SEASONAL VARIATION IN SURVIVAL OF LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, ESTIMATED FROM THE AGE DISTRIBUTION OF JUVENILES

RICHARD D. METHOT, JR.[1]

ABSTRACT

Juvenile northern anchovy, *Engraulis mordax*, collected during autumn of 1978 and 1979 were aged using daily increments in their otoliths. Neither year class was dominated by individuals born during some short period, but March and April had the highest frequency of births in each year. Monthly ichthyoplankton surveys indicated that significant spawning occurred from January through May of each year and peaked in early March. Comparison of the temporal distribution of birth dates with larval abundance indicated that larval survival was similar in the first half of each spawning season and greater during April to May of the 1978 spawning season than the same period in 1979. This difference in seasonal pattern of survival was nearly sufficient to account for the observed greater recruitment in 1978 and is consistent with the hypothesis that offshore transport of larvae influences recruitment.

One goal of fish population dynamics is to understand the processes responsible for annual variation in recruitment. The variation can be more than an order of magnitude and is poorly correlated with abundance of spawners (Cushing and Harris 1973). The concept of a critical period during the early larval stage (Hjort 1926; Marr 1956; May 1974) has structured much of the research. Recent work has focused on the importance of temporal and spatial coincidence of first feeding larvae and concentrations of prey (Beyer and Laurence 1981; Lasker 1978; Vlymen 1977). However, transport of larvae away from juvenile nursery areas can influence recruitment (Nelson et al. 1977; Parrish et al. 1981) and the role of predation is unknown.

Seasonal variation in factors that cause annual variation in recruitment probably influences the average timing of spawning. Support for this hypothesis comes from the latitudinal correlation between duration of the spawning season and the plankton bloom (Wyatt 1980). More direct evidence is found within the North Sea where the short spawning season of each herring population bears a fixed phase relation to the mean date of the local plankton bloom (Cushing 1975). The timing of the most favorable environmental conditions may not be predictable in each year. The match-mismatch hypothesis (Cushing 1975) suggests that variation in the relative timing of spawning and the seasonal plankton bloom contributes to variation in recruitment.

Collection of sufficient years of data to test any recruitment hypothesis is difficult. However, a testable corollary of Cushing's hypothesis is that, in any year, larvae born during favorable environmental periods constitute most of the year class. The age distribution of juveniles—the survivors of the larval stage—is a function of the seasonal distribution of spawning and seasonal changes in larval survival. To test the match-mismatch hypothesis, the birth dates of juvenile northern anchovy, *Engraulis mordax*, were determined from daily increments in otoliths (Brothers et al. 1976; Methot and Kramer 1979; Pannella 1971) and compared with the seasonal distribution of spawning determined from ichthyoplankton surveys conducted during the 1978 and 1979 spawning seasons.

METHODS

Larval Abundance

The seasonal distributions of the northern anchovy larval abundance were estimated from ichthyoplankton surveys (Kramer et al. 1972) on the sampling grid (Fig. 1) of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Seven surveys were conducted between December 1977 and August 1978 and four surveys between January 1979 and May 1979. Only larvae from 2.6 mm (live standard length at hatch) to 5.1 mm (few days after yolk absorption and onset of feeding) were used in the analysis.

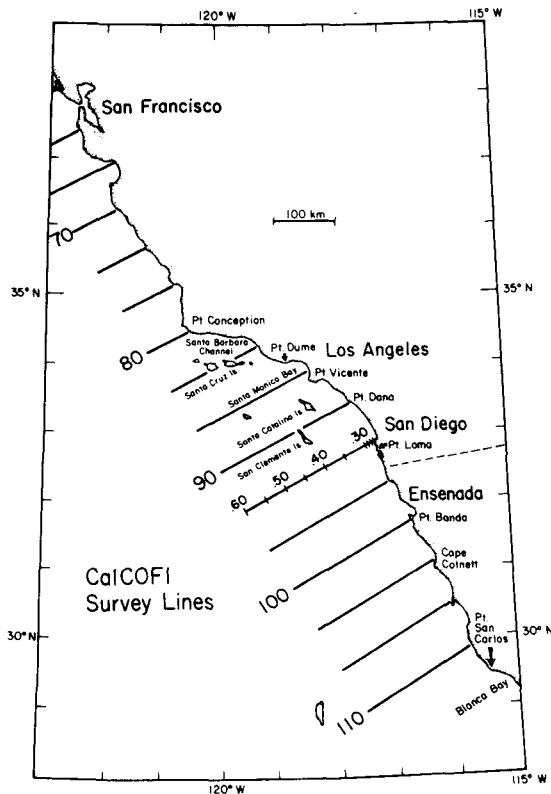Each cruise's larval census was the summed abun-

FIGURE 1.—Geographic region inhabited by the central population of northern anchovy. Ichthyoplankton samples were collected along CalCOFI survey lines. Location of stations is indicated only on line 93.3. Samples of juvenile anchovy were collected along the mainland coast. In 1978 these samples were obtained from the bait fishery from Pt. Conception to the United States-Mexico border. In 1979 samples were collected with a midwater trawl from Pt. Conception to Blanca Bay.

