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Sardine and anchovy larvae biogeography in the southern California Current Ecosystem

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by

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The thesis of Bryant Tran is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

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LIST OF ABBREVIATIONS

CCE	California Current Ecosystem
CalCOFI	California Cooperative Oceanic Fisheries Investigations
IMECOCAL	Investigaciones Mexicanas de la Corriente de California
PDO	Pacific Decadal Osciallation
SHF	Standard Haul Factor
GAM	Generalized Additive Model

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ACKNOWLEDGEMENTS

ABSTRACT OF THE THESIS

Sardine and anchovy larvae biogeography in the southern California Current Ecosystem

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Bryant Tran

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Assessing the spatial and temporal distributions of Northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) is critically important for managing these pelagic forage fish and understanding their roles in marine ecosystems. Here, we examined over 50 years (1963-2015) of larvae data collected across the southern California Current Ecosystem (CCE), focusing on the waters off of California and Mexico. Specifically, we asked where and when these fish larvae were found, whether their geographic distributions were linked to average larvae abundance, and whether or not the abundances of anchovy and sardine larvae were correlated in time. Larvae were found in some periods

primarily in Mexico, California, or both—and in some cases with disjointed distributions—and these patterns were not consistent across species. During the period of extremely low sardine abundance in the U.S. in the 1960s-1990s, sardine larvae were still found in Mexico. We found that sardine and anchovy distributions expanded away from the coast when larval abundance were high for both species. Additionally, the correlation between anchovy and sardine larval abundance was highly dependent on spatial and temporal scale. By combining larval data across a broad section of this globally important coastal upwelling biome, we were able to explore questions regarding biogeography and phenology of these key species.

INTRODUCTION

The California Current Ecosystem (CCE) is an upwelling biome with high primary productivity fueled by strong but variable upwelling of nutrients from below the surface (Rykaczewski & Checkley 2008). This highly productive region is home to large populations of pelagic forage fish, principally *Sardinops sagax* (hereafter Pacific sardine or sardine) and *Engraulis mordax* (northern anchovy or anchovy; Zwolinski et al. 2012; Sydeman et al. 2020). The spatial distribution and overall population size of these species varies through time in this region (MacCall, 1990; Zwolinski et al. 2012; MacCall et al, 2016) in response to environmental factors, ecological processes, predation, and fishing pressure (Chavez et al. 2003; Takasuka et al. 2008; Lindegren et al. 2013; Siple et al. 2020). Tracking these spatial and temporal variations is critically important for understanding the dynamics of marine ecosystems and managing these fisheries (Karp et al. 2019; Sydeman et al. 2020).

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has measured the abundance of larval fish since the 1950s (McClatchie 2016), with data concentrated in the southern CCE from Point Conception to the US-Mexico border, but periodically collected outside this core region (McClatchie 2016; Fig. 1). CalCOFI sampled throughout Baja California for the first three decades of the program but ceased entering Mexican waters in 1984 (McClatchie 2016). The former Mexican CalCOFI stations, however, were reoccupied off Baja California, Mexico since 1997 by Investigaciones Mexicanas de la Corriente de California (IMECOCAL; Funes-Rodríguez et al. 2002; Funes-Rodríguez et al. 2006; Baumgartner et al. 2008), with data collection concentrated from the US-Mexico border to Punta Eugenia, Mexico (Fig. 1). We combine these two larval fish datasets across the southern CCE to study the distribution and phenology of sardine and anchovy larvae. Specifically, we ask the following, linked questions: 1) where and when were sardine and anchovy larvae found in this region?; 2) does the spatial distribution of larvae change with total larval abundance?; and 3) are the abundances of sardine and anchovy larvae correlated, and if so, where and on which spatial scales? We do not, in this study, address

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the underlying environmental and ecological factors causing these patterns, instead documenting patterns of larval distribution.

Our first objective is to assess where (across latitude, nearshore vs. offshore) and when (seasonal and interannual patters) larvae occur on a biome scale. Sardines have relatively low genetic differentiation among geographically separated individuals, and adults can migrate large distances relatively rapidly (Demer et al. 2012; Lecomte et al. 2004; Lo et al. 2011). Anchovy are believed to have distinct stocks or subpopulations (Sydeman et al. 2020), yet genetic differentiation among geographically separated individuals is limited (Lecomte et al. 2004). While the larvae data collected by CalCOFI and IMECOCAL cannot by themselves categorize genetically-distinct subpopulations of sardine and anchovy, they document regional maxima and minima in larval abundance on a spatial scale not previously possible. Phenological shifts in spawning times of both sardine and anchovy have occurred in response to changing environmental conditions (Asch, 2015; Auth et al. 2017; Thompson et al. 2022), but to date no biome-scale analysis has documented seasonal patterns of abundance for anchovy and sardine larvae across the entire southern CCE.

Our second objective is to assess whether the distributions of sardine and anchovy larvae expand latitudinally or perpendicularly to shore with increasing total abundance of larvae. Adult sardine migrate latitudinally seasonally in the CCE, most evidently when the total population size is large (Lo et al. 2011; Demer et al. 2012), but it is not well known whether the centers of larval abundance change position north and south through time. The "basin model" suggests that the ranges of fish expand with favorable environmental conditions but contract with unfavorable conditions to smaller refugia (MacCall, 1990; Barange et al. 2009). By combining the CalCOFI and IMECOCAL larvae data, we can evaluate the hypothesis that the spatial distributions of sardine and anchovy larvae expand latitudinally and offshore with increasing total larval abundance.

Sardine and anchovy populations in the CCE and worldwide exhibit periods of abundance and scarcity occurring on multidecadal timescales (Chavez et al. 2003; Checkley et al. 2017). Adult sardine

have smaller gill raker spacing than anchovies, such that sardines are capable of eating smaller prey than are anchovy (Rykaczewski & Checkley 2008). Strong nearshore to offshore nutrient gradients in the CCE imply that larger phytoplankton and zooplankton are more abundant closer to shore (Rykaczewski 2019; James et al. 2022), and consequently anchovy are thought to be most abundant closer to shore while sardine can be found offshore also (Rykaczewski & Checkley 2008; Sydeman et al. 2020). Chavez et al. concluded that multidecadal shifts in the Pacific Decadal Oscillation (PDO; Mantua 1997) drive opposite patterns of abundance in sardine and anchovy populations in this region. Specifically, negative (colder) phases of the PDO produced environmental conditions more favorable for anchovy, due to increased upwelling/larger plankton abundance, while positive (warmer) phases were more favorable for sardine (Chavez et al. 2003; Sydeman et al. 2020), indicating negative correlation in sardine and anchovy abundance over multidecadal timescales in this region. However, paleorecords of adult sardine and anchovy abundance from the Santa Barbara basin show that the abundance of these fish was generally positively correlated on longer, centennial to millennial timescales (Baumgartner et al. 1992; McClatchie et al. 2017). In addition, Siple et al. recently concluded that the idea that anchovy and sardine populations alternate worldwide (Chavez et al. 2003) is largely a product of bias caused by analysis of fishery-dependent data over short periods of time. Thus, the sign of the correlation between adult sardine and anchovy, if any, is unclear, and it is also unclear whether correlation between sardine and anchovy larvae should follow a similar pattern.

