THE NORTHERN ANCHOVY SPAWNING BIOMASS FOR THE 1982-83 CALIFORNIA FISHING SEASON

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ABSTRACT

The 1982 equivalent larval census estimate of the spawning biomass of the northern anchovy (*Engraulis mordax*) central subpopulation is 1,866,000 MT (2,060,000 short tons). This estimate is based on data gathered by an egg production survey conducted from January 18 to March 9, 1982. The abundance of larvae is projected from the daily production of eggs and the subsequent mortality of eggs and larvae. This equivalent larval census estimate will be the basis of the anchovy fishery optimum yield (OY) for 1982-83.

The egg production method estimate of anchovy spawning biomass is 378,000 MT (417,000 short tons). This is based on a production of 12.30×10^{12} eggs/day and a population (males and females) fecundity of 3.253×10^7 eggs/day/MT. The standard error of the egg production method estimate is 97,200 MT, for a coefficient of variation of 25.7%.

In 1982 the central subpopulation of northern anchovy was geographically distributed in the inshore portion of the Southern California Bight, from the Santa Barbara Channel Islands to northern Baja California. A smaller group was detected between Monterey and San Francisco Bays.

RESUMEN

La biomasa de la puesta en la población de *Engraulis mordax* de la zona central de California, fué de 1.866,000 Toneladas métricas durante 1982, estimación basada en la equivalencia del censo larval. Esta estimación está basada en los datos correspondientes a las exploraciones que desde el 18 de Enero al 9 de Marzo de 1982 se llevaron a cabo para determinar la producción de huevos en la región. La abundancia de larvas se calcula considerando la producción diaria de huevos y la mortalidad de huevos y larvas. Estas estimaciones equivalentes del censo larval serán la base para déterminar el rendimiento que se podrá obtener en la pesquería de anchoa durante el período de 1982-83.

La producción de huevos como método para estimar la biomasa de la puesta de la anchoa resulta de

376,000 Toneladas métricas. Esto se basa en una producción de 12.30×10^{12} huevos diarios y una población (machos y hembras) con fecundidad de 3.253×10^7 Toneladas métricas de huevos diarios. El error normal de las estimaciones por el método de producción de huevos es de 97,200 Toneladas métricas para un coeficiente de variación de 25.7%.

En 1982 la población de anchoa en la zona central de California estaba distribuida por la franja costera del seno del sur de California, desde las islas del Canal de Santa Bárbara, hasta el norte de Baja California. Un grupo de menor importancia se observó entre las Bahías de Monterrey y San Francisco.

INTRODUCTION

The biomass of the central subpopulation of northern anchovy (*Engraulis mordax*) has been assessed periodically using three independent methods: larval census (Smith 1972; Stauffer and Parker 1980; Stauffer 1980; Stauffer and Picquelle 1981); sonar mapping (Smith 1970; Mais 1974; Hewitt et al. 1976); and egg production (Parker 1980; Stauffer and Picquelle[1]). The anchovy management plan adopted by the Pacific Fishery Management Council (PFMC 1978) specifies that harvest quotas will be established by an optimum yield formula based on annual estimates of spawning biomass. Because of technical complexities in converting acoustic returns to fish biomass, the sonar mapping method is most useful for describing the disposition of adult schools. The egg production method is an improvement over the larval census method because it does not require multiple surveys and because it measures and incorporates variability in adult reproductive output. However, the optimum yield (OY) formula was developed based on larval census biomass estimates. The alternative estimation methods mentioned above produce estimates that consistently differ in magnitude from larval census estimates. Consequently, use of one of these estimates would systematically alter the optimum yields calculated from the larval-census-based formula. In order to avoid this

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problem, the PFMC has interpreted the OY formula to require a "larval census equivalent" spawning biomass estimate.

The Scientific and Statistical Committee of the PFMC reviewed egg production and larval census surveys conducted in 1979 and 1980, and recommended that replicate egg production surveys, concurrent with a larval census survey, be conducted in 1981. These were successfully accomplished, and the harvest quotas continued to be established using larval census estimates of biomass. In 1982 the National Marine Fisheries Service, in cooperation with the California Department of Fish and Game, conducted only an egg production survey. This report describes the survey results, the egg production estimate of biomass, and the equivalent larval census estimate of biomass.

The egg production method defines the spawning biomass as the quotient of the daily production of eggs in the sea and the daily fecundity (per ton of spawners) of the population (Parker 1980). The larval census method defines the spawning biomass as proportional to the average standing stock of larvae summed over four quarters of the year, and assumes constant reproductive output (per ton of spawners) and constant survival of the young. The proportionality constant was defined from a regression of sardine biomass on sardine larvae and assumes a relative fecundity between anchovy and sardine (Smith 1972).

No larval census was conducted in 1982; however, an equivalent larval census can be estimated by measuring larval mortality and projecting the number of larvae resulting from the measured egg production.

DESCRIPTION OF SURVEY

The 1982 egg production survey for the central subpopulation of the northern anchovy was conducted on board NOAA ship *David Starr Jordan* and F/V *Oregon Beaver* during the period January 18 through March 9, 1982. (For detailed descriptions of operations, see the respective cruise reports on file at the Southwest Fisheries Center, La Jolla, California, and California Department of Fish and Game, Long Beach, California.) A total of 992 egg samples was obtained on the *Jordan* using a small-mesh plankton net retrieved vertically from 70 m (Figure 1); adults were sampled on the *Beaver* and the *Jordan* with 187 midwater trawls (Figure 2); and the disposition of adult schools was described by sonar operated aboard the *Beaver* (Figure 3). In addition, the larvae were sampled with the 505-micrometer mesh bongo plankton net used for the larval census method. These samples are used to determine the posthatch survival of the larvae. Sea temperature, salinity, and weather observations were also recorded.
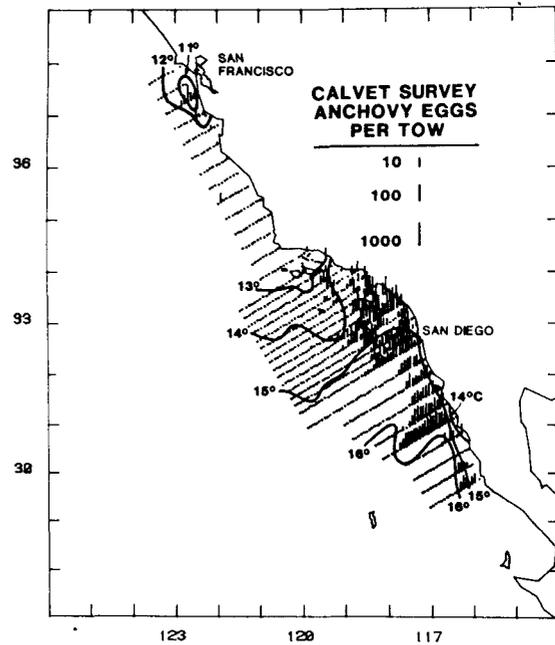