30 samples of northern anchovy were collected from bait receivers at sport fishing docks from San Diego to Pt. Conception, Calif. A total of 1,101 fish were measured, but sample size varied from 11 to 86 fish so each fish's contribution to the overall size distribution was weighted by the inverse of sample size. From 15 of the 30 samples, 141 fish were aged using daily increments in otoliths.

During 1-19 November 1979, specimens were obtained from samples taken with a 15 m midwater trawl on a survey conducted by the California Department of Fish and Game (CFG) to investigate the abundance of juvenile northern anchovy (Mais 1980). Trawls were taken parallel to the coast between the 30 and 90 m isobaths at 7.4 km coastwise intervals between Blanca Bay, Baja California, and Pt. Conception, Calif. Past trawl surveys indicate that the juveniles are concentrated into the nearshore zone (Mais 1974). A total of 2,356 fish were measured from the 93 positive trawls; sample size typically was 25 fish per trawl. In addition, 10 of the 25 fish per trawl were aged by CFG personnel using annual growth marks in otoliths (Collins and Spratt 1969). Juveniles are defined here as those fish with no otolith annuli. The fraction of fish with no annuli in each 5 mm size interval was calculated (Table 1). From 8 of the 93 samples, 129 fish were aged using daily increments in otoliths.

Size distributions were calculated in each of three alongshore regions: North of Pt. Dume (north), San Diego to Pt. Dume (central), and south of San Diego (south). These regions were selected on the basis of the distribution of samples in 1978 and minima in the

dance along CalCOFI lines 60-110. The catch at each station was adjusted for volume of water filtered and weighted by the distance to adjacent stations along the line. Abundances along unsampled lines were estimated from abundance in adjacent lines and cruises. A more complete description and further analyses of these data are in Hewitt and Methot (1982).

The mean and variance of date of larval catch were calculated for each cruise. Each station's contribution to these statistics was weighted by the distance to adjacent stations and by the catch of larvae. The effective duration of each cruise was considered to be ±2 standard deviations of catch date.

Juvenile Northern Anchovy Samples

During the period 28 October-14 December 1978,

TABLE 1.—Frequency of northern anchovy with and without otolith annuli. Specimens were collected by trawl during November 1979 (Mais 1980). Results are stratified by region and 5 mm size interval.

Size interval (mm) N annuli:	North of Pt. Dume		San Diego-Pt. Dume		South of San Diego	
	0	>0	0	>0	0	>0
50					1	
55			4		9	
60	1		7		3	
65	0		12		6	
70	2		11		18	
75	3		28		59	
80	8		23		50	
85	6		13		41	
90	12		8		41	
95	4		4	1	26	26
100	5		5	6	3	71
105	3	5	4	23	2	73
110	2	19	1	66	2	45
115	1	33	1	33		18
120		17		21		3
125		22		8		1
130		7		6		
135		5		5		
140		1				
145		4				

alongshore distribution of juveniles in 1979 (Methot 1981). The regional breakdown was necessary because the overlap in size between juveniles and older fish varied latitudinally (Table 1). Although data in Table 1 are entirely from 1979, they were used to calculate juvenile size distributions from overall size distributions in both 1978 and 1979. In 1978 few adults were collected and no comparable samples were obtained from south of San Diego.[2]

Otolith Preparation

Thawed specimens were measured to the nearest 1.0 mm standard length. Sagittae (largest otoliths) were removed, cleaned in distilled water, dried, and mounted on a microscope slide with a clear methacrylate-based mounting medium. Otoliths of northern anchovy larger than about 40 mm are too thick to transmit sufficient light for viewing the increments. Material was removed from the otolith's medial surface by applying 5-10% HCl to selected regions for about 10 s at a time. Immersion oil, petroleum jelly, or mounting medium were used to mask the outer edge of the otolith and regions already sufficiently thin. The selectively etched surface develops high relief but a thin layer of immersion oil renders this relief nonrefractory and permits examination of the otolith. After most increments became visible, the mounting medium was softened with 80% ethanol, and the otolith was turned over and remounted. Etching of the lateral surface continued until all increments were visible within, but not necessarily at the surface of, the remaining material.

The otoliths in 1978 were prepared by embedding in polyester casting resin and grinding sagittal sections on 400 and 600 grit wet sandpaper. Selective etching was faster and more successful than grinding.

Age Determination

Specimens used for this study also were used to back calculate juvenile growth and a direct count of all increments in an otolith was rarely made. Instead, age was determined from numerical integration of otolith growth (increment width). Increments were measured with a video camera mounted on a compound microscope, an electronic device which positioned a cursor in the video image, and a microcomputer interfaced to the device. All measurements were made along the longest radius of the otolith (towards the posterior margin). The observer positioned the cursor at the outer edge of an increment and keyed in the number of increments between that point and the previous point while the computer recorded the radius to that increment. Increment width usually did not change rapidly so 2-10 increments of similar size were entered together. Data from different regions along the longest radius were recorded at various stages of the etching process.

