

NEARSHORE PRODUCTION OF YOUNG ANCHOVY

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ABSTRACT

The daily production of northern anchovy eggs and larvae is determined for the nearshore region (within ca. 3 mi of the coast) of the Southern California Bight. Stage-specific catches were obtained from monthly Ichthyoplankton Coastal and Harbor Studies (ICHS) cruises during 1979-80. Age-specific production estimates are derived by pooling and adjusting the catches for growth and sampler bias. Hazard functions are introduced, and a production curve is fit to the data. Production of young anchovy was compared with that for the greater Southern California Bight; there was no evidence for greater production inshore. The spawning cycle and survival of young in the nearshore region reflected that occurring throughout the Southern California Bight.

RESUMEN

Se determina la producción diaria de huevos y larvas de anchoa (*Engraulis mordax*) en la zona costera (a menos de tres millas de la costa) en la región del seno de la California Meridional. Los datos utilizados se basan en la serie de fases de desarrollo, que aparecían en las colecciones del programa de Ictioplancton costero y estudios de estuarios y bahías (ICHS), cruceros 1979-80.

Las estimaciones de edades en esta producción se han determinado agrupando las capturas y ajustándolas en relación al crecimiento y a las variaciones ocasionadas por el muestreo. Funciones del azar se incluyen en los cálculos, ajustando así los datos en la curva resultante. Esta producción de anchoa se compara con la obtenida para todo el seno de la California Meridional, y no hay evidencia de que las aguas costeras presenten una mayor producción. El ciclo de puesta y la supervivencia de los jóvenes en la región costera, reflejan lo que acontece en todo el seno de la California Meridional.

INTRODUCTION

The abundance and distribution of several fish populations off the Pacific coast of North America

have been monitored using ichthyoplankton surveys conducted by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) since 1949. These surveys extended from Baja California to Washington state and several hundred km offshore, and were directed at the detection of gross changes in abundance and distribution patterns (Smith 1972). These data have also been used to estimate production and survival of early life stages, with the ultimate goal of explaining and predicting variations in population growth (Smith 1973; Lasker and Smith 1977; Zweifel and Smith 1981; Hewitt 1981; Hewitt and Methot 1982; Hewitt 1982). The principal species of interest has been the northern anchovy (*Engraulis mordax*), partly because of its importance in the natural economy of the California Current and partly because it is typical of clupeoid populations, which are highly productive and support some of the largest fisheries in the world.

Another source of ichthyoplankton data is the Ichthyoplankton Coastal and Harbor Studies (ICHS) (Brewer et al. 1980; Brewer and Smith 1982). During this project the nearshore zone of the Southern California Bight was sampled monthly from June 1978 through July 1980. This zone, within ca. 3 miles of the coast, often harbors high densities of phytoplankton and microzooplankton (Eppley et al. 1978; Beers and Stewart 1967; Lasker 1981) and may also be a region of enhanced larval survival and elevated anchovy productivity.

Brewer and Smith (1982) described the ICHS collections of anchovy and sardine (*Sardinops caerulea*) eggs and larvae. They reported that the seasonal cycle and standing stock of anchovy eggs and larvae in the nearshore zone were comparable to those estimated for the greater Southern California Bight from CalCOFI surveys. The nearshore region accounted for 3.8% of the area and 3% of the larvae contained by the greater Southern California Bight. Brewer and Smith concluded that the nearshore zone was not a preferred spawning habitat; however, they withheld judgment on the importance of the region as a nursery ground.

In this paper we compare the production of larval anchovy in the nearshore zone with that throughout the Southern California Bight. We pooled stage-specific catches through the 1980 spawning season

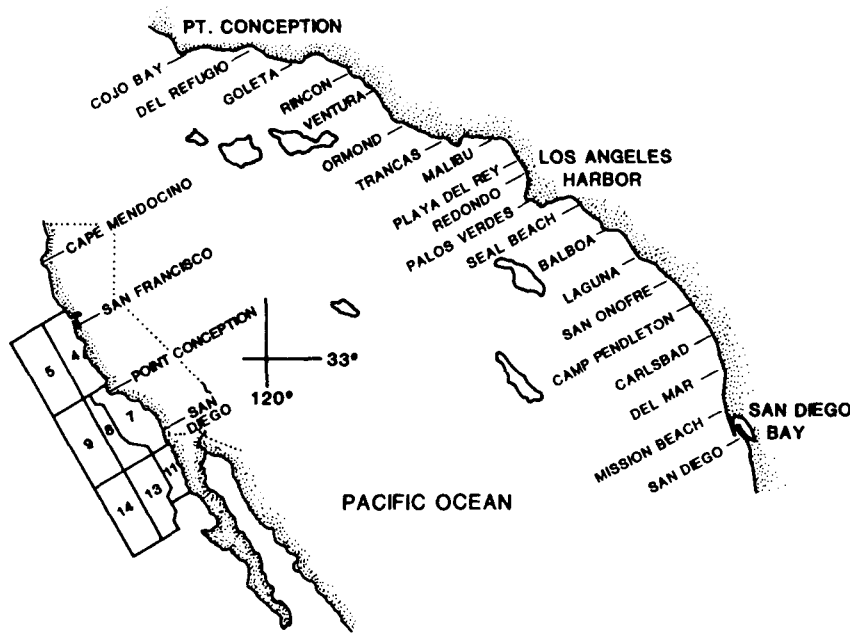


Figure 1. The Ichthyoplankton Coastal and Harbor Studies (ICHS) sampled 20 transects in the nearshore zone (within 3 miles of the coast) of the Southern California Bight between Point Conception and San Diego. Region 7 of the CalCOFI sampling grid is defined here as the greater Southern California Bight (inset).

