

An updated model of potential habitat for northern stock Pacific Sardine (*Sardinops sagax*) and its use for attributing survey observations and fishery landings

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Abstract

Three years after the 2015 collapse of the northern stock of Pacific Sardine that is predominantly located off the west coast of the United States, acoustic-trawl (A-T) surveys documented an increase in the presence and persistence of the southern stock off coastal Southern California. Then in 2020, the biomass of Sardine that was landed in Mexico and attributed to the northern stock exceeded the estimated biomass for the entire northern stock. To investigate if the landings were incorrectly classified, we revisit a model of northern-stock potential habitat and the associated range of sea-surface temperature (SST) used to apportion the A-T survey data and monthly fishery landings to the two stocks, respectively. We update the probabilistic model of potential habitat with data on sardine-egg presence and absence and concomitant satellite-sensed SST and chlorophyll-*a* concentration through 2019 and apply the new model to more accurately attribute the A-T observations and fishery landings data to the northern or southern stock. The addition of recent data, with increased coverage in SSTs between 15°C and 17°C, improves the model accuracy and spatial precision of the stock attribution. The attribution accuracy is critically dependent on the temporal and spatial coincidence of the environmental and survey or landings data and should be corroborated with other characteristics indicative of biological isolation such as spatial separation, distinct spawning areas and seasons, and uncorrelated demographics.

KEYWORDS

oceanographic habitat, operational fisheries oceanography, stock discrimination

1 | INTRODUCTION

Fish stocks or subpopulations are geographically or otherwise distinct components of a fish population between which there is little exchange (Blackhart et al., 2006). Because they have unique spawning areas and migration patterns (Blackhart et al., 2006), fish stocks have independent

reproductive processes on time scales relevant for fisheries management (Berger et al., 2012; Smith, 2005). The population of Pacific Sardine (*Sardinops sagax*) in the northeastern Pacific margin, from the Gulf of California to the Gulf of Alaska, hereafter Sardine, is a small pelagic fish species presumably comprising three stocks with spawning centers in the Gulf of California, Baja California Sur inshore, and Central

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California offshore (Smith, 2005). These stocks are commonly referred to as warm or Gulf stock, temperate or southern stock, and cold or northern stock, respectively (Félix-Uraga et al., 2005; Hill et al., 2019).

In conformance with the prevailing literature (e.g., Demer & Zwolinski, 2014a; Félix-Uraga et al., 2005; PFMC, 2017), and explicitly stated here for preciseness, the northern stock refers to Sardine that, when abundant, spawn predominantly in the spring off Southern and Central California (Figure 1). Valencia-Gasti et al. (2018) indicate that there is sporadic spring spawning of Sardine as far south as Punta Eugenia, Baja California, Mexico. However, it should be noted that the abundance of eggs in the northernmost Mexican waters and hence attributable to the northern stock in the period of 2000 to 2013, is negligible—see Figure 2 in Valencia-Gasti et al. (2018). The northern stock migrates to feed as far north as Canada in summer, and returns south, likely offshore, west of 130°W longitude, in late fall and winter (Clark & Janssen, 1945; Zwolinski et al., 2011). The southern stock resides mostly off Baja California (Enciso-Enciso, Nevárez-Martínez, Sánchez-Cárdenas, Salcido-Guevara, et al., 2023) and migrates seasonally, typically synchronously and separately from the northern

stock (Félix-Uraga et al., 2004; Smith, 2005), recurrently entering the Southern California Bight (SCB) during the summer and occasionally migrating to waters off Central California (Figure 1; Felin, 1954). The Gulf stock seasonally migrates from the Gulf of California to Southern Baja California in summer, returning to the Gulf in winter (Félix-Uraga et al., 2005).

Landings of northern stock Sardine historically occur in six regions: Vancouver Island, Canada; Washington, Oregon, Central and Southern California, USA; and Ensenada, Mexico (Figure 1; Hill et al., 2019). The locations of the catches around each port are generally reported within geographic grid cells or by port of landing. The spatial extent of the Ensenada fishery is unknown, so it is approximated here by a 5-nmi wide coastal band (Figure 1) based on the nearshore distribution of Sardine in the SCB in the spring of 2021 (Zwolinski et al., 2023).

The potential habitat (hereafter habitat) for the northern stock is represented by a generalized additive model (GAM) trained on the presence of Sardine eggs in samples taken off Southern and Central California during the spring from 1998 through 2009 (Zwolinski

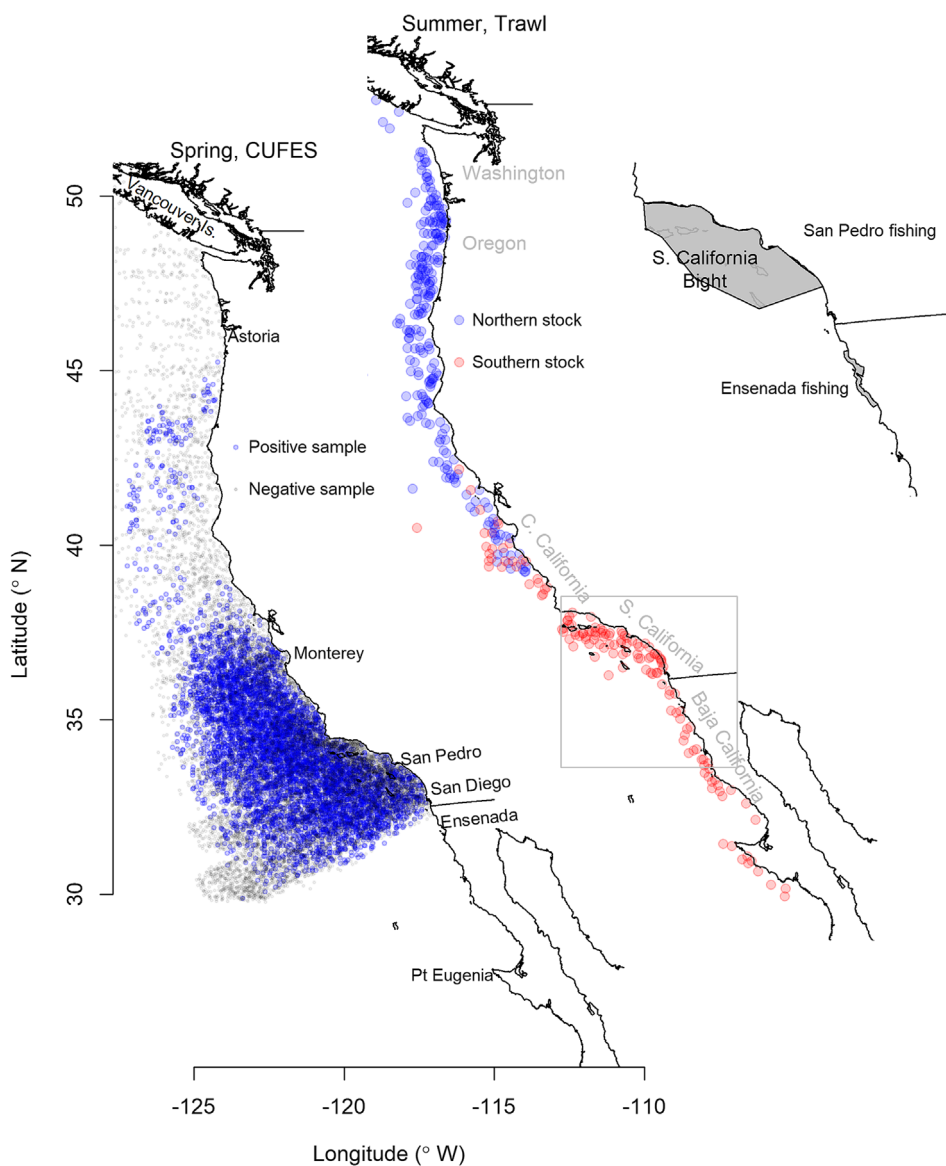


FIGURE 1 Multi-year composite distributions of northern (blue) and southern (red) stock Sardine during spring (left), inferred from egg presences in CUFES samples from 1998 to 2019, and summer (center), inferred from Sardine presence in trawl samples collected during 2012–2022 A-T summer surveys. *Note 1:* Sardine eggs were only sampled in the US exclusive economic zone in spring and were all attributed to the northern stock (left). *Note 2:* Sardine from the southern and northern stocks did not overlap in the same year (center; see Figure 7). The gray polygons on the right plot represent the purported areas of operation of the San Pedro and Ensenada fleets that have targeted northern stock Sardine in the past.

