EGG PRODUCTION AND SPAWNING BIOMASS OF PACIFIC SARDINE (*SARDINOPS SAGAX*) IN 1994, DETERMINED BY THE DAILY EGG PRODUCTION METHOD

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ABSTRACT

The daily egg production method (DEPM) was used to compute spawning biomass of Pacific sardine in a 380,175 km^2 (111,081 n.mi.^{2}) area from San Ignacio Lagoon, south of Punta Abreojos, Baja California Sur, to San Francisco, California, during April–May 1994. The estimated spawning biomass was 111,493 MT (CV = 0.32) with an approximated 95% confidence interval (40,000 MT, 182,800 MT). Daily egg production in the survey area was 0.169 eggs/0.05 m^2/day (CV = 0.22), and daily specific fecundity was 11.53 eggs/gm/day. Estimates for adult parameters were: sex ratio, 0.53 (CV = 0.067); average female weight, 82.49 gm (CV = 0.071); spawning frequency, 0.073 (CV = 0.23); and average batch fecundity, 24,282.52 (CV = 0.11). We estimated peak spawning time for Pacific sardine (9:00 p.m.) and coefficients in a temperature-dependent egg-development model. Egg density in 1994 was similar to that in 1986, indicating that the increase in spawning biomass during 1986–94 was due to expansion of spawning area rather than to increased density of spawners. Most of the eggs collected were found in waters off California and were distributed along temperature gradients formed by upwelling. Surface temperatures of about 13.8°C seemed to limit the inshore distribution of eggs. Food supply, rather than temperature, may have limited the offshore distribution.

INTRODUCTION

The Pacific sardine fishery began to collapse in the early 1950s, and the population declined by the mid-1970s to less than 10,000 MT, or about 1% of the estimated stock in the 1930s (Barnes et al. 1992). The population began to recover in the late 1970s (Watson 1992), and in the 1980s the wetfish fishery began to catch sardine incidentally with mackerel and anchovy (Barnes et al. 1992; Wolf 1992). The sardine population in California waters has increased steadily since 1983 (Deriso et al. 1996).

The daily egg production method (DEPM; Lasker 1985) was first used to estimate sardine spawning biomass off California in 1986–88 when the California Department of Fish and Game (CDFG) conducted surveys off southern California (Wolf 1988a, b; Scannell et al. 1996; table 1). Results from the CDFG spawning biomass surveys were used in conjunction with other information to manage the sardine fishery in U.S. waters (Wolf and Smith 1985, 1986; Wolf 1992).

TABLE 1
Estimates of Egg Production Rates and Adult Reproductive Parameters for Daily Egg Production Method Surveys, 1986–88, 1994

	1986[a]				
Parameters	North	South	1987[b]	1988[c]	1994
Egg production (P_0) (eggs/0.05 m^2/day)	0.276 (.557)[d]	0.513 (.322)	0.657 (.945)	0.33 —	0.169 (0.22)
Area of survey (A) (km^2)	6,616	10,774	37,605	44,339	380,175
Average female weight (W) (gm)	199.9	154.8	163.8	166.3	82.5 (0.07)
Batch fecundity (F)	71,382 (.049)	51,743 (.086)	62,289 (.111)	61,147 (.066)	24,282.52 (0.11)
Spawning fraction (S) (fraction of mature females spawning per day)	.038 (.467)	.189 (.283)	.125 (.062)	.144 (.182)	.0729 (.23)
Sex ratio (R)	.559 (.117)	.603 (.052)	.664 (.062)	.493 (.128)	.537 (.067)
Spawning biomass (B_s) (metric tons)	4,756 (.792)	2,903 (.349)	15,685 (.912)	13,514 —	111,493 (.32)
Daily egg mortality (Z)	Fixed at .05	Fixed at .05			.12 (.97)

[a]Scannell et al. 1996 [b]Wolf 1988a [c]Wolf 1988b [d]Coefficients of variation in parentheses

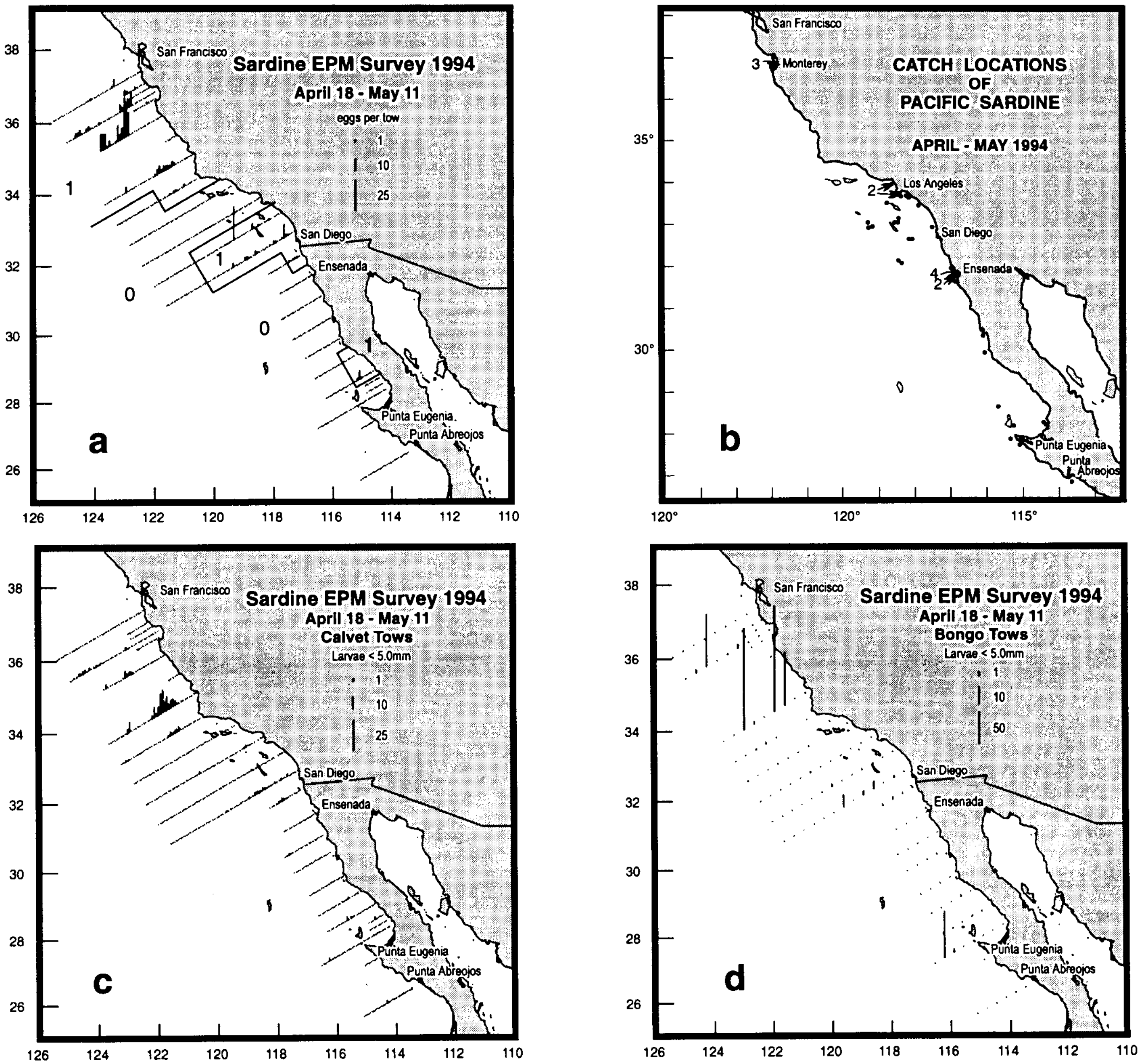

Figure 1. Areas sampled during April–May 1994 daily egg production survey for Pacific sardine. *a*, CalVET stations and egg catches. *b*, Locations for adult samples. *c*, CalVET stations and yolk-sac larval catches. *d*, Bongo stations and yolk-sac larval catches.