Figure 1. Geographic distribution of anchovy eggs in 1982. Spawning did not occur in cold water southeast of Point Conception or immediately adjacent to the northern Baja California coastline; some spawning was evident between Monterey and San Francisco bays.
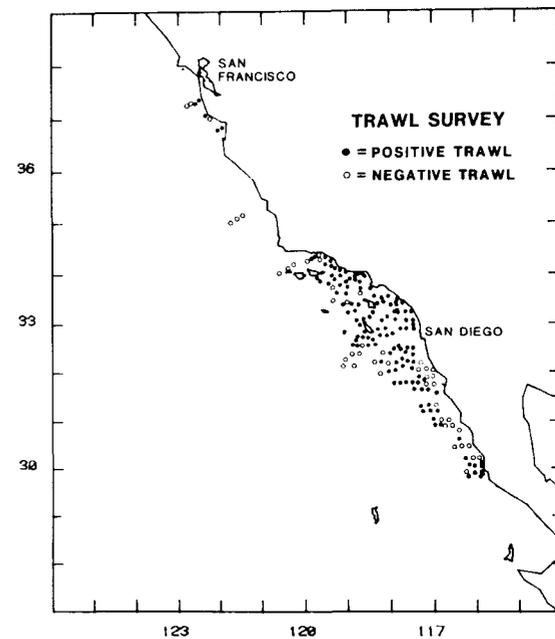

Figure 2. Geographic distribution of trawl sampling effort and trawls that caught adult anchovy (positive trawls). The distribution of adults matched the distribution of eggs (Figure 1).
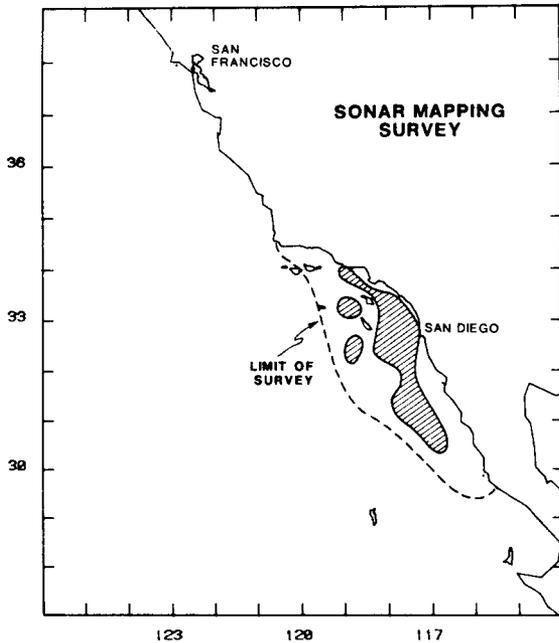
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Figure 3. Geographic areas of heaviest anchovy concentration as mapped by sonar (K. Mais, CDF&G). The general distribution matches those of eggs and adults obtained by direct sampling.

Anchovy eggs were distributed along the northern Baja California coast and in the Southern California Bight as far north as the Santa Barbara Channel Islands (Figure 1). As in previous years, the geographic pattern of spawning was correlated with the pattern of surface temperature isotherms (Lasker et al. 1981). Spawning did not occur in water colder than 14°C south of Point Conception, although this is not considered a lethal temperature. Cold water was observed as a large plume extending southeastward from Point Conception into the Southern California Bight and immediately adjacent to the northern Baja California coastline (Figure 1). A much smaller area of spawning was sampled between Monterey and San Francisco Bays in 11-12°C water.

The geographic distribution of positive trawl samples agrees with the distribution of eggs (Figure 2). Adult fish were caught in the Southern California Bight, along the northern Baja California coast, and between Monterey and San Francisco. Adults were not caught in trawls taken in the Santa Barbara Channel and immediately adjacent to the northern Baja California coastline.

The geographic distribution of fish schools as detected by sonar agrees with the distribution of eggs and positive trawls (Figure 3). The area of heaviest

anchovy concentration extends along the northern Baja California coastline (approximately 50 km offshore) and into the inshore portion of the Southern California Bight as far north as the Santa Barbara Channel Islands. Two smaller areas of heavy concentration were mapped in the offshore portion of the Southern California Bight.

In summary, northern anchovy, in the spring of 1982, were distributed continuously in the Southern California Bight from the Santa Barbara Channel Islands south to Cape Colnett. A second group was distributed between Monterey and San Francisco bays. In both groups fish were spawning, thus facilitating the use of reproductive surveys to estimate adult biomass.

EGG PRODUCTION ESTIMATE

Estimation Equation

The egg production estimate of anchovy spawning biomass, derived by Parker (1980) and modified by Stauffer and Picquelle (1980), is

$$B = P_o A \frac{k W}{R F S} \tag{1}$$

where B = spawning biomass (MT),

P_o = daily egg production, number of eggs produced per 0.05 meter^2,

W = average weight of mature females (grams),

R = sex ratio, fraction of population that are female, by weight (grams),

F = batch fecundity, number of eggs spawned per mature female per batch,

S = fraction of mature females spawning per day,

A = total area of survey (0.05 meter^2 units),

k = conversion factor for grams to metric tons.

An approximate sample variance for the egg production spawning biomass estimator, derived from the delta method (Seber 1973), is a function of the sample variance and covariance of the parameters

$$\text{Var} (B) \cong B^2 \times$$

$$\left\{ \frac{\text{Var} (P_o)}{P_o^2} + \frac{\text{Var} (W)}{W^2} + \frac{\text{Var} (R)}{R^2} + \frac{\text{Var} (F)}{F^2} + \frac{\text{Var} (S)}{S^2} + \right.$$

$$2 \left[\frac{\text{Cov} (P_o,W)}{P_o W} - \frac{\text{Cov} (P_o,R)}{P_o R} - \frac{\text{Cov} (P_o,F)}{P_o F} - \frac{\text{Cov} (P_o,S)}{P_o S} - \frac{\text{Cov} (WR)}{WR} - \right. \tag{2}$$

$$\left. \left. \frac{\text{Cov} (WF)}{WF} - \frac{\text{Cov} (WS)}{WS} + \frac{\text{Cov} (RF)}{RF} + \frac{\text{Cov} (RS)}{RS} + \frac{\text{Cov} (FS)}{FS} \right] \right\}$$

Daily Production of Eggs in the Sea

The parameter P_o, the daily production of eggs in the sea, is the number of eggs spawned per night, per unit area, averaged over the range and duration of the

survey. An ichthyoplankton survey is used to sample anchovy eggs to provide data on the density of the eggs by age. An exponential mortality model is then fit to the data, and the time-zero intercept of the fitted function is the estimate of egg production.

The sampling design of the survey is two-stage sampling with postsurvey stratification. The first stage is a systematic sample of block areas. The total area of the survey is divided into 4 × 20- (or 4 × 10-)nm blocks. The second stage is the selection of a 0.05-m² sampling unit in the center of the block (Stauffer and Picquelle[2]). This sampling design assumes that the distribution of eggs within one block is independent of the distribution within adjacent blocks. This assumption is based on experimental data showing that 4 miles is sufficient distance to ensure a negligible autocorrelation (P. Smith, pers. comm.). Advantages of this sampling plan are convenient and efficient use of ship time, even coverage of the total sample area, and improved precision of abundance estimates by maximizing the heterogeneity between adjacent sampling units (Jessen 1978).

