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 seasonally located off the west coasts of Canada, US, and Mexico, acoustic-trawl (A-T) surveys documented an increase in the presence and persistence of the presently larger southern stock off Southern California. This ecological development renewed attention to the modeled northern-stock potential habitat [Zwolinski et al., 2014, ICES JMS 68:867-879] and associated range of sea-surface temperature [Demer and Zwolinski, 2014, ICES JMS 71:328-335] used to apportion the A-T survey data and monthly fishery landings to the two stocks, respectively. Here, we update the probabilistic generalized-additive-model of potential habitat with data on sardine-egg presence or absence and concomitant satellite-sensed sea-surface temperature and chlorophyll-*a* concentration through 2019, and apply the new model to attribute the A-T observations and fishery landings data to the northern or southern stock. The addition of recent data to the model resulted in more significant and temporally invariant relationships between northern stock Sardine eggs and these oceanographic variables, which improves the accuracy and spatial precision of the attributions of biomass and catch to their respective stocks. The accuracy of the attributions is critically dependent on the temporal and spatial coincidence of the environmental data and the survey or catch data, and should be corroborated with other distinguishing stock characteristics such as spatial separation, length distribution, growth rate, and phenotypes.

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Introduction

A fish stock, or sub-population, is a geographically or otherwise distinct part of a fish population, between which there is little exchange, usually with a particular spawning area and migration pattern, and is subject to a distinct fishery (Blackhart et al., 2006). Fish stocks must have independent reproductive processes, but only on time scales relevant for fisheries management (Berger et al., 2012). 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 coastal pelagic species comprising northern (or cold), southern (or temperate), and Gulf (or warm) stocks (Smith, 2005) (**Figure 1**).

The northern stock refers to sardine that, when abundant, spawn overwhelmingly in the spring off Southern and Central California (**Figure 1**) and sporadically as far south as Northern Baja California, Mexico (Valencia-Gasti et al., 2018), feed as far north as Canada in summer, and return south, mainly offshore, west of 130 °W, in late fall and winter (Clark and Janssen Jr, 1945). The southern stock resides mostly off Baja California, and migrates seasonally, typically synchronously, and separately from the northern stock (Smith, 2005), recurrently entering the Southern California Bight (SCB) during the summer and occasionally migrating to waters off

Central California (**Figure 1**). The Gulf stock seasonally migrates from the Gulf of California to Southern Baja California (Félix-Uraga et al., 2005).

Landings of northern stock sardine historically occur in five regions: Vancouver Island, Canada; Washington and Oregon, Monterey Bay and San Pedro, California; and Ensenada, Mexico (**Figure 1**). The exact locations of the catches around each port are generally unreported or proprietary. The movements of northern stock sardine between these regions is explained by the seasonal availability of suitable northern stock habitat (Demer et al., 2012).

The northern stock habitat is represented by a generalized additive model (GAM) trained on the presence of sardine eggs in samples taken off Southern and Central California during spring 1998 through 2009 (Zwolinski et al., 2011). It is principally characterized by a non-linear combination of satellite-sensed sea-surface temperature (*SST*) and chlorophyll-*a* concentrations (*CHL*). At least 90% of the sardine presences are in the ranges $11.8°C \leq SST \leq 15\ °C$, and $0.2 \leq CHL \leq 1.9$ mg m^{-3}. The model also includes the gradient of sea-surface height to better define the westernmost extent of the potential habitat, but this parameter was less informative than *SST* and *CHL* and is omitted from the operational model (hereafter original model) (https://coastwatch.pfeg.noaa.gov/erddap/griddap/sardine_habitat_modis.graph).

The habitat model indicates that northern stock sardine avoid recently upwelled coastal and oligotrophic oceanic waters, and prefer areas with curl-driven upwelling that have higher zooplankton biomass, lower *CHL*, and sufficiently low turbulence to allow for egg and larval retention (Bakun and Parrish, 1982). This habitat is typically at its northernmost extension during late summer and early fall when historically, peak catches occur off Oregon, Washington and Vancouver Island (Zwolinski et al., 2011). The habitat then recedes south, attaining its southernmost extension in the spring, allowing 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 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 through spring, northern stock sardine may be available at times to all, some, or none of the fisheries at Ensenada, San Pedro and Monterey (**Figure 1**).

When northern stock sardine are landed, the catch biomass and age composition, along with A-T survey estimates of the stock biomass (e.g., Stierhoff et al., 2019; Zwolinski et al., 2016), are input to a stock assessment model (e.g., Kuriyama et al., 2020) and the model outputs are used by the Pacific Fisheries Management Council (PFMC) to manage the stock.

In the 2010s, the northern stock collapsed (Hill et al., 2015), as predicted, due to a cyclical shift in environmental conditions that suppressed recruitment for multiple years (Zwolinski and Demer, 2012) along with increased fishery exploitation (Demer and Zwolinski, 2014b). The fishery was closed in 2015 (PFMC, 2015) and the National Marine Fisheries Service deemed the stock overfished in 2019 (PFMC, 2021). During this period, as the stock abundance diminished, the latitudinal extent of its seasonal migration contracted. Since 2013, no sardine were landed 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 summer A-T surveys suggest that the residual northern stock sardine mostly remained off Oregon and Washington (Stierhoff et al., 2023 and references therein). The model predictions reflect the probability of sardine presence, although the proportion of the habitat utilized by sardine varies with the stock size (Zwolinski et al., 2011).

The potential habitat model has been used to: understand and predict seasonal migration dynamics (Demer et al., 2012); optimize survey-sampling effort (e.g., Zwolinski et al., 2016; Zwolinski et al., 2011); interpret survey results (e.g., Stierhoff et al., 2023; Zwolinski et al., 2023); and attribute fishery landings to stocks (e.g., Demer and Zwolinski, 2014a). However, because the satellite-sensed *CHL* data needed to compute the potential habitat model (Zwolinski et al., 2011) was not available for the entire duration of the 2011 assessment model, a maximum $SST = 16.8$ °C was adopted (Hill et al., 2014) to include 99.9% of the northern stock landings, while potentially attributing some of the southern stock landings to the northern stock (Demer and 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 length distributions, and alter the assessed biomasses (Demer and Zwolinski, 2014b).

In addition to these uses of the potential habitat model, Zwolinski et al. (2011) posited that the accuracy of the model predictions may also serve as an indicator of changes in the state of the ecosystem, or 'regime shifts'. For example, northern stock sardine outside, or southern stock sardine within the modeled northern stock habitat, or both, could indicate changes in habitat preferences. This theory was recently tested.

Since 2014, results of the spring fish-egg surveys indicate that there has been virtually no sardine spawning in the historical spawning area between Bodega Bay and San Diego, CA (**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 the southern stock of sardine increased in US waters, mostly within the SCB (**Table 1**). Collectively, these observations indicate that the northern stock biomass has diminished, the southern stock biomass has increased, and both stocks have shifted northward in the survey area.

Despite these changes, the biomass of sardine landed at Ensenada in 2020, in excess of 30,000 t, assigned to the northern stock using a habitat-associated threshold of $SST = 16.8$ °C (Demer and Zwolinski, 2014a), was larger than the assessed biomass for the entire stock, 28,276 t (Kuriyama et al., 2021). Then, in spring 2021, in the SCB, when and where the northern stock sardine historically tend to spawn, the sampled sardine were almost exclusively nearshore in habitat that was bad or unsuitable for the northern stock (Zwolinski et al., 2023). Those fish were small (modal $L_s \sim 12.5$ cm), likely age-0 and immature, and not spawning. Furthermore, their lengths, growth-projected to summer 2021, matched the lengths of the southern stock sardine sampled in the SCB and not the northern stock sardine sampled farther north (Stierhoff et al., 2023).