In 1994, the National Marine Fisheries Service (NMFS), CDFG, and Instituto Nacional de la Pesca (INP), Mexico, conducted a joint sea survey using the DEPM to assess the spawning biomass of Pacific sardine. The area surveyed extended from San Ignacio Lagoon, south of Punta Abreojos, Baja California Sur, to San Francisco, California (Arenas et al. 1996).

In this paper, we describe the plankton survey design, location of adult samples (Macewicz et al. 1996), the spatial distribution of sardine eggs, and relations with oceanic conditions. We also estimate peak spawning time for Pacific sardine, coefficients in a temperature-dependent egg-development model, daily egg production, egg mortality, and spawning biomass. Macewicz et al. (1996) describe procedures for sampling adults captured in association with the plankton survey and estimate reproductive parameters for adult sardine used to compute the spawning biomass.

MATERIALS AND METHODS

Survey Design

The plankton survey, April 18–May 11, 1994, covered 380,175 km^2 (111,081 n.mi.^{2}) from Punta Abreojos, Baja California Sur, in Mexico to San Francisco, California (table 1, figure 1a). CalVET[1] and bongo nets were used to collect plankton samples (Smith and Richardson 1977; Smith and Hewitt 1985). The survey extended 180 n.mi. offshore in U.S. waters and 80 n.mi. offshore in Mexican waters. The survey grid followed California Cooperative Oceanic Fisheries Investigations (CalCOFI) track lines (east-west transects) at 40-n.mi. spacing. On each line, the distance between stations was 4 n.mi. for CalVET net tows and bucket temperature measurements (except off Monterey, where three short lines were added), 20 n.mi. for bongo net tows (Smith and Richardson 1977; Lasker 1985), and mostly 40 n.mi. for conductivity temperature depth profiler (CTD) casts. The survey was conducted during the primary spawning period for sardine as determined from historical data (Ahlstrom 1966; Hernández-Vázquez 1995).

Two ships were used to collect ichthyoplankton data. The RV *McArthur* started just south of San Francisco on April 18 and ended in San Diego on May 10, covering an area of 253,850 km^2 (CalCOFI lines 63.3 to 93.3). The RV *El Puma* started at Punta Abreojos on April 20 and ended at Ensenada on May 7, covering an area of 126,325 km^2 (CalCOFI lines 130 to 96).

Three research vessels, RV *Mako* (CDFG), RV *David Starr Jordan* (NMFS), and RV *BIP XII* (INP), collected adult sardines (Macewicz et al. 1996). The *David Starr Jordan* and *Mako* used a high-speed midwater trawl (Dotson and Griffith 1996). The *BIP XII* also used a midwater trawl. Also, adult sardine samples were collected from commercial purse seiners. Most adult samples were from the coastal areas or around islands (figure 1b, table 2).

Oceanographic Measurements

CTD casts were made to a nominal depth of 500 m (depth permitting). A Sea-Bird Electronics, Inc. model SBE 911 was used aboard the R/V *McArthur* (calibrated by the Northwest Regional Calibration Center), and a model SBE 19 was used aboard *El Puma*. The SBE 911 data was processed by standard Sea-Bird Seasoft processing software. The data collected by the SBE 19 had sporadic spikes in the conductivity channel (roughly 0.1 to 0.2 Siemens/m) and excessive hysteresis between the down and up casts. Both the conductivity and calculated salinity from the SBE 19 were filtered to reduce the spiking. In addition, the down and up cast data were averaged to eliminate hysteresis. The resulting data were adequate to describe oceanographic conditions.

[1]The diameter of the CalVET net frame is 25 cm; the tow is vertical to minimize the volume of water filtered per unit depth; the mesh size is 0.150 mm, and the depth of tow is 70 m. The diameter of the bongo net frame is 71 cm; the tow is oblique at a 45° wire angle; the mesh size is 0.505 mm; with 300 m of wire out, the depth of tow is 210 m.

TABLE 2
Numbers of Trawl and Purse Seine Samples in U.S. and Mexican Waters Used to Estimate Adult Reproductive Parameters for Pacific Sardine during 1994

		U.S.	Mexico	Total
Trawl	Total	35	34	69
	Usable	13	6	19
Purse seine	Total	11	9[a]	20
	Usable	11	7	18
Total	Total	46	43	89
	Usable	24	13	37

[a]One purse seine sample contained only anchovy.

Sorting and Egg Staging

Sardine eggs were sorted from the plankton and identified on the basis of characteristics described by Ahlstrom (1943) and Miller (1952). Each sample of eggs was placed in a watch glass with water and examined with a dissecting microscope. Eggs were assigned to one of 11 stages based on sequential morphological stages that occur during embryogenesis. Stage criteria were modified from those used for northern anchovy, *Engraulis mordax* (Moser and Ahlstrom 1985). These modified criteria were easier to interpret and more practical than those originally described for Pacific sardine eggs by Ahlstrom (1943).

The use of transmitted light in identifying sardine eggs was essential, since fine structures in the egg could not be seen under reflected light. Most of the preserved eggs for the plankton samples were distorted to some degree, and some were shrunken considerably. We assumed that damage to eggs was an artifact of collection. Stages were therefore assigned to all eggs except those that were amorphous and had no morphological features. Amorphous eggs were assigned stages prorated according to the distribution of egg stages in the sample in which they occurred (Moser and Ahlstrom 1985). Staging criteria used in this study are described briefly below (figure 2).

Stage I: Cell division not yet begun; protoplasm accumulated at one pole of the egg or distributed around granular yolk; the perivitelline space may be small to large; the average diameter of the egg shell (in live eggs, Miller 1952) increases from 1.15 mm at fertilization to 1.38 mm at the end of stage I (ca. 1.5 hours after fertilization), to 1.83 mm at the end of stage II (10 hours after fertilization).

Stage II: Begins with the initial division of the cytoplasm into two cells (or blastomeres), first noticeable as a furrow on the cytoplasmic cap and often marked by tiny bubbles (artifacts produced during preservation) along the cleavage plane. The second cleavage plane is at right angles to the first, and subsequent synchronous divisions produce a blastodisc. Mechanical