Because of time and budget constraints, the sampling intensity was decreased in regions where fewer eggs were expected to be found. In the two 1981 surveys and the 1980 survey, the majority of the anchovy population was found in the Southern California Bight; a narrow band of eggs was typically found off Baja California; and very few eggs were collected off the central California coast. Therefore, the sampling fraction in the bight is increased to one sample per 4 × 10-nm block; elsewhere there is one sample per 4 × 20-nm block. To compensate for the uneven sampling intensity, each station is assigned a weight, w_{ij}, that is proportional to the relative area that the jth station represents in the ith stratum.

The total survey area is divided into two strata in order to reduce the variability about the egg abundance estimates. The geographic area of the survey is specified without knowing the actual area that the anchovy stock is currently occupying. Therefore, a portion of the surveyed area is beyond the range of the stock, contributing a large number of zero stations, which potentially inflates variance estimates. After the data are examined, a boundary for the current anchovy habitat can be drawn. The boundary is determined by following each line seaward until the last positive tow was taken. Thus all stations seaward of the boundary are zero, and all positive stations are shoreward of the boundary, along with many imbedded zero stations. The area within the boundary is allocated to stratum 1, and the area outside the boundary is put into stratum 0.

	Stratum 1	Stratum 0	Total
Area (nm²)	24,190	35,039	59,229
Number of samples	396	596	992

Because the strata can be defined only after the data are collected, this technique is called postsurvey stratification. The area of each stratum, A_i, is not predetermined, so A_i is a random variable, and all variance estimates must be adjusted to include this source of variation (Jessen 1978).

The anchovy eggs from each sample are counted and staged according to the degree of embryonic development. The eggs are then classified into one-day age intervals based on the time of collection, surface water temperature, developmental stage, and laboratory-determined development rates. The ages are then further refined by adding the portion of a day that has elapsed between 2200 (the assumed time of spawning[3]) and the time of collection. This aging procedure is facilitated by the fact that eggs in a particular sample are either spawned on the same evening, or are separated by one-day increments, thus making it easier to separate the modes of egg abundance over stages into one-day age groups. Sea-surface temperatures for the majority of the cruise ranged between 13° and 17°C with an egg-weighted average of 14.9°C. At this temperature, eggs begin to hatch after 2.91 days. Eggs less than 2.67 days old were used in the analysis.

The daily production of eggs, P_o, and its variance are then estimated by regressing the counts of eggs on their age, using the exponential mortality model:

$$P_{ijk} = P_{oi}e^{-Zt_{ijk}} + \varepsilon_{ijk} \qquad (3)$$

where P_{ijk} is the number of eggs in the kth day age category from the jth station in the ith stratum; t_{ijk} is the age in days measured as the elapsed time from the time of spawn for the kth day category eggs to the time of sampling of the jth station in the ith stratum; P_{oi} is the daily production of eggs per unit area (0.05 m²) in stratum i; Z is the daily rate of instantaneous egg mortality; and ε_{ijk} is the additive error term. This model assumes that all eggs are spawned and fertilized each day at time 2200, and eggs have a constant positive rate of instantaneous mortality[4].

The mortality function (equation [3]) is fit to the data by regressing the aged egg counts $\{P_{ijk}\}$ on their age $\{t_{ijk}\}$ for stratum 1 with a weighted nonlinear
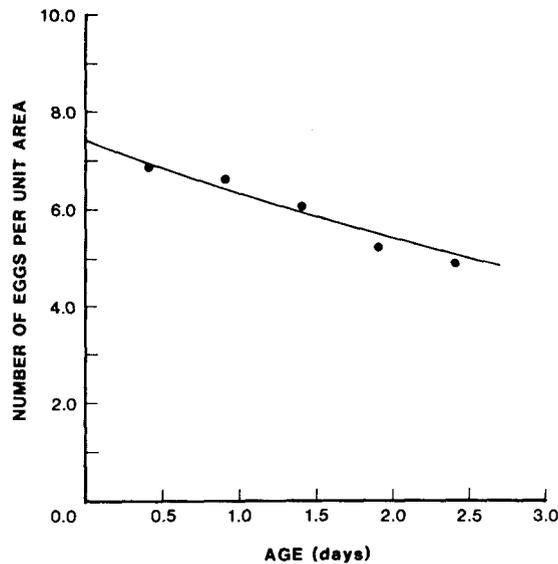
Figure 4. Mean egg production per 12-hour interval for stratum 1 is plotted against age in days. The exponential mortality model was estimated by regressing the individual egg counts on age.

least squares routine using a pseudo-Gauss-Newton algorithm (Dixon and Brown 1979). The individual weighting factors are the station area weights, $\{w_{ij}\}$. The resulting estimate of P_{ol} is 7.40 eggs per day per 0.05 m^2, and Z is 0.158 per day with variances 1.25 and 0.0110, respectively. A plot of the mean egg production per 12-hour interval and the estimated regression for stratum 1 are shown in Figure 4.

The final stratified estimate of P_o is the weighted average of the two strata where the strata weights u_i are proportional to A_i, the area of the ith stratum. P_{oi} for stratum 0 is zero by definition, thus:

$$u_i = \frac{A_i}{A_I + A_O}$$

$$P_o = u_I P_{ol} + u_O P_{oO} = u_I P_{ol}, \qquad (4)$$

and the variance, adjusted for postsurvey stratification (Jessen 1978), is

$$\widehat{\text{Var}}(P_o) = (1 + \frac{1}{n}) \left[\sum_{i=1}^{2} u_i \widehat{(\text{Var}(P_{oi}))} \right] \qquad (5)$$

where n is the total number of observations = 992; $\widehat{\text{Var}}(P_{ol}) = 1.25$ is estimated from the regression (3) for stratum 1, and; $\widehat{\text{Var}}(P_{oO}) = 0$ by definition.

The stratified estimate of P_o is 3.023 eggs per day per 0.05 m^2 for the entire survey area, with an esti-

mated variance of 0.5119 and coefficient of variation of 23.67%. This estimate of P_o applies over the 59,299-nm^2 area of the survey ($A = 4.068 \times 10^{12}$ area units of 0.05 m^2 each).

Adult Parameters W, F, S, and R

The parameters W, F, S, and R are estimated from samples of adult anchovies collected by the midwater trawl survey. The sampling design consists of three stages: (1) placement of trawl stations, (2) trawl catch, and (3) subsample of fish. The statistical technique of judgment sampling is used in selecting the location for the trawls in order to achieve a high proportion of positive trawls. Station locations were selected where concentrations of anchovies were detected by the occurrence of anchovy eggs or larvae in the plankton samples, and the presence of apparent schools on the sonar (Figures 1, 2, and 3). Because more stations are selected where heavy concentrations of anchovies are suspected, the sample design follows the precepts of probability sampling (Cochran 1963).

One trawl is taken at each selected location, and the trawl catch is assumed to be a random sample of fish at the station. Each station is given equal weight by subsampling an equal number of fish from each trawl, m^*. This is appropriate if the probability of choosing a station is exactly proportional to the number of anchovies at the station; however, these probabilities are impossible to enumerate, so that the actual sampling design is only an approximation of the ideal design (judgment sampling rather than probability sampling). If the trawl catch size were a good measure of the abundance of fish at the station, this information could be used to improve the approximation of the ideal sample design. However, trawl catch size and abundance of fish are unrelated for anchovies; catch size depends more on the depth of the school, the avoidance of the net by the fish, and luck. This conclusion is supported by the historical lack of agreement between trawl catch size and the factors that indicate concentrations of anchovies (sonar detection, eggs and larvae in plankton samples).

