SMITH: MONITORING OF PACIFIC SARDINE SPAWNING AREA ColCUFI Rep., Vol. 31, 1990

MONITORING INTERANNUAL CHANGES IN SPAWNING AREA OF PACIFIC SARDINE (SARDINOPS SAGAX)

PAUL E. SMITH National Marine Fisheries Service Southwest Fisheries Center P.O. Box 271 La Jolla, California 92038

ABSTRACT

It is easier to monitor the spawning area of the Pacific sardine than to mount a full-scale effort to precisely estimate spawning biomass. Monitoring the spawning area may be particularly economical when the sardine is extremely rare or extremely abundant. Such imprecise estimates will probably not answer the management question of whether or not to set a specific biomass quota. The spawning area estimate is a candidate — with aerial surveys, scale sedimentation rates, and acoustic-trawl surveys — for use in interpolating between years when the more precise SWFC daily egg production method is used.

RESUMEN

Resulta más fácil monitorear el área de desove de la sardina del Pacífico que montar un estudio a gran escala que estime con precisión la biomasa del desove. El monitoreo del área del desove parece ser una salida económica cuando la abundancia de la sardina es extremadamente baja o extremadamente alta. Estas estimaciones imprecisas probablemente no contesten las preguntas administrativas relacionadas con la posibilidad de imponer una cuota a la biomasa específica. La estimación del área de desove junto con estudios aéreos, determinaciones de velocidad de sedimentación de las escamas, y estudios de arrastres acústicos sea probablemente el mejor método para interpolar datos entre aquellos años cuando el método mas preciso de la producción de huevos del SWFC es utilizado.

INTRODUCTION

The sardine fishery has been thoroughly reviewed by Ahlstrom and Radovich (1970). The fishery began in Monterey in the nineteenth century and grew to a maximum seasonal catch of just over 700,000 metric tons (MT) in the 1936–37 season. The catches began to disappear from the Pacific Northwest and northern California in 1945–46 and were inconsequential by 1952–53. There was a minor resurgence

[Manuscript received February 15, 1990.]

to 115,000 MT in the 1958-59 season; thereafter the fishery declined to very low levels.

There appears to be some recovery of the Pacific sardine stock (Parrish et al. 1989) off southern California (Wolf and Smith 1986; Wolf et al. 1987), as evidenced by the tendency for the spawning area to increase. Since 1986, small quotas for commercial catch have been permitted (907 MT for all use, 317 MT for live bait, 227 MT for dead bait). The incidental catch of sardine has also increased, particularly in the Pacific mackerel fishery (Wolf 1989), If the spawning biomass continues to increase, there will soon be a need for a management plan, and decisions will have to be made about monitoring the size of the stock. The moratorium on sardine catch for all uses was managed informally from 1974 to 1984 with an annual statement that the biomass appeared to be below 20,000 short tons. Currently, the spawning biomass of sardine is estimated from a spawning area relationship published by Wolf and Smith (1985). The quota of 907 MT for all uses has been constant since 1986, but may be increased by the California Department of Fish and Game.

The Southwest Fisheries Center Coastal Division has devised an absolute, instantaneous daily egg production method to estimate spawning biomass of northern anchovy (Lasker 1985). It remains for a management plan to determine how often and how precisely the spawning biomass of sardine must be monitored. Annual management advice is currently based on the stock synthesis model (Methot 1989; Lo and Methot 1989; Jacobson and Lo 1989).

Zweifel (1973) noted that the number of sardine eggs per positive station remained stable from 1951 to 1960, even as the population of sardine declined by nearly an order of magnitude. Smith and Richardson (1977: table 3.10) showed that the mean number of eggs per positive station varied little, even with different quantitative net tows and population sizes varying from 4 million to 200,000 tons. Wolf et al. (1987: table 2) demonstrated that the mean number per positive net tow remained stable, with a sardine spawning biomass estimated at 20,000 tons; thus, over a measured range of 20,000 to 4

SMITH: MONITORING OF PACIFIC SARDINE SPAWNING AREA ColCOFI Rep., Vol. 31, 1990



Figure 1. Locations of net tows taken to search for Pacific sardine eggs in April, May, and June 1929; April, May, and June 1930; February–August 1931; and February, April, and May 1932 (Scofield 1934). Solid circles indicate that the net tow was positive for eggs; open circles indicate that a net tow was taken and examined for eggs but none were found.

