SPRING SPAWNING DISTRIBUTION OF PACIFIC SARDINE IN US AND MEXICAN WATERS

J. A. VALENCIA-GASTI AND R. DURAZO
Facultad Ciencias Marinas
Universidad Autónoma de Baja California
Ensenada, C.P. 22860
Baja California, México
augusto.valencia@uabc.edu.mx

E. D. WEBER AND S. MCCLATCHIE
NOAA
Southwest Fisheries Science Center
8901 La Jolla Shores Drive
La Jolla, CA 92037-1509

T. BAUMGARTNER
Department of Biological Oceanography
CICESE
Ensenada, C.P. 22860
Baja California, México

C. E. LENNERT-CODY
Inter-American Tropical Tuna Commission
8901 La Jolla Shores Drive
La Jolla, CA 92037-1508

ABSTRACT

The Pacific sardine, *Sardinops sagax*, is a highly migratory coastal pelagic species that occurs from the tip of Baja California to the Gulf of Alaska and in the Gulf of California. We used fishery-independent egg surveys to characterize the relative amounts of sardine spawning habitat in the exclusive economic zones (EEZs) of Mexico and the US during spring 2000–13. Most eggs were captured in the US EEZ from San Francisco to the Mexico-US border in all years sampled. A small fraction ranging from 0% to 10% of all eggs captured occurred in the Mexican EEZ, usually from Punta Eugenia north to the border. The abundance and distribution of eggs found in warmer waters between 15˚C to 18˚C off northern Baja California appear to be dependent on periods of more intense flow of the California Current, when sardine belonging to the northern subpopulation found in central and southern California extends southward into the nearshore area off Baja California. However, a small fraction of the southern subpopulation may also have spawned in coastal areas of the US-Mexican border during May in some years.

INTRODUCTION

The Pacific sardine, *Sardinops sagax*, is a coastal pelagic forage fish that inhabits the California Current Ecosystem (CCE) in the northeastern Pacific, ranging from the Gulf of Alaska to the southern tip of Baja California peninsula, Mexico, and into the Gulf of California (Clark 1945; Checkley et al. 2009). It is an important component of the CCE because it occupies an intermediate trophic level, serving as a grazer of plankton and an important prey item for pelagic fish, birds, and mammals (Cury et al. 2000; Kaplan et al. 2013). Sardines also support important fisheries when they are available in the exclusive economic zones of Canada, Mexico, and the US (Radovich 1982; Hill et al. 2015). However, sardine abundance fluctuates greatly in response to environmental conditions in the CCE (Marr 1960; Parrish et al. 1981; Lindegren et al. 2013). Sardine were the most abundant coastal pelagic fish in CCE during the 1930s and 1940s, and from about 1995 to 2005 but the population declined in the last decade to about 1%–2% of its peak abundance in 2007 (Hill et al. 2016). Given these broad population fluctuations, it is important to survey sardine distribution and abundance throughout the entirety of its range for both ecosystem assessment and harvest management.

Two subpopulations or stocks of Pacific sardine, *Sardinops sagax*, exist in CCE and another population occurs mainly in the Gulf of California (Ahlstrom 1960a; Félix-Uraga et al. 2004; Smith 2005). We refer to the two that occur in the CCE as the northern and southern subpopulations. These subpopulations have different morphometric characteristics (Félix-Uraga et al. 2005; García-Rodríguez et al. 2011; Javor et al. 2011), habitat preferences (Félix-Uraga et al. 2004), and spawning aggregations (Marr 1960; Hernandez-Vazquez 1994). However, they cannot be differentiated genetically, suggesting the subpopulations experience some level of interbreeding (Hedgecock 1986; Lecomte et al. 2004; García-Rodríguez et al. 2011). Although the ranges of the northern and southern subpopulations on the Pacific coast overlap, they are spatially segregated during periods of high abundance because the two subpopulations have synchronous north-south annual migration patterns (Félix-Uraga et al. 2004).

