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Publication Date

2025

DOI

10.1139/cjfas-2024-0151

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Temporal dynamics and distributions of sardine and anchovy in the southern California Current Ecosystem

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Abstract

Anchovies and sardines are some of the most economically and ecologically important and well-studied fishes on Earth, but there is still uncertainty regarding how distributions and abundances change through time and space. We bring together larval abundance data for northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) collected by United States and Mexican scientists over 50 years (1963–2015) to test the Basin and Asynchrony hypotheses. The Basin hypothesis states that a species' geographic range and spawning area (R) increase with overall abundance (A) according to a power law, $R = aA^b$, where the exponent (b) is less than ~ 0.5 when the rate of increasing area occupied saturates as population size increases. The Asynchrony hypothesis postulates that anchovy and sardine abundances are negatively correlated through time. We found that the Basin hypothesis was supported for both species but the Asynchrony hypothesis was not during this 53-year period. Due to collaboration between US and Mexican scientists, we were able to better understand how two important fishes utilize their environment.

Key words: Basin hypothesis, Asynchrony hypothesis, CalCOFI, IMECOCAL, coastal pelagic fish

Introduction

Fishery production is vitally important to coastal economies worldwide (Pauly and Christensen 1995). Some of the highest-volume and economically valuable fishery targets are pelagic forage fishes, principally sardines and anchovies (Checkley et al. 2017; Sydeman et al. 2020; FAO 2022). Due to their large biomass during “boom” periods that typically occur on decadal time scales, sardines and anchovies are also essential components of coastal marine ecosystems and greatly affect the reproductive success and survival of a myriad of marine predators (Jahncke et al. 2004; Cury et al. 2011; Santora et al. 2014; McClatchie et al. 2016; Fennie et al. 2023b). From an economic perspective, sardines and anchovies are also important to many coastal economies and thus affect human well-being (Steinbeck 1945; Checkley et al. 2017). For example, just two species of anchovy (anchoveta *Engraulis ringens* and Japanese anchovy *Engraulis japonicus*) and two species of sardine (European pilchard *Sardina pilchardus* and Pacific sardine *Sardinops sagax*) comprised 12% of the global finfish catch in 2020 (FAO 2022). The spatial distribution and overall population size of these species varies by orders of magnitude through time (MacCall 2009; Peck et al. 2013, 2021; MacCall et al. 2016), possibly in response to environmental factors, ecological processes,

or fishing pressure (Chavez et al. 2003; Takasuka et al. 2007; Lindegren et al. 2016; Takasuka et al. 2017; Siple et al. 2020; Giron-Nava et al. 2021). Tracking these spatial and temporal variations is important for understanding the dynamics of marine ecosystems and sustainably managing the fisheries they support (Karp et al. 2019; Sydeman et al. 2020).

Given their importance to economies and ecosystems, the population dynamics of anchovies and sardines have been studied closely for almost a century (Checkley et al. 2017). Major areas of research have included drivers of (1) spatial distribution (MacCall 1990), (2) recruitment (Ryckaczewski and Checkley Jr 2008; Nieto et al. 2014), and (3) interspecific population asynchrony (Chavez et al. 2003). Several hypotheses have been developed over time to define major drivers impacting these three processes.

The Basin hypothesis (also called the “basin model”; MacCall 1990) addresses spatial distribution patterns. It describes how the geographic distribution of a species increases with its total abundance. The Basin hypothesis states that the way that geographic area occupied by an organism changes relative to abundance is analogous to the amount of water that fills, for example, a kitchen sink. As the basin fills, the surface area taken up by the water increases until the basin is full and adding additional water does not result in

increasing area. As the basin drains, the water contracts to a single location that never goes completely dry (unless the species goes extinct). According to the Basin hypothesis, the relationship between area (R) and abundance (A) is described by a power law, $R = aA^b$. MacCall argued that b should be less than ~ 0.5 , implying that the range of a species saturates with increasing abundance. If $b \approx 1$, then the “basin” is not full and fish range expands linearly with abundance. If there is no relationship between abundance and area occupied then the Basin hypothesis is rejected (Barange et al. 1999).

The Basin hypothesis is underpinned by the idea that intraspecific competition for limited resources drives survival. It builds off the ideal free distribution hypothesis (IFDH) (Fretwell and Lucas 1970), which states that if animals have perfect knowledge of resource distribution (their perception of the landscape is “ideal”) and can move uninhibited between patches of habitat (they are “free”), then the number of animals per patch will be proportional to the resource quality of that patch. If population sizes are low, all individuals will be in the patch with the best resources. But, as population sizes increase, animals may obtain more resources per capita in suboptimal patches. Whereas quantifying patch quality is often straightforward in terrestrial environments (i.e., Fretwell and Lucas’s sparrows competed for seeds), the relationship between fishes and habitat in the open ocean is more difficult to quantify. While the IFDH is elegant in its simplicity and adherence to basic ecological principles, it is still unknown if it can explain the relationship between abundance and geographic range in coastal pelagic fishes (Barange et al. 1999; Shepherd and Litvak 2004). Here, we test whether the Basin hypothesis applies to northern anchovy (*Engraulis mordax*) and Pacific sardine (*S. sagax*) populations off the west coast of North America between two well-known marine geographic breakpoints (Bernardi et al. 2003; Pitz et al. 2020), Point Conception, California and Punta Eugenia, Baja California.

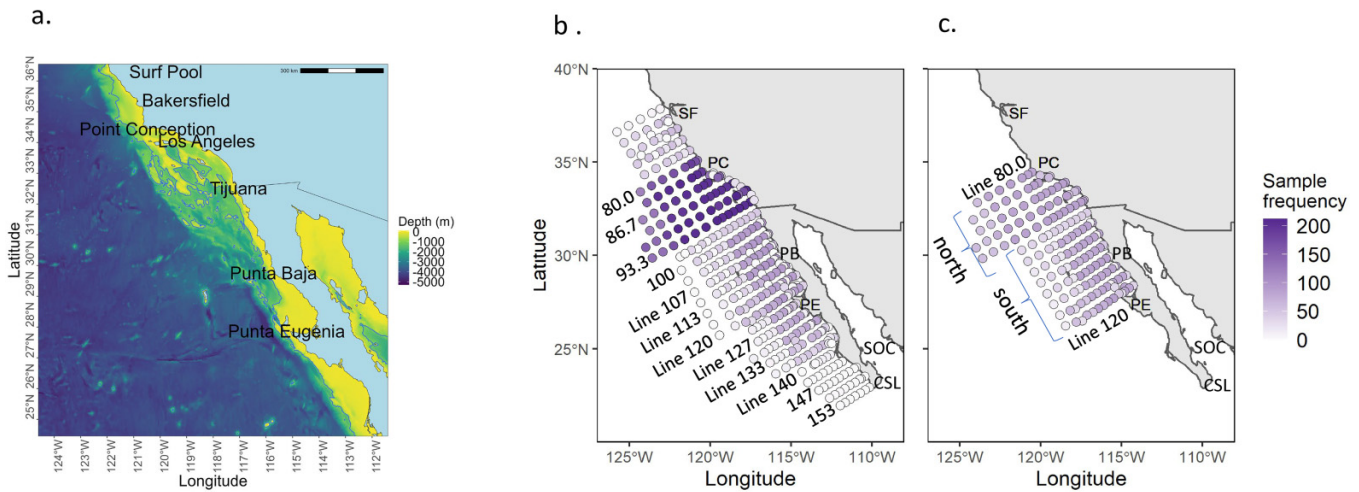
Another hypothesis underpinned by habitat dynamics describing sardine and anchovy population changes is the Asynchrony hypothesis (as articulated by Siple et al. 2020). It states that anchovy and sardine abundances are negatively correlated through time in a given ecosystem (Lluch-Belda et al. 1989, 1992; Schwartzlose et al. 1999; Chavez et al. 2003). Whereas habitat preference presumably controls the distribution of adults and drives the Basin hypothesis, bottom-up, large-scale environmental forcing that differentially affects larval survival and recruitment of anchovy and sardine is the most likely explanation for asynchrony (although factors such as predation, fishing pressure, and competition may also play a role). Chavez et al. (2003) proposed that cyclical changes in oceanographic conditions at the time scale of decades control anchovy and sardine asynchrony, and that anchovy thrive under cold and sardine under warm oceanographic regimes. However, paleorecords that use carbon-dated scale deposits in anoxic sediments to quantify population dynamics over centuries found no evidence for alteration between periods of high anchovy and sardine population sizes in the United States, Peru, or Japan (Baumgartner et al. 1992; Finney et al. 2010; Kuwae et al. 2017; McClatchie et al. 2017; Salvatelli et al. 2018, 2022).