million tons of spawning biomass, the distribution of sardine eggs per positive station remains the same. We believe that this circumstance arises from the schooling habit of adults, regardless of the spawning biomass of the population; the further behavioral concentration of sperm and eggs by the fraction of fish involved in spawning at the time of external fertilization in the open sea; and the subsequent dispersal by turbulent diffusion (Smith 1973; Smith and Hewitt 1985; Mangel 1985; Mangel and Smith, in press). Theoretically, the number of eggs per positive station could decline at high biomass concentrations because filter feeding in schooling fishes like the sardine and anchovy may result in incidental cannibalism and predation of the eggs (Gulland 1971; Alheit 1987; Smith et al. 1990).

It is assumed that the management plan for sardine will be similar to that for anchovy, with two thresholds (PFMC 1983). When the spawning biomass is below the lower threshold, no fishery is permitted; when the spawning biomass is between the lower and upper threshold, a fixed fraction of the spawning biomass, based on demographic considerations, is established as a quota for the ensuing year; and when the spawning biomass is above the upper threshold, no further catch is authorized. The lower threshold is established at the point that the costs of the fisher's search for the remaining fish increase, and where further catches would probably delay the recovery of the stock to higher productivity. The upper threshold is established at the point where fleet and processor capitalization and costs of marketing would not be repaid owing to the temporary nature of high biomass. This requires rather precise monitoring of spawning biomass near the lower threshold, and less precise estimates at all other biomass levels. Also, the policy of using indices of abundance rather than annual absolute measures of abundance reduces management costs for assessing stock at higher levels of abundance while providing for a stable fishery.

It is the purpose of this paper to present data to aid in designing programs to estimate and monitor biomass. These programs should contribute to management of the Pacific sardine fishery and to the understanding of interactions among the sardines, other planktivorous fishes, and their environment. The data used in the original paper on this topic by Zweifel (1973) will be extended from 1940 to the present.

METHODS AND RESULTS

Surveys of sardine eggs and larvae were conducted in 1929–32 (Scofield 1934; figure 1), 1939– 1941 (Ahlstrom 1948; Ahlstrom 1966; Smith 1972;





figure 2); and 1951–89 (CalCOFI on-line data system). Although distributions of eggs and larvae per net tow can be obtained for all these time periods, it is not possible to measure the areal boundaries of the spawning distribution for all sets of years. For this illustration, I have chosen the time series of sardine eggs and larvae for the area surveyed in 1941 (figure 3). At that time, virtual population estimates were based on the assumption that every female over 2 years old was a spawner; maturity and gonadal activity were not checked in each year.

The method used here for estimating biomass is the "index area" method. The quality of this method depends on the assumptions that the area chosen



Figure 3. Contoured abundance of sardine eggs during the period of survey in 1941 (Sette and Ahlstrom 1948). These data are included in the analysis.

contains all the biomass, is a consistent fraction of the total spawning area, or contains a constant fraction of the spawning biomass. It is likely that all time series used will suffer from violation of the same assumptions, since all values contain measurement error, and the values are drawn from an autocorrelated time series. I do not believe the regression methods used (Williams 1983) are valid for direct estimates of spawning biomass for management purposes. Recognizing these limitations, I will use the well-known procedures for linear regression to evaluate the components of indirect measures of population size.

Regression Analysis

Data on egg and larval abundance are available for selected years for a major region of spawning. In a previous analysis of anchovy and sardine (Smith 1972), only the larval data were used. It was noted that larvae can be sampled over 3 weeks and disperse and cover more area than eggs, which can only be sampled over 3 days. In addition, the eggs retain the distributional characteristics of the schooled adults that spawned them. Although larvae have the statistical advantage of dispersal, over 3 weeks' time there may be considerably more variability in mortality than for eggs. In this study I use both egg and larval data as well as the biomass estimates from virtual population methods used for catch analysis from 1932 through 1965 (Murphy 1966: 1932–44; MacCall 1979: 1945-65; table 1). For the remainder of the text I use the notation as follows:

VPM— the biomass (MT) of sardines 2 years old and older;

E—the egg census estimate of abundance in the entire survey area (#/10m²);

