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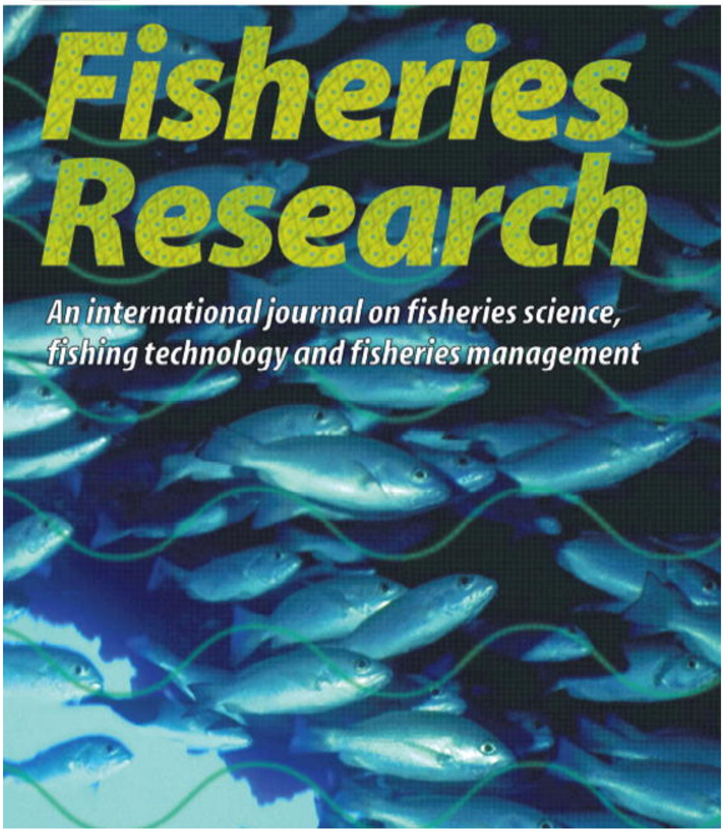

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The spatial structure of the oceanic spawning of jack mackerel (*Trachurus murphyi*) off central Chile (1998–2001)

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Abstract

The jack mackerel population has a widespread oceanic spawning habitat off central Chile, extending more than one thousand nautical miles offshore. In this paper, the spatial structure of jack mackerel eggs density is analyzed on the basis of four surveys carried out in oceanic waters (32°S–39°S, 75°W–92°W), from 1998 to 2001. In each survey, a grid of plankton stations was sampled through vertical hauls with WP2 plankton nets by using several purse-seine fishing ships sampling simultaneously along the E–W transects. With the aim of finding the bulk of the egg distribution within the surveyed area, an exploratory analysis between jack mackerel egg densities, latitude, longitude, and sea surface temperature (SST) was carried out. The spatial structure of the egg distribution was studied using geostatistical techniques. The bulk of the jack mackerel spawning tends to occur offshore between 80°W and 92°W, is maximal at 35°S and associated to SST warmer than 15–16 °C. All of the variograms showed clear spatial autocorrelations without anisotropy, with the range fluctuating between 125 and 252 nautical miles. The range of variograms suggests that the spawning of jack mackerel is a large scale process, probably reflected in the adult behavior of the spawning by favoring a high dispersion of eggs and/or associated with sea surface temperature characterizing the subtropical frontal zone (16–18 °C) off central Chile.

Keywords: Jack mackerel; Oceanic spawning; Spatial pattern; Geostatistics; Southeast Pacific Ocean

1. Introduction

The jack mackerel, *Trachurus murphyi* (Nichols) has a wide distribution in the southeastern Pacific Ocean. In the early 1970s, it was believed that jack mackerel occurred only in coastal waters off Chile and Peru. However, the fishing activity of a distant mid-water trawl fleet during the 1970s and 1980s in the oceanic waters off South America showed that jack mackerel was also distributed between the South American coast and New Zealand (Kawahara et al., 1988; Evseenko, 1987; Parrish, 1989; Bailey, 1989; Elizarov et al., 1993; Grechina, 1998).

According to Serra (1991), there are two self-sustaining populations of jack mackerel within the southeastern Pacific: one located in Peruvian waters and another off Chile, in which the oceanic fraction is included. Serra (1991) described a seasonal migration that would explain jack mackerel availability to the coastal Chilean fisheries. This seasonal migration has been related to both feeding and spawning processes, i.e. offshore migration for austral spring spawning in oceanic waters, and onshore migration during the austral summer-autumn related to food availability in coastal waters (Quiñones et al., 1997; Miranda et al., 1998). According to Arcos et al. (2001) the Chilean jack mackerel population is structured in three different habitats: (a) a nursery habitat northern 30°S, (b) a coastal feeding area off central-south Chile (30°S–40°S); and (c) an oceanic spawning area off central Chile, extending far offshore. The main spawning season extends from October to December, peaking in November during the austral spring (Grechina et al., 1998; Oyarzún et al., 1998). The offshore spawning migration of mature jack mackerel starts at the end of winter (August) into oceanic waters. Jack mackerel is fully mature at 3–4 years of age, and each mature female releases several batches of eggs during the reproductive season (Andrianov, 1985). Furthermore, in the spawning condition the reproductive strategy of jack mackerel is to disperse over a large area in oceanic waters off central Chile, not forming schools or com-

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mercial aggregations (Konchina et al., 1996; Barbieri et al., 1999).

The spawning area of jack mackerel is widespread and located in oceanic waters. Serra (1991) reviewed important reproductive aspects and concluded that jack mackerel spawn off Chile between the Peruvian boundary (18°20′S) and at least 40°S, with the main area between 33°S and 38°30′S. According to Evseenko (1987), the jack mackerel spawning is confined to the Subtropical Convergence Zone (SCZ) extending from the Chilean coast to between 150°W–160°W, which have been verified by Bailey (1989) through samples of juveniles obtained with a dip net and from albacore stomachs from the SCZ of the central South Pacific. During the austral summer, the SCZ is characterized by SST ranging from 15 and 18 °C. Evseenko (1987) found eggs and larvae at 900 nautical miles between 40°S and 42°S, and 80°W to 88°W. Elizarov et al. (1993) reported a high density of jack mackerel eggs (250–500 eggs/m^2) between 80°W and 150°W, suggesting that the southern egg distribution boundary probably occurs approximately at 41°S–42°S. According to Elizarov et al. (1993), the most important concentration of egg was located between 78°W and 90°W off southern Chile (38°S–42°S), suggesting that the position of the 16 °C isotherm could be used as the southern limit for high jack mackerel egg concentration, to the north of 38°S.

