ADULT REPRODUCTIVE PARAMETERS OF PACIFIC SARDINE (*SARDINOPS SAGAX*) DURING 1994

BEVERLY J. MACEWICZ
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

JOSÉ JULIÁN CASTRO-GONZÁLEZ,
CELIA EVA COTERO-ALTAMIRANO
Instituto Nacional de la Pesca
Apartado Postal 1305
Ensenada, B.C.
México

J. ROE HUNTER
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

ABSTRACT

The average female Pacific sardine, *Sardinops sagax*, spawned about once every 15 days along the Pacific coast off California and Baja California during April–May 1994. The relation between batch fecundity and female weight without the ovary (W_{of}) was best estimated by the equation $F_b = -10{,}585 + 439.53W_{of}$. Fifty percent of the females reached sexual maturity by 158.6 mm standard length (95% CI 155 mm–162 mm). Data from surveys off California during 1986–88 combined with the 1994 data indicated that peak daily spawning occurs between 19:00 and 22:59. The spawning cycle of sardine females with active ovaries averaged about one spawning every 7 days during 1986–94 off California. Our interpretation of the literature on sardine spawning indicates that they may spawn at similar rates in Chile, Japan, Australia, and South Africa. Finally, off California differences existed between months in the fraction of females that had active ovaries. These differences may indicate movements of groups of Pacific sardine away from and into the survey area.

INTRODUCTION

To assess spawning biomass using the daily egg production method (DEPM) of Parker (1980, 1985), one must estimate the following adult fish parameters (averages for the spawning population): daily spawning rate of mature females (spawning frequency), number of oocytes released per spawn (batch fecundity), fraction of the population by weight that is female (weight-specific sex ratio), and average weight of mature females. This paper provides estimates of adult Pacific sardine (*Sardinops sagax*) reproductive parameters for the 1994 season to be used in calculating the DEPM spawning biomass (Lo et al. 1996). We also estimate the probability of sexual maturity as a function of standard length and use histological criteria to examine the atretic state of sardine ovaries. We combine our data with those from earlier fecundity studies (MacGregor 1957; Scannell et al. 1996) and the adult reproductive parameters from DEPM estimates (Wolf 1988a, b; Scannell et al. 1996) to establish general relationships for batch fecundity, spawning frequency, and peak time of daily spawning for Pacific sardine. We compare data on Pacific sardine to that on *Sardinops* from around the world to determine if any general patterns in spawning frequency exist.

METHODS

From April 7 to May 14, 1994, adult Pacific sardine were collected from San Ignacio Lagoon (just south of Punta Abreojos), Baja California Sur, Mexico, to Monterey Bay, California, during a joint U.S.–Mexico DEPM survey (Arenas et al. 1996). Thirty-seven trawl or purse seine collections of sardine (taken at night between 1929 and 0500 hours) were usable for determining adult female reproductive parameters (table 1).

Sardine were randomly sampled from the catch. Up to 50 fish from each collection were sexed, and standard length was measured to the nearest millimeter. The first 5 males and first 25 females in each sample were individually weighed to the nearest gram; otoliths were removed for aging (Butler et al. 1996); and gonads were removed and preserved in 10% neutral buffered formalin. If the first 25 females included females with small ovaries in which yolked oocytes were not visible (female potentially immature), more females were taken with the intention of bringing the total number of mature females to 25.

From time to time additional fish were selected after the random sample because they were small, large, or had hydrated ovaries. These fish were used to increase the size range for aging or the number of fecundity samples but were not used to estimate spawning frequency, which requires a representative or random sample from the population.

The female proportion by weight was determined for each collection. The average weight of males and females (calculated from the first 5 males and 25 females) was multiplied by the number of males or females in the random 50-fish subsample to calculate total female and male weights in each subsample. Thus the female proportion by weight in each collection is calculated as total female weight divided by the sum of total female weight and total male weight (table 1). The estimate of the population's weight-specific sex ratio was calculated by methods given in Lo et al. (1996) and Picquelle and Stauffer (1985).

In some instances, on a few vessels included in the survey, only a piece of the ovary was preserved. It was

TABLE 1
Proportion of Female *Sardinops sagax* by Weight[a] Taken in Trawls (T) and Purse Seines (P) during April–May 1994

Collection number	Gear type	Latitude	Longitude	Month/day	Time (h m)	Proportion of females
667	P	36°52.0'N	121°52.2'W	4/22	0402	0.562
666	P	36°37.4'	121°51.2'	4/21	0345	0.433
664	P	36°37.4'	121°54.4'	4/20	0535	0.426
665	P	36°37.2'	121°51.4'	4/21	0109	0.518
663	P	36°36.8'	121°53.6'	4/20	0125	0.587
643	T	33°55.8'	118°33.8'	4/15	0417	0.540
642	T	33°55.4'	118°34.4'	4/15	0247	0.414
660	P	33°41.5'	118°19.5'	5/04	2330	0.619
659	P	33°41.5'	118°19.5'	5/04	2330	0.683
662	P	33°38.6'	118°15.4'	5/04	0309	0.654
655	P	33°37.8'	118°06.1'	4/28	2200	0.622
661	P	33°36.1'	118°02.6'	5/04	0002	0.621
656	P	33°28.2'	117°45.0'	4/30	2300	0.582
657	T	33°09.8'	118°20.2'	5/02	0445	0.294
649	T	33°03.1'	118°23.2'	4/19	2336	0.653
648	T	33°02.8'	118°24.1'	4/19	2117	0.672
645	T	33°00.4'	119°14.8'	4/17	0408	0.212
644	T	32°55.8'	119°06.9'	4/17	0053	0.023
634	T	32°55.7'	117°26.1'	5/07	2223	0.586
646	T	32°55.1'	119°11.9'	4/18	0054	0.892
629	T	32°39.2'	117°59.5'	5/05	1929	0.790
630	T	32°39.1'	118°00.9'	5/06	0037	0.571
611	T	32°05.9'	118°16.8'	4/22	0100	0.467
623	T	32°04.4'	118°15.4'	5/02	2015	0.714
685	P	32°03.0'	116°57.0'	5/14	0100	0.504
683	P	31°48.0'	116°46.0'	5/05	0155	0.597
682	P	31°48.0'	116°46.0'	5/04	0100	0.510
684	P	31°46.0'	116°44.0'	5/07	0355	0.437
687	P	31°36.0'	116°42.0'	4/07	0500	0.513
679	P	31°36.0'	116°42.0'	4/21	0800	0.437
680	P	31°36.0'	116°42.0'	4/22	0255	0.499
675	T	30°20.5'	115°57.8'	5/03	1955	1.000
615	T	28°31.4'	115°32.6'	4/25	0044	0.175
672	T	28°14.8'	114°13.0'	4/27	2203	0.701
673	T	28°03.0'	115°10.6'	4/29	2034	0.430
670	T	27°42.8'	115°11.0'	4/25	0130	0.545
668	T	26°40.1'	113°29.6'	4/22	2015	0.748

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

TABLE 2
Conversion Equations for Pacific Sardine (*Sardinops sagax*) by Location and Maturity