and derived age-specific production estimates by adjusting the catches for growth and sampler bias. We briefly discuss three hazard functions and fit production curves to the data. Finally, we contrast the curves from the two regions and discuss their interpretation.

MATERIALS AND METHODS

We define the greater Southern California Bight as CalCOFI region 7, encompassing the area between Point Conception and the international border at San Diego, and seaward approximately 200 km (Figure 1). The nearshore zone is defined as that portion of the bight within the 43-m isobath and the mainland coast, and contains 2,652 km² (3.8%) of the total 69,055 km² area of CalCOFI region 7. The data reported here were obtained from August 1979 through July 1980 (ICHS Phase II; Brewer and Smith 1982), and the production comparisons were made for the 1980 spawning season (January through June 1980).

The ICHS sampling regime consisted of 46 stations, along 20 transects, that were occupied each month. Stations were positioned over the 8-m and 22-m isobaths on each transect and additionally over the 15-m and 36-m isobaths on the Ormond, Redondo, and San Onofre transects (Figure 1). The sampling gear was a 70-cm diameter bongo frame, fitted with 333-micrometer mesh Nitex nets and an opening-closing device. The gear was deployed to the bottom; the net

apertures were opened; and the gear was retrieved obliquely to the surface, filtering an average of 8.1 m³ of water per m of depth fished. Additional details regarding sampling techniques and laboratory procedures are described by Brewer and Smith (1982).

CalCOFI region 7 was sampled during four cruises conducted in March, April, and May 1980. Two gear types and respective station grids were employed. The first was a 70-cm oblique bongo tow deployed on standard CalCOFI stations; the net was 505-micrometer Nitex with no opening-closing device, fished to 210-m depth and filtering an average of 3.7 m³ per m of depth (see Stauffer and Picquelle 1981, for a description of these cruises, and Kramer et al. 1972, Smith and Richardson 1977, for sampling techniques and laboratory procedures). The second gear was a 25-cm diameter frame, with a 333-micron Nitex net, deployed to 70-m depth and retrieved vertically (see Hewitt, in press, for a brief description of the CalCOFI vertical egg tow-CalVET sampler). The CalVET sampler was deployed over a dense grid of stations with the purpose of intensively sampling anchovy egg production.¹

Plankton samples were preserved and returned to the laboratory, where they were sorted, and the anchovy eggs and larvae were identified and enumer-

¹Stauffer, G. D., and S. J. Picquelle. MS. Egg production estimates of spawning biomass of the northern anchovy for 1980 and 1981.

TABLE 1
 Survey Cruises Contributing to the ICHS Sample of the
 Nearshore Zone and the CalCOFI Sample of the Greater
 Southern California Bight (Region 7)*

Cruise designation	Dates	Number of stations	Percent positive	Egg density (#/m ²)	Larval density (#/m ²)
ICHS					
1979					
15	13-24 Aug	46	98	38	20
16	10-21 Sept	46	100	3	15
17	8-18 Oct	46	85	22	4
18	5-16 Nov	46	54	15	3
19	3-13 Dec	46	78	69	9
1980					
20	7-19 Jan	46	91	70	81
21	11-28 Feb	46	100	191	91
22	10-22 Mar	46	98	295	195
23	7-17 Apr	46	100	124	50
24	12-25 May	46	93	34	22
25	16-26 June	46	87	6	7
26	14-25 July	46	65	4	2
CalCOFI bongo					
8003TK	24 Feb-2 Mar	24	100	—	106
8003JD	27 Mar-6 Apr	20	95	—	204
8005JD	11 Apr-29 Apr	29	90	—	94
8005JD	24 May-30 May	24	71	—	57
CalCOFI CalVET					
8003/04JD	27 Mar-29 Apr	458	64	326	—

*The sample obtained with the CalVET net includes tows made in regions 8 and 11 as well.

ated by developmental stage. Results were expressed in numbers of eggs or larvae under 1 m² of sea-surface area.

RESULTS

Standing Stock

Anchovy eggs and larvae were caught at most stations during every ICHS survey (Table 1). On the other hand, the density of eggs and larvae varied two orders of magnitude as the spawning season progressed. Low spawning activity in the fall is followed by an increase in spawning in December, achieving a maximum in March and declining through July. The bell-shaped seasonal spawning curve (Figure 2) is similar to that found throughout the spawning habitat (Brewer and Smith 1982; Hewitt 1980; Hewitt and Methot 1982).

