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 m^3). 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*) durante 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 m^3). 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 interannual 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 km^2) 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).

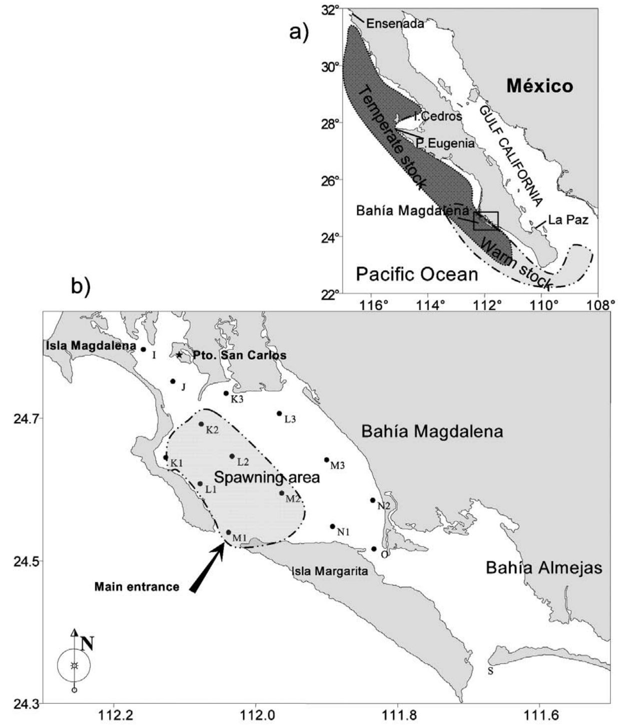

FIG. 1. – Study area and station plan in Bahía Magdalena, Baja California Sur, Mexico. a) Dotted lines represent the previously suggested stock limits of the temperate and warm stocks (Félix-Uraga *et al*. 2005); and b) *Sardinops sagax* spawning area in the western zone (Funes-Rodríguez *et al*. 2001).

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 (m^3/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 m^3) 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 m^2 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 m^3) (Fig. 2i). However, fish larvae quotients never surpassed a value of 1 with any hydrologic variable.