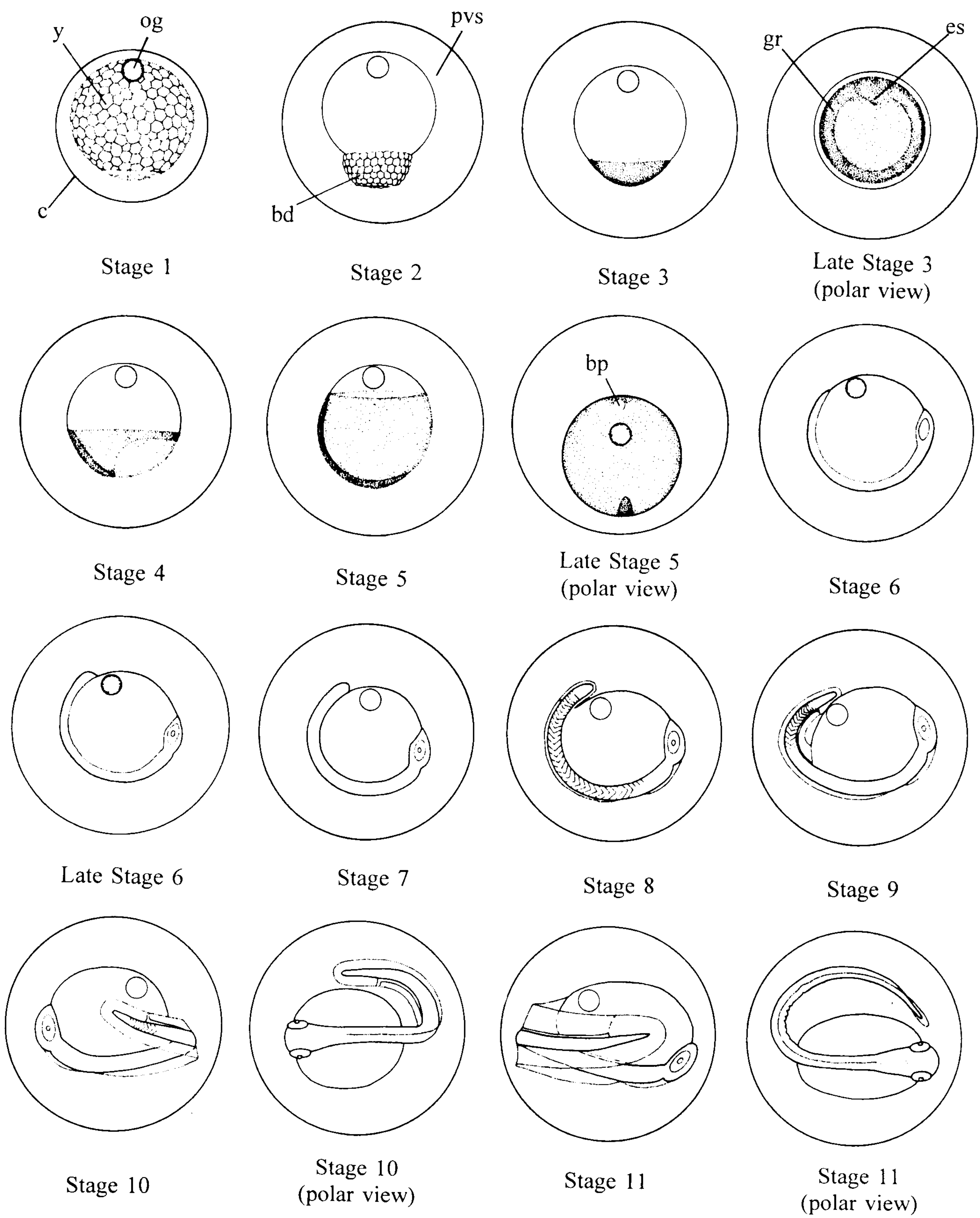

Figure 2. Sardine egg stages. Yolk segmentation is shown only in stage 1. Only a section of the myomeres (muscle segments) is shown beyond stage 8. Symbols: bd, blastodisc; bp, blastopore; c, chorion or shell; es, embryonic shield; gr, germ ring; og, oil globule; pvs, perivitelline space; y, yolk.

stress during the tow may cause the individual cells of the blastodisc to become disassociated and intermingled with yolk granules; however, blastomeres have a different refractive index from yolk granules and appear darker when viewed with transmitted light.

Stage III: Begins when cell division has progressed to the point where individual blastomeres are no longer apparent, and the blastoderm has the appearance of tissue. Late in this stage the cells at the edge of the blastodisc become thickened to form the germ ring; one part of the germ ring becomes thicker to produce an archlike structure (the embryonic shield), which is the first indication of the embryonic axis; the yolk mass begins to be covered by cell proliferation and movement of the blastoderm around the yolk (epiboly).

Stage IV: Begins when the germ ring has enclosed one-third of the yolk mass; embryo forms by further development of the embryonic shield.

Stage V: Begins when the germ ring has enclosed two-thirds of the yolk mass. As epiboly progresses, the uncovered portion of the yolk is referred to as the blastopore. At the end of the stage the brain, optic vesicles, and trunk somites of the embryo are becoming apparent.

Stage VI: Begins with closure of the blastopore at the posterior tip of the embryonic axis. By the end of the stage, somites are present along most of embryo; the brain has begun to differentiate; the lens primordia are forming in the eyes; and the tip of the tail has thickened slightly.

Stage VII: Begins when tip of tail has become rounded and has begun to separate from the yolk mass. The tail becomes pointed as it lengthens.

Stage VIII: Begins when the length of the free section of the tail (the portion that has separated from the yolk mass) is half the length of the head (head length defined for this purpose as the distance from the tip of the snout to the back of the cerebellar lobe of the midbrain).

Stage IX: Begins when the free length of the tail is equal to or greater than the head length.

Stage X: Begins when the free length of the tail has reached halfway around the yolk mass.

Stage XI: Begins when the free length of the tail has reached three-quarters of the way around the yolk mass. The tail continues to lengthen and may extend beyond the front of the head in late-stage specimens just prior to hatching; the stage ends at hatching.

Standardization of Bongo Samples

Counts of eggs and yolk-sac larvae (larvae <5 mm preserved length; Zweifel and Lasker 1976) collected in bongo tows were adjusted for percentage of the sample sorted, multiplied by a standard haul factor (SHF)[2], and adjusted to the units used for CalVET nets (number of eggs or larvae/0.05 m^3/1-m depth). We assumed no extrusion of sardine eggs from bongo tows because the sardine egg diameters (1.35–2.05 mm) were larger than the mesh size (0.505 mm). Some sardine eggs may have been destroyed by the pressure of water in the net during the tow, but we were not able to adjust for this possibility.

Yolk-sac larval production (number/day/0.05 m^2) from bongo tows was computed from the catch in each tow, corrected for larval extrusion and avoidance (Lo 1983; Lo et al. 1989) and the duration of yolk-sac larval stage (Zweifel and Lasker 1976). Extrusion and avoidance correction factors for anchovy larvae were used because this information is not available for sardine. Retention rates for anchovy and sardine larvae are similar (Lenarz 1972; Zweifel and Smith 1981).

Peak Spawning Time within a Day

Peak spawning time of Pacific sardine eggs was estimated to be 10:00 p.m. by Ahlstrom (1950) and midnight by Butler et al. (1993). To refine estimates, we used all available data for sardine eggs collected off California: during 1940–41 (Ahlstrom 1950), 1951–64 (CalCOFI surveys; Smith 1973), 1986–91 (sardine plankton surveys conducted by the CDFG), and 1994 (sardine DEPM survey).

Smith and Hewitt (1985) used 6:00 p.m. as time zero and the proportion of positive tows for anchovy in 2-hour age groups based on tows that caught anchovy eggs to determine the distribution of spawning time within a day. We estimated the peak spawning time based on the peak capture time for stage II sardine eggs. Stage I eggs would be ideal for this purpose, but few stage I eggs were found because of their patchy spatial distribution (Smith 1973, 1981). Cumulative proportions of time-of-tow for stage II eggs were computed starting at sunset (J. R. Hunter, Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, pers. comm.). We used cumulative proportions rather than cumulative abundance of stage II eggs to avoid possible bias caused by a few large catches of stage II eggs. The 50th percentile

[2]SHF is a multiplier used to convert actual catch of a net tow to the equivalent catch per unit of water filtered (catch/10 m^3/1-m depth). SHF = $10/(ab/d)$ where a is the area of the mouth of the net opening in square meters; b is the length of the tow path in meters; d is the maximum depth of tow in meters. The standardized catch is then computed as catch/10 m^3/1-m depth = actual catch * SHF (Smith and Richardson 1977; Zweifel and Smith 1981). To make catches in bongo and CalVET nets comparable, standardized catch in bongo nets was divided by 200 to obtain units of catch per 0.05 m^3/1-m depth (or catch/0.05 m^2).

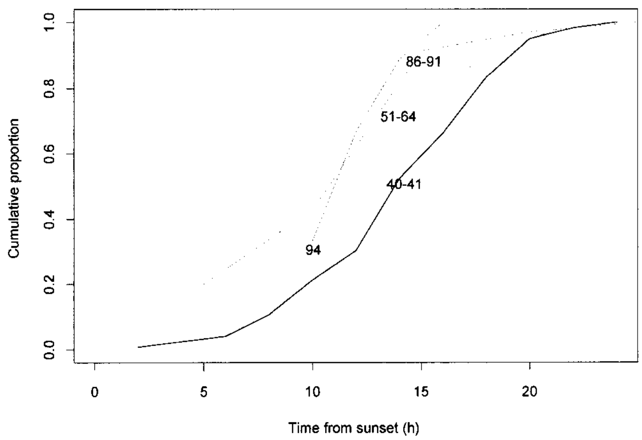

Figure 3. Cumulative proportion of time from sunset (6:00 p.m.) for stage II sardine eggs during 1940–41 (Ahlstrom 1950), 1951–64 (Smith 1973), 1986–91 (Wolf 1988a, b, 1992; Scannell et al. 1996), 1994.