Data from both otoliths and several replicate transects per otolith were combined in the calculation of age. Mean increment width was calculated at all points along the longest radius. Etching errors occasionally produced a region in which increments could not be seen. When this occurred, increment width was interpolated from mean increment width in adjacent intervals by a linear interpolation of increment width on radius. Age was calculated from numerical evaluation of the following expression:

$$\sum_{i=1}^{n} \frac{r_i - r_{i-1}}{G(r_i)}$$

where the following definitions and boundary conditions apply:

r_i = set of all radial distances where increment width changed perceptibly

$G(r_i)$ = average increment width between r_{i-1} and r_i

r_0 = otolith radius at onset of increment formation (6.5 μm)

r_n = maximum otolith radius

$G(r_1)$ = typical initial increment width (0.8 μm per increment)

$G(r_n)$ = $G(r_{n-1})$ if $G(r_n)$ not measurable.

The result converges exactly to the count of increments if each individual increment is measured once. The age estimate was accepted if <20% of the age was from interpolated increments. About 3% of the fish were rejected by this criterion. The mean percentage of interpolated increments for the accepted fish was 4.7% and the median was 2.5%. Usually an independent age estimate could be made from each otolith. When fish were stratified into 50-d age intervals, the coefficient of variation of age between otoliths within fish averaged 4.6% in 1978 and 3.5% in 1979. Thus, the 95% confidence interval for a 250-d-old fish was ±14 d.

743

The birth dates calculated in this study are actually dates of onset of increment formation. The northern anchovy larvae deposit the first increment at about the end of yolk absorption, the fifth day after hatching at 16°C (Brothers et al. 1976). This is close to the mean age of larvae used to estimate larval abundances so no constant was added to the juveniles' ages when calculating birth dates.

The fish in the present study usually had 150-400 increments but the daily deposition of increments in northern anchovy otoliths has been confirmed only to 100 d in the laboratory (Brothers et al. 1976). The accuracy of my interpretation of daily increments in juveniles was tested by comparing birth-date distributions calculated from early samples with distributions calculated from late samples. The distributions should be indistinguishable if the samples were of the same cohort and mortality during the period was not age selective. In addition to the December 1978 samples used in this study, samples were collected at San Diego in September 1978 and February 1979 (Table 2). The three birth-date distributions were compared by the Smirnov test for differences in cumulative probabilities (Conover 1971, p. 309). The September and December distributions were very similar (maximum difference = 0.105, $P < 0.2$) and the February distribution was also not significantly different from September's (0.243, $P < 0.02$). This test is sensitive to aging errors of the same magnitude as the precision of the ages. If ages of February's fish had been overestimated by 15 d (one-half of fish in each month shifted to the following month) the difference between September and February would have increased to 0.376, $P < 0.1$. A 1-mo error in aging the February juveniles would have made the September 1978 to February 1979 comparison highly significant ($P < 0.01$). I conclude that any bias in aging must be less than about 15 d.

were selected to span a wide size range for an analysis of seasonal patterns of juvenile growth (Methot 1981). A less biased estimate of the birth-date distribution was obtained from the size-frequency distribution of a large sample of juveniles and a size/birth-date nomograph (Fridriksson 1934; Kimura 1977). In each year's nomograph, birth-date frequencies (by month) were calculated for fish in each 10 mm size interval. All samples within each year were combined in that year's nomograph.

RESULTS

Larval Abundance

The temporal distributions of northern anchovy larvae differed between the two years (Table 3). The maximum abundance occurred in February-March of each year but the peak was greater in 1978. Larvae were much more abundant during May 1979 than during May 1978. The average larva in 1979 was in water 1°C colder than the average larva in 1978 and was further offshore (Table 3). Larval production per 30-d date interval was calculated by numerical integration of the area under the dashed lines in Figures 2 and 3. Total larval production during January-May 1979 was 2.1% greater than during the same period in 1978.

Size and Birth-Date Distributions

In 1978 and 1979 northern anchovy juveniles, collected north of Pt. Dume, were typically larger (Table 4) and had been born earlier (Table 5) than juveniles collected to the south. The size/birth-date nomograms (Table 6) applied to the juvenile size distributions produced birth-date distributions (Table 7) with peaks in March-April for southern fish and

TABLE 2.—Birth-date frequency of juvenile northern anchovy collected at San Diego between September 1978 and February 1979.

Month		Sept.-Oct. 1978	Dec. 1978	Feb. 1979
	N samples:	2	2	1
	N fish:	28	19	15
	Length (mm): mean	77.8	76.4	82.1
	SD	5.5	6.5	5.9
Jan.		0	2	1
Feb.		3	1	1
Mar.		15	9	4
Apr.		10	6	7
May		0	1	2

Birth-Date Distribution

The selected specimens produce a biased estimate of the juvenile birth-date distribution because they

TABLE 3.—Abundance of northern anchovy larvae. Value in parentheses is the fraction of the abundance that was interpolated. N samples exclude offshore samples with no larvae. Date, distance offshore, and temperature at 10 m were weighted by larval catch at each station.