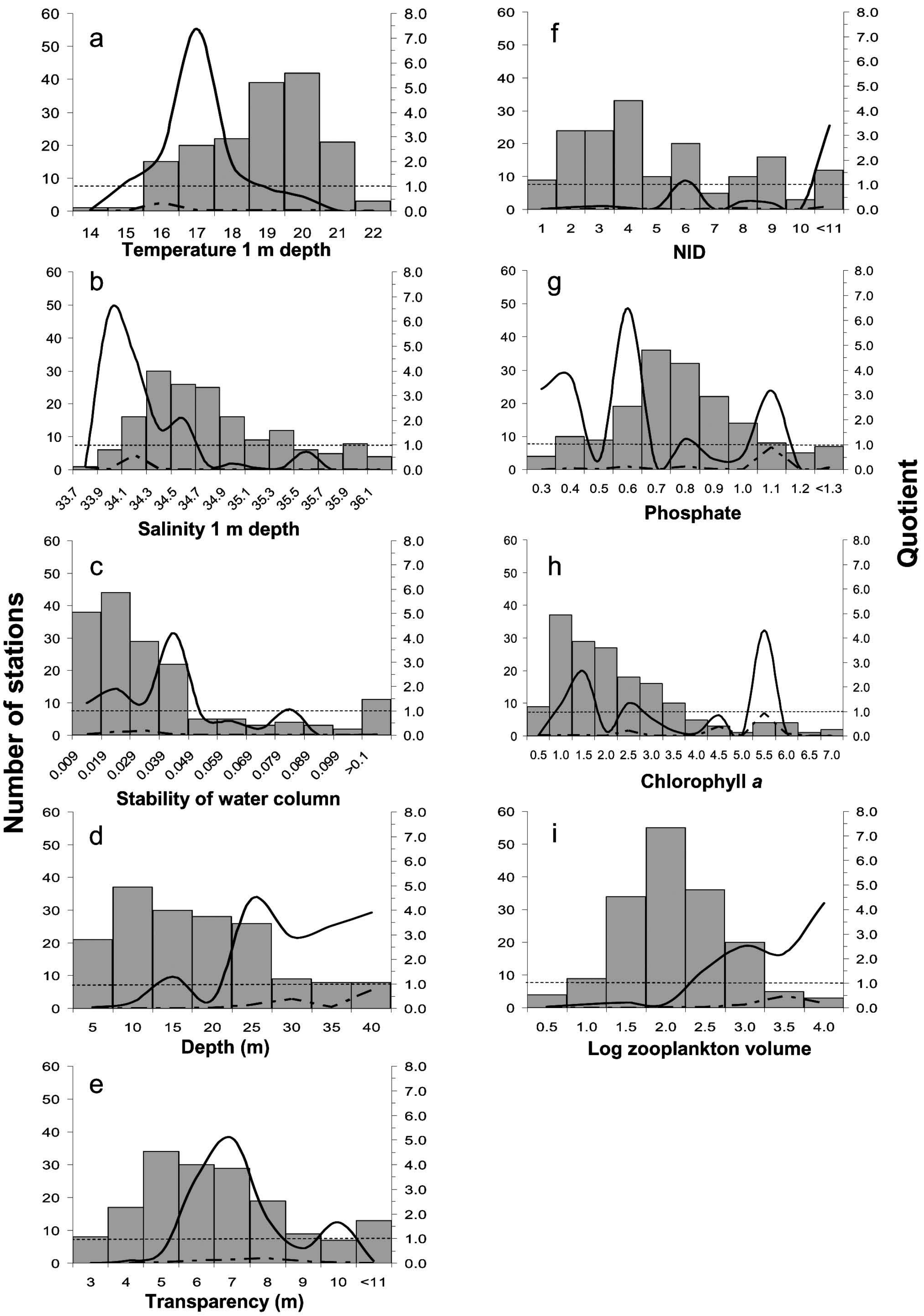

FIG. 2. – Quotient lines of egg (dark line) and larval abundance (dashed line) of *Sardinops sagax* in relation to: a) sea surface temperature; b) salinity; c) density gradient; d) bottom depth; e) transparency; f) NID; g) phosphate; h) chlorophyll *a*; and i) zooplankton volume. Histograms indicate 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).

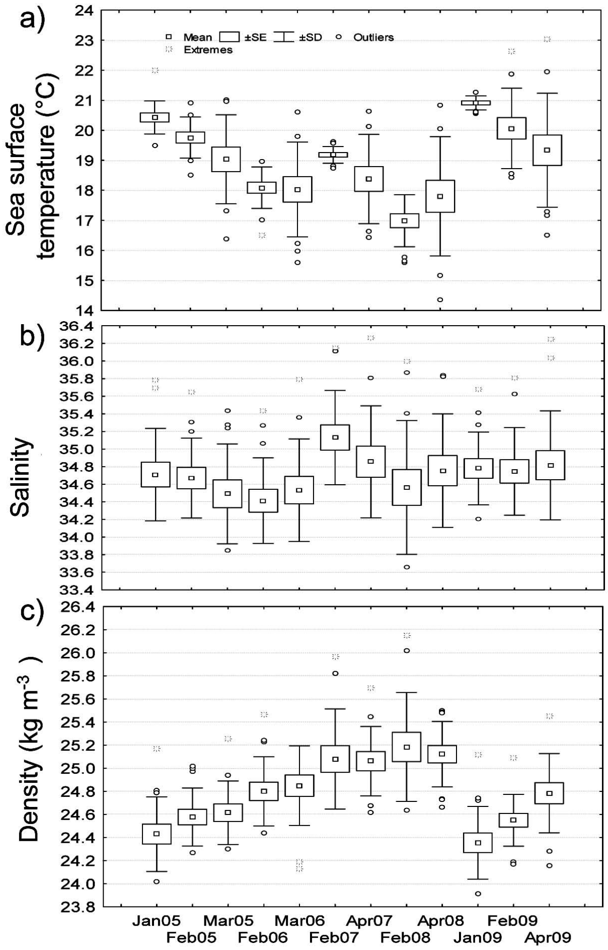

FIG. 3. – Box plots: a) sea surface temperature (°C), b) salinity, and c) density (kg m^{-3}) during winter and early spring 2005-2009 in Bahía Magdalena, Baja California Sur.

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 19ºC 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 µM) (Fig. 4c), while phosphates varied around or above the mean value (≥0.79 µM) 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 m^2), 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 m^3). A second peak in egg abundance (141 eggs per m^2) and a higher larval abundance in early 2008 (12 larvae per m^2) coincided with the lowest SST

