling preserved randomness within a single age or length bin, and helped keep the sample size higher in age or length bins that were less populous than the initial sample. These age and length subsampled data were used in box plots to assess the relationship between hake age and length with latitude. The median age and latitude of the largest hake (≥ 66 cm), was calculated from the “equal-length” subsampled data.

2.3.2 Aggregating specimen data by individual trawl:

The second method of dealing with correlation in biological data aggregated data on the trawl level. We used the presence/absence of hake age classes in each trawl to aggregate the data by trawl and age group, generating a dataset of latitudinal locations for each age class of hake. This dataset was used to generate kernel density estimates of each hake age group over latitude in Matlab (The Mathworks Inc., 2022). The kernel density estimation process generates estimates of probability density functions that are useful for visualizing smoothed histograms of a finite data sample. Each kernel density estimate used 100 points and a bandwidth of 2. As older hake tend to aggregate in multi-age aggregations, five age groupings were chosen: ages 1, 2-3, 4-5, 6-10, and 11-15 (hake older than 15 exist, but are not commonly encountered). In addition, years were categorized as either PDO negative (≤ 0) or positive (> 0) and age-1 hake latitudinal distributions (before kernel density estimation) during negative and positive PDO years were compared using a two-sample t-test.

2.3.3 Aggregating specimen data by trawl stratum

The third method of dealing with correlated length and aged data within catches also used data aggregation and aimed to minimize bias when analyzing broad-scale cross-shelf characteristics of hake distributions. In this method, the individual fish data were grouped by trawl stratum (“trawl-strata aggregated data”) to calculate mean age and length of fish in each trawl and compared to average distance from the shelf break.

2.4 Distance from the shelf break

The distance from the shelf break (characterized by the 200-m bottom depth contour) was calculated for each trawl location and for each kriged spatial estimate of hake biomass. The location of each trawl and acoustic estimate were matched to the NOAA ETOPO 2022 15 Arc-Second Global Relief Model bathymetric data (National Oceanographic and Atmospheric Administration, 2022). The 200-m contour line was calculated from the bathymetric data, and the distance from the shelf break was calculated as the minimum distance from the location of the trawl/acoustic estimate to the 200-m contour line. Due to complicated bathymetry in the most northern part of the survey area (characterized by a large island and shallow strait), the distance from the shelf break analysis was constrained to latitudes less than 51°N. While that removal does exclude the northern-most known extent of hake distribution, it includes the area where the majority of hake are generally found. To evaluate how hake distributes offshore, we calculated the offshore extent of hake as the distance from the 200-m contour that encompassed 95% of the kriged biomass for each survey year. To evaluate hake distribution around the shelf break, the strata-aggregated distance from the shelf break was calculated as the average distance from the shelf break for each trawl in each stratum in each year.

2.5 Survey-level analyses to characterize shifts in distribution

Several survey-level summary statistics were calculated for each survey year using the year-specific biomass data, including the mean age of hake, the offshore extent of hake, the center of latitude of hake biomass (latitude weighted by the biomass at that latitude in that survey year), the proportion of hake biomass in Canada, and the proportion of age 7+ hake.

The proportion of hake in Canada was calculated by taking the biomass north of 48.5°N, and dividing it by the total survey biomass for each year. Denoting south of latitude 48.5°N as being U.S. waters is

approximately correct, except in 1998, when hake occurred further north in Alaskan waters. For the rest of this paper, however, we term hake south of latitude 48.5°N as being in the U.S. and north of latitude 48.5°N as being in Canada. The proportion of age 7+ hake biomass was calculated to quantify the proportion of “older” fish in each survey. Age 7 was chosen because the latitude-at-age boxplot indicated that age 7 was the approximate age at which the median latitude of hake (in equal-age sampled data) could be expected to reach latitude 48.5°N.

2.5.1 Area Occupied:

The square area occupied by hake (nm²) in U.S. and Canada was calculated for each survey year as the number of kriged grid cells containing hake, multiplied by the area of each grid cell (6.25 nm²). This was calculated both south and north of 48.5°N. To test for a trend by year in area occupied as well as the southern and northern extents of where hake were found in the survey, a Mann-Kendall test with Sen’s slope method and pre-whitening (removing autocorrelation and trends) was used (Burkey, 2006; Collaud Coen et al., 2020).

2.6 Niño 3.4 and Pacific Decadal Oscillation data

We used the El Niño Southern Oscillation SST anomaly (°C) from region 3.4 (Niño 3.4) and the PDO to test our hypothesis that shifts in the distribution of hake were related to these parameterizations of the ocean environment. The specific datasets used were the April 1995-2025 Niño 3.4 anomaly data (NOAA Physical Sciences Laboratory, 2025) and the April 1995-2025 PDO data (National Center for Environmental Information, 2025).. April was chosen a priori following previous work done by Cooke et al. (2006) demonstrating the influence of weaker spring upwelling conditions on the northern extent of hake.

2.7 Generalized additive models

Generalized additive models (GAMs, Wood 2017), a generalization of ordinary linear models, are used to model non-linear relationships between one variable (e.g., latitude, distance from shelf break) to another (e.g., age, length, year) without restricting the functional form of the relationship. This type of flexibility allows for depiction of complicated relationships between covariates (e.g., (Swartzman et al., 1992; LaFreniere et al., 2023)). For instance, the standard migration model for hake (Dorn, 1995) predicts that the mean latitude of hake (in the summer) will depend on the age and length of the fish. Using a GAM allows investigation of the partial dependence of each variable used in the model. The package mgcv (Wood, 2017) in the software R (R Core Team, 2023) was used to develop GAMs that assessed relationships at three different data aggregation scales: (1) at the specimen scale, to relate latitude of hake trawls to the covariates age and length of subsampled fish; (2) at the haul-strata scale, to investigate relationships of mean distance from the shelf break to survey year, mean latitude, and age of fish in a trawl stratum (strata-aggregated data); and (3) at the survey scale, to potentially relate parameters such as center of latitude, proportion of hake in Canada, and outer distance to the shelf break to covariates such as mean age of hake in the survey, the April Niño 3.4 anomaly, the April PDO anomaly, survey biomass, and survey year (for survey aggregated data). The mgcv package in R automatically determined the best degree of smoothing. Maximum likelihood was used to automatically estimate the coefficients and smoothness parameter(s) of the model. We also added an extra penalty to each term so that it could be penalized to zero. This allowed the smoothing parameter estimation to completely remove terms from the model to provide a better fit, if necessary. A forward model selection process was used, testing each

parameter in the model individually, and only including the parameter in more complicated models if it was a statistically significant predictor at the $p < .05$ level. The Akaike Information Criterion (AIC) along with estimated p-values were used for model selection. As the GAMs were being used for inference and description instead of predictive forecasting, external cross-validation or “leave-one-out” splitting was not used.

2.7.1 Describing length and age-related differences in latitudinal distribution using GAMs:

The first major set of GAMs were used to visualize latitude vs. age and length for inverse-catch weighted subsampled specimen data, and to determine if using age or length better explained the latitudinal variation of hake. Inverse-catch weighted subsampled data were used to eliminate potential disproportionate influences of trawls with larger catches; they were also used instead of equal-age or equal-length subsampled data so that the same data set could be used for both GAMs. As age and length were strongly correlated, a joint model relating both age and length was not used. As the survey focused on adult biomass, age-2+ fish were used for this analysis. The following GAMs were built using a Gaussian family and identity link: $Latitude \sim s(Age)$ and $Latitude \sim s(Length)$, where $s(Age)$ and $s(Length)$ were the smoothing functions of the predictor variables *Age* and *Length*.

2.7.2 Correlating differences in onshore and offshore distribution with fish age, total biomass, and ocean conditions using GAMs:

The second major set of GAMs used both haul strata-aggregated data and survey aggregated data to investigate how distance from the shelf break was related to total biomass, hake age, the April Niño 3.4 anomaly, and the April PDO value. Haul strata-aggregated data and survey-aggregated data sets were both used in order to investigate relationships at different scales. Haul strata-aggregated data were used instead of data from individual hauls to reduce pseudo-replication, as hauls within a local area in a year tend to have a similar length and age distribution. Haul strata-aggregated data can be used to investigate how different age groupings will vary with distance to the shelf break. There are a number of strata in each year (usually 5-9), each corresponding to a group of hake of different lengths (and by implication, age), so this allows for a finer scale look at the relationship of age to distance from the shelf break. However, survey-aggregated data were useful to test for relationships that vary annually, like total survey biomass, and the April El Niño and PDO indices.

We first used haul strata-aggregated data to explore within and between-year shifts in the onshore and offshore distribution of hake related to strata age by creating GAMs relating distance from the shelf break (of the mean haul distance within a strata) to haul strata-aggregated age, survey total biomass, and the April Niño 3.4 anomaly and PDO values. A gamma family with a log link was used, as haul strata-aggregated distance from the shelf break would be expected to have a number of relatively small values.

Secondly, we used survey-aggregated data to explore interannual shifts in the onshore and offshore distribution of hake by creating GAMs relating the outer distance from the shelf break (distance at which 95% of the biomass was aggregated) to the weighted mean age, survey total biomass, weighted mean latitude, the April Niño 3.4 anomaly and PDO values, and year. A scaled t family with an identity link was used, as the distribution of 95% distance from the shelf-break would be expected to have a long tail. We also used Pearson correlation to compare survey biomass to distance from the shelf break.

2.7.3 Correlating interannual variation in the latitudinal distribution of the hake stock with shifts in mean age, El Niño conditions, and PDO values.

The third major set of GAMS investigated the location of the hake stock was investigated both in terms of the center of latitude and the proportion of hake in Canada. To better understand interannual latitudinal shifts in the stock, we used a GAM model to relate the center of latitude of the stock to the weighted mean age, total biomass, Niño 3.4 anomaly, and PDO value. We also explored whether these variables were related to interannual differences in the proportion of the stock in Canada. The survey-aggregated data for each year consisted of single values of mean age of hake in the survey ($mAge$), total survey biomass, the April Niño 3.4 anomaly of that survey year, the April PDO value of that survey year, and the survey year. GAMs relating survey mean latitude ($wLat$) to covariates used a Gaussian family and identity link. GAMs were built in a similar fashion relating proportion of hake in Canada to survey mean age, year, and April Niño 3.4 anomalies using a beta regression distribution for the GAM to account for proportion data. As the April Niño 3.4 anomalies and April PDO values were correlated, we did not use both of them in any single model.

Additional models were formed to assist in greater understanding of the model results. A GAM relating the proportion of hake in Canada to mean age and April PDO values including an interaction between the two terms was formed $ProportionHakeCanada \sim s(mAge) + s(PDO) + ti(mAge, PDO)$, where ti is a tensor product interaction. In addition, a model relating the proportion of hake in Canada to year and mean age was investigated. "Year" was added as a continuous variable to the model to represent unexplained variation in how the distribution and proportion of the stock in Canada has changed over time. As correlation tests between variables suggested an unexpected correlation between mean age of fish in the survey and the April Niño 3.4 anomaly, models were also formed to investigate if/how shifts in the age structure of the population could be related to interannual shifts in environmental variables. GAMs were built to relate the mean age of hake in the survey to the April Niño 3.4 anomaly, and to the April PDO: $mAge \sim s(Niño\ 3.4\ anomaly)$ and $mAge \sim s(PDO)$

Data from the 16 survey years spanned three decades (1995-2025) and included 43,514 hake specimens with associated age, length, and sex data from 952 hauls. The individual hauls were combined into 143 separate haul strata of similar biological characteristics. Within the years surveyed, the April Niño 3.4 anomalies ranged from -0.77 to 0.78 °C and PDO values ranged from -3.08 to 0.90.

3 Results

3.1 Latitudinal distribution of hake by age and length

The latitudinal distribution of hake was related to fish age and length (Fig. 2). Younger fish had more southern distributions compared to older hake. Age-1 and age-2 hake had the most southern distributions, with the median latitude of both age classes estimated to be south of Cape Mendocino, California (~40.5°N, Fig. 2a); however, age-1 hake had a greater range in distribution along the coast compared with age-2s. In general, older hake are found at higher latitudes, although some old individuals occurred throughout most of the survey area. There were also a few small fish (<20 cm) at relatively high latitudes. Age and length are highly correlated in hake (Fig. S2). In general, larger hake were also found at higher latitudes, except at the shortest and longest lengths (Fig. 2b). Age-1 hake generally range in length between 15 cm and 30 cm. Within this age group, the mean latitude by length varied considerably. Across all survey years, the smallest age-1 hake were generally found north of Cape Mendocino and the largest age-1 hake were generally found farther south (Fig. 2b). The distribution of mid- to large-sized hake in the range of 50 to 65 cm was generally far north into Canadian waters during the survey, although some

of these same sized fish occurred along most of the entire coast. Hake above 60 cm, especially at lower latitudes, tended to be predominantly female (Fig. S1b). The distribution of the very largest hake is more variable and shifts to the south. The median latitude of these largest hake (≥ 66 cm) was 46.0°N, with a median age of 11 ($n = 55$), and 95% were female. Sex-specific differences in the von Bertalanffy growth parameters were found (L_{∞} for females = 52.9 cm, males = 48.5 cm, Fig. S2).

Kernel density estimations of the proportion of hake at latitude by age class showed the same general trend of increased latitude with age (Fig. 3a). A noticeable anomaly was the bimodality of age-1 hake, which sometimes stemmed from true bimodality observed in the survey data (e.g., 1995, 2017), but more often from varying latitudes of unimodality where in some years the single mode was more southerly (e.g., 2013, 2021) and in other years the single mode was more northerly (e.g., 2007, 2015) (Fig. S3). The locations of trawls with age-1 hake ($n = 209$) in positive and negative PDO years was also bimodal, with different mean latitudes ($t_{\text{stat}} = -2.9$, $p < .01$, $df = 262$) and different emphasis on the two modes; the larger age-1 mode occurred in negative, cooler PDO years and was further south, while in positive, warmer PDO years, the larger age-1 mode was further north (Fig. 3b).

The GAMs relating latitude to age or length using “inverse-catch” subsampled specimen data for age-2+ fish indicated that while both length and age were related to the latitude at which hake were found, the model relating latitude to length fit better than the model relating latitude to age (Table 1). Latitude generally increased with length, asymptoting or declining at the longest lengths. The partial effect on latitude generally increased for ages 2-6 and then asymptoted or declined for hake older than age 6 (Fig. S4).

Distribution along the shelf break

Among all survey years, an average of 95% of hake biomass was within 31.3 km of the shelf break. The outer 95th percentile of distance from the shelf break was positively correlated with greater biomass (Pearson correlation $R = 0.55$, $p = 0.033$).