These observations renewed interest in the potential habitat model and its use for attributing survey observations and fishery landings to the northern versus southern stock. Since the original model in Zwolinski et al. (2011), has northern stock sardine altered its habitat preference? Should the habitat model be used instead of a habitat-derived *SST* threshold to more accurately attribute landings, as discussed in Demer and Zwolinski (2014a)? To answer these questions, we update the potential 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, else to the southern stock.

Methods

Data collection

The potential habitat for the northern stock of Pacific 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 putative spawning grounds of the northern stock of Pacific Sardine (**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 ~3 m and collects the plankton in a 200-mm-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 NOAAs Environmental Research Division Data Access Program (ERDDAP, https://coastwatch.pfeg.noaa.gov/erddap/index.html).

SST and *CHL* data were retrieved in 0.2°-latitude by 0.2°-longitude areas around each CUFES sample. When available, 8-day composite images provided most (78%) of the data, else the remainder (22%) was from monthly composites. From 1998-2002, the data were from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) satellites. Subsequently, the data were from Moderate Resolution Imaging Spectroradiometer (MODIS) satellites. 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). The satellite-sensed *SST* is accurate to approximately ±1°C, based on a comparison to measures of surface-water temperatures taken shipboard during egg surveys (**Figure S1**).

Data analysis

Model fitting

The model of potential habitat for the northern stock of sardine was updated using the method described below and further detailed in Zwolinski et al. (2011). The presence of sardine in a CUFES sample was fitted 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:

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

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 smoother (Wood, 2006). The complexity of the smoothers in the GAM were 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 sardine distribution is explored by analyzing the shape of the receiver operating characteristic (ROC) curve (Hanley and McNeil, 1982). For a binary classifier, 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) vs. 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 0.5 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.

Attributing Landings and Biomass

To attribute landings from Ensenada and San Pedro to the northern or southern stock, the putative fishing regions (**Figure 1**) were classified as "northern stock" based on an area index that uses the output of the habitat model and a predetermined probability threshold above which a catch is considered to be from the northern stock. That probability was selected iteratively as the lowest possible in the habitat space in order to maximizes inclusion of the historical northern stock habitat and sardine egg abundances in the training set, while excluding all of the landings of Pacific sardine at Ensenada in 2020 and 2021, when only southern stock sardine were available to the Mexican fisheries.

The optimal probability was found to be 0.18. This threshold correctly classifies 92% of the positive samples in the training set (**Figure 4**), which corresponds to 95% of all eggs, and therefore of the approximate spawning stock biomass. Also, the probability threshold of 0.18 correctly classifies ~50% of the samples with no eggs.

The area index was built from bi-monthly, 8-day satellite composite images obtained on the 1st and 16th day of every month. The final area index for a given month was calculated as the three-point running mean of the bimonthly composites of the area within a fishing region with a probability higher 0.18. If the proportion of the area was higher than 0.5, then all of the landings there that month were attributed to the northern stock, else, they were attributed to the southern stock. For Ensenada, the original area (Demer and Zwolinski, 2014b) was revised to better represent the actual fishing areas based on the 2021 and 20221 observations of nearshore distribution of sardine. The revised Ensenada area extends 5 nmi from the coast, extending to the expected range of a day trip. The other putative fishing areas, e.g., around San Pedro, were unchanged, due to a lack of precise information about contemporaneous fishing areas (**Figure 1**).

For visualization purposes, an additional probability of 0.29 was identified as the threshold above which 80 % of all the positive sardine egg samples are contained, which also correctly classifies ~65% of the samples with no eggs. The probability interval [0.29, 1] is equivalent to the optimal habitat defined in Zwolinski et al. (2011). Visually, the interval [0.18, 0.29[approximates the original model's 'good' habitat class.

Areas corresponding to these probability thresholds were mapped for each month of each year, 2012 through 2022, and compared to those from the original model. Also, for that period, the locations of sardine catches from the A-T surveys were mapped according to their stock attribution, and highlighted if the 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. Then, to corroborate the attributions, the distributions of sardine standard length (L_s) were compared for fish attributed to the two stocks for the period from 2012 to 2021, with the exception

of summer 2017 when the SCB was not surveyed. For 2021, comparison of the two stocks were also made for age-at-length.

Results

Updated Potential Habitat Model

Positive egg samples were contiguously distributed (**Figure 2**) in areas with $11.5 < SST < 15.5$ °C and $0.18 < CHL < 3.2$ mg m^{-3} and, consistent with the original data set, mainly in water where $12 \leq SST \leq 14.5$ °C and $0.3 \leq CHL \leq 1$ mg m^{-3} (**Figure 3**). Lower *SST* (< 11.5 °C) with higher *CHL* (> 3.2 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 °C) and lower *CHL* (< 0.18 mg m^{-3}).

The updated data set (**Figure 3**) and the respective model (**Figure S2**) capture the spawning distribution over a broader environmental space relative to the original counterparts (**Figure 3**).The updated model (**Figure S2**) however, seems to capture the same overarching relationship between the spring-spawning sardine and their habitat as that described by the original mode. The updated model fitted a maximum probability of sardine presence at approximately *SST* = 13 °C, and ln(CHL)= -0.7 (CHL = 0.5 mg m^{-3}), very similar to the original model (**Figure S2**). The updated model (**Figure S2**) had an explanatory AUC of 0.81 (**Figure 4**).

Attributing Landings and Biomass

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 0.29, and 0.18, delimits the boundaries of the habitat containing at least 80%, and 92% of the northern stock sardine eggs, respectively. When these probabilities are applied to the data set and their effect evaluated by year, it can be seen that the rate of false-negatives is spread across all years, without a specific spatial pattern (**Figure 2**). Using these probability thresholds, the updated model shows higher definition in the monthly evolution of northern stock sardine habitat in 2021 compared to the original model, particularly in transition areas such as the SCB (**Figure 5 and S3**), where the *SST* above 16 °C could still be assigned high probability of egg presences in the presence of mid-range *CHL* (**Figure S3**).

From January through April, the northern stock 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. 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.

Using the probability threshold of 0.18 from the updated habitat model, all of the landings at Ensenada in 2020 and 2021 are attributed to the southern stock (**Figure 6**). From 2006 to 2012, northern stock sardine were landed each winter at Ensenada, except 2011. If instead, the probability threshold was 0.22, above which includes at least 89.0% of all the positive egg samples and 92.2% of the sardine egg abundance, only two months of the landings at Ensenada would be attributed to the northern stock.

Using the probability threshold of 0.18, landings at San Pedro 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. However, despite larger proportions of northern stock habitat since 2018, there were almost no landings of the northern stock at this port.

Using probability thresholds from the original (0.32) and updated (0.29) habitat models that contain at least 80% of the northern stock, the attributions of sardine caught in A-T surveys, 2012-2022, changed for four out of ten summer surveys (**Figure 7**). Those that changed are located in the transition zone off Central California, where the attributions, irrespective of the model used, are sensitive to the spatial and temporal coincidence of the catches and environmental data. Furthermore, the cloud cover in this area often limits the availability of the environmental data. Two of the re-attributions, in 2014 and 2017, did not affect the original biomass estimates. The other two, in 2015 and 2018, shifted 3.0 and 7.2% of the originally estimated northern stock biomass to the southern stock, respectively (**Table 1**).

Using the habitat model to attribute A-T trawl catches to stock, statistically significant differences in the L_s of the northern versus southern stock corroborates the separation (**Figure 8**). The growth and longevity of the cohorts in each stock, indicated by modes in their L_s distributions, are observable in the annual time-series (**Figure S4**). For summer 2021, the northern and southern stocks are separated by nearly 500 kilometers, and the lengths for the southern stock generally decrease with increased latitude. The lengths-at-age indicate that northern stock fish grow significantly faster than southern stock fish (**Figure 8**).

Discussion

The Northern and Southern Sardine subpopulations are distinct based on habitat association, separation, recruitments indicated by differences in length distributions, growth indicated by age-at-length, and a lack of mixing (**Figure 8**). To reaffirm the original model of potential habitat for the northern stock (Zwolinski et al., 2011), we updated the model using all available data on sardine-egg presence and absence, and associated environmental conditions, from 1989-2019.