Dependent variable Y	Independent variable X	Area divided at 32°04'N	Mature	Linear equation $Y = a + bX$					Range of X
				a	b	r^2	F	N	
Female wet weight	Ovary-free wet weight	North[a]	Yes	−5.113	1.1055	0.996	79,782.69	362	50.1–269.1
		South	Yes	−1.909	1.0508	0.996	37,802.39	141	19.9–127.4
		North	No	−0.454	1.0136	0.999	132,811.34	28	32.0–88.9
		South	No	−0.1012	1.0079	0.999	861,020.06	68	21.9–108.2
Ovary weight	Ovary-free wet weight	North	Yes	−5.111	0.1054	0.67	725.19	362	50.1–269.1
		South	Yes	−1.820	0.0506	0.49	135.55	141	19.9–127.4
		North	No	−0.437	0.0133	0.47	22.72	28	32.0–88.9
		South	No	−0.1001	0.00791	0.46	56.86	68	21.9–108.2
Ovary weight	Female wet weight	North	Yes	−5.049	0.0994	0.73	971.94	362	53–281
		South	Yes	−1.871	0.0504	0.54	165.60	141	20–133
		North	No	−0.442	0.0134	0.48	24.01	28	32–90
		South	No	−0.102	0.00792	0.47	58.84	68	22–109
Male wet weight	Testis-free wet weight	North	Both	−4.083	1.0954	0.995	17,425.67	96	44.4–203.5
		South	Both	−1.421	1.0408	0.999	283,182.09	173	21.0–240.8

[a]Equation used to predict whole wet weight for females with hydrated ovaries because hydration inflates whole body weight.

therefore necessary to estimate ovary weight from fish weight so that ovary-free female weight could be calculated for females with incomplete ovaries. This is especially important for any mature female used during biomass estimation. In table 2, we provide the conversion equations.

Histological Classification

Each preserved ovary was blotted and weighed to the nearest milligram in the laboratory. A piece of each was removed and prepared as hematoxylin and eosin (H&E) histological slides (Hunter and Macewicz 1985a). All slides were then analyzed and classified.

In Pacific sardine, oocytes develop asynchronously; that is, oocytes in many stages of development occur simultaneously in reproductively active ovaries (Wallace and Selman 1981). Andrews[1] used many histological stages to describe the development and absorption (atresia) of oocytes in Pacific sardine ovaries off southern California. Torres-Villegas (1986), Alarcón et al. (1984), Goldberg et al. (1984), Retamales and González (1984), and Aguilera et al. (1986) used less complex classification systems similar to that developed for the northern anchovy (*Engraulis mordax*) by Hunter and Goldberg (1980) and Hunter and Macewicz (1985a, b) to describe Pacific sardine ovaries off Mexico, Peru, and Chile. We also followed the Hunter and Goldberg (1980) and Hunter and Macewicz (1985a, b) methods of histological classification. With a few modifications for the ovarian structure of Pacific sardine, we recorded the presence or absence of unyolked oocytes; oocytes in early vitellogenic stages (diameters of 0.27–0.6 mm); advanced yolked oocytes (minimum diameter about 0.44 mm); oocytes in migratory-nucleus stage (precursor to hydration, beginning about 0.56 mm in diameter); hydrated oocytes (≥0.8 mm diameter); any atresia; and postovulatory follicles.

Hydrated oocytes in Pacific sardine contain an oil droplet that can be used for staging the ovary. Before vitellogenesis starts, lipid droplets first appear in oocytes of ≥0.25-mm diameter. As the oocyte grows and acquires yolk, the lipid droplets gradually surround the nucleus and begin to fuse. Just before migration of the nucleus, the partially fused lipid droplets move to the side of the nucleus opposite the direction of nuclear migration. The location of the oil droplets on one side of the nucleus is a unique character that signals the onset of the migratory-nucleus stage. For this reason, migratory-nucleus-stage oocytes can be detected much earlier in species with an oil droplet—such as Pacific sardine; Pacific mackerel, *Scomber japonicus*, (Dickerson et al. 1992); or jack mackerel, *Trachurus symmetricus*, (Macewicz and Hunter 1993)—than in species such as the northern anchovy, which lack an oil droplet.

We classified atresia in ovarian sections by using the system of Bretschneider and Duyvene de Wit (1947) and Lambert (1970), as modified by Hunter and Macewicz (1985b). The presence or absence of alpha (α) atresia of previtellogenic, early vitellogenic, or advanced-yolked oocytes, and beta (β) atresia was recorded. We use β atresia in ovaries with only unyolked oocytes and without postovulatory follicles to identify postbreeding females. Postbreeding females are mature females that are no longer active and considered to be incapable of further spawning in the season.

Maturity was calculated as the fraction of all females that were histologically classified as mature. Immature females have ovaries with no β atresia and only unyolked oocytes present (a few oocytes in the earliest stage of yolk deposition may be present). Some ovaries classed as immature may contain α atresia of unyolked oocytes. All females not identified as immature were considered mature. Females were grouped into 10-mm length classes, and the length at which 50% were mature was estimated by logistic regression by means of the computer program BMDPLR (Dixon et al. 1988).

Spawning Frequency

We used aged postovulatory follicles to estimate spawning frequency of Pacific sardine, following the methods of Hunter and Goldberg (1980) and Hunter and Macewicz (1985b). The best method for establishing aging criteria for postovulatory follicles is to spawn fish in the laboratory and sample at known times after spawning, but this has not been done for Pacific sardine. All previous investigators (Goldberg et al. 1984; Alarcón et al. 1984; Retamales and González 1984; Aguilera et al. 1986; and Torres-Villegas 1986) developed their aging criteria by examining a time series of field-collected material and by assuming the peak hour of spawning. We also relied on this method; our resulting histological criteria were essentially the same as those described by Goldberg et al. (1984). Thus the presence of hydrated oocytes or new (without deterioration) postovulatory follicles was used to estimate spawning frequency of females spawning on the night of capture, and the presence of older postovulatory follicles (about 20–30 h old) was used to estimate the spawning frequency of females that had spawned the night before capture.

Batch Fecundity

Batch fecundity (F_b, number of oocytes per spawn) was considered to be the number of migratory-nucleus-stage oocytes or number of hydrated oocytes in the ovary (Hunter et al. 1985). Females that may have lost oocytes

Andrews, C. B. 1931. The development of the ova of the California sardine (*Sardina caerulea*). Unpubl. MS. 88 pp. Stanford University, Stanford, CA 94305.

because they had begun to ovulate and spawn (ovaries with hydrated oocytes and new postovulatory follicles) were not used to determine batch fecundity. We used the gravimetric method to estimate batch fecundity (Hunter et al. 1985, 1992). We teased apart the oocytes in a few drops of 50% glycerin, and identified, counted, and measured them with a digitizer linked by a video camera system to a dissection microscope. We averaged the counts in two or more weighed tissue samples (usually one sample from the central region of each side of an ovary). We estimated mean batch fecundity for 51 females (6 based on counts of hydrated oocytes, and the remaining 45 on counts of migratory-nucleus-stage oocytes) and then determined the relation to female weight (without ovary).

We did not test for how the location of the tissue sample affects batch fecundity estimates. Lo et al. (1986) indicated that such an effect may exist for Peruvian sardine, whereas Clark (1934) and MacGregor (1957) found no such effect for Pacific sardine off California. Our tissue samples came from the central region of the ovary. According to Lo et al. (1986), fecundity estimates based on this location are about 4% higher than the average for hydrated ovaries of Peruvian sardine.