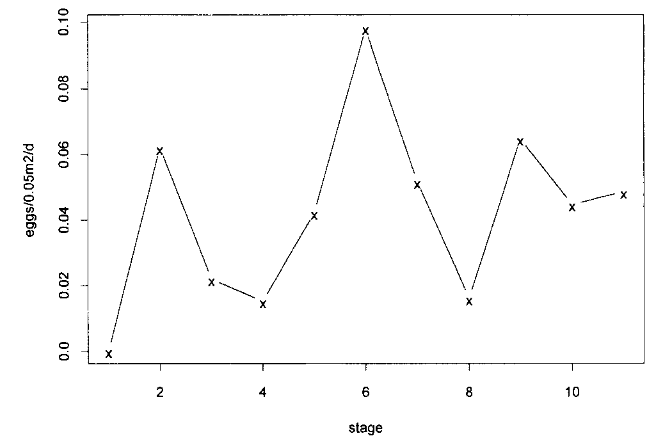

Figure 4. Mean number of Pacific sardine eggs/0.05 m^2 from both CalVET and bongo tows for each developmental stage of Pacific sardine eggs, 1994.

(median) of time from sunset was used to estimate the expected peak capture time for stage II eggs (figure 3). The expected capture time for stage II eggs minus their average age (as estimated by a temperature-dependent egg-development model; see below) approximates the peak spawning time (table 3).

Temperature-Dependent Sardine Egg-Development Model

Nakai (1962) described development rates of Japanese sardine (*Sardinops melanosticta*) eggs at temperatures of 15°, 17°, and 20°C. Zweifel and Lasker (1976) summarized the time to reach stages III, VI, VII–IX, and XI for Pacific sardine eggs at 13.5° to 17° based on field data from Ahlstrom (1950) and laboratory experiments for incubation at 11°–21° (Lasker 1964). We used all the above data sets (table 4) to model the relationship between age and developmental stage for Pacific sardine eggs at various temperatures. The model is (Lo 1985)

$$\hat{y}_{i,t} = \alpha e^{\beta_1 t + \beta_2 i + \beta_{12} i t} i^{\gamma} \tag{1}$$

where $\hat{y}_{i,t}$ is the average age (h) of the ith-stage sardine eggs at temperature t°C; i is egg stage, i = 1,..., 12; and stage 12 represents hatching. All coefficients were estimated by nonlinear regression (Chambers and Hastie 1992) assuming additive errors. The coefficient β_{12} is for the interaction between stage i and temperature t.

Egg Production (P_0) and Egg Mortality (Z)

The number of eggs and yolk-sac larvae per day per unit area, their age, and a negative exponential curve were used to estimate daily egg production, P_0, and egg mortality (Picquelle and Stauffer 1985). Sardine eggs collected from both CalVET and bongo net tows were used

TABLE 3
The Median Time from Sunset (6:00 p.m.) for Positive Tows Containing Stage II Pacific Sardine Eggs, the Corresponding Peak Time of Occurrence, Temperature, and Other Estimates from Four Data Sets

Year	1940–41[a]	1951–64[b]	1986–91[c]	1994
Median time from sunset (h)	14	11	11	12
Peak time of occurrence of stage II	8:00 a.m.	5:00 a.m.	5:00 a.m.	6:00 a.m.
Temperature (°C)	15.12[d]	15.54	16.36	13.8
Age (h)[e] of stage II	8.00	8.00	7.00	10.00
Spawning time	Midnight	9:00 p.m.	10:00 p.m.	8:00 p.m.
Positive tows	122	301	35	9
Egg production (P_0)	0.162	0.169	0.123	0.167
CV	0.40	0.22	0.32	0.22
Embryonic mortality (Z)	0.104	0.12	0.044	0.095
CV	1.96	0.97	3.22	1.11

[a]Ahlstrom 1950
[b]Smith 1973
[c]Wolf 1988a, b, 1992; Scannell et al. 1996
[d]10-m temperature
[e]Rounded to the nearest hour

TABLE 4
Stage and Age of Sardine Eggs Incubated at Various Temperatures (°C) from U.S., Japan, and Mexico Samples

Temperature (°C)	Stage[a]	Age (h)	Data sources
Japan			
20.20	3	5.9	(Nakai 1962)
20.20	4	7.9	
20.20	5	9.9	
20.20	6	12.9	
20.20	6.5	15.9	
20.23	7	18.9	
20.27	8.5	25.9	
20.34	11	33.9	
17.30	3	9.9	
17.30	4	13.4	
17.45	5	16.4	
17.51	6	21.4	
17.50	6.5	26.4	
17.51	7	31.4	
17.56	8.5	42.4	
17.46	11	56.4	
15.21	3	14.6	
15.34	4	19.6	
15.30	5	24.6	
15.24	6	31.6	
15.27	6.5	38.6	
15.28	7	46.6	
15.26	8.5	64.6[b]	
15.23	11	84.6[b]	
United States			
11	12	140	(Lasker 1964)
12	12	115	
13	12	93	
14	12	78.5	
15	12	68.1	
16	12	60.2	
17	12	53.7	
18	12	48.4	
19	12	43.2	
20	12	39.2	
21	12	34	
13.5	3	20.4	
13.5	6	41.8	
13.5	8.5	62.5	
13.5	11	82.6	
14	3	18.9	
14	6	39.1	
14	8.5	58.3	
14	11	77.2	
14.5	3	17.4	
14.5	6	36.6	
14.5	8.5	59.4	
14.5	11	72.2	
United States (continued)			
15	3	16.2	(Ahlstrom 1943)
15	6	34.3	(Zweifel and Lasker 1976)
15	8.5	50.7	
15	11	67.5	
15.5	3	14.9	
15.5	6	32.1	
15.5	8.5	47.2	
15.5	11	63.1	
16	3	13.8	
16	6	30	
16	8.5	44	
16	11	59	
16.5	6	28.1	
16.5	8.5	41.1	
16.5	11	55.1	
17	6	26.3	
17	11	51.5	
Mexico			
19.6	5	2.8	(Ramirez-Sevilla et al. 1992)
19.6	6	7.4	
19.6	7	13.4	
19.6	8	18.0	
19.6	9	18.9	
19.6	10	21.5	
19.6	11	24.8	
19.6	12	26.5	
22.0	5	2.5	
22.0	6	7.0	
22.0	7	12.0	
22.0	8	13.3	
22.0	9	15.3	
22.0	11	19.3	
22.0	12	21.3	
24.0	5	2.5	
24.0	6	6.1	
24.0	7	9.9	
24.0	8	12.0	
24.0	9	13.5	
24.0	10	16.0	
24.0	11	19.4	
24.0	12	20.0	
27.0	5	2.2	
27.0	6	5.1	
27.0	7	8.0	
27.0	8	10.0	
27.0	9	11.1	
27.0	10	14.2	
27.0	11	15.2	
27.0	12	16.0	

[a]Stages of Japanese sardine eggs with decimals are equivalent to multiple stages of Pacific sardine eggs in U.S. data, i.e., stage 6.5 indicates stages 6–7. Stage 12 is end of hatching.
[b]Not used in the analysis because of abnormally high values.

in fitting the negative exponential curve. For a station where both net tows were taken, an average of number of eggs/0.05 m^3/1-m depth for each stage was computed. Yolk-sac larvae were from bongo nets only. Few early-stage eggs were taken in either CalVET or bongo tows during this survey (figure 4), because of their patchy distribution (Smith 1973, 1981). To increase the number of age categories for constructing a mortality curve, we assumed that the mortality rates of eggs and yolk-sac larvae were the same, and we included both in a single embryonic mortality curve (Lo 1986):

$$P_t = P_0 e^{-zt} \qquad (2)$$

where P_t is the number of eggs or yolk-sac larvae produced per day per unit area at age t days; P_0 is daily egg production at age zero; and Z is the daily instantaneous mortality rate.

Age of sardine eggs was calculated based on equation 1, the peak spawning time, and time of tow (Lo 1985). Eggs were grouped by half-day categories, excluding eggs younger than 3 h old and eggs older than the expected hatching time; e.g., 3 d at 15°C (equation 1 and see later section; Smith 1973).

Age of yolk-sac larvae from fertilization was estimated from a temperature-dependent growth curve (Zweifel and Lasker 1976). The average temperature for tows with yolk-sac larvae was 14.5°C and 15.5°C in U.S. and Mexican waters. The age of yolk-sac larvae was 5 d with a duration of 3.7 d in U.S. waters, and 4.6 d with a duration of 3.18 d in Mexican waters. The duration for the yolk-sac larvae was computed from the difference between age at formation of a functional jaw and hatching time, both of which depend on temperature (Zweifel and Lasker 1976).

