RECENT POPULATION TRENDS AND ABUNDANCE ESTIMATES FOR THE PACIFIC SARDINE (*SARDINOPS SAGAX*)

J. THOMAS BARNES
LMR Fisheries Research, Inc.
11855 Sorrento Valley Road, Suite A
San Diego, California 92121

LARRY D. JACOBSON
NOAA, National Marine Fisheries Service
P.O. Box 271
La Jolla, California 92038

ALEC D. MACCALL
NOAA, National Marine Fisheries Service
3150 Paradise Drive
Tiburon, California 94920

PATRICIA WOLF
California Department of Fish and Game
330 Golden Shore, Suite 50
Long Beach, California 90802

ABSTRACT

Five different analytical approaches and several sources of data were used to investigate current sardine abundance and recent changes in population size. Each analysis and all available information show an increasing trend in sardine abundance since the late 1970s. Current estimates indicate that the 1990 spawning biomass fell within the range of 60,000 to 210,000 metric tons (MT). Greater precision may be required for population estimates as a commercial fishery develops. We suggest that an integrated method of stock assessment that combines fishery-dependent and fishery-independent data will best meet future stock assessment and management needs.

RESUMEN

Se investigó la abundancia y cambios recientes en el tamaño de la población de la sardina utilizando cinco enfoques analíticos y varias fuentes de datos. Tanto la información disponible como cada uno de los análisis revelaron que desde finales de los 70 la abundancia mostró una tendencia al alza. Estimaciones recientes indican que en 1990 la biomasa de los reproductores que desovaron fué de entre 60,000 a 210,000 toneladas métricas; las estimaciones podrían requerir mayor precisión al desarrollarse la pesquería comercial. Sugerimos que para satisfacer necesidades futuras de evaluación de stock y manejo se considere un método de evaluación de stock integrado, que combine datos dependientes e independientes de la pesquería.

INTRODUCTION

One characteristic of sardine resources (genera *Sardinops* and *Sardina*) is that the populations can fluctuate widely. Scale-deposition rates for Pacific sardines (*Sardinops sagax*) in California Bight anerobic sediment indicate such fluctuations (Soutar and Isaacs 1974). Depth-related variations in the numbers of sardine scales in sediment suggest periodic changes of significant magnitude in relative abundance, extending back over the past 200 years (Smith and Moser 1988). The study of Pacific sardine population dynamics has also indicated large changes in abundance during this century (Murphy 1966; MacCall 1979). Adjacent year classes have been shown to vary in numbers by more than an order of magnitude (Murphy 1966), presenting the potential for rapid increases or decreases in overall population size, should trends in recruitment develop.

The Pacific sardine resource off the west coast of North America currently extends from the northern part of California to central Baja California. A large fishery was supported by the Pacific sardine many decades ago, when the population ranged from Canada to Mexico. However, abundance declined dramatically from 1945 through 1965 (with some short-lived reversals), and the fishery collapsed (Radovich 1982). In 1967 a moratorium was placed on the taking of sardines along the California coast because of the depressed condition of the stock. Annual landings were negligible from then until recent years, when sardines were once again regularly encountered by California and northern Baja California fishermen.

In 1985 the sardine spawning biomass was estimated to have increased to at least 18,140 MT (Wolf and Smith 1986), and a catch quota of 907 MT was established, allowing a small directed fishery in the United States. At the same time, bait fisheries were allocated a separate quota of 544 MT per year. Total directed and bait fishery quotas were increased to 8,165 MT for the 1991 season in recognition of the continued expansion of the resource. In addition to the directed and bait fisheries, current management regulations allow a 35% maximum incidental take of sardines (by weight) in the California fishery for Pacific mackerel (*Scomber japonicus*) and jack mackerel (*Trachurus symmetricus*). Sardine by-catch in the mackerel fishery usually amounts to about 1,000–3,000 MT per year.

A fishery outside the control of United States authorities operates in Ensenada, Mexico, and proba-

bly harvests the same sardine stock as the southern California fishery. Ensenada sardine landings dominated the fishery in 1990, but were roughly similar in volume to those in the United States during most other recent years (table 1).

In response to apparent increases in sardine abundance and associated public interest in expanding the commercial fishery, a workshop was convened in September 1990 by the California Department of Fish and Game (CDFG) to develop recommendations for assessing and managing the resource. An objective of the workshop was to examine various sources of data concerning the status of sardines. In this paper, we review five independent and complementary analyses used by workshop participants to evaluate the current state of the population. The data, methods, and analyses reported here incorporate some improvements introduced as a result of work done since the workshop. Data employed in the analyses are described in the next section, followed by an explanation of methods and results for each approach. We compare results in the final section and suggest an approach for future assessment of the stock.

DATA

Several sources of information were available. Some were relatively long time series extending back over decades; others were more recent in scope, or fragmentary. Direct estimates of sardine biomass from virtual population analyses (VPA) were available for 1932–59 in Murphy 1966 and for 1945–65 in MacCall 1979. Biomass estimates from MacCall 1979 were used for years when estimates from both sources were available (table 2). No direct VPA biomass estimates were available for years after 1965.

The two general categories of information about sardine biomass during recent years are described in

TABLE 1
Annual Sardine Landings (MT) for Ensenada (Mexico) and California (U.S.), 1983–1990

Year	Ensenada	California Directed	California Incidental	California Total	Grand total
1983	274	192	353	545	819
1984	0	61	238	299	299
1985	3722	14	593	607	4329
1986	243	421	762	1183	1426
1987	2432	600	1711	2311	4743
1988	2035	1034	2801	3835	5870
1989	6224	1400	4409	5809	12033
1990	11375	2035	1329	3364	14739

Data sources were the Instituto Nacional de Pesca for Ensenada; LMR Fisheries Research, Inc. for the 1989 incidental landings; and the California Department of Fish and Game for all other California landings.

detail below. The first category consisted of data types similar to catch-per-unit-effort (egg density, larval density, and tons of sardine sighted per block by fish spotters); the second category consisted of indices that measured sardine biomass by means of presence-absence data (proportion of sea-survey stations positive for eggs and larvae, counts of blocks where sardines were seen by fish spotters, and counts of positive tows from CDFG sea-survey data).

Catch-per-unit-effort (CPUE) indices have lately received much criticism as tools for measuring relative abundance of pelagic fish like sardines because CPUE tends to decline more slowly than abundance (i.e., relationships between CPUE and biomass tend to be nonlinear: see Bannerot and Austin 1983 and references therein). Theory underlying the use of indices of abundance based on presence-absence data is described by Smith (1990), Mangel and Smith (1990), and Wolf and Smith (1985). As with CPUE data, it is possible that indices derived from presence-absence data do not change proportionally with abundance. This is a concern, particularly when data were collected from a geographic area smaller than the range of the stock.

California Cooperative Oceanic Fisheries Investigations

MacCall and Prager (1988) used an analysis of variance approach (ANOVA) to derive an index of abundance for Pacific sardine larvae sampled by California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys from 1951 to 1985. Their ANOVA model consisted of independent additive month, region, and year factors combined to estimate the log of the mean density of larvae in each month, region, and year. MacCall and Prager used antilogs of year factors from the ANOVA to obtain index values of relative annual larval abundance (table 2). This time series is especially valuable because it spans the decline of the 1950s and 1960s, the unfished low period of the 1970s, and the early recovery of the 1980s.