SMITH: MONITORING OF PACIFIC SARDINE SPAWNING AREA ColCOFI Rep., Vol. 31, 1990

TABLE 1

Data for Regression Estimates Using the Census Estimate or the Partitioned Estimates of Eggs or Larvae and the Virtual Population Methods (VPM) for Pacific Sardine

Year	N	E	L	PE	PL	VPM
A. Yea	rs for wl	hich VPM i	s available			
1940	240	699.10	49.13	0.754	0.808	1759.6
1941	210	336.90	36.88	0.629	0.748	2457.1
1951	96	33.33	2.06	0.167	0.146	277.0
1952	152	6.85	3.49	0.099	0.105	136.0
1953	226	0.21	0.07	0.031	0.013	202.0
1954	219	39.67	11.98	0.146	0.110	239.0
1955	142	26.87	7.29	0.169	0.092	170.0
1956	156	47.88	6.90	0.090	0.045	108.0
1957	145	23.00	12.09	0.103	0.097	90.0
1958	171	86.38	8.86	0.298	0.310	177.0
1959	188	182.00	7.88	0.287	0.250	122.0
1960	197	117.14	4.47	0.183	0.168	88.0
1961	73	17.08	1.40	0.164	0.082	54.0
1962	64	1.77	0.95	0.016	0.047	27.0
1963	77	14.22	1.94	0.052	0.039	21.0
1964	183	0.43	0.00	0.022	0.005	11.0
1965	112	4.57	0.79	0.107	0.098	3.0
B. Yea	rs for wh	nich no <i>VP</i>	M is availa	ble		
1966	169	2.01	0.29	0.012	0.053	
1969	147	0.33	0.26	0.027	0.041	
1972	118	0,00	0.03	0,000	0.008	
1975	267	2.54	0.07	0.026	0.007	
1978	189	0.38	0.18	0.026	0.016	
1981	139	0.99	0.23	0.029	0.007	
1984	141	3.40	6.50	0.064	0.043	
1985	99	10.96	8.80	0.061	0.051	
1986	183	3.45	3.62	0.011	0.044	
1987	81	18.73	23.00	0.062	0.111	
1988	85	40.75	2.25	0.082	0.047	
1989	72	61.00	4,96	0.111	0.167	

Key: N = number of net tows included; E = cgg census estimate ofabundance: L = larval census estimate; PE = proportion of net tows containing sardine eggs; PL = proportion of net tows containing sardine larvae; VPM = biomass of sardines 2 years old and older.

L—the larval census estimate (#/10m²; Smith 1972);

PE-the proportion of the net tows containing sardine eggs (positive stations);

PL-the proportion of the net tows containing sardine larvae;

NE — the number of eggs per positive station (#/ $10m^2$); and

NL – the number of larvae per positive station (#/10m²).

NE and NL are not listed in table 1 because they are obtained simply by dividing the census estimate (E) by the proportion of positive stations (PE).

Table 2 lists the parameters, the standard errors of estimate of the parameters, the Student's t value of the estimate, the probability of the t value, the F value of analysis of variance, and the probability of the F value. No constant is less than .05, thus all the equations were redone forcing the zero-intercept.

Omission of the constant when evaluating PE did not materially change the F value of the analysis of variance.

Possibly the most significant result of this analysis for monitoring the sardine biomass is the weakness of number of eggs or larvae per positive station when coupled with the probability of a positive station; in both cases p is greater than .05 and negative in reflecting changes in biomass (PE and NE, PL and NL in table 2; see also NE in figure 4B). As in the previous analysis (Smith 1972), the constants are not important, and the larval time series, with or without inclusion of number per positive station (NL), are marginally better predictors of spawning biomass (actually biomass of age 2+) than the equivalent measures of eggs (table 2). This may simply reflect the longer duration and better mixing with resultant lower variance of the larval estimates. I use the proportion of eggs relationship (PE) to extend the biomass time series to the present (table 3; figure 4A).

Another significant result is that the standard errors of the parameter estimates are all relatively large. This implies than none of these estimates would be adequate for year-by-year management advice during close regulation of the fishery. It seems likely that some of this parameter error is due to the fixed maturation at 2 years of age. The largest deviations occur at the times of significant temperature anomalies. It may be that temperature plays an important role in determining the rate of maturation in sardine, as has been found for anchovy (Methot 1989). If the age at first maturity is shown to be influenced by temperature, it is likely that the VPA series could be adjusted from temperature records on hand (see Methot 1989, table 1).

