

## REVISED ESTIMATES OF HISTORICAL SPAWNING BIOMASS OF THE PACIFIC MACKEREL, *SCOMBER JAPONICUS*

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### ABSTRACT

We present revised spawning biomass estimates for the Pacific mackerel stock off southern California for the years 1929–69. These new estimates include corrected assumptions about fecundity, individual growth, underreporting of catches, and the distribution of fishing effort throughout the season. The time series of new estimates shows a more pronounced spawning population decline preceding the population's collapse.

Spawning appears to be more limited to the older fish than previously thought; cumulative egg production curves reveal an increased impact of exploitation on spawn production. Such a pattern might reduce the stock's stability at high levels of exploitation. In examining the weight-at-age time series, we observed clear evidence of density-dependent growth; fish attained much higher weights at age when the population size was small.

### RESUMEN

Re-estimaciones de la biomasa de desove de la macarela del Pacífico frente al sur de California son presentadas para el período 1929–69. Estos nuevos valores incluyen suposiciones actualizadas en cuanto a fecundidad, crecimiento individual, declaración de capturas inferiores a las reales, y distribución del esfuerzo pesquero a través de la temporada. La serie de tiempo de las nuevas estimaciones indica una disminución más pronunciada de la población de desove que precedió al colapso de la población.

El desove parece estar más restringido a los peces de mayor edad, con respecto a análisis previos. Las curvas acumulativas de producción de huevos revelan un mayor impacto de la explotación sobre la producción de desove. Un patrón de este tipo puede reducir la estabilidad de la población cuando es expuesta a altos niveles de explotación. La serie de tiempo de peso por edad entrega clara evidencia de crecimiento dependiente de la

densidad de la población; los peces alcanzaron mayores pesos a cierta edad cuando el tamaño de la población era chico.

### INTRODUCTION

The California stock of *Scomber japonicus*, known locally as Pacific mackerel and elsewhere as chub mackerel, is one of the most closely monitored fish stocks in the world. A remarkably long record of fishery data has made it possible to compute virtual population analyses for the period from the beginning of the fishery in 1929 until the stock's collapse in the late 1960s. After the California legislature closed the fishery in 1970, the stock rebounded, and the fishery reopened in 1977. This provided a second period of catch data. The stock's population dynamics have been described by Parrish and MacCall (1978), MacCall et al. (1985), and Prager and MacCall (1988).

Recent advances in virtual population analysis (Sims 1982; MacCall 1986; Prager and MacCall 1988), new research about the Pacific mackerel's fecundity by Dickerson and Macewicz<sup>1</sup>, and a critical reanalysis of the existing growth data (this paper) allowed us to compute corrected historical abundance estimates of the stock's spawning biomass. These estimates differ in several respects from the previous ones.

### COMPUTATION OF SPAWNING BIOMASS ESTIMATES

The following formulation was used to compute each year's spawning biomass.

$$B_i = \sum_{j=1}^5 N_{ij} w_{ij} m_j \quad (1)$$

where  $i$  = an index of year,  
 $j$  = an index of age,

<sup>1</sup>Dickerson, T. L., and B. J. Macewicz. MS. Spawning frequency and batch fecundity of chub mackerel, *Scomber japonicus*, during 1985. Available from B. J. Macewicz, Southwest Fisheries Center, P. O. Box 271, La Jolla, CA 92038.

- $B_i$  = the spawning stock biomass estimate in year  $i$ ,
- $N_{ij}$  = the number of fish of age  $j$  in the population at the beginning of year  $i$ ,
- $w_{ij}$  = the mean weight of a single fish of age  $j$  in year  $i$ ,
- $m_j$  = an index of the relative weight-specific egg production (fecundity) of female fish at age  $j$ .

Equation 1 relies upon two main assumptions. First, egg production per gram of total weight is assumed constant for the ages in question, except for the effects of  $m_j$ . Second, the sex ratio is assumed to remain constant. With these assumptions met,  $B_i$  gives relative values of egg biomass spawned from year to year. This quantity is intrinsically relative, both because  $m_j$  is a relative index and because no attempt is made to estimate actual egg production per gram of fish weight. Pacific mackerel exhibit indeterminate fecundity (i.e., the total number of eggs to be spawned is not fixed at the beginning of the season, and new oocytes are recruited if feeding and environment are favorable); therefore actual egg production from a given spawning biomass may vary from year to year.

Estimated spawning biomass, then, comprises three elements (numbers, weights, and fecundities at age), which are treated in the following three sections. We report fish weights and biomasses in the English system of measurement because management and monitoring of this fishery have not yet converted to the metric system.

## NUMBERS AT AGE

### Methods

The estimates of numbers at age were obtained by virtual population analysis (VPA), as in past analyses of this stock's population dynamics (Parrish and MacCall 1978; MacCall et al. 1985). Our first change to past methods was to obtain an estimate of underreporting in the catch statistics. Because no theoretical framework existed for doing this, we relied upon estimates by those involved in management of the fishery (R. Klingbeil, Calif. Dept. of Fish and Game, 245 W. Broadway, Long Beach, CA 90802, pers. comm.). We believe that this approach, while not ideal, is preferable to assuming that no underreporting has taken place (or, almost equivalently, assuming that the degree of underreporting has been constant). Table 1 indicates the degree of underreporting assumed to

TABLE 1  
 Underreporting Percentages Used for Analysis of Pacific Mackerel Catch Data

Years	Underreporting
1929-47	10%
1948-49	9%
1950-51	8%
1952-57	7%
1958-61	6%
1962-69	5%

have taken place, and by which we corrected the catch data before performing VPA.