Distance to the shelf break was best explained by age for haul strata-aggregated hake data (Fig. 4, Table 2), although the model explained only 8% of the deviance. The partial effect plots of the best fit model indicated that on a haul strata basis, the distance from the shelf break increased with age with younger fish being closer to the shelf break and older hake being further from the shelf break, until about age 8, where there was a slight decline with older fish.

For the survey-aggregated analyses, the 95% percentile of distance to the shelf break was correlated with total biomass, the April Niño 3.4 anomaly and the PDO. A more complex model that included total biomass and the April Niño 3.4 anomaly best explained the 95% distance from the shelf break (Table 3), with this full model explaining 64% of the deviance. Years with greater hake biomass were related to a greater 95% distance to the shelf break value (Fig. 5a). Distance from the shelf break showed a dome-shaped relationship with the April 3.4 Niño anomaly (Fig. 5b). Mean age, mean latitude, and year were not significant contributors in hake distance to the shelf break.

Interannual shifts in distribution

We used the survey-aggregated mean age and latitude from 1995 to 2025 to better understand interannual latitudinal shifts in the distribution of the stock. The best fitting model related survey center of latitude to mean age of hake in the survey (Table 4). Age-2+ hake biomass, Niño 3.4 ocean conditions and PDO indices were not significant. The best fit model showed a generally positive relationship of mean age of the hake population to the center of latitude (Fig. 6).

The latitude of hake biomass varied considerably by year (Fig. 7a). The center of latitude and proportion of hake in Canada have been variable between 1995 and 2025, but the proportion of hake in Canada has been especially low in recent years (Fig. 7b). Despite this finding, there were no clear trends in the proportion of older fish in Canada by survey year (Fig. S5).

Southern shifts in hake corresponded with a lesser proportion of the stock biomass in Canada in recent survey years (Fig. 7). Interannual variation in the proportion of hake in Canada was best explained by shifts in mean fish age and the April PDO ocean conditions (Table 5). The partial effects plot indicated a positive, linear relationship between the proportion of the stock biomass in Canada and increasing mean age and warmer PDO ocean conditions (Fig. 8a and b). A linear model of the deviance residuals by year was significant at the $p < 0.1$ level, but not at the $p < 0.05$ level ($R^2 = 0.17$, $F(1,14) = 3.992$, $p = 0.066$, Fig. 8c).

The total area occupied by hake in the survey (Fig. 9) showed a decrease over time (Mann-Kendall's tau test with Sen's slope, slope = -554.5, $p < 0.01$). In addition, the latitude of the northern extent of hake showed a significant decrease over time (northern extent: Mann-Kendall's tau test with Sen's slope, slope = -0.19, $p = 0.021$), but not the southern extent (Mann-Kendall's tau test with Sen's slope, slope = -0.07, $p = 0.55$). The GAM model of the percent of hake in Canada, including an interaction between the PDO and mean age term, was tested, but the interaction was not significant ($p < 0.48$).

Mean age of hake in the survey was found to be positively related to warmer April Niño 3.4 anomalies (Table 6, Fig. 10). Although mean age was also often higher in years with higher April PDO values, the relationship of mean age to April PDO values was not significant.

4 Discussion

Using a 30-year time series, we found that the mean age of hake and warmer PDO conditions contributed to the proportion of hake migrating into Canada, and documented a southward shift in the northern extent of hake that, coupled with a decrease in the area occupied, suggest an overall contraction of the stock. These results have important implications for management of the hake stock and provide insight on interannual shifts in the distribution of hake.

4.1 Latitudinal distribution by fish age and length

We confirm a previously noted relationship between age of hake and how far north they migrate (Dorn (1995). Older, larger hake were typically found farther north than younger, smaller hake. It is not unusual that the largest hake were predominately female, as females older than age 3 are generally larger than males of the same age (Dark, 1975; Beamish et al., 1985). However, not all large hake migrated north; at

least some large fish were found throughout the entire survey area. The very largest hake were found at latitudes further south than expected. These larger fish (≥ 66 cm, median age of 11 years, predominantly female) were found at latitudes more similar to those of 46 cm fish, which have a median age of 6. There have been anecdotal reports from the hake fishing industry of large hake that tend to stay in one location throughout the year – termed “homesteader hake” – and our data support these observations. However, the sample size of larger fish of 66 cm or greater ($n = 55$) was small, so care should be taken with interpretation.

Hake distribution shifted northward with age, with more of the younger fish (ages 2-3) in the south and more of the older fish (ages 11-15) in the north. This latitudinal shift in distribution by age is similar to historical reports (Dorn, 1995). In contrast to historical reports, we found a bimodal distribution of age-1 hake with the first peak around 35°N and a second peak near 46°N ; this bimodality was a combination of true bimodality of fish lengths observed within a survey single year, and individual survey years having distinctly higher or lower latitude single modes than others. Therefore, models that relate age-1 hake to only the southern portion of the hake latitudinal range are improperly simplistic.

The bimodality of age-1 hake latitudinal distributions may stem from a combination of potential expansion of distribution by strong cohorts to reduce density dependence, inter-annual variation in spawning location of adult hake and subsequent variation in larval survival and transport, and changing ocean conditions. True bimodality within a single survey year might stem from a large age-1 cohort spreading out further along the coast, which would reduce competition for resources due to density dependence. For example, the strong 2010 and 2014 cohorts (seen in the 2011 and 2015 surveys; (Johnson et al., 2025) had bimodal age-1 distributions. However, other years with smaller age-1 cohorts had bimodality as well, so other factors may also be at play.

Spawning location of hake is not well characterized, although early models suggested that hake spawn primarily in the southern portion of the California Current Large Marine Ecosystem (Bailey, 1982; Agostini et al., 2006), with the location of the apparent northern front of spawning being correlated to the sea surface temperature (Bailey et al., 1982). Recent models also suggest that spawning occurs at a range of latitudes (Ressler et al., 2007; Head et al., 2025), so variation in latitude of spawning and larval survival might explain why, for instance, 2007 and 2009 had more northerly unimodal age-1 distributions. Interestingly, age-1 hake occurring in the northern part of the survey were smaller than age-1 hake found in the south. This result contrasts both to the general age-2+ relationship of larger, older hake being found further north and to the model of Dorn (1992) showing that increases in sea-surface temperature (more commonly found in the southern portion of the range) were associated with large reductions in growth of younger fish. Also, the asymptotic length at age L_{∞} for males and females (~ 48 -53 cm) in our study (1995-2025) were 8-13 cm less than those found for hake off California, Oregon, and Washington from 1964-1969, ($L_{\infty} \sim 56$ -61 cm) (Kimura, 1979). Since larger hake tend to migrate further north, a reduction in length could potentially lead to reduced northern migration. These results suggest the need for further investigation into hake spawning location and environmental effects on larval and juvenile survival, growth, and transport.

The result of age-1 hake being found further north in warmer, positive PDO conditions is consistent with previous results that found that a portion of the hake stock spawned and remained year-round in Canada

in the 1990's (relatively warm PDO conditions) after a potential 1989 regime shift (Benson et al., 2002). The result is also consistent with the hypothesis that the northerly shift of hake spawning and recruitment in the mid 2000's was related to increased winter/spring temperatures in the Northern California Current (Phillips et al., 2007).

4.2 Distribution along the shelf break

On a finer scale of haul strata-aggregated data, distance from the shelf break depended on mean age of hake within the haul strata, with younger hake closer to the shelf break and older hake more offshore. The model had a poor fit, explaining only 8% of the deviance. However, poor model fits are to be expected when relating distance to the shelf break to haul strata-aggregated data, as a large number of trawls were performed and much of the variation in age for hake is latitudinal along the coast, with minor variations onshore and offshore. The effect of increasing distance from the shelf break with increasing age up to age 8 has not been previously documented, but is consistent with accounts of juvenile hake exhibiting a greater preference for shallow shelf locations than mature fish (Hamel et al., 2015).

On a coarser scale of survey-aggregated data, distance from the shelf break was related to total biomass of the hake population, as well as shifts in the April Niño 3.4 ocean conditions. Distance from the shelf break increased with total hake biomass, peaking in years with neutral El Niño conditions. The relationship of increasing distance from the shelf break with greater biomass may be related to density dependence, with larger fish populations utilizing more space or having to spread out into less desirable habitat to reduce competition. It is not clear why the distance from the shelf break might peak in neutral El Niño conditions. However, as hake have been found to be associated with the poleward flow of the California Undercurrent (Agostini et al., 2006), El Niño-neutral seasons of weaker undercurrent flow may contribute to this peak in distance, with the population spreading out offshore to reduce density dependence and competition. In El Niño years, a narrowed, more shelf-oriented distribution may be the result of the multiple effects an El Niño can exert on the California Undercurrent, such as intensified poleward flow, infusions of warmer and saltier waters at depth deepening the thermocline, and regional variability in the wind fields driving upwelling and hence coastal productivity.

4.3 Interannual shifts in latitude and a decline of hake in Canada

Similar to differences in hake latitudinal distribution by age, interannual shifts in the mean age of hake in the population were correlated with shifts in mean latitude of the stock distribution, corroborating previous studies that demonstrated a correlation between mean age and northward migration of hake (Bailey, 1982; Francis, 1983; Dorn, 1995). The distribution of the hake stock shifted north in years when the mean age of hake in the population was older. The mean age of the population varied by survey year, mainly due to differences in the size of cohorts entering the population, with larger cohorts influencing the mean. In addition to distributional shifts due to differences in mean age of the population, there has been a distinct southern shift in the distribution of the stock since approximately 2011. However, there has not been a clear directional shift in the mean age in that time period. Thus, this southern distributional shift in recent years cannot be explained solely by age. We found that the southern shift of the hake distribution was accompanied by a decline in the area occupied, suggesting a possible contraction of the stock. This may be an example of the "basin hypothesis" (MacCall, 1990), with the hake population contracting into its optimal habitat as the total population size decreases. The contraction of the stock is also associated with a decrease in the northern extent of hake in the survey, further suggesting movement

of the stock south over the years of this study. It should be noted that 1998, near the beginning of the survey time series, was a strong El Niño year, with an associated spatial movement of the stock to its furthest northern extent, which could have affected the interpretation of the trend.

Despite including factors such as survey biomass, Niño 3.4 anomalies and PDO values, only hake age was significant in the model of mean latitude. By contrast, although interannual variation in the proportion of hake biomass in Canada was partially correlated with differences in the mean age of the population, it was also correlated with the April PDO values.

We found that an increasing proportion of hake in Canada was related to positive PDO values, which provides novel insight on hake distribution. Little research has explicitly looked at the relationship of broad-scale shifts in ocean environmental conditions (as characterized by the PDO) with differences in the proportion of hake observed in Canada. Past studies have related upwelling indices and temperature to hake recruitment (Bailey et al., 1985), and upwelling off the West Coast Vancouver Island, Canada (Amphitrite Point) in April was postulated to correlate to the northern limits of migration (Cooke et al., 2006). Warmer years, as determined by elevated sea surface temperatures off Amphitrite Point, were also characterized by an increase in hake biomass in the area off Vancouver Island, Canada (Ware et al. (1995). Other studies have linked an increased northerly hake distribution to El Niño events and the corresponding intensification of poleward transport (Dorn, 1995; Agostini et al., 2006). Our results are in alignment with these past studies, because warmer PDO years tend to be associated with an increase in ENSO events (Tang et al., 2024) and increased subsurface poleward flow.

While the proportion of hake in Canada was related to shifts in PDO values, the center of hake latitude was not significantly related to interannual shifts in El Niño ocean conditions or to shifts in PDO values. There are a few possible explanations for this dichotomy. First, shifts may potentially be more detectable at the extremes of the latitudinal range, and because Canada is at the northern extreme of hake range, this shift may be more detectable there. Secondly, the stock could be potentially contracting but not necessarily shifting with negative El Niño anomalies or cooler PDO regimes. This is consistent with the northern extent of the population moving south, but the southern extent remaining relatively stable through time.

The proportion of hake in Canada clearly reflected the effects of age and/or environmental conditions in some survey years. Peaks in the proportion of the hake biomass found in Canada can be partially attributed to large year classes reaching ~7 years old. For example, a large 1998 cohort was observed in the 2005 survey in Canada, and a large 2010 cohort was observed in the 2017 survey in Canada. Peaks in the proportion of hake biomass in Canada can also be attributed to climate events such as the strong 1998-1999 El Niño associated with a warm PDO that resulted in hake occurring anomalously far north in the 1998 survey.

However, shifts in the age distribution of hake and ocean environmental conditions, as explored with the El Niño and PDO index, do not fully explain a decline of hake in Canada in recent years. For example, some years, such as 2019, had a reasonable proportion of older hake and a positive PDO index, but a relatively low proportion of hake biomass in Canada. The deviance residuals from the GAM relating the proportion of hake in Canada to mean hake age and the April PDO index suggest that there might be

unexplained variation in the model with a possible decreasing trend in the residuals by year. During recent years (2021-2025), the PDO has been fairly cool, and the model results suggest that more hake might stay south and not migrate north into Canada. However, the model residuals for those years were below 0, reflecting that there was even less hake in Canada than the model expected.

If there is a biological or behavioral process explicitly related to year that is driving the recent decrease of hake in Canada, it is not clear what it is. However, new patterns in Pacific Ocean temperature variability are emerging. For example, Cluett et al. (2025) found that although the PDO still exhibits a stable and strong oscillation, a broad, basin-wide warming trend known as the 'pan-basin pattern' (PBP) has been overwhelming sea surface temperature changes in the Pacific Ocean in the recent decade, producing periods during which regional temperature anomalies have diverged from what is expected from the PDO. This divergence from the historical norm appears to have started around 2013 and was in full force by 2017, continuing to the end of the PBP time series in 2024. It is possible that this unexplained recent decrease of hake in Canada may be linked to the PBP.

Several studies have hypothesized that the distribution of hake will shift farther north with increasing temperatures from climate change (Beamish, 2008; Malick et al., 2020; Jacobsen et al., 2021). By contrast, this study showed that the northern extent of hake in each year has been shifting south with time. Our results suggest that the expectation of hake moving north with general ocean warming trends is more complex than previously described, and that hake migration may be more dependent on ocean currents (Dorn, 1995; Malick et al., 2023) than specifically on water temperature. The physical mechanisms involving ocean transport in warm El Niño years are largely driven by remote forcing from the equator (Enfield et al., 1980; Alexander et al., 2002), which can enhance northward transport of hake via the strengthened California undercurrent and winter Davidson current (Dorn, 1995). The forcing mechanisms in warm years due to ocean warming and marine heat events may produce dissimilar or more variable currents with different water types and altered stratification patterns (Jacox et al., 2024), potentially affecting hake migration in unexpected ways. Growing regions of seasonal hypoxia may also play a role. For example, the hypoxic area extending from the mouth of the Strait of Juan de Fuca onto the shelf near the U.S.-Canadian border during the summer has been increasing in recent years (Barth et al., 2024). Areas of hypoxic water could present a barrier to migration if they overlap with the migration route of hake, with potentially increased feeding competition and predation as shelf-wide bottom hypoxia compressed the pelagic habitat above. Other processes, like predation dynamics (e.g. hake-krill interactions), competition dynamics (e.g., hake-pollock interactions) and interactions with fishery, may also explain the southerly shift of the hake stock in recent years. For instance, Phillips et al. (2023) found that hake and krill co-occurrence was ocean temperature-dependent, and Litzow et al. (2014) found that for certain North Pacific biological times series, models performed better when taking into account both ecological and commercial fishing factors.

