SPAWNING BIOMASS OF PACIFIC SARDINE (*SARDINOPS SAGAX*), FROM 1994–2004 OFF CALIFORNIA

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ABSTRACT

The daily egg production method (DEPM) has been used to estimate the spawning biomass of Pacific sardine (*Sardinops sagax*) since 1986. In this paper, we document the current DEPM procedure using as an example the 2004 survey which incorporates the new procedures adopted since 1997. An adaptive allocation survey design used for sardine eggs has been successfully implemented. Yet, other issues associated with estimating spawning biomass of Pacific sardines remain. We also examine the time series of DEPM spawning biomass estimates and associated parameters from 1994 to 2004 and compare them to the spawning stock biomass (SSB) estimates derived from stock assessment models. The spawning biomass estimates off California increased from less than 10,000 mt in 1986 to 118,000 mt in 1994, to nearly 300,000 mt in 2004 and have fluctuated during the recent years. The spatial distribution of Pacific sardine eggs varied with sea surface temperature. The average fish weight doubled in the last 10 years, as has the reproductive rate.

INTRODUCTION

The spawning biomass of Pacific sardines (*Sardinops sagax*) was estimated independently for 1986[1], 1987[2], 1988[3], 1994 (Lo et al. 1996), and 1996 (Barnes et al. 1997), using the daily egg production method (DEPM: Lasker 1985). Before 1997, Pacific sardine egg production was estimated from direct CalVET[4] (CalCOFI Vertical Egg Tow) (Pairovet) plankton net sampling. Adult fish were sampled in various ways to obtain specimens for batch fecundity, spawning fraction, sex ratio, and average fish weight prior to 1996 (Lo et al. 1996; Macewicz et al. 1996)[1, 2, 3].

As the Pacific sardine population increased, the geographic distribution expanded from inshore to offshore and Pacific sardines reappeared along most of the American continent. The location of spawning biomass and the spatial distributions of Pacific sardine eggs off California vary from year to year[5, 6, 7, 8, 9, 10] partially, perhaps, due to migration (Clark and Jansson 1945). To improve the efficiency of collecting samples of Pacific sardine eggs and larvae, an experimental adaptive allocation sampling design was used in combination with the Continuous Underway Fish Egg Sampler (CUFES; Checkley et al. 1997; Checkley et al. 2000) during the 1996 ichthyoplankton survey (Lo et al. 2001; Smith et al. 2004). Since 1997, in addition to CalVET and Bongo nets, the CUFES has been used as a routine sampler for fish eggs to allocate CalVET samples, and data of sardine eggs collected with CUFES have been incorporated in the estimation procedures of the daily egg production in various ways depending on the survey design (Lo and Macewicz 2004). Since 2001, a cost-effective procedure has been adopted to calculate the DEPM biomass, using

[1]Scannel, C. L., T. Dickerson, P. Wolf, and K. Worcester. 1996. Application of an egg production method to estimate the spawning biomass of Pacific sardines off southern California in 1986. Admin. Rep. LJ-96-01. Southwest Fisheries Science Center, National Marine Fisheries Service. La Jolla, CA.

[2]Wolf, P. 1988a. Status of the spawning biomass of Pacific sardine, 1987–1988. Rep. to the legislature. Calif. Dep. Fish. Game, Mar. Res. Div. Department of Fish and Game Headquarters, Sacramento, CA.

[3]Wolf, P. 1988b. Status of the spawning biomass of Pacific sardine, 1988–1989. Rep. to the legislature. Calif. Dep. Fish. Game, Mar. Res. Div. Department of Fish and Game Headquarters, Sacramento, CA.

[4]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.

[5]Hill, K. T., M. Yaremko, L. D. Jacobson, N. C. H. Lo, and D. A. Hanan. 1998. Stock assessment and management recommendations for Pacific sardine in 1997. Admin. Rep. 98-5. Marine Region. California Department of Fish and Game.

[6]Hill, K. T., L. D. Jacobson, N. C. H. Lo, M. Yaremko, and M. Dege. 1999. Stock assessment of Pacific sardine for 1998 with management recommendations for 1999. Admin. Rep. 99-4. Marine Region, California Department of Fish and Game.

[7]Lo, N. C. H. 2001. Daily egg production and spawning biomass of Pacific sardine (*Sardinops sagax*) off California in 2001. Admin. Rep. La Jolla, LJ-01-08. Southwest Fisheries Science Center, National Marine Fisheries Service. La Jolla, CA.

[8]Lo, N. C. H. and B. J. Macewicz. 2002. Spawning biomass of Pacific sardine (*Sardinops sagax*) off California in 2002. Admin. Rep.LJ-02-40. Southwest Fisheries Science Center, National Marine Fisheries Service. La Jolla, CA, 22 pp.

[9]Lo, N. C. H. 2003. Spawning biomass of Pacific sardine (*Sardinops sagax*) off California in 2003. Admin. Rep. LJ-03-11. Southwest Fisheries Science Center, National Marine Fisheries Service. La Jolla, CA.

[10]Lo, N. C. H. and B. Macewicz. 2004. Spawning biomass of Pacific sardine (*Sardinops sagax*) off California in 2004 and 1995. Admin. Rep., LJ-04-08. Southwest Fisheries Science Center, National Marine Fisheries Service. La Jolla, CA.

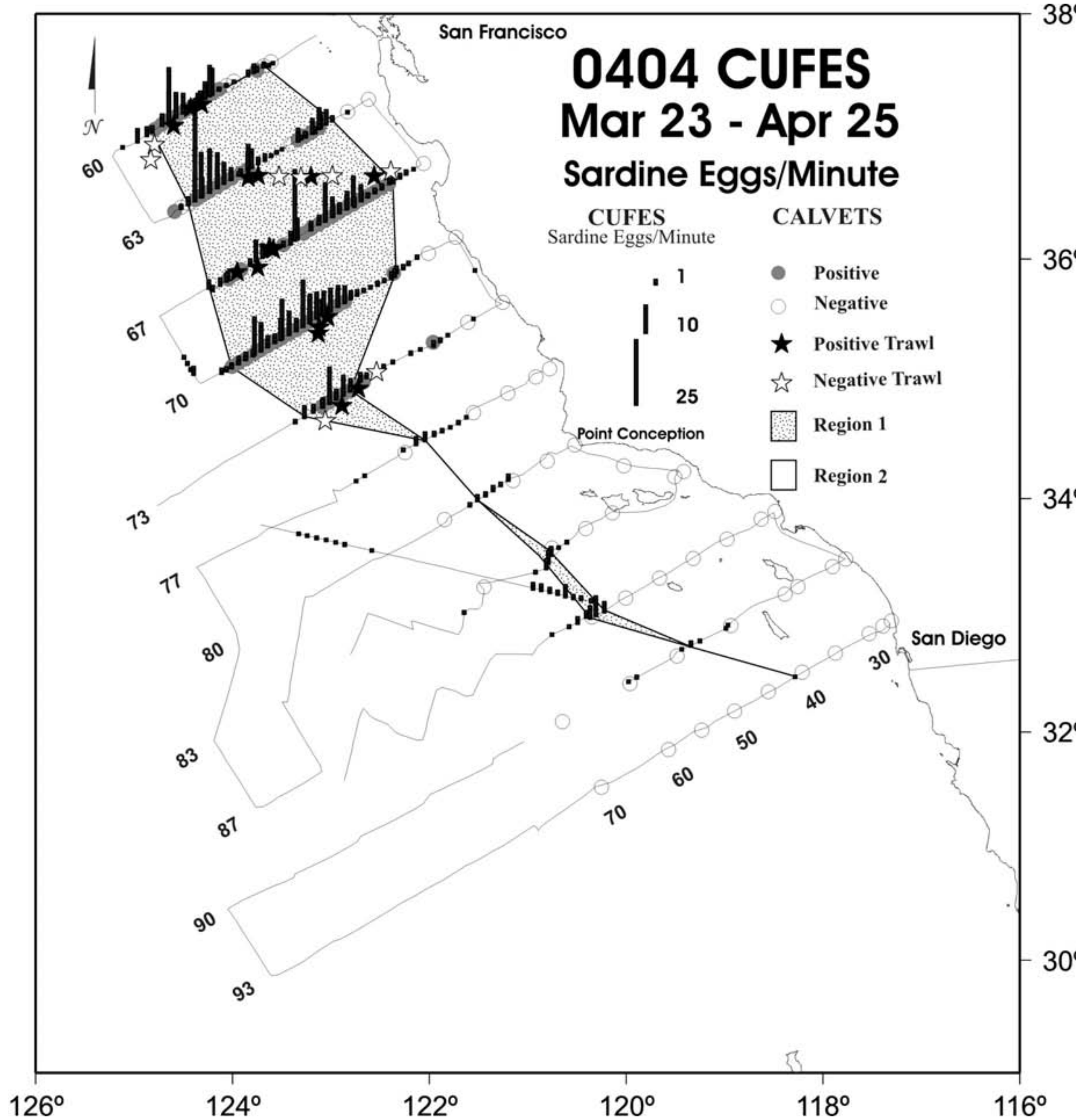

Figure 1. Pacific sardine (*Sardinops sagax*) eggs from the 2004 CalVET (a.k.a. Pairovet) tows and from the 2004 CUFES survey. The numbers on line 93 are CalCOFI station numbers. Trawl survey conducted 21–28 April 2004.

only CalVET samples of eggs and yolk-sac stage larvae in the high-density area (Region 1; fig. 1) defined by the egg density computed from CUFES collections. Data collected from eggs and larvae in Region 1 are used to estimate egg production ($P_{0,1}$) and daily instantaneous embryonic mortality rate in Region 1. The daily egg production in the low density area ($P_{0,2}$) is computed based on $P_{0,1}$ and a correction factor (Lo et al. 2001). The estimate of egg production for the whole survey area is a weighted average of $P_{0,1}$ and $P_{0,2}$.

Although the icthyoplankton survey is conducted yearly, trawl samples were collected only in 1994, 1997, 2001, 2002, and 2004. Except in 1994, sample sizes for trawls were small. For the years 1995–2001, an overall average of the spawning fraction during 1986–94 and estimates of other adult parameters in 1994 were used to estimate daily specific fecundity (number of eggs/gram weight). In 2003, the estimates of adult reproductive parameters from 2002 were used. In 2004, a full-scale survey was conducted to estimate the spawning biomass of Pacific sardine: trawl samples for reproductive output were taken aboard the F/V *Frosti*, and ichthyoplankton samples were taken aboard the R/V *New Horizon* and the NOAA ship *David Starr Jordan*.

