CATCH-AT-AGE ANALYSIS FOR PACIFIC SARDINE (*SARDINOPS SAGAX*), 1983–1995

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ABSTRACT

We used CANSAR (Catch-at-age ANalysis for SARdine, an age-structured stock-assessment model) and a wide range of data to estimate biomass and recruitment of Pacific sardine (*Sardinops sagax*) off California and northern Baja California during 1983–95. Daily egg production method (DEPM) spawning biomass estimates and an abundance index from CalCOFI data based on generalized additive models were important new sources of information. Biomass (344,000 MT of sardine age 1+ during July 1995, CV = 33%) increased by 28% year^{-1}. Fishing mortality (particularly for older ages) after 1991 was high and probably not sustainable under average environmental conditions. DEPM data for sardine during 1986–88 and 1994 may have underestimated spawning biomass due to incomplete coverage of spawning habitat. There was a modest potential for bias in the DEPM data due to nonrepresentative sampling of young age groups by survey gear. On the basis of experience with DEPM data for sardine and northern anchovy (*Engraulis mordax*), we make suggestions about how DEPM data should be used for fish stock assessment and fishery management. Size-at-age declined during 1983–95 and was significantly correlated with sardine biomass.

INTRODUCTION

Pacific sardine (*Sardinops sagax*) along the west coast of North America (stock structure reviewed in Hedgecock et al. 1989) is a small (28–30 cm SL), short-lived (less than nine years in recent years), pelagic schooling fish usually harvested near shore with purse seine gear (Wolf 1992). The historical fishery for Pacific sardine developed during the second decade of the twentieth century (Schaefer et al. 1951). It expanded rapidly; landings exceeded 700,000 MT during the 1936–37 fishing season and often exceeded 500,000 MT season^{-1} during the following years (Radovich 1982). Sardine landings fell off sharply after 1944 as abundance declined to low levels and the fishery collapsed. A minor fishery persisted off California during the 1960s and early 1970s until it was prohibited in 1973.

Sardine biomass began to increase in the late 1970s (Barnes et al. 1992), and sardine became common as by-

catch in fisheries off northern Baja California and California (Wolf 1992). There was immediate commercial interest, and the prohibition on sardine fishing in California waters was lifted in 1986 when a small quota (1,043 MT) was allowed for directed fishing. California and Mexican landings subsequently increased to 5,000 MT in 1987, 48,000 MT in 1993, and 34,000 MT in 1994 (table 1). In California during 1994, Pacific sardine was, next to market squid (*Loligo opalescens*), the second most important species landed in terms of total landings, and the thirteenth most important in terms of ex-vessel revenues ($2.8 million).[2] During 1995, total landings of sardine along the Pacific coast (excluding Mexican landings from the Gulf of California and south of Ensenada) exceeded 70,000 MT (preliminary data). Thus the sardine fishery had grown to again become one of the largest along the coast from Baja California to British Columbia.

Biomass of Pacific sardine is estimated annually and used to set quotas for the California fishery (Wolf 1992). A variety of models and approaches have been used to estimate sardine biomass (Barnes et al. 1992), but none

[2]Revenues include 1,487 MT of live bait sold at $681/MT and 11,933 MT sold at $148/MT primarily for human consumption.

TABLE 1
Pacific Sardine Landings (MT) in the United States (California) and Ensenada, Baja California, Mexico, 1983–1995

Year	First semester U.S.[a]	First semester Mexico	Second semester U.S.	Second semester Mexico	Total
1983	263.0	149.5	89.0	124.1	625.6
1984	159.0	0.1	75.0	0.1	234.2
1985	322.0	3,174.2	271.0	548.1	4,315.3
1986	920.0	99.2	244.0	143.4	1,406.6
1987	1,304.0	975.0	791.0	1,456.6	4,526.6
1988	3,020.0	620.2	766.0	1,414.7	5,820.9
1989	2,154.0	461.0	1,528.0	5,761.2	9,904.2
1990	2,132.0	5,900.0	683.0	5,475.3	14,190.3
1991	5,173.0	9,271.0	2,577.0	22,120.8	39,141.8
1992	6,256.0	3,326.5	11,060.0	31,241.7	51,884.2
1993	12,153.0	18,649.0	4,034.0	13,396.0	48,232.0
1994	8,498.6	5,706.2	4,336.4	15,165.0	33,706.2
1995	28,462.6	18,257.0	12,296.2	15,441.1[b]	74,456.9[b]

[a]U.S. landings include commercial landings and commercial bycatch. Live bait catches (less than 500 MT during 1983–92 and less than 2,000 MT in 1993–94) are excluded.
[b]Preliminary.

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took advantage of all available fishery and fishery-independent data. The purpose of our paper is to describe a stock assessment model (CANSAR for Catch-at-age ANalysis for SARdine; Deriso 1993) that includes all available data. Additionally, we describe a new index of abundance based on CalCOFI data. We also test assumptions about daily egg production method (DEPM) spawning biomass estimates for sardine and evaluate potential bias in DEPM data (Lo et al. 1996).

DATA

Catch-at-age (numbers of fish at age) and mean weight-at-age data for the California fishery during 1983–95 and for the Mexican fishery around Ensenada during 1990–92 were from random stratified port samples. Where catch-at-age data were unavailable, tons landed (table 1) were used instead (see below). Fishery data were aggregated by semester (January–June or July–December) and area (California or Mexico) because of seasonal and spatial differences in catch and weight-at-age. Before use in CANSAR, catch-at-age data were adjusted so that the sum of catch-at-age times weight-at-age was equal to tons landed for both fisheries in each semester of each year. Sardine were aged by counting annuli in whole sagittal otoliths (Yaremko 1996). A birth date of July 1 was assumed.

We used three indices of relative abundance and DEPM spawning biomass estimates for 1986 (Scannell et al. 1996), 1987–88, and 1994 (Lo et al. 1996) in CANSAR to estimate sardine abundance (table 2, figure 1). Indices of relative abundance were from CalCOFI data, fish-spotter reports, and spawning area surveys.

CalCOFI Index

The CalCOFI index measures annual egg production by sardine on a relative basis from ichthyoplankton data collected during 1984–95 (Hewitt 1988). We used data for sardine eggs and larvae taken in bongo nets within the boundaries of the current CalCOFI sampling grid (Lo and Methot 1989) from shore out to station 67.5. The current CalCOFI grid is smaller than the historical range of sardine but is the largest area occupied by the survey in all years. Data from samples taken farther offshore than station 67.5 were omitted because sardine were seldom taken there and the data were highly variable.

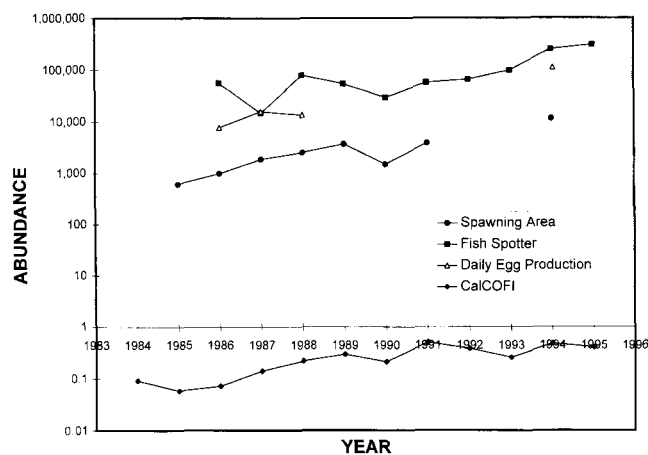Previous studies used four types of aggregated CalCOFI data for sardine: egg density (mean eggs tow^{-1}),

Figure 1. Relative abundance and DEPM data for Pacific sardine used in CANSAR.

