

## Relation between recruitment, sea surface temperature, and density-independent mortality of the Pacific sardine (*Sardinops caeruleus*) off the southwest coast of the Baja California Peninsula, Mexico\*

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**SUMMARY:** The density-independent mortality, considered in the stock-recruitment model of Ricker, was related to the interannual variability of the sea surface temperature (SST) during 1981 to 1993 in Bahía Magdalena, Baja California Sur and Isla Cedros, Baja California, Mexico. From the stock-recruitment curve fitted to the observed data the variation in the density-independent mortality was estimated, maintaining fixed the value of the density-dependent coefficient. The density-independent parameters estimated in this way were related to the SST by using a functional relationship that considers six principal components. This function permitted identification of the changes of the density-independent mortality and its relation to the recruitment of the Pacific sardine *Sardinops caeruleus*. We determined density-independent mortality greater than 3.38 as years with recruitment greater than 25,000 t, and density-independent mortality less than 3.38 as years with recruitment less than 15,000 t. The seasons of greatest influence on the density-independent mortality in relation to the SST were autumn, winter and spring in both regions (Bahía Magdalena and Isla Cedros). In these seasons when the SST > 19.3°C (warmer waters) the variations in recruitment of Pacific sardine were observed.

**Key words:** sea surface temperature, recruitment, density-independent mortality, Pacific sardine.

**RESUMEN:** RELACIÓN ENTRE EL RECLUTAMIENTO, LA TEMPERATURA SUPERFICIAL DEL MAR Y LA MORTALIDAD DENSO INDEPENDIENTE DE LA SARDINA DEL PACÍFICO (*SARDINOPS CAERULEUS*) DE LA COSTA SUROESTE DE LA PENÍNSULA DE BAJA CALIFORNIA, MÉXICO. – La mortalidad denso independiente considerada en el modelo de stock reclutamiento de Ricker fue relacionada con la variabilidad interanual de la temperatura superficial del mar (TSM), durante el periodo de 1981 a 1993 en Bahía Magdalena, Baja California Sur e Isla Cedros, Baja California, México. Ajustando la curva stock reclutamiento a los datos observados, se estimó la variación de la mortalidad denso independiente, manteniendo constante el valor del coeficiente de mortalidad denso dependiente. Los parámetros de denso independencia estimados de ésta forma, fueron relacionados con la TSM usando una relación funcional que considera seis componentes principales. Esta función permitió identificar los cambios en la mortalidad denso independiente y su relación con el reclutamiento de la sardina del pacífico *Sardinops caeruleus*. Se determinó una mortalidad denso independiente > 3.38 como años con reclutamiento > 25,000 t, y mortalidad denso independiente < 3.38 como años con reclutamiento < 15,000 t. Las estaciones de mayor influencia sobre la mortalidad denso independiente en relación a la TSM fueron: otoño, invierno y primavera en ambas regiones (Bahía Magdalena e Isla Cedros). En estas estaciones fueron observadas las variaciones en reclutamiento de la sardina del pacífico cuando la TSM > 19.3°C (aguas cálidas).

**Palabras clave:** temperatura superficial del mar, reclutamiento, mortalidad denso independiente, sardina del Pacífico.

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## INTRODUCTION

Small pelagic fisheries have high interannual variability of abundance and distribution, and these changes can be related to physical variables of the ocean (Lluch-Belda *et al.*, 1989, 1991, 1992a, b). Analyses of scale counts in anaerobic sediments indicate natural cyclical fluctuations in abundance of sardine and anchovy, apparently caused by the environment alone (Baumgartner *et al.*, 1992). Environmental effects on sardine abundance probably affect early life stages and therefore the magnitude of recruitment (Smith *et al.*, 1992; Cisneros-Mata *et al.*, 1996). Sea surface temperature and upwellings may limit sardine recruitment because upwellings induce advection of larvae into offshore areas where survival is poor. This event may be associated with poor reproductive success (Murphy, 1960; Iles, 1973), because sardine spawnings may tend to be unsuccessful in cold water, because spawning is delayed or because the spawning period is shortened (Marr, 1960).