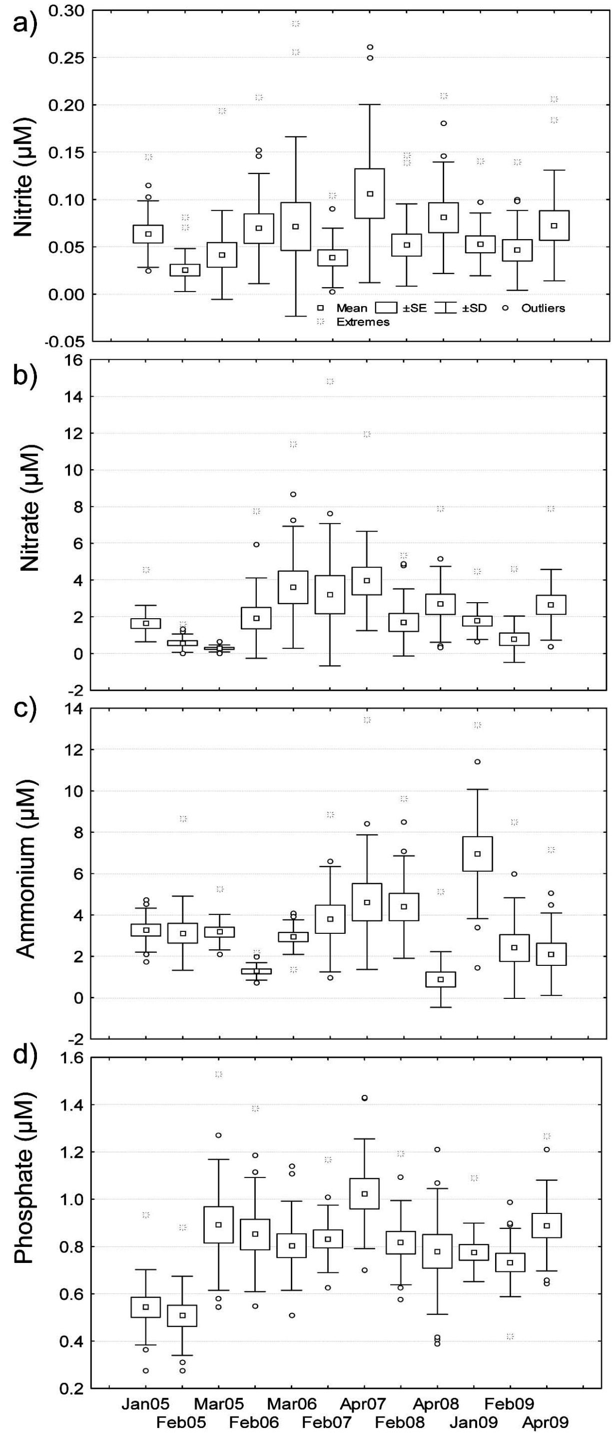

FIG. 4. – Box plots: a) nitrite (µM), b) nitrate (µM), c) ammonium (µM), and d) phosphate (µM) during winter and early spring 2005-2009 in Bahía Magdalena, Baja California Sur.

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.

Survey	N	*S.sagax* eggs/10 m²	sd	*S.sagax* larvae/10 m²	sd	T °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	N	NH_4^+ µM	sd	NID µM	sd	PO_4^{3-} µM	sd	Chl. *a* mg m⁻³	sd	Zoop. ml/1000 m³	sd	Trans. m	sd	Gradient Δσ / Δz	sd
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

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.

	S.sagax larvae 10 m²	Zoop. ml/1000 m³	Depth m	T °C	S	Density kg m⁻³	Chl. *a* mg m⁻³	NH_4^+ µM	NO_2^- µM	NO_3^- µM	NID µM	PO_4^{3-} µM	Trans. m	Gradient Δσ/Δz
S.sagax eggs	**0.535**	**0.199**	**0.378**	–0.135	**–0.235**	–0.116	–0.064	0.072	–0.057	**–0.194**	–0.067	**–0.309**	**0.348**	–0.023
S.sagax larvae		**0.297**	**0.226**	–0.043	–0.125	–0.075	–0.099	**0.156**	–0.015	0.016	0.121	**–0.327**	**0.274**	–0.053
Zoop.			**–0.173**	–0.025	**0.154**	**0.196**	0.096	–0.024	**–0.172**	**–0.251**	**–0.159**	–0.038	**–0.211**	0.066
Depth				**–0.531**	**–0.524**	0.071	**0.228**	0.088	**0.320**	**0.236**	**0.189**	**–0.224**	**0.439**	–0.084
Temperature					**0.582**	**–0.464**	**–0.403**	0.088	**–0.291**	**–0.238**	–0.083	–0.107	–0.029	0.076
Salinity						**0.376**	0.022	–0.015	**–0.339**	**–0.169**	–0.122	0.041	**–0.351**	0.116
Density							**0.499**	–0.117	0.030	**0.181**	0.023	**0.233**	**–0.254**	0.109
Chlorophyll *a*								0.002	0.084	0.119	0.081	**0.186**	**–0.271**	0.086
NH_4^+									–0.049	0.040	**0.733**	–0.094	0.033	0.118
NO_2^-										**0.543**	**0.339**	**0.325**	**0.209**	0.123
NO_3^-											**0.623**	**0.263**	0.087	0.084
NID												**0.159**	0.121	0.139
PO_4^{3-}													**–0.283**	0.015
Transparency														0.057

