ICHTHYOPLANKTON AND ZOOPLANKTON ABUNDANCE PATTERNS IN THE CALIFORNIA CURRENT AREA, 1975

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ABSTRACT

The 1975 CalCOFI data were analyzed to provide a description of regional and seasonal zooplankton and ichthyoplankton abundance patterns. Zooplankton and ichthyoplankton abundances were found to be independent of each other on all scales examined. Zooplankton abundance decreased from north to south and inshore to offshore and appeared to be related to distribution of surface nutrient levels. Greatest ichthyoplankton abundance occurred off southern California and northern Baja California and was due to large spawning stocks of migratory species (anchovy, hake, and jack mackerel); the other ichthyoplankton fraction had complex abundance patterns because of its multispecies composition. Seasonal zooplankton abundance fluctuations along the coast (from Punta Eugenia northward) appeared to follow the northward seasonal progression of coastal upwelling. Maximum ichthyoplankton abundance was associated with periods of relatively stable water conditions prior to the onset of intense coastal upwelling. Persistent high-intensity zooplankton patchiness found off northern Baja California is associated with a zone of surface-layer convergence extending to the coast from offshore areas. This convergence zone may mark a separation of southern California and central-southern Baja California coastal biological regimes.

RESUMEN

Se analizaron los datos obtenidos en 1975 durante el programa CalCOFI, con objeto de obtener información sobre la abundancia regional del zooplancton e ictioplancton a lo largo de las estaciones del año. La abundancia de zooplancton no mantenía relación con la abundancia de ictioplancton, a todas las escalas analizadas. La abundancia de zooplancton decrecía de norte a sur y de la zona costera a la oceánica, y aparecía en cierto modo relacionada con la distribución de los nutrientes en las aguas de superficie. La mayor abundancia de ictioplancton se presentaba frente a la parte meridional de California y la zona norte de Baja California, constituyendo el resultado de las grandes concentraciones de poblaciones de especies migratorias (*Engraulis mordax*, *Merluccius productus* y *Trachurus symmetricus*), mientras que la otra porción de ictioplancton presentaba un patrón complejo debido a su composición multiespecífica. Las fluctuaciones en la abundancia del zooplancton a lo largo de las estaciones del año en la zona costera, al norte de Punta Eugenia, siguen al parecer con el avance de la estación, la progresión hacia el norte de las surgencias costeras. La máxima abundancia de ictioplancton aparecía asociada con períodos de estabilidad relativa de las aguas, antes de desencadenarse las intensas surgencias costeras.

Agregaciones persistentes de zooplancton de elevada cuantía se observaron frente a la parte norte de Baja California, asociadas con una zona de convergencia en superficie, extendiéndose desde la costa hasta mar afuera. Esta zona de convergencia pudiera marcar una separación en los regímenes biológicos costeros del sur de California y la parte centro-meridional de Baja California.

INTRODUCTION

Patterns and processes of oceanic life are sketchily known because of the vastness of oceanic regions, the diversity of oceanic biota, and costs of sustained oceanic study. The importance of abundance variations among certain commercially important oceanic fishes led to the field program of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). This program has provided description of hydrographic conditions in coastal waters and the California Current system (Reid et al. 1958) and has collected a vast amount of information on zooplankton and ichthyoplankton abundances in these waters since 1951.

The CalCOFI zooplankton data have been treated by a variety of researchers, and abundance fluctuations of the entire assemblage as well as its major taxa have been related to both short- and long-term physical processes within the California Current system (Reid et al. 1958; Colebrook 1977; Bernal 1980; Chelton 1981, 1982). The ichthyoplankton data have received comparatively little attention. Although abundance fluctuations among a few commercially important species have been examined in detail, the distribution, abundance, and composition of other ichthyoplankton elements have virtually been ignored.

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Never before have the zooplankton and ichthyoplankton elements been considered together.

Zooplankton and ichthyoplankton are fundamentally different fractions of pelagic communities. Zooplankton individuals spend their entire life cycle as plankton; their distribution and abundance are greatly affected by advective processes within oceanic regions. Larval fishes are the temporary planktonic stages of individuals that are for the most part nektonic and to a large extent zooplanktivorous; ichthyoplankton abundances reflect spawning locales and suitability of conditions for larval survival and recruitment to adult populations. Conditions affecting zooplankton and ichthyoplankton distribution and abundance may be quite different.