The Niño 3.4 anomaly and PDO are “umbrella” indices with many associated variables. Future studies should continue to explore specific environmental factors to better understand the potential for an oscillation in distributional shifts on the decadal scale, directional shifts due to longer-term climate change, and fishery effects on hake distribution, demography, and migration patterns. These covariates might include marine heat waves, dissolved oxygen minimum zones, variability in upwelling, strength and direction of ocean currents, sea surface temperature, depth of the mixed layer, and strength and

distribution of freshwater plumes via river discharge. Upwelling indices such as the Bakun index (Bakun, 1973) or newer, higher resolution indices such as the Coastal Upwelling Transport Index and the Biologically Effective Upwelling Transport Index (Jacox et al., 2018) may also offer additional investigative paths forward.

The relationship of hake age and increasing April Niño 3.4 anomalies is intriguing, as ENSO cycles are usually only 2-7 years. For an environmental driver to have an impact on the mean age of a fish stock, it must be a relatively long-duration driver compared to the life cycle of the fish, especially because hake are only 50% mature at ~2.4 years of age (Head et al., 2025). Although we did not find a significant relationship between mean age of hake in the survey and April PDO values, the relationship of mean age of hake in the survey to April Niño anomalies could still be related to a decadal time scale cycle like the PDO. For instance, Vestfals et al. (2023) found that hake recruitment may be linked to PDO conditions during the adult female preconditioning stage. Analysis of additional data sets and stock assessment model outputs would be useful to explore relationships to ENSO, and would allow the inclusion of time lags in the analysis.

The three-decade-long span of hake survey data used in this study represents a long time series from which to examine patterns in hake distribution, but there are still possible confounding issues. Early in the time series had more years in the warm PDO phase than did recent years, which could be confounded with a recent increase in ocean warming over the last decade. It is possible that some drivers of the relationship between decreased proportion of hake in Canada and more southerly distribution of age-1 fish in recent cool PDO years may actually be a reflection of other ocean warming trends instead of, or in combination with, the PDO. Also, although our analyses sought to reduce the effects of non-random biological sampling from the trawls, the nature of the acoustic-trawl survey design, which was designed to aid in identification of acoustic regions encountered during the survey, meant that biological sampling in the hake survey remained non-random. However, biological sampling occurred coast-wide, covering the range of hake encountered during the survey, so the biological data likely well represents the demography of the stock. In addition, although with ocean warming the usefulness of climate indices like PDO may be diminishing (Litzow et al., 2020), the utility of the index may depend on whether the index is used as a proxy for the relationship of a fish stock with temperature, wind-driven mixing, or ocean currents.

4 Conclusions

We found a relationship between cool PDO years with decreased proportion of hake in Canada and more southerly age-1 fish distributions, as well as relationships of older hake being associated with more northerly distribution in Canada, and a greater distance from the shelf break. Outer (95%) distance from the shelf break was also associated with total survey biomass and had a dome-shaped relationship with the April Niño 3.4 anomaly. The latitudes of the northern and southern extent of hake, as well as the total area occupied, have been decreasing, suggesting both a contraction in the hake stock as well as a potential shift south. Additional research is needed to understand the mechanism behind larger age-1 hake being found further south than smaller age-1 hake, which is opposite to the general trend of larger adult hake being found further north. A greater understanding of seasonal hake migration, with data from multiple seasons within a year, may elucidate some of the questions raised in this study. Additionally, looking beyond mean hake age to the relationship of the proportion of age in the stock relative to factors considered in

this study may be fruitful. Factors not explicitly considered in this study include predator and prey distributions, competitive dynamics with other species, ocean current velocity and direction, and fishing effects. Continuation of past management strategy work investigating the robustness of the current harvest policy to spatial stock structure, shifts in fishery selectivity, and climate-driven distribution shifts (Jacobsen et al., 2021) could also be considered.

Acknowledgements: Many thanks to the crew and volunteers aboard the NOAA Ships *Miller Freeman* and *Bell M. Shimada*, as well as to the CCGS *W.E. Ricker*, the CCGS *John Franklin*, and the F/V *Nordic Pearl*. We also thank C. Wetzel for useful comments on the manuscript. Also much appreciated were the informal conversations with numerous industry members.

Author Contributions: **Rebecca E. Thomas:** Formal analysis, Software, Writing – Original draft. **Julia Clemons:** Data curation, Writing – review & editing, Project administration, **Stéphane Gauthier:** Data curation, Writing – review & editing, Project administration, **Alicia Billings:** Resources, Data Curation, Writing: Review and Editing **Chelsea Stanley:** Data curation, Investigation, **Dezhang Chu:** Software, Writing – Original draft, Validation. **Elizabeth M. Phillips:** Data curation, Investigation, Formal Analysis, Writing: Review and Editing, **John Pohl:** Data curation, Investigation, Writing: Review and Editing, **Sabrina Beyer:** Data curation, Investigation, Formal Analysis, Writing: Review and Editing, **Stephen de Blois:** Data curation, Investigation, Writing: Review and Editing

Data Availability:

The raw acoustic data for the 2003 to 2025 surveys can be accessed through the National Centers for Environmental Information (<https://www.ncei.noaa.gov/maps/water-column-sonar/>). Associated biological data are currently available from the authors upon reasonable request.

Tables

Table 1: Results of generalized additive models using the inverse-catch subsampled specimen data to relate the latitude of age-2+ subsampled specimen hake to age or length. The p-value of each smooth in the model is shown in the smooth column for that individual covariate (e.g., s(Age)).

covariates	ML	R ² (adj)	Deviance Explained	AIC	s(Age)	s(Length)
Age	10,447.8	0.33	33.6%	20,880.72	<0.001***	
Length	10,150.7	0.43	42.1%	20,289.31		<0.001***

Note. Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1. ML = Maximum Likelihood Score; R² (adj) = Adjusted Coefficient of Determination; AIC = Akaike Information Criterion; row in bold represents the better model

Table 2: Results of generalized additive models using haul strata-aggregated data to relate the distance from the shelf break in for each year's haul stratum to mean age in the haul stratum. The p-value of each smooth in the model is shown in the smooth column for that individual covariate (e.g., s(Age)).

covariates	ML	R ² (adj)	Deviance Explained	AIC	s(Age)	s(Biomass)	s(Niño3.4 anomaly)	s(PDO)
Age	398.22	0.06	7.8%	799.51	0.01*			
Biomass	405.88	-0.00	0.0%	815.75		0.83		
Niño3.4 anomaly	405.88	0.00	0.0%	815.75			0.51	
PDO	405.65	0.01	1.7%	815.98				0.20

Note. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. ML = Maximum Likelihood Score; R² (adj) = Adjusted Coefficient of Determination; AIC = Akaike Information Criterion; row in bold represents the best model

Table 3: Results of generalized additive models using survey-aggregated data to relate the 95% percentile (of biomass) survey distance from the shelf break to total survey biomass, mean age of hake in the survey (mAge), mean survey latitude (wLat), the Niño 3.4 anomaly, the April PDO value, and year. The p-value of each smooth in the model is shown in the smooth column for that individual covariate (e.g., s(Biomass)). These analyses used kriged biomass without extrapolation.

covariates	ML	R ² (adj)	Deviance Explained	AIC	s(Biomass)	s(mAge)	s(wLat)	s(Niño3.4 anomaly)	s(PDO)	s(Year)
Total biomass	56.26	0.23	29.8%	117.46	0.02*					
Mean age of hake in the survey	57.26	0.01	1.1%	120.68		0.33				
Mean survey latitude	57.20	0.04	6.2%	120.76			0.20			
Niño3.4 anomaly	56.25	0.27	35.2%	117.94				0.02*		
PDO	56.20	0.23	30.0%	117.54					0.02*	
Year	57.26	-0.00	0.00%	120.52						0.60
Total biomass & Niño3.4 anomaly	54.48	0.54	64.3%	108.10	<0.001***			<0.001***		
Total biomass & PDO	55.90	0.31	41.2%	116.58	0.08.				0.07.	

Note. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. ML = Maximum Likelihood Score; R² (adj) = Adjusted Coefficient of Determination; AIC = Akaike Information Criterion; row in bold represents the best model

Table 4: Results of generalized additive models using survey-aggregated data to relate the center of latitude of hake in the survey to mean age of hake in the survey (mAge), biomass, April Niño 3.4 anomaly, and April PDO value for the 1995-2025 surveys. The p-value of each smooth in the model is shown in the smooth column for that individual covariate (e.g., s(mAge)).

covariates	ML	R ² (adj)	Deviance Explained	AIC	s(mAge)	s(Biomass)	s(Niño3.4 anomaly)	s(PDO)
Mean age	32.40	0.42	45.6%	67.31	0.00*			
Biomass	35.46	0.05	9.1%	75.60		0.28		
Niño3.4 anomaly	35.09	0.12	15.6%	74.14			0.11	
PDO	35.12	0.11	14.9%	74.24				0.12

Note. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. ML = Maximum Likelihood Score; R² (adj) = Adjusted Coefficient of Determination; AIC = Akaike Information Criterion; row in bold represents the best model

Table 5: Results of generalized additive models using survey-aggregated data to relate the proportion of hake in Canada to mean age of hake in the survey (mAge), biomass, April Niño 3.4 anomaly, and April PDO for the 1995-2025 surveys. Year was included as an alternate exploratory variable instead of PDO but was not part of the base model set. The p-value of each smooth in the model is shown in the smooth column for that individual covariate (e.g., s(mAge)).

covariates	ML	R ² (adj)	Deviance Explained	AIC	s(mAge)	s(Biomass)	s(Niño3.4 anomaly)	s(PDO)	s(year)
Mean age	-12.37	0.32	36.2%	-21.73	0.01*				
Biomass	-11.04	0.07	21.4%	-17.61		0.12			
Niño3.4 anomaly	-11.16	0.18	18.3%	-18.40			0.06.		
PDO	-12.15	0.22	39.6%	-20.50				0.01*	
Mean age & PDO	-13.07	0.36	49.3%	-23.08	0.02*			0.04*	
Mean age & year	-15.84	0.63	79.3%	-31.73	<0.001***				<0.001***

Note. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. ML = Maximum Likelihood Score; R² (adj) = Adjusted Coefficient of Determination; AIC = Akaike Information Criterion; row in bold represents the best model from the base model set.

Table 6: Results of generalized additive models using survey-aggregated data to relate the mean age of hake in the survey to the April Niño 3.4 anomaly and the April PDO for the 1995-2025 surveys. The p-value of each smooth in the model is shown in the smooth column for that individual covariate (e.g., s(PDO)).

covariates	ML	R ² (adj)	Deviance Explained	AIC	s(Niño3.4 anomaly)	s(PDO)
Niño3.4 anomaly	24.74	0.21	25.3%	52.91	0.04*	
PDO	25.24	0.17	23.9%	54.74		0.11

Note. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. ML = Maximum Likelihood Score; R² (adj) = Adjusted Coefficient of Determination; AIC = Akaike Information Criterion; row in bold represents the better model

Figures:



Fig. 1: Area of the Joint U.S.-Canada Pacific hake survey off the West Coast of North America. Orange lines are the transects from the 2023 survey. These transects are typical for the hake survey, with 10 nm spacing along most of the coast, 20 nm spacing north of Vancouver Island, and occasional dropped transects for logistical reasons. The grey line represents the 200 m isobath.

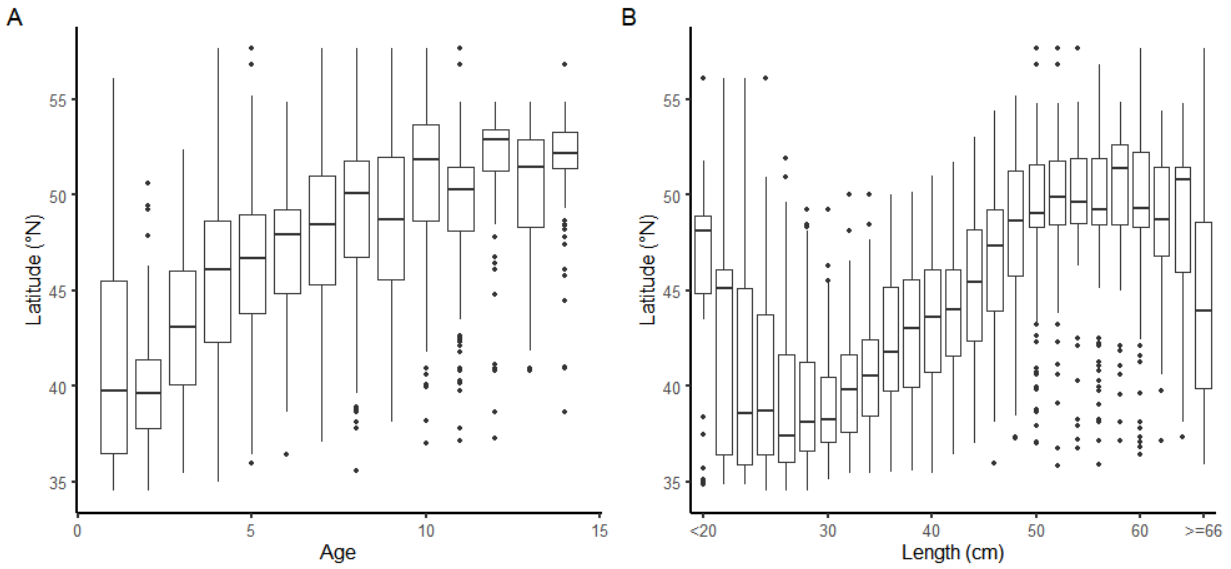


Fig. 2: (a) Box plot of latitude of age from equal-age subsampled trawl data across all survey years and the (b) box plot of latitude of length from equal-length subsampled data across all survey years. The box represents the middle 50% of the values, the horizontal line within the box is the median, and the whiskers extend to 1.5 times the interquartile range. Points outside the box and line are outliers.

