

EGG PRODUCTION OF THE CENTRAL STOCK OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, 1951-82

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ABSTRACT

A model was developed for estimating daily production of eggs of northern anchovy from counts of the total numbers of eggs and size-frequency distribution of larvae. Estimates of egg production using this model were compared with three estimates based on the mortality rates of staged (aged) eggs. The model was used to calculate daily egg production of anchovy for a 24-year time series (1951-82) (data were collected each year from 1951 to 1966 and 1979 to present and every 3 years from 1966 to 1979). Comparisons of this index of stock abundance with ones based on the standing stock of larvae indicate that the present model is a better index of spawning biomass. It was found from the 1979-81 data that the eggs and larvae (< 20 days) have different forms of instantaneous mortality rate (IMR): The larval IMR was age dependent, i.e., $z(t) = \beta/t$ for $t_c < t$ whereas the egg IMR was constant $z(t) = \alpha$ for $t < t_c$ where t_c is incubation time or yolk-sac absorption. Based upon this model, the daily-egg production, and egg-larval mortality rates for larvae < 20 days (< 8 mm preserved length), were estimated for 1951-82 from data collected with 1 m ring nets and bongo nets. Egg production varies with stock size proportionally if the reproduction effort remains constant. The egg production is a better index of stock size than the larval abundance because the latter is subject to the inherent egg and larval mortality in addition to reproductive output.

Ichthyoplankton data have been used extensively for estimating biomass (or spawning biomass) of marine fish stocks (Murphy 1966; Ahlstrom 1968; Smith 1972). One of the tacit assumptions underlying most of the methods used for estimating biomass from ichthyoplankton data is that egg or larval mortality is constant among years. In recent years, however, it has become increasingly evident that egg and larval mortality is quite variable among years and among life stages (Ahlstrom 1954; Marr 1956; Colton 1959; Burd and Parnell 1972; Cushing 1973; Fager 1973; Harding and Talbot 1973). As a result, biomass indices based on standing stock of eggs or larvae are subject to a considerable bias if the interannual variability in mortality is not taken into account. In order to eliminate the bias, attempts were made to estimate the spawning biomass by using the egg production and reproduction parameters (Saville 1964; Beverton and Holt 1965; Ciechowski and Capezzani 1973). The basic model is

$$P_0 = B_\alpha R (E/W) \quad (1)$$

where P_0 = egg production at age zero,
 B_α = spawning biomass,

R = proportion of spawning biomass being female,
 E = average batch fecundity,
 W = average mature female weight.

Equation (1) is adequate for species that spawn only once during a season. But for the multiple spawners, like northern anchovy, *Engraulis mordax*, one needs to include another adult parameter, the proportion of mature spawning female (F), in the equation (Parker 1980). Moreover, Parker chose to use egg production per day, as this could be easily estimated from a single cruise. Thus, the egg production model (EPM) for northern anchovy (or any multiple spawning stock) becomes

$$P_0 = B_\alpha R \cdot F (E/W). \quad (2)$$

Staged eggs are used to estimate the daily egg production (number of eggs per day) of the population (P_0) while adult fish are sampled to estimate the number of eggs produced per fish weight (E/W), sex ratio (R), and proportion of mature spawning female (F). This method is, without doubt, the best of all ichthyoplankton biomass estimation techniques. It is, however, a data rich method requiring both ichthyoplankton and adult sampling plus staging of eggs and various laboratory measurements which may not be available. In this report, I present an alternative method for

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estimating biomass using conventional ichthyoplankton data rather than the extensive sets of specialized information required by the EPM method. This alternative method provides estimates of the daily egg production (P_0) and is referred to as the historical egg production (HEP) to distinguish it from the current EPM. This model for HEP requires only the standing stock of unstaged eggs, and the numbers of larvae in various length classes subsequently transformed into age classes using Gompertz growth curve (Zweifel and Hunter²; Methot and Hewitt³; Lo 1983). Daily egg production varies proportionally with the stock size if the reproduction effort of the population remains constant. The production of eggs by a stock is certainly a better index of stock size than the standing stock of larvae (Smith 1972) because both egg and larval mortality rates are considered in the former case.

In addition to development of the model, I provide a time series of northern anchovy HEP for 1951-82. This historical record of daily egg production rather than the EPM (Equation (2)) was used to estimate anchovy biomass for these past years because data were not available for all the female reproductive parameters until 1980 and none of the eggs have been staged. It would be impractical and take years to do all the staging of eggs that would be required for all the years. The HEP is an unbiased index for the spawning biomass (B_a) of the anchovy population for those years if the annual reproductive output per fish weight has remained constant. I do not have sufficient data to validate the assumption of constant reproductive output although 1981-82 data do indicate so.

ASSEMBLY AND BIAS CORRECTION OF EGG AND LARVAL DATA

The northern anchovy spawning area lies off central and southern California and Baja California. The sampling area was divided into 23 regions covering 17.556×10^{11} m² (Fig. 1). The central anchovy stock is enclosed by eight regions (4, 5, 7, 8, 9, 11, 13, and 14) with a total of 5.703×10^{11} m² (Duke 1976⁴; Huppert et al. 1980). Because the

peak spawning season of northern anchovy was usually February-April, daily egg production for the central stock northern anchovy was computed from egg and larval data (CalCOFI⁵) collected in January-April within these eight regions. The CalCOFI survey was conducted each year until 1966 after which the survey was conducted every 3 yr. Owing to various improvements in the design of the plankton nets over the past 20 yr (Smith and Richardson 1977; Stauffer and Picquelle 1980⁶), different calibration factors were necessary to standardize the catch of eggs and larvae taken in different nets: A 1 m ring net with 0.55 mm silk mesh was used until 1969 when it was replaced by a 1 m ring net with 0.505 mm nylon mesh; this net was used until 1978 when it was replaced by the bongo net of 0.505 mm nylon mesh. Beginning in 1979, a vertical tow of the 0.333 mm mesh, 25.23 cm diameter CalVET net (CalCOFI vertical egg net) (Hewitt 1983) was used along with the 0.505 mm mesh bongo net to collect egg and larval samples in order to estimate the northern anchovy spawning biomass using the egg production method (EPM) (Parker 1980). In addition to the bias in catch caused by the different mesh sizes, biases also existed due to avoidance of the net, water volume filtered through the net (measured by water flowmeter readings), growth rate of larvae, temperature dependent incubation time (in days), and proportion of larvae from each plankton sample sorted (Zweifel and Smith 1981; Lo 1983). All data (counts of eggs and larvae) were adjusted for the above biases, when it was appropriate, following the procedures outlined by Zweifel and Smith (1981).

Egg Data

The counts of unstaged eggs from each tow were adjusted to a standardized volume of water filtered per unit depth ($0.05 \text{ m}^3/1 \text{ m depth} = 0.05 \text{ m}^2$ sea surface area = area sampled by the CalVET net). The adjusted egg counts per 0.05 m^2 sea surface area were then stratified by CalCOFI regions. A weighted mean egg count per 0.05 m^2 was computed as

²Zweifel, J. R., and J. R. Hunter. Unpubl. manuscript. Temperature specific equations for growth and development of anchovy, *Engraulis mordax*, during embryonic and larval stages.

³Methot, R. D., and R. P. Hewitt. 1980. A generalized growth curve for young anchovy larvae: derivation and tabular example. Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. LJ-80-17, 8 p.

⁴Duke, S. 1976. CalCOFI station and region specifications. Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. LJ-76-3, 37 p.