TABLE 2
Abundance, Spawning Biomass, and Mean Three-Season Sea-Surface Temperature Data for Pacific Sardine by Fishing Season

Season[a]	CalCOFI	Fish spotter	CV[b]	California spawning area (nm²)	Daily egg prod. (MT)	CV[b]	Mean three-season[c] Scripps Pier temperature (°C)
1983							17.8
1984	0.0524						17.9
1985	0.0251			670			17.7
1986	0.0175	55,539	0.31	970	7,659	0.51	17.6
1987	0.0519	14,522	0.36	1,850	15,705	0.91	17.2
1988	0.0813	78,605	0.36	2,508	13,526	1.6	17.2
1989	0.1431	54,032	0.39	3,680			17.3
1990	0.0530	29,314	0.36	1,480			17.6
1991	0.2325	56,479	0.32	3,840			17.8
1992	0.1623	65,059	0.32				18.0
1993	0.1370	97,582	0.33				18.0
1994	0.2613	251,862	0.31	11,360	125,537[c]	0.45	18.0[d]
1995	0.2757	306,561	0.34				18.0[d]

[a]Season runs from 1 July of one year to 30 June of the following year; e.g., the 1983 season ran from 1 July 1983 to 30 June 1984.
[b]Coefficients of determination.
[c]Mean three-season sea-surface temperature calculated as in Jacobson and MacCall 1995. For example, the temperature datum for 1983 is used to predict recruitment of age-zero sardine on 1 July 1983 and was calculated from mean daily sea-surface temperatures at Scripps Pier during 1 July 1982–30 June 1985.
[d]Mean three-season temperature assumed to be the same as for 1993.
[e]Preliminary value.

larval density (mean larvae tow^{-1}), proportion of tows positive for eggs, and proportion positive for larvae. A general linear model (GLM) was fit to all four types of CalCOFI data in previous studies to obtain a single index of egg production (Barnes et al. 1992). The index was plagued, however, by problems with trends in residuals, the choice of a small additive constant used to log-transform the data (which includes "zeroes" when no eggs or larvae are taken; MacCall and Prager 1988), and differences in the appropriate statistical distribution for estimating parameters from proportion positive and density data.

To avoid the problems of previous studies, we fit logistic regression models using generalized additive model techniques (GAM; Hastie and Tibshirani 1990) to nonaggregated, tow-by-tow CalCOFI data. The advantages were greater flexibility in modeling, no additive constants, maximum likelihood parameter estimates, and no aggregation of data. The GAM used for sardine presence-absence data was

$$P_{y,m,L,s} = \frac{e^{\eta_{y,m,L,s}}}{1+e^{\eta_{y,m,L,s}}} + \epsilon_{y,m,L,s} \tag{1}$$

where $P_{y,m,L,s}$ was the probability that a tow in year y, month m, at line L and station s would contain at least one sardine egg or larvae, and $\epsilon_{y,m,L,s}$ was a statistical error. The term $\eta_{y,m,L,s}$ is described below.

The variance of statistical errors in equation 1 was modeled with quasi-likelihood techniques (McCullagh and Nelder 1983):

$$\text{VAR}(\epsilon_{y,m,L,s}) = \phi \hat{P}_{y,m,L,s} (1-\hat{P}_{y,m,L,s}) \tag{2}$$

where the scale factor (ϕ) measures how large the actual variance [Var($\epsilon_{y,m,L,s}$)] was relative to that expected under the binomial distribution [($\hat{P}_{y,m,L,s} (1-\hat{P}_{y,m,L,s})$], and hats ($\hat{}$) denote model estimates. The binomial distribution was appropriate because data used to fit model 1 were either zero (if no sardine eggs or larvae were taken in the tow) or one (if at least one egg or larva was taken). Results using just eggs or larvae were similar (correlation coefficient $\rho = 0.9$), so we combined data for eggs and larvae and estimated the probability that a tow was positive for either an egg or a larva.

The term $\eta_{y,m,L,s}$ in equation 1 was a "linear predictor" (McCullagh and Nelder 1983):

$$\eta_{y,m,L,s} = X_y + f(m) + g(L) + h(s) \tag{3}$$

where X_y was a parameter for year y (years were treated as factors), and the components $f()$, $g()$, and $h()$ were smooth, possibly nonlinear, functions of the covariates month, line, and station. Smooth terms were fit with the locally weighted scatterplot smoother (Cleveland

et al. 1988; called "loess" in Cleveland and Devlin 1988 and Hastie and Tibshirani 1990) with a neighborhood size of 75% and quadratic local regressions on the data in each neighborhood. Statistical interactions between month, line, and station probably exist but were omitted from model 3 because they are difficult to specify with loess components. MacCall and Prager (1988) found that interaction terms made little difference in estimation of year effects from CalCOFI data for six fish species.

Models like model 1 for egg and larval density data (numbers tow^{-1}) were fit assuming the Poisson distribution with Var($\epsilon_{y,m,L,s}$) = $\phi \hat{P}_{y,m,L,s}$. We did not report or use the results, however, because the variance of residuals was extreme ($\phi = 9,928$ for larvae and $\phi = 1,950$ for eggs), and estimated trends were erratic. High variance in egg and larvae counts is typical for sardine because of patchiness in the spatial distribution of spawning adults (Mangel and Smith 1990; Smith 1990).

In contrast to results for density data, the variance of residuals for presence-absence data was close to one ($\phi = 0.89$ for proportion-positive larvae and $\phi = 1.4$ for eggs), and trends over time were similar to other abundance indices (figure 1). The CalCOFI index (table 2, figure 1) was calculated for each year during May at line 80 and station 50 (figure 2).

Fish-Spotter Data

An index of schooling biomass for sardine during 1984–95 (table 2, figure 1) was based on fish-spotter data (Squire 1961) and delta-lognormal models (Lo et al. 1992). We used the same procedures to calculate the index as in Lo et al. 1992, except that (1) data for each flight were weighted by the number of blocks searched so that data from long flights were weighted more heavily than data from short flights; (2) July–June annual periods were used to aggregate data (to match time steps used in CANSAR, see below); and (3) years with fewer than 100 positive flights for sardine were excluded. The fish-spotter information for 1995 included only data for July 1994–March 1995.