Although the oceanic spawning of jack mackerel has been described, the spatial structure of the spawning has not been analyzed in terms of the spatial correlation of egg densities. According to Castillo-Jordán et al. (2007), spatial structures and patterns can take several forms due to either exogenous (i.e. transport, physical gradients) or endogenous processes (i.e. egg patchiness as an inherent property). Considering that jack mackerel migrates offshore to spawn by dispersing over a large area off central Chile, the main objective of this paper is to analyze the spawning spatial structure of jack mackerel using information of four egg survey carried out in the spawning area located in oceanic waters off central Chile (31°48′S–39°00′S) between 1998 and 2001. Geostatistical techniques were applied to reveal the spatial autocorrelation of egg densities by examining experimental variograms. The variogram range can be thought of as an indicator of the average dimension of egg patches as well as the average distance between egg patches or clusters (see Petitgas, 1993; Fletcher and Sumner, 1999). In addition, because several authors have postulated that sea surface temperature of 15–16 °C represents a boundary for jack mackerel spawning (Zuta et al., 1983; Elizarov et al., 1993), in this paper an exploratory analysis is also carried out to reveal the influence of sea surface temperature on jack mackerel egg density distribution in oceanic waters.

2. Materials and methods

2.1. Survey data

The study area was located in oceanic waters off central Chile (31°48′S–39°00′S), which represents the main spawning area of jack mackerel (Fig. 1, Table 1). From 1998 to 2001, commercial fishing vessels were used to carry out four surveys in order to determine jack mackerel egg distribution and abundance. A pilot cruise was carried out in 1998 with five fishing vessels and systematic track-lines separated by 75 nautical miles in a zigzag pattern to cover the wide spawning area. From 1999 to 2001, the survey design was changed to a regular grid of plankton stations, where both station and track-line (east–west transect) were separated by 18 nautical miles. Except for the surveys carried out in December 1998, a minimum of nine purse-seine fishing vessels were used to cover the spawning area. Since 1999, the offshore oceanic boundary of the surveys was located at 92°W (*ca.* 1100 nautical miles from the coast). The time needed to cover the survey ranged between six to thirteen days, and therefore we obtained a quasi-synoptic overview of the jack mackerel spawning. A single vessel carried out two track-lines, with each vessel sailing from 75°W to 92°W at a given latitude and returning at another latitude from 92°W to 75°W. The surveys were conducted during the principal jack mackerel spawning period determined from historical data (Andrianov, 1985; Grechina et al., 1998; Oyarzún et al., 1998).

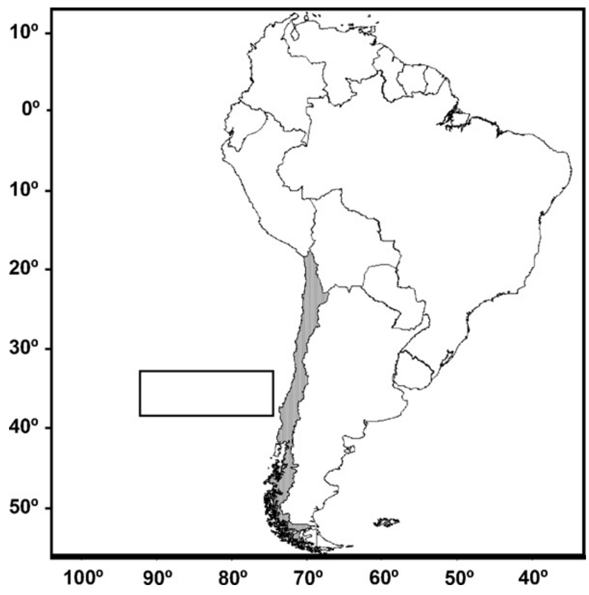

Fig. 1. Scheme of the study area located in oceanic waters off central Chile.

In each vessel, identical WP2 nets were used to collect plankton samples. The diameter of the WP2 net frame was 0.6 m and the tow was vertical to minimize the volume of water filtered per unit depth. A mesh size of 0.33 um, and tow depth of 100 m were used. Sea surface temperature was recorded at each plankton station. All jack mackerel eggs were sorted from the plankton and identified based on characteristics described by Santander and Castillo (1971). Each egg sample was placed in a wash glass with water and examined with a stereoscopic microscope. The density of eggs taken in the WP2 net was expressed as the number of eggs per 10 m^2 of sea surface water.

2.2. Exploratory analysis: egg density and sea surface temperature

Generalized Additive Model technique (Hastie and Tibshirani, 1990) was used to explore probable nonlinear

Table 1
Description of four egg surveys performed in the jack mackerel oceanic spawning area off central Chile between 1998 and 2001

	Survey			
	1998	1999	2000	2001
Date	4–8 December	14–22 November	25 November–4 December	18–30 November
Latitude (°S)	33°00′–39°00′	33°06′–38°12′	32°06′–37°48′	31°48′–36°54
Longitude (°W)	75°00′–86°00′	75°00′–92°00′	75°00′–92°00′	75°00′–92°00′
Study area (na. miles^2)	231 340	284 526	261 815	257 280
No. of vessels	5	9	10	9
Sampling design	Zig zag	Lineal	Lineal	Lineal
Inter-transect distance (na. miles)	75	18	18	18
Number of stations	173	751	880	660

relationships between jack mackerel eggs density and sea surface temperature in each survey. Next, a GAM analysis was performed using data from all surveys combined. The pooled data analysis included year, temperature, and latitude and longitude. We included the year effects to consider interannual changes in mean egg density. The emphasis of this analysis was only exploratory and oriented to find the bulk of the egg distribution within the surveyed area. The egg abundance was log-transformed and regressed against the predictor variables using the non-parametric smooth function 'loess' (Cleveland et al., 1992). The degree of smoothness of the loess term depends on two parameters: the neighborhood span and the degree (linear or quadratic loess) of the weighted regression fitted locally in the neighborhood of each data point. We used span between 0.8 and 0.9 to avoid the influence of very high and few frequent egg densities. The degree of smoothness (linear or quadratic) was investigated by considering the fitted model to the data through an ANOVA test. The GAM output consists of partial regression graphs showing the shape of the estimated relationship between the response and each predictor together with its approximate 95% point-wise confidence intervals and the partial residuals around the prediction line.