Date	N samples	Abundance	Distance (km)	Temp. (°C)
1977-78				
Dec. 15	42	448 (0.08)	119	16.3
Jan. 18	70	558 (0.00)	65	15.5
Feb. 25	87	2,367 (0.00)	65	14.9
Apr. 9	74	686 (0.00)	41	15.8
May 26	64	143 (0.00)	44	15.2
June 30	48	26 (0.00)	72	16.1
Aug. 13	20	26 (0.00)	22	18.1
1979				
Jan. 18	33	448 (0.45)	111	14.0
Mar. 2	71	1,524 (0.00)	65	13.9
Apr. 14	34	1,392 (0.40)	113	14.5
May 10	54	653 (0.00)	54	14.8

TABLE 4.— Size distributions of juvenile northern anchovy calculated from size distributions of all fish and size-specific juvenile fraction (Table 1). The percentage of the population composed of juveniles was also calculated (% juveniles). Area is the surface area (square nautical miles) nearshore of the 50 fathom isobath and excludes the shallow area around islands that was not sampled.

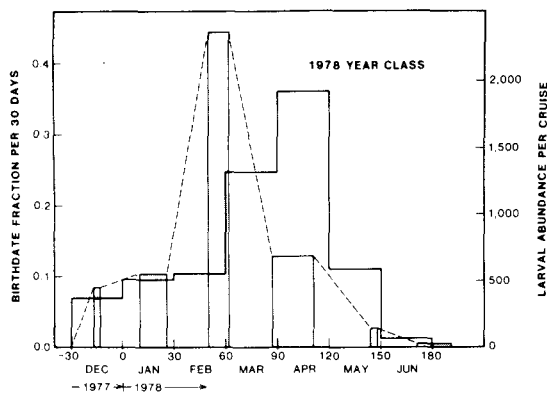|		1978		1979		
		north	central	north	central	south
	Area:	476	484	476	484	1,905
	N samples:	9	21	26	41	66
Size	N fish:	429	724	460	757	1,333
(mm)	% juveniles:	82.0	98.8	28.0	40.8	54.4
40-49		0.0	0.3	0.0	0.0	0.3
50-59		0.0	1.9	0.0	2.9	2.8
60-69		3.3	17.1	3.1	17.8	3.9
70-79		18.3	45.4	10.1	31.7	27.3
80-89		26.9	27.3	22.5	26.9	41.0
90-99		34.3	7.7	31.8	11.3	22.5
100-109		16.7	0.3	24.8	8.4	1.8
110-119		0.5	0.0	7.7	1.0	0.6

FIGURE 2.—Comparison of the seasonal distributions of northern anchovy larval abundance and birth dates of the 1978 year class. The width of the stippled bars is the effective duration of the ichthyoplankton survey (±2 standard deviations of the sample date where each sample is weighted by its catch of northern anchovy larvae). The dashed line was used to interpolate larval abundance per 30-d period. The open histogram indicates the fraction of juvenile's birth dates occurring per 30 d.

TABLE 5.—Frequency of observed birth dates of juvenile northern anchovy stratified by year and region and summarized by 10-d date interval.

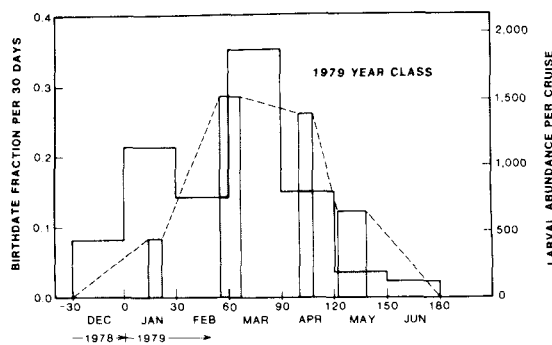| Date interval		1978		1979		
		north	central	north	central	south
	<-30	3	0	7	1	2
Dec.	-30	2	0	0	0	0
	-20	2	0	2	0	0
	-10	6	0	2	1	0
Jan.	0	1	0	4	1	0
	10	5	2	5	0	0
	20	3	1	3	0	1
Feb.	30	1	4	3	0	0
	40	1	0	1	1	0
	50	6	0	2	3	1
Mar.	60	2	9	0	2	4
	70	0	9	7	7	5
	80	1	6	3	7	5
Apr.	90	2	12	2	7	7
	100	0	14	0	1	0
	110	1	16	0	0	0
May	120	0	10	2	1	1
	130	0	7	2	0	0
	140	0	7	0	0	0
June	150	0	2	2	0	0
	160	0	2	1	0	0
	170	0	0	1	1	0
July	>180	0	4	3	13	2

FIGURE 3.—Comparison of the seasonal distributions of northern anchovy larval abundance and birth dates of the 1979 year class. See Figure 2 for explanation.