The central objective of this paper was to document the current DEPM procedure using as an example the 2004 survey which incorporates the new procedures adopted since 1997. A second objective was to examine the time series of DEPM spawning biomass estimates and associated parameters from 1994 to 2004 and to compare them to the spawning stock biomass (SSB) estimates derived from stock assessment models. The DEPM and the stock assessment models[11] provide quite separate measures of spawning biomass; the former is based on direct measurements, while the latter is inferred from modeled relationships between size and age composition of the catch, maturity, natural mortality, and other factors, such as the DEPM estimate as one of many sets of inputs. Comparisons of these quite separate measures of spawning biomass for years prior to 1995 were examined by Deriso et al. (1996) and are useful because understanding the nature of any differences that may exist could lead to a better understanding of spawning dynamics of Pacific sardine and improved methods for determining them.

MATERIALS AND METHODS

Surveys and Data

Egg Production. CUFES was first used off California in 1996 as an experimental tool to collect eggs of small pelagic fish, like Pacific sardine, northern anchovy (*Engraulis mordax*), and jack mackerel (*Trachurus symmetricus*). It was formally used to collect sardine eggs in 1997. The survey area was post-stratified into high-density and low-density 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 during the April CalCOFI cruise each year were used to model embryonic mortality curve and thus to estimate the daily egg production of sardines in the high-density area[12]. In 1998–2000, eggs from both CalVET and CUFES were staged. Since 2001[7], the CUFES data have been used only to map the spatial distribution of Pacific sardine eggs and to allocate extra CalVET tows in high density areas.

Ichthyoplankton surveys before 1985 and since 2003 have sampled the area from San Diego to San Francisco, and since 2003 two research vessels have been used for the spring ichthyoplankton survey. In 2004, the *New Horizon* conducted the regular CalCOFI survey on CalCOFI lines 93 to 77, whereas the *David Starr Jordan* occupied the area north of line 77 (fig. 1). Bongo samples were taken on all CalCOFI survey lines (fig. 2). For the *David Starr Jordan* portion of the cruise, CalVET tows were taken at 4 nm intervals on each line whenever the egg density from each of two consecutive CUFES samples exceeded 1 egg/min, the threshold value, and were stopped when the egg density from each of two consecutive CUFES samples was <1 egg/min. The threshold value was reduced to 1 egg/min from 2 used in years prior to 2002 to increase the size of the high density area and the number of CalVET samples. This adaptive allocation sampling, similar to the 1997 survey (Lo et al. 2001; Smith et al. 2004), was used only aboard *David Starr Jordan*. The number of positive samples for eggs and larvae collected by CalVET and CUFES is quite different between Regions 1 and 2, as expected (tab. 1).

Prior to 2001, eggs collected from both CalVET and CUFES were used to model embryonic mortality. Because CUFES samples at a fixed 3 m water depth, a catch ratio (E), eggs/min = E eggs/0.05 m^2, was calculated to convert abundance of eggs from CUFES to the full water column. Egg densities from each CalVET sample and the CUFES samples taken within an hour before and an hour after the CalVET tows (a total of a two hour interval) were paired. We used a regression estimator to compute the ratio of mean eggs/min from CUFES to mean eggs/tow from CalVET, $E = U_y/U_x$, where y is the eggs/min and x is eggs/tow (Lo et al. 2001). Even though this conversion factor was no longer needed after 2000, it is informative in regard to water mixing and behavior of the spawning population.

Spatial Distribution of Sardine Eggs with Sea Surface Temperature. The CUFES collections of pelagic fish eggs are continuous and can be used to examine their spatial distribution together with oceanographic and biological data (Lynn 2002). For surveys conducted on the NOAA ships *David Starr Jordan* (1996–2004) and *McArthur* (2002), sea surface temperature and salinity were measured continuously at a depth of 2 m with a SBE-21 thermosalinograph (TSG) mounted inside a sea chest in the ships' hulls. Data from the TSG were sent to the ship's scientific computer system (SCS) which provided temperature and salinity values and GPS location related to each CUFES sample to the CUFES software. For samples collected on the R/V *New Horizon* (2004) and R/V *Roger Revelle* (2003), temperature and salinity were measured with a SBE-45 micro TSG using seawater drawn by the CUFES at a depth of 3 m. Data with GPS software were sent to a portable SCS to be stored and distributed to the CUFES software.

Data collected by the CUFES software were mapped to show relative abundance of pelagic eggs over temper-

[11]Conser, R., K. Hill, P. Cone, N. C. H. Lo, and R. Felix-Uraga. 2004. Assessment of the Pacific sardine stock for U.S. management in 2005. Submitted to Pacific Fishery Management Council. Portland, OR. http://swfsc.nmfs.noaa.gov/frd/Coastal%20Pelagics/Sardine/Sardine_Assessment_Nov_2004_revised.pdf

[12]Hill, K. T., L. D. Jacobson, N. C. H. Lo, M. Yaremko, and M. Dege. 1999. Stock assessment of Pacific sardine for 1998 with management recommendations for 1999. Admin. Rep. 99-4. Marine Region, California Department of Fish and Game.

TABLE 1
Number of Positive Tows of Sardine Eggs (*Sardinops sagax*) from CalVET, Yolk-sac Larvae from CalVET and Bongo, and Eggs from CUFES in Region 1 (eggs/min ≥1) and Region 2 (eggs/min <1) for Both *New Horizon* (NH) and *David Starr Jordan* (Jord) Cruises 0404

		Region						Total	NH	Jord
		1			2					
		Total	NH	Jord	Total	NH	Jord			
CalVET eggs	positive	63	0	63	4	0	4	67	0	67
	Total	71	1	70	53	40	13	124	41	83
CalVET yolk-sac	positive	46	0	46	4	1	3	50	1	49
	Total	71	1	70	53	40	13	124	41	83
Bongo yolk-sac	positive	9	0	9	22	15	7	31	15	16
	Total	11	1	10	75	60	15	86	61	25
CUFES eggs	positive	164	10	154	87	29	58	251	39	212
	Total	181	10	171	600	422	178	781	432	349

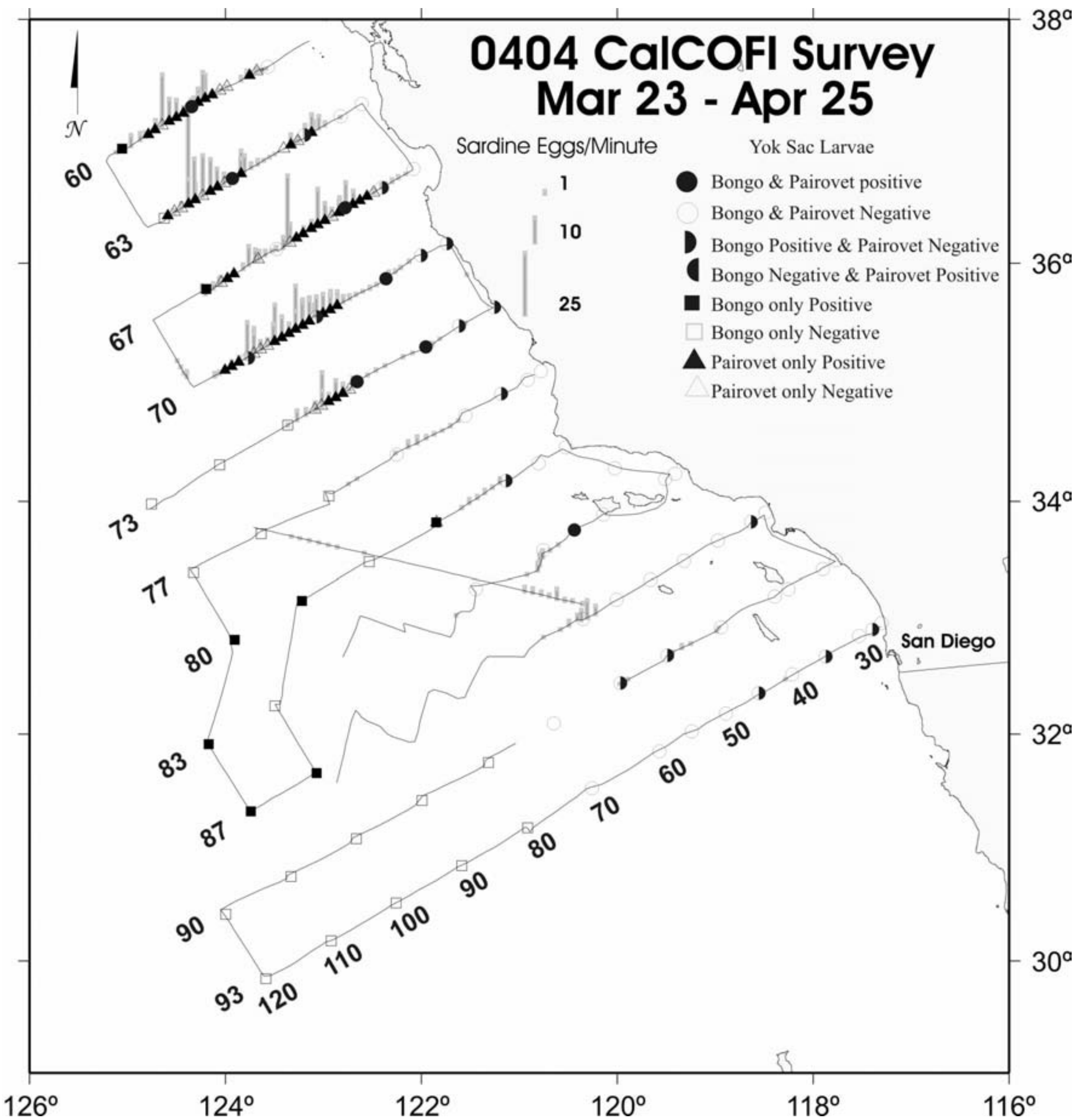

Figure 2. Sardine (*Sardinops sagax*) yolk-sac larvae from CalVET (a.k.a. Pairovet; circle and triangle) and from Bongo (circle and square) in the 2004 surveys.