⁵CalCOFI. California Cooperative Ocean Fisheries Investigation, a program sponsored by the State of California. The cooperating agencies in the program are California Department of Fish and Game, National Marine Fisheries Service, and Scripps Institution of Oceanography, University of California.

⁶Stauffer, G. D., and S. J. Picquelle. 1980. Estimates of the 1980 spawning biomass of central subpopulation of northern anchovy. Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. LJ-80-09.

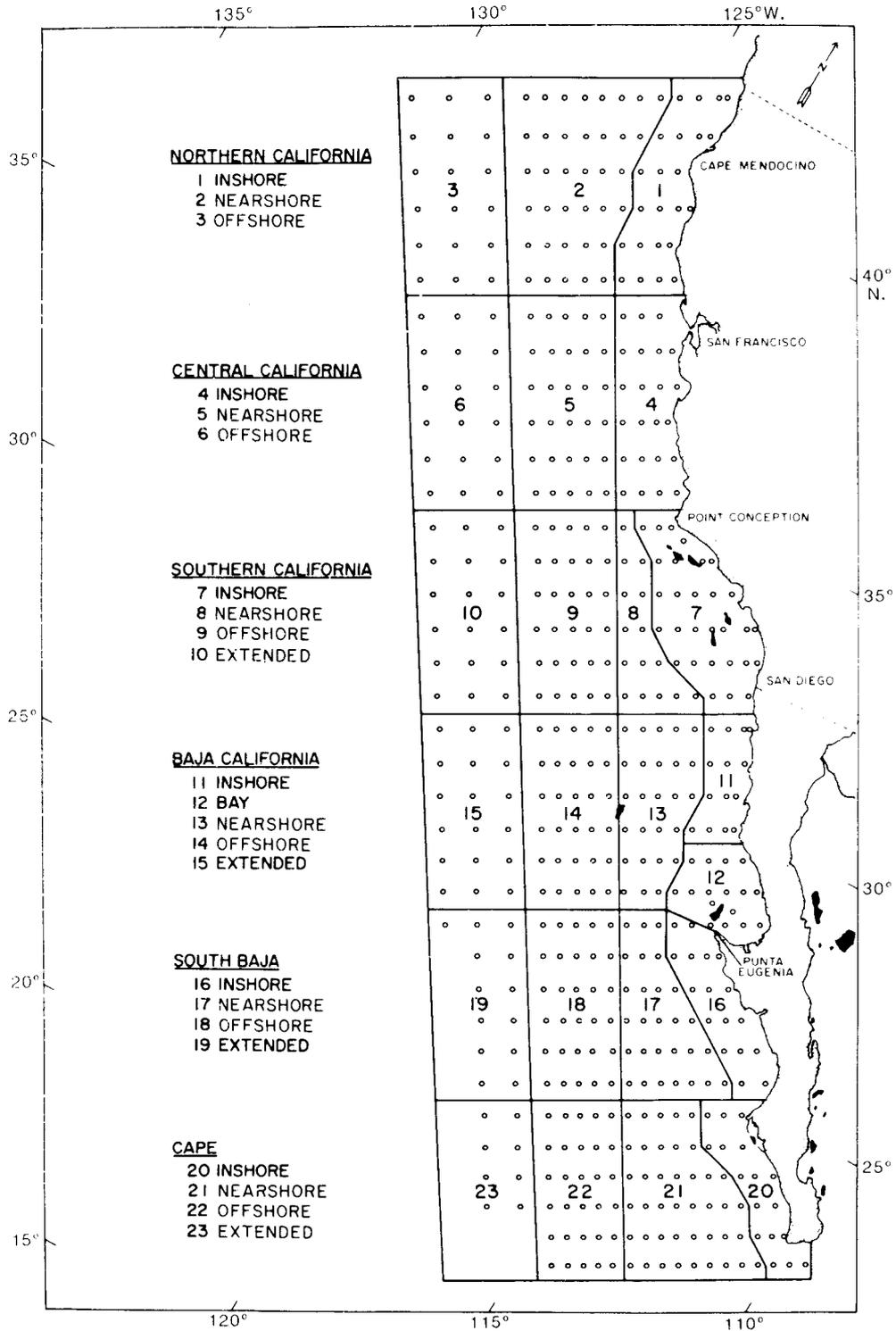


FIGURE 1.—Sampling area for estimating northern anchovy spawning biomass with CalCOFI sampling stations denoted by the open circles, and CalCOFI regions denoted by numbers (from Duke text footnote 4).

$$\bar{x}_w = \sum_i \bar{x}_i W_i, \quad \sum_i W_i = 1$$

where \bar{x}_i is the adjusted mean egg count for region i and W_i is the relative area weight for region i .

Region	$nm_i^2 \times 10^{-3}$	$m^2 \times 10^{-10}$	W_i
4	18	6.105	0.107
5	29	9.878	0.174
7	20	6.896	0.119
8	12	4.116	0.072
9	29	9.878	0.174
11	9	3.171	0.0538
13	21	7.122	0.126
14	29	9.866	0.174
Total	167	¹ 57.031	1.00

¹Sum is not equal to the total due to rounding error.

Zero catch was assumed for regions where no samples were taken because historical records show those regions usually had low densities of eggs and larvae. The weighted \bar{x}_w 's were also corrected for extrusion through the mesh by multiplying the catch by the ratio of the catch in a 0.150 mm CalVET net to the catch in the net used in a particular survey (r): $r = 3.6$ for 0.55 mm mesh silk 1 m ring net (1951-68), $r = 3.04$ for 0.505 mm mesh Nitex⁷ 1 m ring net (1969-76), $r = 12.76$ for 0.505 mm mesh Nitex bongo net (1978-present) (Lo 1983). The 0.505 mm mesh bongo net seems to catch 4 times that of a 1 m ring net. The reason is unknown. (A field experiment was conducted in April 1983 to reestimate the extrusion rate of anchovy eggs from 0.505 mm mesh bongo net. The data have not been analyzed at the time of writing. Although the egg samples from bongo nets were used to compute the HEP, the bongo net is primarily used for catching anchovy larvae, whereas the CalVET net is the egg sampler. The discrepancy between bongo and 1 m ring net is not of major concern for the current anchovy biomass estimation.) The standing stock of eggs per 0.05 m² is then

$$m_{t_l} = \bar{x}_w \cdot r$$

and

$$\text{var}(m_{t_l}) = \text{var}(\bar{x}_w)r^2 + \bar{x}_w^2 \text{var}(r)$$

where m_{t_l} is the standing stock of eggs (and larvae)

⁷Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

up to age t days from fertilization. Here t_l is the duration of incubation.

The size of standing stock of eggs depends on not only egg production rate and mortality rate but also the duration of incubation (or the incubation time), which is a function of sea temperature. The average temperature for all positive egg tows (tows which contain one or more anchovy eggs) over January-April in each year was used to estimate incubation time (t_l) using the equation (Lo 1983)

$$t_l = (18.73 e^{0.125 \text{ temp}})$$

where t_l = incubation time in days,
temp = temperature in degrees centigrade.

Both the standing stock of eggs (m_{t_l}) and the incubation time (t_l) are essential in computing the time series of daily egg production. The temperature in January-April ranges from 11° to 19°C. The long-term average temperature from January to April is 14.25°C, thus the average incubation time is 3.15 d.