Spawning Area Survey

Estimates of spawning area (table 2, figure 1) were used in CANSAR as an index of spawning biomass. The CDFG conducted spawning area surveys in California waters from 1985 to 1991 to measure the surface area of the ocean occupied by spawning sardine (Wolf and Smith 1985, 1986; Barnes et al. 1992). CDFG data were augmented by calculating spawning area during the 1994 DEPM spawning biomass survey (Lo et al. 1996). For consistency, we included only spawning area in California waters during 1994.
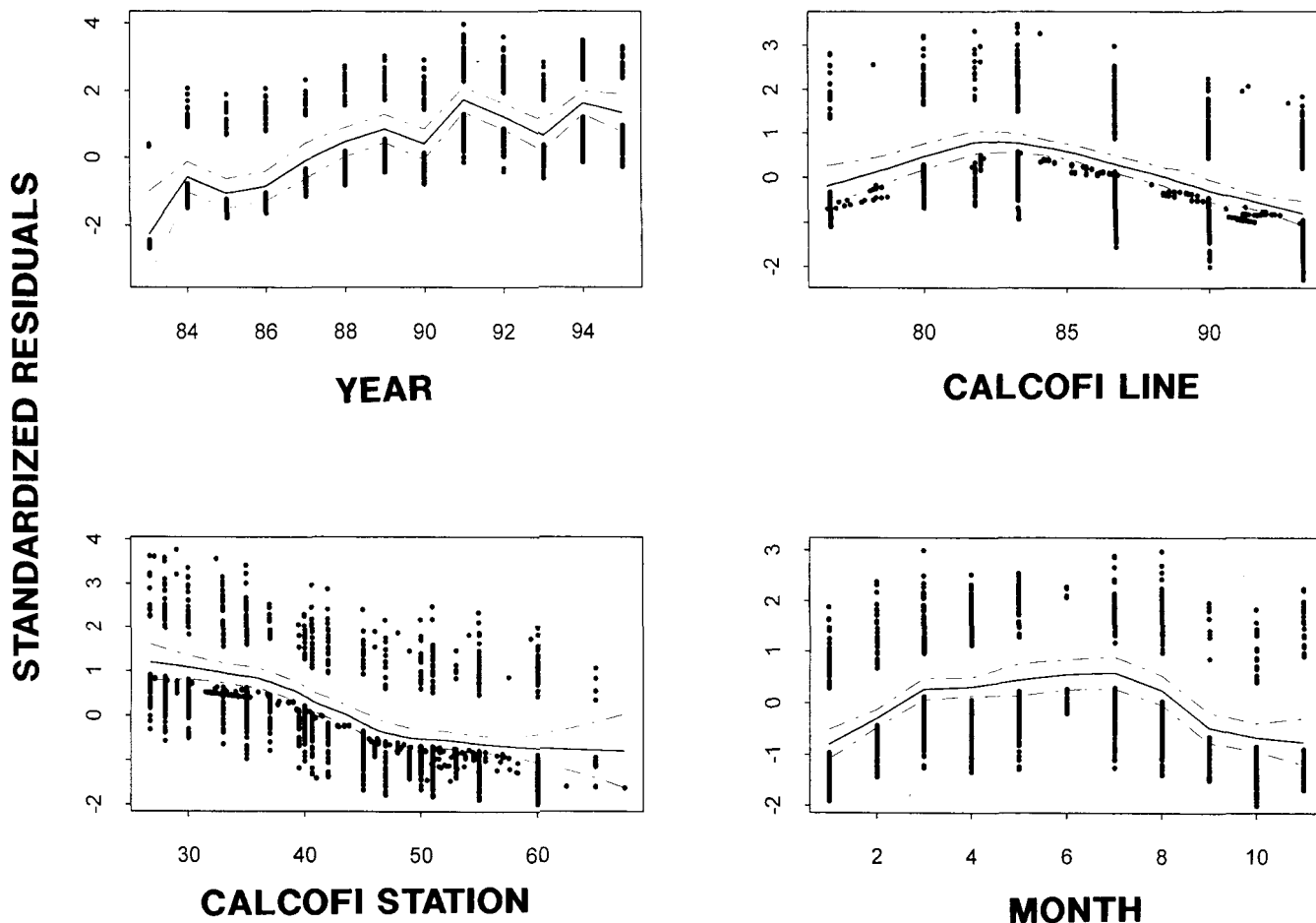
Figure 2.   Fitted values and residuals (with approximate 95% confidence intervals) for a generalized additive model fit to CalCOFI data for Pacific sardine. Plots are scaled so that the mean residual is zero. Many negative residuals occur between major CalCOFI lines because the samples were taken when sardine eggs were rare and no eggs were collected.

MODEL

CANSAR was derived from the CAGEAN program (Deriso et al. 1985). All computer calculations and storage were double precision. The original CAGEAN model used only catch-at-age and catch-per-unit-effort data. Deriso (1993) modified the "observation model" component of CANSAR to accommodate fishery-independent indices of relative abundance, estimates of spawning biomass, and aggregate landings data (without age-composition information). With these modifications, CANSAR was equivalent to other modern age-structured stock-assessment models based on a forward simulation approach (e.g., Methot 1990; Jacobson et al. 1994a).

Semesters were used as time steps in CANSAR; ages were incremented between semesters on 1 July; and spawning was assumed to occur on 1 April (the middle of the first semester). In reality, sardine spawn throughout the year, with a broad peak during March–August (figure 2), but new recruits (age-zero sardine from spawning during the current year) are seldom seen in the fish-

ery before July 1. Ages in the model ranged from zero to 5+ (age five and older, a "plus group"; Megrey 1989). Natural mortality was assumed to be $M = 0.4 \text{ yr}^{-1}$ (MacCall 1979; Barnes et al. 1992). There were obvious seasonal and latitudinal differences in sardine catch-at-age and weight-at-age data, so California and Mexican fisheries during the first and second semesters were modeled separately. In addition, California catch-at-age (selectivity parameters, see below) during the first semester of 1991–95 was modeled separately.

Population Dynamics

Abundance of sardine was modeled with standard equations and techniques (Deriso et al. 1985). For example:

$$N_{a,y,2} = N_{a-1,y,1}\, e^{-Z_{a-1,y,1}} \qquad (4)$$

where $N_{a,y,s}$ is the number of sardine age a alive at the beginning of either the first ($s = 1$) or second ($s = 2$) semesters in year y, and $Z_{a,s,y}$ is an instantaneous total mortality rate. Recruitments (age-zero sardine at the

beginning of the second semester of each year, $N_{0,y,2}$) were parameters estimated in the model.

Population biomass at the beginning of each semester of each year was calculated by summing the products of abundance at age and population weight-at-age. In most instances, population weight-at-age was assumed to be the same as weight-at-age in the California fishery. Fishery samples overestimated weights of age-zero sardine during the second semester of each year (shortly after hatching), however, because only the largest age-zero sardine were large enough to be captured. We therefore assumed a constant value ($w_{0,y,2,POP}$ = 1.5 g, calculated from length data in Butler 1987 and a length-weight conversion formula) for the weight of age-zero sardine in the population during the second semester of each year.

Observation Model

Predicted catch-at-age in the model was given by

$$\hat{C}_{a,y,s,t} = U_{a,y,s,t} \, N_{a,y,s} \qquad (5)$$

where $C_{a,y,s,t}$ was the predicted catch in number of fish by fishery t ($t = 1$ for California and $t = 2$ for Mexico). The exploitation fraction $U_{a,y,s,t}$ was from Baranov's catch equation (Deriso et al. 1985):

$$U_{a,y,s,t} = \frac{F_{a,y,s,t}}{Z_{a,y,s}} \, (1 - e^{-Z_{a,y,s}}) \qquad (6)$$

where $F_{a,y,s,t}$ was an instantaneous fishing mortality rate, and $Z_{a,y,s} = M + F_{a,y,s,US} + F_{a,y,s,MEXICO}$.

