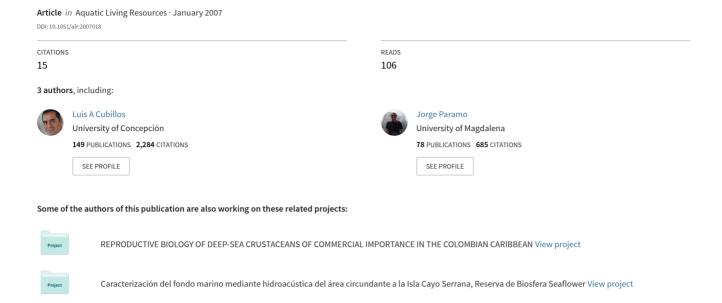
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Aquatic Living Resources

The spawning spatial structure of two co-occurring small pelagic fish off central southern Chile in 2005

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Abstract – Anchovy and common sardine co-occur in the same reproductive and feeding habitat off central southern Chile (33°00′–41°20′S), and have a similar reproductive strategy. Egg-survey data from one survey carried out during the austral winter in 2005 were used to analyze the spawning spatial structure of anchovy (*Engraulis ringens*) and common sardine (*Strangomera bentincki*) through geostatistical techniques and generalized additive models. The spawning spatial structure of both species was characterized by a spatial autocorrelation intensity varying similarly with distance in all directions, ranging between 27.2 and 32.6 km for anchovy and common sardine, respectively. In average, egg density of anchovy was higher than egg density of common sardine, with the bulk of the spawning for both species located in the southern sector of the study area (38°S–40°S). In this sector, both species showed an overlapped distribution, and egg densities were mainly associated to shallow and coastal zones, suggesting that coastal shape and bottom depth are important factors for the spawning of both species. In the south sector, the egg density of both species was positively correlated, indicating that spatial structure of the spawning is not explained by a different strategy of space occupation among anchovy and common sardine.

Key words: Spatial structure / Geostatistics / GAM modeling / Spawning areas / Pelagic fish eggs / Anchovy / Sardine

Résumé – Structure spatiale des pontes de deux petites espèces pélagiques, poissons coexistant au large des côtes du Chili (Centre-Sud) en 2005. L'anchois et la sardine commune fréquentent les mêmes zones de reproduction et d'alimentation au large du Chile (Centre-Sud, 33°00′–41°20′S), et ont des stratégies similaires de reproduction. Les données d'une campagne océanographique de récoltes des oeufs, qui s'est déroulée durant l'hiver austral de 2005, ont été utilisées pour analyser la structure spatiale des pontes de l'anchois (*Engraulis ringens*) et de la sardine (*Strangomera bentincki*), au moyen de techniques géostatistiques et de modèles additifs généralisés. La structure spatiale des deux espèces était caractérisée par une intensité d'autocorrélation spatiale variant avec la distance et de façon similaire dans toutes les directions, s'étendant de 27,2 à 32,6 km respectivement, pour l'anchois et la sardine. En moyenne, la densité en œufs d'anchois était plus élevée que celle de la sardine, avec une zone de forte densité pour les deux espèces, située dans le secteur sud de la zone d'étude (38°S–40°S). Dans ce secteur, les distributions des deux espèces se recouvraient, et les densités en oeufs étaient associées principalement à des zones côtières et peu profondes, suggérant que la forme de la côte et la profondeur sont des facteurs importants pour la reproduction des deux espèces. Dans le secteur sud, la densité en œufs des deux espèces était positivement corrélée, indiquant que la structure spatiale des pontes n'est pas expliquée par une stratégie différente de l'occupation de l'espace entre l'anchois et la sardine.

1 Introduction

In the central-south area off Chile (33°00'S-41°30'S), two commercially important small pelagic fish known as anchovy (*Engraulis ringens*) and common sardine (*Strangomera bentincki*) are coexisting and inhabiting in the coastal zone of a seasonal upwelling system (Cubillos et al. 1998; Cubillos et al. 2002). Anchovy and common sardine are caught by both

small-scale fishermen and industrial fleet of purse-seiners, with Talcahuano as the main port for landings. These species are caught together by fishermen because anchovy and common sardine are co-occurring species and aggregated in mixed schools. Gerlotto et al. (2004) point out that common sardine and anchovy stocks are mixed and concentrated close to the coast in several types of aggregations from small schools to dense layers, which cannot be differentiated acoustically. In addition, the biological characteristics are similar in terms

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of the spatial distribution, growth rate, natural mortality, age composition, reproduction time, spawning area, and recruitment time (Cubillos et al. 2001, 2002; Cubillos and Arcos 2002).