For this study, we used four additional types of CalCOFI data: estimates of sardine egg density (eggs/0.05 m^2); estimates of larval sardine density (larvae/0.05 m^2); the fraction of sampling stations at which eggs were found ("proportion positive for eggs"); and the fraction of stations at which larvae were found ("proportion positive for larvae"). These data were for winter and spring cruises (one cruise per year during January to March and one cruise per year during April to June) and probably covered the period of peak spawning for sardines. The data were

TABLE 2
Data Used in Analyses for Sardine

Year	Number stations	E	L	PE	PL	VPA	SQUIRE	LO	CDFG	ANOVA	WTS	SPT
1916	—	—	—	—	—	—	—	—	—	—	—	16.56
1917	—	—	—	—	—	—	—	—	—	—	—	16.68
1918	—	—	—	—	—	—	—	—	—	—	—	17.35
1919	—	—	—	—	—	—	—	—	—	—	—	16.85
1920	—	—	—	—	—	—	—	—	—	—	—	16.51
1921	—	—	—	—	—	—	—	—	—	—	—	16.50
1922	—	—	—	—	—	—	—	—	—	—	—	16.43
1923	—	—	—	—	—	—	—	—	—	—	—	17.33
1924	—	—	—	—	—	—	—	—	—	—	—	16.52
1925	—	—	—	—	—	—	—	—	—	—	—	16.96
1926	—	—	—	—	—	—	—	—	—	—	—	18.03
1927	—	—	—	—	—	—	—	—	—	—	—	16.84
1928	—	—	—	—	—	—	—	—	—	—	—	16.69
1929	—	—	—	—	—	—	—	—	—	—	—	17.14
1930	—	—	—	—	—	—	—	—	—	—	—	17.40
1931	—	—	—	—	—	—	—	—	—	—	—	18.45
1932	—	—	—	—	—	3,524	—	—	—	—	—	16.27
1933	—	—	—	—	—	3,415	—	—	—	—	—	15.62
1934	—	—	—	—	—	3,625	—	—	—	—	—	17.49
1935	—	—	—	—	—	2,845	—	—	—	—	—	16.67
1936	—	—	—	—	—	1,688	—	—	—	—	—	17.57
1937	—	—	—	—	—	1,207	—	—	—	—	—	17.00
1938	—	—	—	—	—	1,201	—	—	—	—	—	16.64
1939	—	—	—	—	—	1,608	—	—	—	—	—	17.13
1940	240	699.10	49.13	0.75	0.81	1,760	—	—	—	—	—	17.32
1941	210	336.90	36.88	0.63	0.75	2,457	—	—	—	—	—	17.62
1942	—	—	—	—	—	2,065	—	—	—	—	—	16.96
1943	—	—	—	—	—	1,677	—	—	—	—	—	16.95
1944	—	—	—	—	—	1,260	—	—	—	—	—	16.45
1945	—	—	—	—	—	720	—	—	—	—	—	16.57
1946	—	—	—	—	—	566	—	—	—	—	—	16.79
1947	—	—	—	—	—	405	—	—	—	—	—	16.85
1948	—	—	,—	—	—	740	—	—	—	—	—	16.03
1949	—	—	—	—	—	793	—	—	—	—	—	16.48
1950	—	—	—	—	—	780	—	—	—	—	—	16.36
1951	96	33.33	2.06	0.17	0.15	277	—	—	—	16.75	1.00	16.59
1952	152	6.85	3.49	0.10	0.11	136	—	—	—	4.66	1.00	16.23
1953	226	0.21	0.07	0.03	0.01	202	—	—	—	0.48	1.00	16.20

(continued on next page)

"Number stations" is the total number of stations (tows) for CalCOFI data. E is mean number of eggs per 0.05 sq. m. L is mean number of larvae per 0.05 sq. m. PE is proportion of CalCOFI stations positive for sardine eggs. PL is proportion of stations positive for sardine larvae. VPA is biomass (thousand MT) of sardines age two and older from a virtual population analysis. SQUIRE is a catch-per-unit-effort-like index (short tons sighted per block) from fish spotters for nighttime flights over a core area where sardines are normally abundant. LO is the number of blocks in which sardines were spotted by fish spotters during each year. CDFG is California Department of Fish and Game sea-survey data (n.mi.²). ANOVA is analysis-of-variance data from MacCall and Prager 1988; the original ANOVA data were logarithms but are given here in arithmetic units. WTS is for weights from MacCall and Prager (1988, table 2) used to scale the ANOVA data. SPT is for mean annual sea-surface temperatures (centigrade) at Scripps Pier. The symbol — indicates no data available.

from an area of the California Bight much smaller than the historical range of sardines; the boundaries were chosen to coincide with the boundaries of the ichthyoplankton survey conducted during 1941 (figure 3 in Smith 1990). Data for 1940–89 were obtained from table 1 in Smith 1990 and augmented to include data for 1990 (Paul Smith, NMFS, Southwest Fisheries Science Center, pers. comm.). There were 30 observations for each type of CalCOFI data, and a total of 120 CalCOFI observations (table 2).

CalCOFI cruises and sampling procedures are explained in Hewitt 1988. No cruises were conducted in some years, and the number of sampling stations in the study area varied from one survey year to the next. Distance between sampling stations was too great to precisely measure the density of sardine eggs and larvae at low biomass levels. Fortunately, indices of relative abundance based on presence/absence of eggs and larvae are expected to be more robust than density estimates at low biomass and sampling levels (Smith 1990; Mangel and Smith 1990).

Fish-Spotter Data

Fish spotters are pilots employed by commercial fishermen to locate, identify, direct the harvest of,

TABLE 2 continued
Data Used in Analyses for Sardine

Year	Number stations	E	L	PE	PL	VPA	SQUIRE	LO	CDFG	ANOVA	WTS	SPT
1954	219	39.67	11.98	0.15	0.11	239	—	—	—	104.79	1.00	16.81
1955	142	26.87	7.29	0.17	0.09	170	—	—	—	19.77	1.00	16.50
1956	156	47.88	6.90	0.09	0.05	108	—	—	—	3.50	1.00	16.37
1957	145	23.00	12.09	0.10	0.10	90	—	—	—	6.62	1.00	17.36
1958	171	86.38	8.86	0.30	0.31	177	—	—	—	7.79	1.00	17.84
1959	188	182.00	7.88	0.29	0.25	122	—	—	—	6.85	1.00	18.35
1960	197	117.14	4.47	0.18	0.17	88	—	—	—	2.25	1.00	16.61
1961	73	17.08	1.40	0.16	0.08	54	—	—	—	0.39	0.66	16.52
1962	64	1.77	0.95	0.02	0.05	27	—	6	—	1.04	0.48	16.24
1963	77	14.22	1.94	0.05	0.04	21	1.38	51	—	0.95	0.65	16.96
1964	183	0.43	0.00	0.02	0.01	11	1.31	36	—	0.06	0.57	16.42
1965	112	4.57	0.79	0.11	0.10	3	0.02	10	—	0.93	0.66	16.52
1966	169	2.01	0.29	0.01	0.05	—	0.03	9	—	0.25	1.00	17.00
1967	—	—	—	—	—	—	0.00	0	—	0.12	0.28	16.92
1968	—	—	—	—	—	—	0.01	2	—	—	—	16.93
1969	147	0.33	0.26	0.03	0.04	—	0.00	0	—	0.90	0.86	16.64
1970	—	—	—	—	—	—	0.00	4	—	—	—	16.62
1971	—	—	—	—	—	—	0.00	6	—	—	—	16.18
1972	118	0.00	0.03	0.00	0.01	—	0.00	1	—	0.07	0.54	16.87
1973	—	—	—	—	—	—	0.00	2	—	—	—	16.45
1974	—	—	—	—	—	—	0.00	0	—	—	—	16.47
1975	267	2.54	0.07	0.03	0.01	—	0.00	0	—	0.03	0.71	15.53
1976	—	—	—	—	—	—	0.00	0	—	—	—	17.26
1977	—	—	—	—	—	—	0.00	0	—	—	—	17.25
1978	189	0.38	0.18	0.03	0.02	—	0.00	0	—	0.11	0.87	17.42
1979	—	—	—	—	—	—	0.00	0	—	—	—	16.85
1980	—	—	—	—	—	—	0.00	0	—	—	—	16.62
1981	139	0.99	0.23	0.03	0.01	—	0.00	2	—	0.52	0.89	17.62
1982	—	—	—	—	—	—	0.24	8	—	0.09	0.19	17.12
1983	—	—	—	—	—	—	0.33	15	—	2.34	0.10	17.97
1984	141	3.40	6.50	0.06	0.04	—	2.77	20	—	0.62	0.89	18.31
1985	99	10.96	8.80	0.06	0.05	—	97.36	61	670	21.07	0.30	17.21
1986	183	3.45	3.62	0.01	0.04	—	32.35	58	970	—	—	17.72
1987	81	18.73	23.00	0.06	0.11	—	20.12	85	1,850	—	—	17.56
1988	85	40.75	2.25	0.08	0.05	—	145.75	109	2,508	—	—	16.99
1989	72	61.00	4.96	0.11	0.17	—	34.84	78	3,680	—	—	17.18
1990	66	77.89	5.71	0.03	0.08	—	39.03	80	1,480	—	—	17.88
1991	—	—	—	—	—	—	—	—	3,840	—	—	16.97

