DISTRIBUTION AND MORTALITY OF NORTHERN ANCHOVY LARVAE IN 1978 AND 1979

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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.

RESUMEN

Once estudios de ictioplancton realizados durante los trimestres de invierno y primavera en 1978 y 1979 indican que el desove de la anchoveta *Engraulis mordax* en 1978 se produjo relativo al de 1979, tanto espacialmente como temporalmente. Las larvas estaban más lejos de la costa en 1979. El indice de mortalidad instantánea diaria de larvas que se estimó de la inclinación de la distribución de frecuencias de edades (vitelo hasta 15 mm, alrededor de 25-30 días) varió insignificativamente entre 1978 y 1979, con un promedio de 0.168. Una comparación con un modelo simple de desove sugiere que cambios temporales en las inclinaciones se deben únicamente a un sesgo sistemático y no a cambios verdaderos en el indice de mortalidad.

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 occurrió 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 porqué 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 contribuído 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 larvae 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-

bution maps, abundance estimates, and mortality are reported for each of 11 surveys.

METHODS AND MATERIALS

The data presented here were obtained during 11 cruises (Table 1) conducted off the coast of the Californias (Figure 1) in 1978 and 1979, as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Plankton samples were taken obliquely from a depth of 210 m with 0.505-mm mesh nylon nets mounted on a bongo frame (see Kramer et al. 1972, for detailed methodology). Samples were preserved in a buffered Formalin solution and an ethyl alcohol solution. A subsample of the alcohol-preserved specimens of anchovy larvae was aged using daily increments in the otoliths (Methot 1981). Anchovy larvae in Formalin-preserved samples were enumerated in 1-mm classes of standard length. Preserved larval lengths were adjusted to live lengths using the shrinkage factors reported by Theilacker (1980).

We use two different summarization procedures. The first will be presented on a fine spatial scale but will not take into account extrusion, avoidance, and growth that affect the relation between larval production and the catch in each 1-mm size class. The results of this first summarization are used to describe the distribution and relative abundance of larvae. The second procedure incorporates factors affecting the relation between larval production and catch but requires a large sample size, so no within-cruise stratification was possible. The age-specific larval productions resulting from the second summarization are used to calculate mortality rates of larvae.

Only samples from the central population of anchovy are considered in the quantitative analyses. Electrophoretic and morphometric data indicate that anchovy along southern Baja California constitute a separate population (Vrooman and Smith 1971). We exclude samples collected south of CalCOFI line 110 (Figure 1). A third population occurs primarily along

the coasts of Oregon and Washington.

In the first summarization, larval catches were stratified into four classes of live length (2.6-4.9 mm, 5.0-8.3 mm, 8.4-11.3 mm, and 11.4-14.3 mm) and expressed as numbers of larvae under 10 m^2 of sea surface. Distribution maps of these summarized data were prepared. Each station's contribution to the larval census was weighted by the distance to adjacent stations along the CalCOFI line. Offshore stations were 40 miles apart; inshore stations were as close as 4 miles. The weighted sum of larvae was calculated for each line. Sums of unsampled lines were extrapolated from sums in adjacent lines and cruises. The total of the sums for CalCOFI lines 60-110 was the cruise's larval census.

Each station's contribution to the mean distance offshore of larvae was weighted by the distance to adjacent stations and by the catch of larvae at the station.

The second summarization procedure fits a negative binomial weighted model (Bissell 1972) to the frequency distributions of each 1-mm length class. The procedure was adapted for use on fish larvae by Zweifel and Smith (1981). The negative binomial distribution is described by two parameters: the mean, m; and the contagion parameter, k. The variance is related to these parameters by:

$$\text{Var} = m + \frac{m^2}{k}$$

According to the weighted model, the frequency distribution of actual catches depends not only on the underlying m and k but also on the individual effective sampler volume w_i. We consider two factors affecting each sample: volume of water filtered per unit depth and avoidance of the net by larger larvae during the day (Smith 1972). We include a third factor, extrusion of small larvae through the mesh, to permit quantitative comparison between size classes. This extrusion factor does not vary between samples. A fourth factor, temperature-and-month-dependent growth rate, corrects for variation in the period larvae remain in each size class. This duration factor transforms the results from a standing crop in each size class to production or flux through the size class. Each of the above factors is defined to be typically about 1.0. The product of the 4 factors is the effective sample volume w_i, for the ith sample.

The correction for volume of water filtered was calculated as:

$$f_1 = \left(\frac{V}{D}\right)\frac{1}{3.5}$$

where V is volume filtered, D is maximum depth sampled, and 3.5 is the standard sample of 3.5 m^3 per m of depth.

TABLE 1
CalCOFI Surveys 1977 through 1979

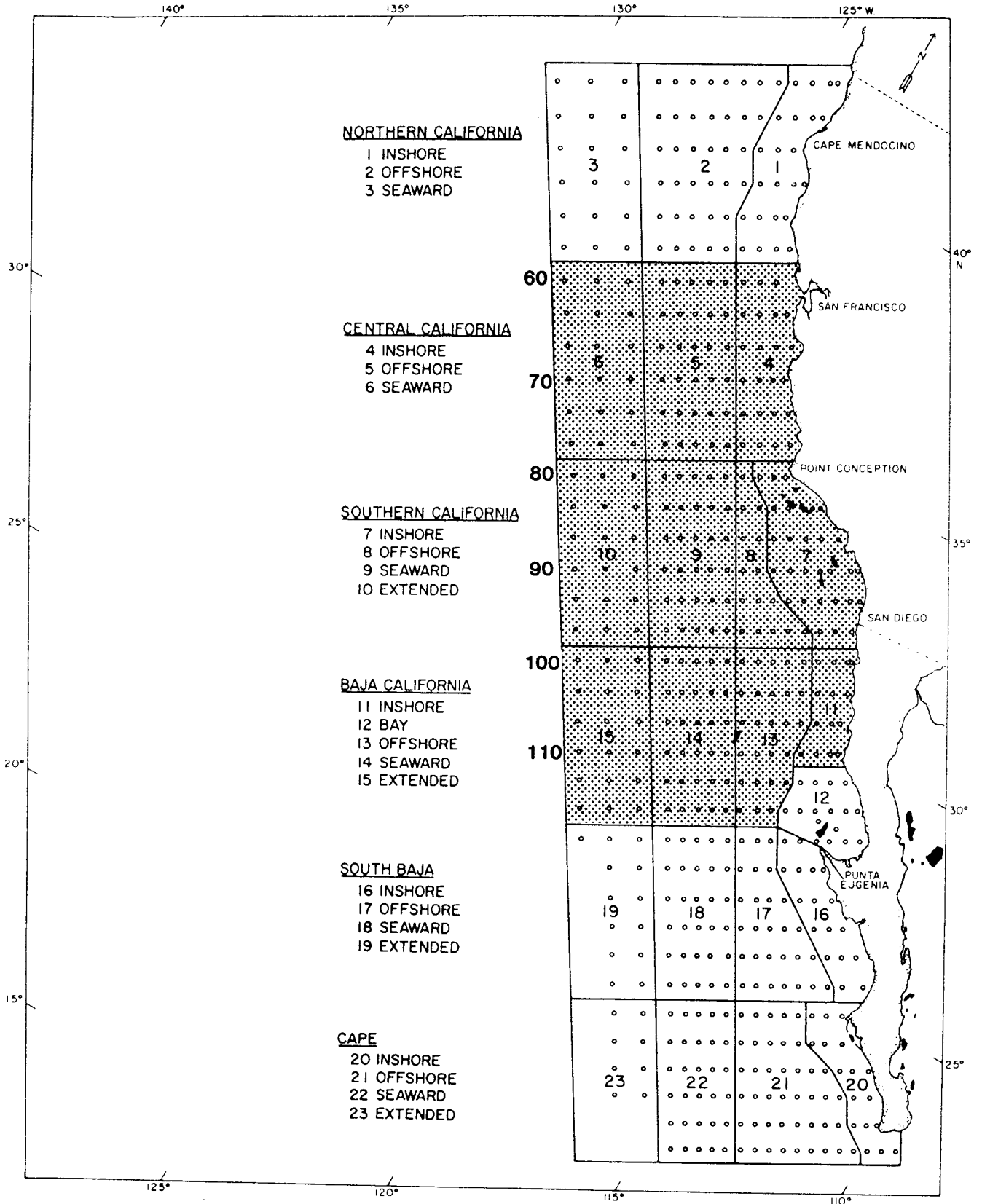| Cruise	Dates	Number of stations occupied	% positive for anchovy larvae
7712	Dec 8-Dec 19	80	54
7801	Jan 5-Jan 31	211	46
7803	Feb 18-Mar 15	208	59
7804	Mar 29-Apr 25	147	48
7805	May 14-Jun 10	132	39
7807	Jun 20-Jul 17	219	23
7808	Jul 31-Aug 26	118	17
7901	Jan 12-Jan 22	46	67
7903	Feb 25-Mar 13	95	66
7904	Apr 1-Apr 17	61	54
7905	Apr 30-May 21	102	51

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:

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

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:

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

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

Figure 2. The night/day larval catch ratio increases with larval length. The dots were calculated from the 1978 and 1979 surveys using the bridle-free bongo net. The stars are similar ratios for anchovy larvae using the bridled 1-m net (Smith 1981). The solid line is a regression fit to the night/day catch ratios for sardine larvae using a bridled 1-m net (Ahlstrom 1954).