According with Cubillos et al. (2001), the reproductive strategy of these two species is to spawn at the end of southern winter (August), when environmental conditions are characterized by an alternation between northerly winds and southerly winds. The northerly winds produce onshore transport and convergence at the coast, favoring concentration and retention of eggs and larvae at the coast, while southerly winds generate moderate upwelling events favoring biological enrichment of the surface waters. This reproductive strategy of the species is coherent with the triad hypothesis of Bakun (1996).

Although the reproductive strategy seems to be similar for both species, the spatial structure in terms of the spatial correlation of egg densities, as well as the dependence of physical variables in the reproductive habitat over egg density could be different for each species. Indeed, spatial structures and patterns can take several forms due to either exogenous or endogenous processes. Exogenous processes can induce spatial patterns by factors independent of the variable of interest (e.g. physical gradients, transport, or the spatial configuration of habitats). Instead, endogenous ecological processes can determine also a spatial structure, where the more relevant is egg patchiness as an inherent property. In fact, eggs of a species are more likely to be spatially adjacent in a patchy fashion or exhibiting an "inherent" spatial autocorrelation because the spawning. This means that nearby values of egg density are more likely to be similar than they would be by chance. The goal of this paper is to analyze the spawning spatial structure of the common sardine and anchovy, using information of one egg survey carried out in winter 2005 in the central-south area off Chile (33°00′S–41°19′S). Geostatistical techniques are 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; Maravelias et al. 1996). In addition, generalized additive models are used to analyze the influence of sea surface temperature and the spatial configuration of the physical reproductive habitat. The results should be of interest for inferring and understanding differences in the aggregative strategies of the spawning of co-occurring species.

2 Material and methods

2.1 Study area and data

In order to determine the egg distribution and abundance of anchovy and common sardine, a survey was carried out from August 21th to September 22th 2005, covering an area of 32 523 km². The study area was located in the central-south area off Chile (33°00′S–41°19′S), which represents the main spawning area for both species. According to Cubillos et al. (1999, 2001), spawning extends from July to September, peaking between August and September for both anchovy and common sardine. In this way, a single survey is enough to characterize the spawning process of the two species. The

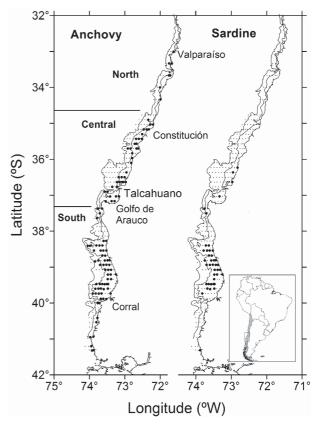


Fig. 1. Study area of the egg survey (August 21–September 22, 2005), showing plankton stations (small dots) and positive stations with eggs for anchovy (left) and common sardine (right). The bottom depth of 100 m (inner) and 200 m (outer) is also shown along the coastal line.

study area was separated into three geographic zones, defined according with the orientation and shape of the coastal line and the extension and distribution of the continental shelf (i.e. the 200 m bottom depth, Table 1, Fig. 1). The area between 33°00'S and 34°20'S was considered an exploratory zone because egg abundance practically have been not observed in this zone previously (Castro et al. 1997; Castillo et al. 2002; Cubillos et al. 2005). In this zone transect lines were separated by 20 nautical miles, with stations every 4 nautical miles along each transects. In the other two zones, the grid of plankton stations were design to quantify egg densities of the species with transect lines separated by 8 nautical miles and plankton stations located 4 nautical miles apart. The central zone was allocated between 34°46'S and 37°10'S, while the south zone was allocated between 37°20'S and 41°19'S (Fig. 1).

In each plankton station eggs were collected by vertical hauls with a CalVET net (25 cm diameter, 0.150 mm mesh size, Smith et al. 1985) from 70 m or close to the sea-bed for depths lower than 70 m. Egg abundance was standardized to number of egg per $0.05~\text{m}^2$. In addition, in each plankton stations sea surface temperature was recorded.