In fecundity preparations from formalin-preserved material, migratory-nucleus-stage and hydrated oocytes are easily identified. Hydrated oocytes are very large and translucent, with faint segmentation resulting from the fusing of yolk globules into "large plates." Oocytes with late-stage migratory nuclei are larger and less opaque than the other yolked oocytes and may have a wide, clearish, peripheral band that results from the fusion of some yolk globules. In addition, a reflective oil drop (or several if lipid droplets are still fusing) is prominent in the migratory-nucleus and hydrated-oocyte stages. Migratory-nucleus-stage oocytes are detectable in whole oocyte material only after most of the lipid droplets have accumulated and begun to fuse. Earlier stages involving movement and fusion of lipid droplets can be consistently detected only in histological sections.

RESULTS AND DISCUSSION

Size, Sex, and Maturity

Standard length of sardine in the samples ranged from 131 to 284 mm for females and from 128 to 283 mm for males (figure 1). The proportion by weight of the population that was female was 0.537 (Lo et al. 1996). Following the recommendation of Picquelle and Stauffer (1985), we adjusted for bias in female weight caused by females with hydrated ovaries by using the linear regression equation (table 2) for the area north of 32°04'N latitude, where all the hydrated females were taken. The

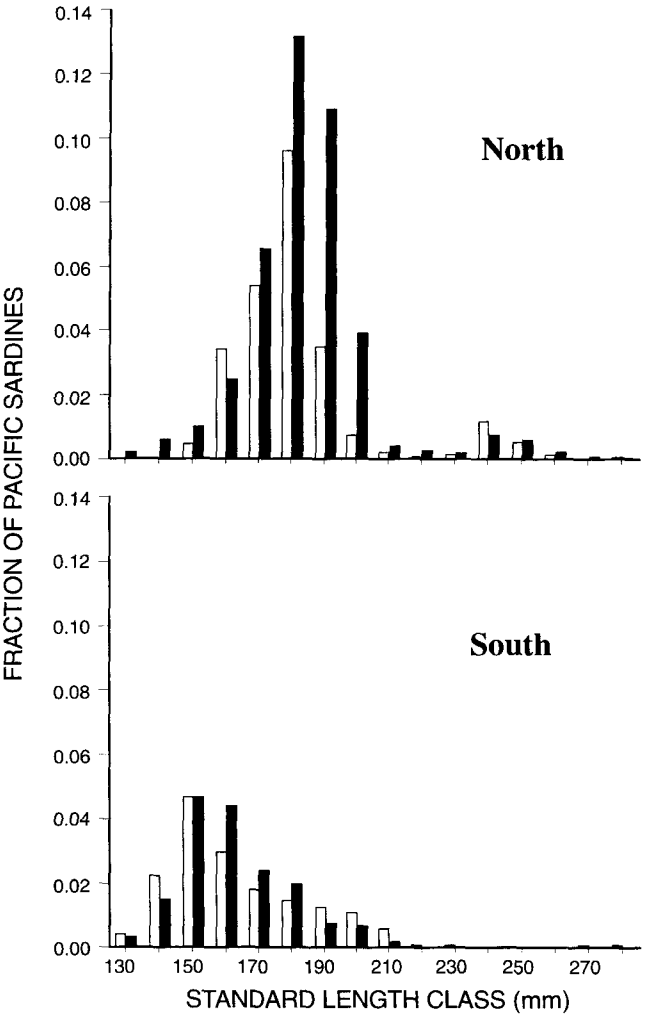

Figure 1. Length distribution for Pacific sardine (total N = 1,343) in the random subsamples taken by trawls and purse seines during 1994, for areas north and south of 32°04'N latitude. Males = *open bar*; females = *closed bar*.

mean whole wet weight and ovary-free wet weight of the mature females (N = 583) used to estimate spawning frequency was 82.5 grams and 79.3 grams, respectively (table 3).

According to logistic regression results (table 4), 50% of the females taken in the survey were sexually mature at a standard length of 158.6 mm (figure 2). We divided the females into the same three latitudinal areas used by Butler et al. (1996) and determined the length at 50% mature and the 95% confidence interval (CI) for each area (table 4). We compared two methods of using CI to detect differences in population means (Lo 1994), and neither detected a difference in the populations. Therefore we feel confident that we can pool the data and that our estimate (158.6 mm) is acceptable over the whole area studied during 1994.

TABLE 3
Parameters for Mature Female *Sardinops sagax* Used in Estimation of 1994 Biomass from Individual Samples

Collection number	Number of mature females	Average whole weight (g)	Average ovary-free weight (g)	Average batch fecundity (oocytes)	Number of females spawning	
					Night of capture	Night before capture
667	23	78.0	75.7	22,704	0	0
666	9	83.8	81.4	25,180	0	0
664	24	98.7	94.6	31,014	0	0
665	25	89.2	86.0	27,196	0	0
663	25	95.6	91.7	29,725	0	0
643	25	79.7	77.4	23,449	6	2
642	2	85.0	82.3	25,593	0	1
660	25	86.4	84.2	26,416	0	0
659	25	87.0	84.6	26,592	0	0
662	22	73.8	71.8	20,953	0	1
655	18	83.9	82.2	25,545	0	0
661	8	77.0	74.0	21,937	0	0
656	15	75.7	74.0	21,956	0	0
657	2	61.0	59.2	15,442	0	0
649	16	70.8	67.1	18,909	2	3
648	25	65.4	62.4	16,827	8	3
645	5	100.2	94.2	30,833	1	2
644	8	88.2	83.7	26,190	5	0
634	25	86.9	83.0	25,907	1	5
646	25	84.6	79.0	24,130	0	0
629	25	80.1	76.9	23,212	0	6
630	25	82.9	79.0	24,148	2	4
611	25	192.9	178.2	67,738	0	0
623	2	215.5	192.8	74,181	0	0
685	4	34.9	34.8	4,694	0	0
683	25	52.6	52.0	12,278	0	6
682	25	36.9	36.7	5,545	0	0
684	1	33.4	33.3	4,043	0	0
687	6	61.8	60.6	16,045	0	0
679	2	29.0	28.9	2,099	0	0
680	3	27.7	27.6	1,551	0	0
675	1	63.0	62.2	16,762	0	0
615	25	106.0	101.6	34,076	11	4
672	25	49.4	48.3	10,630	0	3
673	6	60.0	59.6	15,621	0	0
670	6	51.7	51.2	11,930	0	0
668	25	77.8	77.3	23,382	0	3
All	583	82.5	79.3	24,282	36	43
SE		1.4	1.2	2,617		

TABLE 4
Logistic Model[a] Parameters and Estimated Standard Length at Which 50% of Pacific Sardine Females Were Sexually Mature

Latitudinal area[b]	Length at 50% mature (mm)	95% CI	*a*	SE	*b*	SE	*N*
26°35'–36°55'N	158.6	155–162	−18.16	1.55	0.1145	0.0094	632
36°35'–36°55'N	160.6	128–191	−22.31	4.72	0.1389	0.0277	125
31°35'–33°59'N	159.3	156–162	−19.53	1.92	0.1226	0.0117	443
26°35'–30°25'N	159.1	154–163	−18.60	3.83	0.1169	0.0237	103

[a] $P = \frac{e^{a+bL}}{1+e^{a+bL}}$

[b] Data from whole 1994 survey and divided into three areas.