In addition, recent analyses of global records of anchovy and sardine abundances concluded that the negative relationships found by Lluch-Belda and others may be products of the analysis of short time series data and/or reliance on fishery-dependent data (Izquierdo-Peña et al. 2019; Siple et al. 2020; Ong et al. 2021). The validity of the Asynchrony hypothesis is thus still in question.

In the northeast Pacific Ocean, the California Current Ecosystem (CCE) is home to Pacific sardine (hereafter “sardine”) and northern anchovy (hereafter “anchovy”) (Checkley et al. 2017). Both species are capable of being the most abundant fish in the CCE. Sardine live approximately 8 years and reach a maximum size of 41 cm, although fishery catches are rarely over 30 cm (Kuriyama et al. 2020). When abundant, sardine migrate north from southern/central California to the Pacific northwest during summer and return south in winter. In the US, sardine is currently managed as two separate stocks, one ranging from approximately northern Baja and into the US, and the second distributed from approximately northern Baja California to Bahia Magdalena in Baja California Sur. However, the biological validity of the sardine stocks has recently been called into question (Craig et al. under review). Anchovy are smaller and shorter-lived than sardine, reaching a size of approximately 18 cm and 4 years of age (Kuriyama et al. 2022). Anchovy are managed as three separate stocks (Sydemann et al. 2020). The northern group lives between Queen Charlotte Island, British Columbia in the north to Cape Mendocino, California in the south. The central stock ranges from approximately San Francisco, California, to Punta Eugenia, Mexico, while the southern stock is south of Punta Eugenia and into the Sea of Cortez.

The CCE is one of the best-monitored marine ecosystems in the world (Gallo et al. 2022). In particular, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program is the world’s longest-running fishery-independent monitoring survey and has systematically measured the abundance of larval fishes since 1951 (McClatchie 2014; Gallo et al. 2019). CalCOFI collects larval fish with plankton nets and sampling is currently concentrated in the southern CCE from approximately Point Conception to the US/Mexico border (McClatchie 2014; Fig. 1, Fig. S1). CalCOFI also sampled throughout Baja California for the first three decades of the program but ceased entering Mexican waters in 1984 (McClatchie 2014). The former Mexican CalCOFI stations, however, were reoccupied off Baja California, Mexico from 1997 to 2018 by Investigaciones Mexicanas de la Corriente de California (IMECOCAL; Funes-Rodriguez et al. 2002; Funes-Rodriguez et al. 2006). The IMECOCAL program regularly collected data from just south of the US/Mexico border to Punta Eugenia, Mexico, although it occasionally went south to Cabo San Lucas (Fig. 1, Fig. S1). In this study, we combine these two larval fish datasets across the southern CCE to reassess two classic hypotheses of sardine and anchovy dynamics: the Basin and Asynchrony hypotheses. To date, joint analyses of CalCOFI and IMECOCAL data have been limited (but see Bautista-Romero et al. 2018), and this, to the best of our knowledge, is the first study to examine anchovy and sardine dynamics at such broad temporal (53 years) and spatial scales (Point Conception to Punta Eugenia; ~ 1100 km) in the CCE.

Fig. 1. (a) Bathymetry in the study region. The base map was obtained using the R package *naturalearth* (Massicotte and South 2025) and the bathymetry from *marmap* (Pante and Simon-Bouhet 2013). The map projection is GCS, the datum WGS84, and coordinate system latitude–longitude in decimal degrees. (b) Geographic extent and sampling frequency of the CalCOFI and IMECOCAL programs from 1951–1984 and 1984–2022. (c) Set of stations with sufficient sampling to be analyzed in this study. Acronyms in panels b and c stand for San Francisco (SF), Point Conception (PC), Punta Baja (PB), Punta Eugenia (PE), Cabo San Lucas (CSL), and Sea of Cortez (SOC). The base map was obtained using the R package *naturalearth*.



To provide insight on anchovy and sardine population dynamics in the northeast Pacific Ocean, we first examine larval abundance patterns off California, Mexico, and both areas combined from 1962 to 2015. Next, we test the Basin hypothesis by estimating the exponent (b) of the power law linking geographic area occupied and mean larval abundance. We also examine weighted means of centers of latitude and distance from shore against larval abundance to discern where populations are centered when population sizes are low, as these areas may serve as refugia and be particularly important for conservation. Finally, we test the Asynchrony hypothesis by correlating abundances of anchovy versus sardine off California, Mexico, and both areas combined.

Methods

Ichthyoplankton sampling

CalCOFI has conducted systematic, quarterly, cruises in the CCE since 1951 (sampling frequency and spatial extent were greater in the 1950s), with transects roughly perpendicular to the coast extending outward approximately 200–280 nautical miles (370–518 km; Fig. 1a). These transects, or “lines”, are spaced 40 nautical miles (74 km) apart, with the distance between stations being either 20 (stations on the shelf) or 40 (stations off the shelf) nautical miles (37 or 74 km; McClatchie 2014). 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 (Fig. 1, Fig. S1). CalCOFI sampled off Baja California from 1951–1984 but ceased sampling south of line 93.3 in 1985. In 1997, IMECOCAL began reoccupying the former Mexican CalCOFI stations. Here, we refer to stations at line 93.3 and north to be “northern”

or “US” stations, while stations south of line 93.3 “southern” or “Mexican” stations. To avoid spatial biases, we focused on the best-sampled portion of the grid (Fig. 1b). Cruises were grouped seasonally by the months in which station sampling occurred. Months that fell into each season were organized as such: (winter) December, January, February; (spring) March, April, May; (summer) June, July, August; and (fall) September, October, November. In (very rare) cases of overlap, where the duration of a cruise passed through two seasons, the cruise was grouped into the season where the majority of station sampling occurred. 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 combined CalCOFI and IMECOCAL cruises (e.g., 142 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. These criteria eliminated samples from the 1950s and early 1960s, and hence we began with data from 1963, when sampling patterns were more consistent with the modern CalCOFI cruises. Our sampling criterion also excluded CalCOFI and IMECOCAL data after 2015, as IMECOCAL sampling has been sparse in recent years. Our final data set thus spanned 53 years (1963–2015). However, samples were not necessarily present in each season in each year. For example, between 1969 and 1983 samples were collected every third year and sporadic mechanical issues with a ship limited sampling in some years. Nevertheless, 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.

