

THE RELATIVE MAGNITUDE OF THE 1985 PACIFIC SARDINE SPAWNING BIOMASS OFF SOUTHERN CALIFORNIA

PATRICIA WOLF California Department of Fish and Game 245 West Broadway Long Beach, California 90802 PAUL E. SMITH National Marine Fisheries Service Southwest Fisheries Center P.O. Box 271 La Jolla, California 92038

ABSTRACT

The spawning biomass of the Pacific sardine off southern California during 1985 is considered to be at least 20,000 short tons¹. This determination was made using an inverse egg production or "egg production area" method, which estimates the area over which a specified spawning biomass (20,000 tons) would be expected to occur. Our survey had a 95% probability of detecting the spawning area within the survey area if at least 20,000 tons of adults were present. This method was developed from the egg production method, which estimates adult biomass from measurements of egg production in the spawning area and from the egg production rate of the adult population. Using estimates of the components of egg production and specific fecundity for sardines from previous studies, we predicted that 20,000 tons of spawning biomass would cover a spawning area of about 500 n.mi².

A total of 86 sardine eggs was collected at 11 of 419 stations during the May 1985 survey, which ranged from San Diego to Point Conception and extended from within one mile of the coast to approximately 80 miles offshore. Spawning occurred mainly along the Santa Barbara Ventura coast and covered an estimated 670 n.mi². A total of 1,170 anchovy eggs and 266 anchovy larvae were found at 114 and 69 of the stations, respectively.

As provided by state law when the sardine biomass reaches 20,000 tons, a 1,000-ton fishery for sardines was opened on January 1, 1986. This is the first directed tishery allowed for California sardines since a moratorium on sardine fishing was enacted in 1974. Adult reproductive parameters and egg survival must be determined for absolute biomass estimation.

RESUMEN

La biomasa de desove de la sardina del Pacifico frente al Sur de California fue estimada en por lo menos 20,000 toneladas cortas (1 tonelada corta = 0.907

toneladas métricas) en 1985. Esta determinación fue hecha por medio del método inverso de producción de huevos o "área de producción de huevos." Este método estima el área en la cual una biomasa de desove dada (20,000 toneladas) supuestamente tendrá lugar. Nuestro estudio permitiría localizar el área de desove dentro del área de estudio con un 95% de probabilidad si hubieran, al menos, 20,000 toneladas de adultos. Este método está basado en el método de producción de huevos el cual evalúa la biomasa de adultos a partir de medidas de la producción de huevos en el área de desove, y de la tasa de producción de huevos por la población de adultos. Sobre la base de estudios previos sobre la producción de huevos y la fecundidad específica de las sardinas, se pronostican 20,000 toneladas de biomasa de desove en un área de desove de alrededor de 500 mi.n².

Se colectaron 86 huevos de sardinas en 11 de 419 estaciones ubicadas entre San Diego y Point Conception, y que se extendían entre 1 y aproximadamente 80 millas mar afuera, durante mayo de 1985. El desove ocurrió a lo largo de la costa entre Santa Barbara y Ventura principalmente, cubriendo un área estimada en 670 mi.n^2 . Se encontraron 1,170 huevos y 266 larvas de anchoveta en 114 y 69 de las estaciones, respectivamente.

De acuerdo con la legislación estatal, cuando la biomasa de sardina alcanzó 20,000 toneladas, se abrió una pesquería para 1,000 toneladas de este recurso el 1° de enero de 1986. Esta es la primera pesquería dirigida que se permite para las sardinas de California desde la implementación, en 1974, de una veda de esta pesquería. Para obtener una estimación absoluta de la biomasa, los parámetros reproductivos de los adultos y la sobrevivencia de los huevos deben ser determinados.

INTRODUCTION

This report assesses the 1985 spawning biomass of the Pacific sardine. Legislation closing the sardine fishery in 1974 requires the Department of Fish and Game to determine annually whether the spawning biomass is more than 20,000 tons. This legislation imposes a moratorium on fishing sardines while the biomass remains below 20,000 tons and allows a 1,000-

[[]Manuscript received February 14, 1986.]

