# THE 1983 SPAWNING BIOMASS OF THE NORTHERN ANCHOVY 

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#### Abstract

The 1983 equivalent larval census estimate of the spawning biomass of the northern anchovy (Engraulis mordax) central subpopulation is $1,405,000$ MT. This estimate is based on data gathered by an egg production survey conducted from February 4 to April 1, 1983. 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 is the basis of the anchovy fishery optimum yield for 1983-84.

The egg production method estimate of anchovy spawning biomass is $652,000 \mathrm{MT}$. This is based on the summation of three regional estimates of daily egg production and population fecundity. The standard error of the total estimate is 137,000 MT, for a coefficient of variation of $21 \%$.

In 1983 the central subpopulation of northern anchovy was geographically distributed more offshore and poleward than in recent years. Spawning was extensive throughout the Southern California Bight (with the exception of the Santa Barbara Channel); spawning was evident along a narrower coastal band adjacent to the northern Baja California coast inside of Guadalupe Island; a small amount of spawning was detected adjacent to the coast north of Point Conception.


## RESUMEN

La estimación, por medio del censo larval correspondiente, de la biomasa de reproductores en la subpoblación de la anchoveta del norte, Engraulis mordax, que habita las aguas de la California Central es de $1.405,000 \mathrm{Tm}$ para 1983. Esta estimación se basa en los datos sobre producción de huevos obtenidos durante exploraciones realizadas desde el 4 de Febrero al $1^{\circ}$ de Abril de 1983. La abundancia de larvas es derivada de la producción diaria de huevos y la mortalidad consiguiente de huevos y larvas. Esta estimación equivalente del censo larval sirve de base para obtener la producción óptima de anchovetas para 1983-84.

Por el método basado en la producción de huevos se estima que la biomasa de la población reproductora es

[^0]de $652,000 \mathrm{Tm}$, para lo cual se considera la suma de tres estimaciones regionales de producción diaria de huevos y fecundidad de la población. El error estándar para la estimación total es de $137,000 \mathrm{Tm}$, para un coeficiente de variación del $21 \%$.

La distribución de la población central de E. mordax aparecía en 1983 más alejada de las aguas costeras y se extendía más al norte que en años anteriores. La puesta se extendía por todo la Bahía del Sur de California (excepto en el Canal de Santa Bárbara); además, se observó en una franja costera a lo largo de la zona norte de Baja California, mar adentro de la Isla Guadalupe, y algo de puesta aparecía en la zona costera al norte de Punta Concepción.

## INTRODUCTION

This report documents the 1983 spawning biomass estimate of the central subpopulation of northern anchovy (Engraulis mordax), as required by the Anchovy Management Plan, adopted by the Pacific Fishery Management Council (PFMC 1978). In recent years, anchovy biomass has been assessed using two ichthyoplankton-based methods: larval census (Smith 1972; Stauffer and Parker 1980; Stauffer 1980; Stauffer and Picquelle 1981); and egg production (Parker 1980; Stauffer and Picquelle 1980; Picquelle and Hewitt 1983). The larval census method assumes a constant of proportionality between larval abundance and spawning biomass, whereas the egg production method measures and incorporates variability in this proportionality parameter; these two methods produce estimates that consistently differ in magnitude.

This year, as well as last year, we estimated anchovy biomass using the egg production method because it is a more accurate and efficient estimator than the larval census method. However, the management plan's harvest quota is determined by an optimum yield formula based on larval census biomass estimates. The PFMC has interpreted the optimum yield formula to require a "larval census equivalent", spawning biomass estimate (Picquelle and Hewitt 1983).

This report describes the survey results, the egg production biomass estimate, 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 quarterly average standing stock of larvae summed over four quarters of the year, and assumes constant quarterly reproductive output (per ton of spawners) and constant survival of the young (Smith 1972). An equivalent larval census can be estimated by measuring larval mortality and projecting the number of larvae resulting from the measured egg production (Stauffer 1983; Picquelle and Hewitt 1983).

## DESCRIPTION OF SURVEY

The 1983 survey of the central subpopulation of the northern anchovy was conducted aboard the NOAA R/V Townsend Cromwell from February 4 through April 1, 1983. The survey ran from north to south, starting at San Simeon, California, (CalCOFI line 73.3) and ending at Bahia del Rosario, Baja California (CalCOFI line 110.0). The southern end of the survey was truncated because of the expiration of the Mexican sampling permit. Plankton samples were taken at 850 stations using a $25-\mathrm{cm}$ diameter net of 150 -micron mesh, retrieved vertically from a depth of 70 m ; of these plankton samples, 482 contained anchovy eggs (Figure 1). Midwater trawl samples were taken at 62 stations using a $15-\mathrm{m}^{2}$ trawl with a $2-\mathrm{mm}$ mesh liner;


Figure 1. Geographic distribution of anchovy eggs from CaIVET samples and surface isotherms.