and estimate the size of fish schools (Squire 1961, 1972). Analogous to CalCOFI data, two indices of relative abundance based on fish spotter data were available: densities of sardines observed by fish spotters, and the proportion of total blocks searched by fish spotters in which sardines were observed (table 2).

An index of relative density (biomass per block sighted by fish spotters in each year) was calculated from flights conducted at night over a "core" area where sardines were relatively abundant (Squire 1972). There were 28 annual records for the period 1963–90 (table 2). Unpublished sardine density data from fish spotters used in this analysis were developed and provided by Jim Squire (NMFS, Southwest Fisheries Science Center, pers. comm.).

N. C. H. Lo (NMFS, Southwest Fisheries Science Center, pers. comm.) developed the proportion-positive-blocks index of relative abundance. Lo's index was calculated by counting "positive blocks"

for sardines from 1962 to 1990 (29 annual records) where positive blocks were unique blocks in which sardines were seen by fish spotters (e.g., sardines were seen in six blocks by fish spotters during 1962; table 2). The proportion-positive index from fish-spotter data was calculated annually from all flights. Fish spotters covered a broader geographic area than the sardine stock in each year (N. C. H. Lo, unpublished data) so that counts of positive blocks were measures of the areal extent and size of the sardine stock.

Landings

Sardines commonly occur both in "pure" schools (sardines only) and in "mixed" schools with Pacific or jack mackerel. In recent years, incidental sardine catches in the mackerel fishery were a primary source of sardines in the southern California landings (table 1).

In 1988, LMR Fisheries Research, Inc. instituted a

program to collect fishery-based data other than tons landed. Each year from 1988 through 1990, data were collected from the San Pedro fresh fish market and a Terminal Island cannery. Samples were collected at both locations during the directed sardine fishery in January, and during the year-round mackerel fishery. Species composition data were collected from about 30.5% of all wetfish fleet landings during the study period. When sardines were present, biological samples consisting of 25 randomly selected fish were collected from individual deliveries. These fish were measured (standard length to the nearest mm, appendix table A), weighed (round weight to the nearest 0.1 g, appendix table B), and examined for sex and maturity. Otoliths were removed for age determination (appendix table C). Ages were estimated by examining otoliths with reflected light under 18× magnification (Sunada, undated; Mosher 1954).

The fishery data included information about the volume and age composition of landings during 1988–90, but were not suitable for standard VPA-based population estimates because the time series of catch-at-age data were short, and cumulative fishing mortalities during recent years may have been low (Pope 1972).

Sardine Egg Survey

From 1985 to 1991, CDFG conducted annual sea surveys to collect sardine eggs (Wolf and Smith 1986; Wolf et al. 1987). The extent of spawning area, defined by the number of sampling stations at which sardine eggs were found, was used to measure the areal extent and relative size of the spawning biomass. This approach allowed managers to track trends in biomass levels while the sardine population was relatively small and difficult to measure with conventional techniques (Wolf and Smith 1985). Smith's (1990) results and other analyses described in this paper indicate that spawning area is a useful index of biomass for sardines. Spawning area estimates for 1985–91 are given in table 2.

CDFG sea-survey design and sampling techniques are discussed in Wolf and Smith 1985 and 1986. Surveys were designed to take place during peak spawning and to cover waters in which spawning was likely to occur. The geographic extent of the surveys varied somewhat each year to accommodate new information about the range of sardine spawning. After the 1986 survey, which used a dense station plan over a relatively small area (Wolf et al. 1987), surveys encompassed the Southern California Bight and adjacent waters. Because the survey area increased slightly each year, a minor portion of the

increase in observed spawning area may be due to eggs detected in areas not surveyed the year before. Also, spawning was observed at the edge of the survey grid in some years, indicating that some fish may have spawned outside the survey area. However, annual CalCOFI surveys (which cover a larger area) found few sardine eggs outside the areas identified by CDFG surveys during each year for 1985–91 (unpublished data), indicating that the actual spawning area was probably identified by the CDFG surveys each year.

Sea-Surface Temperatures (SST)

Scripps Pier SST data, which are the longest time series of uninterrupted oceanographic data for Pacific sardine habitat, were used in this analysis (table 2). MacCall and Prager (1988) identified three major regimes in the data for 1916 to the late 1980s: warm water from 1916 to the early 1940s, followed by cool water until the mid-1970s, and then warm water until the late 1980s. Additional data through 1991 indicate that warm conditions have continued.

METHODS AND RESULTS

Indices used in our analyses to measure sardine biomass (table 2) were generally consistent with one another and indicated similar trends in abundance. Correlation coefficients were positive except in two cases where the sample size was small (table 3). Correlations among CalCOFI indices and between VPA biomass estimates and CalCOFI indices were particularly high (correlation coefficients >0.8). Correlation coefficients between other pairs of indices were also high but not reliable because sample sizes were small.

Historical CalCOFI Larval Abundance

MacCall's (1979) VPA estimates of sardine biomass were used to calibrate MacCall and Prager's (1988) CalCOFI larval index to units of sardine biomass (age 2 and older). The two data sets overlap from 1951 to 1965, but with incomplete monthly and regional coverage by the 1961–65 CalCOFI surveys. Index values from MacCall and Prager's 1988 ANOVA model were scaled by a multiplicative constant (25,072 MT) so that the index had the same weighted geometric mean and units of measurement as VPA biomasses over the period of overlap. Weights were taken from table 2 of MacCall and Prager 1988; data for 1951–60 were given unit weight, and weights for 1961–65 ranged from 0.482 to 0.659 (table 2).