The northern subpopulation ranges from Vizcaino Bay (Punta Eugenia, Baja California, Mexico; fig. 1) to the Gulf of Alaska (Clark 1945). The subpopulation inhabits subarctic water mass with salinities in the range of about 32.5 to 33.7 and sea-surface temperatures (SSTs) in the range of about 12˚ to 17˚C (Checkley et al. 2000; Lynn 2003), although off Oregon/Washington, sardine occur in lower salinity water near the Columbia River plume (Emmett et al. 2005). In the 1930–40s, individuals attained total lengths up to 30 cm with life spans greater than 13 years and reaching sexual maturity at 2 years of age (Murphy 1966; Schwartzlose et al. 1999). However, since the early 1990s, the

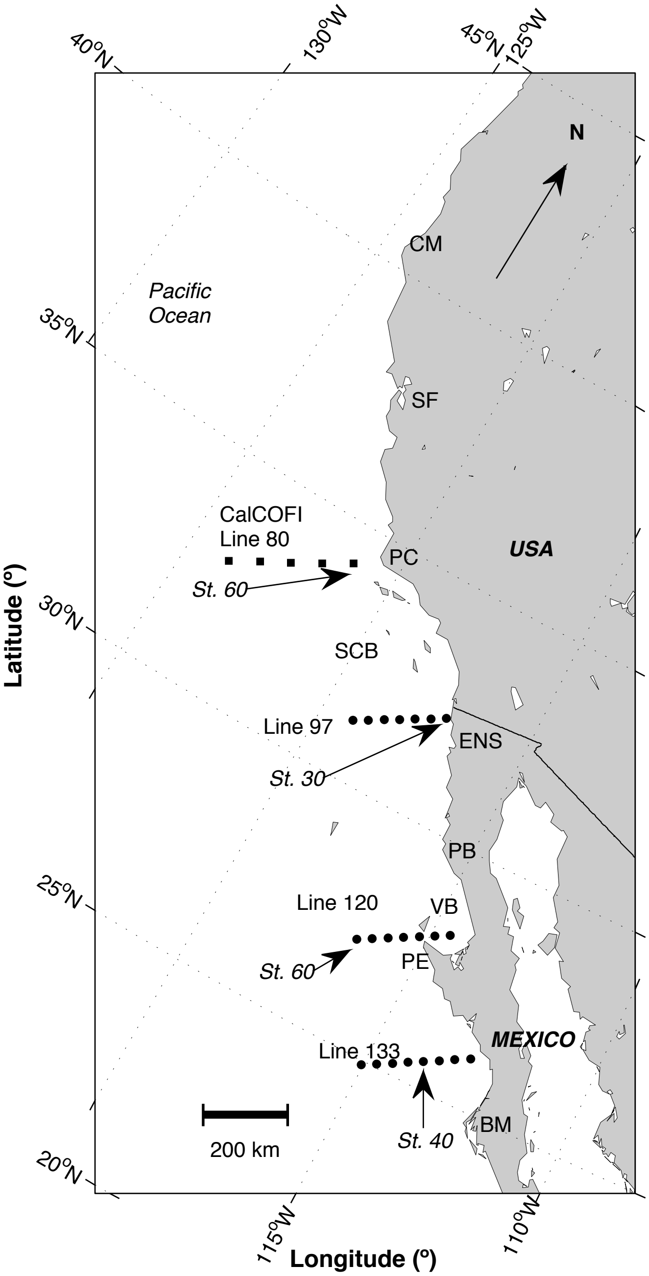

Figure 1. Map of the west coast of North America from Oregon (US) to Baja California (México) showing the location of the sites mentioned in the text; Cape Mendocino (CM), San Francisco (SF), Point Conception (PC), Southern California Bight (SCB), Ensenada (ENS), Punta Baja (PB), Vizcaino Bay (VB), Punta Eugenia (PE), Bahía Magdalena (BM). Some CalCOFI Lines are indicated by square and circles with the numeric ID to the right.

size of sardines caught by the commercial fishery have been less than 27 cm, and reach ages of five or six years with younger age-at-maturity (Lo et al. 2005; McDaniel et al. 2016). These sexually mature sardines aggregate in the southern portion of their range in spring and migrate northward in summer and early fall (Clark and Marr 1955). Spawning occurs in both waters off Baja California, Mexico, and off California in spring, and sporadically off Oregon (42˚–46˚N) in early summer (Lo et al. 2010).