Our purpose in this paper is to use the 1975 CalCOFI survey data of zooplankton and ichthyoplankton abundances to identify major seasonal and regional features within the California Current system. Zooplankton and ichthyoplankton abundance patterns are compared to each other and related to physical processes within the current system.

METHODS

The 1975 ichthyoplankton and zooplankton data were derived from standard CalCOFI oblique plankton tows taken with a 1-m diameter net (mesh size, 505 μm) fished from 0 to 210 m. Samples were collected according to the basic CalCOFI station plan (Figure 1), with increased numbers of inshore sampling locations (Lasker 1978). All larval fishes were sorted out, identified, and counted. The larvae of five commercially important pelagic schooling species (anchovy, hake, sardine, jack mackerel, and Pacific mackerel) were sorted and treated separately from the 200+ other larval fish taxa collected. The five species are herein grouped together and referred to as the "PL" ("pelagic" larvae); the remaining taxa are considered together as the "OL" ("other" larvae). Ichthyoplankton abundances used are "total larvae" (all species lumped), the five combined PL species, and the OL fraction. The PL and OL fractions are treated separately because abundances of the PL (especially anchovy and hake) mask abundance relations of the OL. Data on individual PL species are included in tables, figures, and the Appendix, but receive only cursory treatment here; absolute and relative abundances of individual taxa are considered in Loeb et al., 1983a, b. Larval fish abundances are expressed as numbers of larvae per 10 m^2 sea-surface area; macrozooplankton ($\geq$ 5 μm) abundance is wet displacement volume (cc per 1,000 m^3) (Kramer et al. 1972).

Absolute regional abundance estimates are mean numbers of larvae per m^2 sea surface multiplied by sea-surface area of the region. These are summed to provide the total estimated larval fish abundance within the CalCOFI survey area by cruise and for all six 1-month cruises (Appendix).

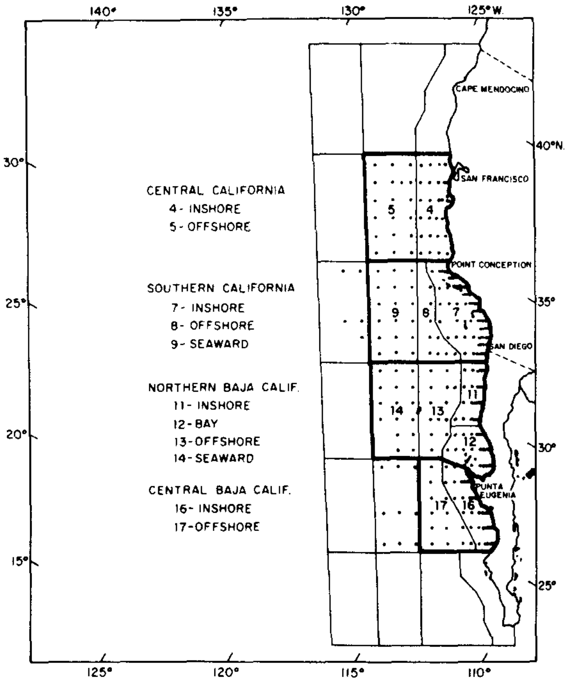

Figure 1. CalCOFI stations, regions, and areas sampled during the 1975 survey.

Data from 1,504 samples were formatted by cruise and standard CalCOFI regions. Thirteen regions were sampled (Figure 1); however, two of these (regions 10 and 18) received relatively less intensive coverage (< 10 samples per region; Table 1) and are not included in the analysis. The 11 regions considered were sampled during at least six 1-month cruises, and most were represented by $\geq$ 10 samples per cruise (Table 1). Most regions were sampled in December, January, March, May, July, and October; central California regions 4 and 5 were sampled in November rather than October. November data for southern California regions 7, 8, and 9 were used rather than October data, because larger numbers of samples were available (Table 1). For overviews of abundance and diversity patterns, regional data were combined into four latitudinal areas (central and southern California, northern and central Baja California; Figure 1) and into inshore, offshore, and seaward areas.

