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Spawning, daily egg production, and spawning stock biomass estimation for common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*) off central southern Chile in 2002

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Abstract

In this paper, the first daily egg production method (DEPM) parameters were estimated for anchovy and common sardine stocks distributed in the central-south area off Chile (33–40°S). The study area was stratified according to the topography, shape and orientation of the coastal line, and the survey was carried out on the continental shelf during the main spawning peak (August–September, 2002). The bulk of the spawning of both species was successfully covered, which was characterized by a coastal distribution within the first 20 nautical miles, and following the inner zone associated with the 100 m bottom depth. The coastal distribution of the spawning can be related to the oceanographic conditions occurring during the transition from winter to spring (southern Hemisphere), which are characterized by the alternation between northerly and southerly winds. Probably, these factors are interacting to produce enrichment, concentration and retention of egg in coastal zones in the study area. The daily egg production rate (P_0) was estimated for two geographic strata, and was different in each region. Also, the length frequency and adult reproductive parameters were different between geographic strata, specially the daily spawning fraction. For anchovy, the P_0 was lower in comparison with available estimates for the same species in Peru and in the north area off Chile. Also, the relative fecundity of anchovy was lower, probably because anchovy in the study area have bigger eggs as compared with the anchovy in Northern Chile. The DEPM parameters estimated for common sardine in the investigated area were similar to the range of existing values for the *Engraulis* genus in other upwelling areas. The stratified spawning stock biomass estimate was 133,031 t (CV = 44%) for anchovy and 706,792 t (CV = 68%) for common sardine. Probably, daily egg production and adult reproductive parameters of both species are highly variables and further research is suggested for improvements future DEPM application for the species.

Keywords: Daily egg production; Spawning; Reproductive parameters; Small pelagic fish; DEPM; Central-south Chile

1. Introduction

Two small pelagic fish, locally known as common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*), are important fish resources for both industrial and small-scale purse-seine fleet in the central-south area off Chile (34–40°S), with Talcahuano as the main port for landings (Cubillos et al., 1998, 2002). *S. bentincki* is an endemic species distributed from northern Coquimbo (29°S) to Puerto Montt (42°S), while *E. ringens* is distributed from northern Peru to southern Chile (Arrizaga, 1981; Serra, 1983). In the central-south area off Chile, these small pelagic species are caught together by fishermen because anchovy and common sardine are co-occurring species and aggregated in mixed schools (Gerlotto et al., 2004). In addition, the biological characteristics are similar in terms of the spatial distribution, growth rate, reproduction time, spawning area, and recruitment time (Cubillos et al., 2001, 2002).

The spawning season of the species tends to occur in winter (southern Hemisphere) and extends from July to September, with a peak between August and September (Cubillos et al.,

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1999). Three to four months after the spawning, the surviving juveniles are recruiting into the population from November to January at a modal length between 5 and 6 cm total length (Cubillos et al., 2001, 2002). The fishery is heavily dependent on the annual pulse of recruitment, which is due to the higher abundance, availability and accessibility of recruits in bays and gulfs from January to March (Cubillos et al., 1998).

Stock assessments of common sardine and anchovy have been done through cohort analysis on a monthly basis due to their short-life cycle and the seasonal behavior of the fishery (Cubillos et al., 2002). Since 2000, hydroacoustic surveys have been carried out to assess the annual pulse of recruitment in January every year (Castillo et al., 2001, 2002, 2003a,b, 2004), and only one hydroacoustic survey was carried out in August 2001 to estimate total and spawning stock biomasses (Castillo et al., 2002). In the former, the acoustic survey estimated a total biomass of 564 thousand t for anchovy and 261,000 t for common sardine, from which 41 and 60% represented the mature biomass of anchovy and common sardine respectively (Castillo et al., 2002).

However, the spawning stock biomass of both species can be assessed by applying the daily egg production method (DEPM, Lasker, 1985; Hunter and Lo, 1993). In fact, both species have a coastal and well defined spawning area (Castro et al., 1997), and they are species with asynchronous oocyte development (undetermined fecundity) (Arancibia et al., 1994; Cubillos et al., 1999). Biomass estimation by DEPM has several advantages over hydroacoustic assessment because DEPM provides information about the reproductive condition of females, distribution of the spawning, reproductive habitat, egg production and mortality during the peak of spawning. These parameters are important for stock assessment and fisheries management if DEPM estimates can be keeping on sufficiently long-time periods, and particularly when DEPM parameters can be compared across species and genus (Alheit, 1993; Somarakis et al., 2004).

In 2002, a DEPM was applied for spawning stock biomass estimation of common sardine and anchovy off central southern Chile. This is the first application of DEPM for the southern stocks of anchovy and common sardine in the Humboldt Current System, providing important and new information in terms of the spatial distribution of the spawning, the daily egg production, egg mortality, as well as the reproductive adult parameters. In this paper, results are compared with the daily egg production and the adult reproductive parameters available for other clupeoids stocks in upwelling areas particularly on Northern anchovy (*E. mordax*) off California, *E. ringens* off Peru and northern Chile, and *E. encrasicolus* off South Africa.

2. Materials and methods

2.1. Study area and survey description

The study area was located off central southern Chile (33–40°S) covering 27,837 km^2, 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 study area was divided in three strata: (a) northern zone, from Valparaiso to northern Constitución (33–35°S), (b) central zone, from Constitución to Gulf of Arauco (35–37°10′S), and (c) south zone, from Lebu to south of Corral (37°28′–40°S) (Fig. 1). Plankton stations were distributed regularly on the continental shelf (200 m depth) with stations spaced by two nautical miles apart along E–W transects, and transects separated by five nautical miles. The northern zone was considered an exploratory area in which transects were spaced by 10 nautical miles apart, because egg abundance practically has been not observed in this zone previously (Castro et al., 1997; Castillo et al., 2002). During 15 August–9 September 2002, two ships were used to collect ichthyoplanktonic data by means of vertical hauls of Pairovet nets (25 cm diameter, 0.150 mm mesh size, Smith et al., 1985) from 70 m or near the seabed in depth less than 70 m. The research vessel "KAY KAY" of the "Universidad de Concepción" operated in the central zone, while the fishing vessel "FOX" operated in northern and southern zones.

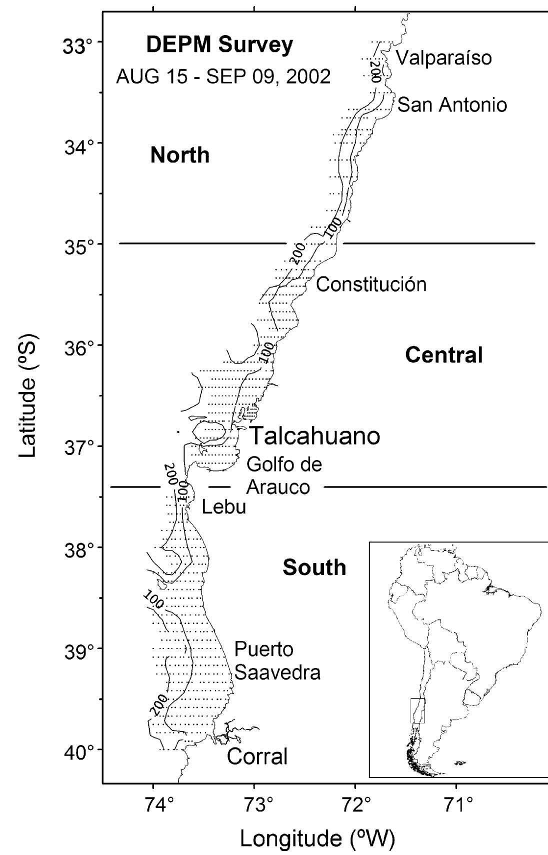

Fig. 1. Study area showing the location of the plankton stations and depth contour.