December-January for northern fish. The calculated birth-date distributions were similar to the observed birth-date occurrences in the two regions in 1978; the calculated differed from the observed in 1979 because selection of specimens was highly nonrandom in 1979. A substantial fraction of 90-110 mm fish in 1979 were assigned to birth dates before December 1978. Because these fish had no otolith annulus they are considered part of the 1979 year class.[3]

[3]Among the 95-105 mm anchovy examined in 1979, all those with an annulus (1978 year class) had 400-510 daily increments so had been born during summer of 1978. Among the similar-sized fish without an otolith annulus, some had been born in December 1978 and some as early as late summer 1978. This observation indicates the occasional ambiguity of assigning year classes when some spawning occurs throughout the year.

TABLE 6.— Size/birth-date nomograms stratified by 10 mm size interval and 30-d date interval (labeled by approximate month).

Size interval (mm)	Birth month								
	<Dec.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	>June
				1977-78					
40								1	2
50							4	2	1
60			1	0	2	14	10	0	1
70				2	7	20	5	1	
80			4	4	15	10			
90	2	5	4	4	3	1			
100	1	5	3	2					
				1978-79					
30									4
40									6
50								1	6
60					3	0	4	3	2
70				2	19	9	1	1	
80	1	2	7	6	17	8	1		
90	7	3	6	2	1				
100	2	0	1	1					

TABLE 7.—Birth-date distributions calculated from size/birth-date nomograms (Table 6) and regional juvenile size distributions (Table 4). Distributions are presented as %/30-d date intervals (labelled as approximate months). Combined birth-date distribution is mean of regional distributions with weighting factors proportional to nearshore shallow area (Table 4). Mortality correction factor accounts for the greater duration that the early born fish are exposed to juvenile mortality (see text). After multiplying the combined distributions by the mortality correction factors, the distributions are presented only for those months with larval abundance data.

	<Dec.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	>June	Weight factor
Regional distributions:										
1978										
central	0.8	2.1	5.5	7.6	23.7	41.9	15.4	2.0	1.0	83.4
north	5.2	16.8	15.3	14.7	21.5	21.8	4.1	0.5	0.1	16.6
1979										
south	10.5	5.5	14.5	10.5	34.9	15.5	3.1	2.2	3.3	66.5
central	9.5	3.1	10.4	9.3	34.7	14.0	7.6	5.9	5.5	16.9
north	28.5	6.1	21.9	15.4	17.0	7.6	1.9	1.1	0.5	16.6
Combined distributions:										
1978	1.5	4.6	7.1	8.8	23.4	38.5	13.5	1.7	0.9	
1979	13.3	5.2	15.0	11.1	32.0	13.8	3.7	2.7	3.2	
Mortality correction factors:										
		2.09	1.85	1.64	1.45	1.28	1.13	1.0		
Combined distributions corrected for juvenile mortality:										
1978		7.0	9.6	10.4	24.7	35.9	11.1	1.3		
1979		8.5	21.8	14.2	36.3	13.9	3.2	2.1		
1979			24.4	15.9	40.6	15.5	3.6			

Combining the regional results to produce an overall juvenile birth-date distribution is problematic, especially in 1978 when no samples were collected south of San Diego. Each region's weighting factor should be proportional to the abundance of juveniles in the region. Because local abundance of a pelagic schooling fish is measured crudely by a trawl survey, the areas of the primary juvenile habitat (Table 4) were used as weighting factors. The north region has only 16.6% of the total area nearshore of the 90 m (50 fathom) isobath, so contributes little to the total. Although the north region contributed nearly 50% of the total area from which samples were obtained in 1978 (Table 4), I assume that the unsampled fish from Baja California had birth dates similar to those of San Diego-Pt. Dume fish so I use

16.6% for the north's weighting factor in 1978. The combined birth-date distributions are in Table 7.

Correction for Juvenile Mortality

The birth-date distributions for the northern anchovy presented above represent the birth dates of those fish which survived until November. A monthly cohort's contribution to the birth-date distribution of its year class is a function of the spawning rate during that month, the mortality rates experienced by that cohort, and the age of that cohort when sampled. Northern anchovy juveniles which had been born during January are expected to be less abundant in November than juveniles born in May because the older juveniles experienced mortality as juveniles for

a longer period. A correction for this difference in age is necessary before differences between the seasonal distribution of larval abundance and the resultant distribution of juvenile birth dates can be interpreted as differences in larval survival. Few juveniles collected in November were <5-mo-old so the relative abundance of older juveniles need only be adjusted by the inverse of survival from age 5 mo to age at capture. Age-specific survival rate was assumed to increase from 64% per month at age 3 mo to 88% at 10 mo (calculated from preliminary estimates of juvenile mortality rates in Smith 1981). If one assumes no seasonality in juvenile survival, the resultant birth-date distributions are as if all the monthly cohorts had been sampled at the same age rather than at variable ages in November. Because most juveniles were between 6 and 10 mo old, corrected birth-date distributions are similar to the uncorrected distributions (Table 7).