2.3. Geostatistical analysis

Geostatistical techniques (Matheron, 1963; Cressie, 1993; Petitgas, 1993) were used to describe the spatial structure of the egg distribution, and to estimate the correlation range as an estimator of the average distance between egg patches as well as the mean egg density and its variance. Previously the coordinate system (latitude and longitude) was transformed to nautical miles into Easting and Northing spatial components by using UTM (Universal Transverse Mercator). The experimental variogram is defined as the variance of difference between values that are h units apart and is a function of variance and covariance, i.e.

$$\hat{\gamma}(\boldsymbol{h}) = \frac{1}{2N(\boldsymbol{h})}\sum_{i=1}^{N(\boldsymbol{h})}[z(x_i) - z(x_i + \boldsymbol{h})]^2 \qquad (1)$$

where $\hat{\gamma}(\boldsymbol{h})$ is semivariance, $\mathbf{h}$ is a vector of distance and direction, and $N(\mathbf{h})$ is the number of pairs of observations at distance h and given direction, $z(x_i)$ is the egg density for the ith data point. The experimental variogram described by Eq. (1) was applied only to the 1998 survey because large sample values were distributed within a small portion of the area with smaller and denser neighboring aggregations (Mello and Rose, 2005). Instead, for the other surveys we chose the robust (or stable) variogram estimator because egg density was characterized for very many small and few large values, which can impact the variogram pattern and parameters (Mello and Rose, 2005). According to Cressie and Hawkins (1980) and Cressie (1993), the robust variogram is expressed by

$$2\hat{\gamma}(\boldsymbol{h}) = \frac{\left(\sum_{i=1}^{N(\boldsymbol{h})}|z(x_i) - z(x_i + \boldsymbol{h})|^{0.5}\right)^4}{(0.457 + 0.494/|N(\boldsymbol{h})|)N(\boldsymbol{h})^4} \qquad (2)$$

In order to explore and to detect whether the intensity of spatial autocorrelation varies according to direction (anisotropic process), experimental variograms were calculated for raw data in four directions (0°, 45°, 90° and 135°). Once analyzed the directional variograms, omni-directional experimental variograms were computed for raw data. Several lag distances were explored to best resolve spatial continuity, and asymptotic functions such as the Spherical, Gaussian, and Exponential models were fitted and selected according to the weighted least-square minimization criterion of Cressie (1993). In the models of variogram, the nugget is the y-intercept, while the range and the sill are both determined by the upper inflection point where the line becomes flat. The x-coordinate of this inflexion point is the range, while the y-coordinate is the sill. The spherical model of variogram was the best in explaining the experimental variograms, i.e.

$$\gamma(\boldsymbol{h}) = \begin{cases} C_0 & |\boldsymbol{h}| = 0 \\ C\left(1.5\dfrac{|\boldsymbol{h}|}{r} - 0.5\dfrac{|\boldsymbol{h}|^3}{r^3}\right) & 0 < |\boldsymbol{h}| \le r \\ C & |\boldsymbol{h}| > r \end{cases} \qquad (3)$$

where C_0 is the nugget effect, C is the sill; r represents the range, and $|\mathbf{h}|$ the Euclidean distance. In addition, cross-validation (Isaaks and Srivastava, 1989) was used to determine two kriging neighborhood parameters: the number of sectors and the number of neighboring points used in the interpolation by kriging. The mean squared error of residuals was used to select the best combination of the parameters (see Maravelias et al., 1996). Finally, ordinary point kriging was used to reproduce the stochastic processes across the region of interest. This method provides the best linear, unbiased estimators of local density, which are best in the sense of having less residual variance (Isaaks and Srivastava, 1989). The estimated jack mackerel egg density at any given locality within the region was given by

$$z^*(x_0, y_0) = \sum_{i \in \eta} \lambda_i z(x_i, y_i) \tag{4}$$

where η defines a local neighborhood and λ is a weight assigned to each observation within η. During kriging, the weights were obtained by using the estimated variogram model and minimizing the kriging variance (Isaaks and Srivastava, 1989). The mean jackmackerel egg density across the region R was obtained by

$$z^*(R) = \frac{1}{M} \sum_{m}^{M} z_m^* \tag{5}$$

where M is the number of nodes in a pre-determined kriging grid and m indexes those nodes. To estimate the variance of the mean jack mackerel egg density, the intrinsic geostatistical method was applied in which the variance is computed by

$$\sigma_E^2 = 2\bar{\gamma}(V, v) - \bar{\gamma}(V, V) - \bar{\gamma}(v, v) \tag{6}$$

where $\bar{\gamma}(V, v)$ represents the mean of the variogram and involves all the distances between each sample, considering sample position in the V area. The term $\bar{\gamma}(V, V)$, the variance in V taking into account the shape of the area in V, is the population variance inside V and it is called the dispersion variance. Finally, $\bar{\gamma}(v, v)$ takes into account the sampling design. In this way, the variance is dependent on the geometry in V, the sampling design, and the variogram structure (Petitgas and Prampart, 1995; Rivoirard et al., 2000). We used the spatial module in S+ Spatial Stats software (Insightful Corporation) for exploring empirical variograms, and also for fitting models of variograms, and the EVA2 software (Petitgas and Prampart, 1995; Petitgas and Lafont, 1997) for variance estimation. The geostatistical mean egg densities and precision of estimates, in terms of the coefficient of variation of the mean (CV), were compared with the single arithmetic mean and CV.