VPA spawning biomass estimates and scaled CalCOFI index values are shown in figure 1. Index

TABLE 3
Correlation Coefficients for Indices Used to Measure Sardine Biomass in a General Linear Model

	E	L	PE	PL	VPA	SQUIRE	LO
L	0.88						
	(30)						
PE	0.92	0.87					
	(30)	(30)					
PL	0.93	0.89	0.98				
	(30)	(30)	(30)				
VPA	0.81	0.91	0.89	0.93			
	(17)	(17)	(17)	(17)			
SQUIRE	0.47	0.22	0.36	0.20	0.86		
	(16)	(16)	(16)	(16)	(3)		
LO	0.74	0.57	0.44	0.54	0.091	0.78	
	(16)	(16)	(16)	(16)	(3)	(28)	
CDFG	0.56	−0.13	0.82	0.79	★	−0.006	0.56
	(6)	(6)	(6)	(6)		(6)	(6)

Column and row headings are defined in table 2. Sample sizes are given in parentheses. The asterisk is used where there was insufficient data to calculate a correlation.
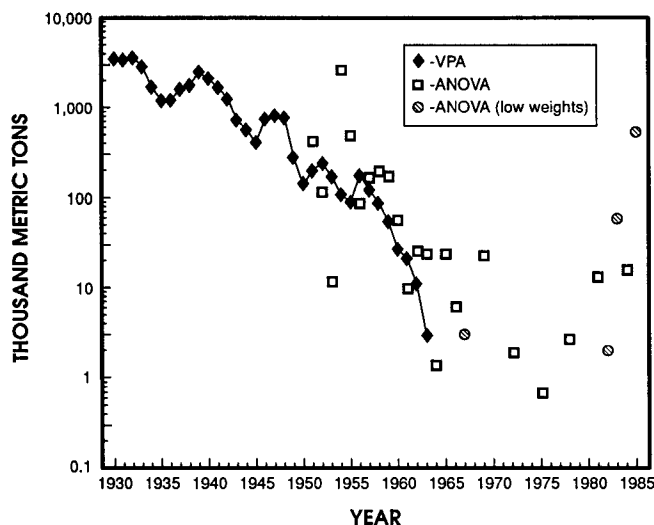

Figure 1. Sardine biomass (age 2 and older) estimated by VPA and ANOVA. ANOVA estimates are based on CalCOFI data and have been rescaled to the same units as VPA estimates. *Circles* indicate ANOVA estimates that are unreliable because of inadequate sampling (low-weight years).

values based on less than 30% coverage of the spawning months and regions (i.e., with weights <0.30) should be assumed unreliable. The remaining larval index values are still very imprecise, since errors appear as large as tenfold in some years. Nonetheless, long-term trends are clearly apparent in the time series of index values. The sardine population reached bottom during the mid-1970s. The recovery seems to have started in the late 1970s, but is not clearly apparent until the early 1980s.

General Linear Model Analysis

All of the data types in table 2 (with the exceptions of "Number Stations," "ANOVA," "WTS," and "SPT") were used in a statistical model to estimate recent levels of sardine biomass. The model was:

$$B_{t,y} = T_t Y_y z_{t,y} \qquad (1)$$

where $B_{t,y}$ was biomass (in absolute or relative units) of sardines in year y as measured by data type t; T_t was the effect for data type t; Y_y was the effect for year y; and $z_{t,y}$ was a statistical error. Taking logs gave the linear form:

$$\ln(B_{t,y}) = \ln(T_t) + \ln(Y_y) + \ln(z_{t,y}) \qquad (2)$$

which was the same as would be assumed in a two-way analysis of variance on log-transformed sardine biomass data with data types and years as factors. Statistical interactions between years and data types were not considered when equation 2 was fitted because of the scarcity of data for some years and to avoid complications in interpreting the results. Interactions are, however, biologically plausible and have been demonstrated elsewhere (MacCall and Prager 1988).

Models like equation 2 are known as general linear models or log-linear models. They are often used by fishery scientists and managers to derive a single index of relative abundance for a fish population from two or more types of data (e.g., catch rates from two types of fishing vessels) or data that were similar but collected from two or more temporal or spatial strata (Gulland 1956; Robson 1966; Kimura 1981, 1988; MacCall and Prager 1988). The general linear model (2) was fitted by standard linear regression techniques (Weisberg 1980) including residual plots, outlier analyses, and Cook's (1977, 1979) distance.

Statistical errors $(z_{t,y})$ in the general linear model (2) were assumed to be independent and lognormally distributed with variance constant over years

(y) and data types (t). The assumptions of normality and constant variance were required primarily for interpretation of statistical tests, which were not an important part of the analysis. The assumption of independence was more important (see below).

Abundance estimates for each year from model 2 were expressed in the same units as VPA biomass estimates (weight of sardines age 2 and older). The expected value for log-scale biomass was computed as:

$$\beta_{VPA,y} = \tau_{VPA} + \Omega_y, \tag{3}$$

where $\beta_{VPA,y}$ was the estimate of log-scale VPA biomass for sardines $[\ln(B_{VPA,y})]$ from model 2 for year y; τ_{VPA} was the estimate of the log-scale effect for VPA data $[\ln(T_{VPA})]$; and Ω_y was the estimate of the log-scale effect for year y $[\ln(Y_y)]$. Estimates of the expected value for sardine biomass on an arithmetic scale were obtained by taking exponents:

$$\Phi_{VPA,y} = \exp(\beta_{VPA,y} + \sigma^2/2) \tag{4}$$

where $\Phi_{VPA,y}$ (which estimates $B_{VPA,y}$) is the index for year y (units MT of fish age 2 and older), and σ^2 is the variance of residuals from the fit of model 2. The factor $\sigma^2/2$ corrects for bias due to log transformation (Beauchamp and Olson 1973). An unbiased estimate of median biomass can be obtained from equation 4 by neglecting the correction factor.

Variances for log-scale indices of sardine biomass were calculated from sums of variances and covariances for estimates of parameters on the right-hand side of equation 3, which were obtained from the regression output. Arithmetic-scale confidence intervals for estimates of sardine biomass in each year were calculated from the log-scale confidence intervals by taking exponents and correcting for bias as in equation 4.

The CalCOFI and fish-spotter data used to fit the general linear model (2) were probably not completely independent, since all of the CalCOFI indices were based on data collected during the same ichthyoplankton surveys, and both fish-spotter indices were derived from data collected during the same flights. The practical consequence of this problem would be biased estimates of biomass for sardines, because the statistical errors for CalCOFI or fish-spotter indices in a particular year ($z_{t,y}$) would tend to be either all positive or all negative and would not "cancel each other out." The magnitude of this problem could not be determined from the available data, but it is necessary to consider potential bias when interpreting results.

We used weights for CalCOFI data when fitting model 2 in an effort to avoid potential problems with lack of independence. Weights used were 0.5 for CalCOFI data and 1.0 for all other data types, so that each CalCOFI observation would receive half the weight used for VPA, fish-spotter, or CDFG sea-survey data during parameter estimation. We considered it unnecessary to use weights to account for lack of independence among the two types of fish-spotter indices, because differences in their geographic and temporal scope should result in some degree of independence.

Model 2 was initially fit to data for all available years, but residual plots indicated nonlinear relationships between sardine biomass and most of the indices. The initial estimate of sardine biomass during 1990 was 200,000 MT. In order to limit bias from the linear model due to nonlinear relationships in the data, we omitted years for which the initial sardine biomass estimate was much smaller (<50,000 MT during 1964–83) or much larger (>500,000 MT during 1940–41) than the 1990 level, and fitted the model again. This approach confined the analysis to a range of sardine biomass levels within which the linear model was approximately valid. An additional advantage in excluding years with very low biomass is that "zeroes" (e.g., egg density data for 1972) were not used to estimate parameters. When zeroes are present, a positive constant must be added to all observations before the data are log-transformed (e.g., MacCall and Prager 1988). Approaches to choosing additive constants are well developed when log-linear models are used for hypothesis testing (Berry 1987) but not for estimation or measurement.

Model 2 was fitted to the data for 1951–63 and 1984–90 after data for high and low biomass years were omitted, and one anomalous observation (VPA biomass in 1953) was identified as an outlier (t test = 4.43, Bonferroni probability value for mistakenly rejecting the null hypothesis of no outlier <0.05; see Weisberg 1980). The model was fitted again after the outlier was omitted. There were 114 observations in the data set finally used.

