DISTRIBUTION OF EGGS AND LARVAE FROM SARDINE AND ANCHOVY OFF CALIFORNIA AND BAJA CALIFORNIA, 1951–1989

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ABSTRACT

The CalCOFI data set for sardine and anchovy eggs and larvae from 1951 to 1989 formed the basis of this analysis. The seasonal pattern is described on a monthly basis; for the geographical analysis the CalCOFI area was divided into alongshore regions and offshore-onshore regions. The percentage of positive stations was used to describe the seasonal and geographical patterns of sardine and anchovy eggs and larvae. Two seasonal spawning patterns for sardine are described: one associated with the Southern California Bight area (northern pattern) and another located off Punta Eugenia, Baja California Sur (B.C.S.), Mexico (southern pattern). The northern pattern takes place from February to June–July; the southern pattern occurs from August to October. The transition zone between patterns could be Punta Baja, Baja California, Mexico. In contrast, the spawning pattern described for anchovy shows no geographical variations from Point Conception, California, to Magdalena Bay, B.C.S., and takes place from December to April, with high numbers of eggs and larvae in the Southern California Bight; there is, however, a secondary spawning center in the Punta Eugenia region.

RESUMEN

El presente análisis se fundamenta en la base de datos de "CalCOFI" de huevos y larvas de sardina y anchoveta de 1951 a 1989. Se describen los patrones estacionales sobre una base mensual. Para el análisis geográfico, se usaron diversos criterios: el área total abarcada por los muestreos "CalCOFI", y subdivisiones de ésta área, por región a lo largo de la costa, y por regiones costeras *vs.* regiones en mar adentro. Se usó el porcentaje de estaciones con presencia de huevos y larvas de sardina y anchoveta para describir los patrones estacionales y geográficos. Se describen dos patrones estacionales de desove para la sardina. El patrón "norteño" ocurre de febrero a junio–julio al sur de California, mientras que el "sureño" ocurre de agosto a octubre en Punta Eugenia, Baja California Sur (B.C.S.), México. La zona de transición entre ambos patrones podría ser Punta Baja, Baja California, México. En contraste, el patrón de desove de la anchoveta no varía geográficamente desde Point Conception, California, hasta Bahía Magdalena, B.C.S., y ocurre de diciembre hasta abril con máximos de huevos y larvas en el sur de California. Existe asimismo un punto de desove secundario en el área de Punta Eugenia.

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INTRODUCTION

The distribution and abundance of sardine (*Sardinops sagax*) and anchovy (*Engraulis mordax*) eggs and larvae in the California Current system have been intensely studied since the end of the 1940s, when the California Cooperative Oceanic Fisheries Investigations Program (CalCOFI) was established. This program was designed to obtain information about the causes of the great decline in sardine catches (Chelton et al. 1982). CalCOFI carried out oceanographic/biológical cruises on a monthly basis from Cape Mendocino, California, to Cabo San Lucas, Baja California Sur (B.C.S.), Mexico, to more than 200 nautical miles offshore.

In this paper I use the extensive CalCOFI data set to describe the distributional and abundance patterns of sardine and anchovy eggs and larvae observed during the 1951–89 period. Moser et al. (1993) presented a global analysis of the whole CalCOFI area; here I explore detailed area/time windows to find seasonal trends. No interannual variations are accounted for because they are the subject of a second paper in preparation. The seasonal variation is described, and its possible causes are discussed.

Sardine and Anchovy Fishery/ Population Fluctuations

Even a superficial review of catch statistics of the small pelagic fishes of eastern boundary currents shows one feature: great fluctuations in their catches (and certainly in their abundance) on annual and decadal scales. The years considered in this analysis (1951–89) do not include the period when great concentrations of sardine existed in the northern half of the CalCOFI area (California). In the 1930s and 1940s, the sardine catches in California were more than 500,000 tons in some years, but the fishery dramatically decreased at the beginning of 1950s. In the 1960s the California sardine fishery virtually disappeared, but a small Mexican fishery, less than 50,000 tons per year, was maintained on the west coast of Baja California. Barnes et al. (1992) present data on

the fluctuations of sardine biomass off California and northern Baja California from 1933 to 1991, and show that the sardine population began to decline in the early 1940s and reached its lowest levels in the mid 1970s. Thus it must be realized that the information described in this paper was primarily taken while the sardine population off California and northern Baja California (B.C.) was low.

The highest catches for the California anchovy fishery were made in the mid 1970s, with a maximum of 141,000 tons in the 1975–76 season. In the last ten years (1982–92), the annual average California catches were not over 3,000 tons; the Mexican fishery at Ensenada, B.C., fluctuated between 170,000 and 100 tons.

Sardine and Anchovy Spawning Range and Seasonality

It is known that in the 1930s, when a large Canadian sardine fishery existed, sardines spawned during summer as far north as British Columbia (Walford and Moser 1941). But sardines have been virtually absent from the region north of California since the 1950s and have only recently reappeared there. Clark (1934) showed that sardines spawn off California from February to August, with a peak in April–May. Scofield (1934) reported that the main areas of spawning were located between San Diego and Point Conception, with sporadic spawning as far north as San Francisco and as far south as Magdalena Bay, B.C.S. The cruises analyzed by Scofield were carried out during spring and early summer in 1929–32; only a few stations were located along the Mexican coast. The importance of the Scofield study is that it was made when sardine populations were at a high level in California. Before the development of the CalCOFI program, several authors suggested that sardine spawning off California was concentrated during spring and summer (Tibby 1937; Janssen 1937; Sette and Ahlstrom 1948).

Based on the more extensive coverage of the CalCOFI program, Ahlstrom (1954) described two main spawning areas for the sardine. The first is an area of intensive spawning off the central part of the Baja California peninsula. In this area spawning peaks from February to May, but eggs appear throughout the year in the Vizcaino, B.C., region. The second, larger area includes the Southern California Bight (SCB) and northern portion of the Baja California peninsula. In this region spawning peaks in April–June. Ahlstrom (1954) reported that during 1950–51 more than 80% of sardine spawning was concentrated off of central Baja California.

Ahlstrom (1960) suggested that a group of sardines spawns in the Southern California Bight from April to June, and from January to June in warmer years; another group spawns off the central and southern part of Baja California throughout the year, with peaks in both winter and summer. Also, he mentioned sporadic sardine spawning north of Point Conception from May to August.

Kramer and Smith (1971) used the CalCOFI 1951–60 data set for sardine eggs and larvae to suggest that "Two major centers of spawning are evident first in January in small areas off central Baja California and southern California . . . With the passage of time the southern groups spread northward and seaward; then in May and June, they intermix with the northern group, which spreads somewhat southward. In July, the two groups are separate again and, in October, heavy spawning occurs only off central Baja California."

Lluch et al. (1992) analyzed sardine spawning during the 1950s off California and Baja California and found that spawning started early in the year near Punta Eugenia, B.C.S. During spring, sardine populations expand both northwards and southwards; in the north they reach the Southern California Bight from March to July. When spawning ceases there, sardine distribution contracts again to the Punta Eugenia area, where spawning takes place year-round. Moser et al. (1993) present the patterns for sardine eggs and larvae for 1951–84. Moser et al. found a major spawning area in the Punta Eugenia region, where spawning occurs throughout the year, with a maximum from January to September. Moser et al. also show a spawning center in the Southern California Bight area during April–June, although some eggs are present there all year. Off central Baja California eggs are concentrated in the first ten nautical miles; in the northern part of the peninsula and in the Southern California Bight eggs have a broader offshore distribution.

Regarding anchovy, Ahlstrom (1966) showed that larvae are distributed from Oregon to Punta San Juanico, B.C.S. A number of researchers have described the seasonal pattern of anchovy spawning in the southern California and northern Baja California region, using the presence of eggs and larvae in the CalCOFI data set, and gonad maturity information from adult anchovies. Lasker and Smith (1977), Chavez et al. (1977), Parrish et al. (1986), and Moser et al. (1993) state that anchovy spawning is concentrated from February to April in the Southern California Bight, although anchovy eggs and larvae and actively spawning adults are present throughout the year. Chavez et al. (1977) found mature anchovies during February–May in the Ensenada region.