CalCOFI and IMECOCAL collected fish larvae (ichthyoplankton) with obliquely-towed ring nets (1951–1977) and bongo nets (1978 to present; [Ohman and Smith 1995](#); [Thompson et al. 2017](#)). Detailed sampling protocols can be found in [Kramer et al. \(1972\)](#) and [Smith and Richardson \(1977\)](#), but, briefly, nets were towed to 140 m (or within 15 m of the bottom at shallow stations) from 1951–1968 and then to 210 m after 1968 ([Ohman and Smith 1995](#)). Plankton in ring nets and starboard side of the bongo net were preserved in 5% buffered formalin, while, beginning in 1997, contents of the port side net were preserved in 100% ethanol ([Gold et al. 2024](#)); here, we focus on just formalin-preserved samples. In the laboratory, all larval fishes were sorted from the rest of the plankton and identified to species. Whereas it is not possible to identify all ichthyoplankton to species (e.g., rockfishes; [Thompson et al. 2016](#)), anchovy and sardine are readily identifiable at all life stages. To account for any differences in tow depths or the amount of water filtered, raw abundances were standardized by multiplying by standard haul factor which accounts for the volume of water that was filtered (standard haul factor; [Smith and Richardson 1977](#)) and divided by the percent of the sample sorted (100% of most samples were sorted but in cases where zooplankton biomass was very high a fraction was sorted). These adjustments make it possible to directly compare samples across the time series despite some changes to sampling methodology through time ([Thompson et al. 2017](#)). The units of abundance from the net tows are reported as “number under 10 m²”, which is the number of larvae in a column of water with area 10 m² extending downwards to the depth of the tow.

Long-term trends in abundance and distribution

Larval fish abundance is often used as a proxy for adult spawning stock biomass (SSB; [Richardson et al. 2009](#); [Ingram Jr. et al. 2010](#); [Adamski et al. 2011](#)). To verify that larval abundance reflected SSB, we used linear models (Fig. S2) to evaluate the significance of correlation estimates of SSB from stock assessments (anchovy: [Hinchliffe et al. 2025](#); sardine: [MacCall 1979](#); [Hill et al. 2010, 2016](#)) and mean larval abundance of all stations in spring (the peak spawning season for both species) in the years when larval data and assessment estimates overlapped (anchovy: 1969–2012; sardine: 1963–1965, 1981, and 2000–2012). We recognize that the spatial domain for our larval data and the stock assessment did not completely overlap, but we determined that this analysis was appropriate as our goal was to discern if the larval data was capable of differentiating periods with greatly different SSB. All statistical analyses were performed using R-4.3.1 ([R Core Team 2023](#)) and graphing and mapping was completed using the package `ggplot2` ([Wickham 2016](#)).

To qualitatively evaluate temporal dynamics, we plotted mean larval abundance of anchovy (Fig. 2a) and sardine (Fig. 2b) per station per cruise for each quarterly sample from the northern (<line 94) and southern (>line 94) stations combined, the northern stations alone, and the southern stations alone. To visualize the relationship between larval abundance and time on decadal scales, we fit a generalized

additive model (GAM) with the package “`mgcv`” ([Wood 2006](#)). To ensure that trends over a short period of time were visible, we iteratively explored how changing knots affected the shape of the line and eventually set the number of knots in the GAM to six. Our purpose was not to assess statistical relationships between year and abundance, and we thus do not report GAM statistics nor plot standard errors.

To further visualize changes through space and time, we created heatmaps of log₁₀ average larval abundance within 0.5° latitudinal bins for each season from 1962 to 2015 to examine the yearly weighted mean latitudinal abundance between adjacent seasons.

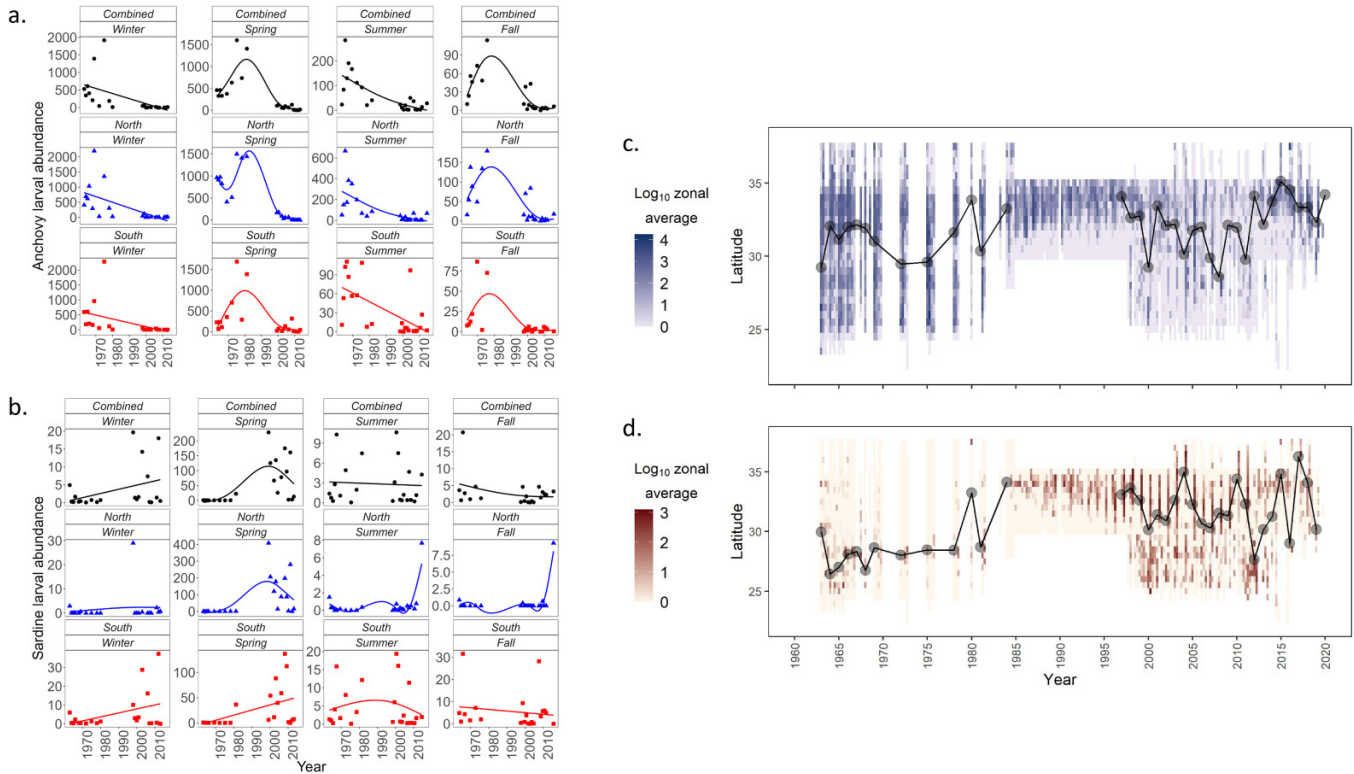
Basin hypothesis

We determined the area occupied by sardine and anchovy larvae in spring (the season when abundances tended to be highest). Notably, we assume that larval distribution is a suitable proxy for adult distribution as most larvae are less than a week old and likely had not moved far from their mothers ([Hewitt 1980](#)). We first drew a polygon around the periphery of stations where at least one individual was found using the R packages “`alphahull`” ([Pateiro-Lopez and Rodriguez-Casal 2022](#)) and “`igraph`” ([Csardi et al. 2023](#)). If positive stations were more than 100 km from one another, we did not consider area occupied to be contiguous and drew multiple polygons. We then determined the area within each polygon (km²) using the package “`sf`” ([Pebesma and Bivand 2023](#)) after using the “`PBSmapping`” package ([Schnute et al. 2022](#)) to convert longitude and latitude into UTM coordinates (which are meters rather than decimal degrees). For sardine, there were 4 years (1964, 1966, 1972, and 1975) when less than three stations had sardine larvae in spring, which precluded determination of area. In these cases, we determined the area occupied from the nearest season when at least three stations had sardine larvae (winter 1964 and 1966, summer 1972, and fall 1975). The exponent *b* in the power law linking abundance to area ($R = aA^b$) is the slope of the linear relationship between the log₁₀ transformed area and abundance data, estimated using a linear least squares approach. Ninety five percent confidence intervals for the slope and intercept (log₁₀ a) were also estimated.