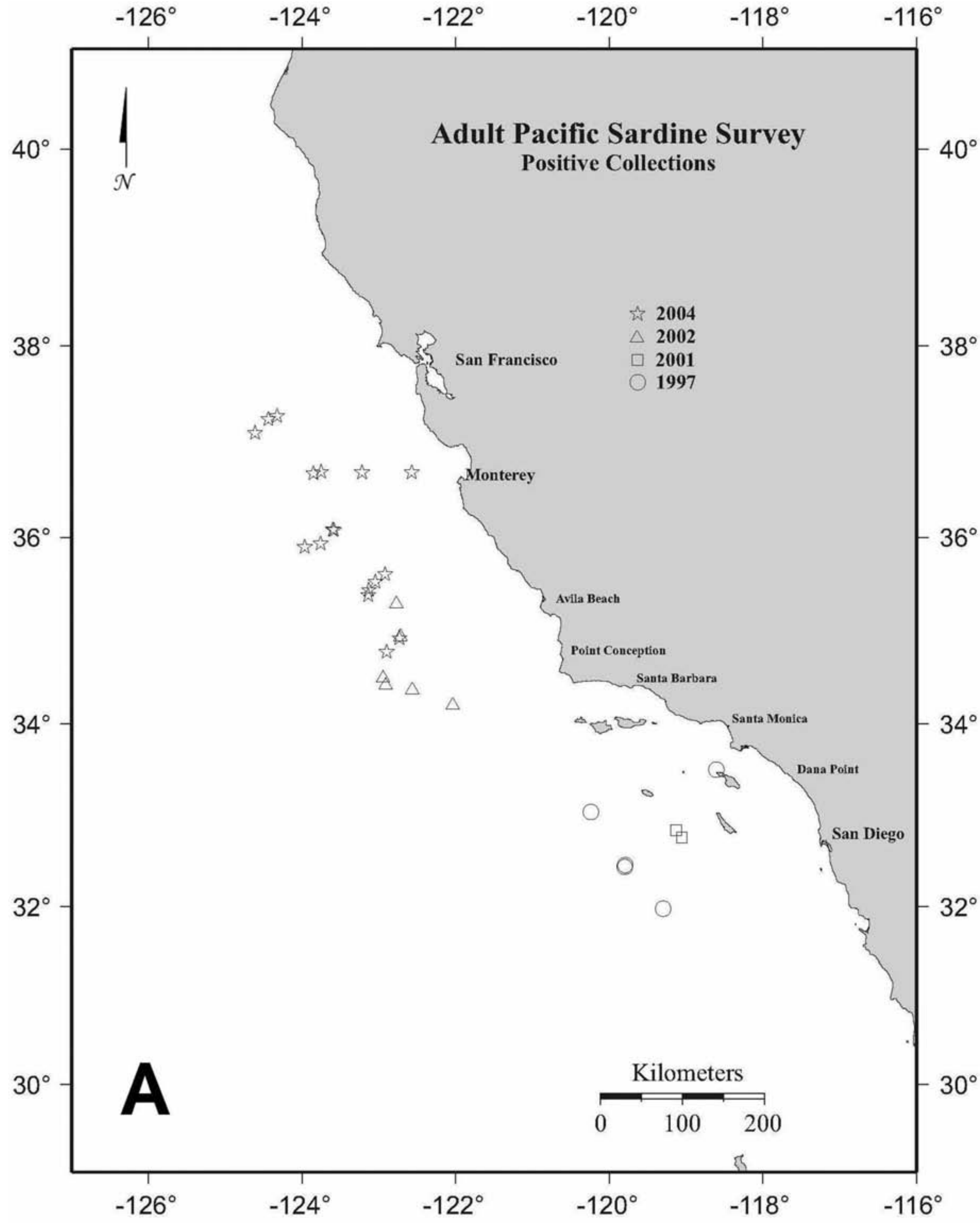

Figure 3A. Locations of adult Pacific sardine (*Sardinops sagax*) samples. A - adults taken by trawls.

ature contours. These contours were created with General Mapping Tools software using a blockmedian transformation for arbitrarily located x, y, and z values and smoothed using a surface tension adjustment (Smith and Wessel 1990).

Adult Pacific Sardine Sampling. Adult Pacific sardines were collected from San Diego to as far north as San Francisco during 1997, 2001, 2002, and 2004 (fig. 3). During 1997–2002, samples were taken aboard the NOAA ship *David Starr Jordan* using a high-speed mid-

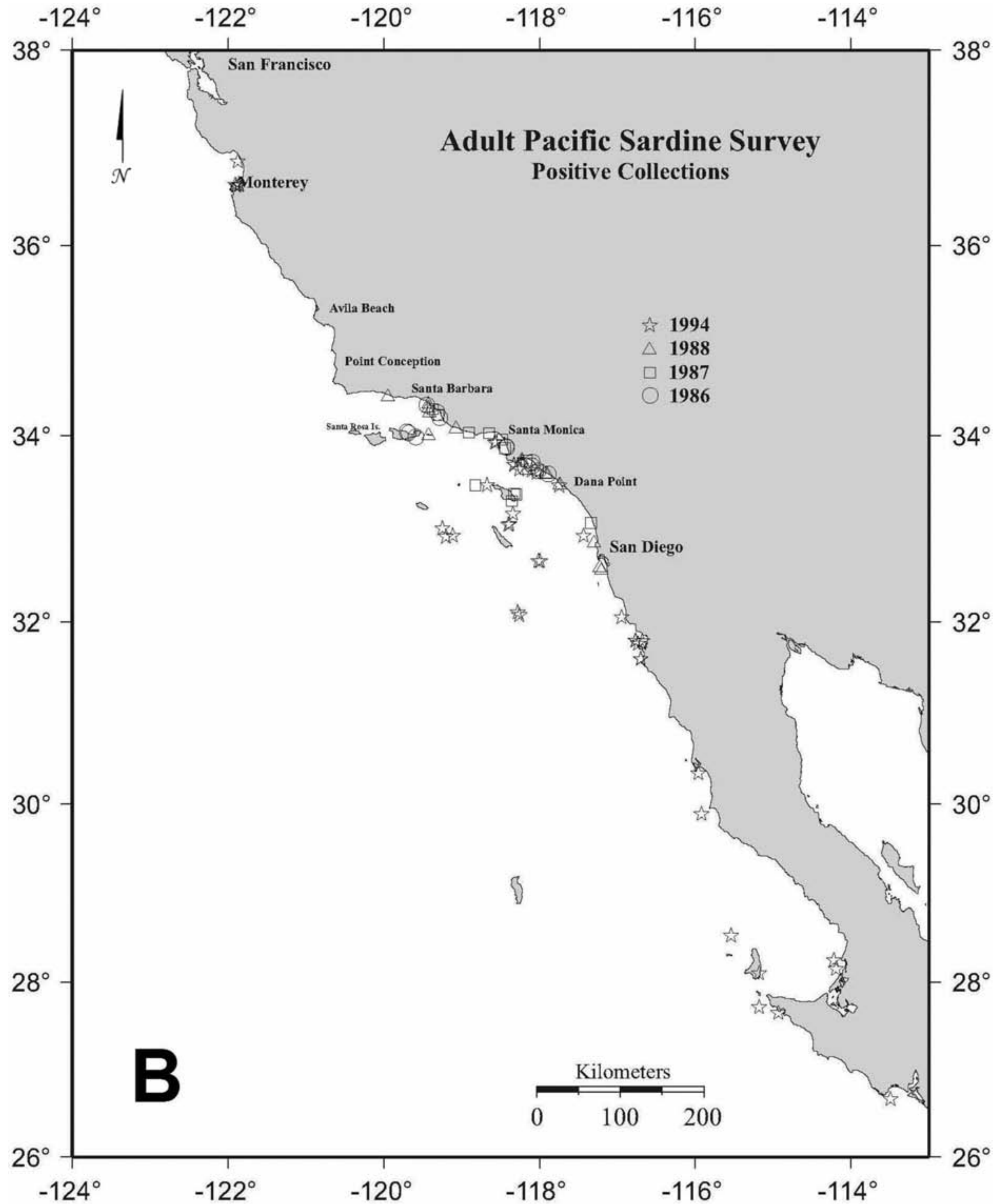

Figure 3B. Locations of adult Pacific sardine (*Sardinops sagax*) samples. B - adults taken by trawls and purse seines (1994) or only purse seines (1986–88).

water trawl, while in 2004 sardine samples were collected aboard the F/V *Frosti* using a Nordic 264 midwater trawl. Allocation of trawls was based on evidence of schools on echosounder or sardine eggs in CUFES samples. Collections of sardines were taken at night between 2017 and 0431 hours (tab. 2). Up to 50 fish randomly sampled from each collection were sexed and standard length was measured to the nearest millimeter. All fish sampled were individually weighed to the nearest gram, except in 1997 when the first 25 fish and all

TABLE 2
Proportion of Female Pacific Sardine (*Sardinops sagax*) by Weight[a] Taken in Trawls, and Collection Information during 1997, 2001, 2002, and 2004

Year	Month	Day	Time (h m)	Collection number	Latitude ˚N	Longitude ˚W	Surface temp. ˚C	Headrope depth	Random sample size	Proportion of females
1997	4	6	313	1809	33.5062	118.6067	15.8	25	18	0.281
	3	16	2121	1805	33.0407	120.2433	13.4	15	10	0.391
	4	3	2205	1807	32.4522	119.7933	13.8	20	50	0.618
	4	4	236	1808	32.4398	119.7983	13.7	37	50	0.396
	3	12	2021	1804	31.9723	119.2967	14.7	17	50	0.754
2001	5	2	340	5004	32.8393	119.1287	13.1	15	5	0.690
	5	1	2347	5003	32.7621	119.0579	12.8	25	11	0.670
2002	4	23	2017	5016	35.2867	122.7767	12.7	30	1	1.000
	4	21	2108	5010	34.9400	122.7183	12.5	30	2	0.472
	4	22	216	5011	34.4950	122.9500	13.0	31	14	0.458
	4	22	355	5012	34.4200	122.9133	13.3	31	7	0.565
	4	18	146	5006	34.3683	122.5700	12.6	25	12	0.096
	4	21	431	5009	34.2017	122.0417	12.6	30	25	0.399
2004	4	22	109	2111	37.2700	124.3280	13.3	0	50	0.565
	4	27	2049	2132	37.2402	124.4380	13.5	0	1	0.000
	4	27	2359	2133	37.0968	124.6120	14.0	0	10	0.621
	4	23	2248	2118	36.6876	123.7520	13.4	0	3	0.741
	4	22	2221	2113	36.6828	122.5750	12.3	0	1	1.000
	4	23	414	2115	36.6802	123.2190	13.1	0	50	0.611
	4	24	25	2119	36.6740	123.8550	13.6	0	3	1.000
	4	26	2049	2128	36.0815	123.5990	13.8	0	50	0.827
	4	26	2253	2129	36.0730	123.5890	13.8	20	50	0.536
	4	27	124	2130	35.9343	123.7570	13.6	0	50	0.813
	4	27	353	2131	35.8958	123.9650	13.6	0	50	0.351
	4	24	2046	2120	35.6080	122.9200	13.7	0	7	0.745
	4	24	2250	2121	35.5260	123.0460	13.8	0	49	0.560
	4	25	130	2122	35.4382	123.1310	13.8	0	50	0.512
	4	25	330	2123	35.3840	123.1400	13.7	0	50	0.725
	4	25	2311	2125	34.9271	122.7340	14.1	0	50	0.618
	4	26	140	2126	34.7815	122.9020	13.9	0	50	0.599

[a]Sex ratio based on average weights (Picquelle and Stauffer 1985).

females in each sample were individually weighed. Otoliths were removed for aging and gonads were removed and preserved in 10% neutral buffered formalin. After the random subsample, additional fish were processed following procedures used in 1994 (Macewicz et al. 1996).