Larval Data

The anchovy larvae from all years were measured to the nearest 0.5 mm preserved length. For the purpose of estimating mortality rate, larval data were grouped into 2.5 mm, ranging 2-3.0 mm; 3.75 mm, 3.5-4.0 mm; 4.75 mm, 4.5-5.0 mm; ... for larvae < 30 mm. Each preserved length was first converted to a live standard length using a shrinkage formula based on the tow duration (Theilacker 1980), and then converted to age (t days) using a two-cycle Gompertz growth curve. The first cycle is from hatching to yolk-sac absorption, a temperature-dependent growth curve, and the second cycle is from yolk-sac absorption to 22 mm larvae, a food-dependent growth curve (Zweifel and Hunter footnote 2; Methot and Hewitt footnote 3; Lo 1983). Larval abundance by length (age) group was estimated using a negative binomial weighted model (Bissell 1972; Zweifel and Smith 1981) which incorporates the "effective sampler size" (relative sampler bias). All larval abundance data were adjusted to conform to the following standard conditions: no extrusion, no day-night difference in avoidance, and a constant water volume filtered per unit depth. These data were converted to daily production (P_t) by dividing the total number of larvae in each length group by the duration (the number of days larvae remain within each length

group). It was necessary to compute a weighted mean of larval production (${}_wP_t$) because the number of net tows was not proportional to the area size: The daily larval production (P_{t_j}, t_j) was estimated first for each of the three subareas ($j = 1$: inshore = regions 7 and 11; $j = 2$: nearshore = regions 4, 8, and 13; and $j = 3$: offshore = regions 5, 9, and 14) (Fig. 1). The data set (${}_wP_t, t$) was used for final fitting of the mortality curve where ${}_wP_t = \sum_{j=1}^3 P_{t_j} u_j$, and $u_j = 0.17, 0.31,$ and 0.52 for $j = 1, 2,$ and 3 , the relative area sizes. The unweighted average age \bar{t} over three areas was used because little variation exists among t_j 's (Fig. 2).

DAILY LARVAL PRODUCTION PER 0.05 m² (${}_wP_t$) AT AGE t , 1979

PRESERVED SIZE (mm)	LIVE SIZE (mm)	AVE. AGE (day)	DAILY LARVAL PROD./0.05 m ²
2.50	3.26	4.91	0.518
3.75	4.57	8.60	0.121
4.75	5.69	11.58	0.0838
5.75	6.27	14.15	0.0665
6.75	7.63	16.41	0.0481
7.75	8.87	18.62	0.036

$${}_wP_t = 1.364 (t/3.16)^{-2.217}$$

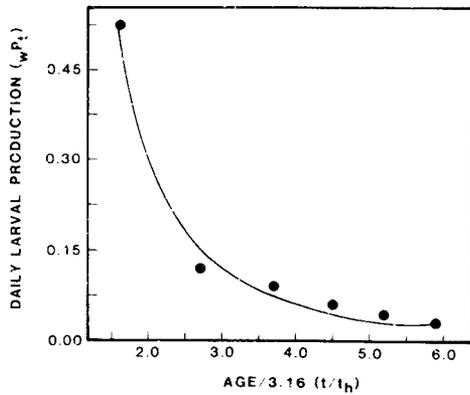


FIGURE 2.—Weighted daily larval production (${}_wP_t$) and age in days (t) of northern anchovy and the fitted larval mortality curve based upon Equation (8B) for larvae < 20 d old, 1979.

MODEL

If a cohort of eggs (larvae) is followed and N_t is defined as the number of eggs (larvae) at age t (days), then the ratio N_t/N_0 measures the survival probability at age t : $S(t; z(t)) = P(T > t; z(t))$. The sample ratio n_t/n_0 estimates the survival probability $S(t)$ where $z(t)$, the instantaneous mortality rate (IMR), is defined as $\lim_{\Delta t \rightarrow 0} \frac{P(t < T < t + \Delta t | T > t)}{\Delta t}$. If the sample data (n_t, t) are taken from a single cohort and the form

of $S(t)$ is known, both N_0 and $z(t)$ can be estimated through $n_t = n_0 S(t; z(t))$. Assuming that the standing stock of eggs and larvae represents a single cohort (with stable age distribution) as it ages, then (N_t, t) can be estimated from the number of eggs and larvae in various stages (lengths) which are later converted to age in the sample. Hewitt (1982) conducted a simulation study to check for possible bias in larval mortality rate caused by seasonal changes in the intensity of spawning of northern anchovy which violates the assumption of a stable age distribution. He found that mortality was overestimated in the beginning (January-February) of a season when spawning was increasing and underestimated at the end (May-July) when spawning was decreasing. When the larval numbers were accumulated over the entire season, these two biases tended to cancel out. Therefore, the stable age distribution is a reasonable assumption if the egg and larval sample covers the entire season. To compute larval mortality for each year, I chose larval data from January to April to be consistent with the current sampling scheme. According to Hewitt's study, the larval mortality may be overestimated. However, because only young larvae (< 8 mm preserved length) were considered in the model, the upward bias is slight. The number of eggs and larvae at various stages or length classes (n_{t_i}), as mentioned in a previous section, was further adjusted for the duration in days that eggs (larvae) remained in a particular stage or length class (t_i), i.e., $P_{t_i} = n_{t_i}/d_i$. The quantity P_{t_i} is egg (larval) production per day per unit area (e.g., 0.05 m²) at age t_i , the average age of eggs (larvae) in the i th stage (length) class (Farris 1960; Saville 1964; Harding and Talbot 1973; Ciechomski and Capezani 1973). (In later sections, the subscript i is dropped, thus (P_t, t) is used in place of (P_{t_i}, t_i) .)

The model is based on the form of the mortality curves of northern anchovy eggs and those for anchovy larvae, the form of the curve for eggs and larvae being distinctly different. The daily egg and larval production P_t is modeled by three survivorship functions $S_1, S_2,$ and S_3 :

$$P_t = P_0 S(t) = \begin{cases} P_0 S_1(t; z_1(t)) & t \leq t_c \\ P_{t_c} S_2(t; z_2(t) | T > t_c) & t_c < t < 20 \text{ d} \\ P_{t_k} S_3(t; z_3(t) | T > t_k) & t_k < t \end{cases} \quad \begin{matrix} (3A) \\ (3B) \\ (3C) \end{matrix}$$

with the IMR

$$z(t) = \begin{cases} z_1(t) & t \leq t_c \\ z_2(t) & t_c < t < 20 \text{ d} \\ z_3(t) & t_k < t \end{cases}$$

where $S_2(t; z(t) | T > t_c) = P(T > t; z(t) | T > t_c)$, t_c is the age when the form of IMR changes, t_k is $\max t_i$ for $t_i < 20$ d where t_i is the average age for the i th length class.

The quality of larval data for larvae older than 20 d is questionable because older larvae avoid the net (Hewitt 1982). The forms of $z_3(t)$ and $S_3(t)$ for $t > 20$ d are unknown at the present time. Therefore, only the mortality of eggs and larvae < 20 d old was assessed.