Several authors have postulated environmental mechanisms that may explain the distribution and timing of sardine and anchovy spawning in the California Current. Parrish et al. (1983) suggested a strong relationship between the sea-surface temperature, turbulence and transport, and reproductive success. Lluch-Belda et al. (1991) proposed a hypothesis relating the upwelling index and

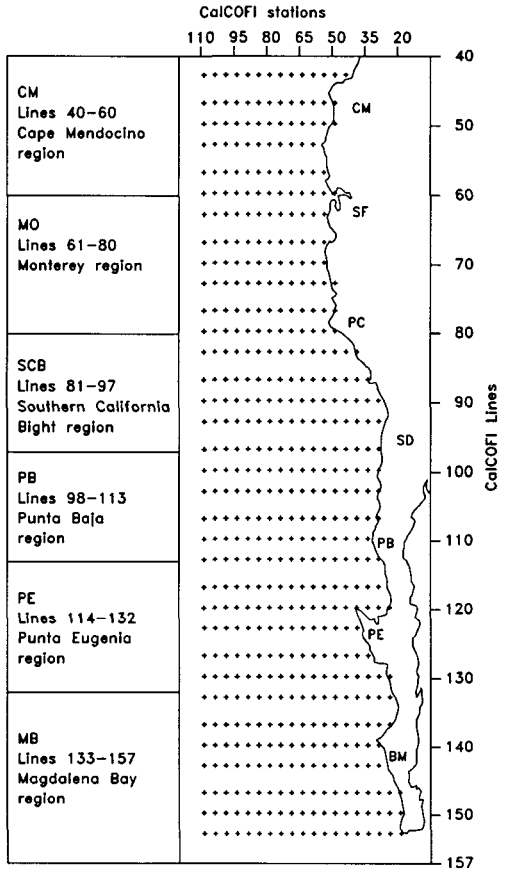

Figure 1. Basic CalCOFI grid, with the geographic areas used in this analysis (1951–89). CM = Cape Mendocino, Calif.; SF = San Francisco; PC = Point Conception; SD = San Diego; PB = Punta Baja, B.C.; PE = Punta Eugenia, B.C.S.; and MB = Magdalena Bay).

sea-surface temperature to the distribution of sardine eggs and larvae on a yearly basis.

DATA AND METHODOLOGY

The CalCOFI data set for sardine and anchovy eggs and larvae for the 1951–89 period formed the basis of this analysis. The CalCOFI basic grid consists of an array of lines and stations (Eber and Hewitt 1979). Lines are perpendicular to the coast at intervals of 40 nautical miles (n.mi.). Stations are parallel to the coast, and separated by 4 n.mi. (figure 1). For each CalCOFI station the data base includes the date (year, month, and day), time, geographical position (CalCOFI line/station code), sea-surface temperature (0–10 m), and the number of sardine and anchovy eggs and larvae (standardized to 10 m^2 of sea surface).

For the purpose of this paper the seasonal pattern is described on a monthly basis, and the geographical analyses utilize four different criteria as follows (figure 1):

1. All CalCOFI stations combined (global analysis).
2. The CalCOFI area divided by alongshore regions: Cape Mendocino (CM) region, 40–60 lines; Monterey (MO) region, 61–80 lines; Southern California Bight (SCB) region, 81–97 lines; Punta Baja (PB) region, 98–113 lines; Punta Eugenia (PE) region, 114–132 lines; and Magdalena Bay (MB) region, 133–157 lines.
3. By CalCOFI line.
4. Cross-shelf analysis: distance to the coast.

The CalCOFI line analysis used the standard CalCOFI lines (90, 93, 97 . . . .) because these lines were systematically sampled, whereas the intermediate lines—91, 92, 96—were omitted (of all stations sampled during the 1951–89 period only 5.6% were located in these intermediate CalCOFI lines). The other three analyses included all CalCOFI lines.

The percentage of positive stations was used to describe the seasonal and geographical pattern of occurrence of sardine and anchovy eggs and larvae for each of the four criteria. Some authors have used egg and larval density (the average number per station); others, however, have expressed doubts, because density may be biased if a sample is taken near a spawning adult. Nevertheless, both indices are very well correlated; to be certain, I analyzed all of the series and found them to be correlated beyond the 0.01 level.

The geographical and temporal coverage of the CalCOFI surveys varied widely during the 1951–89 period covered by this analysis. From 1951 to 1960, surveys were made monthly (only 6 months were not covered) and the latitudinal coverage was best from the north of Magdalena Bay (CalCOFI line 133) to Point Conception (CalCOFI line 80). Only 25% of surveys extended to the north and/or south of this area. Hewitt (1988) graphically described the temporal and spatial coverage surveys for the 1949–87 CalCOFI period. In summary, the geographical and seasonal coverage of the CalCOFI surveys is best from the Punta Eugenia area to the Monterey area and in the months from January to July; data are poorest in the Cape Mendocino region and in the months of September, November, and December.

The number of stations sampled per month was greatest in the first part of the year (table 1). From January to July more than 2,500 stations were sampled each month, whereas from August to December (except October), no more than 1,300 stations were sampled per month. The number of stations per CalCOFI line, in general, was less than 100 from August to December (except October), but lines 90–93 (located in the Southern California Bight region) had more than 100 stations sampled per line. From January to July, more than 100 stations per line were sampled from line 80 (Point Conception) to line 130 (Punta Eugenia).

The surveys generally occupied stations as far offshore as station 90 (150 to 300 n.mi., depending on CalCOFI

TABLE 1
Number of Stations Sampled in the CalCOFI Area, by Line and Month, 1951–1989

CalCOFI line	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total line	Areas*	Total areas
40	11	6		9	18	8	23	6		7	2		90		
43	10	1		6	4	3	15	3		6			48		
47	8	1	2	3	3	3	14	2					36		
50	8	9		7	17	19	26	5		7	7		105		
53	6	8		4	3	11	13	3		3			51		
57	6	8		4	3	12	15	3		3			54		
60	113	37	44	144	72	64	147	30	25	67	40	13	796		
63	72	46	37	95	61	43	87	23	5	40	20	11	540		
67	73	53	39	101	57	50	88	25	6	41	22	12	567		
70	118	47	50	129	96	69	125	33	17	54	38	12	788		
73	72	58	63	88	68	43	76	21	5	44	21	10	569		
77	88	88	84	105	105	63	97	47	16	65	42	14	814		
80	177	125	122	171	140	97	145	84	70	104	68	52	1355		
83	156	142	119	175	179	122	164	57	56	131	69	45	1415		
87	159	208	127	212	203	139	189	67	68	148	69	71	1660		
90	234	216	192	251	258	191	222	125	135	192	103	108	2227	CM	1204
93	201	237	221	230	245	205	220	101	127	201	94	91	2173	MO	4771
97	167	185	167	208	121	223	202	57	50	169	39	61	1649	SCB	9746
100	182	172	149	224	140	195	208	73	52	167	49	64	1675	PB	7218
103	137	153	110	221	119	186	172	49	39	126	17	53	1382	PE	6242
107	120	144	106	205	122	158	184	45	39	125	17	60	1325	MB	2716
110	141	174	138	187	157	148	183	96	50	131	44	65	1514	Sum*	31897
113	99	154	105	191	119	137	172	54	49	117	3	61	1261		
117	111	163	114	199	136	127	207	62	62	114	17	58	1370		
120	136	196	164	208	170	134	215	112	72	160	49	79	1695		
123	57	111	90	115	79	58	129	57	33	83	20	43	875		
127	46	122	81	117	81	58	124	67	27	90	19	39	871		
130	64	153	100	132	105	68	124	95	37	115	41	44	1078		
133	65	124	79	137	74	53	107	79	22	95	19	34	888		
137	70	120	79	120	85	56	105	65	22	89	31	27	869		
140	35	50	18	36	10	20	6	15	7	7	21	6	231		
143	36	29	17	24		9		10	3	7		6	141		
147	34	33	13	34		5		9	4	9		6	147		
150	35	33	18	17		22		9	10	9	14	6	173		
153	34	29	7	28		9		2	3	12		3	127		
157	37	28	9	12		20			2		11	3	122		
Total*	3338	3580	2788	4224	3137	2936	3903	1679	1234	2821	1050	1207			

*Includes intermediate CalCOFI lines (41, 42, . . . , 55, 56, . . . , 98, 99, . . . etc.)

line), but 14% of the surveys did not extend beyond CalCOFI station 80 (table 2).

