DISTRIBUTION OF LARVAL PACIFIC SARDINE, SARDINOPS SAGAX, IN SHALLOW COASTAL WATERS BETWEEN OCEANSIDE AND SAN ONOFRE, CALIFORNIA: 1978–1986

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ABSTRACT

Spatial and temporal distributions of larval Pacific sardine, *Sardinops sagax*, were investigated at two nearshore sites between San Onofre and Oceanside, California. Neuston, midwater, and epibenthic samples were collected at night with plankton nets towed at a randomly selected isobath within each of five sampling blocks between the 6-m and 75-m isobaths at each site. The San Onofre site was sampled from January 1978 through September 1986; the site near Oceanside was sampled from July 1979 through September 1986. Sampling frequency varied from weekly to quarterly, depending on other requirements of the study.

The average cross-shelf distribution of larvae differed little from year to year: abundance usually was highest between the 12-m and 45-m isobaths, particularly for yolk-sac and preflexion larvae. Densities were typically highest in midwater. Vertical and cross-shelf distributions were similar at both study sites.

Larvae were found nearly year-round, but were most abundant in summer and fall. Seasonal abundance patterns differed relatively little between sites or from year to year. Abundance was quite low from 1978 to 1980, then increased dramatically to a peak in 1984.

The results of this study, together with other published reports, suggest that the resurgence of the Pacific sardine off southern California in the early 1980s began in 1981 in shallow waters along the central southern California coast.

RESUMEN

Se investigó la distribución espacio-temporal de las larvas de *Sardinops sagax*, la sardina del Pacífico, en dos estaciones costeras entre San Onofre y Oceanside, California. Se colectaron muestras durante la noche en el neuston, a media agua y en el epi-bentos; en cada localidad se hicieron arrastres en curvas isobatas elegidos aleatoriamente en cada uno de cinco bloques de muestreo (entre las curvas isobatas de 6 y 75 m). El sitio en San Onofre fué muestreado de Enero de 1978 a Septiembre de 1986, y el cercano a Oceanside de Julio de 1979 a Septiembre de 1986. La frecuencia de muestreo fué variada, de semanal a trimestral, dependiendo de otros requerimentos del estudio.

La distribución promedio de las larvas en sentido perpendicular a la costa varió poco de año a año, encontrandose la máxima abundancia entre las curvas isobatas de 12 y 45 m; esto fué particularmente cierto para los estadios de saco vitelino y pre-flexión. Las densidades más altas se encontraron a media agua. Las distribuciones vertical y en sentido perpendicular a la costa fueron similares en ambos sitios de estudio.

Se encontraron larvas durante todo el año, con máximos en verano y otoño. Los patrones de abundancia estacional difirieron relativamente poco entre los distintos sitios o de año a año. La abundancia larval fué relativamente baja en 1978–80 y subsecuentemente se incrementó de manera substancial hasta alcanzar un máximo en 1984.

Los resultados de este estudio, aunados a otros reportes ya publicados, sugieren que el repunte a principio de los 80 de la sardina del Pacífico en el Sur de California empezó en 1981 en aguas someras de la costa central del Sur de California.

INTRODUCTION

The rise and fall of the Pacific sardine fishery along the west coast of the United States between about 1915 and the mid 1960s has been extensively documented and discussed (e.g., Murphy 1966; Ahlstrom and Radovich 1970; MacCall 1979; Radovich 1982). A minor fishery continued after the mid 1960s until 1974, when a moratorium was declared. In the early 1980s Pacific sardine again began to increase in California waters (e.g., Bedford et al. 1982; Wolf and Smith 1985), and in 1986 a small directed fishery once again was permitted (e.g., Wolf and Smith 1986; Wolf et al. 1987).

Lavenberg et al. (1986), reporting on nearshore ichthyoplankton surveys along the southern California coast, suggested that this resurgence may have begun in shallow coastal waters, as would be

[[]Manuscript received February 3, 1992.]

predicted by MacCall's (1983) model of habitat selection by declining fish populations. The purpose of this report is to further document the spatial and temporal distributions of larval Pacific sardine in shallow coastal waters of southern California in the years just before, and during, the resurgence of the early 1980s. This report is based on a longer time series (1978–86) and more complete water-column coverage than have been documented before from the shallow coastal zone.