51 trawls caught anchovies (Figure 2). For a detailed description of field operations see Cruise Report 8304TC, dated May 18, 1983, William Flerx, Southwest Fisheries Center, La Jolla, California.)

The distribution of anchovy eggs differed greatly from recent years: the range extended much farther offshore, and a smaller proportion of eggs was taken in Mexican waters. Also unlike previous years, there was a lack of correlation between the geographic pattern of eggs and the pattern of surface temperature isotherms (Figure 1) (Lasker et al. 1981; Picquelle and Hewitt 1983). One possible explanation is the occurrence of unusually warm water over the entire range of the survey.

The occurrence of positive trawls agreed well with the distribution of eggs (Figure 2). Unfortunately, there was a lack of trawl stations in the San Pedro Channel region, even though there was a high density of eggs in this area. Another shortcoming of the survey was the decision to sample only to CalCOFI line 110, the assumed southern extent of the central subpopulation. The two largest samples of eggs were taken from the southernmost line of the survey (Figure 1), suggesting that a local high density of anchovies occurred there and presumably extended farther south. It is impossible to estimate the amount of biomass residing south of the survey, or whether these fish


Figure 2. Geographic distribution of trawl stations and positive trawls within each region.
would be from the central subpopulation. With these two possible exceptions, the egg and trawl surveys appear to have provided good sample coverage of the central subpopulation of northern anchovy in 1983.

## EGG PRODUCTION BIOMASS ESTIMATE

## Biomass Model

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

$$
\begin{equation*}
B=P_{o} A \frac{k W}{R F S} \tag{1}
\end{equation*}
$$

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 is 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 $^{2}$ ),
$k=$ 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 variances and covariances of the parameters

$$
\begin{gather*}
\operatorname{Var}(B) \cong B^{2} \times \\
\left\{\frac{\operatorname{Var}\left(P_{o}\right)}{P_{o}{ }^{2}}+\frac{\operatorname{Var}(W)}{W^{2}}+\frac{\operatorname{Var}(R)}{R^{2}}+\frac{\operatorname{Var}(F)}{F^{2}}+\frac{\operatorname{Var}(S)}{S^{2}}+\right. \\
2\left[\frac{\operatorname{Cov}\left(P_{o} W\right)}{P_{o} W}-\frac{\operatorname{Cov}\left(P_{o} R\right)}{P_{o} R}-\frac{\operatorname{Cov}\left(P_{o} F\right)}{P_{o} F}-\frac{\operatorname{Cov}\left(P_{o} S\right)}{P_{o} S}-\frac{\operatorname{Cov}(W R)}{W R}-\right.  \tag{2}\\
\left.\left.\quad \frac{\operatorname{Cov}(W F)}{W F}-\frac{\operatorname{Cov}(W S)}{W S}+\frac{\operatorname{Cov}(R F)}{R F}+\frac{\operatorname{Cov}(R S)}{R S}+\frac{\operatorname{Cov}(F S)}{F S}\right]\right\} .
\end{gather*}
$$

The quantity $P_{o} A$ is the daily production of eggs in the sea. Estimating this parameter requires the assumption that the rate of instantaneous egg mortality is constant over the range and duration of the survey; mortality was not measured with sufficient precision to test this hypothesis. The quantity $\operatorname{RFS} /(\mathrm{kW})$ is the daily fecundity (per ton of spawners) of the population; the model assumes that this parameter is also constant over the range and duration of the survey. It was possible to test this hypothesis, and for this survey it was rejected. The value of average female weight


Figure 3. Subdivision of CaIVET survey into strata (0-beyond the range of anchovy spawning, 1 -within the range of anchovy spawning) and regions (north, bight, and south).
decreased from north to south while spawning fraction increased.

The survey area was divided into three regions (Figure 2 ), within which each parameter was relatively constant. The north region was the area north of the boundary line drawn halfway between CalCOFI lines 82.5 and 83.3; it contained 150 egg samples and 10 positive trawl samples. The northern boundary for the south region corresponded roughly to the U.S.Mexican border and was drawn halfway between CalCOFI lines 95.0 and 95.8 ; this region contained 263 egg samples and 11 positive trawl samples. The bight region, everything between the north and south regions, contained 437 egg samples and 30 positive trawl samples (Figures 2 and 3). We estimated the spawning biomass separately for each region. The total estimated spawning biomass is the sum of the three regional biomasses, and the total variance is the sum of the three regional variances.