Larval fish diversity is expressed in two ways: as the mean number of fish taxa per tow, and as the total number of fish taxa taken in 60 randomly selected

TABLE 1
Regional Sampling Effort, 1975 CalCOFI Survey

Area	Region	Cruise/month 7412 Dec.	7501 Jan.	7503 Mar.	7505 May	7507 July	7510 Oct.	7511 Nov.	Total no. samples
Central	4	26	26	23	13	24	—	25	137
California	5	10	4	18	9	12	—	11	64
Southern	7	80	81	81	79	77	7	74	479
California	8	10	8	9	9	9	4	4	53
	9	18	18	16	18	18	—	14	102
	10	2	2	—	—	—	—	—	4
Northern	11	26	26	19	27	26	28	—	152
Baja	12	28	28	18	28	28	29	—	159
California	13	13	13	10	13	13	12	—	74
	14	4	12	4	12	15	15	—	62
Central	16	38	38	18	2	37	37	—	170
Baja	17	13	12	4	1	13	13	—	56
California	18	—	2	1	2	2	2	—	9

samples (10 samples/cruise) from each region. Regions 8 and 17 were represented by 53 and 56 samples, and those diversities may be underestimated.

Sample variability due to patchiness within each region is described by an index of dispersion based on variance to mean ratios ($S^2/\bar{x}$) and compared to an expected chi-square distribution (Pielou 1977). Here chi-square $P \leq 0.05$ implies aggregation, $0.05 < P < 0.95$ implies no significant departure from randomness, and $P \geq 0.95$ implies regularity of distribution. Extremely large index-of-dispersion values reflect high-intensity patchiness (Haury et al. 1978). Index-of-dispersion values for zooplankton abundances are based on biomass, and those of larval fishes are based on numbers of individuals per 10 m^2; consequently, comparisons cannot be made between these values.

Day-night abundance comparisons are based on day (1 hour before sunrise to 1 hour after sunset) and night samples. Differences of these (and other) mean abundances are tested with a 2-tailed Z test (Dixon and Massey 1969).

Comparisons of zooplankton and ichthyoplankton geographical and seasonal abundance patterns are made using Kendall's tau and concordance tests (Tate and Clelland 1957) on ranked regional and cruise abundances. Kendall's tau provides a correlation coefficient that is a measure of the similarity between the order of rankings within two data sets (e.g., between zooplankton and ichthyoplankton ranked regional abundances within a cruise or ranked cruise abundances within a region). The concordance test is a nonparametric analysis of variance performed on several sets of rankings; it is used here to test for similarity of zooplankton, PL, and OL seasonal abundances rankings within areas.

Kolmogorov-Smirnov (K-S) tests (Conover 1971) are based on the maximum differences between cumulative percent curves for two sets of data. They are used here to identify significant differences in the timing of the zooplankton and ichthyoplankton abundance increases.

TAXONOMIC PROBLEMS

The 1,504 samples yielded 104 species, and 100 higher taxa (50 generic, 45 familial, and 5 ordinal). Many abundant larvae (especially the Myctophidae and Bathylagidae) are identified to species, but identification of many coastal larvae, especially *Sebastes* spp (Scorpaenidae) and subtropical forms, is difficult. These identification problems limit analyses, especially the interpretation of diversity indices where inclusion of multispecies groupings certainly underrepresents the actual species richness of a region. This is a major problem only in nearshore and southern regions, but suggests caution in between-region comparisons of diversity.

RESULTS

Abundance and Diversity Estimates

Tables 2 and 3 and the Appendix present 1975 zooplankton and ichthyoplankton abundances by cruise and for all cruises combined for each region. The zooplankton, total larvae, and OL categories all exhibit large sample variances; standard deviations range from 0.3-2.3 times the mean values. Index of dispersion values for zooplankton biomass (Table 4A) and for numbers of total larvae and OL (Table 4B) by region and cruise predominantly indicate extreme aggregations of these categories (X^2 probabilities

≤ 0.05 for 77% of zooplankton, 94% of total larvae, and 85% of OL indices of dispersion). Because of tow-to-tow sample variability caused by patchiness, only large differences in abundance within and between regions can be detected as significant with standard statistical tests.