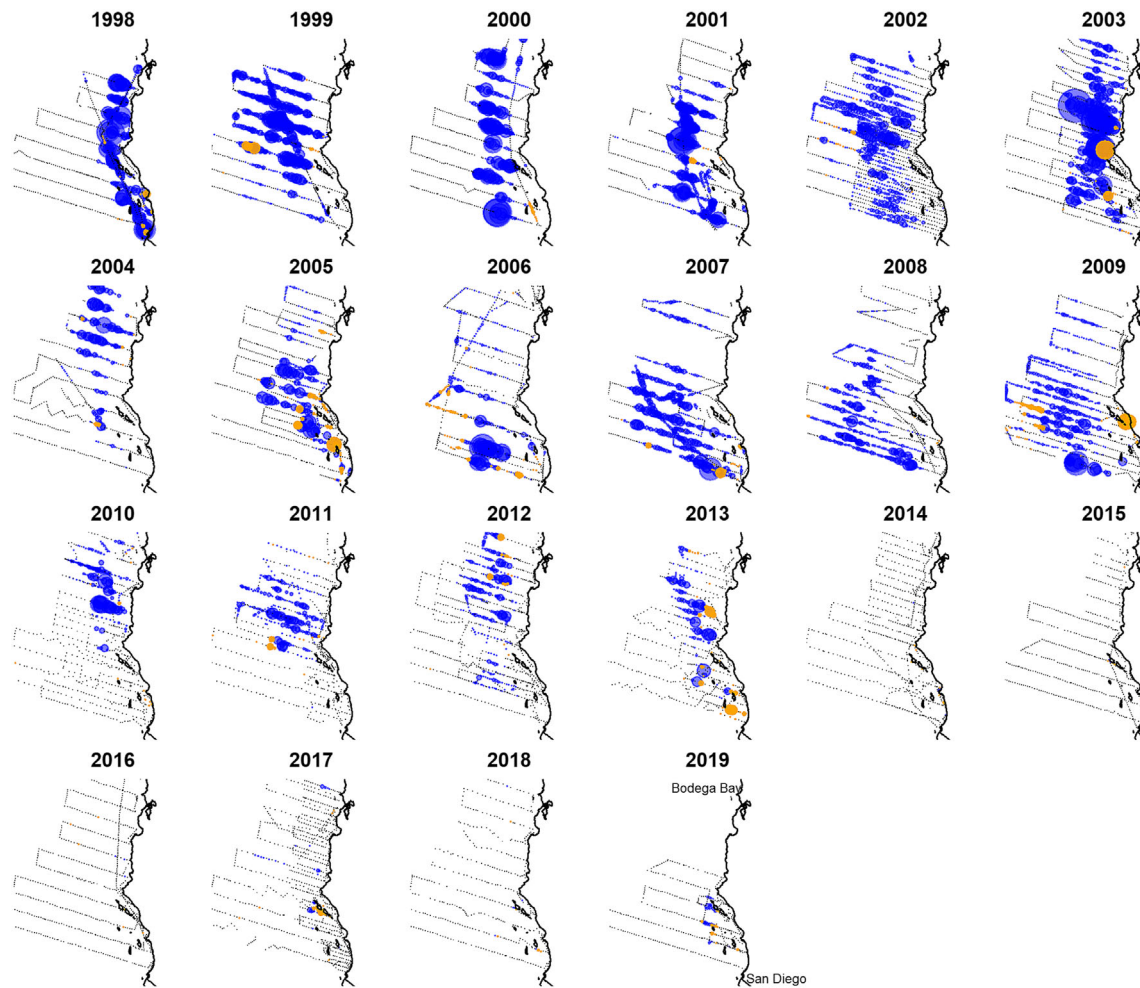


FIGURE 2 Relative sardine-egg abundance in continuous underway fish-egg sampler (CUFES) data collected during SWFSC, CalCOFI, and other spring surveys, generally April, 1998–2019, from San Diego (Lat $\sim 32.7^\circ\text{N}$) to Bodega Bay (Lat $\sim 38.34^\circ\text{N}$), California. Since 2014, after the northern stock collapsed (Hill et al., 2015), it has not been spawning in this area. A probability threshold of .18 in the updated habitat model retains 95% of the Sardine eggs (blue) and excludes 5% (orange). *Note:* The geographic positions were distorted to allow for improved graph legibility.

et al., 2011). It is principally characterized by a nonlinear combination of satellite-sensed sea-surface temperature (*SST*) and chlorophyll-*a* concentration (*CHL*). At least 90% of the Sardine egg presences are in the ranges $11.8^\circ\text{C} \leq \text{SST} \leq 15^\circ\text{C}$, and $.2 \leq \text{CHL} \leq 1.9 \text{ mg m}^{-3}$. The model also includes the gradient of sea-surface height but this parameter was less informative than *SST* and *CHL* and is omitted from the operational model (https://coastwatch.pfeg.noaa.gov/erddap/griddap/Sardine_habitat_modis.graph; hereafter original model).

The original habitat model indicates that during spring, when the northern stock is spawning, Sardine avoid both coastal upwelling and oligotrophic oceanic waters, preferring mesotrophic waters with moderate turbulence that favor egg and larval retention (Bakun & Parrish, 1982). From January to April, the habitat is typically offshore and south of Oregon. Beginning in April, the habitat moves northwards and compresses towards the coast. Throughout most of the summer, warm, oligotrophic waters offshore and to the south compress a narrow band of habitat along the coast, from Oregon to Vancouver Island (Zwolinski et al., 2011). Although the habitat model is

based on the oceanographic conditions conducive to spring spawning, it also predicts the habitat of the entire mature stock and its movements between these regions (Demer et al., 2012; Zwolinski et al., 2011). In synchrony with the available habitat, peak catches historically occurred off Oregon, Washington, and Vancouver Island during late summer and early fall (Zwolinski et al., 2011).

In the early autumn, the Sardine habitat expands and, from October through November, recedes towards the south, first departing from the coast of Vancouver Island. The offshore southwards movement continues through the winter and the habitat reaches a southern extreme during February and March. It attains its southernmost extension in the spring, which allows for the northern stock to spawn off Central and Southern California (Zwolinski et al., 2011) and occasionally off Northern Baja California (Valencia-Gasti et al., 2018). In some years, the model predicts the presence of spring spawning habitat in the coastal waters off Northern Baja California and, in other years, a year-round absence of nearshore habitat for the northern stock in the SCB. Therefore, from winter to spring, northern stock

TABLE 1 Acoustic-trawl survey estimates of northern and southern stock Sardine biomasses loosely attributed using the original habitat model (Zwolinski et al., 2011), and revised using closer inspection of the updated habitat model, corroborated by length distributions (Figure S5).