¹ Commercial landings, tonnages specified in legislation, and tonnages in this paper are reported in short tons.

ton fishery when the biomass exceeds this level. Earlier assessments of the sardine spawning biomass were based on ichthyoplankton surveys, aerial observations, trawl surveys, and incidental landings in mackerel and live bait fisheries, and have shown signs of increase since 1980 (Wolf 1985; Klingbeil and Wolf 1984; Klingbeil 1981, 1982, 1983).

Because the sardine population appeared to increase, a quantitative method for detecting recovery and determining whether the biomass had exceeded 20,000 tons was required. Estimates of the sardine population biomass during the fishery were based on analysis of catch and age data (Murphy 1966; MacCall 1979). The egg production method (Parker 1980) is currently used to estimate spawning biomass of anchovies off California (Picquelle and Hewitt 1983) and anchovies and sardines off Peru (Santander et al. 1982). However, available methods of biomass estimation are not applicable at low biomass levels; the cost and effort necessary to achieve meaningful levels of precision are too high.

We developed the egg production area method to allow a cost-efficient, quantitative determination of the relative magnitude of spawning biomass while levels remain low. Details of the method and survey design are described by Wolf and Smith (1985). Here we apply the egg production area method to assess the relative magnitude of the sardine spawning biomass during 1985.

EGG PRODUCTION METHOD

The egg production method estimates spawning biomass as

$$B = P_o A \frac{kw}{RFS}$$

where B = spawning biomass (MT)

 P_o = daily egg production, number of eggs produced per 0.05 m² of sea-surface area,

W = average weight of mature females (g),

R = sex ratio, fraction of population that is female, by weight (g),

F = batch fecundity, number of eggs spawned per mature female per batch,

S = fraction of mature females spawning per day.

 $A = \text{total area of survey } (0.05 \text{ m}^2), \text{ and}$

k = conversion factor from grams to metric tons.

This method was derived by Parker (1980), and applied by Picquelle and Hewitt (1983, 1984) and Hewitt (1985) to estimate northern anchovy biomass.

EGG PRODUCTION AREA METHOD

In the egg production method, daily egg production and population fecundity parameters are measured during the survey. An exponential mortality model is fit to counts of aged eggs, and P_o is estimated by extrapolating back to the number of eggs at the time of spawning. Parameters W, F, S, and R are estimated from samples of adult fish collected during the survey.

In the egg production area method, the spawning biomass is specified and the equation solved for A_1 :

$$A_1 = \frac{B_1 R F S m}{P_0 k_1 W}$$

where A_1 = spawning area of biomass B_1 in nautical miles².

 B_1 = spawning biomass, in short tons,

 $k_1 =$ conversion factor from grams to tons,

m = conversion factor from 0.05 m² to nautical miles².

The procedure for estimating sardine spawning area differs from that used for anchovy² in that occasional stations with no eggs are incorporated for anchovy: a slight increase in area is compensated by a slight decrease in mean abundance of eggs. For the sardine spawning area estimate, only stations with eggs are included. We assumed that an area represented by a single sample is not entirely covered, but that this is compensated by the fact that eggs might be present in another area represented by a sample containing no eggs.

We used information from previous studies to estimate the parameters, P_o , W, F, S, and R for sardines rather than collecting measurements during the survey. These values (Table 1) are not known or have not been measured recently for California sardines; we adapted existing information concerning sardines and related species (Wolf and Smith 1985).

Estimates of daily egg production for sardines and anchovies off Peru³ indicate that egg production rates are lower for sardines than for anchovies by a factor of 1:2. We applied this relationship to annual estimates from 1980 through 1984 (Hewitt 1985) of daily egg production rates for anchovies (approximately 10 eggs/ 0.05 m^2) to obtain an estimate of sardine daily egg production of about 5 eggs/ 0.05 m^2 . Historical CalCOFI egg surveys yielded an estimated California sardine daily egg production rate of approximately 1.5 eggs/ 0.05 m^2 . This value is thought to be low, however, be-

² Lasker, R. (ed.) MS. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchosy (*Energalis mordas*).