Here, we combine larval abundance data from CalCOFI and IMECOCAL in order to address the three outlined questions above, namely: 1) where and when are larvae from sardine and anchovy found in this region?; 2) does the distribution of larvae change with total larval abundance?; and, 3) are the abundances of sardine and anchovy larvae correlated, and if so, where and on what scales? We quality control and harmonize both data sets so that they are directly comparable, and focus our analyses on larval data collected from Point Conception, California to Punta Eugenia, Baja California Sur, as this is the area most consistently sampled over the duration of both surveys.

METHODS

CalCOFI and IMECOCAL sampling

Since the 1950s, CalCOFI has conducted quarterly cruises in the CCE, with transects roughly perpendicular to the coast extending outward approximately 200-280 nautical miles (370.4-518.56km) (Fig. 1a). These transects, or "lines", are spaced 40 nautical miles (74.08 km) apart, with the distance between stations being either 20 or 40 nautical miles (37.04-74.08 km; McClatchie 2016). The actual number of stations and lines occupied seasonally by CalCOFI has varied considerably over time, with the region between Point Conception and the USA-Mexico border being sampled most consistently. Additionally, IMECOCAL has conducted research cruises off the coast of Baja California since 1997, focusing on seasonal cruises and adapting the survey grid previously managed by CalCOFI. To avoid spatial biases in our larval biogeography analysis, we focused on the best-sampled portion of the grid (Fig. 1b). We included cruises and stations that met the following criteria: 1) only cruises with station coverage greater than or equal to 60% of the most intensely sampled cruise (141 stations, summer of 2014) were used, 2) cruises that surveyed a region spanning from line 80 to line 120 (Point Conception to Punta Eugenia) were included, and 3) stations sampled less than 10 total times from 1963 onwards were not included. We also began with data from 1963, when sampling patterns were more consistent with the modern CalCOFI cruises. While the filtered set of stations and cruises (Fig. 1b) is a subset of the full number of stations (Fig. 1a), it is the most robustly-sampled portion of the programs and results inferred from this subset of data are less likely to be influenced by spatial and temporal variations in sampling intensity.
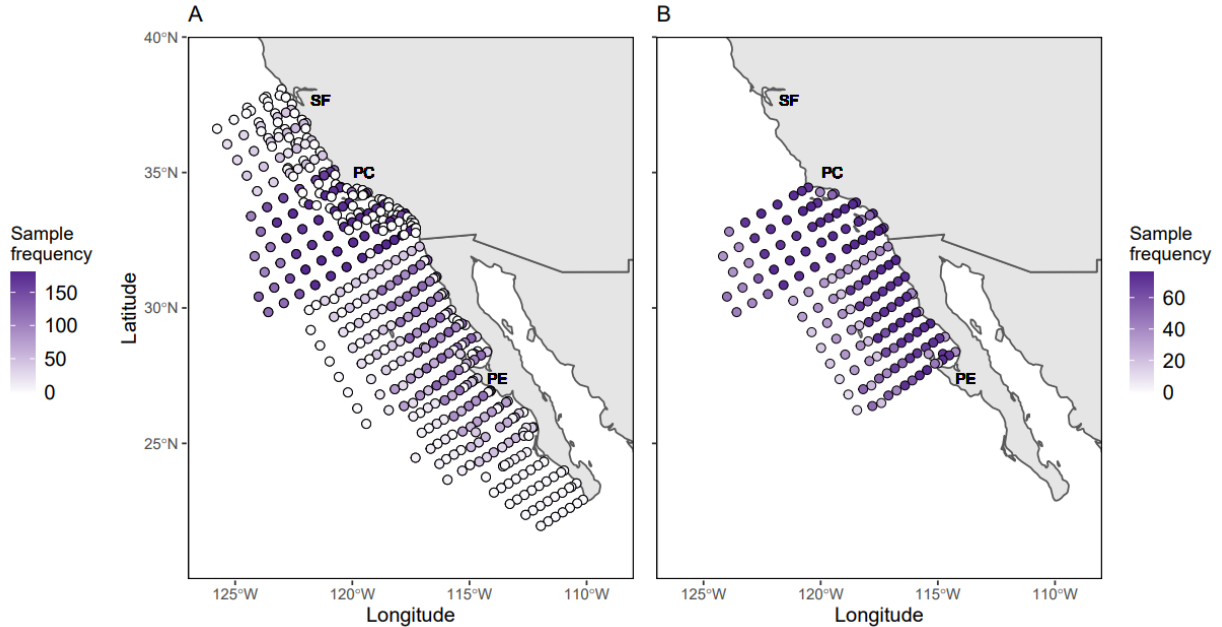
Figure 1. Total number of cruises where larvae were sampled per station from 1963-2020 over CalCOFI and IMECOCAL sampling areas (A). Total number of larvae samples per station for the same data sets, but only with data from cruises that had greater than or equal to 60% station coverage (based on the cruise with the most sampled stations), surveyed from Point Conception to Punta Eugenia (line 80-120), and with data from stations sampled greater than 10 times from 1963 onwards (B). SF = San Francisco, PC = Point Conception, and PE = Punta Eugenia. Data in (B) form the core region of analysis for this paper.

CalCOFI collected fish larvae (ichthyoplankton) at each station using ring net (1951 to 1977) and bongo net trawls (1978-present; Ohman & Smith 1995; Thompson et al. 2017). Initially, nets were towed in a 45° angle at 140 meters and gradually lifted to the surface, although the maximum tow depth was adjusted to 210 meters after 1968 (Ohman & Smith 1995). Ichthyoplankton were then collected and filtered out from the nets. Identification was determined through ontogenetic analysis of the morphology, meristics, and coloration of the samples, which was then compared to distinct identifying features of known fish species (Sumida et al. 1987). To account for any differences in tow depths or the amount filtered from the nets between stations, values were standardized by a standard haul factor (SHF; Thompson et al. 2017). Essentially, the raw larvae count for each station was divided by the proportion actually sorted, and then multiplied by the calculated SHF, which gave the calculated number of individuals per $10m^2$ of sea surface (Thompson et al. 2017).

Determining spatial distributions

For each season from 1963-2015 that met our data frequency and distribution thresholds (see above), we calculated the weighted average latitudinal position ($\bar{Y}$; ° latitude) of the larval distribution from the combined CalCOFI and IMECOCAL data, weighting the latitude of each station i (Y_i; ° latitude) by the larval abundance at that station (A_i; units):

$$\bar{Y} = \frac{\sum_i^n Y_i A_i}{\sum A_i}$$

where n is the total number of samples. We also used the weighted average longitudinal position ($\bar{X}$; ° longitude) for some of the data, which was calculated by weighting the longitude of each station i (X_i; ° longitude) by its larval abundance (A_i; units):

$$\bar{X} = \frac{\sum_i^n X_i A_i}{\sum A_i}$$

The geographic spread of the larvae was estimated by calculating a weighted standard deviation in latitudinal position:

$$\sigma_Y = \sqrt{\frac{\sum_i^n A_i (Y_i - \bar{Y})^2}{\sum A_i}}$$

as well as the weighted standard deviation in longitudinal positon:

$$\sigma_X = \sqrt{\frac{\sum_i^n A_i (X_i - \bar{X})^2}{\sum A_i}}$$

The weighted mean variance in latitudinal/longitudinal position is σ_Y^2 and σ_X^2, respectively. Each station's distance from the coastline was estimated by calculating the planar distance to the nearest coastline point,

using the dist2line() function from the R package "geosphere" (Hijmans 2019). The weighted mean distance from the coast ($\overline{\Delta x}$; km) is:

$$\overline{\Delta x} = \frac{\sum_i^n \Delta x_i A_i}{\sum A_i}$$

where i is the station in the sampling grid, Δx_i is the distance (km) from the coast for station i, and A_i is the larval abundance at station i. The weighted variance in distance to the coast ($\sigma^2_{\Delta x}$; km^2) is:

$$\sigma^2_{\Delta x} = \frac{\sum_i^n A_i(\Delta x_i - \overline{\Delta x})^2}{\sum A_i}$$