Effects of years and data types were statistically significant (probability of no differences among years or data types <0.00). There were seven observations with large standardized residuals (absolute magnitude greater than 2.0), but none could be rejected as an outlier on statistical grounds. No observations had an unusually large influence on predicted values as indicated by Cook's distance. Standard deviations for residuals from the seven data types were similar.
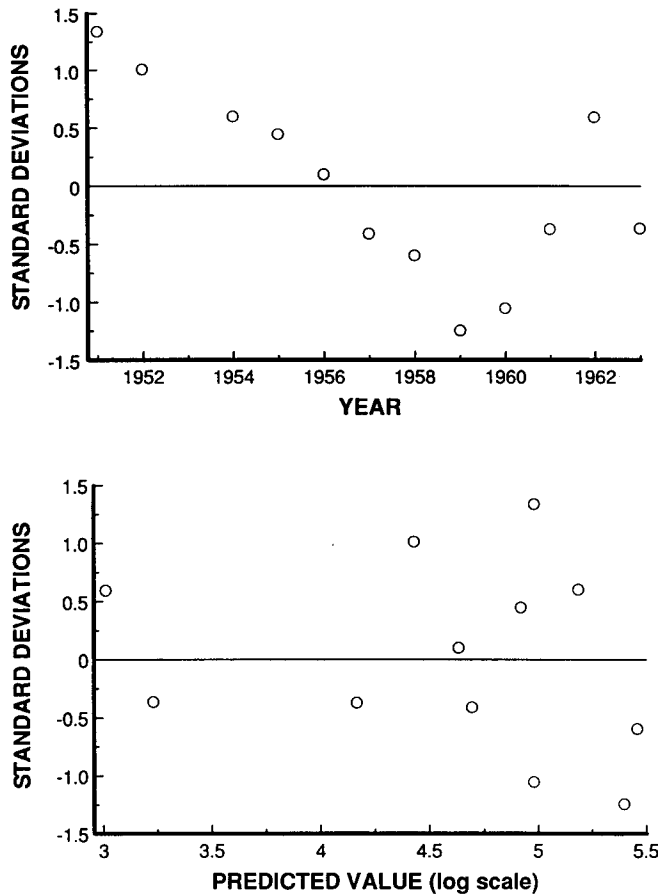
Figure 2. Studentized residuals from a general linear model. Residuals for sardine VPA data are plotted against year (*top*) and predicted log sardine biomass (*bottom*). Positive residuals occur where predicted values are too small; negative residuals occur where predicted values are too large.

TABLE 4

Sardine Biomass Estimates from GLM Analysis
(Thousand MT of Fish Age Two and Older), with Upper
and Lower Bounds for 95% Confidence Intervals

Year	Lo 95%	Biomass	Hi 95%
1951	84	176	371
1952	48	101	213
1953	2	6	14
1954	103	216	455
1955	79	166	349
1956	59	124	261
1957	63	132	278
1958	135	284	597
1959	127	267	561
1960	83	176	370
1961	37	78	164
1962	12	24	52
1963	16	30	58
1984	14	30	65
1985	49	99	202
1986	28	57	117
1987	58	119	243
1988	78	160	326
1989	78	160	326
1990	62	115	214

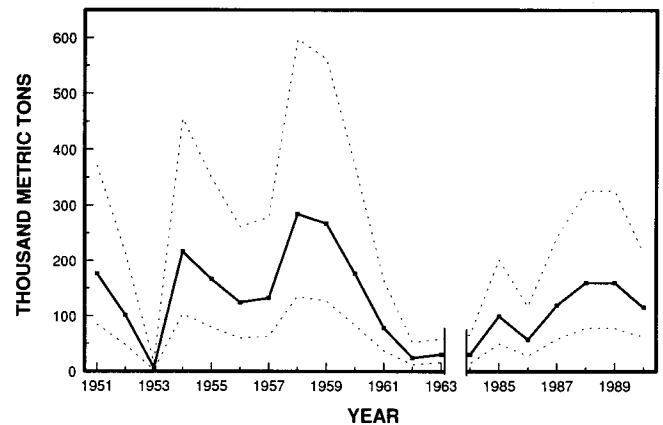Figure 3. Sardine biomass estimates (age 2 and older) with 95% confidence intervals from a general linear model.

Residual plots indicated that the linear model (2) was adequate for the reduced data set, although there was a trend in the plot of residual values for the VPA data versus time with predicted values being smaller than observed values (positive residuals) for 1940–55 (figure 2). This result indicates that estimates of VPA biomass for sardines from the model were generally too small (biased low) for 1951–55 and too high (biased high) for 1957–65.

Estimates of sardine biomass ($\Phi_{VPA,y}$) from the general linear model (table 4 and figure 3) indicated that sardine biomass increased after 1984, although the trend was somewhat erratic. Sardine biomass increased from about 30,000 MT in 1984 to about 160,000 MT in 1988–89 and then fell to 115,000 MT in 1990. These results were similar to trends reported by MacCall (1979), MacCall and Prager (1988), and Smith (1990), although similarity would be expected since the same data were used. Confidence intervals for the estimates of sardine biomass were quite broad, particularly for years in which sardine biomass was estimated to be large (figure 3). The

95% confidence interval for sardine biomass during 1990 was 62,000–214,000 MT.

Egg Production Area Method

Since 1985, CDFG has used an egg production area method (Wolf and Smith 1985) and sea-survey data (table 2) to determine if sardine spawning biomass exceeded the 18,156-MT level necessary to allow a directed fishery. The area over which a specified or "threshold" spawning biomass would be expected to occur was:

$$A = \frac{B\,R\,F\,S\,m}{P_o\,k\,W}, \tag{5}$$

where A is the spawning area occupied by the sardine population at biomass B, in nautical miles^2 (n.mi.^{2}); B is the spawning biomass (MT); P_o is the daily egg production, number eggs/0.05 m^2/day; W is the average weight of mature females (g); R is the sex ratio (fraction female, by weight); F is the batch fecundity (number eggs spawned/mature female/batch); S is the fraction mature females spawning per day; k is the conversion factor from g to MT; and m is the conversion factor from 0.05 m^2 to n.mi.^{2}. Equation 5 is derived from the original egg production method formula (equation 4 in Parker 1985) that expresses spawning biomass as a function of spawning area and other variables (Wolf and Smith 1986).

If the observed spawning area was equal to or greater than the threshold spawning area, then a quota was allotted for directed fishing. Using estimates for the parameters in equation 5, and assuming a sex ratio of 50% females by weight (table 5), the spawning area corresponding to 18,156 MT is 2,300 n.mi.^{2} (7,900 km^2). This may be an underestimate of threshold spawning area, since females may constitute slightly more than 50% of the population by weight. The estimate of 62% for sex ratio was based on a small number of samples and is assumed to be high. The observed spawning area exceeded the 2,300-n.mi.^{2} threshold in 1988, 1989, and 1991.

Sardine spawning area increased in each year after 1986, except in 1990 when it dropped below the level observed in 1987 (figure 4). The spawning biomass for sardines during 1990 (estimated by inverting
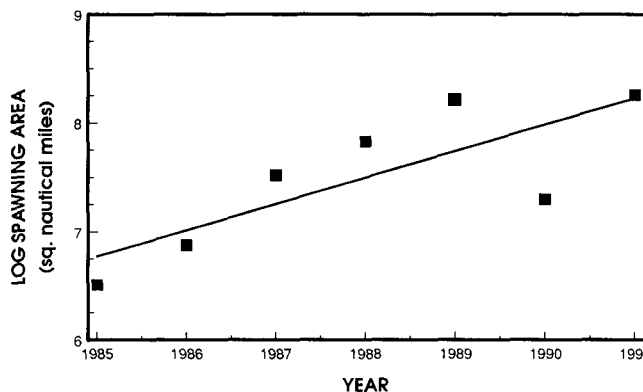

Figure 4. Sardine spawning area from CDFG sea surveys, 1985–91. Line was fitted by linear regression.

equation 5) that corresponds to the observed spawning area of 1,480 n.mi.^{2} (5,083 km^2) is 12,000 MT. This estimate seems low relative to total sardine landings during 1990 (14,739 MT) as well as to biomass estimates from other sources for 1989 and 1990. Apparently the current best estimates for the parameters in equation 5 are imprecise, or the parameter values have changed over time. Additional research will be required if this approach is used in the future.

