SCIENTIA MARINA 76(2) June 2012, 247-257, Barcelona (Spain) ISSN: 0214-8358 doi: 10.3989/scimar.03442.20C

Abundance patterns of early stages of the Pacific sardine (*Sardinops sagax*) during a cooling period in a coastal lagoon south of the California Current

RENÉ FUNES-RODRÍGUEZ, RAFAEL CERVANTES-DUARTE, SILVERIO LÓPEZ-LÓPEZ, ALEJANDRO HINOJOSA-MEDINA, ALEJANDRO ZÁRATE-VILLAFRANCO and GABRIELA M. ESQUEDA-ESCÁRCEGA

Centro Interdisciplinario de Ciencias Marinas (CICIMAR-IPN), Av. IPN s/n, Col. Playa Palo de Sta. Rita, La Paz, Baja California Sur 23096, Mexico. E-mail: rfunes@ipn.mx

SUMMARY: Abundance patterns of eggs and larvae of the Pacific sardine, *Sardinops sagax* (Jenyns, 1842), in Bahía Magdalena, Baja California Sur, were analysed during a cooling period south of the California Current from 2005 to 2009. The thermohaline characteristics and zooplankton abundance were good descriptors of the potential spawning habitat. Individual quotient analyses showed a predominance of eggs and larvae within a SST range of 16 to 18° C, at low salinities (33.9-34.1) and at low density gradient variability (0.009-0.029), associated with deeper waters (25-40 m) near the main entrance, where the transparency was intermediate (6-8 m) and zooplankton abundance was relatively high (>316 ml/1000 m³). Increments within different class intervals meant that neither dissolved inorganic nitrogen (DIN), phosphates nor chlorophyll *a* predominated. The large interannual fluctuations in sardine spawning activity and preferential temperatures observed in historical and recent data suggest that two sardine stocks spawn in Bahia Magdalena: one stock spawned in the period 1981-1989 and one stock spawned in the period 1997-2009. The influence of cooling and warming periods as additional components of the regional environmental framework is analysed and discussed.

Keywords: Pacific sardine, small pelagic fishes, fish eggs and larvae, hydrologic conditions, Bahia Magdalena, California Current.

RESUMEN: PATRONES DE ABUNDANCIA DE LOS ESTADIOS TEMPRANOS DE LA SARDINA DEL PACÍFICO (*SARDINOPS SAGAX*) DU-RANTE UN PERIODO DE ENFRIAMIENTO EN UNA LAGUNA COSTERA AL SUR DE LA CORRIENTE DE CALIFORNIA. – Los patrones de abundancia de huevos y larvas de la sardina del Pacífico, *Sardinops sagax*, en Bahía Magdalena, Baja California Sur, fueron analizados durante un periodo de enfriamiento al sur de la Corriente de California de 2005 a 2009. La combinación de las características termohalinas y abundancia del zooplancton fueron buenos indicadores del hábitat potencial del desove. El análisis individual de cocientes mostró una predominancia de huevos y larvas en el intervalo de temperatura superficial del mar entre 16 y 18°C, a baja salinidad (33.9-34.1), y valores bajos de la diferencia del gradiente de densidad (0.009-0.029) asociados a las aguas profundas (25-40 m) cercanas a la entrada principal, donde la profundidad de transparencia fue intermedia (6-8 m), y la abundancia del zooplancton fue relativamente alta (>316 ml/1000 m³). El Nitrógeno Inorgánico Disuelto (DIN), fosfatos y clorofila *a* no revelan una clara predominancia, debido a incrementos en diferentes intervalos de clases. La amplia fluctuación interanual de la actividad reproductiva de la sardina y temperaturas preferenciales observadas en datos históricos y recientes sugiere la reproducción de dos poblaciones en Bahía Magdalena (1981-1989 y 1997-2009). La influencia de los periodos de enfriamiento y calentamiento como complemento de marco ambiental regional es analizada y discutida.

Palabras clave: sardina del Pacífico, peces pelágicos pequeños, huevos y larvas, condiciones hidrológicas, Bahía Magdalena, Corriente de California.

