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SUMMARY

The spawning biomass of the Pacific sardine (*Sardinops sagax*) in April - May 2009 was estimated by the daily egg production method (DEPM) to be 185,084 mt (CV = 0.26) for an area of 274,895 km² off California from San Diego to south of San Francisco (CalCOFI lines 95.0-63.3). The daily egg production estimate (P_0) was 0.59/.05m² (CV = 0.22), with the majority of eggs found south of Point Conception. The daily specific fecundity was calculated as 17.53 (number of eggs/population weight (g)/day) using the estimates of reproductive parameters from 467 mature female Pacific sardine collected from 29 positive trawls: F, mean batch fecundity, 29,790 eggs/batch (CV = 0.06); S, fraction spawning per day, 0.11 females spawning per day (CV = 0.15); W_f , mean female fish weight, 112.4 g (CV = 0.04); and R, sex ratio of females by weight, 0.602 (CV = 0.04).

The estimates of spawning biomass of the Pacific sardine off California in 1994 - 2008 were 127,000 mt, 80,000 mt, 83,000 mt, 410,000 mt, 314,000 mt, 282,000 mt, 1.06 million mt, 791,000 mt, 206,000 mt, 485,000 mt, 300,000 mt, 600,000 mt, 837,000 mt, 392,00 mt, 117,000 mt and 185,000mt (for the standard DEPM area), respectively. Therefore, the estimates of spawning biomass have been fluctuating, peaking in 2000 and 2006 and have been declining over the last three years. Starting in 2009, the time series of female spawning biomass and the total egg production starting from 1985 are two of the fishery-independent inputs to the annual stock assessment of the Pacific sardine.

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INTRODUCTION

The spawning biomass of Pacific sardine (*Sardinops sagax*) during 1986 (Scannel et al. 1996), 1987 (Wolf 1988a), 1988 (Wolf 1988b), 1994 (Lo et al. 1996), and 1996 (Barnes et al. 1997) was estimated independently using the daily egg production method (DEPM: Lasker 1985). The DEPM estimates spawning biomass by: 1) calculating the daily egg production (P_0) from ichthyoplankton survey data, 2) estimating the maturity and fecundity of females from adult fish samples, and 3) calculating the biomass of spawning adults. Before 1996, sardine egg production was estimated from CalVET plankton net samples and adult fish were sampled in various ways to obtain specimens for batch fecundity, spawning fraction, sex ratio, and average female fish weight (Wolf 1988a, 1988b; Scannell et al. 1996; Macewicz et al. 1996; Lo et al. 1996).

Since 1996, in addition to CalVET and Bongo nets, the Continuous Underway Fish Egg Sampler (CUFES; Checkley, et al. 1997) has been used as a routine sampler for fish eggs. Data of sardine eggs collected with CUFES have been incorporated in various ways, depending on the survey design, in the estimation procedures of the daily egg production. In the 1997 sardine egg survey (Hill et al. 1998, Lo et al. 2001), CUFES was used to allocate CalVET tows in an adaptive sampling plan. From 1998 to 2000, data of sardine eggs collected with both CalVET and CUFES during each April California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruise were used to estimate daily egg production (Hill et al. 1999). Use of the full data sets from both samplers in the DEPM can be time consuming and since the CUFES samples are collected exclusively from 3 m depth, it is not clear whether the distributions of sardine egg stages from CUFES samples are representative. Use of the CUFES data also requires an estimated conversion factor from eggs/min to eggs/0.05m². Starting with the 1999 April CalCOFI survey, an adaptive allocation survey design similar to the 1997 survey was implemented. In this design CalVET tows are added in areas where they were not pre-assigned, if sardine egg densities in CUFES collections are high.

Since 2001, a cost-effective alternative has been adopted to retain the DEPM index, but in a revised form that reduces effort in calculation and egg staging for CUFES collections. This revised DEPM index only uses CalVET samples of eggs and yolk-sac larvae and Bongo samples of yolk-sac larvae in the high density area (Region 1) to provide an estimate of P_0 , the variance of which can be large due to small sample size (fewer than 100 plankton tows). Adult samples were collected sporadically in 1997, 2001 and 2002. The egg production estimates for 1998-2000 were recomputed excluding data of staged eggs from CUFES to be consistent with later years.

Starting in 2004, full-scale surveys have been conducted for collection of Pacific sardine eggs, larvae, and adults to estimate the spawning biomass in the area off California from San Diego to San Francisco (Lo and Macewicz 2004; Lo et al. 2005; Lo and Macewicz 2006; Hill et al. 2006 a,b; Lo et al. 2007a,b, 2008). In 2004 the adult samples were taken primarily in the high density area, but beginning in 2005 adult Pacific sardine samples for reproductive output were taken in both high and low density areas. The ichthyoplankton samples taken during regular April CalCOFI cruises were also included in the spawning biomass computation. During 2006 and 2008, the survey area was extended north to the US-Canadian border and spawning biomass was computed for both the whole survey area and the standard DEPM survey area, e.g. from San Diego to San Francisco.

In 2009, in addition to the estimates of spawning biomass based on the past procedure by which, the P_0 was a weighted average with weights being the area size (km²) of each region, whereas the adult parameters were estimated from all trawl samples in the entire survey area. An alternative estimator based on the stratified sampling for each parameter was also included (Hill et al. 2009) for years when adequate adult samples were available. This alternative method was used to estimate the female spawning biomass, an input time series for the stock assessment. Here, we report the time series of spawning biomass based on the original method and the stratified estimates for comparison purposes.

MATERIALS AND METHODS

Data

Sardine eggs were collected aboard the chartered fishing vessel *F/V Frosti* using CalVET, CUFES, and Bongo nets during the April 15 -May 9 2009 sardine biomass survey. The survey was conducted south of San Francisco down to San Diego (CalCOFI lines 63.3 to 95.0) and extended offshore to CalCOFI station 90 and 100 in the areas north and south of Point Conception, respectively (Figure 1). As the spring CalCOFI cruise was conducted from March 7-22, only data from the DEPM survey were used for estimating the daily egg production of Pacific sardine. In addition to sardine eggs and yolk-sac larvae collected with the CalVET net, yolk-sac larvae collected with the Bongo net have been included to model the sardine embryonic mortality curve since 2000. Beginning in 2001 (Lo 2001), the CUFES data from the ichthyoplankton surveys are used only to map the spatial distribution of the sardine spawning population with the survey area post-stratified into high density (Region 1) and low density (Region 2) areas according to the egg density from CUFES collections. Staged eggs from CalVET tows and yolk-sac larvae from CalVET and Bongo tows in the high density area are used to model the embryonic mortality curve in the high density area and later converted to the daily egg production for the whole survey area.

CalVET and Bongo tows were taken at each pre-determined station. Additional CalVET tows were taken at 4 nm intervals on each line after the egg density from each of two consecutive CUFES samples exceeded 1 egg/min and CalVET tows were stopped after the egg density from each of two consecutive CUFES samples was less than 1 egg/min. One egg/min is equivalent to two to seven eggs/CalVET tow, depending on the degree of water mixing. The threshold value was reduced to 1 egg/min from 2 used in years prior to 2002 to increase the area of the high density area and, subsequently, to increase the number of CalVET samples. This adaptive allocation sampling was similar to the 1997 survey (Lo et al. 2001).

