ABSTRACT

Eleven ichthyoplankton surveys, conducted during the winter and spring quarters of 1978 and 1979, indicate that spawning of the northern anchovy, *Engraulis mordax*, was contracted both spatially and temporally in 1978 relative to 1979. Larvae were farther offshore in 1979. Instantaneous daily larval mortality rate estimated from slope of the age-frequency distribution (yolk sac through 15 mm, ca. 25-30 days) varied insignificantly between 1978 and 1979 and averaged 0.168. Comparison to a simple model of spawning suggests that seasonal changes in the slopes are due solely to a systematic bias and not to real changes in the mortality rate.

Seasonal larval production was compared with birthdate distributions of fish surviving to the juvenile stage. In both years March had the greatest larval production and was the commonest month of birth among the survivors of the larval stage. Larval survivorship tended to increase within the 1978 spawning season and decrease within the 1979 season. Low survivorship in winter 1978 is consistent with the hypothesis that winter storms disrupted aggregations of prey necessary for larval feeding, but does not explain why apparent recruitment was greater in 1978 than 1979. Variation in larval survivorship could not be attributed to larval mortality. The offshore distribution of larvae in 1979 may have contributed to the relatively low survival.

La producción larval temporal fue comparada con distribuciones de fechas de nacimiento de peces que sobrevivieron hasta la etapa juvenil. En ambos años, la mayor producción de larvas ocurrió en marzo, y el haber nacido en este mes era más común entre los sobrevivientes de la etapa larval. La supervivencia larval tendía a aumentar en la época de desove de 1978 y a descender en la época de 1979. La supervivencia baja del invierno de 1978 es consistente con la hipótesis de que tormentas de invierno interrumpieron conjuntos de presas necesarias para alimentar las larvas, pero no explica porque el reclutamiento era mayor en 1978 que en 1979. La variación en la supervivencia larval no se pudo atribuir a la mortalidad larval. La distribución de larvas fuera de la costa en 1979 pudo haber contribuido a la supervivencia relativamente baja.

INTRODUCTION

The planktonic phase of a schooling fish’s life history is considered the most amenable to quantitative sampling (Smith and Richardson 1977). Egg and larval surveys have been used to estimate the number of adults responsible for their production (e.g., Sette and Ahlstrom 1948; Saville 1964; Smith 1972). Fish larvae are also of interest because they are the link between the present adult stock and some future recruitment to the adult stock. The lack of a clear relationship between stock and recruitment has focused attention on events during the larval stage and their ultimate effect on survival to the juvenile and adult stages.

The literature on the pelagic fishes of the California Current is particularly rich. Smith (1981) summarized the influences on northern anchovy larval survival: (1) the availability of suitable prey for larvae exhausting their yolk sacs (Lasker 1978); (2) interspecific and intraspecific predation (Hunter 1976; Hunter and Kimbrell 1981); (3) starvation (Hunter 1976; O’Connell 1980); (4) effect of adult nutritional state on quality of eggs and fitness of larvae (Smith and Lasker 1978; Hunter and Leong 1981); (5) preschooling dispersal (Smith 1973; Hewitt 1981); and (6) larval transport to or from favorable areas (Sette 1950; Parrish et al. 1981).

In this report we describe the results of ichthyoplankton surveys conducted in 1978 and 1979, and discuss what may be inferred about factors affecting larval anchovy survival during those 2 years. Distri-
The results of this first summarization are used to describe the distribution and relative abundance of larval anchovy but requires a large sample size, so no within-cruise stratification was possible. The age-specific larval production and the catch in each 1-mm size class. The correction for volume of water filtered was calculated as:

\[ f_i = \left( \frac{V_i}{D} \right) \left( \frac{1}{3.5} \right) \]

where \( V \) is volume filtered, \( D \) is maximum depth sampled, and 3.5 is the standard sample of 3.5 m³ per m of depth.
Figure 1. CalCOFI survey grid is divided into 23 regions. The central subpopulation of the northern anchovy is contained within the shaded regions (Vrooman and Smith 1971).
The correction for avoidance of the net during daylight was calculated by a sinusoidal function:

\[ f_2 = \frac{(1 + DN_L) + (1 - DN_L) \cos \left( \frac{2\pi t}{24} \right)}{2} \]

where \( DN_L \) is the midday-to-midnight catch ratio of \( L \)-length larvae, and \( t \) is the hour of the tow. The factor is 1.0 at midnight and declines to a size-specific minimum \( DN_L \) at noon. The ratios of mean catch during night (2030-0230 h) to mean catch during day (0830-1630 h) are presented in Figure 2 along with similar curves derived from catches by the 1-m bridled net (Ahlstrom 1954; Smith 1981).

The correction for extrusion of small larvae through 0.505-mm mesh was calculated as:

\[ f_3 = 0.3311 \exp \left\{ 1.10526[1 - \exp(-0.0165L^3)] \right\} \]

where \( L \) is the preserved length of the larvae. This correction was derived by Zweifel and Smith (1981) from the catch rates of nets with 0.333-mm mesh compared to paired catches by 0.505-mm mesh. The factor increases asymptotically to 1.0.