To evaluate where population centers within our sample frame occur over time, we calculated the abundance-weighted average distance from shore ($\overline{\Delta x}$, km) and latitudinal position (\overline{Y} , °latitude) of the larval distribution from the combined northern and southern data. We removed years when the number of stations with at least one larva was less than four to reduce the potential influence of spurious data. 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 2024](#)). We ignored detached land masses, such as islands, and focused on the mainland coastline only. The weighted mean distances from the coast ($\overline{\Delta x}$) and latitude (\overline{Y}) are:

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

Fig. 2. Mean larval abundance per station per cruise (No. under 10 m^2) for all stations (top row), stations just in the north (middle row) and stations just in the south (bottom row) for (a) anchovy and (b) sardine. Generalized additive model (GAM) fits were added to each subplot to highlight variations through time. Mean \log_{10} abundance per 0.5°N latitude through time and center of latitudinal abundance (points) for (c) anchovy and (d) sardine. Center of latitudinal abundance is the annual average larval abundance for each species weighted by the latitudinal position of the station where they were collected. This was calculated only for periods where we had data from stations above and below the US/Mexico border. A line was added to visualize trends over time.



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

where i is the station in the sampling grid, n is the total number of stations, Δx_i is the distance (km) from the coast for station i , Y_i is the latitude for station i , and A_i is the larval abundance at each station.

We used linear models to determine if there was a significant relationship between mean larval abundance and weighted mean latitude and distance for shore. We also used the acf function in R software to test for temporal autocorrelation in the residuals, but there was no sign of strong autocorrelation and hence we did not further adjust p -values.

Asynchrony hypothesis

We used Spearman's rank correlation to assess if there was a negative correlation between sardine and anchovy average \log_{10} larval abundances. We conducted analyses using larval data averaged over the combined northern and southern data, and northern and southern regions alone. To evaluate if there was a seasonal effect, we also analyzed each quarter separately. A sequential Holm-Bonferroni adjustment to p -values was applied to account

for multiple runs of the Spearman rank correlation tests (Holm 1979).

Results

Long-term trends in abundance and distribution

Larval abundances in spring and SSB estimates from stock assessments were highly linearly correlated for both species (Fig. S2; $p = 0.001$, $R^2 = 0.54$ for anchovy; $p = 0.002$, $R^2 = 0.48$ for sardine). We were therefore justified in using larval abundance as an index of SSB.

Temporal changes in larval abundances in the northern and southern regions were mostly similar for anchovy (Figs. 2a and 2c). Larval abundances were highest in winter and spring, moderate in summer, and lower in fall. Spring and fall larval abundances were high in the 1960s and 1970s, and peaked in the mid-1980s. Larval anchovy abundance generally was lower from 1998 to 2015 than in the preceding decades. Notably, larval anchovy abundance was low in all seasons subsequent to 2005.

The temporal patterns of sardine larval abundance were also similar in the north and south but less so than for

anchovy (Figs. 2b and 2d). Peak sardine larval abundance was generally lower than anchovy larval abundance (Fig. S1). In both the north and south in winter and spring, there were no larvae in most years/seasons from 1963 to 1984. When sampling in the south resumed in 1997, sardine larval abundances were high in both the northern and southern areas, but the highest year/season was almost three times higher in the north (average of 408 larvae under 10 m²; spring 1999) than the south (average of 137 larvae under 10 m²; spring 2008). In summer and fall, there was little change in larval abundance through time in either the north or south (with the exception of a spike in abundances in the north in summer and fall of 2015). Larval abundances in these seasons were always lower than the peak years in winter and spring, but abundances tended to be higher in the south than the north. In summer, peak larval abundance was 3.5 times higher in the south (average of 19 larvae under 10 m²; fall, 1965) than the north (average of 8 larvae under 10 m²), and in fall, maximal abundance was 2.5 times higher in the south (average of 32 larvae under 10 m²; fall 1965) than the north (average of 9 larvae under 10 m² fall 2015). Moreover, in summer, there was never a year without any sardine larvae at all in the south but larvae were completely absent in seven summers in the north. This pattern was more pronounced in fall as sardine larvae were absent in 16 years in the north but only 2 years in the south.

Basin hypothesis

The geographic area occupied by anchovy and sardine increased with larval abundance for both species in a manner consistent with the Basin hypothesis. For both species, geographic area occupied increased steeply at lower abundances and then saturated. A power law equation with an exponential term, b , of less than 0.5 explained more than double the variation (anchovy $R^2 = 0.68$, sardine $R^2 = 0.45$; Fig. 3a, Table 1) of linear equations (anchovy $R^2 = 0.23$, sardine $R^2 = 0.22$; Fig. 3b, Table 1). Notably, spring 2011 was a major outlier for sardine (Fig. 3b), but b was still less than 0.5 ($b = 0.28$) when this year was excluded, indicating that the outlier did not qualitatively affect the result.

The weighted mean distance from shore ($\overline{\Delta x}$) and latitude (\bar{Y}) correlated with larval abundance for sardine but not anchovy (Fig. 4; Table 2). Anchovy mean distance from shore did not change with abundance and was centered at 68 km from shore when anchovy populations size was low (Fig. 4a). For sardine, the weighted distance from shore of larval occurrences increased with larval abundance ($R^2 = 0.49$; Table 2, Fig. 4b). When population sizes were very low, sardine larvae were centered at 121 km from shore (Table 2).

Anchovy center of abundance did not significantly change as abundance increased (Table 2, Figs. 2b and 4c, Fig. S3a). Anchovy latitudinal center of abundance was at approximately 32°N, about 33 km south of the US/Mexico border (Table 2, Figs. 1 and 4c). Sardine latitudinal center of abundance shifted north as population size increased ($R^2 = 0.60$, Table 2, Figs. 2d and 4d, Fig. S3b). When sardine abundance was low, the population was centered at 29.4°N, which is off

central Baja California between Punta Baja and Punta Eugenia (Fig. 1).

Asynchrony hypothesis

There was no significant Spearman rank correlation between anchovy and sardine larval abundances at any spatial scale considered in any season after correcting for multiple testing (Fig. 5, Table 3).

Discussion

Long-term patterns of larval abundance and distribution

Coastal pelagic fishes worldwide are characterized by radical swings in abundance (Peck 2021), and anchovy and sardine in the southern CCE are no exception. Our research attempted to broaden the view of anchovy and sardine population dynamics in the CCE by jointly analyzing larval abundances from two geographically contiguous datasets that have rarely been analyzed together in the past 40 years (but see Bautista-Romero et al. 2018). Whereas the dynamics of larval anchovy abundance were very similar in the north and the south, there were important differences for sardine. When the sardine population collapsed in the northern portion of its range in the late 1940s (Checkley Jr. et al. 2017), they were still consistently found in more southerly locations (centered between Punta Baja and Punta Eugenia), albeit at lower abundances.