In addition, 10 small purse-seine boats (18 m length) were used to obtain adult samples of anchovy and common sardine during the study period. Five boats were allocated to the central zone and five to the southern zone. A total of 106 fishing sets were conducted from which 17 were without fish, and the majority of the sets occurred in the daytime, mainly between 6:30 and 18:00 h. The sets covered a wide geographic area between Con-

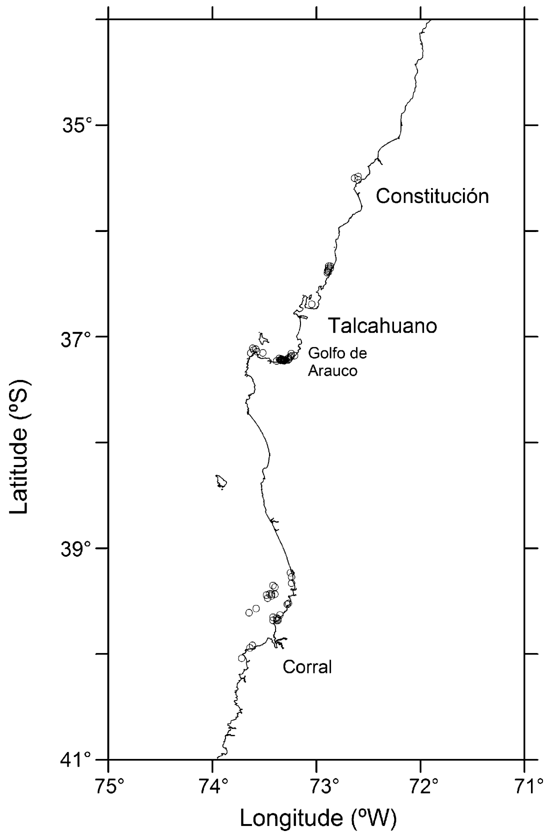

Fig. 2. Geographic distribution of sampling effort that caught adult anchovy and common sardine (positive fishing sets), August–September 2002.

stitución and Corral, within 10 nautical miles from the coast (Fig. 2).

2.2. Staging and ageing eggs

Anchovy and common sardine eggs were sorted from the plankton and identified under a stereoscopic microscope according to the characteristics described by Moser and Ahlstrom (1985), Santander et al. (1984), and Herrera et al. (1987). Eggs were counted and their abundance standardized to number per $0.05\,\mathrm{m}^2$, and assigned to one of 11 developmental stages on the basis of sequential morphological stages that occur during embryogenesis as described for anchovy by Moser and Ahlstrom (1985) and Santander et al. (1984). The sequential morphological egg stages for common sardine, as described by Herrera et al. (1987), were adapted from those established for anchovy.

According to Santander et al. (1984) and Alheit et al. (1984), peak of spawning time of both anchovy and common sardine eggs was assumed to occur at 22:00 h within a day cycle. Age of eggs was calculated by means of the automated procedure described by Lo (1985), on the basis of stage-temperature-dependent models obtained for both anchovy and common sardine through incubation of eggs (see below), the station surface temperature, peak of spawning time, and time of tow. Eggs were grouped into daily cohorts, and the average age of egg weighted by egg densities was computed. Eggs younger than 4 h and older than 90% of the expected hatching time were discarded to avoid possible biases caused by incomplete recruitment of eggs to the plankton or hatching (Somarakis and Tsimenides, 1997).

2.2.1. The stage-temperature-dependent egg-development model

Eggs of common sardine and anchovy were collected from plankton samples taken at night and near shore of Coliumo Bay (36°32′–72°57′S) during the austral spring (September–October 1999) by using WP2 plankton net (0.6 diameter, 0.33 mm mesh size). In the laboratory, eggs were identified and sorted on the basis of 11 embryonic characteristics, and incubated at constant temperatures ranging from 10 to 17 °C. An average of 30 eggs of anchovy and 10 of common sardine were put in sterile glasses of 20 ml filled with filtered sea water (0.5 μm). The incubation system was located in an isolated room, where photoperiod was automatic controlled and environmental temperature was kept constant. Three thermo-regulated baths, consisting of a circular recipient of 20 l filled with sea water and a thermoregulator Haake (model C1 or C10) were used in the incubation of eggs. For common sardine the incubation was carried out at 10, 11.5, 13, 15, 16 and 17 °C, while for anchovy eggs were incubated at 11, 15, 16 and 17 °C by using several replicates. The embryonic development was sampled regularly each 1–3 h during the whole development duration at each temperature. Because eggs were collected from plankton samples, most of egg embryonic development started at stage III. To obtain average ages and the parameters of the Lo (1985) model, the algorithms in the packages *egg* and *eggsplore* were used. The packages were written for the statistical language and environment R (Ihaka and Gentleman, 1996; http://www.r-project.org/), which are available in the Sourceforge project ichthyoanalysis (http://sourceforge.net/projects/ichthyoanalysis).

2.3. Daily egg production

Egg numbers were assumed to decline at a constant exponential rate according to the model:

$$P_t = P_0 \exp(-Zt) \tag{1}$$

where P_t is the egg abundance at age t (egg per $0.05\,\mathrm{m}^2$ per day), P_0 the daily egg production per $0.05\,\mathrm{m}^2$ per day, and Z is the daily total mortality rate. The daily egg production was computed only for the positive stratum (spawning area) in the North-Central and South sub-zones. Polygons enclosing the positive stations were considered in the computation of the spawning areas, including a few negative stations within these polygons. Eggs from the North and Central zones were pooled because the eggs abundance in the North zone was low, with few positive stations (see Section 3). In each sub-zone, the fitting procedure of Eq. (1) to observed data was based on a generalized linear model (GLM), instead of the traditional weighted or unweighted non-linear least square procedure, according to:

$$E[P_t] = \mathrm{g}^{-1}[\log P_0 + Zt] \tag{2}$$

where $E[P_t]$ is the expected value of the density of eggs of age t and g^{-1} is the inverse of the link function. In the fitting procedure, the link function used natural logarithm and a negative binomial family, which accounts for increasing variance as the density of eggs increases (Bernal et al., 2001). The negative binomial distribution has an extra parameter, which was iteratively estimated in the fitting procedure according with Venables and Ripley (2002). The parameters, $\log(P_0)$ and Z, are estimated as intercept and slope of the GLM model. The daily egg production is estimated as the exponential of the intercept of the model. We used the package MASS (Venables and Ripley, 2002), written for the statistical language and environment R (Ihaka and Gentleman, 1996; http://www.r-project.org). Finally, the stratified estimates of daily egg production and variance in the total survey area of each stratum were computed according to procedures described in Picquelle and Stauffer (1985).