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 $\log_e$ (production) on age:

$$\log_e (m_t) = \log_e (m_o) - z(t)$$

Where m_t is the mean production of the size class with mean age t, z is the instantaneous mortality rate, and m_o 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.
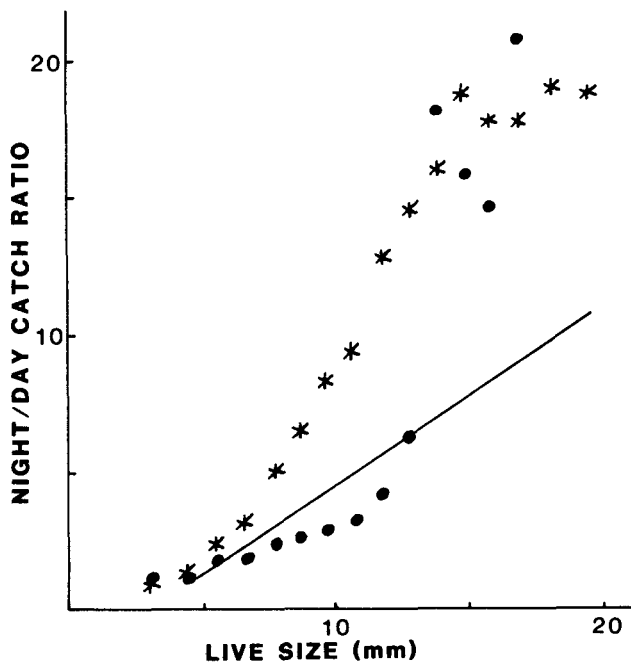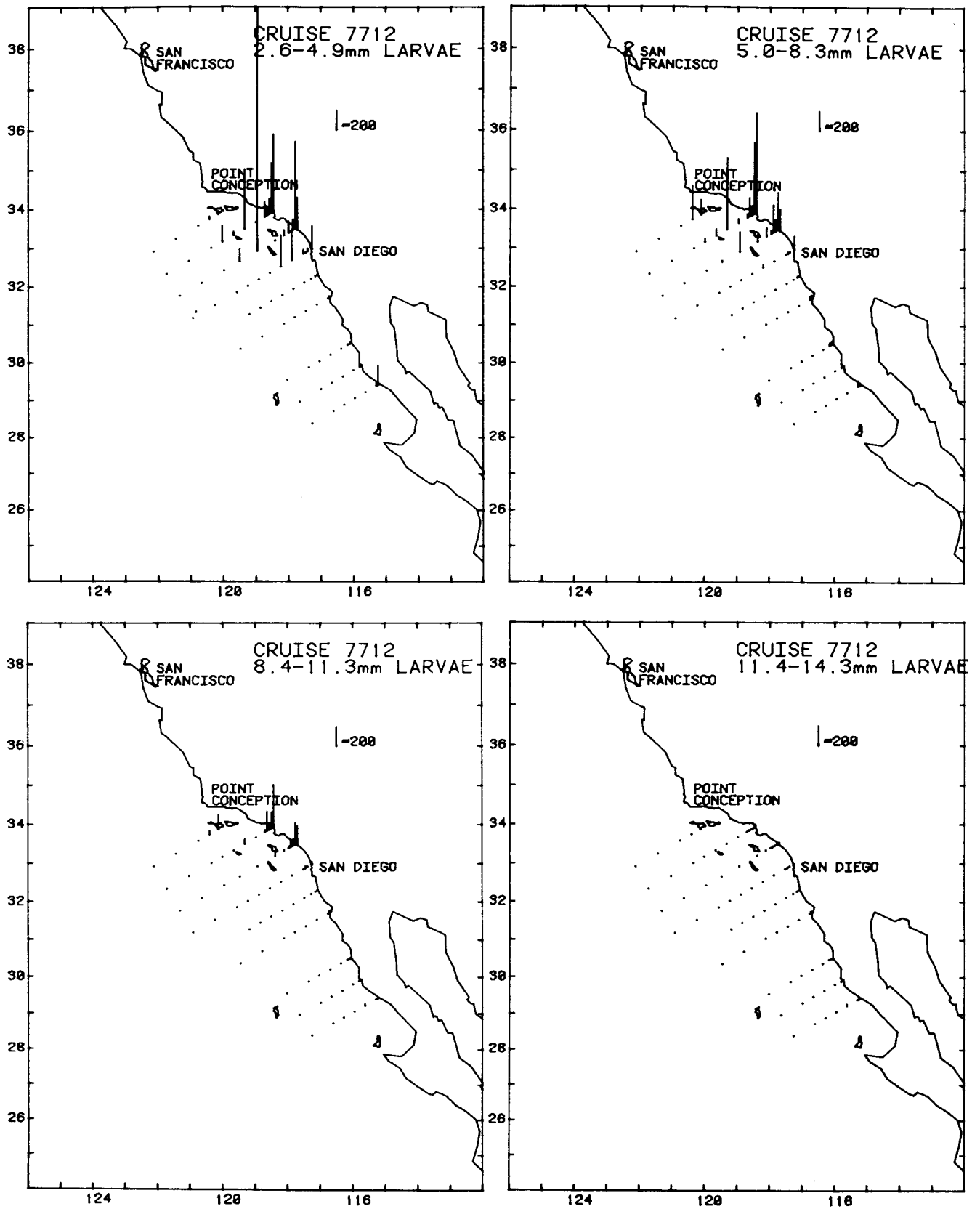
Figures 3 through 13. "Orchard" charts depict spatial