Year	Original		Revised		Reference
	Northern (t)	Southern (t)	Northern (t)	Southern (t)	
2012	341,000	0	—	—	(Zwolinski et al., 2014)
2013	314,000	0	—	—	(Zwolinski et al., 2014)
2014	26,300	0	—	—	(Hill et al., 2015)
2015	14,795	0	14,351	445	(Stierhoff et al., 2021a)
2016	80,092	323	—	—	(Stierhoff et al., 2021b)
2017	14,103	—	—	—	(Zwolinski et al., 2019)
2018	25,148	33,093	23,345	34,896	(Stierhoff et al., 2019)
2019	33,632	14,890	—	—	(Stierhoff et al., 2020)
2021	47,721	196,609	—	—	(Stierhoff, Renfree, et al., 2023)
2022	69,506	107,468	—	— </tr	

Note: Estimates from 2012 to 2019 are for US waters only, and those from 2021 and 2022 include waters off the United States and Mexico.

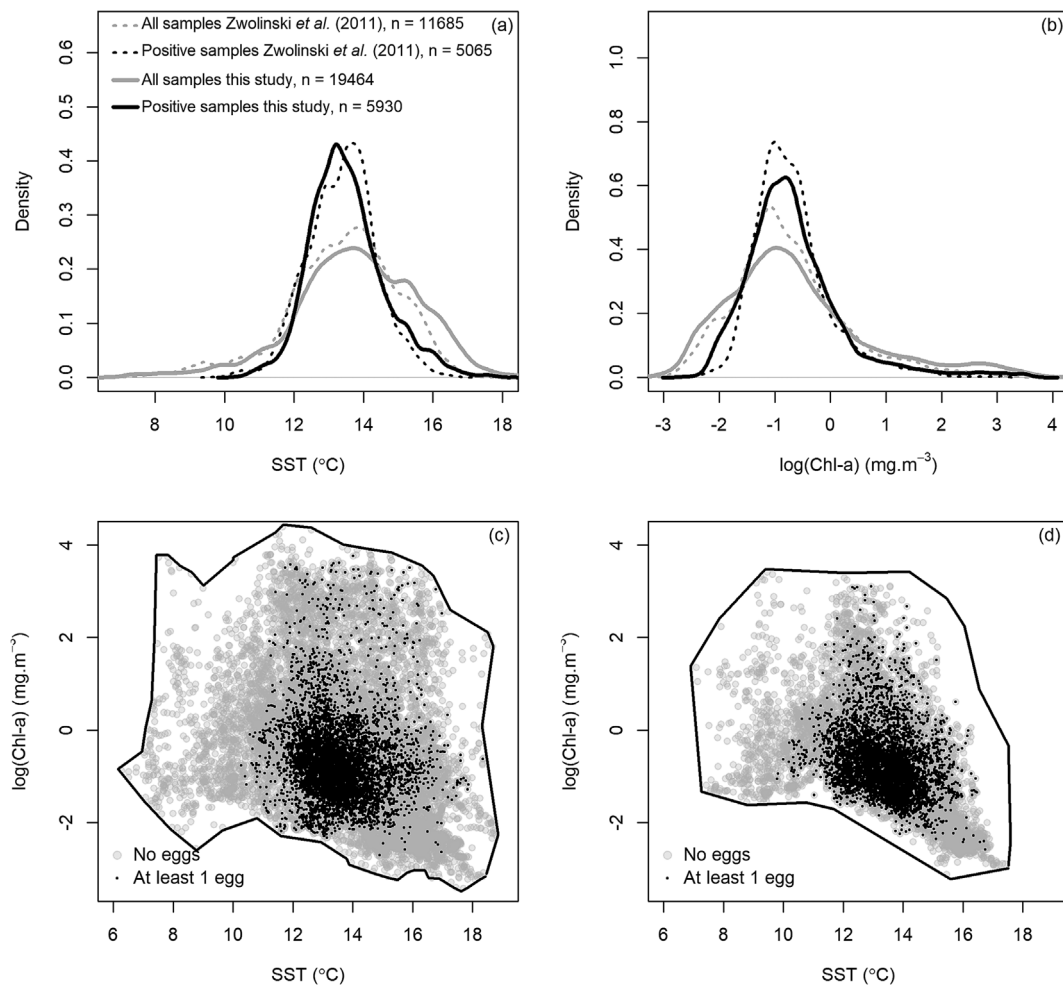


FIGURE 3 Empirical probability density functions for CUFES samples with Sardine eggs (black lines) and for all CUFES samples (gray lines) versus satellite-sensed SST (a), and log (CHL) (b) for the data used in (Zwolinski et al., 2011) (dashed) and the updated data set (solid) shown on Figure 2. Also shown are the bi-dimensional distribution of the CUFES samples used in this study (c) and those from Zwolinski et al. (2011) (d), each with polygons (black line) around the training data.

Sardine may be available at times to all, some, or none of the fisheries at Ensenada, San Pedro, and Monterey.

A-T survey estimates of the stock biomass of sardine age 1 year and older (e.g., Stierhoff et al., 2019; Zwolinski et al., 2016), landed biomass, and age composition from the fisheries, are input to a stock assessment model (e.g., Kuriyama et al., 2020). The Pacific Fisheries Management Council (PFMC) uses the model outputs to provide management recommendations. In the 2010s, the northern stock collapsed (Hill et al., 2015) likely due to a cyclical shift in environmental conditions that suppressed recruitment for multiple years (Zwolinski & Demer, 2012) along with increased fishery exploitation (Demer & Zwolinski, 2014b). During this period, as the stock abundance diminished, the latitudinal extent of its seasonal migration contracted. Since 2013, no Sardine were available off Vancouver Island, Canada, and since 2014, virtually no spring spawning from the northern stock was observed in the SCB (Figure 2). Since 2015, the results of the spring CalCOFI (Figure 2) and summer A-T surveys (Stierhoff, Renfree, et al., 2023, and references therein) suggest that the residual northern stock Sardine have restricted their seasonal migration between Northern California and Washington, despite the existence of suitable habitat beyond that range. The main US directed fishery was closed in 2015 and the stock was deemed overfished in 2019 (PFMC, 2021).

The habitat model has been used to understand and predict seasonal migrations (Demer et al., 2012), optimize survey-sampling effort (e.g., Zwolinski et al., 2016, 2011), interpret survey results (e.g., Stierhoff, Renfree, et al., 2023; Zwolinski et al., 2023), and attribute fishery landings to stocks (e.g., Demer & Zwolinski, 2014a). However, because the satellite-sensed *CHL* data needed to compute the habitat model (Zwolinski et al., 2011) was not available for the entire duration of the 2011 assessment model, a maximum $SST = 16.7^{\circ}C$ was adopted (Hill et al., 2014) to include an estimated 99.9% of the northern spawning stock landings, while potentially attributing some of the southern stock landings to the northern stock (Demer & Zwolinski, 2014a). Depending on the number of misclassified landings, inclusion of southern stock landings could positively bias the estimated fishery exploitation rates, skew the Sardine demographics, and alter the assessed biomasses (Demer & Zwolinski, 2014b). But because the reduced time span of current assessments models no longer requires landings prior to 2006 (e.g., Kuriyama et al., 2021), instead of the above-mentioned *SST* rule to separate catches, a habitat-based index can be used to inform the stock identity of both commercial catches and landings.