The principal species of small pelagics in the commercial fishery between Isla Cedros and Bahía Magdalena, Mexico is the Pacific sardine (*Sardinops caeruleus* Girard 1854) (Fig. 1). The fleet size in the fishing area varies between 5 and 7 boats per year, the fleet is composed of boats with a carrying capacity of between 60 and 120 t, and the fishing grounds are mostly located within Bahía Magdalena. Pacific sardine has been harvested commercially along the western coast of Baja California Peninsula since 1951, but when the sardine fishery collapsed in Cal-

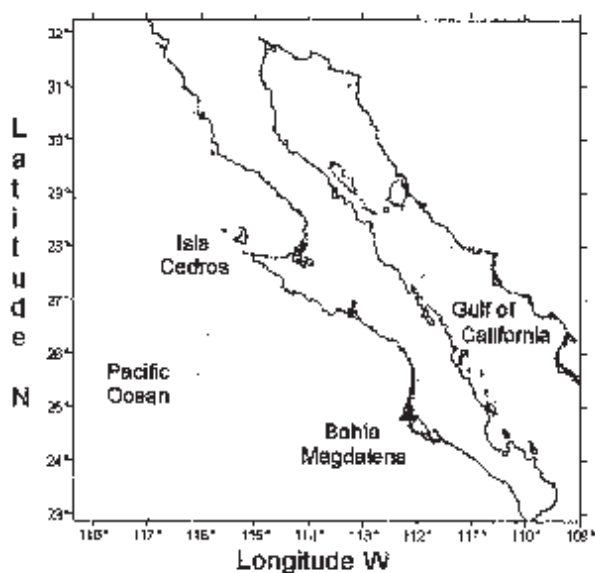


FIG. 1. – Study zone along the southwest coast of the Baja California Peninsula, Mexico.

ifornia, the Mexican fishery was established at Isla Cedros (1961) and Bahía Magdalena (1972) (Félix-Uraga *et al.*, 1996). The fishing season is throughout the year; it has two periods of maximum catches, from late spring to early summer, and from late fall to early winter. *S. caeruleus* has a seasonal reproductive cycle from winter to early summer, and the species shows two spawning periods, the most important peak being observed during January and February, with another small spawning peak during July and August (Torres-Villegas *et al.*, 1995). For the Pacific sardine, a few annual classes are present (Félix-Uraga *et al.*, 1996) and the abundance of the population depends strongly on recruitment. Therefore, the relation between the environment and abundance of the resource is a close one.

Statistical models between recruitment and environment for some exploited populations have been developed by Tang (1985), who proposed in the prawn (*Panaeus orientalis*) a modification to the stock-recruitment model of Ricker through a multiple linear function associated with the density-independent mortality coefficient. Gardiner and Shachley (1991) showed that sea surface temperature (SST) is related to the size of the stock, growth, and survival of juveniles in a population of salmon (*Salmo salar*). Clark (1992) and Hannah (1993) used regression models to evaluate the influence of the environmental variability on the recruitment of arctic grayling (*Thymallus arcticus*) and ocean shrimp (*Pandalus jordani*). Jacobson and MacCall (1995) analysed models of the stock-recruitment relation for Pacific sardine, taking into account the SST variability, and showing that fluctuations in the recruitment were influenced by the changes in the SST. The relation between environmental factors and sardine population may be affected by other physical regimes such as mixing, upwelling, and thermal stratification processes (Hemingway, 1979; Huato-Soberanis and Lluch-Belda, 1987; Lluch-Belda *et al.*, 1989). In this paper, we investigate the relation between recruitment of Pacific sardine off the southwest coast of Baja California Peninsula, Mexico, and environmental conditions related to the interannual variability of the sea surface temperature.

## MATERIAL AND METHODS

The estimates of the stock size and recruitment for the southern stock of *S. caeruleus* off the southwest coast of the Baja California Peninsula, Mexico

TABLE 1. – Recruitment and adult stock estimated with VPA. (Morales-Bojórquez, 1999).