The IMR, $z(t)$, relates to the survivorship function $S(t)$, by definition, in the form of

$$S(t) = e^{-\int_0^t z(u) du} \tag{4}$$

$$= \begin{cases} e^{-\int_0^t z_1(u) du} & = S_1(t) & t \leq t_c \\ e^{-\int_0^{t_c} z_1(u) du - \int_{t_c}^t z_2(u) du} & = e^{-\int_0^{t_c} z_1(u) du} S_2(t | T > t_c) & t_c < t < 20 \\ & = S_1(t_c) S_2(t | T > t_c) & \\ & = S_2(t). & \end{cases}$$

The critical age t_c was defined as the age before

which $z(t) = z_1(t)$, after which $z(t) = z_2(t)$. P_t and t from larval data were used to estimate both P_{t_c} and $z_2(t)$ through Equation (3B) after $S(t)$ is specified. Both larval production (P_{t_c}) and the standing stocks of eggs and larvae up to age t_c (m_{t_c}) were then used to estimate P_0 and $z_1(t)$ through Equation (3A) as below:

$$m_{t_c} = \int_0^{t_c} P_t dt = \int_0^{t_c} P_0 S_1(t; z_1(t)) dt \tag{5A}$$

and

$$P_{t_c} = P_0 S_1(t_c; z_1(t)). \tag{5B}$$

Now I have two Equations (5A) and (5B) to be solved simultaneously for the unknowns P_0 and the parameters in $z_1(t)$. An iterative procedure was used to obtain estimates of P_0 and $z_1(t)$. Clearly, the selection of the function forms of $z_1(t)$ and $z_2(t)$ are important in obtaining accurate estimates of P_0 and P_{t_c} .

Anchovy Mortality Curves and Estimation of Egg Production

Daily egg and larval production per 0.05 m² and their ages (P_t, t) were estimated for 1979-81 to model the mortality curves $P_0 S_1(t)$ and $P_{t_c} S_2(t | T > t_c)$ (Equation (3)). The egg data were collected in vertical net tows from 70 m with the

TABLE 1.—Daily egg and larval production per 0.05 m² (P_t) at various ages in days (t) sampled from CalVET and bongo tows, and the estimates of five parameters: egg production at age zero (P_0), egg mortality ($\hat{\alpha}$), larval mortality coefficient ($\hat{\beta}$), larval production at hatching (\hat{P}_l) and incubation time in days (t_l) in CalCOFI regions 4, 7, 8, and 11, January-April 1979-81.

	1979 ¹			1980		1981		Live standard length (mm) ²		
	t	P_t	Live standard length (mm)	t	P_t	t	P_t			
Eggs	0.4167	10.79		0.4167	9.34	0.4167	5.64	CalVET net		
	0.9167	4.36		0.9167	9.22	0.9167	7.66			
	1.4167	4.91		1.4167	6.34	1.4167	4.87			
	1.9167	4.58		1.9167	4.71	1.9167	6.05			
	2.4167	6.87		2.4167	5.14	2.4167	4.84			
	2.9167	3.63								
Larvae	3.73	2.64	3.03	2.94	2.26	3.14	3.23	3.03	Bongo net	
				4.08	2.39	4.35	2.99	3.59		
				5.91	0.99	6.25	2.10	4.13		
				7.69	0.86	8.08	1.84	4.66		
				4.72	1.96	3.26	3.05	2.35		3.10
				8.32	0.48	4.17	5.65	1.04		5.86
			11.49	0.35	5.69	8.90	0.49	9.22		
			13.90	0.25	6.77	11.47	0.39	11.79		
			16.24	0.19	7.83	13.83	0.26	14.01		
			18.31	0.13	8.87	15.91	0.21	16.01		
						17.99	0.15	18.22		
\hat{P}_c		9.76	³ (2.82)	11.46	(1.27)	6.73	(1.32)			
$\hat{\alpha}$		0.33	(0.28)	0.38	(0.09)	0.11	(0.13)			
$\hat{\beta}$		1.83	(0.14)	1.24	(0.17)	1.19	(0.17)			
\hat{P}_l		3.59	(0.18)	2.51	(0.19)	4.81	(0.42)			
t_l		3.21		2.96		2.85				

¹Not weighted by area size.

²For both 1980 and 1981 larval data.

³Asymptotic standard error in parentheses.

CalVET net, and the larval data were collected with both bongo oblique tows and the CalVET nets. The egg and larval catches by age group were standardized, that is, corrected for possible biases caused by extrusion through the mesh, day-night difference in avoiding the net, variation in the amount of water filtered, and the variation of larval growth rates which is both temperature and food dependent (Methot 1981; Lo 1983). The standardized daily egg and larval production estimates per 0.05 m² sea surface area in CalCOFI regions 4, 7, 8, and 11 for January-April 1979-81 are given (Table 1, Fig. 3).

The IMR for the egg stage was believed to be constant, $z_1(t) = \alpha$, (Stauffer and Picquelle footnote 6), whereas the IMR for larval stage was found to be age dependent $z_2(t) = \beta/t$ (a Pareto hazard function, Johnson and Kotz 1970). I first calculated sample IMR $z(t_i) = (P_{t_{i-1}} - P_{t_i}) / (t_i - t_{i-1}) / P_{t_i}$ which is an approximation of $dS(t)/dt / S(t)$ at various t for $0 < t < 20$ d using 1980 standardized egg and larval data listed in Table 1. The 1980 egg and larval production and age data were further combined so that $z(t) > 0$ for all t . The relationship between $z(t)$ and t determined the function form of $z(t)$ (Table 2). The $z(t)$'s were