RESULTS

The results are presented for four geographical perspectives, from a global CalCOFI view to regional cross-shelf views for both sardine and anchovy; each perspective includes a seasonal analysis. The larvae/egg ratio for the global and subarea analyses is also presented.

Global Analysis for Entire CalCOFI Area

For both sardine and anchovy, larvae were taken at more stations than were eggs. The total number of sampled stations during 1951–89 was 31,897; 2,089 (6.5%) were positive for sardine eggs; 2,877 (9.0%) for sardine larvae; 7,147 (22.4%) for anchovy eggs; and 15,012 (47.0%) for anchovy larvae. The corresponding values for the mean number of eggs and larvae per station were

TABLE 2
Frequency of Occurrence of Each Station as the Most Offshore Location Sampled, 1951–1989

CalCOFI station	Percent
40	1.47
50	1.10
60	3.68
70	4.04
80	3.68
90	30.51
100	23.16
110	3.68
120	12.87
130	1.47
140	3.68
150	0.74
160	1.47
170	0.37
180	1.10
190	0.00
200	6.99

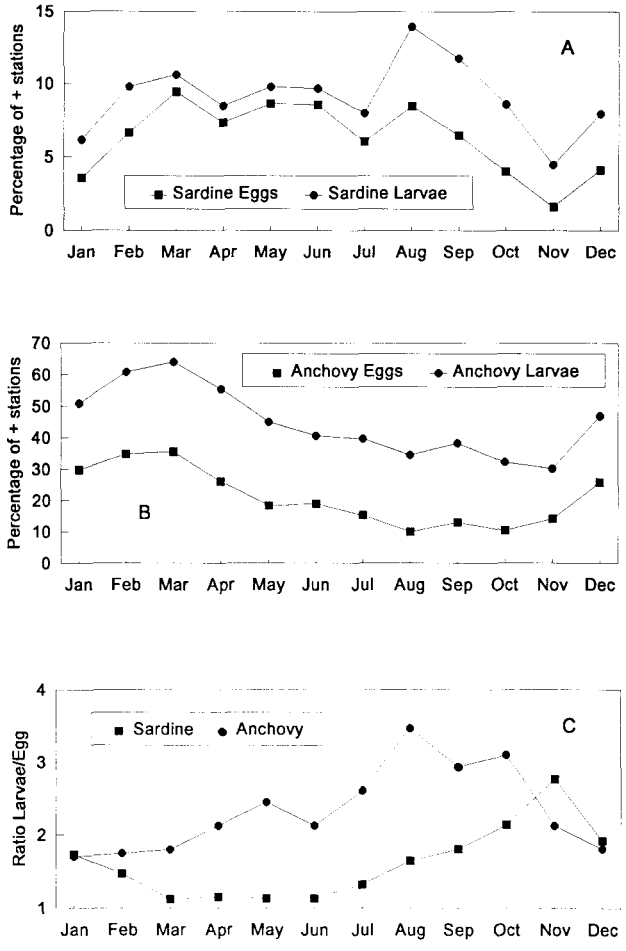

Figure 2. Monthly percentage of positive stations for eggs and larvae of (*A*) sardine and (*B*) anchovy. *C*, larvae/egg ratio for global analysis.

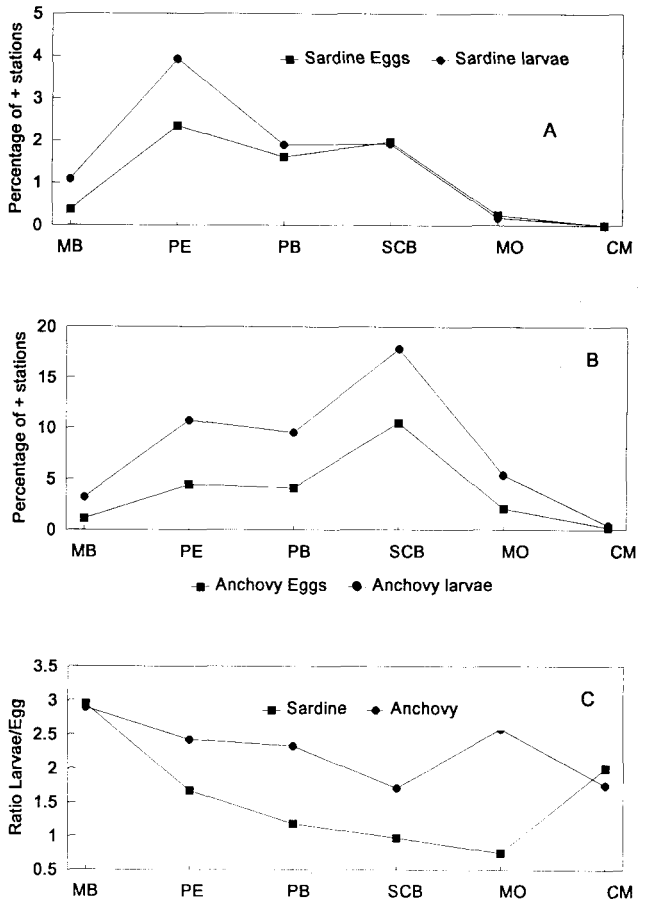

Figure 3. Percentage of positive stations for eggs and larvae of (*A*) sardine and (*B*) anchovy. *C*, larvae/egg ratio for analysis of areas (MB = Magdalena Bay; PE = Punta Eugenia; PB = Punta Baja; SCB = Southern California Bight; MO = Monterey; CM = Cape Mendocino).

13.86, 2.63, 65.81, and 64.82. Anchovy eggs and larvae occurred at more stations than sardine eggs and larvae.

Sardine eggs and larvae. As described by earlier workers, sardine eggs and larvae are present throughout the year along Baja California and California (figure 2A), but it appears that the spawning season along the whole coast is more extended than that described in earlier studies, because the percentage of positive stations for sardine eggs remains in the 6% to 9% range from February until September. The percentage decreases to less than 4% in October, to an annual low of 1.7% in November, and then rises to almost 4% in December and January. The highest percentages for sardine larvae are during August (14%) and September (12%). During the earlier peak of eggs and larvae (February to July), the percentage of positive stations is only slightly higher than that for eggs, but starting in August and continuing into the winter there are about twice as many positive stations for larvae as there are for eggs. As shown below, general patterns for the entire coast are due to complex seasonal patterns in different areas.

The larvae/egg ratio for sardine (figure 2C) shows low values from March to July (i.e., less than 1.5 larvae per egg), but the ratio increases to a maximum in November (highest ratio: 2.7).

Anchovy eggs and larvae. Both anchovy eggs and larvae are present throughout the year along the whole coast, with a peak from December to April (i.e., 28%–35% for eggs and 48%–65% for larvae; figure 2B). Percentages decline to a minimum of about 10% for eggs in August to October and about 30% for larvae in November. High larvae/egg ratios occur from July to October (highest value in August: 3.4). The ratio declines to less than 2 from November to March. From April to June the ratio again increases above 2 (figure 2C).

Analysis by Areas

This section describes latitudinal stratification of the seasonal patterns for sardine and anchovy eggs and larvae. It appears that sardine and anchovy larvae have quite different geographical patterns (figure 3). The highest values of occurrence of sardine larvae were in the Punta

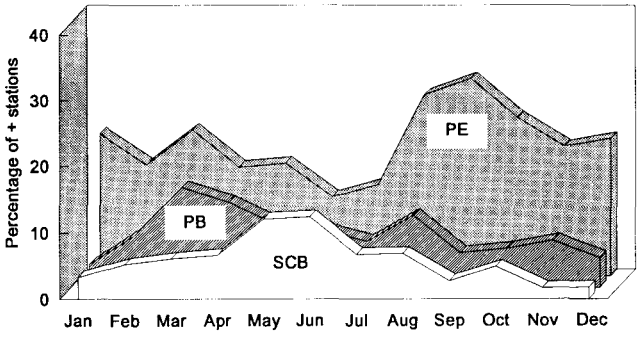

Figure 4. Monthly percentage of positive stations for sardine larvae, by area (PB = Punta Baja; SCB = Southern California Bight; PE = Punta Eugenia).