Linear regression was used to fit a line to the CDFG sea-survey data, with years as the independent variable, and the natural logarithm of relative spawning areas as the dependent variable (figure 4). Log-transformed spawning-area data increased in an approximately linear fashion during 1986–91, indicating that sardine spawning biomass increased exponentially. If the slope of the log-scale linear regression is b, then $\exp(b) - 1$ gives the average percent annual increase in spawning area from 1986 to 1991. The estimate of b obtained from the regression (0.242) corresponds to an average annual increase of 27% in sardine spawning area and biomass. The 95% confidence interval for the average annual increase was 8%–50%.

Life-Table Estimates

Sardine abundance during 1989 was estimated by simulation in a life table using three types of data: age composition of landings, tons landed, and CDFG estimates of spawning area. The most important assumptions in the simulation were that recruitment increased at a constant rate for the 1981–87 year classes and that total mortality rates for sardine did not change from 1983 to 1989.

Age-composition data for 1988–90 were combined because data and catch curves for individual years were similar, as would be expected under conditions such as those assumed for the simulation

TABLE 5

Best Estimates for Parameters Used to Estimate Area Occupied by Spawning Sardines at the Threshold Level of Spawning Biomass (18,156 MT or 20,000 Short Tons)

Parameter	Symbol	Best estimate and units
Sex ratio	R	
Measured		62% females, by weight
Assumed		50%
Batch fecundity	F	62,500 eggs/batch/ mature female/day
Spawning fraction	S	11.5% spawning females/mature females/day
Conversion factor (0.05 m^2 to n.mi.^{2})	m	1.458×10^{-8} n.mi.^{2}/ 0.05 m^2
Conversion factor (0.05 m^2 to km^2)	m_1	5×10^{-8} km^2/0.05 m^2
Egg production	P_0	2.4 eggs/0.05 m^2/day
Conversion factor (g to MT)	k	1×10^{-6} MT/g
Female weight	W	172 g

Figure 5. Sardine catch curve from commercial landings in southern California, 1988–90.

$$N_{a,t} = N_{a-1,t-1}\, e^{-Z} \text{ and} \tag{6}$$

$$R_t = N_{2,t} = 100/\alpha^{1989-t} \tag{7}$$

where $N_{a,t}$ is the number of fish age a ($a > 2$) in year t (e.g., 1987); R_t is the number of recruits (2-year-old sardines) in year t; Z is the total mortality rate; and α is the proportional annual increase for recruitment.

We converted relative numbers of fish in each age during each year to relative biomass for each age group using mean weight-at-age data for sardines taken by the commercial fishery from 1988 to 1990:

$$B_{a,t} = N_{a,t} w_a \tag{8}$$

where w_a is the weight of fish age a. We derived weight at age from data in appendix B by using the mean of the monthly values for each year, then using the mean of the three annual estimates to obtain w_a.

	Age						
	2	3	4	5	6	7	8
w_a (Average weight [g] per fish)	139.1	161.8	173.5	181.5	193.3	191.6	192.8

Relative total biomass in each year was obtained by summing $B_{a,t}$ for each age. Relative spawning biomass in each year was calculated from relative biomass at age, assuming that one-half of sardines age 2 spawn and that all sardines age 3 and older spawn (Clark 1934; MacGregor 1957). We calculated the slope of the catch curve (Z_a) for sardines in the simulation by applying Heinke's method to the simulated age-composition data for 1988 to 1989.

We used an iterative approach to systematically vary the annual increase in recruitment (α) in the simulation until the ratio of spawning biomass in 1985 and in 1989 agreed with that actually observed. For each iteration we specified a new value of α, and adjusted the mortality rate in the model until the slope of the actual and simulated catch curves matched exactly. The simple ratio of beginning/ending year biomasses was suitable for solving the iteration because annual spawning area increased at a nearly constant rate from 1985 to 1989, making it unnecessary to match biomass estimates for each year in between. Intermediate years were fit by the simulation because of the assumption that recruitment also increased at a constant rate during those years. The closest match between the observed and simulated data was for $\alpha = 160\%$ and $Z = 0.65$ yr^{-1}.

(Ricker 1975). Sardines age 3 and older were fully recruited to the fishery (figure 5 and appendix table C). The slope of the catch curve for fully recruited sardines during 1988–90 estimated by Heinke's method (Ricker 1975) from the combined data set was $Z_a = 1.13$ yr^{-1}. If the number of sardine recruits had been constant in recent years, then 1.13 yr^{-1} would be a reasonable estimate of the actual instantaneous mortality rate (Z) experienced by fully recruited individuals in the stock. The assumption of constant recruitment was not plausible, however, because CDFG sea-survey data indicate that sardine spawning area and biomass increased by about 549% from 1986 to 1989. Density-dependent effects on recruits per unit of spawning biomass are thought to be minimal at low biomass levels, so it is likely that recruitment increased in proportion to spawning biomass and spawning area. Consequently, the slope of the catch curve (Z_a) was greater than the actual mortality experienced by the fully recruited ages (Z).

A simulated life table was constructed to account for the effect of increasing recruitment on age composition of landings and the slope of the catch curve. Recruitment in the life table was assumed to increase at a constant but unknown rate for the 1981–87 year classes, which were present as age-2 and older fish during 1983–89. The number of age-2 sardines in the simulation during 1989 (the 1987 year class) was assigned the arbitrary value of 100, and the number of recruits in previous years was calculated assuming a constant proportional rate of increase (α). Once the number of recruits in each year was specified, and assuming constant mortality (Z), the number of sardines in each year class from 1983 to 1989 could be calculated by standard methods:

	Observed	Life-table simulation
Ratio 1985/1989		
spawning biomass	549%	535%
Slope from catch curves	1.13	1.13

An estimate of the fishing mortality rate (F) for sardines during 1983–89 was obtained from the estimate of total mortality:

$$F = Z - M \qquad (9)$$

where M is the rate of natural mortality. The rate of natural mortality (M) for sardines is uncertain. Murphy (1966) and MacCall (1979) used $M = 0.4$ yr^{-1} for VPA analyses, although Murphy used $M = 0.8$ yr^{-1} for 1951 and later year classes. In this analysis we used a range of 0.3–0.6 yr^{-1} for M. Biomass in 1989 was calculated from the ratio of fishing mortality rate (annualized) and landings:

$$B_a = C/F \qquad (10)$$

where B_a is the average biomass (MT) and C is total landings during 1989. Sardine landings during 1989 (C), assuming that the southern California and Ensenada fisheries exploit the same stock, amounted to 12,033 MT, and biomass estimates for 1989 ranged from 41,000 to 247,000 MT.

Z	M	F	Biomass (landings/F)
0.65	0.3	0.35	40,747
0.65	0.4	0.25	54,399
0.65	0.5	0.15	86,387
0.65	0.6	0.05	246,727

No particular value of M within the indicated range is thought to be the best estimate under current conditions. However, for the specific purpose of comparison with the historical biomass estimates given in table 2, the current biomass estimate associated with $M = 0.4$ (54,399 MT) is probably the most appropriate, because it is based on the same estimate of M that was adopted for the earlier VPA analyses.

The precision of life-table estimates for sardine biomass was not calculated, because the number of observations used to fit the model (spawning area in 1985 and 1989) were too few to obtain meaningful results from approaches based on asymptotic theory or bootstrap methods.