METHODS

Ichthyoplankton samples were collected from January 1978 through September 1986 along an onshoreoffshore transect approximately 1 km south of the San Onofre Nuclear Generating Station (SONGS), and from July 1979 through September 1986 along a similar transect off Stuart Mesa, approximately 17 km south of the SONGS transect (figure 1). The sampling methodology, which was the same at both sites, was described by Barnett et al. (1984), Walker et al. (1987), and Moser and Watson (1990). Briefly, a stratified random design (Snedecor and Cochran 1967) was used to sample the neustonic (top 16 cm), epibenthic (bottom 67 cm), and remaining midwater layers of the water column along a randomly selected isobath within each of five blocks at each site on each survey date. These blocks were defined by bottom depth: (A) 6-9 m, (B) 9-12 m, (C) 12-22 m, (D) 22-45 m, and (E) 45-75 m.

Three different nets, equipped with 0.333-mmmesh Nitex and flowmeters, were used to sample the entire water column. A Manta net, 88 cm wide



Figure 1. Locations of the study sites along the southern California coast, with schematic profiles of the bathymetry at each site. On each survey date, a sample was taken at a randomly selected isobath within each of the five blocks (A-E) at each site.

by 16 cm deep, was used to sample the neuston; a 71cm bongo net was used for a stepped-oblique tow through the midwater column; and an Auriga net (MBC Applied Environmental Sciences, 947 Newhall Street, Costa Mesa, CA 92627) 2 m wide by 0.5 m high was used in the epibenthic stratum. All tows were taken at night along the chosen isobaths, at about 1 m/s for a fixed time selected to filter a target volume of 400 m³. Samples were not collected in block E on two dates in 1985 because of equipment problems. All samples were preserved in the field in 10% Formalin in seawater.

Although this study yielded information on the temporal and spatial distributions of larval Pacific sardine, acquiring such information was not its specific intent. Instead, the study was designed to predict, and subsequently measure, how two new SONGS units would affect the plankton. Consequently, sampling frequency varied considerably, according to the changing requirements of the power plant study. Sampling frequency ranged from approximately weekly toward the end of the predictive phase of the study (1980) to quarterly during the 3-year interim between the plant's preoperational and operational phases (1981–83). Most sampling was done in spring and summer (March–September).

In the laboratory, most samples were subsampled with a Folsom plankton splitter before being sorted for fish larvae (average for all samples = 25%sorted, range = 3.1%-100%). After sorting, each subsample was checked to ensure that at least 90% of the larvae were removed. Larval Pacific sardine were counted in four developmental stages (yolksac, preflexion, notochord flexion, postflexion) for a subset of the 1978-79 samples (one transect per survey) and for all subsequent samples. A small proportion of the larvae were too damaged to allow unequivocal identification of developmental stage; since most of those were small, all were arbitrarily assigned to the preflexion class. The count data were converted to number per 100 m³, and these density data were used to calculate abundance (number under 10 m² in each block and number in a 1-m-wide strip between the 6-75-m isobaths at each site). No corrections were made for the missing block E values on the two 1985 surveys; for those dates cross-shelf abundance values may be somewhat underestimated.

The density data and abundance-per-block data were transformed by log (x + 0.1) and analyzed using ANOVA and Student-Neuman-Keuls (SNK) multiple range tests to examine spatial patterns (results evaluated at $\alpha = 0.05$). The surveys lacking block E samples were deleted from the statistical analyses in order to maintain a balanced design, and surveys during which sardine larvae were not collected were deleted because they contained no information about location. Incidence was calculated as the percentage of total tows that contained Pacific sardine larvae.

Seasonal patterns and interannual changes in abundance were examined qualitatively with the cross-shelf abundance values (number/m between the 6–75-m isobaths); these patterns are presented in figures.

RESULTS

Spatial Distribution

Overall, larval Pacific sardine at both study sites were most abundant in block D, between the 22-m and 45-m isobaths; abundance decreased at the shoreward and seaward stations. The most shoreward station (6–9-m depth) had the lowest abundance. Cross-shelf patterns varied somewhat from year to year, but in general they were similar at both sites throughout the study (figure 2).

There was slight evidence of a possible ontogenetic seaward shift in a cross-shelf distribution at both sites, with yolk-sac larvae most abundant in block C, preflexion and flexion larvae most abundant in block D, and postflexion larvae slightly more abundant in block E (figure 3). However, most of these patterns were not statistically detectable (table 1). At San Onofre, only the high abundance of preflexion larvae in block D could be distinguished from their low abundance in block A. At Stuart Mesa, higher abundances of preflexion larvae in blocks C, D, and E were distinguishable from lower abundance in blocks A and B, whereas for flexion larvae the higher abundance in block D was distinguishable from the lower abundance in block A (table 1).