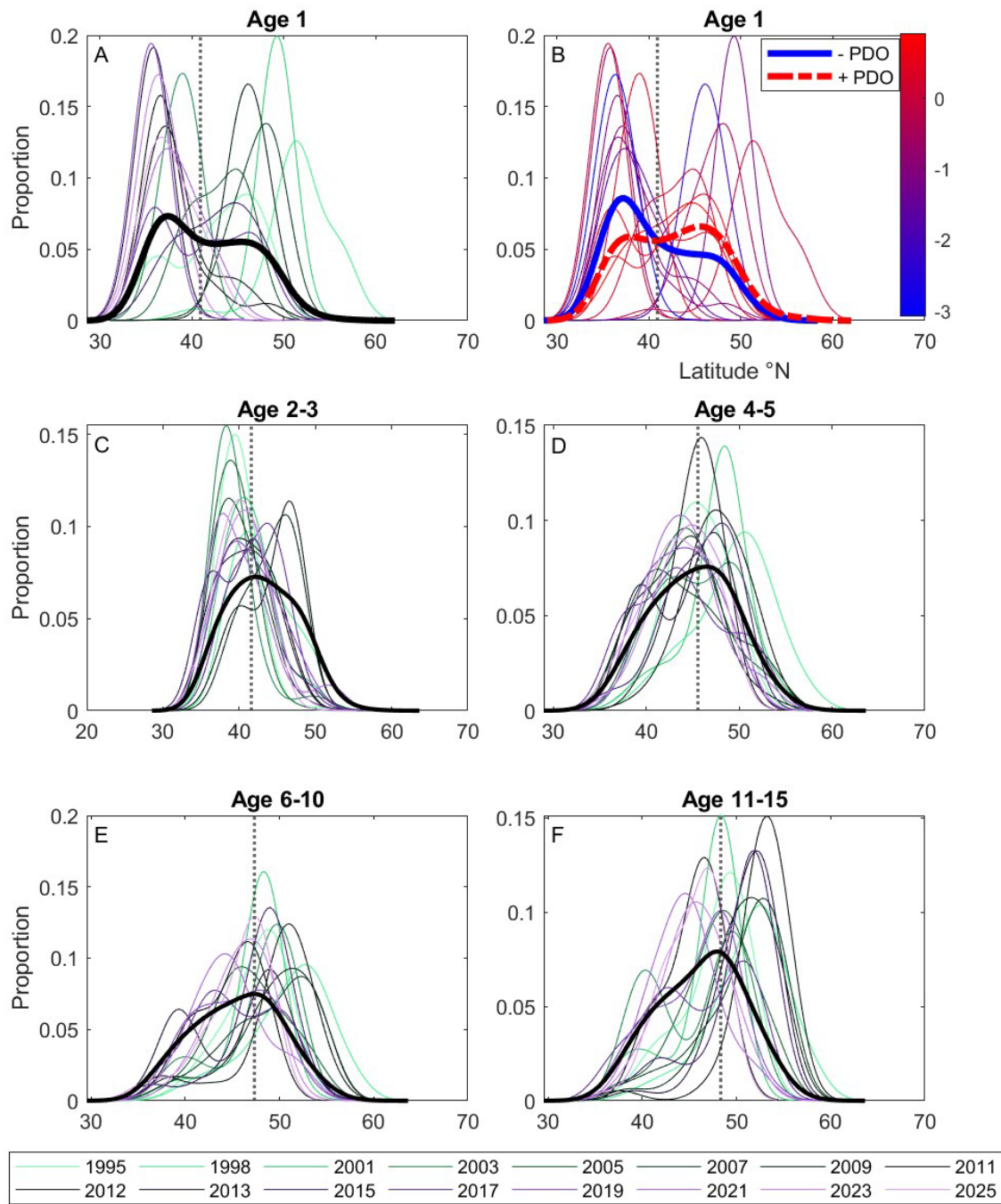


Fig. 3: (a),(c),(d),(e) Kernel density estimations of proportion of hake trawls by latitude by age class across all years of available biological data. The thin lines are the kernel density color coded by individual year. The thick black line is the composite across all years (b) Kernel density estimations for proportion of hake trawls by latitude for trawls containing age-1 hake during years with low vs high April PDO values. The red dashed line is the composite from years with positive April PDO values, and the blue line is the composite for years with negative April PDO values. Individual years are shown as light lines, with the lines color coded by the April PDO value for that year.

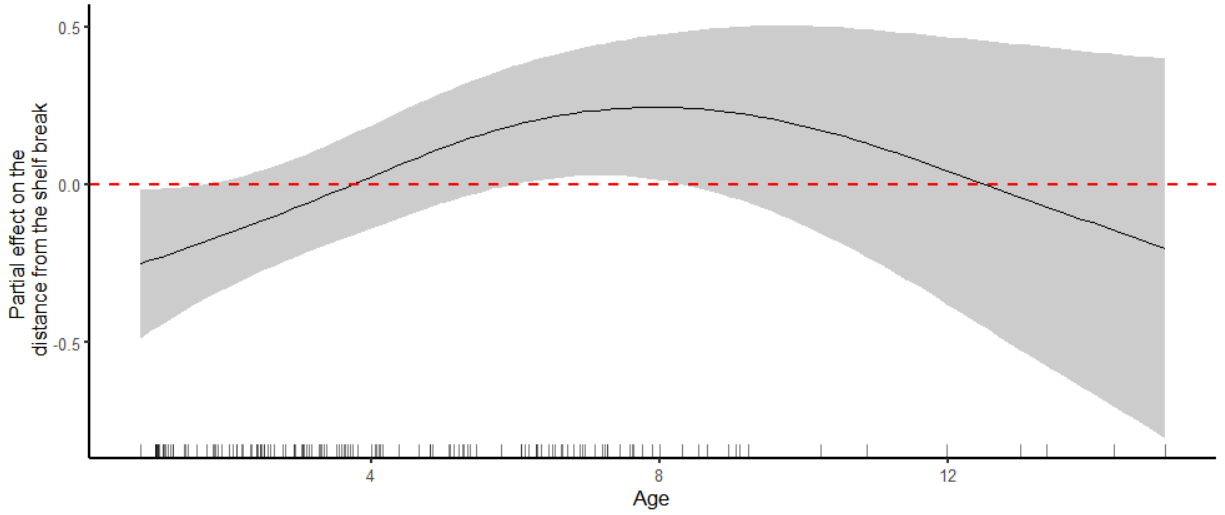


Fig. 4: Generalized additive models showing the partial effect of mean age in the haul stratum on distance from the shelf break for each year-haul stratum.

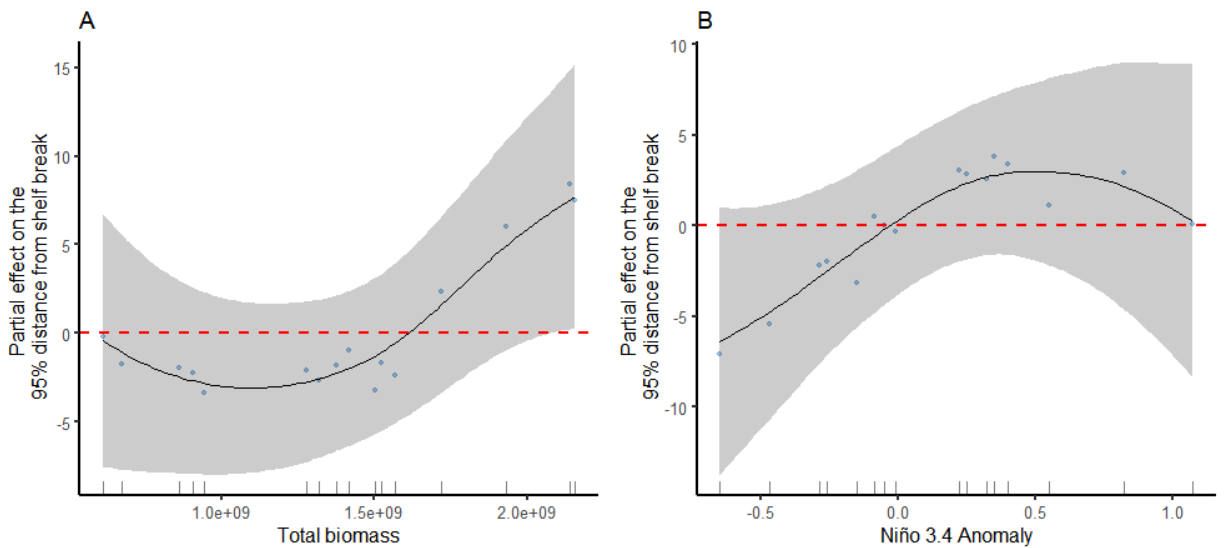


Fig. 5: Generalized additive models showing the partial effect of (a) total biomass (the outliers are 2009 and 2019), and (b) April Niño 3.4 anomaly (the outlier is 2009), on outer 95% distance from the shelf break. Residuals are plotted as blue circles. The dashed red line indicates the threshold at which the additive effect is 0.

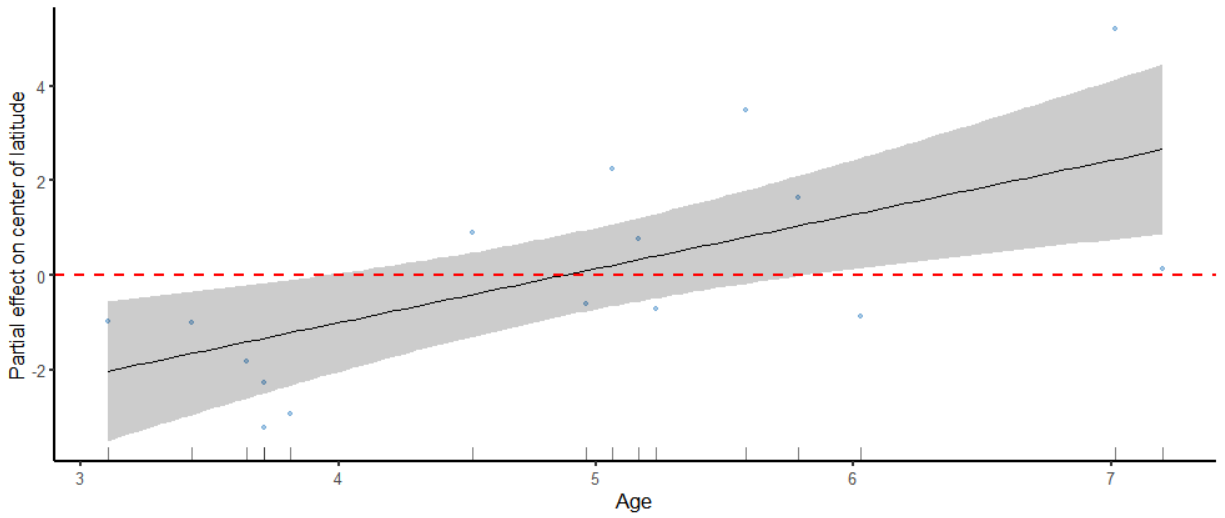


Fig. 6: Generalized additive model of the partial effect of age on center of latitude of hake in the survey using survey-aggregated data. Residuals are plotted as blue circles. The dashed red line indicates the threshold at which the additive effect is 0.

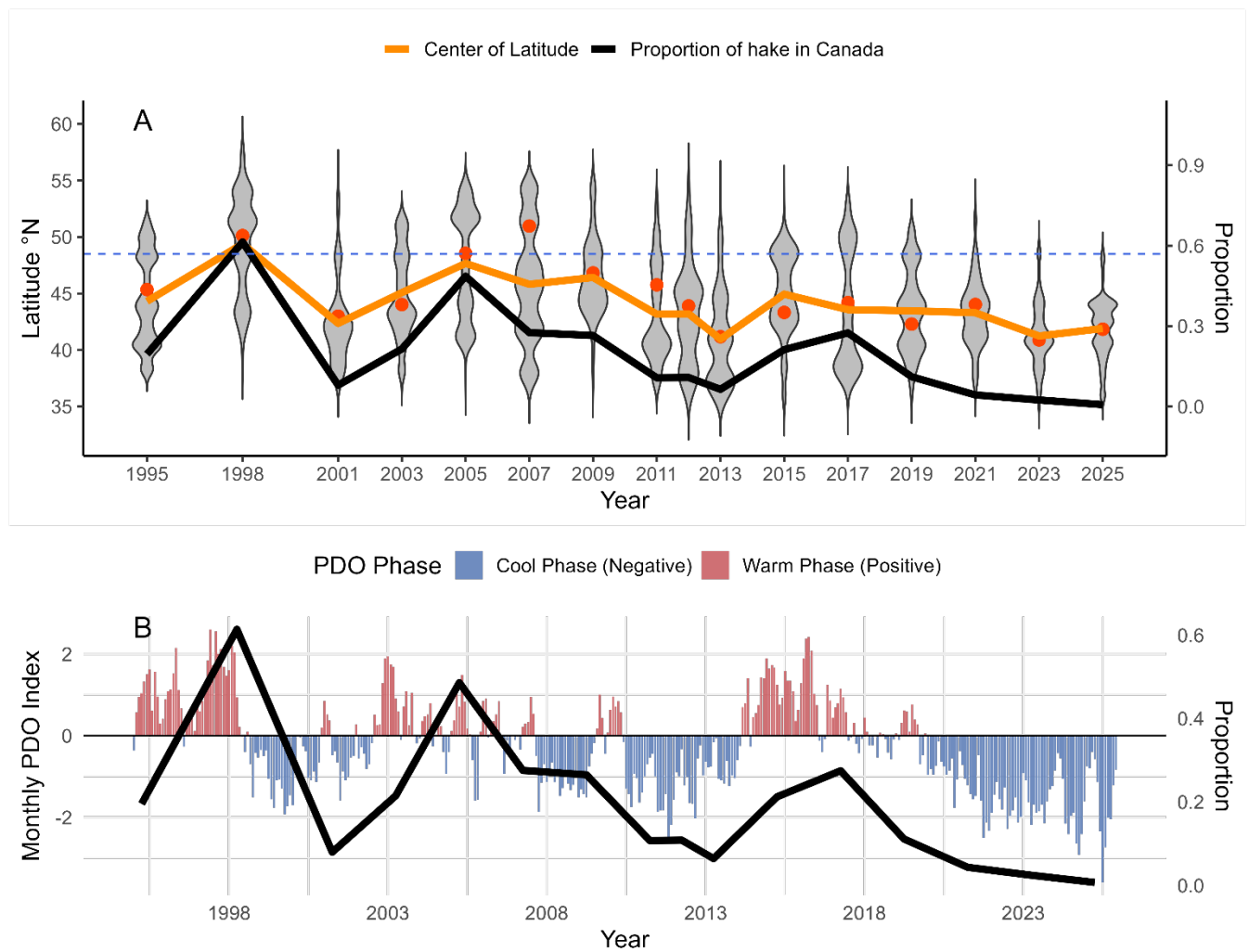


Fig. 7 (a) A "violin" plot of latitude of hake biomass in each survey year, weighted by the biomass at each latitude. The median latitude of biomass is shown as a red dot. The dotted horizontal line is at 48.5°N, roughly the latitude of the U.S./Canada border. Also plotted are the center of latitude (orange line) and proportion of hake in Canada (north of 48.5°N) (black line) based on annual survey biomass estimates. (b) PDO values from 1975 to 2024 where red bars are positive values and blue bars are negative values, with the proportion of the survey biomass in Canada (north of 48.5°N) overlaid in black.