Even with the improvement in accuracy, it does not appear from table 3 that useful estimates can be obtained from the level of sampling effort now being conducted in the quarterly CalCOFI surveys. Although the trend of recovery may be essentially correct, the spawning biomasses indicated may well be overestimates (Wolf and Smith 1986; Wolf et al. 1987). In the absence of an adequate SWFC daily egg production method estimate to provide a recent calibration, it does not seem likely that spawning area estimates alone will be adequate for setting quotas for the Pacific sardine fishery (figure 4A). The spawning area estimate would be useful for monitoring the sardine stock at high levels, and the area and VPM or stock synthesis estimates may be useful for examining this population's impact on the ecosystem. If the stock recovers to more than a million tons it may be necessary to conduct wide-ranging

Predictor	Coef	SD	Student's (р	F-ratio	P
A. With constant						
Constant	51.2	113.5	0.45	0.659	29.05	0.000
E	3.0976	0.5747	5.39	0.000		
Constant	- 68.40	88.15	-0.78	0.450	68.12	0.000
L	45.489	5.511	8.25	0.000		
Contrant	- 225 5	108.7	- 2.07	0.056	57.00	0.000
PF	2046.9	390.3	7.55	0.000	57.00	0.000
	27-0.7		7.33	0.000		
Constant	143.87	83.06	-1.73	0.104	88.96	0.000
PL	2651.7	281.1	9.43	0.000		
Constant	-77.5	214.0	-0.41	0.722	6.98	0.018
NE	1.4407	0.5453	2.64	0.018		
Constant	296 A	252 3	1 17	0 258	0.08	0 780
NL	1 114	3 971	0.28	0.250	0.00	0.700
		5.72.	0.20	0.700		
Constant	- 85.78	91.08	-0,94	0.362	33.89	0.000
Ê	- 1.034	1.188	-0.87	0.399		
L	58.22	15.64	3.72	0.002		
Constant	- 158.8	115.2	-1.38	0,190	31.42	0,000
PE	3559.9	574.2	6.20	(),()(X)		
NE	-0.6284	0.4432	-1.42	0,178		
Constant	- 175 0	111.4	- 1 57	0 139	47 17	0.000
PL	2647.8	289.2	9.16	0.000		
NL	0.669	1.536	0.44	0.670		
Constant	-67.0	113.7	- 0 59	0 565	28 39	0.000
PE	- 2425	2019	-1.20	0.253	20.07	
PL	5214	1669	3.12	0.009		
NÉ	-0.6225	0.3882	-1.60	0.135		
NL	2.183	1.519	1.44	0.176		
B. No constant						
E;	3.2239	0.4891	6.59	0.000	43.44	0.000
L	43.032	4.455	9.66	0.000	93.30	0,000
PÉ	2379.4	305.9	7.78	0.000	60.52	0.000
PL.	2345.1	231.6	10.12	0.000	102.50	0.000
N/F	1 2015	0 3476	3 73	0.000	17.90	0.000
IVE	1.2915	0.5470	3.72	0.002	15.80	0.002
NL	4.527	2.663	1.70	0.109	2.89	0.109
E	- 0.789	1.154	-0.68	0.505	45.33	0.000
L	52.27	14.26	3.67	0.002		
PE	3469.8	587.3	5.91	0.000	38.98	0.000
NE	-0.8776	0.4166	-2.11	0.052		
PL.	2437.8	268.7	9.07	0.000	49.93	0,000
NL	-0.881	1.234	-0.71	0.486		
	20/2	1750	1.40	0.114	20.12	0.000
~ <u>C</u> D1	- CONC -	1758	3 79	0.002	37.12	0.000
NE NE	-0.6318	0.3781	-1.67	0.119		
NI	1 832	1 364	1.34	0.202		

TABLE 2
Comparison and Evaluation of Regression Parameters for Indirect Estimation of Spawning Biomass of Pacific Sardine

Key: E = egg census estimate of abundance; L = larval census estimate; PE = proportion of net tows containing sardine eggs; NE = number of eggs per positive station; PL = proportion of net tows containing sardine larvae; NL = number of larvae per positive station.