For modeling purposes, fishing mortality was separated into annual mortality and age-specific selectivity components (Megrey 1989):

$$F_{a,y,s,t} = s_{a,y,s,t} \, f_{y,s,t} \qquad (7)$$

where $s_{a,y,s,t}$ was a selectivity parameter for age, year (see below), semester (first or second), and fishery (U.S. or Mexico); and $f_{y,s,t}$ was a fishing mortality rate. Selectivities were scaled to a value of one at age 5+ (Deriso et al. 1985). Selectivities (see below) and fishing mortality rates for each fishery and semester were parameters estimated by the model.

First semester selectivities for the U.S. fishery were assumed constant during 1983–90 and 1991–95. The change from 1990 to 1991 accounted for a change in the United States from a first semester incidental fishery (sardine as a bycatch) to a directed fishery with sardine as the main target species (table 1 in Wolf 1992). Selectivities for the first semester Mexican (directed) as well as second semester fisheries in the United States (incidental) and Mexico (directed) were assumed constant during 1983–95. Preliminary runs with simpler selectivity patterns had trends in residuals. Preliminary runs that as-

sumed more complicated selectivity patterns had convergence problems associated with overparameterization.

Catch-at-age data were not available for Mexican and California fisheries during some semesters, so we modeled total landings instead:

$$\hat{C}_{0+,y,s,t} = \sum_{a=0}^{5+} U_{a,y,s,t} \, N_{a,y,s,t} \, w_{a,y,s,t} \qquad (8)$$

where $\hat{C}_{0+,y,s,t}$ was predicted total landings in weight, and the $w_{a,y,s,t}$ were weights-at-age. Ratios of mean weight-at-age in the Mexican and California fisheries during 1991–92 (first semester) and 1990–92 (second semester) were used to calculate weight-at-age in the Mexican fishery where necessary. For the first semester, the ratio of Mexican to California weight-at-age was 0.74 for age zero and 0.95 for ages 1–5+. For the second semester, the ratios were 0.56 for age zero and 0.89 for ages 1–5+.

In CANSAR, predicted DEPM spawning biomass was calculated:

$$\hat{I}_{DEP,y} = Q_{DEPM} \sum_{a=0}^{5+} m_a \, N'_{a,y} \, w_{a,y,1,US} \qquad (9)$$

where Q_{DEPM} was a scaling parameter; m_a was sexual maturity of sardine age a; $w_{a,y,s,t}$ was weight-at-age in the U.S. fishery during the first semester; and $N'_{a,y}$ was the abundance of sardine (males and females) in the middle of spawning season (April 1). The scaling parameter Q_{DEPM} was theoretically equal to one and unnecessary (because the DEPM method estimates spawning biomass), but we included it so that assumptions could be tested. For modeling purposes, sexual maturity (m_a) is defined as the probability that a female sardine has already spawned, is spawning, or will spawn during the current spawning season.

Data from fishery and research trawl samples during the 1994 DEPM survey indicate that maturity of young sardine was lower for samples collected north of the Southern California Bight near Monterey, California (Butler et al. 1996). Because the number of sardines collected near Monterey during the DEPM cruise was small, we used a larger set of fishery data collected during 1991–93 (Hester 1993) to estimate maturity-at-age for sardine. Results (table 3) confirm that maturity at age zero is lower in fishery samples taken near Monterey.

All of the maturity data available for sardine taken near Monterey were from the fishery, which operates near shore, usually within 10 km of the coast. It is possible that lower maturity for young sardine near Monterey was due to a tendency for smaller sardine (with lower

TABLE 3

Maturity-at-Age Data for Female Sardine in Fishery and Research Catches during March–April, 1994 (Butler et al. 1996) and from Fishery Samples during March–June, 1990–92 (Hester 1993)

	Southern California Bight			Monterey, California			Population estimated maturity
Age	Mature females	Total females	Estimated maturity	Mature females	Total females	Estimated maturity	
0	136	238	0.65	9	29	0.50	0.58
1	720	794	0.87	136	184	0.71	0.79
2	763	798	0.96	48	51	0.86	0.91
3	441	450	0.99	25	30	0.94	0.97
4	244	245	1.00	12	12	0.97	0.99
5+	164	165	1.00	12	13	0.99	1.00

Note: Southern data include sardine collected between 31° and 34° N. Lat., primarily at Terminal Island, Calif., and Ensenada, Mexico. Maturity was determined by visual inspection of gonads (Hjort 1914); females with eggs visible to the eye were recorded as mature. Estimated maturities were by logistic regression; slope and intercept parameters for logistic regressions fit to Monterey and southern samples were significantly different ($p < 0.05$). Population maturities were estimated by averaging southern and Monterey values.

maturity) to occur near shore (Parrish et al. 1985), rather than to effects of latitude on the population (Hedgecock et al. 1989). In addition, we had no way of knowing how to combine maturity estimates for northern and southern areas to calculate age-specific maturity for the sardine population as a whole. We ignored these problems and used the simple average of maturity-at-age for northern and southern samples in CANSAR (table 3).

Predicted values for CalCOFI data in each year ($I_{CalCOFI,y}$) were calculated:

$$\hat{I}_{CalCOFI,y} = Q_{CalCOFI}\, E_y \qquad (10)$$

TABLE 4

Estimates of Relative Fecundity-at-Age (f_a) Used in CANSAR for Pacific Sardine

Age (years)	Fecundity-at-age data for mature females (eggs batch^{-1} mature fish^{-1})	Predicted fecundity-at-age for mature females (eggs batch^{-1} mature fish^{-1})	Predicted fecundity-at-age for all females (eggs batch^{-1} fish^{-1})	Rescaled fecundity-at-age for all females (eggs batch^{-1} fish^{-1})
0	15,794 ($N = 62$)	10,408	6,037	0.075
1	23,101 ($N = 256$)	24,498	19,354	0.239
2	28,164 ($N = 168$)	38,588	35,515	0.434
3	52,140 ($N = 18$)	52,678	51,098	0.632
4	77,777 ($N = 6$)	66,768	66,100	0.817
5+	76,823 ($N = 1$)	80,858	80,858	1.00

Note: Fecundity estimates were calculated from data for female sardine collected during the 1994 DEPM survey and aged (Macewicz et al. 1996; Butler et al. 1996). For each female sardine, batch fecundity (B) was calculated from ovary-free body weight (O) using $B = -108585. + 439.53$ O (B. Macewicz, Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, pers. comm.). Average batch fecundities for each age class were regressed on age. Predicted batch fecundities from the regression on age were multiplied by maturity-at-age (table 3) and rescaled to a maximum value of 1.0 to calculate relative fecundity for female sardine. The sample size for each age group (N = number of female sardine) is given in parentheses.

where $Q_{CalCOFI}$ was a scaling parameter and E_y was relative egg production on 1 April. Predicted values for the CDFG spawning area index were obtained in the same manner except that a different scaling parameter (Q_{CDFG}) was used.