Larvae occurred most frequently in midwater (incidence overall 20% at San Onofre and 28% at Stuart Mesa), secondarily in the neuston (15% at San Onofre, 22% at Stuart Mesa), and least in the epibenthos (8% at San Onofre, 11% at Stuart Mesa). All stages appeared more frequently in midwater than in the other strata. Yolk-sac and preflexion larvae were somewhat less common in the neuston and relatively uncommon in the epibenthos, while flexion and postflexion larvae appeared almost equally frequently in neustonic and epibenthic samples.

Mean larval density values largely reflected the incidence values, and apparently differed little between study sites. Yolk-sac and preflexion larvae



Figure 2. Mean number of larval Pacific sardine under 10 m² of sea surface in each sampling block. The very low abundances in 1978–80 are not shown. All larval stages are pooled. a = San Onofre; b = Stuart Mesa.

typically were most numerous in midwater and neuston samples (figures 4 and 5). Yolk-sac larvae were rare in epibenthic samples, but preflexion larvae were moderately dense in the epibenthic stratum of the more shoreward blocks (figures 4 and 5). Flexion and postflexion larvae were distributed more uniformly through the water column, although somewhat lower near shore and higher farther from shore (figures 4 and 5).

Analysis of variance demonstrated significant differences in density among vertical strata for yolksac and preflexion larvae at both sites, but failed to indicate significant differences among strata for the older larvae at San Onofre (table 2). There were no statistically significant differences between blocks (block main effects) at San Onofre, and only one significant block X stratum interaction at either site



Figure 3. Mean number of larval Pacific sardine under 10 m² of sea surface in each sampling block. Each developmental stage is plotted separately; all years are pooled. a = San Onofre; b = Stuart Mesa.

(postflexion larvae at Stuart Mesa), although some block main effects and interactions approached significance (0.10 > p > 0.05; table 2).

Temporal Distribution

Seasonal pattern. Larval sardines were collected in every month except January and February, with a distinct maximum in summer and fall (figure 6). Incidence (percent positive collections, all years at both sites pooled) increased from 7%-27% between March and May to 60%-79% during June-September, then declined to the winter nadir, except during December, when six of seven transects yielded sardines. Although incidence varied somewhat from year to year and increased substantially beginning in 1981, there were no consistent changes to suggest a shift in the seasonal pattern over the nine years of the study (figure 7). Incidence at the

TABLE 1 Results of ANOVA and SNK Analyses on Cross-Shelf Distributions of Larval Pacific Sardine

	ANOVA result							
Stage	N	F	P	SNK result				
San Onofre Yolk-sac	17	0.67	>.05	E	A	В	D	С
Preflexion	32	2.44	<.05	Α	E	В	С	D
Flexion	21	1.83	>.05	Α	B	D	С	Ε
Postflexion	22	0.61	>.05	Α	В	D	E	С
Stuart Mesa Yolk-sac	21	1.96	>.05	E	A	B	D	С
Preflexion	30	8.19	<.05	Α	В	<u>C</u>	E	D
Flexion	22	2.25	>.05; <.10	Α	В	Е	С	D
Postflexion	19	0.49	>.05	E	C	D	В	Α

Only positive survey dates (*N*) were included in the analyses. SNK results are shown with sampling blocks (A–E) ordered from lowest geometric mean abundance (left) to highest geometric mean abundance (right). Sampling blocks joined by underlines are statistically indistinguishable (evaluated at $\alpha = 0.05$).

Stuart Mesa site tended to be a little lower than at San Onofre in spring (typically 50%–90% of San Onofre values), but a little higher in summer (usually 110%–140% of San Onofre values).

Abundance largely mirrored incidence, with none to few larvae in winter and spring, rapidly increasing abundance to a maximum in September and October, then a rapid decline to the winter nadir (figure 6b). Apart from a substantial increase in abundance that began in 1981, there were no consistent year-toyear changes that would suggest a shift in seasonal pattern (appendix). Patterns were similar at both study sites, except that the summer-fall peak was smaller and earlier at San Onofre than at Stuart Mesa (figure 6b). The high larval incidence in December surveys noted above was attributable to consistent collection of small numbers of larvae.