Our second revision concerned the VPA methodology used to estimate numbers at age from the catch data. VPA methodology has been well described (Murphy 1965; Pope 1972; MacCall 1986), and thus is not reviewed here. However, we made several modifications to the VPA techniques used in prior analyses of this stock. VPA, since it assumes that the fishing effort is uniformly distributed throughout the fishing season, can produce biased results in a fishery with strongly seasonal fishing effort (Sims 1982). We accommodated this fact by using a variant of MacCall's (1986) approximation that took the seasonal nature of the fishery into account. We used the VPA estimator:

$$\hat{N}_i = N_{i+1} \exp(M) + kC_i \quad (2)$$

- where  $\hat{N}_i$  = the estimate of population (in numbers) at the start of year  $i$ ,
- $C_i$  = the catch (in numbers) during year  $i$ ,
- $M$  = the instantaneous rate of natural mortality (assumed constant),
- $k$  = a constant depending on  $M$  and the temporal distribution of catch throughout the year.

In most VPA applications,  $k$  is held constant. In contrast, we developed a procedure to find annual values of  $k$  fitting the distribution of each year's catch, which increased the accuracy of our population estimates. To do this, we performed an iterative monthly VPA on the unaged catch data, and found for each year the  $k_i$  that caused equation 2 to hold on an annual basis (MacCall 1986). These values of  $k_i$  were then used in the analysis of the aged annual catches by equation 2. Since the Pacific mackerel fishery is highly seasonal, this gave more accurate estimates of population number than did the standard iterative solution based on constant fishing effort over the full year.

**Results of Virtual Population Analysis**

The catch data after correction for underreporting are given in Table 2. The new VPA estimates of population number (Table 3) are slightly higher than the estimates of Parrish and MacCall (1978), especially in the years before 1940. This occurs because the correction for underreporting slightly outweighs the seasonal VPA correction in those years.

**WEIGHTS AT AGE**

The second data component used to estimate spawning biomass was the matrix of age- and year-specific weights at the nominal mean spawning date, May 1. This section describes our procedures for revising these weights for the years 1928-69 and 1974-84. Although spawning biomass estimates were not computed for the years 1974-84, weights for these years were needed to estimate earlier values.

The weight data fell into three groups: (1) no data for 1929 to 1938; (2) average weight of the season's catch by age for 1939 to 1969; (3) monthly weights at age beginning in 1977. Accordingly, we divided our analysis into the same three groups of years. For ease of narrative, we begin with the most recent period.

**Years 1977-1984**

Weights at age for each year, 1977-84, were based on monthly weight measurements of fish from the catch (R. Klingbeil, California Dept. of Fish and Game, unpubl. data). These were recorded from April through June of each year; we estimated May 1 weights as means of the recorded April and May entries (which, as monthly means, approximate mid-month weights). In years missing data from April or May, we assumed linear growth in weight during the season, interpolated the missing values, and took the mean of April and May

TABLE 2  
 Adjusted Catch Statistics for Pacific Mackerel in Numbers of Fish (Multiply by 1000)

Year	Age 1	Age 2	Age 3	Age 4	Age 5+
1929	12,743	23,027	21,338	5,338	9,073
1930	1,360	6,996	4,724	1,871	721
1931	942	9,834	6,093	1,287	1,310
1932	144	3,221	5,843	1,393	1,701
1933	4,162	17,132	28,727	21,048	11,286
1934	3,743	40,807	27,227	31,211	18,610
1935	8,468	9,921	48,061	49,709	33,609
1936	1,894	17,197	14,664	27,866	36,522
1937	1,414	2,484	7,701	15,249	36,690
1938	12,262	33,859	17,506	4,564	22,422
1939	30,304	31,916	42,246	12,711	13,757
1940	24,051	80,182	29,219	15,674	3,582
1941	15,093	31,924	30,967	6,180	1,833
1942	35,770	11,208	15,462	6,418	1,318
1943	15,378	66,767	12,532	8,802	1,822
1944	19,600	22,550	40,140	9,130	2,439
1945	16,941	12,233	12,152	12,216	5,681
1946	11,588	32,072	14,746	5,789	5,939
1947	1,867	10,816	14,831	6,894	4,839
1948	77,374	3,879	924	1,351	881
1949	26,987	60,924	5,292	851	1,102
1950	5,064	25,268	20,798	1,232	278
1951	1,920	5,371	16,825	13,497	451
1952	60	677	1,672	12,334	3,627
1953	1,102	774	951	262	1,237
1954	65,034	6,324	338	115	63
1955	6,986	41,490	11,806	400	278
1956	75,425	22,852	22,341	5,556	95
1957	7,273	35,604	13,234	9,530	3,871
1958	1,428	6,614	12,148	3,905	1,583
1959	62,281	4,618	1,151	1,407	612
1960	22,049	24,804	9,579	2,504	839
1961	35,576	18,143	12,934	2,719	381
1962	31,826	14,669	10,585	4,071	462
1963	4,042	23,458	13,626	8,315	1,272
1964	7,375	5,695	10,747	14,239	1,992
1965	1,321	801	1,777	5,772	10,698

weights as in other years. Values of  $w_{5+}$  were estimated as weighted means of weights at ages 5 and 6, namely

$$w_{5+} = 0.8w_{5} + 0.2w_{6}$$

This ad hoc relationship was suggested by the relative frequencies of 5- and 6-year-old fish in the catch.