In the laboratory, each preserved ovary was processed (Hunter and Macewicz 1985). We analyzed oocyte development, atresia, and postovulatory follicle age to assign female maturity and reproductive state (Macewicz et al. 1996). Immature females were defined as those having ovaries with no β atresia and only unyolked oocytes present (a few oocytes may be in the earliest stage of yolk deposition). Some immature ovaries may contain α atresia of unyolked oocytes. Mature females were classified as active or postbreeding. Active, mature females are capable of spawning and are identified as having ovaries containing oocytes with yolk or postovulatory follicles less than 60 hours old. Postbreeding females are considered incapable of further spawning in the season and are identified by the presence of β atresia in ovaries with only unyolked oocytes and without postovulatory follicles (Macewicz et al. 1996). Sufficient numbers of immature and mature females for estimating the length at which 50% were mature were collected only during 2004. Females from 2004 were grouped into 10 mm length classes, and the length at which 50% were mature was estimated by logistic regression.

Daily Egg Production (P_0)

Since 2001, we have used the net tow instead of the transect line as the sampling unit (Lo et al. 2001)[7] because eggs from CUFES are not used to model the embryonic mortality curve. Eggs classified into developmental stages from CalVET tows and yolk-sac larvae from both CalVET and Bongo tows in Region 1 were used to compute egg production (figs. 1 and 4). The modeling procedures were modified from Lo et al. (2001). We used individual egg counts at age, and not half-day age groups, as input to fit an exponential embryonic mortality curve for the high-density area using a weighted nonlinear regression (Picquelle and Stauffer 1985; Lo et al. 1996).

The final estimate of $P_{0,1}$ was corrected for a bias introduced from the nonlinear regression. A simulation

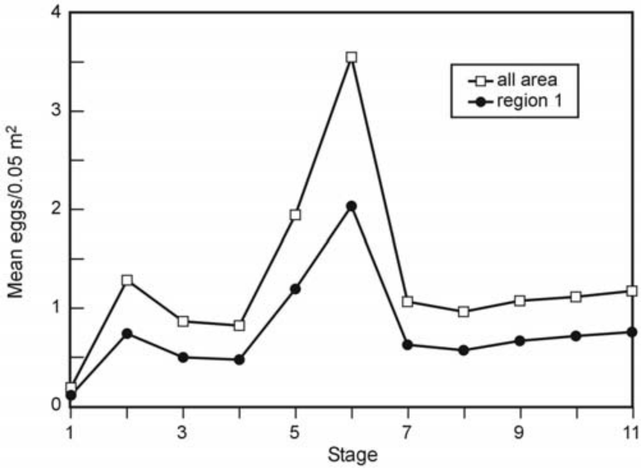

Figure 4. Pacific sardine (*Sardinops sagax*) eggs/0.05 m² for each developmental stage from March–April 2004.

study[7] 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 RB = (mean of 1,000 estimates – true value)/mean of 1,000 estimates. Therefore, the bias-corrected estimate is $P_{0,1,c} = P_{0,1} * (1- \mathrm{RB}) = P_{0,1} * 1.04$, and $\mathrm{SE}(P_{0,1,c}) = \mathrm{SE}(P_{0,1}) * 1.04$. The daily egg production in the low-density area ($P_{0,2}$) is $P_{0,1,c} * q$; where q is the ratio of eggs/min in the low-density area to that of the high-density area based on CUFES data. The estimate of egg production for the whole survey area is a weighted average of $P_{0,1}$ and $P_{0,2}$ where the weight is the area size of each region (Lo et al. 2001).

Adult Parameters

We followed methods in Macewicz et al. (1996) to evaluate the adult parameters (Picquelle and Stauffer 1985): fraction of the population by weight that is female (weight-specific sex ratio, R); average weight of mature females (W_f); number of oocytes released per spawn (batch fecundity, F); and daily spawning rate of mature females (spawning fraction, S). Two minor variations in the methods were necessary. First, for the daily spawning fraction in 2002, the number of spawning females per trawl (the numerator) was computed as an average of the number of females spawning two nights before capture and those spawning the night after capture[8, 10, 13]. Secondly, since females necessary for determining the relationship between batch fecundity and ovary-free female weight (W_{of}) were scarce before 2004 (two in 2002), we used the regression equation from 1994 (Macewicz et al. 1996) to estimate F, while in 2004 we used the relationship from 39 females collected that year. We compared the 2004 results with batch fecundity data from 1986–1994 (Macewicz et al. 1996)[1]. The basic formulas for the population mean and variance for the adult reproductive parameters are in Picquelle and Stauffer (1985) and Lo et al. (1996).

Spawning biomass (B_s)

The spawning biomass was computed according to:

$$B_S = \frac{P_0 AC}{RSF/W_f} \qquad (1)$$

where A is the survey area in units of 0.05 m², C is the conversion factor from gm to 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 as a function of the coefficient of variation (CV) of the estimate for each parameter and the covariance for adult parameter estimates (Parker 1985):

$$VAR(\hat{B}_s) = \hat{B}_s{}^2[CV(\hat{P}_0)^2 + CV(\hat{W}_f)^2 + CV(\hat{S})^2 + CV(\hat{R})^2 + CV(\hat{F})^2 + 2COVS] \qquad (2)$$

The covariance term is:

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

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 is positive if both parameters are in the numerator or denominator of B_S (equation 1); otherwise, the sign is negative.

When the estimates of adult reproductive parameters are not available, $CV^2(\hat{B}_s) = var(\hat{B}_s)/(\hat{B}_s)^2$ (equation 2) could be approximated by $CV(\hat{P}_0)^2 + allCVsCOV$ where the equation $allCVsCOV = CV(\hat{W})^2 + CV(\hat{S})^2 + CV(\hat{R})^2 + CV(\hat{F})^2 + 2COVS$ is computed from data collected during the previous trawl survey[9].

Spawning Stock Biomass from the Stock Assessment Model

The recent stock assessment model used for Pacific sardine is the Age-Structure Assessment Program (ASAP) model (Legault and Restrepo 1998)[11]. This model uses a general estimation approach, which is a flexible forward-simulation that allows for the efficient and reliable estimation of a large number of parameters. For Pacific sardine, a number of fishery-independent spawning biomass-related time series was used as indices in the model, among which is the time series of the annual estimates

[13]Chen, H., N. Lo, and B. Macewicz. 2003. MS ACCESS programs for processing data from adult samples, estimating 86 adult parameters and spawning biomass using daily egg production method (DEPM). Admin. Rep. LJ-03-14. Southwest Fisheries Science Center, National Marine Fisheries Service. La Jolla, CA.

from DEPM from 1983–2004. The predicted spawning stock biomass (SSB) was calculated basically following that of Deriso et al. (1996):

$$\hat{I}_{DEPM} = qS\hat{SB}$$

where I_{DEPM}, the DEPM spawning biomass index, and q, a scaling parameter, were estimated from the model. The index was taken to represent sardine SSB. The modeled selectivity pattern was set using the proportion of sardines mature at age (tab. 9 in Conser[11]). For the time series of spawning stock biomass, while the historical data (1932–1965) were not formally used in the model, the historical VPA biomass estimates derived from them were qualitatively used to establish the scale of virgin SSB in the ASAP modeling of the contemporary period.

RESULTS

Eggs

Egg Production (P_0). The embryonic mortality curve of egg production of Pacific sardine (*Sardinops sagax*) off California from San Diego to San Francisco in 2004 included $P_{0,1}$ = 3.78/0.05 m² (CV = 0.23) and the instantaneous daily mortality rate z = 0.25 (CV = 0.04) for Region 1 (fig. 5). $P_{0,1,c}$ after correction for bias was 3.92/0.05 m² (CV = 0.23). The egg production for Region 2, $P_{0,2}$ was 0.16/0.05 m² (CV = 0.43), and the egg production for the entire survey area was 0.96/0.05 m² (CV = 0.24) in 2004. The egg production increased from 0.193/0.05 m² (CV = 0.22) in 1994 to close to 1/0.05 m² (CV = 0.24) in 2004, with the peak of 4.23 eggs/0.05 m² (CV = 0.4) in 2000 (tab. 3). Daily embryonic mortality rates ranged from 0.10 (CV = 0.6) in 1999 to 0.48 (CV = 0.08) in 2003 (tab. 3).

Catch Ratio between CUFES and CalVET (E). In 2004, the catch ratio of eggs/min to eggs/tow (E) computed from 66 pairs of CalVET tows and CUFES collections (excluding a tow with 200 eggs, as the maximum in all other tows was <50) was 0.22 (CV = 0.09) (fig. 6). A ratio of 0.22 means that one egg/tow from CalVET tow is equivalent to approximately 0.22 egg/min from a CUFES sample, or one egg/minute from the CUFES is equivalent to 4.54 eggs/tow from a CalVET sample. Although this ratio is no longer needed in the estimation procedure, we compute it for comparison purposes every year (see discussion).

Spatial Distribution of Sardine Eggs and Sea Surface Temperature

The spatial distribution of spawning for Pacific sardines in relation to temperature contours from 1996–2004 appears to follow some general trends (figs. 7–9). Pacific sardines spawned within the temperature range of 12°C to 14°C, with occasional spawning activity at 15°C.

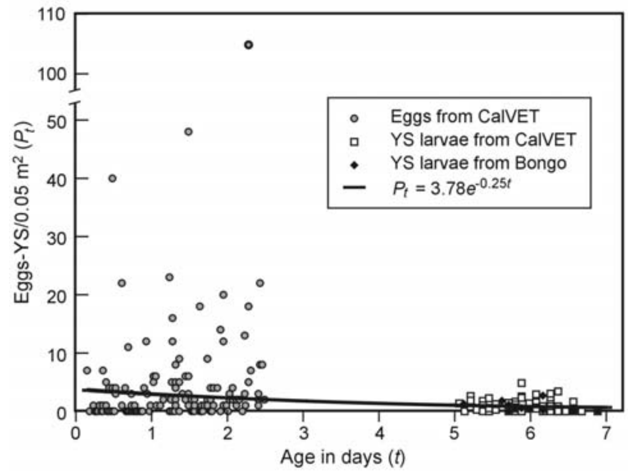

Figure 5. Pacific sardine (*Sardinops sagax*) embryonic mortality curve for eggs and larvae during March–April survey in 2004. The number, 3.78, is the estimate of daily egg production before correction for bias.

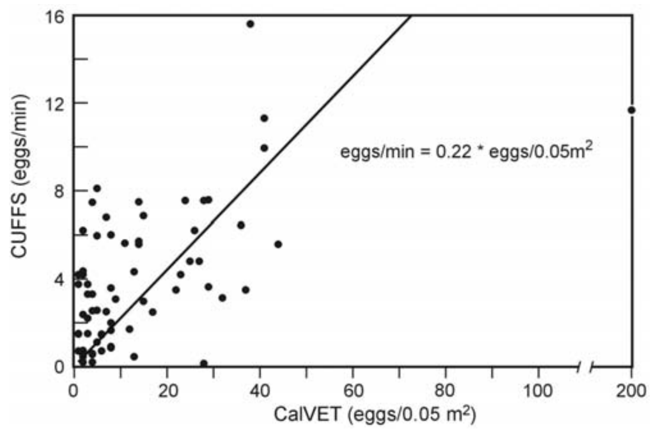

Figure 6. The catch ratio (0.22) of Pacific sardine (*Sardinops sagax*) egg density from paired CUFES and CalVET samples in 2004 (n = 66, p<0.01).