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 sharper boundaries serve to more accurately identify the survey biomass and fishery landings, notably in the SCB and at Ensenada, respectively, especially during recent years when the biomass and residency of the southern stock of sardine has increased in these areas.

As shown, the updated habitat model can be used to attribute both biomass (**Figure 8**) and landings (**Figure 6**) to their respective stocks. A probability threshold was designed to reject all northern stock landings at Ensenada in 2020 and 2021, when there were no northern stock sardine south of Point Conception. The same probability threshold, 0.18, serves to attribute both biomass and landings. It is important to ensure, however, that the environmental data, survey samples, and catches are matched sufficiently closely in both space and time. Also, these attributions should be routinely corroborated with other information, such as geographic separation (e.g., Zwolinski et al., 2023; and Stierhoff et al., 2023), and differences in life history parameters such as length distributions (**Figure 8, S4**), growth rates, and perhaps other phenotypical metrics such as vertebral

counts (Reyes Corral and Aguirre, 2019) and otolith shape (Soeth et al., 2022), and stable isotope ratios (Espinasse et al., 2020).

Prior to 2021, incomplete habitat information and a lack of corroborating evidence may have led to inaccurate stock differentiations (**Figure S4**). For example, in summer 2018, incomplete habitat information off Central California due to cloud cover may have caused a portion of the southern stock to be incorrectly attributed to the northern stock. A similar mis-attribution may have occurred in summer 2019.

As noted in Zwolinski et al. (2011), if northern stock sardine are observed outside, or if southern stock sardine are sampled within the modeled northern stock habitat, or both, their habitat preferences may have changed, in which case further investigation is warranted. Unless or until such a change in the state of the ecosystem is detected, sardine sampled in the A-T surveys can be attributed to their stock using the updated model of northern stock potential habitat. Moreover, landings may be attributed to the northern and southern stocks using indices 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.

Acknowledgments

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Tables

*Table 1. Acoustic-trawl survey estimates of northern and southern stock sardine biomasses, loosely attributed using the original habitat model (Zwolsinski et al., 2011), and revised using closer inspection of the updated habitat model, corroborated by length distributions (**Figure S5**). Estimates from 2012-2019 are for US waters only, and those from 2021 and 2022 include waters off U.S. and Mexico.*

Year	Original Northern (t)	Original Southern (t)	Revised Northern (t)	Revised Southern (t)	Reference
2012	341,000	0	341,000	0	Zwolinski et al. (2014)
2013	314,000	0	314,000	0	Zwolinski et al. (2014)
2014	26,300	0	26,300	0	(Hill et al., 2015)
2015	14,795	0	14,351	445	(Stierhoff et al., 2021)
2016	80,092	323	80,092	323	Stierhoff et al. (2021)
2017	14,103	-	14,103 t	-	Stierhoff et al. (2018)
2018	25,148	33,093	23,345	34896	Stierhoff et al. (2019)
2019	33,632	14,890	33,632	14,890	Stierhoff et al. (2020)
2021	47,72	199,724	47,72	199,724	Stierhoff et al. (2023)
2022	69,506	107,468	69,506	107,468	Stierhoff et al. (*in prep.*)