INTRODUCTION

Most small pelagic fishes along the northeast Pacific coast show variations in the extent and duration of spawning in relation to water masses (Moser and Smith 1993, Smith and Moser 2003, Emmett *et al.* 2005). The spatial range and location of spawning can be critical for eggs and larvae due to interan-

nual changes in population structure and geographic variations in environmental conditions (Planque *et al.* 2007, Smith and Moser 2003, Emmett *et al.* 2005, Bernal *et al.* 2007, Ibaibarriaga *et al.* 2007, Coombs *et al.* 2006). However, few comprehensive surveys of eggs and larvae are available to determine preferred spawning locations and little is known of the stock structures of various important species (Agostini and Bakun 2002), which are influenced by physical processes that provide favourable habitat requirements for larval growth and survival (Lasker 1978, Parrish *et al.* 1981, Bakun 1996, Logerwell and Smith 2001, Lynn 2003, McClatchie *et al.* 2007, Planque *et al.* 2007, Aceves-Medina *et al.* 2009).

The spawning season and temperature range of the Pacific sardine, Sardinops sagax, show marked latitudinal variation over its wide distribution range as there are a number of stocks (Parrish et al. 1989, Lluch et al. 2003) separated by distinct preferential ranges of sea surface temperature (SST) in the Northeast Pacific (Tibby 1937, Ahlstrom 1954, 1965, Lluch et al. 1991, Funes-Rodríguez et al. 1995) and the Gulf of California (Hammann et al. 1998, Aceves-Medina et al. 2004). In the vicinity of Bahía Magdalena (BM), in the southern part of the California Current, two stocks (warm and temperate) of Pacific sardine overlap because temperate stock migrates in the winter with the strengthening of the California Current to its southern distribution limit, as evidenced by increased catches in spring-summer, conversely its northward movement begins in summer with the onset of the equatorial countercurrent (Félix-Uraga et al. 1996, Félix-Uraga et al. 2004, 2005). Morphometric results showed differences between the two stocks associated with different SST intervals along the Pacific coast of the Baja California Peninsula. These differences suggest that there are different morphotypes, but the current molecular data do not clearly support the existence of a phylogeographically structured population (García-Rodríguez et al. 2010).

The presence of two stocks coincides with a winter spawning period in BM (Torres-Villegas *et al.* 1995), probably associated with the warm stock and, a second period during summer outside the bay (Moser *et al.* 1993, Hernández-Vázquez 1994) related with the temperate stock. The spawning season of the winter stock in BM (warm stock) occurs in a preferential temperature range between 19 and 20°C (Saldierna-Martínez *et al.* 1987, Funes-Rodríguez *et al.* 2001, 2004, 2007), similar to the temperature range in the Gulf of California (Hammann *et al.* 1998, Aceves-Medina *et al.* 2004). However, the temperate stock in the area during the summer may not spawn inside the bay due to the high water temperature reached in this season (>25.0°C) (Funes-Rodríguez *et al.* 2007).

The abundance and recruitment of the Pacific sardine are highly variable, probably due to long-term environmental processes (Lluch-Belda *et al.* 1992, Deriso *et al.* 1996, Félix-Uraga *et al.* 1996, Schwartzlose *et al.* 1999, Rodríguez-Sánchez et al. 2001, Melo-Barrera et al. 2010, Cota-Villavicencio et al. 2010). There is a good correspondence between the warming periods from 1956-1959 and 1976-1980 and the expansion northwards of sardine spawning. The main difference is that while there was a sustained cooling trend after 1959, sardine spawning was progressively restricted to the south (Lluch et al. 2003). The Pacific sardine fishery collapsed in California and Ensenada in the early 1950s, which coincided with the Mexican fishery moving south towards new fishing areas, such as Isla Cedros, BM and the Gulf of California (Félix-Uraga et al. 1996). Sardine eggs and larvae were most abundant (1951-1984) towards the southern part of the sardine distribution range, south of Punta Eugenia and north of BM (Moser et al. 1993, Hernández-Vázquez 1994, Lluch et al. 2003). Subsequently, the sardine fishery showed signs of recovery in California in the early 1980s (Deriso et al. 1996) but not in BM during this same decade (Félix-Uraga et al. 1996). Catches have increased in the last decade (Félix-Uraga et al. 2007, Melo-Barrera et al. 2010), coinciding with a cooling period (Peterson and Schwing 2003). Populations of small pelagic planktivores generally have wide interannual variability in reproductive success, which results in extreme variability in their population sizes. This has large effects on the trophic levels and may be critical for biological communities with trophic structures that exhibit a striking "wasp waist" configuration (Bakun et al. 2010).

This study analysed the relationship between hydrographic fluctuations and the abundance of eggs and larvae of the Pacific sardine, *Sardinops sagax*, during a cooling period from 2005 to 2009 in Bahía Magdalena, Baja California Sur. The study assesses for the first time the sardine's potential spawning habitat in this bay, based on the occurrence ranges of early developmental stages in relation to various explanatory variables (SST, salinity, nutrient concentration, chlorophyll *a* concentration, water column density gradient and zooplankton biomass). The likelihood of spawning activity of different sardine stocks in BM is discussed in relation to interannual variations in commercial catches and the abundance of spawning products recorded in historical and current data.