Even though equal subsample sizes are attempted, they are not always attainable: the catch may have few mature females, or the catch may be extremely small. In these cases the stations should receive less weight to compensate for the error in judgment sampling; if there are few mature females in the catch then it is assumed that there are few mature females at the station, and if the catch is very small then it is assumed that the actual number of anchovies at the station is relatively small. Thus,

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each station is given a weight of the relative sub-sample size.

The estimates and variances, $(\bar{\bar{y}})$ and $\text{var}(\bar{\bar{y}})$, of the four parameters—W, R, F, and S—are the weighted sample mean and sample variance (Cochran 1963)

$$\bar{\bar{y}} = \sum_{i=1}^{n} \left(\frac{m_i}{n\bar{m}}\right) \bar{y}_i \qquad (6)$$

$$\widehat{\text{Var}(\bar{\bar{y}})} = \frac{\sum_{i=1}^{n} \left(\frac{m_i}{\bar{m}}\right)^2 (\bar{y}_i - \bar{\bar{y}})^2}{n(n-1)} \qquad (7)$$

where m_i is the number of fish subsampled from the ith trawl, $\bar{m}$ is the average number of fish subsampled per trawl, n is the number of positive trawls, y_{ij} is the observed value for the jth fish in the ith trawl, and $\bar{y}_i = \sum_{j}^{m_i} y_{ij}/m_i$ is the average for the ith trawl.

The method described by equations (6) and (7) is used in the succeeding sections to estimate parameters W, F, S, and R and their respective variances.

Average Female Weight

The average female weight, W, is calculated as the weighted average of W_{ij}, the weight of the jth mature female from trawl i, using equation (6). The weight of females with hydrated eggs in their ovaries is temporarily inflated because of water retention, therefore their weight is adjusted using the regression of whole-body weight on ovary-free weight estimated from females that do not have hydrated eggs,

$$\hat{W}_{ij} = -0.0701 + 1.06 \, W_{ij}^* \qquad (8)$$

where W_{ij}^* is the ovary-free weight; the regression has an $r^2 = 99.6\%$. The desired subsample size is $m^* = 15$ mature females. The estimated average female weight is 18.83 g with a variance of 0.1319 (equation [7]) and coefficient of variation of 1.93%. The mode of the frequency distribution of W_i, the average weight of mature female anchovies in the ith trawl, is at 19 g (Figure 5).

Batch Fecundity

For the estimate of batch fecundity, F, the individual observations, F_{ij}, are not observed directly but are estimated from a relationship between batch fecundity and ovary-free weight. This relationship is estimated from a sample of 109 hydrated females that were collected over the duration of the cruise. These hydrated females have a distribution of adjusted weights (equation [8]) similar to the weight
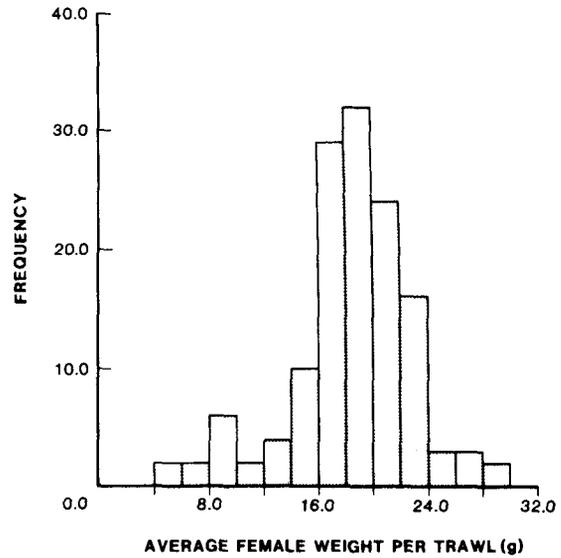

Figure 5. The frequency distribution of the average weight of mature females per trawl.

distribution of females for the whole cruise (Figure 6). A linear regression of fecundity on weight was selected because the fitted exponent for the power function was not significantly different from one, indicating that any curvature present in the data is
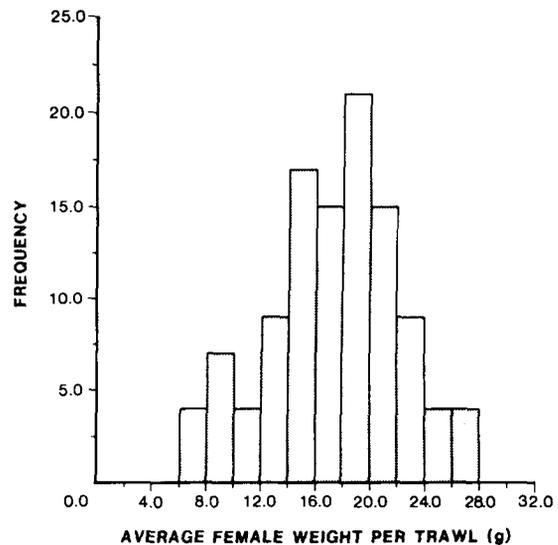

Figure 6. The frequency distribution of whole body weights for the hydrated females used in regression (9). The weights of the hydrated females were adjusted to nonhydrated weights using regression (8). The frequency distribution of adjusted weights is similar to that of the average weights of mature females (Figure 5).

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very slight. The selected regression model is

$$\hat{F}_{ij} = -179.7 + 617.2\ W_{ij}^* \qquad (9)$$

with an $r_2 = 52.4\%$ (Figure 7).

Based on this regression, the F_{ij} are estimated for each of the $m^* = 15$ mature females from each trawl. Estimated average batch fecundity is 10845 (equation [6]), with a variance of 171730 (equation [10]) and coefficient of variation of 3.82%. Because the trawl averages ($\bar{F}_i$) are not based on actual observations, but are estimates with their own variance, the variance estimate for F includes this additional source of variation (Draper and Smith 1966):

$$\widehat{\text{Var}}\,(\bar{\bar{F}}) = \overset{n}{\underset{i=1}{\Sigma}} \qquad (10)$$

$$\frac{\left(\frac{m_i}{\bar{m}}\right)^2 \left[\frac{(\bar{F}_i - \bar{\bar{F}})^2}{n-1} + \frac{S_h^2}{109} + (\bar{W}_i^* - \bar{W}_h^*)^2\ \widehat{\text{Var}}(b)\right]}{n}$$

where $S_h^2 = 6658675$ is the variance about the regression (9); $\bar{W}_i^*$ is the average ovary-free weight for the ith trawl; $\bar{W}_h^* = 16.54$ is the average ovary-free weight for the 109 hydrated females; $\widehat{\text{Var}}(b) = 3172$ is the variance of the slope of regression (9); and $n = 135$ positive trawls.

Specific fecundity, expressed as eggs per gram of whole-body weight, is similar to those observed in 1981.

Year	1980	1981	1981	1982
Survey	8003/4	8102	8104	8202
Mean weight (g)	17.4	13.4	16.2	18.8
Eggs/gram	444.4	623.0	546.0	575.9

Spawning Fraction

Spawning fraction, S, is estimated from $m^* = 15$ mature females, and $S_{ij}^l = 1$ if the ovary of the jth mature female in the ith trawl is classified as having day-1 postovulatory follicles (day-1 spawners), and $S_{ij}^l = 0$ otherwise (see Hunter and Macewicz 1980 for histological definition of day-1 and day-0 spawners). Thus $\bar{S}_i^l$ is the proportion of mature females in the ith trawl that are in the day-1 spawning category (S^1).