Factors Affecting Sardine Biomass

There has been a long and colorful debate (Radovich 1982) about the relative importance of environment, ecology, and fishing on short- and long-term changes in sardine abundance (Smith and Moser 1988). Water temperatures are believed to affect abundance (Radovich 1982), although a variety of other environmental factors have also been identified (Kondo 1980). The transition from warm to cold water in the early 1940s corresponds approximately to the decline in abundance at that time.

Data and results from our analyses, and new Scripps Pier temperature data extend the historical record for sardines (figure 6). Like the historical data, our new data indicate that water temperatures and fishing both affect abundance. The historical record (pre-1965) indicates that sardine biomass decreased in the late 1930s and early 1940s, when exploitation increased beyond 20% annually and sea-surface temperatures declined to or below the historical average (16.9°C). Exploitation rates during 1941–65, when sardine biomass declined consistently, were generally higher than 30% and, in 1958, as high as 68%. Temperatures during the same period were generally well below the historical average except during the 1957–59 El Niño.

Data and results for recent years (1965 and after) indicate that sardine biomass remained low during 1965–74, when recorded landings were nil and temperatures were generally below average. Biomass began to increase in about the late 1970s, when water temperatures increased beyond the historical average and exploitation rates remained near zero. Sardine biomass continued to increase from the late 1970s to 1990 as warm-water conditions continued and exploitation rates remained less than 10% per year. Thus, since the early 1930s, sardine biomass increased with warm water and low exploitation rates, and decreased with cold water and higher exploitation rates (>20% per year).

DISCUSSION

Sardine analyses prepared for the September 1990 workshop provided a foundation for discussions about the status and management of sardines. The workshop approach offered an effective format for assembling current data from diverse sources and developing timely population estimates needed for management during the initial stages of recovery. Concerns about weaknesses in individual analyses were alleviated by general agreement among the independent lines of evidence.

All of the analyses presented at the workshop indicated a generally increasing trend in sardine bio-
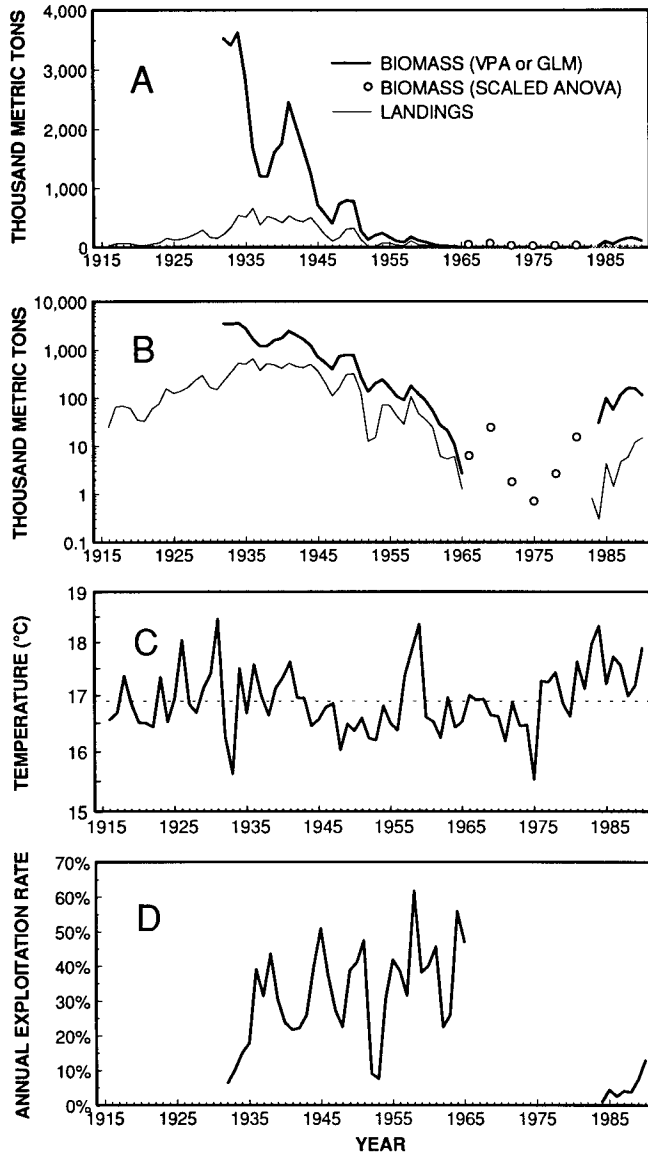
Figure 6. (A,B) Biomass estimates and landings data for Pacific sardines; (C) mean annual sea-surface temperature data from Scripps Pier; and (D) annual exploitation rates for sardines. Biomass estimates for 1932–44 are from VPA analysis by Murphy (1966); estimates for 1945–65 are from VPA analysis by MacCall (1979); estimates for 1966, 1969, 1972, 1975, 1978, and 1983 are scaled ANOVA values from figure 1 and MacCall and Prager (1988), with low-weight years omitted; estimates for 1984–90 are from a general linear model (table 4). Landings data for 1916–49 are from Murphy (1966); data for 1950–65 are from MacCall (1979); and data for 1983–90 are from table 1. Landings data for 1916–65 are for fishing seasons (e.g., the data for 1916 are for landings from June 1916 to May 1917); landings data for 1983–90 are for calendar years. The effects of mixing landings data from calendar years and fishing seasons are insignificant. A crude measure of annual exploitation for sardines in each year was obtained by dividing annual sardine landings (California plus Ensenada) by sardine biomass.

mass from the late 1970s to 1989. The rate of recovery slowed during 1990–91, but there was no indication of year-class failure.

The range of biomass estimates from our analyses was broad, illustrating the uncertainty about current sardine abundance levels. A subjective conclusion

based upon a majority of the data and findings at the workshop was that the 1990 spawning biomass probably fell within the 95% confidence limits of the general linear model analysis, i.e., 60,000–210,000 MT.

The analyses described in this paper were designed to make simultaneous use of a variety of data, although no single assessment used all of the available data. The results we obtained indicate that more completely integrated models (Deriso et al. 1985; Gavaris 1988; Methot 1989) based on fishery-dependent and fishery-independent data will be useful for sardine assessments. We expect that one facet of sardine research will be to develop better population models of this type.

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APPENDIX

TABLE A
Sardine Length-Frequency Data (SL, mm) from Landings at Terminal Island and San Pedro, 1988–1990

Length (mm)	1988 Jun	Jul	Aug	Sep	Oct	Nov	Dec	1989 Jan	Feb	Mar	Apr	May	Jun	Jul
<151	1	—	—	—	—	—	—	4	—	—	—	—	—	—
151–155	—	—	—	1	—	—	—	6	—	3	2	—	—	—
156–160	—	—	—	—	—	1	—	1	—	3	6	—	2	1
161–165	—	—	—	1	—	1	—	2	—	22	12	—	8	3
166–170	—	—	—	3	—	—	1	—	1	17	19	—	7	8
171–175	—	—	—	3	—	3	—	2	—	12	20	—	10	7
176–180	1	2	—	9	—	9	—	4	—	7	16	—	4	3
181–185	3	5	1	5	—	7	—	1	—	11	9	—	7	17
186–190	7	—	1	9	—	10	—	7	—	5	8	—	13	43
191–195	11	—	4	4	—	4	1	17	5	9	4	—	9	63
196–200	29	—	3	14	—	3	—	21	4	16	13	—	7	45
201–205	23	1	16	23	2	5	—	13	5	8	14	1	12	39
206–210	20	—	29	36	5	9	1	26	11	19	12	—	24	28
211–215	19	3	51	46	10	13	3	27	20	25	23	2	20	39
216–220	7	9	39	71	8	21	7	58	33	36	37	—	32	43
221–225	4	16	29	36	5	8	6	39	47	39	46	3	40	28
226–230	—	12	11	31	3	17	5	33	28	29	41	8	17	12
231–235	—	7	3	9	2	14	4	18	27	13	32	5	13	5
236–240	—	7	5	6	—	7	4	11	7	5	26	1	7	4
241–245	—	1	—	1	—	1	1	2	4	1	10	3	3	—
246–250	—	1	2	2	—	—	1	2	3	1	12	2	—	—
251–255	—	—	1	—	—	—	—	1	1	—	3	—	—	—
256–260	—	—	—	—	—	—	—	—	—	—	4	—	—	—
261–265	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	125	64	195	310	35	133	34	295	196	281	369	25	235	388