Figures

Figure 1 – Synoptic distributions of northern stock sardine during spring (left panel) inferred from egg presences in CUFES samples from 1998-2019 and, summer distributions (center panel) of both northern (blue) and southern (red) stocks inferred from sardine presences in trawl samples collected during 2012-2022 A-T summer surveys. The upper-right panel indicates the purported regions of operation of the San Pedro and Ensenada fisheries. Note: the presence of southern and northern stock off Central California in the center plot is not a sign of simultaneous presence (see Figure 7).
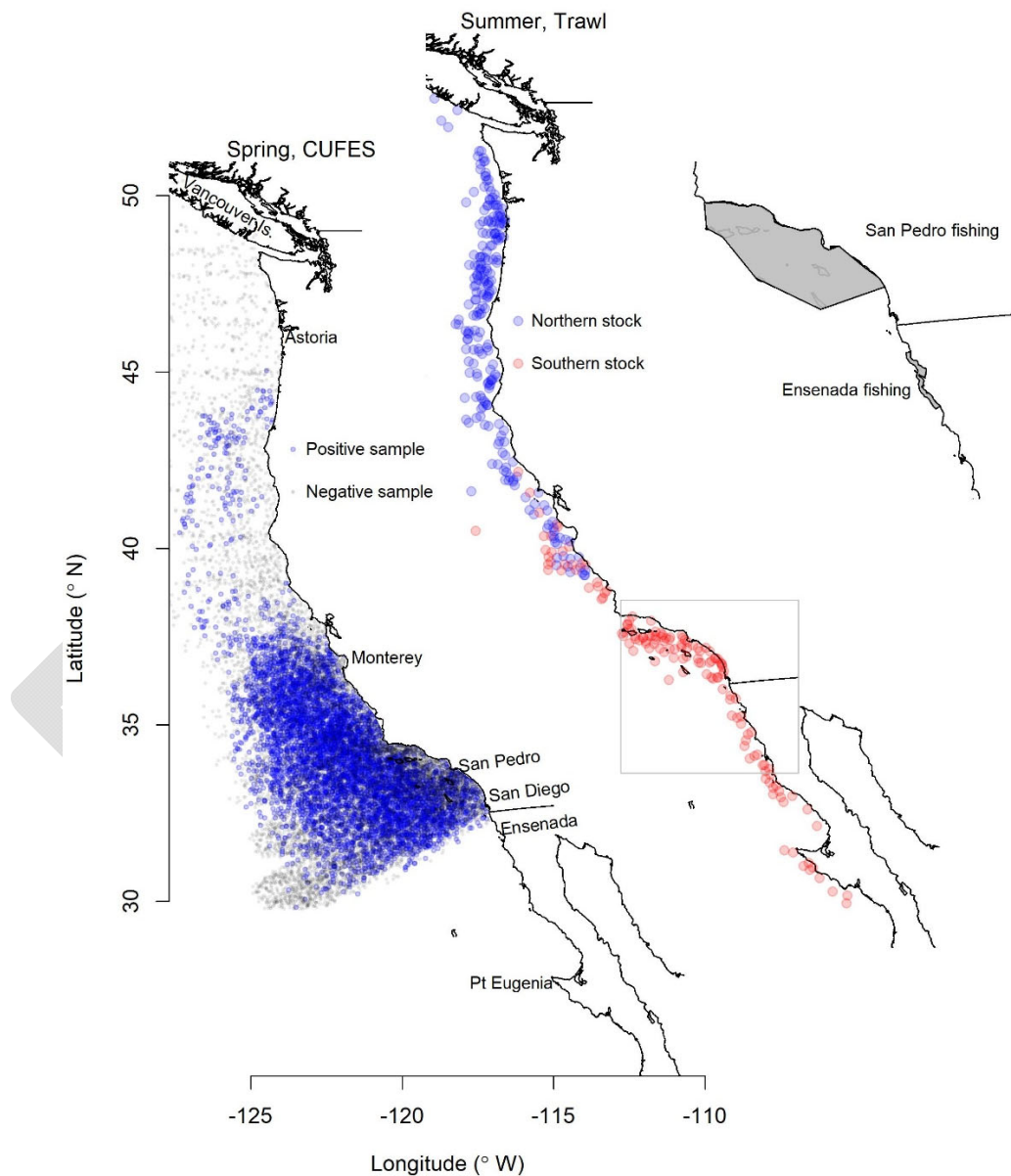
Figure 2 – Relative sardine-egg abundance in continuous underway fish-egg sampler (CUFES) data collected during SWFSC, CalCOFI, and other spring surveys, generally April, 1998-2019, San Diego to Bodega Bay, California. Since 2014, after the northern stock collapsed (Hill et al., 2015; Zwolinski and Demer, 2012), it has not been spawning in this area. A probability threshold of 0.18 in the updated habitat model retains 95% of the sardine eggs (blue) and excludes 5% (orange).