Another measure of spawning activity is the proportion of mature females that are classified as day-0 spawners, S^0. In past surveys, it has been suspected that the proportion of day-0 females is a biased estimate because of oversampling of females that spawn on the night of capture. This was indicated by a large discrepancy between S^1 and S^0, with the deviation between these two measures reaching a max-
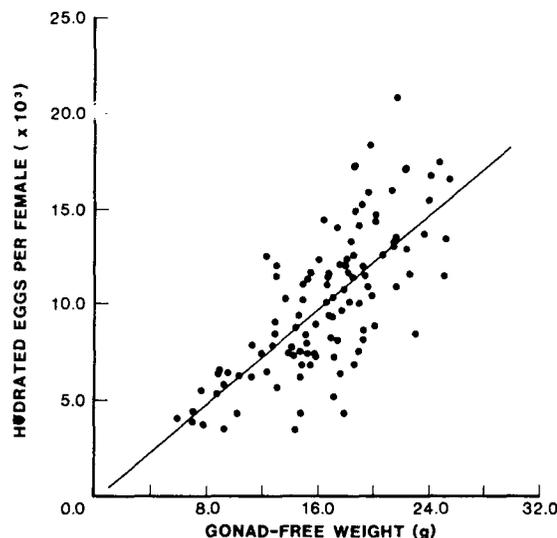

Figure 7. Batch fecundity regressed on ovary-free weight of 109 hydrated females using a linear model (equation [9]).

imum during the peak hours of spawning. There was also a co-occurrence of high values of S_i^0 and low values for sex ratios for trawls taken during these hours, which suggested that males and day-0 spawning females segregate out from other females at the peak hours of spawning at a depth where they are more vulnerable to the midwater trawl[5]. In previous surveys, m_i was adjusted by assuming that the actual number of day-0 females is the same as the observed number of day-1 females.

The apparent oversampling of day-0 females was reduced in this year's data; this may have been due to a slight change in the trawl gear. The difference between S^1 and S^0 is still greatest during the peak spawning time 2200-2259 (Figure 8), and there is still a dip in the sex ratio over the time 2000-2259 (Figure 9), but the discrepancy is very small relative to past years. In fact, the values of S^1 and S^0, 0.120 and 0.127, respectively, are not significantly different from each other. Thus, we concluded that day-0 spawning females were not oversampled this year. Hence, m_i is not adjusted and is simply the number of mature females in the ith trawl. The estimate of spawning fraction is 0.120 (equation [6]) with variance $= 9.47 \times 10^{-5}$ (equation [7]) and coefficient of variation $= 8.13\%$.

Sex Ratio

The parameter R, sex ratio, is the fraction of females in the anchovy stock based on fish weight.
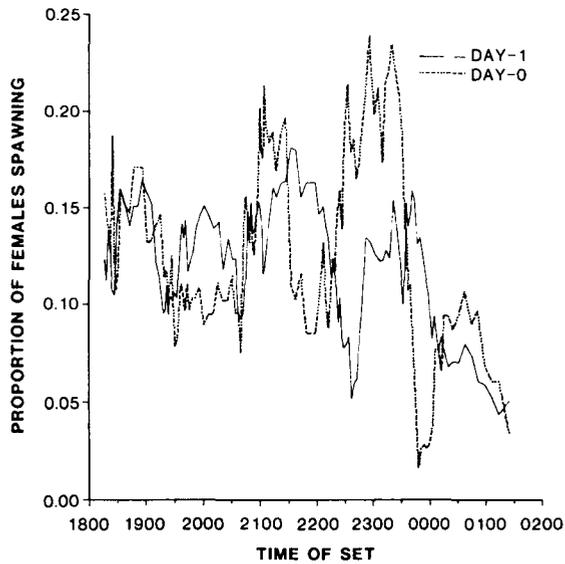
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[5]See footnote 1 on page 16.

Figure 8. The running averages for S^0 (day-0 spawning fraction) and for S^1 (day-1 spawning fraction) plotted against the time of trawl. The running averages are based on 10 observations. The discrepancy between S^0 an S^1 is largest during the time interval 2200-2259, the peak time of spawning.
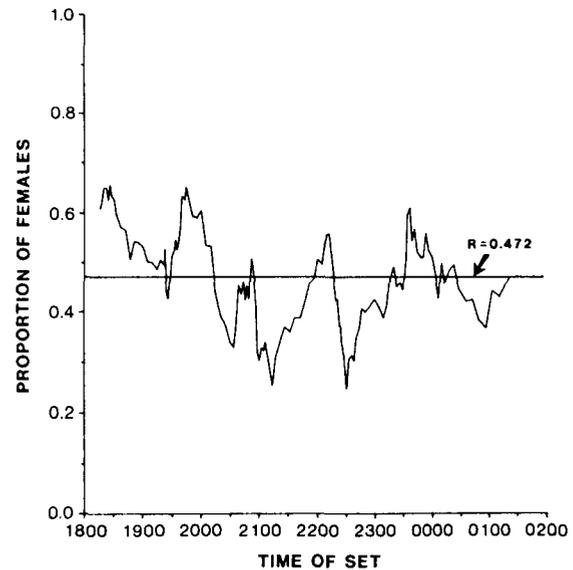

Figure 9. The changes of observed sex ratio with time. The running average for sex ratio is based on 10 observations. The horizontal line is the estimated mean sex ratio.

The sex ratio for each trawl is determined from the first 50 fish. Average weights by sex per trawl are estimated from the first 5 males and the first 20 females, where the weight of hydrated females is adjusted using equation (8). The trawl average, $\bar{R}_i$, is the estimated total weight of the females in the first 50 fish subsampled, divided by the estimated total weight of the first 50 fish. The m_i in equations (6) and (7) for this parameter is the estimated total weight of the first 50 fish. For both sexes, both mature and immature fish are included because of the difficulty of distinguishing between mature and immature males. The estimate for sex ratio is 0.472 (equation [6]), and its estimated variance (equation [7]) and coefficient of variation are 4.90×10^{-4} and 4.69%, respectively.

Biomass Estimate and Variance

The parameter estimates and their variances given above are summarized in Table 1. The resultant estimate of anchovy spawning biomass using equation (1) is 378,000 MT (417,000 short tons). The approximate variance is calculated according to equation (2), where covariance terms are included only for those pairs of variables with sample correlations that are significantly different from zero. The sample correlations between P_o and the adult parameters are assumed to be zero because they are

TABLE 1
**Estimates of Egg Production Parameters and
Spawning Biomass for 1982**

Parameter	Symbol	Mean	Variance	Coefficient of Variation
Egg production (eggs/0.05 m²-day)	P_o	3.023	0.5119	0.237
Area of survey (0.05 m² units)	A	4.068×10^{12}	—	—
Average female weight (grams)	W	18.8	0.132	0.0193
Sex ratio by weight (females/total)	R	0.472	4.90×10^{-4}	0.0469
Batch fecundity (eggs per batch per mature female)	F	10845	171730	0.0382
Fraction of mature females spawning per day	S	0.120	9.47×10^{-5}	0.0813
Spawning biomass (MT)	B_e	378,000	945×10^9	0.257

derived from two different surveys (the plankton survey and the trawl survey) and thus cannot be estimated. Of the adult parameters, only cov(W,F), cov(R,W), and cov(F,R) are significant, with values of 110, 0.00271, and 1.57, respectively. The approximate variance of the biomass estimate is 9.45×10^9, and standard error is 97,200 MT, for a coefficient of variation of 25.7%. The approximate 95% confidence interval is ± 194,000 MT.