SMITH: MONITORING OF PACIFIC SARDINE SPAWNING AREA ColCOFI Rep., Vol. 31, 1990



Figure 4. Time series plot of sardine 1932–89 (Murphy 1966: 1932–44; MacCall 1979: 1945–65). A, estimates using virtual population methods or egg incidence correlates (PE); B, estimated egg abundance per unit surface area at positive stations (NE).

TABLE 3 Virtual Population Estimates of Sardine Spawning Biomass (2+) Derived from Regression on the Proportion of Positive Egg Stations in 1940–41 and 1951–65

Year	N	PE	VPMHAT
1940	240	0.754	1800
1941	210	0.629	1500
1951	96	0.167	400
1952	152	0.099	240
1953	226	0.031	74
1954	219	0.146	350
1955	142	0.169	-400
1956	156	0.090	210
1957	145	0.103	250
1958	171	0.298	710
1959	188	0.287	680
1960	197	0.183	440
1961	73	0.164	390
1962	64	0.016	38
1963	77	0.052	120
1964	183	0.022	52
1965	112	0.107	250
1966	169	0.012	29
1969	147	0.027	64
1972	118	0.000	0
1975	267	0.026	62
1978	189	0.026	62
1981	139	0.029	69
1984	141	0.064	150
1985	99	0.061	150
1986	183	0.011	26
1987	81	0.062	150
1988	85	0.082	200
1989	72	0.111	260

Key: N = number of net tows; PE = proportion of net tows containing sardine eggs; VPMHAT = estimate of sardine biomass

containing sardine eggs; VPMHAT = estimate of sardine biomass 2 years old and older based on the regression estimate of table 2, no constant. surveys (figures 1 and 2) to accomplish a daily egg production estimate based on the extent of spawning in the 1929–32 and 1939 surveys (Scofield 1934; Ahlstrom 1948).

DISCUSSION

Monitoring sardine biomass for fisheries management and ecosystem time series can be done with precise, but elaborate and expensive, egg production methods as used for the baseline studies of northern anchovy (Lasker 1985). Alternatively, indirect methods could be used, such as the deposition rate of scales (Soutar and Isaacs 1974) in anoxic sediments or traps; aerial surveys (Squire 1972); incidence and abundance of eggs or larvae; or trawl-acoustic methods in a mixed technique model (Methot 1989). Sardine stocks in the California Current region and other regions in the world fluctuate by orders of magnitude (Smith and Moser 1988; Lluch-Belda et al. 1989), and rough estimates of biomass may be sufficient for management plans during many periods of the species time sequence.

ACKNOWLEDGMENTS

I thank Patty Wolf, John Hunter, Izadore Barrett, Marc Mangel, Alec MacCall, and an unnamed reviewer for offering suggestions for materially improving the text. I am particularly grateful to Richard Charter and Cindy Meyer for maintaining the CalCOFI data base and writing special programs for extracting the data.

LITERATURE CITED

- Ahlstrom, E. H. 1948. A record of pilchard eggs and larvae collected during surveys made in 1939 to 1941. Spec. Sci. Rep. U.S. Fish and Wildl. Serv. Fisheries (54), 82 pp.
- -. 1966. Distribution and abundance of sardine and anchovy larvae in the California Current region off California and Baja California, 1951-64, a summary. Spec. Sci. Rep. U.S. Fish and Wildl. Serv. Fisheries (534), 71 pp.
- Ahlstrom, E. H., and J. Radovich. 1970. Management of the Pacific sardine. In A century of fisheries in North America, N. G. Benson, ed. Special Publication No. 7, American Fisheries Society, Wash. D.C., pp. 183-193
- Alheit, J. 1987. Cannibalism versus egg predation: their significance in anchovies. In The Benguela and comparable ecosystems, A. I. L. Payne, J. A. Gulland, and K. H. Brink, eds. S. Afr. J. Mar. Sci. 5:467-
- Gulland, J. A. 1971. Ecological aspects of fishery research. In Advances in ecological research, volume 7, J. B. Cragg, ed. New York: Academic Press, pp. 115–176.
- , and N. C. H. Lo. 1989. Spawning biomass of the Jacobson, L. D. northern anchovy in 1989. Southwest Fisheries Center Administrative Report LJ-89-17.
- Lasker, R., ed. 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *En-*graulis mordax. NOAA Tech. Rep. NMFS 36, 99 pp.
- Lluch-Belda, D., R. J. M. Crawford, T. Kawasaki, A. D. MacCall, R. H. Parrish, R. A. Schwartzlose, and P. E. Smith. 1989. Worldwide fluctuations of sardine and anchovy stocks: the regime problem. S. Afr. J. Mar. Sci. 8:195-205.
- Lo, N. C. H., and R. D. Methot. 1989. Spawning biomass of the northern anchovy in 1988. Calif. Coop. Oceanic Fish. Invest. Rep. 30:18-31
- MacCall, A. D. 1979. Population estimates for the waning years of the Pacific sardine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 20:72-82.
- Mangel, M. 1985. Search models in fisheries and agriculture. Lect. Notes Biomath. 61:105-138.
- Mangel, M., and P. E. Smith. In press. Presence-absence sampling for fisheries management. Can. J. Fish. Aquat. Sci. 47.
- Methot, R. D. 1989. Synthetic estimates of historical abundance and mortality for northern anchovy. In Mathematical analysis of fish stock dynamics, E. F. Edwards and B. A. Megrey, eds. Am. Fish. Soc. Symp. 6:66-82.
- Murphy, G. I. 1966. Population biology of the Pacific sardine (Sardinops caerulea). Proc. Calif. Acad. Sci. Fourth Series 34:(1)1-84.
- Parrish, R. H., R. Serra, and W. S. Grant. 1989. Monotypic sardines, Sardina and Sardinops: their taxonomy, distribution, stock structure, and zoogeography. Can. J. Fish. Aquat. Sci. 46:2019-2036.