## Daily Production of Eggs in the Sea

The parameter $P_{o} A$, the daily production of eggs in the sea, is the total area multiplied by the number of eggs spawned per night, per unit area, averaged over the range and duration of the survey, or in this case, region. The plankton samples provide counts of eggs
of each age for each station (Figure 1). We estimated egg production by fitting an exponential mortality function to the egg data and then extrapolating back to the number of eggs at the time of spawning.

We analyzed the egg counts using a two-stage systematic sampling scheme (see Picquelle and Hewitt 1983, for a complete description of the sample design). First, we gave each station a weight proportional to the area the station represents. Second, we stratified the stations by location to decrease the variance. Many of the stations were beyond the spawning range of the anchovy and contributed a large number of zero counts to the egg data set, thus inflating the variance. This effect was minimized by defining a stratum to contain those stations that were determined after the survey to be located beyond the geographic area of spawning; this was called stratum 0 . Stratum 1 was the geographic area that included all stations where anchovy eggs were found. These two strata were created for each region (Figure 3); the area ( $\mathrm{nm}^{2}$ ) and number of samples ( $n$ ) for each stratum within each region were:

|  |  | Region |  |  |  |
| :---: | :---: | ---: | :---: | ---: | :---: |
| Stratum |  | North | Bight | South | Total |
| 1 | area | 3,480 | 14,800 | 9,340 | 27,620 |
|  | $n$ | 86 | 351 | 126 | 563 |
| 0 | area | 2,640 | 4,600 | 10,420 | 17,660 |
|  | $n$ | 64 | 86 | 137 | 287 |
| Total | area | 6,120 | 19,400 | 19,760 | 45,280 |
|  | $n$ | 150 | 437 | 263 | 850 |

The mortality function is fit to the egg data by regressing egg counts on age. The eggs for each sample are assigned an age that is determined by the developmental stage, water temperature, and the time the sample was collected. It is assumed that all eggs are spawned and fertilized each night at time 2200 (Stauffer and Picquelle 1980). Water temperatures range from $14^{\circ}$ to $17^{\circ} \mathrm{C}$; at these temperatures hatching begins at the age of 2.5 days, hence only eggs up to 2.5 days old are used in the regression. The data are then tabulated by age for each station, with each station contributing up to three observations (one count for each age). The exponential mortality model

$$
\begin{equation*}
P_{i j k}=P_{o i} e^{-z_{i j k}}+\varepsilon_{i j k} \tag{3}
\end{equation*}
$$

was then fit to the data by a weighted nonlinear least squares regression (Dixon and Brown 1979),
where $P_{i j k}$ is the number of eggs in the $k$ th day age category from the $j$ th station in the $i$ th stratum, $t_{i j k}$ is the age in days measured as the elapsed time from the time of spawn for the $k$ th day category eggs to the time of sampling of the $j$ th station in the $i$ th stratum,
$P_{o i}$ is the daily production of eggs per unit area $\left(0.05 \mathrm{~m}^{2}\right)$ in stratum $i$,
$Z$ is the daily rate of instantaneous egg mortality, and
$\epsilon_{i j k}$ is the additive error term.

Egg mortality, $Z$, is difficult to estimate precisely, so we pooled the data from stratum 1 for all regions to produce a single estimate of $Z$. This value was 0.1836 / day with standard error $0.1302 /$ day. Next, we fit the model to the data from stratum 1 for each region separately, where $Z$ was fixed at $0.1836 /$ day. This produced an estimate of $P_{o 1}$ for each region (Figure 4). The stratified estimate of $P_{o}$ for each region was calculated as the weighted average of $P_{o 1}$ and $P_{o o}$, where $P_{o o}$ is zero by definition, and the weights are the relative areas of the two strata. Thus

$$
\begin{equation*}
P_{o}=\frac{A_{1}}{A} P_{o 1}+\frac{A_{o}}{A} P_{o o} \tag{4}
\end{equation*}
$$

and the variance, adjusted for postsurvey stratification (Jessen 1978), is
$\operatorname{Var}\left(P_{o}\right)=\left(1+\frac{1}{h}\right)\left[\left(\frac{A_{1}}{A}\right)^{2} \operatorname{Var}\left(P_{o l}\right)+\left(\frac{A_{o}}{A}\right)^{2} \operatorname{Var}\left(P_{o o}\right)\right]$
where $A_{i}$ is the area of stratum $i$ for each region,
$n$ is the total number of observations by region,
$\operatorname{Var}\left(P_{o 1}\right)$ is estimated for each region from the regression (3), and
$\operatorname{Var}\left(P_{o o}\right)=0$ by definition.
The estimates for $P_{o 1}$ and $P_{o}$, their standard errors, and total production $A_{i} P_{o}$ for the three regions were:

