SPAWNING HABITAT OF THE PACIFIC SARDINE (*SARDINOPS SAGAX*) IN THE GULF OF CALIFORNIA: EGG AND LARVAL DISTRIBUTION 1956–1957 AND 1971–1991

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ABSTRACT

The distribution of Pacific sardine eggs and larvae in the Gulf of California was studied from 38 cruises carried out during 1956–57 and 1971–91. Eggs and larvae were found throughout the gulf, but spawning was more intense in the central region. Contrary to previous hypotheses, spawning was not restricted to the coasts. Pacific sardine spawn in the Gulf of California from November to May, most intensely during December and January. Spawning habitat is inferred from the sea-surface temperature (SST) where early-stage (I–III) eggs are present; spawning occurred at 18.9° ± 1.9°C. Water is rarely colder than 14° in the gulf, so cold water is not likely to limit spawning, but the probability of finding Pacific sardine eggs is lower than 5% in waters warmer than 24° at the surface. It is suggested that Pacific sardine spawning in the Gulf of California is limited by the strong seasonality in sea-surface temperature caused in part by the summer intrusion of warm, subtropical water. Furthermore, eggs and larvae appear to be retained by the central anticyclonic gyre found in the gulf during winter, and spawning close to the eastern coast could be detrimental because of transport to the warm, subtropical conditions in the south.

INTRODUCTION

The Pacific sardine, *Sardinops sagax* (Jenyns, 1842), is a coastal pelagic schooling fish found from the Gulf of California, Mexico, to British Columbia, Canada (Whitehead 1985). In the Gulf of California, it has typically been the dominant species in the multispecies "sardine" fisheries. Yearly landings have exceeded 275,000 metric tons, and there is concern that the stock may have been overexploited (Cisneros-Mata et al. 1995). Hedgecock et al. (1989) found no genetic differences between sardine sampled from the Gulf of California and four other widely separated localities on the Pacific Coast. Nevertheless, there may be regional differences in life-history traits and population dynamics that occur on shorter time scales.

The Gulf of California is a semienclosed sea, unique in being the only large evaporation basin in the Pacific Ocean (Roden and Groves 1959). It is characterized by great seasonality in temperature, circulation, winds, upwelling, and productivity (Rosas-Cota 1977; Badan-Dangon et al. 1985; Robles and Marinone 1987; Valdéz-Holguín and Lara-Lara 1987; Bray 1988; Ripa and Marinone 1989; Alvarez-Borrego and Lara-Lara 1991; Paden et al. 1991; Cervantes-Duarte et al. 1993; Castro et al. 1994; Santamaría-del-Angel et al. 1994a, b; Lavín et al. 1995).

There have been many reports of sardine eggs and larvae collected from ichthyoplankton cruises in the Gulf of California (Sokolov and Wong-Ríos 1972, 1973; De la Campa and Gutierrez 1974; Gutierrez 1974; Gutierrez and Padilla 1974; Moser et al. 1974; Sokolov 1974; Wong-Ríos 1974; De la Campa and Ortiz 1975; Molina-Valdez and Pedrin 1975; De la Campa et al. 1976; Padilla-Garcia 1976a, b, 1981; Olvera-Limas 1981; Olguin et al. 1982; Molina-Valdez et al. 1984; Olvera-Limas and Padilla 1986). However, egg stages have not been presented to better define the spawning season, and the overall seasonality of Pacific sardine spawning has not been described.

The purpose of this paper is to analyze the seasonality in the distribution of Pacific sardine eggs and larvae collected on 38 cruises from 1956 to 1991 in the Gulf of California and to determine the relation of spawning to sea-surface temperature. Early-stage eggs are a good index of spawning, and their presence can be used to define the thermal limits under which spawning tends to occur (Tibby 1937; Ahlstrom, 1943; Lasker 1964; Lluch-Belda et al. 1991).

MATERIALS AND METHODS

Historical raw data come from seven California Cooperative Oceanic Fisheries Investigations (CalCOFI,

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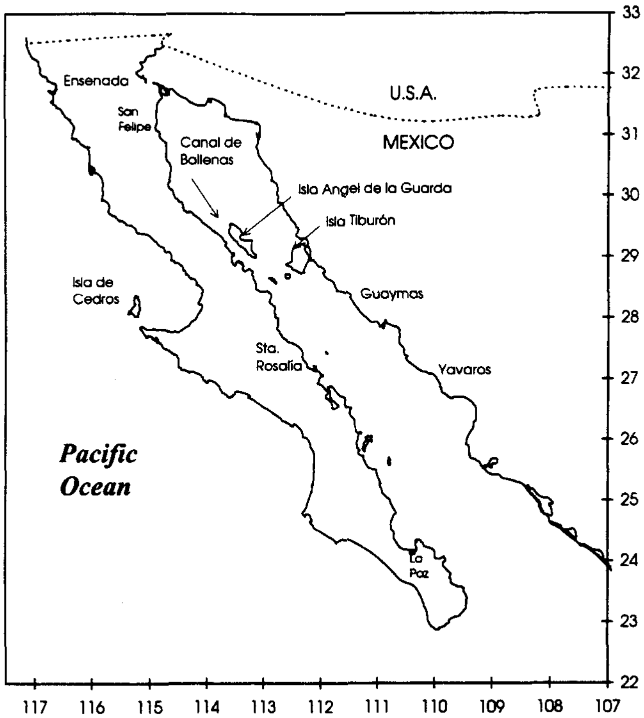

Figure 1. The Gulf of California.