	Recruits (MT)	Adult stock (MT)
1981	15,506	69,427
1982	24,236	10,357
1983	14,226	14,022
1984	34,753	15,417
1985	38,156	27,436
1986	26,978	33,349
1987	39,635	23,161
1988	34,759	34,533
1989	21,849	36,885
1990	16,745	31,123
1991	15,045	15,263
1992	32,867	7,633
1993	24,997	22,733

during 1981-1993 were obtained through virtual population analysis (VPA) (Pope, 1972). The individuals in the catch from Bahía Magdalena and Isla Cedros were combined in the VPA. Sagittae otoliths were used to estimate age of fish in the catch (Félix-Uraga *et al.*, 1996). Adult stock and recruitment were estimated with tuned VPA using criteria for effort (Table 1) (Hilborn and Walters, 1992; Morales-Bojórquez, 1999). The natural mortality ( $M = 0.6/\text{year}$ ) was estimated using the Silliman method (Ricker, 1975). The sea surface temperature was obtained from the Comprehensive Ocean Atmosphere Data Set (COADS) (Roy and Mendelssohn, 1994),  $24^\circ\text{N}$ ,  $113^\circ\text{W}$  for Bahía Magdalena (MB), and  $27^\circ\text{N}$ ,  $116^\circ\text{W}$  for Isla Cedros (CI) (Fig. 1). We used the monthly average of the SST for each year and each region, building a matrix of 13 years by 24 values of SST.

The VPA was tuned to include auxiliary information into the cohort analysis; the index ( $I$ ) was CPUE data (Quinn II and Deriso, 1999). In this case, the estimated index at time  $t$  denoted as  $I_t^E$  was computed as  $I_t^E = I_t^O + \varepsilon_t$ , where  $I_t^O = \delta_0 + \delta_1 N_{a,t}$ ; therefore,  $I_t^O$  represents the observed index at time  $t$ ,  $\delta_0$  and  $\delta_1$  are calibration coefficients,  $N_{a,t}$  is number of individuals at age  $a$  and time  $t$ , and  $\varepsilon_t$  is error term distributed normally with mean and variance of  $I_t^O$ . Parameter  $\delta_0$  is an optional intercept term, which allows an index to be linearly related to abundance  $N_{a,t}$  without being directly proportional (Hilborn and Walters, 1992; Quinn II and Deriso, 1999). Given initial estimates of abundance, the tuned abundance and calibration coefficients were estimated by minimizing the next objective function:

$$RSS_{N_{a,t}} = \sum_I \sum_a \sum_t \lambda_{I,a,t} (I_t^E - I_t^O)^2 \quad (1)$$

where  $RSS_{N_{a,t}}$  is a residual sum of squares between the estimated and observed index. The  $\lambda$  value is a ratio of variance (variance of observed logarithm catch  $\sum_a \sum_t N_{a,t}$  divided by the variance of observed logarithm index  $I_t^O$ ); therefore, we consider  $\lambda$  to be a weighting factor that adjusts the amount of influence of auxiliary information (Deriso *et al.*, 1985; Quinn II and Deriso, 1999).

## Model

The stock-recruitment model of Ricker (1975) uses a parameter ( $\beta$ ) related to the density-dependent mortality and one ( $\alpha$ ) associated with the density-independent natural mortality:

$$R = \alpha S \exp(-\beta S) \quad (2)$$

Our approach assumed the density-dependent parameter  $\beta$  was an intrinsic characteristic of the stock that was constant from year to year (Harris, 1975; Tang, 1985; Tang *et al.*, 1989). In our analysis, variations in  $\alpha$  were related to density-independent effects, like the fluctuations of SST expressed as principal components (Doi, 1973). The parameters  $\alpha$  and  $\beta$  were estimated using a nonlinear fit (Cisneros-Mata *et al.*, 1995). A nonlinear sum of squares was used, fitting the model to the data with log transformation of the recruitment data. The log transformation stabilizes the variance of residuals and the objective function was the following (Hilborn and Walters, 1992):

$$SSQ = \sum_{t=1}^n (\ln R_{Obs} - \ln R_{Est})^2 \quad (3)$$

where  $R_{obs}$  = observed recruitment,  $R_{est}$  = estimated recruitment, and  $t$  = fishing season. Parameters  $\alpha$  and  $\beta$  were used to build the classical stock-recruitment curve for *S. caeruleus*. Maintaining  $\beta$  constant, the theoretical value of the coefficient  $\alpha_t$  at year  $t$  was calculated from the following expression:

$$\alpha_t = R_t / [S_t \exp(-\beta S_t)] \quad (4)$$

The values of  $\alpha_t$  were related to principal components ( $Pc_i$ ). In this way, the  $\alpha_t$  coefficient was described by the multiple linear equation (Doi, 1973):

$$\alpha_t = a_0 + \sum_{i=1}^m a_i Pc_i \quad (5)$$

In the analysis of multiple regression we did not use as independent variables the SST values, but the values of  $Pc_i$  (as vectors) estimated with multivariate analysis.  $Pc_i$  has the characteristic of being orthogonal and uncorrelated, avoiding the regression on residuals (Mardia *et al.*, 1989; Morrison, 1990; Milstein, 1993). Orthogonality is defined as perfect non-association between variables (Manly, 1994; Krzanowski, 1993). If two or more variables are orthogonal, the correlation between them is zero (Tabachnick and Fidell, 1989).