|  | North | Bight | South |
| :--- | :--- | :--- | ---: |
| $P_{o 1}$ (eggs $\left./ 0.05 \mathrm{~m}^{2}\right)$ | 2.85 | 9.54 | 10.71 |
| Standard error | 1.44 | 0.625 | 2.43 |
| $P_{o}$ (eggs $\left./ 0.05 \mathrm{~m}^{2}\right)$ | 1.62 | 7.28 | 5.06 |
| Standard error | 1.09 | 0.547 | 1.68 |
| $A_{i} P_{o}\left(\times 10^{12} \mathrm{eggs}\right)$ | 0.682 | 9.70 | 6.87 |

The egg densities, $P_{o 1}$, of the bight and south regions were similar, but the eggs were much less dense in the north region. The variance of egg densities was very small in the bight region; the large variance for the north region was partially due to the small number of positive egg samples; the large variance for the south region was due to a few samples with extremely large egg counts.


Figure 4. Exponential mortality model for estimating $P_{\mathrm{o}_{1}}$, daily egg production for stratum 1, plotted with egg abundances for each region.

## Adult Parameters W,F,S, and R

The parameters $W, F, S$, and $R$ were estimated from samples of adult anchovies collected by the midwater trawl survey (Figure 2). The sample design consisted of three stages: (1) selection of trawl stations, (2) sample of fish at the station using the midwater trawl, and (3) subsample of fish from the trawl catch. (See Picquelle and Hewitt 1983, for a complete description of the sample design.)

We estimated each parameter for each region by a weighted sample mean ( $\overline{\bar{y}}$ ) and with a weighted variance (Cochran 1963):

$$
\begin{align*}
\overline{\bar{y}} & =\sum_{i=1}^{n}\left(\frac{m_{i}}{m n}\right) \bar{y}_{i}  \tag{6}\\
\operatorname{Var}(\overline{\bar{y}}) & =\frac{\sum_{i=1}^{n}\left[\left(\frac{m_{i}}{m}\right)^{2}\left(\overline{y_{i}}-\overline{\bar{y}}\right)^{2}\right]}{n(n-1)} \tag{7}
\end{align*}
$$

where $m_{i}$ is the number of fish subsampled from the $i$ th trawl,
$\bar{m}$ is the average number of fish subsampled per trawl,
$n$ is the number of positive trawls,
$y_{i j}$ is the observed value for the $j$ th fish in the $i$ th trawl, and
$\bar{y}_{i}=\sum_{\mathrm{j}=1}^{m_{i}} y_{i j} / m_{i}$ is the average for the $i$ th trawl.

## Average Female Weight

The average female weight, $W$, was calculated for each region using equations (6) and (7), where $\bar{y}_{i}$ was the average female weight for the $i$ th trawl within the region. The desired subsample size was $m_{i}=25$ mature females from each trawl; however, this was not always attainable for small trawl catches or for catches composed mostly of immature fish.

The weight of females with hydrated eggs in their ovaries is inflated because of water retention in their ovaries. To correct for this, we adjusted their weight using the regression of whole body weight on ovaryfree weight. We estimated this regression using mature females without hydrated eggs from the entire survey,

$$
\begin{equation*}
\hat{W}_{i j}=0.0972+1.05 W_{i j}{ }^{*} \tag{8}
\end{equation*}
$$

where $\hat{W}_{i j}$ is the estimated whole body weight in grams, and
$W_{i j}{ }^{*}$ is the ovary-free weight in grams;
the regression had an $r^{2}=0.998$.


Figure 5. Frequency distribution for average whole-body weight (in grams) of mature females for each region.

The estimated average female weights and standard deviations for each region were:

|  | North | Bight | South |
| :--- | :---: | :---: | :---: |
|  | (grams) | 12.9 | 11.2 |
| Standard error | 1.56 | 0.790 | 0.371 |
| $n$ | 10 | 30 | 11 |

The frequency distributions of average weight per trawl were quite different among regions (Figure 5). The weights for the north region had the same range as the weights for the bight region, but there was no clear mode, and a high standard error. The distribution of the weights for the bight region was symmetrical, with both mean and mode at 11 grams. The distribution of fish in the south region was truncated, with no average weights greater than 12 grams; the average southern weight was significantly smaller than both the bight and northern average weights (one-tailed test, $p=$ 0.10 ).