The spawning regions tended to shift to the north over the years. Pacific sardines spawned closer to the shore in years with high temperature, e.g. in 1998. However, when the average temperature was low (in 1999 and 2001), the spawning was more offshore (tab. 3; figs 7–9). The egg distributions of northern anchovy and jack mackerel were included in Figures 7–9 for comparison purposes.

Adult Parameters

The average whole wet weight of mature females, adjusted for bias (tab. 4), ranged from 75.58 to 228 g, and ovary-free wet weight ranged from 71.69 to 216.13 g (tab. 5). The estimates of W_f and W_{of} were highest in the 2004 survey (tab. 6). The ranges in standard length (SL) are fairly similar despite small sample sizes in 2001 and 2002 (tab. 6). A logistic regression indicated that fifty percent of females in 2004 were sexually mature at 193.34 mm SL (fig. 10).

TABLE 3
Estimates of Pacific Sardine 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 Sardine (*Sardinops sagax*), and Average Sea Surface Temperature for the Years 1994 to 2004

Year	P_0 (CV)	*Z* (CV)	Area (km²) (Region 1)	$\frac{RSF}{W}$	Spawning biomass (mt) (CV)[b]	Ave. temperature for positive egg or yolk-sac samples (°C)	Mean temperature (°C)
1994	0.193[c] (0.22)	0.120 (0.97)	380,175 (174,880)	11.52	127,102 (0.32)	14.3	14.7
1995	0.830 (0.5)	0.400 (0.4)	113,188.9 (113,188.9)	23.55[d]	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[e]	409,579[e] (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 (.24)	0.250 (0.04)	320,620 (68,234)	21.86[f]	281,639[f] (0.31)	13.4	13.7

[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 of 1.14 was used (appendix Lo 2001).
[b]$CV(B_s) = (CV^2(P_0) + allCVsCOV)^{1/2} = (CV^2(P_0) + 0.054)^{1/2}$. For 1995–2001 allCVsCOV was from 1994 data (Lo et al. 1996). For 2003, allCVsCOV was from 2002 data (Lo and Macewicz 2002).
[c]bias correction (1.14; appendix Lo 2001) of original result (0.169; Lo et al. 1996).
[d]23.55 was from computation for 1994 based on $S = 0.149$ (the average spawning fraction (day 0 and day 1) of active females from 1986–1994; Macewicz et al. 1996).
[e]is 25.94 when calculated from parameters in table 6 and estimated spawning biomass is 371,725 with CV = 0.36.
[f]uses R = 0.5 (Lo and Macewicz 2004); if using actual R = 0.618, then value is 27.0 and biomass is estimated as 227,746.

The relationship between female weight (without ovary, W_{of}) and batch fecundity (F_b) in the 2004 was $F_b = 356.46W_{of}$ ($n = 39$)[10]. This equation was used to estimate batch fecundity for each of the 290 mature females in 2004, and the estimated mean batch fecundity was 55,711 (tab. 6). For estimates of mean batch fecundities in 1997, 2001, and 2002, we used the 1994 fecundity equation ($F_b = -10585 + 439.53W_{of}$), with 1994 data for comparison purposes (tab. 6).

We used analysis of covariance to test the differences in the relationship between batch fecundity and female weight (W_{of}) among 1986, 1987, 1994, and 2004 (fig. 11). We included data from fish between 69 and 200 g because this range encompassed data from each of the four years. The difference among slopes from the four data sets was barely significant ($p = 0.058$). Assuming the slopes were equal, covariance analysis indicated that the adjusted group means were not different at the 10% significant level ($F_{3,158} = 2.55$, $p = 0.097$). Combining the data from all five years yielded the equation: $F_b = -12042 + 452.69W_{of}$, where $n = 190$, $r^2 = 0.799$ and W_{of} ranged from 39 to 244 grams (fig. 11).

TABLE 4
Relation of Wet Weight (*W*) and Ovary-free Wet Weight (W_{of}) for Non-hydrated Female Pacific Sardine (*Sardinops sagax*) for 1997, 2002, and 2004

	Linear equation $W = a + bW_{of}$					
Year	*a*	*b*	r^2	*F*	*N*	Range of *W* in grams
1997	0	1.069		182143	107	82–191
2002	0	1.088		20480	17	120–197
2004	–4.24	1.094	0.989	30303	324	31–261

The average fraction of mature female sardine spawning per day, when the estimate was based on females spawning on the night of capture, was 0.133 in 1997 and 0.131 in 2004 (tab. 6). No female in 2002 was identified as spawning on the night of capture (tab 5); the estimate in that year was 0.174 mature females spawning per day (Lo and Macewicz 2002).

Spawning Biomass

The spawning biomass in 2004 was estimated to be 281,639.27 mt ($CV = 0.3$) for an area of 320,619.8 km²,

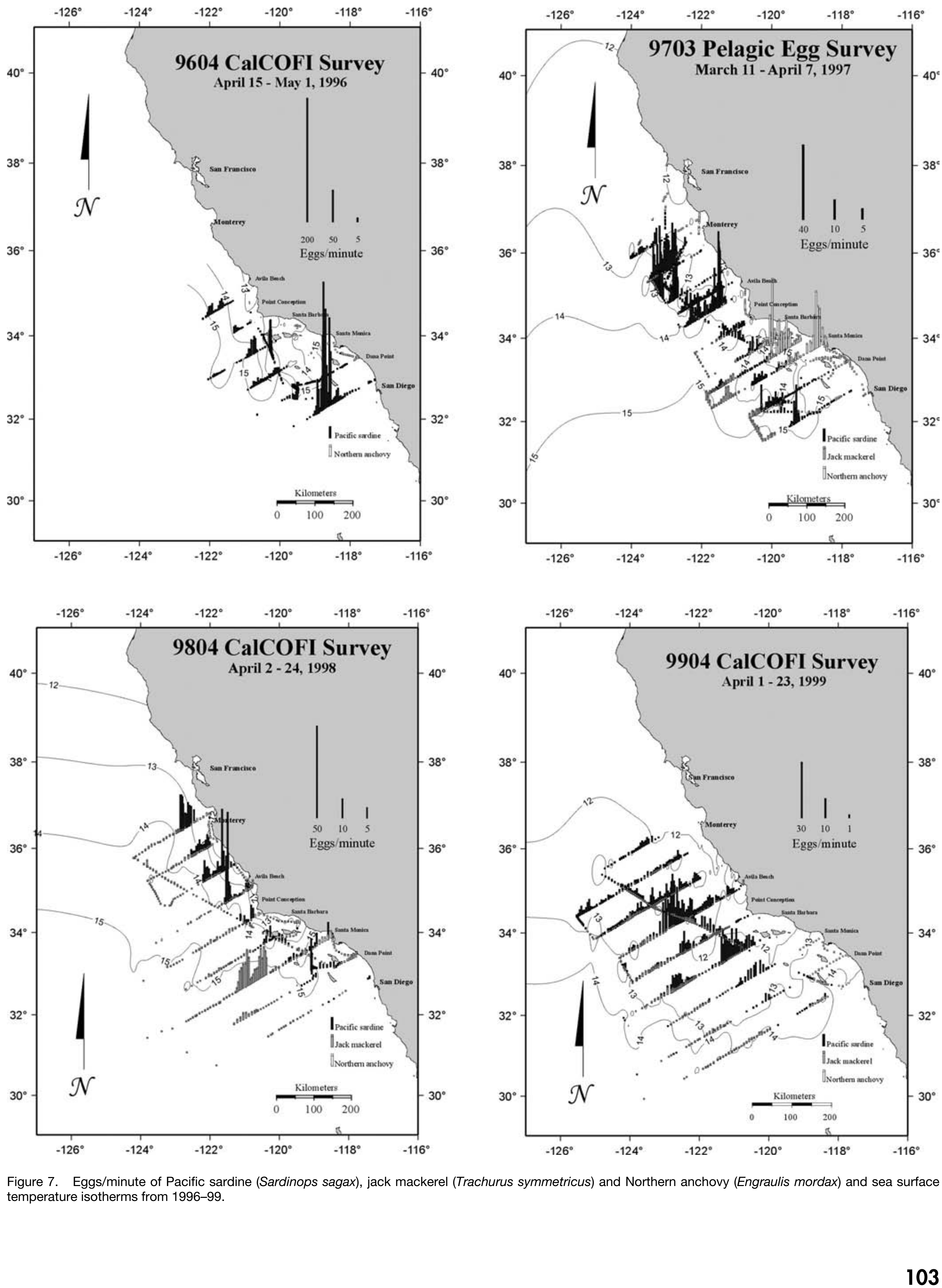

Figure 7. Eggs/minute of Pacific sardine (*Sardinops sagax*), jack mackerel (*Trachurus symmetricus*) and Northern anchovy (*Engraulis mordax*) and sea surface temperature isotherms from 1996–99.