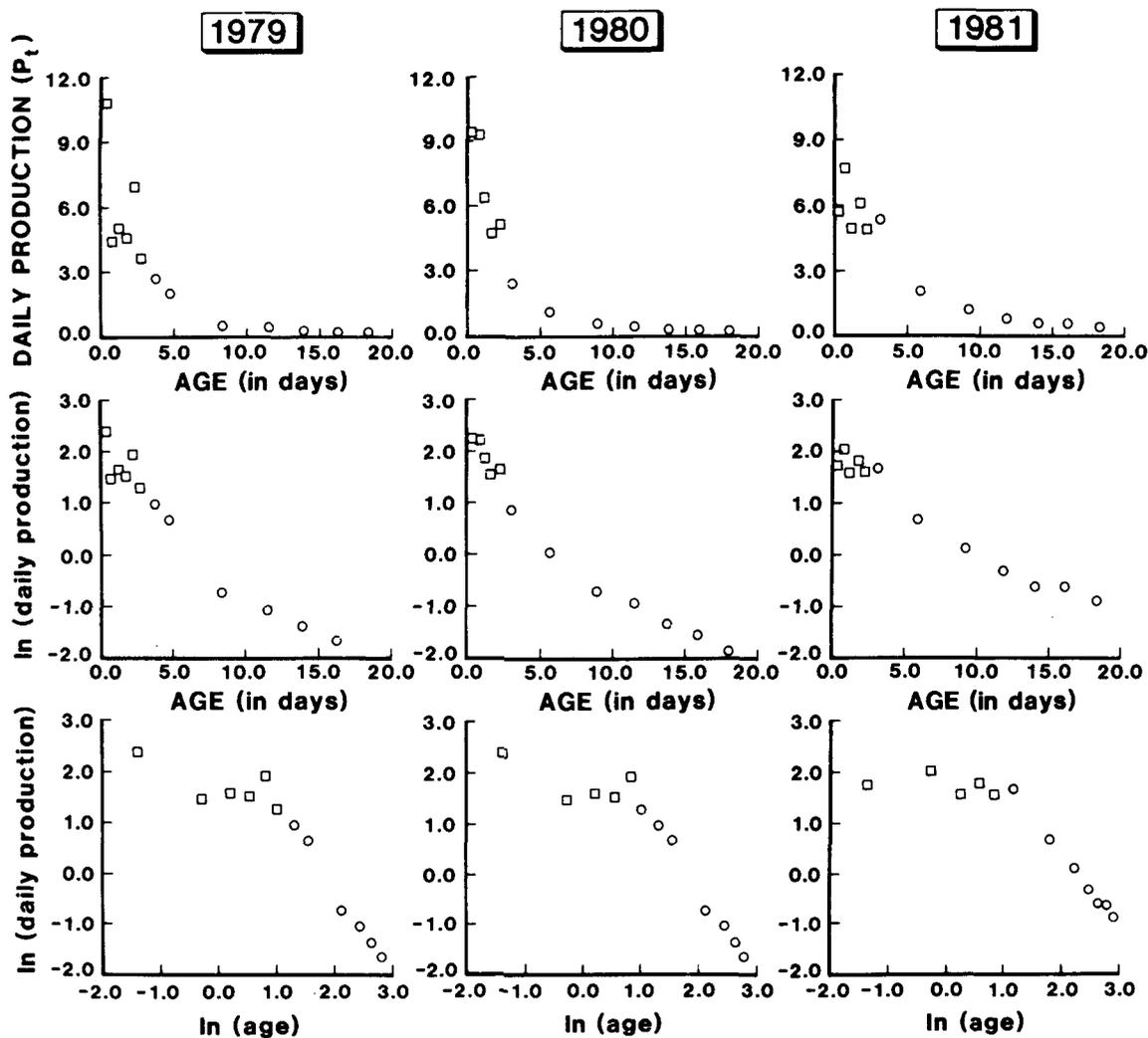


FIGURE 3.—Daily egg and larval production of northern anchovy per 0.05 m² (P_t) by age in days (t) and their log transformations ($\ln(P_t)$), 1979-81. A linear relationship between $\ln(P_t)$ and t indicates a constant instantaneous mortality rate (IMR) and a curvilinear relationship between $\ln(P_t)$ and t indicates an age dependent IMR. Squares are egg data and open circles are larval data.

TABLE 2.—The instantaneous mortality rates of anchovy eggs and larvae < 20 days ($z(t_i)$) by age in days (t_i) computed from the daily egg and larval production estimates (P_{t_i}) and age (t_i), 1980. $z(t) = 0.0060 + 1.63/t$ is the function fitted to the data in the last two columns for $t > 4.5$ d.

<i>i</i>	t_i (d)	Daily egg and larval production	$\bar{t}_i =$			
		P_{t_i}	$P_{t_{i-1}} - P_{t_i}$	$t_i - t_{i-1}$	$(t_i + t_{i-1})/2$	$z(t_i)$
1	0.67	9.28				
2	1.67	5.53	3.75	1.00	1.17	0.40
3	2.60	3.70	1.83	0.93	2.14	0.36
4	3.57	2.37	1.33	0.97	3.09	0.37
5	5.65	1.04	2.28	2.08	4.61	0.46
6	5.91	0.99	0.05	0.26	5.78	0.18
7	7.69	0.86	0.13	1.78	6.80	0.07
8	8.90	0.49	0.37	1.21	8.30	0.36
9	11.47	0.39	0.10	2.57	10.19	0.08
10	13.83	0.26	0.13	2.36	12.65	0.14
11	15.91	0.21	0.05	2.08	14.87	0.09
12	17.99	0.15	0.06	2.08	16.95	0.14

$$^1z(t_i) = (P_{t_{i-1}} - P_{t_i}) / (t_i - t_{i-1}) / P_{t_i}$$

quite constant for egg and larvae < 4.5 d old and decreased thereafter. For t values > 4.5 d, the function $z(t) = a + b/t$ fit the data best. Based upon the function relationship $z(t) = b/t$ (the intercept a is not distinguishable from zero and thus was dropped), I have the IMR $z(t)$:

$$z(t) = \begin{cases} \alpha & t \leq t_c \\ \beta/t & t_c < t < 20. \end{cases} \quad (6)$$

Applying Equation (6) to Equation (4) leads to

$$S(t) = \begin{cases} S_1(t) = e^{-\alpha t} & t \leq t_c \\ S_2(t) = e^{-\alpha t_c} \left(\frac{t}{t_c}\right)^{-\beta} & t_c < t < 20. \end{cases} \quad (7)$$

Combining Equations (3) and (7) one has

$$P_t = \begin{cases} P_0 e^{-\alpha t} & t \leq t_c \\ P_0 e^{-\alpha t_c} \left(\frac{t}{t_c}\right)^{-\beta} & t_c < t < 20 \end{cases} \quad (8A)$$

$$= P_{t_c} \left(\frac{t}{t_c}\right)^{-\beta} \quad (8B)$$

To validate both Equations (8A) and (8B), logarithms of P_t and t were plotted: $\ln(P_t)$ against t should be a straight line for $t \leq t_c$ (Equation (8A)) and $\ln(P_t)$ against $\ln(t)$ should be a straight line for $t_c < t < 20$ (Equation (8B)) (Fig. 3). This was true for egg and larval production from 1979 to 1981. The determination of t_c , the age at which

IMR changes, was subjective. Two values of t_c were used: One was the time of hatching or the duration of incubation (t_I) which is temperature dependent and the other was the average age of yolk-sac larvae (embryonic period) $t_c = t_{ys} : t_{2.5 \text{ mm}} = \text{age at preserved length 2.5 mm (about 5 d old)}$. When t_c was considered equivalent to the incubation time ($t_c = t_I$), the egg stages were considered as one group with constant IMR; and when t_c was equivalent to average age of the yolk-sac larvae ($t_c = t_{ys}$), egg stages and yolk-sac length class(es) were considered as one group with constant IMR. In either case, P_{t_c} was estimated from the fitted curve

$$P_t = P_{t_I} \left(\frac{t}{t_I}\right)^{-\beta}, \text{ i.e., } \hat{P}_{t_c} = \hat{P}_{t_I} \left(\frac{t_c}{t_I}\right)^{-\beta}.$$

Substitution of Equation (7) in Equation (5) gives

$$m_{t_c} = \begin{cases} \int_0^{t_c} P_0 e^{-\alpha t} dt = P_0(1 - e^{-\alpha t_c})/\alpha & \alpha > 0 \\ t_c \cdot P_0 & \alpha = 0 \end{cases} \quad (9A)$$

$$P_{t_c} = P_0 e^{-\alpha t_c} \quad (9B)$$

where m_{t_c} is the standing stock of eggs and larvae up to age t_c . Equation (9A) divided by Equation (9B) results in

$$q = \begin{cases} m_{t_c}/P_{t_c} = (e^{\alpha t_c} - 1)/\alpha = h(\alpha) & \alpha > 0 \\ t_c & \alpha = 0 \end{cases} \quad (10)$$

where $t_c = t_I$ or t_{ys} and q is the ratio of standing stock of eggs and larvae up to age t_c to the larval production P_{t_c} . The estimated IMR, $\hat{\alpha}$, was obtained by an iterative procedure using Equation (10). The estimated egg production obtained by rearranging the terms in Equation (9B):

$$\hat{P}_0 = \hat{P}_{t_c} \cdot e^{\hat{\alpha} t_c}.$$

The approximate variance of $\hat{\alpha}$ and $\hat{\beta}$ were computed in the appendix.

TIME SERIES ESTIMATES OF HISTORICAL EGG PRODUCTION (HEP)

The HEP per 0.05 m² (P_0) and the egg IMR (α) for the central stock of northern anchovy in the first 4 mo of the year, 1951-82, were estimated based upon Equations (9B) and (10). For years after 1978, catch data were available for CalVET and bongo nets, but I chose to use samples from

bongo nets because only bongo or similar nets (1 m ring nets) were used for sampling eggs and larvae prior to 1978.

Two series of HEP estimates were constructed. Series 1 assumed a constant IMR for the egg stage with $t_c = t_I$, whereas series 2 with $t_c = t_{ys}$ assumed a constant IMR throughout the embryonic period (Table 3). Both P_{tI} and $P_{t_{ys}}$, the daily larval production at hatching and yolk-sac stage, were obtained from the fitted line of Equation (8B) with $t_c = t_I$.