Seasonal catches by stage are described in Figure 3. Nine percent of the year's catch was taken between August and November. The early fall spawning peak, apparent in the August survey, was limited to the western portion of the Santa Barbara Channel. Very little spawning occurred in September and October, and larger larvae (10-mm mode in September, 15-mm mode in October) were encountered in Santa Monica Bay. Some spawning and small larvae were detected

DENSITY OF ANCHOVY EGGS AND LARVAE

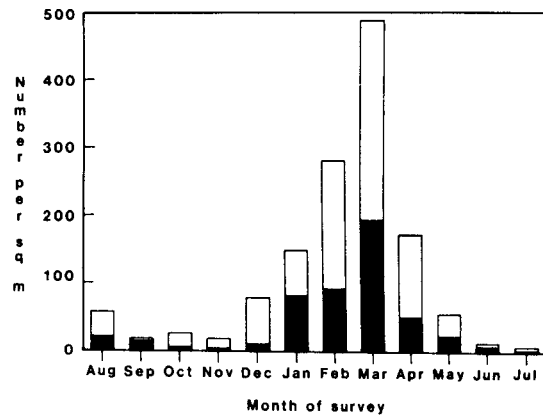


Figure 2. Densities (number under 1 m² of sea-surface area) of anchovy eggs (clear) and larvae (shaded) in the nearshore zone by survey month. The bell-shaped spawning curve is similar to that observed throughout the spawning habitat.

in the Santa Barbara Channel in November. By December, spawning increased in intensity and spread south and east to Santa Monica Bay. In January spawning extended from the Santa Barbara Channel to the Los Angeles harbor, and larger larvae were evident from the December spawning. By February, spawning was evident from the Santa Barbara Channel to San Diego and peaked in March with extensive spawning all along the coast. In April, May, and June spawning was progressively reduced and displaced southward. By July very little reproduction was evident; catches of large larvae from the previous months' spawning were made along the coast between Los Angeles and San Diego.

Data from the January through June cruises were pooled to draw the composite catch curve (Figure 4). These data constitute 85% of all the eggs and larvae retained, and describe the rise, peak, and decline of the spawning cycle.

Production

To appreciate trophic dynamics, and more specifically to assess the biological importance of a region, one must consider the flux of organic material (or production) rather than the simple standing stock. To do so we assumed that the average standing stock by stage was representative of a single cohort as it progressed through the larval period. This is the critical assumption and implies steady-state production of eggs and a stable age distribution. That eggs are continually produced in the population is supported by estimates that the average female spawns every 7 to 10 days during the spawning season (Hunter and Gold-