EQUIVALENT LARVAL CENSUS ESTIMATE OF BIOMASS

The anchovy management plan presently requires that the annual harvest quota for the U.S. fishery be based on an annual estimate of spawning biomass (Smith 1972; Huppert et al. 1980). The PFMC has interpreted the plan to require an equivalent larval census biomass estimate. The 1982 survey was designed to generate an estimate of the biomass based on the egg production and fecundity of the population, but was not designed to directly generate a larval census estimate of biomass.

It is possible to generate an equivalent larval census estimate of biomass by estimating the number of larvae resulting from the measured production of eggs (Stauffer 1983). To do so, the mortality rates of both eggs and larvae are required. The abundance of larvae can then be extrapolated to an annual census using historical proportions of quarterly abundances. The spawning biomass is assumed to be proportional to the annual census; the constant of proportionality was determined from a regression of adult sardine biomass on the annual census of sardine larvae, and an assumption of sardine to anchovy annual fecundity of 1:2 (Smith 1972).

During the 1982 egg production cruise, 96 plankton samples were obtained using the bongo net at standard CalCOFI stations (Figure 10). Anchovy larvae were found at 69 of the stations. In the following sections we discuss: (1) the production curve of the larvae derived from the size-specific catch curve; (2) an equivalent annual larval census derived from the population production of eggs and the subsequent mortality of both eggs and larvae; and (3) the discrepancy between the egg production estimate of biomass and the equivalent larval census estimate.

Production Curve

The larvae were grouped into 12 size categories (yolk-sac to 15 mm), and catches were adjusted for variations in the volume of water filtered per m of depth. Bias corrections were also applied for extrusion of small larvae through the meshes of the net and avoidance of the net by large larvae. The adjusted catches were divided by the duration of growth, through each size class, to estimate the age-specific production of larvae (P_t). The adjustments were accomplished by fitting a weighted negative binomial model to the sample frequency distributions of each size class. Each observation is weighted by a factor that is the product of the various adjustments, and the means of the final distributions are unbiased estimates of production (P_t). The pro-
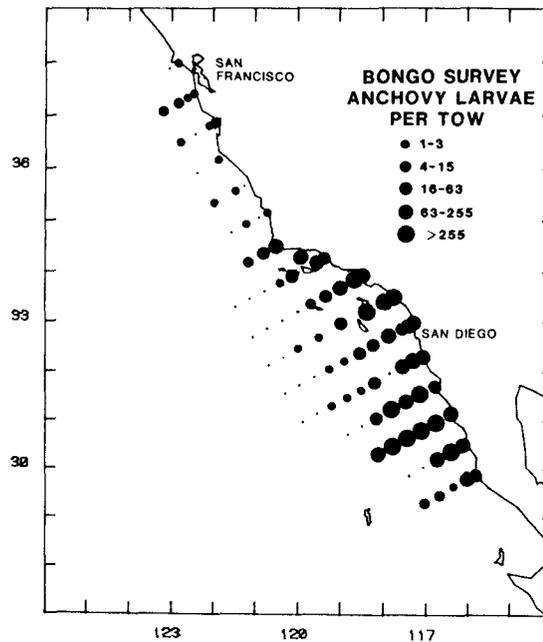

Figure 10. Geographic distribution of anchovy larvae as determined from standard CalCOFI ichthyoplankton bongo tows taken at 96 stations during the 1982 egg production survey.

cedure was developed in a series of papers: Bissel 1972; Zweifel and Smith 1981; Hewitt 1981, 1982; Hewitt and Methot 1982; Hewitt and Brewer 1983. The calculations are summarized in Table 2, and the results are described in Figure 11.

It is clear, from a log-transform plot, that a constant mortality model, $dp/dt = -cP$ will not adequately describe the data. A variable mortality model may be devised by defining c as a function of age.[6] Several forms would adequately describe the data, but for reasons of mathematical tractability we may use:

$$\frac{dP}{dt} = -\frac{\beta}{t}P . \tag{11}$$

As t increases, the instantaneous rate of change of production decreases (improving survival with age). The above expression may be rearranged, integrated, and the integration constant determined at the age of hatching (t_h):

$$P_t = P_h \left(\frac{t}{t_h}\right)^{-\beta} \text{ for } t \geqslant t_h. \tag{12}$$

[6] Variable mortality rate may be defined as a function of age, size, or population abundance. The important point is that the number of deaths is modeled as a portion of those living. N. Lo, SWFC, suggested the form used here.

TABLE 2
Size-Specific Catches of Anchovy Larvae and Age-Specific Estimates of Daily Production

Preserved size (mm)	Fraction retained by net[1]	Average adjustment for sampling and sorting variability[2]	Average duration of growth[3] (days)	Average catch $\left(\dfrac{\text{larvae}}{\text{tow}}\right)$	P_t[4] $\left(\dfrac{\text{larvae}}{\text{m}^2\text{-day}}\right)$	Age[3] since fertilization (days)
2.50	0.21	1.91	3.59	29.99	20.82	4.42
3.75	0.51	1.99	3.51	26.91	7.56	8.00
4.75	0.69	1.98	2.58	16.91	4.80	11.07
5.75	0.73	2.18	2.38	12.12	3.20	13.62
6.75	0.73	2.18	2.24	8.93	2.51	15.74
7.75	0.68	2.20	2.16	6.75	2.09	18.13
8.75	0.61	2.22	2.12	5.10	1.78	20.24
9.75	0.60	2.09	2.11	3.38	1.28	22.67
10.75	0.54	2.86	2.12	1.70	0.52	24.92
11.75	0.56	2.27	2.14	1.06	0.39	27.01
12.75	0.46	1.75	2.19	0.51	0.29	28.88
13.75	0.57	2.11	2.29	0.33	0.12	31.93

[1]Extrusion corrections are based on relative retention rates between 75-micrometer and 505-micrometer mesh nets (Lo, SWFC pers. comm.) Avoidance corrections are based on night and day catch comparisons using bongo data from 1978 and 1979 (Hewitt and Methot 1982). Fraction of larvae retained in the net is estimated as Σ col. $5/\Sigma$ (col. 5/col. 2); $r = 0.4$.

[2]Accounts for partial sorting of samples and standardizes sampling volume to 1 m^2 per m of depth.

[3]Temperature-dependent embryonic growth is determined from laboratory experiment (Lo, SWFC pes. comm.), and post-yolk-sac growth follows Methot's (1981) description.

[4]Production rates (P_t) may be estimated by dividing the average catch by the product of columns 2, 3, and 4. In practice, however, P_t is the mean of a weighted negative binomial model fit to the distribution of individual observations (ie., plankton tows).