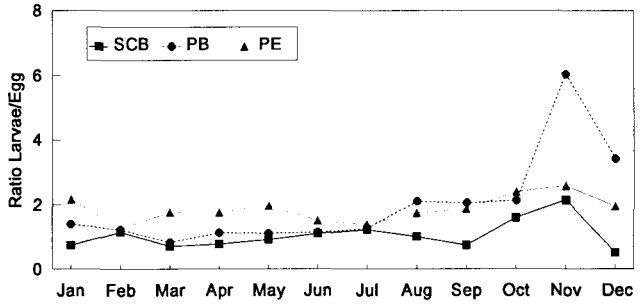

Figure 5. Monthly larvae/egg ratio for sardine, by area (SCB = Southern California Bight; PB = Punta Baja; PE = Punta Eugenia).

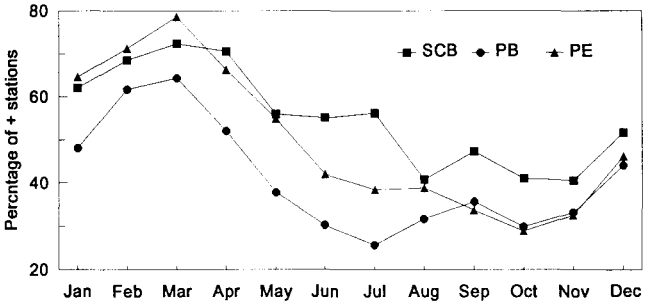

Figure 6. Monthly percentage of positive stations for anchovy larvae, by area (SCB = Southern California Bight; PB = Punta Baja; PE = Punta Eugenia).

Eugenia region, whereas for anchovy the highest values were in the Southern California Bight region. The occurrence of sardine eggs from the Southern California Bight to the Punta Eugenia region varied little except for diminishing northward and southward. However, the occurrence of sardine larvae in the Punta Eugenia region was almost twice that in the Punta Baja region and the SCB. Geographical patterns were similar for anchovy eggs and larvae, but larvae had higher percentages by region, except for Cape Mendocino, where the percentages were similar.

The lowest sardine larvae/egg ratios were in Monterey, with an increase toward the south (figure 3C). The ratio for the CM region is undoubtedly biased because of the low number of stations sampled. The ratios for anchovy increase both to the south and the north from SCB.

Sardine eggs and larvae. The seasonal patterns for eggs and larvae were similar for the three regions selected; I present only the data for larvae (figure 4). The Southern California Bight region shows the typical pattern described in the earlier papers; that is, the spawning season for the sardine begins in February and ends in June–July; some larvae, however, are present throughout the year. The adjacent Punta Baja region has its spawning peak two months earlier (March) than the SCB peak (May–June); there is also a small increase in positive stations during August. The Punta Eugenia region shows high values for all months except May and June. The maximum values of occurrence in the Punta Eugenia region (August–October) are much higher than those observed elsewhere.

The larvae/egg ratios for sardine have low values (with little variation) from February to September in the SCB region, and highest values during October and November (figure 5). The Punta Baja region has a sharp peak in November and a decline from December to July, when ratios show the lowest values and variability. Punta Eugenia also has a maximum ratio in November, and lower ratios from February to September.

Anchovy eggs and larvae. Because anchovy, like sardine, have the same seasonal patterns for eggs and larvae, again I present only the data for larvae (figure 6). In general, the three regions with maximum abundance of anchovy larvae (SCB, PB, and PE) have a similar seasonal pattern: the principal spawning season extends from December to July, as described by previous researchers. The Southern California Bight region shows a high number of positive stations from December to April, with a small decrease from May to July. The lowest values for the SCB region occur during October and November. The spawning seasons for anchovy in PB and PE are shorter than in the SCB (i.e., peak occurrence from December to March), but there were higher occurrences in PE than in PB. A comparison of monthly values of the percentage of positive stations among regions indicates that PB had lower values, while the SCB and PE had similar values.

Seasonally, the larvae/egg ratios for anchovy vary less for the SCB than for PE and PB (figure 7). For the SCB, ratios are lower from December to April, increase slightly from May to September, and decrease once again to November. PB has the lowest ratios from November to March, but there is a sustained increase from April to October. The seasonal pattern found for PE shows some similarity to that for PB, but instead of a sustained increase, there is a higher variability.

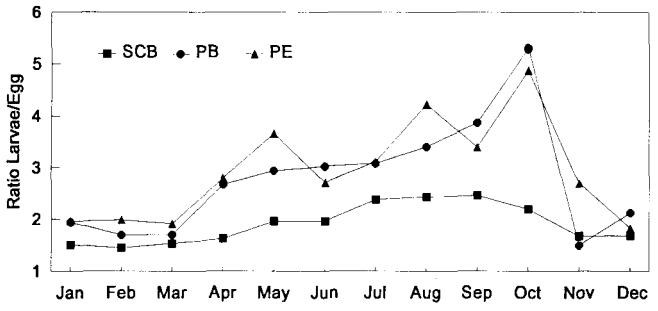

Figure 7. Monthly larvae/egg ratios for anchovy, by area (SCB = Southern California Bight; PB = Punta Baja; PE = Punta Eugenia).

Analysis by CalCOFI Lines

The geographical analysis by CalCOFI line may be biased from CalCOFI line 140 (Magdalena Bay) to the south, as well as from line 77 (north of Point Conception) to the north, since fewer than 300 stations were sampled per line, whereas from Point Conception to the north of Magdalena Bay, from 800 to 2,200 stations were sampled per line (table 1).

The percentage of positive stations by CalCOFI line for sardine and anchovy eggs and larvae differs considerably for the two species (figure 8). The occurrence of sardine eggs is even from just south of Point Conception (line 80) to just north of Magdalena Bay (line 140), except for a sharp peak in the Punta Eugenia region (line 120). Occurrence is very low to the north of Point Conception and south of Magdalena Bay. Sardine larvae have a similar latitudinal pattern, but from the Magdalena Bay region to the south the percentage of positive stations increases, suggesting an additional important spawning area; this pattern could, however, be due to the low number of stations sampled in this region (not more than 240 stations per line).

Sardine larvae/egg ratios show an increasing trend from north to south, with a sharp increase in the Punta Eugenia area (figure 9). In the northern areas the ratios vary from 0.77 to 1.11 (lines 80 to 97); the ratios observed at the northern portion of Baja California (lines 100 to 115) range from 0.84 to 1.6, whereas the values observed at the Punta Eugenia region (lines 117 to 130) vary from 1.36 to 2.52. The highest ratios (3.57 to 23) come from the southern part of the CalCOFI area (south of the Magdalena Bay region); again, the highest values might be biased because of the low number of stations taken in this region.