Each principal component is a linear combination of the physical factors ( $X_j$ ):

$$Pc_i = \sum_j \lambda_{ij} [(X_j - \bar{X}_j) s_j^{-1}] \quad (6)$$

where  $\lambda_{ij}$  is the eigenvector's  $j$ -th coordinate of the  $i$ -th principal component. It therefore represents the contribution of each physical factor  $X_j$  (with mean  $\bar{X}_j$  and variance values  $s_j^2$ ) (Pielou, 1984; Tabachnick and Fidell, 1989; Ortega-García and Gómez-Muñoz, 1992). For the  $m$  principal components that explain a high percentage of the total variability and are highly correlated with  $\alpha_t$ , we used the following stock recruitment model:

$$R_t = \left[ \left( a_0 + \sum_{i=1}^m a_i Pc_i \right) * S_t \right] * \exp(-\beta S_t) \quad (7)$$

Principal Component Analysis permitted a ranking and simplification of the new variables called principal components, determining the total variation of the data, and explaining it with a few factors

(factor loadings  $\geq 0.7$ ). The criterion used to determine the number of the independent variables  $Pc_i$  in sequential way was the test of confidence statistics of  $r^2$  of Sokal and Rhoif (1981).

## RESULTS

The Ricker model showed values of the mortality coefficients  $\alpha = 3.38$  and  $\beta = -4.19 \times 10^{-5}$ . The variations in the estimation of value  $\alpha_t$  showed the same trends as the observed recruitment for *Sardinops caeruleus* during each year analysed (Fig. 2). The estimation of  $\alpha_t$  with the principal components showed that six principal components of a total of 24 computed ( $r^2 = 0.93$ ,  $P < 0.05$ ) participated, explaining 91% of the total variation of the information in terms of variance accumulated (Table 2).

The analysis of the principal components that participated in the model (expression 7) showed the seasons of main statistical importance (factor loadings  $\geq 0.7$ ; Table 2). The first principal component had a contribution of 42.28% of variance, where October, November, and December (autumn) in MB, and November, and December (autumn) in CI were months with SST  $> 23.4^\circ\text{C}$  in MB, and SST  $> 20.8^\circ\text{C}$  in CI. In the second principal component (with variance of 19.9%) January, February, and March (winter) in MB, and January, and February (winter) in CI were identified as months with SST  $> 21.7^\circ\text{C}$  in MB, and SST  $> 19.3^\circ\text{C}$  in CI. Finally, the third principal compo-