2.4. Adult sampling and laboratory procedures

On board, adult anchovy and common sardine were randomly sampled from 32 and 52 fishing sets, respectively. In the Central zone, 14 fishing sets were available for anchovy and 32 for sardine, while in the South sector 18 fishing sets were for anchovy and 20 for sardine. Total length (cm) of adult fish was measured with the aim of obtaining length-frequency distributions by sex. A random sub-sample of mature females was taken from each set, and each fish was dissected by mid-ventral incision, and preserved in 10% buffered formaldehyde solution for subsequent histological analysis of the ovary. In addition, any extra females macroscopically detected with hydrated ovaries were preserved in formaldehyde solution for subsequent analysis of batch fecundity. These extra females were not used in adult parameter analysis. Finally, a random sub-sample of 200 fish was also preserved to determine sex proportion by weight.

Each preserved adult sub-samples was analyzed in the laboratory by measuring total length and both total and gonad free weight (body weight). Also, the sex of every fish was determined and each ovary from the mature females in each sub-sample was weighed ($\pm$0.01 g) and preserved in 10% buffered formaldehyde solution, and subjected to histological analysis. Ovaries of mature females were sectioned and stained with haematoxylin and eosin. Oocyte development and maturation was subdivided into eight stages according to characteristics described by Wallace and Selman (1981). Similarly, ovaries of hydrated females available for batch fecundity estimation were weighed and preserved to subsequent histological analysis to confirm this particular stage according to Hunter et al. (1985) and Hunter and Macewicz (1985). A correction factor was obtained to convert formalin weight to alive wet weight based on a sample of 30 fish per species according to procedures described by Hunter (1985). On average, preservation in 10% buffered formaldehyde solution caused a 5.2% increase in anchovy wet weight and a 3.91% increase in sardine wet weight during a period of 63 days.

2.5. Adult parameters

The mean weight (W) of mature females in the ith fishing set was computed and corrected by factors associated to preservation, as well as the total weight of hydrated females was corrected for the increase in weight due to hydration of the ovaries. The sex ratio (R) in the ith fishing set was computed from the weight of females divided by the sum of total weight of females and males. The weight of males was also corrected by factors associated to preservation in formaldehyde solution.

The spawning fraction (S), i.e. the fraction of mature females spawning per day in each sample, was assessed by ageing postovulatory follicles (POFs) according to the criteria developed by Hunter and Goldberg (1980) and Hunter and Macewicz (1985). Day-0, day-1 and day-2 POFs were observed. Day-0 POFs are females that spawned in the night of capture (0–9 h), day-1 and day-2 between 9 and 32 (the night before the capture) and 33–56 h after the spawning peak respectively (Alheit et al., 1984). Spawning fraction was estimated from the proportion of 1-day old POFs for samples captured mainly during daytime (mainly from 6:30 to 18:00 h). We used day-1 because day-2 POFs may appear the same in histology for a longer period than 24 h. This is just an inaccuracy in ageing old POFs, and not a bias that needs to be adjusted. In this way, we do not apply any adjust to the number of mature females and spawning fraction was estimated as the proportion between day-1 POF and mature females.

The batch fecundity (F, number of eggs to be spawned as a batch) of females with hydrated oocytes was estimated using the gravimetric method suggested by Hunter et al. (1985). Only ovaries with hydrated oocytes (early hydratation, fully hydrated) but no POFs were used which had previously been analyzed through histology of one ovary. Three sub-sections were cut from an ovary, weighed, and the number of hydrated oocytes in each counted. The total number of eggs per batch was computed by multiplying the mean number of oocytes per gram of ovary subsection by the total weight of the ovaries. Batch fecundity was related to ovary-free weight of hydrated females by considering a linear model, i.e.

$$F_j = a + bW_j^* \quad (3)$$

where W_j^* is the ovary-free weight of the jth female, a and b are parameters estimated by linear regression. The mean batch fecundity for mature females in each set was estimated by

$$\bar{F}_i = \frac{1}{m_i} \sum_{j=1}^{m_i} \hat{F}_{ij} \quad (4)$$

where $\hat{F}_{ij}$ is the estimate batch fecundity for the jth female in the ith fishing set, computed from Eq. (3). The whole population batch fecundity ($\bar{\bar{F}}$) was estimated through ratio estimator (Eq. (6)), while variance estimator of the batch fecundity was givenby

Hunter et al. (1985), i.e.

$$\mathrm{Var}(\bar{\bar{F}})=\frac{\sum_{i=1}^{n}\left[(F_i-\bar{\bar{F}})^2/(n-1)+s_{\mathrm{h}}^2/n_h+(\bar{W}_i^*-\bar{W}_{\mathrm{h}}^*)s_{\mathrm{b}}^2\right]}{\left(\sum_{i=1}^{n}(m_i/n)\right)^2 n} \quad (5)$$

where s_{h}^2 is the variance about the regression (Eq. (3)), n_{h} the number of hydrated females used to fit the regression, $\bar{W}_i^*$ the average ovary-free weight in the ith fishing set, $\bar{W}_{\mathrm{h}}^*$ the average ovary-free weight of the n_{h} hydrated females, and s_{b}^2 is the variance of the slope of the regression (Eq. (3)).

The whole population adult parameters were computed by ratio estimator (Picquelle and Stauffer, 1985), i.e.

$$\bar{\bar{y}}=\frac{\sum_{i=1}^{n}m_i\bar{y}_i}{\sum_{i=1}^{n}m_i} \quad (6)$$

and sample variance

$$\mathrm{Var}(\bar{\bar{y}})=\frac{\sum_{i=1}^{n}m_i^2(\bar{y}_i-\bar{\bar{y}})^2}{(\bar{m})^2 n(n-1)} \quad (7)$$

where $\bar{\bar{y}}$ is the estimate of the population mean for adult parameters (W, R, S, and F), n the number of fishing set, $\bar{y}=\sum_{j=1}^{m_i}y_{ij}/m_i$ the mean of the ith fishing set, m_i the number of mature females sampled in each fishing set, and y_{ij} the value computed for the jth female in the ith fishing set.