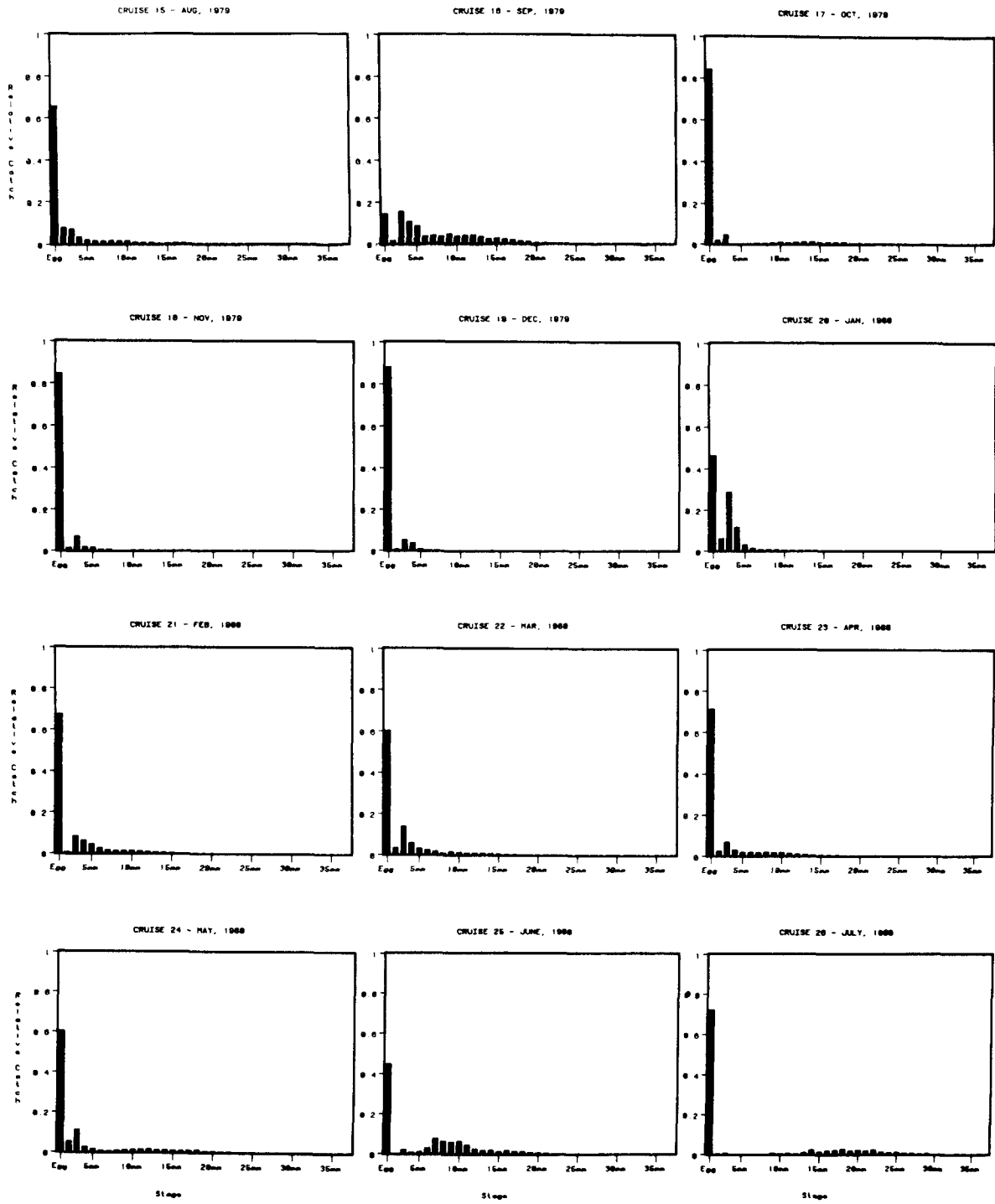


Figure 3. Relative catches by stage for each ICHS survey month reflect the seasonal spawning curve. Egg production in August resulted in catches of large larvae in September and October; large larvae again became a substantial portion of the catch in May, June, and July when egg production rapidly declined.

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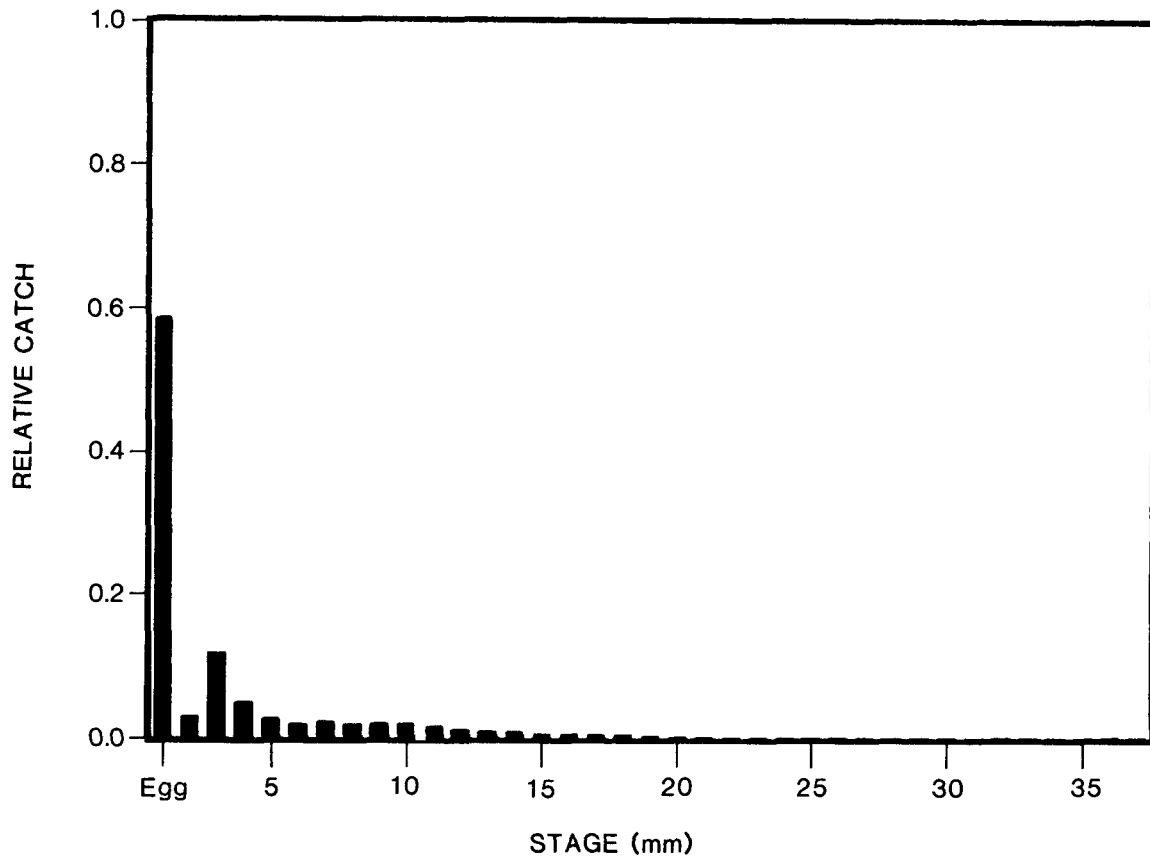


Figure 4. The average catch curve for the ICHS surveys conducted during the period January through June accounts for 85% of all eggs and larvae retained. These data were collected through the rise, peak, and decline of the spawning season. We assumed that the average standing stock by stage was representative of a single cohort as it passed through the larval period.