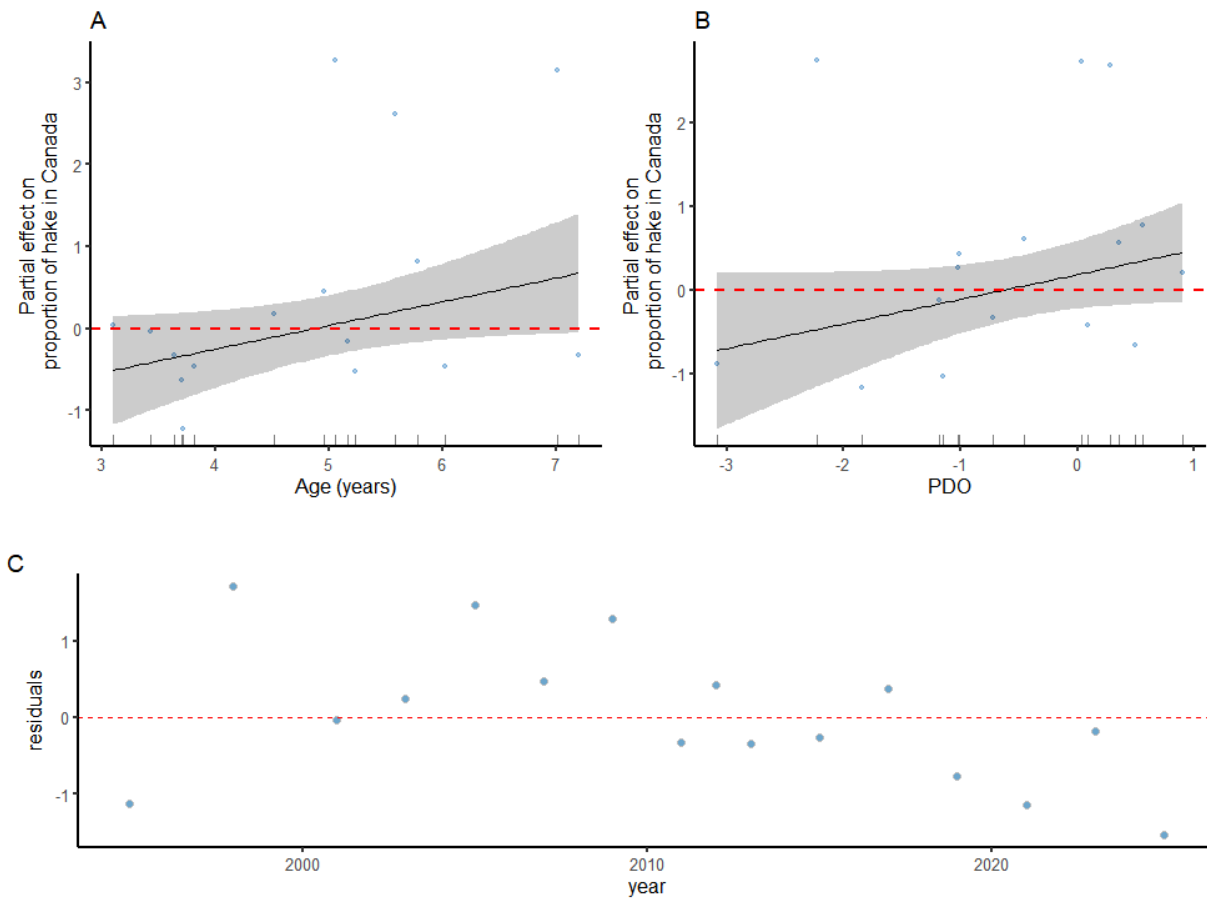


Fig. 8: Generalized additive models of the partial effects of (a) mean hake age and (b) April PDO on the proportion of hake biomass in Canada (north of 48.5°N). Residuals are plotted as blue circles. The dashed red line indicates the threshold at which the additive effect is 0. (c) The deviance residuals from the GAM plotted by year. The red dashed line represents a residual of 0.

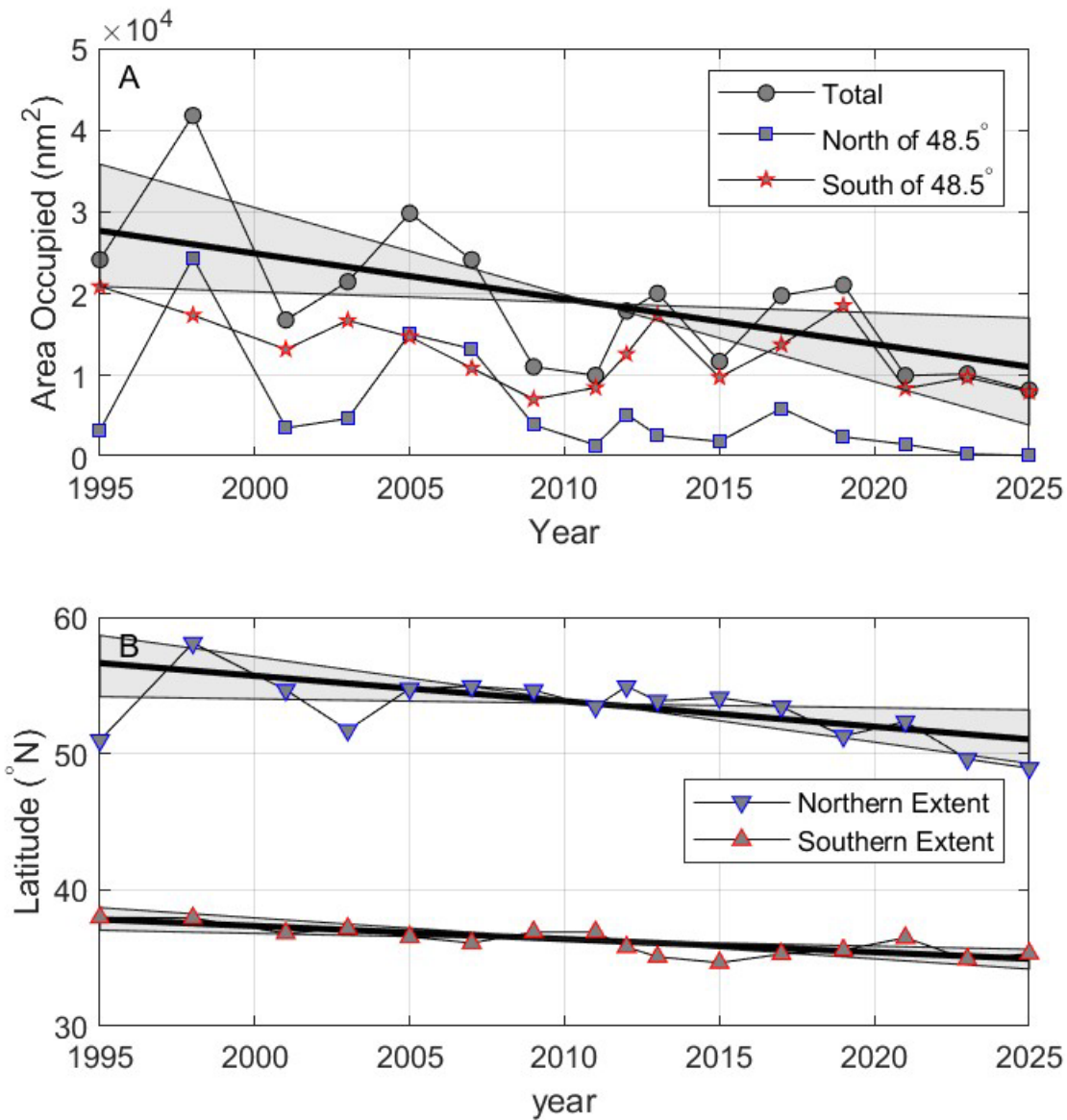


Fig. 9: (a) Survey area occupied from kriged biomass estimates between 1995 and 2025. Blue squares denote the area occupied by hake south of 48.5°N (generally U.S.), red stars denote north of 48.5°N (generally Canada), and the black squares are the survey-wide total. The dark black line and shaded area are the slope of the trend line to the total and the associated confidence interval area. (b) Latitudes of southern (red triangles) and northern (blue upside down triangles) extent of hake in the survey (from unextrapolated kriged biomass estimates) between 1995 and 2025. The dark black lines and shaded areas are the slope of the trend lines to each of the southern and northern extent and the associated confidence interval areas

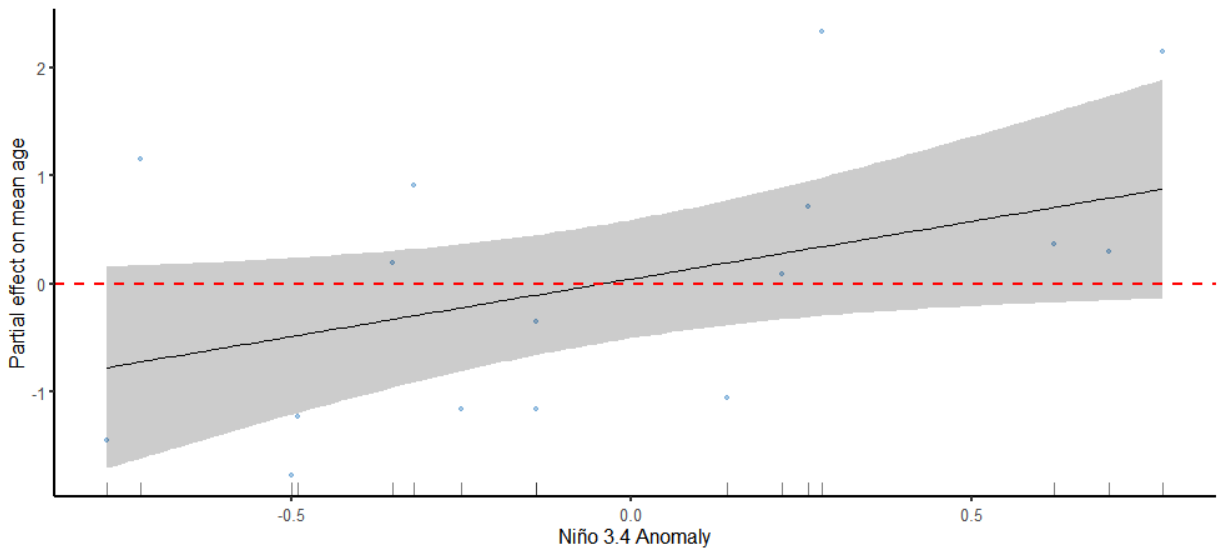


Fig. 10: Generalized additive model of the partial effect of April Niño 3.4 anomaly on mean hake age. Residuals are plotted as blue circles. The dashed red line indicates the threshold at which the additive effect is 0.

Supplemental Material:*Derivation of biomass density:*

The TS-length equation for hake used in the survey is:

$$TS = 20 \log(l) - 68 \quad (S1)$$

where l is fish fork length in cm (Traynor, 1996). A recent study based on survey data spanning 15 years suggested a b20 (intercept) of -67.9 (a difference of only 0.1 dB from the Traynor model). This change was not implemented in this study. By definition $TS \equiv 10(\sigma_{bs})$ dB re 1m^2 (MacIennan et al., 2002), so the differential backscattering cross section for stratum $s < \sigma_{bs} >_s$ can be calculated as:

$$< \sigma_{bs} >_s = \sum_i f_{is} 10^{\{[-68+20 \log l_{is}]/10\}} \quad (S2)$$

where l_{is} is the fork length (in cm) of length class i in stratum s and f_{is} is the frequency of the length class i in stratum s (sum of $f_{is} = 1$). Lengths are binned in 2 cm increments.

The number density (ρ_A , numbers nmi^{-2}) for an acoustic region and associated estimate of $< \sigma_{bs} >$ can be calculated as:

$$\rho_A = \frac{S_A}{4\pi < \sigma_{bs} >} \quad (S3)$$

This number density can be converted to biomass density (ρ_W , kg/nmi^2) as:

$$\rho_W = \frac{S_A}{4\pi < \sigma_{bs} >} \hat{W}_s \quad (S4)$$

where $\hat{W}_s$ is the average weight in kg of fish in stratum s . The average weight of fish in stratum s , $\hat{W}_s$, is given by:

$$\hat{W}_s = \sum_i f_{is} w_{is} \quad (S5)$$

where w_{is} is the weight of a fish of length i in stratum s . Therefore, the biomass density for an acoustic region associated with stratum s on transect X and interval I is:

$$\rho_W^{X,I} = \frac{S_A^{X,I}(s)}{4\pi < \sigma_{bs} >_s} W_s \quad (S6)$$

where W_s is the weight of fish at each length bin for stratum s , and $< \sigma_{bs} >_s$ is the averaged differential backscatter cross-section in stratum s .

Data transformation:

To attain the pseudo-isotropy needed for quality kriged estimates, spatial data were transformed before kriging onto a normalized, distance-based coordinate system. Hake distribution is often centered along the 200 m shelf break, so the first data transformation step transformed the original longitude coordinates ($Lon_{Orig}(p, lat)$) into shelf break-relative coordinates ($Lon_{Trans}(p, lat)$):

$$Lon_{Trans}(p, lat) = Lon_{Orig}(p, lat) - Lon_{200m}(lat) + Lon_{Ref} \quad (S7)$$

for each datum or mesh grid point p (function of latitude Lat) in the spatial data set, given $Lon_{Ref} = -125^\circ$ (longitude $125^\circ W$).