TABLE 1
Cruises in the Gulf of California

Cruise	Institution	Dates	Number of stations
CC5602	CalCOFI, USA	Feb. 1956	93
CC5604	"	Apr. 1956	129
CC5612	"	Dec. 1956	79
CC5702	"	Feb. 1957	70
CC5704	"	Apr. 1957	125
CC5706	"	June 1957	132
CC5708	"	Aug. 1957	81
AA7101	INP, Mexico	Apr. 1971	50
AH7110	"	Sept. 1971	80
AA7204	"	Apr. 1972	77
AH7206	"	Nov. 1972	79
AA7302	"	Mar. 1973	79
AH7303	"	Mar. 1973	15
AA7305	"	Apr.–May 1973	75
AA7308	"	July 1973	103
AA7402	"	Feb.–Mar. 1974	52
AA7403	"	Apr. 1974	12
AA7405	"	Dec. 1974	19
AA7501	"	Jan. 1975	66
AA7503	"	Mar.–Apr. 1975	50
AA7504	"	Apr. 1975	39
AA7601	"	Jan. 1976	65
AH7605	"	Apr. 1976	66
AA7605	"	July 1976	58
AA7701	"	Feb. 1977	24
AH7703	"	Sept. 1977	58
AA7704	"	Aug.–Sept. 1977	50
AA7708	"	Dec. 1977	48
AA7802	"	Feb.–Mar. 1978	59
AA7810	"	Sept.–Oct. 1978	59
AA8103	"	Mar.–Apr. 1981	78
PU8403	"	Mar.–Apr. 1984	87
PU8611	"	Nov. 1986	187
AA8701	"	Jan.–Feb. 1987	56
PU8711	"	Nov. 1987	22
AL9002	CICESE	Feb.–Mar. 1990	200
BIPXI9008	"	Aug.–Sept. 1990	38
PU9109	"	Sept. 1991	110

USA) and 28 Instituto Nacional de Pesca (INP, Mexico) cruises in the Gulf of California (fig. 1) during 1956–57 and 1971–87; three additional cruises were carried out by the Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE, Mexico) during 1990 and 1991 (table 1).

The number of cruises per year, number of stations, sampling gear, and station plan varied among cruises (fig. 2, table 2); there were no cruises during the 1960s. During the 38 cruises, 3,631 tows from 2,667 stations were made with a surface neuston net, a standard CalCOFI net, a bongo net, or a CalVET net, following ichthyoplankton techniques described by Kramer et al. (1972), Smith and Richardson (1977), and Lasker (1985).

Pacific sardine eggs and larvae were separated; eggs were staged following Ahlstrom (1943); and larvae were measured to ±0.5 mm. Egg abundance data were standardized to numbers/m^2; larval abundances were standardized to numbers/10 m^2. The high variability of water volume filtered in the surface neuston tows caused by the net breaking the surface, and the overestimation of abundance from surface samples does not allow for standardization, so for neuston samples we used presence or absence, not actual abundance.

During summer months in the Gulf of California, Pacific sardine eggs could be confused with those of thread herring (*Opisthonema* spp.; Matus-Nivón et al. 1989 [for *O. libertate*]), but slight differences between the number of myomeres and pigmentation of the larvae have been reported (Watson and Sandknop 1996). Nevertheless, it is unlikely that thread herring eggs and larvae occurring in the summer would have been misidentified as Pacific sardine for several reasons. Adult distribution of Pacific sardine during the summer is restricted to the region of the large islands, north of the central gulf (Cisneros-Mata et al. 1988). Adult maturity studies have shown that Pacific sardine preferentially spawn in cooler temperatures during winter and spring (Torres-Villegas et al. 1986), and thread herring spawn in warm temperatures during summer (Torres-Villegas et al. 1985; Rodriguez 1987). The relative abundance of thread herring adults in the Gulf of California is usually lower than that of Pacific sardine (Cisneros-Mata et al. 1988). As an example, thread herring scales were not sufficiently abundant to appear in laminated sediments in the Gulf of California (Holmgren and Baumgartner 1993), even though they are quite different from Pacific

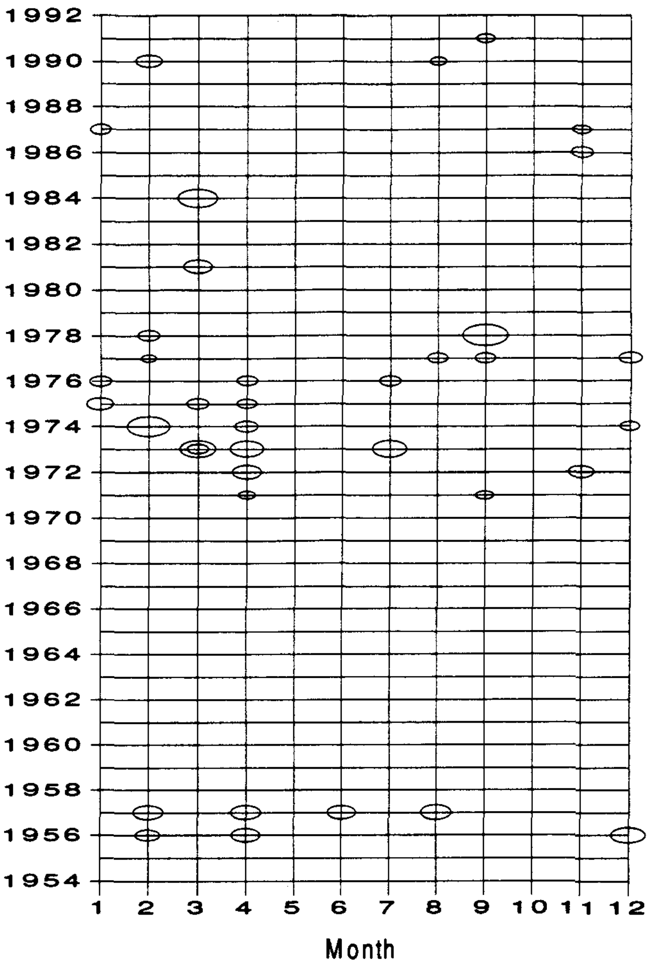

Figure 2. Time distribution of cruises in the Gulf of California. Ellipses indicate individual cruises, with size proportional to cruise duration (5 to 31 days).