The southern subpopulation ranges from the southern tip of Baja California into the southern California Bight. It inhabits Pacific subarctic water mixed with warmer and saltier waters from the south and west. The range of salinity of this water is 33.6 to 34.6 and sea surface temperature vary from 18˚ to 22˚C (Durazo and Baumgartner 2002). Fish from the southern subpopulation tend to be smaller than their northern counterparts and they reach sexual maturity at an earlier age (Butler et al. 1996). This is because the warmer water that they inhabit results in greater metabolic demands (Peck et al. 2013). The southern subpopulation spawns throughout the year along the coast of southern Baja California. Most spawning occurs in summer (July) and the least during the fall (Ahlstrom 1960b; Hernandez-Vazquez 1994). Environmental preferences of the southern subpopulation have usually been evaluated using data from the fishery (Félix-Uraga et al. 2004). Thus, their reported ranges of preferred temperature conditions may be biased by the limited spatial sampling pattern of the commercial fleet. However, preferred spawning habitat conditions have been documented by collection of temperature and salinity data with the continuous underway fish egg sampler (CUFES; Checkley et al. 1997, 2000) used on Mexican fishery-independent surveys (Valencia-Gasti et al. 2015).

The distribution pattern of Pacific sardines has important implications for management because the US stock assessment is assumed to address only the northern subpopulation (Hill et al. 2016). The assessment excludes the monthly catch attributed to the southern subpopulation in the fisheries off northern Baja California and in the Southern California Bight. However, invalid assumptions about the distribution of sardines from each subpopulation and their interannual variability could bias estimates of recruitment and fishing mortality, resulting in inaccurate assessments (Demer and Zwolinski 2014). Recent US sardine stock assessments have relied on acoustic/trawl (Demer et al. 2012) and daily-egg-production (DEPM; Lo et al. 2005) methods combined with an assessment model to estimate sardine biomass of the northern subpopulation. Surveys have been conducted in the spring when the majority of the northern subpopulation is typically aggregated offshore between San Francisco and the Mexico-US border, and in summer when sardine are concentrated farther north in shelf waters along the US West Coast.

Total annual harvest by the Mexican fishery is not regulated by quotas, but there is a minimum legal size limit for sardine to prevent the capture of juveniles (DOF 1993; Sagarpa 2012). Mexico implemented a formal management plan in 2012 and is considering modifica-

TABLE 1.
CUFES samples conducted in US and Mexican waters: the total number of stations recorded (N) from waters off central California to the southern Baja California peninsula by the research programs: CalCOFI (US) and IMECOCAL (Mexico). The number (n) and percentage (%) of stations at which sardine eggs were found (sardine presence), the mean and standard error (SE) for egg density and their water temperature.