2.2 Geostatistics

Geostatistical techniques (Cressie 1993; Petitgas 1993) were used to describe the spatial structure of the egg density

	Study area (33°S–41°19′S)				
	North sector (33°00′S–34°20′S)	Central sector (34°46′S–37°10′S)	South sector (37°22′S–41°19′S)		
Date	21 Sep.–22 Sep.	30 Aug15 Sep.	21 Aug.–31 Aug.		
Transect lines	4	21	32		
Number of stations	18	130	140		
Positive stations:					
anchovy	7 (38.9%)	39 (30.0%)	63 (45.0%)		
common sardine	0	4 (3.1%)	36 (25.7%)		
Total egg counts:					
anchovy	55	1815	4856		
common sardine	0	10	1093		
Sea surface temperature (°C)	13.4 (11.5–14.5)	12.3 (11.0–14.8)	11.7 (10.5–13.5)		

Table 1. Description of the egg survey performed in the central-south spawning area of anchovy and common sardine off Chile in 2005.

of anchovy and common sardine, 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.

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

where h is a vector of distance and direction, and N(h) is the number of pairs of observations at distance h and given direction. However, we also chose the robust (or stable) variogram estimator (Cressie and Hawkins 1980; Cressie 1993) since it permitted a better definition for the variogram pattern for common sardine:

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

In order to explore and to detect whether the intensity of spatial autocorrelation vary according to direction (anisotropic process), experimental variograms were calculated for log transformed data in four directions (0°, 45°, 90° and 135°). The range and sill of these directional variograms were similar in both species (results not shown), reason for which omnidirectional experimental variograms were computed for raw data, this means including higher and zero densities. 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 these functions, 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. In addition, crossvalidation (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). Ordinary point kriging was used to reproduce the stochastic processes across the region of interest to estimate the egg density at any given locality within the study area. We used the spatial module in S+ Spatial Stats software (Insightful Corporation) for exploring empirical variograms, and also for fitting models of variograms, while the EVA2 software (Petitgas and Prampart 1995; Petitgas and Lafont 1997) was used for variance estimation. The precision is given in terms of the coefficient of variation (CV).

2.3 GAM modeling

To explore the dependence of egg density with environmental variables, we used Generalized Additive Models (GAM) with a quasipoisson error distribution and a log link by using the "mgcv" library (v. 1.1-8) of Wood (2002, 2003) for the language and software R v. 2.0.2 (Ihaka and Gentleman 1996; http://www.r-project.org). The general form of the model was:

$$D = \alpha + s(Long, Lat) + s(Depth) + s(SST)$$
 (3)

where α is the intercept, and $s(\bullet)$ represent a smooth function (penalized regression splines), D is egg density (egg per 0.05 m²), Long and Lat is the geographic longitude and latitude respectively; *Depth* is the bottom depth (m), and *SST* is the sea surface temperature (°C). We used the "mgcv" library because it implements an automatic selection of the smoothing parameters associated with each smooth term on the basis of generalized cross-validation (GCV). Crudely, cross-validation involves leaving one of the data-points out, fitting the model to the remaining data, and then computing the squared difference between those points. This procedure is repeated for all data-points and for several amounts of smoothing, and hence the smaller squared differences mean a better model. Also, one advantage of "mgcv" is the possibility of taking into account the dependence on spatial location as an isotropic bivariate function of longitude and latitude (Wood and Augustin 2002). In fact, the correlation between Latitude and Longitude was high (r = 0.884, n = 288), deserving this treatment. Instead, the coefficients of correlation between Depth-Latitude (r = 0.207) and Depth-Longitude (r = 0.043) were lower, and

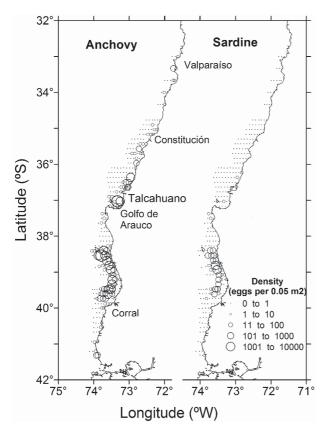


Fig. 2. Egg density of anchovy and common sardine in the study area, August-September 2005.

can be considered as an independent variable. In addition, SST was correlated better with Latitude (r = 0.534) and Longitude (r = 0.472) than with Depth (r = 0.185). First, Equation (3) was applied without temperature, and this model was named as Model 1. Instead, when temperature was included the relationship was named as Model 2.

3 Results

According with the incidence of positive stations, the bulk of the spawning of both species was more important in the south sector of the study area (Table 1, Fig. 1). Similar pattern was evident in terms of raw egg densities (Fig. 2). Indeed, the egg density of common sardine was practically null in the north and central sectors of the study area, except in some stations in which egg counts were very low (Table 1, Fig. 2). Because this is a limitation for the application of geostatistical techniques and GAM modeling, these techniques were applied only for the south sector for common sardine.