Since 2014, results of spring fish-egg surveys indicate that there has been virtually no Sardine spawning in the historical spawning area between Bodega Bay and San Diego, California (Figure 2). Since 2016, results of the summer A-T surveys show that there has been no northern stock habitat in the SCB and hence there were no attributions of northern stock Sardine in that area. Meanwhile, since 2018, the abundance and persistence of southern stock Sardine increased in US waters, mostly within the SCB (Table 1, Zwolinski et al., 2023). The latter coincides with more than a two-fold increase in annual catches in the Ensenada region between 2016 and 2021

(Enciso-Enciso, Nevárez-Martínez, et al., 2022). Collectively, these observations indicate that the northern stock biomass has diminished and its migration has been abbreviated, and the southern stock biomass has increased and expanded northwards more persistently. Sardine landed at Ensenada in 2020, in excess of 30,000 t, assigned to the northern stock using a habitat-associated threshold of $SST = 16.7^{\circ}C$ (Demer & Zwolinski, 2014a), was larger than the assessed biomass of age 1 years and older northern stock Sardine of 28,276 t (Kuriyama et al., 2021). Then, in spring 2021, no sardine were found in the historical northern stock habitat, and the sardine sampled in the SCB were almost exclusively nearshore (Zwolinski et al., 2023). Those fish had a modal standard length (L_s) of approximately 12.5 cm, indicating being age 0 and immature. Furthermore, their lengths were compatible with the lengths of the southern stock Sardine sampled in the SCB just 4 months later, in waters with *SSTs* conducive to southern stock presence (Stierhoff, Renfree, et al., 2023). These results confirm the year-round presence of southern stock Sardine in SCB waters.

These conflicting observations, between the low biomass estimated for the northern stock and the relatively large landings in Mexican waters attributed to that stock using an *SST* rule (Demer & Zwolinski, 2014a), prompted us to revisit the habitat model as a better way of attributing landings and A-T survey data to the northern stock

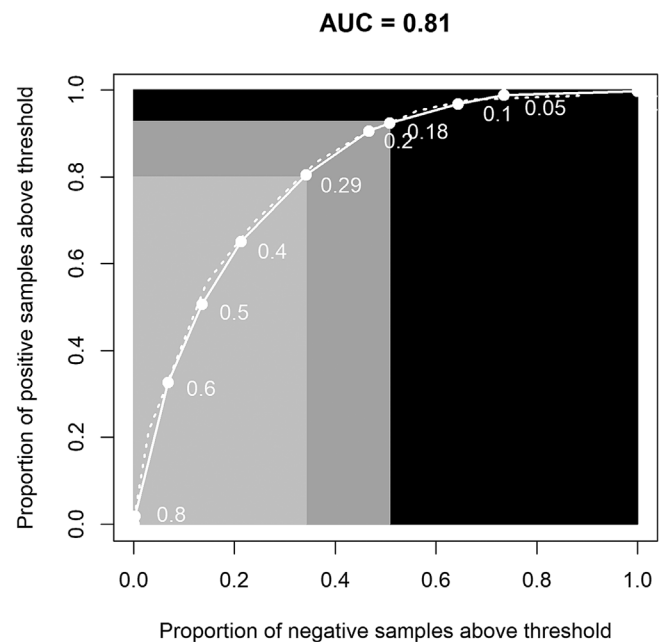


FIGURE 4 Receiver operating characteristic (ROC) curve for the updated habitat model (continuous line, $AUC = .81$), showing the sequential levels of fitted probability versus the proportion of false positives (negative samples classified as positive) and the proportion of true positives (positive samples classified as positive). The observations with probabilities higher than .29 and .2 contain 80% and 90% of all positive samples, respectively. The observations with probabilities .18 or higher contain approximately 92% of all positive samples and 95% of all eggs in the data set and exclude approximately 50% of the samples with no eggs. The dashed line represents the ROC curves for the original model ($AUC_{original} = .832$).

as discussed in Demer and Zwolinski (2014a). We update the habitat model using all of the available egg-presence data, 1998 through 2019, compare the original and updated models, and apply the updated model to attribute both A-T observations and fishery landings to the northern stock.

2 | METHODS

2.1 | Data collection

The potential habitat for northern stock Sardine was inferred from the oceanographic environment associated with their egg presence sampled during spring surveys, 1998–2019 (Crone et al., 2019; Demer et al., 2013; Hill et al., 2012; Hill et al., 2009, and references there in; Stierhoff et al., 2017; Zwolinski et al., 2012; Zwolinski et al., 2014; Zwolinski et al., 2016). The surveys had different sampling designs, but they all spanned the spawning grounds of northern stock Sardine in US waters (Figure 2). Fish eggs were collected with a continuous, underway fish-egg sampler (CUFES; Checkley et al., 2000), which pumps water from a depth of approximately 3 m and collects the plankton in a 200- μ m-mesh sieve. Sardine eggs were visually

identified and counted. The median CUFES sampling interval (CSI) was generally 30 min, corresponding to 5–6 miles at a ship speed of 10–12 knots. The CUFES samples were spatially and temporally indexed by their central geographic positions and times. The CUFES data were accessed through NOAA's Environmental Research Division Data Access Program (ERDDAP, <https://coastwatch.pfeg.noaa.gov/erddap/index.html>).

All of the oceanographic data were obtained from ERDDAP using the routines in the packages `rerddap` (Chamberlain, 2021) and `rerddapXtracto` (Mendelssohn, 2021) for R (R Core Team, 2022). SST and CHL data were retrieved in $.2^\circ$ latitude by $.2^\circ$ longitude areas around each CUFES sample. When available, 8-day composite images were used, providing 78% of the data. For the samples for which no 8-day composite information was available due to cloud coverage, monthly composites were used. From 1998 to 2002, CHL data were retrieved from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) satellites, and SST from NOAA's AVHRR instruments (Pathfinder). From 2003 onwards, both SST and CHL data were sourced from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellites. The satellite-sensed SST is accurate to approximately $\pm 1^\circ\text{C}$, based on a comparison to measures of surface-water temperatures taken ship-board during egg surveys (Figure S1).