The survey area was post-stratified into two regions: Region 1, the high density area, and Region 2, the low density area. Region 1 encompassed the area where the egg density in CUFES collections was at least 1 egg per minute. The sizes of Region 1 and the total survey area were calculated using the formula for trapezoid area. The area of Region 1 was 74,966 km², 27% of the total survey area of 274,895 km². The rest of the survey area was Region 2 (Figure 1).

A total of 663 CUFES samples was collected. CUFES sampling intervals ranged from 1 to 67 minutes with a mean of 27 minutes and median of 30 minutes. A total of 136 CalVET samples was collected, of which 70 contained at least one sardine egg (Table 1). Egg densities from each CalVET sample and from the CUFES samples taken within an hour before and after the CalVET tow, were paired and used to derive a conversion factor (*E*) from eggs/min of CUFES sample to CalVET catch. We used a regression estimator to compute the ratio of mean eggs/min from CUFES to mean eggs/tow from CalVET: $E = \mu_y / \mu_x$ where y is the eggs/min and x is eggs/tow.

For adult samples, the survey plan was to conduct 3-5 trawls a night at the regular CalCOFI stations if possible on the survey line regardless of the presence of sardine eggs in

CUFES collections from April 15 - May 8, 2009. A Nordic 264 rope trawl with 3.0 m^2 foam core doors was towed at the surface at night for a duration of 30 minutes. The trawl was modified for surface trawling with Polyform floats attached to the head rope and trawl wings. The trawl was modified with a marine mammal extruder device placed midsection just forward of the codend. Pacific sardines were caught in 34 of the 61 trawls that were conducted at night near the surface (0-6 fathoms).

Up to 50 sardines were randomly sampled from each positive trawl with more than 75 fish or all if less than 75 fish (Table 2). If necessary, additional mature females were collected to obtain 25 mature females per trawl for reproductive parameters or for use in estimating batch fecundity. Each fish was sexed, standard length (mm) and weight (g) were measured, otoliths were removed for aging, tissue was preserved in 95% ethanol for genetics, and for females their ovaries were removed and preserved in 10% neutral buffered formalin. Each preserved ovary was blotted and weighed to the nearest milligram in the laboratory. Ovary wet weight was calculated as preserved ovary weight times 0.78 (unpublished data, CDFG 1986). A piece of each ovary was removed and prepared as hematoxylin and eosin (H&E) histological slides. All slides were analyzed for oocyte development, atresia, and postovulatory follicle age to assign female maturity and reproductive state (Macewicz et al. 1996).

Daily egg production (P_0)

Similar to the 2001-2008 procedure (Lo 2001), we used the net tow as the sampling unit. Eggs from CalVET tows and yolk-sac larvae from both CalVET and Bongo tows in Region 1 were used to compute egg production based on data from 10 transects (lines 63.3-95) (Figure 1). A total of 56 of the 70 CalVET samples in this region contained at least 1 sardine egg; these eggs were examined for their developmental stages (Figure 2).

Based on aboard-ship counts of eggs in CUFES samples, 335 of the 663 collections were positive for sardine eggs. In Region 1, there were 159 positive CUFES collections out of 200 total collections. In Region 2, 176 of the total 463 collections were positive (Table 1).

For modeling the embryonic mortality curve, yolk-sac larvae (larvae ≤ 5 mm in preserved length) were included assuming the mortality rate of yolk-sac larvae was the same as that of eggs (Lo 1986). Yolk-sac larval production was computed as the number of yolk-sac larvae/0.05m² divided by the duration of the yolk-sac stage (number of larvae/0.05m²/day), and the duration was computed based on the temperature-dependent growth curve (Table 3 of Zweifel and Lasker 1976) for each tow. For yolk-sac larvae caught by the Bongo net, the larval abundance was further adjusted for size-specific extrusion from 0.505 mm mesh (Table 7 of Lo 1983) and for the percent of each sample that was sorted. The adjusted yolk-sac larvae/0.05 m² was then computed for each tow and was termed daily larval production/0.05 m². In the entire survey area, 54 of 136 CalVET and 43 of 81 Bongo samples had at least one yolk-sac larva (Figure 3). In Region 1, 41 of 70 CalVET and 10 of 15 Bongo samples were positive for yolk-sac larvae. In Region 2, 13 of 66 CalVET and 33 of 66 Bongo samples were positive for yolk-sac larvae (Table 1).

Daily egg production in Region 1 ($P_{0,1}$)

Sardine eggs and yolk-sac larvae and their ages were used to construct an embryonic mortality curve (Lo et al. 1996). Sardine egg density for each developmental stage was computed based on CalVET samples (Figure 2). The density of eggs in 2009 was slightly higher than that of 2008 and lower than some of the previous years (Lo 2003; Lo and Macewicz 2002, 2004, 2006; Lo et al. 2005, 2007a,b and 2008). Like most of the past data, the density of eggs at stage 6 was highest. A temperature-dependent stage-to-age model (Lo et. al. 1996) was used to assign age to each stage. Sardine egg abundances and estimated ages were used directly in a nonlinear regression. Eggs \leq 3-h old and eggs older than 2.5 days were excluded because of possible bias. The average sea surface temperature for CalVET tows with \geq 1 egg was 13.54°C, higher than 13.3°C in 2008, lower than 14.95°C in 2006 and 14.2°C in 2005, and similar to 13.4°C in 2004 and 13.8°C in 2003.

The sardine embryonic mortality curve was modeled by an exponential decay curve (Lo et al. 1996):

$$P_t = P_0 e^{-zt}$$
^[1]

where P_t is either eggs/ $0.05m^2$ /day from CalVET tows or yolk-sac-larvae/ $0.05m^2$ /day from CalVET and Bongo tows, and t is the age (days) of eggs or yolk-sac larvae from each tow. A weighted nonlinear regression was used to estimate two parameters in equation (1) where the weights were 1/SD. The standard deviation (SD) of eggs was 2.51, 8.65, and 2.73, for day one, day two and day three age groups respectively. The SD of yolk-sac larval production from CalVETs was 0.47 and the SD of yolk-sac larval production from Bongo samples was 0.53.

A simulation study (Lo 2001) indicated that $P_{0,1}$ computed from a weighted nonlinear regression based on the original data points has a relative bias (RB) of -0.04 of the estimate where the RB = (mean of 1,000 estimates - true value)/mean of 1,000 estimates. Therefore the bias-corrected estimate of egg production in Region 1: $P_{0,1,c} = P_{0,1} * (1 - RB) = P_{0,1} * (1.04)$, and SE ($P_{0,1,c}$) = SE($P_{0,1}$) * 1.04.