berg 1980; Hunter and Macewicz 1980; Picquelle and Hewitt 1983). Hewitt and Methot (1982) showed that an unbiased age distribution may be obtained by pooling data collected through the spawning season.²

The pooled catch curve (Figure 4) was then adjusted for sampling bias and variability: individual observations were adjusted for variations in the volume of water filtered per m of depth; bias corrections were applied for extrusion of small larvae through the meshes of the net; and the adjusted catches were divided by the duration of growth, through each stage, to estimate the age-specific production rate (P_t). The

adjustments were accomplished by fitting a weighted negative binomial model to the sample frequency distributions of each size class. Each observation was 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. The calculations are summarized in Table 2, and the results are described in Figure 5.

Estimates of production declined with age as the larvae starved or were preyed upon (Figure 5); initial mortality was severe and abated somewhat as the larvae developed. Our intention was to describe these data with a functional form; this curve is sometimes referred to as the mortality curve or, conversely, the survival curve; here we label it the production curve.

²Alternatively one may plot the seasonal curves of daily production for each stage and estimate total seasonal production as the area under the curves (Bamister et al. 1974). This method and the one described in the text yield essentially the same results, i.e., total seasonal production estimated from the seasonal curves of daily production is not different from the average daily production summed over the averaging period. Furthermore, the rate of decline in production with age is also the same.

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

Preserved size (mm)	Fraction retained in net ¹	Average adjustment for sampling and sorting variability ²	Average duration of growth ³	Average catch ($\frac{\text{number}}{\text{tow}}$)	P_t ($\frac{\text{number}}{\text{m}^2 \cdot \text{day}}$) ⁴	Age since fertilization (days)
Egg	0.917	15.848	2.43	1978.61	56.03	1.22
1.75	0.630	1.087	0.38	5.98	22.99	2.63
2.75	0.630	0.998	2.93	25.12	13.64	4.28
3.75	0.630	1.214	3.34	12.36	4.84	7.44
4.75	0.950	1.244	2.48	6.36	2.17	10.34
5.75	1.000	1.457	2.28	4.55	1.37	12.74
6.75	1.000	1.699	2.13	4.09	1.13	14.76
7.75	1.000	1.957	2.05	3.65	0.91	16.91
8.75	1.000	1.862	2.01	3.93	1.05	18.85
9.75	1.000	1.954	1.99	3.85	0.99	20.88
10.75	1.000	2.084	1.99	3.11	0.75	22.78
11.75	1.000	2.040	2.00	2.53	0.62	24.80
12.75	1.000	2.199	2.06	2.31	0.51	26.73
13.75	1.000	2.246	2.12	2.00	0.42	28.80

1. Extrusion corrections are based on relative retention rates between 75-micrometer and 333-micrometer mesh nets (Lo, in press).
2. Accounts for partial sorting of samples, and standardizes sampling volume to 1m³ per m of depth. An average of 17% of the larvae were sized.
3. Temperature-dependent embryonic growth is determined from laboratory experiment (Lo, in press), 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 (i.e., plankton tows).

To begin, we model the mortality as a portion of those living:

$$\frac{dp}{dt} = P Z(t)$$

where *P* is the production rate, *t* is age, and *Z(t)* is the hazard function (Watson and Leadbetter 1964), also referred to as the conditional failure rate, age-specific

death rate, or instantaneous mortality rate. By integrating the expression from 0 to *t* we can express the probability of an animal's living to time *t* as:

$$\frac{P_t}{P_o} = \exp\left(\int_0^t z(t) dt\right)$$

By rearrangement the production curve is:

$$P_t = P_o \exp\left(\int_0^t z(t) dt\right)$$

Several forms may be used for *Z(t)*; here we describe the consequences of three. Because animals are dying, the hazard function is always negative.

Case 1: $Z(t) = -Z$ (a constant)

This is the well-known constant mortality or exponential decay model. The production curve becomes:

$$P_t = P_o e^{-Zt}$$

If the population followed this model, the logarithm of the production rate would be a linear function of age, and the slope would be equal to $-Z$. With no increase in the number of parameters, the hazard function can be modeled to decrease with age³:

$$\text{Case 2: } Z(t) = \frac{-\beta}{t}$$

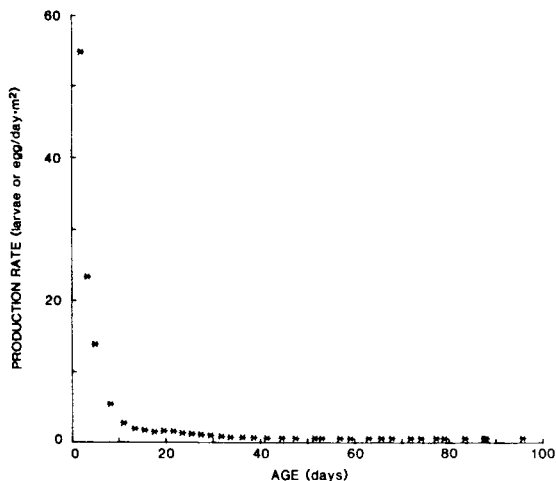


Figure 5. Estimates of age-specific production rates were derived from the pooled catch curve by adjusting the catches for growth and sampler bias. A production curve fit to these data must describe initially severe mortality, which abates somewhat as the larvae develop.