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

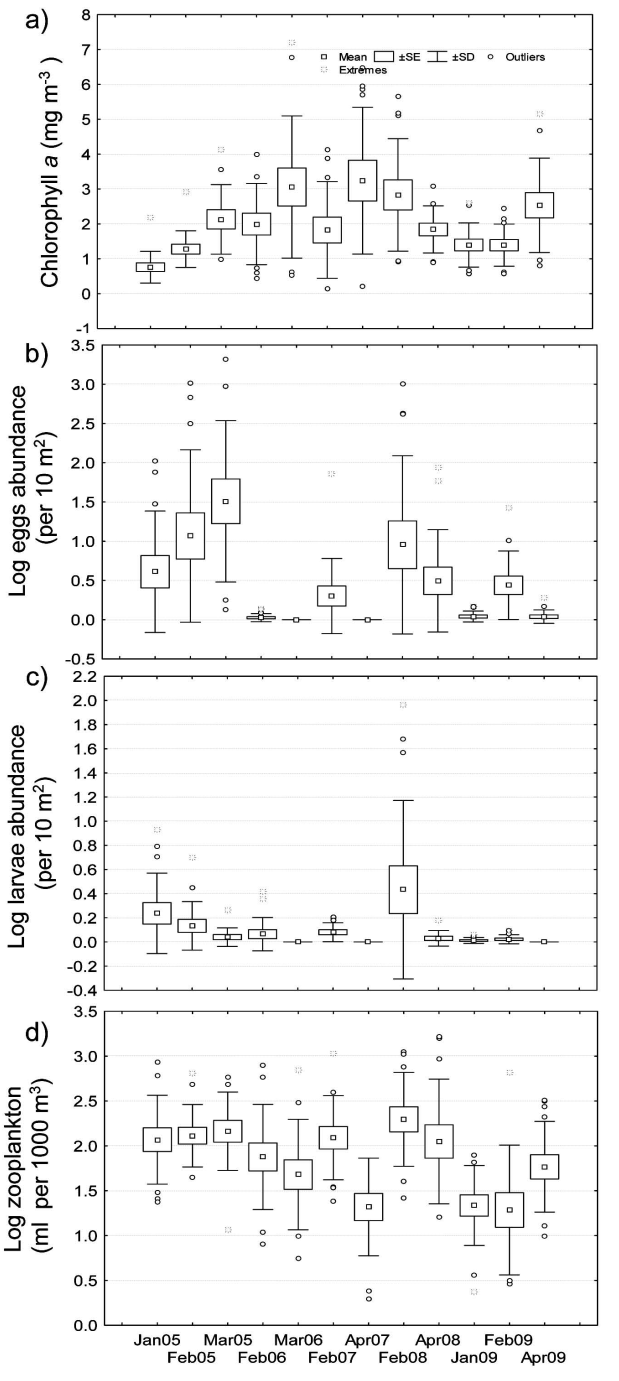

FIG. 5. – Box plots: a) chlorophyll *a* (mg m^{-3}), b) *Sardinops sagax* eggs (numbers per 10 m^2), c) larvae, and d) zooplankton (ml/ 1000 m^3) during winter and early spring 2005-2009 in Bahía Magdalena, Baja California Sur.

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

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

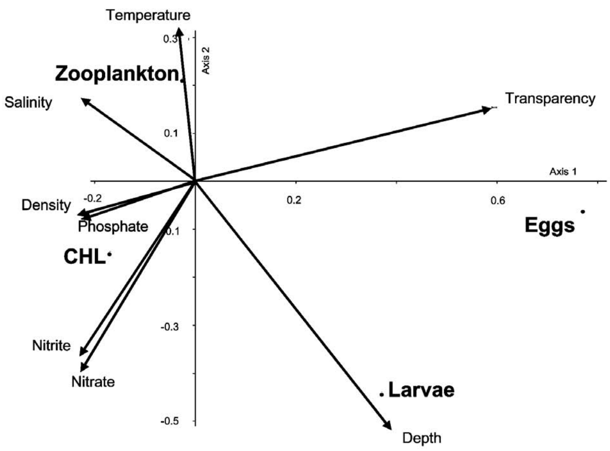

FIG. 6. – CCA ordination diagram using *Sardinops sagax* egg and larval abundance, chlorophyll *a* concentration and zooplankton volume (points) during winter and early spring 2005-2009 in Bahía Magdalena, Baja California Sur. Arrows represent significant explanatory factors; arrowheads indicate the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

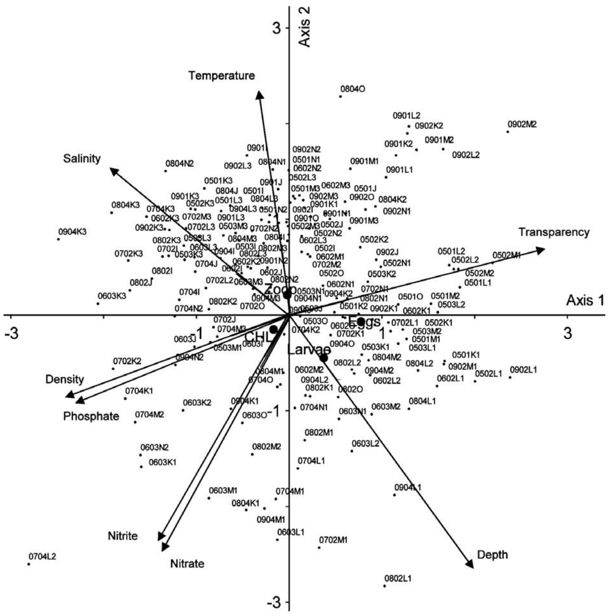

FIG. 7. – CCA ordination diagram using the same matrix with sites and environmental variables during winter and early spring 2005-2009 in Bahía Magdalena, Baja California Sur. Arrows represent significant explanatory factors; arrowheads indicate the positive direction for the different variables. Station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