³ Smith, P.E., H. Santander, and J. Alheit. MS. Comparison of the mortality and dispersal of sardine (*Sardinops sugar sagar*) and anchosy (*Engraulis ringens*) eggs off Peru.

TABLE 1 Parameters Used to Estimate Spawning Area, and Resulting Estimates

B ₁	W	R	F	<i>P</i> ,,	<u>S</u>	A1
Spawning biomass (short tons)	Average female weight (g)	Sex ratio (females/total)	Batch fecundity (eggs batch/ female)	Egg production (eggs: .05m ² -day)	Spawning fraction (spawning females/ total females)	Spawning area (nautical miles ²)
20,000	120	0.5	32,000	5.0	0.02	141
					0.05	353
					0.10	706
					0.15	1,058
				1.5	0.02	470
					0.05	1,176
					0.10	2,352
					0.15	3,528

cause the sampling technique (oblique tows instead of vertical tows) may have overestimated the surface area of water sampled. Both values of P_{ρ} were used (Table 1). Average weight of mature females, W, was estimated to be 120 grams, and batch fecundity, F. was estimated at 32,000 eggs (MacGregor 1957). The female fraction of the population by weight, R, was assumed to be half. Spawning fraction, S, for other pelagic species ranges from 0.02 females spawning per day (spawning once every 50 days) for Pacific sauries (Hatanaka 1956) to 0.14 females spawning per day (spawning once every 7 days) for anchovies (Hunter and Macewicz 1980). Spawning fraction for sardines off Peru (J. Alheit, Instituto del Mar del Perú, pers. comm.) and for sardines off the west coast of Baja California (J.R. Torres-Villegas, CICIMAR, unpublished data) has been estimated at about 0.06 females spawning per day. The range values of S was used (Table 1).

The calculated area, A_1 , over which 20,000 tons of Pacific sardines could be expected to spawn ranges from 141 to 1,058 n.mi.², for an estimated daily egg production rate of 5 eggs/0.05 m² and an estimated range of values for spawning fraction, and from 470 to 3,525 n.mi.² for a daily egg production rate of 1.5 eggs/ 0.05 m² and the same range of values for spawning fraction (Table 1). With available information, we consider the higher value of P_o —5.0 eggs/0.05 m²—and a value of S ranging between 0.05 and 0.10 females spawning per day to be the best estimates of these parameters for sardines. Therefore, 500 n.mi.² was selected as a useful estimate of A_1 .

SURVEY DESIGN

The survey area and time of year over which sardine spawning would be likely to occur were determined from occurrences of sardine eggs and larvae in historical CalCOFI survey data (Wolf and Smith 1985). The critical spawning area, A_1 , estimated at 500 n.mi.², was approximately 2% of the survey area, which in-

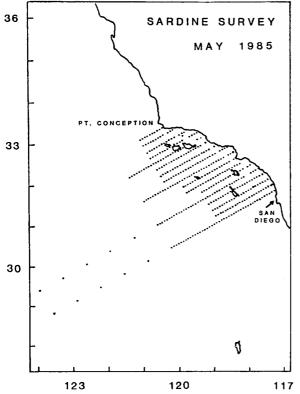
cluded CalCOFI regions 7 and 8 and covered an estimated 32,000 n.mi.² (Smith et al. 1976). Using a table for determining confidence limits of a proportion (Natrella 1963), we determined the number of stations (374) representing the minimum effort required to locate the spawning area within the survey area, with a high probability (95%) of detecting the spawning area if 20,000 tons of spawning adults were actually present. The stations were spaced 4 n.mi. apart offshore and 10 n.mi. apart alongshore according to standard anchovy egg production procedures. Because each station represents 40 n.mi.², the calculated spawning area that 20,000 tons of sardines would cover was expected to contain 12 or 13 positive stations.