TABLE 2
Number of Stations and Tows per Cruise in the Gulf of California

Cruise	Stations	Oblique tows*	Neuston tows
CC5602	93	93	0
CC5604	129	129	0
CC5612	79	79	0
CC5702	70	70	0
CC5704	125	125	0
CC5706	132	132	0
AA7101	50	50B	50
AH7110	80	80C	80
AA7204	77	77C	77
AH7206	79	79C	79
AH7302	79	71C	61
AA7303	15	15C	4
AA7305	75	73C	70
AA7308	103	66C	103
AA7402	52	40C	52
AA7403	12	8C	12
AA7405	19	16C	17
AA7501	66	37C	66
AA7503	50	50C	50
AA7504	39	32C	39
AA7601	65	39C	65
AH7605	66	49C	66
AA7605	58	39C	58
AA7701	24	21C	24
AH7703	58	48C	58
AA7704	50	50C	0
AA7708	48	48C	0
AA7802	59	59C	0
AA7810	59	59C	0
AA8103	78	78C	0
PU8403	87	87B	0
PU8611	187	187CV	0
AA8701	56	56B	0
PU8711	22	22B	0
AL9002	200	200CV	0
AL9002	200	110B	0
BIP9008	47	47M	0
PU9109	79	79B/71M	0

*B = bongo net; C = CalCOFI net; CV = CalVET net; M = Kidd-Methot net.

sardine scales and easily identifiable (Holmgren 1993). During the June cruise clupeoid eggs were found and thought to be thread herring (12.3% positive from NMSF/SWFC raw data notes) because thread herring larvae were the most abundant larval fish and no Pacific sardine larvae were found (Moser et al. 1974); using later life stages as a taxonomic aid for earlier life stages is a common practice. Furthermore, although Pacific sardine eggs and larvae were reported from the two cruises during July, no thread herring eggs were reported. Thread herring larvae were reported for the cruises during August and September, but not thread herring eggs.

Seasonality in the spawning of Pacific sardine is described as the average percentage of positive stations per month for eggs and larvae. Distribution and abundance data for Pacific sardine eggs and larvae in the Gulf of California are combined for all cruises, as well as for each month when spawning occurred.

Sea-surface temperature (SST) was taken at each station during the cruises. Station SST data for the CalCOFI cruises are from SIO (1963 and 1965). The surface thermal characteristics of the spawning habitat were described by comparing the frequency distribution of SST for stations positive for egg stages I–III and IV–XI, and larvae. Eggs are 13 to 8 hours old at the end of stage III at 17° and 21°C, respectively (calculated from data in Lasker 1964). Using all egg stages to increase the sample size, we calculated the probability of finding Pacific sardine eggs at different SSTs.

RESULTS

Average SST in the Gulf of California ranged from 17° in February to 30° in August; no cruises were made in October, so that point was interpolated (fig. 3).

Pacific sardine spawn in the Gulf of California from November to May, most intensely during December and January (fig. 4, table 3). Owing to their more dispersed distribution (Smith 1973; Hewitt 1981), larvae (20%–50%

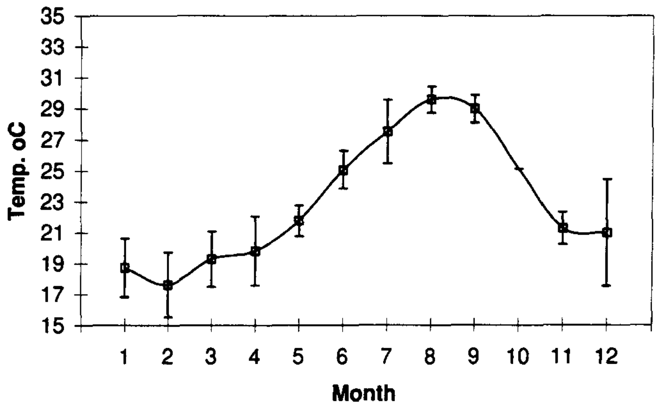

Figure 3. Average monthly sea-surface temperature in the Gulf of California from cruise data ±1 SD.

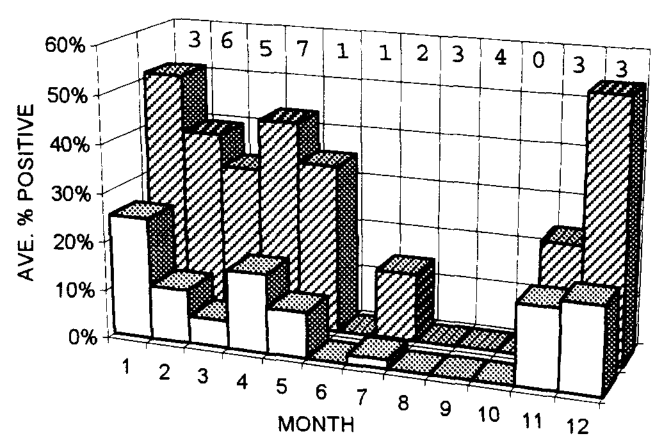

Figure 4. Monthly average percentage of positive stations for all egg stages (open bars) and larvae (hatched bars) of Pacific sardine in the Gulf of California, 1956–91. Numbers at top indicate the number of cruises per month.