Relative egg production for sardine was calculated:

$$E_y = \sum_{a=0}^{5+} f_a\, N'_{a,y} \qquad (11)$$

where f_a is relative fecundity at age for female sardine in units of eggs batch^{-1} fish^{-1} (table 4). Ideally, fecundities would be calculated from the product of age-specific batch fecundity (eggs batch^{-1}) and spawning frequency (batches day^{-1}), but estimates for spawning frequency were not available. Scaling parameters (e.g., $Q_{CalCOFI}$) made it possible to calculate egg production (equation 11) in terms of male and female abundance ($N'_{a,y}$), assuming that the sex ratio was constant.

Predicted values for the fish-spotter index were calculated:

$$\hat{I}_{SPOTTER,y} =$$
$$Q_{SPOTTER} \sum_{a=0}^{5+} \overline{s}_{a,y,US}\, N_{a,y,2}\, w_{a,y,2,US} \qquad (12)$$

where $\overline{s}_{a,y,US}$ was the geometric mean during year y of selectivities for sardine age a in the U.S. fishery during semester 2 and fish age a-1 during semester 1. Fish spotters locate and direct harvesting operations in the U.S. commercial fishery. Thus it was reasonable to use the same age-specific selectivities for both the U.S. fishery and fish–spotter data.

CANSAR included a modified Ricker (1975) spawner-recruit function that constrained recruitment estimates:

$$\tilde{R}_y = Z_y\, e^{\alpha + \beta\, Z_y + \gamma\, T_y} \qquad (13)$$

where $\tilde{R}_y$ was the number of age-zero sardine on 1 July of year y predicted by the spawner-recruit model; Z_y

was a measure of spawning biomass during April; and T_y was temperature. The spawner-recruit parameters α, β, and γ could, in principle, have been estimated by CANSAR, but this proved difficult because so few years of data were available. Jacobson and MacCall (1995) fit a model like model 13 to a longer series of spawner-recruit data using biomass of sardine age 1+ in July to measure spawning biomass (S_y), and "mean three season" sea-surface temperatures at Scripps Pier in San Diego, California, to measure temperature (T_y). In CANSAR, we fixed spawner-recruit parameters at values from Jacobson and MacCall (1995) after adjusting for differences in units ($\alpha = -14.02$, $\beta = 3.147 \times 10^{-7} \, MT^{-1}$, $\gamma = 0.961°C^{-1}$). To correspond as closely as possible with Jacobson and MacCall 1995, spawning biomass for spawner-recruit calculations was the biomass of sardine age 1+:

$$Z_y = \sum_{a=1}^{5+} N'_{a,y} \, \bar{w}_{a,1,US} \qquad (14)$$

where $\bar{w}_{a,1,US}$ were average first semester weights-at-age for sardine in the California fishery. The definition of sardine spawning biomass for spawner-recruit calculations was similar, but not identical to, the definition of spawning biomass for DEPM calculations (equation 9).

Parameter Estimation in CANSAR

Parameters in CANSAR (selectivities $s_{a,s,t}$; fishing mortalities $f_{s,y,t}$; scaling parameters $Q_{CalCOFI}$, Q_{CDFG}, $Q_{SPOTTER}$; and recruitments R_y) were estimated by nonlinear least squares as described by Deriso et al. (1985). All parameters were estimated after log transformation, and calculations were mostly log scale (to facilitate calculation of derivatives). Parameter estimates minimized the sum of squares:

$$L = \sum_{r=1}^{R} \lambda_r \sum_{j=1}^{N_j} \delta_{r,j} [\ln(D_{r,j}) - \ln(\hat{D}_{r,j})]^2 \qquad (15)$$

where λ_r was a weight applied to data of kind r; $\delta_{j,r}$ was a weight for observation j of kind r; and $D_{r,j}$ was a datum. For the spawner-recruit constraint, "observed" values were the models' current best estimates of recruitment (R_y), and "predicted" values $(\tilde{R}_y)$ were from equation 13. By definition (Deriso et al. 1985), λ_1 was one for U.S. fishery data in CANSAR. The search for best parameter estimates was terminated in CANSAR when either the change in the objective function (equation 15) or the relative change in all parameter estimates between steps was less than 10^{-6}. Problems with false minima were reduced by using these relatively stringent convergent criteria. Bootstrap procedures (2,000 iterations)

were used to calculate variance and bias of sardine biomass and recruitment estimates from CANSAR (Deriso et al. 1985).

Theoretically, the weights λ_r account for differences in precision among different kinds of data, whereas the weights $\delta_{r,j}$ account for differences in precision or variance among observations of the same kind (Deriso et al. 1985). The theory is simple but difficult to implement because variance estimates for data are difficult to obtain independently of the model (Deriso et al. 1985; Conser and Powers 1989; Jacobson et al. 1994a). In practice λ_r is often used to increase or decrease the influence of a data type on parameter estimates, while $\delta_{r,j}$ is used to increase or decrease the influence of a single observation. We set λ_{SR} for spawner-recruit estimates to a small value (0.1) because recruitment variability is large for sardine (Jacobson and MacCall 1995). Weights (λ_i) for other kinds of data were set to 1.0 except during sensitivity analyses. Weights for individual data and spawner-recruit estimates $(\delta_{r,j})$ were set to 1.0 (but see below).

RESULTS

Initial CANSAR runs gave estimates of sardine recruitment and biomass that were anomalously high for the most recent seasons, and gave estimates of abundance for sardine age 5+ in 1983 that were near zero. Very low abundance of old fish during 1983 was reasonable because the stock had just begun to recover and few old fish were present. In final runs, the abundance of sardine age 5+ during 1983 was fixed at a small value and not estimated in CANSAR.

To obtain more reasonable estimates of recruitment and biomass for sardine during recent years, we increased weights on spawner-recruit predictions in CANSAR for 1993–95 to $\delta_{r,j} = 5.0$, 7.5, and 10.0, which, with $\lambda_{SR} = 0.1$, gave total effective weights on spawner-recruit predictions of 0.1, 0.5, 0.75, and 1.0 for 1993–95. Thus the spawner-recruit calculations for 1995 were given the same weight in parameter estimation as a catch or abundance datum.

An interesting result from our study was evidence that DEPM data for 1986–88 and 1994 underestimated spawning biomass in the sardine population. Preliminary runs with $Q_{DEPM} = 1$ had large positive residuals (predicted DEPM > observed value) for each year (figure 3). This result was not definite, however, because the final scaling parameter estimate $(Q_{DEPM} = 0.34$, CV = 1.5) was not significantly different from one and because spawning biomass estimates from CANSAR were imprecise. Residual patterns from runs with $Q_{DEPM} = 1$ may have been due to model miss-specification, errors in assumptions about maturity (i.e., the relation between spawning and total biomass), or other problems. We calculated sums-of-squares profiles (Mittertreiner
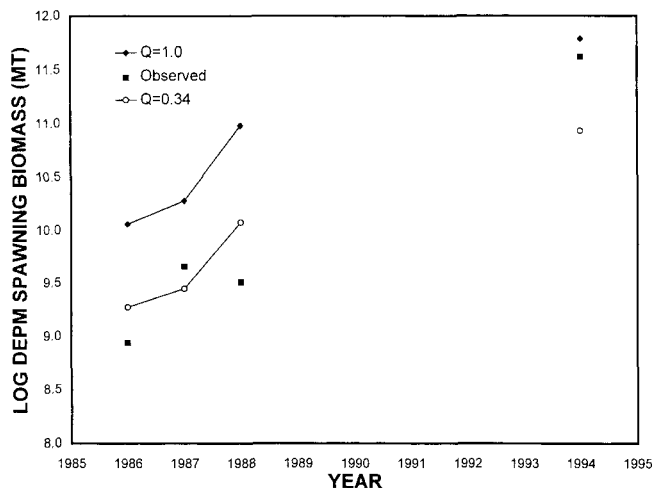
Figure 3. Observed and predicted DEPM data for models assuming DEPM data are an absolute (scaling parameter $Q_{DEPM} = 1$) and relative ($Q_{DEPM} = 0.34$) measure of spawning biomass for Pacific sardine.