Incidence and abundance of yolk-sac larvae were examined in order to better estimate the spawning season. Almost all yolk-sac larvae were collected between May and October (one transect occupancy each in March 1980 and December 1983 also yielded yolk-sac larvae). Incidence increased steadily from 16% in May to 50% in August, then declined steadily to the winter minimum, indicating that spawning takes place principally in summer (figure 8a). There were no consistent differences in seasonal incidence over the years to suggest a shift in spawning season. Incidence was higher at Stuart Mesa than at San Onofre (typically 130%–200% of San Onofre values) in summer and fall.

Abundance of yolk-sac larvae differed somewhat from incidence (figure 8). Abundance did generally



Figure 4. Mean number of larval Pacific sardine per 100 m³ of water in each stratum (neuston, midwater, epibenthos) in each sampling block at San Onofre. Each developmental stage is plotted separately; all years are pooled. Neustonic and epibenthic strata are vertically exaggerated in these schematic representations. Shading indicates rankings of the geometric mean densities from the ANOVA on density: dark = the five highest-ranked means; light = the five middle-ranked means; white = the five lowest-ranked means.

increase from spring to a fall maximum, but with two or three smaller peaks at about 2-month intervals during the spring and summer. The minor peaks were about one month earlier at San Onofre than at Stuart Mesa, but the major peak was in October at both sites (figure 8b). The abundance of yolk-sac larvae varied considerably from year to year, but there were no consistent changes to suggest a shift in spawning season.

Interannual change. Larval Pacific sardine were collected in relatively few of the 1978–80 samples (figures 7, 9, 10): incidence in those years ranged from a low of 2% in 1979 to 6% in 1980. Incidence increased dramatically in 1981 (to 39%), reached a maximum of 44% in 1984, and remained above 20% through 1986.

Larval abundance likewise was quite low in 1978– 80, especially in 1979, then increased substantially, peaking in 1984 (figures 9a, 10a; appendix). The initial increase was somewhat larger at San Onofre, but subsequently tended to be higher at the Stuart Mesa site.

These initial increases of larval Pacific sardine in 1981 were largely attributable to preflexion and older stages. The incidence of yolk-sac larvae did not begin to increase until 1982 (figures 9a, 10a); yolk-sac abundance did not increase markedly until 1984 (figures 9b, 10b). Yolk-sac larval incidence peaked near 20% at both sites in 1984, then by 1986 returned to the low levels (<5%) typical of the early years of the study. Yolk-sac larval abundance also peaked at San Onofre in 1984, but at Stuart Mesa it continued to increase to a much higher peak in 1985. At both sites, 1986 abundances were quite low, comparable to the levels characteristic of the first years of the study.



Figure 5. Mean number of larval Pacific sardine per 100 m³ of water in each stratum (neuston, midwater, epibenthos) in each sampling block at Stuart Mesa. Each developmental stage is plotted separately; all years are pooled. Neustonic and epibenthic strata are vertically exaggerated in these schematic representations. Shading indicates rankings of the geometric mean densities from the ANOVA on density: dark = the five highest-ranked means; light = the five middle-ranked means; white = the five lowest-ranked means.

DISCUSSION

Spatial Distribution

Lavenberg et al. (1986, 1987) showed that over the southern California continental shelf, Pacific sardine eggs were more abundant shoreward from the 36-m isobath than at the 75-m isobath during 1978–86, suggesting that the shallow coastal zone was an important spawning area in those years. In both the Lavenberg et al. 1986 study and this one, Pacific sardine larvae were most abundant in this same zone. This was particularly true for younger larvae in this study: yolk-sac and preflexion larvae were usually most abundant in samples collected between the 12-m and 45-m isobaths, and least abundant in samples collected shoreward and seaward of those depths.

Cross-shelf patterns were much less consistent for the older larvae, suggesting that they were more patchily distributed and that the patches were more

widely dispersed across the inner half of the continental shelf. There was no evidence that larvae attempted to remain in the shallow zone, and only a slight suggestion that the older larvae made any directed movement away from it. CalCOFI ichthyoplankton surveys in 1978, 1981, and 1984 yielded few larval Pacific sardines along the transect lines (80-97) off southern California (Ambrose et al. 1988; Sandknop et al. 1988; Stevens et al. 1990), except in March, June, and July 1984, when a few relatively large catches were made, mainly at nearshore stations (Stevens et al. 1990). Together, these studies suggest that between 1978 and 1984-86 sardines spawned chiefly in the zone bounded by the 12-m and 45-m isobaths, and that larvae slowly dispersed from this spawning center, but remained primarily over the continental shelf.