3. Results

3.1. Exploratory analysis: sea surface temperature and spawning

The distribution of the sea surface temperature (SST) is shown in Fig. 2 for all of the surveys. In 1998, SST ranged between 12.8 and 19.6 °C (average: 16 °C, S.D. = 1.4 °C), with higher temperatures observed in the north–west sector of the study area. In 1999, SST fluctuated between 14 and 21.7 °C, with an average of 17 °C (S.D. = 1.1 °C), without important gradients and dominated by 17 °C in the central sector of the study area. In 2000, SST was warmer than the previous years with an average of 17.7 °C (S.D. = 1.7 °C), and ranging from 14.4 to 23.5 °C. The isotherm of 18 and 19 °C were distributed toward the south and close to the 82°W. Instead, in 2001 the SST was the coldest with an average of 16.1 °C (S.D. = 0.9 °C), and fluctuating only between 13.9 and 18 °C.

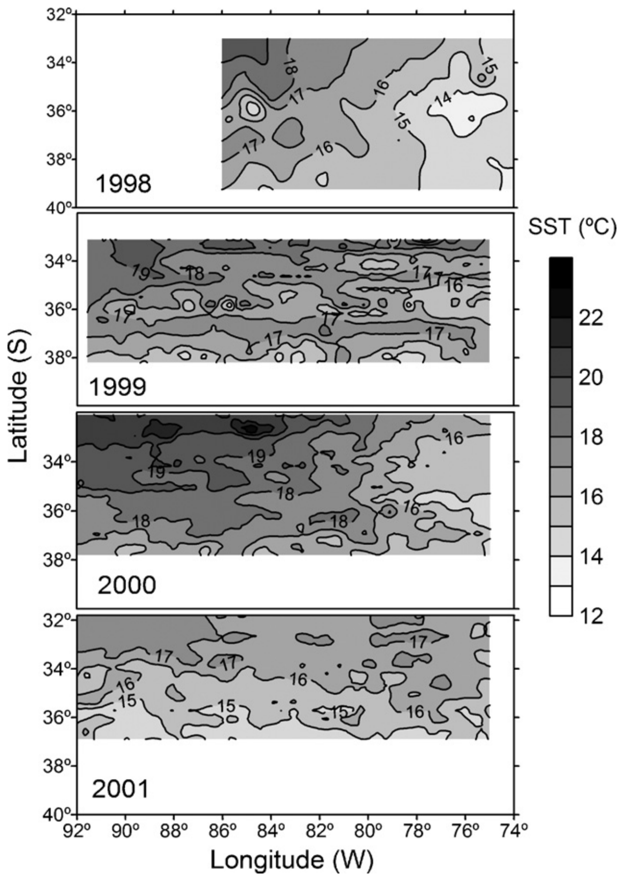

Fig. 2. Distribution of the sea surface temperature in December 1998, November 1999, November 2000, and November 2001.

The relationship between egg density and SST were dome-shaped for all the surveys (Fig. 3). In fact, models with degree quadratic were better than linear (Table 2). In 1998, higher egg densities were located in water ranging between 16 and 17 °C and declined abruptly at higher SST. In 1999 and 2000, egg densities peaked in waters ranging between 18 and 19 °C while in 2001 higher abundance of eggs was found in waters ranging between 14 and 16 °C, peaking at 15 °C and then egg density declined at higher SST (Fig. 3).

For pooled data, the relationship between egg density, latitude, longitude and sea surface temperature revealed that egg density exhibited a dome-shape relationship with latitude and an asymptotic relationship with longitude and SST (Fig. 4). This model was significant (null deviance = 19314.8 on 2460 d.f., residual deviance = 11051.3 on 2447.8 d.f.) and characterized by the quadratic degree for latitude. It can be inferred that jack mackerel spawning is maximal at 35°S and is associated with SSTs higher than 15–16 °C. According to GAM, the offshore spawning boundary was not determined during the surveys due to the continuous increases in egg density with longitude (Fig. 4).

3.2. Spatial structural analysis and spawning patterns

For the survey carried out in November 1998, a classical experimental variogram was computed, while robust experimental variograms were calculated for the other three surveys. All

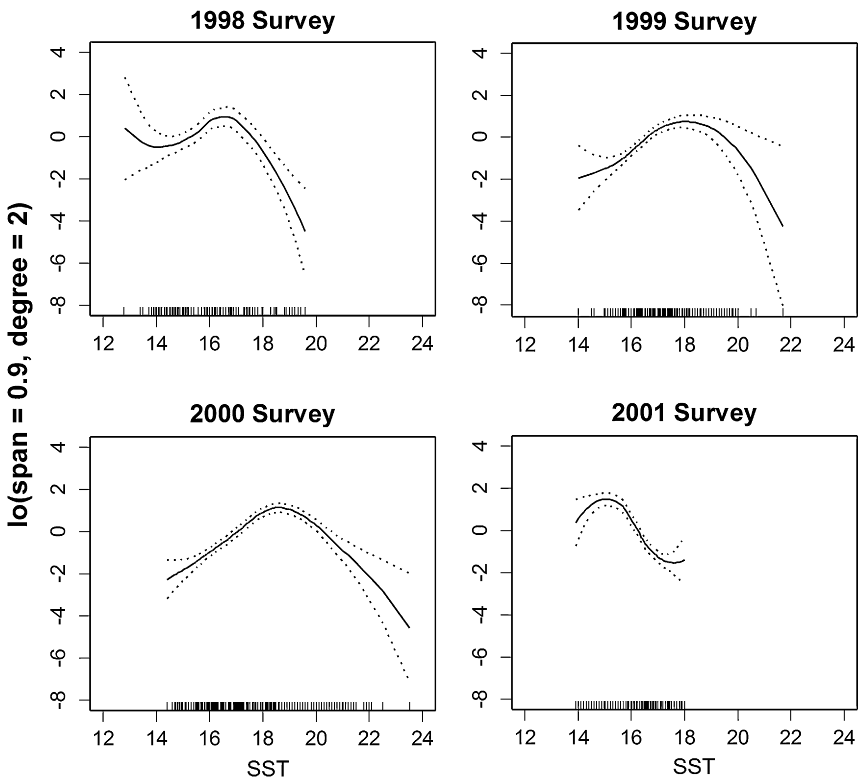

Fig. 3. Relationships between jack mackerel eggs density and sea surface temperature obtained by GAM models with loess smoother.