and Schnute 1985) for a wide range of maturity-at-age parameters to determine if problems with lack of fit to DEPM data were due to the assumptions about maturity used to interpret DEPM, CalCOFI, and spawning area data. The sums-of-squares surface was relatively flat, indicating that reliable estimates of maturity could not be obtained from our data. Moreover, maturity patterns that gave the lowest sums-of-squares (best fit) corrected the problem with residuals but were biologically unreasonable (i.e., maturity declined with age). In final runs, we used default maturity-at-age values (table 3), estimated Q_{DEPM}, and assumed that DEPM data were a relative, rather than an absolute, measure of spawning biomass for sardine.

Fishery selectivities from final runs made sense with asymptotic selectivity patterns estimated for the directed fisheries in Mexico and in California during the first semester of 1991–95. Selectivity patterns for the incidental California fishery during the first semesters of 1983–90 and second semesters of 1983–95 were domed.

We found that CANSAR sometimes converged to local, rather than global, minima in the sums-of-squares surface, a common problem in complicated nonlinear models estimated from limited data (Jacobson et al. 1994a). We reran CANSAR repeatedly, starting with different initial parameter values to confirm that our final parameter estimates were at the global minima.

The model used for final runs included 104 parameters, of which 101 were actually estimated in CANSAR. Mean squared log-scale residuals (calculated instead of variances because degrees of freedom were unknown; Jacobson et al. 1994a) were similar (0.2–0.4) for all data types except spawning area, which appeared to be more precise than other types of abundance data for sardine (see below). Recruitment estimates for sardine from

CANSAR did not fit the spawner-recruit function precisely.

Data type	Number of observations	Mean squared log-scale residual
Calif. fishery	120	0.30
Mex. fishery	50	0.29
CalCOFI	12	0.19
Spawning area	8	0.12
Spotter	10	0.37
DEPM	4	0.24
Spawner-recruit	13	1.3

Like Jacobson et al. (1994a) and Bence et al. (1993), we found that biomass and recruitment estimates for sardine from CANSAR were generally biased high. Final estimates (table 5 and figure 4) were corrected for consistent bias according to Efron (1982) and log-transformation bias (Jacobson et al. 1994a). Consistent bias, measured by comparing biomass and recruitment estimates to mean values from bootstrap runs, ranged 6% to 12%

TABLE 5
Sardine Biomass and Recruitment on 1 July 1983–1995, Corrected for Bias

Year	Biomass (age 1+ MT)	CV[a]	Recruits (10^6 fish)	CV[a]
1983	9,061	0.33	227	0.27
1984	23,533	0.24	246	0.23
1985	32,021	0.22	167	0.24
1986	44,071	0.20	550	0.19
1987	68,683	0.17	414	0.19
1988	83,984	0.16	666	0.17
1989	99,534	0.14	441	0.19
1990	103,333	0.14	1,442	0.20
1991	164,159	0.16	1,648	0.22
1992	151,403	0.17	1,623	0.29
1993	148,191	0.23	3,751	0.29
1994	245,625	0.25	4,863	0.35
1995	344,141	0.33	6,912	0.43

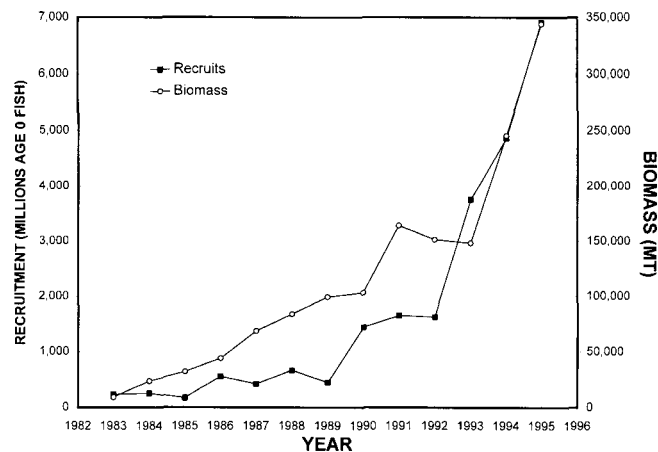[a]Arithmetic scale coefficient of variation.

Figure 4. Estimated biomass (MT age 1+ on 1 July) and recruitment (10^6 age-zero fish) for Pacific sardine during 1983–95.

and averaged 8%. Log-transformation bias (from exponentiating log-scale biomass and recruitment estimates in CANSAR) ranged from -9% to -1% and averaged -3%. Consistent and log-transformation biases tended to cancel one another; total bias ranged from 4% to 8% and averaged 6%. All three types of bias in biomass and recruitment estimates were correlated with variance. CVs and bias in estimates from CANSAR were comparable to those from other models for pelagic fish (Lo et al. 1992; Jacobson et al. 1994a, b) and indicate reasonable model performance.

Sensitivity Analysis

We varied weights (λ_t) on different data types to determine how differences among data affected estimates of sardine biomass (ages 1+ on 1 July) during 1990–94 from CANSAR. Results (table 6) indicate that average estimated sardine biomass during 1990–95 was not sensitive (change $< 10\%$) to halving or doubling weights on different types of data or the spawner-recruit constraint. The estimate of sardine biomass during 1995 was, however, sensitive (change $> 10\%$) to halving the weight on fish-spotter data and doubling the weight on CalCOFI data or the spawner-recruit constraint. Biomass estimates were more strongly affected (change $>10\%$) when weights were increased to ten times their default values or set to zero (i.e., the data type was removed from the model;

table 6). Results for the spawner-recruit constraint (decreased biomass estimates when the weight on the spawner-recruit constraint was increased) indicate that sardine recruitment in recent years has been stronger than would have been predicted on the basis of Jacobson and MacCall's (1995) spawner-recruit model.

DISCUSSION

The available data (figure 1) and biomass estimates from CANSAR (figure 4) indicate that Pacific sardine increased in abundance and were highly productive during 1983–95. Estimated sardine biomass (fish age 1+ on 1 July) increased exponentially from about 9,000 (CV 33%) to 344,000 MT (CV = 33%) at an average rate of 28% $year^{-1}$ (calculated as in Barnes et al. 1992). This impressive rate of increase occurred in the presence of fishing. Fishing mortality rates for sardine increased (table 7) in 1991 when total landings increased from about 14,000 to almost 40,000 MT $year^{-1}$ (table 1).