Daily egg production in Region 2 ($P_{0,2}$)

Although 66 CalVET samples were taken in Region 2, only 14 tows had ≥ 1 sardine egg, ranging from 1 to 9 eggs per tow (Table 1) as compared to the maximum 63 eggs in region 1. Therefore, we estimated daily egg production in Region 2 ($P_{0,2}$) as the product of the bias-corrected egg production in Region 1 ($P_{0,1,c}$) and the ratio of egg density in Region 2 to Region 1 (q) from CUFES samples, assuming the catch ratio of eggs/min from CUFES to eggs/tow from CalVET is the same for the whole survey area:

$$P_{0,2} = P_{0,1,c}q$$
 [2]

$$q = \frac{\sum_{i} \frac{x_{2,i}}{\overline{x_{1,i}}} m_i}{\sum_{i} m_i}$$
[3]
$$[n/(n-1)] \sum_{i} m_i^2 (q_i - q)^2$$

$$\operatorname{var}(q) = \frac{[n/(n-1)]\sum_{i} m_{i}^{2} (q_{i} - q)^{2}}{\left(\sum_{i} m_{i}\right)^{2}}$$

where q is the ratio of eggs/min between the low density and high density areas, m_i was the total CUFES time (minutes) in the ith transect, $\overline{x}_{j,i}$ is eggs/min of the ith transect in the jth Region, and $q_i = \frac{\overline{x}_{2,i}}{\overline{x}_{1,i}}$ is the catch ratio in the ith transect.

Daily egg production for the whole survey area (P_0)

 P_0 was computed as the weighted average of $P_{0,1}$ and $P_{0,2}$:

$$P_{0} = \frac{P_{0,1,c}A_{1} + P_{0,2}A_{2}}{A_{1} + A_{2}}$$

$$= P_{0,1,c}w_{1} + P_{0,2}w_{2}$$

$$= P_{0,1,c}[w_{1} + qw_{2}]$$
[4]

and

$$mse(P_0) = mse(P_{0,1,c})(w_1 + w_2q)^2 + P_{0,1,c}^2w_2^2V(q) - mse(P_{0,1,c})w_2^2V(q)$$

(Goodman 1960) where *mse* $(P_{0,1,c}) = v(P_{0,1}) + bias^2 = v(P_{0,1}) + (P_{0,1} RB)^2$

and $w_i = \frac{A_i}{A_1 + A_2}$, and A_i is the area size for i = 1 or 2.

Adult parameters

Four adult parameters are needed for estimation of spawning biomass: 1) daily spawning fraction or the number of spawning females per mature female per day (*S*); 2) the average batch fecundity (*F*); 3) the proportion of mature female fish by weight (sex ratio, *R*); and 4) the average weight of mature females (g, W_f). Population values for *S*, *R*, *F* and W_f were estimated by methods in Picquelle and Stauffer (1985). Daily specific fecundity (number of eggs per population weight (g) per day) is (*RSF*)/*W*_f. The parameters were estimated for the whole area and separately for sardine females caught in each region. Correlations among all pairs of adult parameters were calculated for computing the variance of the estimate of spawning biomass (Parker 1985). In the past, the predicted batch fecundity for each female fish was calculated as y = a + bx where x is the female weight (without ovary) and y is the predicted value. In reality, most of the batch fecundities we estimated gravimetricly are scattered around the regression line and not on it. Therefore, to account for the deviation of batch fecundity from the regression line, we added an error term to the predicted value as y = a + bx + e where error term e was a random number generated from a normal distribution with mean zero and a variance of the error terms from the regression analysis. An MS ACCESS¹ Visual Basic program (Chen et al. 2003) was modified accordingly to more accurately describe batch fecundity variance, and was used to summarize the trawl adult parameters, calculate adult parameter correlations and covariance, and to estimate spawning biomass and its coefficient of variation.

Spawning fraction (S). A total of 467 mature female sardines was analyzed and considered to be a random sample of the population in the area trawled. Histological criteria can be used to identify four different spawning nights: postovulatory follicles aged 44-54 hours old indicated spawning two nights before capture (A) (day-0 female) postovulatory follicles aged about 20-30 hours old indicated spawning the night before capture (B) (day-1 female); hydrated oocytes or new (without deterioration) postovulatory follicles indicated spawning the night of capture (C) (day-2 female); and early stages of migratory-nucleus oocytes indicated that spawning would have occurred the night after capture (D). The daily spawning fraction can be estimated by using the number of females spawning on one night, an average of several nights, or all nights. We used the average of the number of females identified as having spawned the night before capture (B) and those having spawned two nights before capture (A) and the adjusted number of mature females caught in each trawl (Table 2) to estimate the population spawning fraction (S₁₂) and variance (Picquelle and Stauffer 1985, Hill et al. 2009).

Batch fecundity (F). Batch fecundity (number of oocytes per spawn) was considered to be the number of migratory-nucleus-stage oocytes or the number of hydrated oocytes in the ovary (Hunter et al., 1985). We used the gravimetric method (Macewicz et al. 1996; Hunter et al. 1985, 1992) to estimate mean batch fecundity for 65 females caught during the April-May 2009 survey. The relationship of batch fecundity (F_b) to female weight (without ovary, W_{of}), as determined by simple linear regression, was $F_b = -4598 + 326.78W_{of}$ where $r^2 = 0.734$, variance of the slope was 612.56, and W_{of} ranged from 54 to 216g (Figure 4), although the intercept did not differ from zero (P = 0.135). We used the equation $F_b = -4598 + 326.78W_{of} + e$ where the error term, e, was generated from a normal distribution with mean zero and variance of 36,309,756 to estimate batch fecundity for each of the 467 mature Pacific sardine females analyzed to estimate spawning frequency.

Female weight (W_f). The observed female weight was adjusted downward for females with hydrated ovaries because their ovary weights were temporarily inflated. We obtained the adjusted female weight by the linear equation $W_f = -1.35 + 1.06W_{of}$ where W_f is wet weight and

¹ Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

 W_{of} is ovary-free wet weight based on data from non-hydrated mature females taken during the April-May 2009 survey.

Sex ratio (R). The female proportion by weight was determined for each trawl (or each collection). The average weight of males and females (calculated from the first 10 males and 25 females) was multiplied by the number of males or females in the collection of 50 randomly selected fish to calculate total weight by sex in each collection. Thus, the female proportion by weight in each collection (Table 2) was calculated as estimated total female weight divided by estimated total weight in the sample. The estimate of the population's sex ratio by weight was calculated (Picquelle and Stauffer, 1985).

Spawning biomass (B_s)

The spawning biomass was computed according to:

$$B_s = \frac{P_0 A C}{RSF / W_f}$$
[5]

where A is the survey area in unit of 0.05 m², S is the number of females spawning per mature females per day, F is the batch fecundity (number of eggs per mature female), R is the fraction of mature female fish by weight (sex ratio), W_f is the average weight of mature females (g), and C is the conversion factor from grams (g) to metric tons (mt). P_0A is the total daily egg production in the survey area, and the denominator (*RSF/W_f*) is the daily specific fecundity (number of eggs/population weight (g)/day).