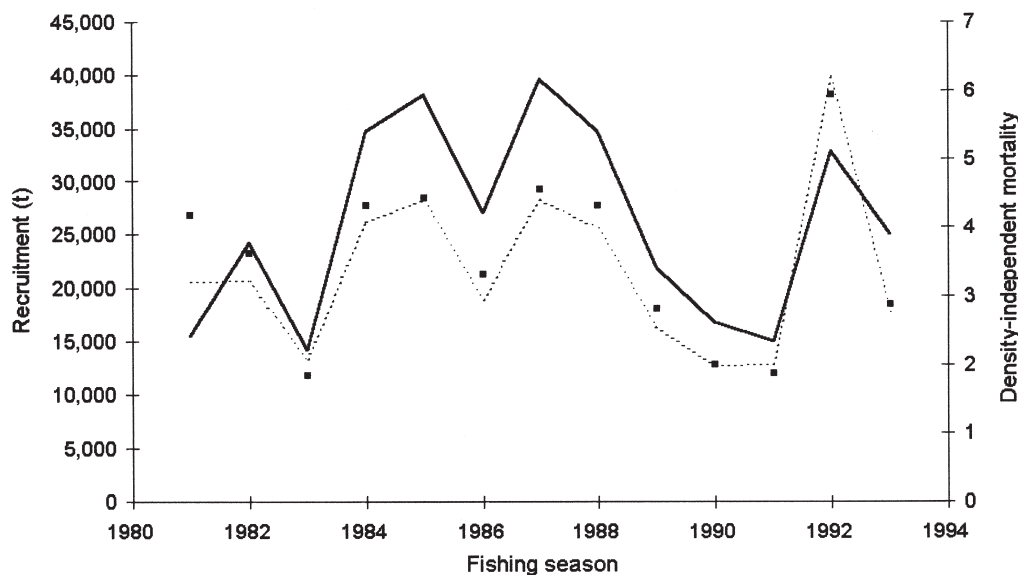


FIG. 2. – Interannual variations of the density-independent mortality observed (filled squares), estimated density-independent mortality (dotted line), and recruitment (solid line).

TABLE 2. – Eigenvectors (Eigv) estimated with principal components with confidence level  $P < 0.05$ . Only the eigenvectors of the principal components that were used in the multiple linear model as independent variables are shown. The first column has the key: JAN = January, T = SST, MB = Bahía Magdalena and CI = Isla Cedros. Eig. = Eigenvalue, Var. = Variance (%), Varac. = Variance accumulated (%).

	Eigv 1	Eigv 2	Eigv 3	Eigv 4	Eigv 5	Eigv 6
JANTMB	-0.05	0.95	0.06	0.07	0.02	-0.03
FEBTMB	-0.09	0.94	-0.20	-0.02	-0.08	0.00
MARTMB	0.00	0.82	0.18	0.10	0.12	0.49
APRTMB	-0.04	0.40	0.70	0.36	0.28	0.13
MAYTMB	0.15	0.37	0.73	0.42	0.20	0.07
JUNTMB	0.27	0.32	0.45	0.57	0.14	0.13
JULTMB	0.28	0.10	0.57	0.65	-0.02	-0.05
AUGTMB	0.28	0.09	0.32	0.86	0.15	0.01
SEPTMB	0.46	-0.08	0.13	0.82	0.05	-0.02
OCTTMB	0.76	0.04	-0.10	0.28	-0.17	0.07
NOVTMB	0.88	0.10	0.05	0.37	0.05	0.03
DECTMB	0.92	0.15	0.09	0.20	0.16	-0.01
JANTCI	0.12	0.89	0.09	0.28	0.00	-0.04
FEBTCI	0.13	0.89	0.23	0.09	0.01	-0.06
MARTCI	-0.07	0.50	0.76	-0.07	0.26	-0.02
APRTCI	0.09	-0.13	0.95	0.10	0.08	-0.04
MAYTCI	0.16	-0.03	0.90	0.23	0.06	0.04
JUNTCI	0.07	-0.05	0.73	0.17	-0.13	0.02
JULTCI	-0.12	0.04	0.52	0.39	-0.03	0.01
AUGTCI	0.28	-0.01	0.41	0.42	0.75	0.04
SEPTCI	0.27	0.29	0.19	0.83	0.15	-0.01
OCTTCI	0.46	0.20	0.03	0.75	0.05	0.10
NOVTCI	0.75	-0.14	0.21	0.39	0.22	0.02
DECTCI	0.76	-0.29	0.18	0.19	0.00	-0.12
Eig.	10.63	4.78	3.49	1.35	0.98	0.64
Var.	44.28	19.90	14.55	5.61	4.09	2.68
Varac.	44.28	64.18	78.73	84.34	88.44	91.12

ment with variance of 14.55% showed the influence of spring in both regions (SST > 24.2°C in MB, and 20.3°C in CI), April, and May in MB, and March, April, May, and June in CI. The variance accumulated for these principal components was 78.73%, and their coefficients were positives in all cases, and higher than the mean (19.3°C). Thus, during autumn, winter and spring for both regions the variations in recruitment of Pacific sardine was related to warmer waters. The principal components 4, 5 and 6 showed a contribution in accumulated variance of 12.38%, so their coefficients were not analysed.

The parameters of the multiple linear model that relate the principal components to  $\alpha_t$  are shown in Table 3. The values of the principal components for each year allow one to estimate a new value of  $\alpha_t$  as a function of the interannual variability of the SST. It was compared with the observed values of  $\alpha_t$  ( $r^2 = 0.96$ ,  $P < 0.05$ ) (Fig. 2) in the Ricker model (expression 5). In this model, we determined  $\alpha_t = 3.38$  as the standard curve of stock recruitment relation in the Ricker model. Values of  $\alpha_t > 3.38$  showed high recruitment, greater than 25,000 t, and the low recruitment was obtained with values of  $\alpha_t < 3.38$ , lower than 15,000 t. Two examples of this condition

TABLE 3. – Coefficients of the multiple linear model among  $\alpha_t$  and principal components estimated.