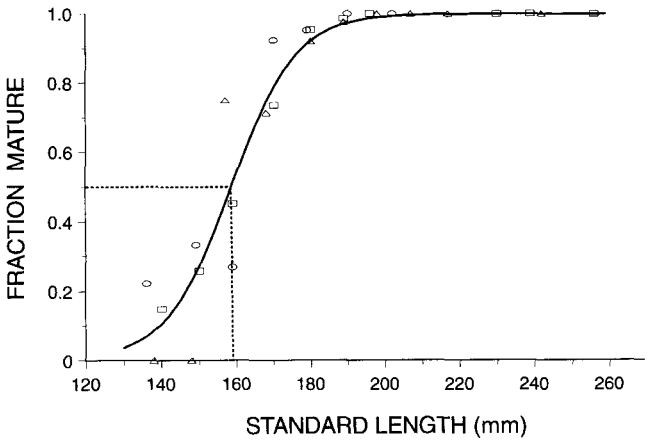

Figure 2. Fraction of Pacific sardine females that were sexually mature as a function of standard length (logistic curve parameters: $a = -18.16$; $b = 0.1145$). *Dotted line*, estimated length at which 50% of the females were mature (158.6 mm). Curve estimated from random females caught within entire 1994 survey area. Symbols represent actual fraction mature within 10-mm length classes for females in each latitudinal area: *triangle* = 36°35'N–36°55'N; *square* = 31°35'N–33°59'N; and *circle* = 26°35'N–30°25'N.

Batch Fecundity

The relation between female weight (without ovary, W_{of}) and batch fecundity (F_b) for the 51 females taken in the 1994 survey (table 5), as determined by simple linear regression, was

$$F_b = -10{,}585 + 439.53 W_{of}$$

where $r^2 = 0.92$, and W_{of} ranged from 39 to 231 g (table 6). We tried using a power function to model the relationship, but it did not fit the data as well ($r^2 = 0.85$). Additionally, a linear function is easier to use in comparisons and during computations for biomass estimation. Thus we used the above equation to predict batch fecundity for each of the 583 mature Pacific sardine females used to estimate spawning frequency. The mean predicted batch fecundity for these females was 24,282 oocytes (table 3), equivalent to a relative fecundity of 306 oocytes per gram fish weight (24,282 oocytes/79.3-g female).

We used covariance analysis to test for differences in the relation between batch fecundity and female weight (without ovary) in sardine from 1986, 1987, and 1994. California Department of Fish and Game (CDFG) provided the data sets for females collected during past Pacific sardine surveys off southern California in 1986 ($N = 44$) and 1987 ($N = 56$). No statistical difference existed among slopes from the three data sets ($P = 0.234$). Assuming that the slopes were equal, covariance analysis indicated that the adjusted group means were not different at the 5% significant level ($F_{2, 147} = 3.00$, $P = 0.053$). Combining the data from all three years (figure 3) yielded the equation

$$F_b = -13{,}677 + 471.79 W_{of}$$

TABLE 5
Batch Fecundity[a] of 51 *Sardinops sagax* Females Taken in 1994

Collection number	Fish number	Standard length (mm)	Body weight without ovary (g)	Ovary weight (g)	Batch fecundity (oocytes)
672	26	149	39.13	2.400	6,012
672	65	158	47.20	2.300	8,492
648	63	161	50.00	15.380	19,553
648	23	160	51.83	4.060	12,863
672	63	167	53.74	2.900	7,177
648	37	168	57.63	4.318	16,885
683	02	183	58.00	5.400	13,434
649	40	168	59.88	5.301	17,578
648	51	170	61.06	23.005	28,027
649	29	171	63.78	5.404	17,776
648	10	172	64.56	8.260	22,863
672	70	174	65.57	4.400	19,711
646	15	170	66.50	8.330	23,880
648	22	171	67.42	4.599	14,473
630	27	181	70.66	5.568	16,921
646	30	174	73.70	8.072	24,676
646	07	175	74.15	10.067	25,097
646	06	176	75.22	6.126	22,284
630	39	182	75.81	9.217	27,262
648	27	182	76.59	19.762	22,035
646	24	184	76.71	10.632	29,928
646	28	185	78.36	7.224	25,516
646	02	180	78.69	6.809	23,258
648	05	192	79.76	29.789	31,698
630	18	192	80.20	8.724	29,920
646	10	184	80.76	11.850	26,955
661	07	184	81.49	8.349	25,757
634	08	187	81.71	4.219	12,376
646	13	178	81.90	7.821	24,728
661	05	186	82.99	5.140	23,583
630	21	189	86.84	10.456	25,510
615	11	191	87.25	7.375	22,930
646	12	189	88.40	9.740	26,767
634	05	192	89.47	7.095	25,141
615	19	197	92.24	9.957	28,842
615	57	197	95.48	7.072	21,116
644	55	200	98.22	9.969	31,637
645	30	197	99.17	12.599	31,453
648	01	202	104.85	36.085	32,152
615	37	200	105.69	9.388	30,993
615	59	208	112.78	11.815	32,260
611	37	237	149.73	14.446	48,305
611	30	238	151.93	18.035	51,265
662	54	242	162.49	18.605	57,233
611	66	247	169.00	24.354	75,422
611	39	251	183.12	21.635	60,301
611	18	250	184.95	26.990	76,034
623	02	255	196.88	32.211	82,695
611	59	265	197.20	24.103	64,647
611	27	267	198.87	28.375	91,603
611	52	290	230.67	40.169	94,486

[a]Batch fecundity—number of oocytes to be spawned in the batch—was determined from counts of hydrated oocytes or migratory-nucleus-stage oocytes in the ovary.

TABLE 6

Linear Regression Coefficients for the Relation between Female Weight (W_{of}, Ovary-Free, in g) and Batch Fecundity (F_b) for Pacific Sardine, *Sardinops sagax*, from 1946 (MacGregor 1957), 1986, 1987, 1994, and the Three Recent Years Combined

	Linear equation $F_b = a + bW_{of}$								Estimate for 130-g	Female weight	
Year	a	SE	b	SE	r^2	F	s^a	N	female	Mean	Range
1994	−10,585	1,907	439.53	17.78	0.93	611	5,844	51	46,554	97	39–231
1986	−21,018	9,330	495.76	52.65	0.68	89	11,890	44	43,430	174	103–244
1987	−21,088	10,564	531.83	62.72	0.57	72	14,763	56	48,050	165	97–237
1986–94	−13,677	2,874	471.79	18.73	0.81	634	11,735	151	47,658	145	39–244
1946	3,300	NA	250.00	NA	0.60	NA	5,100	40	35,800	132	95–169

[a] s is the square root of the MS error of the regression line.