2.6. Spawning biomass

The daily egg production model was used to estimate the spawning stock biomass, which according to Stauffer and Picquelle (1980) is expressed by

$$B=\frac{P_0AW}{RSF}k \quad (7)$$

where B is the spawning stock biomass (t), P_0 the daily egg production (number of eggs per m^2 per day), A the total survey area (m^2), W the average weight of mature females (g), k the conversion factor from grams to tons, R the fraction of mature females by weight, S the fraction of mature females spawning per day, and F is the batch fecundity (mean number of eggs per mature female per spawning). Variance estimator for spawning biomass was computed by

$$\mathrm{Var}(B)\cong\hat{B}^2\times(\mathrm{CV}(P_0)^2+\mathrm{CV}(W)^2+\mathrm{CV}(F)^2+\mathrm{CV}(S)^2+\mathrm{CV}(R)^2+2\mathrm{COVS}) \quad (8)$$

where CV denotes coefficient of variation and COVS the sum of terms involving covariance. The covariance formulas are standard, and are expressed by

$$\mathrm{COVS}=\sum_{i}\sum_{i<j}\mathrm{sign}\frac{\mathrm{COV}(x_i,x_j)}{x_ix_j} \quad (9)$$

where x represents adult parameters, and i and j are indices for different parameters, e.g. $x_i=F$ (fecundity) and $x_j=W$ (female weight). The term sign denotes the sign, positive when both parameters are in the numerator or in the denominator, and negative in any other case. The correlation function is the variance–covariance matrix, e.g. the correlation between fecundity (F) and weight (W) is given by

$$r(\bar{\bar{F}},\bar{\bar{W}})=\frac{\sum_{i}m_i(\bar{F}_i-\bar{\bar{F}})k_i(\bar{W}_i-\bar{\bar{W}})}{\{\bar{m}\bar{k}n(n-1)\}\sigma_F\sigma_W} \quad (10)$$

where m_i and k_i represent the number of mature females in the ith fishing set for each parameter, and σ the standard error of each parameter (Eq. (7)). Without considering the standard error product in the denominator, the equation represents the covariance.

3. Results

3.1. Spawning patterns and environmental conditions

A description of the egg survey is summarized in Table 1. The spawning of both species was very sparse in the north with a few positive stations of very low egg abundance (Fig. 3). In the central sector, the average eggs abundance of common sardine was higher than anchovy eggs (Table 1), but the spawning distribution of anchovy was more continuous along the coast (Fig. 3). In the South sector, the spawning of both species was very coastal (Fig. 3), and the average abundance of anchovy was lower than sardine (Table 1). Basically, the bulk of the spawning distribution of both species was fully covered by the survey (Fig. 3).

The spatial distribution of sea surface temperature (SST) revealed typical winter conditions for the study area, with SST ranging between 7 °C in the South sector to 13.8 °C in offshore

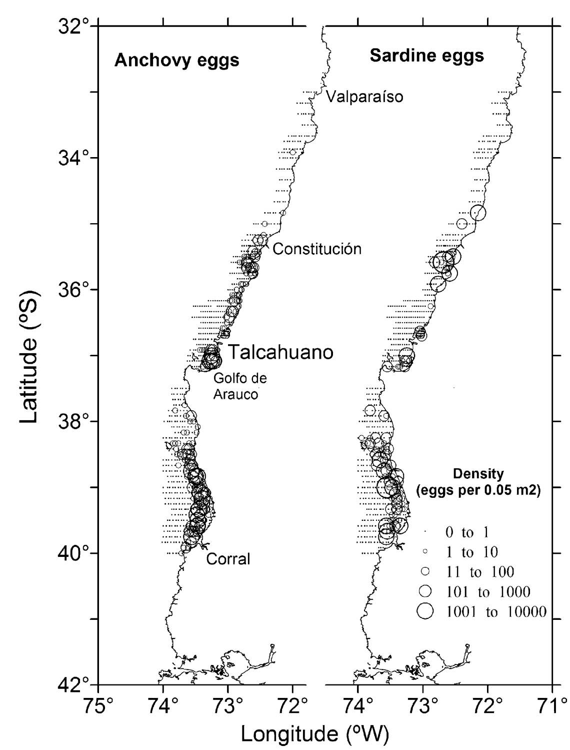

Fig. 3. Distribution of anchovy and common sardine eggs (egg per 0.05 m^2) in the surveyed area.

Table 1
Description of the egg survey carried out off central southern Chile in 2002

	Study area (33°S–40°S)		
	North sector (33°00′S–35°15′S)	Central sector (35°19′S–37°09′S)	South sector (37°30′S–40°00′S)
Date	15 August–18 August	29 August–9 September	21 August–30 August
Transect lines	17	23	31
Number of stations	129	308	358
Positive stations			
Anchovy	8 (6.2%)	82 (26.6%)	103 (28.8%)
Common sardine	2 (1.6%)	25 (8.1%)	84 (23.5%)
Average density and S.D. (egg/0.05 m^2)			
Anchovy	0.3 (0.3)	4.0 (18.1)	9.9 (38.9)
Common sardine	2.3 (19.8)	8.5 (86.2)	12.2 (86.6)
Sea surface temperature (°C) and range	12.4 (11.8–13.3)	12.4 (10.0–13.8)	11.6 (7.0–13.1)

waters in the North-Central sector of the study area (Fig. 4). The SST in the central sector (35°20′S–37°10′S) showed surface frontal structures associated with the runoff of freshwater or plumes of the main rivers like the Itata and Bio–Bio rivers. Nevertheless, a great area of the central sector presented SST lower than 12.5 °C (ranging between 11.5 and 12.5 °C), except a small area within the Gulf of Arauco with SST higher than 13 °C. In the South sector (37°30′S–40°S), the SST distribution showed two different zones. The first one was located to the north of 39 °S with SST higher than 11.5 °C (range 11.5–12 °C), and the second one located to the south of 39 °S with SST lower than 11.5 °C. In the latter, the lowest SST was registered near the coast (7–9 °C, 39°30′S–73°20′W).

During the survey, wind conditions were characterized by an alternation between northerly and southerly winds with periods ranging between 2 and 3 days. The southerly winds were more important in the central zone. These winds were moderate, and related with offshore transport and weak upwelling events. On the contrary, northerly winds were related with convergence events in the coast, and they were active in both the north and south zones of the study area, with 2–3 days of duration.

3.2. Egg development model from incubation

The results obtained from the incubation experiments are showed in Figs. 5 and 6 for anchovy and common sardine, respectively. The temperature-stage dependent egg-development model for anchovy was:

$$Y_{D,T} = 19.39\exp(-0.0876T - 0.0557D)D^{1.346}$$

and for common sardine expressed by:

$$Y_{D,T} = 15.21\exp(-0.0593T - 0.0192D)D^{1.038}$$

where $Y_{D,T}$ is the age (hours) of eggs, as a function of the development stage (D) and temperature (T). All coefficients of the models were significant at $p < 0.05$, with residual standard error of 2.562 for anchovy (29 degrees of freedom) and 2.58 for common sardine (39 degrees of freedom).