The correction for duration of each size class was calculated from temperature-specific growth of yolk-sac larvae (2.6-4.1 mm) in the laboratory (Zweifel and Lasker 1976; Zweifel and Hunter, unpubl. data) and growth of feeding larvae measured in the sea by daily increments in otoliths (Methot and Kramer 1979). Methot (1981) found that growth was similar to temperature-specific growth in the laboratory, but a month-specific model, which we use here (Methot and Hewitt 1980), was a more precise description. We divide the durations by a standard duration of 2 d/mm.

The slope of the relation between larval production (duration-corrected mean larval abundance) and age is an estimate of larval mortality rate. We calculate the linear regression of \( \log_e (m_t) \) (production) on age:

\[ \log_e (m_t) = \log_e (m_0) - z(t) \]

where \( m_t \) is the mean production of the size class with mean age \( t \), \( z \) is the instantaneous mortality rate, and \( m_0 \) is the estimated production rate of hatching larvae (per 2 days). Interpretation of the slope as the mortality rate requires the assumption that the spawning rate is constant. Later we evaluate consequences of violating this assumption.

Hewitt (1982) makes use of patchiness indices derived from the contagion parameter, \( k \).

Some selection of stations was necessary for the second summarization procedure. Samples with no larvae presented a problem because they cannot be clearly interpreted: some result from sampling outside the habitat entirely, and others result from low densities within the habitat. The zero samples do not influence the census estimates, but they do influence the fit of the negative binomial model to the frequency distribution of larval catch for each size class. We defined the habitat as those areas where a larva of any size was found, and excluded samples containing no larvae. In the Los Angeles Bight (Pt. Conception to San Diego), and within 20 miles of the coast, sampling effort was often increased. To correct for the effect of oversampling, data from up to 6 stations on the inshore end of a station line were averaged to a composite station.

RESULTS

The geographic distribution of spawning differed between the 2 years. In 1978 larvae were found throughout the surveyed region, but most occurred between Pt. Conception and San Diego (Figures 3-9). During May to August all larvae of the central population were in this subregion. In 1979 the distribution of spawning was displaced southward (Figures 10-13). In the region north of Pt. Conception (CalCOFI lines 60-77) the census of 2.6-4.9-mm larvae for the 4 cruises between January and May was 587 in 1978 and 109 in 1979 (Tables 2 and 3). In the region including lines 80-97 the censuses were 19,853 in 1978 and 13,240 in 1979. In the south, lines 100-110, only 2 cruises, March and May, can be compared. In 1978 the census for 2.6-4.9-mm larvae in March and May was 418; in 1979 it increased to 6258.
Figures 3 through 13. "Orchard" charts depict spatial disposition of four groups of larvae for each cruise. Height of "tree" is proportional to the number of larvae per 10 m$^2$ of sea surface.
Figure 5.
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Figure 6.
Figure 7.

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Figure 8.
Figure 9.
Figure 10.
Figure 12:
Figure 13.
In addition to being displaced southward, larvae were farther offshore in 1979 (Table 4). Few larvae were collected offshore of the islands in 1978 (Figures 3-9), and offshore larvae commonly occurred in 1979 (Figures 10-13). The mean distances offshore of larvae for the 4 cruises between January and May (with larval census as weighting factor) were as follows:

<table>
<thead>
<tr>
<th>Size group</th>
<th>2078</th>
<th>2079</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.0-8.3</td>
<td>584</td>
<td>584</td>
</tr>
<tr>
<td>8.4-11.3</td>
<td>584</td>
<td>584</td>
</tr>
<tr>
<td>11.4-14.3</td>
<td>584</td>
<td>584</td>
</tr>
</tbody>
</table>

The trend with size differs between the years; however, the magnitudes of the trends are small unless one includes values for large larvae, which are based on few positive samples. The temporal distribution of spawning also differed between the years. In 1978, anchovy spawning was moderately low during December and January, increased to a pronounced peak in early March, and decreased to a low level in May; larval abundance was very low by July and August (Table 2). In 1979, spawning was moderately low in January, and increased to a peak in early March. The peak was not as sharp as in 1978, and spawning was sustained at a
moderate level through May (Table 3). Integrated over January, March, April, and May, anchovy larvae were 1.2 times more abundant in 1979 than in 1978.

To summarize: spawning during 1978 was compressed spatially and temporally relative to 1979. Spawning during 1978 was displaced southward and offshore, and took place later in the year.

An example of the second summarization procedure is presented in Figure 14. The frequency distributions are highly skewed but adequately described by the mean, m, and contagion parameter, k, of the negative binomial distribution. The slopes of the regressions of loge (m) on t ranged from 0.23 to 0.15 during December 1977 and the first 4 months of 1978 (Table 5). We will not interpret slopes based on the low and probably sporadic level of spawning during the summer. During the first 5 months of 1979 the slopes ranged from 0.19 to 0.13.