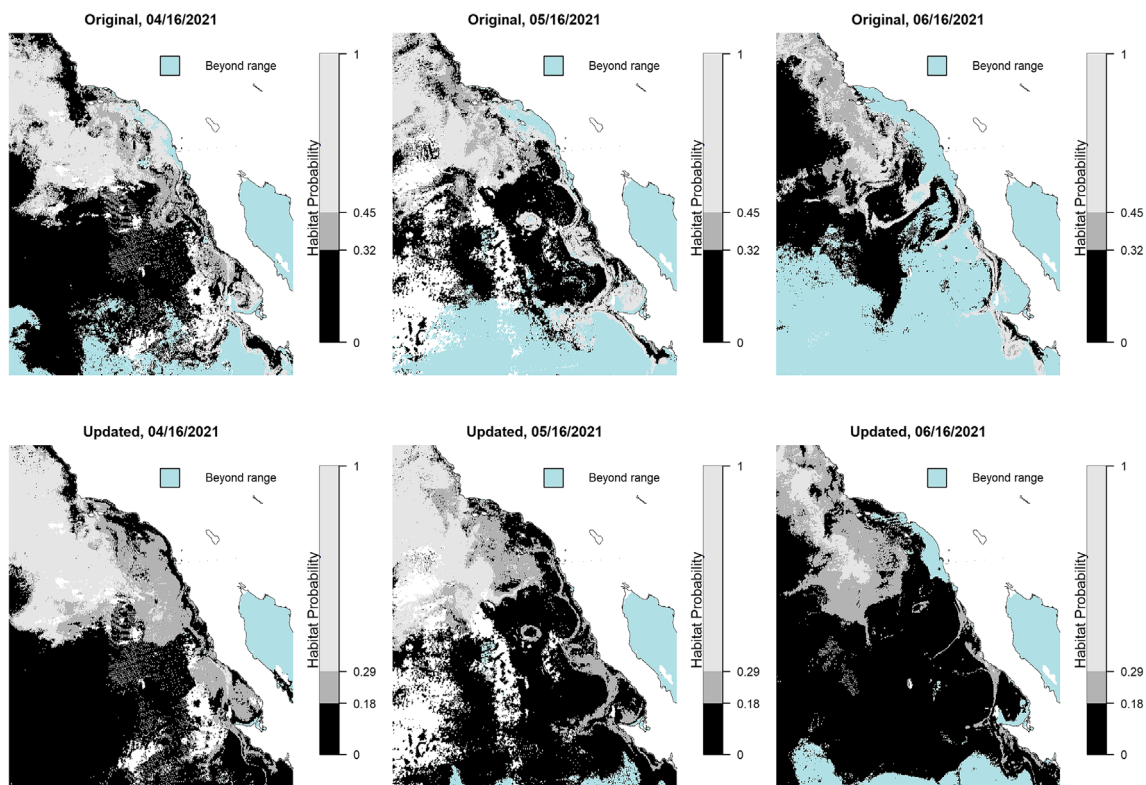


FIGURE 5 The original (top) and updated (bottom) model results showing the spring evolution of northern stock Sardine habitat during 2021. For the original model, the habitat probability intervals $[0, .32]$, $[.32, .45]$, and $[.45, 1]$ contain 10%, 10%, and 80%, respectively, of all the positive samples from 1998 to 2009. For the updated model, the habitat probability intervals $[0, .18]$, $[.18, .29]$, and $[.29, 1]$ contain 8%, 12%, and 80%, respectively, of all the positive samples from 1998 to 2019 (cf. Figure 4). Both sets of intervals were shown as black, dark gray, and light gray regions, respectively. Some of the environment data are beyond the fitted data ranges (light blue), and some areas have no satellite-sensed environmental data (white).

2.2 | Data analysis

2.2.1 | Model fitting

The model of potential habitat for northern stock Sardine was updated using the method described below and further detailed in Zwolinski et al. (2011). The presence of Sardine eggs in a CUFES sample was fit as a function of a two-dimensional (2-D) smoother of SST and the natural logarithm (\ln) of CHL and the addition of a one-dimensional (1-D) smoother of CSI to account different sampling intensities. The linear predictor was linked to the response variable via the logit link function:

$$\ln\left(\frac{\hat{p}}{1-\hat{p}}\right) = te(SST, \ln(CHL)) + s(CSI), \quad (1)$$

and the model was fit using the gam function from the mgcv package (Wood et al., 2016) for R. The 2-D smoother for SST and CHL was fit using the tensor-product smooth function, and the 1-D smoother for CSI was fit using the default spline basis function. The former allows the fitting of variables measured at different scales within the same 2-D function (Wood, 2006). The complexity of the smoothers in the GAM was adjusted by varying the dimensions of the basis functions.

Models with too many parameters fit the training data set well but failed on out-of-sample performance (Zwolinski et al., 2011). A model with the best balance between overfitting and prediction resulted from starting values of $k = 6$.

The utility of the habitat model for predicting northern stock Sardine distribution is explored by analyzing the shape of the receiver operating characteristic (ROC) curve (Hanley & McNeil, 1982). For a binary classifier informed from a continuous probability response, an ROC curve is a plot of the model's sensitivity (the proportion of positive outcomes whose fitted probabilities are above a certain discriminant threshold: true positives) versus the model's 1-specificity (the proportion of negative outcomes below the same discriminant threshold: true negatives). This relationship is summarized by the area under the ROC curve (AUC). An AUC of .5 indicates that the classifier does not perform better than random, and a value of 1 indicates that there is at least one probability threshold that results in a sensitivity of 1 and a 1-specificity of 0.

2.2.2 | Attributing landings and biomass

To attribute landings from Ensenada and San Pedro to the northern stock, the putative fishing regions (Figure 1) were classified as

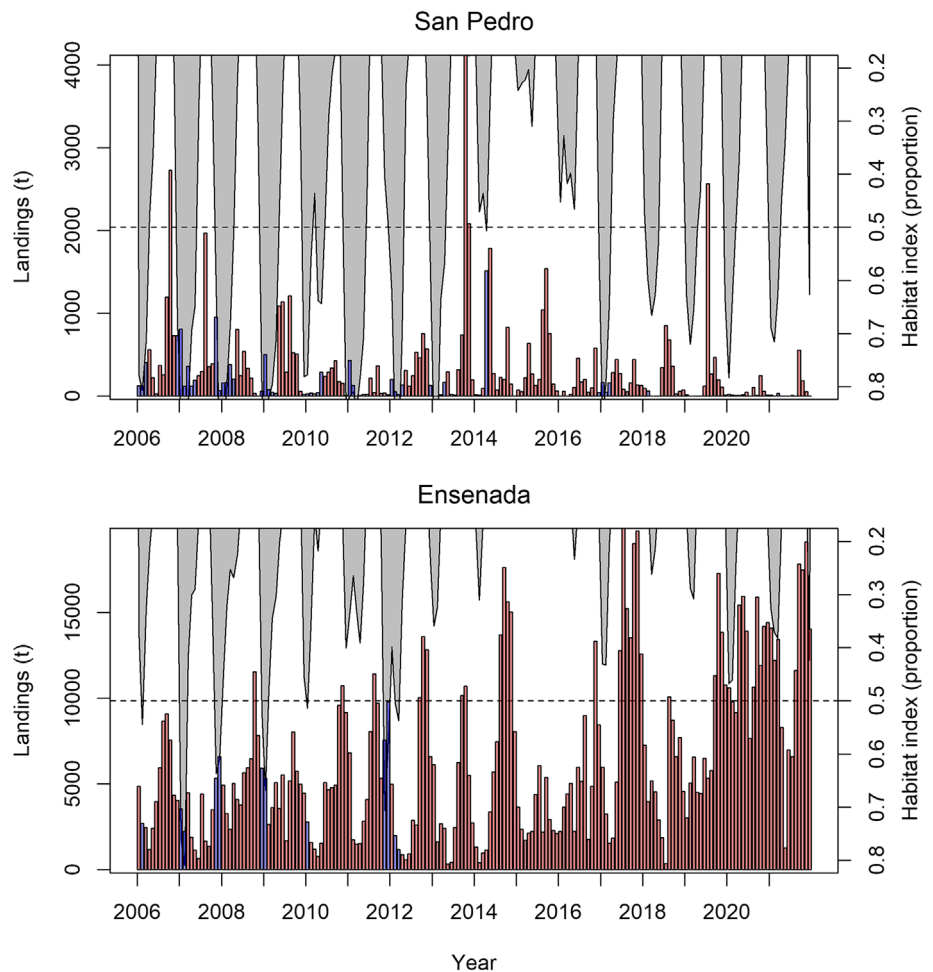


FIGURE 6 Landings at San Pedro (top panel) and Ensenada (bottom panel) attributed to the northern stock (blue) when more than 50% of the fishing area (Figure 1) includes northern stock habitat with a probability of .18 or more (gray), else the landings are assigned to the southern stock (red). Since 2015, the US sardine fishery has been closed, except for landings by the bait fishery, through experimental fishing permits, and from incidental takes.