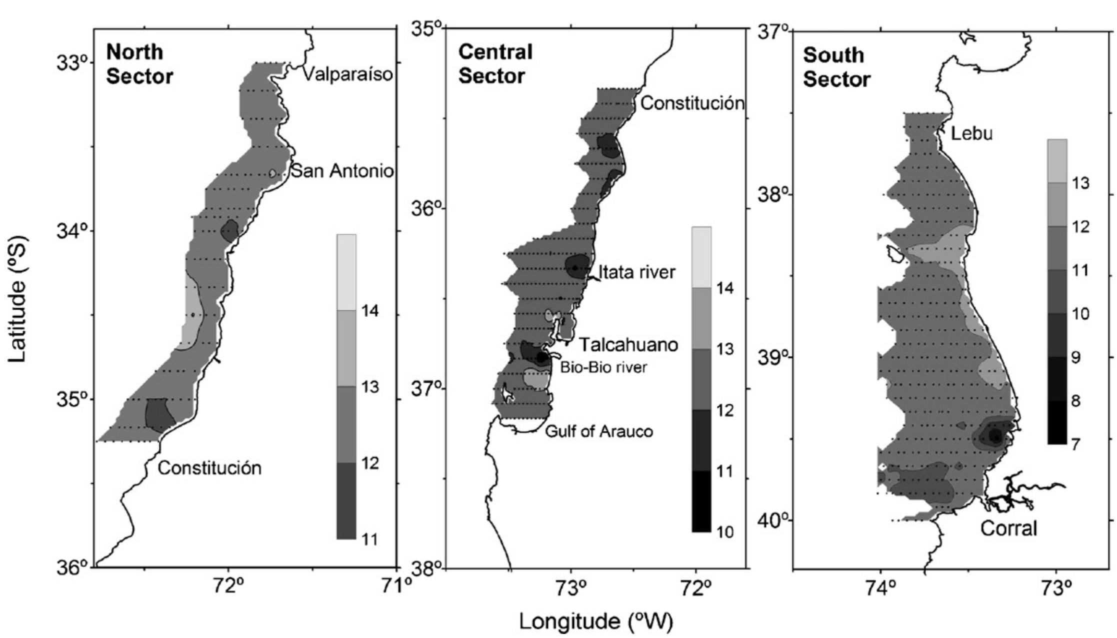

Fig. 4. Horizontal distribution of sea surface temperature (°C) in the three sub-areas of the study area.

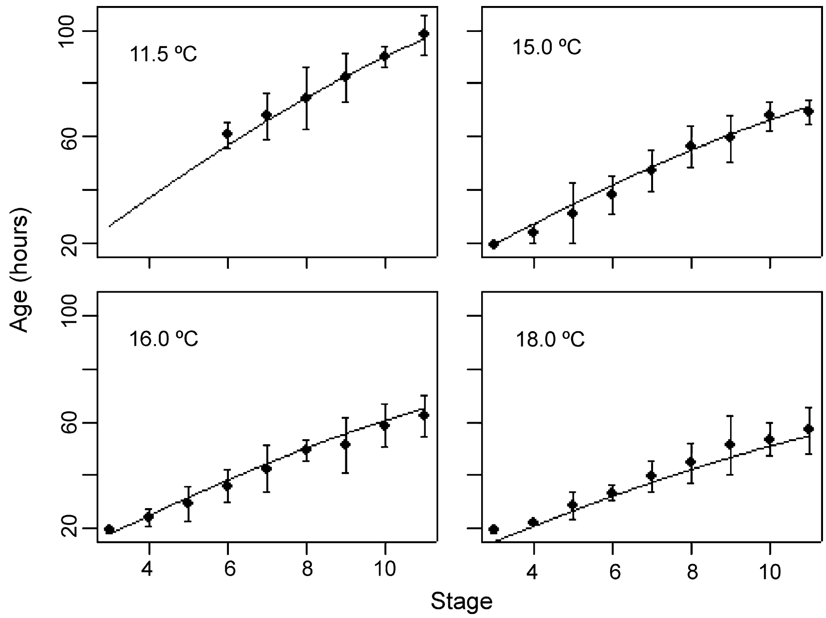

Fig. 5. Anchovy temperature-dependent egg-development obtained from incubation experiments.

3.3. Daily egg production

In the North-Central sector, the positive spawning area of anchovy was estimated as 2737 km^2 (17.8% of the stratum), while the common sardine spawning area was estimated as 999 km^2 and covered only 6.3% of the stratum. In the South sector, the spawning area was estimated as 4553 and 3528 km^2 for anchovy and common sardine respectively (Table 2).

The daily egg production was computed for two zones, the North-Central and South sectors. The North-Central stratum included the few positive stations observed in the north sub-zone (Table 1). A plot of eggs density against the mean age within each daily cohort for each sampled station in the spawning area is shown in Fig. 7, with the density axis in log scale to allow for better interpretation. In anchovy, the density of eggs with ages less than 24 h was lower than sardine (Fig. 7). The daily egg production (P_0) was estimated as 5.5 eggs per 0.05 m^2 per day for anchovy, and 93.7 eggs per 0.05 m^2 per day for common sardine in the positive North-Central area. In the South sector, the P_0 of anchovy was estimated as 16.9 egg per 0.05 m^2 per day, while the P_0 of common sardine was estimated as 46.8 egg per 0.05 m^2 per day (Table 2). The estimates of mortality rate

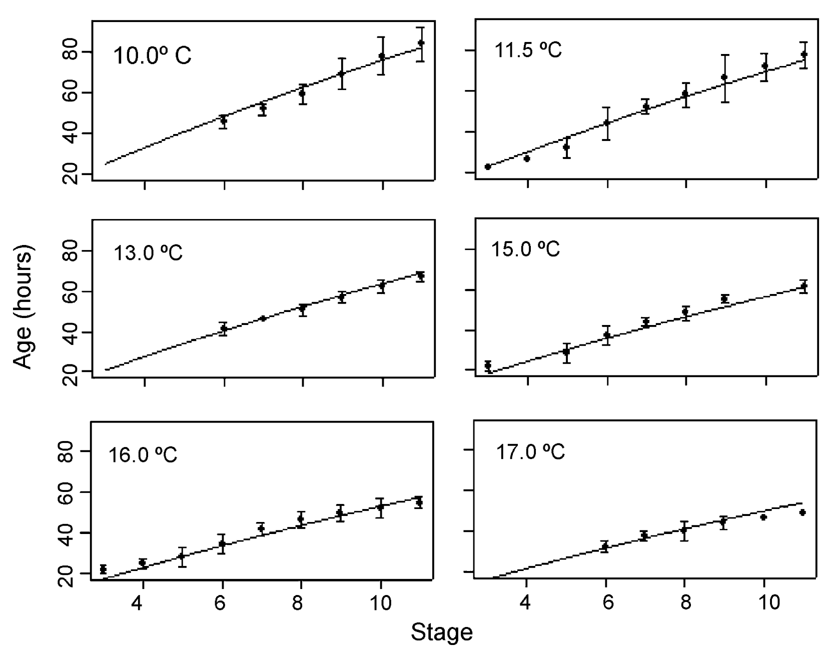

Fig. 6. Common sardine temperature-dependent egg-development obtained from incubation experiments.

Table 2
Estimates of daily egg production (P_0) and daily total mortality rate (Z) for anchovy and common sardine using GLM with binomial negative family and log link in the spawning area (A_1) of each stratum

	Anchovy		Common sardine	
	North and Central	South	North and Central	South
Survey area (A, km^2)	15367	12468	15367	12468
Spawning area, (A_1, km^2)	2737	4553	999	3528
P_0 (egg/0.05 m^2/day)	5.5 (0.281)	16.9 (0.275)	93.7 (0.615)	46.8 (0.331)
Z (day^{-1})	0.22[a] (0.660)	0.47 (0.285)	0.98 (0.343)	0.80 (0.201)
Dispersion parameter for binomial negative (θ)	0.183	0.132	0.105	0.137
P_0 (egg/m^2 day)	19.7 (0.666)	123.6 (0.457)	121.8 (2.416)	264.6 (0.549)

The coefficient of variation is shown in parenthesis, and the stratified daily egg production for the survey area in each stratum.
[a] Non-significant.

ranged between 0.22 and 0.47 day^{-1} for anchovy, and between 0.8 and 0.98 day^{-1} for common sardine. Only the mortality rate of anchovy was not significant in the North-Central sector (Table 2). Finally, the daily egg production for the whole surveyed area in each stratum ranged between 19.7 and 123.6 egg per m^2 per day for anchovy and between 121.8 and 264.6 egg per m^2 per day for common sardine (Table 2).