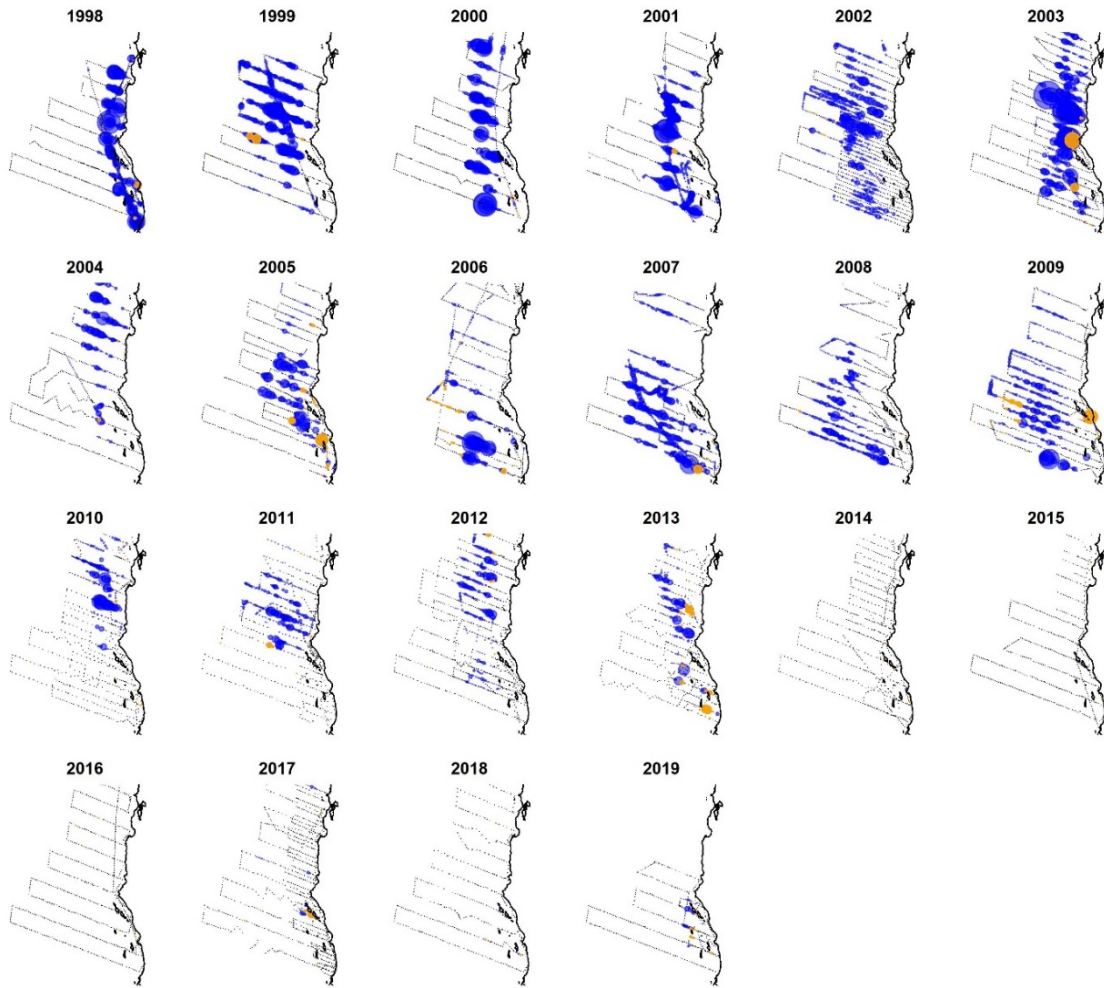
Figure 3 - Empirical probability density functions (epdf) for CUFES samples with sardine eggs (dashed lines) and without sardine eggs (solid lines) versus satellite-sensed SST (a), and log(CHL) (b) for the data used in (Zwolinski et al., 2011) (gray) and the updated data set (black) shown on Figure 2. 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.
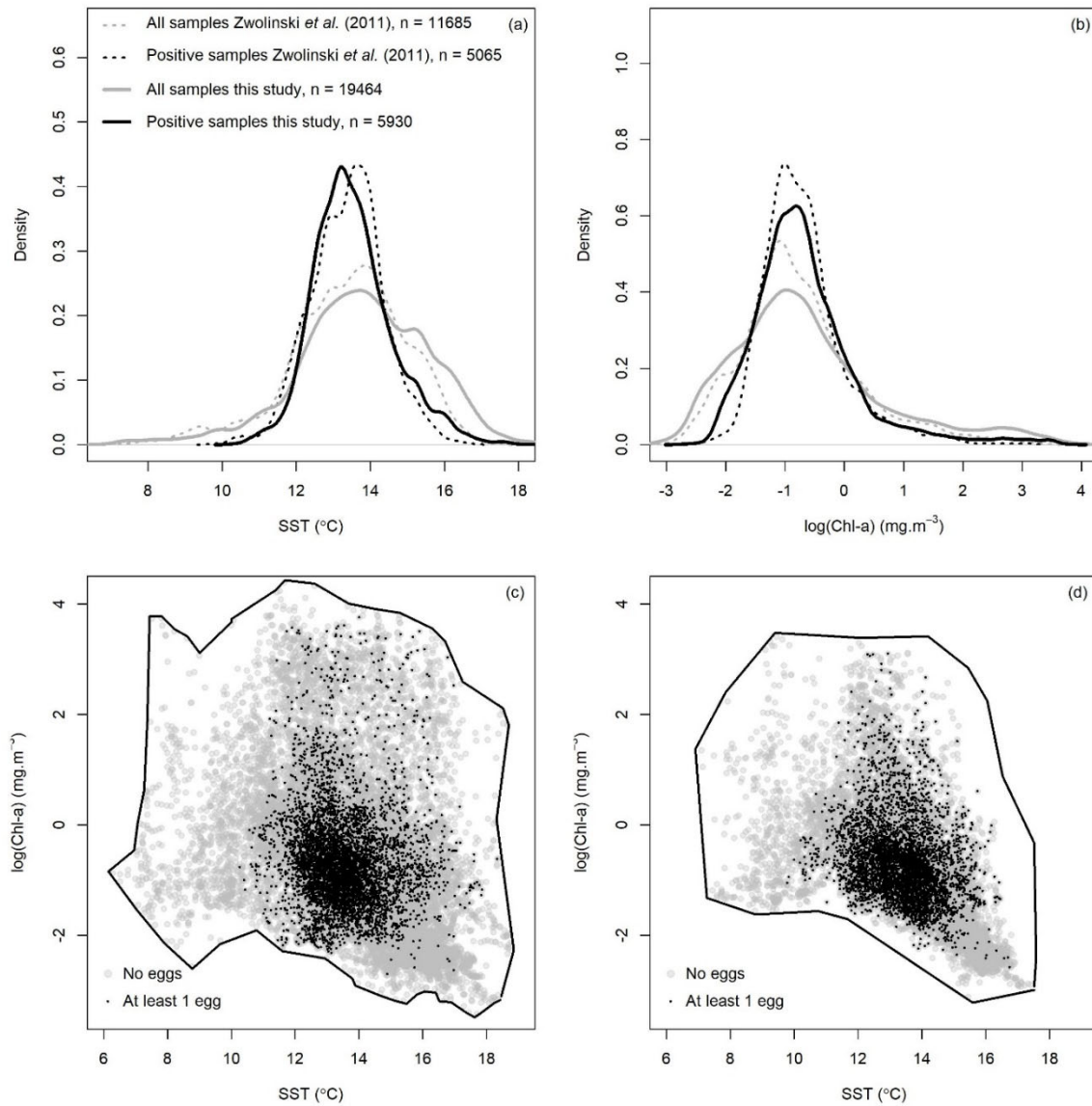
Figure 4 - Receiver operating characteristic (ROC) curve for the updated habitat model (continuous line, AUC = 0.81), showing the sequential levels of fitted probability versus the proportion of false positives (negative samples classified as positive) and the proportion of true positives (positive samples classified as positive). The observations with probabilities higher than 0.29 and 0.2 contain 80% and 90% of all positive samples, respectively. The observations with probabilities 0.18 or higher contain ~92% of all positive samples and 95% of all eggs in the data set, and exclude ~50% of the samples with no eggs. The dashed line represents the ROC curved for the original model (AUC = 0.832).