Assessing correlation between sardine and anchovy larvae

Spearman's rank correlation coefficient was used to determine the relationship between sardine and anchovy larval abundances. In order to test the impact of spatial variation, the studied region was separated into distinct subsections. Considering the impact of nutrient gradients on anchovy and sardine distributions in the CCE, where strong nearshore upwelling implies larger phytoplankton and zooplankton are more abundant closer to shore (Rykaczewski 2019; James et al. 2022), we decided to partition the data between a nearshore (<200 km) and offshore (>=200km) region. Besides this, data was divided between stations found in California and those found in Mexico. In doing so, we hoped to discern any distinct patterns between the two areas. Spearman's rank correlation was tested on combinations of the above restrictions, as well as versions where the entire dataset was considered.

In order to understand the influence of data availability on correlation, bootstrapping was done to create a correlation sample distribution for each subregion. This was done to compare expected correlation values against the actual value that was obtained from the original data. We randomly sampled 80% of the available data from each subregion and determined the correlation coefficient for that data

chunk. In total, this was repeated 1000 times, and a distribution of these correlation coefficients was created.

<div align="center">RESULTS & DISCUSSION</div>

Where and where were larvae found?

Sardine and anchovy larvae abundance varied considerably in space and time, both latitudinally and along a nearshore-offshore gradient and on seasonal to decadal timescales (Figs. 2-5). The most consistently sampled region was located between 30ºN-35ºN, with frequency of data coverage decreasing outside of this core, intensely-sampled region (Fig. 2A, C). Fig. 2A, C show larval abundances averaged into half degree latitude bins, over time, using all available CalCOFI and IMECOCAL larvae data, not just cruises and stations meeting our data distribution and frequency criteria. In the 1960s through early 1980s, anchovy larvae abundance was relatively high in two disconnected regions (Fig. 2A): one local maxima was found between 25ºN-30ºN in Mexico and one further north between 30ºN-35ºN in the USA, with a region of relatively low larvae abundance located between the two. During this same period, overall sardine larval abundance was relatively low with local maxima in waters off Punta Eugenia and very few larvae in California (Fig. 2C). In the mid-1980s through the late 1990s, samples were not available off Mexico, so inference is limited to southern California. Here, larvae for both species were relatively high from 32-35ºN but low from 30-32ºN (Fig. 2A, C). In the 2000s to early 2010s, when Mexican data was again available, anchovy larvae abundance was lower in California compared with previous years, but larvae were found widely, including in Mexican waters (Fig. 2A). During this same period, sardine larvae were found in both California and Mexico (Fig. 2C). When averaging larvae abundance over only stations and cruises that met our data distribution and frequency criteria (thus restricting the spatial coverage; Fig. 2B, D), local maxima off Punta Eugenia and in the northern Southern California Bight were seen for each species.

The weighted average and variance in latitudinal position ($\bar{Y}$ and σ_Y^2, respectively) characterize the overall north-south distribution and spread of sardine and anchovy larvae (Fig. 3A-B). The weighted average and variance in distance from the shore ($\overline{\Delta x}$ and $\sigma_{\Delta x}^2$, respectively) indicate the overall onshore-offshore distribution and spread of sardine and anchovy larvae (Fig. 3C-D). These analyses used only data meeting our criteria for data frequency and distribution, so are insensitive to changes in sampling intensity over time. Neither anchovy nor sardine showed a significant trend in weighted latitudinal position over time (Fig. 3A; Spearman rank correlation $r = 0.0961$, $p = 0.4021$ for anchovy, $r = 0.1999$, $p = 0.0834$ for sardine). The weighted mean latitudinal position of anchovy in the 2000s varied considerably from cruise to cruise, while the overall latitudinal spread in anchovy distribution was relatively low during this period (Fig. 3B, Spearman rank correlation $r = -0.3522$, $p = 0.0017$), suggesting that anchovy larvae distribution in this period was patchy compared with the 1960s to 1980s (also seen in Fig. 2A). Anchovy and sardine larvae exhibited opposite temporal trends in weighted average distance from the shore ($\overline{\Delta x}$; Fig. 3C); sardine larvae were found further from the shore in the 2010s (Spearman rank correlation $r = 0.4939$, $p = 5.7886e-05$), while anchovy were found further from the shore in the 1960s and 1970s (Spearman rank correlation $r = -0.5412$, $p = 4.9561e-07$). Anchovy and sardine larvae exhibited significant and inverse temporal trends in variance in distance from the shore (Fig. 3D; Spearman rank correlation $r = -0.4181$, $p = 0.0002$ for anchovy, $r = 0.3755$, $p = 0.0008$ for sardine), such that when the larvae were found, on average, further from shore, the variance in distance from the shore was also greater. These results imply that larvae distributions expand and contract to and away from shore to a greater extent that by moving north and south.

When averaging larvae abundance over only stations and cruises that met our data distribution and frequency criteria, a nearshore to offshore decrease in average larvae abundance was seen for both anchovy (Fig. 2B) and sardine (Fig. 2D). The highest average larvae abundance for anchovy was observed in the nearshore stations off of California and the nearshore stations close to Punta Eugenia, and the highest average larval abundance for sardine was observed further offshore off of California and in the

nearshore stations close to Punta Eugenia. These results show that larvae abundance (over the entire

utilized timescale) was highest in the northern Southern California Bight and near Punta Eugenia, on

average, suggesting that these particular regions were hotspots for anchovy and sardine spawning, had

particular environmental and biotic conditions that allowed larvae to persist until collection, and/or had

higher spawning stock biomass. Near Point Conception, sardine larvae were found well and further

offshore than anchovy larvae, on average. Near Punta Eugenia, sardine larvae were concentrated

nearshore, while anchovy larvae were found offshore in addition to nearshore. These patterns suggest that

the nearshore-offshore distribution of anchovy and sardine larvae did not neatly follow a cross-shore

gradient in vertical nutrient supply, primary productivity, and plankton community composition

(Rykaczewski, 2019; James et al. 2022).

Collectively, these results indicate that, within the constraints of available data, anchovy and

sardine larvae spatial distributions are dynamic through time, and that larvae data collected within just

Mexico or the USA would provide an incomplete picture of their distributions. Larvae were found in

some periods primarily in Mexico, California, or both—and in some cases with disjointed distributions—

and these patterns were not consistent across species. While these data alone cannot identify spatially

disconnected and genetically distinct subpopulations (e.g., Lecomte et al. 2004), the occurrence of

spatially separated maxima in larvae abundance of each species may be consistent with separate

subpopulations.