Discerning the causes of dynamics in the abundance of sardines, anchovies, and other small pelagic fishes has been a major objective of fisheries ecology for over a century (Hjort 1914), but the mechanistic drivers of population swings are typically elusive (Hare 2014). There is general consensus that the survival of larvae to a recruitment life history stage sets population sizes in coming years (Houde 1987, 2016). Chavez et al. (2003) postulated that when ocean water at a basin scale was warm, sardine thrived, and vice-versa for anchovy. In the CCE, it was predominantly cool from 1950 to 1976, warm from 1977 to 1998, and cool from 1999 to 2013 (Peabody et al. 2018). However, these periods do not line up well with periods of high anchovy (approximately 1960–1990) and sardine (1985–2013) abundances. In the last decade, the idea that anchovy thrive under cool and sardine under warm ocean conditions was further undermined. 2014–2016 was the warmest 3-year period on record in the north east Pacific (Jacox et al. 2018), and prolonged anomalously warm conditions persisted in the CCE from 2014–2022 (Thompson et al. 2024). While sardine abundance did not rebound during this warm decade, larval anchovy abundance in spring rose to record high levels from 2015 to 2022 (Thompson et al. 2022).

Although the mechanistic drivers of anchovy and sardine population dynamics have not yet been resolved, some recent progress has been made with anchovy. Swalethorp et al. (2023) used compound-specific stable isotope analysis to quantify the trophic position of larval anchovy prey using preserved larvae collected by CalCOFI from 1960 to 2015. They found that the population boomed when larvae

Fig. 3. Relationship between mean larval abundance per station per cruise (No. under 10 m²) and geographic area occupied (km²) for (a) anchovy and (b) sardine. The lines are the best fit power functions (see Table 1).

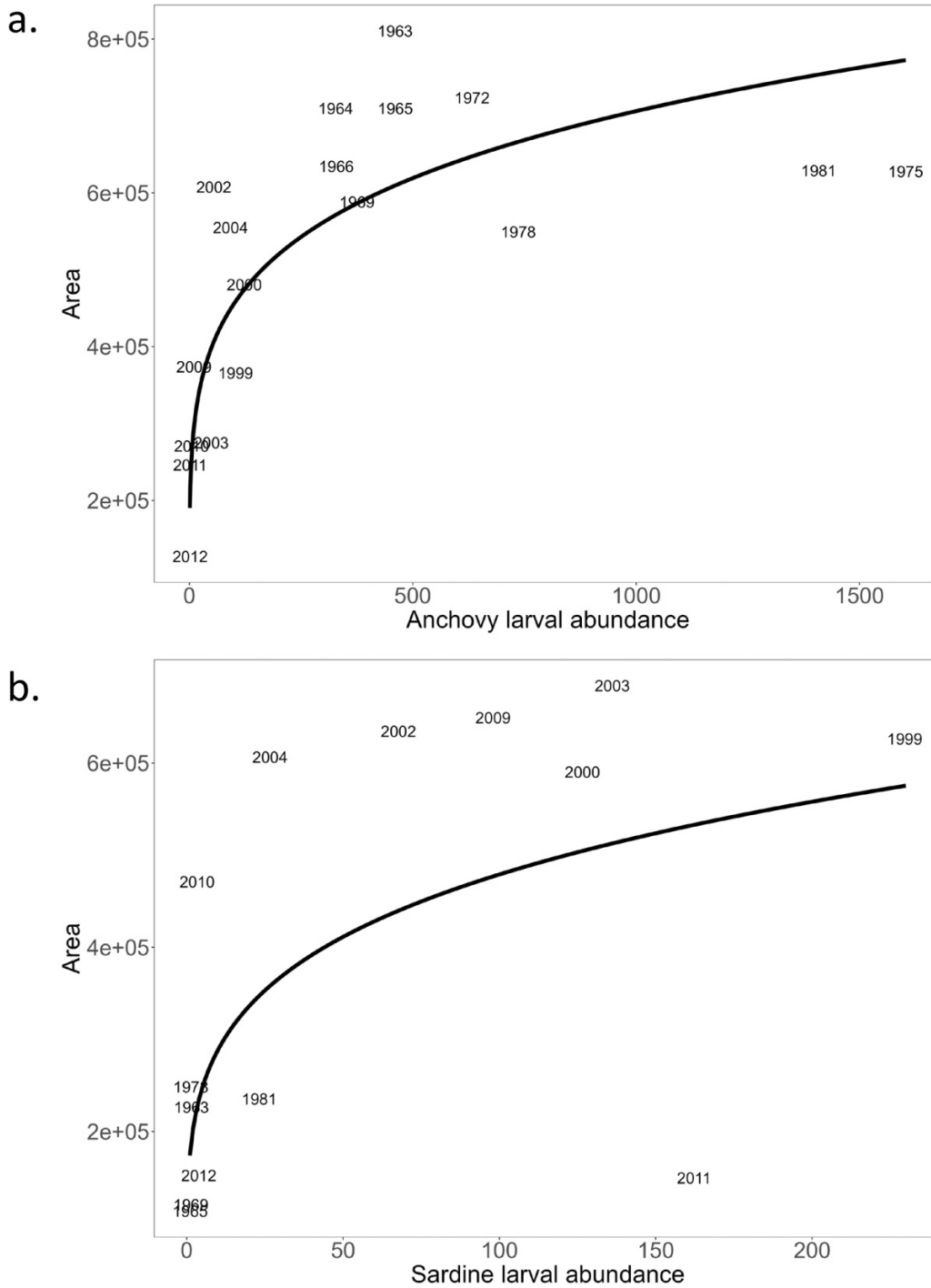


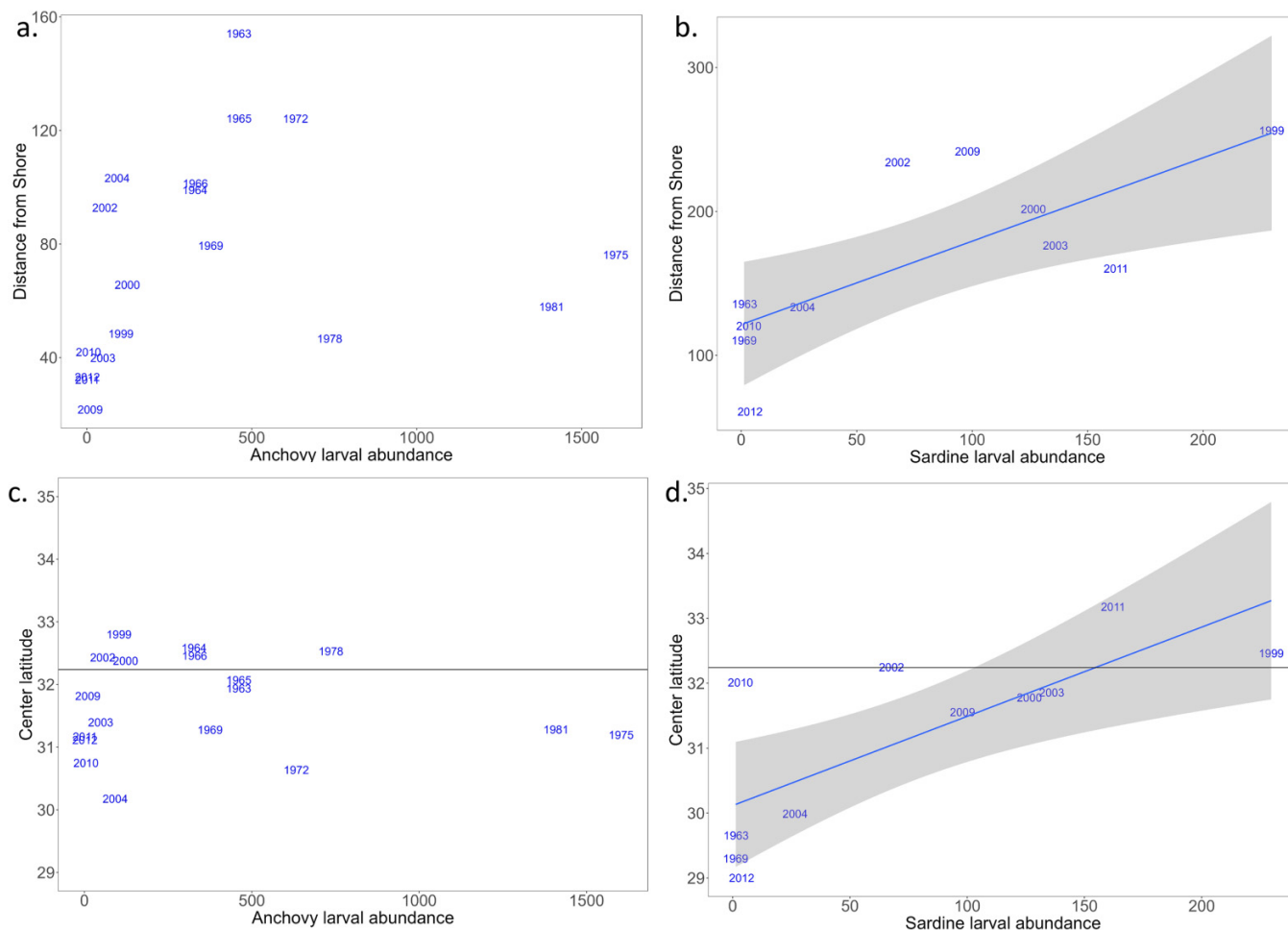
Table 1. Estimates of coefficients m and b in linear ($R = mA + b$) and a and b in power ($R = aA^b$) models, where R is the geographic area occupied (km²) and A is the larval abundance (No. 10 m⁻²).