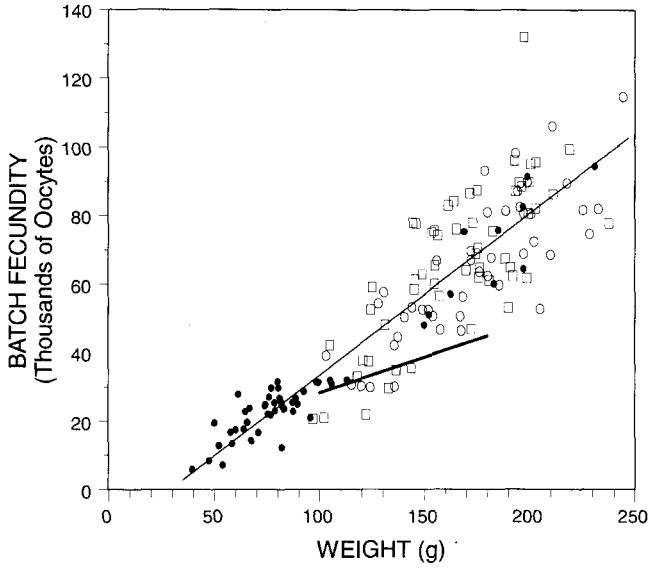

Figure 3. Batch fecundity (F_b) of *Sardinops sagax* as a function of female weight (W_{of}, without the ovary) for 151 females taken during 1994 (*closed circle*), 1986 (*open circle*), and 1987 (*open square*). The batch was estimated from numbers of migratory-nucleus-stage oocytes or hydrated oocytes. The fitted regression line was $F_b = -13{,}677 + 471.79\ W_{of}$ where $r^2 = 0.81$ (*thin line*). For comparison, we include the regression $F_b = 3{,}300 + 250W_{of}$ (*thick line*) for 40 sardine females taken in 1946 (MacGregor 1957).

where $r^2 = 0.81$, and W_{of} ranged from 39 to 244 grams (table 6).

MacGregor (1957) estimated that the relation between batch fecundity and female ovary-free weight for 40 Pacific sardines captured in February 1946 was $F_b = 3{,}300 + 250W_{of}$ ($r^2 = 0.60$). We compared the slope of his regression to the slope of the regression for the combined data ($N = 151$) from the recent studies and the estimated batch fecundity from each model for a 130-g fish (without ovary). Both the slopes and predicted value for batch fecundity differed significantly (slopes, $t = -4.94$; estimated fecundity at 130 g, $t = -9.25$).

It is possible that the difference in batch fecundity may be due to the techniques used by MacGregor (1957). He states that he estimated fecundities only for ovaries with a distinct group of advanced-yolked ova differentiated by size from the smaller-yolked ova. This could cause an underestimate of fecundity if the oocytes destined to form the hydrated batch were not fully recruited into the modal group counted by MacGregor.

Alternatively, this difference may be related to the biomass of the stock, since the estimated biomass of Pacific sardine in 1986, 1987, and 1994 was 44, 69, and 246 thousand MT, respectively (age 1+, Deriso et al. 1996); whereas in 1946, when MacGregor took his samples, it was estimated to be 566 thousand MT (age 2+, MacCall 1979). Both batch fecundity and somatic growth (see Butler et al. 1996) were apparently lower when the population of Pacific sardine was higher. Thus, more food may have been available per sardine in recent times (1986–94) than in the past.

Spawning Frequency

The average percentage of female sardine spawning per day was 6.2% when the estimate was based on females spawning on the night of capture, and 7.4% when based on females that had spawned the night before capture (table 3). Thus both estimates of spawning frequency for sardine were similar. This was not the case for northern anchovy: females spawning on the night of capture were believed to be more vulnerable to the trawl and thus oversampled (Picquelle and Stauffer 1985). Although frequencies estimated for female Pacific sardine spawning on the night of capture may be less reliable (see discussion on time of day and spawning), we found no indication of overestimation due to sampling bias. Combining the rates for the two nights resulted in an average estimate of 6.8% of the mature females spawning per day. Thus in April–May of 1994 the average mature female in the population spawned about once every 15 days.

A geographic pattern may exist in spawning rates, with sardine in the most southern section of the pattern (26°38'N–30°25'N latitude) spawning at nearly twice the rate of females farther north (table 7). Strangely, none of the fish taken at the northern end of the pattern had spawned recently; in fact, most females were in a post-breeding condition. The northern samples were taken on a commercial vessel that fished nearshore in Monterey Bay. Considering the small number of collections and the opportunistic nature of our sampling, it seems premature to conclude that a fixed geographic trend existed

TABLE 7
Average Percentage of Mature Pacific Sardine Females Spawning per Day during 1994 in Three Areas

Latitudinal area	Female ovarian state[a]	Number of females	Mature females percent spawning: Night of capture	Mature females percent spawning: Night before capture	Average fraction spawning per day
36°35'–36°55'N	Active	13	0.0	0.0	0.000
	All mature	106	0.0	0.0	0.000
31°35'–33°59'N	Active	270	9.3	12.2	0.107
	All mature	389	6.4	8.5	0.074
26°38'–30°25'N	Active	44	25.0	22.7	0.233
	All mature	88	12.5	11.4	0.120
Total	Active	327	11.0	13.1	0.121
	All mature	583	6.2	7.4	0.068

[a]Active mature females are capable of spawning and have ovaries containing oocytes with yolk or postovulatory follicles less than 48 hours old. "All mature" females include mature females that are postbreeding and incapable of further spawning this season.

in reproductive traits. It seems likely, however, that there was strong local patchiness in reproductive traits.

The spawning rates described above are our best estimates of the population rate during the 1994 survey period. The population rate (spawning females divided by all mature females) is a requirement of the DEPM model (Picquelle and Stauffer 1985) and includes in the denominator not only females with reproductively active ovaries, but also mature females classed as postbreeding (inactive). If the postbreeding females are excluded from the denominator, one obtains a measure of the spawning rate of the reproductively active females in the population. The average active female spawning rate was 12.1%, about twice the population spawning rate, because nearly half the females were in postbreeding condition (table 7). Thus the average Pacific sardine female may have spawned once every 8 days during her reproductive season in 1994.

Comparisons of Sardine Spawning Frequency Estimates

In making comparisons, it is better to use the spawning frequency for active females rather than the population rate. Population spawning rates not only depend on the spawning rate of active females but are also a function of the fraction of active females, which varies seasonally. We compared the spawning frequency of active female sardine in the 1994 survey to rates from CDFG surveys in 1986, 1987, and 1988. The average fraction of active females spawning per day (table 8) was 12%–13% in 1986, 1987, and 1994, and 20% in 1988, with a grand mean of 14.9%. The mean based only on females spawning the night before capture, possibly a more reliable method, was 13.7%. Thus, over the 1986–94 period, the average duration of the spawning cycle for active Pacific sardine off California seems to have been about 7 days.

To compare spawning rates for active sardine off California with values from the literature for sardines from around the world, we made the following assumptions:

1. Population rates are equivalent to the active rate of spawning, since they are not usually distinguished in the literature.