Seasonal and interannual patterns of larvae abundance

When averaging across the entire sampling region, anchovy larvae were most abundant in the

decades between the 1960s and 1990s, but decreased in the 2000s (Fig. 4). During this period of relatively

low average regional abundance, the decline was greatest in the northern part of the survey region (32-

35ºN; Fig. 2A). Further south (30-32ºN; Fig. 2A), anchovy larvae abundance increased from the mid-

1980s and 1990s to the 2000s. Comparing across decades in waters west of Punta Eugenia (Fig. 2A), anchovy abundance was considerably higher in the 1960s and 1970s compared with the 2000s. Sardine larval abundance was very low in the 1960s to 1980s, on average over the whole region, but increased in the 2000s (Fig. 4). During the period of very low sardine larvae abundance in the 1960s and 1970s, sardine larvae were more common off of Mexico than in the USA. In the 2000s, a similar contrast was observed. Overall, the average regional abundance of anchovy and sardine larvae (Fig. 4) are negatively correlated (Spearman rank correlation, $r = -0.2354$, $p = 0.0407$; see section below about correlation), but this signal overlooks considerable regional and decadal variability.
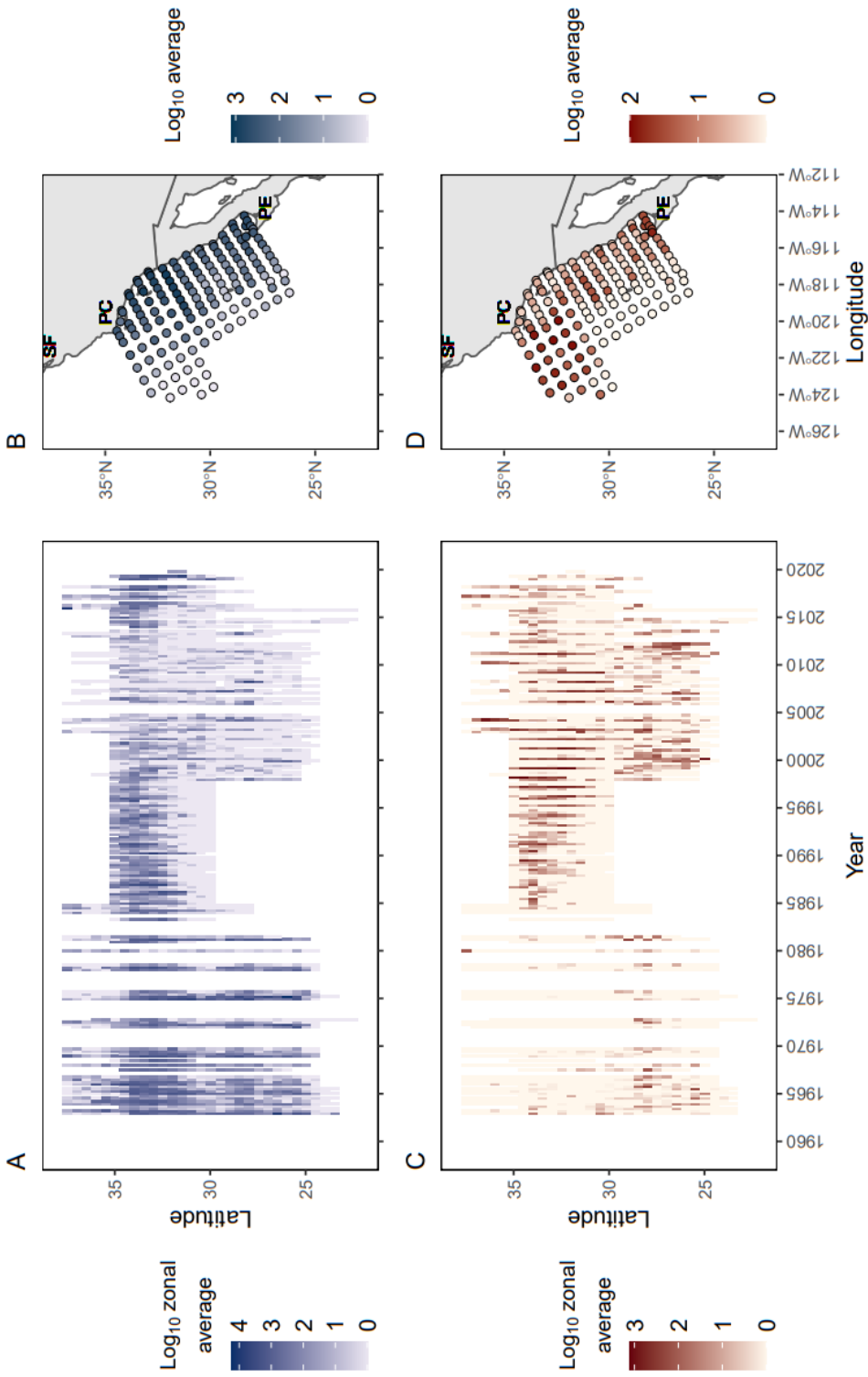
Figure 2. Abundance of northern anchovy (A) and Pacific sardine (C) larvae over time, averaged in half-degree latitude bins, using all available data from CalCOFI and IMECOCAL. Abundance of northern anchovy (B) and Pacific sardine (D) larvae by station from 1963-2015, averaged over all years and cruises that met our data distribution and frequency criteria. For plots (A) and (C), stations within every half-degree latitude were grouped together and had their larvae counts averaged and then converted to a $\log_{10}$ scale, per cruise. For (B) and (D), larvae counts for each individual station were averaged over the entire time series, and then converted to a $\log_{10}$ scale. White areas in (A, C) indicate no data coverage. SF = San Francisco, PC = Point Conception, and PE = Punta Eugenia.
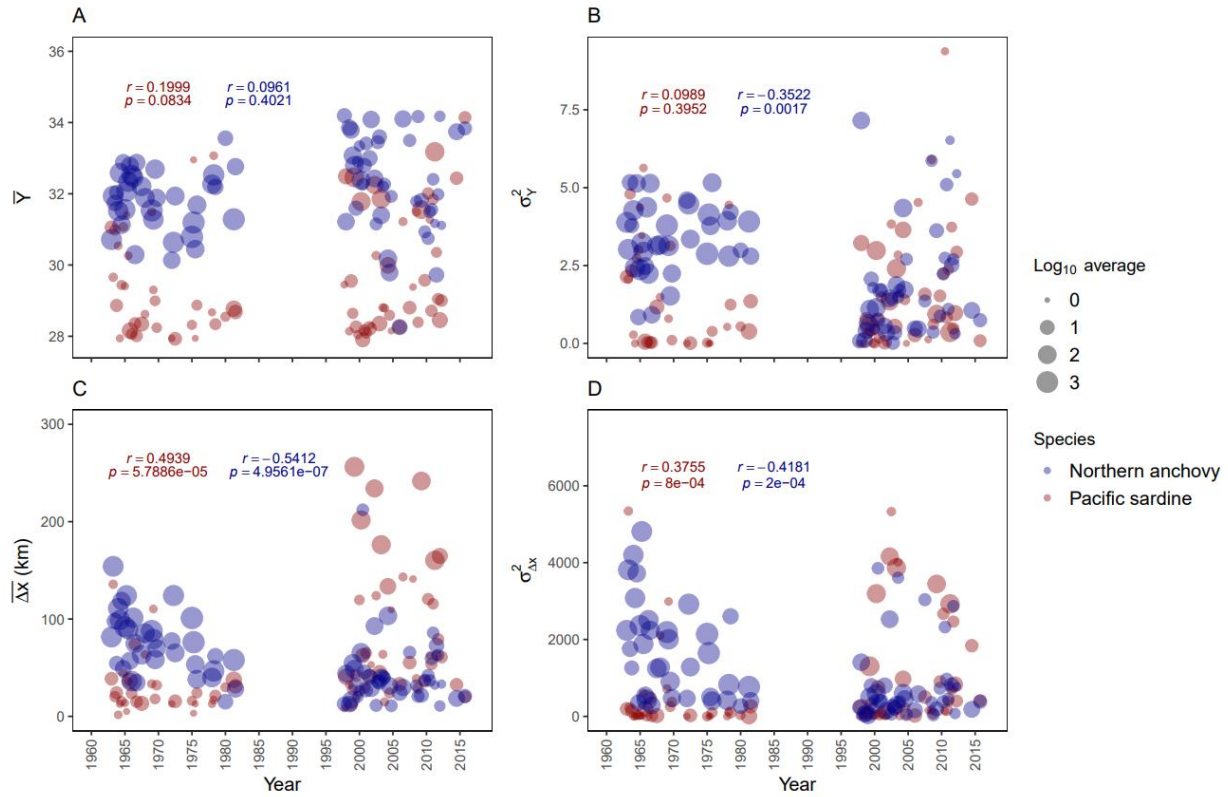
Figure 3. Weighted average latitudinal position (A) and distance from the coastline (C) for northern anchovy (blue) and Pacific sardine (red) from 1963-2015. The size of each point represents the regional average larvae abundance within a single season/cruise. Only stations and cruises that met our criteria for data distribution and frequency were used here. The weighted variance of latitude (B) and distance from the coastline (D) indicate the geographic spread in the population. For each plot, Spearman's rank correlation (*r*) and p-value (*p*) were tracked for both species, and organized by color.