Under series 1, nearly half of the egg IMR ($\hat{\alpha}$)

were negative (11 out of 24 yr). This was because the egg IMR depended on the value of q through Equation (10) where $q = m_{tI}/P_{tI}$. However, judging from Equation (10), $q = t_I$ for $\alpha = 0$. Therefore for those years where $q < t_I$, egg IMR would be less than 0. The small q 's could result from the underestimated m_{tI} or overestimated P_{tI} or both. The poor results of IMR ($\hat{\alpha}$) were likely due to the underestimation of m_{tI} . As a result, the standing stock of eggs and that of yolk-sac larvae were combined into one group in series 2, to eliminate the negative IMR's.

TABLE 3.—Two time series of estimated historical egg production (\hat{P}_0), and egg mortality ($\hat{\alpha}$), larval mortality coefficient ($\hat{\beta}$), mean egg abundance (m_{tI}), mean egg and yolk-sac larval abundance ($m_{t_{ys}}$), January-April, and mean larval abundance (L_a) per 0.05 m², 1951-82 with standard error in parentheses.

Year	Series 1		Series 2		Larval mortality coeff. $\hat{\beta}$	Mean egg abundance m_{tI}	Mean yolk-sac larval abundance $m_{t_{ys}}$	Mean larval abundance ² L_a
	Daily egg production \hat{P}_0	Egg mortality $\hat{\alpha}$	Daily egg production \hat{P}_0	Egg mortality $\hat{\alpha}$				
1951	0.006 (0.024)	0.03 (1.34)	0.012 (0.116)	0.23 (2.18)	0.85 (0.15)	0.02 (0.03)	0.03 (0.03)	0.04
1952	0.002 (0.003)	-0.57 (0.35)	0.017 (0.107)	0.09 (1.27)	0.88 (0.20)	0.02 —	0.07 (0.01)	0.04
1953	0.026 (0.019)	-0.08 (0.20)	0.066 (0.180)	0.19 (0.54)	0.95 (0.10)	0.11 (0.03)	0.21 (0.03)	0.011
1954	0.031 (0.026)	-0.48 (0.26)	0.168 (0.188)	0.12 (0.24)	1.16 (0.07)	0.24 (0.08)	0.61 (0.08)	0.17
1955	0.026 (0.028)	-0.77 (0.32)	0.316 (0.393)	0.07 (0.26)	1.01 (0.17)	0.39 (0.12)	1.27 (0.14)	0.19
1956	0.122 (0.114)	0.33 (0.26)	0.146 (0.647)	0.33 (0.88)	0.88 (0.24)	0.25 (0.12)	0.36 (0.12)	0.11
1957	0.148 (0.040)	-0.12 (0.31)	0.364 (0.423)	0.20 (0.25)	0.94 (0.10)	0.54 (0.23)	1.09 (0.24)	0.26
1958	0.966 (0.481)	0.40 (0.18)	1.274 (1.182)	0.43 (0.23)	0.88 (0.08)	1.61 (0.45)	2.44 (0.93)	0.33
1959	0.444 (0.267)	-0.11 (0.21)	0.992 (0.822)	0.23 (0.20)	1.18 (0.16)	1.47 (0.36)	2.68 (0.38)	0.34
1960	0.678 (0.535)	-0.18 (0.26)	1.765 (0.774)	0.24 (0.10)	1.80 (0.06)	2.78 (0.99)	4.85 (0.99)	0.34
1961	0.446 (0.669)	0.25 (0.43)	0.653 (0.635)	0.29 (0.22)	1.55 (0.16)	0.94 (0.28)	1.59 (0.28)	0.26
1962	0.443 (0.297)	-0.18 (0.18)	1.314 (1.171)	0.19 (0.18)	1.08 (0.23)	2.09 (0.50)	4.15 (0.58)	0.67
1963	1.404 (0.690)	0.16 (0.15)	2.275 (0.991)	0.28 (0.09)	0.81 (0.04)	3.57 (0.93)	5.92 (0.93)	0.95
1964	3.681 (1.956)	0.43 (0.15)	4.147 (2.681)	0.42 (0.13)	1.44 (0.21)	6.39 (1.80)	8.55 (1.81)	0.65
1965	0.778 (0.559)	-0.45 (0.21)	4.019 (1.176)	0.19 (0.06)	2.42 (0.12)	6.48 (1.75)	12.78 (1.75)	1.04
1966	3.540 (1.660)	0.26 (0.14)	5.256 (1.799)	0.42 (0.07)	1.84 (0.04)	7.82 (2.11)	10.61 (2.11)	0.80
1969	0.876 (0.557)	-0.42 (0.19)	3.821 (1.062)	0.19 (0.06)	2.15 (0.08)	6.16 (1.53)	12.14 (1.53)	0.67
1972	0.639 (0.356)	-0.09 (0.16)	1.657 (0.804)	0.25 (0.11)	1.73 (0.11)	2.56 (0.66)	4.52 (0.67)	0.62
1975	15.320 (11.608)	0.36 (0.22)	19.691 (10.364)	0.44 (0.11)	1.88 (0.20)	30.06 (4.40)	39.14 (14.41)	0.81
1978	10.524 (4.566)	0.64 (0.15)	10.738 (4.484)	0.59 (0.10)	1.66 (0.10)	13.58 (3.67)	16.60 (3.67)	0.29
1979	4.258 (2.215)	0.36 (0.16)	5.426 (2.616)	0.48 (0.10)	2.22 (0.15)	8.06 (2.39)	10.05 (2.39)	0.39
1980	2.338 (1.427)	0.37 (0.22)	2.671 (1.260)	0.36 (0.08)	1.22 (0.03)	4.12 (1.46)	6.48 (1.46)	0.40
1981	3.95 (2.658)	0.36 (0.24)	4.376 (2.084)	0.38 (0.08)	1.53 (0.03)	6.88 (2.70)	10.29 (2.70)	0.63
1982	1.941 (1.230)	0.15 (0.20)	3.294 (1.367)	0.36 (0.09)	1.81 (0.04)	4.93 (1.70)	7.33 (1.70)	0.46

¹Series 1 and 2 are two methods used for estimating daily egg production (P_0). Series 1 assumed a constant IMR for egg stage whereas series 2 assumed a constant IMR for egg through yolk-sac larval stage.
²Computed from annual larval abundance for the central subpopulation (Table 2, Stauffer and Charter 1982).

Under series 2, P_0 and α were estimated based upon $q = m_{t_{ys}}/P_{t_{ys}}$ (Equations (9B) and (10)), with $t_c = t_{ys}$. The average age of yolk-sac larvae ($t_{ys} = t_{2.5 \text{ mm}}$) was 4.7 d. All q 's were greater than t_{ys} , thus $\hat{\alpha}$'s were all positive.

The HEP (P_0) for both series have the same trend: a gradual increase from the early 1950's to middle 1960's, thereafter fluctuating until 1975 when it reached the peak value at 15.32/day per 0.05 m² (series 1) or 19.69/day per 0.05 m² (series 2). From 1978, HEP decreased to the present level of 1.94/day per 0.05 m² (series 1) and 3.29/day per 0.05 m² (series 2) (Table 3, Fig. 4). The approximate standard error of the estimated HEP (P_0) and egg mortality ($\hat{\alpha}$) is large for the early years and small for the recent years, possibly because of the poor quality of early egg data, or an insufficiency of the delta method to estimate the variance.