TABLE 8
Summary of Estimated Percent Spawning for Pacific Sardine off California and Baja California during 1986–1994

Adult survey midpoint date & organizations[a]	Survey area (# of collections)	Gear type[b]	Female ovarian state[c]	Number of females	Mature females percent spawning: Night of capture	Mature females percent spawning: Night before capture	Average fraction spawning per day
April 22, 1994 NMFS, INP, CDFG	Monterey Bay, USA, to San Ignacio Lagoon, Mexico (37)	P, T	Active	327	11.0	13.1	0.121
			All mature	583	6.2	7.4	0.068
Aug. 9, 1986 CDFG	Point Conception, USA, to international border (12)	P, T	Active	322	14.0	11.5	0.127
			All mature	323	13.9	11.4	0.127
July 26, 1987 CDFG	Point Conception, USA, to international border (13)	P	Active	409	7.1	17.1	0.121
			All mature	431	6.7	16.2	0.115
May 13, 1988 CDFG	Monterey Bay, USA, to international border (19)	P, HL	Active	557	27.1	12.9	0.200
			All mature	746	20.2	9.6	0.149
All			Active	1615	16.2	13.7	0.149
			All mature	2083	12.5	10.6	0.116

[a]National Marine Fisheries Service (NMFS), Mexican National Fisheries Institute (INP), California Dep. of Fish and Game (CDFG)
[b]Sardine were collected by purse seine (P), midwater trawls (T), or hook and line (HL).
[c]"Active" mature females are capable of spawning and have ovaries containing oocytes with yolk or postovulatory follicles less than 48 hours old. "All mature" females include mature females that are postbreeding and incapable of further spawning this season.

TABLE 9
Comparison of Spawning Rates for *Sardinops* around the World

Species	Area	Percent spawning per day[a]	Reference
S. sagax	California & Baja Calif.	13.7	Table 8, this paper (mean of 1986–94)
S. sagax	N. Chile	17.8	Retamales and González 1984
S. sagax	S. Chile	10.6[b]	Aguilera et al. 1986
S. melanostictus	SW. Japan	11.5[b]	Aoki and Murayama 1993 Murayama et al. 1994 Matsuyama et al. 1994
S. neopilchardus	W. Australia	11.0	Fletcher, in press (mean of 1991–92)
S. ocellatus	South Africa	10.5[b]	Le Clus 1989 (Sept. 1973–Feb. 1974)
	All	12.5	

[a]In these comparisons, we averaged only midseason peak values if multiple values were given.
[b]We calculated the spawning rate from data in the references.

2. A female with migratory-nucleus-stage (MN) oocytes will most likely spawn the night after capture (considered one spawning event).
3. Hydrated, or final-maturation, oocytes and new postovulatory follicles occur only on the night of spawning.
4. When the number of females with postovulatory follicles (not aged separately) is added to the number of hydrated females, two spawning nights are indicated (thus the combined number is divided by 2).
5. "Beyond the commencement of hydration" (Le Clus 1989) includes the earliest stages of MN oocytes as well as fully hydrated oocytes (thus the combined number is divided by 2).

These assumptions lead us to conclude that the overall mean sardine spawning rate from California and Baja California, northern Chile, southern Chile, South Africa, western Australia, and Japan was 12.5%, which is equivalent to each female spawning about once a week (table 9). We assumed that 12.5% spawning per day is a midseason rate for active female sardine.

Time of Day and Spawning

The time of peak spawning each night is essential to DEPM spawning biomass estimates because the assumed peak time affects how ages are assigned to egg stages, and ultimately the estimates of egg mortality and daily production of eggs (Picquelle and Stauffer 1985). Females identified as spawning on the night of capture (ovaries containing hydrated oocytes, new postovulatory follicles 0–5 h old, or both) can be used to estimate when the time of daily peak spawning occurs (Hunter and Macewicz 1980). The number of females in the 1994 survey was insufficient to carry out a meaningful analysis of occurrence of histological stages by hour. We therefore combined the 1994 data with the original data from the 1986–88 CDFG sardine DEPM surveys off California. The time of day for each collection was assumed to be the midpoint between the time at the beginning and end of the trawl or purse seine set. All sardine were captured between 1929 at night and 0825 in the morning.

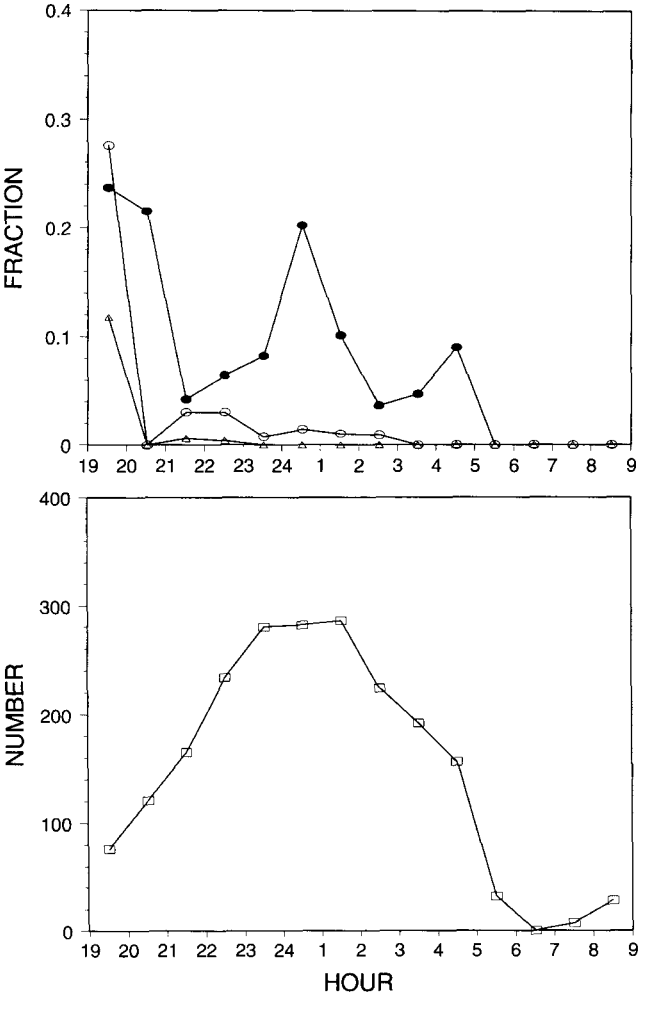

Figure 4. *Top*, Fraction of mature females caught in each hour that were identified as spawning on the night of capture by the histological presence in the ovaries of hydrated oocytes (*triangles*), hydrated oocytes and new postovulatory follicles (*open circles*), or only new postovulatory follicles (*closed circles*). *Bottom*, Number of mature sardine females sampled in each hour; mature females from four surveys taken in 1986, 1987, 1988, and 1994.