### Years 1940–1968

For the 1939–69 seasons, publications of the California Department of Fish and Game tabulated each season's catches in weight and numbers by age (Fitch 1951, 1953a, 1953b, 1955, 1956, 1958; Hyatt 1960; Knaggs 1972; Parrish and Knaggs 1971, 1972). From these publications, each season's average (not May 1) weights  $w_{ij}^*$  at age were obtained by dividing catches in weight by catches in numbers. To estimate weights on May 1, we first calculated the mean harvest date of each fishing season

from the monthly distribution of landings. We then assumed that the recorded mean weights at age occurred on that date. Finally, by assuming linear growth from one mean harvest date to the next, we estimated the May 1 weights at age ( $w_{ij}$ ) by interpolation. Because 1939 was the first season with weight information, the first interpolation was for 1940. To estimate weights at age 5<sup>+</sup>, we increased weights at age 5 by 5%, a value suggested by examining a few years for which both  $w_5$  and  $w_{5+}$  were known.

The interpolation could not be done for age 1 in 1943 and 1945 because we lacked catch data for age 0, and for age 5 in 1954 because we lacked catch data for age 5. Therefore, these mean weights were estimated indirectly by referring to the relative weight of an adjacent cohort at the same age. For example, in 1953 the age 4 mean weight was approximately equal to the mean of age 4 weights in the preceding and following years; thus the age 5 mean weight in 1954 was estimated as the mean of

TABLE 3  
 Revised VPA Population Estimates of Pacific Mackerel in Numbers of Fish (Multiply by 1000)

Year	Age 1	Age 2	Age 3	Age 4	Age 5 <sup>+</sup>
1929	352,430	224,170	168,150	27,994	47,584
1930	754,120	204,480	119,190	86,449	33,317
1931	987,320	456,360	118,690	68,694	69,940
1932	1,094,400	598,120	269,220	67,294	82,159
1933	768,830	663,650	360,380	158,940	85,224
1934	276,090	463,280	390,010	197,600	117,820
1935	120,520	164,720	251,200	216,680	146,500
1936	151,650	66,824	92,559	116,750	153,020
1937	325,570	90,604	28,064	45,508	109,500
1938	237,380	196,400	53,076	11,199	55,014
1939	380,930	134,600	93,238	18,810	20,357
1940	246,870	206,630	55,927	22,517	5,146
1941	215,060	130,690	61,836	10,785	3,200
1942	458,450	118,680	54,396	13,380	2,747
1943	166,870	249,720	63,104	20,742	4,294
1944	150,350	89,142	99,071	28,440	7,597
1945	157,890	76,000	36,590	28,980	13,478
1946	47,175	82,465	36,491	12,651	12,979
1947	39,432	19,372	24,441	10,374	7,281
1948	396,570	22,498	3,527	3,548	2,316
1949	216,890	182,590	10,741	1,447	1,875
1950	24,255	111,590	65,693	2,601	588
1951	10,167	10,932	48,826	24,324	813
1952	6,226	4,737	2,630	17,082	5,023
1953	126,370	3,734	2,394	414	1,950
1954	311,330	75,759	1,641	686	378
1955	131,130	138,890	41,094	736	512
1956	229,670	74,130	52,130	15,787	269
1957	44,260	80,090	27,023	14,080	5,719
1958	67,801	21,210	20,994	6,137	2,488
1959	221,770	39,991	7,618	3,097	1,346
1960	192,800	85,817	20,645	3,721	1,247
1961	330,760	99,062	31,939	4,756	666
1962	168,500	173,080	46,041	9,360	1,063
1963	28,322	77,701	93,687	19,778	3,025
1964	16,632	14,205	29,875	46,802	6,546
1965	6,644	4,762	4,503	10,358	19,199

the preceding and following age 5 weights. A similar procedure was used for age 1 fish in 1943 and 1945; variations in relative weight of age 2 fish were used as the basis for comparison.

### Years 1929–1939

Because no weight data had been collected, Parrish and MacCall (1978) had assumed that weights at age were constant before 1939. However, an examination of data from other years indicated that *Scomber japonicus* weights at age are quite variable, and appear to be density-dependent. The use of constant weights during a period of high abundance is likely to have produced biased estimates of spawning biomass.