of the variograms showed clear spatial autocorrelations without anisotropy (Fig. 5, Table 3). In fact, the ratio between the maximum and minimum values of the range was lower than 2 and suggests absence of anisotropy (Table 3). In this way, the omni-directional spherical variograms proved to be the best model for all the surveys (Fig. 6). The variogram models and kriging parameters resulting from cross-validation are shown in Table 4, indicating that the omni-directional spherical variograms plus a nugget effect with similar neighborhood search strategies were the best (other results are not shown). The spatial correlation was satisfactorily determined, with the range fluctuating between 125 and 252 nautical miles. The nugget as a percentage of the sill, this mean the unresolved spatial variability, was 43.0, 36.3, 27.6, and 18.8% for the years 1998 through 2001, respectively (Table 4).

The egg distribution patterns for the four surveys are shown in Fig. 7. In November 1998, important aggregations of jack mackerel eggs were detected in the survey area, and four of them were distributed from 79°W to 84°W along the 36°30′S (Fig. 7). Two other centres of high egg densities were located one at 34°S–78°30′W and another close to the coast at 35°S. In November 1999, important high-density hotspots of jack mackerel eggs were found, some of them very close to the offshore boundary of the survey area (Fig. 7). In November 2000, a wide extension of eggs was observed and distributed in several small nuclei with the bulk of eggs distributed west of 78°W (Fig. 7). The offshore boundary of egg distribution was not determined. Similar results were observed in November 2001, but in this survey the most important aggregations of eggs were distributed north of 35°S and to the west of 80°W (Fig. 7).

Table 2
Comparison of GAM models fitted to egg density (D) as a function of sea surface temperature (SST) by loess smother, lo(•)

Survey	Model	Residual d.f.	Residual deviance	Test	d.f.	Deviance	$P(\chi^2)$
1998	A: log(D) = 1 + lo(SST, span = 0.9, degree = 1)	1002.9	1169.1	A vs. B			
	B: log(D) = 1 + lo(SST, span = 0.9, degree = 2)	947.8			1.27	55.2	<0.05
1999	A: log(D) = 1 + lo(SST, span = 0.9, degree = 1)	5524.9	5905.7	A vs. B			
	B: log(D) = 1 + lo(SST, span = 0.9, degree = 2)	5474.3			1.66	50.7	<0.05
2000	A: log(D) = 1 + lo(SST, span = 0.9, degree = 1)	5667.2	6475.5	A vs. B			
	B: log(D) = 1 + lo(SST, span = 0.9, degree = 2)	5566.0			1.41	101.2	<0.05
2001	A: log(D) = 1 + lo(SST, span = 0.9, degree = 1)	4971.5	5692.4	A vs. B			
	B: log(D) = 1 + lo(SST, span = 0.9, degree = 2)	4878.6			1.32	96.9	<0.05

A span = 0.9 was used to avoid a noisy surface curvature, and only the degree of the loess smother was evaluated (linear vs. quadratic).

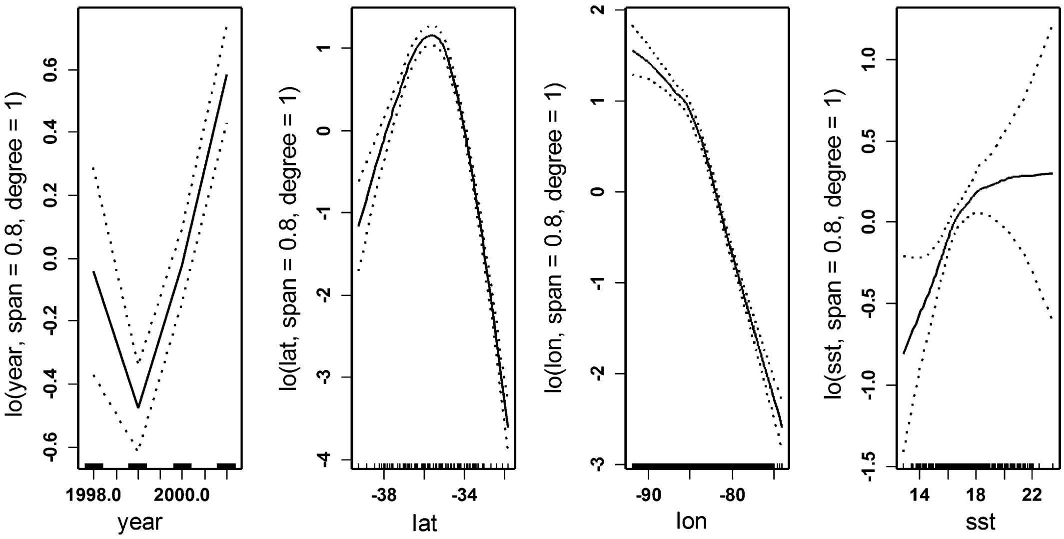

Fig. 4. Partial regression GAM plots explaining the jack mackerel eggs density. The solid line indicates the fitted model and the dashed lines are 95% confidence intervals.

Table 3
Analysis of anisotropy, spherical variogram model fitted to the direccional empirical variogram

Survey	Parameter	0°	45°	90°	135°
December 1998	Nugget	3258	183021	8916	208031
	Nugget (% sill)	0.8	43.6	2.1	52.2
	Sill	414445	419579	431972	398420
	Range	103	141	118	122
	Ratio	1.4	1.0	1.2	1.2
November 1999	Nugget	64059	55118	56401	58962
	Nugget (% sill)	38.5	31.7	29.4	33.1
	Sill	166219	174065	191677	178398
	Range	186	197	238	208
	Ratio	1.3	1.2	1.0	1.1
November 2000	Nugget	52366	51185	44425	49982
	Nugget (% sill)	30.8	28.7	23.3	28.2
	Sill	170035	178038	191027	177486
	Range	256	268	288	275
	Ratio	1.1	1.1	1.0	1.1
November 2001	Nugget	67608	63878	76872	71297
	Nugget (% sill)	19.0	17.3	19.7	19.5
	Sill	356053	368477	389755	366310
	Range	169	182	230	196
	Ratio	1.4	1.3	1.0	1.2

Ratio represents the maximum range value divided by the range value at a given direction.