## Batch Fecundity

Fecundity for each mature female was estimated by the regression of fecundity on ovary-free weight esti-
mated from a sample of 83 females with hydrated eggs that were collected over the duration of the survey. This sample was selected so that its weight distribution was similar to the weight distribution of females for the whole cruise (Figure 6). The fitted linear regression is

$$
\begin{equation*}
\hat{F}_{i j}=-942+582 W_{i j}^{*} \tag{9}
\end{equation*}
$$

where $\hat{F}_{\mathrm{ij}}$ is the estimated fecundity for a female with
$W_{i j}{ }^{*}$ ovary-free weight; $r^{2}=0.83$ (Figure 7).
Batch fecundity is then estimated for each region using equation (6) where the $y_{i j}=\hat{F}_{i j}$ are estimated using equation (9). Again, the desired $m_{i}$ was 25 mature females. The variance estimate (equation [7]) is modified to include the extra source of variance resulting from trawl averages being estimated rather than observed directly (Draper and Smith 1966):
$\operatorname{Var}(\overline{\bar{F}})=\frac{\sum_{i=1}^{n}\left\{\left(\frac{m_{i}}{m}\right)^{2}\left[\frac{\left(\overrightarrow{F_{i}}-\overline{\bar{F}}\right)^{2}}{n-1}+\frac{S_{h}{ }^{2}}{83}+\left(\vec{W}_{i}{ }^{*}-W_{h}{ }^{*}\right)^{2} \operatorname{Var}(b)\right]\right\}}{n}$


Figure 6. Frequency distribution for whole-body weight (in grams) of mature females. The top histogram is for all mature females; the bottom histogram is for those females used to estimate the fecundity regression


Figure 7. The linear regression of batch fecundity on ovary-free weight fit to 83 females with hydrated eggs.
where $S_{h}{ }^{2}=867,000$ is the variance about the regression (9),
$\bar{W}_{i}{ }^{*}$ is the average ovary-free weight for the $i$ th trawl,
$\bar{W}_{h}{ }^{*}=11.6$ grams is the average ovary-free weight for the 83 hydrated females used in regression (9),
$\operatorname{Var}(b)=1040$ is the variance of the slope of regression (9), and
$n$ is the number of positive trawls.
The resulting means and standard errors for fecundity for each region were:

|  | North | Bight | South |
| :--- | ---: | ---: | ---: |
|  |  |  |  |
| $\bar{F}$ (eggs per | 6285 | 5295 | 4423 |
| $\quad$ batch) | 879 | 467 | 252 |
| Standard error | 10 | 30 | 11 |
| $n$ |  |  |  |

Fecundity follows the same pattern over regions as weight because it was positively correlated with weight.

Specific fecundity, expressed as eggs per gram of whole body weight, was calculated for the entire survey without regionalization to allow for easy comparison to previous years (these values were not used to estimate biomass):

| Year | 1980 | 1981 | 1981 | 1982 | 1983 |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Survey | $8003 / 4$ | 8102 | 8104 | 8202 | 8302 |
| Mean weight (g) | 17.4 | 13.4 | 16.2 | 18.8 | 11.2 |
| Eggs/gram | 444 | 623 | 546 | 576 | 473 |

## Spawning Fraction

To estimate spawning fraction, $S$, for each region, we again used equation (6), where $\bar{y}_{i}=S_{i}$ was the proportion of mature females in the $i$ th trawl that spawned one night prior to capture (day-1 spawners). (See Hunter and Macewicz 1980, for histological definition of day- 1 and day- 0 spawners.) The desired $m_{i}$ was again 25 mature females.
The proportion of day- 0 spawners (females that spawn on the night of capture) can also be used to estimate spawning fraction. However, it was suspected that these females are overrepresented in the trawl catches, thus biasing the proportion of day-1 spawners. Hence, the value of $m_{i}$ in equations (6) and (7) is adjusted by deleting day-0 spawners from the sample and equating the number of day- 0 spawners to the number of day- 1 spawners, thus reducing the average subsample size, $\bar{m}$.
The adjusted estimates of spawning fraction for each region are:

|  | North | Bight | South |
| :---: | :---: | :---: | :---: |
|  | 0.0346 | 0.103 | 0.126 |
| $\overline{\bar{S}}$ | 0.0178 | 0.0299 |  |
| Standard error | 0.0195 | 0.0178 | 11 |
| $n$ | 10 | 30 |  |

Spawning fraction varied greatly among regions (Figure 8), violating the assumption of the egg production model that all parameters were constant. This observation necessitated regionalizing the survey so that the parameters within each region were constant. Spawning fraction to the north region was significantly smaller than that for the bight and south regions (two-tailed test, $p=<0.10$ ). The estimated mean spawning fractions for the bight and south regions were similar, although their observed distributions were quite different (Figure 8).