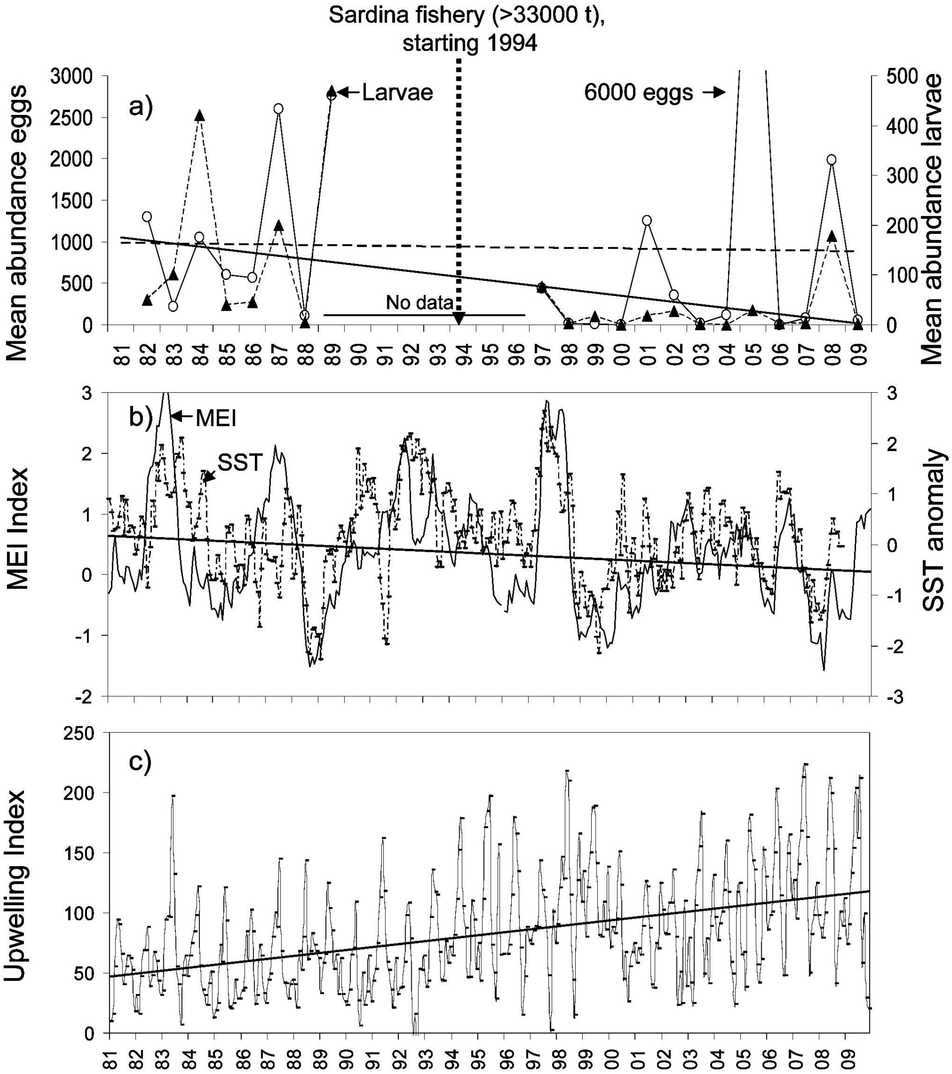

FIG. 8. – a) *Sardinops sagax* egg and larval abundance (numbers per 10 m^2); b) Multivariate El Niño-Southern Oscillation Index and SST anomalies; and c) upwelling index (m^3/s/100 m coastline) at 24°N and 113°W. Horizontal lines indicate linear regressions (trendline).

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 m^2 in 2001, 2005, 2008), drastic decreases occurred in consecutive years (100 eggs and 15 larvae per 10 m^2 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 m^2), 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].

REFERENCES

Aceves-Medina G., Hinojosa-Medina A., Jiménez-Rosenberg S.P.A., Funes-Rodríguez R., Saldierna-Martínez R. 2004. Fish larvae assemblages in the Gulf of California. *J. Fish Biol*. 65: 1-16.

Aceves-Medina G., Palomares-García R., Gómez-Gutiérrez J., Robinson C., Saldierna-Martínez R. 2009. Multivariate characterization of spawning and larval environments of small pelagic fishes in the Gulf of California. *J. Plankton Res*. 31: 1283-1297.

Agostini V.N., Bakun A. 2002. 'Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). *Fish. Oceanogr*. 11: 129-142.

Ahlstrom E.H. 1954. Distribution and abundance of egg and larval populations of the Pacific sardine. *Fish. Bull*. 93: 1-140.

Ahlstrom E.H. 1965. A review of the effects of the environment of the Pacific sardine. *ICNAF Special Pub*. 6: 53-76.

Arthur D.K. 1976. Food and feeding and larvae of three fishes occurring in the California current, *Sardinops sagax, Engraulis mordax*, and *Trachurus symmetricus*. *Fish. Bull*. 74: 517-530.