For sardine egg samples, the survey area was post-stratified into stratum 1 (which included the area containing positive tows), and stratum 0 (which was devoid of eggs). Stratum 1 included 64% of the U.S. survey area and 10% of the Mexican survey area (46% of the total area; figure 1a). Egg production in each half-day age group for the whole survey area was obtained as egg production at age in stratum 1 times the fraction of the total area belonging to stratum 1. The stratification was not applied to yolk-sac larvae because yolk-sac larvae are less patchy than sardine eggs.

Biomass Computation

The spawning biomass was estimated (Parker 1985) as

$$B_s = \frac{P_0 A C}{R S F / W_f} \tag{3}$$

where P_0 is daily egg production per 0.05 m^2; A is the survey area in units of 0.05 m^2; S is the proportion of mature females that spawned per day; F is the batch fecundity; R is the fraction of mature female fish by weight (sex ratio); W_f is the average weight of mature females (gm); and C is the conversion factor from g to MT. $P_0 A$ in equation 3 is the total daily egg production in the survey area, and the denominator in equation 3 is the daily specific fecundity (number of eggs/population weight (gm)/day). F, R, W, and S are adult parameters.

The variance of the spawning biomass estimate (B_s) was computed from the Taylor expansion and in terms of the coefficient of variation (CV) for each parameter estimate and covariances for adult parameter estimates (Parker 1985):

$$\begin{aligned} \text{VAR}(\hat{B}_s) = \hat{B}_s^2\, [&CV(\hat{P})^2 + CV(\hat{W})^2 + \\ &CV(\hat{S})^2 + CV(\hat{R})^2 + \\ &CV(\hat{F})^2 + 2COVS] \end{aligned} \tag{4}$$

The 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 $x_j = W$. The sign of any two terms is positive if they are both in the numerator of B_s or denominator of B_s (equation 3); otherwise, the sign is negative.

We used a ratio estimator (Cochran 1977; Picquelle and Stauffer 1985) for adult parameters F, R, W, and S:

$$\begin{aligned} \bar{y} &= \sum_{i=1}^{n} \sum_{j=1}^{m_i} \bar{y}_{ij} \Big/ \sum_{i=1}^{n} m_i \\ &= \sum_{i=1}^{n} m_i \bar{y}_i \Big/ \sum_{i=1}^{n} m_i \end{aligned} \tag{5}$$

with sample variance

$$s^2(\bar{y}) = \sum_i^n m_i^2 (\bar{y}_i - \bar{y})^2 / [\bar{m}^2 n(n-1)]$$

where y_{ij} is the measurement of the jth female fish in the ith trawl; m_i is the number of mature females; $\bar{y}_i$ is the sample mean for F, S, or W in the ith trawl; and n is number of trawls. For sex ratio (R), m_i is the sample total weight, and $\bar{y}_i$ is the sex ratio in the ith trawl.

The correlation between two adult parameter estimates, say fecundity ($\hat{F}$), and female weight ($\hat{W}$) from equation 5, was

$$correlation\ (\hat{F}, \hat{W}) = \frac{\sum_i^n m_i(\bar{F}_i - \hat{F}) k_i (\bar{W}_i - \hat{W})}{[\bar{m}\bar{k} n(n-1)] se(\hat{F}) se(\hat{W})} \tag{6}$$

where m_i and k_i are number of mature females sampled in the ith trawl for each parameter. $\bar{F}_i$ and $\bar{W}_i$ are $\bar{y}_i$ in equation 5 where se is the standard error of an adult parameter estimate.

For simplicity, all estimates will be written in this paper without the symbol ˆ. For example, $\hat{P}_0$ will be written as P_0.

RESULTS

Oceanography and Distribution of Sardine Eggs

Most sardine eggs were distributed in a narrow range of sea-surface temperatures (SST; figures 5 and 6a). Nine percent of the sardine eggs were found at SSTs of 13.7°C and below (only three eggs were found below 13.0°); sixty-five percent were found at SSTs between 13.8° and 14.5°; and the remainder were over a range from 14.6° to 16.6°. All eggs found at SST above 14.5° were within

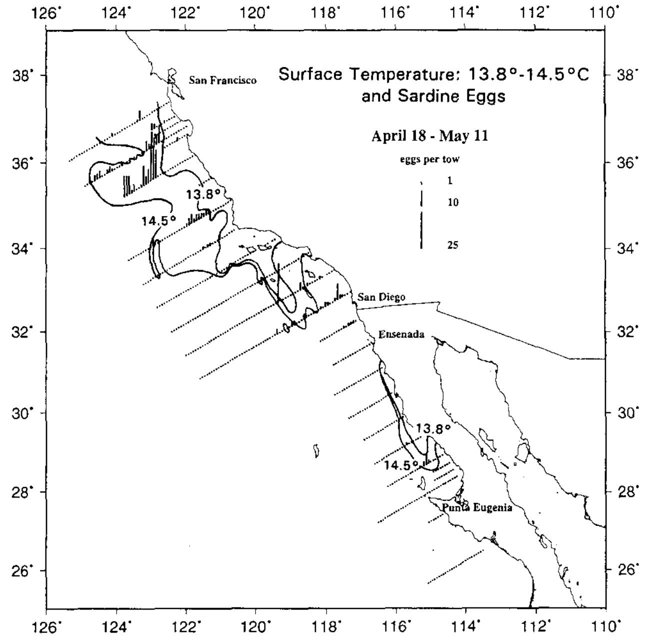

Figure 5. Pacific sardine eggs from CalVET tows and 13.8° and 14.5°C sea-surface isotherms.

and offshore of the southern portion of the Southern California Bight (SCB). The median SST at stations where sardine eggs were found was 14.3°, slightly below the temperature of 14.6° described by Lluch-Belda et al. (1991) as the lower of two peaks in the ratio of frequency distributions for SST and sardine eggs based on 39 years of CalCOFI data.

The greatest number of sardine eggs was found in a region south of Monterey Bay and associated with a filament of relatively cold water. The filament of cold water extended offshore from the coastal headlands north and south of Monterey Bay (figures 6a and 7a). The association of eggs with the offshore extension of the filament was particularly strong in samples along CalCOFI line 70 off Point Sur, where the filament coincided with a station track that extended 240 km offshore. A second, smaller concentration of eggs was associated with a smaller filament south of Point Piedras Blancas. A few sardine eggs were also found at four stations south of the coastal upwelling around Punta San Antonio (figures 5, 6a, and 7b).

Peak Spawning Time within a Day

We chose 9:00 p.m. as the peak spawning time for Pacific sardine, based on data from 1951 to 1964. Our estimate is similar to the 10:00 p.m. stated by Ahlstrom (1950). The cumulative proportion of time from sunset for stage II eggs in the 1940–41 data set was quite different than in the other three data sets (figure 3, table 3). Temperature measurements for the 1940–41 data set were made at 10-m depth. If the sea-surface temperature used in some years of the three other data sets were warmer than the temperature at 10 m, our estimate of the age of stage II eggs, based on surface temperature, would have been smaller, and the peak spawning time may have been earlier (Macewicz et al. 1996).