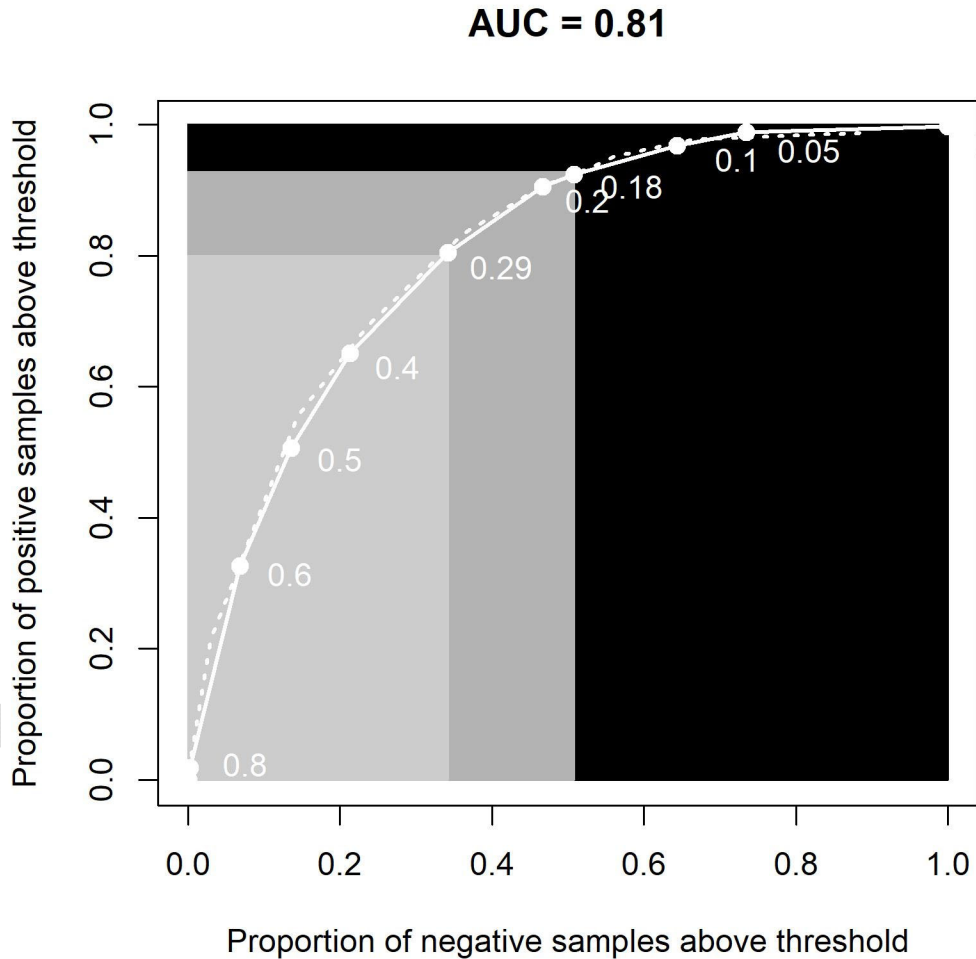
*Figure 5 – The updated (top) and operational (original sans GRAD; bottom) model results showing the monthly evolution of the northern stock habitat during 2021. For the updated model, the habitat probability intervals [0, 0.18[, [0.18, 0.29[, and [0.29, 1] contain 8, 12, and 80% of all the positive samples from 1998-2019 (cf. **Figure 4**). For the original model, the habitat probability intervals [0, 0.32[, [0.32, 0.45[, and [0.45, 1] contain 10, 10, and 80% of all the positive samples from 1998-2009 (cf. **Figure 4**). Both sets of intervals shown as black, dark grey, and light grey regions, respectively. Some of the environment data is beyond the fitted data ranges (blue), and some areas have no satellite-sensed environmental data (white).*
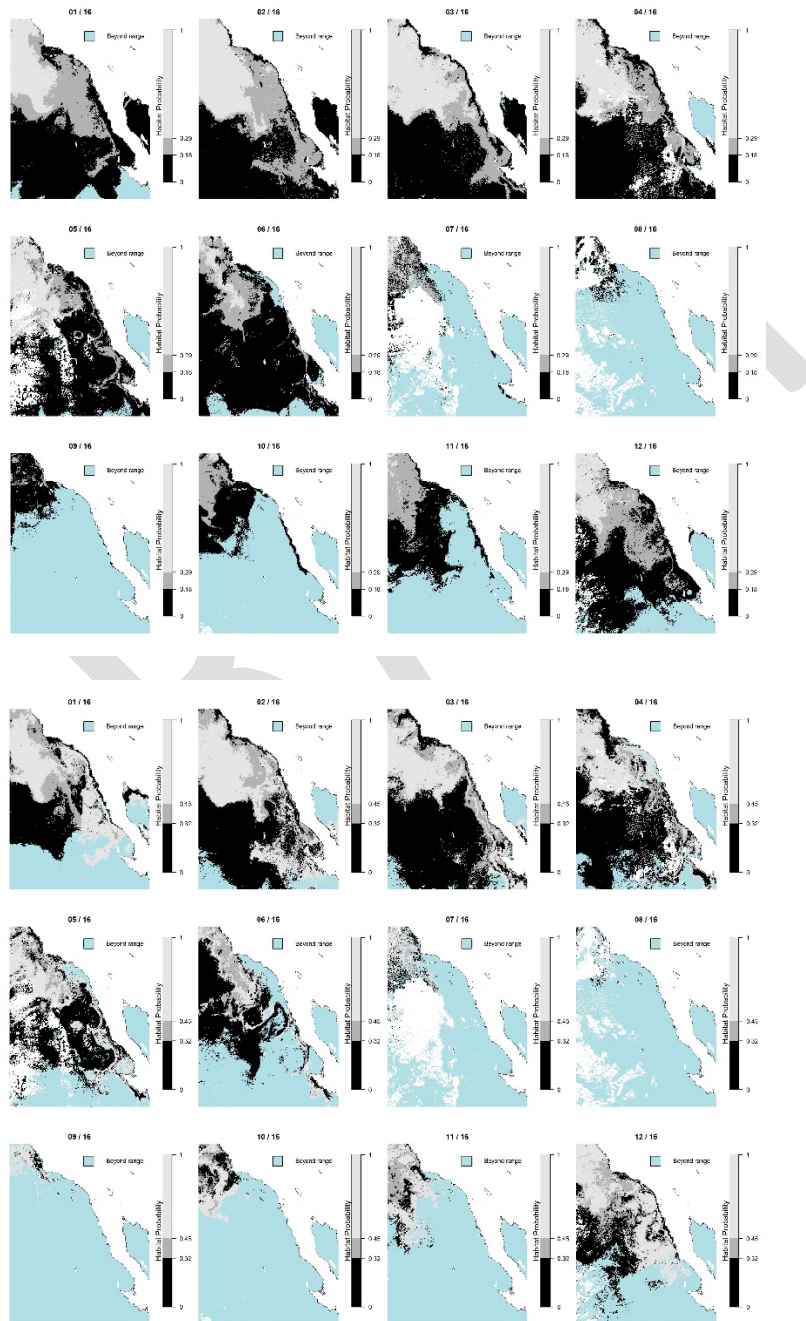
*Figure 6 - Landings at San Pedro (top) and Ensenada (bottom) attributed to the northern stock (blue) when more than 50% of the fishing area (**Figure 1**) includes northern stock habitat with a probability of 0.18 or more (grey), else