## Sex Ratio

The parameter sex ratio, $R$, was measured as the fraction of females in the population based on fish weight. We again used equations (6) and (7) by setting $\bar{y}_{i}=\bar{R}_{i}$ where $\bar{R}_{i}$ is the estimated total weight of females in the first 50 fish subsampled divided by the estimated total weight of the 50 fish; and $m_{i}$ is the estimated total weight of the first 50 fish (Picquelle and Hewitt 1983). The average weights for each sex for each trawl were estimated from 5 males and from 25 females; again the weight of any females with hydrated eggs was adjusted using equation (8).

The estimated sex ratios for the three regions were similar (Figure 9).

|  | North | Bight | South |
| :---: | :---: | :---: | :---: |
| $\overline{\bar{R}}$ | 0.523 | 0.559 | 0.549 |
| Standard error | 0.0496 | 0.0411 | 0.0703 |
| $n$ | 10 | 30 | 11 |

## Biomass Estimate and Variance

The parameter estimates and their coefficients of variation are summarized by region in Table 1. The biomass estimates for each region were calculated using equation (1), and approximate variances were calculated using equation (2). The sample covariance terms in equation (2) were calculated only for adult parameters; $P_{o}$ was derived from a separate survey than that for the adult parameters (the plankton survey


Figure 8. Frequency distributions of spawning fractions for each region.
vs the trawl survey), hence the sample covariances between $P_{o}$ and the adult parameters were assumed to be zero.

The sample correlations among the adult parameters that were significantly different from zero are (by region):

North $-\operatorname{corr}(W F)=0.978, \operatorname{corr}(W S)=0.735$, corr $(F S)=0.714$
Bight $-\operatorname{corr}(W F)=0.930, \operatorname{corr}(W R)=0.473$, corr
$(F R)=0.439$
South $-\operatorname{corr}(W F)=0.824$
The correlation between weight and fecundity was high for each region because fecundity was estimated by a linear regression on weight. Weight and spawning fraction were highly correlated for the north region, implying that the larger females spawned more


Figure 9. Frequency distributions of sex ratio for each region.

TABLE 1
Estimates of Egg Production Parameters and Spawning Biomass by Region for 1983

| Parameters |  | North | Bight | South | Total |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Egg production | $P_{o}$ |  |  |  |  |
| (eggs/0.05m ${ }^{2}$-day) |  | (0.671) | (0.0751) | (0.332) |  |
| Area of survey (* $10^{12} 0.05 \mathrm{~m}^{2}$ ) | A | 0.420 | 1.33 | 1.36 |  |
| Average female weight (grams) | W | $\begin{aligned} & 12.9 \\ & (0.121) \end{aligned}$ | $\begin{aligned} & 11.2 \\ & (0.0705) \end{aligned}$ | $\begin{aligned} & 9.63 \\ & (0.0385) \end{aligned}$ |  |
| Batch fecundity (eggs per batch per mature female) | $F$ | $\begin{aligned} & 6285 \\ & (0.140) \end{aligned}$ | $\begin{aligned} & 5295 \\ & (0.0882) \end{aligned}$ | $\begin{aligned} & 4423 \\ & (0.0570) \end{aligned}$ |  |
| Spawning fraction (spawning females/ total females) | $S$ | $\begin{aligned} & 0.0346 \\ & (0.563) \end{aligned}$ | $\begin{aligned} & 0.103 \\ & (0.174) \end{aligned}$ | $\begin{aligned} & 0.126 \\ & (0.237) \end{aligned}$ |  |
| Sex ratio (females/total) | $R$ | $\begin{aligned} & 0.523 \\ & (0.0949) \end{aligned}$ | $\begin{aligned} & 0.559 \\ & (0.0736) \end{aligned}$ | $\begin{aligned} & 0.549 \\ & (0.128) \end{aligned}$ |  |
| Spawning biomass (metric tons) | $B$ | $\begin{aligned} & 77,500 \\ & (0.897) \end{aligned}$ | $\begin{aligned} & 358,000 \\ & (0.214) \end{aligned}$ | $\begin{aligned} & 216,000 \\ & (0.419) \end{aligned}$ | $\begin{aligned} & 652,000 \\ & (0.211) \\ & \hline \end{aligned}$ |

