

REVISED ESTIMATES OF HISTORICAL SPAWNING BIOMASS
OF THE PACIFIC MACKEREL, *SCOMBER JAPONICUS*MICHAEL H. PRAGER
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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 Parish 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 Macewicz¹, 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,

¹Dickerson, 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 (Parish 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 , that caused equation 2 to hold on an annual basis (MacCall 1986). These values of k , 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

$$w_{5+} = 0.8w_{55} + 0.2w_{56}$$

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+, 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+ |
|------|-----------|---------|---------|---------|---------|
| 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, $w_{i1} = f\{N_{i1}, \dots, N_{i5}\}$.)
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_i) 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⁺:

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

Here Φ_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 |
|---------|---------|-------|-------|-------|-------|
| 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 α 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 .

α = 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^a

$$\begin{aligned} \hat{w}_{11} &= 0.469 - 0.000208N_{11} - 0.000252N_{12} \\ \hat{w}_{12} &= 0.166 + 0.651w_{11} + 0.585w_{1-1,1} + 0.000243N_{11} - 0.00087N_{12} \\ \hat{w}_{13} &= -0.313 + 1.055w_{12} + 0.829w_{1-1,2} \\ \hat{w}_{14} &= 0.435 + 0.780w_{1-1,3} \\ \hat{w}_{15} &= 0.122 + 0.613w_{14} + 0.544w_{1-1,4} \end{aligned}$$

^aSubscripts refer to year and age, in that order. Symbols are defined in the text.

Recent histology by Dickerson and Macewicz² 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

²Dickerson, 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 ₁₁ | 35 | 0.443 | 14.9 | < 0.0001 |
| w ₁₂ | 35 | 0.79 | 33.4 | < 0.0001 |
| w ₁₃ | 35 | 0.63 | 30.4 | < 0.0001 |
| w ₁₄ | 34 | 0.89 | 282 | < 0.0001 |
| w ₁₅ | 33 | 0.84 | 89.0 | < 0.0001 |

(1 through 5⁺) 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-

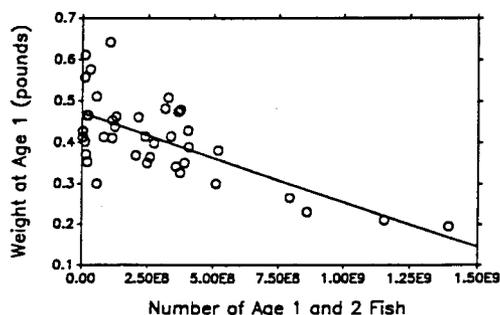


Figure 1. Density-dependence of weight at age 1 in the Pacific mackerel stock. Data shown cover years 1940-84, and do not include weights estimated by regression analysis. The regression line is shown for illustration. Other ages are similar.

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

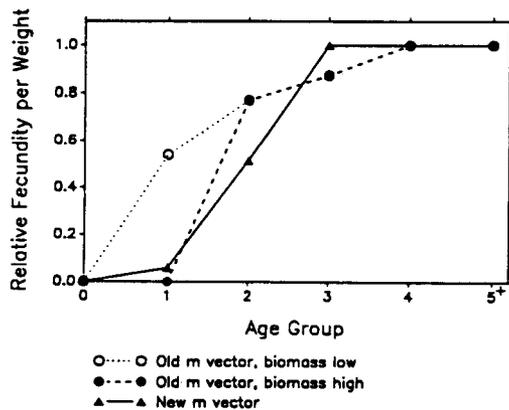


Figure 2. Spawning ogives under new and revised fecundity schedules (m vectors). The new schedule reveals that spawning is more concentrated among the older ages.

7 were all very similar, we averaged them and rescaled 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 . 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 $F = 1.0$; Φ , was set to 0.26, an average