SURVEY DESCRIPTION

The survey was conducted by NOAA ship *David* Starr Jordan from April 29 through May 19, 1985. Stations were occupied from south to north, beginning at San Diego and ending at Point Sal, and extending offshore an average distance of about 80 miles (Figure 1). Plankton samples were collected at 419 stations using a 25-cm-diameter CalVET (vertical egg tow) net of 150micron mesh that was retrieved vertically from 70 m (when depth allowed) to the surface. Samples were collected at all hours. No stations were occupied in established shipping lanes.

Sardine and anchovy eggs and larvae were identified, sorted, and counted. A total of 86 sardine eggs occurred at 11 stations, with the number of eggs per station ranging from 1 to 42 (Figure 2). Most of the positive stations occurred along the coast near Santa Barbara, and in the eastern portion of the Santa Barbara Channel, from Port Hueneme to Anacapa and Santa Cruz islands. Two positive stations occurred off Newport Beach. Sardine larvae occurred at 10 stations, in approximately the same areas as eggs. Eggs and larvae in combination occurred at 16 stations.

Evidence of anchovy spawning (1,710 eggs and 266





larvae at 114 and 69 stations, respectively) was considerably more common but occurred in different areas than sardine spawning. Anchovy eggs and larvae were concentrated mostly in the southern portion of the survey near San Diego.

Two of the samples had to be discarded because of inadequate preservation. Neither were adjacent to or near stations at which sardine eggs occurred (Figure 2).

SPAWNING AREA

Spawning area was determined by multiplying the number of egg-positive stations by the area represented by each station (40 n.mi.²). Some stations that were positive for sardine eggs were adjacent to areas that were not sampled, either because the area occurred in the shipping lanes or was close to shore and aligned in such a way that the station plan did not call for a sample. In order to consider these areas in the spawning area estimate, we adjusted the area of positive stations adjacent to an unsampled area to include half of the adjacent unsampled area, averaged along lines in order of station occupation and estimated by eye. The area of positive stations too near to shore to include an entire

 40 n.mi.^2 were also adjusted to reflect the portion of the 4 by 10 n.mi.^2 actually sampled.

An unadjusted estimate of the spawning area equals 440 n. mi². An estimate of the spawning area adjusted as described above is 670 n.mi.² (Figure 2). Both of these estimates are within the range of spawning area calculated for 20,000 tons of spawning biomass of sardines and are close to the selected estimate of A_1 (Table 1).

DISCUSSION

The egg production area method allows detection of the onset of sardine recovery and provides an objective, quantitative technique for determining the relative magnitude of spawning biomass. This is particularly useful when the management plan requires determining whether a specified spawning biomass level has been exceeded, but either the level to be ascertained remains low enough that developing a direct estimate with reasonable precision is cost- and effortprohibitive, or information beyond the relative magnitude of biomass is unnecessary.

Because the spawning area observed during the survey was close to that predicted for 20,000 tons of adult sardines, the spawning biomass of sardines off California is considered to be at least 20,000 tons in 1985. As specified by state law, this determination allowed the initiation of a 1,000-ton fishery in January 1986. The provision for a fishery was included in the 1974 moratorium legislation because of concern that a total moratorium would preclude detecting the onset of recovery. Also, simulations of a 5% fishery at that biomass level projected no deleterious effects (W. Lenarz, NMFS, Tiburon, pers. comm.). MacCall's (1979) estimates of apparently lower recruitment rates at low biomass levels suggest that Lenarz's projections may be optimistic.

The large range of values calculated for A_1 resulted from using a range of values to estimate parameters P_{o} (daily egg production rate) and S (spawning fraction). These parameters are not known for Pacific sardines. Two other parameters—W (average female weight) and F (batch fecundity)—were estimated from sardines taken from the 1945-46 commercial catch. The average monthly mean weight of mature female sardines occurring incidentally with mackerel during 1985 was 142 grams. As discussed below, all of the components of egg production and specific fecundity are dynamic and have been shown to vary from year to year for northern anchovy (Hewitt 1985). Daily egg production rate and spawning fraction must be determined for Pacific sardines; the adult parameters should be obtained simultaneously. The egg production area method, however, uses historical information.