Constant	Value	Standard Error	P-level
$a_0$	3.36	0.083	0.000
$a_1$	-0.34	0.086	0.056
$a_2$	-0.48	0.085	0.030
$a_3$	0.55	0.086	0.023
$a_4$	0.34	0.086	0.058
$a_5$	-0.22	0.101	0.152
$a_6$	0.14	0.106	0.304

are shown in Figure 3. Values of  $\alpha_t = 6.19$  (1992) were related to recruitment of 32,000 t, and  $\alpha_t = 1.98$  (1990) to recruitment of 16,000 t.

## DISCUSSION

We have shown a relation between the variations of the coefficient  $\alpha_t$  and the recruitment of *S. caeruleus*, but the explanation of this dependency is difficult to interpret. Lluch-Belda *et al.* (1989, 1991, 1992a, b) showed that there is a relation between SST, abundance, distribution, and the possible relation of these to the recruitment of *S. caeruleus*, explaining an expansion and contraction pattern of

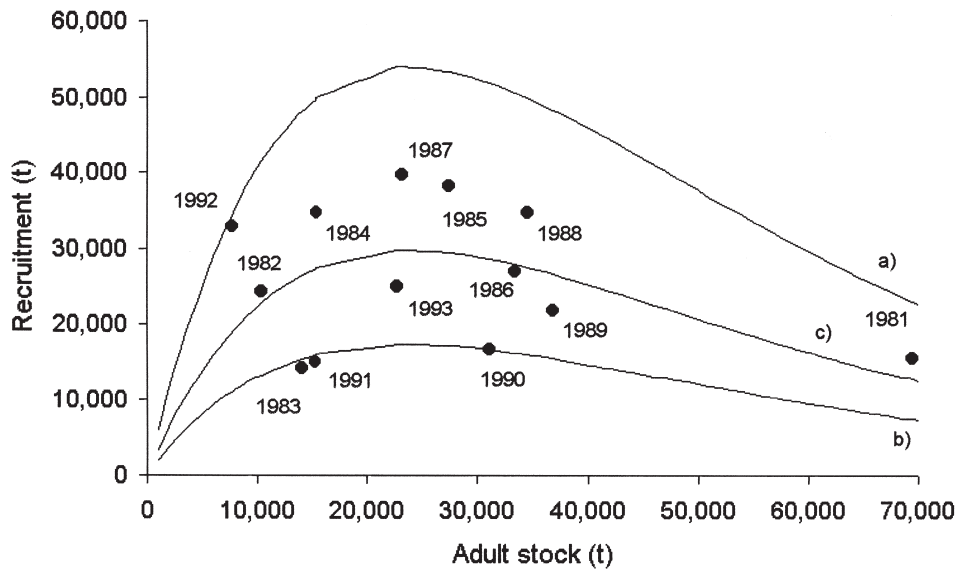


FIG. 3. – Ricker model estimated with two different conditions of the SST; a) 1992 was estimated with  $\alpha = 6.19$ , b) 1990 was estimated with  $\alpha = 1.98$ , and c) shows the Ricker model estimated with nonlinear fit.

the population in the California Current. Furthermore, Félix-Uraga *et al.* (1996) showed a local movement between Bahía Magdalena, Isla Cedros, and Ensenada associated with SST. Kawasaki (1983, 1992) proposed an ecological model of the interaction between the marine environment and the survival of the communities of phytoplankton and zooplankton. The changes in these communities directly affect the population of Pacific sardine. Among the variables, SST is important in the regulation of development, growth, and larval survival (Ramírez-Sevilla *et al.*, 1992; Bloomer *et al.*, 1994), whereas in adults, the SST mainly modifies spawning through a change in the distribution of the spawning areas along the California Current (Hernández-Vázquez, 1994).