Relative Larval Survival

The juveniles' birth-date distributions, corrected for juvenile mortality, and the seasonal distributions of larval production for the northern anchovy are presented in Figures 2 and 3. The ratio of monthly birth-date frequency to monthly larval production is an index of larval survival relative to survival from other months in the same spawning season. Survival tended to increase within the 1978 season and decrease within the 1979 season (Fig. 4). In both years the only anomalies to the trends were low relative survival of larvae born in February.

DISCUSSION

This study has documented seasonal changes in survivorship of larval northern anchovy. Both the magnitude and the timing of changes are important. The magnitude of the seasonal changes determines whether annual variation in recruitment could be caused by short seasonal events. The timing of the changes in survival relative to environmental events elucidates the linkage between oceanographic conditions and recruitment.

Temporal Patterns in Larval Survival

To evaluate the importance of seasonal changes in larval survival of the northern anchovy requires estimates of annual variation in recruitment. The age composition of the central population of northern anchovy is monitored through the fishery and trawl
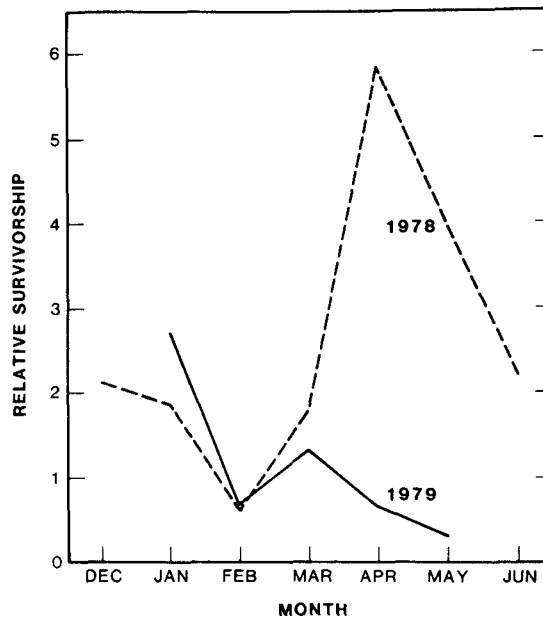

FIGURE 4.—Relative survivorship is the ratio of the fraction of northern anchovy juvenile's birth dates to the fraction of annual larval production per 30 d. To enable comparison between years the relative survivorship for 1978 has been scaled by the ratio of recruitment (2.0) and the ratio of annual larval production (0.98) between the 2 years.

surveys. Mais (1981a) analyzed the age composition of the commercial fishery in southern California and suggested the following ranking of recent year classes: 1974 weak, 1975 weak, 1976 mediocre-strong, 1977 weak, and 1978 very strong. During the 1978-79 fishing season the 1978 year class of the northern anchovy contributed 65% of the southern California catch and in the following season the 1979 year class contributed 35% (Mais 1981a). In the spring 1979 trawl survey the 1978 year class contributed 62% and in spring 1980 the 1979 year class contributed 35% (Mais 1980, 1981b). Thus the fishery and the survey indicate that the 1978 year class was about twice as large as the 1979 year class.

This difference in recruitment cannot be explained by the abundance of young northern anchovy larvae. Northern anchovy larval production in 1979 was 2.1% greater than in 1978. Thus the larger 1978 year class resulted from higher survival because larval abundance was less in 1978 than in 1979.

The critical question is whether the recruitment variation described above requires more annual variation in larval survival than is caused by the seasonal changes described in this study. I evaluated this question by scaling the northern anchovy larval abundance estimates (Figs. 2, 3) with the ratio of lar-

747

val abundance between the 2 years (0.979), and the monthly fractions of juvenile birth dates (Table 7) were scaled by the ratio of recruitments (2.0). The ratio, (scaled birth date fraction)/(scaled larval abundance fraction), estimates relative survival of a month's spawn (Fig. 4). Because of the scaling, these ratios can be compared both between and within years. Survival of winter spawn in 1979 was similar to survival of winter spawn in 1978, but survival was much greater in April-May 1978 than April-May 1979. Thus, the larger 1978 year class was not necessarily the result of greater survival throughout the spawning season. The increase in survival during the last 2 major months of the 1978 spawning season was sufficient to cause a large increase in recruitment.

Detection of Changes in Survival

Detection of a match between spawning and favorable environmental conditions of the northern anchovy seems more likely than detection of an event which results in poor survival. If a short-duration favorable environmental period results in a doubling of year class abundance, then more than half of the year class would have been born during that period. Such a concentration of birth dates could have been, but was not, detected in 1978 and 1979. A particular match apparently was not necessary for these two year classes. Conversely, a short-duration unfavorable environmental period that destroys all northern anchovy larvae born during the period may cause only a small reduction in year class abundance and a short gap in the birth-date distribution that would be difficult to detect with small sample sizes.

The effect of other environmental events will be more difficult to detect. Long-duration events or events that affect larvae of a wide age range will have little effect on the birth-date distribution. Secondly, environmental events which do not extend over the geographic range of spawning may not be detected even though they have important local effects.