The percentage of positive stations for anchovy eggs and larvae indicates two areas of increased spawning: the Southern California Bight region and northern Baja California (figure 8). A second, broader peak occurs in the region from north of Punta Eugenia to north of Magdalena Bay. Between these two spawning areas, in the Punta Baja area, there is a small decrease. Anchovy

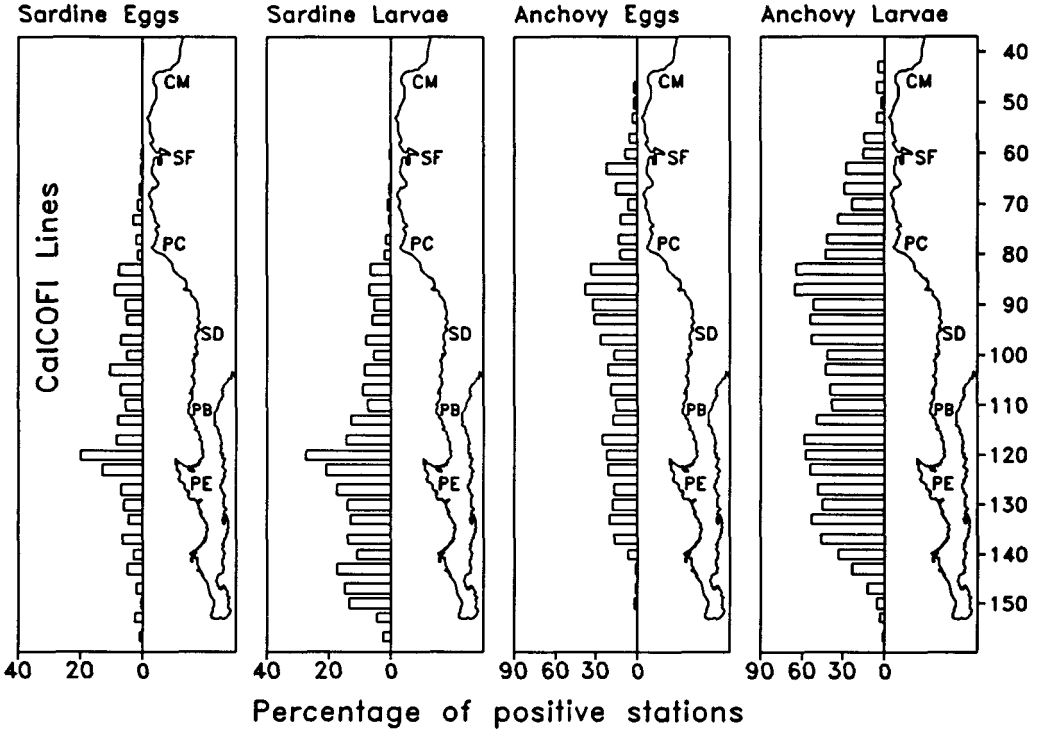

Figure 8. Percentage of positive stations for sardine and anchovy eggs and larvae per CalCOFI line.

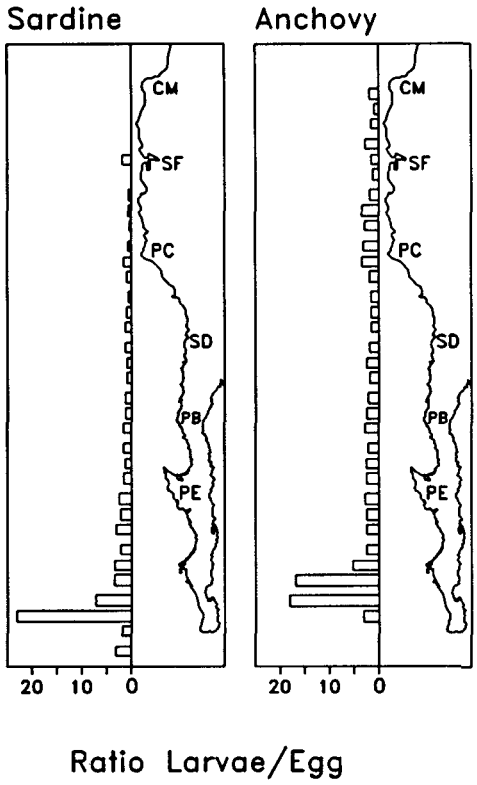

Figure 9. Larvae/egg ratio for sardine and anchovy per CalCOFI line.

eggs and larvae occur more frequently than those of sardine in the Point Conception area and extend into the northern areas (as far as Cape Mendocino).

The anchovy larvae/egg ratios, like the sardine ratios, diminish from south to north, except for CalCOFI lines 61–80, north of Point Conception (figure 9). Also, the ratios increase markedly (3.0 to 18.01) south of Magdalena Bay (where sample sizes were small).

Sardine eggs and larvae. Because the geographical and monthly percentages of positive stations for eggs and larvae by CalCOFI line exhibit essentially the same pattern, I present only the data for larvae (figure 10). The region to the north of Punta Baja shows the same seasonal pattern that was described by earlier workers; the highest occurrence of sardine larvae is from February to July. But the peak appears about two months earlier in the Mexican portion of this area (April) than in the California portion (June). The region south of Punta Baja shows very little seasonal variation in the percentage of sardine larvae, with only a moderate decrease in November and December. The strong peak that was previously shown for the Punta Eugenia region is obvious throughout the year. The Magdalena Bay region appears to be an important spawning area, with high occurrences during winter months and June, but the low number of stations taken in this region does not allow definitive conclusions (see table 1).

Anchovy eggs and larvae. Seasonal patterns for eggs and larvae are similar, therefore I show only those for larvae (figure 11). Anchovy larvae are present throughout the year from San Francisco (line 67) to Magdalena Bay (line 140). From January to May there are two modes, one in the Southern California Bight and one in the Punta Eugenia region. From June to November the southern mode shifts northward to the Punta Baja area, while the northern mode remains in the same location. In general, the seasonal pattern of larval occurrence shows higher values from December to July over the entire study area.

Inshore-Offshore Analysis

Offshore, more sardine and anchovy larvae are found than eggs, but in general the highest values appear near the coast for both eggs and larvae off California and Baja California (first 20 n.mi.; figure 12). The offshore occurrence of sardine eggs and larvae varies considerably among areas. The Magdalena Bay and Punta Eugenia regions show high percentages of positive stations for sardine eggs in the first 20 n.mi. The Punta Baja area seems to be a transitional region, since there is a moderate presence off 80–100 n.mi. In the Southern California Bight and central California areas there are only minor inshore peaks and little other variation within the first 100 n.mi.; values are quite low in the central California area. The few positive stations in the Cape Mendocino region exhibit little pattern. The offshore patterns for sardine eggs and larvae are different only in the Punta Eugenia region: there larvae have a high occurrence out to 80–100 n.mi., but the eggs are more concentrated in the first 20 n.mi.

Anchovy eggs and larvae are found more frequently within the first 40 n.mi. for all areas except Magdalena Bay, where more eggs are found in the 20 n.mi. fringe (figure 12, right side). In general, there are two offshore patterns. In the first—from the Southern California Bight to the north—the occurrence of eggs and larvae decreases as far as 100 n.mi. offshore. In the second pattern—from Punta Baja to the south—there is higher occurrence as far as 60 n.mi.

In order to demonstrate the seasonal offshore patterns for sardine and anchovy eggs and larvae, I use contour plots to show the percentage of positive stations by months and by distance offshore for each geographical region.

Sardine eggs and larvae. The seasonal offshore patterns for eggs and larvae are similar in all regions, but because larval occurrence is higher than that of eggs, I illustrate only the pattern for larvae (figure 13). The few stations in the Cape Mendocino area do not exhibit any pattern. Two general patterns are present off California and Baja California: the first corresponds to the Southern California Bight, in which high occurrence of sardine