To eliminate this source of bias, we estimated the 1929–39 May 1 weights at age by using linear regression models of known May 1 weights on May 1 abundances at age. The modeling procedure was similar for estimating weights at each age. (Although all weights are year-specific, the subscript for year is omitted below unless required for clarity.) The procedure for modeling  $w_1$  was:

1. We computed all possible regressions of weight on population numbers of each age. (That is,  $\hat{w}_{i1} = f\{N_{i1} \dots N_{i5}\}$ .)
2. By examining goodness-of-fit statistics, including Akaike's information criterion (Akaike 1969), Mallows's  $C_p$  (Mallows 1964), and the  $R^2$  and adjusted  $R^2$  statistics (Kvalseth 1985), we chose one or two potential models from those computed for each age.
3. We plotted the selected models to examine goodness of fit and detect any possible outliers or other ill behavior.
4. Favoring simpler models, we chose one regression model and computed predicted values of  $w_1$  where missing.

Models of  $w_2$  through  $w_{5+}$  were constructed in a similar way, except that the weight of the same cohort at the previous age was included among the independent variables. For example, in predicting  $w_{i3}$ , we included  $w_{i-1,2}$  among the possible regressors. In addition, we found it useful to include the same year's weight at the next younger age among the possible regressors. May 1 weights used for fitting the models were from the procedures described above for 1940–68 and 1977–84.

*Special cases.* The model for  $w_1$  included  $N_2$ , which was unrecorded before 1926. Therefore no weight at age 1 was estimated for 1925. Similarly, the model for weight at age 2 included the popula-

tion number at age 4, which was unrecorded before 1928. In order to estimate  $w_2$  in 1927, we used a separate regression not including  $N_4$ . This made it possible to estimate  $w_3$  starting in 1928,  $w_4$  starting in 1929, and  $w_{5+}$  starting in 1930.

A value of  $w_{5+}$  for 1929 was necessary so that the year's data could be used for further analysis. A separate regression of  $w_{5+}$  on  $w_4$  was used for 1929 only. This was possible because, for the older fish, the weights at age were correlated within a single year—in this case, Pearson's  $r = 0.85$ .

The  $w_{5+}$  value for 1965 (1.228), derived as discussed above through interpolation, was considered an outlier. The value of  $w_{5+}$  predicted from the regression model (1.495) was substituted for the interpolated 1965 value.

### Results of Weight Analysis

The new series of estimated May 1 weights is given in Table 4. Equations for the regression models used to estimate pre-1939 weights are given in Table 5, with model statistics in Table 6. A plot of weight versus population size (Figure 1) illustrates the density-dependence in the stock.

### FECUNDITIES AT AGE

Because of data limitations, we used estimated mean fecundities ( $m_j$ ) that were not year-specific. This is similar to the methodology of Parrish and MacCall (1978), who used the following vector of age-specific fecundities, corresponding to age groups 1, 2, 3, 4, and 5<sup>+</sup>:

$$m = \{\Phi_i, 0.77, 0.88, 1.0, 1.0\} \quad (3)$$

Here  $\Phi_i$ , the fraction of age 1 biomass which is mature ( $m_{i1}$ ), was the only year-specific element. It was given by:

$$\Phi_i = 0.54 \exp(-0.00717 B_i^*) \quad (4)$$

where  $B_i^*$  is the total stock biomass, in millions of pounds, in year  $i$ .

This  $m$  vector was based on gonad observations from samples of the catch taken in 12 fishing seasons from 1958 through 1969 (Knaggs and Parrish 1973). Female mackerel gonads from those samples were classified into three categories: immature ("I," no eggs present); maturing ("g," eggs present); and mature ("G," large translucent eggs present). To derive the  $m$  vector, Parrish and MacCall combined the mean proportions of fish of each age falling into the g and G categories, which they considered to be equal indicators of maturity, and mul-

TABLE 4  
 Revised May 1 Weights (Pounds) at Age of Pacific Mackerel

Year	Age 1	Age 2	Age 3	Age 4	Age 5 <sup>+</sup>
1925	—	—	—	—	—
1926	0.396	—	—	—	—
1927	0.369	0.705	—	—	—
1928	0.348	0.613	0.918	—	—
1929	0.368	0.655	0.887	1.152	1.355
1930	0.306	0.664	0.931	1.127	1.330
1931	0.252	0.609	0.880	1.161	1.337
1932	0.178	0.611	0.836	1.121	1.332
1933	0.182	0.442	0.660	1.087	1.289
1934	0.313	0.436	0.513	0.950	1.186
1935	0.409	0.479	0.553	0.836	1.041
1936	0.425	0.626	0.745	0.867	0.998
1937	0.389	0.700	0.945	1.016	1.107
1938	0.383	0.683	0.988	1.172	1.284
1939	0.371	0.695	0.986	1.206	1.389
1940	0.429	0.575	0.795	0.984	1.280
1941	0.482	0.685	0.883	1.113	1.322
1942	0.381	0.703	0.900	1.143	1.465
1943	0.479	0.617	0.944	1.132	1.384
1944	0.461	0.739	0.903	1.182	1.422
1945	0.369	0.728	0.965	1.181	1.440
1946	0.411	0.654	0.966	1.204	1.423
1947	0.510	0.796	1.048	1.211	1.450
1948	0.351	0.741	1.060	1.275	1.484
1949	0.327	0.577	0.864	1.262	1.480
1950	0.462	0.564	0.804	1.059	1.437
1951	0.353	0.692	0.846	1.051	1.311
1952	0.611	0.785	1.058	1.213	1.442
1953	0.438	0.790	0.959	1.219	1.471
1954	0.342	0.740	1.075	1.227	1.484
1955	0.350	0.556	0.889	1.159	1.497
1956	0.398	0.652	0.899	1.092	1.403
1957	0.453	0.662	0.931	1.134	1.342
1958	0.413	0.697	0.844	1.093	1.294
1959	0.414	0.735	0.968	1.136	1.409
1960	0.364	0.690	1.044	1.285	1.521
1961	0.389	0.668	1.017	1.236	1.455
1962	0.508	0.751	1.039	1.236	1.480
1963	0.642	0.873	1.093	1.291	1.560
1964	0.576	0.827	1.119	1.312	1.616
1965	0.402	0.745	1.008	1.254	1.289
1966	0.371	0.717	1.070	1.292	1.715
1967	0.413	0.605	1.004	1.266	1.583
1968	0.427	0.712	1.051	1.240	1.524
1969	0.557	0.801	1.044	1.371	1.614
1970	—	—	—	1.250	1.524
1971-74 No data					
1975	0.465	—	—	—	—
1976	0.465	0.741	—	—	—
1977	0.415	0.940	1.840	—	—
1978	0.473	0.880	1.730	1.920	2.221
1979	0.195	0.865	1.255	1.715	2.205
1980	0.230	0.420	1.010	1.340	1.732
1981	0.265	0.610	0.650	1.250	1.537
1982	0.210	0.500	0.660	0.860	1.357
1983	0.300	0.520	0.745	1.010	1.222
1984	0.300	0.455	0.690	0.855	0.991