Interpretation of the slopes of the above regressions as mortality rates requires the assumption of a stable age distribution (i.e., continuous and constant production of newly hatched larvae). The March larval abundance peak clearly violates this assumption, so we set up a hypothetical population to examine the extent of bias that may arise. The simulated population had a seasonal spawning cycle approximated by the normal curve, with peak spawning occurring at the end of March. A number of larvae were hatched each day, according to the distribution, and allowed to die at an instantaneous mortality rate of 0.15. Numbers of surviving larvae by age were summarized by month, and the instantaneous mortality was recalculated. Mortality is overestimated when spawning is increasing and underestimated when spawning is declining; the bias increases with seasonal contraction in spawning (Table 6). The bias is asymmetrical, greater when spawning is increasing; however, when larval numbers are accumulated over the entire season, the biases tend to cancel out. The observed seasonal decline in the slope of the larval catch curve (Table 5) is exactly as expected from constant mortality and the observed seasonal changes in larval production.

We calculated an annual estimate of mortality using the larval catch accumulated over each spawning season. The instantaneous mortality of young larvae in 1978—0.175—was not significantly different from that for 1979—0.161.

DISCUSSION

The ultimate importance of events in the larval stage is their effect on survival into the juvenile stage. We have information regarding the between-year and also within-year variation in survival. Differences in larval anchovy survival between 1978 and 1979 may be inferred from the age distribution of the commercial landings of anchovy; despite greater production of larvae in 1979, the 1978 year class was about twice the size of the 1979 year class (J. Sunada, California Department of Fish and Game, pers. comm.). Methot (1981) described the temporal distributions of birthdates of juvenile fish sampled from these 2 year classes. In both years larval abundance peaked in March, and March was the commonest birthmonth (Figure 15). Neither year class was dominated by individuals born during some short period. Thus survivorship within 1978 and 1979 was proportional, for the most part, to larval production. Deviations from constant survivorship may be characterized as greater survivorship of spring 1978 spawn relative to winter 1978 spawn and the reversed seasonal pattern in 1979. This pattern of deviations was not evident in our estimates of early larval mortality. The twofold difference in survivorship between the years appears to be at least as large as the survival variability within the years.

In discussing the above survival patterns, we must consider the environmental conditions during these 2 years. Winter mixed-layer temperatures were cooler in 1979 than 1978; the Los Angeles Bight temperature ranged from 14° to 15°C in March 1978 and 12° to 13°C in March 1979. The incursion of a cold-water tongue into the Los Angeles Bight was evident in April 1978 and not in April 1979; the southern shift of spawning in 1979 may have been a reaction to thermal conditions or avoidance of an upwelled water mass.
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CRUISE 7803

Avg. weight 0.286 0.623 0.423 0.432 0.377 0.367 0.370 0.365 0.333 0.350 0.320 0.327
m 256.59 95.22 64.53 41.65 28.18 21.31 13.60 11.17 0.34 5.82 3.42 1.63
k 0.1473 0.2069 0.2018 0.3118 0.2947 0.2604 0.3006 0.3827 0.1951 0.1555 0.0904 0.0853

Figure 14. The sample distributions of sized larvae, from cruise 7803, can be approximated by negative binomial distributions defined by the parameters m and k.

(Lasker et al. 1981). By May of both years, a tongue of cool water extended southeastward off Pt. Conception; pockets of cold water were adjacent to the central California and northern Baja California coasts; and a warm-water plume trailed to the southeast off Santa Catalina Island. There were no obvious differences in
winter 1978, and remained below normal through May 1978. Upwelling was again low during winter 1979 but returned to normal by spring. Parrish, Nelson, and Bakun (1981) suggest low upwelling will entrain larvae closer to shore and lead to higher survivorship. Changes in the onshore-offshore distribution of larvae need not affect our estimates of early larval mortality rates. The important affected factor is the fraction of larvae capable of being recruited to the nearshore juvenile habitat. The seasonal pattern of survivorship in 1978 is not consistent with the drift hypothesis, but the seasonal pattern in 1979, the offshore distribution of larvae in 1979, and the relative year-class strengths do support this hypothesis.

We conclude that, in 1978 and 1979, significant variations in survival occurred during the late larval through juvenile stages. We also conclude that there is reason to doubt that larval surveys alone are sufficient to consistently predict recruitment.

In addition to the factors affecting survival of spawn, attention should be addressed to the factors affecting the production of spawn and its distribution in time and space. Since 1966, the central population of the northern anchovy has contracted spatially, expanded the spawning season, exhibited north/south shifts in the spawning center, and varied the month of peak spawning activity from January to May (Hewitt 1980).

ACKNOWLEDGMENTS

The material presented here has been extracted from our Ph.D. dissertations. The work was accomplished with the support and encouragement of our doctoral committees and the Southwest Fisheries Center. We especially wish to thank Drs. Reuben Lasker, John Hunter, and Paul Smith for their advice and critical review.

LITERATURE CITED


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