“northern stock” based on a fishing-area index that uses the output of the updated habitat model and a predetermined probability threshold above which monthly landings are considered to be from the northern stock. The probability threshold was chosen to be sufficiently high enough to exclude all of the 2020 and 2021 Ensenada landing, when only southern stock Sardine were thought to be available to the Mexican fisheries, but low enough to include at least 90% of the Sardine eggs in the training set. The fishing-area index is a three-point running mean of 8-day-composite satellite images, from the 1st and 16th day of each month. If more than half of the fishing area includes a probability greater than the threshold, then all of the landings there that month are attributed to the northern stock. When the proportion of the fishing area suitable for the northern stock is less than 50%, all of the monthly landings are assumed to be from the southern stock. For Ensenada, the original area (Demer & Zwolinski, 2014b) was revised to better represent the actual fishing area. Based on the observed distributions of Sardine in 2021 (Stierhoff, Renfree, et al., 2023), the area extends 5 nmi from the coast (Figure 1), and north and south to the expected range of a day trip. The other

putative fishing areas around San Pedro were unchanged due to a lack of precise information about contemporaneous fishing locations (Figure 1).

For each summer from 2012 to 2022, maps of updated habitat were overlaid with the locations of Sardine catches in trawls from the A-T surveys. These catches were attributed to the northern or southern stock using the updated habitat model, and it was noted if their original attribution changed, either from an improved spatial-temporal match of the survey data to the modeled habitat or due to differences in the original versus the updated habitat model. Also, to add support to the stock attributions, the L_5 from the northern stock were compared to those from the complement southern stock to investigate if the habitat informed-separation is also matched with a disjoint length distribution. Finally, in 2021, coast-wide ages for sardine were available from SWFSC collaborative A-T survey (see Renfree et al., 2022, for details) and the demographic structure of both groups was investigated for signs of different growth patterns by comparing the respective lengths-at-age using the Wilcoxon rank sum test.

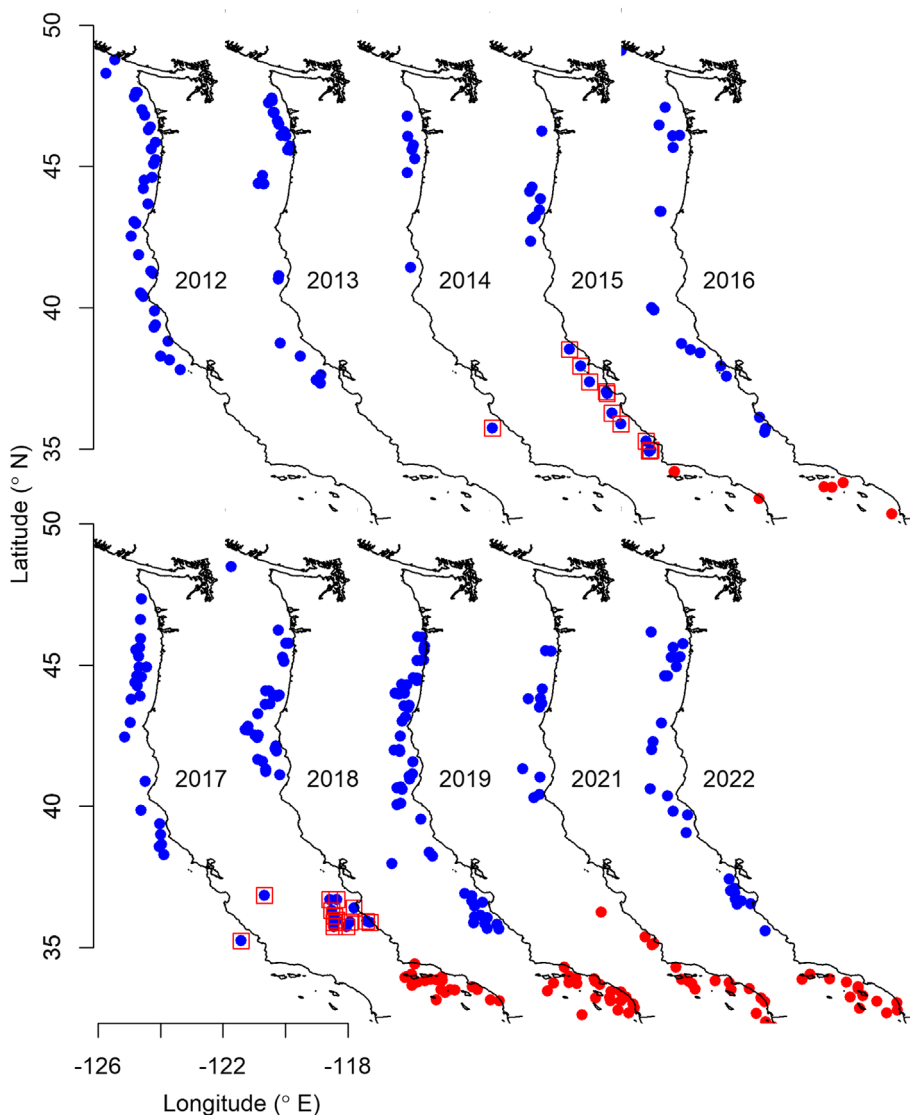


FIGURE 7 Locations of trawl catches including Sardine during A-T surveys, 2012–2022, attributed to the northern (blue) and southern (red) stock, loosely using the original northern stock habitat model (dot), or re-classified as not northern stock, and by complement as southern stock, upon further inspection using the updated habitat model (red square; see Figure S4). The SCB was not sampled in summer 2017. The surveys in 2021 and 2022 spanned Mexican waters south of the depicted area and all the Sardine sampled there were attributed to the southern stock.

3 | RESULTS

3.1 | Updated potential habitat model

Positive egg samples were contagiously distributed (Figure 2) in areas with $11.5 < SST < 15.5^{\circ}\text{C}$ and $.18 < CHL < 3.2 \text{ mg m}^{-3}$ and, consistent with the original data set, mainly in water where $12 < SST < 14.5^{\circ}\text{C}$, and $.3 < CHL < 1 \text{ mg m}^{-3}$ (Figure 3). Lower $SST (< 11.5^{\circ}\text{C})$ with higher $CHL (> 3.2 \text{ mg m}^{-3})$ is indicative of freshly upwelled waters and defines the inshore limit of northern stock Sardine eggs. Offshore, the presence of eggs is bounded by oceanic water with higher $SST (> 15.5^{\circ}\text{C})$ and lower $CHL (< .18 \text{ mg m}^{-3})$.

The updated data set (Figure 3) and model (Figure S2) capture the spawning distribution over a broader environmental space relative to the original counterpart (Figure 3). The updated and original models (Figure S2), however, capture the same general relationship between spring-spawning Sardine and their habitat. The updated model fitted a maximum probability of Sardine presence at approximately $SST = 13^{\circ}\text{C}$, and $\ln(CHL) = -.7$ ($CHL = .5 \text{ mg m}^{-3}$), very similar to the

original model (Figure S2). The updated model (Figure S2) had an explanatory AUC of .81 (Figure 4).