multiplied the resulting  $m$  vector by a constant  $\alpha$  to scale  $k_s$  to unity.

$$m_j = \alpha\{P_j(g) + P_j(G)\} \quad (5)$$

where  $m_j$  = the estimated mean proportion mature at age  $j$ .

$\alpha$  = the scaling constant described above,

$P_j(g)$  = the fraction of fish of age  $j$  in classification  $g$ ,

$P_j(G)$  = the fraction of fish of age  $j$  in classification  $G$ .

TABLE 5  
 Regression Models of Pacific Mackerel Weights at Age<sup>a</sup>

$\hat{w}_{i1}$	$= 0.469 - 0.000208N_{i1} - 0.000252N_{i2}$
$\hat{w}_{i2}$	$= 0.166 + 0.651w_{i1} + 0.585w_{i-1,1} + 0.000243N_{i1} - 0.00087N_{i4}$
$\hat{w}_{i3}$	$= -0.313 + 1.055w_{i2} + 0.829w_{i-1,2}$
$\hat{w}_{i4}$	$= 0.435 + 0.780w_{i-1,3}$
$\hat{w}_{i5+}$	$= 0.122 + 0.613w_{i4} + 0.544w_{i-1,4}$

<sup>a</sup>Subscripts refer to year and age, in that order. Symbols are defined in the text.

Recent histology by Dickerson and Macewicz<sup>2</sup> indicates that the three gonad classifications have a different interpretation from that of Parrish and MacCall. Examination of gonads taken during the 1985 spawning season showed that the G category represented hydrated eggs, indicating spawning imminent within a few hours, whereas the g category was the normal state of mature, spawning fish. Dickerson and Macewicz also report that, in the 1985 spawning season, the average mature female's mean spawning frequency was about once per 12 days, while fish at maximum egg production spawned approximately once per 1.3 days. We assumed that fish in category g were average mature females, and that those in category G were at maximum egg production. (This interpretation, although it may not be accurate, appears better than the previous assumption that g and G represent equally important indicators of maturity.) This leads to a new expression, replacing equation 5, for establishing the  $m$  vector, and a new interpretation; i.e., that  $m_j$  reflects relative fecundity, not just maturity, at age. The new expression is:

$$m_j = \frac{P_j(g)}{12} + \frac{P_j(G)}{1.3} \quad (6)$$

where  $m_j$  = the new relative fecundity index for age  $j$ ,

$P_j(g)$  = the fraction of fish of age  $j$  in classification g,

$P_j(G)$  = the fraction of fish of age  $j$  in classification G.

Equation 6 allowed us to reevaluate the  $m$  vector (equations 3 and 4) established by Knaggs and Parrish (1973); their original data were kindly provided us by Richard Klingbeil (Calif. Dept. of Fish and Game, Long Beach, pers. comm.). The 12 years of data were tabulated by the five age groups

<sup>2</sup>Dickerson, T. L., and B. J. Macewicz. MS. Spawning frequency and batch fecundity of chub mackerel, *Scomber japonicus*, during 1985. Available from B. J. Macewicz, Southwest Fisheries Center, P. O. Box 271, La Jolla, CA 92038.

TABLE 6  
 Statistics from Regression Models of Pacific Mackerel Weights at Age

Weight estimated	$n$	Adjusted $R^2$	$F$ statistic	Prob. of larger $F$
$w_{i1}$	35	0.443	14.9	< 0.0001
$w_{i2}$	35	0.79	33.4	< 0.0001
$w_{i3}$	35	0.63	30.4	< 0.0001
$w_{i4}$	34	0.89	282	< 0.0001
$w_{i5}$	33	0.84	89.0	< 0.0001

(1 through 5<sup>+</sup>) and eight months (March through October) in which spawning tends to occur. Of these 480 cells, only 280 contained data, of which 86 were zero observations; thus, only 40% of the cells contained nonzero values for  $m$ .