Table 4
Omnidirectional spherical model of variogram and cross-validation results for the number of sectors and the maximum number of points to be used during kriging

	Surveys			
	December 1998	November 1999	November 2000	November 2001
Nugget	179833	64353	49955	69258
Sill (egg 10 m^{-2})^2	418489	177086	181210	368395
Range (nautical miles)	125	193	252	172
Number of sectors	1	1	1	1
Maximum number of points	5	5	5	7
Bias (eggs 10 m^{-2})	3.6	5.1	−1.8	5.1
Residual SD (eggs 10 m^{-2})	348.4	1244.3	375.6	22.4
MSE (eggs 10 m^{-2})^2	121390.6	1548338.7	141072.2	902508.1

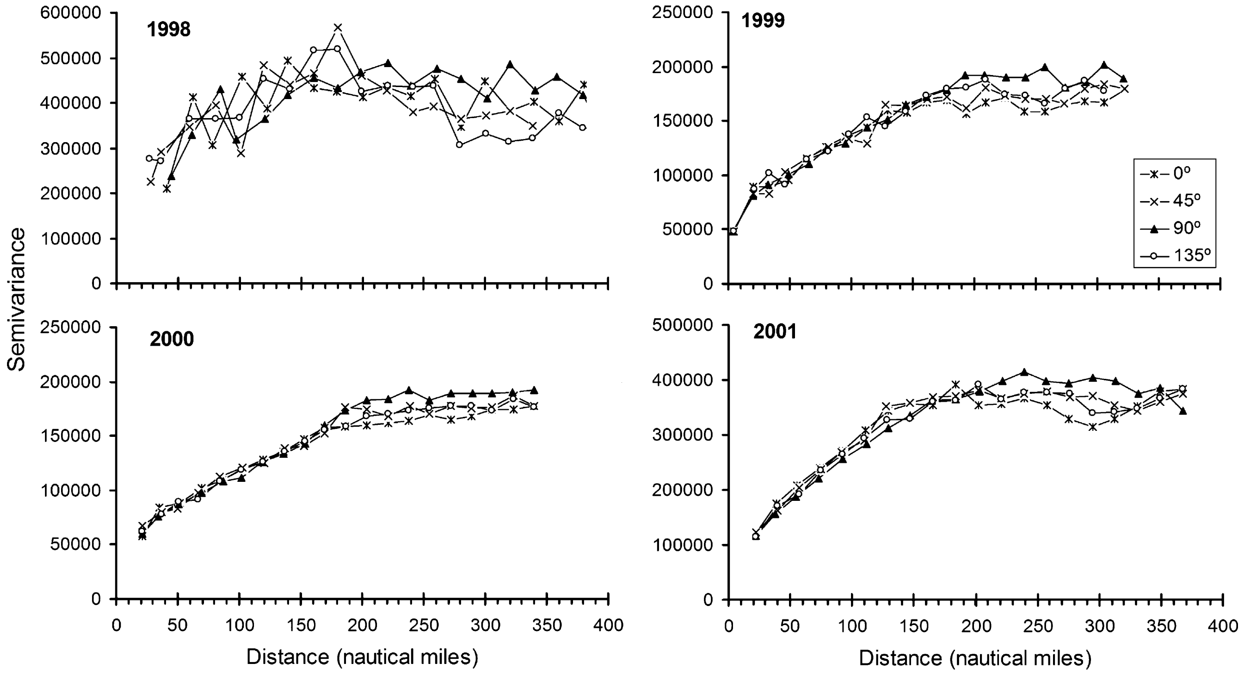

Fig. 5. Directional experimental variograms obtained for each survey showing an isotropic process in the jack mackerel eggs density (eggs per 10 m^2).

From the geostatistical analysis, the estimates of the mean egg density for each year have fluctuated between 372 and 735 eggs per 10 m^2 with a precision between 2.5 and 14.4% in terms of the coefficient of variation (Table 5). These estimates are consistently higher than the simple arithmetic mean, but the geostatistical estimates provided lower coefficient of variation, except in 1998.

In general terms, the jack mackerel spawning took place in a large oceanic area. However, the densest concentrations of eggs were consistently located between 80°W and 92°W, and according to the geostatistical analysis, these dense egg patches were identified at spatial scales varying between 125 and 252 nautical miles (Table 5, Fig. 7).

4. Discussion

Although jack mackerel spawn all along the South American coast between 7°S and 41°S in oceanic waters (Evseenko,