Figure 4. Average Pacific sardine (red) and northern anchovy (blue) larvae abundance from 1963-2015, averaged over all cruises and stations that met data distribution and frequency criteria. Each point is the average from all the available stations in a given season/cruise. A generalized additive model (GAM) with a 95% confidence interval (gray shading) was added to illustrate the overall changes in abundance through time. Years that had less than 2 total cruises had their GAM line removed for that period.
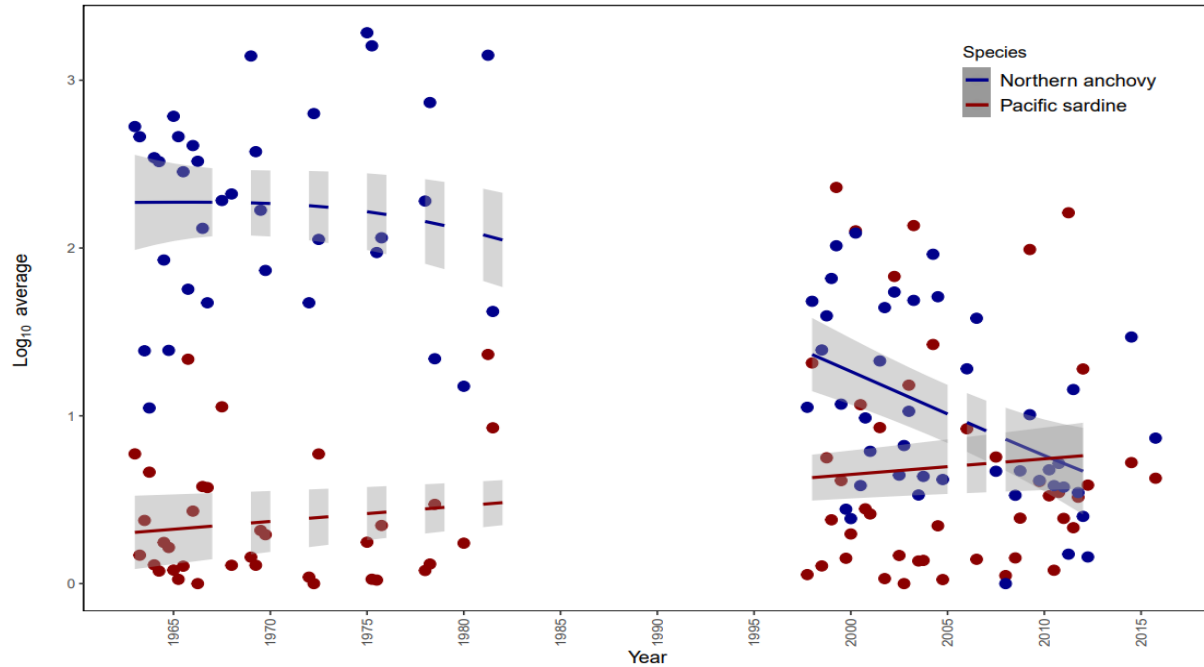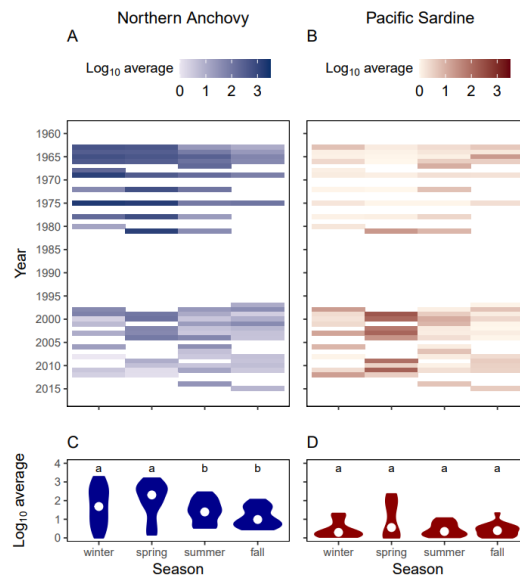

Figure 5. Seasonal average abundance of northern anchovy (A) and Pacific sardine larvae (B) from 1963-2015, and the average across all years for northern anchovy (C) and Pacific sardine larvae (D). The median seasonal larvae abundance across all years is denoted by a white dot. Months that fell into each season were organized as such: (winter) December, January, February; (spring) March, April, May; (summer) June, July, August; (fall) September, October, November. Within each species, the Mann-Whitney U test was applied to denote statistically significant differences between seasonal averages, and used the labels "a" and "b" to group seasonal averages that were similar.

The abundance of anchovy and sardine larvae varied seasonally, but this pattern was not constant through time (Fig. 2, 5). Anchovy larvae were found across all seasons, but were typically more abundant in winter and spring than in summer and fall (Fig. 5C). In the 1960s, in particular, anchovy larvae were most abundant in winter and spring (Fig. 5A). Sardine larvae were also found in all seasons, and no significant differences between seasons were found (Fig. 5B). However, in the 2000s, sardine larvae were particularly abundant in spring and less abundant at other times of year. The peak of sardine larvae in spring in the 2000s is apparent in the vertical bars in Fig. 2. Anchovy may spawn throughout the year, but most often in February and March (Parrish et al. 1986; Sydeman et al. 2020). Sardine are also thought to spawn in spring (Zwolinski & Demer, 2012), but this clearly varied over 1963-2015.