TABLE 3
Percentages of Positive Stations for Pacific Sardine Eggs and Larvae in the Gulf of California

Cruise	Stations	Eggs	Larvae
CC5602	93	17.4	35.5
CC5604	129	16.7	35.8
CC5612	79	13.7	52.9
CC5702	70	29.2	42.4
CC5704	125	17.5	68.2
CC5706	132	0.0	0.0
CC5708	81	0.0	0.0
AA7101	50	30.0	32.0
AH7110	80	0.0	0.0
AA7204	77	10.4	40.3
AH7206	79	0.0	2.5
AA7302	71	5.1	36.7
AA7303	15	0.0	13.3
AA7305	73	9.3	34.7
AA7308	66	1.9	17.5
AA7402	40	11.3	51.9
AA7403	8	33.3	50.0
AA7405	16	31.6	89.5
AA7501	37	6.1	43.9
AA7503	50	10.0	36.0
AA7504	32	2.6	56.4
AA7601	39	16.9	33.8
AH7605	49	3.0	18.2
AA7605	39	1.7	10.3
AA7701	21	4.2	41.7
AH7703	48	3.4	0.0
AA7704	50	0.0	0.0
AA7708	48	8.3	18.7
AA7802	59	0.0	28.8
AA7810	59	1.7	0.0
AA8103	78	12.8	41.0
PU8403	87	0.0	35.6
PU8611	187	31.0	0.0
AA8701	56	51.8	75.0
PU8711	22	18.2	68.2
AL9002	110	4.0	35.0
BIP9008	38	0.0	0.05
PU9109	110	0.0	0.0

stations positive) were captured in more stations than eggs (5%–25%).

The central gulf is the most important area for spawning in the Gulf of California (fig. 5); spawning is not restricted to the coasts, but appears more related to the central gyre(s). Spawning was irregular in both the northern and southern gulf. More larvae than eggs were collected in the samples, and larvae were more widely distributed throughout the central gulf.

Monthly distribution maps for eggs and larvae are shown for November to May, when most spawning occurred (figs. 6 and 7). When spawning was most intense, higher concentrations appeared in the central gulf and became less dense and generally more coastal as spawning declined. Comparison of the distribution of eggs and larvae reveals little evidence for east–west transport, although transport of larvae to the south is suggested.

The SST interval within which eggs of stages I–III, IV–XI, and larvae were collected in the gulf clearly differed from that of the general gulf environment (fig. 8). Of the 1,209 stations sampled for eggs, only 59 were positive for stage I–III eggs. The average SST for those stations was 18.9° ± 1.9°. One standard deviation below and above the mean SST for these early-stage eggs is between 16.9° and 20.8°. A total of 213 stations were positive for eggs of any stage.

Older eggs (stages IV–XI) become dispersed over the SSTs found in this environment, and generally occur in warmer waters and within a wider SST interval than stage I–III eggs (Kolmogorov-Smirnov *t* test, $p < 0.07$). Larvae were found in significantly cooler water (19.0° ± 2.1°) than stage IV–XI eggs (Kolmogorov-Smirnov *t* test, $p < 0.008$), and no significant difference was found from the SST interval of stage I–III eggs. All egg stages and larvae were found in SSTs significantly cooler than