³Lo, N. MS. Egg production of central stock of northern anchovy, 1951-82.

As t increases, $Z(t)$ decreases, describing improving survival with age. The production curve becomes:

$$P_t = P_h \left(\frac{t_h}{t} \right)^\beta \quad \text{for } t \geq t_h$$

Although this form is attractive because only two parameters are required (P_h and β), it cannot be extrapolated to time zero. Picquelle and Hewitt (1983) applied this model to larval production data where t_h is the age of hatching, and time zero is the moment of fertilization. If the population followed this model, the logarithm of the production rate would be a linear function of the logarithm of age. The production curve may be extended to the origin by adding a third parameter (α):

$$\text{Case 3: } Z(t) = \frac{-\beta}{\alpha+t}$$

This form also describes improving survival with age; in addition, as t approaches zero, $Z(t)$ remains finite. The production curve becomes:

$$P_t = P_o \left(\frac{\alpha}{\alpha+t} \right)^\beta$$

As with Case 2, a linear plot of the logarithm of the production rate on the logarithm of age would be consistent with this model.

A semilog plot of production on age (Figure 6A) is nonlinear, particularly at ages less than 20 days, suggesting that a constant mortality model (Case 1) would not be appropriate. During this period aggregated eggs are disbursing and hatching; yolk-sac larvae are developing locomotor abilities; and post-yolk-sac larvae are rapidly acquiring sensory capabilities. Given the rapid ontogeny compressed into this phase of the life history, it may be biologically unreasonable to expect constant mortality. A log-log plot of the data (Figure 6B) is linear with a break at approximately 30 days of age; either of the decreasing mortality models described as Case 2 and Case 3 would be appropriate to describe the first 30

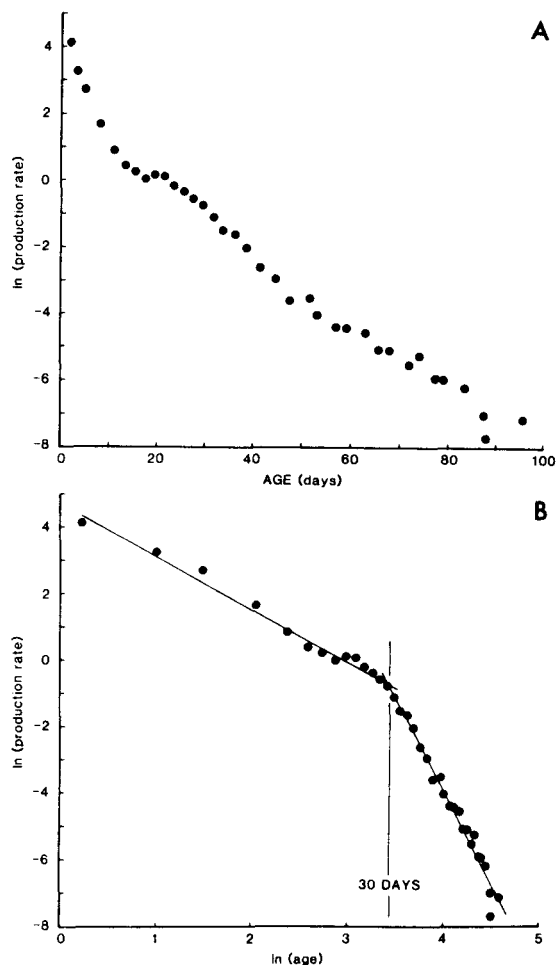


Figure 6 A. The semilog plot of production rate on age is nonlinear for the youngest stages, suggesting that the constant mortality model described as Case 1 would be inappropriate.

B. The log-log plot of production rate is linear with an abrupt change in slope at 30 days post fertilization. The lines are drawn by eye for the purpose of emphasizing the linearity and the break point.

TABLE 3
 Parameter Values and Production Rate Estimates for
 Production Curves Fit to the ICHS and CalCOFI Samples

Parameter	ICHS		CalCOFI	
	Parameter value	(Std. error)	Parameter value	(Std. error)
α	1.5	0.42	16.4	9.01
β	2.0	0.22	6.3	2.85
P_{10}	187.6	24.6	230.2	11.3
\hat{P}_{10}	3.0	—	11.4	—
\hat{P}_{20}	0.8	—	1.5	—
\hat{P}_{30}	0.4	—	0.4	—

days. We fit the Case 3 model to the age-specific production rates for animals less than 30 days old using a nonlinear least squares method. The resulting production curve is described in Figure 7; parameter values are listed in Table 3. Average egg production over the spawning season (January to June) in the nearshore zone was approximately 190 eggs per day per m^2 (standard error = 25).