Recent fishing mortality rates for sardine probably could not be sustained under average environmental conditions. Average instantaneous fishing mortality rates for sardine age 2+ (weighted by number of fish in each age group) ranged from 0.52 to 0.84 yr^{-1} and averaged 0.68 yr^{-1} during 1991–95. Sardine productivity is positively correlated with sea-surface temperatures (Jacobson and MacCall 1995), and F_{msy} (the fishing mortality rate

TABLE 6
Sensitivity of Biomass Estimates for Pacific Sardine to Weights (λ_t) Used in CANSAR

Multiplier	U.S. fishery	Mexican fishery	CalCOFI	Spawning area	Fish spotter	Daily egg production method	Spawner-recruit
Mean 1991–95 biomass							
0.0	71%	116%	13%	0%	−29%	0%	35%
0.5	1%	−1%	3%	0%	−10%	0%	1%
2.0	−5%	0%	−10%	1%	5%	2%	−7%
10.0	7%	−5%	−34%	15%	56%	27%	−11%
1995 biomass							
0.0	−31%	88%	20%	0%	−48%	0%	96%
0.5	−4%	−3%	5%	0%	−16%	0%	1%
2.0	−9%	−3%	−17%	2%	9%	3%	−15%
10.0	5%	−19%	−54%	22%	87%	32%	−24%

Note: Discrepancies between best fit estimates and estimates with different weights are given in the table as percentages of best fit estimates. For each run, base case weights (λ_t = 0.1 for spawner-recruit calculations and 1.0 for other data types) were scaled by the multiplier in the first column. Bias corrections were not used.

TABLE 7
Annual Fishing Mortality Rates (yr^{-1}) for Pacific Sardine, 1983–95, Estimated in CANSAR

Age	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
0	0.01	0.00	0.04	0.00	0.00	0.00	0.00	0.01	0.02	0.02	0.04	0.02	0.04
1	0.18	0.03	0.23	0.01	0.04	0.03	0.05	0.06	0.15	0.19	0.29	0.18	0.30
2	0.59	0.11	0.59	0.04	0.13	0.10	0.18	0.19	0.42	0.62	0.71	0.48	0.65
3	0.57	0.09	0.73	0.04	0.16	0.11	0.24	0.25	0.69	1.08	1.04	0.80	0.93
4	0.40	0.04	0.70	0.03	0.14	0.08	0.20	0.22	0.68	1.02	1.05	0.80	0.94
5	0.46	0.06	0.71	0.03	0.14	0.09	0.21	0.23	0.64	0.94	0.96	0.74	0.82

giving the maximum sustained yield or MSY) at current temperatures (three-season average of 18°C, table 2) is about 0.6 yr^{-1}, so recent fishing mortality rates were near the MSY level. In contrast, F_{msy} at average three-season temperatures (17°C) is about 0.2 yr^{-1} (Jacobson and MacCall 1995).

Weight-at-age data for sardine indicate that individual growth rates decreased as abundance increased. Correlations between sardine biomass and weight-at-ages 2 to 5+ in the second-semester U.S. fishery were, for example, all between −0.7 and −0.9. This result suggests that weight-at-age might be used as an index of abundance for sardine. In addition, it appears that sardine biomass is currently large enough to affect growth rates in the stock.

Uncertainty

Bootstrap CVs for sardine biomass and recruitment indicate substantial uncertainty (table 5), but there were sources of uncertainty in our analysis not included in bootstrap calculations. Parma (1993) found that bootstrap calculations underestimated variances for abundance of Pacific halibut (*Hippoglossus stenolepis*) because serial correlation in residuals (also present in results for sardine) was not included in the bootstrap procedure. Variances from CANSAR probably understated uncertainty about sardine biomass because bootstrap calculations included the spawner-recruit constraint, which reduced variability in biomass and recruitment estimates for recent years. In addition, uncertainties about natural mortality, age-specific fecundity, maturity-at-age, and other parameters estimated outside of the model were not included in the bootstrap procedure (Restrepo et al. 1992).

Sardine age 4+ were seldom observed in the recent fishery but were common in the historical sardine fishery (Murphy 1966; MacCall 1979). Absence of older sardines from recent landings may be due to relatively high fishing mortality rates on older fish (table 7) or movement of large, old sardine to areas outside the range of the current fishery. In statistical terms, effects of movement and fishing mortality may be confounded in selectivity parameters estimated by CANSAR.

Effects of uncertainty about relationships between DEPM data and sardine biomass were substantial. Biomass estimates with $Q_{DEPM} = 0.34$ were larger by 6%–25% than biomass estimates with $Q_{DEPM} = 1$, and the discrepancy was largest for recent years.

Nonlinear relationships between abundance data and sardine biomass are a potentially major source of uncertainty that we were not able to fully evaluate. This source of uncertainty may become more important as sardine biomass expands. Fish-spotter, CalCOFI, and other abundance data for sardine were collected from areas smaller than the current distribution of the sar-
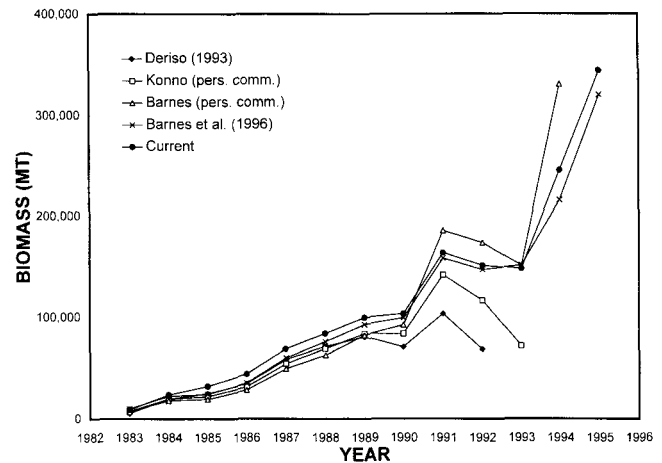

Figure 5. Historical record of biomass estimates (MT age 1+ on 1 July) from CANSAR used to manage the California sardine fishery. Estimates labeled "pers. comm." are from E. Konno (California Department of Fish and Game, 330 Golden Shore, Suite 50, Long Beach, CA 90802) and T. Barnes (California Department of Fish and Game, Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038). Estimates labeled "Current" are from this paper.

dine stock. Abundance indices will "saturate" to the extent that increased biomass outside the survey area is not reflected by proportional increases in the data. Residuals from final runs were plotted against time and predicted value, and there was no evidence for saturation, but the possibility remains.

We evaluated retrospective bias (Sinclair et al. 1991) in CANSAR by running it with 1990–95 data omitted (Jacobson et al. 1994a). Results indicated little or no retrospective bias. Although CANSAR did not suffer from retrospective bias in a statistical sense, there is historical evidence that errors in biomass estimates for recent years are usually correlated (figure 5). In addition, results from CANSAR appear sensitive to changes in data (e.g., the 1994 DEPM observation and information about maturity-at-age), environmental conditions (e.g., 1991–93 El Niño; Lynn et al. 1995), and changes in modeling approaches routinely introduced from one year to the next.

Bias in DEPM Data from Nonrepresentative Sampling

Several studies have investigated bias in DEPM spawning biomass estimates for northern anchovy due to nonrepresentative sampling of adult fish (Parker 1985; Picquelle and Stauffer 1985; Smith and Hewitt 1985; Alheit 1985). We used a different approach to examine this question for sardine. Mathematical symbols used in this section for DEPM calculations are from Parker (1985) and not the same as used elsewhere in this paper.