3.1 Spatial structural analysis and spawning patterns

For egg densities of anchovy a classical variogram was computed, while for the common sardine the robust experimental variogram was better. The directional variograms showed the same spatial autocorrelations in all directions (results not showed), and according with the cross-validation,

the omni-directional spherical variogram was better for both species (Fig. 3). The range of the variograms was satisfactorily determined in 14.7 and 17.6 nautical miles for anchovy and common sardine, respectively (27.2 and 32.6 km, respectively). The nugget is variability smaller than the sampling unit distance, as an effect not explained by spatial scale. In the case of anchovy, the nugget was null while for common sardine the nugget was low (17% of the sill). The sill was higher for anchovy (= $14\,634.56\,$ egg per $0.05\,$ m 4) than for sardine (= $62.42\,$ egg per $0.05\,$ m 4) because anchovy showed many small and few very large values inflating the variance.

According with the kriging, in the south sector of the study area, an important aggregation of anchovy and common sardine eggs was detected, with the bulk of the spawning distributed from $38^{\circ}16'S$ to $40^{\circ}S$ for both species in the coastal sector (Figs. 4 and 5). In the north and central sectors, the spawning of anchovy revealed one centre of low egg densities located between Valparaiso and San Antonio, and another one more important within the Gulf of Arauco at $37^{\circ}05'S$ (Fig. 4). The geostatistical average egg density of anchovy for the entire study area was 32.8 eggs per 0.05 m² (CV = 14.9%) while for the southern sector the average egg density of sardine was 15.6 eggs per 0.05 m² (CV = 6.04%).

3.2 GAM analysis

GAM modeling was carried out by separating two sectors for anchovy because of differences in egg densities, and only the south sector for common sardine. The results are summarized in Table 2. According with the general cross-validation scores (GCV), egg density of both species was better explained by a bivariate function of Longitude and Latitude plus the bottom depth. Sea surface temperature was not significant for anchovy in the North-Central sector of the study area, and although significant effect was found in the south sector, its contribution to the overall fit was marginal. Similar results were observed in common sardine for the south sector (Table 2).

The effect of the bottom depth on the egg densities was very similar for both species (Fig. 6), the bulk of the spawning tend to occur in waters lower than 75 m depth and peaking around 50 m depth of the sea bottom. In other words, the spawning of both species is restricted to the more coastal zone of the study area.

The reproduction of the spatial distribution generated by GAM models was similar to the geostatistical results obtained through kriging (results not shown). The spawning pattern of anchovy had moderate egg density inside the Gulf of Arauco. Instead, in the south sector a similar spawning pattern was revealed for both species, with the bulk distributed between 38° and 40°S. It should be considered that both species showed a high co-occurrence of egg densities in the south sector, and although average egg density of common sardine was lower than the average anchovy egg density a good relationship between log-transformed egg density values of both species was found in the south sector ($r^2 = 0.699$, F = 321.9, p < 0.001, n = 140, Fig. 7).

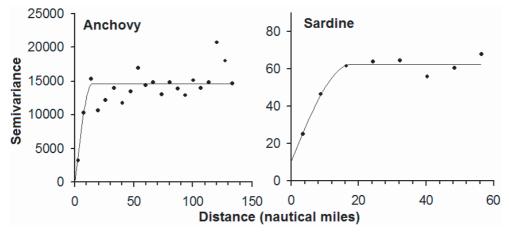


Fig. 3. Omni-directional spherical model fitted to experimental variograms for total egg densities (eggs per 0.05 m²) of anchovy and common sardine egg densities.

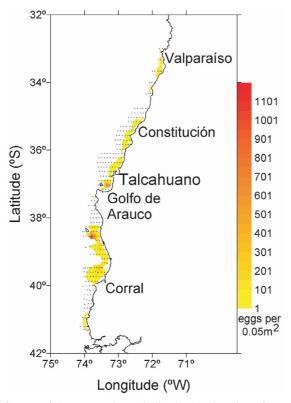


Fig. 4. Map of the surveyed area indicating the location of plankton stations and spatial distribution of anchovy eggs density (eggs per 0.05 m^2) as the reproduction of a spatially stochastic process by kriging.