For the purpose of verification, HEP (P_0) from the two series based upon the egg-larval mortality model and the egg production at age 0 estimated from the current EPM (Stauffer and Picquelle footnote 6) were compared for 1980-82 where adequate egg and larval samples were available (Table 4). The P_0 's from the two series of HEP and the current EPM were not significantly different, nor were the egg mortality rates. However, the

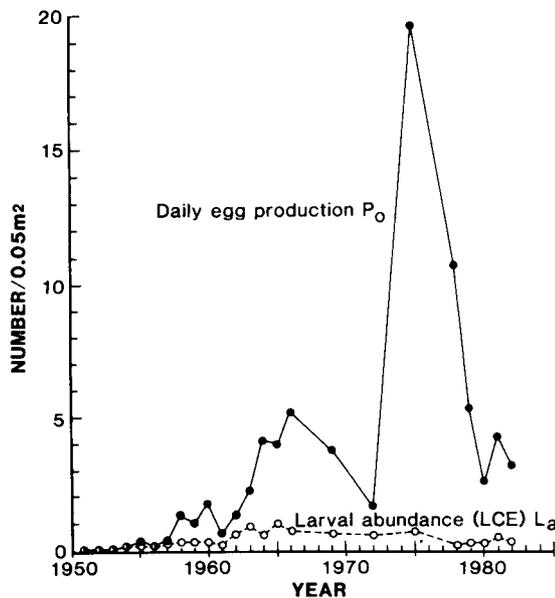


FIGURE 4.—Estimates of historical egg production of the central stock of northern anchovy using the series 2 method (P_0) and the larval abundance (L_a) of the larval census estimates, 1951-82.

TABLE 4.—Daily egg production per 0.05 m² (\hat{P}_0), egg instantaneous mortality ($\hat{\alpha}$), egg abundance (m_{tj}) of northern anchovy, and number of tows (n) in CalCOFI regions 4, 5, 7, 8, 9, 11, 13, and 14, January-April 1980-82.

	1980		1981		1982	
	\hat{P}_0 (SE)	$\hat{\alpha}$ (SE)	\hat{P}_0 (SE)	$\hat{\alpha}$ (SE)	\hat{P}_0 (SE)	$\hat{\alpha}$ (SE)
Historical egg production						
Series 1	2.33 (1.46)	0.37 (0.21)	3.95 (2.70)	0.36 (0.24)	1.94 (1.70)	0.15 (0.20)
Series 2	2.67 (1.46)	0.36 (0.08)	4.37 (2.70)	0.38 (0.08)	3.29 (1.70)	0.36 (0.09)
Current egg production method ¹	2.29 (0.51)	0.45 (0.11)	1.82 (0.31)	0.14 (0.08)	1.18 (0.32)	0.15 (0.104)

	1980		1981		1982	
	n	m_{tj} (SE)	n	m_{tj} (SE)	n	m_{tj} (SE)
Egg abundance per 0.05 m ² (m_{tj})						
CalVET (0.333 mm) ²	961	3.20 (0.52)	1,134	4.72 (0.72)	992	3.48 (0.62)
Bongo (0.505 mm)	97	4.12 (1.46)	403	6.88 (2.70)	113	4.93 (1.70)

¹ Picquelle, see text footnote 8.
² Mesh size.

point estimates of P_0 's from the current EPM were lower than those estimated from the two series. The reason for the lower values is unknown at the moment. This could be due to random fluctuation of the statistics. The current EPM estimates of P_0 were much more precise than those derived from the historical egg-larval mortality model, whereas the precision of egg mortality rate from both methods was similar.

As to the estimates from the two series of HEP, the point estimates of P_0 from series 2 were always higher than those estimated from series 1. Recall that the assumption of series 2 was that the egg through yolk-sac larval stage suffers a constant mortality rate. However, if in fact the yolk-sac larvae suffer a higher mortality rate than eggs, the mortality rate of eggs and larvae when combined (series 2) would overestimate egg mortality as well as egg production (P_0) (Equation (9B)).

DISCUSSION

Historical production (P_0) and egg IMR (α) of the central stock of northern anchovy for the first 4 mo of the year from 1951 to 1982 were estimated based upon the information of total number of eggs and yolk-sac larvae per 0.05 m² and the egg-larval mortality model. Two series of P_0 and α were produced. Series 1 assumed a constant IMR for only the egg stage whereas series 2 assumed a constant IMR for the entire embryonic period. Both series of P_0 showed the same trend (Table 3, Fig. 4) with a peak in 1975. The high daily egg

production estimate (P_0) in 1975 was caused by the high standing stock of eggs ($m_{tI} = 30.06/0.05 \text{ m}^3$ per m depth) which was more than 10 times that of other years, and the high egg IMR ($\hat{\alpha} = 0.36$) (Table 3). The high daily egg production in 1975 reflects either a high fecundity (high spawning frequency) or a high spawning biomass or some combination of these effects. The present level of egg production is the same as that in the middle 1960's. Both egg IMR ($\hat{\alpha}$) and larval IMR coefficient $\hat{\beta}$, $z(t) = \beta/t$, vary from year to year (Fig. 5).

In addition to providing a 24-yr time series of HEP for the northern anchovy, two important conclusions can be drawn from this analysis:

1. The form of IMR of eggs (and yolk-sac larvae) is different from that of older larvae (6-20 d).
2. Egg production is a better index of stock abundance than is the standing stock of larvae.

Little doubt exists that mortality rates change sometime between the hatching of the eggs and the onset of feeding. Analysis of the daily egg and larval production by age for 1979-81 (Fig. 3) suggested a constant IMR for eggs (or eggs and yolk-sac larvae) and an age-dependent IMR of Pareto form for older larvae ($z(t) = \beta/t$ for $t_c < t < 20 \text{ d}$) (Table 2). The age t_c in Equation (3) could be

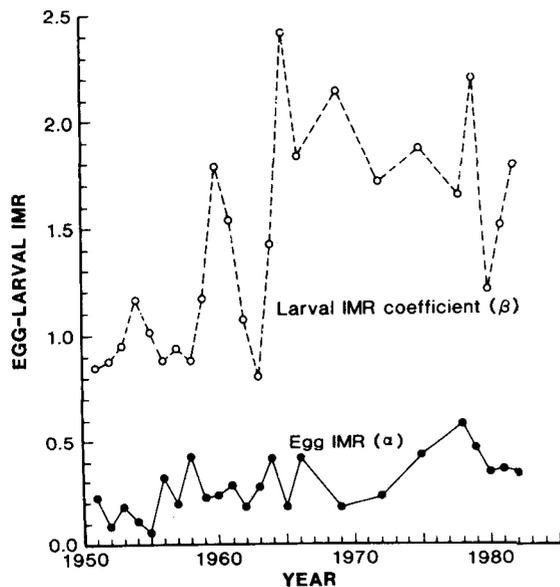


FIGURE 5.—Estimated egg instantaneous mortality rate (IMR) ($\hat{\alpha}$) from series 2 method of estimating egg production and the larval mortality coefficient ($\hat{\beta}$) of the central stock of northern anchovy, 1951-82.

considered to mark the end of the critical period after which mortality decreases (Ahlstrom 1954; Marr 1956; Farris 1960; Saville 1964). Series 1 assumed $t_c =$ incubation time and series 2 assumed $t_c =$ average age of yolk-sac larvae. From the existing data, I could not ascertain which assumption was the more likely, but it was evident that larvae at hatching or near first-feeding (yolk absorption) suffer higher mortality than do older larvae.