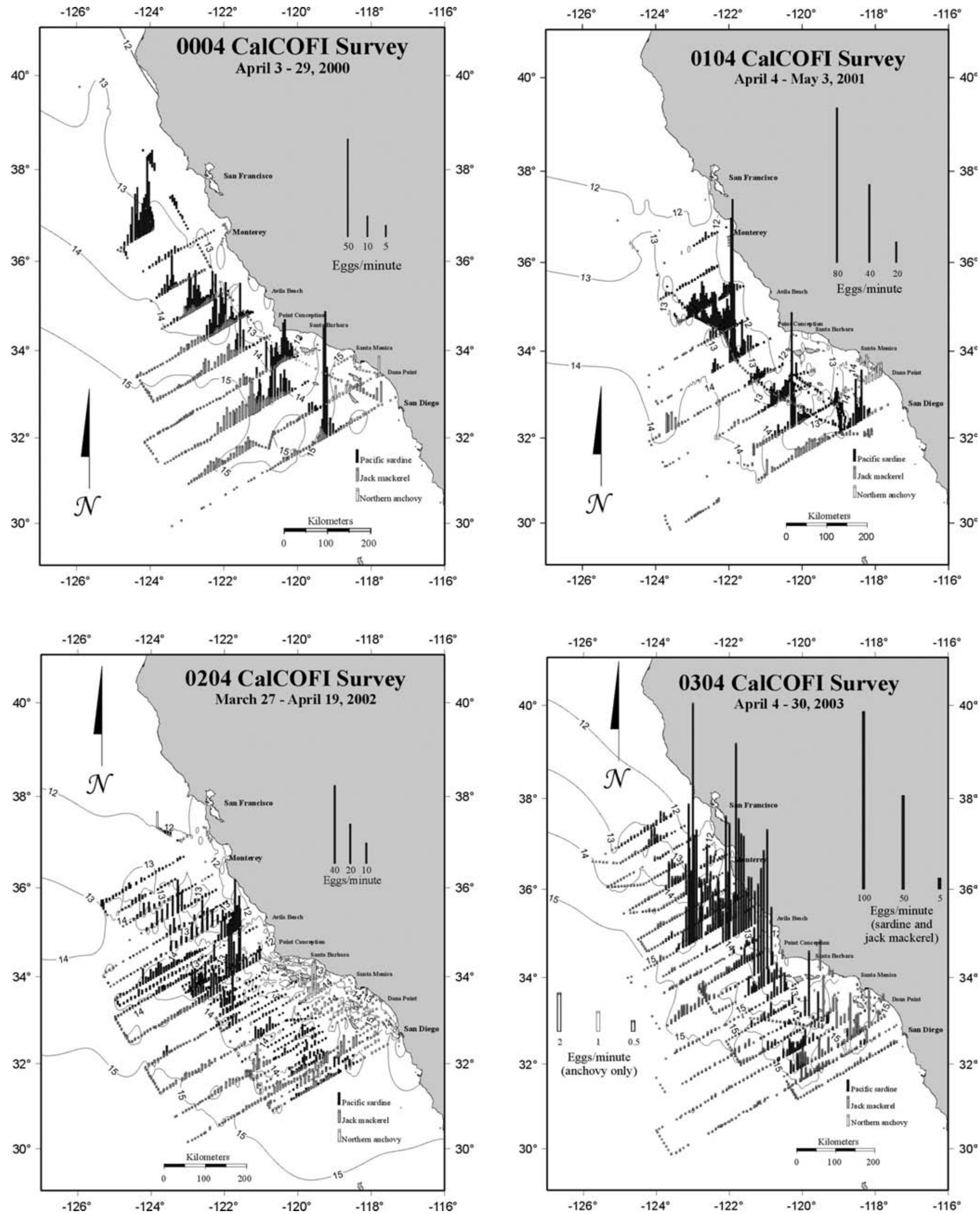

Figure 8. Eggs/minute of Pacific sardines (*Sardinops sagax*), jack mackerel (*Trachurus symmetricus*) and Northern anchovy (*Engraulis mordax*) and sea surface temperature isotherms from 2000–03.

TABLE 5
Parameters for Mature Female Pacific Sardine (*Sardinops sagax*) Used in Estimation of Biomass from Individual Samples

Year and collection number	Number	Average wet weight (g)	Average ovary-free weight (g)	Average batch fecundity	Number of females spawning: Night of capture	Night before capture	Two nights before capture	No spawn within last 60 hours	Spawning fraction: Night of capture "Day 0"	Night before capture "Day 1"[a]	Number of mature females adjusted[b]
1997											
1809	5	104.20	na	na	na	na	na	na	na	na	na
1805	3	95.51	88.51	28317	1	0	0	2	0.333	0.000	2
1807	25	132.40	124.92	44319	3	3	3	16	0.120	0.120	25
1808	24	115.58	108.66	37174	8	6	2	8	0.333	0.273	22
1804	25	138.68	128.66	45964	0	1	7	17	0.000	0.038	26
all	77				12	10	12	43			75
2001											
5004	3	86.07	82.15	25520	0	0	0	3	0	0	3
5003	6	75.58	71.69	20923	1	0	0	5	0.167	0	6
all	9				1	0	0	8			9
2002											
5016	1	178.74	178.74	53721	1	0	0	0	1.000	0.000	1
5010	1	142.37	142.37	42811	1	0	0	0	1.000	0.000	1
5011	6	170.83	159.43	47930	2	0	3	1	0.333	0.025	6
5012	4	147.00	136.42	41026	2	0	0	2c	0.500	0.025	4
5006	1	188.00	163.91	49274	0	0	0	1c	0.000	0.500	1
5009	10	149.73	141.34	42503	6	0	2	2	0.600	0.100	10
all	23				12	0	5	6			23
2004											
2111	25	178.72	167.80	59815	2	3	3	17	0.080	0.115	26
2132	0	0.00	0.00	0	0	0	0	0	0.000	0.000	0
2133	6	178.05	167.65	59761	4	1	0	1	0.667	0.333	3
2118	2	180.71	169.11	60282	1	0	0	1	0.500	0.000	1
2113	1	228.00	216.13	77041	0	0	0	1	0.000	0.000	1
2115	25	176.48	165.97	59160	2	1	3	19	0.080	0.042	24
2119	3	201.67	189.17	67430	0	2	0	1	0.000	0.400	5
2128	25	148.88	140.19	49972	0	5	7	13	0.000	0.167	30
2129	25	155.60	147.10	52435	0	5	6	14	0.000	0.167	30
2130	25	170.44	160.18	57098	5	8	1	11	0.200	0.286	28
2131	25	144.72	137.02	48841	15	3	3	4	0.600	0.231	13
2120	5	185.60	175.29	62484	0	0	0	5	0.000	0.000	5
2121	25	174.20	161.70	57641	0	3	2	20	0.000	0.107	28
2122	23	151.78	141.54	50453	1	1	4	17	0.043	0.043	23
2123	25	173.04	161.22	57469	2	2	1	20	0.080	0.080	25
2125	25	176.56	163.08	58133	3	2	4	16	0.120	0.083	24
2126	25	171.20	158.30	56429	3	2	3	17	0.120	0.083	24
all	290				38	38	37	177			290

[a]Values in 2002 are an average based on females that will spawn the night after capture and those that spawned two nights before (Lo and Macewicz 2002; Chen et al. 2003).
[b]Number adjusted during biomass estimation per Picquelle and Stauffer 1985; in 2001 and 2002 values equal actual number of mature analyzed .
[c]These females will spawn the night after capture because their ovaries contained migratory-nucleus stage oocytes (Lo and Macewicz 2002, Chen et al. 2003).

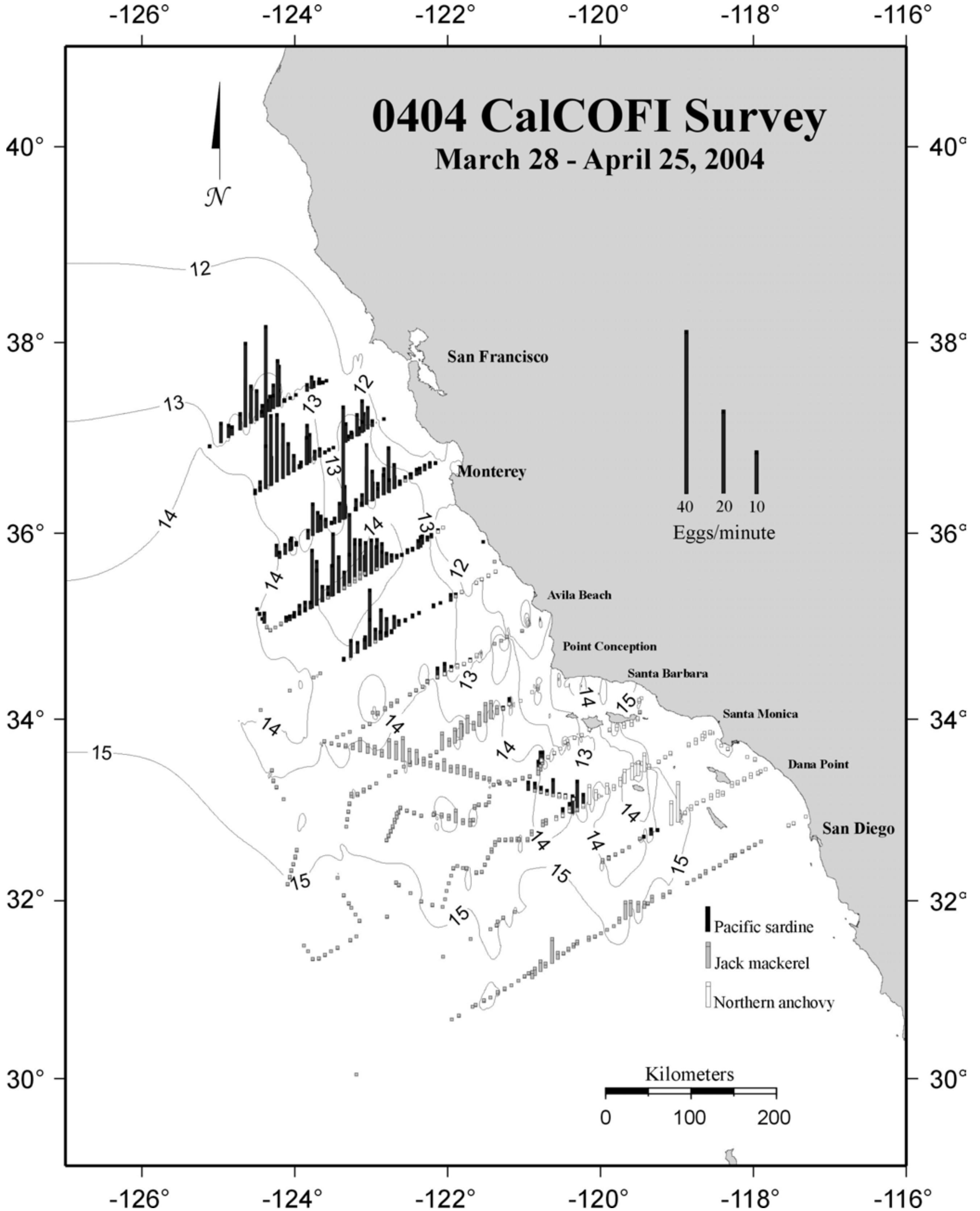

Figure 9. Eggs/minute of Pacific sardine (*Sardinops sagax*), jack mackerel (*Trachurus symmetricus*) and Northern anchovy (*Engraulis mordax*) and sea surface temperature isotherms in 2004.

TABLE 6
Estimates of Adult Pacific Sardine (*Sardinops sagax*) Parameters from Surveys Conducted in 1994, 1997, 2001, 2002, and 2004

		1994	1997	2001	2002	2004
Midpoint date of survey		April 22	March 25	May 1	April 21	April 25
N collections with mature females		37	4	2	6	16
Average surface temperature (°C)						
at collection locations		14.36	14.28	12.95	12.75	13.59
Female fraction by weight	R	0.538	0.592	0.677	0.385	0.618
Mature female weight (grams):						
with ovary	W_f	82.53	127.76	79.08	159.25	166.99
without ovary	W_{of}	79.33	119.64	75.17	147.86	156.29
Batch fecundity[a]	F	24283	42003	22456	54403	55711
N mature females analyzed[b]		583	77	9	23	290
Spawning fraction of mature females[c]	S	0.073	0.133	0.111	0.174	0.131
Spawning fraction of active females[d]	S_a	0.131	0.130	0.111	0.174	0.131
Daily specific fecundity	RSF/W	11.5	25.9	21.3	22.9	27.0
Standard length (mm) females						
mean		176	221	185	236	243
min.		131	187	161	216	142
max.		284	261	199	250	278
Standard length (mm) males						
mean		175	209	172	233	238
min.		128	129	160	213	171
max.		283	236	188	250	271

[a]1994–2001 estimates were calculated using $F_b = -10858 + 439.53W_{of}$, (Macewicz et al. 1996); 2004 estimate calculated using $F_b = 356.46W_{of}$ (Lo and Macewicz 2004).
[b]Mature females include females that are active and those that are postbreeding (incapable of further spawning this season).
[c]Fractions in 1994, 1997, and 2004 are based on females that spawned the night before capture and the number of mature females adjusted (Picquelle and Stauffer 1985). The 2001 fraction is based on one spawning female; the 2002 fraction is an average of two nights (Lo and Macewicz 2002); and the number of mature females was not adjusted in either 2001 or 2002.
[d]Active mature females are capable of spawning and have ovaries containing oocytes with yolk or postovulatory follicles less than 60 hours old. Calculation does not adjust the number of active mature females.