We postulated a model in which multiplicative year and age parameters produce a predicted value for the annual spawning output, defined as the sum of the monthly cells for the year. The age factors of this model form the  $m$  vector. Although the model could have been fit directly to the data by maximum likelihood, the effort for that approach exceeded our resources, so we chose instead to estimate parameters by analysis of variance (ANOVA) of log-transformed data. To remove month effects, we conducted the ANOVA on yearly sums.

It was necessary to fill missing cells before computing the yearly sums. To accomplish this, we used a second ANOVA based on additive year, month, and age effects to estimate values for the empty cells. This ANOVA was weighted according to the square root of the number of observations in each cell. (Independence of data would warrant weighting by the number of observations; however, the samples of fish came from schools, within which spawning condition was probably corre-

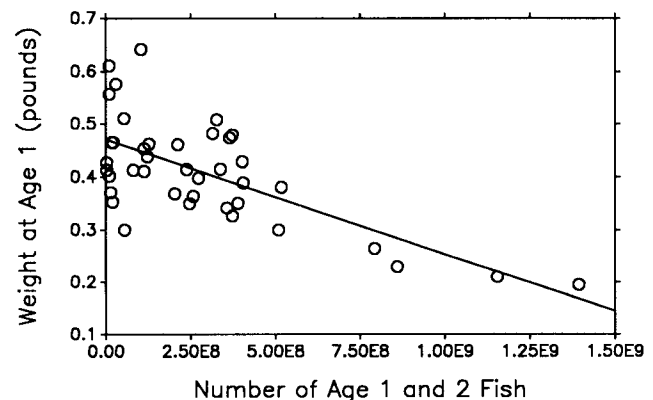


Figure 1. Density-dependence of weight at age 1 in the Pacific mackerel stock. Data shown cover years 1940–84, and do not include weights estimated by regression analysis. The regression line is shown for illustration. Other ages are similar.

lated. By means of the square root weighting, we attempted to acknowledge this fact while also recognizing that larger sample sizes should nonetheless provide more precise index values.) Very large *F* statistics from this ANOVA suggested that year, month, and age effects were all meaningful; however, lack of normality, the nonstandard weighting scheme, and the additive model, which is probably misspecified, prevented computation of parametric significance probabilities.

After empty monthly cells were replaced by predicted values, the yearly sums formed a data matrix of 12 years by five ages. Negative values in this matrix were treated as missing values. Because abundances from 1966 to 1969 were the lowest on record, and spawning activity the highest, these years were deleted as possibly reflecting an atypical level of spawning activity. Data from 1958 and 1965 were also deleted, because their yearly indices were based on fewer than seven actual (i.e., not estimated) monthly values. The six-year period from 1959 to 1964 remained as the data available to estimate the age specific *m* vector.

**Results of Fecundity Analysis**

The model of year and age effects was estimated by ANOVA of log-transformed values with equal cell weights. Large *F* values, although not strictly statistically significant, indicated likely biological significance. Exponentiating the age effects from the ANOVA gave an *m* vector of:

$$m = \{0.0586, 0.4837, 0.9107, 0.9118, 1.0\} \quad (7)$$

Because the age 3, 4, and 5+ elements of equation

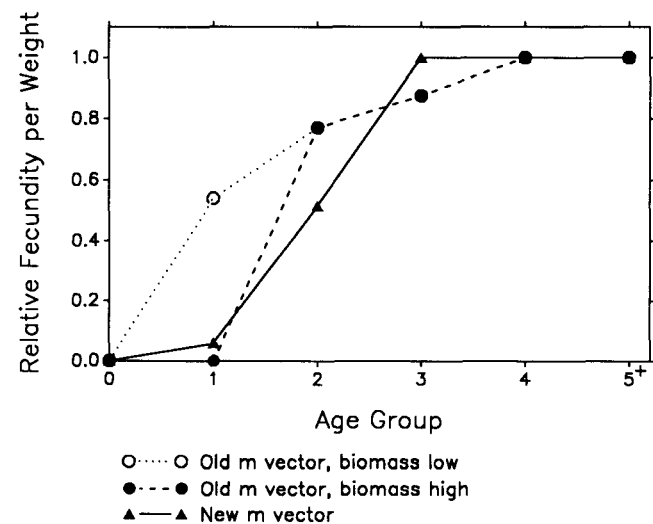


Figure 2. Spawning ogives under new and revised fecundity schedules (*m* vectors). The new schedule reveals that spawning is more concentrated among the older ages.

7 were all very similar, we averaged them and re-scaled them to unity. This gave a final *m* vector of

$$m = \{0.062, 0.514, 1.0, 1.0, 1.0\} \quad (8)$$

We found little evidence of density-dependent changes in *m*<sub>1</sub>. Its small magnitude supports Fry's (1936) observation that yearling fish do not spawn.

In view of the new fecundity schedule (*m* vector), it appears that Parrish and MacCall overestimated the contributions of ages 1 and 2 to egg production, even though it was correct that relatively large fractions of these age groups were mature and capable of spawning. The new schedule shifts the spawning biomass to a slightly older mean age, as illustrated in Figure 2, which gives spawning ogives under the old and new *m* vectors.