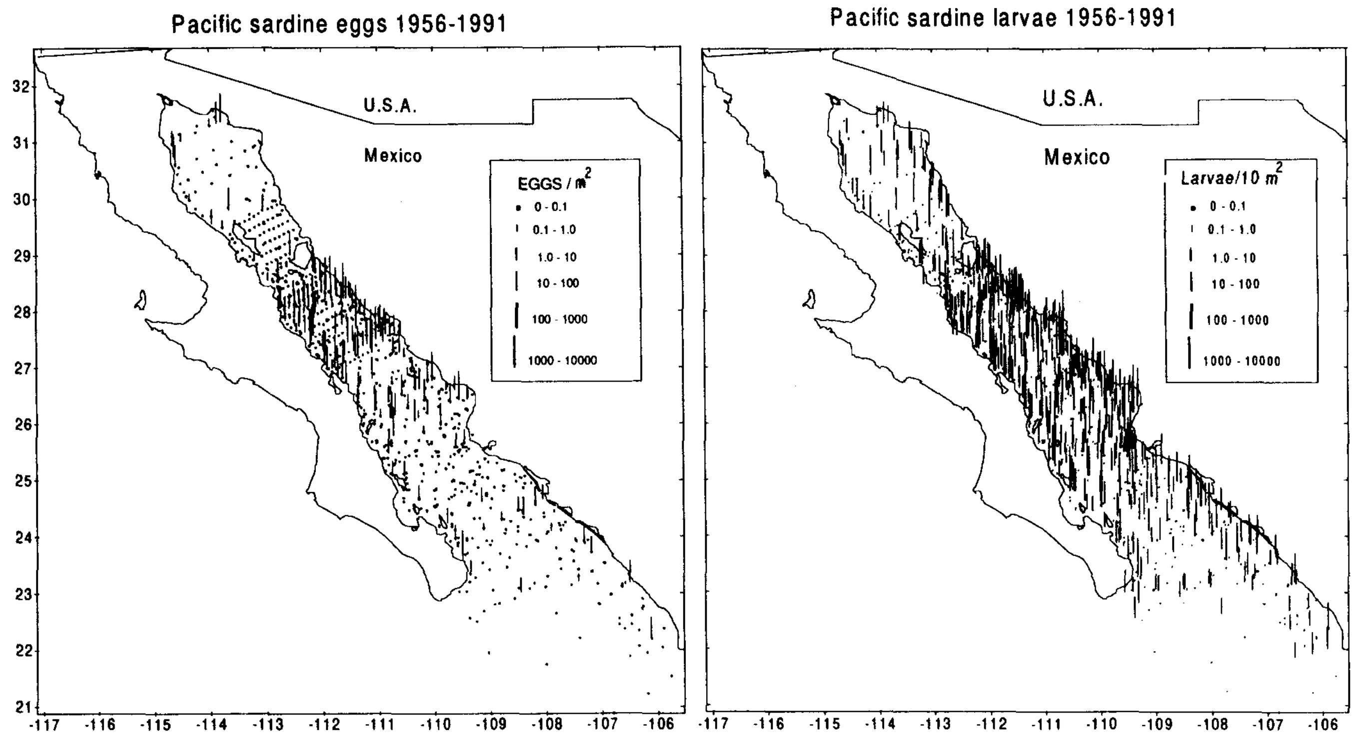

Figure 5. Distribution and abundance of Pacific sardine eggs and larvae collected on 38 cruises in the Gulf of California, 1956–57 and 1971–91.

the gulf's average SST of 22.3° ± 4.7° (Kolmogorov-Smirnov *t* test, $p < 0.001$).

The probability of collecting eggs at different SSTs available in the Gulf of California is truncated below 14°, and skewed toward higher SSTs (fig. 9). For eggs of any stage, 95% of positive stations are found between 15° and 23° SST. Dispersion of eggs into warmer, and possibly unfavorable, waters, as suggested by figure 8, is also shown here by the skewness of the curve; the wider SST interval is due to the inclusion of late-stage eggs.

DISCUSSION

This study incorporated historical data from 38 cruises of varying design; standard techniques were not always used, nor was the gulf equally represented in time and space. Recently, disparities between CalCOFI and INP egg staging showed that INP underestimated the numbers of early stages because many eggs were assumed to be damaged, and were not aged. For the purpose of the present paper, however, more emphasis was given to total eggs and their percentage of occurrence.

Because of these shortcomings in the database, interannual comparisons of distribution, abundance, and spawning biomass cannot be made. Nevertheless, by combining cruises and thus increasing sample size, it is possible to reach some conclusions about spawning habitat in relation to SST conditions of the gulf.

Dispersal of eggs and larvae is shown by the greater geographical area over which larvae were collected (see figs. 5–7), and by the increased SST range over which older eggs and larvae were found. Smith (1973) defined diffusion and transport as the only feasible causes of dispersal until larvae can swim well enough to determine their own distribution. Hewitt (1981) described a decrease in patchiness after spawning as eggs are dispersed passively; when larvae begin to form schools and swim, patchiness increases. The significant decrease in mean SST of stations positive for larvae compared to eggs, despite higher overall SST in the gulf, also suggests this pattern of dispersal and then schooling.

Optimal physical conditions for larval survival and growth occur where physical forces provide retention, concentration, and enrichment (Parrish et al. 1981; Lasker 1985; Cury and Roy 1989; Bakun et al. 1991; Hunter and Alheit 1995; Bakun 1996). The circulation in the Gulf of California provides an ideal combination of factors for larval survival, by aiding the retention of eggs and larvae in the highly productive central gulf region. Two major gyre systems have been described, one in the upper gulf, and the other in the central/southern region (Bray 1988; Marinone and Ripa 1988; Beier 1997; Marinone, unpubl. data). In the upper 100 m of the central gulf gyre, currents near the coast can be as strong as 60 km per day (70 cm s^{-1}), diminishing to almost zero about 30 km offshore (Beier 1997). During winter, flow is southward on the eastern coast and northward on the peninsular coast; during summer the flow reverses (Beier 1997). Both Beier (1997) and Marinone (unpubl.