TABLE 2
Mean and Standard Deviations of Zooplankton Displacement Volume (cc/1000m^3) and Ichthyoplankton Abundance (no./10^2 sea-surface area) by Region and Cruise for 1975

Cruise 7412		Region 4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	260.7	176.2	85.2	93.4	132.7	85.1	56.6	83.0	53.2	44.5	50.8
	σ	117.0	108.0	49.1	64.1	131.0	70.9	30.6	42.6	11.6	28.9	40.2
Total larvae	χ	132.4	75.7	213.8	83.4	53.2	177.3	93.4	128.1	106.5	679.2	70.4
	σ	247.0	68.9	201.0	100.0	33.7	236.0	119.0	58.4	127.0	884.0	87.1
Anchovy	χ	2.2	8.5	123.2	9.4	—	88.4	62.0	4.5	—	597.6	—
	σ	4.6	18.4	154.0	18.3	—	180.0	112.0	9.0	—	878.0	—
Hake	χ	0.9	—	1.8	—	—	—	—	—	—	0.6	—
	σ	3.1	—	0.8	—	—	—	—	—	—	1.8	—
Sardine	χ	—	—	—	—	—	—	—	—	—	7.5	—
	σ	—	—	—	—	—	—	—	—	—	20.8	—
Other larvae	χ	129.3	67.2	88.8	74.0	53.2	88.9	31.4	123.6	106.5	73.5	70.4
	σ	247.0	53.6	135.0	84.7	33.7	80.6	34.8	61.7	127.0	64.7	87.1
No. tows		26	10	80	10	18	26	28	13	4	38	13
Cruise 7501		**Region 4**	**5**	**7**	**8**	**9**	**11**	**12**	**13**	**14**	**16**	**17**
Zooplankton	χ	206.6	117.5	104.8	89.1	84.2	159.5	130.3	62.2	68.7	51.4	42.8
	σ	152.0	40.0	55.2	35.5	58.4	174.0	83.3	20.7	31.6	41.0	23.4
Total larvae	χ	425.0	127.5	1943.3	4628.4	1886.9	2183.2	2539.1	2133.1	193.8	625.3	201.8
	σ	344.0	122.0	2155.0	2730.0	4248.0	4341.0	4293.0	3096.0	92.5	1443.0	296.0
Anchovy	χ	11.8	—	1463.5	4027.0	189.9	1997.1	2374.5	2059.5	24.2	554.6	109.1
	σ	24.5	—	2123.0	3123.0	584.0	4320.0	4166.0	3097.0	35.9	1438.0	272.0
Hake	χ	28.9	—	89.0	449.2	1593.0	25.9	1.3	5.5	—	5.6	1.0
	σ	55.6	—	370.0	833.0	4120.0	50.7	5.1	14.0	—	10.5	3.5
Jack mackerel	χ	—	—	0.2	—	—	—	—	—	—	—	—
	σ	—	—	1.4	—	—	—	—	—	—	—	—
Sardine	χ	—	—	—	—	—	—	7.5	—	—	8.7	—
	σ	—	—	—	—	—	—	17.2	—	—	39.3	—
Other larvae	χ	384.3	127.5	390.7	152.1	104.0	160.2	155.8	68.2	169.6	56.6	91.7
	σ	328.0	122.0	433.0	119.0	60.8	134.0	152.0	34.8	96.2	69.8	73.5
No. tows		26	4	81	8	18	26	28	13	12	38	12
Cruise 7503		**Region 4**	**5**	**7**	**8**	**9**	**11**	**12**	**13**	**14**	**16**	**17**
Zooplankton	χ	187.1	143.6	284.1	145.4	115.4	346.3	488.7	94.9	63.8	252.9	97.0
	σ	80.5	121.0	208.0	61.0	61.6	454.0	389.0	45.8	39.1	198.0	24.0
Total larvae	χ	311.1	151.0	2494.4	2721.4	659.9	2857.9	2112.8	941.9	876.2	1656.2	1307.3
	σ	203.0	102.0	2405.0	2665.0	1113.0	1931.0	3845.0	1036.0	1056.0	1911.0	1263.0
Anchovy	χ	1.9	0.4	2047.4	1973.4	15.3	2054.0	1883.6	313.2	2.5	1569.1	1068.5
	σ	5.1	1.9	2344.0	2178.0	40.1	1768.0	3755.0	688.0	3.3	1882.0	1345.0
Hake	χ	2.0	1.1	82.8	548.3	525.0	617.0	36.3	529.1	297.8	5.7	1.8
	σ	4.0	3.1	269.0	978.0	1053.0	957.0	58.5	921.0	541.0	8.4	3.5
Jack mackerel	χ	—	0.2	—	—	8.3	4.6	1.3	22.0	333.5	2.4	13.5
	σ	—	0.7	—	—	21.7	13.2	3.9	19.0	414.0	6.0	20.3
Sardine	χ	—	—	0.7	—	—	—	—	—	—	—	—
	σ	—	—	0.7	—	—	—	—	—	—	—	—
Other larvae	χ	307.1	149.3	364.1	199.7	111.3	182.4	191.6	77.6	242.5	79.1	223.5
	σ	203.0	101.0	318.0	182.0	97.8	106.0	335.0	43.3	276.0	69.5	226.0
No. tows		23	18	81	9	16	19	18	10	4	18	4

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TABLE 2 (Cont.)