- PFMC: Pacific Fishery Management Council. 1983. Northern anchovy fishery management plan. PFMC, 526 S. W. Mill St., Portland, Oregon 97201
- Scofield, E. C. 1934. Early life history of the California sardine (Sardina caerillea), with special reference to distribution of eggs and larvae Calif. Dep. Fish Game Fish Bull. 41:1-48
- Sette, O. E., and E. H. Ahlstrom. 1948. Estimations of abundance of the eggs of Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941. J. Mar. Res. 7:511-542.
- Smith, P. E. 1972. The increase in spawning biomass of northern an-chovy. Engrandis mordax. Fish. Bull. U.S. 70:849–874.
- , 1973. The mortality and dispersal of sardine eggs and larvae Rapp. P. -V. Reun. Cons. Int. Explor. Mer 164:282-292.
 Smith, P. E., and R. P. Hewitt. 1985. Anchovy egg dispersal and mortality as inferred from close-interval observations. Calif. Coop.
- Oceanic Fish. Invest. Rep. 26:97-110.
- Smith, P. E., and H. G. Moser. 1988. CalCOFI time series: an overview of fishes. Calif. Coop. Oceanic Fish. Invest. Rep. 29:66-78. Smith, P. E., and S. L. Richardson. 1977. Standard techniques for pe-
- lagic fish egg and larva surveys. FAO Fisheries Tech. Pap. 175, FAO Rome, 100 pp. Smith, P. E., H. Santander, and J. Alheit. 1990. Comparison of mortal-
- ity rates of Pacific sardine, Sardinops sagax, and Peruvian anchovy,
- Engraulis ringens, eggs off Peru. Fish. Bull. U.S. 87:497-508. Soutar, A., and J. D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. Fish. Bull. U.S. 72;257-273.
- Squire, J. L., Jr. 1972. Apparent abundance of some pelagic marine fishes off the southern and central California coast as surveyed by an air-
- borne monitoring program. Fish. Bull. U.S. 70:1005-1019. Williams, B. K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology 64:1283-1291.
- Wolf, P. 1989. Review of some California fisheries for 1988. Calif. Coop. Oceanic Fish. Invest. Rep. 30:7-17. 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.
- 1986. The relative magnitude of the 1985 Pacific sardine spawning biomass off southern California. Calif. Coop. Oceanic Fish. Invest. Rep. 27:25-31.
- Wolf, P., P. E. Smith, and C. L. Scannell. 1987. The relative magnitude of the 1986 Pacific sardine spawning biomass off California. Calif. Coop. Oceanic Fish. Invest. Rep. 28:21-26.
- Zweifel, J. R. 1973. A non-parametric approach to the estimation of relative change in fish population size from egg and larval surveys. Rapp. P. -V. Reun. Cons. Int. Explor. Mer 164:276-281.