Spatial Pattern

This study was designed to study temporal changes in frequency of juvenile birth dates but a strong spatial pattern also was detected. Northern anchovy juveniles collected north of Pt. Dume were larger than southern juveniles because of earlier birth dates. Hewitt and Methot (1982) showed that spawning contracted towards the San Diego area as the 1978 and 1979 spawning seasons progressed. This trend would contribute to an earlier mean birth date

for northern fish, if currents and eddies did not substantially redistribute the larvae. In addition, if juveniles routinely move northward along the coast, early born fish will be further north by November. There are no data on the distribution of late larvae with which to investigate the cause of latitudinal pattern in juvenile birth dates. Geographic pattern in birth date will contribute to geographic pattern in size at age of adults.

Relation to Environmental Conditions

Two oceanographic factors, stability of the upper water column (Lasker 1978) and offshore transport (Parrish et al. 1981), have been suggested as factors in recruitment of northern anchovy. These factors should have had different effects on recruitment in 1978 and 1979.

Lasker (1975, 1978) suggested that northern anchovy larvae are likely to encounter adequate prey concentrations only when the upper water column is stable and prey are aggregated into layers. Of particular importance is the inshore chlorophyll maximum layer which may be composed of dinoflagellates suitable as prey for first feeding larvae. These layers are homogenized as storms or upwelling events destroy the stratification of the upper tens of meters of the water column. The winter of 1977-1978 was particularly stormy (Lasker 1981) and the isothermal surface layer was as deep as 50 m until stratification was restored in March. This hypothesis correctly predicts lower larval survival in winter 1978 than in spring 1978, but incorrectly predicts a poor year class in 1978.

Any hypothesis concerning the availability of prey will predict increasing survival through the major spawning season (December to June). Zooplankton biomass increases to its seasonal maximum in June (Smith and Lasker 1978). Stratification (differences between temperature at 10 and 30 m) increases so the prey of larval fish probably are increasingly aggregated into layers. Day length increases so that larvae can feed longer per day (Hunter 1972). A measurable response of northern anchovy larvae to the above factors is an increase in growth rate from 0.43 mm/d in January to 0.55 mm/d in June (Methot 1981) despite trivial changes in mean temperature (Table 3). If food availability is important to larval survival then survival should consistently increase through the spawning season.

The second major hypothesis concerns offshore transport and coastal upwelling caused by the predominantly northwest winds (Parrish et al. 1981).

748

Northern anchovy larvae which are transported offshore may experience higher larval mortality rates, and the survivors may be unable to return to the inshore juvenile nursery areas. Monthly indices of upwelling (Bakun 1973) at lat. 30° and 33°N, relative to long-term monthly means, were exceptionally low during January-March 1978 (downwelling occurred) and remained below normal through May 1978 (McLain and Ingraham 1980). Seckel et al. (1978) suggested that these conditions entrained larvae close to shore and correctly predicted an abundant 1978 year class. However, the results obtained here suggest that larval survival was higher during late spring 1978 than during the winter when downwelling occurred.

Upwelling was as low in December 1978 and January 1979 as in winter 1978, but the storms were less severe in 1979. Later in 1979, upwelling was near normal. The increased upwelling in 1979 relative to 1978 may have been responsible for the greater offshore displacement of northern anchovy larvae in 1979 (Table 4). The transport hypothesis correctly predicts a poorer year class in 1979 relative to 1978 and decreasing larval survival through the 1979 spawning season.

This brief examination of environmental data does not completely account for the patterns of recruitment of the northern anchovy in 1978 and 1979. Indices of offshore transport seem more important than indices of food availability, but the seasonal pattern of survival in 1978 could not be explained by transport. It is simplistic to assume that only one factor is involved in recruitment and that the effect of this factor is linear. One plausible scenario is that the winter storms of 1978 caused high mortality of early larvae, but the low upwelling throughout the year permitted high entrainment of late larvae and resulted in the good year class. It is also possible that the extremely low upwelling during winter 1978 did not have a proportionally greater effect than the low upwelling of spring 1978. Relatively low upwelling late in the spawning season may be important because absolute upwelling and transport typically increase through the spring (Smith and Lasker 1978). The spawning season may be timed to avoid low food availability in winter and high transport in late spring.

Other evidence indicates that survival of early northern anchovy larvae was nearly constant during the 1978 and 1979 spawning seasons. Hewitt and Methot (1982) inferred larval mortality from the slopes of the larval age-frequency distributions and found no significant seasonal changes. This evidence is consistent with the hypothesis that the significant change in survival which caused the difference in recruitment occurred after the early larval stage. Adverse larval drift would not necessarily cause increased mortality during the age interval examined by Hewitt and Methot but may affect the fraction of the surviving larvae which are entrained in the range of the juvenile habitat.

LITERATURE CITED

BAKUN, A.
1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.

BEYER, J. E., AND G. C. LAURENCE.
1981. Aspects of stochasticity in modelling growth and survival of clupeoid fish larvae. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178:17-23.

BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.

COLLINS, R. A., AND J. D. SPRATT.
1969. Age determination of northern anchovies, *Engraulis mordax*, from otoliths. In J. D. Messersmith (editor), The northern anchovy (*Engraulis mordax*) and its fishery 1965-1968, p. 39-55. Calif. Dep. Fish Game, Fish Bull., 147.

CONOVER, W. J.
1971. Practical nonparametric statistics. Wiley, N.Y., 462 p.

CUSHING, D. H.
1975. Marine ecology and fisheries. Camb. Univ. Press, Camb., Engl., 278 p.

CUSHING, D. H., AND J. C. K. HARRIS.
1973. Stock and recruitment and the problem of density dependence. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 164:142-155.

FRIDRICKSSON, A.
1934. On the calculation of age-distribution within a stock of cod by means of relatively few age determinations as a key to measurements on a large scale. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 86:1-15.

HEWITT, R., AND R. D. METHOT, JR.
1982. Distribution and mortality of northern anchovy larvae in 1978 and 1979. CalCOFI Rep. 23:226-245.

HJORT, J.
1926. Fluctuations in the year classes of important food fishes. J. Cons. Int. Explor. Mer 1:5-38.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.

KIMURA, D. K.
1977. Statistical assessment of the age-length key. J. Fish. Res. Board Can. 34:317-324.

KRAMER, D., M. J. KALIN, E. G. STEVENS, J. R. THRAILKILL, AND J. R. ZWEIFEL.
1972. Collecting and processing data on fish eggs and larvae in the California Current region. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 370, 38 p.

LASKER, R.
1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.

1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173:212-230.

1981. The role of a stable ocean in larval fish survival and subsequent recruitment. In R. Lasker (editor), Marine fish larvae: Morphology, ecology, and relation to fisheries, p. 80-87. Wash. Sea Grant Program, Univ. Wash. Press.

MCLAIN, D. R., AND W. J. INGRAHAM, JR.
1980. Marine environmental conditions in the eastern North Pacific Ocean. In E. D. Haynes (editor), Marine environmental conditions off the coasts of the United States January 1978 - March 1979, p. 5-39. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-OF-5.

MAIS, K. F.
1974. Pelagic fish surveys in the California Current. Calif. Fish Game, Fish Bull. 162, 79 p.
1980. California Department of Fish and Game sea survey cruises 1979. CalCOFI Data Rep. 22:82-87.
1981a. Age-composition changes in the anchovy, Engraulis mordax, central population. CalCOFI Rep. 22:82-87.
1981b. California Department of Fish and Game sea survey cruises 1980. CalCOFI Data Rep. 30:1-64.

MARR, J. C.
1956. The "critical period" in the early life history of marine fishes. J. Cons. Int. Explor. Mer 21:160-170.

MAY, R. C.
1974. Larval mortality in marine fishes and the critical period concept. In J. H. S. Blaxter (editor), The early life history of fish, p. 3-20. Springer, Heidelberg.

METHOT, R. D., JR.
1981. Growth rates and age distributions of larval and juvenile northern anchovy, Engraulis mordax, with inferences on larval survival. Ph.D. Thesis, Univ. California, San Diego, 200 p.

METHOT, R. D., JR., AND D. KRAMER.
1979. Growth of northern anchovy, Engraulis mordax, larvae

in the sea. Fish. Bull., U.S. 77:413-423.
NELSON, W. R., M. C. INGHAM, AND W. E. SHAAF.
1977. Larval transport and year-class strength of Atlantic menhaden, Brevoortia tyrannus. Fish. Bull., U.S. 75:23-41.

PANNELLA, G.
1971. Fish otoliths: daily growth layers and periodical patterns. Science (Wash., D.C.) 173:1124-1127.

PARRISH, R. H., C. S. NELSON, AND A. BAKUN.
1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175-203.

SECKEL, G. R., A. BAKUN, AND R. PARRISH.
1978. Large-scale atmospheric circulation and the west coast upwelling regime in 1976/77 and 1977/78. In Proceedings of the Third Annual Climate Diagnostics Workshop: Cooperative Institute for Marine and Atmospheric Studies, University of Miami, Miami, Florida, October 31-November 2, 1978, p. 7-1—7-12. U.S. Dep. Commer., NOAA, Natl. Clim. Program Off., Rockville, Md.

SMITH, P. E.
1981. Sampling to determine anchovy larval mortality in the sea. In R. Lasker (editor), Marine fish larvae: Morphology, ecology, and relation to fisheries, p. 12-17. Wash. Sea Grant Program, Univ. Wash. Press.

SMITH, P. E., AND R. LASKER.
1978. Position of larval fish in an ecosystem. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173:77-84.

VLYMEN, W. J.
1977. A mathematical model of the relationship between larval anchovy (Engraulis mordax) growth, prey microdistribution, and larval behavior. Environ. Biol. Fishes 2:211-233.

WYATT, T.
1980. The growth season in the sea. J. Plankton Res. 2:81-97.