The DEPM estimator for spawning biomass (Parker 1985; Lo et al. 1996) is proportional to:

$$\frac{W}{FS} \tag{16}$$

where W is average weight of mature females (g); F is batch fecundity for actively spawning females (eggs batch^{-1} active female^{-1}); and S is spawning frequency (fraction mature females that are actively spawning per day; one batch day^{-1} female^{-1} assumed). Adult parameters (W, F, and S) may vary in sardine with age and size, but the bias in equation 16 is minimal when adult parameters are estimated from representative samples of the mature female population (Parker 1985). Comparison of age-composition data for all sardine (mature and immature) sampled during the DEPM survey (Butler et al. 1996) as well as estimates for the population during April, 1994, from CANSAR indicate that age-zero sardine were undersampled during the DEPM survey by about 70% (see below).

	Age composition		
Age	DEPM	CANSAR	CANSAR CV
0	0.21	0.71	0.29
1	0.41	0.19	0.30
2	0.28	0.073	0.30
3	0.063	0.021	0.39
4	0.026	0.002	0.56
5+	0.003	0.004	0.76

Estimates from CANSAR may be misleading because they were imprecise (CVs > 29%) and affected by a spawner-recruit constraint and other assumptions. It seems likely, however, that age-zero sardine were more common in the population than in the DEPM samples because sardine abundance has been increasing (figure 1) due to strong recruitment during recent years.

Estimates of population maturity-at-age and batch fecundity-at-age (F) were taken from tables 3 and 4. Weight-at-age (W) was assumed to be the same as in the U.S. fishery during the first semester of 1994. Unfortunately, no data were available to estimate age-specific spawning frequency (S). We therefore calculated potential bias under two scenarios: (1) S constant, and (2) S increasing from 1.0 at age 0 to 1.5 at age 5+. The choice of 1.5 at age 5+ was arbitrary.

For each scenario, simulated sample means for adult parameters W, F, and S were calculated assuming representative and nonrepresentative sampling. In our calculations, the age composition for nonrepresentative samples was the same as the population age composition except that

$$q_0 = \pi_0 \, \kappa \qquad (17)$$

where q_0 was the proportion of age-zero sardine in DEPM samples; π_0 was the proportion of age-zero sardine in the population; and κ measured survey gear selectivity for age-zero sardine. Gear selectivity ranged from $\kappa = 0$ (no age-zero fish sampled) to $\kappa = 1$ (representative sampling).
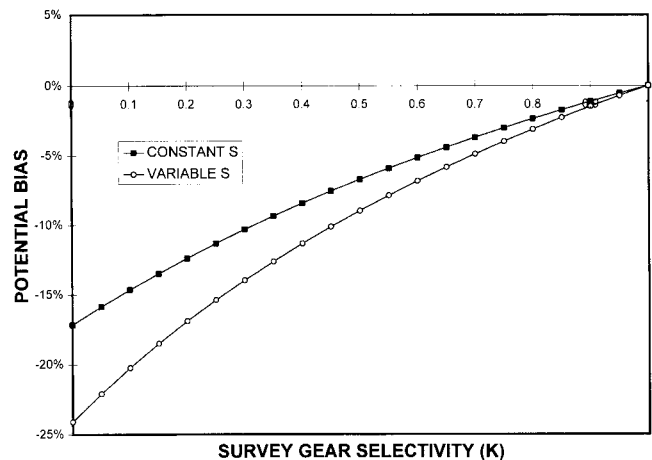

Figure 6. Potential bias in DEPM spawning biomass estimates due to non-representative sampling of age-zero sardine. Age-zero fish are not sampled by survey gear (100% undersampling) when $\kappa = 0$, and are sampled in proportion to their abundance when $\kappa = 1$.

Results (figure 6) indicate the possibility of modest bias in the 1994 DEPM estimate due to nonrepresentative sampling. When the proportion of age-zero sardine in DEPM samples was 30% of the proportion in the population ($\kappa = .30$ for 70% undersampling), potential bias was -10% for the constant S scenario and -14% for the increasing S scenario. Bias due to nonrepresentative sampling was not large enough to account for the difference between DEPM data and spawning biomass estimates from CANSAR.

Bias in DEPM data was probably not as great as indicated in our calculations because mature age-zero sardine were probably undersampled to a lesser extent than smaller, immature age-zero fish. In addition, sampling gear may have taken large, mature age-zero sardine preferentially, leading to estimates of maturity at age zero that were biased high. Maturity-at-age is not important in DEPM calculations but was used in our bias calculations. Potential bias was lower when the assumed maturity at age zero was reduced. On the other hand, our potential bias calculations did not include nonrepresentative sampling of fish ages 1+, which would likely increase estimates of potential bias.

Use of DEPM Data for Fisheries Management

DEPM spawning biomass estimates have been used directly to set catch quotas and manage fisheries (e.g., Priede and Watson 1993). The precision of advice to managers may be enhanced, however, when DEPM and all fishery and fishery-independent information, including DEPM data, are combined in a single stock-assessment model. Estimates of total biomass for sardine from CANSAR during 1986 and 1994 (table 5) were substantially more precise than the DEPM data on which they were based (table 2). Jacobson et al. (1994a) ob-

tained CVs of about 0.14–0.20 for northern anchovy (*Engraulis mordax*) spawning biomass estimates during 1981–86, while CVs for DEPM data ranged from 0.17 to 0.26. In addition, use of DEPM data in a model makes it possible to adjust estimates based on DEPM data for spawning habitat that was not surveyed.

Use of DEPM Data in Stock-Assessment Models

As in Methot (1989) and Jacobson et al. (1994a), DEPM spawning biomass estimates for sardine were used as "tuning" data in CANSAR. A problem with this approach is that there are assumptions about population age structure and adult parameters in both the DEPM estimate (equation 16) and the model (equation 9) which may be contradictory (see above). It may be better to tune future models to total egg production rather than to spawning biomass. Adult parameters could be modeled individually or collapsed into single age-specific parameters (e.g., $s_a = R_a F_a S_a$). External estimates of adult parameters could be used either directly, as starting values for further parameter estimation, or as Bayesian constraints on feasible parameter values (Jacobson et al. 1994a; Dorn 1995). This approach would be more flexible and would allow more consistent interpretation of data. In line with Methot's (1990) approach and recent modeling trends, our suggestion makes the "model look like the data," rather than the reverse.

It seems likely that DEPM data underestimated spawning biomass for the sardine population because of incomplete coverage of the spawning area during DEPM surveys. Sardine occur along the coast to the north (Hargreaves et al. 1994) and south (Félix-Uraga et al. 1996) of the areas surveyed during DEPM cruises. Relative underestimation of spawning biomass by DEPM data (figure 3) was smallest in 1994, when the survey extended over the widest geographic range. In modeling, we chose to assume that DEPM data were proportional ($Q_{DEPM} \neq 1$) rather than absolute ($Q_{DEPM} = 1$) measures of spawning biomass for sardine. A more accurate assumption would probably be that DEPM data measured spawning biomass within the area surveyed in absolute terms. Apparent underestimation of spawning biomass for the population as a whole probably resulted from the fact that not all of the spawning habitat was surveyed.

ACKNOWLEDGMENTS

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