Data representing the greater Southern California Bight are drawn from two sources: CalVET and bongo samples (Figure 8). The CalVET sample is a collection of observations made with a small vertical tow designed to sample pelagic fish eggs. These

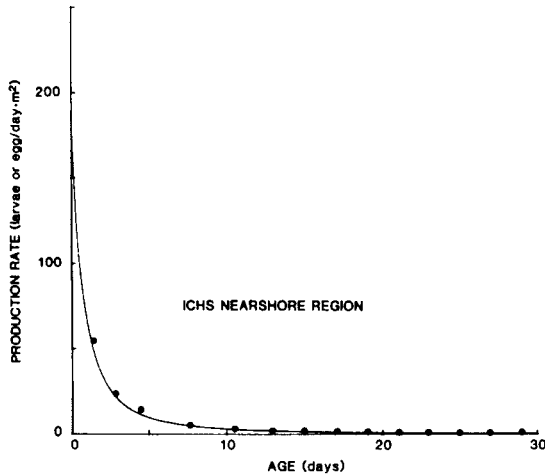


Figure 7. The production curve for the ICHS nearshore zone is of the form described as Case 3, and is fit to the production rate estimates for larvae less than 30 days old.

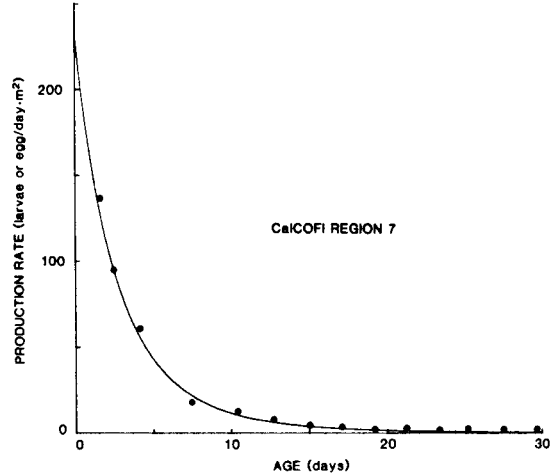


Figure 9. The production curve for the greater Southern California Bight (CalCOFI region 7) is of the form described as Case 3, and is fit to production rate estimates derived from both the CalVET and bongo samples.

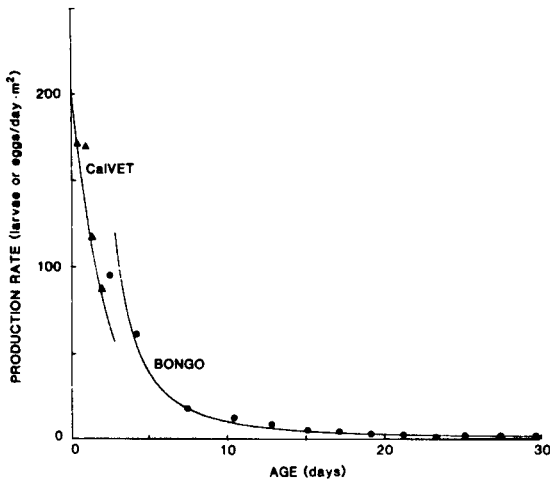


Figure 8. Anchovy egg and larvae production rates for the greater Southern California Bight are estimated from CalVET and bongo net samples obtained in CalCOFI region 7 during March, April, and May. The production curve fit to the CalVET data is of the form described as Case 1; the production curve fit to the bongo data is of the form described as Case 2.

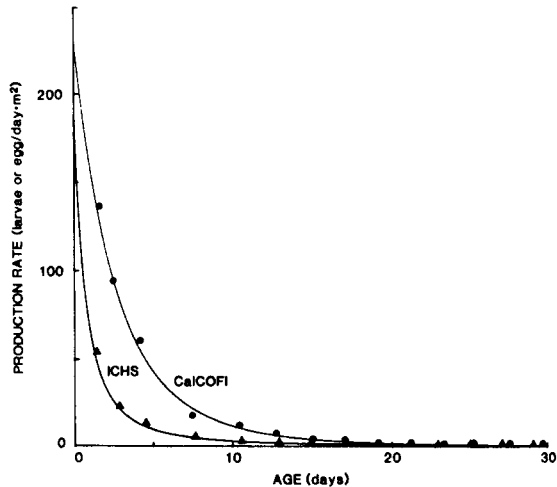


Figure 10. Initial egg production rates in the nearshore zone (ICHS sample) and the greater Southern California Bight (CalCOFI sample) are comparable. Mortality on eggs and yolk-sac larvae appears to be more severe in the nearshore zone; however, the production of 30-day-old larvae is again comparable between the two regions.

data are presented as estimates of egg production in half-day increments over the incubation period (2.8 days at an average temperature of 15.15°C). Stauffer and Picquelle⁴ fit the egg-production curve using the constant mortality model described as Case 1. The bongo sample is a collection of observations made with a larger, oblique tow designed to sample larvae. The production curve is the functional form

described as Case 2 proposed by Lo⁵ and is analogous to analyses reported by Picquelle and Hewitt (1983). Although the sampling gears are quite different in design, they generate complementary and consistent data (Figure 8). The data were merged, and a single production curve (Case 3 functional form) was fit (Figure 9 and Table 3). Although a constant mortality for eggs and variable mortality for larvae may be

⁴See footnote 1 on page 236.