disposition of four groups of larvae for each cruise. Height of "tree" is proportional to the number of larvae per 10 m² of sea surface.
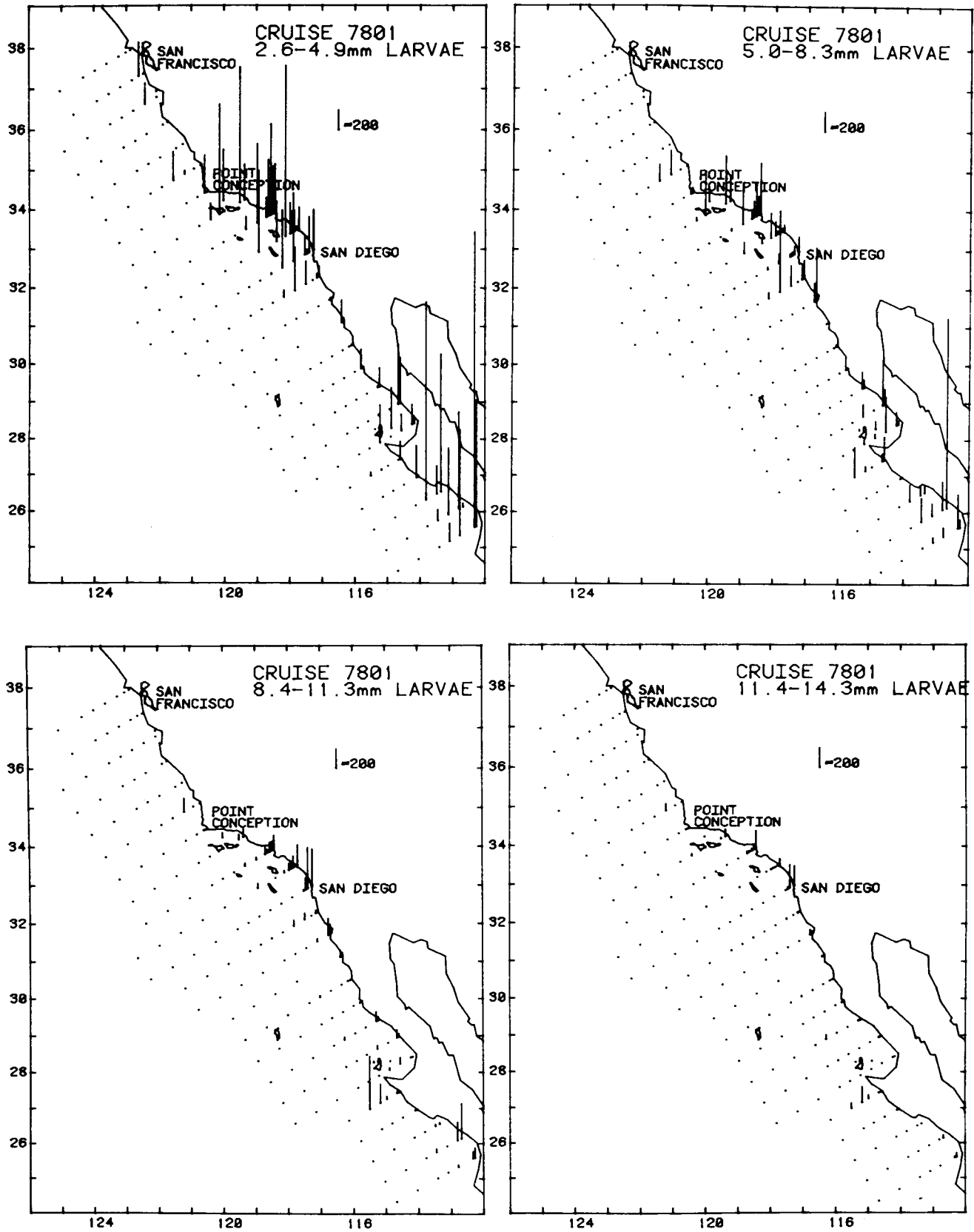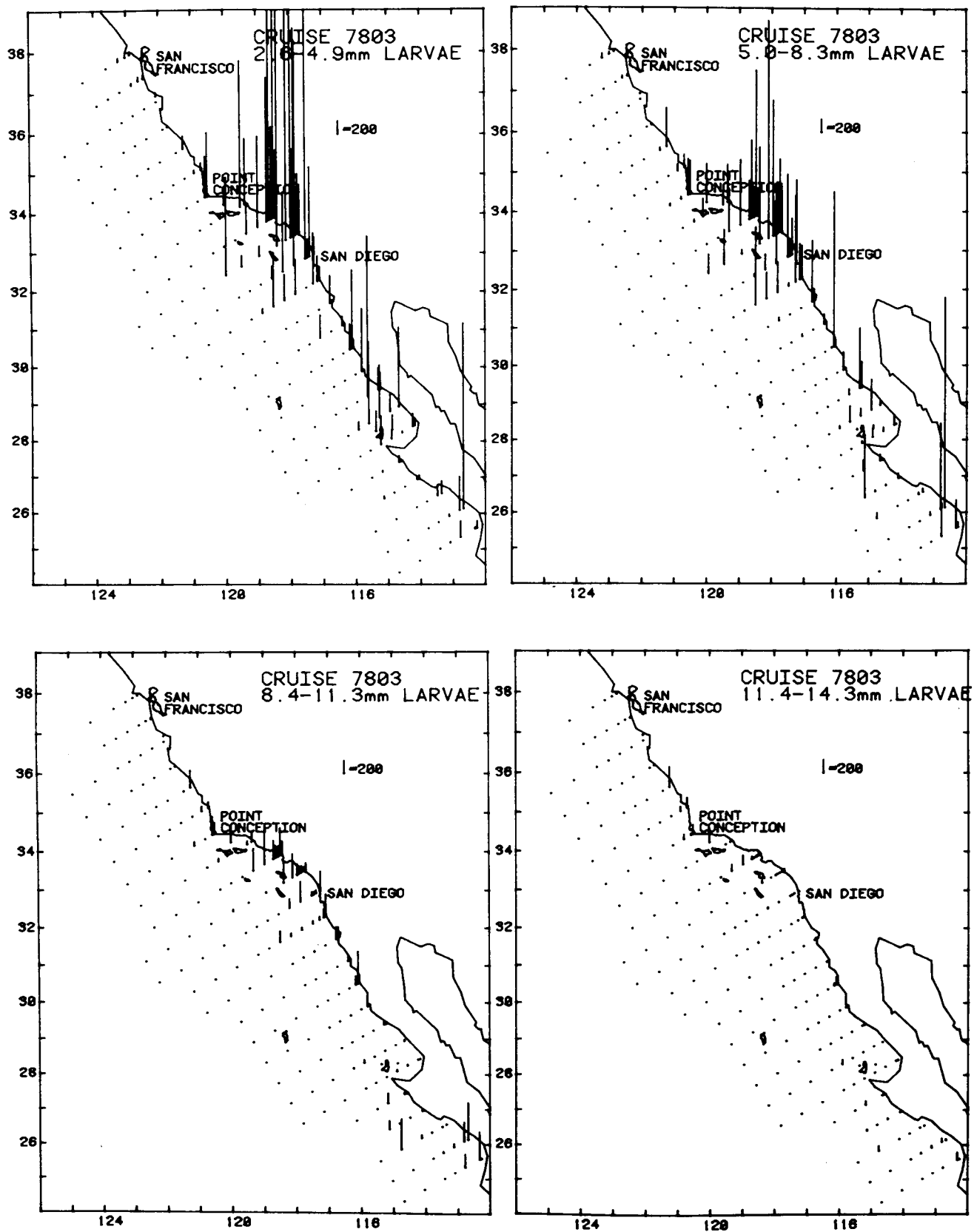