| Species | Linear | | | | Power | | | |
|---------|----------------------------|--------------------|-------|-------|----------------------------|--------------------|-------|----------|
| | m [95% CI] | b [95% CI] | R^2 | p | a [95% CI] | b [95% CI] | R^2 | p |
| Anchovy | 0.0013 [0.00027, 0.0023] | -280.7 [-833, 271] | 0.23 | 0.024 | 239 100 [150 390, 327 809] | 0.15 [0.09, 0.22] | 0.68 | 0.000002 |
| Sardine | 290 504 [148 690, 432 318] | 1634 [157, 3111] | 0.22 | 0.051 | 216 200 [80 842, 351 558] | 0.19 [0.047, 0.33] | 0.45 | 0.00001 |

Table 2. Linear models for abundance-weighted mean distance from shore ($\overline{\Delta x}$, km) and abundance-weighted mean latitude (\overline{Y} , °N) ~ mean larval abundance per season per year (No. 10 m⁻²) for anchovy and sardine.

| Model | Intercept [95% CI] | Slope [95% CI] | Model R ² | p-value |
|--|----------------------|----------------------------|----------------------|---------|
| $\overline{\Delta x} \sim$ anchovy abundance | 68 [45, 90] | 0.02 [-0.02, 0.056] | 0.04 | 0.39 |
| $\overline{\Delta x} \sim$ sardine abundance | 121.35 [83.9, 158.8] | 0.58 [0.23, 0.93] | 0.49 | 0.010 |
| $\overline{Y} \sim$ anchovy abundance | 31.72 [31.24, 32.19] | -0.00013 [-0.0009, 0.0007] | 0.01 | 0.75 |
| $\overline{Y} \sim$ sardine abundance | 29.4 [28.32, 30.52] | 1.26 [0.59, 1.93] | 0.60 | 0.005 |

Fig. 4. Relationship between weighted mean distance from shore ($\overline{\Delta x}$, km) and mean abundance per cruise per station (No. under 10 m²) for (a) anchovy and (b) sardine, and weighted mean latitude (\overline{Y} , °N) and mean abundance per cruise per station (No. 10 m²) for (c) anchovy and (d) sardine. The horizontal line in panels (c) and (d) depicts the US/Mexico border at shore. Blue font depicts winter, green spring, red summer, and orange fall cruises.



consumed lower trophic position prey (presumably facilitating efficient energy transfer) and busted when food chain length abruptly increased in the late 1980s. This finding suggested that bottom up forcing drives the availability of optimal prey for larvae that impacts recruitment and, ultimately, adult population size. Maternal provisioning is another factor that may affect recruitment. Recent research on anchovy in the CCE (Robidas 2023), European sardine (*Sardina pilchardus* off Portugal; Garrido et al. 2015), and rockfishes (*Sebastes* spp.; Fennie et al. 2023a; Walsh 2023) in the CCE found that individual larvae that were relatively large when first hatched or

extruded had a higher probability of surviving to post flexion stages. Larval quality (e.g., size at hatch, size at length, and growth rate) may be a function of maternal condition (Sogard et al. 2008; Hixon et al. 2014), and elucidating factors that affect maternal condition may be a promising area of research to better understand forces driving recruitment and population dynamics.

Basin hypothesis

MacCall’s Basin hypothesis states that if something (predation, intraspecific or interspecific competition for resources)

Fig. 5. Relationship between mean \log_{10} (anchovy abundance + 1) per cruise per station and \log_{10} (sardine abundance + 1) per cruise per station (No. 10 m²) for each season (columns) for (a–d) all stations combined, (e–h) just the north and (i–j) just the south. We display the values on a \log_{10} scale to keep the scales the same on all panels and enable visualization of both the lower and upper values.