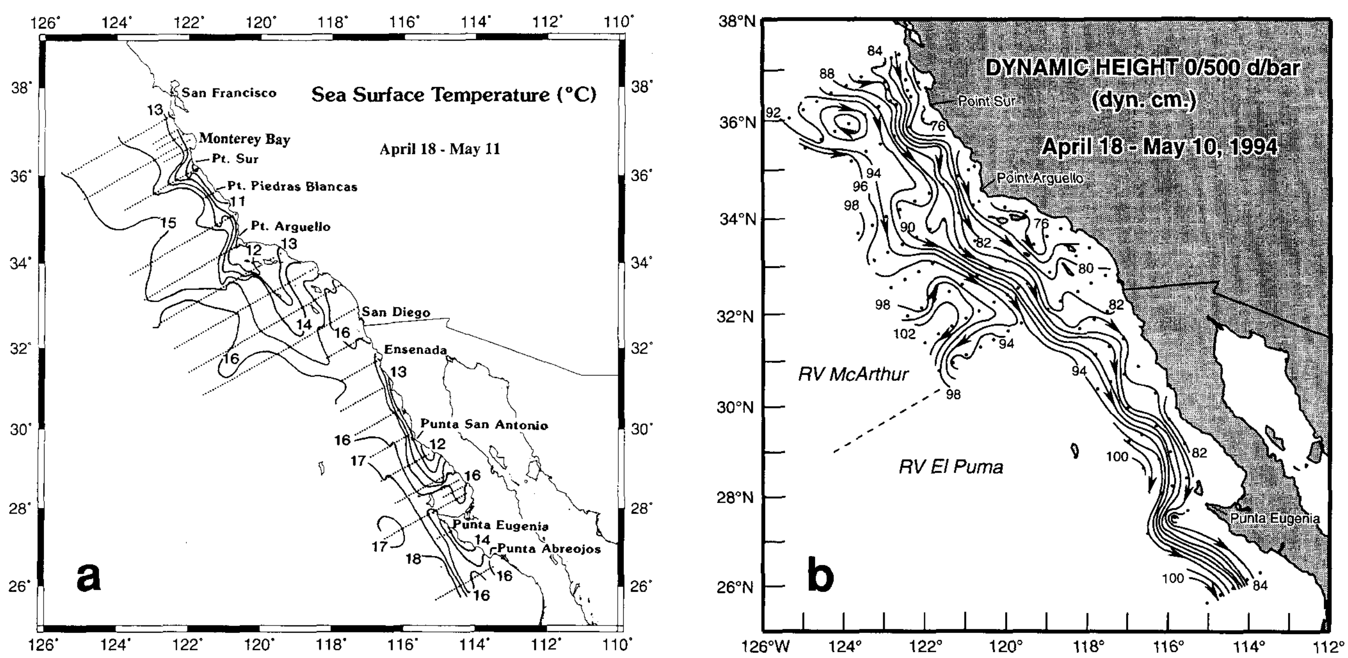

Figure 6. Oceanographic data for daily egg production method survey area: *a*, sea-surface temperature (°C), and *b*, dynamic height of the sea surface relative to a level of 500 decibars (in dynamic centimeters). *Arrows* indicate the direction of geostrophic flow.

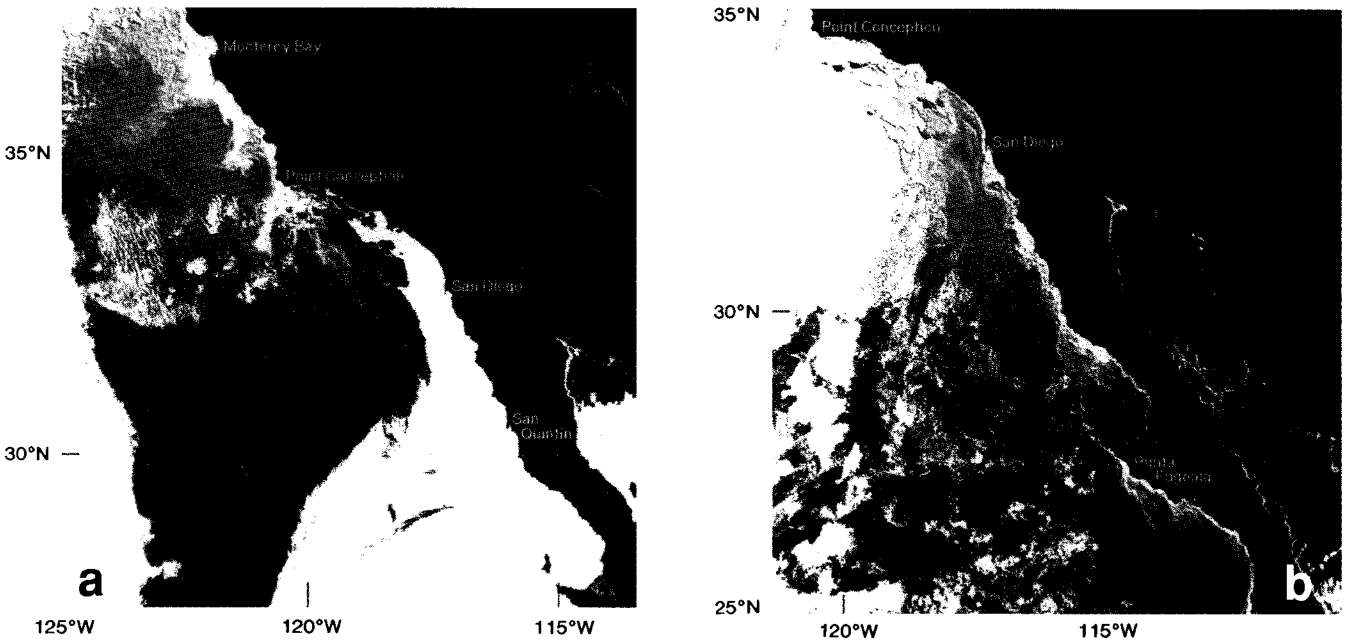

Figure 7. Infrared sea-surface temperature images from NOAA 11 channel 4 AVHRR satellite on (*a*) April 19, 1994, when the RV *McArthur* was at the western end of the northernmost line and (*b*) a combined image for April 28 and 29, 1994, when the RV *El Puma* was at the western end of the station line off Punta Eugenia. The images were provided by the *CoastWatch* node at La Jolla, California.

Temperature-Dependent Sardine Egg-Development Model

Estimates and the standard errors of coefficients for the temperature-dependent egg-development model (equation 1, figure 8) from data of Japan and United States are[3]:

Coefficient	Estimates	CV	*t* values
Intercept (α)	30.66	0.186	5.4
Stage (β_1)	−0.037	0.54	1.8
Temperature (β_2)	−0.145	0.026	38.5
Stage (γ)	1.41	0.12	8.33

The residual standard error was 3.0 on 58 degrees of freedom.

We also computed the expected age (hours) and expected peak time of occurrence for sardine eggs at different developmental stages and temperatures ranging from 10° to 22°C (table 5; Lo 1985). The expected age can be computed directly from equation 1. However, the peak time for each stage at various temperatures is a function of peak spawning time. Therefore the expected peak time, together with field data, can be used for checking the accuracy of staging of field-collected sardine eggs, as well as the accuracy of an assumed peak spawning time.

[3]Ramirez-Sevilla et al. (1992) reported the development rates of *Sardinops sagax caerulea* from 19.6° to 27°C. We were unaware of this report while we computed the spawning biomass of Pacific sardine. The following estimates of coefficients for equation 1 were computed from combined data of Japan, U.S., and Mexico, and are recommended particularly if temperature is higher than 21°C (table 4).

Coefficient	Estimates	CV	*t* values
Intercept (α)	82.832	0.4	2.47
Temperature (β_1)	−0.1139	0.35	2.80
Stage (β_2)	−0.2103	0.11	9.52
Temperature x Stage (β_{12})	0.0050	0.4	2.52
Stage (γ)	1.4024	0.15	6.55

The residual standard error was 3.82 on 88 degrees of freedom.

Embryonic Mortality Curve and Daily Egg Production

A total of 684 CalVET tows were taken, 462 off California and 222 off Mexico (figure 1a). There were 66 CalVET tows positive for sardine eggs off the United States, and 8 off Mexico (figure 1c). Bongo tows were taken at 91 stations off California and at 45 stations off Mexico (figure 1d). When CalVET and bongo tows are combined, the number of positive stations for sardine eggs was 82, of which 74 were in U.S. waters. Sardine eggs were not caught in bongo tows taken off Mexico.

The number of positive CalVET tows for yolk-sac larvae was 49 in U.S. waters and 8 in Mexican waters (figure 1c). Nineteen bongo tows in U.S. waters and 6 in Mexican waters caught yolk-sac larvae (figure 1d). The number of positive stations (CalVET and bongo) was 76, of which 62 were in U.S. waters and 14 were in Mexican waters (table 6).