Phytoplankton and microzooplankton biomass usually display onshore-offshore gradients along the southern California coast, with higher values nearer

Sampled at Each Location						
Larval stage	Source	d.f.	M.S.	F	Р	
San Onofre						
Yolk-sac	Blocks	4	0.66	1.72	>0.10	
	Strata	2	6.01	15.77	< 0.01	
	Interaction	8	0.25	0.67	>0.10	
	Error	225	0.38			
Preflexion	Blocks	4	1.32	2.26	>0.05; <0.10	
	Strata	2	4.68	8.02	< 0.01	
	Interaction	8	0.33	0.56	>0.10	
	Error	480	0.58			
Flexion	Blocks	4	0.85	2.31	>0.05; <0.10	
	Strata	2	0.72	1.95	>0.10	
	Interaction	8	0.39	1.06	>0.10	
	Error	300	0.37			
Postflexion	Blocks	4	0.43	1.97	>0.05; <0.10	
	Strata	2	0.14	0.64	>0.10	
	Interaction	8	0.37	1.72	>0.05; <0.10	
	Error	315	0.22			
Stuart Mesa						
Yolk-sac	Blocks	4	0.88	1.79	>0.10	
	Strata	2	7.67	15.56	< 0.01	
	Interaction	8	0.56	1.13	>0.10	
	Error	300	0.49			
Preflexion	Blocks	4	4.63	8.73	< 0.01	
	Strata	2	7.81	14.73	< 0.01	
	Interaction	8	0.70	1.33	>0.10	
	Error	435	0.53			
Flexion	Blocks	4	2.24	5.86	< 0.01	
	Strata	2	0.30	0.78	>0.10	
	Interaction	8	0.48	1.26	>0.10	
	Error	315	0.38			
Postflexion	Blocks	4	0.53	2.47	< 0.05	
	Strata	2	0.25	1.16	>0.10	
	Interaction	8	0.44	2.03	< 0.05	
	Error	270	0.22			

TABLE 2
Summary of ANOVA on Density (Number per 100 m ³) in
the 15 Strata (3 Vertical Strata × 5 Cross-Shelf Blocks)
Sampled at Each Location

Only positive dates were included in the analyses.

shore (e.g., Mullin 1986). The high rates of phytoplankton production, and the high concentrations of microzooplankton and macrozooplankton near shore (e.g., Beers and Stewart 1967; Lasker 1978; Petersen et al. 1986; Barnett and Jahn 1987) should provide a good feeding environment for Pacific sardine, and might have enhanced egg quality or production as well as larval survival during the study period. MacCall (1983, 1990) predicted that just such a productive nearshore zone would support the remnants of a depleted population such as the Pacific sardine, and that any subsequent resurgence of the population would originate from this core area. This may partially explain the observed increase.

In the shallow nearshore zone there was little evidence of strong vertical stratification, except that the younger larvae (yolk-sac and, to a lesser extent, preflexion) were rare in the lower 0.5 m of the water column. (These samples, however, were all collected at night, and the vertical distributions observed may not reflect daytime patterns; e.g., Silliman 1943).



Figure 6. *a*, Monthly mean incidence (percent positive collections) and *b*, abundance (number under a 1-m-wide strip between the 6-m and 75-m isobaths) of larval Pacific sardine. All developmental stages and all years are pooled.



Figure 7. Incidence (percent positive collections) of larval Pacific sardine, 1978–86, plotted by quarter. All developmental stages, and data from both study sites are pooled.



Figure 8. *a*, Monthly mean incidence (percent positive collections) and *b*, abundance (number under a 1-m-wide strip between the 6-m and 75-m isobaths) of yolk-sac larval Pacific sardine. All years are pooled.

Postflexion larvae, on the other hand, tended to appear in the lower 0.5 m, but usually only at shallower depths (≤ 22 m). By avoiding the epibenthic stratum, the small larvae may avoid being eaten by the many large larval and small juvenile fishes resident on the shallow shelf (e.g., croakers, gobies: Barnett et al. 1984; Brewer and Kleppel 1986; Jahn and Lavenberg 1986). The postflexion larvae may be large enough to avoid this danger. But whether predator avoidance does actually limit the vertical distribution of larval Pacific sardine in nearshore waters is purely speculative at this point.