Does the distribution of larvae change with total larval abundance?

The distribution of sardine and anchovy has shifted over time (Figs. 2-3). We found that the weighted average latitudinal position ($\overline{Y}$) for anchovy larvae (Fig. 6A) were significantly correlated with average larval abundance. Sardine larvae (Fig. 6B) were not correlated with average larval abundance in the region, but that average distance from the shore ($\overline{\Delta x}$) for anchovy (Fig. 6A) and sardine larvae (Fig. 6B) increased with average larvae abundance. In other words, when there were more larvae present, they were found further offshore. This expansion offshore with increasing population size is consistent with the "basin model", where the ranges of fish expand with favorable environmental conditions but contract towards shore with unfavorable conditions to smaller refugia (MacCall, 1990; Barange et al. 2009).
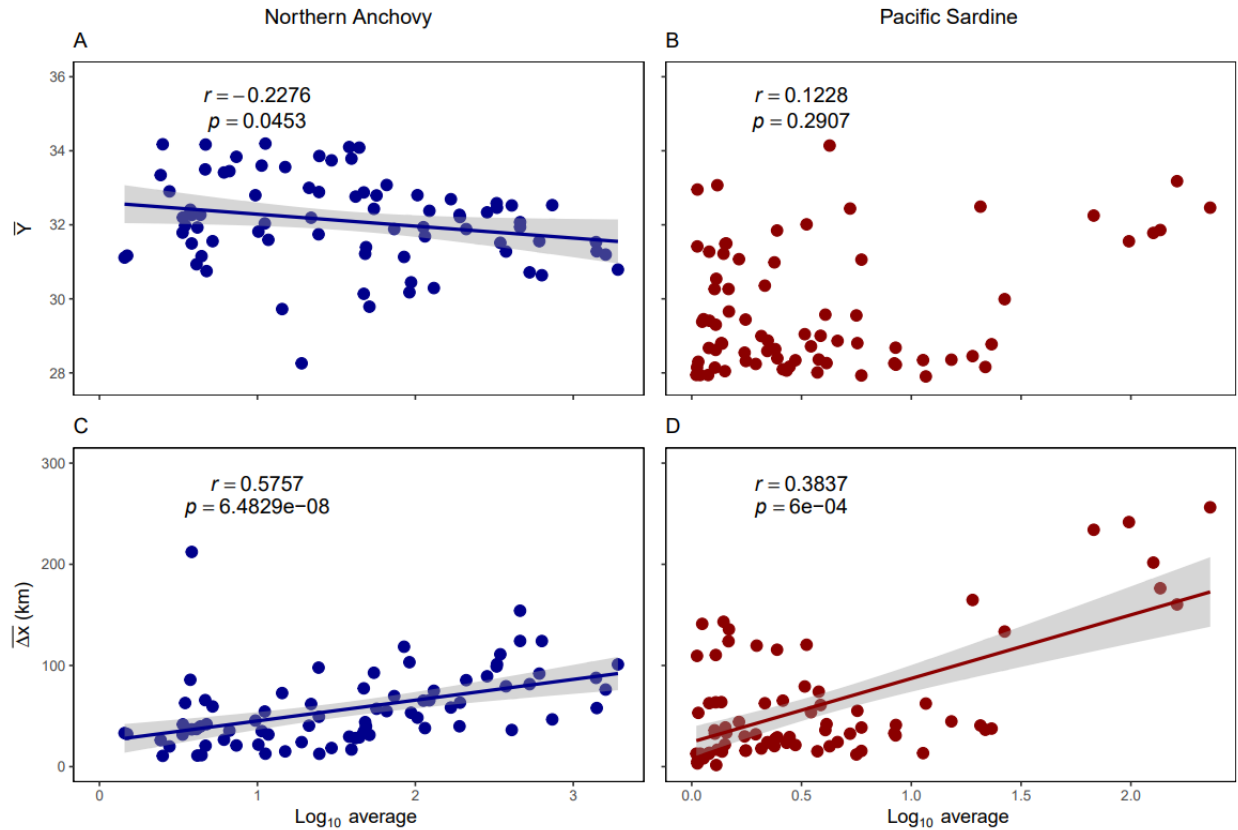
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Figure 6. Weighted mean latitudinal position for northern anchovy (A) and Pacific sardine (B) plotted against average larvae abundance. Each dot represents a season/cruise. Northern anchovy distance from coastline (C) and Pacific sardine distance from coastline (D) plotted against species abundance, per cruise. Spearman correlation (r) was calculated for each plot, and the significance shown by the p-value (p). A generalized additive model (GAM) with a 95% confidence interval (gray shading) was added to illustrate the trend in abundance through time. Plots with $p > 0.05$ did not have a trend line included.

When and where are sardine and anchovy larvae correlated, if at all?

Correlation between sardine and anchovy larvae varied with the area sampled (Fig. 7), and was highly sensitive to the availability of data through time (Fig. 8). We calculated Spearman rank correlation coefficients between anchovy and sardine larvae abundance for 1963-2015 using data from stations in both California and Mexico, Mexico only, and California only, and also separated regions based on distance from the coastline, which were labeled "full region", "nearshore", and "offshore". Stations within a cruise that were between CalCOFI lines 80 to 93.3 were considered to be in California, while stations between line 96.7 to 120 were considered to be in Mexico. Nearshore stations included any

stations less than 200 kilometers from the coastline, and offshore stations were those greater than or equal to that distance. When comparing sardine and anchovy larval data across the whole region, we found a significant, weak, negative relationship between anchovy and sardine larvae (Fig. 7A, $r = -0.2354$, $p = 0.0407$). The correlation between anchovy and sardine larvae was not significant when including only data from California or Mexico (Figs. 7B-C). In the nearshore area, the correlation was weakly significant and negative when combining data from California and Mexico (Fig. 7D, $r = -0.2350$, $p = 0.0410$), but the correlation was not significant when using only California or Mexico larvae data (Fig. 7E-F). In no case was there a significant correlation in the offshore region (Fig. 7G-I). When we randomly sampled 80% of the cruises through time, and calculated the Spearman rank correlation for each subsample of data, we found that the correlation coefficient varies strongly based upon the selection of data, for all regions and distances from shore (Fig. 8). We conclude that the apparent negative correlation between anchovy and sardine larvae depends strongly on the temporal and spatial scale sampled in the CCE. Longer paleorecords indicate that anchovy and sardine abundances are generally but not always positively correlated (Baumgartner et al. 1992), but neither did we find evidence for a positive correlation between anchovy and sardine larvae. Though very long in duration by scientific standards, the CalCOFI/IMECOCAL program is not long relative to the decadal fluctuations of anchovy and sardine populations, and it is difficult, potentially impossible, to robustly assess correlation patterns between these species based upon these records.