The estimated daily egg production (P_0) was 0.169 eggs/0.05 m^2/day (CV = 0.22), and the estimated daily embryonic mortality rate (Z) was 0.12/day (CV = 0.97; figure 9 and tables 1 and 7). The relatively high CV of

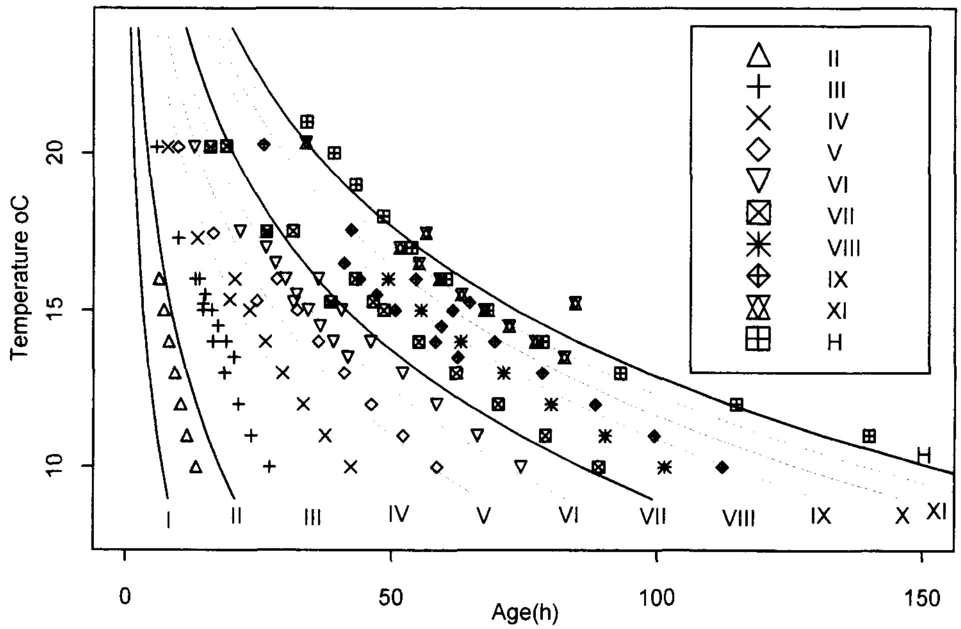

Figure 8. Age for each developmental stage of sardine eggs, based on a temperature-dependent model. Stage XII is end of hatching (H). Symbols are data for Japan and U.S. (table 4).

TABLE 5
Average Age (h) and Expected Time of Peak Occurrence for Pacific Sardine Eggs for Stages I to XI, and Temperatures between 10° and 22°C

Average age (hour)

	Stage										
Temp. (°C)	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
10	6	16	28	40	53	66	80	93	106	118	131
11	5	14	24	35	46	57	69	80	91	102	113
12	4	12	21	30	40	50	60	69	79	88	97
13	4	10	18	26	34	43	51	60	68	76	84
14	3	9	15	22	30	37	44	52	59	66	73
15	3	7	13	19	26	32	38	45	51	57	63
16	2	6	11	17	22	28	33	39	44	49	54
17	2	5	10	14	19	24	29	33	38	43	47
18	2	5	8	12	16	21	25	29	33	37	41
19	1	4	7	11	14	18	21	25	28	32	35
20	1	3	6	9	12	15	18	21	24	27	30
21	1	3	5	8	10	13	16	18	21	24	26
22	1	2	4	7	9	11	14	16	18	20	22

Expected peak time of occurrence (hour)

	Stage										
Temp. (°C)	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
10	3	13	1	13	2	15	5	18	7	19	7
11	2	11	21	8	19	6	18	5	16	3	14
12	1	9	18	3	13	23	9	18	4	13	22
13	1	7	15	23	7	16	00	9	17	1	9
14	00	6	12	19	3	10	17	1	8	15	22
15	00	4	10	16	23	5	11	18	00	6	12
16	23	3	8	14	19	1	6	12	17	22	3
17	23	2	7	11	16	21	2	6	11	16	20
18	23	2	5	9	13	18	22	2	6	10	14
19	22	1	4	8	11	15	18	22	1	5	8
20	22	00	3	6	9	12	15	18	21	00	3
21	22	00	2	5	7	10	13	15	18	21	23
22	22	23	1	4	6	8	11	13	15	17	19

Peak spawning time was assumed to be 9:00 p.m. Each entry was computed at the midpoint of temperature.

TABLE 6
Summary of Data Used to Compute Yolk-Sac (YS) Larval Production for Pacific Sardine from Bongo and CalVET Samples

	YS larvae /d/0.05 m^2	Positive tows	Total stations	% of survey area
United States				
Bongo	0.11	19	91	
CalVET	0.077	49	462	
Bongo and CalVET	0.098	62[a]	462	67
Mexico				
Bongo	0.0312	6	45	
CalVET	0.018	8	222	
Bongo and CalVET	0.024	14	222	33
Total bongo and CalVET	0.0735[b]	76	684	100

The average of standard haul factor for bongo tows was 4.8 for U.S. samples and 9.0 for Mexican samples.
[a]62 is the number of tows that caught yolk-sac larvae with either or both bongo and CalVET nets.
[b]An average weighted by survey area.

the estimate of egg mortality was due in large measure to patchiness of early-stage eggs (figure 4; Smith 1973, 1981).

Spawning Biomass

Of the 43 collections positive for adult sardine, 37 were usable; most of the positive collections were in coastal or insular areas (figure 1b). The sex ratio for sardine sampled during the survey was 0.53 (CV = 0.068); mean batch fecundity was 24,282.52 eggs/batch (CV = 0.11); spawning frequency was 0.073/d (CV = 0.23); and mean female fish weight was 82.53 gm (CV = 0.071; table 1; Macewicz et al. 1996). The daily specific fecundity was 22.53 eggs/gm/day. The correlation matrix for the adult parameter estimates (equation 3) is:

	F	S	R
W	.89	−.22	−.29
F		−.2	−.27
S			−.07

The biomass was 111,493 MT (CV = 0.32), with an approximated 95% confidence interval of 40,000 to 182,800 MT.

DISCUSSION

During April 1994, oceanographic conditions were close to seasonal norms. Upwelling as measured by Bakun's index (1973) in April 1994 was very close (within 0.5 units of standard deviation) to its long-term (1963–93) mean value from Oregon to southern Baja California. There is strong evidence that the large-scale cold-water filaments, especially common off northern and central California and Baja California in late spring and early summer, are associated with a meandering current jet (Strub et al. 1991). A strong coastal jet during the survey coincided with nearshore temperature and salinity gradients from San Francisco to Punta Abreojos (figure 6b). Sardine eggs were found mainly in waters between 13.0° and 14.5°C in association with the high-flow region of the current jet. Eggs associated with the eddy in the northwest corner of the survey (figure 7) were found in waters between 14.3° and 14.5°. Eggs found in waters of temperatures above 14.5°C were within the bight in the low-flow region. During July 1994, off Oregon, sardine eggs were found in the 1–10-m depth temperature range of 14° to 16°, which was a sharp temperature gradient (Bentley et al. 1996).

The SST range (13.8°–14.5°) in which most (65%) of the sardine eggs were found occurred within the strong SST and salinity gradients that develop immediately offshore of coastal upwelling centers during spring. With only a few exceptions, sardine avoided spawning in waters of less than 13.0°, a temperature fatal to sardine larvae in laboratory experiments (Lasker 1964). Studies conducted on the large cold-water filaments show that the current jet associated with these features is a boundary between coastal eutrophic waters and the offshore

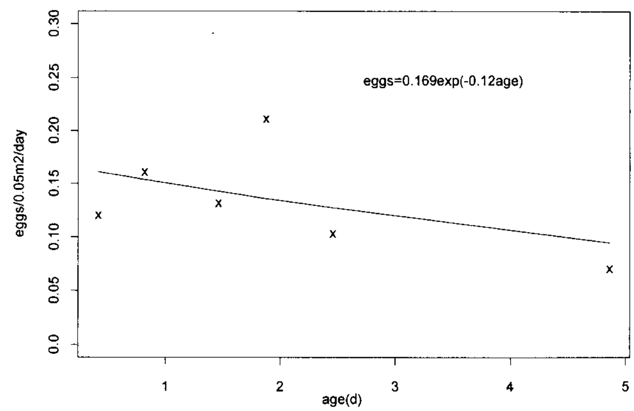

Figure 9. Embryonic mortality curve for Pacific sardine eggs and yolk-sac larvae during the daily egg production method survey, 1994.