Temporal Distribution

Ahlstrom (1960, 1967) showed that off southern California in the 1950s, Pacific sardines spawned largely in spring and summer, and occasionally at other seasons during warmer years. From 1978 to



Figure 9. *a*, Annual mean abundance (number under a 1-m-wide strip between the 6-m and 75-m isobaths) and *b*, incidence (percent positive collections) of larval Pacific sardine off San Onofre.

1986, spawning was nearly year-round, but was almost always highest in summer or fall (Brewer and Smith 1982; Lavenberg et al. 1986, 1987; this study). It has been speculated that this shift in the principal spawning season represented a movement into southern California waters of a later-spawning southern stock (Brewer and Smith 1982; Lavenberg et al. 1986), perhaps facilitated by the somewhat warmer temperature regime during those years.¹ An alternative suggestion that the warmer temperature may have allowed more extended spawning by the local population (e.g., Lavenberg et al. 1986), as happened in the late 1950s (Ahlstrom 1960), seems

^{&#}x27;S. Hernández-Vázquez, D. Lluch-Belda, D. Lluch-Cota, and C. Salinas-Zavala. Interannual variability of sardine and anchovy eggs and larvae in the Southern California Bight related to sea surface temperature, upwelling index and small zooplankton biomass: 1951–1988. Calif. Coop. Oceanic Fish. Invest. Ann. Conf. 22–24 October 1991, Lake Arrowhead, Calif.



Figure 10. a, Annual mean abundance (number under a 1-m-wide strip between the 6-m and 75-m isobaths) and b, incidence (percent positive collections) of larval Pacific sardine off Stuart Mesa.

unlikely to solely account for the strong summerfall spawning peak, but it may well have contributed to both the extended spawning season and the shift in timing. Lavenberg et al. (1987) noted a return to spring-summer spawning in 1986; no such shift was apparent in this study.

The resurgence of the Pacific sardine began in the early 1980s (Wolf and Smith 1985; Lavenberg et al. 1986, 1987); I suggest that it started in 1981. The initial increase near San Onofre apparently was not attributable to local spawning, since increases for yolk-sac larvae lagged total larvae by a considerable period. Lavenberg et al. (1986) reported that sardine larval abundance first increased north of San Onofre, primarily in the Seal Beach area in 1982, and subsequently spread north and south along the coast in 1983. Because nearshore currents along the southern California coast usually flow alongshore toward the south (Winant and Bratkovich 1981), it seems reasonable to speculate that the early increases in larval abundance in the San Onofre vicinity represented southward alongshore advection of larvae from some spawning site farther north (but probably not as far north as Seal Beach, since an egg spawned there would be a well-developed larva or juvenile 2 to 5 weeks old by the time it reached San Onofre). Alternatively, yolk-sac larvae may simply have not been collected, or not retained in the nets if they were collected, during the early years of this study. Although it seems likely that yolk-sac sardine larvae were not quantitatively sampled by the 0.333mm-mesh nets used (because of extrusion), no systematic change during the course of the study would have caused the yolk-sac larvae to be undersampled more in some years than in others. The precipitous decline in larval abundance in 1986 is consistent with the report by Lavenberg et al. (1987) that no Pacific sardine eggs were collected off San Onofre in 1986 (although they were abundant at the Santa Monica Bay and San Pedro Bay sites).

In summary, on the basis of this and other studies, it appears that the resurgence of the Pacific sardine off southern California began in 1981 in shallow waters off the central coast.

ACKNOWLEDGMENTS

This study was based on a larger study of ichthyoplankton in the vicinity of San Onofre, California, conducted by MEC Analytical Systems, Inc. for the Marine Review Committee of the California Coastal Commission. The Marine Review Committee does not necessarily accept the results, findings, or conclusions stated herein.

I thank the many technicians at MEC Analytical Systems, Inc. who spent long hours collecting and processing the samples that provided the basis for this study. I thank H. G. Moser for reviewing an earlier draft of the manuscript, and D. Foster for typing it.