The second step transformed the shelf break-transformed longitude and original latitude (Lat) coordinates into a distance coordinate system (x, y).

$$\begin{cases} x = 60 * Lon_{Trans} \cos(Lat) \\ y = 60 * Lat \end{cases} \text{ (nmi).} \quad (S8)$$

The third step normalized the coordinates (x, y) by the maximum longitudinal ($D_x = x_{max} - x_{min}$) and latitudinal ($D_y = y_{max} - y_{min}$) extents, respectively:

$$x_n = \frac{x - x_{min}}{D_x} \text{ and } y_n = \frac{y - y_{min}}{D_y}. \quad (S9)$$

D_y will vary slightly each survey year depending on distribution. Hake are correlated over a longer distance in the N/S direction than in the E/W direction due to the general N/S orientation of the bathymetry along the U.S. and Canada West Coasts. Therefore, the final step in coordinate transformation was to transform the normalized, shelf break-relative, distance coordinates into a pseudo-isotropic system using an aspect ratio transformation. Ideally, the y (latitude) direction values would be normalized by the aspect ratio of the hake spatial distribution, R_{aspect} , defined as the ratio of the two length scales

$$L_y = R_{aspect} L_x \quad (S10)$$

where L_y and L_x are correlation lengths in x (longitude) and y (latitude). In reality, given discrete transects arranged along the y dimension, and nearly continuous sampling along the x dimension, the sample spatial resolution in y is much lower than that in x . Therefore, we used the aspect ratio from the survey region to approximate the real aspect ratio, i.e.

$$R_{aspect} \equiv \frac{D_y}{D_x} \quad (S11)$$

to transform

$$x_c = x_n \text{ and } y_c = \frac{y_n}{R_{aspect}} \quad (S12)$$

to obtain x_c and y_c , the final transformed coordinates to go into kriging.

2.3 Geostatistical Analysis:

Kriging is a technique that provides the best linear unbiased estimator of unknown quantities (Journel et al., 1976; Kitanidis, 1997). It is a local estimator that can provide the interpolation and extrapolation of the original sparsely sampled data that are assumed to be reasonably characterized by the Intrinsic Statistical Model (ISM). An ISM does not require the quantity of interest to be stationary, i.e., its mean

and standard deviation are independent of position, but rather that its covariance function depends on the separation of two data points only:

$$E[(z(x) - m)(z(x + h) - m)] = C(h) \quad (\text{S13})$$

where $E[]$ stands for expectation, $z(x)$ is the quantity to be kriged, m is the mean of $z(x)$, and $C(h)$ is the covariance function with lag h , with h being the distance between two samples (e.g. grid cells) at x and $x+h$:

$$h = \|x - (x + h)\| \quad (\text{S14})$$

Another way to characterize an ISM is to use a semi-variogram,

$$\gamma(h) = 0.5 * E[z(x) - z(x + h)]^2 \quad (\text{S15})$$

The relationship between the covariance function and the semi-variogram is

$$\gamma(h) = C(0) - C(h) \quad (\text{S16})$$

The general Gaussian exponential-Bessel experimental model, a commonly used semi-variogram model, was chosen due to its simplicity. The analytical expression of the semi-variogram (also called variogram) model is:

$$\gamma(h) = \gamma(\infty) \left[1 - \exp\left(-\frac{h}{L}\right)^p \right] \quad (\text{S17})$$

where h is the lag, representing the distance between two sample points, L is the length scale, p is the power, and $\gamma(\infty)$ is the sill, the value of the semi-variogram when $h \rightarrow \infty$ and is finite if $\gamma(h)$ is stabilized as $h \rightarrow \infty$. The lag (h) and the length scale (L) are dimensionless quantities in a normalized coordinate system (see Section **Methods**); therefore, the length scale, L , is a quantity derived from the model and data fitting.

The variograms used for these analyses assumed 0 for the semi-variogram at zero lag ($\gamma(0)=0$).

The ordinary kriging method finds a local estimate of the quantity at a specified location, x_L . This estimate is a weighted average of the N adjacent observations:

$$\hat{z}(x_L) = \sum_{\alpha=1}^N \lambda_{\alpha} z(x_{\alpha}) \quad (\text{S18})$$

The weighting coefficients λ_{α} can be determined based on the minimum estimation variance criterion:

$$E\{[z(x_L) - \hat{z}(x_L)]^2\} = C(0) - 2 \sum_{\alpha} \lambda_{\alpha} C(\|x_{\alpha} - x_L\|) + \sum_{\alpha} \sum_{\beta} \lambda_{\alpha} \lambda_{\beta} C(\|x_{\alpha} - x_{\beta}\|) \quad (\text{S19})$$

subject to the normalization condition

$$\sum_{\alpha=1}^N \lambda_{\alpha} = 1 \quad (\text{S20})$$

Note that we do not know the exact value at x_L , but we are trying to find a predicted value that provides the minimum estimation variance. Differentiating Eq. (S13) with respect to λ_{α} results in

$$\begin{aligned} \sum_{\beta=1}^N \lambda_{\beta} C_n(\|\mathbf{x}_{\alpha} - \mathbf{x}_{\beta}\|) - \mu &= C_n(\|\mathbf{x}_{\alpha} - \mathbf{x}_L\|) \\ \sum_{\beta=1}^N \lambda_{\beta} &= 1 \end{aligned} \quad (\text{S21})$$

where μ is the Lagrangian coefficient. In addition, we have replaced the covariance function with the normalized covariance function [normalized by $C(0)$]. Equivalently, by using Eq. (S10), we can also express the kriging equation in terms of the semi-variogram as

$$\begin{aligned} \sum_{\beta=1}^N \lambda_{\beta} \gamma_n(\|\mathbf{x}_{\alpha} - \mathbf{x}_{\beta}\|) + \mu &= \gamma_n(\|\mathbf{x}_{\alpha} - \mathbf{x}_L\|) \\ \sum_{\beta=1}^N \lambda_{\beta} &= 1 \end{aligned} \quad (\text{S22})$$

where we have used the normalized semi-variogram, i.e., the semi-variogram normalized by $C(0)$ as we did in deriving Eq. (S15).

To avoid numerical difficulties associated with solving a huge linear equation system, we chose a moving, localized kriging scheme, i.e., instead of using all the available spatial data points to estimate the value at a specified location, we used only those within the search radius centered at that specified location. In our applications, the search radius was chosen to be $3L$, and a minimum of 3 points and a maximum of 10 data points within that search radius were used to constitute a valid estimate.

In addition, we limited extrapolation beyond the offshore survey boundary (west side of the survey transects). The extrapolation was exponentially attenuated beyond $3L$ west of the survey boundary. The resultant biomass estimated for the i th grid cell beyond the survey boundary was weighted by

$$\begin{cases} w_i = 1, & r_{kmin} \leq SR \\ w_i = \exp(-r_{kmin}/SR), & r_{kmin} > SR \end{cases} \quad (\text{S23})$$

with $SR = 3L$. An exponential function ensures an exponential decayed weighting factor, w_i to avoid an abrupt change in the region beyond SR .

The total biomass estimated was then calculated by

$$\hat{B}_{tot} = \sum_{L=1}^{N_g} \hat{\rho}(\mathbf{x}_L) A_L, \quad (\text{S24})$$

Where $\hat{\rho}(\mathbf{x}_L)$ is the biomass density (i.e., $\hat{z}(\mathbf{x}_L)$ in Eq. (S12)), N_g is the total number of grid cells of the kriging region and A_L was the area (nmi²) of grid region L . In our application, $A_L = 2.5 \times 2.5 = 6.25$ nmi² and was constant throughout the survey region and survey years. The averaged CV from kriging is

$$CV = \frac{\sqrt{\sum_{L=1}^{N_L} \sigma_L^2(\mathbf{x}_L)}}{\sum_{L=1}^{N_L} \hat{\rho}(\mathbf{x}_L)}. \quad (\text{S25})$$

Having obtained the weighting coefficients (λ_β) and the Lagrangian coefficient (μ) by solving either Eq. (S15) or Eq. (S16), the kriging variance can be expressed as:

$$\begin{aligned}\sigma_L^2 &= E\{[z(x_L) - \hat{z}(x_L)]^2\} = C(0) + \mu - \sum_{\alpha} \lambda_{\alpha} C(\|x_{\alpha} - x_L\|) \\ &= \mu + \sum_{\alpha} \lambda_{\alpha} \gamma(\|x_{\alpha} - x_L\|) - \gamma(0).\end{aligned}\quad (\text{S26})$$

Tables:

Table S1: Characteristics of nets used by different vessels during the Pacific hake acoustic-trawl survey between 1995-2025.

Location	Net Type	Ship (years) – bold US	Average Vertical Opening	Codend Liner Size (mm)	Door Specifications
	Aleutian Wing Trawl (AWT)	NOAA Ship Miller Freeman (1995-2009) NOAA Ship Bell M Shimada (2011-2023) F/V Forum Star (2012) F/V Nordic Pearl (2021) CCGS Sir John Franklin (2023)	27 m (1995); 22 m (1998 & 2005); 24 m (2001, 2007, & 2009) 19 m (2011); 18 m (2013); 21 m (2015); 23 m (2017); 26 m (2019, 2021, & 2023)	NOAA – 32mm (11x 12 mm in 2001) DFO – 6mm	6'x9' steel V or 5 m ² "Fishbuster"; 4 m ² "Fishbuster" (2005–2023); USA Jet (2023 on <i>Franklin</i>)
Midwater	Canadian Diamond-7	CCGS W.E. Ricker (1995-2015)	21 m (2012) 13.5m	38mm	Superkrub 5 m ²
	RS 250/550/14 Cantrawl	CCGS W.E. Ricker (2013) F/V Nordic Pearl (2017–2019)	21 m	6 mm	USA jet (2013); Thyborøn Type-2 (2017–2019)
	Polish rope	CCGS W.E. Ricker (2003)	20 m	10 mm	5-m ² USA JET (Model P)
	Multi-Function Trawl (MFT)	NOAA Ship Bell M Shimada (2025) CCGS Sir John Franklin (2025)	25 m	8 mm	4 m ² Thyborøn Type 22
Bottom	Poly-Yankee 36	CCGS <i>W.E. Ricker</i> (2003)	4–5 m	25 mm	5-m ² USA JET (Model P)
	Nylon Nor'eastern	NOAA Ship Miller Freeman (1995)	6 m	32 mm	5 m ² "Fishbuster"

Poly Nor'eastern	NOAA Ship Miller Freeman (1995– 2001)	7 m (1995 & 2001); 6 m (1998); 10 m (2005); 8 m (2007); 3 m (2011)	32 mm	6'x9' steel V or 5 m ² "Fishbuster"
---------------------	---	---	-------	---

Table S2: Characteristics of primary echosounders used by different vessels during the Pacific hake acoustic-trawl survey between 1995-2025.

Ship/survey	NOAA Ships Miller Freeman (1995–2009), Bell M. Shimada (2011–2025)	CCGS W. E. Ricker (1995–2015), F/V Nordic Pearl (2017-2021)	CCGS Sir John Franklin (2023-2025)
Transceiver	EK500: 1995–2001* EK60: 2005–2023 EK80: 2025	EK500: 1995–2003 EK60: 2005–2021	EK80: 2023–2025
Transducer	38 kHz (Simrad ES38B)	38 kHz (Simrad ES38B)	38 kHz (Simrad ES38B, ES38-7 (2023–2025))
Ping interval	≤ 4 s ping-1	≤ 4 s ping-1	≤ 4 s ping-1
Power	2,000 W	2,000 W	2,000 W
Nominal 3 dB beam angles	Along: 6.8 Athwart: 6.9 (offsets=0)	Along: 7.1 Athwart: 7.1 (offsets=0)	Along: 7.1 Athwart: 7.1 (offsets=0)
Transducer depth	9.15 or 7.0 m	4.5, 4.0 m	9.15 m
Vessel speed	5.6-6.1 m/sec (9-12 knots)	4.6-5.1 m/sec (9-10 knots)	5.6-6.1 m/sec (11-12 knots)

* no U.S. vessel in 2003

Supplemental Figures:

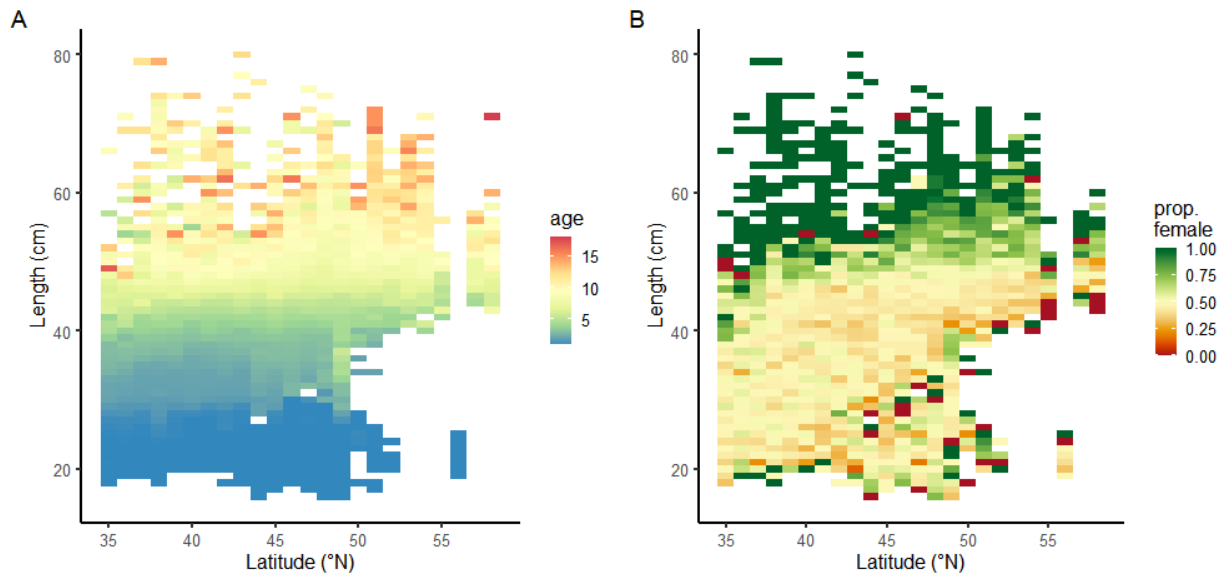


Fig. S1: Heatplots of (a) the age of hake by length and latitude and (b) proportion of female hake by length and latitude. The heat plots of hake age by length and latitude, and proportion of female hake by length and latitude were made from the complete data set of age-1+ hake aged individuals.