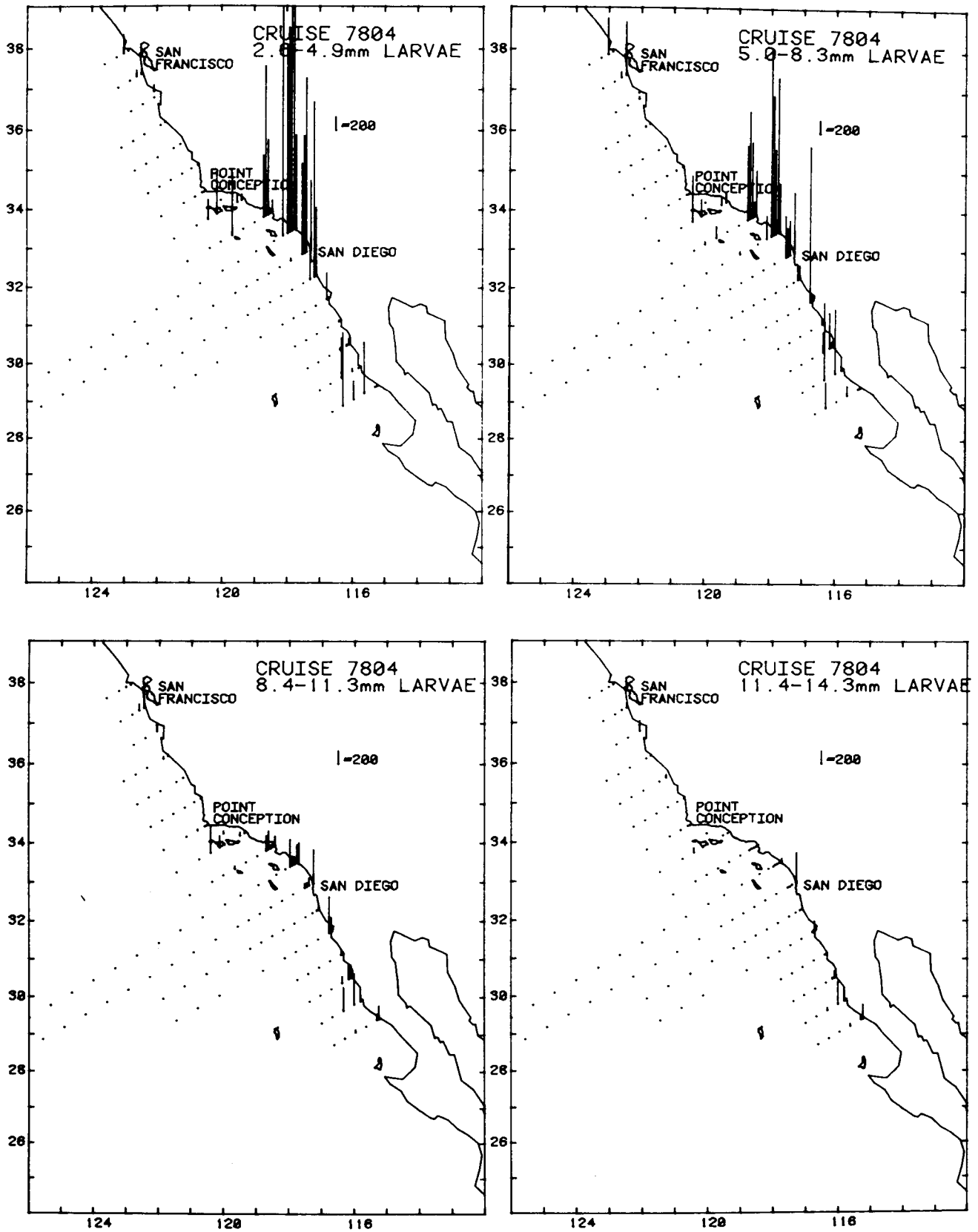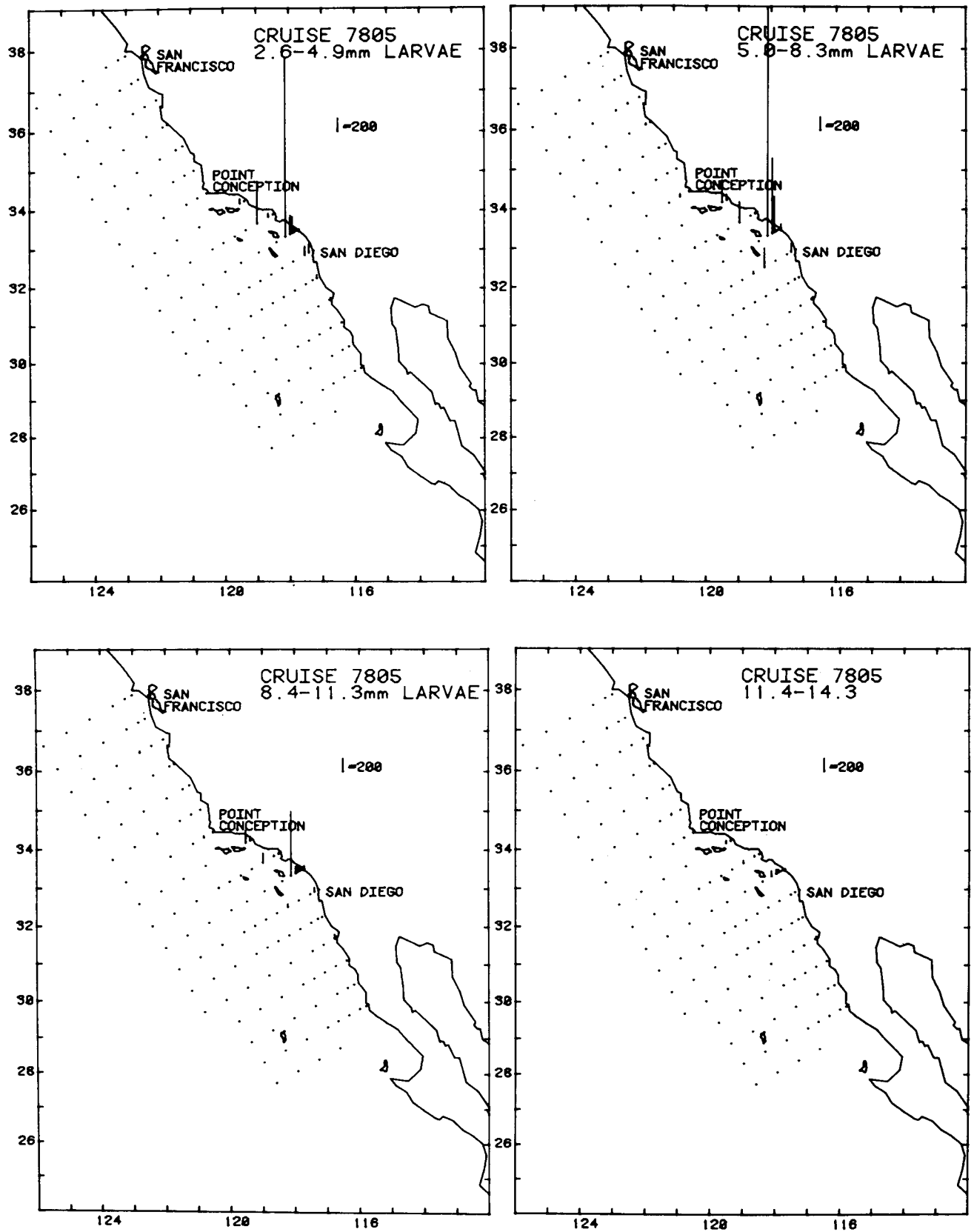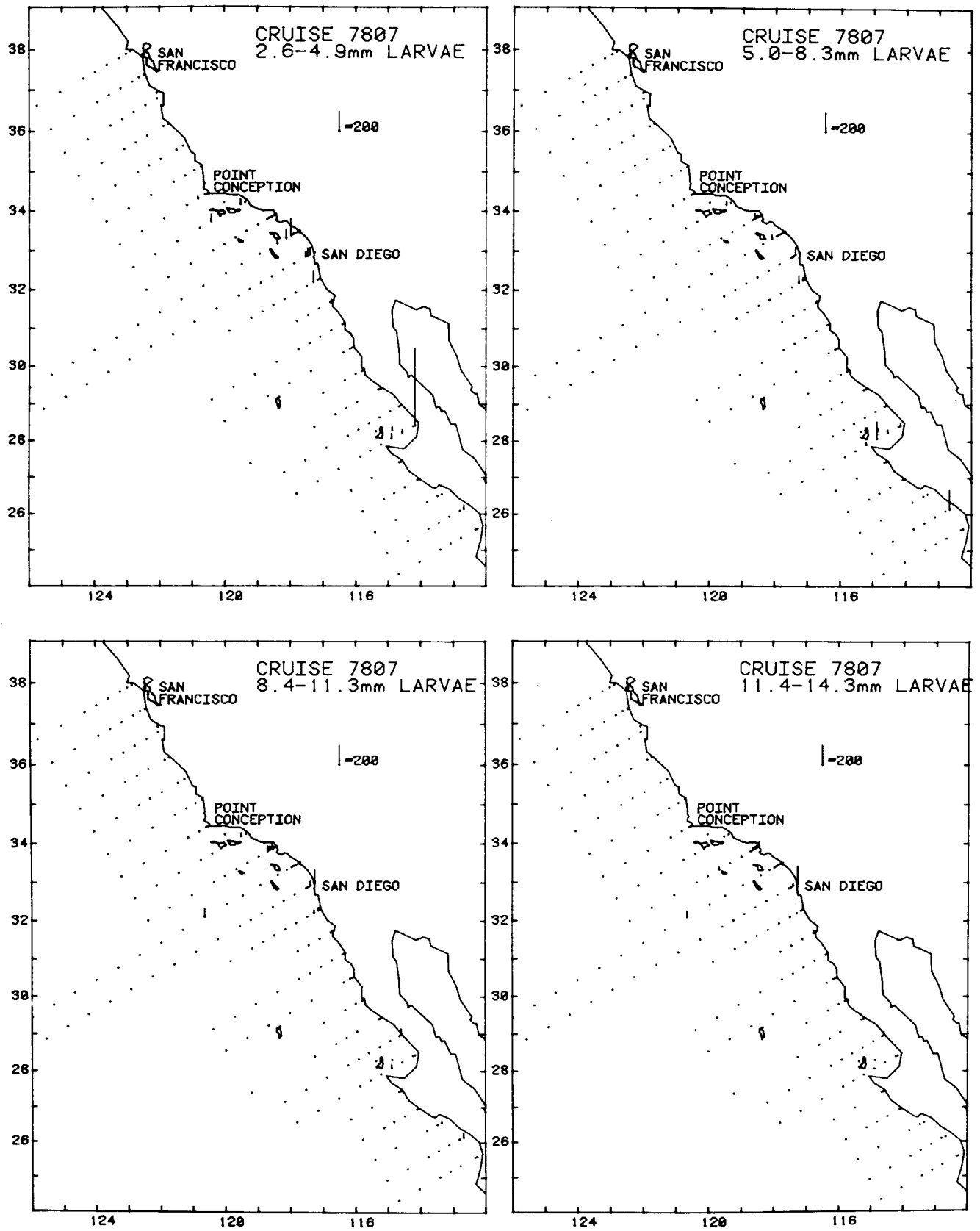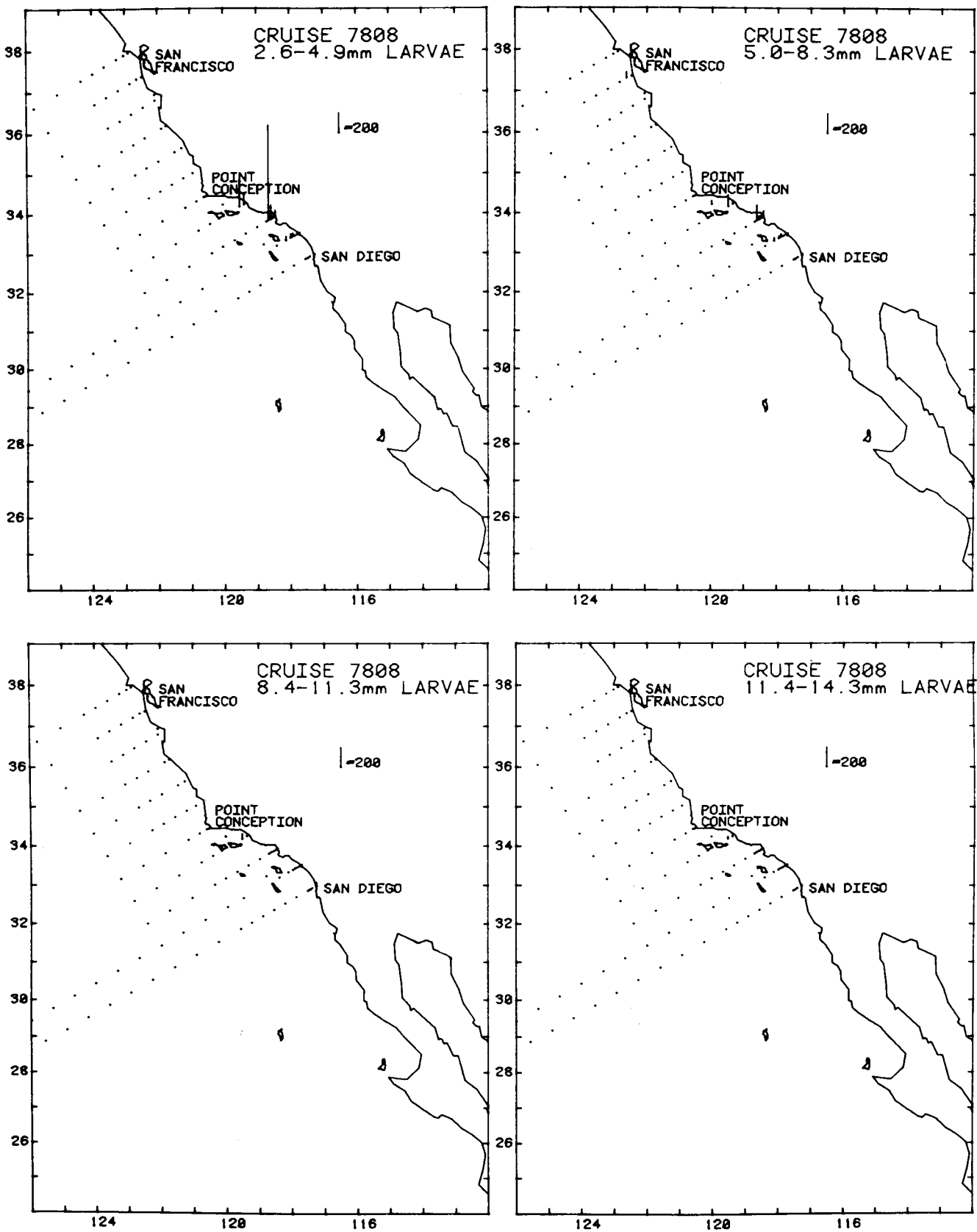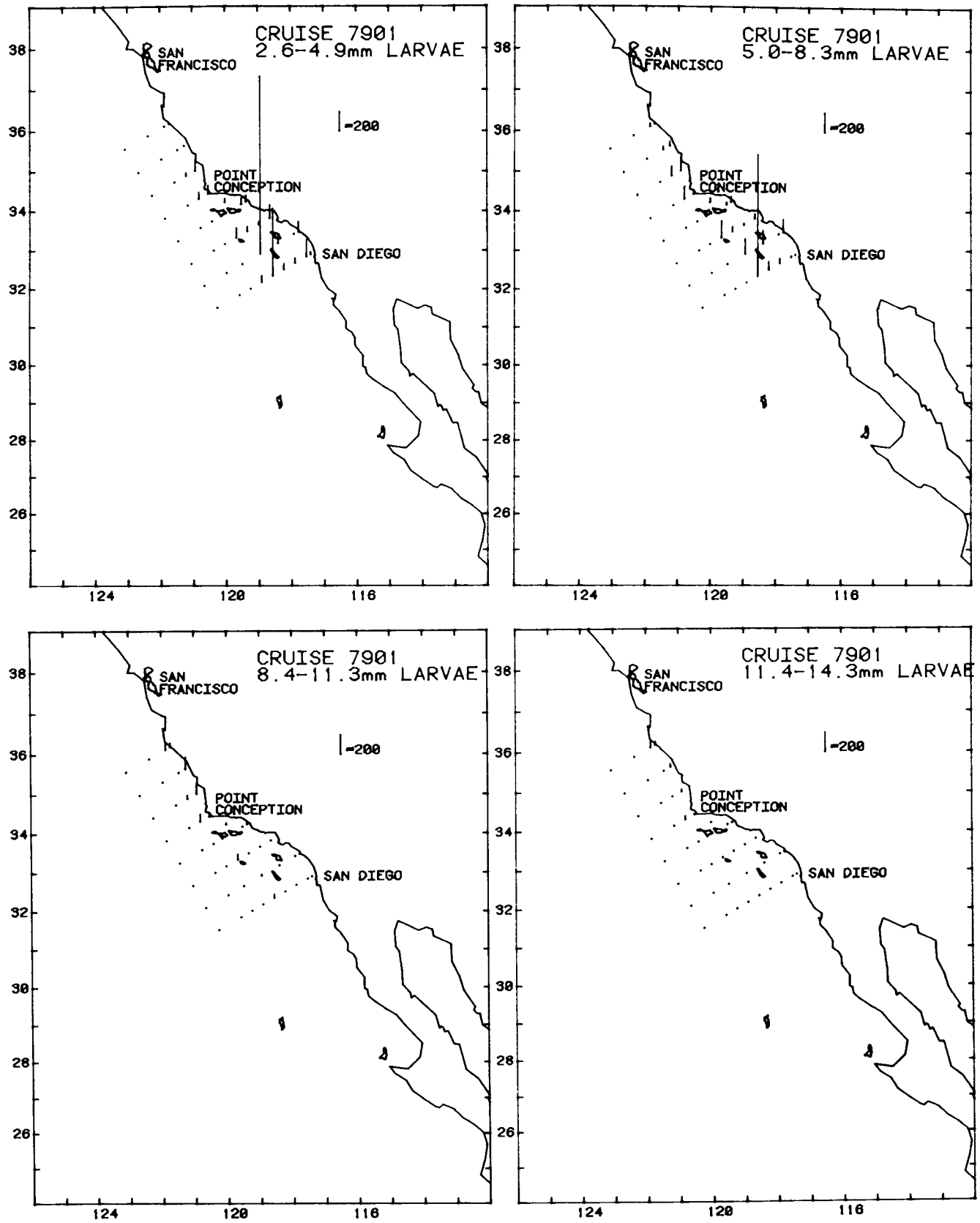
Figure 4.