MATERIALS AND METHODS

Bahía Magdalena, Baja California Sur, is one of the most extensive areas in Mexican Pacific waters. The system is located to the south of the area of influence of the California Current, on the west coast of Baja California Peninsula, Mexico (24°15'N 25°20'N and 112°30'W 112°12'W). Bahía Magdalena (BM) (649.7 km²) comprises three zones: A northern zone with shallow channels (3.5 m, average depth) surrounded by estuaries bordered by mangroves; a western zone connected to the neritic zone (4.5 km wide and 40 m maximum depth); and a shallow eastern zone with sandy bottoms (3.5 m depth) (Fig. 1).



FIG. 1. – Study area and station plan in Bahía Magdalena, Baja California Sur, Mexico. a) Dotted lines represent the previously suggested stock limits of the temperate and warm stocks (Félix-Uraga et al. 2005); and b) Sardinops sagax spawning area in the western zone (Funes-Rodríguez et al. 2001).

Between 2005 and 2009, 12 oceanographic surveys were carried out at 14 stations during the Pacific sardine spawning season from winter to early spring (Total of 166 plankton tows). Temperature and salinity (psu) were recorded with a CTD (Seabird 19) to 40m maximum depth. Nutrient (nitrites, nitrates, ammonium and phosphates) and chlorophyll a (CHL) concentrations were determined following Strickland and Parsons (1972) and Venrick and Hayward (1984), respectively. The sum of nitrites, nitrates and ammonium was considered to be the dissolved inorganic nitrogen (DIN). Samples were collected at the surface, filtered under less than one third of atmospheric pressure and then frozen (-40°C) prior to analyses. The stability of the water column was estimated by calculating the vertical density gradient (Peterson et al. 1988). A Secchi disc was used to measure water transparency (m). As supplementary information on the region's environmental framework, time series of the multivariate ENSO index (NOAA, Earth System Research Laboratory, Physical Science Division, www.esrl.noaa.gov), the average monthly upwelling index (m³/s 100 m of coastline) and SST anomalies (24°N, 113°W) (Pacific Fisheries Environmental Laboratory, www.pfeg.noaa.gov) were obtained to assess interannual environmental variations. Zooplankton samples were collected with a conical net with a standard 0.5 m mouth diameter and 0.505 mm mesh size, fitted with a calibrated flowmeter, towed at the surface (1 m depth) following a semicircular trajectory at about 1 m/s for five minutes. Integrated vertical plankton tows were not possible due to equipment limitations. However, high velocities that were measured and modeled (up to 1.1 m/s) suggest a well-mixed water column during the flood, when a strong tidal flow produced intense vertical mixing of near-bottom cold water with upper layer water, which led to reduced SST values (Zaytsev et al. 2010). Samples were preserved in 4% formalin with sodium borate as buffer. Zooplankton volume (ml/1000 m³) was determined by measuring the displaced volume (Beers 1976). Eggs and larvae of S. sagax were sorted and their abundances expressed as number of individuals per 10 m² of sea surface. Historical information about the abundance of S. sagax (January to April) in BM (1982-1989 and 1997-2004) was obtained from the Centro Interdisciplinario de Ciencias Marinas database, La Paz, Baja California Sur, Mexico. Analyses of Variance (ANOVA) and box plots were applied to test for monthly differences (winter-spring 2005-2009) in abundance and environmental variables. These analyses were carried out for each data set, 12 months at 14 stations (N=166 stations). Spearman's rank correlation tests were conducted to identify relationships between abundance and environmental variables (each environmental variable was tested separately; P < 0.05). The spawning season was characterized in terms of the explanatory variables recorded by means of quotient analysis. This technique is commonly used to identify preference or avoidance of spawning zones by assessing the distribution of eggs and larvae in relation to covariates of interest (Emmet et al. 2005, Bernal et al. 2007, Ibaibarriaga et al. 2007). A canonical correspondence analysis (CCA) was applied to correlate egg and larval abundance with environmental variables. Prior to analysis, S. sagax and zooplankton abundance data were log transformed as $\ln(x+1)$.