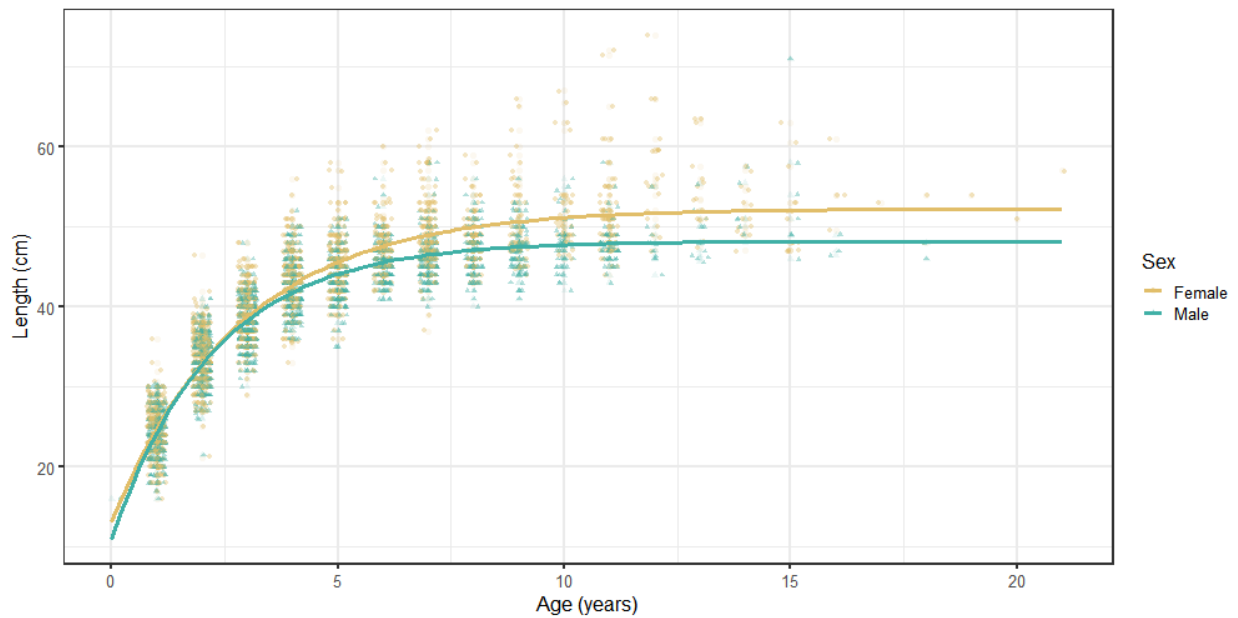


Fig. S2: Plot of hake length by age and sex (yellow=female, green=male) from inverse-catch subsampled specimen data. The fitted von Bertalanffy growth curves relating age to length by sex are shown as colored lines. For females, $L_{\infty} = 52.87$ cm, $k = 0.34$, $t_0 = -0.88$ and for males, $L_{\infty} = 48.5$ cm, $k = 0.43$, $t_0 = -0.61$.

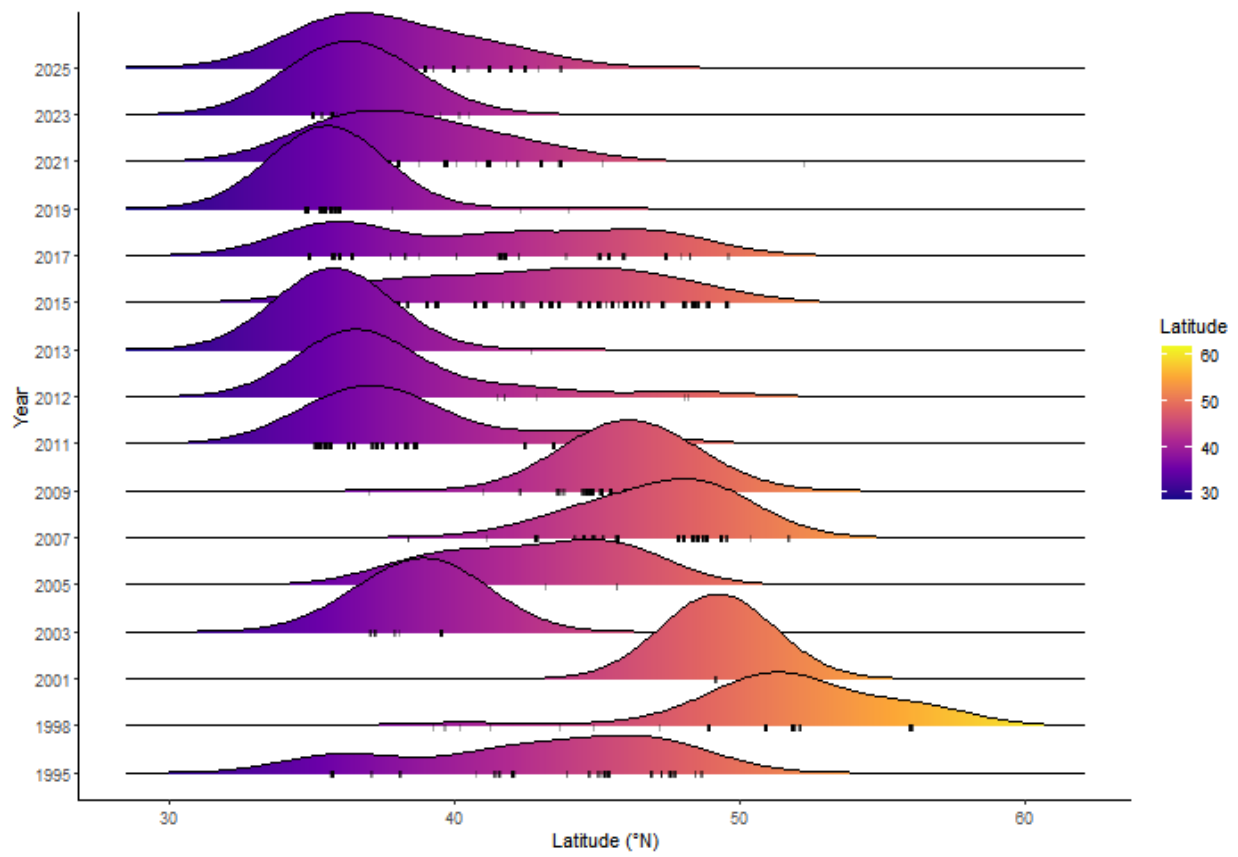


Fig. S3: Ridgeline plot of latitudes of trawls with age-1 fish between 1995 and 2025.

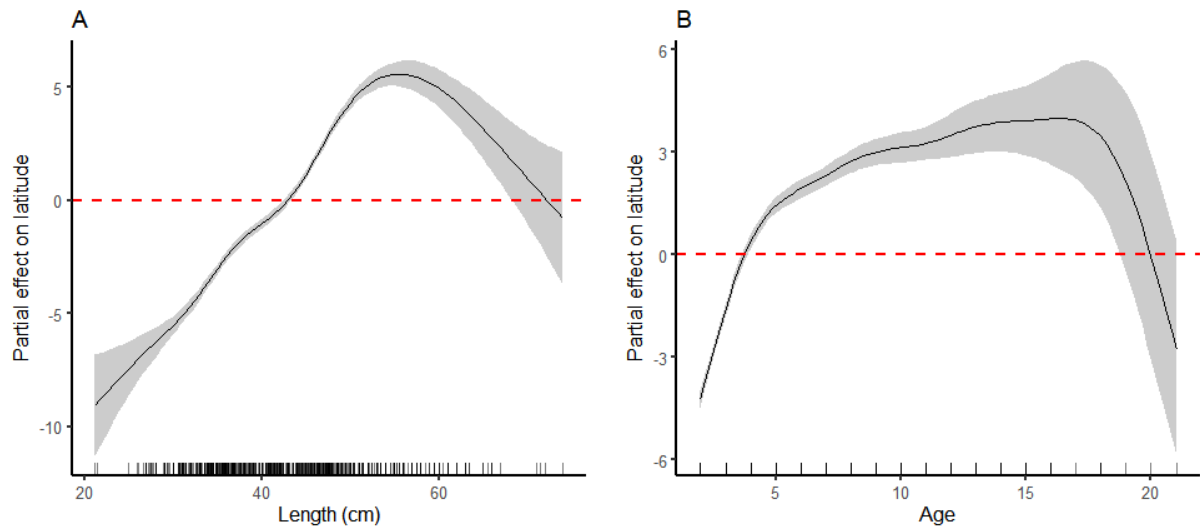


Fig. S4: Generalized additive models showing the (a) partial dependence of latitude of fish vs. length and the (b) partial dependence of latitude of fish vs. age. (a) and (b) are from separate GAM models

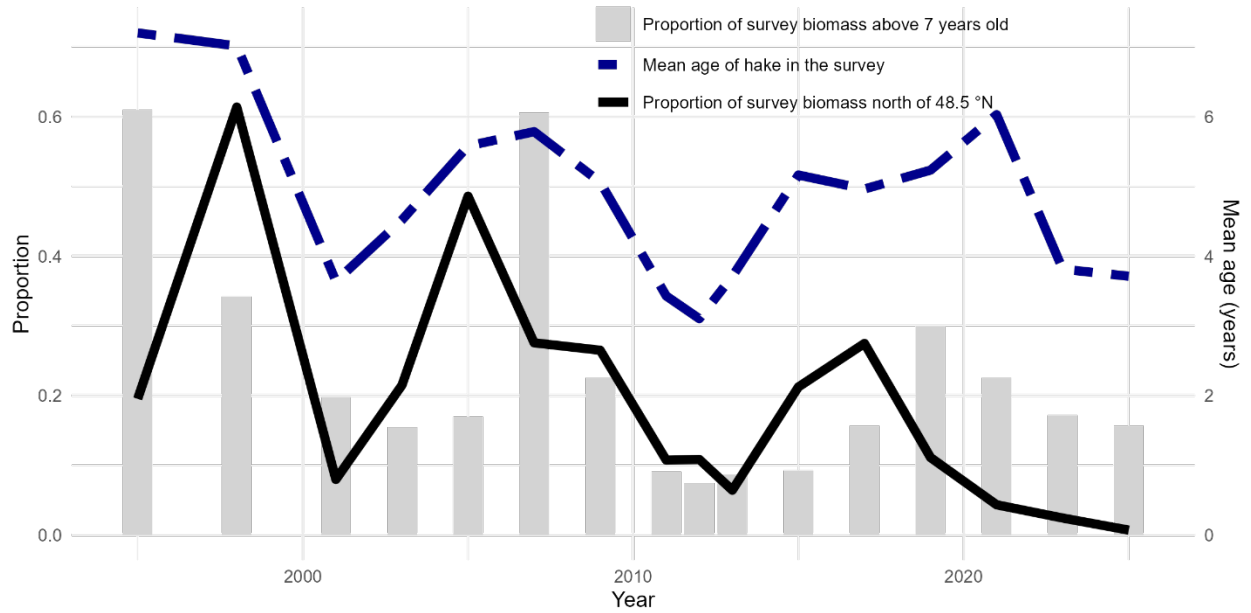


Fig. S5: Proportion of the survey biomass older than age 7 (grey bars) by year, with the proportion of biomass in Canada (north of 48.5°N) overlaid in black and the mean age of hake in the survey overlaid in dotted blue.

References:

- Agostini, V. N., Francis, R. C., Hollowed, A., Pierce, S. D., Wilson, C. D., & Hendrix, A. N. (2006). The relationship between Pacific hake (*Merluccius productus*) distribution and poleward subsurface flow in the California Current system. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 2648-2659.
- Agostini, V. N., Hendrix, A. N., Hollowed, A. B., Wilson, C. D., Pierce, S. D., & Francis, R. C. (2008). Climate–ocean variability and Pacific hake: A geostatistical modeling approach. *Journal of Marine Systems*, 71(3), 237-248.
- Alexander, M. A., Bladé, I., Newman, M., Lanzante, J. R., Lau, N.-C., & Scott, J. D. (2002). The Atmospheric Bridge: The Influence of ENSO Teleconnections on Air–Sea Interaction over the Global Oceans. *Journal of Climate*, 15(16), 2205-2231. doi:[https://doi.org/10.1175/1520-0442\(2002\)015<2205:TABTIO>2.0.CO;2](https://doi.org/10.1175/1520-0442(2002)015<2205:TABTIO>2.0.CO;2)
- Bailey, K. M. (1982). The early life history of the Pacific hake, *Merluccius productus*. *Fishery Bulletin*, 80(3), 589-598.
- Bailey, K. M., & Francis, R. C. (1985). Recruitment of Pacific whiting, *Merluccius productus*, and the ocean environment. *Marine Fisheries Review*, 47(2), 8-15.
- Bailey, K. M., Francis, R. C., & Stevens, P. R. (1982). The life history and fishery of Pacific whiting, *Merluccius productus*. *California Cooperative Oceanic Fisheries Investigations Reports*, XXIII, 81-98.
- Bakun, A. (1973). Coastal upwelling indices, west coast of North America, 1946-71.
- Barth, J. A., Pierce, S. D., Carter, B. R., Chan, F., Erofeev, A. Y., Fisher, J. L., Feely, R. A., Jacobson, K. C., Keller, A. A., Morgan, C. A., Pohl, J. E., Rasmuson, L. K., & Simon, V. (2024). Widespread and increasing near-bottom hypoxia in the coastal ocean off the United States Pacific Northwest. *Scientific Reports*, 14(1), 3798. doi:10.1038/s41598-024-54476-0
- Beamish, R. J. (2008). Impacts of climate and climate change on the key species in the fisheries in the North Pacific.
- Beamish, R. J., & McFarlane, G. A. (1985). Pacific whiting, *Merluccius productus*, stocks off the west coast of Vancouver Island, Canada. *Marine Fisheries Review*, 47(2), 75-81.
- Benson, A. J., McFarlane, G. A., Allen, S. E., & Dower, J. F. (2002). Changes in Pacific hake (*Merluccius productus*) migration pattern and juvenile growth related to the 1989 regime shift. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 1969-1979.
- Burkey, J. (2006). A non-parametric monotonic trend test computing Mann-Kendall Tau, Tau-b, and Sen's slope written in Mathworks-MATLAB implemented using matrix rotations. *King County, Department of Natural Resources and Parks, Science and Technical Services section, Seattle, Washington, USA*.
- Caserta, V., Punt, A. E., Arneri, E., Berginc, T., Kec, V. C., Costantini, I., De Felice, A., Donato, F., Leonori, I., & Santojanni, A. (2025). Incorporating key environmental drivers in European anchovy (*Engraulis encrasicolus*) stock assessment model in the Adriatic Sea. *ICES Journal of Marine Science*, 82(9), fsaf171.
- Chavez, F. P., Ryan, J., Lluch-Cota, S. E., & Niquen C, M. (2003). From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science*, 299(5604), 217-221.
- Cluett, A. A., Bograd, S. J., Jacox, M. G., Buil, M. P., & Hazen, E. L. (2025). Pan-basin warming now overshadows robust Pacific Decadal Oscillation. *Nature Climate Change*, 1-8.
- Collaud Coen, M., Andrews, E., Bigi, A., Martucci, G., Romanens, G., Vogt, F. P. A., & Vuilleumier, L. (2020). Effects of the prewhitening method, the time granularity, and the time segmentation on the Mann–Kendall trend detection and the associated Sen's slope. *Atmos. Meas. Tech.*, 13(12), 6945-6964. doi:10.5194/amt-13-6945-2020