⁵See footnote 3 on page 240.

biologically reasonable, a two-phase production curve is indistinguishable from the single curve for this data set. Average egg production over March, April, and May in the greater Southern California Bight was approximately 230 eggs per day per m^2 (standard error = 11).

The production curves for the nearshore zone (ICHS) and for the greater Southern California Bight (CalCOFI region 7) are superimposed in Figure 10. Initial production of eggs is comparable in both areas, although early mortality appears to be more severe in the nearshore zone. Later mortality in the nearshore zone is less severe, and the production of 30-day-old larvae is comparable between the two areas.

DISCUSSION

The primary conclusion that may be drawn from these data is that there is no evidence for enhanced production of young anchovy larvae in the nearshore zone. In addition, differences between the shapes of the production curves (Figure 10) are provocative. Anchovy eggs and yolk-sac larvae appear to suffer a more severe mortality in the nearshore zone than in the Southern California Bight. These are also the stages that are most contagious (patchy) in their distribution patterns (Hewitt 1981, 1982), and the most proximate to the adult schools that spawned them. Cannibalism on anchovy eggs is a significant source of mortality (Hunter and Kimbrell 1980), and it may be that the restricted depth range of the nearshore zone acts to increase the incidence of cannibalism. Higher densities of juvenile anchovy and general planktivores in the nearshore zone may cause heavier predation on these stages, which are very aggregated and not yet fully mobile.

Nearshore survival of feeding larvae appears to improve so that the production of 30-day-old larvae in the nearshore zone is comparable to that in the greater Southern California Bight at 0.4 larvae per day per m^2 . The improved survival in the nearshore zone may be due to better feeding conditions, although Methot (1981) reported that most young anchovy were growing at the maximum rate, suggesting that food may not be limiting their survival. Increased turbidity of nearshore water may enhance protection from visually oriented predators, but this advantage must be offset partially by the increased density of predators. Regardless of the cause, if the difference in survival rates continued into the juvenile stage, then the nearshore zone would be an area of enhanced anchovy productivity. This question cannot be addressed until methods are developed to effectively sample late larvae and juvenile fish.

Large larvae were caught during the ICHS cruises, although the downward bend in the production curve at 30 days (Figure 6B) suggests that larvae either entered a region of higher mortality or they were increasingly able to avoid the sampling gear. The CalCOFI data also displayed a change in the slope of the production curve at 30 days, and because of the causal ambiguity we eliminated older larvae from the analyses. After comparing the day and night catches of successively larger larvae, Hewitt and Methot (1982) suggested that anchovy larvae, 30 days and older, are increasingly able to avoid capture at night as well as during the day. The ICHS sample contained a greater fraction of large larvae than the CalCOFI sample, although less than would be expected from an extension of the production curve beyond 30 days. Larger larvae become increasingly aggregated as they adopt the schooling habit (Hewitt 1981), and it may be that the difference between the data sets is because the ICHS gear samples a much larger volume of water per tow and thus increases the probability of encountering an aggregation of large larvae. With this interpretation, the difference in catch rates of large larvae may not represent a density difference so much as an example of a problem with sampler threshold. Alternatively, the density of large larvae may indeed be higher in the nearshore zone; again this question cannot be addressed until more appropriate samplers are developed.

The critical assumption involved in deriving a production curve from catch data is that a stable age distribution prevails. The errors introduced by seasonal variation in egg production can be minimized by pooling data collected throughout the spawning season (Hewitt and Methot 1982), as we have done with the ICHS surveys.

Immigration and emigration of eggs and larvae to and from the nearshore zone may also upset the assumption of a stable age distribution. Because we are comparing production between regions, we cannot pool spatially as we did temporally and must therefore examine the monthly distribution maps and catch curves for evidence of larvae moving in or out of the nearshore zone. There was nothing to suggest significant immigration or emigration: larvae were more dispersed but encountered in the same general area as eggs; egg production in August resulted in catches of large larvae in September and October; large larvae again became a substantial portion of the catch in May, June, and July, when egg production rapidly decreased. If there was constant transport into the nearshore zone, the apparent mortality would tend toward that of the bight;

whereas constant transport out of the nearshore zone would tend to exaggerate the apparent mortality relative to that of the bight. In fact, neither transport nor spawning are steady through the season and may interact to produce a complex pattern of effects. However, the continuity of geographic patterns between stages and from survey to survey suggests that these effects are not great.

The survey data presented here suggest that production of young anchovy (less than 30 days old) in the nearshore zone is representative of production throughout the greater Southern California Bight. The seasonal production cycle, the density, and the survival of spawn are comparable between the regions. We emphasize, however, our lack of knowledge regarding the late larval and juvenile stages; until this can be improved, the significance of the nearshore zone to anchovy production cannot be fully appreciated.

ACKNOWLEDGMENTS

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