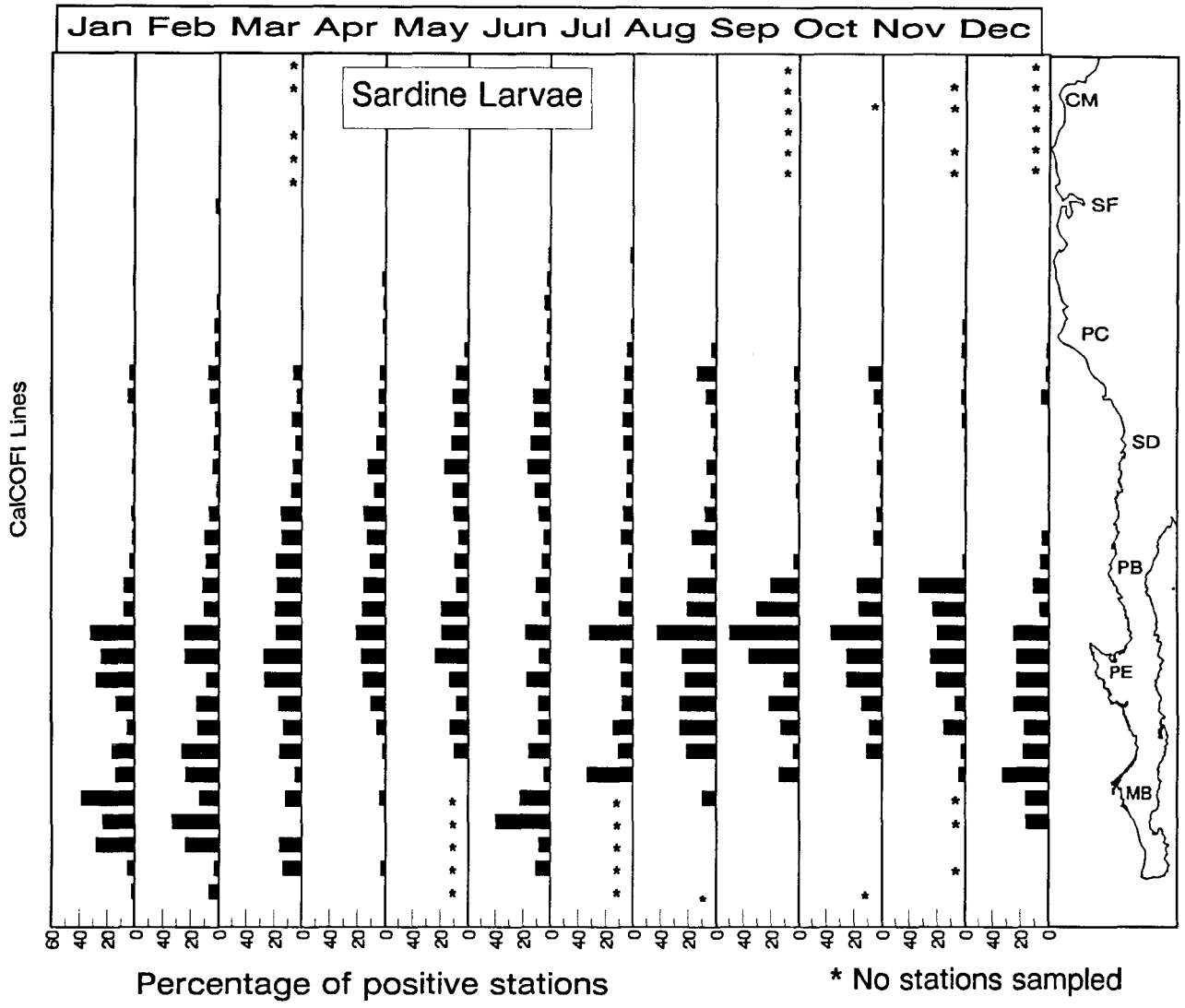

Figure 10. Monthly percentage of positive stations for sardine larvae per CalCOFI line.

larvae begins in April and extends until August, with the highest values during May and June. This region also shows a relatively homogenous offshore occurrence during those months. After August, low percentages (less than 5%) of positive stations extend as far as 90 n.mi. offshore in the SCB. In contrast, the Punta Eugenia area exhibits a high inshore occurrence of sardine larvae from August to February (more than 50%). From March to July moderate occurrence is evident (less than 30%), but the offshore distribution is homogenous as far as 90 n.mi. for this region.

The Punta Baja region seems to be a transitional area between the southern (Punta Eugenia region) and the northern patterns (SCB area), since features of both patterns are present: nearshore occurrence is highest from July to September, and there is a secondary, smaller, peak in February–March (associated with the northern pattern).

In the Magdalena Bay area the low number of offshore stations sampled did not allow a comparison with the Punta Eugenia region. In the Monterey area, there are high offshore values during June and July and low inshore values during the winter.

Anchovy eggs and larvae. Anchovy larvae are present throughout the year in all areas. Highest concentrations are nearshore from February to March (figure 14). Larvae show, in general, a more oceanic distribution than eggs for each area. In the area from Monterey to Magdalena Bay, high concentrations of anchovy larvae begin in November–December (near the coast) with a rapid increase until February–March. From April to May–June the presence of larvae decreases, reaching the lowest values in September and October. Regarding the inshore-offshore monthly distribution of larvae, the 50% contour shows higher offshore values from January to April (corresponding to the spawning peak), whereas in

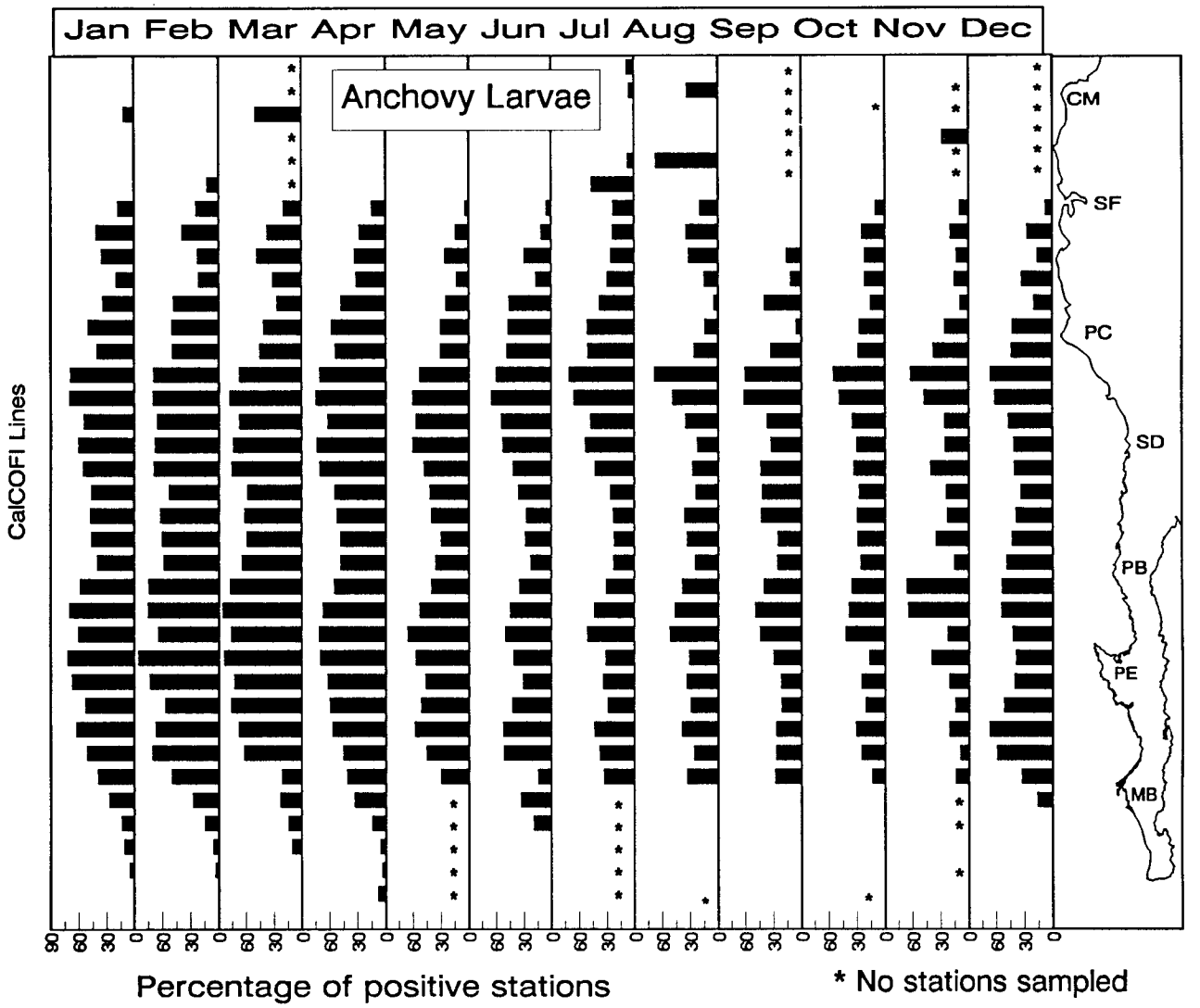

Figure 11. Monthly percentage of positive stations for anchovy larvae per CalCOFI line.

September and October the larvae are concentrated nearshore.

For particular regions, some specific features can be observed. There is a homogenous offshore distribution during June and July for the Monterey region. Offshore of Cape Mendocino, a high concentration nucleus at 70 n.mi. is evident during July.