This expression defines the larval production curve. The average standing stock of larvae is the area under the curve, and it may be determined by integrating the above expression between t_h and 30 days (the maximum age effectively caught with a standard plankton tow). Thus:

$$N = A \int_{t_h}^{30} P_h \left(\frac{t}{t_h}\right)^{-\beta} dt$$

$$= A \frac{P_h t_h}{\beta - 1}\left(1 - \left(\frac{t_h}{30}\right)^{\beta-1}\right) \qquad (13)$$

where N is the average standing stock of larvae and A is the area of the survey.

Equivalent Annual Larval Census

An equivalent larval census estimate of biomass may be derived by reducing the production of eggs to the production of hatching larvae via egg mortality and then integrating the larval production curve over age to estimate average standing stock of larvae. The average standing stock is converted to the annual larval census by a factor[7] of 2.12. The standard sampler would retain a fraction (r) of these larvae; the remainder are extruded through the meshes, and a small portion avoid capture. Finally, the annual larval census is converted to spawning
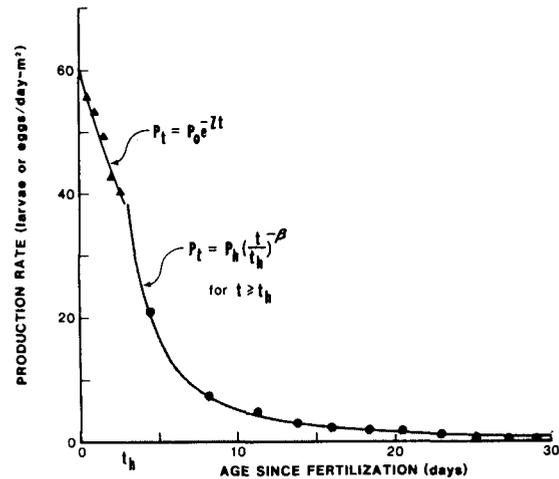

Figure 11. Changes in the production rate of eggs and larvae with time since fertilization. Production of eggs (triangles) was estimated from the CalVET sample, and the production of larvae (dots) was estimated from the CalCOFI bongo sample. The shaded area under the larval production curve is the average standing stock of larvae (N).

biomass using the historical conversion factor of 8.9 $\times$ 10^{-8} MT/larva. Thus:

$$\hat{B}_t = N(2.12)\ r(8.9 \times 10^{-8}) \qquad (14)$$

where: r = fraction of larvae retained in standard sampler,

$$P_h A = P_o A s$$

$$N = P_o A s \left(\frac{t_h}{\beta-1}\right)\left(1 - \left(\frac{t_h}{30}\right)^{\beta-1}\right)$$

[7]The annual larval census is the sum of the average standing stock in each quarter. Stauffer and Picquelle (1980) describe the historical proportions of the quarterly values as 1.1.06 .06, so that the annual larval census is equal to 2.12 times the average standing stock over the first 2 quarters.

TABLE 3
Projected and Observed Larval Census Estimates of Spawning Biomass and Related Parameters

	1980	1981 Feb.	1981 Apr.	1982
Population production P_oA of eggs (eggs/day)	23.97×10^{12}	19.07×10^{12}	11.46×10^{12}	12.30×10^{12}
Egg mortality rate z	0.453	0.138	0	0.158
Time to hatch (days) t_h	2.71	2.75	2.75	2.91
Survival to hatch $s = e^{-zt_h}$	0.293	0.684	1.000	0.631
Coefficient in larval mortality β model	1.7999	1.7058	1.7058	1.7085
Retention r	0.4	0.4	0.4	0.4
Projected larval census B_l estimate of spawning biomass (MT)	1.533×10^6	3.126×10^6	2.746×10^6	1.866×10^6
Larval census estimate of B_l spawning biomass (MT)	1.611×10^6	2.544×10^6	2.544×10^6	—
Daily fecundity $\left(\frac{eggs/day}{ton}\right) q$	30.28×10^6	33.03×10^6	33.84×10^6	32.53×10^6

and P_hA is the population production of hatching larvae, P_oA is the population production of eggs, s is the fraction of egg production surviving to hatch, and $\hat{B}_l$ is the equivalent larval census estimate of spawning biomass (MT).

When equation (14) was applied to 1980 and 1981 surveys, which generated both egg production and larval census estimates, the larval census was similar to that estimated from the production of eggs (average ratio = 1.09; range 0.95 to 1.23; Table 3). By rewriting equation (1) as:

$$B_e = \frac{P_oA}{q}$$

where B_e is the egg production estimate of spawning biomass, P_oA is the daily population production of eggs, and q is the daily fecundity on a weight basis $= RFS/kW$, we may relate the equivalent larval census estimate of biomass ($\hat{B}_l$) to the egg production estimate of biomass (B_e) using equation (14):

$$\hat{B}_l = B_e \, qs$$

$$\left(\frac{t_h}{\beta-1}\right)\left(1-\left(\frac{t_h}{30}\right)^{\beta-1}\right) r \, (18.9 \times 10^{-8}). \quad (15)$$

Thus the equivalent larval census estimate of spawning biomass may be calculated from the egg production estimate of biomass by adjusting the latter for fecundity, egg survival, larval survival, and larval retention in the standard ichthyoplankton sampler historically used for larval census estimates. Because the larval census estimate of biomass assumes a fixed fecundity, $\hat{B}_l$ may be calculated from the population production of eggs, without consideration of the adult reproductive parameters, using equation (14).

Equation (14) was applied to the data presented in this report; the parameter values are listed in Table 3. The 1982 equivalent larval census estimate of spawning biomass is 1.866×10^6 MT (2.060×10^6 short tons); the equivalent annual larval census is $20,966 \times 10^9$ larvae.

Discrepancy between the Biomass Estimates

The equivalent larval census estimate of spawning biomass (1.866×10^6) is nearly five times the egg production estimate of spawning biomass (0.378×10^6 MT). One or more of three factors may be the cause of this discrepancy: (1) sampling errors between the ichthyoplankton gears; (2) variability in the conversion factor relating the larval census to the spawning biomass (resulting from variability in the population fecundity and survival of young, which are assumed to be constant in the larval census method); and (3) systematic inaccuracy in the conversion factor relating anchovy larvae to anchovy spawners.

The projected abundance of larvae and the measured abundance of larvae agree reasonably well for three surveys (Table 3). This indicates that the two sampling gears (CalVET net, used to sample eggs, and the CalCOFI bongo net, used to sample larvae) yield consistent and compatible estimates of ichthyoplankton production. It is possible to predict the catch of one gear from the catch of the other. The discrepancy between the biomass estimates is thus not due to inaccuracy or imprecision in the ichthyoplankton sampling.