4 Discussion

The main objective of this study was to detect differences in the spatial structure in egg density of two co-occurring small pelagic fish, which have a similar reproductive strategy in the central-south area off Chile (Cubillos et al. 2001). In the area between Valparaiso (33°S) and Gulf of Arauco (37°10'S), the spawning of common sardine was practically null. Instead, the bulk of the spawning of both species was important in the

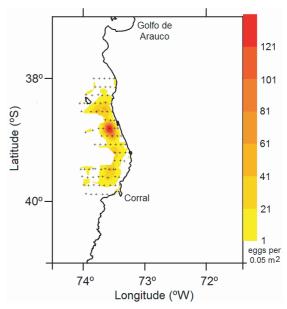


Fig. 5. Map of the south surveyed area indicating the location of plankton stations and spatial distribution of common sardine eggs density (eggs per 0.05 m²) as the reproduction of a spatially stochastic process by kriging, August–September 2005.

south sector of the study area (37°22′S–41°19′S). In the survey sampling design, the inter-transect distance (North-South direction) was 8 nautical miles (14 km), while plankton stations were 4 nautical miles (7.4 km) in the East-West direction. Because the maximum range was 32.6 km for sardine (17.6 nautical miles), eggs collected more than 32.6 km apart should be considered uncorrelated. In this way, inter-transect and inter-station distances were smaller than the patch size, allowing detecting, characterizing and quantifying the spatial pattern in the data. Therefore, the average egg density and variance computed by conventional methods based on inference may be biased because that requires that observations are independent.

According with the structural analysis, the range of the variograms indicates that spatial autocorrelation fluctuates

Table 2. Summary of GAM models used to analyze the spatial egg density of anchovy and common sardine. Intercept represents the overall mean, and s(Long, Lat), s(Depth) and s(Temp) are the smooth terms associated to latitude-longitude, depth bottom (m), and sea surface temperature, respectively. The standard error is showed in parenthesis, GCV score is the general cross-validation score for each fitted model.

		Anc	Sardine			
	North and	central zone	South zone		South zone	
	ZC	one				
	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
Intercept	-6.168*	-5.892*	-0.331*	-0.545^*	-3.969*	-9.017*
	(3.978)	(4.714)	(0.6103)	(0.6422)	(3.743)	(8.102)
s(Long,Lat)	21.94**	20.37**	21.43**	22.13**	16.81**	21.8**
s(Depth)	2.319**	1.911**	6.871**	6.477**	5.176**	5.027**
s(Temp)	_	4.431*	_	1.494**	_	1**
Deviance explained (%)	92.6	94.7	96.1	96.8	92.7	96.3
R^2 (adj.)	0.941	0.946	0.957	0.973	0.897	0.949
GCV score	19.631	36.374	13.935	16.007	10.897	11.167
n	148	148	140	140	140	140

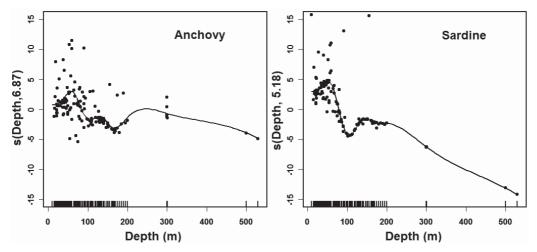


Fig. 6. Partial effects of the bottom depth (m) on egg densities of anchovy and common sardine in the south sector of the study area, August–September 2005.

between 27.2 and 32.6 km for anchovy and common sardine, respectively (i.e. 14.7 and 17.6 nautical miles, respectively). A similar range (22 km) was found by Lo et al. (2001) for Pacific sardine (Sardinops sagax) off California. In addition, the nugget effect was null in anchovy and lower in sardine (<17%), indicating that small-scale variability was not significant. The range is almost similar, and therefore the spatial spawning pattern of both species is almost the same and probably related with and endogenous "inherent" ecological process. Probably the aggregative behavior of the spawner are producing the subsequent egg patches, meaning that there is not further differences in the reproductive strategy of the species in terms of spatial dependence. Indeed, the spawning process of both species was characterized by an isotropic process, because the intensity and range of spatial autocorrelation varied similarly with distance in all directions. In addition, the distribution of very high egg density of both species was lower, and it was more important in the south sector of the study area. Therefore, small-scale variability and randomness should be important only when the number of high-density nuclei is considerable and when they are distributed within the entire surveyed area.