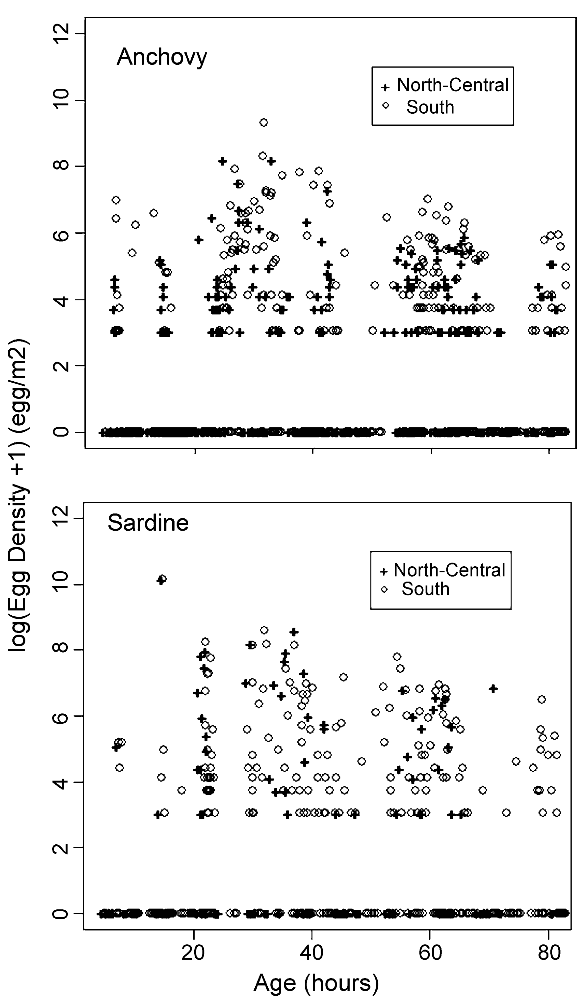

Fig. 7. Log-transformed egg density (eggs per m^2) against average age of daily cohorts for anchovy and common sardine in the spawning area of each geographic area of the study area.

3.4. Adult reproductive parameters and spawning biomass estimation

The length structure of anchovy was estimated from 4884 specimens ranging from 6 to 17.5 cm total length, with 2501 males and 2383 females. In the central sector, anchovy presented a mode at 10 cm while in the South sector the mode was located at 14.5 cm for males and 15.5 cm for females (Fig. 8). In the case of common sardine, the length composition was determined from 11569 specimens ranging from 6 to 17.5 cm, with 6321 males and 5248 females. Clearly, the length structure among strata differ for anchovy, while common sardine presented a similar length structure among zones, with a main mode centered at 10 cm and a secondary mode between 14 and 15 cm (Fig. 8).

The main reproductive parameters, as used in the DEPM, were evaluated from 1384 mature females in 32 fishing sets of anchovy, from which 14 were allocated in the North-Central stratum and 18 in the South sector (Table 3). In the case of common sardine, reproductive parameters were evaluated from 1265 mature females in 52 fishing sets, from 32 allocated in the North-Central sector and 20 in the South sector (Table 3).

During the survey, females of both species were reproductively active and collected mainly during daytime, and hence very few new postovulatory follicles (day-0 POFs) were observed. The spawning fraction computed on the basis of day-2 POFs was 1.8 times larger than day-1 POFs for anchovy in the South sector and for common sardine in the North-Central sector (Table 3). Instead, in the South sector, the spawning fraction of sardine based on day-2 was 3.1 times larger than spawning fraction based on day-1 POFs. The higher incidence of day-2 POFs might be due to inaccuracy in ageing older POFs. In this way, the spawning fraction estimates must be based on day-1 POFs. The estimates of spawning fraction were lower for both species in the South stratum, and were significantly different among geographic areas (ANOVA based on binomial family and logit link in a generalized linear model, $p < 0.01$).

The average weight of mature females was higher for the South sector in both species (Table 3). A linear relationship between batch fecundity and body weight was established, from 158 anchovy and 116 sardine females (Fig. 9). Because the low

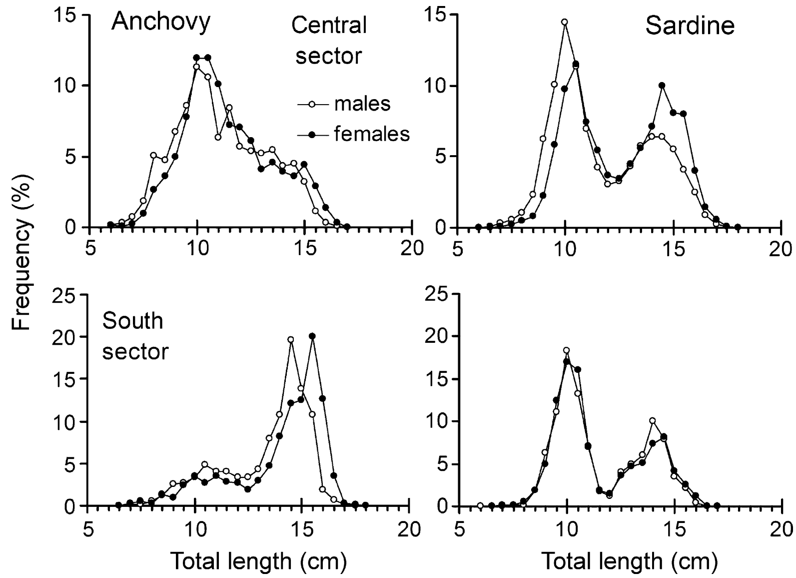

Fig. 8. Length frequency distribution per sex of anchovy and common sardine in each geographic area of the study area.

number of hydrated specimens, it was not possible to estimate a different relationship for each sub-zone. However, the average batch fecundity is computed from mature female body weight. In this way, the average batch fecundity was estimated as 4989 for anchovy (CV = 12.3%) in the North-Central, and 8497 eggs per females in the South sector (CV = 4.9%). In the case of common sardine, the average batch fecundity ranged between 8239 (CV = 4.8%) and 10414 (CV = 3.2%) eggs per females for the North-Central and South sectors, respectively (Table 3). The fraction of females by weight of anchovy ranged between 49 and 51% for anchovy, and between 52 and 40% for common sardine.

A summary of the reproductive parameters used as input in the daily egg production method for estimating spawning stock biomass is showed in Table 4. Clearly, the daily egg production and the reproductive parameters differed between the North-Central and South sectors. Therefore, the spawning stock biomass was estimated for each stratum and these can be considered as independent estimates. The estimates of spawning stock biomass were higher in the South sector of the study area for both species. The total stratified biomass estimates, which are the sum of the biomass, were 133,031 t for anchovy and 706,792 t for common sardine.