The variance of the spawning biomass estimate (\hat{B}_s) was computed from the Taylor expansion and in terms of the coefficient of variation (CV) for each parameter estimate and covariance for adult parameter estimates (Parker 1985):

$$VAR(\hat{B}_{s}) = \hat{B}_{s}^{2} \left[CV(\hat{P}_{0})^{2} + CV(\hat{W}_{f})^{2} + CV(\hat{S})^{2} + CV(\hat{R})^{2} + CV(\hat{F})^{2} + 2COVS \right]$$
[6]

The last term involving covariance term on the right-hand side is

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

where *x*'s are the adult parameter estimates, and subscripts *i* and *j* represent different adult parameters; e.g., $x_i = F$ and $x_j = W_f$. The sign of any two terms is positive if they are both in the numerator of B_S or denominator of B_S (equation 5); otherwise, the sign is negative. The covariance term is

$$\operatorname{cov}(x_{i,}x_{j}) = \frac{[n/(n-1)]\sum_{k} m_{k}(x_{i,k} - x_{i})g_{k}(x_{j,k} - x_{j})}{\left(\sum_{k} m_{k}\right)\left(\sum_{k} g_{k}\right)}$$

where k refers to k^{th} tow, and k=1,...,n. The terms of m_k and g_k are sample sizes and $x_{i,k}$ and $x_{j,k}$ are sample means from the k^{th} tow for x_i and x_j respectively.

As the survey area was post-stratified into two regions based on the presence of sardine eggs: region 1 (high density area) and region 2 (low density area), equation (5) can be applied to the whole survey area and/or to each of the two regions depending on the availability of data. For the female spawning biomass (fs. biomass), one of the inputs to the stock assessment, the sex ratio (R) was excluded from equations (5) and (6).

RESULTS

Daily egg production (P_0)

In Region 1, the daily egg production ($P_{0,1}$) was 1.69/0.05m²/day(CV=0.22); equation 1 and Figure 5). The bias-corrected egg production ($P_{0,1,c}$) was 1.76/0.05 m²/day (CV = 0.22;Table 3) compared to 1.45/0.05 m²/day (CV = 0.18) in 2008 for the standard DEPM survey area, egg mortality was Z = 0.25 (CV = 0.19) compared to 0.13 (CV = 0.29) in 2008, and the area of region 1 was 74,966km² (21,903nm²) compared to 53,514 km² (20,447 nm²) in 2008 (Table 4). The point estimate of egg mortality was slightly higher than the past two years (Table 4). The ratio (q) of egg density between Region 2 and Region 1 from CUFES samples was 0.087 (CV = 0.17) (equation 3). In Region 2, the egg production ($P_{0,2}$) was 0.15 /0.05 m²/day (CV = 0.27) for an area of 199,929 km² (58,416 nm²). The estimate of the daily egg production for the entire survey area was 0.59/0.05 m² (CV = 0.22) (equation 4) for a total area of 274,895 km² (80,320 nm²) (Table 3).

Catch ratio between CUFES and CalVET (E)

Although this ratio is no longer needed in the current estimation procedure, we computed it for comparison purposes. The catch ratio of eggs/min to eggs/tow (eggs/min = $E * \text{eggs}/0.05 \text{ m}^2$) was computed from 53 pairs of CalVET tows and CUFES collections (Figure 6). The eggs/min corresponding to each positive CalVET tow was the mean of all CUFES collections taken from one hour before to one hour after each positive CalVET tow. The catch ratio was 0.158 (CV=0.12), compared to the 2008 estimate of 0.19 (CV = 0.06). A ratio of 0.158 means that one egg/tow from a CalVET tow was equivalent to approximately 0.158 egg/min from a CUFES sample, or one egg/minute from the CUFES was equivalent to 6.32 eggs/tow from the CalVET sample.

Adult parameters

Standard length (SL) of the randomly obtained sardines in each trawl ranged from 163 to 256 mm for 398 males and from 159 to 259 mm for 559 females (Figure 7). The smallest mature female was 170 mm SL. The length at which 50% of females are mature (ML_{50}) was not calculated because only one immature female sardine (159 mm SL) was captured in the survey.

Reproductive parameters of the 467 mature female sardines for the individual trawls (25 maximum per trawl) are given in Table 2. The estimate of April-May 2009 population sex ratio (*R*), was 0.602 (CV = 0.04) (Table 5). Estimates of the other female sardine parameters were: *F*, mean batch fecundity,29,790 eggs/batch (CV = 0.06); *S*, spawning fraction, 0.11 per day (CV = 0.15); and W_f , mean female fish weight, 112.4 grams (CV = 0.04). The average interval between spawning (spawning frequency) was about 9 days (inverse of spawning fraction or 1/0.11), and the daily specific fecundity was 17.53 eggs/gm/day (Table 5). The correlation matrix for the adult parameter estimates is shown in Table 5.

Spawning biomass (B_s)

The final estimate of spawning biomass of sardine in 2009 (equation 5, Table 4) was 185,084 mt (CV = 0.28) or 203,593 short tons (st) (= 185,084 x 1.1) for an area of 274,895 km² (80,320 nm²) from San Diego to San Francisco. The point estimates of spawning biomass of Pacific sardine in 1994-2009 are, respectively: 127,102; 79,997; 83,176; 409,579; 313,986; 282,248; 1,063,837; 790,925; 206,333; 485,121; 281,639; 621,657; 837,501; 392,492; 117,426; and 185,084 mt (Table 4).

DISCUSSION

Pacific sardine eggs

Sardine eggs were distributed throughout the survey area with a slightly higher density in the southern area between CalCOFI lines 81.7 and 95 (Figure 1). The average egg density (0.5 egg/min (CV = 0.23, Table 3) from CUFES samples in 2009 was similar to 2008 (0.49 egg/min (CV=0.03). The egg densities by stage are much lower than those in previous years. There seemed to be less spawning activity in the northern part of the survey area during 2009, similar to 2006 -2008 and unlike 2002 - 2005.

The adaptive allocation sampling procedure was used to allocate additional CalVET tows for the whole survey and a higher percentage of positive tows was seen for all gear types in region 1 than region 2 (Table 1). Again, we highly recommend that the adaptive allocation sampling be applied aboard the research vessel that conducts the routine spring (March-April) CalCOFI survey in the future to improve the quality of the estimate of the spawning biomass of Pacific sardine.

Embryonic mortality curve

The estimates of the daily egg production at age 0 ($P_0/0.05 \text{ m}^2$) was similar to that of 2008 and lower than those of previous years. The daily embryonic mortality was slightly higher than that of 2008 and lower than many other years. The density among egg developmental stages peaked at stage 6 similar to many previous years. The combined data of staged eggs and yolk-sac larvae in the embryonic mortality curve enabled us to obtain a robust estimate of the mortality rate (Table 4).

Catch ratio between CUFES and CalVET (E)

The 2009 catch ratio between CUFES and CalVET (0.15) was lower than most of those obtained in recent years: 1998 (0.32), 1999 (0.34), 2000 (0.277), 2001 (0.145 (CV = 0.026)), 2002 (0.24 (CV = 0.06)), 2003 (0.39 (CV = 0.11)), 2004 (0.22 (CV = 0.09), 2005 (0.18 (CV = 0.28)). and 2006 (0.32 (CV = 0.12)),2007 (0.15(CV=0.09) and 2008(0.19(CV=0.06)). This 2009 value was quite different from the 1996 estimate of 0.73. This could be because the 1996 CalVET samples were taken only in the southern area near San Diego while after 1997 CalVET samples were taken in a larger area extending far north of San Diego.