RESULTS

Individual quotient analyses applied to identify the range of those variables considered relevant in the Pacific sardine spawning habitat showed a predominance of eggs within a SST range between 16 and 18°C, at low salinity (33.9-34.1) and low density gradient variability in the water column (0.009-0.029) associated with deeper waters (25-40 m) near the access inflow, where the transparency was intermediate (6-8 m) (Fig. 2a-e). The egg quotients in relation to dissolved inorganic nitrogen (DIN), phosphates and chlorophyll a (CHL) did not show a clear trend because there were increments within different class intervals (Fig. 2f-h). In contrast, the shift in quotients towards the right of the zooplankton class intervals evidenced a predominance of spawning products associated with an increase in zooplankton (>316 ml/1000 m³) (Fig. 2i). However, fish larvae quotients never surpassed a value of 1 with any hydrologic variable.



FIG. 2. – Quotient lines of egg (dark line) and larval abundance (dashed line) of *Sardinops sagax* in relation to: a) sea surface temperature; b) salinity; c) density gradient; d) bottom depth; e) transparency; f) NID; g) phosphate; h) chlorophyll *a*; and i) zooplankton volume. Histograms indicate the number of samples taken in each class interval during winter and early spring 2005-2009 in Bahía Magdalena, Baja California Sur. Quotient=1 (horizontal dashed line).



FIG. 3. – Box plots: a) sea surface temperature (°C), b) salinity, and c) density (kg m⁻³) during winter and early spring 2005-2009 in Bahía Magdalena, Baja California Sur.

The Analyses of Variance (ANOVA) and box plots revealed significant monthly and inter-annual differences (P<0.05) in most hydrologic and biological characteristics. The sea surface temperature showed interannual variation with values above 19°C in 2005, 2007 and 2009 (except for April 2007) and lower values in 2006 and 2008 (Fig. 3a). Salinity and average density showed less variation than SST (34.71 and 24.7 kg m⁻³, respectively); however, density decreased as a result of the increase in SST (2005 and 2009) (Figs. 3a, 3b and 3c). Nitrites and nitrates increased mainly in April (0.07 and 2.06 µM, respectively) and were usually lower early in the year (Figs. 4a and 4b). Ammonium increased in 2007 and early 2008 and 2009 (>3.7 μ M) (Fig. 4c), while phosphates varied around or above the mean value ($\geq 0.79 \ \mu M$) during the study period, decreasing in early 2005 (Fig. 4d).

Chlorophyll *a* (>2.00 mg m⁻³) generally followed the increase in nutrients and phosphates (Table 1; Figs. 4a-4d and 5a). The abundance of zooplankton and sardine early stages increased in 2005 and 2008 (Figs. 5b-5c). In 2005, *S. sagax* eggs peaked (152-279)





eggs per 10 m²), coinciding with a relatively high SST (>19.0°C) and a simultaneous increase in zooplankton abundance, with values around the average (180-210 ml/1000 m³). A second peak in egg abundance (141 eggs per m²) and a higher larval abundance in early 2008 (12 larvae per m²) coincided with the lowest SST