Figure 3 compares eggs-per-recruit (EPR) curves (fecundity multiplied by survivorship; Prager et al. 1987) for unexploited and exploited populations under old and new schedules, given fishing availabilities from MacCall et al. (1985). The EPR curves with no fishing were scaled to unity; exploitation was at *F* = 1.0;  $\Phi_1$  was set to 0.26, an average

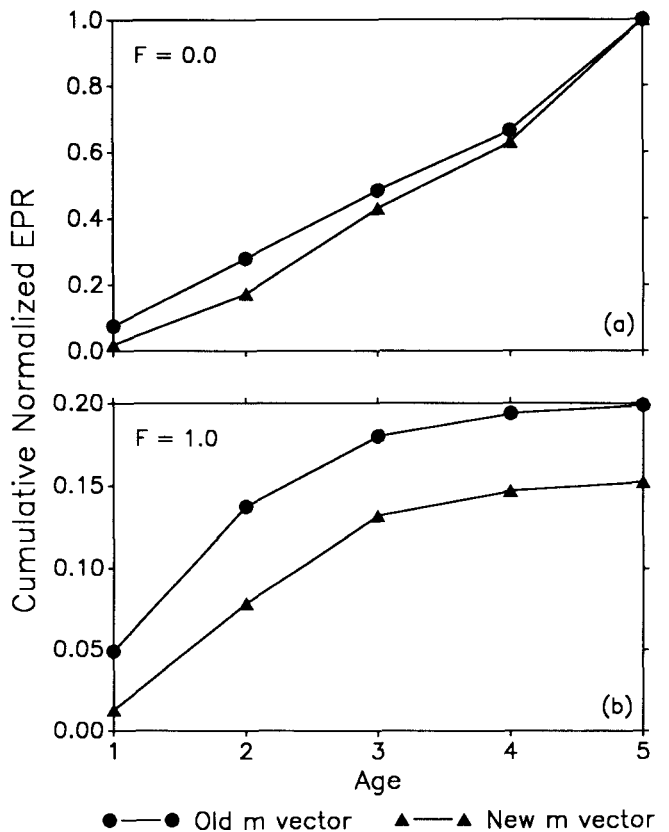


Figure 3. Cumulative eggs-per-recruit (EPR) curves for the Pacific mackerel stock under old and new fecundity schedules (*m* vectors). Curves have been normalized so that each yields EPR = 1.0 with no exploitation. (a). Unexploited stock; (b), stock exploited at annual *F* = 1.0.



value, for the old  $m$  vector. With exploitation, the new cumulative EPR curve reaches 0.15, whereas the old curve reaches 0.20. In other words, at  $F = 1.0$ , spawning output is about 75% of what we thought under the old schedule; thus, slightly less harvestable productivity might be expected. Certainly, these results suggest that the population's spawning productivity is more affected by fishing than was previously believed.

**SPAWNING BIOMASS ESTIMATION**

The final spawning biomass estimates (Table 7) are presented with approximate 95% confidence intervals in Figure 4. The standard deviation of the estimates was computed by the delta method (Seber 1973; Prager and MacCall 1988); we assumed a 5% coefficient of variation on each element of the  $m$  vector; confidence intervals were computed as  $\pm 2$  standard deviations. Figure 5 presents the old (Parrish and MacCall 1978) and new (this paper)

TABLE 7

**Revised Spawning Biomass Estimates for Pacific Mackerel in Pounds (Multiply by 1000)**

Year	Spawning biomass	Std. deviation of sp. biomass	Coefficient of variation
1929	329,400	308,350	93.6%
1930	336,800	299,583	89.0%
1931	435,900	318,591	73.1%
1932	609,800	370,675	60.8%
1933	679,900	344,674	50.7%
1934	636,700	277,471	43.6%
1935	516,100	192,120	37.2%
1936	348,400	114,978	33.0%
1937	234,400	67,535	28.8%
1938	210,700	53,703	25.5%
1939	199,700	46,787	23.4%
1940	140,800	17,804	12.6%
1941	123,300	21,347	17.3%
1942	122,000	29,215	23.9%
1943	173,100	35,539	20.5%
1944	172,000	30,077	17.5%
1945	121,000	20,888	17.3%
1946	97,870	13,122	13.4%
1947	57,910	6,829	11.8%
1948	28,900	6,046	20.9%
1949	72,430	11,925	16.5%
1950	89,460	14,244	15.9%
1951	72,050	9,346	13.0%
1952	32,890	3,986	12.1%
1953	10,620	2,858	26.9%
1954	38,580	9,596	24.9%
1955	80,690	13,513	16.7%
1956	94,990	12,919	13.6%
1957	77,290	8,817	11.4%
1958	36,980	4,969	13.4%
1959	33,590	6,777	20.2%
1960	63,020	10,635	16.9%
1961	81,320	18,218	22.4%
1962	133,100	34,943	26.3%
1963	168,600	36,878	21.9%
1964	112,000	19,593	17.5%
1965	44,270	5,828	13.2%