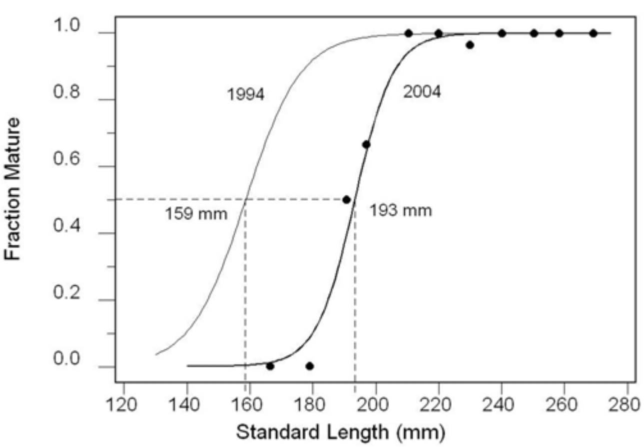

Figure 10. Fraction of Pacific sardine (*Sardinops sagax*) females that were sexually mature as a function of standard length. 2004 logistic curve parameters are $a = -31.605$ and $b = 0.16347$. Symbols represent actual fraction mature within 10 mm length classes for 2004. 1994 logistic curve parameters were $a = -18.16$ and $b = 0.1145$ (Macewicz et al. 1996).

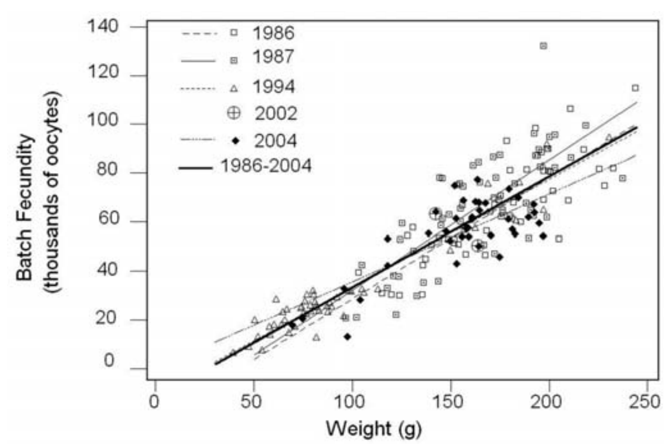

Figure 11. Batch fecundity (F_b) of Pacific sardine (*Sardinops sagax*) as a function of female weight (W_{of}, without ovary) for 191 females from trawl surveys in 1986–2004; fitted regression is $F_b = -12042 + 452.69\ W_{of}$, where $r^2 = 0.799$ (bold line). 1986, 1987, and 1994 (Macewicz et al. 1996) and 2004 (Lo and Macewicz 2004) regression lines are plotted for comparison.

using the daily specific fecundity (number of eggs/population weight (g)/day) of 21.86 (tab. 3).

The estimates of spawning biomass of Pacific sardine in 1994–2004 are 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, and 300,000 mt, respectively (tab. 3, fig. 12). Therefore, the estimate of spawning biomass fluctuated and tripled from 1994 to 2004. The size of the high-density area varied from 57,525 km² in 2000 to 130,890 km² in 1999 excluding 1994, which included Mexican waters, and 1995 and 1998, when the stratification methods were different from those used in other years.

Spawning Biomass from the Stock Assessment Model

The time series of SSB was around 1 million mt for biological years 1996–2005[11] which is much higher than most of the DEPM spawning biomass (fig. 12). An approximate simple *t* statistic was computed for each year: $t = (DEPM\text{-}SSB)/sqrt([SE(DEPM)]^2 + [SE(SSB)]^2)$. Except for 2000, 2001, and 2003, all *t* values were less than –2.5, which is significant at the 5% level with 2 d.f. (in reality, the degree of freedom should be larger). This means for those years with a *t* value <–2.5, the population mean of SSB was significantly higher than that of DEPM at the 5% level. Using the criterion of overlapped confidence intervals is not recommended because this decision-making process based on overlapped confidence intervals is likely to lead to the conclusion that there is no difference even when there is (Lo 1994), e.g. 1997 and 2004. Because the DEPM estimates were computed from field data, these differences indicate that the procedures of both methods should be examined (see discussion section).

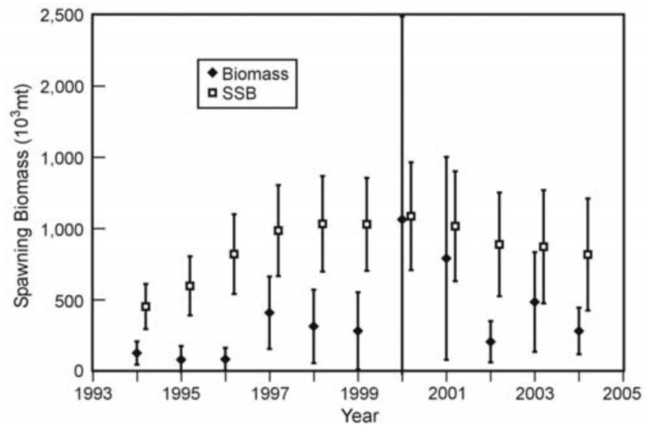

Figure 12. Time series of the estimates of spawning biomass of Pacific sardine (*Sardinops sagax*) off California from DEPM (biomass) and the estimates of spawning stock biomass (SSB) from the ASAP model (Conser et al. 2004). Lines indicate ± 2 standard error.

DISCUSSION

Eggs

Density. Developmental stage-specific egg densities are the basis for estimation of the egg-mortality curve and, thus, the egg production at age 0. On the population level, the density of eggs decreases as the stage increases. However, for Pacific sardines, the egg density seems always to peak at stage 6 (e.g. fig. 4 and Lo et al. 1996)[7, 8, 9, 10], possibly because the spatial distribution of stage 6 eggs is less aggregate than early stages, and stage 6 eggs are still abundant enough for the current sampling intensity. This hypothesis needs to be tested with available data.

Production (P_0). We used a weighted nonlinear regression to estimate P_0. A generalized additive model (GAM) has been used to estimate the annual egg production of Atlantic mackerel (*Scomber scombrus*) (Augustin et al. 1998) and the daily egg production of Atlantic mackerel (*Scomber scombrus*) and horse mackerels (*Trachurus trachurus*) (Borchers et al. 1997; ICES 2003a) and Atlanto-Iberian sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) (ICES 2003b; Stratoudakis et al. 2004). Comparisons between the two procedures for estimating P_0 of sardine and anchovy off Spain and Portugal indicate that although the GAM takes into consideration the spatial distribution of eggs and environmental variables, while the weighted nonlinear regression does not, the point estimates of P_0 from these two methods are similar (fig. 13; ICES 2003b).

A Bayesian procedure has been considered for P_0 in Region 1. The estimate is a weighted average of P_0 of the current year and that of the prior distribution where the weight is the inverse of each variance. As the prior distribution of P_0 is hard to obtain, we opted to use the estimate of P_0 of the previous year as the prior. Therefore, the Bayesian estimate of P_0 becomes the weighted average of P_0 of the current year and P_0 of the previous year. Preliminary work indicated that the time series of Bayesian estimates is much smoother than that of the individual annual estimates in Region 1 from 1997–2004 (fig. 14). The major difference between these two estimates of P_0 was in 2000; the estimate using the Bayesian procedure was much lower than the conventional method, primarily due to the large standard error of the estimate of P_0 from the nonlinear regression in 2000.

Catch Ratio between CUFES and CalVET (E). The 2004 catch ratio between CUFES and CalVET was 0.22, similar to those since 1997 but quite different from the 1996 estimate of 0.73 (fig. 15). The higher ratio in 1996 indicates that the water was more stratified because more eggs were collected at the 3 m CUFES depth. In theory, if there is complete mixing of the water column, the catch ratio would simply be the ratio of the volumes of water filtered by the different nets (Lo et al. 2001). In our study, the data indicated that the catch ratio is positively correlated with the SST, perhaps reflecting increased stratification at higher SST. The only exception to the relationship was in 1999 when the SST was low (12.5°C) and the catch ratio remained similar to those of other years.

A mixing model with environmental covariates for converting CUFES counts to full water column counts has been developed to determine whether CUFES may be used as the primary egg sampler (Sundby 1983; Williams et al. 1983; ICES 2002; ICES 2003b), but the results were not satisfactory. Additional research is currently underway to provide more conclusive results on

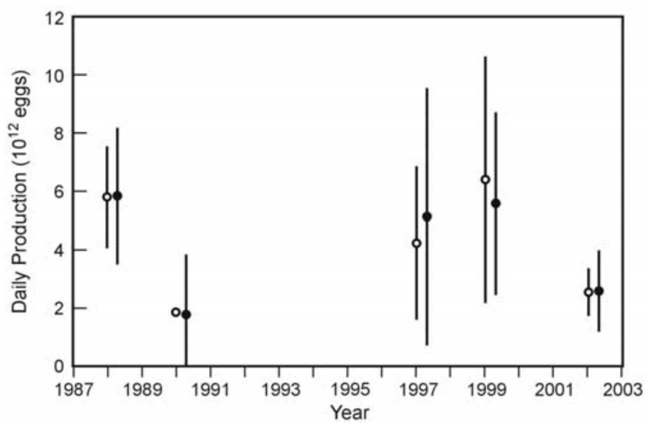

Figure 13. Time-series of estimates of sardine (*Sardina pilchardus*) daily egg production based on the new GAM method (left) and the traditional method (right) for Atlanto-Iberian surveys. Lines are approximate 95% confidence intervals (2SE), which for the traditional method are based on an assumed normal distribution and in the GAM-method on a log-normal distribution. Traditional method estimates have been shifted to the right for presentation. GAM SE is not available in 1990. (Table 2.3.1.3, in ICES 2003b).