Bakun A. 1996. *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics*. California, USA: Univ. California Sea Grant, San Diego, CIBNOR, La Paz, Baja California Sur, México, 323 pp.

Bakun A., Babcock E.A., Lluch-Cota S.E., Santora C., Salvadeo C.J. 2010. Issues of ecosystem-based management of forage fisheries in ''open'' non-stationary ecosystems: the example of the sardine fishery in the Gulf of California. *Rev. Fish Biol. Fish*. 20: 9-29.

Beers J.R. 1976. Volumetric methods. In: Steedmann H.F. (ed.), *Zooplankton Fixation and Preservation*. Monogr. Oceanogr. Method. UNESCO Press, Paris, pp. 56-60.

Bernal M., Stratoudakis Y., Coombs S., Angelico M.M., Lago de Lanzós A., Porteiro C., Sagarminaga Y., Santos M., Uriarte A., Cunha E., Valdés L., Borchers D. 2007. Sardine spawning off the European Atlantic coast: Characterization of and spatio-temporal variability in spawning habitat. *Prog. Oceagr*. 74: 210-227.

Cervantes-Duarte R., López-López S., González-Rodríguez E. 2007. Características hidrológicas de Bahía Magdalena, B.C.S. México, en el periodo 2001-2003. *CICIMAR Oceánides* 22: 1-11.

Cervantes-Duarte R., López-López S., González-Rodríguez E., Futema-Jiménez S. 2010. Ciclo estacional de nutrientes, temperatura, salinidad y Clorofila *a* en Bahía Magdalena, BCS, México (2006-2007). *CICIMAR Oceánides* 25: 111-120.

Coombs S.H., Smyth T.J., Conway D.V.P., Halliday N.C., Bernal M., Stratoudakis Y., Alvarez P. 2006. Spawning season and temperature relationships for sardine (*Sardina pilchardus*) in the eastern North Atlantic. *J. Mar. Biol. Ass. U.K*. 86: 1245-1252.

Cury P., Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci*. 46: 670-680.

Cota-Villavicencio A., Troncoso-Gaytán R., Romero-Martínez M., Nevárez-Martínez M.O. 2010. Situación de la pesquería de pelágicos menores en la costa noroccidental de Baja California durante las temporadas de pesca 2007 y 2008. *Cienc. Pesq.* 18: 19-32.

Deriso R., Barnes T., Jacobson L., Arenas, P. 1996. Catch-at-age analysis for Pacific sardine (*Sardinops sagax*), 1983-1995. *Calif. Coop. Ocean. Fish. Invest. Rep*. 37: 175-187.

Emmett R.L., Brodeur R.D., Miller T.W., Pool S.S., Krutzikowsky G.K., Bentley R.J., McCrae J. 2005. Pacific sardine (*Sardinops sagax*) abundance, distribution and ecological relationships in the Pacific northwest. *Calif. Coop. Ocean. Fish. Invest. Rep*. 46: 122-143.

Félix-Uraga R., Alvarado-Castillo R. M., Carmona-Piña R 1996. The sardine fishery along the western coast of Baja California, 1981 to 1994. *Calif. Coop. Ocean. Fish. Invest. Rep*. 37: 188-192.

Félix-Uraga R., Gómez-Muñoz V.M., Quiñónez-Velázquez C., Melo-Barrera F.N., García-Franco. W 2004. On the existence of Pacific sardine groups off the west coast of the Baja California Peninsula and southern California. *Calif. Coop. Oceanic Fish. Invest. Rep*. 45: 146-151.

Félix-Uraga R., Gómez-Muñoz V.M., Quiñonez-Velázquez C., Melo-Barrera F.N., Hill K., García-Franco W. 2005. Pacific sardine stock discrimination in the west coast of Baja California and southern California, using otolith morphometry. *Calif. Coop. Oceanic Fish. Invest. Rep*. 46: 113-121.

Félix-Uraga R., Melo-Barrera F.N., Quiñonez-Velázquez C. 2007. Parámetros poblacionales de la sardina del Pacífico *Sardinops sagax* y su contribución a la pesquería de Bahía Magdalena: enfoque de stocks. In: Funes-Rodríguez R., Gómez-Gutiérrez J., Palomares-García R. (eds.), *Estudios ecológicos en Bahía Magdalena*. CICIMAR-IPN, La Paz, Baja California Sur, México, pp. 223-234.

Funes-Rodríguez R., González-Armas R., Esquivel-Herrera A. 1995. Abundancia y composición específica del ictioplancton en la costa del Pacífico frente a Baja California Sur (1983-1985). *Hidrobiológica* 5: 125-131.

Funes-Rodríguez R., Hinojosa-Medina A., Avendaño-Ibarra R., Hernández-Rivas M.E., Saldierna-Martínez R., Watson, W. 2001. Spawning of small pelagic fish in Magdalena, Baja California Sur, México, at the beginning of the 1997-1998 El Niño event. *Est. Coast. Shelf Sci*. 53: 653-664.