The analysis of the stock-recruitment relation with environmental variability has in some cases shown an understanding of the variability of the recruitment (Anthony and Fogarty, 1985; Clark, 1992; Hannah, 1993). However, the methods used are generalised models having an empirical approximation of the interpretation of the recruitment-environment relation. Roy *et al.* (1992) and Cury and Roy (1989), using simulation models, showed that the success of the recruitment is related to optimal environmental conditions. In this study, the influence of the variability of the SST has been defined in two different regions, describing the seasons with greater influence on the density-independent mortality of *S. caeruleus*. The combined effect of this variability in the marine environment may be explained

by the presence of the events that cause fluctuation in the recruitment of *S. caeruleus*. Félix-Uraga *et al.* (1996) showed that periods of warming cause a redistribution of the population northward in the California Current, observing that a change of this type has the effect of low catch in the zone between Bahía Magdalena and Isla Cedros. Alvarado-Castillo *et al.* (1994) presented a theoretical model of annual distribution in the zone studied, showing that high SST values are associated with movement of the population of Pacific sardine northward of Bahía Magdalena during the summer and autumn, and that a low SST in winter and spring causes movement southward from Isla Cedros. This effect could be increased on a spatial and temporal scale by the influence of warming events (ENSO) (Wolf, 1992).

The Ricker model has a large compensatory density-dependent term, which implies that at high biomass, recruitment is low. We used an analytical approach to incorporate environmental effects into the stock recruitment model, and through this approach we have identified SST seasons that are important in determining recruitment for the Bahía Magdalena sardine population. An interesting observation is that the recruitment during 1981 was lower at a higher adult stock level (Fig. 3). In this year, we observed an overcompensation occurring when the recruitment decreases as the spawning stock increases (Quinn II and Deriso, 1999). In the Gulf of California, Mexico a strong overcompensation was observed when stock-recruitment data of Pacific sardine were analysed (Cisneros-Mata *et al.*,

1995). The mechanism off the southwest coast of the Baja California peninsula is that when cooling occurs, sardine spawning is restricted to Punta Eugenia and Bahía Magdalena, Mexico. However, if a warmer period is observed the spawning stock shows a change in distribution toward the north. The recruitment is thus based on the spawning temperature and modification in the adult stock distribution (Lluch-Belda *et al.*, 1992a; Alvarado-Castillo *et al.*, 1994).

The statistical evidence observed in  $\alpha_t$  during autumn, winter, and spring in Bahía Magdalena, and Isla Cedros can be related to environmental variability of SST (temporal and spatial) on a local scale (Cohen *et al.*, 1991). The changes in upwelling are principally seasonal, and the pattern is strong upwelling during winter and spring, and weak upwelling during summer and fall (Martínez *et al.*, 2000). Associated with these oceanographic conditions, the species shows two spawning periods, the most important peak being observed during winter (January and February), with another small peak during early summer (July and August) (Torres-Villegas *et al.*, 1995). Hernández-Vázquez (1994) concluded that Bahía Magdalena is an important spawning area, with high occurrence during winter months and June. The offshore occurrence of sardine eggs and larvae in Bahía Magdalena and Punta Eugenia (Isla Cedros region) showed high percentages of positive stations for sardine eggs in the first 20 n. mi. (from 1951 to 1989). Nonetheless, the Punta Eugenia region shows high values for all months except May and June. The maximum values of occurrence in the Punta Eugenia region (August-October) are much higher than those observed in Bahía Magdalena; the spawning zones are therefore well identified.

The results of this study indicate that temporal changes in sea surface temperature coincide with the most important spawning period of *S. caeruleus*, and if the success in survival of early stages is due to SST, then they are the ultimate regulators of year class strength of *S. caeruleus*. In this case, temperature can be related to deviations from the stock-recruitment relationship, explaining the apparent stochastic behavior and variance of the data (Morales-Bojórquez, 1999). Given the previous background, it is possible that the match-mismatch hypothesis (Cushing, 1982) provides an explanation for fluctuations in recruitment of *S. caeruleus*. Similarly, Lasker (1975) also concluded that survival rates of larval northern anchovy *Engraulis mordax* depend not so much on plankton density as on the

timing and intensity of upwellings and the production cycle of larvae and their food supply. Evidences from other small pelagic fishes also indicated that hydrographic events were ultimate factors influencing larval mortality and recruitment. Although empirical support for the match-mismatch hypothesis based on statistical evidence alone may be questionable (Bakun y Parrish, 1980), the match-mismatch hypothesis can be further corroborated.

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