Adult parameters

The 2009 Pacific sardine DEPM survey was the first survey since 1994 to collect a large number of trawls (29) with mature female sardines out of a total of 60(Table 1 and 6). The relative high number of positive trawls was because every night 3-5 trawls were conducted, few extreme weather days occurred, and the ship did not have to reduce trawling days by conducting lines missed during the spring CalCOFI survey. The increase in trawling resulted in an almost equal number of trawl samples (Table 2) collected in areas of high (Region 1) and low (Region 2) egg density to yield a better estimate of spawning biomass for the whole population in the large oceanic area from San Diego to San Francisco. The fraction of females spawning per day was higher in Region 1 (0.141 females/day (SE = 0.02)) than in Region 2 (0.085 females per day (SE = 0.02)), however, the difference in the fraction of females spawning was not statistically significant (t = 1.79, df = 26, p > 0.05). The regional difference in the fraction of females spawning was similar to past DEPM surveys in 2005, 2006 (Lo and Macewicz 2006, Lo et al. 2007a), 2007 (when one unusual trawl is removed, Lo et al. 2007b) and 2008 (Lo et al. 2008). Because the spawning rates differed between the two regions, it is necessary to continue to take trawls in both regions to ensure an unbiased estimate of spawning biomass for the whole population.

The increase in the number of trawl samples of mature females to 29 in 2009 was the major factor in the improvement of the spawning fraction CV (0.15). In the past, spawning fractions had high CVs (CVs of 0.33 in 2007 and 0.31 in 2005 and 2008) which were most likely due to the low number of trawls with sardine (12 - 14) and high variability of spawning. Another factor was the change in the calculation of daily spawning fraction. In the past (1994, 1997, 2004, 2005, 2007, and 2008), the daily spawning fraction was based on the number of day-1 females (night B) (S₁), a procedure used for Northern anchovy (Pcquelle and Hewitt, 1983) to replace the day-0 females (night A) (S₀) and the number of total mature females was adjusted accordingly. In 2009 we used the daily spawning fraction (S₁₂) based on the mean number of day-1 and day 2

spawning females captured for each trawl. We chosed S_{12} to estimate daily spawning fraction because of the higher precision of S_{12} than S_1 (Hill et al. 2009) although the point estimates of the two were similar ($S_{12} = 0.1098$ and $S_1 = 0.1047$). Therefore, we recommend to use S_{12} , and that similar numbers of positive tows (~ 29 trawl samples with mature females) be obtained in both high and low egg density areas, for future biomass surveys.

We examined the sardines taken in 2009 and compared them to those taken during a similar period in the standard DEPM area in 2008. The mean size of sardines (male and females) was similar (Figure 7). Only one immature female was found in 2009 and none was found in 2008. We believe the scarcity of immature females is because both survey's samples were from offshore areas and sardines are always larger offshore (Lo et al. 2007). Port samples or samples from observers on commercial vessels could contain the smaller fish that predominately occur inshore for maturity information but, generally, the samples are not preserved and could not be used for estimation of daily spawning fraction which requires histological analysis. We recommend that to improve the whole population adult parameter analyses more trawls should be added in the inshore areas to obtain spawning and maturity information on smaller fish.

Finally, weighing fresh sardine body onboard vessels has improved over the years since 1994 and fish in the random sample can be weighed individually. After adjusting the body weight of females with hydrated ovaries (see methods) we summed the individual weights of females and males for each trawl and estimated sex ratio as sum of female weights divided by the total weight of males and females. Sex ratio by individual weights was 0.598 similar to 0.602 from the original method using average weights from a subsample in each trawl (Picquelle and Stauffer 1985). We recommend that estimation of sex ratio by sum of individual weights be re-examined and possibly used in the future.

Spawning biomass

The 2009 estimate of spawning biomass is similar to that of 2008 and considerably lower than that in 2006 and most previous years. The 2009 egg production $(0.59 \text{ eggs}/0.05\text{m}^2)$ was lower than that in the 2006 standard DEPM survey area $(1.94 \text{ eggs}/0.05\text{m}^2)$ and many other years. The adult daily reproductive output (daily specific fecundity) was similar to that in 2007 (15.68 eggs/g/day) and the adjusted 2006 estimate (15.57 eggs/g/day), and lower than estimates in 2008 and during 1997-2004 (Table 4). The higher values in early years were due to the fact that trawl samples were taken in the high density area only while since 2005 trawl samples were taken in both Region 1 and Region 2. For the stock assessment, we provided the estimates of the female spawning biomass for years when adequate adult samples were available (Table 7).

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		Reg	gion	
		1	2	Total
CalVET eggs	Positive	56	14	70
	Total	70	66	136
CalVET-yolk-sac	Positive	41	13	54
	Total	70	66	136
BONGO-yolk-sac	Positive	10	33	43
	Total	15	66	81
CUFES eggs	Positive	159	176	335
	Total	200	463	663
Trawls	Positive	16	18	34
	Total	21	40	61

Table 1. Number of positive tows and total number of tows of Pacific sardine eggs from
CalVET, yolk-sac larvae from CalVET and Bongo, eggs from CUFES, and trawls in
Region 1 (eggs/min \geq 1) and Region 2 (eggs/min <1) for *R/V Frosti* cruise 0904.

Table 2. Sardine egg density region, individual trawl information, sex ratio^a, and parameters for mature female *Sardinops sagax*, used in the estimation of the April-May 2009 spawning biomass. Trawls are listed from north to south.