Funes-Rodríguez R., Hinojosa-Medina A., Aceves-Medina G., Saldierna-Martínez R., Hernández-Rivas M.E. 2004. Diagnosis Taxonómica y Distribución de la Abundancia de los Primeros

Estadios de Vida de los Peces Pelágicos Menores. In: Quiñónez-Velázquez C., Elorduy-Garay J.F. (eds.), *Ambiente y pesquería de pelágicos menores en el noroeste de México*. CICIMAR-IPN, La Paz, Baja California Sur, México, pp. 27-56.

Funes-Rodríguez R., Leal-Espinoza J.D., Hinojosa-Medina A., Hernández-Rivas M.E., Flores-Coto C. 2007. Composición, distribución y abundancia de larvas de peces en Bahía Magdalena. In: Funes-Rodríguez R., Gómez-Gutiérrez J., Palomares-García R. (eds.), *Estudios ecológicos en Bahía Magdalena*. CICIMAR-IPN, La Paz, Baja California Sur, México, pp. 205-219.

Gárate-Lizárraga I., Siqueiros-Beltrones D.A. 1998. Time variation in phytoplankton assemblages in a subtropical lagoon system after the 1982-83 "El Niño" event (1984 to 86). *Pac. Sci*. 1: 79-97.

García-Rodríguez F.J., García-Gasca S.A., De La Cruz-Agüero J., Cota-Gómez V.M. 2010. A study of the population structure of the Pacific sardine *Sardinops sagax* (Jenyns, 1842) in Mexico based on morphometric and genetic analyses. *Fish. Res*. 107: 169-176.

Gómez-Gutiérrez J., Palomares-García J.R., De Silva-Dávila R., Carballido-Carranza M.A., Martínez-López A. 1999. Copepod daily egg production and growth rates in Bahía Magdalena, Mexico. *J. Plankton Res*. 21: 2227-2244.

Gómez-Gutiérrez J., Martínez-Gómez S., Robinson, C. J. 2007. Influence of tidal fronts on surface zooplankton aggregation and community structure in a subtropical bay, Bahía Magdalena, Mexico. *Mar. Ecol. Progr. Ser*. 346: 109-125.

Hammann M.G., Nevárez-Martínez M.O., Green-Ruíz Y. 1998. Spawning habitat of the Pacific sardine (*Sardinops sagax*) in the Gulf of California: egg and larval distribution 1956–1957 and 1971–1991. *Calif. Coop. Oceanic Fish. Invest. Rep*. 39: 169-179.

Hernández-Vázquez S. 1994. Distribution of eggs and larvae from sardine and anchovy off California and Baja California, 1951-1989. *Calif. Coop. Oceanic Fish. Invest. Rep.* 35: 94-107.

Ibaibarriaga L., Irigoien X., Santos M., Motos I., Fives J.M., Franco C., Lago de Lanzós A., Acevedo S., Bernal M., Bez N., Eltink G., Farinha A., Hammer C., Iversen S.A., Milligan S.P., Reid D.G. 2007. Egg and larval distributions of seven fish species in north-east Atlantic waters. *Fish. Oceanogr*. 16: 284-293.

Lasker R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer* 173: 212-230.

Logerwell E., Smith P.E. 2001. Mesoscale eddies and survival of late stage Pacific sardine (*Sardinops sagax*) larvae. *Fish oceanogr*. 10: 13-25.

Lluch-Belda D., Lluch-Cota D.B., Hernández-Vázquez S., Salinas-Zavala C.A., Schwartzlose R.A. 1991. Sardine and anchovy spawning as related to temperature and upwelling in the California Current system. *Calif. Coop. Oceanic Fish. Invest. Rep*. 32: 105-111.

Lluch-Belda D., Hernández-Vázquez S., Lluch-Cota D. 1992. The recovery of the California sardine as related to global change. *Calif. Coop. Oceanic Fish. Invest. Rep*. 33: 50-59.

Lluch-Belda D., Lluch-Cota D.B., Lluch-Cota S.E. 2003. Baja California's Biological Transition Zones: Refuges for the California Sardine. *J. Oceanogr*. 59: 503-513.

Lynn R.J. 2003. Variability in the spawning habitat of Pacific sardine (*Sardinops sagax*) off southern and central California. *Fish. Oceanogr*. 12: 541-553.

McClatchie S., Rogers P.J., McLeay L. 2007. Importance of scale to the relationship between abundance of sardine larvae, stability, and food. *Limnol. Oceanogr*. 52: 1570-1579.

Melo-Barrera F.N., Félix-Uraga R., Quiñonez-Velázquez C. 2010. Análisis de la pesquería de *Sardinops sagax* en la costa occidental de Baja California Sur, México, durante 2006-2008. *Cienc. Pesq.* 18: 33-46.

Moser H.G., Charter R.L., Smith P.E., Ambrose S.R., Charter C.A., Meyer E.M., Watson W. 1993. *Distributional atlas of fish larvae and eggs in the California Current region: taxa with 1000 or more total larvae, 1951 through 1984. Calif. Coop. Oceanic Fish. Invest,* Atlas 31. Scripps Inst. of Oceanog. La Jolla, CA, 233 pp.