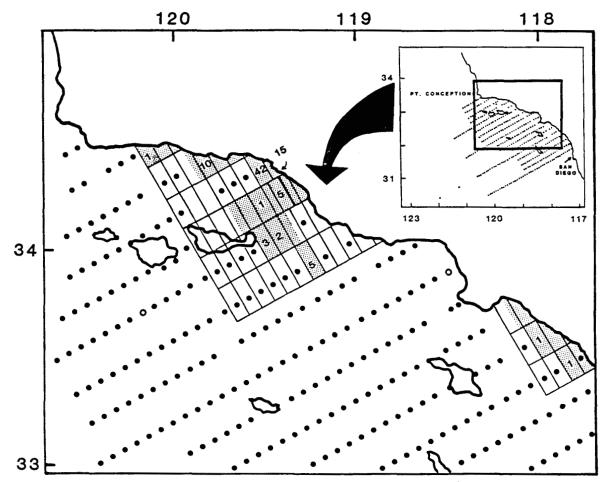


Figure 2. Number of eggs per station and location of stations that contained sardine eggs. Rectangles outline 4-by-10-n.mi.² areas represented by each station to illustrate spawning area adjustment. Shaded area is adjusted sardine spawning area. Open circles are discarded samples.

Several other sources provide additional information concerning the status of the adult Pacific sardine population during 1985. Incidental landings of sardines with mackerel during 1985 totalled 652 tons, the largest annual take in 20 years ("Review of Some California Fisheries for 1985," this volume). Sardines have become increasingly more common in mackerel landings, occurring in 50% of observed landings in 1985 compared to 30% in 1984. Catch length frequencies of incidental sardines show a trend from 1983 through 1985 of a broader length distribution, indicating recruitment in 1985 (Figure 3). Sardines from the 1985 year class were detected in early 1966 in Monterey Bay, indicating that spawning occurred north of Point Conception and beyond the range of the survey. Sardines ranked first in biomass and third in abundance in purse seine hauls from Long Beach Harbor during 1983

and the first half of 1984 (C. Mitchell, MBC Applied Environmental Sciences, pers. comm.). No detectable trend, however, was observed in the mean number of sardines captured by purse seine off San Onofre from 1983 through 1985 (E. DcMartini, UCSB Fish Program, pers. comm.).

The abundance of sardine eggs and larvae in four nearshore ichthyoplankton transects in the Southern California Bight increased two to three orders of magnitude from 1978-79 through 1982-84, and sardines ranked third in overall abundance during that period (R.J. Lavenberg, Los Angeles County Natural History Museum, pers. comm.). From 1978 through 1984, monthly mean numbers of sardine larvae in coastal waters near San Onofre increased steadily (W. Watson, Marine Ecological Consultants of Southern California, pers. comm.). Both of these studies indicate that a sub-

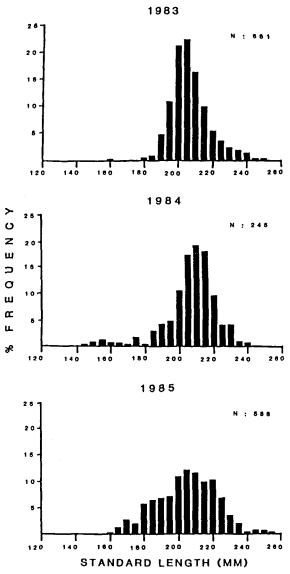


Figure 3. Catch length frequencies of sardines landed incidentally with mackerel in 1983, 1984, and 1985. Mean weights of modal length classes for each year are: 1983, 130 g, 205-209 mm SL; 1984, 147 g, 210-214 mm SL; 1985, 143 g, 205-209 mm SL.

stantial portion of sardine spawning in recent years has occurred relatively near to shore (within the 75-m contour) and during summer and fall.