4. Discussion

During the survey period, the weather conditions were characterized by an alternation between northerly and southerly winds with at least 2 to 3 days of duration each one. The northerly winds are typical in winter time, and they are able to produce onshore transport and convergence in the coast, particularly when the wind intensity is strong (Arcos and Navarro, 1986). Cubillos et al. (2001) concluded that the reproductive strategy of anchovy and common sardine is to spawn at the end of the austral winter (August), when oceanographic conditions are producing retention and concentration of eggs and larvae near the coast (i.e. onshore transport and convergence by northerly winds). These conditions are alternating with moderate southerly winds, which are able to produce moderate upwelling events. One month later, only southerly winds are dominating and the enrichment of the coastal waters by upwelling takes place (Arcos and Navarro, 1986; Castro et al., 2000; Cubillos et al., 2001).

In 2002, during the winter-to-spring transition (southern Hemisphere), the bulk of the spawning of anchovy and common sardine was very coastal, within 20 nautical miles and at depths less than 100 m bottom depth. In this context, the design of the grid stations successfully covered the spawning area of

Table 3
Summary of the average adult reproductive parameters for anchovy and common sardine, obtained from samples collected during daytime (mainly 6:30 to 18:00 h) between 19 and 31 August (North-Central sector) and between 31 August and 9 September (South sector)

Parameters	Anchovy		Common sardine	
	North-Central	South	North-Central	South
Spawning fraction, Day-1 females, S_1	0.15 (0.220)	0.07 (0.151)	0.14 (0.169)	0.03 (0.427)
Spawning fraction, Day-2 females, S_2	0.15 (0.201)	0.12 (0.136)	0.24 (0.100)	0.09 (0.160)
Weight of mature females, W (g)	14.2 (0.108)	22.2 (0.040)	19.5 (0.052)	24.6 (0.031)
Batch fecundity, F (egg per mature female)	4989 (0.123)	8239 (0.048)	8497 (0.049)	10414 (0.032)
Fraction of females by weight, R	0.49 (0.044)	0.52 (0.056)	0.51 (0.036)	0.40 (0.056)
No. of fishing set	14	18	32	20
No. of mature females	459	702	771	494

Table 4
DEPM parameter and spawning stock biomass estimates for anchovy and common sardine in the "North-Central" and "South" strata off central southern Chile (August–September 2002)

DEPM Parameters	Anchovy		Common sardine	
	North-Central	South	North-Central	South
Daily egg production, P_0 (egg/m^2/day)	19.7	123.6	121.8	264.6
Weight of mature females, W (g)	14.2	22.2	19.5	24.6
Sex ratio, R (fraction of females by weight)	0.49	0.52	0.51	0.40
Batch fecundity, F (eggs per mature females)	4989	8239	8497	10414
Spawning fraction, S	0.15	0.07	0.14	0.03
Relative fecundity, RF[a] (eggs per g)	351	371	436	424
Daily specific fecundity, DSF[b] (eggs per g)	25.6	12.7	30.4	5.1
Survey area, A (km^2)	15367	12468	15367	12468
Spawning biomass, B (t)	11840 (0.70)	121191 (0.48)	61635 (2.42)	645157 (0.71)
Total spawning stock biomass, B (t)	133031 (0.44)		706792 (0.68)	

The coefficient of variation is shown in parenthesis for the spawning stock biomass estimates.
[a] RF = F/W.
[b] DSF = SFR/W.

the species. The coastal shape and the bottom depth seem to be important factors for the spawning distribution of both species. In the central sector, the continental shelf is wide and the three bays located there ("Golfo de Arauco", "Bahía de Concepción", and "Bahía Coliumo") are acting as important spawning zones probably through retention and concentration processes (Bakun, 1996). In the South sector, the coastal shape is also acting as a big bay between 38°30′ and 40°S.

The spawning distribution is in agreement with recent results available in terms of the spatial distribution of eggs, larvae, recruits, and adults (Castro et al., 1997; Castillo et al., 2002, 2003a,b, 2004). These studies have revealed the absence of recruits and adults of anchovy and common sardine in the northern sector of the study area, i.e. from Valparaiso (33°S) to 34°30′S (northward Constitución). Castro et al. (1997) found higher eggs concentrations of both species in neritic zones (continental shelf), with nuclei well defined around the mouth of the Itata river (36°05′S–36°45′S), within the Gulf of Arauco, and between 37°40′S and 39°40′S. Although these results are confirmed in this study, we used a more dense grid of stations and therefore obtained a better spatial resolution of the spawning. According to Castillo et al. (2002), the biomass quantified acoustically in winter 2001 (August) was mainly confined to the neritic sector of the study area, with 100% of the biomass of both species concentrated between the coast and 10 nautical miles offshore.

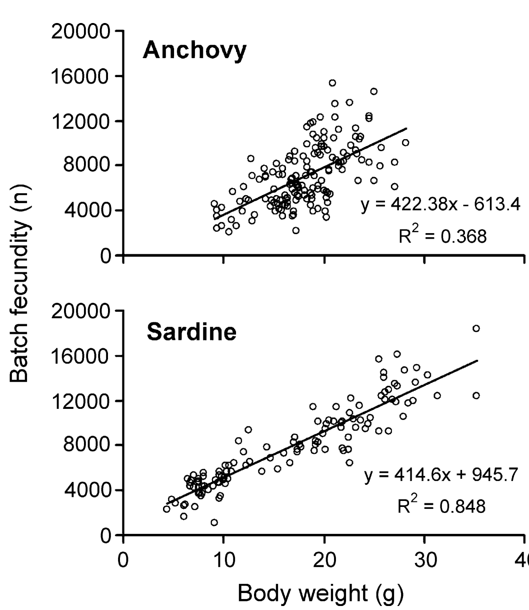

Fig. 9. Regressions of batch fecundity on ovary-free weight of females of anchovy and common sardine.

Although the survey revealed two main important spawning areas, one located in the central sector from Constitución to Gulf of Arauco (34°30′S–37°10′S) and the other one located in the South sector between 37°20′S and 40°S, the daily egg production was higher in the central sector for common sardine and in the South sector for anchovy. Nevertheless, the spatial distribution of the spawning of common sardine was more continuous in the South sector. In fact, the spawning of common sardine was patchy with two very high eggs density nuclei in the central sector. In contrast, the spawning of anchovy showed a continuous distribution along the coast in both sectors.