According with the range of the variograms, the egg patches or egg clusters of common sardine seems to be a little wider than anchovy. However, the spatial structure could be also density-dependent. Maybe when the spawning stock biomass is in a situation of high abundance, could be possible to observe an increase in the "hotspots" of very high-density, rather than an increase in the positive stations. Barange et al. (2005) studying the strategies of space occupation by anchovy (Engraulis encrasicolus) and sardine (Sardinops sagax) populations in southern Benguela, observed an increase in the number of hotspots during the spatial expansion of these two species in a high-density year. In Benguela, both species were spatially segregated in the low-biomass year, but overlapped extensively in the high-biomass year. Unfortunately, at present we do not known the magnitude of the spawning stock biomass during the survey carried out in 2005. However, in January 2005 an acoustic survey was carried out to assess the recruitment fraction in both species. The biomass of anchovy at the beginning of the year was 909 664 t, while the biomass of common sardine was 399 936 t (Castillo et al. 2005 available on line at http://www.fip.cl). In addition, from February to July, an intense fishing mortality has been applied on recruits of

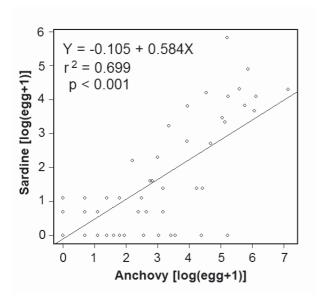


Fig. 7. Relationship between the common sardine and anchovy egg densities (log-transformed values) in the south sector of the study area.

both species, particularly in the central sector of the study area. In 2005, the catch obtained during the first half of the year was 361 795 t of anchovy and 218 781 t of common sardine (SERNAPESCA 2006). This implies that the survival spawning stock biomass in August could be lower for both species, and particularly for common sardine. Therefore, the low egg density of common sardine in the North-Central and South sectors could be explained by a lower spawning stock biomass. In this way, we can conclude that the spawning of both species was not spatially segregated during a year in which the spawning stock biomass was probably low.

According with GAM models, the best model to explain the egg densities depend almost exclusively on geographic predictors (longitude, latitude and bottom depth). Since egg densities depend exclusively on quantities that are not sensitive for fish, the results could be not completely satisfactory from a biological point of view. In fact, often temperature is of biological interest even if it is not the most important variable in model results. Nevertheless, Giannoulaki et al. (2006) analyzed the effect of coastal topography on the spatial structure of anchovy and sardine in the eastern Mediterranean Sea; they suggest that environmental spatial heterogeneity attributable to coastal topography affected the way fish schools were organized into aggregations. Stratoudakis et al. (2003) used generalized additive model to explain sardine (Sardina pilchardus) egg distribution data. They used only spatial covariates such as latitude, longitude, distance along the coastline, closest distance to the coastline, and depth bottom.

In central southern Chile, the spatial reproductive strategy of both species seems to be similar, and also the spatial distribution of the spawning, which is dependent on the physical characteristics of the spawning habitat. For instance, the bulk of the spawning is occurring in shallow waters and restricted to the more coastal sector. The spatial differences between the north, central, and south sectors of the study area

are associated with differences in the extension of the continental shelf, the shape of the coastal line, the bottom depth distribution, and also the presence of bays and protected zones like the Gulf of Arauco at 37°05'S. These factors associated with some environmental variables such as wind regimes during the winter to spring transition (e.g. Cubillos et al. 2001) probably are more important for the spawning of both species, than physical variables as for example temperature, that can be detected directly by spawner. In fact, the sea surface temperature during the survey was distributed homogeneously and fluctuating in a narrow range (11 and 13 °C, Table 1). This narrow range of sea surface temperature is probably the optimum for spawning, and to detect an important effect on egg densities a wide enough range of temperatures outside the biological optimum are required for GAM modeling. In addition, probably the river runoff and precipitation could be also important factors for spawning, because these factors are affecting coastal salinity during August to September in the study area (Castro and Hernández 2000; Castro et al. 2000; Quiñones and Montes 2001).

According with the evidence showed in this paper, the coastal shape and the bottom depth are important factors to take into account for the spawning distribution of both species. In the central sector, the continental shelf is wide and the three bays located there (Gulf of Arauco, "Bahía de Concepción", and "Bahía Coliumo") are acting as important spawning zones, probably through retention and concentration processes driven for winds regimes (Bakun 1996). In the southern sector, the coastal shape is also acting as a big bay between 38°20' and 40°S. The overlapped distribution of the spawning in the south sector, as well as the correlation between eggs density of both species, are indicating that the spatial structure of the spawning is not explained by a different strategy of space occupation by anchovy and common sardine. Nevertheless, although more studies are required to validate this statement our results can be considered a first study for determine differences in the aggregative strategies of co-occurring species like anchovy and common sardine in central southern Chile.

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