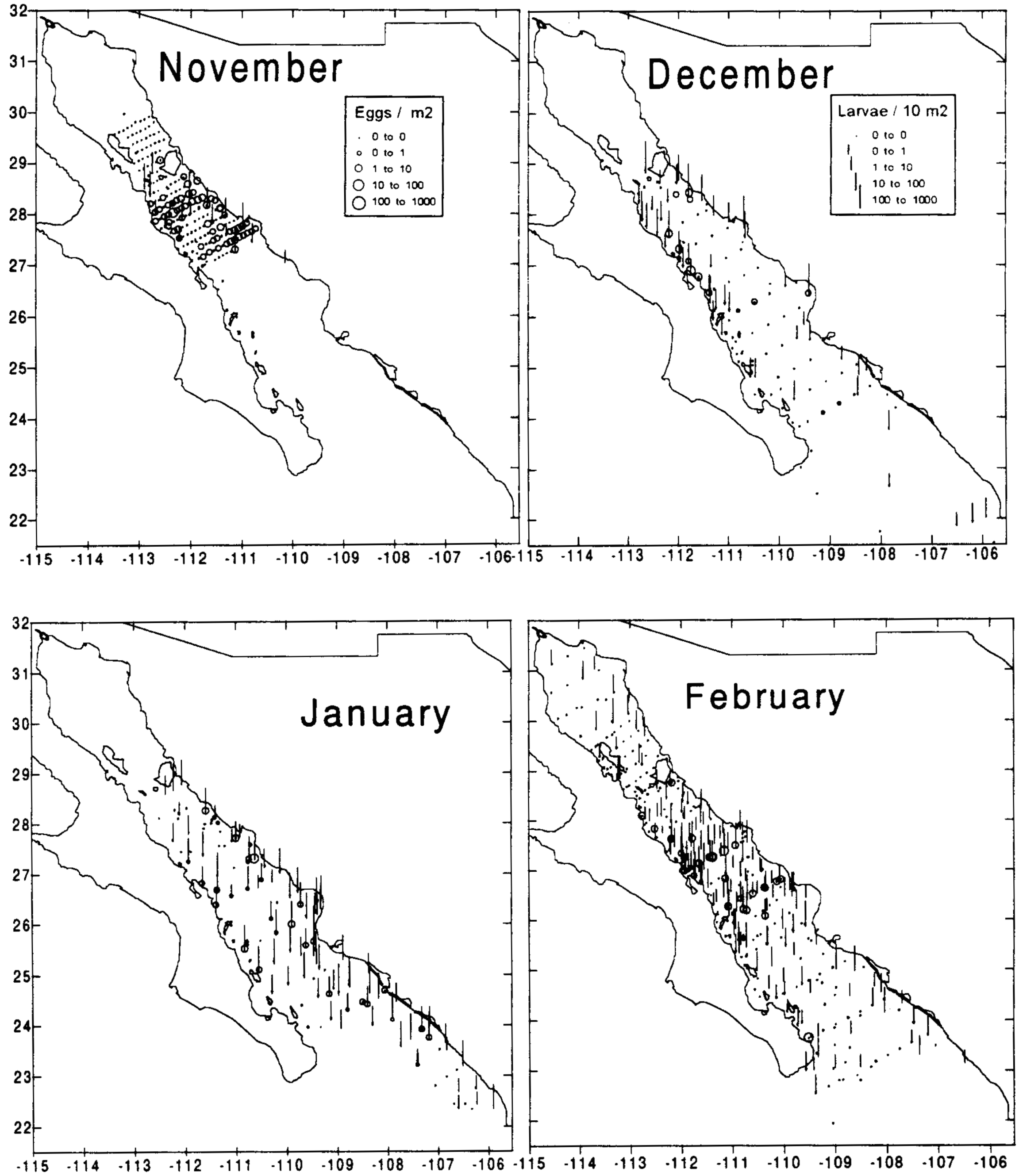

Figure 6. Monthly distribution combined for all years of Pacific sardine eggs (circles) and larvae (lines) in the Gulf of California, 1956–57 and 1971–91: November, December, January, February.

data) predicted weak east–west currents on the order of 1–2 km per day, which also change direction seasonally; flow is from east to west during winter. Mesoscale fronts and filaments in the central gulf were observed in satellite imagery and reported by Badan-Dangon et al. (1985) and Hammann et al. (1988). Similar filaments have been studied in the California Current and could represent flow velocities up to 50 km per day (Flament et al. 1985).

Pacific sardine eggs hatch in fewer than three days (Ahlstrom 1943), and 20 mm larvae are about 40 days old (Butler 1987). Although average east–west flow would cause only a net transport of about 40 km before larvae can swim and school, eggs and larvae near filaments could reach the western coast in a few days, where they would be entrained in the central gyral circulation. Some southern loss is evident, however, and could represent the eggs and larvae of adults that spawned too close to the east coast, where currents are fastest.