The population fecundity and survival of larvae did not vary considerably among the three surveys (Table 3). Egg survival, however, did vary, ranging from an estimated 29% survival in 1980 to 100%

TABLE 4
Adjustment of Larval Census Estimates of Spawning Biomass for Variability in Egg Survival

Year	1980	1981		1982
		Feb.	Apr.	
S	0.293	0.684	1.000	0.631
B_e	792×10^3	577×10^3	339×10^3	378×10^3
B_l	1611×10^3	2544×10^3	2544×10^3	1866×10^3
$\dfrac{0.650}{s}$	2.218	0.950	0.650	1.030
Adj. B_l	3573×10^3	2417×10^3	1654×10^3	1922×10^3
$\dfrac{\text{Adj. } B_l}{B_e}$	4.5	4.2	4.9	5.1
$\dfrac{0.300}{s}$	0.977	0.439	0.300	0.475
Adj. B_l	1574×10^3	1117×10^3	763×10^3	886×10^3
$\dfrac{\text{Adj. } B_l}{B_e}$	2.0	1.9	2.3	2.3
$\dfrac{1.000}{s}$	3.412	1.462	1.000	1.585
Adj. B_l	5498×10^3	3719×10^3	2544×10^3	2957×10^3
$\dfrac{\text{Adj. } B_l}{B_e}$	6.9	6.4	7.5	7.8

survival in April 1981. Low egg survival implies that a low larva-to-spawner ratio actually existed and that spawner biomass was underestimated relative to surveys where egg survival was high. To investigate this effect, we assumed that an egg survival rate of 65% prevailed during all the surveys, and we proportionally adjusted the larval census estimates of spawning biomass (Table 4). The adjusted larval census estimates of spawning biomass are consistently 4 to 5 times greater than the egg production estimates of spawning biomass, indicating a systematic bias. If we assume an egg survival of 30%, the ratio decreases to 2; whereas an egg survival of 100% implies that the larval census overestimates spawning biomass by a factor of 7 (Table 4). Thus by considering variability in egg survival we have shown that the discrepancy between the two biomass estimates can be reconciled by a single factor for all the surveys.

Finally, we consider the conversion factor relating the annual census of anchovy larvae to anchovy spawners. This factor was determined for the sardine by regressing virtual population estimates of the adult stock on the annual sum of quarterly larval census estimates (Smith 1972). The proportionality was extended to the anchovy by estimating the relative annual fecundity (anchovy: sardine) to be 2 (Smith 1972); i.e., each anchovy larva represented only half the weight of adult fish that a sardine larva did. We demonstrated above that the larval census estimate of biomass (when adjusted for variations in egg survival) exceeds the egg production estimate of biomass by a fixed factor. We suggest that this bias

results from inaccuracy in the anchovy/sardine relative annual fecundity (on a weight basis). The average of the four observations of egg survival is our best estimate of the long-term average egg survival (65%); use of this value implies that the relative fecundity is approximately 4.5 times the previously accepted value. We suggest that the anchovy spawns approximately 9 times as many eggs per gram throughout the year as does the sardine. This may be explained by increasing the batch fecundity per gram and shortening the interval between spawnings (these relationships between the reproductive parameters of anchovies and sardines have been observed in Peru by P. Smith [pers. comm.]).

Thus the discrepancy between the larval census estimates and the egg production estimates of spawning biomass can be explained by variation in egg survival and inaccuracy in estimating the average proportionality between the larval census and the spawning biomass. We further consider the egg production method to be more precise (because it considers the rate at which eggs die) and more accurate (because of the underestimate of anchovy fecundity) than the larval census method.

ACKNOWLEDGMENTS

LITERATURE CITED

Bissell, A. F. 1972. A negative binomial model with varying element sizes. Biometrika 59:435-441.

Cochran, W. G. 1963. Sampling techniques. John Wiley and Sons, Inc., New York, 413 p.

Dixon, W. J., and M. B. Brown, eds. 1979. Biomedical computer programs, P-series. University of California Press, Berkeley.

Draper, N. R., and H. Smith. 1966. Applied regression analysis. John Wiley and Sons, Inc., New York, 407 p.

Hewitt, R. P. 1981. The value of pattern in the distribution of young fish. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:229-236.

———. 1982. Spatial pattern and survival of anchovy larvae: implications of adult reproductive strategy. Ph.D. dissertation, University of California, San Diego, 187 p.

Hewitt, R. P., and G. D. Brewer. 1983. Nearshore production of young anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 24:(this volume).

Hewitt, R. P., and R. D. Methot. 1982. Distribution and mortality of northern anchovy larvae in 1978 and 1979. Calif. Coop. Oceanic Fish. Invest. Rep. 23:226-245.

Hewitt, R. P., P. E. Smith, and J. C. Brown. 1976. Development and use of sonar mapping for pelagic fish stock assessment in the California Current area. Fish. Bull., U.S. 74:281-300.

Hunter, J. R., and B. J. Macewicz. 1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy Engraulis mordax, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139-149.

Huppert, D. D., A. D. MacCall, G. D. Stauffer, K. R. Parker, J. A. McMillan, and H. W. Frey. 1980. California's northern anchovy fishery: biological and economic basis for fishery management. NOAA Tech. Memo, NOAA-TM-NMFS-SWFC-1, 234 p.

Jessen, R. J. 1978. Statistical survey techniques. John Wiley and Sons, Inc., New York, 500 p.

Lasker, R., J. Peláez, and R. M. Laurs. 1981. The use of satellite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy, Engraulis mordax. Remote Sensing of Environment 11:439-453.

Mais, K. F. 1974. Pelagic fish surveys in the California Current. Cal. Fish. Game, Fish. Bull. 162, 79 p.

Methot, R. D. 1981. Growth rates and age distributions of larval and juvenile northern anchovy, Engraulis mordax, with inferences on

larval survival. Ph.D. dissertation, University of California, San Diego, 203 p.

Pacific Fishery Management Council (PFMC). 1978. Northern anchovy fishery management plan. Fed. Reg. 43(141)Book 2:31655-31879.

Parker, K. 1980. A direct method for estimating northern anchovy, Engraulis mordax, spawning biomass. Fish. Bull., U.S. 78:541-544.

Seber, G. A. F. 1973. The estimation of animal abundance and related parameters. Hafner Press, New York, 506 p.

Smith, P. E. 1970. The horizontal dimensions and abundance of fish schools in the upper mixed layer as measured by sonar. In G. B. Farquhar (ed.), Proc. Inter. Symp. on Biol. Sound Scattering in the Ocean, Maury Center for Ocean Science. Dept. Navy, Washington, D. C., p. 563-591.

———. 1972. The increase in spawning biomass of northern anchovy, Engraulis mordax. Fish. Bull., U.S. 70:849-874.

Stauffer, G. D. 1980. Estimate of the spawning biomass of the northern anchovy central subpopulation for the 1979-80 fishing season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:17-22.

———. 1983. Calibration of northern anchovy spawning biomass estimates derived by egg production larval census methods. Calif. Coop. Oceanic Fish. Invest. Rep. 24:(this volume).

Stauffer, G. D., and K. Parker. 1980. Estimate of the spawning biomass of the northern anchovy central subpopulation for the 1978-79 fishing season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:12-16.

Stauffer, G. D., and S. J. Picquelle. 1980. Estimates of the 1980 spawning biomass of the central subpopulation of northern anchovy. SWFC Admin. Rep. LF-80-09, 41 p.

———. 1981. Estimate of the spawning biomass of the northern anchovy central subpopulation for the 1980-81 fishing season. Calif. Coop. Oceanic Fish. Invest. Rep. 22:8-13.

Zweifel, J. R., and P. E. Smith. 1981. Estimates of abundance and mortality of larval anchovies (1951-75): application of a new method. Rapp. R.-v. Réun. Cons. int Explor. Mer 178:248-259.