Compared to the original model, the probability thresholds for the updated model are lower. For example, the ROC curve for the updated model (Figure 4), evaluated at probability thresholds of .29 and .18, delimits the boundaries of the habitat containing at least 80% and 92% of the CUFES samples with northern stock Sardine eggs, respectively. To compare maps of the original and revised habitat models, .29 was identified as the probability threshold that contains 80% of the positive Sardine egg samples and 35% of the samples with no eggs. Areas defined by the probability thresholds [.29, 1] and [.18, .29], approximating the “optimal” and “good” habitat classes defined in Zwolinski et al. (2011), were mapped for the spring months of 2021 (a cold year) and 2015 (a warm year) and compared to the original model. Using these probability thresholds, the updated model shows higher definition in the monthly evolution of northern stock habitat in 2021 compared to the original model, particularly in transition areas such as the SCB (Figures 5 and S3), where the SST above 16°C could still be assigned high probability of egg presences in the

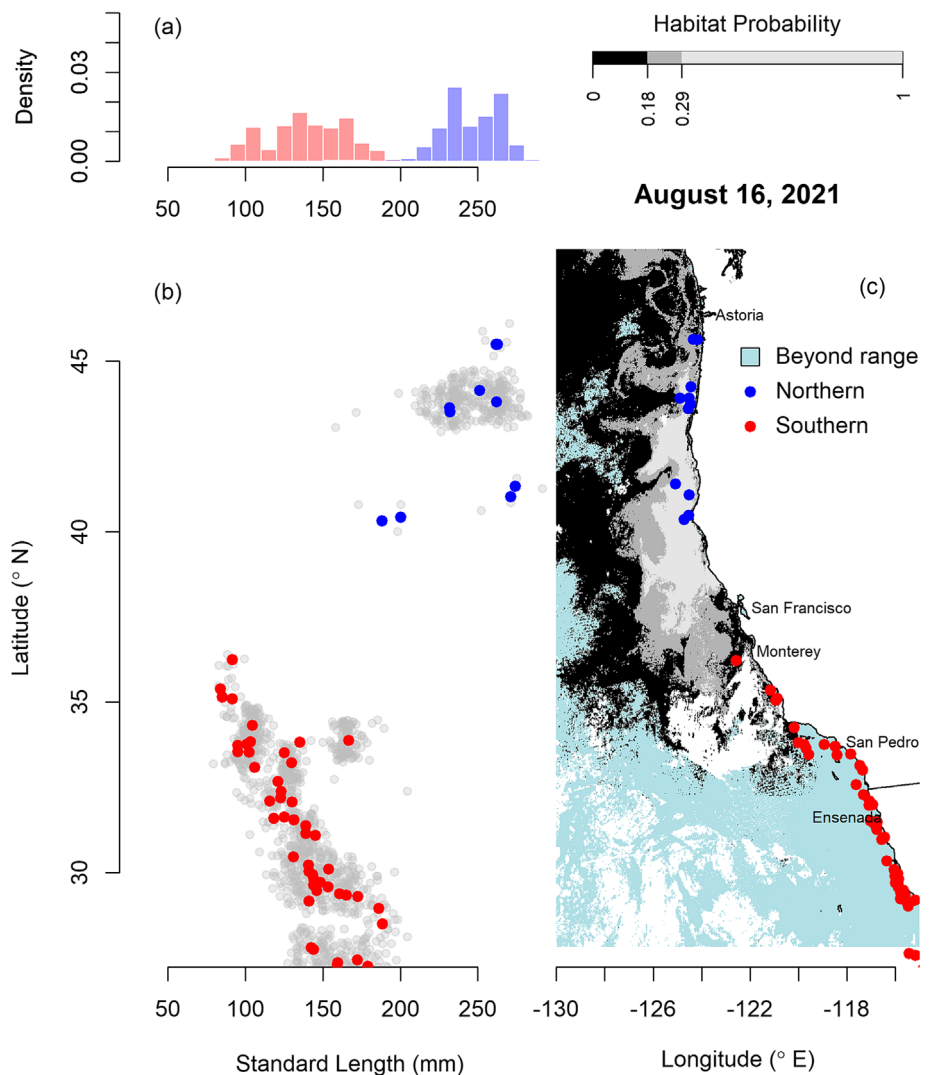


FIGURE 8 During summer 2021: (a) histogram of Sardine standard lengths for the northern (light blue) and southern (pink) stocks sampled from FSV Reuben Lasker and Mexican Research Vessel Dr. Jorge Carranza Fraser (see Renfree et al., 2022 for details on the sampled area by the two vessels); (b) the individual length measurements for the two stocks (gray points jittered around the respective latitude and length) and the actual centroids of the length and latitude distributions for each Sardine catch (blue for northern stock and red for southern stock); and (c) catch locations overlaid on a map of the updated habitat model centered at August 16. Some of the environment data is beyond the fitted data ranges (blue), and some areas have no satellite-sensed environmental data during the 8-day average (white).

presence of mid-range *CHL* (Figure S3). The approximately 8% of false-negatives below the .18 probability threshold are spread across all years, without a spatial pattern (Figure 2), indicating that no single year is heavily influential or uninformative in the model fit. The samples with probabilities above .18 contained around 50% of all negative samples, with that number being largely dominated by the latter years, when the northern stock Sardine biomass was low.

3.2 | Attributing landings and biomass

The fishing area index using a habitat probability of .18 classified all 2020 and 2021 landings from Ensenada as non-northern stock (Figure 6). Simultaneously, the .18 probability threshold retained 92% of the positive samples in egg data set (Figure 4), which corresponds to 95% of all eggs (not shown). Therefore, .18 was selected as the probability cutoff above which Sardine, both from commercial catches or scientific A-T surveys, were considered to belong to the northern stock. The fishing area index indicates that northern stock was captured in Ensenada only from 2006 through 2012. In San Pedro, landings from 2006 to 2014 and 2017 are attributed to the northern stock each winter and spring (Figure 6). In 2015 and 2016, during a marine heat wave (Weber et al., 2021), the proportion of northern stock habitat in the San Pedro fishing area was relatively low.

Using probability thresholds of .32 from the original model, which corresponds to the classification of good plus optimal habitat, and the optimized probability of .18 from the updated model, the attributions of Sardine caught in A-T surveys in US waters between 2012 and 2022, changed in 4 of 10 summer surveys (Figure 7). Those that changed are located off Central California, where the attributions, irrespective of the model used, are sensitive to rapid temporal variability of the environmental data, particularly SST. Furthermore, the cloud cover in this area often limits the availability of the environmental data. Prior to 2021, incomplete habitat information due to cloud coverage and the lack of supporting length and age evidence may have led to uncertain stock differentiations (Figure S4). The biomass affected by that uncertainty is small, however. Two of the re-attributions, in 2014 and 2017, did not affect the original biomass estimates. The other two, in 2015 and 2018, were reduced by 3.0% and 7.2% of the originally estimated northern stock biomass, respectively (Table 1).

The habitat-model attributions of A-T catches are often supported by statistically significant differences in L_s for the northern versus southern stock (Figures 8 and S4). In summer 2021, for example, the stocks are separated by nearly 500 km, and L_s have disjoint distributions, with the lengths of the southern stock decreasing with increasing latitude. The lengths-at-age (Figure 9), $N = 283$ and $N = 935$ from the northern and southern stocks, respectively, show significant smaller lengths (p value $< .05$) for ages 1, 2, and 3 years of the southern stock (ages 0 and 4 years not tested). The ages of the northern stock Sardine extend to 11 years, but only to 4 years in the southern stock, and the northern stock appears to have a significantly larger asymptotic length.