it is attributed to the southern stock (red). Since 2015, the U.S. sardine fishery has been closed, except for landings by the bait fishery, through experimental fishing permits, and from incidental take.*
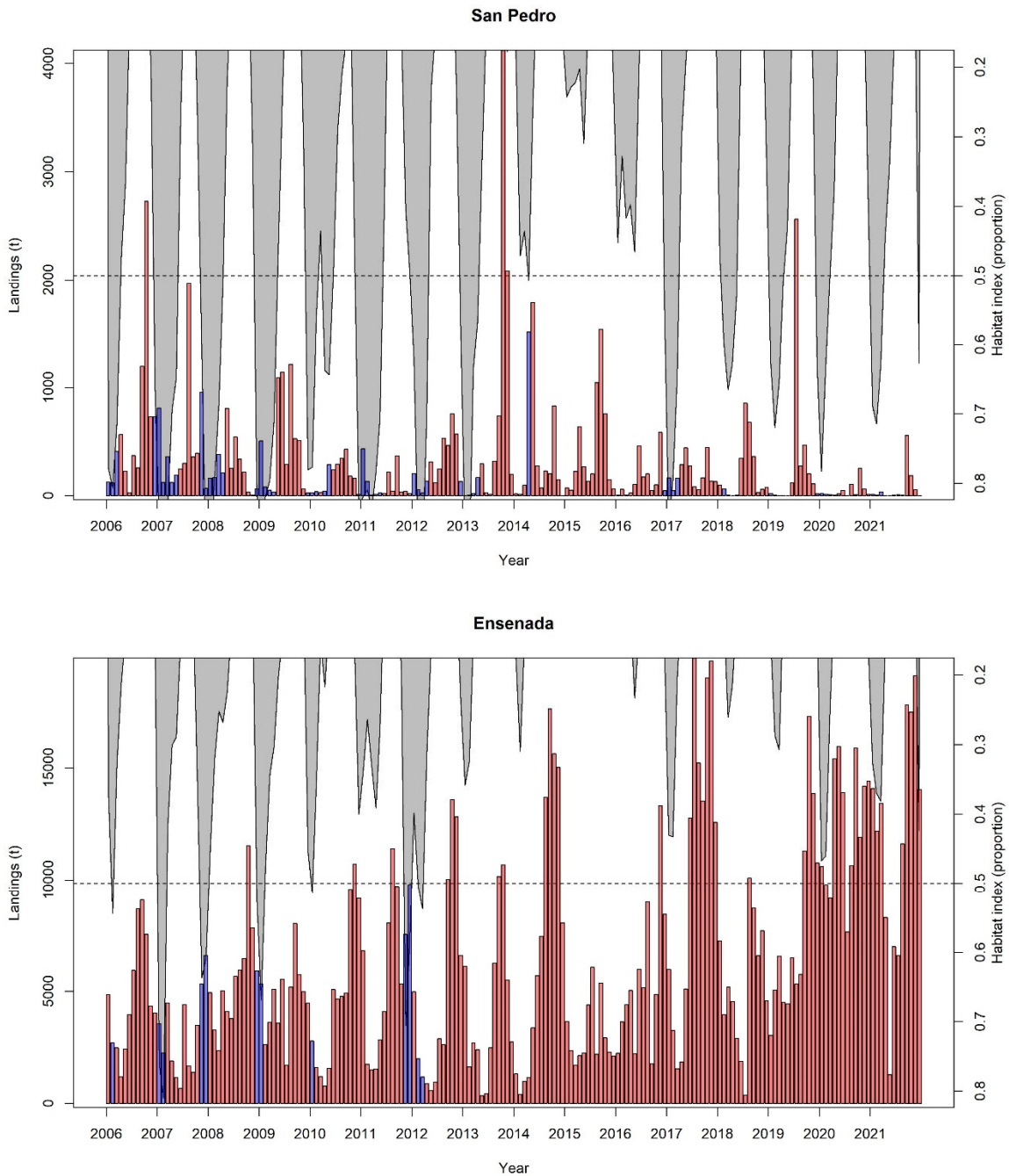
*Figure 7. Locations of trawl catches including sardine during A-T surveys, 2012-2022, attributed to the northern (blue) and southern (red) stock, loosely using the original habitat model (dot), or reassigned to the southern stock, upon further inspection using the updated habitat model (box; see **Figure S4**).*
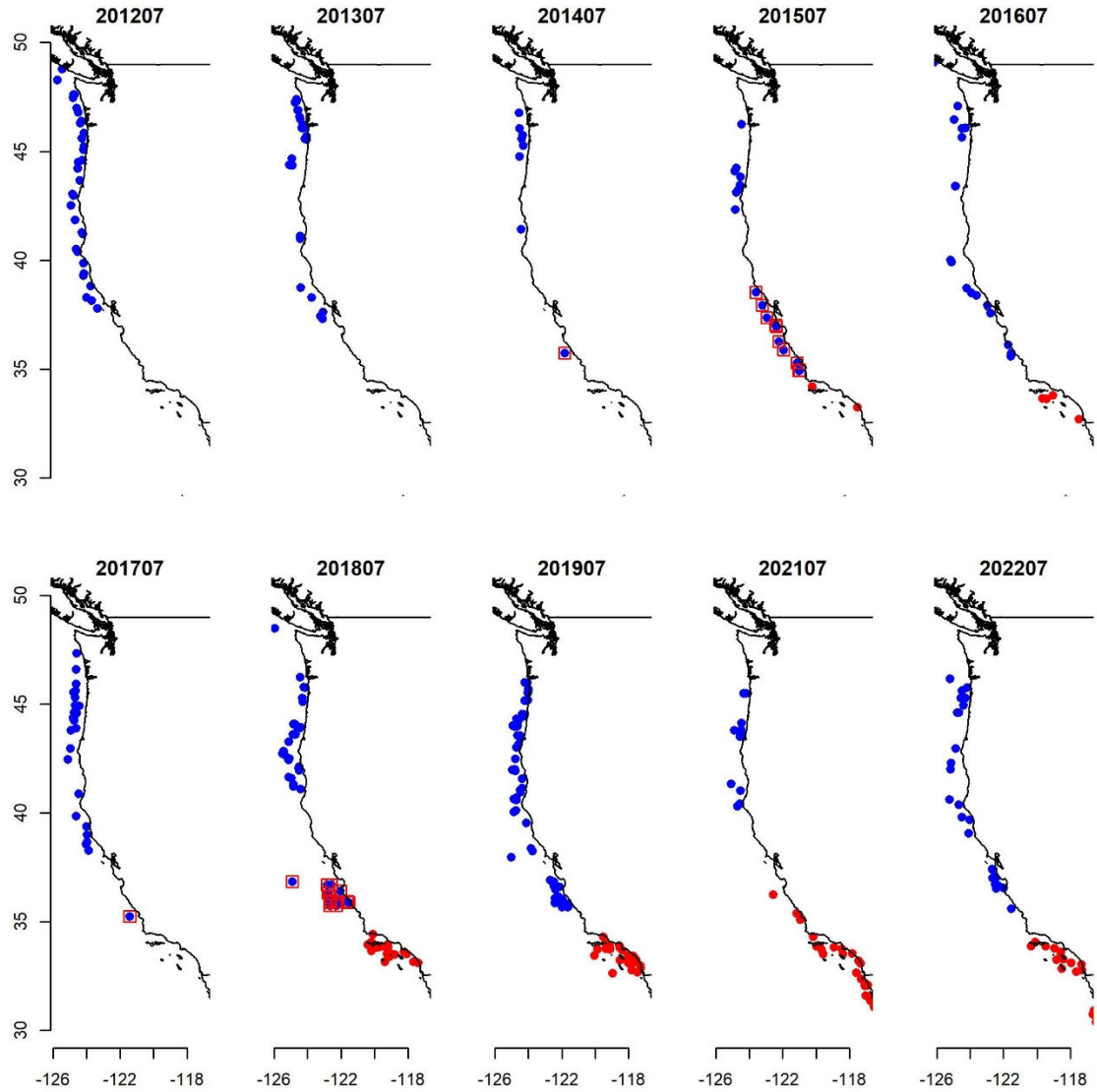
Figure 8. During summer 2021: (a) sardine standard length distributions for the southern (red) and northern (blue) stocks; (b) the individual length measurements for the two stocks (gray points) and the centroids of the distributions for each sardine catch (blue and red points); (c) the lengths at age; and (d) catch locations overlaid on a map 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).
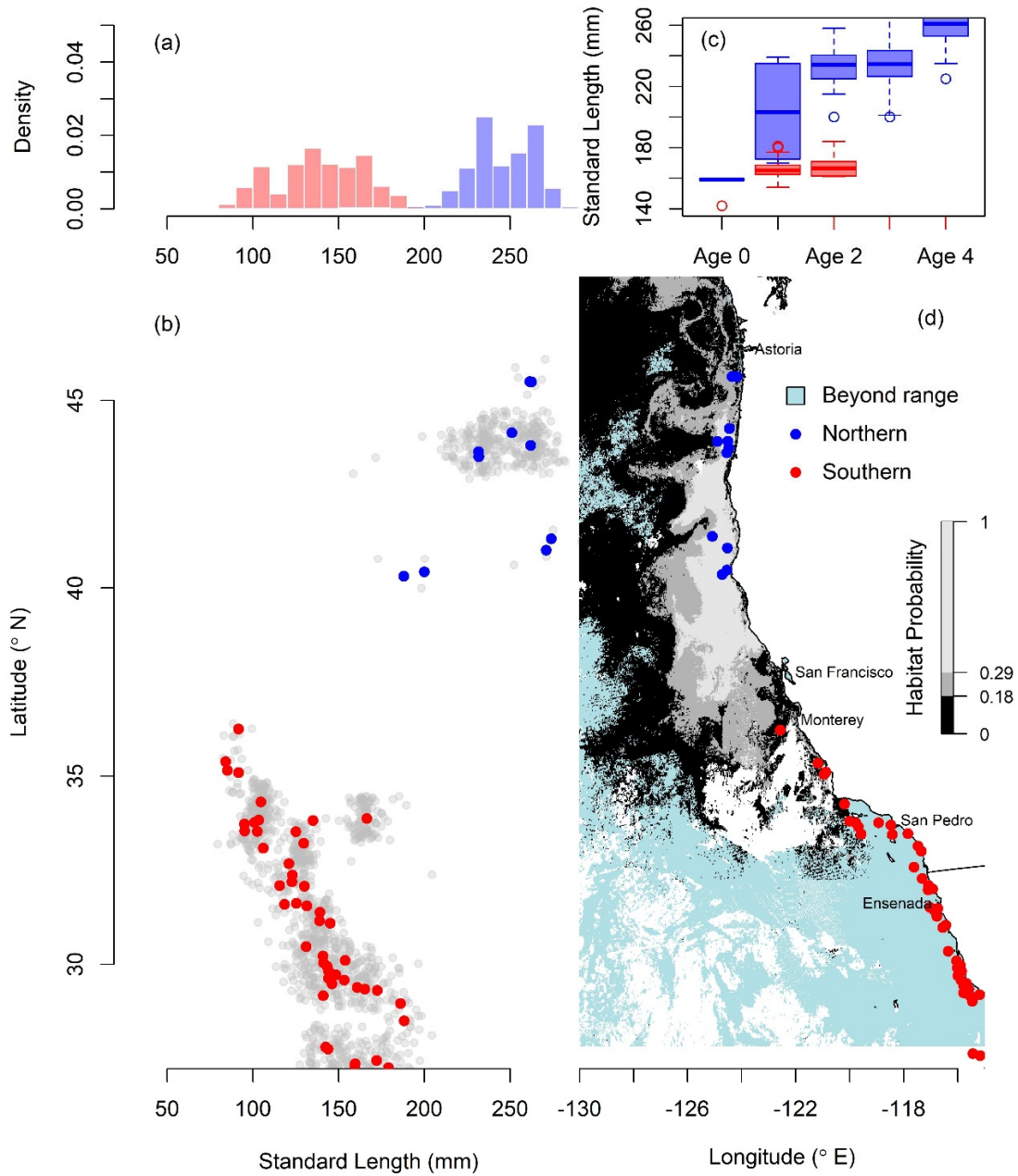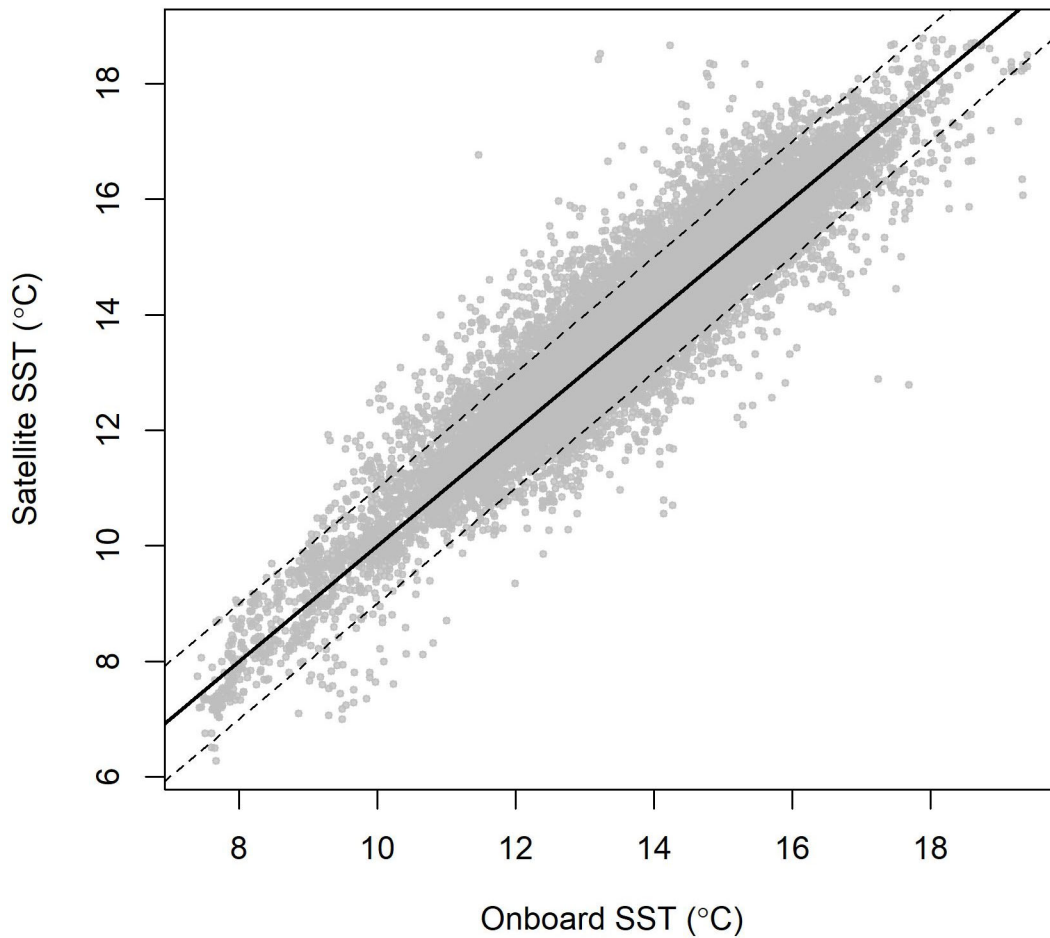
Supplementary Material