TABLE 7
Number of Eggs and Yolk-Sac Larvae Used to Estimate the Parameters of the Embryonic Mortality Curve for Pacific Sardine during 1994 Survey

	Age (d)	Number/0.05 m^2/d	
1	0.41	0.123	Eggs
2	0.82	0.163	
3	1.46	0.134	
4	1.87	0.213	
5	2.45	0.105	
6	2.84	0.206	
7	3.35	0.105	
8	3.80	0.079	
9	4.76	0.073	Larvae

Eggs younger than 3 h and older than 2.8 d were excluded from the analysis.

oligotrophic waters (Hood et al. 1991; Mackas et al. 1991). Thus the absence of sardine eggs in warmer water offshore beyond the 14.5° isotherm suggests that the availability of food rather than temperature might limit the offshore extent of spawning. Eggs found within the SCB at temperatures above 14.5° (up to 16.6°) are in a biologically richer environment than eggs found in similar temperature in the offshore waters. Sardine eggs have been found in waters as warm as 27° (Lluch-Belda et al. 1991).

We may have underestimated daily egg production, P_0, and the spawning biomass because sardine eggs destroyed in the net were not accounted for. Future studies are needed to quantify the proportion of eggs destroyed, and to correct spawning biomass estimates for this effect.

The variance for our spawning biomass estimate may be underestimated because the peak spawning time was estimated but its variance not included in the variance estimates for egg production. We computed P_0 and Z for four spawning times: 8:00 p.m., 9:00 p.m., 10:00 p.m., and midnight. P_0 and Z were similar for all estimated peak spawning times except 10:00 p.m. (table 3). There was no trend between P_0 and estimated spawning time. We concluded that the estimates of P_0 and Z were not biased by our assumption about the spawning time. The peak spawning time for sardine estimated by Macewicz et al. (1996; 8:00–10:00 p.m.) was similar to the value we assumed.

The low abundance of sardine eggs off Mexico was probably because our survey was conducted before the peak August spawning time there (Hernández-Vázquez 1995). The low abundance of sardine eggs collected in Mexican waters during our survey does not indicate low Pacific sardine abundance there.

The CV for our spawning biomass estimate (CV = 32%) was due mostly to an uncertainty about the estimated egg production (CV = 0.22) and the estimated spawning frequency (CV = 0.23). Although 684 CalVET tows were taken in the survey, the embryonic mortality rate of 0.12/d was imprecise (CV = 0.97), primarily because eggs at young stages were not captured efficiently because of their patchy distribution (Smith 1973, 1981) and relatively short duration (Picquelle and Stauffer 1985). The patchy distribution of early-stage eggs is primarily due to the aggregation of adult females. The spatial distribution of older-stage eggs becomes less patchy because of dispersal as eggs age (Smith 1973). Smith (1973) computed number of positive tows for 6-hour age groups for sardine eggs and found that 6-hour-old sardine eggs were lowest among all age groups. Smith (1981) computed the number of tows required to estimate production for one-day categories of anchovy eggs for a given level of precision. He showed that sample size should be four times larger for day-one anchovy eggs than for day-two anchovy eggs. Similarly, early-stage sardine eggs will require more tows than later-stage eggs, due to high variance, which is a direct result of patchiness. Other potentially more efficient sampling schemes, like adaptive sampling (Thompson 1992) or Bayesian approaches, might yield more efficient and unbiased estimates of egg production for the youngest sardine eggs.

TABLE 8
Comparison of Sardine Parameters and Estimates during 1986 and 1994

	1986	1994
Area	17,390 km^2	380,175 km^2 253,850 km^2 (U.S.)
North	Point Conception	San Francisco
South	San Diego	Punta Abreojos
CalCOFI lines	80–93.3	63.3–130
Month	August	April–May
Number of CalVET tows (positives)	330 (59)	462 (66) (U.S.) 222 (8) (Mex.) 684 (74) (total)
Eggs/tow	0.78	0.7 (U.S.) 0.07 (Mex.) 0.64 (total)
Peak spawning	10:00 p.m.	9:00 p.m.
Number of positive trawls	11	24
Number of positive purse seine samples	—	19
Batch fecundity		
Intercept	−21,000	−10,585
Slope	495.67	439.53
Density of spawning biomass	0.44 MT/km^2	0.27 MT/km^2 0.4 MT/km^2 (U.S.) assuming 90% of population is in U.S. waters

We compared estimates from our survey with values obtained in 1986 by CDFG (Scannell et al. 1996), the first year when the DEPM was used to estimate the spawning biomass of sardine off California. Significant changes between parameter estimates in 1986 and 1996 may shed light on the dynamics of sardine population in this ten-year period (Wolf 1988a, b, 1992; Barnes et al. 1992).

The survey area in 1994 was 22 times larger than during the 1986 survey, and the 1986 survey covered a more inshore area (tables 1 and 8). The survey in 1994 was conducted in April–May, whereas the 1986 survey was conducted in August. The dates for each survey were based on the best estimates of the spawning season. The spawning time for California sardine has shifted from summer to spring. Based on CalVET tows only, the number of eggs/0.05 m^2 was 0.64 during 1994 (0.7 in U.S. waters) and 0.78 during 1986. Percentage of positive tows was 0.1 during 1994 (0.14 for U.S.) and 0.18 during 1986. The percentage of positive tows during

1986 was higher because the survey area was closer to shore and intentionally near the center of the spawning grounds. Egg production (P_0) was 0.169/0.05 m^2 during 1994 and 0.27–0.513/0.05 m^2 during 1986. In 1994, the estimated egg mortality was 0.12/d (CV = 0.97). An assumed value of 0.05/d was used for 1986.

Most of the adult parameter estimates were similar for 1986 and 1994, except that the average female fish weighed less in 1994 (83 gm) than in 1986 (150–200 gm; tables 1 and 8). Deriso et al. (1996) also report reductions in average weight during 1983–95. The spawning biomass and survey area for 1986 were 7,659 MT and 17,390 km^2, compared to 111,493 MT and 380,175 km^2 in 1994. If one assumes that 90% of the 1994 spawning biomass of sardines was in U.S. waters, then the density in U.S. waters during 1994 would be 0.4 MT/km^2, which is similar to 0.45 MT/km^2 in 1986. Therefore the increase in the spawning biomass of Pacific sardine from 7,659 MT in 1986 to 111,493 MT was due to the expansion of area (either spawning area or survey area) rather than to an increase in the density of spawning biomass.

ACKNOWLEDGMENTS

We thank the scientific and ships' crews of the RV *El Puma*, RV *David Starr Jordan*, RV *McArthur*, RV *Mako*, and *BIP XII* for their work during the 1994 egg production survey. We are grateful to Richard Charter and his staff at the Southwest Fisheries Science Center (SWFSC), NMFS, for plankton sorting and database management. We thank David Ambrose, Sharon Charter, Elaine Acuna, and William Watson of SWFSC for providing data on sardine egg stages needed to calculate mortality rates. We thank Jose Luis Cerecedo, Ramón Sánchez, and Guillermo Ortuño of INP-Mexico City, and Gilberto Valdéz and Erick Varela of Centro Regional de Investigación Pesquera (CRIP)-Mazatlán for plankton sorting. We thank Miguel Angel Valdéz of CRIP-Mazatlán for processing temperature data. We thank Kenneth Bliss of SWFSC for processing CTD data, Richard Cosgrove of Scripps Institution of Oceanography for supplying the *CoastWatch* satellite AVHRR images, and Larry Jacobson of SWFSC for editorial suggestions. We thank three referees for constructive reviews of the paper.

Part of this study was supported by Consejo Nacional de Ciencia y Tecnología (ICECXNA-060568) under the project "Evaluación de las Poblaciones de Sardina y Anchoveta en la Costa Occidental de Baja California."

We thank Rosa María Olvera Limas of INP for coordination between Mexico City and Mazatlán Laboratories. We thank John Hunter of SWFSC, Pablo Arenas of INP, and Walterio García of CRIP-Ensenada for coordinating work between Mexico and the United States.

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