COLLECTION INFORMATION

MATURE FEMALES

Location							Body	Weight			Nun	nber spa	wning			
Region						Surface	No.		No.	weight	without	Batch			Night	2 Nights
1=hiah		Month-		Latitude	Lonaitude	Temp.	of	Sex	anal-	(a)	ovarv	Fecundity	Adi.	Niaht of	before	before
2=low	No.	Dav	Time	°N	°W	°C	fish	Ratio	vzed	Ave.	(q) Ave.	Ave.	No. ^b	capture	capture	capture
2	2490	4-18	22:45	36.539	122.671	10.5	9	0.887	8	148.94	140.95	41400	8.0	0	0	0
2	2489	4-18	20:01	36.467	122.789	10.9	50	0.634	25	142.26	136.88	38425	25.0	0	0	0
2	2487	4-17	21:34	35.941	125.275	11.6	50	0.483	23	154.13	145.10	42848	18.5	6	1	2
2	2493	4-19	22:53	35.577	123.082	12.9	26	0.729	19	122.44	115.63	31861	16.0	5	2	2
2	2494	4-20	1:41	35.477	123.268	12.9	45	0.617	24	118.44	113.56	31137	24.5	4	5	4
2	2488	4-18	1:50	35.474	124.920	11.9	50	0.628	25	139.84	130.96	36602	25.0	3	3	3
2	2495	4-20	3:44	35.390	123.459	12.6	18	0.511	9	113.94	108.69	29517	9.5	1	1	2
2	2499	4-21	3:01	34.744	123.171	13.5	34	0.691	23	115.57	109.37	30377	23.5	1	1	2
2	2498	4-21	0:19	34.654	123.394	13.5	50	0.717	25	124.04	116.53	34810	17.5	8	1	0
2	2497	4-20	22:00	34.522	123.626	14.0	19	0.697	13	114.91	110.30	30731	13.0	3	4	2
2	2496	4-20	19:48	34.413	123.832	14.3	1	0.000	-	-	-	-	-	-	-	-
2	2503	4-22	21:25	34.044	122.561	13.9	70	0.615	25	117.58	111.89	32839	6.5	19	1	0
2	2504	4-22	23:58	33.935	122.828	14.4	1	0.000	-	-	-	-	-	-	-	-
2	2513	4-25	1:39	33.913	120.799	12.3	50	0.540	25	110.90	106.45	31509	25.0	0	0	0
2	2512	4-24	22:41	33.851	120.946	13.3	64	0.645	25	112.54	108.02	28553	27.5	0	1	4
1	2511	4-24	19:36	33.733	121.196	13.4	53	0.694	25	111.39	105.77	28056	23.5	3	1	2
1	2514	4-27	19:44	32.844	121.440	12.9	39	0.335	13	100.14	95.52	25433	10.5	4	2	1
2	2509	4-24	2:14	32.834	123.009	13.9	2	0.000	-	-	-	-	-	-	-	-
2	2508	4-24	0:17	32.782	123.204	13.9	4	0.506	2	119.43	113.60	29927	1.0	1	0	0
1	2515	4-27	22:00	32.765	121.594	13.1	50	0.481	23	105.80	100.56	27860	8.0	15	0	0
1	2523	4-30	1:44	32.705	120.158	12.8	9	0.469	4	83.75	79.99	18794	4.0	1	1	1
2	2507	4-23	22:10	32.673	123.353	13.9	1	0.000	-	-	-	-	-	-	-	-
1	2516	4-28	0:29	32.671	121.756	13.2	50	0.445	25	92.34	88.05	22634	26.0	0	1	1
1	2517	4-28	3:54	32.566	122.005	13.1	20	0.243	5	93.20	88.63	23401	4.0	1	0	0
1	2525	5-01	19:42	32.270	119.455	13.0	50	0.799	25	81.66	77.69	21161	30.0	0	5	5
1	2526	5-01	21:58	32.199	119.604	12.2	6	0.823	5	98.27	95.10	30369	5.5	1	2	1
1	2527	5-01	23:57	32.142	119.763	12.7	50	0.706	25	93.12	89.33	22616	30.0	0	4	6
1	2528	5-02	3:26	32.023	120.013	13.0	50	0.559	25	89.02	85.15	23559	29.0	2	5	7
1	2538	5-05	20:08	31.517	119.519	13.8	8	0.622	5	83.45	80.16	22789	5.5	1	0	3
1	2539	5-05	22:00	31.470	119.597	13.6	7	0.548	4	78.00	74.84	20764	6.0	0	3	1
1	2535	5-04	23:00	31.470	119.502	13.5	1	0.000	-	-	-	-	-	-	-	-
1	2536	5-05	0:50	31.443	119.572	13.6	11	0.651	7	84.50	78.56	22945	6.5	1	0	1
1	2537	5-05	2:57	31.404	119.665	13.6	6	0.685	4	94.25	89.44	24250	3.5	1	1	0
1	2541	5-06	2:20	31.376	119.775	13.4	3	0.314	1	78.50	75.88	29546	0.0	1	0	0
									467				432.5	85	45	50

^aSex ratio, proportion of females by weight, based on average weights from subsamples and number of fish sampled in each trawls (Picquelle and Stauffer 1985). ^bMature adjusted by the average number of females spawning the night before capture and females spawning 2 nights before capture.

Parameter	Region 1	Region 2	Whole a	Whole area			
CUFES samples	463	200	663	663			
Calvet samples	70	66	136	136			
$P_0/0.05 \text{m}^2$	1.76	0.15	0.59	0.59			
CV	0.22	0.27	0.22	0.22			
Area (km ²)	74966	199929	274895	274895			
%	27	63	100	100			
Year for adult samples	2009	2009	2009	2008			
Trawls with females	15	14	29	12			
Female fish wt (W_f)	94.3	125.5	112.4	102.22			
Batch fecundity(F)	24236	33806	29790	28964			
Spawning fraction (S)	0.141	0.085	0.110	0.1136			
Sex ratio (R)	0.564	0.624	0.602	0.631			
Eggs/g biomass/day (RSF/W_f)	20.37	14.34	17.53	20.31			
Spawning biomass (mt) ^b	129520	41816	185084	159694			
CV	0.31	0.38	0.28	0.42			
Daily mortality (Z)	0.25	-					
CV	0.19	-					
eggs/min	1.60	0.12	0.50				
CV	0.26	0.21	0.23				
q = eggs/min in Region 2 / eggs/n	nin in Region	1	0.087				
CV			0.17				
E = eggs.min/eggs/tow			0.158				
CV			0.12				
Bongo samples	15	66	81				
Area in nm ²	21903	58416	80320				
Spawning biomass							
(short ton)	142472	40572	203592				

Table 3. Pacific sardine egg production (P_0), adult parameters, and spawning biomass estimates in Region 1 (eggs/min \ge 1), in Region 2 (eggs/min < 1) and for the whole area of the 2009-DEPM surveys.

^a 1.76 was corrected for bias of P₀. ^b biomass was computed from estimates of parameters in each column, i.e. 2009 whole area is an average of adult parameters and $185084 \neq 129520 + 41816$.

Table 4. Estimates of daily egg production $(P_0)^a$ for the survey area, daily instantaneous mortality rates (Z) from high density area (Region 1), daily specific fecundity (RSF/W), spawning biomass of Pacific sardines and average sea surface temperature for the years 1994 to 2009.

Year	$P_{\theta}(\mathrm{CV})$	Z (CV)	Area (km ²) (Region 1)	$\frac{RSF^{h}}{W}$	Spawning biomass (mt) (CV) ^b	Mean Temp. for positive egg or yolk-sac samples	Mean temperature all CalVETs
1994	0.193 (0.21)	0.120 (0.91)	380,175 (174,880)	11.38	127,102 (0.32)	14.3	14.7
1995	0.830 (0.5)	0.400 (0.4)	113,188.9 (113188.9)	23.55 ^c	79,997 (0.6)	15.5	14.7
1996	0.415 (0.42)	0.105 (4.15)	235,960 (112,322)	23.55	83,176 (0.48)	14.5	15.0
1997	2.770 (0.21)	0.350 (0.14)	174,096 (66,841)	23.55 ^d	409,579 (0.31)	13.7	13.9
1998	2.279 (0.34)	0.255 (0.37)	162,253 (162,253)	23.55	313,986 (0.41)	14.38	14.6
1999	1.092 (0.35)	0.100 (0.6)	304,191 (130,890)	23.55	282,248 (0.42)	12.5	12.6
2000	4.235 (0.4)	0.420 (0.73)	295,759 (57,525)	23.55	1,063,837 (0.67)	14.1	14.4
2001	2.898 (0.39)	0.370 (0.21)	321,386 (70,148)	23.55	790,925 (0.45)	13.3	13.2
2002	0.728 (0.17)	0.400 (0.15)	325,082 (88,403)	22.94	206,333 (0.35)	13.6	13.6
2003	1.520 (0.18)	0.480 (0.08)	365,906 (82,578)	22.94	485,121 (0.36)	13.7	13.8
2004	0.960 (0.24)	0.250 (0.04)	320,620 (68,234)	21.86 ^e	281,639 (0.3)	13.4	13.7
2005	1.916 (0.417)	0.579 (0.20)	253,620 (46,203)	15.67	621,657 (0.54)	14.21	14.1
2006	1.936 (0.256)	0.31 (0.25)	336,774 (98,034)	15.57 ^f	837,501 ^f (0.46)	14.95	14.5
2007	0.864 (0.256)	0.133 (0.36)	356,159 (142,403)	15.68	392,492 (0.45)	13.7	13.6
2008 ^g	0.43 (0.21)	0.13 (0.29)	297,949 (53,514)	21.82	117,426 (0.43)	13.3	13.1
2009	0.59 (0.22)	0.25 (0.19)	274895 (74966)	17.53	185,084 (0.28)	13.6	13.5

a Weighted non-linear regression on original data and bias correction of 1.04, except in 1994 and 1997 when grouped data and a correction factor of 1.14 was used (appendix Lo 2001).