			Sardine presence		Temperature (°C)		Egg density	
Year	N	Dates	n	%	Mean	SE	Mean	SE
U.S.								
2000	801	April 7 to April 29	262	33	13.88	0.05	9.66	0.95
2001	928	April 6 to May 2	425	46	13.13	0.03	5.99	0.57
2002	1622	March 21 to April 14	825	51	13.61	0.02	2.67	0.18
2003	1287	April 4 to April 30	514	40	13.76	0.04	9.78	0.95
2004	780	March 23 to April 22	251	32	13.5	0.04	4.89	0.44
2005	961	March 28 to May 1	297	31	14.25	0.05	3.41	0.41
2006	1385	April 6 to May 8	477	34	13.73	0.07	4.05	0.54
2007	959	March 28 to April 30	606	63	13.74	0.03	2.51	0.18
2008	1628	March 25 to May 1	556	34	13.14	0.03	2.18	0.14
2009	1127	March 8 to May 7	578	51	13.59	0.03	2.57	0.3
2010	1058	April 2 to May 16	242	23	13.64	0.05	2.57	0.42
2011	923	March 25 to April 26	333	36	13.22	0.04	1.38	0.14
2012	962	April 1 to April 28	274	28	12.95	0.03	1.33	0.13
2013	686	April 7 to May 3	179	26	13.27	0.11	2.41	0.34
Mexico								
2000	654	April 4 to April 21	58	9	15.68	0.14	1.36	0.36
2001	426	April 5 to April 14	79	19	14.69	0.12	1.95	0.41
2002	839	April 19 to May 8	82	10	15.85	0.05	0.71	0.09
2003	648	April 4 to April 23	37	6	16.22	0.11	0.44	0.16
2004	735	April 15 to May 7	79	11	16.33	0.12	0.6	0.14
2005	584	April 14 to May 6	3	1	16.63	1.17	0.17	0.12
2006	425	April 20 to May 2	29	7	16.62	0.2	0.69	0.32
2007	334	April 26 to May 7	12	4	15.58	0.21	0.1	0.02
2008	465	April 16 to May 1	15	3	15.23	0.42	0.58	0.43
2009	456	April 9 to April 24	5	1	16.6	0.16	0.11	0.03
2010	512	March 30 to April 17	5	1	16.54	0.6	1.77	1.5
2011	506	April 20 to May 7	42	8	15.48	0.12	0.95	0.32
2012	342	March 8 to March 24	39	11	15.75	0.17	1.06	0.33
2013	377	May 23 to June 7	30	8	16.36	0.32	0.65	0.29

tions to the plan that would include a harvest control rule and monitoring of biomass, similar to the US management plan. These modifications are currently undergoing review by stakeholders and the general public to improve efforts towards sustainable fisheries of small pelagic fish, with the eventual goal of obtaining certification from the Marine Stewardship Council, as was obtained by the sardine fishery in the Gulf of California (SCS 2016).

The goal of this study is to characterize the distribution of spring spawning sardines in the CCE off Mexico and the US. The specific objectives are: 1) Quantify the abundance and distribution of eggs during spring surveys conducted over a 14-year period; and, 2) Qualitatively estimate the fraction of spring-spawning sardines in waters off Mexico relative to the US to provide supporting information for stock assessment.

MATERIALS AND METHODS

Sardine eggs were collected using the CUFES during spring 2000–13 cruises as part of the Investigaciones Mexicanas de la Corriente de California (IMECOCAL; http://imecocal.cicese.mx) program in the Mexican EEZ, the California Cooperative Oceanic Fisheries Investigations program (CalCOFI; reviewed by McClatchie 2013) and sardine acoustic/trawl surveys and DEPM in the US. Sampling extended from central Oregon to southern Baja California. Cruises occurred in March through May but usually were centered on April (table 1).

The CUFES draws samples from 3 m depth with a continuous flow of approximately 640 l/min and filters ichthyoplankton by using an agitator with 200 µm mesh (Checkley et al. 2000). Samples were collected underway at speeds of 7–8 knots off Mexico, and 8–14 knots off the US. Samples generally were collected every 30 min (mean; ±12 SD) but were collected more frequently when the sampling mesh was becoming clogged by debris or large amounts of krill. Longer samples were collected occasionally (fewer than 29% of samples) when no eggs were captured in the mesh for an extended period. Overall, sample times ranged from less than 1 min to 192 min. However, all counts were standard-