LITERATURE CITED

- Ahlstrom, E. H. 1960. Synopsis on the biology of the Pacific sardine (Sardinops caerulea). FAO Fish. Biol. Synop. FB/S17.
- . 1967. Co-occurrence of sardine and anchovy larvae in the California Current and Baja California, Calif. Coop. Oceanic Fish. Invest. Rep. 11:117–135.
- Ahlstrom, E. H., and J. Radovich. 1970. Management of the Pacific sardine. In A century of fisheries in North America, N. G. Bensen, ed. Amer. Fish. Soc. Spec. Publc. No. 7, pp. 183–193.
- Ambrose, D. A., R. L. Charter, H. G. Moser, and B. S. Earhart. 1988. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1981. NOAA Tech. Memo., NMFS, SWFC, No. 112, 170 pp.

- Barnett, A. M., and A. E. Jahn. 1987. Patterns and persistence of a nearshore planktonic ecosystem off southern California. Cont. Shelf Res. 7:1–25.
- Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. 1984. Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. Fish. Bull., U.S. 82:97–111.
- Bedford, D., S. Crooke, T. Jow, R. Klingbeil, R. Read, J. Spratt, and R. Warner. 1982. Review of some California fisheries for 1980 and 1981. Calif. Coop. Oceanic Fish. Invest. Rep. 23:8–14.
- Beers, J. R., and G. L. Stewart. 1967. Microzooplankton in the euphotic zone at five locations across the California Current. J. Fish. Res. Board Can. 24:2053–2068.
- Brewer, G. D., and G. S. Kleppel. 1986. Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California. Mar. Ecol. Prog. Ser. 27:217–226.
- Brewer, G. D., and P. E. Smith. 1982. Northern anchovy and Pacific sardine spawning off southern California during 1978–80: preliminary observations on the importance of the nearshore coastal region. Calif. Coop. Oceanic Fish. Invest. Rep. 23:160–171.
- Jahn, A. E., and R. J. Lavenberg. 1986. Fine-scale distribution of nearshore suprabenthic fish larvae. Mar. Ecol. Prog. Ser. 31:223-231.
- Lasker, R. 1978. The relation between occanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P-V. Réun. Int. Explor. Mar 173:212-230.
- Lavenberg, R. J., A. E. Jahn, G. E. McGowen, and J. H. Petersen. 1987. Sampling for eggs of sardine and other fishes in the coastal zone using the CalVET net. Calif. Coop. Oceanic Fish. Invest. Rep. 28:178–182.
- Lavenberg, R. J., G. E. McGowen, A. E. Jahn, J. H. Petersen, and T. C. Sciarrotta. 1986. Abundance of southern California nearshore ichthyoplankton: 1978–1984. Calif. Coop. Oceanic Fish. Invest. Rep. 27:53–64.
- MacCall, A. D. 1979. Population estimates for the waning years of the Pacific sardine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 20: 72–82.
- . 1990. Dynamic geography of marine fish populations. Washington Sea Grant Prog., Seattle, 153 pp.
- Moser, H. G., and W. Watson. 1990. Distribution and abundance of early life history stages of the California halibut, *Paralichthys californicus*, and comparison with the fantail sole, *Xystreurys liolepis*. Calif. Dep. Fish Game Fish Bull. 174:31-84.

- Mullin, M. M. 1986. Spatial and temporal scales and patterns. *In* Plankton dynamics of the Southern California Bight, 15. Lecture notes on coastal and estuarine studies, R. W. Eppley, ed. New York: Springer-Verlag, 353 pp.
- Murphy, G. I. 1966. Population biology of the Pacific sardine, Sardinops sagax. Proc. Calif. Acad. Sci. 34:1-84.
- Petersen, J. H., A. E. Jahn, R. J. Lavenberg, G. E. McGowen, and R. S. Grove. 1986. Physical-chemical characteristics and zooplankton biomass on the continental shelf off southern California. Calif. Coop. Oceanic Fish. Invest. Rep. 27:36–52.
- Radovich, J. 1982. The collapse of the California sardine fishery: what have we learned? Calif. Coop. Oceanic Fish. Invest. Rep. 23:56–78.
- Sandknop, E. M., R. L. Charter, H. G. Moser, C. A. Meyer, and A. E. Hays. 1988. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1978. NOAA Tech. Memo., NMFS, SWFC, No. 111, 216 pp.
- Silliman, R. P. 1943. Thermal and diurnal changes in the vertical distribution of eggs and larvae of the pilchard (*Sardinops caerulea*). J. Mar. Res. 5:118-130.
- Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. 6th ed. Ames: Iowa State Univ. Press, 593 pp.
- Stevens, E. G., R. L. Charter, H. G. Moser, and C. A. Meyer. 1990. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1984. NOAA Tech. Memo., NMFS, SWFC, No. 141, 157 pp.
- Walker, H. J., Jr., W. Watson, and A. M. Barnett. 1987. Seasonal occurrence of larval fishes in the nearshore Southern California Bight off San Onofre, California. Estuarine Coastal Shelf Sci. 25:91–109.
- Winant, C. D., and A. W. Bratkovich. 1981. Temperature and currents on the southern California shelf: a description of the variability. J. Phys. Oceanogr. 11:71–86.
- Wolf, P., and P. E. Smith. 1985. An inverse egg production method for determining the relative magnitude of Pacific sardine spawning biomass off California. Calif. Coop. Oceanic Fish. Invest. Rep. 26: 130–138.
- ------. 1986. The relative magnitude of the 1985 Pacific sardine spawning biomass off southern California. Calif. Coop. Oceanic Fish. Invest. Rep. 27:25–31.
- Wolf, P., P. E. Smith, and C. L. Scannell. 1987. The relative magnitude of the 1986 Pacific sardine spawning biomass off California. Calif. Coop. Oceanic Fish. Invest. Rep. 28:21–26.