Length (mm)	1989 Aug	Sep	Oct	Nov	Dec	1990 Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Total*
<151	—	—	—	—	—	5	—	—	—	—	—	—	—	10
151–155	—	—	—	—	—	—	—	—	—	—	—	—	—	12
156–160	—	—	—	—	—	1	—	—	—	—	—	—	—	15
161–165	1	—	—	—	—	—	—	—	—	—	—	—	1	51
166–170	2	—	2	—	—	—	—	—	—	—	—	—	2	62
171–175	8	—	6	—	—	—	—	—	—	—	—	—	1	72
176–180	27	14	21	1	5	2	—	1	—	—	—	—	2	128
181–185	46	25	55	3	9	14	2	—	—	—	—	—	4	224
186–190	85	23	118	15	35	39	4	5	6	—	—	—	3	436
191–195	149	47	190	20	46	93	6	21	7	—	—	—	2	712
196–200	177	50	223	30	64	115	19	49	4	—	—	—	—	886
201–205	127	51	101	15	51	108	41	77	13	1	2	2	—	751
206–210	134	37	37	7	17	132	39	131	16	1	5	4	5	785
211–215	173	39	23	4	7	93	40	103	12	2	23	24	12	856
216–220	148	43	23	2	8	85	48	155	14	8	32	42	14	1,023
221–225	104	36	11	2	4	56	52	118	8	5	57	41	36	876
226–230	47	25	4	—	2	36	26	91	10	6	63	47	40	644
231–235	14	15	—	—	—	14	22	32	1	4	48	30	22	354
236–240	6	12	—	—	—	7	9	15	1	6	34	23	17	220
241–245	2	5	—	—	—	1	4	6	2	1	18	10	3	79
246–250	—	1	1	—	—	—	3	2	1	1	6	13	4	58
251–255	—	—	—	—	—	—	—	3	—	—	4	7	1	21
256–260	—	1	—	—	—	—	—	—	—	—	—	—	2	7
261–265	—	—	—	—	—	—	1	—	—	—	—	—	—	1
Total	1,250	424	815	99	248	801	316	809	95	35	292	243	171	8,283

*June 1988–August 1990

TABLE B

Average Round Weight (g) by Age of Sardines from Landings at Terminal Island and San Pedro, 1988–1990

	Year class											Weighted average*
	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980	
1988												
Jun			—	96.0	137.2	163.8	146.0	—	—	—	—	136.6
Jul			—	133.0	194.0	197.7	202.1	175.0	230.0	—	—	194.5
Aug			—	117.3	152.0	166.4	185.9	205.0	218.0	—	—	155.5
Sep			—	105.1	155.4	175.1	188.0	—	—	—	—	157.6
Oct			—	—	146.4	162.2	—	168.0	—	—	—	151.5
Nov			55.0	90.2	153.6	180.3	196.8	201.0	183.0	184.5	—	152.7
Dec			—	—	136.3	146.7	152.0	—	—	—	—	173.9
1989												
Jan		—	110.4	116.2	141.7	161.5	184.4	199.0	—	—	—	154.9
Feb		—	80.5	116.8	173.2	197.7	200.7	203.0	213.0	167.5	—	176.6
Mar		—	69.2	108.0	163.6	170.2	185.1	—	—	—	—	139.9
Apr		—	75.5	104.5	164.5	204.2	217.1	230.8	195.4	197.0	182.0	150.9
May		—	—	149.0	186.5	164.5	192.3	—	—	—	—	181.2
Jun		64.3	98.3	133.6	162.2	164.6	186.6	201.2	—	—	—	149.5
Jul		83.9	106.2	119.8	150.3	158.5	169.2	192.8	—	—	—	132.6
Aug		111.1	111.8	127.9	148.5	156.4	166.0	—	—	—	—	134.5
Sep		—	108.3	133.2	153.4	180.1	185.1	175.4	—	—	—	132.9
Oct		84.8	101.3	116.0	138.4	160.8	138.2	148.1	—	—	—	104.9
Nov		—	108.6	122.3	125.2	—	159.3	—	—	—	—	112.2
Dec		—	103.8	117.9	120.0	153.3	131.4	—	—	—	—	108.1
1990												
Jan	—	89.4	123.4	147.8	158.3	170.2	160.5	147.9	—	—	—	134.2
Feb	—	121.9	130.1	157.8	170.0	168.2	160.2	—	—	—	—	148.1
Mar	—	116.0	134.2	157.4	162.9	165.3	170.4	185.7	192.4	—	—	151.7
Apr	—	110.4	134.8	156.5	167.4	185.8	—	—	—	—	—	148.3
May	—	—	128.4	168.9	183.2	197.9	—	—	—	—	—	171.7
Jun	—	—	163.0	177.7	184.5	197.8	190.5	210.4	—	—	—	180.9
Jul	—	—	156.3	171.6	176.1	185.6	189.3	200.9	214.3	—	—	173.0
Aug	60.5	—	162.1	163.7	172.7	176.4	189.3	—	—	—	—	166.5

*All ages combined

TABLE C

Age Composition (Number of Fish) of Sardines from Landings at Terminal Island and San Pedro, 1988–1990

	Year class											Sample size
	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980	
1988												
Jun			1	2	99	6	2	—	—	—	—	110
Jul			—	6	9	24	17	4	1	—	—	61
Aug			—	6	142	12	10	2	1	—	—	173
Sep			3	30	206	34	20	—	—	—	—	293
Oct			—	—	28	5	—	1	—	—	—	34
Nov			1	29	64	16	15	3	1	2	—	131
Dec			—	—	4	3	1	—	—	—	—	8
1989												
Jan		—	15	25	73	15	8	3	—	—	—	139
Feb		—	2	4	142	22	11	6	1	2	—	190
Mar		—	63	38	140	16	15	—	—	—	—	272
Apr		—	41	13	58	17	24	9	5	1	1	169
May		—	—	3	16	2	4	—	—	—	—	25
Jun		7	18	55	62	7	8	1	1	—	—	159
Jul		7	56	178	117	20	7	2	—	—	—	387
Aug		5	51	184	197	45	10	—	—	—	—	492
Sep		—	143	112	75	19	5	2	—	—	—	356
Oct		7	670	81	30	4	1	1	—	—	—	794
Nov		—	75	19	3	—	1	—	—	—	—	98
Dec		—	173	60	6	1	1	—	—	—	—	241
1990												
Jan	—	48	386	218	78	13	15	1	—	—	—	759
Feb	—	1	132	120	43	10	5	—	—	—	—	311
Mar	—	5	298	285	127	47	23	5	1	—	—	791
Apr	—	7	44	25	11	8	—	—	—	—	—	95
May	—	—	4	16	12	3	—	—	—	—	—	35
Jun	—	—	56	84	105	27	14	5	—	—	—	291
Jul	—	—	48	79	76	22	12	5	1	—	—	243
Aug	5	7	56	45	40	10	6	—	—	—	—	169
Total	5	94	2,336	1,717	1,963	408	235	50	12	5	1	6,826