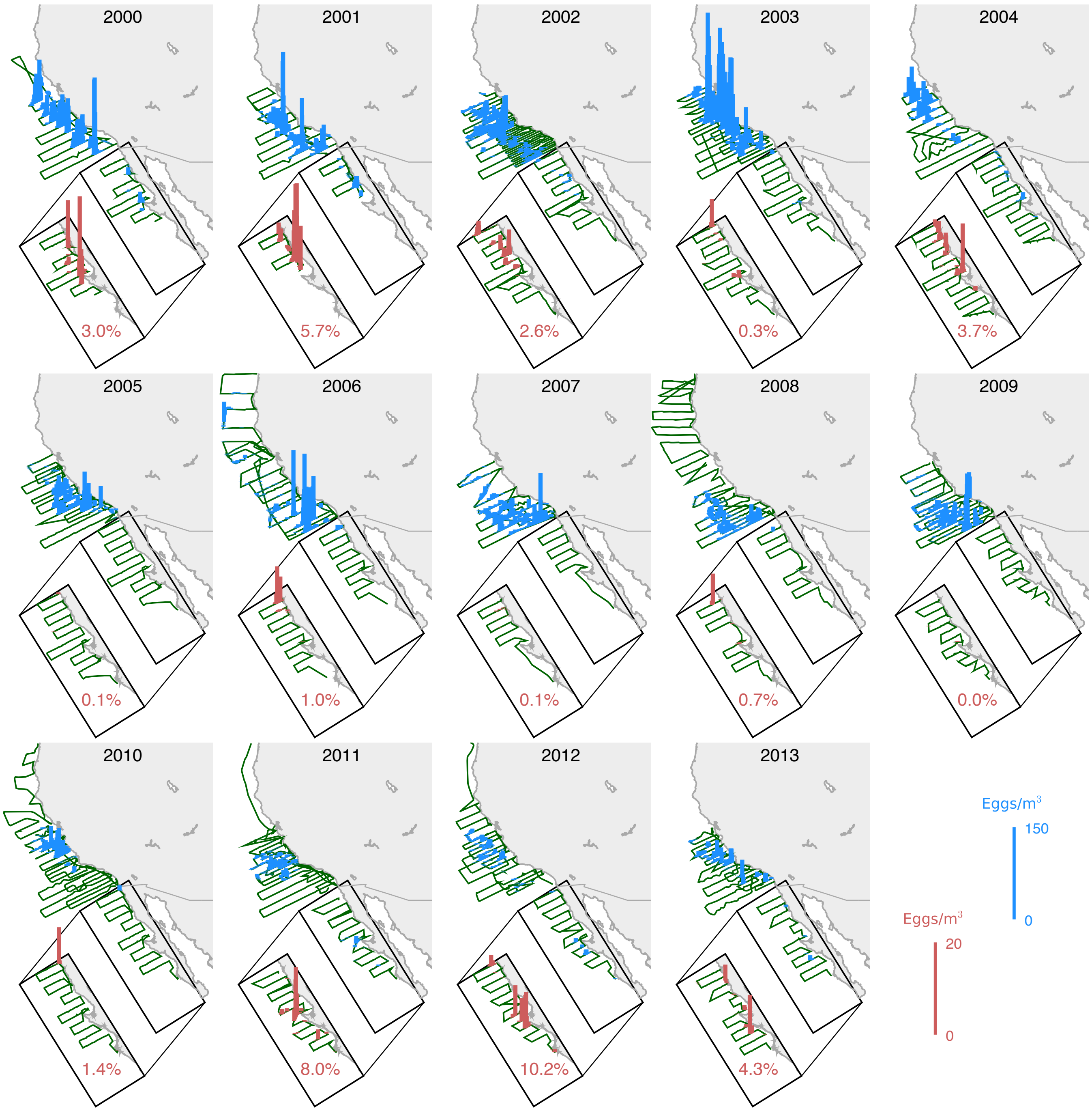

Figure 2. Observed Pacific sardine spatial distribution of eggs in the California Current System during the spring, centered on April from 2000 to 2013. Blue bars indicate sardine eggs per m^{-3} of water filtered for the entire study. Insets depict egg densities in the IMECOCAL region at greater magnification to show structure (red bars). The percentage in each panel expresses the fraction of the total number of eggs recorded in the Exclusive Economic Zone of Mexico. The paths of ships where continuous egg sampling by CUFES is performed are shown as green lines. The year of sampling is indicated at the top of each panel.