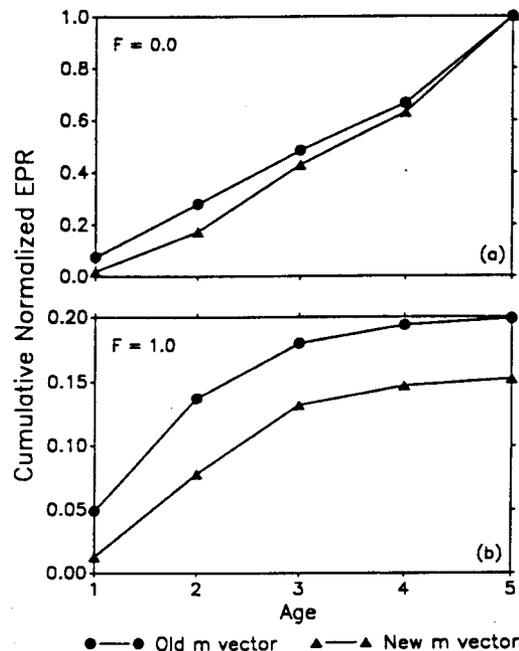


Figure 3. Cumulative eggs-per-recruit (EPR) curves for the Pacific mackerel stock under old and new fecundity schedules (m vectors). Curves have been normalized so that each yields EPR = 1.0 with no exploitation. (a), Unexploited stock; (b), stock exploited at annual $F = 1.0$.

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 ± 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% |

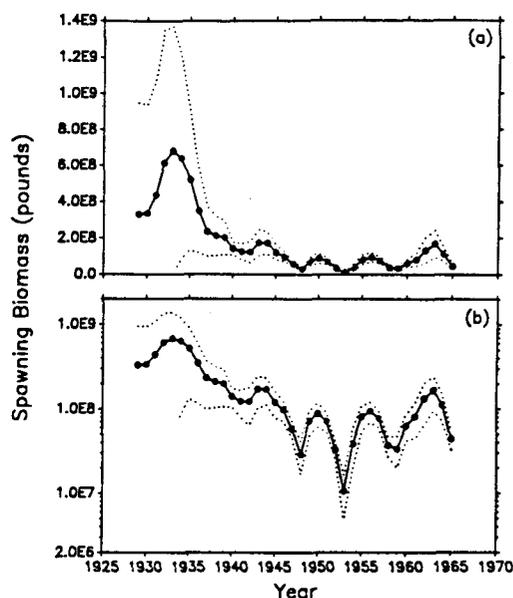


Figure 4. Revised spawning biomass estimates for Pacific mackerel stock, with approximate 95% confidence interval (dotted line). (a), Linear scale; (b), log scale. Large confidence bounds before 1940 reflect less precise knowledge of age structure and weights at age.

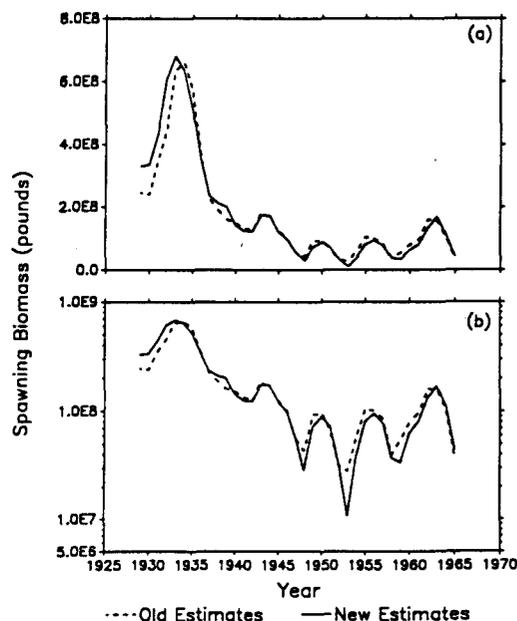


Figure 5. Old and revised spawning biomass estimates for Pacific mackerel stock: (a), linear scale; (b), log scale.

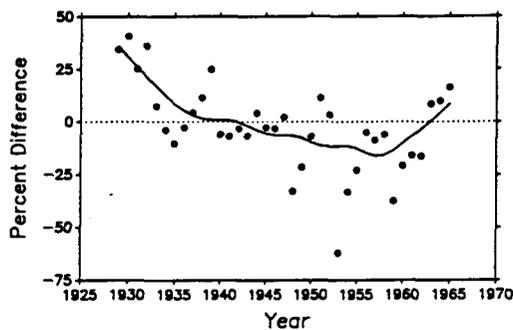


Figure 6. Difference between old and revised spawning biomass estimates, expressed as percent difference from the old to the new estimate [i.e., $(\text{old} - \text{new}) \times 100 / \text{old}$]. Smoothed line is locally weighted robust regression (LOWESS).

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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