Coefficient of variation indicated by ().
frequently or that the smaller females had a much shorter spawning season. The partial correlation of fecundity and spawning fraction would be negligible if adjusted for weight.
The total biomass is estimated by the sum of the regional biomasses. The variance of the total biomass is the sum of the regional variances. These are:

|  | North | Bight | South | Total |
| :--- | ---: | ---: | ---: | ---: |
|  |  |  |  |  |
| (MT) | 77,500 | 358,000 | 216,000 | 652,000 |
| Standard error | 69,500 | 76,800 | 90,500 | 137,000 |
| Coefficient of variation | 0.897 | 0.214 | 0.419 | 0.211 |

The 1983 biomass estimate increased substantially from 1982 and is approximately midway between the 1980 biomass and the first 1981 biomass estimate (Stauffer and Picquelle 1980; Picquelle and Hewitt 1983). In 1983 the mesh size of the plankton net used to sample eggs was reduced from 0.333 mm to 0.150 mm . Experimentation has shown that the previously used larger mesh net retains $91 \%$ of the eggs caught by the smaller mesh net (Lo 1983). The previous spawning biomass estimate should be corrected for net retention, giving the second series of biomasses in the table below:

| Year | 1980 | 1981 | 1981 | 1982 | 1983 |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Cruise | $8003 / 4$ | 8102 | 8104 | 8202 | 8302 |
| Reported $B$ (MT) | 792,000 | 577,000 | 339,000 | 378,000 | 652,000 |
| Coefficient of <br> variation | 0.262 | 0.216 | 0.187 | 0.057 | 0.211 |
| Retention-cor- <br> $\quad$ rected $B$ (MT) | 870,000 | 635,000 | 372,000 | 415,000 | 652,000 |

The increase in biomass was probably due to a very large 1982 year class. This conclusion is supported by
a shift in the weight distribution towards much smaller fish. In 1982 the modal mature female weight was 19 grams; in 1983 it was 11 grams. The 1982 year class constituted the major portion ( $75 \%$ ) of a trawl survey conducted by the California Department of Fish and Game in February, 1983 (K. Mais, Cruise Report 83-X-1, dated March 21, 1983, Calif. Dept. of Fish and Game, Long Beach CA).

## EQUIVALENT LARVAL CENSUS ESTIMATE BIOMASS

The best estimate of the 1983 anchovy spawning biomass is the quotient of the production of eggs and the adult fecundity by weight as described above. However, the Anchovy Management Plan requires that the biomass estimate be based on the larval census method, which assumes that spawning biomass is simply proportional to the annual census of larvae.
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 by the adults and constant survival of the young. The proportionality constant was defined from a regression of sardine biomass on sardine larvae and extended to the anchovy by assuming a constant relative fecundity between the two species (Smith 1972).

During the 1983 biomass survey, 850 vertical tows for eggs (CalVET) and 78 oblique tows for larvae (CalBOBL) were conducted during the anchovy spawning season. These samples are adequate to determine the daily production of eggs and larvae during the sampling period, but not adequate to measure the annual census of larvae. Instead, the annual census of larvae may be estimated by integrating the larval production curve and extrapolating the resulting estimate of standing stock to an annual census using historical proportions of quarterly abundances.

In order to correctly use Smith's (1972) proportionality constant, the estimate of standing stock of larvae must be reduced to that portion which would have been retained by a standard plankton net. Thus:
$\hat{B}_{1}=N(2.12)(r)(k)$ (Picquelle and Hewitt 1983)
where $\hat{B}_{1}$ is the equivalent larval census estimate of spawning biomass (MT),
$N$ is the average standing stock of larvae during the spawning season estimated as the integral of the larval production curve over the age period which is vulnerable to capture (larvae), 2.12 is the average factor by which the annual census has exceeded the standing stock of lar-
vae during the spawning season, (Picquelle and Hewitt 1983)
$r$ is the retention of larvae in the net (Picquelle and Hewitt 1983), estimated as the ratio of the raw catch and the catch adjusted for extrusion and avoidance (size-specific retention from Lo 1983, weighted by abundance at size), $r=$ 0.30 ,
$k$ is Smith's (1972) proportionality constant $=$ $8.9 \times 10^{-8}$ (MT/larva).

The distributions of anchovy eggs and larvae describe the same general geographic pattern (Figure 10): extensive spawning throughout the Southern California Bight with the exception of the Santa Barbara Channel, spawning along a narrower coastal band adjacent to the northern Baja California coast inside of Guadalupe Island, and measurable but reduced spawning adjacent to the coast north of Point Conception. Larvae were distributed more extensively over the survey area than were eggs. Both eggs and larvae were distributed farther offshore in 1983 than in 1982.