Limitations

Our study featured several important limitations. First, the CalCOFI and IMECOCAL programs, though incredible in coverage, had varied sampling intensity in time and space. To account for this in our biogeographic analyses, we applied strict criteria for data frequency and distribution, which removed some stations and cruises, as well as data north of Point Conception and south of Punta Eugenia, from further analysis. Both anchovy and sardines are resident or migrate outside this range (Lo et al. 2011; Demer et al. 2012; Sydeman et al. 2020). Additionally, we did not include any of the data after 2015,

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when southern California experienced a large marine heatwave from 2014-2016 (Kintisch 2015) and when anchovy exhibited historically high abundance and recruitment (Thompson et al. 2022). Unfortunately IMECOCAL data was sparse after 2015. Regional maxima of both sardine and anchovy populations were seen in the upper and lower extremes of our data. In situations where regional maxima occurred in both these areas, using values such as the weighted mean latitude/longitude, which would approximate the stock location in the central region of observed stations, which is not as heavily populated. Using one averaged stock location, consequently, does not adequately address disjointed populations. We also made an effort to solely study larval distributions, and did not attempt to study other environmental factors in greater detail. However, this may be an area of research for subsequent papers.
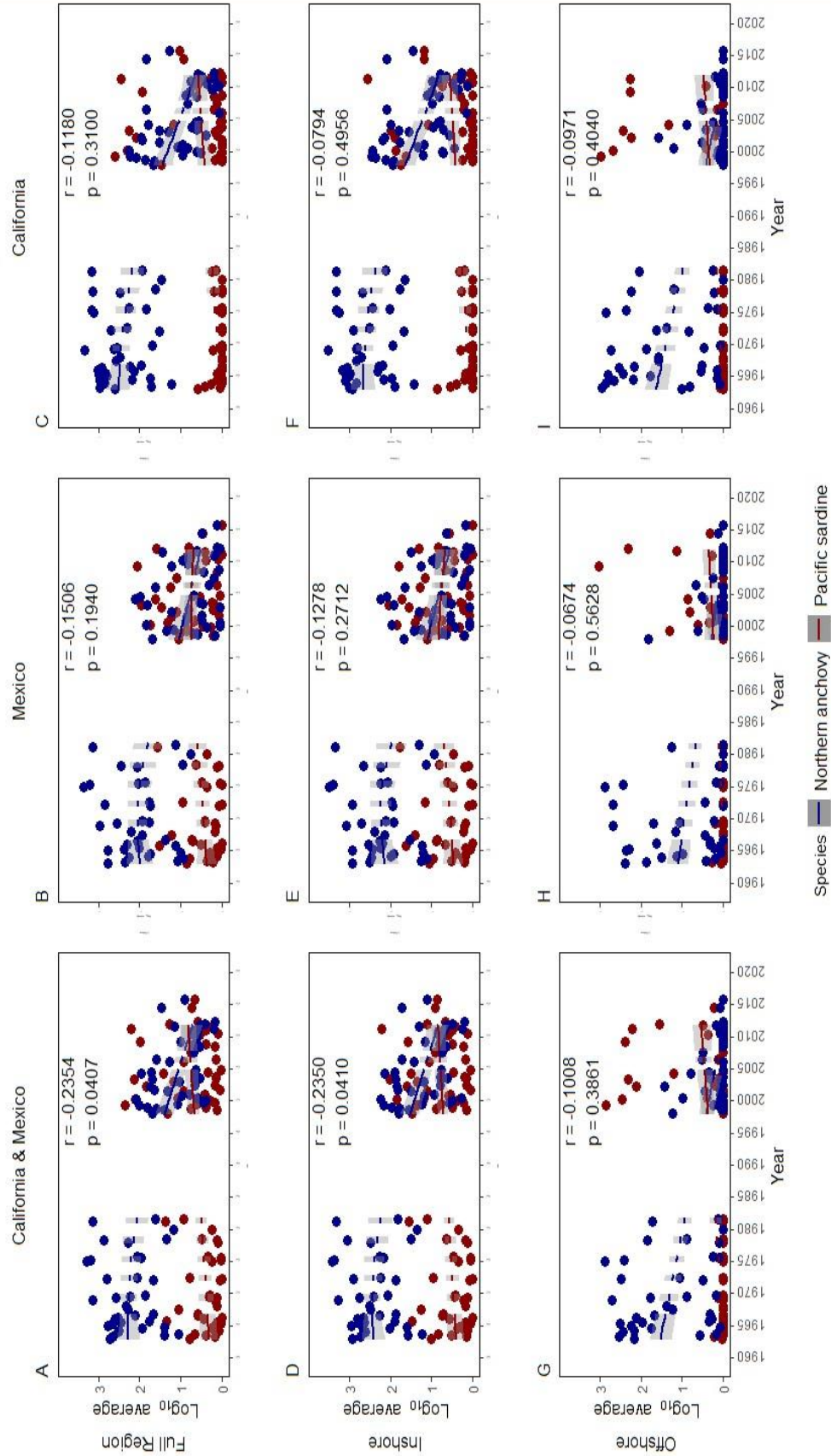
Figure 7. Average larval abundance of northern anchovy (blue) and Pacific sardine (red) from 1963-2015, separated by region (columns) and distance from shore (rows). Only cruises and stations meeting our criteria for data distribution and frequency were included. For illustrative purposes, a generalized additive model (GAM) with a 95% confidence interval (shading) was generated for both species to depict trends through time. Years that had less than 2 total cruises had their GAM line removed for that period. Spearman correlation (r) was calculated for each plot, and the significance is shown by the p-value (p).