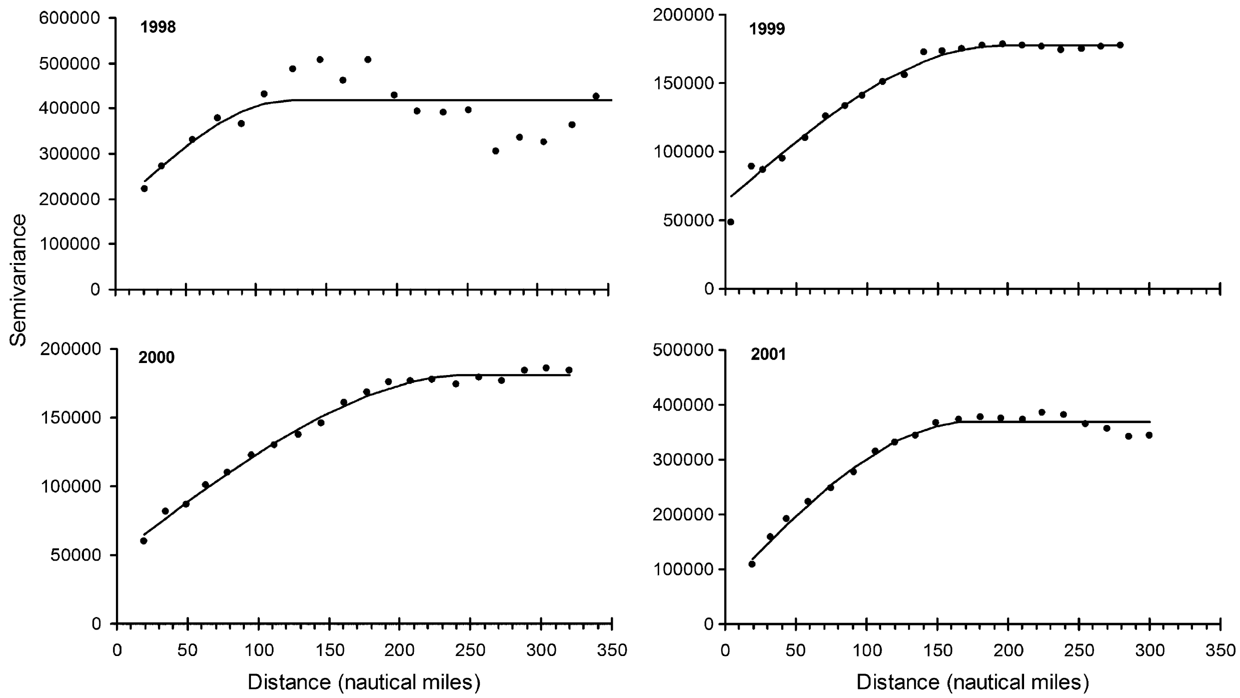

Fig. 6. Omnidirectional spherical model fitted to experimental variograms for egg densities (eggs per 10 m^2) of jack mackerel.

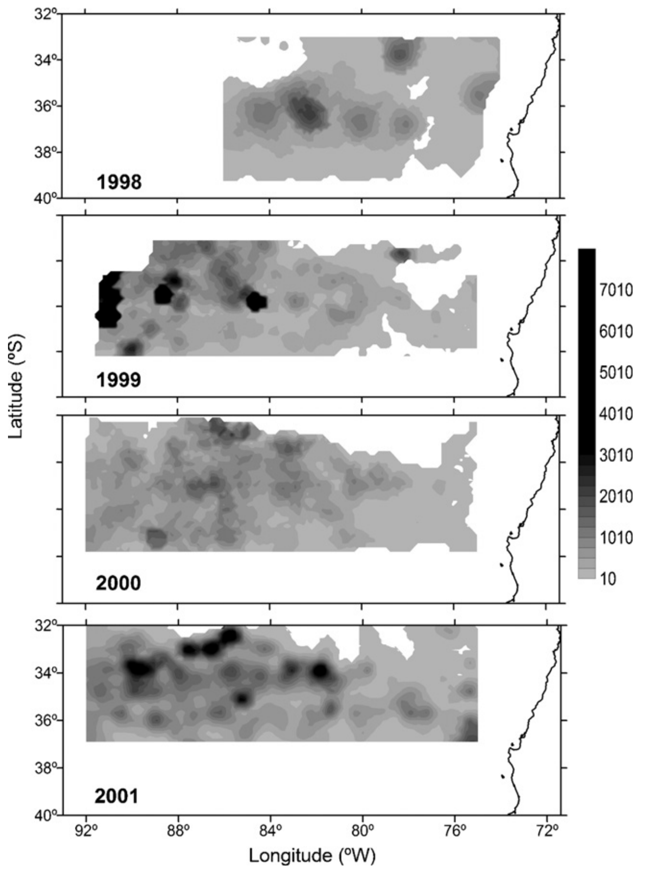

Fig. 7. Spatial distribution of jack mackerel egg densities (eggs per 10 m^2) as the reproduction of a spatially stochastic process by kriging: December 1998, November 1999, November 2000, and November 2001.

1987; Serra, 1991), the egg densities found in oceanic waters off central Chile are much higher than those in Peru (Santander and Flores, 1983; Gorbunova et al., 1985; Muck et al., 1987), and northern Chile (Grechina et al., 1998). Thus, the surveyed area in oceanic waters off central Chile can be considered one of the most important spawning areas of jack mackerel.

Zuta et al. (1983), Muck et al. (1987) and Elizarov et al. (1993) have suggested that jack mackerel spawning is associated with sea surface temperature higher than 15–16 °C. We found a dome-shape relationship between egg density and sea surface temperature (SST) for each survey, excepting 2001. In the former, a narrow range of SST was found and probably within the optimum for spawning, influencing the relationship. In fact, to detect an important effect on egg densities a wide enough range of temperatures outside the biological optimum is required for GAM modeling such as in the case of 1999 and 2000, which were similar. Probably these relationships only reflect interannual differences in SST affected partially by the sampling period, and further analysis will be required to establish the effects of SST on egg density because the emphasis of our analysis was rather exploratory and not quantitative. Indeed, the GAM results for the pooled data analysis suggest an asymptotic relationship between egg density and SST when location is accounted for (latitude and longitude). In this way, suitable conditions for spawning could be related to SSTs higher than 15–16 °C. In fact, it is probable that these temperatures are related to the 'subtropical frontal zone', to the north of 40° S and characterized by small food items (less than 2–3 mm), without seasonal changes in plankton biomass (Vinogradov et al., 1991; Konchina et al., 1996).

In terms of the spawning boundaries, the offshore boundary was never resolved by the surveys, but the main spawning was maximal at 35° S and sea surface temperatures higher than 15–16 °C. Our exploratory analysis with GAM verified an early suggestion of Elizarov et al. (1993) in terms of using the position of the 15–16 °C isotherms as the southern limit of egg concentration of jack mackerel. Probably, for future surveys the most cost-effective approach would be use real-time SST from satellite imagery to guide the selection of transect-line and set the outer boundaries. However, since egg density is probably affected by spawning behavior, it could be necessary to formalize the process by establishing rules based on the probability of finding eggs at a specific temperature by presence-absence rather than egg densities. Nevertheless, because the geostatistical structural analysis is suggesting that the oceanic spawning of jack mackerel off central Chile is a large scale process (see below) probably other environmental conditions than sea surface temperature could be more important in terms of the egg distribution at the scale of several hundred nautical miles. Further research is needed to investigate the environmental conditions of the jack mackerel spawning habitat, and the aspects here discussed should be considered only a first step.