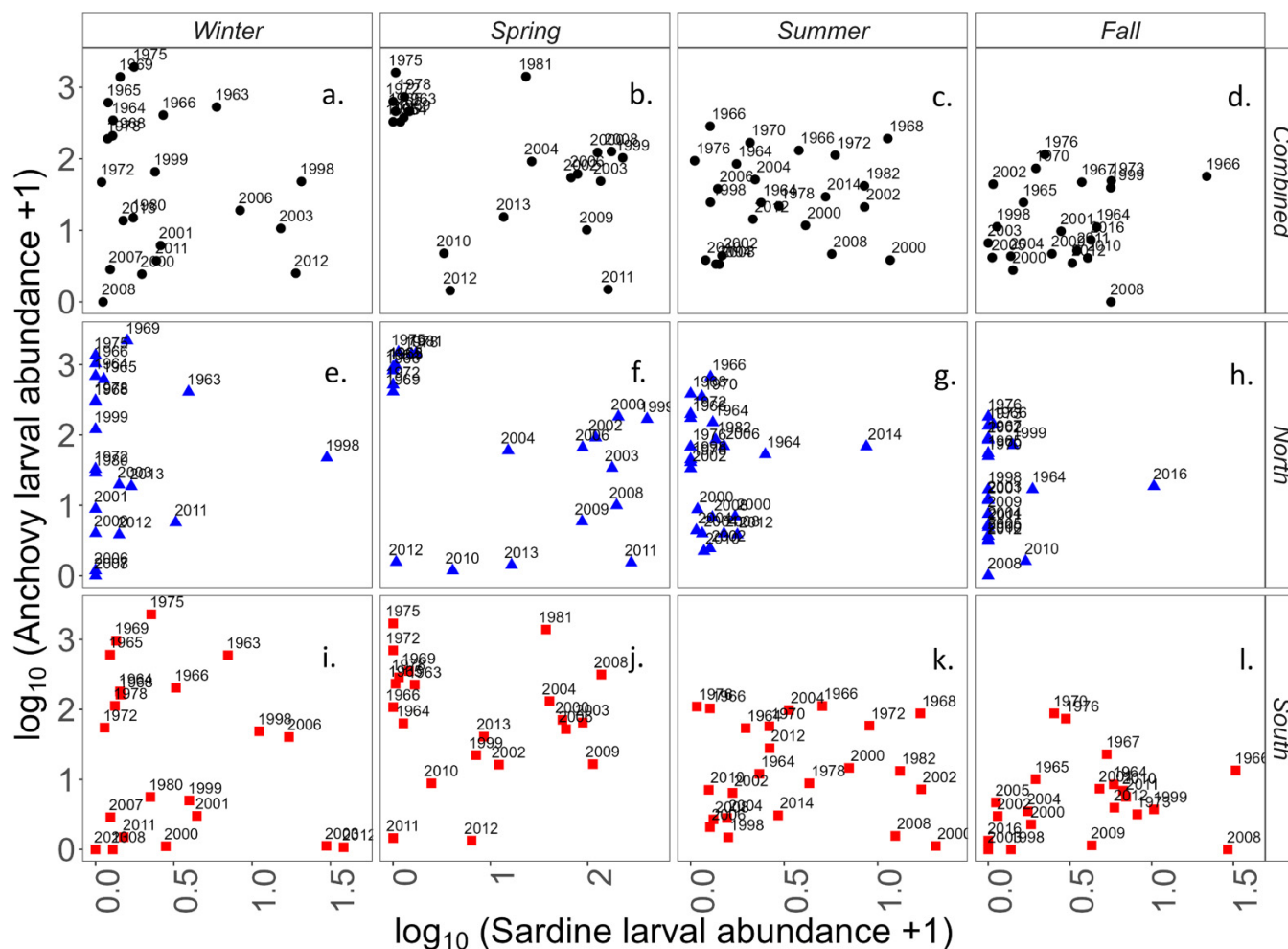


Table 3. Spearman ρ , p -value, and p -value adjusted after sequential Bonferroni correction from seasonal comparisons between all stations combined, just Mexico (southern), and just the US (northern).

| Spatial scale | ρ | p -value | p -value adjusted |
|-----------------|--------|------------|---------------------|
| Combined winter | -0.1 | 0.66 | 1 |
| Combined spring | -0.56 | 0.01 | 0.11 |
| Combined summer | 0.06 | 0.78 | 1 |
| Combined fall | 0.14 | 0.54 | 1 |
| Northern winter | 0.07 | 0.75 | 1 |
| Northern spring | -0.51 | 0.02 | 0.19 |
| Northern summer | -0.21 | 0.33 | 1 |
| Northern fall | 0.11 | 0.62 | 1 |
| Southern winter | -0.08 | 0.72 | 1 |
| Southern spring | -0.2 | 0.38 | 1 |
| Southern summer | 0 | 0.99 | 1 |
| Southern fall | 0.29 | 0.21 | 1 |

limits the expansion of a population there should be a power relationship (with the exponential term well below 1) between population size and area (MacCall 1990; MacCall 2009). Our results are consistent with this idea as we find a saturating response (i.e., $b < 1$) between abundance and area occupied for both anchovy and sardine. This finding aligns with previous analysis in the CCE, where MacCall (1990) used anchovy as a model species when developing the Basin hypothesis and found a very similar relationship between area occupied and anchovy SSB to our results. However, MacCall (2009) interpreted the findings of Smith (1990) to conclude that sardine population size and area occupied were geometric (i.e., linear with a slope of 1). Notably, Smith's data ended in 1989, and it is possible that this data set covered time periods of steep expansion and steep decline and did not include periods when sardine increased to much higher abundances the region. It is also conceivable that there is a linear relationship for sardine at a spatial scale larger than the approximately 1100 kms between Point Conception and Punta Eugenia. Adult sardine are strong swimmers relative to

anchovy, and can undergo seasonal migrations as far north as Vancouver Island, Canada in summer and fall to feed before swimming back to California to spawn in winter and spring (Checkley et al. 2017).

Whereas our results show a saturating response between abundance and area, it is important to note that the “basin” we evaluated may not contain the entire population of anchovy and/or sardine in the CCE. However, the latitudinal boundary of the area we studied is bookended by two well established biogeographic barriers (Pitz et al. 2020). In the north, Point Conception is the southern limit of the distribution of over 60 coastal fish species (Horn and Allen 1978). In the south, Punta Eugenia also serves as a barrier in fish distribution as tropical species are rarely found north of this location (Bernardi et al. 2003; Funes-Rodríguez et al. 2006, 2011; Peiro-Alcantar et al. 2016; Aceves-Medina et al. 2019). The underwater region between Point Conception and Punta Eugenia is also physically demarked by movement of the continental shelf and deep ridges and canyons bound this region. As such, the geographic range of our study makes it an ecologically relevant region to test the Basin hypothesis.

Worldwide, the Basin hypothesis for sardine and anchovy has been mostly supported. Off Japan, several studies found that Japanese sardine (*Sardinella zumasi*; Wada and Kahiwai 1991; Kobayashi and Kuroda 1991) and Japanese pilchard (*Sardinops melanostictus*; Zenitni and Yamada 2000) adhered to density-dependent habitat use, and the relationship between population size and area was well fit with a power function with an exponent term < 0.5 . Similar to our findings, Barange et al. (1999) found a curvilinear relationship between biomass and area for South African anchovy (*Engraulis capensis*) in the southern Benguela Current Ecosystem. However, they found no relationship between biomass and area for Benguela sardine (also *Sardinops sagax*). In addition to small coastal pelagic fishes, the relationship between area occupied and abundance of Atlantic cod (*Gadus morhua*) and yellowtail flounder (*Pleuronectes ferruginea*) largely adhered to the Basin hypothesis (Swain and Wade 1993; Atkinson et al. 1997; Brodie et al. 1998; Zenitani and Yamada 2000; Simpson and Walsh 2004).

Both our study and MacCall (1990) found that anchovy were centered near the US/Mexico border. MacCall reasoned that southern California was a region where larval retention and thus larval survival is high. By contrast, very similar to Lluch-Belda et al. (2003) who analyzed egg abundances collected between 1951 and 1967, we found that sardine larval distribution contracted to Baja California between Punta Baja and Punta Eugenia when abundance was low. Thus, these areas may serve as refuge habitats during times of low population sizes and may be particularly important for conservation (Brown and Kodric-Brown 1977; MacCall 1990; Lluch-Belda et al. 2003). For both species, an important next step would be to discern the habitat features that allow them to persist in these regions when absent or so low that they are undetectable elsewhere.

The US NOAA National Marine Fisheries Service currently manages sardine under the assumption that two genetically distinct subpopulations (Pacific Fisheries Management Council 2023) occupy US waters based on a hypothesis proposed

by Marr (1960). Under this idea, a putative northern subpopulation occurs in US water year-round while the southern subpopulation is in Mexican waters during winter and spring, and then moves into southern California in summer and fall (Smith 2005; Kuriyama et al. 2020; Pacific Fisheries Management Council 2023). Analyses based on morphometrics and otolith shape also supported the two-population idea in the CCE (Felix-Uraga et al. 2005; Vergara-Solana et al. 2013). However, there is some debate as to whether these stocks should be considered separate populations, as phenotypic plasticity in response to a gradient in water temperature could affect both body shape and otolith development (Craig et al. in prep). In addition, there is no genetic evidence differentiating sardine captured off Mexico versus the US (Lecomte et al. 2004; Adams 2023), and previous rationales for separation based on variables such as vertebral count and blood type have failed to consistently separate subpopulations in recent reanalysis of the original data (Craig et al. in prep). Modern whole genome sequencing of sardine collected in the US and Mexico should help resolve the population status of sardine in the CCE (Longo et al. in prep).