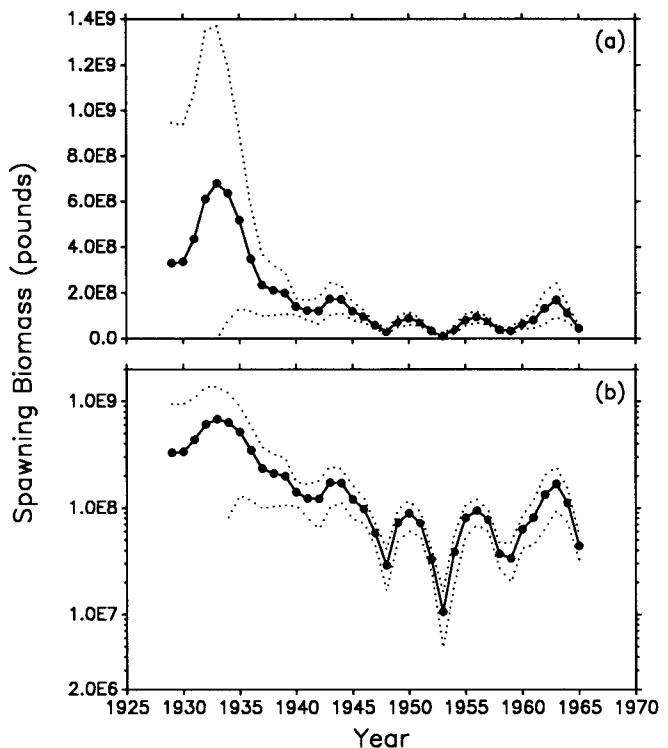


Figure 4. Revised spawning biomass estimates for Pacific mackerel stock, with approximate 95% confidence interval (dotted line). (a), Linear scale; (b), log scale. Large confidence bounds before 1940 reflect less precise knowledge of age structure and weights at age.

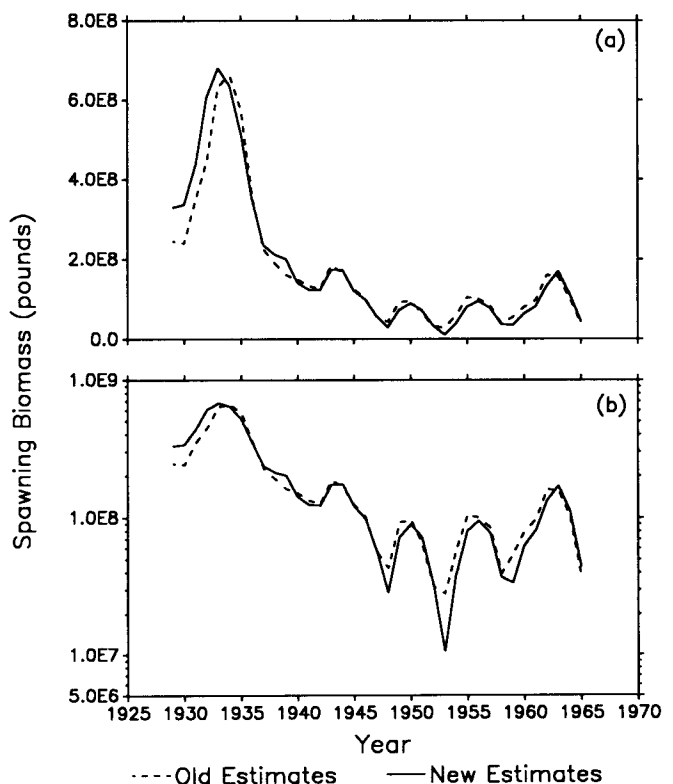


Figure 5. Old and revised spawning biomass estimates for Pacific mackerel stock: (a), linear scale; (b), log scale.

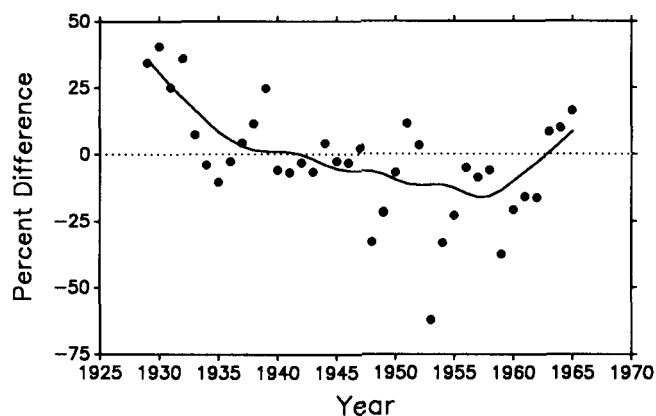


Figure 6. Difference between old and revised spawning biomass estimates, expressed as percent difference from the old to the new estimate [i.e.,  $(\text{old} - \text{new}) \times 100 / \text{old}$ ]. Smoothed line is locally weighted robust regression (LOWESS).

spawning biomass estimates. Although they appear quite similar, a closer look presents a different picture. Figure 6, which shows the differences (between new and old estimates) as percentages of the old estimates, illustrates that the declining trend of the spawning biomass from 1925 to 1962 is more clearly seen under the new estimates. This clearer vision is a direct result of increased knowledge of the Pacific mackerel's spawning biology. We hope that our clearer view of the stock's population dynamics will help to lessen the probability of another collapse.

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