Figure 5.

Figure 6.

Figure 7.

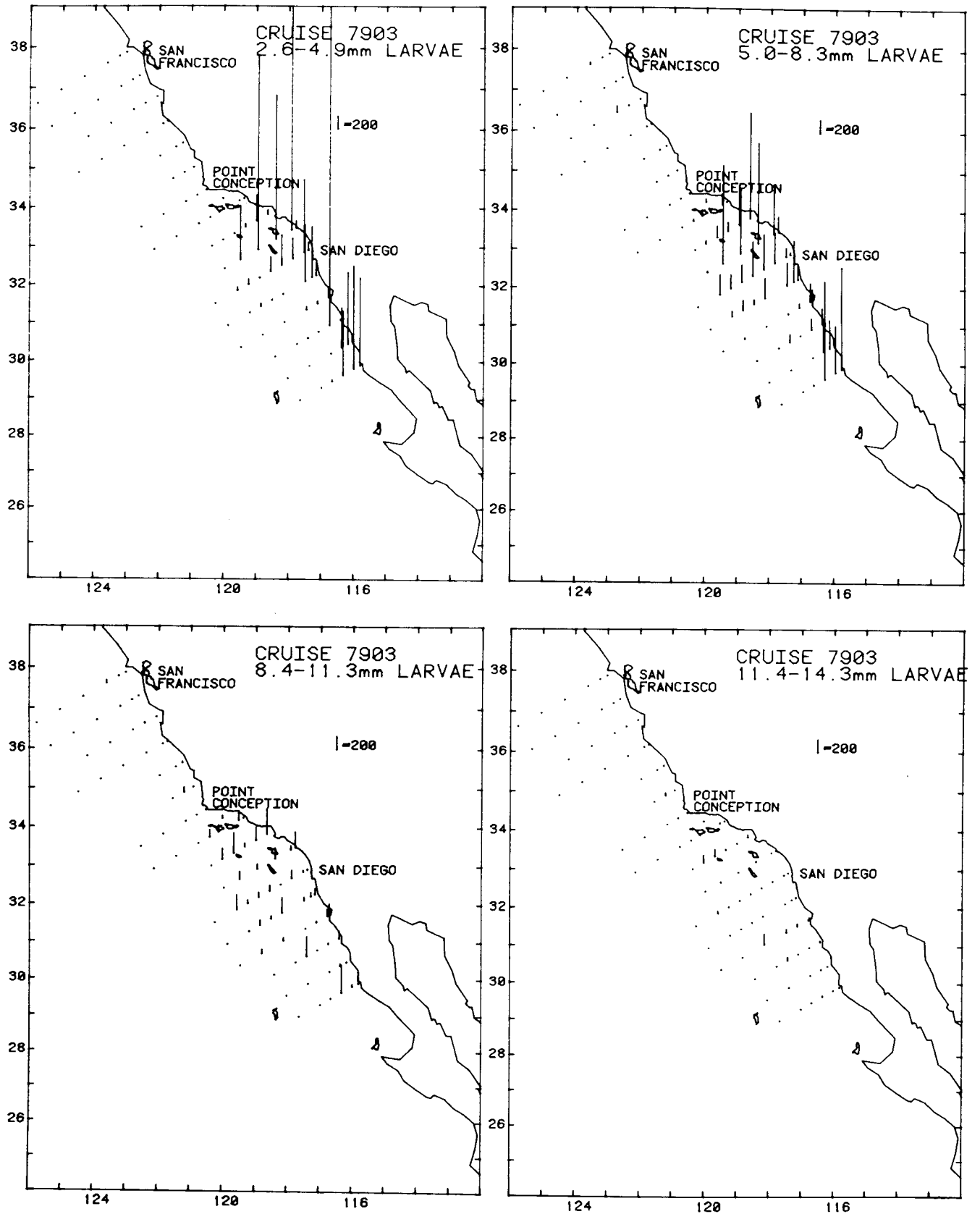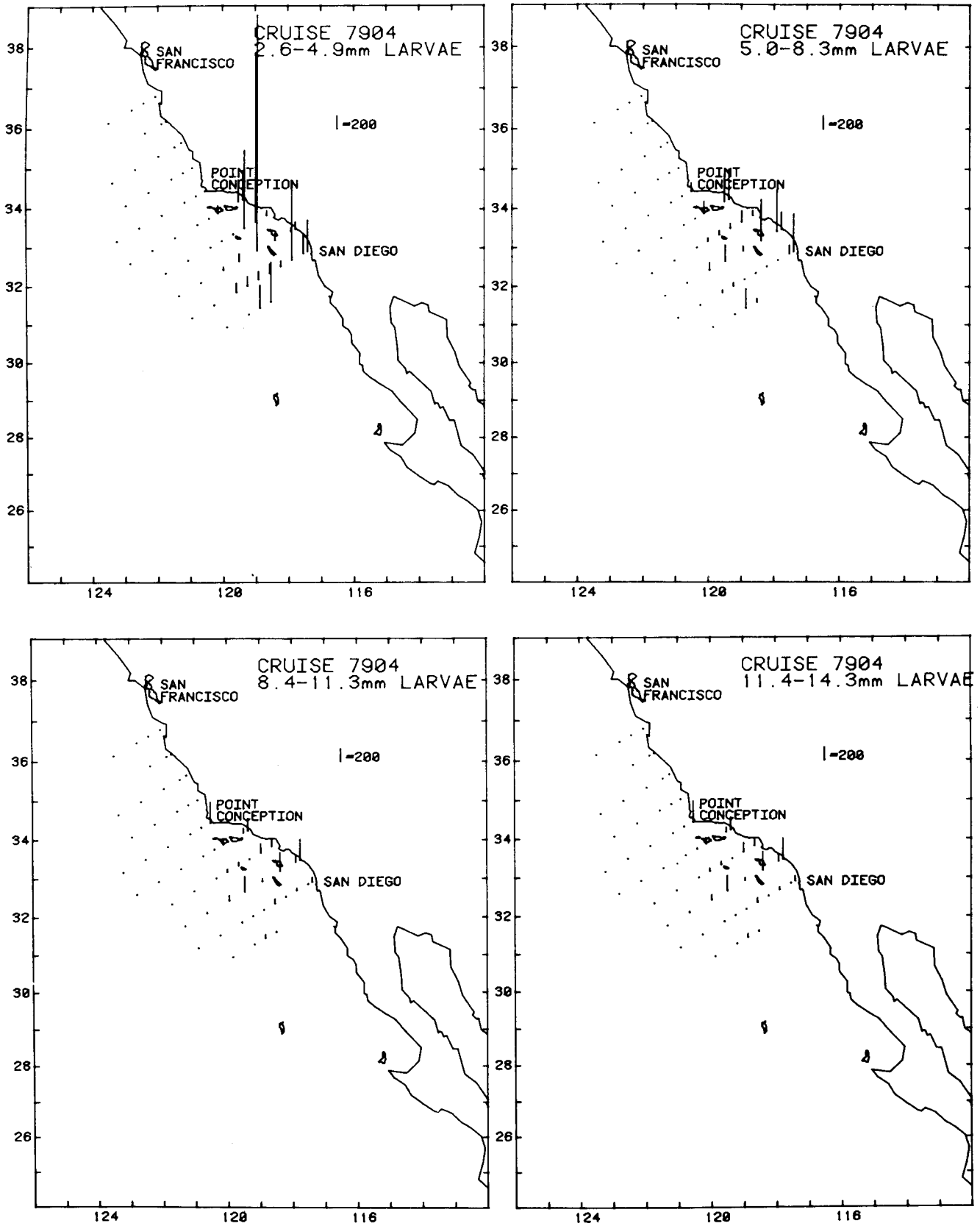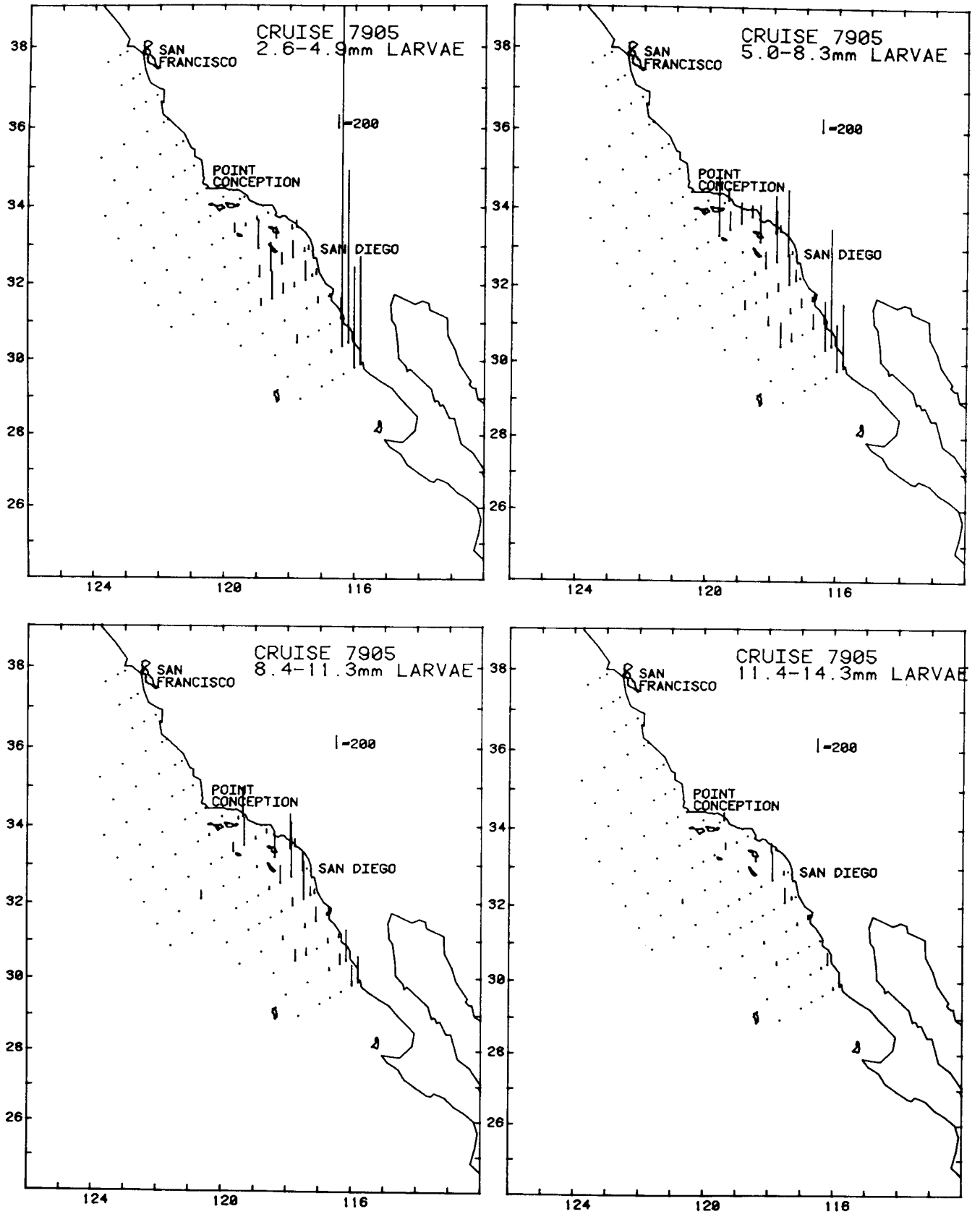Figure 8.