Females with hydrated ovaries were caught until 2259, with the highest fraction occurring just after sunset, between 1900 and 1959 (figure 4). Females in the act of spawning (both hydrated oocytes and new postovulatory follicles present in ovary) were captured from 1900 to 0259, with a peak between 1900 and 2259 (figure 4). Analyses of staged Pacific sardine eggs (Lo et al. 1996) indicated that the time of peak spawning was about 2100, which agrees with our findings. Peak spawning time for

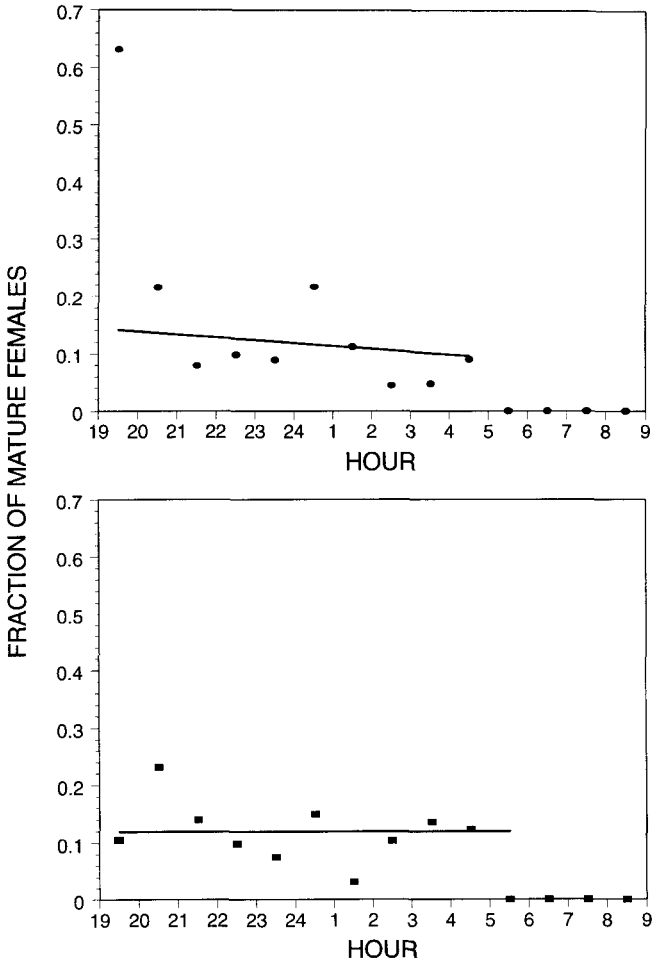

Figure 5. Fraction of mature females caught in each hour that were spawning on the night of capture (*upper panel*) or had spawned the night before capture (*lower panel*). The slope of the regression line was not significant (calculated over 1900–0459 h; $P = 0.417$) for females that spawned the night before capture (ovaries contained 18–31-h-old postovulatory follicles), but for females spawning the night of capture, the line indicated a decreasing trend with time ($P = 0.050$).

sardines off California is similar to the peak times reported for Pacific sardine, *Sardinops sagax musica*, off Ecuador (2000–2300; Coello 1988) and northern Chile (2100–2359; Retamales and Gonzâlez 1984) and for the Japanese sardine, *Sardinops melanostictus*, off southwestern Japan (2000–2300; Morimoto 1993; Matsuyama et al. 1994).

The data for Pacific sardine off California during 1986–88 and 1994 were also examined to determine if biases existed in estimates of reproductive states due to sampling time. The fraction of females judged to have spawned the night before capture (ovaries with ~24-h-old postovulatory follicles) was not affected by time of capture (figure 5, lower panel); in fact, the slope of the trend line did not differ from 0 ($P = 0.417$). This result indicates that the use of females with ~24-h-old postovulatory follicles provides an unbiased estimate of spawning rate.

In some pelagic species, females with hydrated ovaries may be oversampled, presumably because of increased vulnerability to the trawl or purse seine (*Engraulis mordax*; Picquelle and Stauffer 1985; *Engraulis ringens*; Alheit 1985). When the numbers of sardine females with hydrated oocytes, new postovulatory follicles, or both are combined, there is a significant ($P = 0.050$) decreasing slope with time (figure 5, upper panel). If all stages were equally vulnerable to the capture gear at all times, there should be no trend, because the decline in number of females with hydrated ovaries should be offset by an increase in the number of females with new postovulatory follicles (0–5-h old). The trend is largely due to very high values for all three stages during 1900 h (figure 4), when only 2 collections were taken. We recommend that additional adult collections be taken between 1700 h and 2000 h before conclusions about vulnerability of hydrated females are drawn.

Incidence of Postbreeding Females, Indicator of Sardine Movements?

A striking feature of the April 1994 survey was the high incidence of postbreeding females. Since peak spawning of sardine in the Southern California Bight (1951–89) is thought to be May–June (Hernández-Vázquez 1994), these results are counterintuitive. The percentage of postbreeding females by month from surveys during 1986–88 and 1994 was calculated from table 8 as: April (1994) 44%; May (1988) 25%; July (1987) 5%; and August (1986) 0.3%. Thus the three surveys carried out by CDFG also indicate counterintuitive seasonal trends in the incidence of postbreeding females.

Why does the number of postbreeding females decrease as the season progresses? We hypothesize that after spring spawning in the bight, sardine move north, and may be replaced by sardines migrating into the bight from the south. Two sources of information support our hypothesis: first, the peak spawning season of sardine in the south (Punta Eugenia region) is in August and September (Hernández-Vázquez 1994); and second, tagging results and timing of the historical sardine fishery indicate that sardine from the bight migrate north after spawning (Clark 1952).

Another possible hypothesis is that the apparent monthly trend in postbreeding females occurred by chance—the result of the extreme patchiness of reproductive traits (including the seasonality of spawning) and our partially opportunistic sampling of adult sardine in the north and south.

Thus the results can be best explained either by contagion in the regional timing and duration of the spawning season, or by movements of adult sardines along

the coast (or by a combination of these effects). Both hypotheses involve levels of biological complexity that we do not yet fully understand.

ACKNOWLEDGMENTS

Our ability to interpret data from the cruise was greatly enhanced by the addition of adult sardine reproductive data from 1986–88 provided by the California Department of Fish and Game (CDFG). We wish to thank the CDFG and, in particular, P. Wolf, T. Dickerson, K. Mais, K. Worcester, R. Reed, E. Konno, T. Bishop, and M. Larson. We thank all on shipboard who helped collect Pacific sardine ovaries during the 1994 survey: A. Ruiz, J. Sanchez, R. Sanchez, M. L. Granados, P. Diaz, B. Leos, T. Barnes, T. Bishop, E. Konno, W. Chou, H. Fish, E. Acuna, D. Ambrose, S. Charter, R. Dotson, and D. Griffith. O. Tapia V. assisted in the laboratory. N. C. H. Lo gave statistical advice. R. Charter and D. Prescott updated computer programs.

LITERATURE CITED

Aguilera, E. A., C. Oyarzún, and J. Chong. 1986. Reproductive cycle of the Pacific sardine, *Sardinops sagax musica* (Girard, 1854) from the fishery area of Talcahuano, Chile (1983–1984). Biología Pesquera 15:45–53.

Alarcón, V. H., S. R. Goldberg, and J. Alheit. 1984. Histología de folículos postovulatorios de la sardina (*Sardinops sagax*) del Perú. Bol. Inst. Mar Perú-Callao 8(1):1–16.

Alheit, J. 1985. Spawning frequency of Peruvian anchovies taken with a purse seine. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*), R. Lasker, ed. NOAA Tech. Rep. NMFS 36, pp. 59–61.

Aoki, I., and T. Murayama. 1993. Spawning pattern of the Japanese sardine *Sardinops melanostictus* off southern Kyushu and Shikoku, southwestern Japan. Mar. Ecol. Prog. Ser. 97:127–134.