DISCUSSION

In order to describe the long-term average geographic and seasonal distributions for sardine and anchovy eggs and larvae off California and Baja California it is important to briefly discuss several considerations. First, sardine and anchovy live in a highly productive and variable habitat. In the California Current they extend over three coastal zoogeographic provinces, an entire coastal upwelling zone, and three oceanic water masses (Moser et al. 1993). The large geographic range where these fishes live places them in regions with different seasonal and geographic patterns of abiotic and biotic parameters (SST, productivity, zooplankton biomass, etc.). The different patterns of these parameters along the extended range of sardine and anchovy could be a major factor in determining these fishes' reproductive behavior on a geographical/monthly basis. On the other hand, during the period studied (1951–89), the California Current experienced a series of warm and cold events. Also, natural fluctuations in abundance (on a decadal basis) of these populations, as well as the fisheries on them, could have altered the population structure and hence their reproductive processes.

Sardine Eggs and Larvae

The CalCOFI line and subarea analysis clearly demonstrates that sardine eggs and larvae are most concentrated in the southern portion of the range, from south of Punta

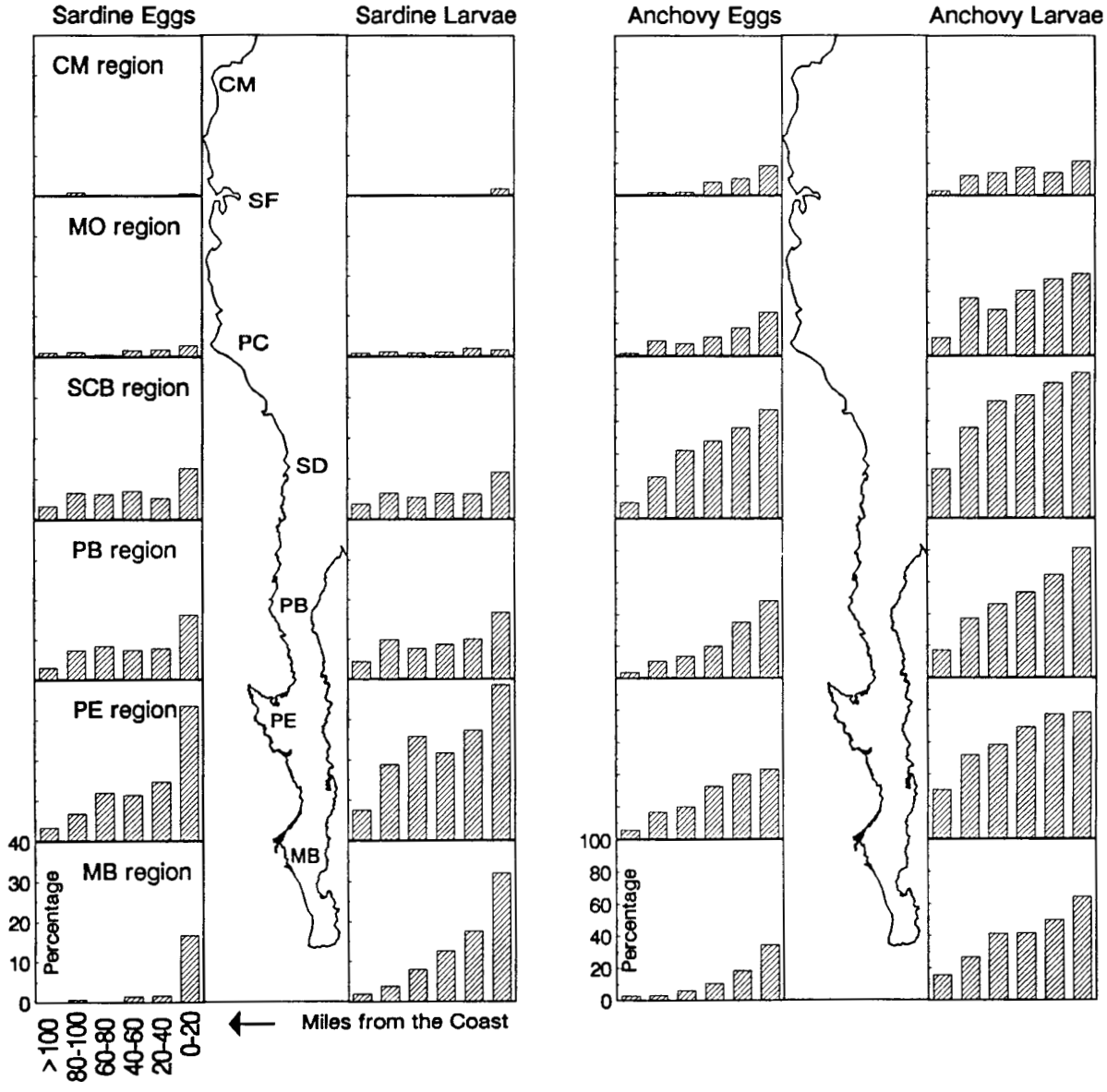

Figure 12. Inshore-offshore patterns for sardine and anchovy eggs and larvae by geographic region.

Baja, B.C., to north of Magdalena Bay, B.C.S. Eggs and larvae occur over the entire area studied, from San Francisco to Cabo San Lucas, B.C.S., but south of Magdalena Bay and north of Point Conception their values are relatively low. This geographic pattern agrees, in part, with the findings of Ahlstrom (1960) and Kramer and Smith (1971) that the Punta Eugenia region and the Southern California Bight are important spawning centers. Moser et al. (1993) also show that the Punta Eugenia area has the highest concentration of eggs and larvae.

The slight southward increase in the larvae/egg ratio (increasing southward) observed in analyses by CalCOFI line and subareas could be associated with higher SSTs observed in the south. Also the higher larvae/egg ratio from July to November could be associated with the high SST during these months. These patterns can be observed, generally, from Punta Eugenia to southern California. Incubation time is shorter at high SST (Lasker 1965).

The global seasonal analysis, which is very similar to that described in Moser et al. (1993) presents a misleading picture of the seasonality of sardine spawning. Both analyses are a composite of the two quite different seasonal patterns in the southern California–northern Baja California region and the central–southern Baja California region. In the northern pattern, spawning takes place from February to July, whereas the southern pattern shows two spawning peaks: a strong one from August to September and a small one in March.

The results presented in this paper have established that sardine eggs and larvae can be observed during any