Figures

Figure S1 – *Satellite-sensed SST versus concomitant shipboard measures of surface-water temperatures taken during egg surveys, 1998-2019, (a) combined and (b) for each survey. The full black line represents y = x, and the black dotted lines indicate y = x ± 1 °C.*
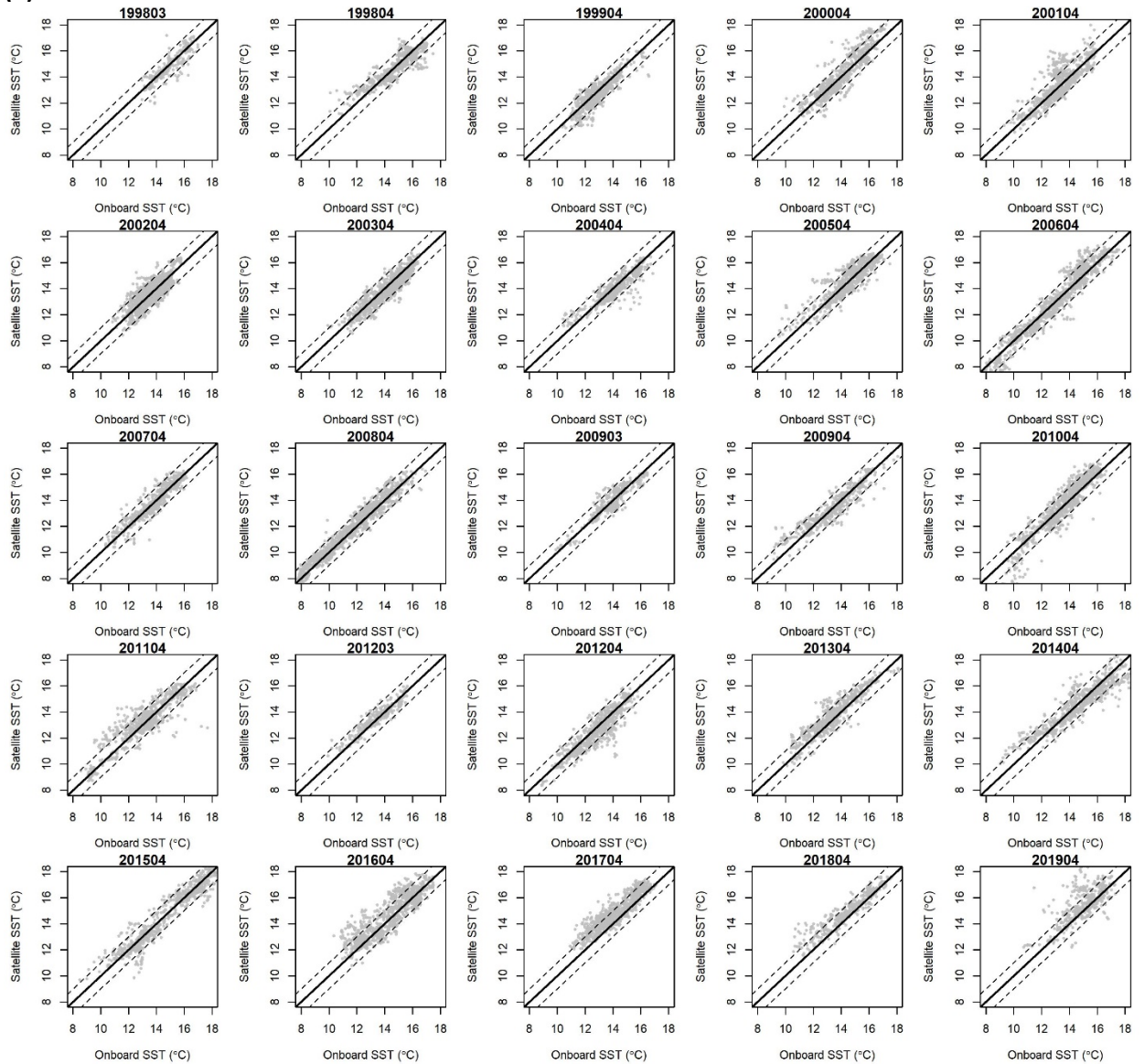
(a)

(b)

***Figure S2** – 2-dimensional surface for the probability of finding at least one northern stock sardine egg in a CUFES sample with a standard duration of 30 min as a function of SST and log(Chl-a) for the updated (left) and original (right) model.*
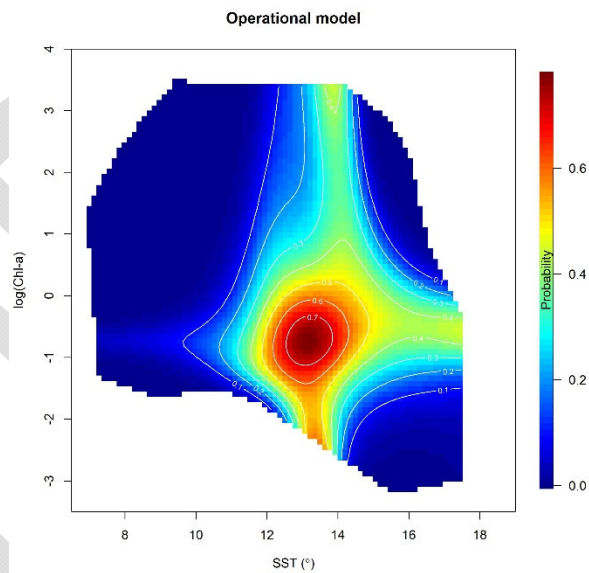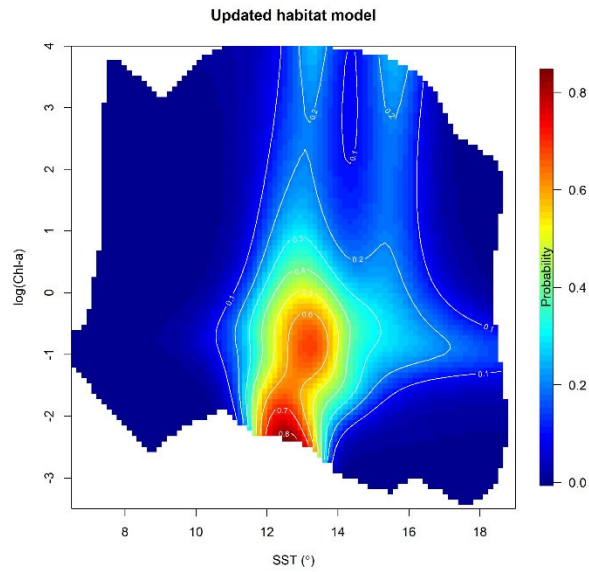
Figure S3 –*The updated (top) and operational (original sans GRAD; bottom) model results showing the monthly evolution of the northern stock habitat during 2015. For the updated model, the habitat probability intervals [0, 0.18[, [0.18, 0.29[, and [0.29, 1] contain 8, 12, and 80% of all the positive samples from 1998-2019 (cf.* **Figure 4**). *For the original model, the habitat probability intervals [0, 0.32[, [0.32, 0.45[, and [0.45, 1] contain 10, 10, and 80% of all the positive samples from 1998-2009 (cf.* **Figure 4**). *Both sets of intervals shown as black, dark grey, and light grey regions, respectively. Some of the environment data is beyond the fitted data ranges (blue), and some areas have no satellite-sensed environmental data (white).*

Figure S4. For summer surveys during 2022 through 2012: (a) sardine standard length distributions for the southern (red) and northern (blue) stocks during the respective summer survey; (b) the individual length measurements for the two stocks (gray points) and the centroids of the distributions for each sardine catch (blue and red points); and the catch locations overlaid on a map of the updated habitat model.

(a)

Habitat Probability

August 1, 2019

(b)

(c)

Beyond range
Northern
Southern