b $CV(B_s) = (CV^2(P_0) + \text{allotherCOV}^2)^{1/2} = (CV^2(P_0) + 0.054)^{1/2}$. For 1995-2001 allotherCOV² was from 1994 data (Lo et al. 1996). For 2003, allotherCOV was from 2002 data (Lo and Macewicz 2002).

c 23.55 was from computation for 1994 based on S = 0.149 (the average spawning fraction (day-0 + day-1) of active females from 1986-1994; Macewicz et al. 1996).

d Would be 25.94 when calculated from parameters in table 6 and estimated spawning biomass is 371,725 mt with CV = 0.36.

e Uses R = 0.5 (Lo and Macewicz 2004); if use actual R = 0.618, then value is 27.0 and biomass is estimated at 227,746 mt.

f Value for standard DEPM sampling area off California when calculated using S = 0.126, the average of females spawning the night before capture ("day-1") from 1997, 2004, 2005, and 2007. When survey S of 0.0698 was previously used (Lo et al. 2007a), the 2006 DEPM spawning biomass was estimated as 1,512,882 mt (CV 0.46) and the 2006 coastwide spawning biomass was estimated as 1,682,260 mt.

g Standard DEPM sampling area off California from San Diego to CalCOFI line 66.7; for the 2008 survey area off the west coast of North America from about 31°N to 48.47°N latitude, spawning biomass was estimated as 135,301 (CV = 0.43).

h RSF/W for 2009 is based on S_{12} : average of day-1 and day 2 females

Table 5. Estimated 2009 adult parameters and correlations for each region and the whole area outputted from the EPM program (Chen et al. 2003).

	Average	Variance		COF	RELATIONS							
Whole Body Weight	94.347378857	10.958367687	Parameter	w	F	s	R -					
Gonad Fee Weight	89.933763776	9.6793531474				0.5535055			COR	RELATIONS		
Batch fecundity	24236.059148	2476780.0094	Whole - Body Weight (W))	0.93350517	-0.55/5255	-0.1128					
Spawners, Day 0	0.1581632653	0.0051885145	Batch Fecundity (E)			-0 3897159	-0 1390	<u>Parameter</u>	w	F	S	<u> </u>
Spawners Day 1	0.1406252214	0.0005686459	SI	pawners Ave	(1+2)	0.3097139	0.1550	Whole - Body Weight (W)		0.95755022	-0.1284791	-0.3569017
Sex Ratio	0.5639930694	0.0025579735	Fraction Spawning (S)				0.26514					
Spawners Ave (1+2)	20.373664531							Batch Fecundity (F)			-0.2711574	-0.4236005
Number of Sets	15		Sex Ratio (R)					Fraction Spawning (S)				0.03862498
		9 										
								Sex Ratio (R)				
		Whole	e area				R	legion 2				
	Statistic Res	ults:										
)	Average	Variance										
Whole Body Weight 🛙	112.40387620	17.943259872		сс	ORRELATIONS							
Gonad Fee Weight	106.93256424	15.638148064										
Batch fecundity	29789.625833	2784107.5839	<u>Parameter</u>	w	F	S	F	<u>R</u>				
Spawners, Day 0).1755888651	0.0023525602	Whole - Body Weight (\	N)	0.98009752	-0.4268618	-0.028	2056				
Spawners Day 1	0.1098266439	0.0002709884										
Sex Ratio	0.6021279075	0.0005465396	Batch Fecundity (F)	Spawners Av	ve (1+2)	-0.4360751	-0.038	5191				
Daily specific fecundity	17.525895972											
Number of Sets	29		Fraction Spawning (S)				0.1384	108A				
			Sex Ratio (R)									

Region 1

Table 6. Pacific sardine female adult parameters for surveys conducted in the standard daily egg production method (DEPM) sampling area off California (1994 includes females from off Mexico).

		1994	1997	2001	2002	2004	2005	2006	2007	2008	2009
Midpoint date of trawl survey		April 22	March 25	May 1	April 21	April 25	April 13	May 2	April 24	April 16	April 27
Beginning and ending dates of positive collections		04/15- 05/07	03/12- 04/06	05/01- 05/02	04/18- 04/23	04/22- 04/27	03/31- 04/24	05/01- 05/07	04/19- 04/30	04/13- 04/27	04/17- 05/06
N collections with mature females		37	4	2	6	16	14	7	14	12	29
N collection within Region 1		11	4	2	6	16	6	2	8	4	15
Average surface temperature (°C) at collection locations		14.36	14.28	12.95	12.75	13.59	14.18	14.43	13.3	12.4	12.93
Female fraction by weight Average mature female weight (grams):	R	0.538	0.592	0.677	0.385	0.618	0.469	0.451	0.515	0.631	0.602
with ovary	$\mathbf{W}_{\mathbf{f}}$	82.53	127.76	79.08	159.25	166.99	65.34	67.41	81.62	102.21	112.40
without ovary	Wof	79.33	119.64	75.17	147.86	156.29	63.11	64.32	77.93	97.67	106.93
Average batch fecundity ^a (mature females, oocytes estimated)	F	24283	42002	22456	54403	55711	17662	18474	21760	29802	29790
Relative batch fecundity (oocytes/g)		294	329	284	342	334	270	274	267	292	265
N mature females analyzed		583	77	9	23	290	175	86	203	187	467
N active mature females		327	77	9	23	290	148	72	187	177	463
Spawning fraction ^b of mature females ^c Spawning fraction of active females ^d	S S _a	0.074 0.131	0.133 0.133	0.111 0.111	0.174 0.174	0.131 0.131	0.124 0.155	0.0698 0.083	0.114 0.134	0.1186 0.1187	0.1098 0.1108
Daily specific fecundity	<u>RSF</u> W	11.7	25.94	21.3	22.91	27.04	15.67	8.62	15.68	21.82	17.53

^a 1994-2001 estimates were calculated using F_b = -10858 + 439.53 W_{of} (Macewicz et al. 1996), 2004 used F_b = 356.46 W_{of} . (Lo and Macewicz 2004), 2005 used F_b = -6085 + 376.28 W_{of} (Lo and

Macewicz 2006), 2006 used $F_b = -396 + 293.39 W_{of}$ (Lo et al. 2007a); 2007 used $F_b = 279.23 W_{of}$. (Lo et al. 2007b), and 2008 used $F_b = 305.14 W_{of}$. (Lo et al. 2008).