APPENDIX

Number of Larval Pacific Sardine under a 1-m-Wide Strip between the 6-m and 75-m Isobaths off San Onofre and Stuart Mesa on Each Survey Date: 1978–86

	Number of la	Number of larvae (thousands)		Number of larvae (thousands)		
Starting date	San Onofre	Stuart Mesa*	Starting date	San Onofre	Stuart Mesa*	
1978			1980, cont'd.			
24 Jan.	0		4 Aug.	4.156	4.482	
16 Feb.	0		11 Aug.	0.793	0	
6 Mar.	0.231		18 Aug.	1.367	3.256	
21 Mar.	0		25 Aug.	0.059	1.103	
3 Apr.	0		1 Sept.	0	0.320	
26 Apr.	0		8 Sept.	0.022	0	
8 May	0		22 Sept.	0.002	0	
22 May	0		26 Sept.	0	0	
5 June	0		29 Sept.	0.002	0	
21 June	0		6 Oct.	0	0	
7 July	0.355		13 Oct.	0	0.003	
17 July	0.002		1981			
2 Aug.	0.002		7 July	24.831	9.080	
16 Aug.	0		15 Sept.	1.194	0.432	
7 Sept.	0.851		17 Nov.	0	0.185	
3 Oct.	0		1982			
8 Nov.	0.001		9 Mar.	0	0	
28 Nov.	0		13 July	5.127	1.965	
27 Dec.	0		26 Aug.	0.099	0.373	
1979			10 Dec.	4.677	0.314	
3 Feb.	0		1983			
26 Feb.	0		12 May	0	0	
26 Mar.	0		19 July	1.018	0.954	
25 Apr.	0		23 Aug.	86.468	89.389	
23 May	0.002		14 Dec.	0.423	0.587	
25 June	0		1984			
24 July	0	0	13 Mar.	0.886	1.411	
22 Aug.	0	2.527	7 May	0	0	
23 Aug.	0	0	30 May	6.104	2.805	
20 Sept.	0	0	19 June	0.903	0.987	
21 Sept.	0	0	23 Aug.	13.770	11.067	
1980			13 Sept.	196.829	197.311	
10 Mar.	1.783	0	4 Oct.	26.251	85.524	
17 Mar.	0	0	21 Dec.	0.025	0.473	
24 Mar.	0	0	1985			
4 Apr.	0	0	21 Jan.	0	0	
14 Apr.	0	0	22 Apr.	0	0	
23 Apr.	0	0	13 May	0.056	0.051	
5 May	0	0	4 June	4.624	7.667	
12 May	0	0	25 June	0.920	0.001	
19 May	0	0	18 July	54.868	3.971	
26 May	0	0	6 Aug.	0.028	0.327	
2 June	1.389	1.384	26 Aug.	2.108	126.126	
9 June	0	0	12 Sept.	38.030	40.550	
17 June	1.350	0	1986			
24 June	0	0	5 Mar.	0	0	
30 June	0.002	21.332	1 Apr.	0	0.001	
7 July	0	2.421	30 Apr.	0.055	0	
14 July	0	0	21 July	1.687	7.748	
21 July	0	0.001	2 Sept.	4.283	4.355	
28 July	0	0	25 Sept.	0.518	0.516	

*Sampling began at the Stuart Mesa site in July 1979.