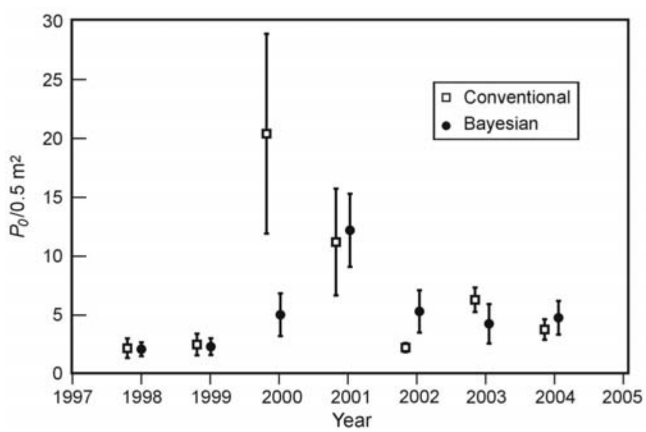

Figure 14. Estimates of Pacific sardine (*Sardinops sagax*) egg production (P_0/0.05 m^2) and ± one standard error using the conventional and the Bayesian method for the high density area (Region 1), 1998–2004.

the applicability of CUFES as a quantitative sampler of egg abundance in the water column[14].

Adaptive Allocation Sampling. The spatial distribution of Pacific sardine eggs varies from year to year (figs. 7–9). The adaptive allocation sampling design, using the eggs collected by the CUFES as a guide, allowed us to allocate CalVET tows where eggs were mostly likely to be found. The efficiency of this survey design was confirmed by data collected in years after 1997 (Lo et al. 2001; Smith et al. 2004). For example, even though the number of net tows used in the 2004 survey was only 18% of that used in 1994, when a conventional survey design was used, the precision of P_0 was similar between these two surveys (tab. 7). A similar adaptive allocation sampling strategy has been used in the Iberian DEPM survey since 2002 (ICES 2002, 2003b).

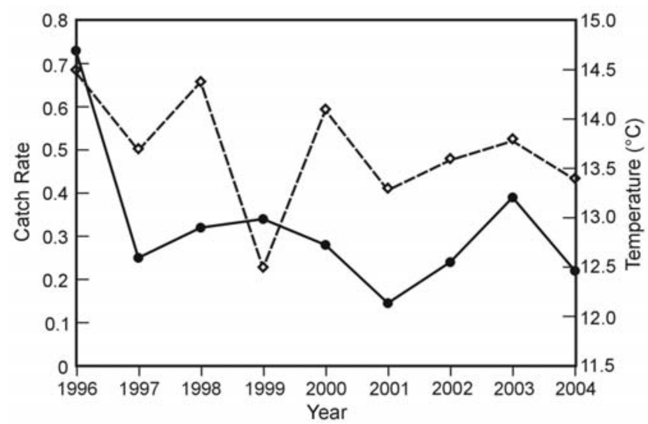

Figure 15. Catch ratio for Pacific sardine (*Sardinops sagax*) (eggs/min to eggs/tow, circle) and sea surface temperature (°C, diamond), 1996–2004.

Spatial Distribution of Pacific Sardine, Jack Mackerel and Northern Anchovy Eggs

The spatial distribution of Pacific sardine spawning fluctuates from year to year, but it consistently occurs within 12°C–14°C SST. It appears that the bulk of the spawning distribution is located within these temperature limits (figs. 7–9). Checkley et al. (2000) characterized the spawning habitat of Pacific sardine as the transition zone between the colder, more saline, upwelled inshore waters and the warmer, less saline waters of the California Current for the years 1996 and 1997. Checkley et al. (2000) also suggested that Pacific sardine and northern anchovy spawn in different types of water; the Pacific sardines occupy the transition zone while northern anchovies spawn in water characterized by upwelled water, which can be either recently upwelled (cooler) water or older upwelled (warmer) water, which is identified by a higher salinity. Temperature salinity plots of the years 1997 to 2002 uphold these trends seen for Pacific sardine and northern anchovy but do not show a distinct trend for jack mackerel (D. Griffith, unpub. data), which tends to span both water types with no relative affinity to either. Jack mackerel spawn in slightly warmer waters but salinity does not appear to be a factor.

Lynn (2002) examined the 1996–1999 Pacific sardine egg distributions off California together with SST and the mean volume backscatter strength (MVBS), which was measured by a 150 kHz acoustic Doppler current profiler (ADCP), a strong indicator of zooplankton volume. He indicated that the inshore distribution of Pacific sardine spawning appears to be limited by the low temperatures of freshly upwelled waters and, in some years (e.g. 1997), the abrupt offshore decrease in MVBS coincides with the offshore boundary of Pacific sardine eggs. Although the MVBS data were not included in our analysis, it appears that SST, salinity, and plankton

[14]A. Uriarte, pers. comm.

TABLE 7
Pacific Sardine (*Sardinops sagax*) Daily Egg Production (P_0) from a Conventional Survey (1994), Compared with an Adaptive Allocation Sampling in 2004

Year: 1994		Year: 2004	
Area	380,175 km²	Area	320,619 km²
CalVET tows		CalVET tows	
Total	684	Total	124
Positive for eggs	72	Positive for eggs	67
Positive percent	11	Positive percent	54
CUFES samples	None	CUFES samples	
		Total	781
		Percent positive	32
		High density area	87
		Low density area	15
Daily egg production		Daily egg production	
P_0	0.176/0.05 m²	P_0	0.96/0.05 m²
CV	0.22	CV	0.24
Spawning biomass:	117,593 mt	Spawning biomass	281,639 mt

volume all are related to the Pacific sardine egg distributions. The effect of temperature limits on Pacific sardine spawning was especially apparent during the El Niño year of 1998 where the transition zone was drastically narrowed and pushed inshore, with little or no coastal upwelling.

Adult Reproductive Parameters

We estimated the adult parameters for the surveys in 1997, 2001, 2002, and 2004 (tab. 6). Adult size varied by location over the years (tabs. 2 and 5, fig. 3). In 1986–1988, when biomass was low, the average weight of mature females was 154.8–199.9 g (Lo et al. 1996), and adults were caught close to shore or near the islands (fig. 3). By 1994, the sardine population had expanded and the average female weight was small (82.5 g) except for two offshore collections (32°N and 118°W) with mean female weights of 192.9 and 215.5 g (Macewicz et al. 1996). Since 1994, larger females have appeared offshore, and smaller females near shore or close to the islands (tabs. 2 and 5). The length at 50% maturity has increased from 159 mm (age 1) in 1994 to 193 mm (age 2) in 2004 (fig. 10; age estimates from Butler et al. 1996). The increase in length at 50% maturity may be due to location of sampling (most were inshore in 1994 but offshore in 2004; fig. 3), a delay in maturation because of increasing population size, different growth rates, and/or sampling fish schools which migrate through the survey area. In order to distinguish among these, we need to increase the number of samples of adults to cover the entire spawning area.

Spawning fraction can also be expressed as the spawning rate of active females (S_a) times the fraction of active females: $S = S_a (N_a / N_m)$ where N_a is the number of active females and N_m is the number of all mature females, including active and postbreeding females. Macewicz et al. (1996) found that the average fraction of active females spawning per day, based on females spawning the night before capture, was 0.137 during 1986–1994. The average of the fraction of active females spawning the night before capture in 1997 and 2004 was 0.132 (tab. 6); the estimate in 2002, 0.174, was high due to a bias introduced by the survey design[8]. Hence, the estimate of spawning fraction for active females (S_a) is fairly stable, averaging 0.13. However, the fraction of active females changes through the spawning season and is close to 100% during peak spawning. If ovary samples are unavailable for histological analysis, we recommend setting S to 0.13. If samples are not taken during peak spawning, or if the spawning population is patchily distributed (figs. 7–9) and adults are only sampled in Region 1, an estimate of the fraction of active females by other methods such as port sampling would be necessary to adjust S downward. Again, increasing the quantity of adult samples and number of locations from which they are collected to cover the entire area of egg production should minimize bias in estimation of S.

The relationship of female weight (W_{of}) and batch fecundity is similar among the years 1986–2004 (fig. 11). If females with ovaries containing hydrated or migratory-nucleus stage oocytes are not available, we recommend using the overall equation ($F_b = -12042 + 452.69 W_{of}$) to estimate fecundity of each mature female used in the spawning biomass computation.

Spawning Biomass

The fluctuation of spawning biomass among years could be due to 1) a real change of spawning biomass off California; 2) migration of the adult population along the western coast of North America; 3) change in the estimates of egg production, P_0, for years when trawl surveys were not conducted and an average of spawning fraction was used; and 4) any combination of the above. The 2004 estimate of spawning biomass is considerably lower than that in 2003 but similar to 2002. These differences are primarily due to the change of the egg production estimate, 0.96 eggs/0.05 m² over a smaller Region 1 area in 2004 compared to 1.52 eggs/0.05 m² in 2003 and 0.728 eggs/0.05 m² in 2002 (tab. 3). The daily specific fecundity of 21.86 eggs/g/day used for the 2004 estimate of spawning biomass was based on trawl samples taken from Region 1, but the daily egg production per day for the entire survey area was a weighted average of the estimates from regions with high and low egg density. Thus, the spawning biomass may have been underestimated because the daily specific fecundity may be lower in Region 2 than Region 1. The degree of underestimation may be minimal unless the daily specific fecundity or the spawning fraction in Region 2 was substantially lower than that in Region 1, as the number of eggs produced per day in Region 1 was 87% of the total produced per day in the entire survey area. To estimate the degree of bias of the spawning biomass estimate when trawl samples are taken only from Region 1, it is necessary to collect adult samples in the low-density area in future years. Data from adult samples in the low-density area will be also useful to ascertain the presence of an adult population because a low density of eggs may result from either a low abundance of adults or a high abundance of adults with low spawning activities.

Sardine Stock Assessment and Spawning Biomass

The DEPM estimate is used in assessments of the Pacific sardine as an index of abundance, and it has not been treated in the assessment model as an absolute measure of spawning biomass. Nevertheless, it is important to compare this direct measure of spawning biomass to that derived from age-based assessment models to see what can be learned regarding both the DEPM and the assessment models. When we did this (fig. 12), we found that, except for the 2000, 2001, and 2003 surveys, the population means of SSB estimated by the sardine stock assessment model were significantly higher than those of the DEPM biomass estimates, despite the high variance in both of SSB and the DEPM estimates.

A variety of potential biases exist in the application of the DEPM that could lead to underestimating spawning biomass (Deriso et al. 1996). These include movement of postspawning adults out of the sampling area, egg contagion affecting the slope of egg-embryonic mortality curve, changes in the age of first maturity, failure of the DEPM survey to cover all spawning habitats, and changes in the seasonality of spawning. On the other hand, the potentially biased age composition (Deriso et al. 1996), and/or the change of the maturity ogive to older fish in 2004 from younger fish in 1994 (fig. 10), may result in an overestimate of the SSB from the stock assessment model and thus affect the inter-comparisons of the estimates from the two methods. We conclude that the comparison between DEPM and the current ASAP model indicates that it is necessary to address the basis for the differences in estimates between methods and thereby improve our understanding of sardine biology and improve future DEPM and assessment models.

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