Figure 9.

Figure 10.

Figure 11.

Figure 12.

Figure 13.

TABLE 2

Temporal and Spatial Distribution of Anchovy Larvae during 1978

Between lines	Size group	7712	7801	7803	7804	7805	7807	7808
60-70	2.6-4.9	93	110	44	77	0	0	0
	5.0-8.3	44	0	44	214	16	0	11
	8.4-11.3	19	5	16	110	16	0	0
	11.4-14.3	0	0	0	16	11	0	0
	Total	159	115	104	429	44	0	11
70-80	2.6-4.9	93	137	203	11	5	5	0
	5.0-8-3	44	121	264	11	27	0	0
	8.4-11.3	19	49	154	16	49	5	0
	11.4-14.3	0	22	115	11	33	5	0
	Total	159	324	814	49	181	22	0
80-90	2.6-4.9	2002	2156	9355	2574	737	110	170
	5.0-8.3	726	654	2755	1391	1023	33	66
	8.4-11.3	231	132	643	352	368	93	38
	11.4-14.3	5	38	104	22	60	66	11
	Total	3025	3129	13249	4609	2299	379	302
90-100	2.6-4.9	209	660	3283	1039	49	33	0
	5.0-8.3	27	429	1765	671	115	16	0
	8.4-11.3	5	137	346	148	44	16	0
	11.4-14.3	0	44	33	22	0	16	0
	Total	264	1369	5676	1969	236	104	0
100-110	2.6-4.9	16	165	418	203	0	0	0
	5.0-8.3	38	5	302	715	5	0	0
	8.4-11.3	5	49	93	308	5	0	0
	11.4-14.3	0	11	33	132	0	0	0
	Total	60	269	913	1485	11	0	0
60-110	2.6-4.9	2413	3129	13303	3904	791	148	170
	5.0-8.3	879	1209	5130	3002	1186	49	77
	8.4-11.3	279	372	1252	934	482	114	38
	11.4-14.3	5	115	285	203	104	87	11
	Total	3667	5206	20951	8541	2771	505	313

Values are x 10^9 larvae; parentheses denote extrapolated values.

TABLE 3

Temporal and Spatial Distribution of Anchovy Larvae During 1979

Between lines	Size group	7901	7903	7904	7905
60-70	2.6-4.9	0	16	0	0
	5.0-8.3	22	60	0	0
	8.4-11.3	88	33	0	0
	11.4-14.3	66	5	0	0
	Total	198	132	0	0
70-80	2.6-4.9	71	0	22	0
	5.0-8.3	132	0	55	0
	8.4-11.3	82	33	11	0
	11.4-14.3	27	16	0	0
	Total	319	49	93	5
80-90	2.6-4.9	968	3894	3003	374
	5.0-8.3	253	2805	1017	924
	8.4-11.3	49	544	544	671
	11.4-14.3	11	155	137	176
	Total	1369	7771	4884	2266
90-100	2.6-4.9	858	1116	2373	654
	5.0-8.3	1171	1325	639	924
	8.4-11.3	33	495	236	737
	11.4-14.3	16	181	92	269
	Total	2145	3377	3718	2794
100-110	2.6-4.9	858	3536	2384	2722
	5.0-8.3	1171	1149	961	1138
	8.4-11.3	33	297	363	434
	11.4-14.3	16	33	111	88
	Total	2145	5115	3993	4636
60-110	2.6-4.9	2755	8562	7782	3750
	5.0-8.3	2749	5339	2672	2986
	8.4-11.3	285	1402	1154	1842
	11.4-14.3	136	350	340	533
	Total	6176	16444	12688	9701

Values are x 10^9 larvae; parentheses denote extrapolated values.

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:

	2.6-4.9mm	5.0-8.3	8.4-11.3	11.4-14.3
1978	60 km	56	53	46
1979	85	86	89	117

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, in-

creased 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

TABLE 4

Average Distance Offshore (km) of Anchovy Larvae

	Cruise						
	7712	7801	7803	7804	7805	7807	7808
2.6-4.9 mm	119	65	65	41	44	72	22
5.0 to 8.3	83	61	67	39	48	52	26
8.4 to 11.3	70	39	60	46	57	174	56
11.4 to 14.3	126	41	46	33	74	172	41

	7901	7903	7904	7905
2.6 to 4.9 mm	111	65	113	54
5.0 to 8.3	104	89	89	63
8.4 to 11.3	59	104	104	74
11.4 to 14.3	41	130	174	91

moderate level through May (Table 3)[1]. 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 1979 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 $\log_e (m)$ 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

TABLE 5
Regressions of Larval Production Rates on Age

	7712	7801	7803	Cruise 7804	7805	7807	7808
A	4.87+.36	4.39+.18	5.53+.11	4.82+.17	2.87+.30	1.13+.35	3.62+.24
B	0.23+.03	0.16+.01	0.18+.01	0.15+.01	0.11+.02	0.03+.03	0.22+.02
C	.91	.96	.98	.95	.72	.01	.92

	7901	7903	7904	7905
A	4.23+.26	5.32+.16	5.10+.36	4.82+.16
B	0.19+.02	0.17+.01	0.19+.02	0.13+.01
C	.93	.97	.88	.93

A = ln (m₀)+s.e.
B = z +s.e.
C = r²

[1]No eggs and a few small larvae were detected during a nonstandard cruise in June 1979 (Methot, unpubl. data).