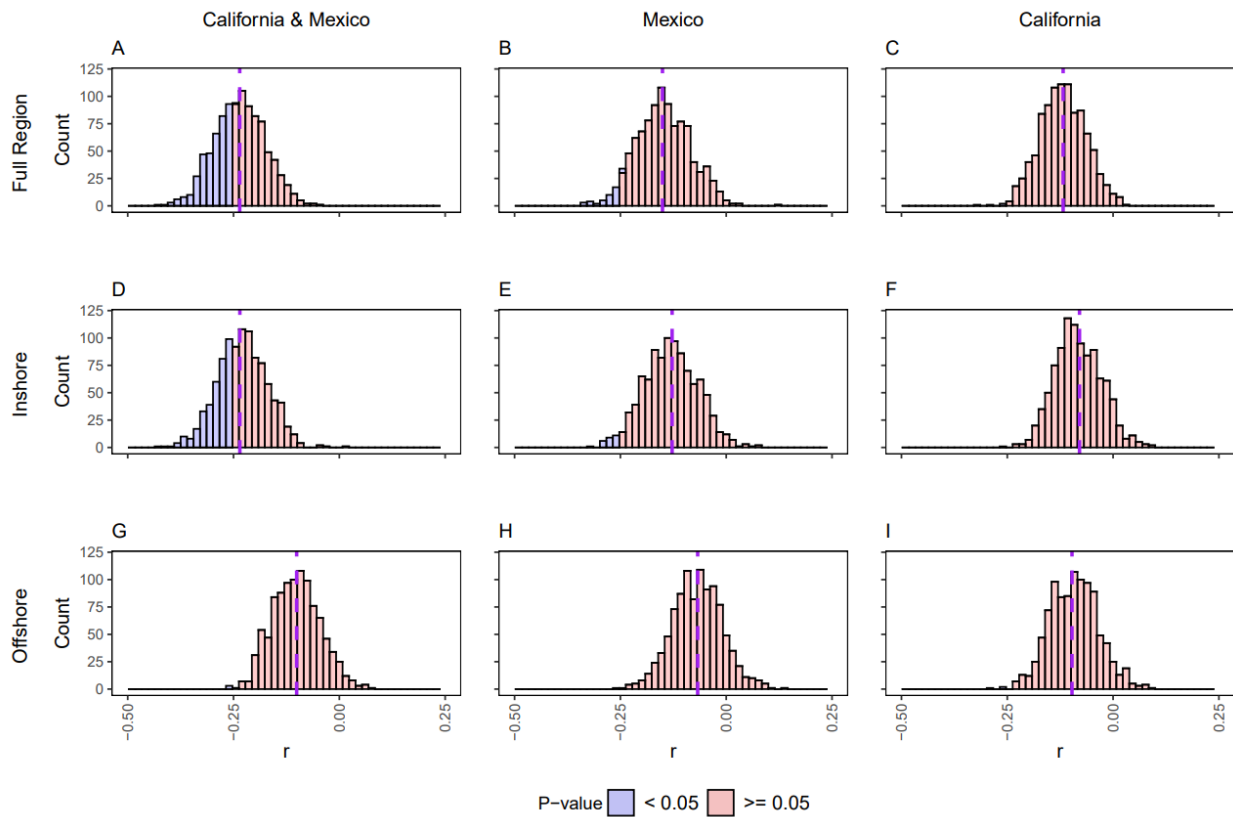Figure 8. Histograms of bootstrapped Spearman rank correlation results (denoted by "r") comparing Pacific sardine and northern anchovy larvae counts per cruise across each region; 80% of the data over time from each region was sampled randomly and repeated 1000 times, and r calculated on each subset of data. The vertical purple dashed line denotes the actual r calculated value for each region. All Spearman correlation results were included, regardless of the results respective p-value. Significant results (p-value < 0.05) were colored blue, while non-significant results (p-value $>= 0.05$) were colored red.

CONCLUSION

Sardine and anchovy populations shifted through time, appearing in California, Mexico, and occasionally both areas at once. However, these distributions were not identical between both species, with environmental and biotic conditions acting as potential drivers for larvae abundance. Larvae distributions expanded and contracted from the coast to a greater extent than moving northward and southward. Additionally, offshore expansion was positively correlated with increasing larval abundance for both species. The apparent negative correlation between anchovy and sardine larvae depended strongly on the temporal and spatial scale sampled in the CCE, and the significance of this correlation was

extremely variable. Inversely, we also did not find evidence of positive correlation between the two species. Though very long in duration by scientific standards, the CalCOFI/IMECOCAL programs only provide a snapshot of the decadal fluctuations of anchovy and sardine populations. It is difficult to robustly assess correlation patterns between these species based upon these records, but there is clearly no strong evidence for a negative relationship in population size between these species.
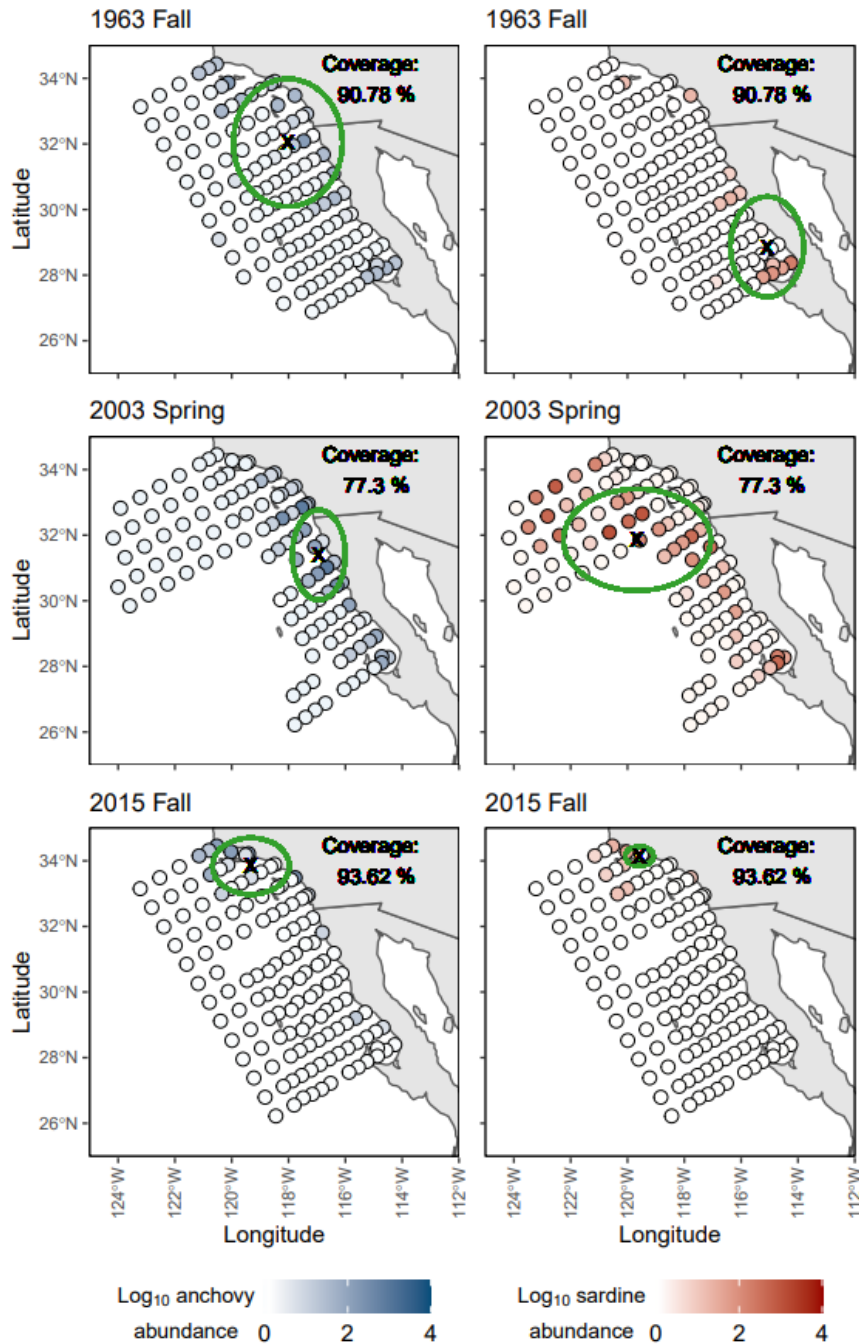
ACKNOWLEDGEMENTS

Figure S1. Northern anchovy (left) and Pacific sardine (right) larval distributions for a selection of cruises, with abundances by station. Station coverage varied per cruise, but these data include cruises and stations that met our data distribution and frequency criteria. "X" denotes the weighted mean central location calculated through the weighted average latitude and longitude. Additionally, the general spread of each species, denoted by a green circle, was determined by the weighted standard deviation of latitude and longitude. "Coverage" refers to the number of stations within that cruise compared to the number of stations of the most intensively sampled cruise (141 stations, spring of 2014), described as a percentage. These cruises were chosen as they show the shifting distributions for both species near the beginning, middle, and end of the time series data utilized.

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