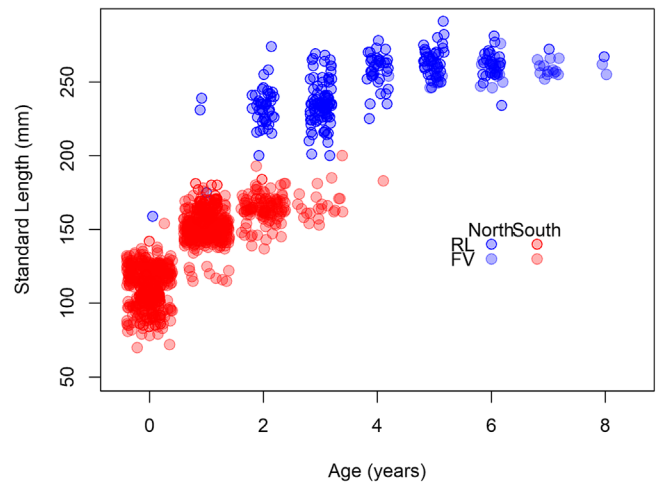


FIGURE 9 During summer 2021: the lengths-at-age for the northern (blue, $n = 283$) and southern (red, $n = 935$) stocks sampled using Reuben Lasker (RL) and two fishing vessels (FV), Lisa Marie north of San Francisco and Long Beach Carnage to the south (see Renfree et al., 2022, for details on the sampled area by the various vessels). The southern stock shows significant smaller lengths than the northern stock for ages 1, 2, and 3 years (p value $< .05$). Note: The age data were randomized around the discrete age for easier visualization.

4 | DISCUSSION AND CONCLUSION

Our observations of two groups of Sardine geographically separated and differentiated by oceanographic habitat, demographics, and growth patterns (Figure 8), agree with the long-standing hypothesis of two stocks off the Pacific Coast of the US and Mexico (e.g., Félix-Uraga et al., 2004; MacCall, 1979; Murphy, 1966; Smith, 2005; Vrooman, 1964). To validate the habitat model for the northern stock (Zwolinski et al., 2011) during the current period of low northern stock biomass, we updated the original habitat model for the northern stock using all available data on Sardine-egg presence and absence, and associated environmental conditions, from 1989 to 2019.

The values of *SST* and *CHL* associated with Sardine presence in this study are similar to those described previously (Zwolinski et al., 2011), but the addition of more recent data has served to better define the habitat boundaries, particularly at higher *SST* and *CHL*. The clearer boundaries of the updated model more accurately attribute the survey biomass and fishery landings, notably in the SCB and at Ensenada, respectively, especially during recent years when the residency and biomass of the southern stock of Sardine has increased in these areas (Enciso-Enciso, Nevárez-Martínez, Sánchez-Cárdenas, Salcido-Guevara, et al., 2023; Stierhoff, Renfree, et al., 2023; Zwolinski et al., 2023). As shown, the updated habitat model can be used to attribute both biomass from surveys (Figure 8) and landings (Figure 6) to their respective stocks. An optimized probability threshold rejects all northern stock landings at Ensenada in 2020 and 2021, when there were no northern stock Sardine south of Point Conception.

The well-defined northern stock habitat appears to impose a physical separation between the adult sardine that live within the environmental confines of the habitat and those that live outside it and presumably belong to the southern stock (Stierhoff, Renfree, et al., 2023; Zwolinski et al., 2023). This separation may explain the reported differences in phenotypical traits such as growth patterns (this study; Anon, 1952; Felin, 1954; Murphy, 1967) and otolith shape (Félix-Uraga et al., 2005). Southern stock Sardine, which are smaller for their age or “stubbier” than northern stock Sardine (this study; Anon, 1952), principally spawn off southern Baja California (Smith, 2005), but have been seasonally present off southern California (Demer & Zwolinski, 2014a; Felin, 1954; Phillips, 1948), as expected from the seasonal warming of the SCB.

The northern and southern stocks occupy SSTs centered at 13°C and 19°C, respectively, and an SST between 16°C and 17°C separates the two stocks (Félix-Uraga et al., 2004; Weber & McClatchie, 2010; Zwolinski et al., 2011). Because this transition temperature is unlikely to induce a significant physiological response (Pribyl et al., 2016), their preferences for different environmental conditions may be learned from water masses in which they have been entrained in as juveniles. Then, without a hard physical or physiological barrier, some mixing of the stocks may occur off Southern California (Anon, 1952; Clark & Marr, 1955; Murphy, 1967). Significant differences in vertebral counts, a meristic characteristic that might indicate reproductive isolation (Cadrin, 2020), were observed between young Sardine caught off California versus Southern Baja California. However, those counts from the adult population were not significantly different (Clark, 1947) suggesting that there may have been some post-recruitment exchange between the two reproductive groups. Murphy (1967) also reported mixing between the two Sardine stocks (identified as races or subpopulations in that publication) after the collapse of the northern stock in the mid-1900s.

Mixing, when it occurs, might begin with non-migrating juvenile Sardine (McDaniel et al., 2016). Young Sardine from either stock that recruit to the SCB or waters off Central California may experience alternations in habitat and encounter adults from the associated stocks. Therefore, depending on the timing of recruitment and habitat alternation, the recruits may school and mix with migrating adults from either stock. Such admixing is low when the northern stock is abundant (Murphy, 1967). After 2014, following the collapse of the northern stock, five of seven surveys (Figure S4) have disjoint length distributions for the northern and southern stocks. However, in 2016 and 2019, the lengths distributions partially overlap. Because this could occur due to either mixing, or spawning time and differences in growth, additional analyses of demography are needed. Periodic sampling from commercial landings or frequent scientific surveys may provide information on the heterogeneity in life history traits indicative of stock separation, whether of genotypic or phenotypic origin (Cadrin et al., 2023; Smith, 2005).

Presently, northern stock Sardine have a well-defined oceanographic habitat, but this may change. Therefore, as noted in Zwolinski et al. (2011), if northern stock Sardine are observed outside of their

habitat in improbable quantities, or if suspected southern stock Sardine are sampled within the modeled northern stock habitat, or both, further investigation is warranted. However, unless or until such a change in the state of the ecosystem is detected, Sardine sampled in the A-T surveys can be classified by using the updated model of northern stock potential habitat and its complement. These attributions should be corroborated by evaluations of the latitudinal separation of samples from the two stocks, and differences in their respective length and age-at-length distributions, and consistency in their length distributions and those projected from past observations. Moreover, landings may be attributed to the northern stock using an index derived from the updated habitat model, evaluated in the fishing areas. Repeated for emphasis, the accuracy of these attributions will depend on the temporal and spatial coincidence of the SST and CHL data, and the catches and the attributions should be corroborated by metrics of phenotypic variation.

AUTHOR CONTRIBUTIONS

David A. Demer: methods conceptualization and writing. **Juan P. Zwolinski:** methods conceptualization, data curation and analysis, and writing.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest to report.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in CalCOFI Continuous Underway Fish-Egg Sampler at <https://coastwatch.pfeg.noaa.gov/erddap/index.html>. These data were derived from the following resources available in the public domain: - <https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMBsstd8da>, <https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMBsstd8day.html>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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