- Cooke, K. D., Holmes, J., Fleischer, G., Thomas, R., & Ressler, P. (2006). Distributional changes observed in the geographic range of Pacific hake (*Merluccius productus*) in association with ocean conditions off the Pacific coast of Canada and the United States. *ICES CM* 2006.
- Cooper, A. B., & Weir, K. (2006). A guide to fisheries stock assessment: from data to recommendations.
- Dark, T. (1975). Age and growth of Pacific hake, *Merluccius productus*. *Fishery Bulletin*, 73(2), 336-355.
- Denechaud, C., Smoliński, S., Geffen, A. J., Godiksen, J. A., & Campana, S. E. (2020). A century of fish growth in relation to climate change, population dynamics and exploitation. *Global Change Biology*, 26(10), 5661-5678. doi:<https://doi.org/10.1111/gcb.15298>
- Dorn, M. W. (1992). Detecting environmental covariates of Pacific whiting *Merluccius productus* growth using a growth-increment regression model. *Fishery Bulletin*, 90, 260-275.
- Dorn, M. W. (1995). The effects of age composition and oceanographic conditions on the annual migration of Pacific whiting, *Merluccius productus*. *California Cooperative Oceanic Fisheries Investigations Reports*, 36, 97-105.
- Edwards, A. M., Berger, A. M., Grandin, C. J., Wetzel, C. R., Johnson, K. F., & Oken, K. L. (2026). *Status of the Pacific Hake (whiting) stock in U.S. and Canadian waters in 2026*. Prepared by the Joint Technical Committee of the U.S. and Canada Pacific Hake/Whiting Agreement, National Marine Fisheries Service and Fisheries and Oceans Canada.
- Enfield, D. B., & Allen, J. S. (1980). On the Structure and Dynamics of Monthly Mean Sea Level Anomalies along the Pacific Coast of North and South America. *Journal of Physical Oceanography*, 10(4), 557-578. doi:[https://doi.org/10.1175/1520-0485\(1980\)010<0557:OTSADO>2.0.CO;2](https://doi.org/10.1175/1520-0485(1980)010<0557:OTSADO>2.0.CO;2)
- Ferriss, B. E., Connors, B. M., Crozier, L. G., Anderson, S. C., Boldt, J. L., Cheng, W., Edwards, A. M., Freshwater, C., Gertseva, V., & Huff, D. D. (2026). Leveraging transboundary science to support Northeast Pacific fisheries and protected species management. *ICES Journal of Marine Science*, 83(3), fsag019.
- Fleischer, G. W., Cooke, K. D., Ressler, P. H., Thomas, R. E., de Blois, S. K., & Hufnagle, L. C. (2008). The 2005 integrated acoustic and trawl survey of Pacific hake, *Merluccius productus*, in U.S. and Canadian waters off the Pacific coast. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-94. 57 p.:
- Francis, R. C. (1983). Population and trophic dynamics of Pacific whiting, (*Merluccius productus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 40, 1925-1943.
- Hamel, O. S., Ressler, P. H., Thomas, R. E., Waldeck, D. A., Hicks, A. C., Holmes, J. A., & Fleischer, G. W. (2015). Biology, fisheries, assessment, and management of Pacific hake (*Merluccius productus*). In H. Arancibia (Ed.), *Hakes: biology and exploitation* (pp. 234-262): John Wiley & Sons, Ltd.
- Hare, S. R., & Mantua, N. J. (2000). Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, 47(2-4), 103-145.
- Head, M. A., Billings, A. A., Tuttle, V. J., Johnson, K. F., Berger, A. M., & Heppell, S. A. (2025). Decade-scale spatio-temporal variability in maturity of Pacific hake, *Merluccius productus*, along the US West Coast. *Environmental Biology of Fishes*, 108(3), 317-338.
- Hilborn, R., & Walters, C. J. (1992). *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. London: Chapman and Hall.
- Jacobsen, N. S., Marshall, K. N., Berger, A. M., Grandin, C. J., & Taylor, I. G. (2021). Management strategy evaluation of Pacific hake: Exploring the robustness of the current harvest policy to spatial stock structure, shifts in fishery selectivity, and climate-driven distribution shifts.

- Jacox, M. G., Bograd, S. J., Fiechter, J., Pozo Buil, M., Alexander, M., Amaya, D., Cordero Quiros, N., Ding, H., & Rykaczewski, R. R. (2024). Linking upwelling dynamics and subsurface nutrients to projected productivity changes in the California Current System. *Geophysical Research Letters*, 51(10), e2023GL108096.
- Jacox, M. G., Edwards, C. A., Hazen, E. L., & Bograd, S. J. (2018). Coastal upwelling revisited: Ekman, Bakun, and improved upwelling indices for the US West Coast. *Journal of Geophysical Research: Oceans*, 123(10), 7332-7350.
- Johnson, K., Edwards, A., Berger, A., Grandin, C., & Wetzel, C. (2025). Status of the Pacific Hake (whiting) stock in US and Canadian waters in 2025.
- Journel, A. G., & Huijbregts, C. J. (1976). Mining geostatistics.
- Kimura, D. K. (1979). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin*, 77(4), 765.
- King, J. R., Agostini, V. N., Harvey, C. J., McFarlane, G. A., Foreman, M. G. G., Overland, J. E., Di Lorenzo, E., Bond, N. A., & Aydin, K. Y. (2011). Climate forcing and the California Current ecosystem. *ICES Journal of Marine Science*, 68(6), 1199-1216. doi:10.1093/icesjms/fsr009
- Kitanidis, P. K. (1997). *Introduction to geostatistics: applications in hydrogeology*: Cambridge university press.
- LaFreniere, B. R., Peters, R., Donahue, B., McBride, R., & Mohan, J. A. (2023). What the hakes? Correlating environmental factors with hake abundance in the Gulf of Maine. *Journal of Northwest Atlantic fishery science*, 54.
- Litzow, M. A., Hunsicker, M. E., Bond, N. A., Burke, B. J., Cunningham, C. J., Gosselin, J. L., Norton, E. L., Ward, E. J., & Zador, S. G. (2020). The changing physical and ecological meanings of North Pacific Ocean climate indices. *Proceedings of the National Academy of Sciences*, 117(14), 7665-7671.
- Litzow, M. A., Mueter, F. J., & Hobday, A. J. (2014). Reassessing regime shifts in the North Pacific: incremental climate change and commercial fishing are necessary for explaining decadal-scale biological variability. *Global Change Biology*, 20(1), 38-50.
- MacCall, A. D. (1990). *Dynamic geography of marine fish populations*. Seattle: Washington Sea Grant Program.
- MacIennan, D. N., Fernandes, P. G., & Dalen, J. (2002). A consistent approach to definitions and symbols in fisheries acoustics. *ICES Journal of Marine Science*, 59(2), 365-369. doi:10.1006/jmsc.2001.1158
- Malick, M. J., Hunsicker, M. E., Haltuch, M. A., Parker-Stetter, S. L., Marshall, K. N., Pohl, J. E., Berger, A. M., Siedlecki, S. A., Gauthier, S., & Hermann, A. J. (2023). Spatially varying effects of the California Undercurrent on Pacific hake distribution. *Canadian Journal of Fisheries and Aquatic Sciences*, 81(2), 154-165.
- Malick, M. J., Siedlecki, S. A., Norton, E. L., Kaplan, I. C., Haltuch, M. A., Hunsicker, M. E., Parker-Stetter, S. L., Marshall, K. N., Berger, A. M., & Hermann, A. J. (2020). Environmentally driven seasonal forecasts of Pacific hake distribution. *Frontiers in Marine Science*, 7, 844.
- Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. R., & Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, 78(6), 1069-1079.
- Marquez, J. F., Sæther, B. E., Aanes, S., Engen, S., Salthaug, A., & Lee, A. M. (2021). Age-dependent patterns of spatial autocorrelation in fish populations. *Ecology*, 102(12), e03523.
- McClure, M. M., Haltuch, M. A., Willis-Norton, E., Huff, D. D., Hazen, E. L., Crozier, L. G., Jacox, M. G., Nelson, M. W., Andrews, K. S., Barnett, L. A. K., Berger, A. M., Beyer, S., Bizzarro, J., Boughton, D., Cope, J. M., Carr, M., Dewar, H., Dick, E., Dorval, E., Dunham, J., Gertseva, V., Greene, C. M., Gustafson, R. G., Hamel, O. S., Harvey, C. J.,

- Henderson, M. J., Jordan, C. E., Kaplan, I. C., Lindley, S. T., Mantua, N. J., Matson, S. E., Monk, M. H., Moyle, P., Nicol, C., Pohl, J., Rykaczewski, R. R., Samhour, J. F., Sogard, S., Tolimieri, N., Wallace, J., Wetzel, C., & Bograd, S. J. (2023). Vulnerability to climate change of managed stocks in the California Current large marine ecosystem. *Frontiers in Marine Science*, 10, 1103767.
- Melnichuk, M. C., Baker, N., Hively, D., Mistry, K., Pons, M., Ashbrook, C. E., Minto, C., Hilborn, R., & Ye, Y. (2020). *Global trends in status and management of assessed stocks: achieving sustainable fisheries through effective management* (Vol. 665): Food & Agriculture Org.
- Methot, R. D., & Dorn, M. W. (1995). Biology and fisheries of North Pacific hake (*M. productus*). In J. Alheit & T. J. Pitcher (Eds.), *Hake: biology, fisheries and markets* (pp. 389-414). London: Chapman and Hall.
- National Center for Environmental Information. (2025). *ERSST PDO Index*. Retrieved from: <https://www.ncei.noaa.gov/pub/data/cmb/ersst/v5/index/ersst.v5.pdo.dat>
- National Oceanographic and Atmospheric Administration. (2022). *NOAA 2022 ETOPO 2022 15 Arc-Second Global Relief Model*. Retrieved from: <https://www.ncei.noaa.gov/products/etopo-global-relief-model>
- NOAA Physical Sciences Laboratory. (2025). Niño 3.4 SST Index.
- Pepin, P., King, J., Holt, C., Gurney-Smith, H., Shackell, N., Hedges, K., & Bundy, A. (2022). Incorporating knowledge of changes in climatic, oceanographic and ecological conditions in Canadian stock assessments. *Fish and Fisheries*, 23(6), 1332-1346.
- Perryman, H. A., Hansen, C., Howell, D., & Olsen, E. (2021). A review of applications evaluating fisheries management scenarios through marine ecosystem models. *Reviews in Fisheries Science & Aquaculture*, 29(4), 800-835.
- Petitgas, P. (1993). Geostatistics for fish stock assessments: a review and an acoustic application. *ICES Journal of Marine Science: Journal du Conseil*, 50(3), 285-298.
- Petitgas, P. (2001). Geostatistics in fisheries survey design and stock assessment: models, variances and applications. *Fish and Fisheries*, 2(3), 231-249.
- Phillips, A. J., Ralston, S., Brodeur, R. D., Auth, T. D., Emmett, R. L., Johnson, C., & Weststad, V. G. (2007). Recent pre-recruit Pacific hake (*Merluccius productus*) occurrences in the northern California current suggest a northward expansion of their spawning area. *CalCOFI Reports*, 48, 215-229.
- Phillips, E. M., Malick, M. J., Gauthier, S., Haltuch, M. A., Hunsicker, M. E., Parker-Stetter, S. L., & Thomas, R. E. (2023). The influence of temperature on Pacific hake co-occurrence with euphausiids in the California Current Ecosystem. *Fisheries Oceanography*, n/a(n/a). doi:<https://doi.org/10.1111/fog.12628>
- R Core Team. (2023). R: A Language and Environment for Statistical Computing. Vienna, Austria: Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Ressler, P. H., Holmes, J. A., Fleischer, G. W., Thomas, R. E., & Cooke, K. C. (2007). Pacific hake, *Merluccius productus*, autecology: a timely review. *Marine Fisheries Review*, 69(1-4), 1-24.
- Rivoirard, J., Simmonds, J., Foote, K., Fernandes, P., & Bez, N. (2008). *Geostatistics for estimating fish abundance*: John Wiley & Sons.
- Simmonds, E., & MacLennan, D. (2005). *Fisheries Acoustics: Theory and Practice*: Oxford: Blackwell Science.
- Steiner, E., Phillips, A., & Chen, A. (2025). Economic Status of the Pacific Hake Fishery, 2009-23.
- Swartzman, G. (2001). Spatial patterns of Pacific hake (*Merluccius productus*) shoals and euphausiid patches in the California Current ecosystem. *Spatial processes and management of marine populations. Alaska Sea Grant College Program, AK-SG-01-02*, 495-511.

- Swartzman, G., & Huang, C. (1992). Spatial analysis of Bering Sea groundfish survey data using generalized additive models. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 1366-1378.
- Tang, H.-S., Zhang, Y., Kosaka, Y., Yang, J.-C., Shu, Q., Liu, Y., & Lin, X. (2024). Positive feedback between the negative phase of interannual component of the Pacific Decadal Oscillation and La Niña. *Climate Dynamics*, 62(8), 8319-8332. doi:10.1007/s00382-024-07346-4
- The Mathworks Inc. (2022). Natick, Massachusetts: The MathWorks Inc. (Version 9.12.0.1884302 (R2022a)). Retrieved from <https://www.mathworks.com>
- Traynor, J. J. (1996). Target-strength measurements of walleye pollock (*Theragra chalcogramma*) and Pacific whiting (*Merluccius productus*). *ICES Journal of Marine Science*, 53(2), 253-258.
- Agreement Between the Government of the United States of America and the Government of Canada on Pacific Hake/Whiting, Treaty Doc. 108-24 C.F.R. (2003).
- Vestfals, C. D., Marshall, K. N., Tolimieri, N., Hunsicker, M. E., Berger, A. M., Taylor, I. G., Jacox, M. G., & Turley, B. D. (2023). Stage-specific drivers of Pacific hake (*Merluccius productus*) recruitment in the California Current Ecosystem. *Fisheries Oceanography*, 32(4), 352-389.
- Ward, E. J., Anderson, S. C., Barnett, L. A., English, P. A., Berger, H. M., Commander, C. J., Essington, T. E., Harvey, C. J., Hunsicker, M. E., & Jacox, M. G. (2024). Win, lose, or draw: Evaluating dynamic thermal niches of northeast Pacific groundfish. *PLOS Climate*, 3(11), e0000454.
- Ware, D. M., & McFarlane, G. A. (1995). Climate-induced changes in Pacific hake (*Merluccius productus*) abundance and pelagic community interactions in the Vancouver Island upwelling system. In R. J. Beamish (Ed.), *Climate change and northern fish populations* (Vol. 121): Canadian Journal of Fisheries and Aquatic Sciences (Spec. Publ.).
- Woillez, M., Rivoirard, J., & Fernandes, P. G. (2009). Evaluating the uncertainty of abundance estimates from acoustic surveys using geostatistical simulations. *ICES Journal of Marine Science: Journal du Conseil*, fsp137.
- Wood, S. N. (2017). *Generalized additive models: an introduction with R*: chapman and hall/CRC.