Although the limited interpretation of the 1985 survey is conclusive in the original objectives relative to 20,000-ton spawning biomass, we resist broadening these few results for a biomass estimate or fishery quota. The spawning area of 670 n.mi.² is nearly identical to the 500 n.mi.² criterion adopted for this tech-

nique. This means that any deviation from the assumed adult parameters could change the evaluation. Another critical feature is that we can estimate only the standing crop of eggs from this small set, not the egg production. The two unevaluated factors are mortality rate of the eggs and the precision of the intercept estimate. Future surveys must quantify the mortality rate and the frequency distribution of eggs.

The estimated mean of positive samples in the 1985 survey is high relative to samples of the 1930s to 1950s (Table 2). It appears that the high value is due to the chance encounter of more observations with high values. We believe the cause of this difference is technical rather than biological, although this cannot be determined from these few samples. It is important to note that all the other distributions result from oblique or horizontal tows and that the new results are from a vertical tow. The scale of the integration is 25 cm for the CalVET net and on the order of meters for all but one of the other nets, and kilometers for the highspeed net used in 1950. The smaller CalVET net will have a greater probability of sampling zero eggs. Also, the sampling threshold of the CalVET net (1 egg in a CalVET is equivalent to 50 eggs in a 1-m oblique tow) might cause the lower end of the frequency distribution of egg densities to be undersampled. Both of these characteristics would cause the mean observed density of positive samples to be inflated. This would imply that the entire area of sardine spawning was not detected and that 20,000 tons is a conservative estimate.

The high mean value could also result from a lower than normal mortality or higher than normal per capita egg production rate, which would imply a lower spawning biomass. These biological factors will all have to be separately assessed for the absolute biomass to be estimated from egg production rates.

Analogous data from the anchovy egg production procedure indicate the great importance of the adult sampling effort for biomass estimation. If the interval between batches of eggs is long, for example 20 days, the ratio of gonads with evidence of spawning in the previous day is only 5%. This ratio would require many independent samples to precisely determine the spawning fraction. Individual samples of anchovy females range from 0% spawning to over 40% when the mean is 15%. Thus the overall precision of spawning biomass estimates may be determined by the ability to obtain a sufficient number of independent samples of adult females.

In summary, at least one more year of field and laboratory work on additional egg samples and adult collections will be required before the procedure for an absolute biomass estimate can be designed. WOLF AND SMITH: MAGNITUDE OF SARDINE SPAWNING BIOMASS CalCOFI Rep., Vol. XXVII, 1986

		Net types and years								
$\frac{\frac{\#}{10} \text{ m}^2}{x \qquad \ln(x)}$		CalVET 1985	CF&G 2-m 1931-32	l-m 1941	0.5-m 1941	Hi-speed 1950	l-m 1959			
.125	5 - 2.08	b	2							
.5	-0.69	_	4			—				
2	0.69		6	21	_		28			
8	2.08		7	22	8		28			
32	3.47	_	14	16	15		30			
128	4.85	4	12	31	29	77	23			
512	6.24	4	13	27	14	20	12			
2,048	7.62	2	5	17	10	7	5			
3,192	9.01	ī	2	3	2	I	4			
Estin	nated									
mean		1,564	544	569	619	406	410			
	s (MT) ^c	0.02	3.9	2.7	2.7	1.0	0.2			

TABLE 2 Pacific Sardine Egg Sample Frequency Distributions at Different Levels of Spawning Biomass^a

"(Smith and Richardson 1977)

^bValue below sampler threshold

"(Murphy 1966)