TABLE 6
Estimated Mortality Rates from Age Distributions Pooled over 30 Days When Actual Mortality is Constant at 0.15, and Spawning Follows a Normal Distribution in Time

Std. deviation of spawning curve	Jan.	Feb.	Mar.	Apr.	May	June	Summed over season
30 days	0.24	0.20	0.17	0.14	0.11	0.08	0.15
45	0.22	0.18	0.16	0.15	0.13	0.12	0.15
60	0.21	0.16	0.15	0.15	0.14	0.13	0.15

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 survival 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
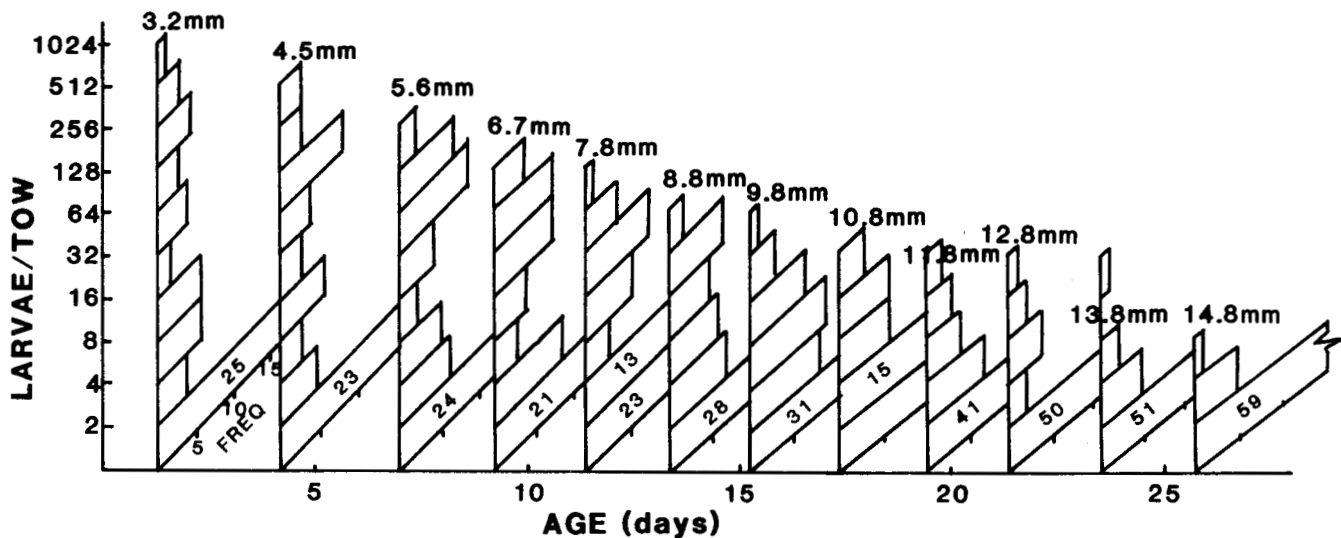
CRUISE 7803

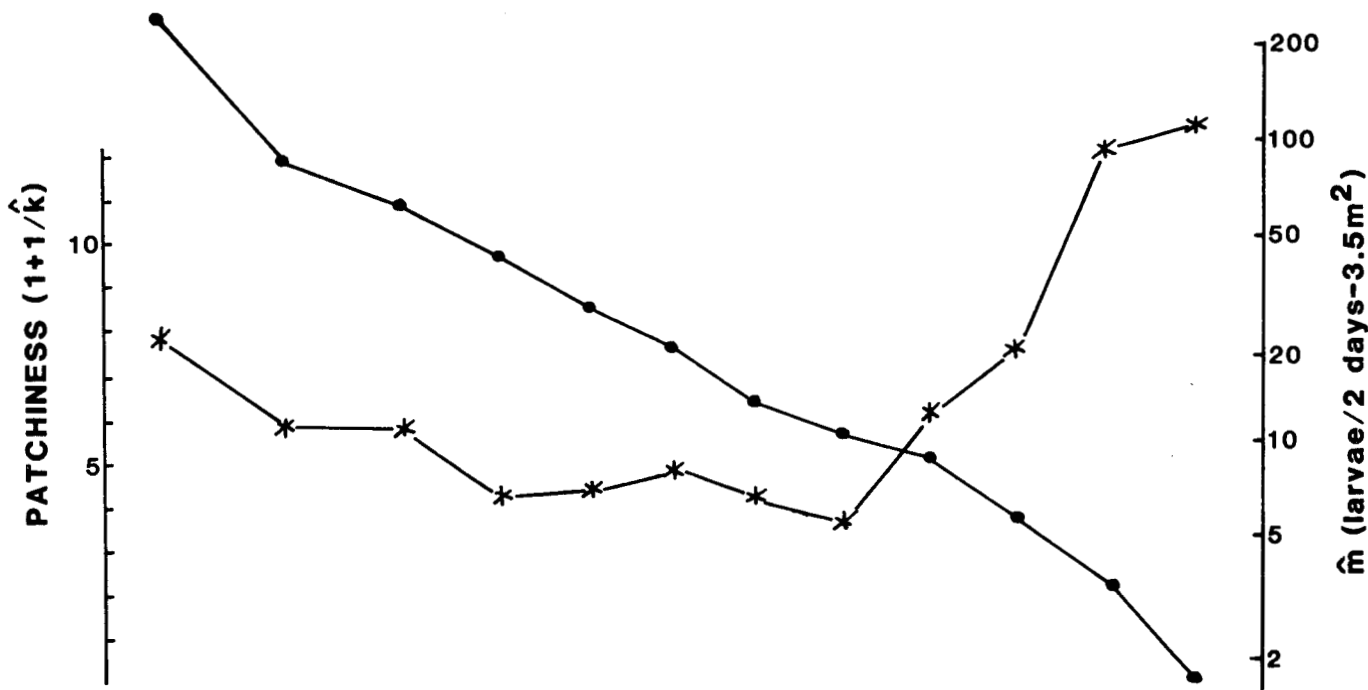| Avg. weight	0.286	0.523	0.423	0.432	0.377	0.367	0.370	0.365	0.333	0.350	0.320	0.327
m	256.59	95.22	64.53	41.65	28.18	21.31	13.60	11.17	9.34	5.62	3.42	1.63
k	0.1473	0.2069	0.2018	0.3118	0.2947	0.2604	0.3006	0.3827	0.1951	0.1555	0.0904	0.0853

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
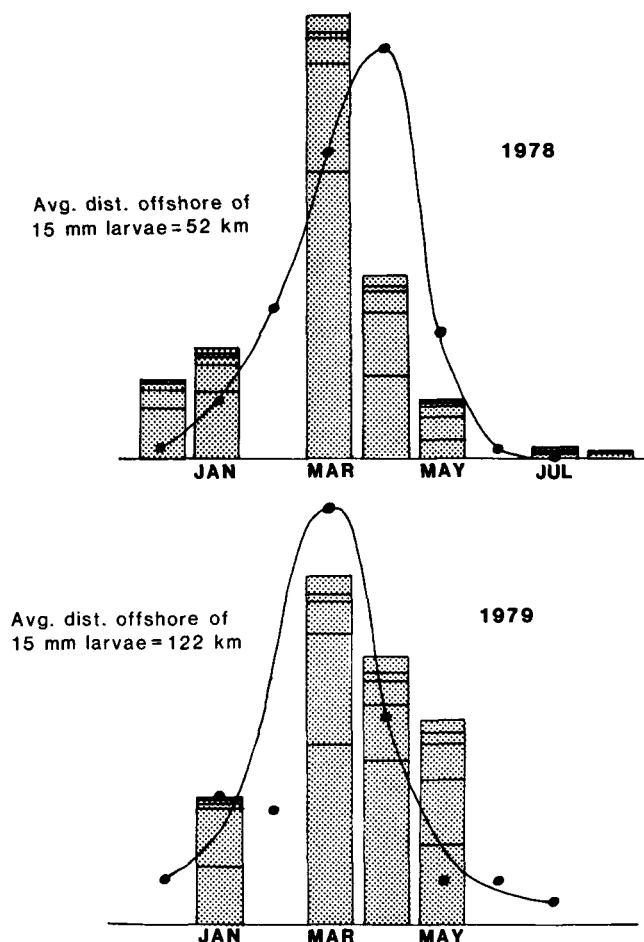
Figure 15. The seasonal distribution of larvae (bars) agreed generally with the birthdate distribution of survivors (line). The height of the bars is proportional to the abundance of larvae; bar subdivisions are proportional to the abundance of four size groups of larvae. The dots represent the fraction of juvenile fish that were spawned in each month.

the May temperature distributions that correlated with the dramatic difference in spawning activity.

Strong storms occurred during the winter of 1978, and substantial stratification of the upper water column was delayed until March 1978. Lasker (1981) suggests that this turbulence prevented formation of prey aggregations considered necessary to anchovy larvae. We did not find increased larval mortality during winter 1978, but Methot (1981) did find that survivorship increased during the 1978 spawning season. However, if larval survival was low during winter 1978 then postlarval survival must have been high throughout 1978 because the 1978 year class was abundant. Also, the winter of 1979 was less stormy, and the 1979 year class was only half as abundant as that from 1978.

Transport of larvae may be responsible for the difference in survivorship between 1978 and 1979. Upwelling and offshore transport of surface water caused by the stress of NW winds were extremely low during

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).

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