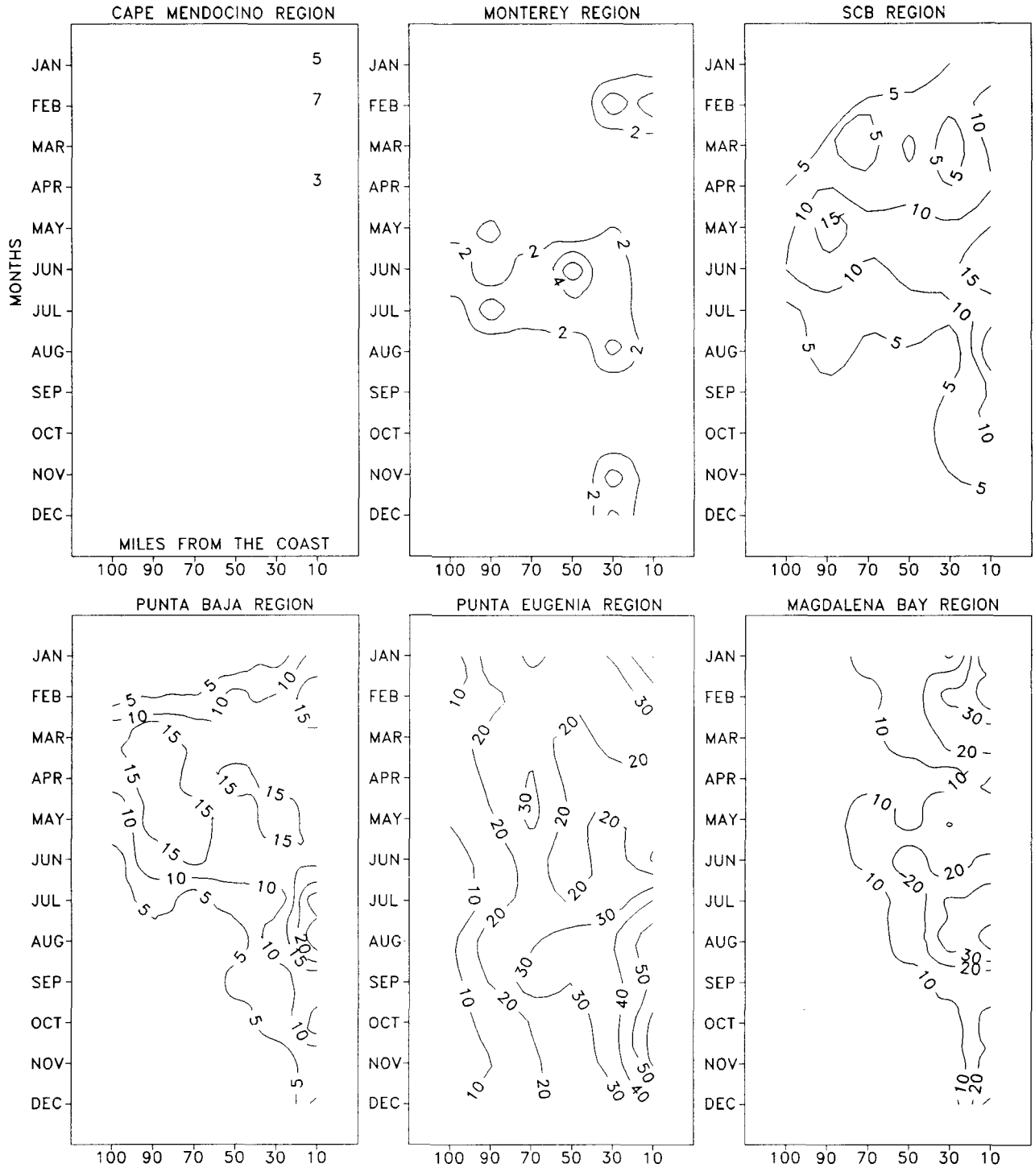

Figure 13. Monthly percentage of positive stations for sardine larvae by area and offshore.

month in at least one place off California and Baja California. The geographical-temporal analysis indicates in which months and areas high or low concentrations are found.

The analyses by CalCOFI line (geographical/seasonal) and subarea suggest that the Punta Baja region is a transition zone between the Punta Eugenia region and the Southern California Bight, because the Punta Baja seasonal pattern shows higher occurrence of larvae from February to March (as in southern California) and a small peak of spawning in August (the Punta Eugenia pattern).

The results for the geographical offshore analyses agree with those of Moser et al. (1993). High inshore

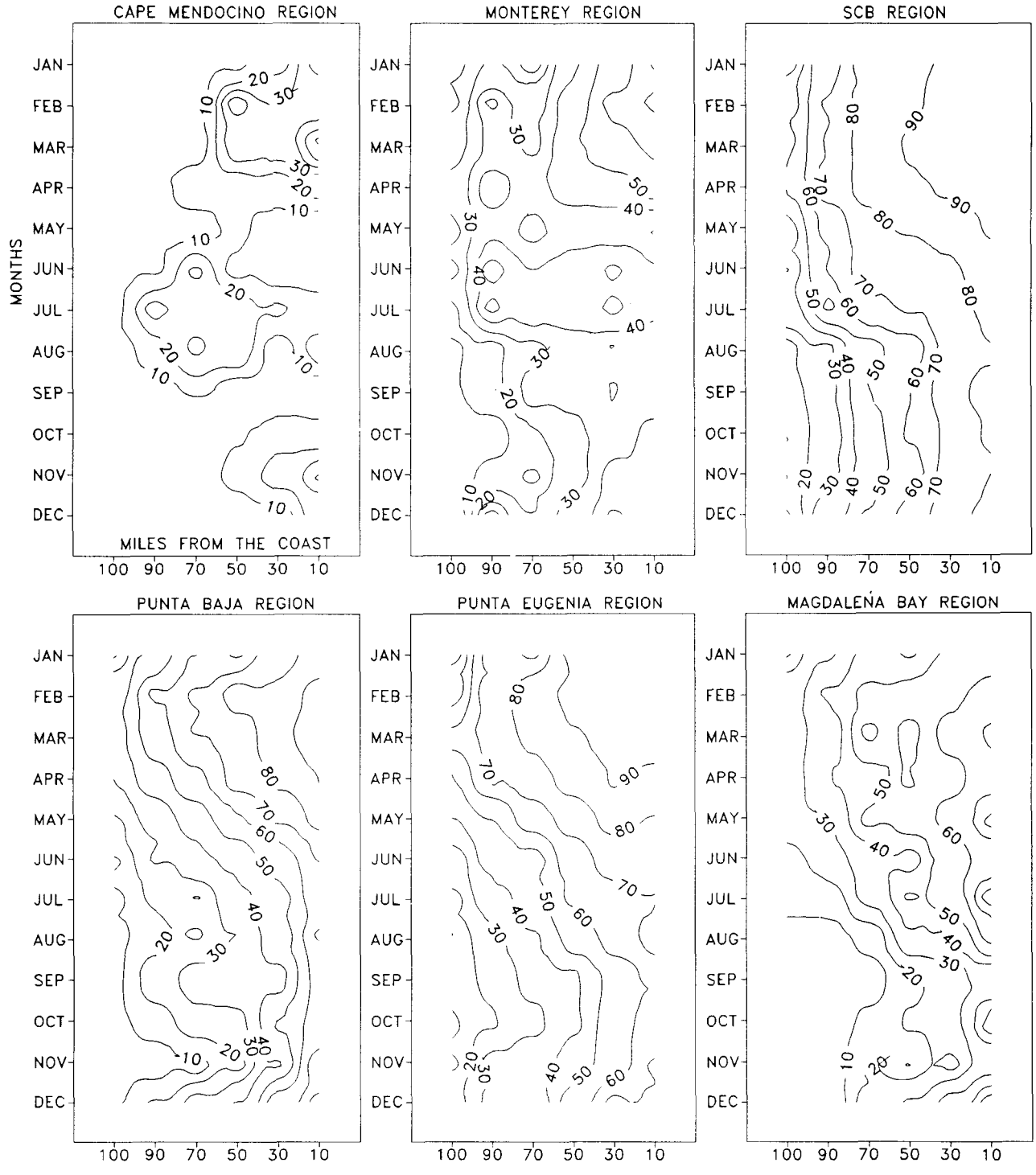

Figure 14. Monthly percentage of positive stations for anchovy larvae by area and offshore.

concentrations of sardine eggs and larvae are observed in the southern areas (Punta Baja south), and broader offshore presence of spawning is observed from southern California to the north. In the geographical/seasonal offshore analyses the pattern changes seasonally. From March to July, there is a homogenous presence of eggs and larvae from the coast to 100 n.mi. (from southern California to the Punta Eugenia region), which could be associated with upwelling processes during those months. From August to February, the offshore occurrence virtually disappears in the southern California and Punta Baja regions, but not in the Punta Eugenia area.

It can be concluded that the patterns found in the southern areas (Magdalena Bay and Punta Eugenia) are

different from those found in the northern areas (Punta Baja and the Southern California Bight).

Anchovy Eggs and Larvae

The main anchovy spawning center is clearly located in the Southern California Bight, but there is a secondary center in the Punta Eugenia area. As observed for the sardine, the higher larvae/egg ratio for anchovy from July to October could be associated with higher SSTs during these months, but the geographical effect on the ratios is not clear.

The spawning peak stretches from December to April in the global seasonal analyses, as has been previously described by several workers. The results of subarea and CalCOFI line analyses suggest no latitudinal differences for anchovy; the same seasonal pattern could be seen from southern California to the Punta Eugenia region.

It is evident that sardine and anchovy have different geographical and seasonal patterns in spawning. Although the sardine has its main spawning center in the Punta Eugenia region, anchovy are located in the Southern California Bight area. The main spawning season of the anchovy is restricted in time (December to April), whereas that of the sardine differs geographically.

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