Moser H.G., Smith P.E. 1993. Larval fish assemblages of the California current region and their horizontal and vertical distributions across a front. In Moser, H. G., Smith P. E. and Fuiman L. A. (eds), *Advances in the early life history of fishes, Part 1.* Larval fish assemblages and oceanic boundaries. *Bull. Mar. Sci*. 53: 283-289.

Palomares-García R., Gómez-Gutiérrez J. 1996. Copepod community structure at Bahia Magdalena, Mexico during El Niño 1983-1984. *Est. Coast. Mar. Sci*. 43: 583-595.

Palomares-García R., De Silva-Dávila R. 2007. Variación estacional de la producción de huevos de copépodos en Bahía Magdalena. In: Funes-Rodríguez R., Gómez-Gutiérrez J., Palomares-García R. (eds.), *Estudios ecológicos en Bahía Magdalena*, CICIMAR-IPN, La Paz, Baja California Sur, pp. 175-188.

Parrish R.H., Nelson C.S., Bakun A. 1981. Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogr*. 1: 175-203.

Parrish R.H., Serra R., Grant W.S. 1989. The monotypic sardines, Sardina and Sardinops: Their taxonomy, distribution, stock structure, and zoogeography. *Can. J. Fish. Aquat. Sci*. 46: 2019-2036.

Peterson W.T., Arcos D.F., McManus G.B. 1988. The nearshore zone during coastal upwelling: daily variability and coupling between primary and secondary production off Central Chile. *Progr. Oceanogr*. 20: 1-40.

Peterson W.T., Schwing F.B. 2003. A new climate regime in Northeast Pacific ecosystems. *Geophys. Res. Let*. 30: 1-4.

Planque B., Bellier E., Lazure P. 2007. Modelling potential spawning habitat of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. *Fish. Oceanogr*. 16: 16-30.

Rodríguez-Sánchez R., Lluch-Belda D., Villalobos-Ortíz H., Ortega-García S. 2001. Large-Scale Long-Term variability of small pelagic fish in the California current system. In: Kruse G.H., Bez N., Booth A., Dorn M.W., Hills S., Lipcius R.N., Pelletier D., Roy C., Smith S.J., Witherell D. (eds.), *Spatial Processes and Management of Marine Populations*. University of Alaska, Fairbanks, AK, pp. 447-462.

Saldierna-Martínez R., Sánchez-Ortíz C.A., Vera-Alejandré G.R. 1987. *Estudios sobre los primeros estadios de vida de las sardinas crinuda Opisthonema libertate y monterrey, Sardinops sagax, en Bahía Magdalena, B. C. S.* Professional Thesis, Univ. Autón. Baja California Sur, México, 217 pp.

Schwartzlose R.A., Alheit J., Bakun A., Baumgartner T.R., Cloete R., Crawford R.J.M., Fletcher W.J., Green-Ruíz Y., Hagen E., Kawasaki T., Lluch-Belda D., Lluch-Cota S.E., MacCall A.D., Matsuura Y., Nevárez-Martínez M.O., Parrish R.H., Roy C., Serra R., Shust K.V., Ward M.N., Zuzunaga J.L. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *S. Afr. J. mar. Sci*. 21: 289-347.

Smith P.E., Moser G.H. 2003. Long-term trends and variability in the larvae of Pacific sardine and associated fish species of the California Current region. *Deep-Sea Res*. 50: 2519-2536.

Strickland J.D., Parson T.R. 1972. *A practical handbook of seawater analysis. J. Fish. Res. Board Can.* Bull. 167 pp.

Tibby R.B. 1937. The relation between surface water temperature and the distribution of spawn of the California sardine (*Sardinops caerulea*). *Cal. Fish. Game* 23: 132-137.

Torres-Villegas J.R., Ochoa-Báez R.I., Perezgómez-Álvarez L., García-Melgar G. 1995. Comparison of seasonal variability in reproduction of Pacific sardine (*Sardinops sagax*) from Baja California Sur, Mexico, in the years 1982-1992. *Sci. Mar*. 59: 255-264.

Turner J.T. 1984. *The feeding ecology of some zooplankters that are important prey items of larval fish.* NOAA Tech. Rep. NMFS 7, 28 pp.

Venrick E., Hayward T. 1984. Determining chlorophyll on the 1984 CalCOFI surveys. *Calif. Coop. Oceanic Fish. Invest. Rep*. 25: 74-79.

Zaytsev O., Cervantes-Duarte R., Sánchez-Montante O., Gallegos-García A. 2003. Coastal upwelling activity of the Pacific shelf of Baja California Peninsula. *J. Oceanog*. 59: 489-502.

Zaytsev O., Sánchez-Montante O., Saldivar-Reyes M 2010. Seasonal variations of the thermohaline structure in the Magdalena-Almejas Bay lagoon system and adjacent sea. Cienc. Mar. 36: 413-432.

Scient ed.: I. Palomera.
Received June 8, 2011. Accepted November 9, 2011.
Published online February 20, 2012.