This is the first study in estimating the parameters of the Daily Egg Production Method for anchovy and common sardine in the central-south area off Chile. Estimates of the daily egg production were different in the two geographic areas sampled, and also the adult reproductive parameters, particularly the spawning fraction. In this way, the survey area had to be geographically stratified and we estimated DEPM parameters separately for the North-Central and South strata of the surveyed area. The daily egg production (P_0) of anchovy ranged between 5.5 and 16.9 eggs per 0.05 m^2 in the positive area. These values are low as compared with P_0 estimates available for the same species off northern Chile, but they are within the range of values reported for the same species in Peru, *E. mordax* in California, and *E. encrasicolus* in South Africa (Table 5). In the north area off Chile (18°20′S–24°S), the daily mortality rate has been estimated between 0.44 and 1.15 per day, which is higher when compared to our estimation of 0.22 to 0.47 per day for anchovy off central southern Chile. In the case of the common sardine, the P_0 found in this species ranged between 46.8 and

Table 5
Summary of DEPM data for *Engraulis* genus in upwelling regions. P = daily egg production (eggs per 0.05 m^2 per day), Z = mortality rate (day^{-1}), W = average weight of mature females (g), F = average batch fecundity (eggs per mature females), S = average spawning fraction, R = fraction of females by weight, DSF = daily specific fecundity (eggs per g)

Species	Area	Year	*P*	*Z*	*W*	*F*	*S*	*R*	DSF
E. mordax	California[a]	1980	11.1	0.45	17.4	7751	0.14	0.48	30.3
		1981	8.0	0.14	13.4	8329	0.11	0.50	33.0
		1982	3.3	0.16	18.8	10845	0.12	0.47	32.5
		1983	5.6	0.18	11.2	5297	0.09	0.55	24.4
		1984	3.8	0.17	12.0	5485	0.16	0.58	42.4
		1985	4.8	0.29	14.5	7343	0.12	0.61	37.1
E. ringens	Peru[b]	1981	23.7	1.04	25.8	15401	0.16	0.56	53.4
		1990	3.0	1.30	26.7	13487	0.05	0.51	12.9
		1994	15.1	1.14	23.3	12723	0.08	0.53	22.0
		1995	19.0	0.63	25.6	12701	0.12	0.54	32.2
		1996	n.a	n.a	29.8	18495	0.09	0.52	25.2
E. ringens	Northern Chile[c] (18°20′S–24°S)	1992	41.8	1.15	20.7	14917	0.16	0.48	55.3
		1995	20.0	0.63	29.2	15405	0.18	0.42	39.9
		1996	15.8	0.48	30.0	19658	0.19	0.46	57.2
		1997	14.9	0.44	21.7	12102	0.13	0.51	37.2
		1999	23.0	0.78	22.7	10600	0.17	0.46	36.5
		2000	29.7	0.77	30.9	16279	0.19	0.50	50.1
		2001	30.2	0.80	32.4	15911	0.19	0.47	43.3
		2002	15.9	0.62	21.3	16761	0.14	0.51	55.2
		2003	37.1	0.83	25.2	13327	0.18	0.49	47.1
E. encrasicolus	South Africa[d]	1984	19.5	0.02	15.1	7953	0.15	0.51	40.1
		1985	16.3	0.22	14.2	7991	0.19	0.48	50.3
		1986	24.4	0.28	11.7	5627	0.10	0.55	25.3
		1987	15.2	0.26	11.0	6490	0.08	0.56	26.5
		1988	15.7	0.40	12.0	5878	0.09	0.55	22.7
		1989	8.7	0.06	14.6	9045	0.13	0.49	37.9
		1990	17.7	0.13	11.5	6967	0.06	0.55	21.1

[a] Picquelle and Stauffer (1985) and Lo (1997).
[b] Santander et al. (1984), Hunter and Lo (1997), Lo (1997) and Ayon and Buitron (1997).
[c] Braun et al. (2004).
[d] Armstrong et al. (1988) and Shelton et al. (1993).

93.7 eggs per 0.05 m^2. These estimates are higher than anchovy even when they are compared with the estimates available for *E. ringens* in other upwelling areas (Table 5). Unfortunately, we do not have other any common sardine reference to compare our estimation.

According to the length frequency distributions, the size composition of anchovy was substantially different between the two geographic strata, while the length composition of common sardine was more similar. At present, it is not possible to establish whether the differences in the length composition of anchovy are due to the spatial structure or the population dynamics of this species in the study area (i.e. migration processes), and further research is required.

The estimates of average batch fecundity of anchovy were lower in comparison with available estimates for the same species in the northern area off Chile (Table 5). Because average fecundity is a size-dependent parameter, it is possible that the differences could be explained by the size of anchovy in each region. Nevertheless, in central-south Chile the size of anchovy eggs is larger than off northern Chile (Llanos-Rivera and Castro, 2004). In this way, the lower relative fecundity (351–371 eggs per gram of female) estimated in this study for anchovy could be off set by their bigger eggs.

In terms of the daily spawning fraction, we used the day-1 postovulatory follicles (POFs) because we think that day-2 POFs may have longer degeneration time. Also it is known that the degeneration rate of POFs is affected by temperature (Fitzhugh and Hettler, 1995; Ganias et al., 2003), and the low temperature range (11–12 °C) observed during the survey could be affecting the accuracy of ageing older POFs, particularly in the South sector of the study area (SST range: 7–13 °C). Although the estimates of spawning fraction in the North-Central stratum were similar to those values reported for the genus (Table 5), the estimates of daily spawning fraction were substantially lower in the South sector for both species. Considering that the fishing sets for adults were carried out outside of the bulk of the spawning in the South sector (Figs. 2 and 3), probably the estimates of spawning fraction could be also underestimated. Nevertheless, estimates of spawning fraction as low as 0.05 have been reported for anchovy in Peru and South Africa (Table 5). Also, Somarakis et al. (2002) estimated a daily spawning fraction of 0.061 for *E. encrasicolus* in the Ionian Sea. In this way, probably the reproductive parameters of anchovy and common sardine are highly variable in the central-south area off Chile, and further research is recommended to verify this statement.

The total stratified spawning stock biomass estimate was approximately 133,000 t for anchovy, and 707,000 t for common sardine. Acoustic biomass estimates carried out in January 2002 were 1.5 and 0.87 million t for anchovy and common sardine, respectively (Castillo et al., 2003a). It must be mentioned that both species are recruiting from November to January in central-south Chile. In this way, the acoustic biomass carried out at the beginning of the year is characterized by a high proportion of recruits (51% in anchovy and 99% in common sardine, Castillo et al., 2003a). Also, the fishery is strongly dependent on the annual pulse of recruitment with the highest catches obtained between January and April, contributing to at least 75% of total annual catch (Cubillos et al., 1998, 2002). In this context, the surviving adult biomass at the beginning of the spawning season must be strongly reduced by fishing and natural mortality. In addition, Cubillos et al. (2002) carried out monthly biomass estimates through cohort analysis. The estimates of total biomass for August in the period 1990–1998 ranged between 173 and 586,000 t in common sardine, and between 285 and 781,000 t for anchovy. In consequence, our estimates of spawning biomass seem to be reasonable according to previous assessment, and the seasonal changes occurring in the abundance of the species in the central-south area off Chile.

Finally, we want to note that this is the first DEPM applied to two small pelagic fish off central southern Chile. In this way, some suggestions for improvements are necessary for future DEPM estimation. It will be necessary to keep the stratified scheme developed in this study, particularly to verify the differences founded in the daily egg production and the adult reproductive parameters. Estimates of spawning fraction require special attention because of inaccuracy in ageing older POFs, and probably a review of the criteria used deserves care for anchovy and common sardine, specially the former. Experiments of degeneration rate of POFs are highly recommended by considering the low environmental temperature founded in the spawning habitat of the species. Adult reproductive parameters will improve with every annual repetition, as well as daily egg production. In fact, the DEPM estimates are better for stock assessment and fishery management when they are kept for a sufficiently long period.

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