ACKNOWLEDGMENTS

We would like to acknowledge the editorial assistance of two anonymous reviewers. Rocky French and Terry Palmisano helped with graphics. We thank the crew of NOAA ship David Starr Jordan and her captain, M. Roll. J. Thrailkill of the National Marine Fisheries Service (NMFS) was responsible for cruise logistics. The team of scientists participating on the survey included W. Flerx, J. Metoyer, D. Abramenkoff of NMFS; T. Dickerson of the California Department of Fish and Game; W. Bryan, S. Cummings, and C. Walker of Scripps Institution of Oceanography; E. Isidro of the University of Azores, Portugal; and S. Mildner and J. Mildner from Australia. Dennis Gruber and Evelyn Conley sorted the CalVET samples and staged the sardine eggs. Betsy Stevens, Elaine Sandknop, and Barbara Sumida MacCall provided assistance with egg staging. Celeste Santos Methot entered and edited the data. Rich Charter and Cindy Meyer helped with data management.

LITERATURE CITED

- Hatanaka, M. 1956. Biological studies on the population of the saury, Cololabis saira (Brevoort) Part I: reproduction and growth. Tohoku J. Agr. Res. V1(3):227-269.
- Hewitt, R.P. 1985. The 1984 spawning biomass of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 26:17-25.
- Hunter, J.R., and B. 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.
- Klingbeil, R.A. 1981. Status of the spawning biomass of the Pacific sardine, 1980-81. Calif. Dept. Fish and Game, Mar. Resources Admin. Rep. No. 81-1, 6 p.

1982. Status of the spawning biomass of the Pacific sardine. 1981 82. Calif. Dept. Fish and Game. Mar. Resources Admin. Rep. No. 81-2,
7 p.

- . 1983. Status of the spawning biomass of the Pacific sardine. 1982-83. Calif. Dept. Fish and Game. Mar. Resources Admin. Rep. No. 83-1, 5 p.
- Klingbeil, R.A., and P. Wolf. 1984. Status of the spawning biomass of the Pacific sardine, 1983-84. Calif. Dept. Fish Game. Mar. Resources Admin. Rep. No. 84-1, 7 p.
- MacCall, A.D. 1979. Population estimates for the waning years of the Pacific sardine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 20:72-82.
- MacGregor, J.S. 1957. Fecundity of the Pacific sardine (Sardinops caerulea). Fish. Bull. 121:427-449.
- Murphy, G.I. 1966. Population biology of the Pacific sardine (Sardinops caerulea), Proc. Cal. Acad. Sci. 34:1-84.
- Natrella, M.G. 1963. Experimental statistics. National Bureau of Standards Handbook 91, U.S. Supt. Doc.
- Parker, K. 1980. A direct method for estimating northern anchovy. Engraulis mordax, spawning biomass. Fish. Bull. 78:541-544.
- Picquelle, S.J., and R.P. Hewitt. 1983. The northern anchovy spawning biomass for the 1982-83 California fishing season. Calif. Coop. Oceanic Fish. Invest. Rep. 24:16-28.
- . 1984. The 1983 spawning biomass of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 25:16-27.
- Santander, H., P.E. Smith, and J. Alheit. 1982. Determination of sampling effort required for estimating egg production of anchoveta (*Engratulis ringens*) off Peru. Bol. Inst. Mar. Peru Callao 7:9-18.
- Smith, P.E., S. de la Campa, and J.R. Thrailkill. 1976. Instituto National de Pesca and CalCOFI statistical regional divisions for ichthyoplankton surveys. Southwest Fisheries Center Admin. Rep. LJ-36-31.
- Smith, P.E., and S.L. Richardson. 1977. Standard techniques for pelagic fish egg and larva surveys. FAO Tech. Paper No. 175, 100 p.
- Wolf, P. 1985. Status of the spawning biomass of the Pacific sardine, 1984-85. Calif. Dept. Fish and Game. Mar. Resources Admin. Rep. No. 85-1, 20 p.
- Wolf, P., and P.E. Smith. 1985. An inverse egg production method for determining the relative magnitude of Pacific sardine spawning biomass off California. Calif. Coop. Oceanic Fish. Invest. Rep. 26:130-138.