We used the CalVET sample to estimate the egg production curve, as described earlier and shown in Figures 4 and 11. We used the CalBOBL sample to estimate the larval production curve (Figure 11). The larvae were grouped into twelve size categories (yolk-


Figure 11. Production rate of anchovy eggs and larvae as a function of age since fertilization. The egg production curve was fit to the CaIVET samples (Figure 4); the larval production curve was fit to the CaIBOBL samples.
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


Figure 10. The distributions of anchovy eggs from CaIVET samples and anchovy larvae from CalBOBL samples. The distributions of eggs and larvae describe the same general geographic pattern, with the larvae distributed more extensively over the survey area.
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 procedure was developed in a series of papers: Bissel 1972; Zweifel and Smith 1981; Hewitt 1981, 1982; Hewitt and Methot 1982; Hewitt and Brewer 1983; Picquelle and Hewitt 1983.

Estimates of larval production $\left(P_{t}\right)$ decline at a decreasing rate with age ( $t$ ) (Figure 11). An unweighted nonlinear least squares method was used to fit the following two-parameter function to the data:

$$
\begin{equation*}
P_{t}=P_{h}\left(\frac{t}{t_{h}}\right)^{-\beta} \text { for } t>t_{h} \tag{12}
\end{equation*}
$$

where $t_{h}$ is the age (since fertilization) at hatch, and $P_{h}$ is the production of hatching larvae. (This form results from expressing the mortality rate as continually decreasing with age: $d P / P d t=-^{\boldsymbol{\beta}} / t ;$ Lo, in press.) The average standing stock of larvae $(N)$ is the integral of the production curve from the age at hatch to 30 days, multiplied by the area of the survey:

$$
\begin{equation*}
N=\frac{A P_{h} t_{h}}{\beta-1}\left(1-\left(\frac{t_{h}}{30}\right)^{\beta-1}\right) \tag{13}
\end{equation*}
$$

where $A=$ the area of the survey.
Because the egg production curve is derived from more observations than the larval production curve, the former may be expected to yield a more precise estimate of production at age of hatch. For this reason we used the CalBOBL data to determine the shape of the larval production curve and the CalVET data to scale the curve. To do this, we substituted $P_{o} s$ for $P_{h}$ in the above expression for $N$, where $P_{o}$ is the initial production of eggs and $s$ is the fraction surviving to hatch. ${ }^{2}$ As it turned out, the two production curves lined up reasonably well (Figure 11) with $P_{h}=81 / \mathrm{m}^{2}$ and $P_{o} s=69 / \mathrm{m}^{2}$ (see also Table 2). In constraining the larval production curve to be consistent with the egg production curve, we improve the precision of the estimate of the larval standing stock (time integral of the larval production curve).

[^1]TABLE 2
Parameters Used to Estimate Larval Census Equivalent Spawning Biomass

| Parameters |  | Estimates |
| :--- | :---: | :--- |
| Area of survey | $A$ | $155.5^{*} 10^{9} \mathrm{~m}^{2}$ |
| Initial production of eggs | $P_{o}$ | $110.95 \mathrm{eggs} / \mathrm{m}^{2}$ |
| Egg mortality rate | $Z$ | 0.18356 |
| Time to hatch | $t_{h}$ | 2.56 days |
| Survival to hatch | $s=e^{-Z_{l} h}$ | 0.6251 |
| Production of eggs |  |  |
| $\quad$ surviving to hatch | $P_{o} s$ | $69.35 \mathrm{eggs} / \mathrm{m}^{2}$-day |
| Retention factor | $r$ | 0.30 |
| Larval mortality coefficient | $\beta$ | 2.0229 |
| Production of hatching larvae | $P_{h}$ | $80.49 \mathrm{larvae} / \mathrm{m}^{2}$-day |
| Standing stock of larvae | $N$ | $24,813^{*} 10^{9}$ larvae |
| Equivalent larval census |  | $15,800^{*} 10^{9}$ larvae |
| Estimate of spawning biomass | $B_{l}$ | $1.405^{*} 10^{6} \mathrm{mt}$ |

Parameter values are listed in Table 2. The 1983 equivalent larval census estimate of anchovy spawning biomass is $1.405 \times 10^{6} \mathrm{MT}$; the equivalent annual larval census is $15,800 \times 10^{9}$ larvae. The observations were not stratified; rather, all were treated in an equal manner regardless of their geographic position. The retention factor, $r$, was lower in 1983 because larval population was composed of a relatively large number of small larvae, which are more easily extruded through the net meshes.

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[^1]:    ${ }^{2}$ The fraction surviving to hatch, $s$, is estimated by applying the egg mortality rate over the incubation period. The incubation period (time to hatch in Table 2) is calculated using Lo's (1983) expression and the mean temperature at 10 m depth weighted by egg abundance $\left(15.9^{\circ} \mathrm{C}\right)$.