The main objective of this study was to detect the spatial structure in egg density of jack mackerel in the oceanic spawning habitat off central Chile. The spawning process was characterized by a process in which intensity and range of spatial autocorrelation varied similarly with distance in all directions. In addition, the range of variograms was consistently wide in all surveys, and suggests that the spawning of jack mackerel is a large scale process in oceanic waters off central Chile. As corroborated by other studies (Barange and Hampton, 1997;

Table 5
Total number of samples, positive samples (%), and mean egg density of jack mackerel eggs

Cruise	Total stations	Positive stations (%)	Mean egg density (eggs 10 m^{-2}) and CV (%)	
			Arithmetic	Geostatistic
December 1998	173	72.3	317.9 (14.5)	372.2 (14.4)
November 1999	751	72.7	561.7 (10.7)	662.4 (2.5)
November 2000	880	75.0	444.1 (4.6)	515.7 (2.6)
November 2001	660	72.3	640.2 (6.6)	734.9 (3.4)

The coefficient of variation of the mean (%) is shown in parentheses.

Fletcher and Sumner, 1999), the results found here indicate that jack mackerel eggs have a wider distribution that reflects the spawning behavior of the adults. According to Barbieri et al. (1999), jack mackerels do not maintain a compact aggregation and remain scattered in the spawning area. Probably jack mackerel is favoring a high dispersion of eggs by developing a highly scattered spawning behavior (M.A. Barbierie, personal communication), explaining the wide range of variograms.

According to Mello and Rose (2005), the range, sill, and nugget values depend on the size, number, and proximity of aggregations and the degree of variability in sample values within aggregations. In 1998, large sample values were distributed within a small portion of the area with smaller and denser neighboring aggregations, which resulted in the smallest range and high proportion of the nugget. Also, in 1998, the distance between stations and transects was wider and it could has an impact on the nugget. The variograms computed for 1999, 2000, and 2001 were similar. These surveys covered a larger area than the 1998 survey, and it seems that the variogram range and sill is reflecting cluster size and a large spatial heterogeneity in sample values rather than the spatial properties of any single aggregation.

According to Swartzman et al. (1999), marine habitats often contain directional gradients with which fish might be associated. The isotropic process found in jack mackerel egg density distribution, and the average distance between egg clusters (range), suggests that in the oceanic reproductive habitat there is not directional gradients affecting the spatial pattern. Indeed, the jack mackerel spawning is not confined or associated to the shelf-break like other *Trachurus* species such as *T. declivis* in Eastern Tasmanian waters (Jordan et al., 1995), as well as *T. trachurus* in the Northeast Atlantic Ocean (Borchers et al., 1997). Mello and Rose (2005) found differences in distribution between inner and outer bay in Placentia Bay cod, where the variograms for the inner bay tended to have smaller ranges throughout the year than in the outer bay. Similarly, Giannoulaki et al. (2006) demonstrated the significant effect of area and land enclosure on the spatial structures of anchovy and sardine, concluding that coastal topography affected the way fish schools were organized into aggregations. In our case, the range of variograms is wider as compared with small pelagic fish such as sardine and anchovy, which have a coastal reproductive habitat. In fact, Lo et al. (2001) found a range of 22 km (12 nautical miles) for Pacific sardine (*Sardinops sagax*) off California. Castillo-Jordán et al. (2007) found a spatial autocorrelation of 27 and 32 km for anchovy (*Engraulis ringens*) and sardine (*Strangomera bentincki*) off central-southern Chile (i.e. 14.7 and 17.6 nautical miles, respectively). Fletcher and Sumner (1999) estimated a size patch between 8 and 10 nautical miles for day 1 eggs of sardine (*Sardinops sagax*) off the south coast of Western Australia. A patch size of less than 10 nautical miles was also estimated for pilchards off South Africa on the basis of acoustic data (Barange and Hampton, 1997), and range estimated between 30.5 and 36.6 nautical miles for a period of high abundance of anchovy and sardine (Barange et al., 2005). In this way, the range of variograms (125–254 nautical miles) of jack mackerel suggests that the average distance between egg clusters of jack mackerel is not constrained in oceanic waters because this species is not confined to or associated with the coastal domain like other pelagic species. Rather, the jack mackerel is related to large scale oceanic processes likely associated with the sea surface temperature distribution and characterizing the subtropical frontal zone, as suggested by the nonlinear relationships here obtained. Furthermore, according with our results and those found in similar studies, it is probable that the scale of detected spatial structure in many species tend to be related to the spatial scale of specific or dominant hydrographic/topographic features in both coastal and offshore domains of the habitats.

According to the range of variograms, eggs collected more than 125–252 nautical miles apart should be considered not spatially correlated. Since 1999 we have performed egg surveys using the same regular grid of stations (18 × 18 nautical miles). In this way, inter-transect and inter-station distances were smaller than the patch size or distance between egg clusters allowing us to detect, to characterize and to quantify the spatial pattern in the data. In fact, the sampling interval should be smaller than its diameter to ensure that egg patches are sampled at least once. The geostatistical average egg density was consistently higher than the arithmetic mean. This can be explained by a sampling egg density that is slightly lower compared with the kriged egg density estimate, and also because observed egg density was characterized by many small and few large values. Nevertheless, the geostatistical coefficient of variation of the mean was generally lower, indicating better estimates in terms of the precision. Future surveys could take our results in order to modify the survey design to cover a larger area by spacing transect-line and station distances further apart than the current 18 nautical miles. Although it is clearly impractical to carry out a survey that totally closes the oceanic spawning area of jack mackerel, it is highly recommended to modify the survey design area because at present samples taken are not spatially independent.

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