Here, we are agnostic to the population structure of sardine. In years when larval sardine were very low in abundance or absent in US waters, larvae were still found off Mexico year round (a pattern also detected by Hernandez-Vazquez (1994)). If there are actually two biological subpopulations of sardine, this means that the northern stock fell to levels that were undetectable by CalCOFI sampling. Because CalCOFI uses relatively large (the current vessel RV Reuben Lasker is 63.6 m long) ships, its capacity to sample very close to shore is limited. MacCall (1990) speculated that the northern sardine subpopulation collapsed very close to shore and even in bays and estuaries following the crash in the late 1940s. Alternatively, it is possible, as suggested by our findings, that a single stock retracted to central Baja (where spawning occurs year-round; Ahlstrom 1959) and then expanded out of Mexico as population sizes increased (Lluch-Belda et al. 2003). The lack of larval data from Mexico during the recovery in the late 1980s and most of the 1990s unfortunately prohibits us from determining if the recovery in Mexico predated that in the US.

Asynchrony hypothesis

The idea that anchovy and sardine exhibit asynchronous temporal patterns of biomass within regions is widespread in the field of fisheries ecology. This notion was described as the “Regime Problem” by Lluch-Belda et al. (1989). They detailed sardine and anchovy catch data from Japan, California, the Humboldt Current, the Canary Current, and the Benguela Current from as early as 1890 (Canary Current) to the mid-1980s and concluded that catches were asynchronous in each system. A subsequent paper expanded the time series through the 1990s arrived at the same conclusion (Lluch-Belda et al. 1992). However, we did not find evidence for asynchrony (or synchrony) between larval sardine and anchovy abundances in the CCE between 1963 and 2015 (Fig. 5; Table 3). While we observed times when sardine larvae were abundant and anchovy larvae scarce and vice versa, there were also years when their abundances were both low

and both high. As in the 1950s, anchovy and sardine larvae were both scarce in the mid-2010s (Thompson et al. 2022). Both species were also common in the mid-2000s. Our results do not support general asynchrony between anchovy and sardine, which suggests that results from previous studies in the CCE (e.g., Chavez et al. 2003) may have been influenced by using data from a smaller geographic region over a limited period of time.

Our findings support recent global analyses of sardine/anchovy dynamics that also did not detect widespread examples of asynchrony in abundance. For example, Izquierdo-Peña et al. (2019) reanalyzed the time series from Lluch-Belda et al. (1989) with an additional quarter century of data and concluded that there was no evidence of consistent alteration between sardine and anchovy abundances within any of the analyzed ecosystems. Similarly, there was no correlation between anchovy and sardine catch in the southeast Atlantic, northwest Pacific, or eastern central Pacific (Ong et al. 2021). In the most complete analysis of sardine/anchovy correlation, Siple et al. (2020) found no significant correlation between sardine and anchovy abundances in the Benguela, California, Humboldt, Kuroshio-Oyashio, or NE Atlantic systems from either fishery dependent or biomass data. The only significant result they found was a positive correlation between anchovy and sardine recruitment in the Benguela system. Thus, our findings seem to match those from around the world in failing to detect a significant correlation between anchovy and sardine abundances.

Siple et al. (2020) identified two probable causes for concluding that anchovy and sardine populations are negatively correlated: short time series and reliance on fishery-dependent data. Through a power analysis, they concluded that there is a high probability of a Type I error (mistakenly detecting a pattern when there is none) when analyzing multi-decadal cycles with less than 100 years of data. For example, in the CCE, CalCOFI sampling began in 1951 and has thus spanned one period of high sardine abundance that lasted from about 1990–2012, and two periods of high anchovy abundance (1960–1989 and 2016 to present). Therefore, although there is over 70 years of data, the number of observed cycles is only one or two (MacCall 2009; McClatchie et al. 2017). Much longer time series are needed to accurately assess relationships between sardine and anchovy abundance, and historical data from paleorecords generally do not find alteration between anchovy and sardine scale deposits. For example, there was no overall correlation between Japanese sardine (*Sardinops melanostictus*) and Japanese anchovy from approximately 900 BC to 2000 AD (Kuwae et al. 2017). In the Humboldt Current Ecosystem, there was also no correlation between anchoveta and sardine based on sediment cores collected from three locations off Peru that covered the years 1850–2000, as both species were simultaneously abundant for decades at a time at all three sites (Salvatteci et al. 2018). In the CCE, McClatchie et al. (2017) found that anchovy and sardine scale depositions were positively correlated from 1000 to 1500 AD. To date, all studies that have analyzed data from time periods spanning multiple centuries found no evidence for asynchrony between anchovy and sardine.

Utilization of landings data can also bias results towards the conclusion of asynchrony. In many fisheries, the choice of target species is not based solely on abundance (i.e., availability), but also on economic factors. For example, during the 1930–1940's, sardine were a far more valuable commodity in the CCE for fishers than anchovy. Following the collapse of the sardine population in the northern portions of its range and contraction to the south in the late 1940s, the sardine fishery was closed for almost half a century. When the sardine population increased in the 1980s and the fishery reopened, sardine were again broadly fished as far north as Canada until the fishery closed again in 2015. The fishery for anchovy in the CCE, however, has responded differently to changes in anchovy abundance. From the 1960s–1980s, there was a moderate reduction fishery during these high abundance years (Jacobson et al. 1994). Following the recent anchovy resurgence that began in approximately 2015, a significant US fishery has not redeveloped as fishers have deemed anchovy not worth pursuing based on economic forces. Thus, if fishery data (i.e., landings) were used to evaluate sardine-anchovy dynamics over the last decade in the US, the anchovy estimates would not reflect actual abundance or biomass. Notably, the current anchovy boom in the CCE may provide one of the only examples of any location on earth where anchovy abundance is very high but not heavily fished over at least the last half century.

Conclusion

Sardine and anchovy are iconic coastal pelagic species that are vitally important to marine ecosystems and human economies globally. In the CCE and other parts of the world, these species undergo fluctuations in population size (Peck et al. 2013, 2021). Our findings show that there are similar relationships between habitat utilization and population size for anchovy and sardine in the CCE. Our results also did not support Asynchrony hypothesis. This is important, because if anchovy and sardine systematically replaced one another, then there would consistently be resources for either fishers or marine predators. If asynchrony does not exist, then there can be profound ecological and economic consequences, particularly if the abundance of both species is low for extended periods and other prey that can nourish marine predators are also low. For example, the dearth of coastal pelagic fishes in the mid-2010s had large ecosystem impacts, such as the starvation of sea lion pups (McClatchie et al. 2016) and loss of fishery revenue (Free et al. 2023). Most importantly, our findings demonstrate the importance of international cooperation to gain a deeper understanding of fish dynamics in a world where fish do not respect anthropogenic borders.

Acknowledgements

We extend our deepest gratitude to Alec MacCall and Margaret Siple who inspired this work and worked with us to help improve the paper. Anela Choy also helped formulate the ideas in this paper. We are also appreciative of everyone who dedicated time and effort contributing to this research. None of this work could have been done without the efforts

of hundreds of people in the United States and Mexico that collected and processed the larval fish samples.

Article information

History dates

Received: 27 May 2024

Accepted: 23 December 2024

Accepted manuscript online: 15 January 2025

Version of record online: 19 February 2025

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Data availability

The analyzed data can be found on Dryad: <https://dx.doi.org/10.5061/dryad.zcrjdfnfm>.

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Competing interests

There are no competing interests associated with this document.

Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2024-0151>.

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