Survey	Ν	<i>S.sagax</i> eggs/10 n	sd n ²	<i>S.sagax</i> larvae/10 r	sd	°C ℃	sd	S	sd	Density kg m ⁻³	sd	Nitrite µM	sd	Nitrate µM	sd
Jan-05	14	17.40	32.45	1.40	2.40	20.43	0.55	34.71	0.53	24.43	0.32	0.06	0.04	1.63	0.99
Feb-05	14	152.42	317.90	0.55	1.10	19.76	0.69	34.67	0.45	24.58	0.25	0.03	0.02	0.57	0.50
Mar-05	13	279.49	597.38	0.11	0.24	19.03	1.48	34.49	0.57	24.61	0.28	0.04	0.05	0.28	0.19
Feb-06	14	0.07	0.14	0.23	0.52	18.09	0.69	34.41	0.49	24.80	0.30	0.07	0.06	1.93	2.18
Mar-06	14		0.00		0.00	18.03	1.58	34.53	0.58	24.85	0.34	0.07	0.09	3.61	3.32
Feb-07	14	5.72	19.07	0.22	0.23	19.18	0.28	35.13	0.54	25.08	0.43	0.04	0.03	3.20	3.87
Apr-07	13	0.02	0.06		0.00	18.38	1.49	34.86	0.64	25.06	0.30	0.11	0.09	3.95	2.70
Feb-08	14	141.73	292.73	12.78	27.01	16.99	0.86	34.56	0.76	25.18	0.47	0.05	0.04	1.69	1.83
Apr-08	14	11.74	26.61	0.08	0.18	17.80	1.98	34.76	0.65	25.12	0.28	0.08	0.06	2.68	2.06
Jan-09	14	0.12	0.20	0.03	0.06	20.91	0.24	34.78	0.41	24.35	0.31	0.05	0.03	1.77	1.00
Feb-09	14	3.81	6.85	0.06	0.10	20.06	1.34	34.75	0.50	24.55	0.22	0.05	0.04	0.78	1.26
Apr-09	14	0.11	0.27		0.00	19.34	1.90	34.82	0.62	24.78	0.34	0.07	0.06	2.65	1.93
Survey	Ν	NH4+	sd	NID	sd	PO ₄ ³⁻	sd	Chl. a	sd	Zoop.	sd	Trans.	sd	Gradien	t sd
2		μM	μΜ		μŴ		$mg m^{-3}$ ml/1000 m ³			m		$\Delta\sigma$ / Δz			
Jan-05	14	3.27	1.06	4.97	1.48	0.54	0.16	0.76	0.46	210.17	247.2	7.44	1.87	0.04	0.03
Feb-05	14	3.12	1.79	3.71	1.89	0.51	0.17	1.28	0.53	180.87	176.4	6.79	1.60	0.02	0.02
Mar-05	13	3.17	0.86	3.49	0.86	0.89	0.28	2.13	1.00	207.33	165.3	5.45	1.55	0.02	0.02
Feb-06	14	1.27	0.43	3.27	2.22	0.85	0.24	2.00	1.16	164.91	231.3	7.29	2.35	0.01	0.01
Mar-06	14	2.93	0.84	6.61	3.28	0.80	0.19	3.06	2.04	117.36	186.7	5.57	1.64	0.01	0.01
Feb-07	14	3.79	2.55	7.03	4.28	0.83	0.14	1.83	1.39	213.75	271.2	5.86	1.79	0.02	0.02
Apr-07	13	4.62	3.26	8.67	4.75	1.02	0.23	3.24	2.10	34.37	27.0	5.00	0.98	0.04	0.03
Feb-08	14	4.38	2.47	6.13	3.17	0.82	0.18	2.83	1.61	357.51	376.3	6.00	1.51	0.04	0.03
Apr-08	14	0.88	1.34	3.64	2.42	0.78	0.27	1.84	0.67	368.53	582.5	8.32	2.20	0.35	0.56
Jan-09	14	6.95	3.12	8.77	3.37	0.78	0.12	1.40	0.63	31.12	23.4	9.51	3.02	0.04	0.05
Feb-09	14	2.40	2.43	3.22	2.95	0.73	0.14	1.39	0.60	76.26	170.2	9.18	3.18	0.03	0.04
Apr-09	14	2.10	1.99	4.83	2.64	0.89	0.19	2.53	1.35	106.84	118.0	5.41	1.17	0.02	0.01
*															

 TABLE 1. – Sardinops sagax egg and larval mean abundance, and mean and standard deviation (sd) of hydrological variables during winter and early spring 2005-2009 in Bahía Magdalena, Baja California Sur. Chl. a, chlorophyll a; S, salinity; T, temperature; Trans., transparency; Zoop., zooplankton.

Bold numbers indicate singnificant differences between means (±95% confidence interval).

 TABLE 2. – Spearman's rank order correlations between Sardinops sagax egg and larval abundance and hydrological variables during winter and early spring 2005–2009 in Bahía Magdalena, Baja California Sur. Chl. a, chlorophyll a; S, salinity; T, temperature; Trans., transparency; Zoop., zooplankton.

	<i>S.sagax</i> larvae 10 m ²	Zoop. ml/1000 n	Depth n ³ m	T °C	S	Density kg m ⁻³	Chl. a mg m ⁻³	${}^{NH_4^+}_{\mu M}$	$\stackrel{NO_2^-}{\mu M}$	$NO_3^- \mu M$	NID μM	PO4 ³⁻ μM	Trans. m	Gradient $\Delta\sigma/\Delta z$
S.sagax eggs S.sagax larvae Zoop. Depth Temperature Salinity Density Chlorophyll a NH ₄ ⁺ NO ₂ ⁻ NO ₃ ⁻ NID PO ₄ ³⁻ Transparency	0.535	0.199 0.297	0.378 0.226 -0.173	-0.135 -0.043 -0.025 - 0.531	-0.235 -0.125 0.154 -0.524 0.582	-0.116 -0.075 0.196 0.071 -0.464 0.376	-0.064 -0.099 0.096 0.228 - 0.403 0.022 0.499	0.072 0.156 -0.024 0.088 0.088 -0.015 -0.117 0.002	-0.057 -0.015 -0.172 0.320 -0.291 -0.339 0.030 0.084 -0.049	-0.194 0.016 -0.251 0.236 -0.238 -0.169 0.181 0.119 0.040 0.543	-0.067 0.121 -0.159 0.189 -0.083 -0.122 0.023 0.081 0.733 0.339 0.623	-0.309 -0.327 -0.038 -0.224 -0.107 0.041 0.233 0.186 -0.094 0.325 0.263 0.159	0.348 0.274 -0.211 0.439 -0.029 -0.351 -0.254 -0.271 0.033 0.209 0.087 0.121 -0.283	$\begin{array}{c} -0.023\\ -0.053\\ 0.066\\ -0.084\\ 0.076\\ 0.116\\ 0.109\\ 0.086\\ 0.118\\ 0.123\\ 0.084\\ 0.139\\ 0.015\\ 0.057\end{array}$