Arenas, P. R., J. R. Hunter, and L. D. Jacobson. 1996. The 1994 Mexico–U.S. spawning biomass survey for Pacific sardine (*Sardinops sagax*) and the 1995 CalCOFI sardine symposium. Calif. Coop. Oceanic Fish. Invest. Rep. 37 (this volume).

Bretschneider, L. H., and J. J. Duyvene de Wit. 1947. Sexual endocrinology of non-mammalian vertebrates. Monogr. Prog. Res., vol. II. New York: Elsevier.

Butler, J. L., B. J. Macewicz, M. L. Granados G., J. T. Barnes, and M. Yaremko. 1996. Age composition, growth, and maturation of the Pacific sardine (*Sardinops sagax*) during 1994. Calif. Coop. Oceanic Fish. Invest. Rep. 37 (this volume).

Clark, F. N. 1934. Maturity of the California sardine (*Sardina caerulea*), determined by ova diameter measurements. Calif. Dep. Fish Game, Fish Bull. 42, 49 pp.

———. 1952. A review of the California sardine fishery. Calif. Fish Game 38(3):367–380.

Coello, S. 1988. Time of day of spawning in *Sardinops sagax* (Jenyns). J. Fish Biol. 33:655–656.

Deriso, R. B., J. T. Barnes, L. D. Jacobson, and P. R. Arenas. 1996. Catch-at-age analysis for Pacific sardine (*Sardinops sagax*), 1983–95. Calif. Coop. Oceanic Fish. Invest. Rep. 37 (this volume).

Dickerson, T. L., B. J. Macewicz, and J. R. Hunter. 1992. Spawning frequency and batch fecundity of chub mackerel, *Scomber japonicus*, during 1985. Calif. Coop. Oceanic Fish. Invest. Rep. 33:130–140.

Dixon, W. J., M. B. Brown, L. Engelman, M. A. Hill, and R. I. Jenrich. 1988. BMDP statistical software manual, vol 2. Los Angeles: Univ. Calif. Press, 1,234 pp.

Fletcher, R. In press. Use of the daily egg production method to estimate the stock size of Western Australian sardines (*Sardinops sagax*). Aust. J. Mar. Freshwater Res. 48.

Goldberg, S. R., V. H. Alarcón, and J. Alheit. 1984. Postovulatory follicle histology of the Pacific sardine, *Sardinops sagax*, from Peru. Fish. Bull., U.S. 82:443–445.

Hernández-Vázquez, S. 1994. Distribution of eggs and larvae from sardine and anchovy off California and Baja California, 1951–1989. Calif. Coop. Oceanic Fish. Invest. Rep. 35:94–107.

Hunter, J. R., and S. R. Goldberg. 1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641–652.

Hunter, J. R., and B. J. Macewicz. 1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139–149.

———. 1985a. Measurement of spawning frequency in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*), R. Lasker, ed. NOAA Tech. Rep. NMFS 36, pp. 79–94.

———. 1985b. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 83:119–136.

Hunter, J. R., N. C. H. Lo, and R. J. H. Leong. 1985. Batch fecundity in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*), R. Lasker, ed. NOAA Tech. Rep. NMFS 36, pp. 67–77.

Hunter, J. R., B. J. Macewicz, N. C. H. Lo, and C. A. Kimbrell. 1992. Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. Fish. Bull., U.S. 90:101–128.

Lambert, J. G. D. 1970. The ovary of the guppy *Poecilia reticulata*. The atretic follicle, a *Corpus atreticum* or a *Corpus luteum praeovulationis*. Z. Zellforsh 107:54–67.

Le Clus, F. 1989. Size-specific seasonal trends in spawning of pilchard *Sardinops ocellatus* in the northern Benguela system, 1973/74. S. Afr. J. Mar. Sci. 8:21–31.

Lo, N. C. H. 1994. Level of significance and power of two commonly used procedures for comparing mean values based on confidence intervals. Calif. Coop. Oceanic Fish. Invest. Rep. 35:246–253.

Lo, N. C. H., J. Alheit, and B. Alegre. 1986. Fecundidad parcial de la sardina Peruana (*Sardinops sagax*). Bol. Inst. Mar. Perú-Callao 10(2):45–60.

Lo, N. C. H., Y. A. Green R., M. J. Cervantes, H. G. Moser, and R. J. Lynn. (1996). Egg production and spawning biomass of Pacific sardine (*Sardinops sagax*) in 1994 determined by the daily egg production method. Calif. Coop. Oceanic Fish. Invest. Rep. 37 (this volume).

MacCall, A. D. 1979. Population estimates for the waning years of the Pacific sardine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 20:72–82.

Macewicz, B. J., and J. R. Hunter. 1993. Spawning frequency and batch fecundity of jack mackerel, *Trachurus symmetricus*, off California during 1991. Calif. Coop. Oceanic Fish. Invest. Rep. 34:112–121.

MacGregor, J. S. 1957. Fecundity of the Pacific sardine (*Sardinops sagax*). U.S. Fish. Wildl. Serv. Fish. Bull. 57(121):427–449.

Matsuyama, M., T. Fukuda, S. Ikeura, Y. Nagahama, and S. Matsuura. 1994. Spawning characteristics and steroid hormone profiles in the wild female Japanese sardine *Sardinops melanostictus*. Fish. Sci. 60:(6)703–706.

Morimoto, H. 1993. Time of maximal oocyte hydration and spawning in the Japanese sardine in Tosa Bay, southwestern Japan. Nippon Suisan Gakkaishi 59:7–14.

Murayama, T., M. Shiraishi, and I. Aoki. 1994. Changes in ovarian development and plasma levels of sex steroid hormones in the wild female Japanese sardine (*Sardinops melanostictus*) during the spawning period. J. Fish. Biol. 45:235–245.

Parker, K. 1980. A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass. Fish. Bull., U.S. 78:541–544.

———. 1985. Biomass model for the egg production method. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*), R. Lasker, ed. NOAA Tech. Rep. NMFS 36, pp. 5–6.

Picquelle, S., and G. Stauffer. 1985. Parameter estimation for an egg production method of northern anchovy biomass assessment. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*), R. Lasker, ed. NOAA Tech. Rep. NMFS 36, pp. 7–15.

Retamales, R., and L. González. 1984. Fecundidad de sardina española (*Sardinops sagax musica*). Programa Estudio de Recursos Pelágicos. Corporación. Gerencia de Desarrollo. Instituto de Fomento Pesquero, Chile AP84–5.

Scannell, 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. SWFSC Admin. Rep., La Jolla, LJ-96-01, 37 pp.

Torres-Villegas, J. R. 1986. Evaluación de *Sardinops sagax* por el método de producción de huevos, en Bahía Magdalena, B.C.S., México. Tesis MS CICIMAR-I.P.N. La Paz, B.C.S. México, 116 pp.

Wallace, R. A., and K. Selman. 1981. Cellular and dynamic aspects of the oocyte growth in teleosts. Am. Zool. 21:325–343.

Wolf, P. 1988a. Status of the spawning biomass of the Pacific sardine, 1987–1988. Calif. Dep. Fish Game, Mar. Res. Div., Rep. to the legislature, 9 pp.

———. 1988b. Status of the spawning biomass of the Pacific sardine, 1988–1989. Calif. Dep. Fish Game, Mar. Res. Div., Rep. to the legislature, 14 pp.