^b In 1994, 1997, 2004, 2005, 2007, and 2008 spawning fraction (S_B) calculation used the number of females spawning the night before capture (night B) and the adjusted number of mature females, 2001 used a female spawning on the night of capture, 2002 used the average of females spawning 2 nights before capture (night A) and those spawning the next night (night D), and 2006 used the average of night B and Night A spawning females

^c Mature females include females that are active and those that are postbreeding (incapable of further spawning this season).

^d Active mature females are capable of spawning and have ovaries containing oocytes with yolk or postovulatory follicles less than 60 hours old.

Calendar year	Season	Region	¹ <i>P₀</i> /0.05 m² (cv)	<i>Z</i> (CV)	² RSF/W based on S ₁	³ RSF/W based on S ₁₂	⁴ Area (km²)	⁵ Spawning biomass (cv)	S. biomass (Sum of R1andR2) (cv)	S. biomass females (cv	total egg productio n (TEP)	Mean temperature (°C) for positive eggs	Mean temperature (°C) from Calvet
1986(Aug)	1986	⁶ S	1.48(1)	1.59(0.5)	38.31	43.96	6478	4362 (1.00)		2632 (1)	9587.44		
		Ν	0.32(0.25)		8.9	13.34	5333	2558 (0.33)		1429 (0.28)	1706.56		
		whole	0.95(0.84)		23.61	29.89	11811	7767 (0.87)	6920 (0.64)	4491 (0.86)	11220.45	18.7	18.5
1987(July)	1987	1	1.11(0.51)	0.66(0.4)	38.79	37.86	22259	13050 (0.58)		8661 (0.56)	24707.49		
		2	0				15443	0		0	0		
		whole	0.66(0.51)		38.79	37.86	37702	13143 (0.58)	13050 (0.58)	8723 (0.56)	25637.36	18.9	18.1
1994	1993	1	0.42(0.21)	0.12(0.91)	11.57	11.42	174880	128664 (0.30)		69065 (0.30)	73449.6		
		2	0(0)	-			205295	0		0	0		
		whole	0.193(0.21)		11.57	11.42	380175	128531 (0.31)	128664 (0.30)	68994 (0.30)	73373.775	14.3	14.7
2004	2003	1	3.92(0.23)	0.25(0.04)	27.03	26.2	68204	204118 (0.27)		126209 (0.26)	267359.68		
		2	0.16(0.43)		27.03	26.2	252416	30833 (0.45)		19065 (0.44)	40386.56		
		whole	0.96(0.24)		27.03	26.2	320620	234988 (0.28)	234951 (0.24)	145297 (0.27)	307795.2	13.4	13.7
2005	2004	1	8.14(0.4)	0.58(0.2)	31.49	25.6	46203	293863 (0.45)		161685 (0.42)	376092.42		
		2	0.53(0.69)		3.76	3.2	207417	686168 (0.86)		298258 (0.89)	109931.01		
		whole	1.92(0.42)		15.67	12.89	253620	755657 (0.52)	980031 (0.62)	359209 (0.50)	486950.4	14.21	14.1
2007	2006	1	1.32(0.2)	0.13(0.36)	12.06	13.37	142403	281128 (0.42)		136485 (0.36)	187971.96		
		2	0.56(0.46)		24.48	23.41	213756	102998 (0.67)		61919 (0.62)	119703.36		
		whole	0.86(0.26)		15.68	16.17	356159	380601 (0.39)	384126 (0.36)	195279 (0.36)	306296.74	13.7	13.6
2008	2007	1	1.45(0.18)	0.13(0.29)	57.4	53.89	53514	29798 (0.20)		22642 (0.19)	77595.3		
		2	0.202(0.32)		13.84	12.6	244435	78359 (0.45)		43753 (0.42)	49375.87		
		whole	0.43(0.21)		21.82	20.31	297949	126148 (0.40)	108157 (0.33)	79576 (0.35)	128118.07	13.1	13.1
2009	2008	1	1.76(0.22)	0.25(0.19)	19.50	20.37	74966	129520 (0.31)		73048 (0.29)	131940.16		
		2	0.15(0.27)		14.25	14.34	199929	41816 (0.38)		26114 (0.38)	29989.35		
		whole	0.59(0.22)		17.01	17.53	274895	185084 (0.28)	171336 (0.25)	111444 (0.27)	162188.05	13.6	13.5

Table 7. The spawning biomass related parameters: daily egg production/ $0.05m^2$ (P_0), daily mortality rate (z), survey area (km²), daily specific fecundity (RSF/W), spawning biomass, total egg production (TEP) and sea surface temperature for 1986, 1987, 1994 and 2004-2009

1: P_0 for the whole is the weighted average with area as the weight.

2. The estimates of adult parameters for the whole area were unstratified and RSF/W was based on original S₁ data of day-1 spawning females. For 2004, 27.03 was based on sex ratio = 0.618 while past biomass used RSF/W of 21.86 based on sex ratio = 0.5.(Lo et al. 2008)

3. The estimates of adult parameters for the whole area were unstratified. Batch fecundity was estimated with error term. For 1987 and 1994, estimates were based on S₁ using data of day-1 spawning females. For 2004, all trawls were in region 1 and value was applied to region 2,

4. Region 1, since 1997, is the area where the eggs/min from CUFES ≥1 and prior to 1997, is the area where the eggs/0.05m² >0 from CalVET tows

5: For the spawning biomasses, the estimates for the whole area uses unstratified adult parameters

6. 1986: Within southern and northern area, the survey area was stratified as region1 (eggs/0.05m2>0 with embedded zeros) and region 2 (zero catch)



Figure 1. Location of Pacific sardine eggs from CalVET, a.k.a. Pairovet; (solid circle denotes positive catch and open circle denotes zero catch) and from CUFES (stick denotes positive collection) in 2009. Trawl locations (solid star is catch with sardine adults and open star is catch without sardines). The numbers on line 95.0 are CalCOFI station numbers. Region 1 is stippled area.



Figure 2. Pacific sardine eggs per 0.05 m^2 for each developmental stage for April 15-May 9, 2009. Symbols: o = Region 1 and x = entire survey area.



Figure 3. Locations of Pacific sardine yolk-sac larvae from CalVET (or Pairovet; circle and triangle) and from Bongo (circle and square) in 2009. Solid symbols are positive and open symbols are zero catch.



Figure 4. Batch fecundity (F_b) of *Sardinops sagax* as a function of female body weight $(W_{of},$ without the ovary) for 65 females taken during April-May 2009. The batch was estimated from numbers of hydrated or migratory-nucleus-stage oocytes.



Figure 5. Embryonic mortality curve of Pacific sardine. Staged egg data were from CalVET and yolk-sac larval data were from CalVET and Bongo in 2009. The intercept, 1.69, is the estimate of daily egg production before correction for bias.



Figure 6. Catch ratio of eggs/min from CUFES to eggs/0.05m² from CalVET during April – May 2009.



Figure 7. Length distribution and mean length of Pacific sardines caught in the 2009 and 2008 survey. Males indicated by dotted bars and females by solid bar.

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