Bold font indicate significant correlations (P<0.050).

(16.9-17.8°C) recorded over the study period. However, the increase in zooplankton abundance was consistently observed in both 2005 and 2008, in contrast with 2006, 2007 and 2009, when zooplankton abundance was below the mean and eggs and larvae were scarce (Table 1; Fig. 5).

Spearman's rank correlations (P<0.05) revealed a significant correlation between phosphates and the CHL concentration but no significant correlations with nitrite and nitrate concentrations. Nevertheless, the chlorophyll a, nitrite and nitrate concentrations as well as the egg and larval abundances in the area around the inflow were correlated with both depth and transparency, which suggests an oceanic influence. Phosphate concentration and zooplankton abundance were negatively correlated with depth (Table 2).

The first two axes of the canonical correspondence analysis (CCA) accounted for 23.5% of the total variation. The first canonical axis revealed an environmental gradient related to salinity, density, transparency and phosphate concentration (-0.592, -0.566, 0.611 and -0.65, respectively). The second canonical axis



TABLE 3. – Axis eigenvalues and explained variance (%) from a canonical correspondence analysis using *Sardinops sagax* egg and larval abundance, chlorophyll *a* and zooplankton at each of the 92 stations during winter and early spring 2005-2009 in Bahía Magdalena, Baja California Sur.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.072	0.033	0.016
Explained variance (%)	16.0	7.4	3.6
Accumulated variance (%) 16.0	23.5	27.1
Correlation values	·		
Depth	0.535	-0.696	0.237
Temperature	-0.072	0.661	-0.516
Salinity	-0.592	0.443	-0.073
Density	-0.566	-0.171	0.455
Ammonium	0.031	-0.196	0.308
Nitrite	-0.283	-0.441	0.194
Nitrate	-0.323	-0.552	-0.466
NID	-0.197	-0.514	-0.087
Phosphate	-0.650	-0.219	0.071
Secchi	0.611	0.154	0.111
Density gradient	-0.054	0.252	-0.021
Montecarlo test, 999 runs			
Mean	0.022	0.010	0.004
Minimum	0.006	0.002	0.000
Maximum	0.056	0.032	0.011
P	0.001	0.001	0.001



FIG. 6. – CCA ordination diagram using Sardinops sagax egg and larval abundance, chlorophyll a concentration and zooplankton volume (points) during winter and early spring 2005-2009 in Bahía Magdalena, Baja California Sur. Arrows represent significant explanatory factors; arrowheads indicate the positive direction for the different variables (matrix 92 stations).

salinity. Egg and larval abundances were correlated with transparent and deep waters (Fig. 6) in accordance with the outcome of the Spearman's rank correlations (Table 2). The CCA of sites and environmental variables indicated that stations near the main entrance (stations, K1, L1, M1, N1, L2, M2) were largely related to transparent and deep waters (Axis 1, right), while shallow stations (Axis 1, left) were related to warmer waters with higher salinities, which indicates that there is high evaporation in the northern and eastern zones (I, J, K2, K3, M3, N1, N2, O). For some years, the relative positions of stations with respect to density and nutrient vectors have corresponded to sites located near the main entrance (Fig. 7).

FIG. 5. – Box plots: a) chlorophyll a (mg m⁻³), b) Sardinops sagax eggs (numbers per 10 m²), c) larvae, and d) zooplankton (ml/ 1000 m³) during winter and early spring 2005-2009 in Bahía Magdalena, Baja California Sur.

was directly associated with SST (0.661), nitrate concentration and DIN (-0.552 and -0.514, respectively). There was a low correlation with nitrite, ammonium and the density gradient in the water column (-0.441, -0.196 and 0.252, respectively) (Table 3). The chlorophyll *a* concentration was associated with intermediate values of nutrients and density, whereas zooplankton abundance was associated with an increase in SST and



FIG. 7. – CCA ordination diagram using the same matrix with sites and environmental variables during winter and early spring 2005-2009 in Bahía Magdalena, Baja California Sur. Arrows represent significant explanatory factors; arrowheads indicate the positive direction for the different variables. Station points (year, month, station).