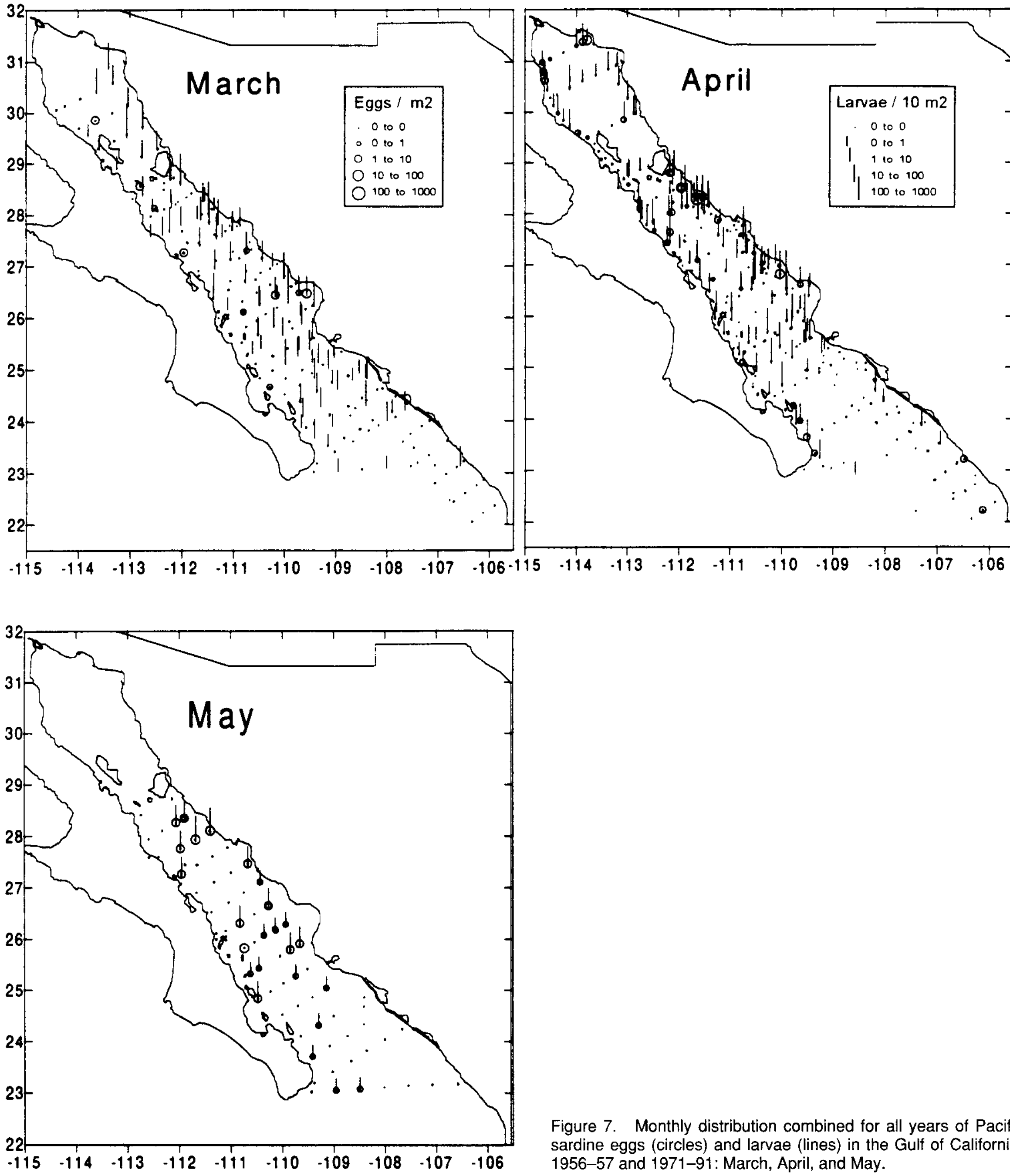

Figure 7. Monthly distribution combined for all years of Pacific sardine eggs (circles) and larvae (lines) in the Gulf of California, 1956–57 and 1971–91: March, April, and May.

Summer thermal conditions (SST) are accompanied by changes in the wind and circulation regime, and the central gyre reverses direction; larvae could be transported south toward unfavorable conditions. A similar mechanism for larval retention was described for haddock (*Melanogrammus aeglefinus*) in Georges Bank (Smith and Morse 1985). For the Southern California Bight, Parrish et al. (1981) related the spawning of several species of small pelagic fishes to weak offshore transport and coastal gyre circulation patterns. Nakata et al. (1989) found that eggs and larvae of *Sardinops melanosticta* were transported from offshore spawning grounds and concentrated in the frontal zone in Sagami Bay, Japan.

Our study shows that spawning was not restricted to the cool upwelled waters (<16°C) off the mainland coast but was more intense in the central gulf, within a range of 16.9° to 20.8° SST. Furthermore, the distribution of Pacific sardine eggs and larvae in the Gulf of California indicates retention near the spawning area in the central gulf. The difference observed in figure 8 between the temperature distribution of early- and late-stage eggs suggests spawning near fronts; at temperatures below 21°,

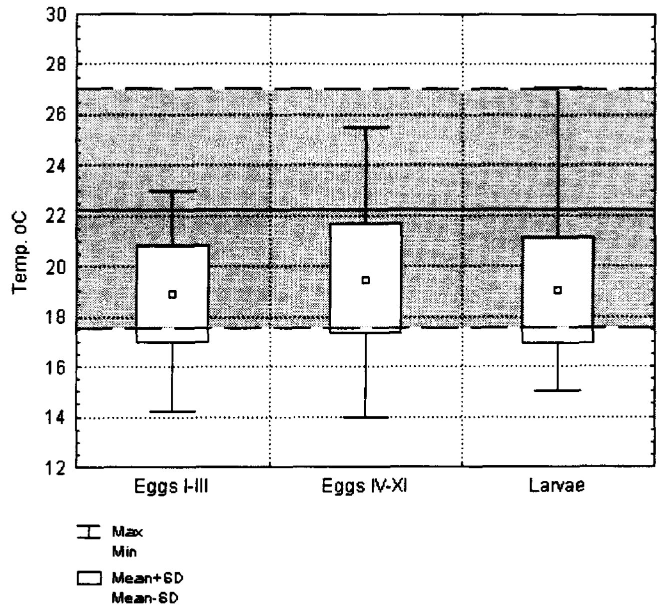

Figure 8. Sea-surface temperature for Pacific sardine egg stages I–III and IV–XI, and larvae collected in the Gulf of California on 38 cruises, 1956–57 and 1971–91. Mean overall environmental sea-surface temperature ±1 SD is shown in the shaded background.

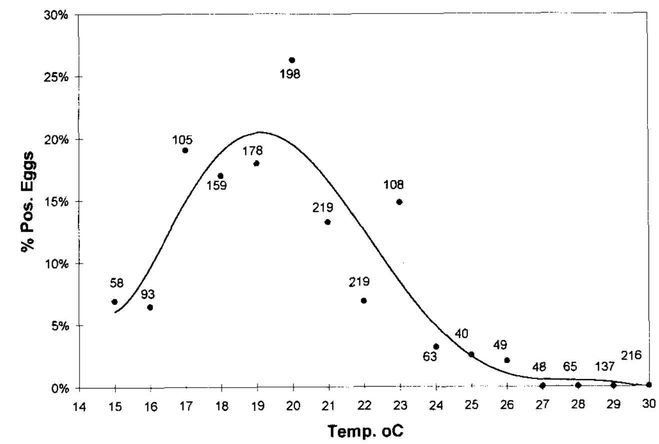

Figure 9. Probability of collecting Pacific sardine eggs of any stage at various sea-surface temperatures in the Gulf of California. Data are from the percentage of positive stations for all tows across all years at each temperature. The line represents the best fit with a polynomial model for the data from 38 cruises during 1956–57 and 1971–91.

stage I–III eggs mature in fewer than 13 hours. The model for the Pacific sardine life cycle in the Gulf of California proposed by Sokolov (1974) included winter spawning on the eastern coast, and transport of eggs and larvae toward the western coast. That study was based on fisheries and ichthyoplankton data collected during 1970–73, a period of low population size (Cisneros-Mata et al. 1995), which might explain the contrast with our study. Nevertheless, during those early years, the sardine fisheries operated only near the coast, and the ichthyoplankton surveys were concentrated in areas of known sardine abundance.