The HEP (P_0) is certainly preferable to larval standing stock (larval census estimate = LCE) for use as an index of spawning biomass. Egg production is related to the spawning biomass through Equation (2), i.e., $P_0 = B_a \cdot C$, where the proportionality C is the reproductive output ($R \cdot F \cdot E/W$). If the reproductive output remains constant between years, as shown by 1980-82 anchovy data (Picquelle⁸), the HEP will be an unbiased index of the spawning biomass. The LEC assumes $B_a = K \cdot L_a$ where L_a is the larval abundance and K is a constant proportionality (Smith 1972; Stauffer and Charter 1982) (Table 3, Fig. 4). Thus to provide an unbiased index of biomass, the method requires that not only the reproductive output be constant from year to year but also the egg and larval mortality must remain constant as well. Using Equation (8), the larval abundance (age < 30 d old) can be written as

$$L_a = \int_{tI}^{30} P_t dt$$

$$= \int_{tI}^{30} P_0 S(t; z(t)) dt$$

$$= B_a \left(\frac{R \cdot F \cdot E}{W} \right) g(\alpha, \beta, tI)$$

$$\text{where } g(\alpha, \beta, tI) = \begin{cases} e^{-\alpha tI} \frac{tI}{\beta - 1} \left[1 - \left(\frac{30}{tI} \right)^{-(\beta - 1)} \right] & \text{for } \beta \neq 1 \\ e^{-\alpha tI} (\ln 30 - \ln tI) & \beta = 1 \end{cases}$$

α is the egg IMR and β is the larval mortality coefficient.

The larval abundance (L_a) is proportional to the spawning biomass (B_a) with constant proportionality only if the reproductive output

⁸S. J. Picquelle, Statistician, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard E, Seattle, WA 98112, pers. commun. July 1983.

($R \cdot F \cdot E / W$) and the egg and larval mortality rates through the function $g(\alpha, \beta, t_l)$ remain constant from year to year. It is clear that from 1951 to 1982 time series (Table 3) that the assumption of constant egg and larval mortality has not been met by the central California anchovy population. The HEP requires constant reproductive output. The validity of this assumption can only be tested with future data.

In addition to the ichthyoplankton data, several other indices of anchovy biomass exist: acoustic trawl surveys conducted by California Department of Fish and Game, aerial survey records from aircraft associated with the fishery, catch-effort analysis (CPUE), and cohort analysis from the catch of the United States and Mexican fishery. In a recent management plan, all of these indices except cohort analysis have been calculated and compared with the time series of egg production presented in this paper (MacCall et al.⁹). The estimates of egg production covaried with these other indices from year to year and appeared to be the most consistent index of spawning biomass among these indices (Table 5).

Selection of the appropriate method for estimating biomass depends upon the data availability and knowledge of the growth of eggs and larvae. If nothing is known of the age of eggs and larvae and no information exists on reproductive parameters, the LCE is the only method available

⁹MacCall, A. D., R. D. Methot, D. D. Huppert, H. W. Frey, and O. Mathisen. 1983. Northern anchovy second draft revised fishery management plan incorporating DEIS/RIR. Pac. Fish. Manage. Council.

TABLE 5.—Correlations among various indices of anchovy spawning biomass. Upper value is correlation coefficient, lower value is number of observations. (Reproduced from table 4.3-2 of MacCall et al. (text footnote 9).)

Historical egg production					
0.458	Larval				
(23)	census				
0.807	0.708	Acoustic			
(8)	(7)	survey			
0.818	0.327	0.659	Aerial		
(9)	(9)	(9)	index		
0.791	0.004	0.512	0.379	Spring	
(4)	(4)	(10)	(9)	CPUE	
0.395	0.865	0.290	0.655	0.256	Fall
(4)	(4)	(10)	(10)	(9)	CPUE
Spawning biomass index		Consistency ¹		Rank	
Historical egg production		0.654		1	
Larval census		0.480		5	
Acoustic survey		0.606		2	
Aerial index		0.583		3	
Spring CPUE		0.388		6	
Fall CPUE		0.517		4	

¹Consistency is average of correlation coefficients.

although subject to major biases. If egg and larval age data exist but no data on reproductive parameters are available, then the HEP is the preferable method. The EPM is the best method; it requires not only knowledge of egg mortality but accurate estimates of adult reproductive parameters as well. In many time series, both growth and abundance of eggs and larvae are available but reproductive parameters are not. In these cases, the HEP is probably the most accurate means of creating a historic time series of biomass.

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APPENDIX

The approximate variances of $\hat{\alpha}$ and \hat{P}_0 were derived from the delta method (Seber 1973):

$$\begin{aligned} \text{var}[f(x_1, \dots, x_I)] &\doteq \sum_{i=1}^I \left[\frac{\partial}{\partial x_i} f(x_1, \dots, x_I) \right]^2 \text{var}(x_i) \\ &+ 2 \sum_{i < j} \frac{\partial}{\partial x_i} f(x_1, \dots, x_I) \frac{\partial}{\partial x_j} f(x_1, \dots, x_I) \text{cov}(x_i, x_j) \Big|_{\hat{E}x_i, i=1, \dots, I} \end{aligned}$$

$\text{var}(\hat{\alpha})$ was computed based upon Equation (10), i.e.,

$$\text{var}(q) \doteq \left(\frac{\partial h(\alpha)}{\partial \alpha} \right)^2 \text{var}(\hat{\alpha}).$$

$$\begin{aligned}
\text{Thus } \text{var}(\hat{\alpha}) &\doteq \text{var}(q) \cdot \left(\frac{\partial h(\alpha)}{\partial \alpha} \right)^{-2} \\
&\doteq \text{var}(\hat{m}_{t_c} / \hat{P}_{t_c}) \left(\frac{\partial h(\alpha)}{\partial \alpha} \right)^{-2} \\
&= \frac{\text{var}(\hat{m}_{t_c}) + q^2 \text{var}(\hat{P}_{t_c}) - 2q \text{cov}(\hat{m}_{t_c}, \hat{P}_{t_c})}{\hat{P}_{t_c}^2} \cdot \left[\hat{\alpha}^4 / \{ e^{\hat{\alpha} t_c} (\hat{\alpha} t_c - 1) + 1 \}^2 \right]
\end{aligned}$$

where $\text{cov}(m_{t_c}, P_{t_c})$ was estimated from the 1951-82 time series. $\text{Var}(P_0)$ was computed based upon Equation (9B)

$$\begin{aligned}
\hat{P}_0 &= \hat{P}_{t_c} e^{\hat{\alpha} t_c} \\
\text{var}(\hat{P}_0) &\doteq \left\{ \frac{\partial P_0}{\partial \alpha} \right\}^2 \text{var}(\hat{\alpha}) + \left\{ \frac{\partial P_0}{\partial P_{t_c}} \right\}^2 \text{var}(\hat{P}_{t_c}) + 2 \left(\frac{\partial P_0}{\partial \alpha} \right) \left(\frac{\partial P_0}{\partial P_{t_c}} \right) \text{cov}(\hat{P}_{t_c}, \hat{\alpha}) \Big|_{\hat{\alpha}, \hat{P}_{t_c}} \\
&= e^{2\hat{\alpha} t_c} \left[t_c^2 \hat{P}_{t_c}^2 \text{var}(\hat{\alpha}) + \text{var}(\hat{P}_{t_c}) + 2\hat{P}_{t_c} \cdot t_c \cdot \text{cov}(\hat{P}_{t_c}, \hat{\alpha}) \right]
\end{aligned}$$

where $\text{cov}(\hat{P}_{t_c}, \hat{\alpha})$ was estimated from the 1951-82 time series.