DISCUSSION

Early stages of small pelagic fishes display latitudinal differences separated by preferential SST intervals in different ecosystems around the world (Parrish et al. 1989, Lluch et al. 1991, Bernal et al. 2007, Coombs et al. 2006, Ibaibarriaga et al. 2007). In the northeast Pacific, spawning of the Pacific sardine, Sardinops sagax, occurs over a wide SST range (13-25°C) across the area of influence of the California Current and Gulf of California. In California, the early stages of sardine occur in a temperature range between 13.5 and 16.5°C (Ahlstrom 1954, 1965), with a second peak between 19 and 23.5°C, which corresponds to the warmer part of its distribution range off the west coast of Baja California (Lluch et al. 1991). This second peak is similar to the that observed in BM (19 to 20°C) during the 1980s (Saldierna-Martínez et al. 1987) and in the Gulf of California (Hammann et al. 1998, Aceves-Medina et al. 2004), which was even slightly higher during the El Niño years in 1983 and 1997 (19.0 to 21.5°C) (Saldierna-Martínez et al. 1987, Funes-Rodríguez et al. 1995, 2001). However, under the current cooling conditions (2005-2009), the SST range includes lower temperatures (14 to 22°C) off Baja California (unpublished data) and in BM, with similar preferential temperature ranges (15.5-16.0°C and 16-18°C, respectively).

Physical processes that combine to yield a favourable reproductive habitat for coastal pelagic fishes have been called the 'ocean triad' (enrichment, concentration and retention) (Bakun 1996, Agostini and Bakun 2002). In this case, food production determines survival and re-

productive success of small pelagic larvae (Lasker 1978, Lynn 2003, Logerwell and Smith 2001, McClatchie et al. 2007, Planque et al. 2007, Aceves-Medina et al. 2009). Survival of first-feeding larvae improves when there is food of an adequate size and layered concentrations associated with a stable water column (Lasker 1978). However, the evidence of a correlation between water column stability and larval survival varies (Cury and Roy 1989, Planque et al. 2007). In Sardina pilchardus from the Bay of Biscay, egg abundance drops as water stratification increases (Planque et al. 2007), while the egg abundance of S. sagax in South Australia is significantly related to water column stability (McClatchie et al. 2007). In this study, sardine eggs and larvae were more abundant in non-stratified waters, although this was not statistically significant, probably because larvae occurred at stations both close to the bay entrance and in stable and shallow waters inside the bay. Intense coastal upwelling takes place in spring (Zaytsev et al. 2003, 2010) so that sardines are caught mainly in spring and summer in BM (Félix-Uraga et al. 2007), but they do not spawn inside the bay due to the high water temperatures reached in summer (>25.0°C) (Funes-Rodríguez et al. 2007). This implies that the high seasonal variability in sardine egg and larval abundance in BM is mainly related to temperature and the migratory movements of different stocks.

The biological productivity that characterizes BM results from nutrient enrichment entering from the adjacent sea and also nutrient regeneration in the bay itself (Gómez-Gutiérrez et al. 1999, Gómez-Gutiérrez et al. 2007, Palomares-García and De Silva-Dávila 2007). In line with this, the stations near the bay entrance were positively correlated with nutrient and CHL concentrations, whereas shallow waters were associated with phosphates. However, the correlations between spawning products and nutrient and CHL concentrations were not significant. This seems reasonable because spawning takes place mainly from January to March before the onset of the intense coastal upwelling in April and May (Zaytsev et al. 2003, 2010) that leads to a peak in CHL (Cervantes-Duarte et al. 2007, 2010) and phytoplankton (Gárate-Lizárraga and Siqueiros-Beltrones 1998).

Although a direct relationship between spawning products and zooplankton was observed, zooplankton abundance and diversity are known to be relatively low during the winter and high in the summer (Palomares-García and Gómez-Gutiérrez 1996). Thus, this relationship between sardine spawning and zooplankton might be related to food type. Early larvae feed on copepod nauplii (Arthur 1976, Turner 1984), which might correspond to the temperate species typical of the California Current that are usually present at the bay entrance (*Acartia clausi, Calanus pacificus*), including the euphausid *Nycthiphanes simplex*, or the species that are abundant inside the bay (*Paracalanus parvus* and *A. lilljeborgii*) (Palomares-García and Gómez-Gutiérrez 1996, Gómez-Gutiérrez *et al.* 1999).