Although Pacific sardine biomass in the Gulf of California varied greatly from 1956 to 1991 (Moser et al. 1974; Cisneros-Mata et al. 1995), individual cruise reports show a similar distribution for eggs and larvae. A pattern of geographic habitat suitability related to population biomass, as suggested by MacCall's basin model (MacCall 1990), could bias a study of habitat usage. Nevertheless, in the Gulf of California, the seasonal variation in SST is much greater than the interannual variability, and thus should not greatly affect these results, especially when all years are combined. Furthermore, no trend was observed in percentage of stations positive for eggs during the study period (table 3). The relation between habitat availability and fluctuations in the sardine population will be explored in another paper.

The spawning season of Pacific sardine in the Gulf of California (November to May) can be related to the observed seasonality in SST and circulation, and matches the spawning seasonality reported in adult maturity studies by Torres-Villegas et al. (1986). Although small numbers of sardine eggs and larvae were reported during July, they could have been confused with *Opisthonema* spp. But as mentioned previously, it is not likely that the *Opisthonema* spp. eggs and larvae reported in summer months were in fact Pacific sardine; we merely suggest that there is a possibility of limited Pacific sardine spawning in localized areas during summer.

Early southerly intrusion of warm water may affect recruitment by compressing the sardine's adult distribution northward, reducing available spawning habitat, and shortening the spawning season. There are few places in the world where populations of temperate sardines (*Sardinops, Sardina*) are as geographically limited as in the Gulf of California. North–south seasonal migration of the Pacific sardine has been described for the Gulf of California (Sokolov and Wong-Rios 1973) and the California Current (Clark and Janssen 1945). The land barriers to the north, west, and east, and the subtropical water to the south of the gulf, however, limit living space and the potential for population growth.

When habitats are compressed, cannibalism may increase (Hunter and Kimbrell 1980; Santander et al. 1983; Alheit 1987; Hammann et al. 1988), and increased food competition among juveniles may affect their mortality, growth rate, and future fecundity. Cisneros-Mata et al. (1996) demonstrated the importance of density-dependent and environmental factors for the population dynamics of Pacific sardine in the Gulf of California. Huato-Soberanis and Lluch-Belda (1987) suggested strong recruitment of Pacific sardine in the gulf after cool, anti-El Niño years, conditions which would represent an increase in available habitat. For adult Pacific sardines, Hammann et al. (1991) explained the three-fold summer

TABLE 4
Temperature Ranges for Peak Spawning of Sardine Species in Different Regions

Species	Region	Range (°C) for peak spawning	Reference
Sardinops sagax	Gulf of California	17–20.8 mean ±1SD	This paper
Sardinops sagax	Calif. Current	15–18	Tibby 1937
Sardinops sagax	Calif. Current	13–16	Ahlstrom 1959
Sardinops sagax	Calif. Current	15 and 23 (2 peaks)	Lluch-Belda et al. 1991
Sardinops sagax	Magdalena Bay, B.C.S.	16.1–25.6 (min/max)	Lluch-Belda et al. 1991
Sardinops neopilchardus	Australia	14–21 (min/max)	Whitehead 1985
Sardinops ocellatus	South Africa		Crawford et al. 1987
	23°S	12–16.5	
	20°S	16.5–22.8	

increase in the catch per unit of effort (CPUE, t/trip) in the large island region in the gulf by increased school density caused by habitat compression.

By comparing the SST intervals over which sardines have been found spawning or commercially captured around the world, one can see that as temperate species, all sardines live between 10° and 25°C and spawn mostly between 15° and 20° (table 4). The warmest peak spawning reported is in the Gulf of California and Bahía Magdalena, Mexico, and—late—in the California Current (Lluch-Belda et al. 1991). Warm-water spawning should benefit larval growth and mortality as long as there are sufficient food resources (Hunter and Alheit 1995). This combination may not be common in other areas of the world because warm temperatures do not often coincide with high food abundance. Finally, Lasker (1964) reported, from laboratory experiments on how temperature affects development rate, that few Pacific sardine eggs or larvae survive below 13°. The upper thermal limit, however, is unknown because the eggs survived the highest temperature tested (21°); field data presented here suggest the upper limit to be near 27° (fig. 9).

In this paper, the SST interval over which Pacific sardine spawn in the Gulf of California is defined, as is the probability of spawning at the temperatures available in the environment. Ninety-five percent of positive egg stations had SSTs between 15.1° and 22.7°, and there is less than a 5% probability of finding eggs in waters warmer than 24°. This information could be important for egg production cruises if real-time temperature data were available, for example from satellite imagery. Water temperatures lower than 14° are rare in the Gulf of California, and we suggest that Pacific sardine spawning is limited by habitat because of the summer intrusion of warm water. Furthermore, the relation of spawning to winter circulation patterns suggests that eggs and larvae are retained by the central anticyclonic gyre in the gulf, and that spawning close to the eastern coast could be detrimental.

In conclusion, Pacific sardine spawning is related to the strong seasonality in thermal and circulatory conditions in the Gulf of California, and the temperature relationship presented here could be useful for monitoring seasonal and interannual changes in thermal habitat for spawning.

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