ized to densities (number of eggs m^{-3} of water sampled). Sardine eggs were identified using the morphometric characteristics described by Moser (1996).

There were 22,410 observations (stations sample) in the data set. Of those, eggs were present in 6,334 (~28%) of the samples (table 1). Sea surface temperature was collected using a thermosalinometer between each CUFES stations. Mean temperatures and standard error are also summarized in Table 1.

RESULTS

From 2000 to 2013 nearly all spawning in spring occurred between San Francisco (38°N) and Punta Eugenia, Mexico (~28°N; fig. 2). The core of the spawning area was located in waters around Point Conception (34˚N) but tended to shift northward and inshore during El Niño events as well as the warm years in the California Current (2003, 2005, and 2010), and southward to offshore of the Southern California Bight during the cooler years from 2006 to 2009. Sampled egg densities were greatest in the early years of the study, 2000–03, when they commonly exceeded 55 eggs/m^3 and reached densities as high as 175 eggs/m^3 in core spawning areas (fig. 2; table 1). Sampled egg densities generally declined during the study period, falling to densities of 12–29 eggs/m^3 in core spawning areas during 2011–13. The mean annual sea-surface temperature in which eggs were captured in US waters ranged 13.0–14.3˚C.

Spring spawning in the Mexican EEZ was primarily scattered in coastal areas between Punta Eugenia and the US-Mexican border. In the early 2000s, when egg densities were high, most spring spawning off Baja California occurred between Punta Baja (30˚N) and Punta Eugenia (28˚N) producing egg densities greater than 4 eggs/m^3. Egg densities sampled in Mexican waters were an order of magnitude lower than mean egg densities during the same period off California. During the period 2011–13, when egg densities were low off California, most spawning in the Mexican EEZ occurred around Punta Eugenia with egg maximum densities in the range of 7–10 eggs/m^3 (table 1). Some spawning also occurred to the south between Punta Eugenia and Bahía Magdalena (~25˚N) during 2011–13. The maximum densities of eggs were higher in 2011–13 (8–10 eggs/m^3) than in 2000–03 (4–17 eggs/m^3) off Mexico, while the opposite was true off California where maximum egg densities were 12–29 eggs/m^3 in 2011–13 and 55–176 eggs/m^3 in 2000–03. Most eggs were captured at temperatures between 15˚ and 17˚C.

Only a small portion of the total spring spawning occurred in the Mexican waters off Baja California, ranging from 0.02%–10% of all eggs captured per year, as depicted in Figure 2. The proportion of spring spawning in Mexico was greatest (4%–10%) when overall egg density in the CCE was at its lowest during 2011–13. The proportion of spawning sardine in Mexico was least (0.02%–1%) in 2005–09 when overall egg densities were intermediate.

DISCUSSION

Our study combined high resolution egg survey data from Mexican and US surveys to delimit the spatial distribution of spawning sardines in the spring in greater detail than previous studies using commercial catch data (Félix-Uraga et al. 2004). Our results indicated that most spring spawning, primarily by the northern subpopulation, occurred in US waters. Only 0.0%–10.2% of all eggs captured occurred in Mexican waters during any year of the study (fig. 2), and less than 5% occurred in Mexican waters in 11 of 14 years. The US sardine management currently assumes that 13% of the northern subpopulation occurs in the Mexican EEZ (Hill et al. 2015). Assuming the distribution of the entire population is proportional to the egg densities observed (i.e., nonspawners are not congregating disproportionately in Mexican waters), our results suggest the true fraction of the northern subpopulation off Mexico rarely exceeds 10% and usually is less than 5%.