FIG. 8. – a) Sardinops sagax egg and larval abundance (numbers per 10 m²); b) Multivariate El Niño-Southern Oscillation Index and SST anomalies; and c) upwelling index (m³/s/100 m coastline) at 24°N and 113°W. Horizontal lines indicate linear regressions (trendline).

In BM, the sardine fishery decreases with anomalous warming events (El Niño) but recruitment increases the following year (1983-84, 1992-93 and 1998), particularly in the case of the warm stock (Félix-Uraga et al. 1996, 2007). A similar trend was observed in spawning products, which decreased with intense El Niño warming events (1982-1983, 1997-1998) and increased after the warming event (Fig. 8a). Nevertheless, changes in the abundance of small pelagic species are associated with distribution shifts that occur over decades and in large geographic areas (Lluch-Belda et al. 1992, Deriso et al. 1996, Félix-Uraga et al. 1996, Schwartzlose et al. 1999, Rodríguez-Sánchez et al. 2001). This suggests that during the warm period (1981-1988) the main reproductive group in BM is the warm stock (winter – spring). Due to its distribution south of the Peninsula, this stock can only be caught in BM, whereas sardines from the temperate stock can be caught in any of the three fishing areas (BM, Isla Cedros and Ensenada)

(Félix-Uraga *et al.* 2004, 2005). In fact, even though commercial catches in BM were relatively small during the warm period (10000 t; 1981-1989), they were comparatively smaller (5000 t) in Isla Cedros and Ensenada during the 1980s (Félix-Uraga *et al.* 1996). Consistently, a winter spawning season in BM corresponds to the warm stock (Torres-Villegas *et al.* 1995, Funes-Rodríguez *et al.* 2001, 2004, 2007), whereas the temperate stock, located between Punta Eugenia and BM (Moser *et al.* 1993, Hernández-Vázquez 1994), is caught in spring and summer in BM (Félix-Uraga *et al.* 2007) but does not spawn in the bay due to the high SST in the summer (Funes-Rodríguez *et al.* 2007).

Over the last decade, a cooling period off BM (Peterson and Schwing 2003), which has been confirmed by climatic indices (Figs. 8b and 8c), markedly impacted the sardine spawning activity in BM. This is evidenced by the comparatively low preferential SST ranges. More recently, although peaks in egg abundance were

observed to alternate every two or three years (>1000 eggs per 10 m² in 2001, 2005, 2008), drastic decreases occurred in consecutive years (100 eggs and 15 larvae per 10 m² in 2000, 2003, 2004, 2006, 2007, 2009). In contrast, the warm period between 1981 and 1988 had marked peaks (in 1984, 1987, 1989) but smaller interannual decreases (<500 eggs; >50 larvae per 10 m²), except in 1983 and 1988 when intense El Niño and La Niña events occurred (Fig. 8b). Under the current cooling conditions (2000-2009) and a likely expansion of the temperate stock, the total catch of Pacific sardine increased in the fisheries located on the peninsula's western coast, and particularly in BM (50000 t) between 2000 and 2008 (Félix-Uraga et al. 2007, Melo-Barrera et al. 2010). Based on these observations, reproduction of the warm stock might be delimited in BM, whereas the temperate stock may be making a larger contribution in the present conditions. This is related to the presence of mature and post-spawning individuals throughout the year (2006-2008), although there is a larger percentage (90%) of males and females early in the year in addition to a second, smaller peak in June-July (Melo-Barrera et al. 2010). However, the reasons why large increases followed by drastic decreases in the early stages of sardine have been observed during the present cooling period (2000-2009), seem to be related to migration processes, fluctuations in SST anomalies and moderate El Niño events.

ACKNOWLEDGEMENTS

The authors thank the fish larvae staff at the Depto. de Plancton y Ecología Marina, Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional. The stability of the water column was estimated by MS. Sonia Futema from the Depto. Oceanología, and editorial suggestions were made by María Elena Sánchez Salazar. This study was supported by grants from the Instituto Politécnico Nacional [SIP: 20100180, 20110103] and Investigaciones Mexicanas de la Corriente de California [CONACyT: 47044, 23947, 99252].

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Scient ed.: I. Palomera.

- Received June 8, 2011. Accepted November 9, 2011.
- Published online February 20, 2012.