Pairing Mexican and US CUFES data provided insight about the spatial structure of the sardine population that could not be gleaned from fishery-dependent data. The sardine spawning habitat stretches latitudinally from waters around Cape Mendocino in the US, to Bahía Magdalena in Mexico, and reaches 500 km offshore in the Southern California bight. In Mexican waters, the spawning area is characterized by a relatively small wedge-shaped distribution in which eggs occur mostly in coastal waters associated with the bifurcation to the south of the California Current (CC) near the coast. During most years, a large gap in egg abundance occurred off northern Baja California, which may have been the intermediate area between the northern and southern subpopulations (fig. 2). If so, the southern subpopulation generally was restricted to Mexican waters with SST greater than about 17˚C, as proposed by Félix-Uraga et al. (2004). A limitation of this study is that we cannot differentiate between the northern and southern subpopulations. If CUFES data were available for the peak spawning season of the southern subpopulation in summer off Baja California, it would be possible to model the habitat use and spatial extent both subpopulations throughout the year. The IMECOCAL program does collect such data but has not yet processed a sufficient number of samples to complete such modeling. This future research will be an important step in advancing our understanding of the dynamics of the two subpopulations.

Despite the extension of spawning area southward in 2000–04, there is an offshore gap in sardine spawning distribution across the US-Mexico border in the rest of the time series suggesting that the southern branch of the Southern California eddy may be a physical barrier to the continuity of the habitat some 550 km from the coast. The positive wind stress curl south of Point Conception (34˚N) induces a cyclonic circulation in the SCB region that separates the north central region of California from the southern California basin and the Baja California waters (Durazo 2015). The southern border of this large eddy is known as the Ensenada Front (centered at ~31˚N) and accounts for the presence of relatively low chlorophyll concentrations in the northern coastal area of the Baja California peninsula. The eddy's southern limb advects oligotrophic ocean and CC water to the coast, changing the composition and abundance of phytoplankton (Venrick 2015). Consequently, the phytoplankton community in the SCB coastal zone, dominated by diatoms, is replaced by coccolithophorids transported in warm oligotrophic water from the ocean area by the eddy. As a result, primary production decreases in the southern SCB and the Ensenada Front becomes an ecological and hydrographic boundary for the fauna (Santamaría-del-Ángel et al. 2011). A change in its physical properties at interannual and decadal scales has been related to fluctuations in sardine catches (Rykaczewski and Checkley 2008), and has highlighted the importance of this mechanism in restructuring the pelagic ecosystem when changes in environmental conditions occur. High temperatures and salinities at the southern border of the front and also the lower prey quality (see fig. 11 in Lo et al. 2005) may also produce physiological stress in sardine, reducing their fecundity and lead to a lower population density.

It is unknown whether the relatively large proportion of eggs captured in Mexican coastal waters during 2011 and 2012 was due to movement of sardines into Mexican waters or increased production in the coastal area off Bahía Magdalena. Water temperatures in the southern California Bight were relatively cold in 2011, and below average in 2012 (http://sccoos.org/data/el-nino). Such conditions have been associated with poor recruitment of sardine (e.g., Marr 1960; Zwolinski and Demer 2014). However, no similar change in egg distributions occurred when conditions were similar in 2008. Densities of sardine eggs collected by the IMECOCAL program in summer, likely belonging the southern subpopulation, have increased in recent years (Valencia-Gasti, unpublished data) as the northern subpopulation has declined to about 1%–2% of its peak abundance in 2007 (Hill et al. 2016). It is possible that the additional spawning in Mexican waters was due to fish from the southern subpopulation spawning outside of their peak season. These results highlight the need to better understand sardine subpopulation dynamics to better manage the fishery.

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