Mean and Standard Deviations of Zooplankton Displacement Volume (cc/1000m^3) and Ichthyoplankton Abundance (no./10^2 sea-surface area) by Region and Cruise for 1975

Cruise 7505		Region 4	5	7	8	9	11	12	13	14	16	17
Zooplankton	$\bar{x}$	338.7	258.8	322.9	512.0	203.1	486.9	196.4	172.2	88.9	177.0	—
	σ	397.0	174.0	463.0	568.0	160.0	618.0	124.0	91.3	28.0	42.4	—
Total larvae	$\bar{x}$	103.2	119.1	293.8	76.4	97.3	1396.1	1510.8	248.0	221.2	1319.5	400.0
	σ	83.4	75.7	410.0	57.0	69.3	2527.0	3549.0	195.0	126.0	251.0	—
Anchovy	$\bar{x}$	2.9	—	243.0	2.7	—	1324.3	1210.1	60.1	0.5	1186.0	—
	σ	10.5	—	404.0	5.7	—	2504.0	3067.0	161.0	1.7	124.0	—
Hake	$\bar{x}$	2.7	11.2	0.04	—	1.6	0.4	—	1.0	—	—	—
	σ	4.6	17.6	0.34	—	3.1	2.1	—	3.6	—	—	—
Jack mackerel	$\bar{x}$	—	—	—	—	—	5.3	0.3	76.0	10.8	—	—
	σ	—	—	—	—	—	9.9	1.7	112.0	9.6	—	—
Sardine	$\bar{x}$	—	—	—	—	—	—	6.9	—	—	—	—
	σ	—	—	—	—	—	—	36.5	—	—	—	—
Other larvae	$\bar{x}$	97.6	107.9	50.8	73.8	95.7	66.2	293.5	110.9	210.0	133.5	400.0
	σ	78.3	61.6	49.0	59.0	68.0	60.7	530.0	60.7	124.0	127.0	—
No. tows		13	9	79	9	18	27	28	13	12	2	1

Cruise 7507		Region 4	5	7	8	9	11	12	13	14	16	17
Zooplankton	$\bar{x}$	276.9	292.8	165.3	179.4	197.6	179.3	169.1	78.8	50.5	118.5	64.3
	σ	194.0	259.0	199.0	124.0	123.0	292.0	166.0	35.7	19.5	121.0	67.3
Total larvae	$\bar{x}$	62.4	56.1	198.9	119.2	79.9	331.9	641.0	228.9	343.5	284.5	343.7
	σ	44.0	43.0	281.0	124.0	59.1	621.0	996.0	298.0	233.0	341.0	293.0
Anchovy	$\bar{x}$	1.5	—	163.6	3.7	0.2	263.2	160.2	17.4	0.1	68.0	34.0
	σ	5.0	—	277.0	9.9	0.7	580.0	216.0	25.8	0.5	175.0	121.0
Hake	$\bar{x}$	—	—	—	—	—	—	1.7	—	0.2	0.1	—
	σ	—	—	—	—	—	—	4.0	—	0.8	0.6	—
Jack mackerel	$\bar{x}$	—	1.2	0.7	49.3	18.3	2.7	—	12.6	17.5	1.1	0.2
	σ	—	4.3	4.1	127.0	19.9	6.4	—	11.9	13.5	3.9	0.6
Sardine	$\bar{x}$	—	—	—	—	—	—	0.2	—	—	20.3	—
	σ	—	—	—	—	—	—	0.9	—	—	71.5	—
Other larvae	$\bar{x}$	61.0	54.8	34.6	66.2	61.4	66.0	478.9	198.9	325.7	194.9	309.4
	σ	42.7	41.7	34.1	28.6	50.5	64.2	864.0	300.0	238.0	261.0	248.0
No. tows		24	12	77	9	18	26	28	13	15	37	13

Cruise 7510		Region 4	5	7	8	9	11	12	13	14	16	17
Zooplankton	$\bar{x}$	—	—	139.7	40.2	—	126.0	118.1	45.6	43.8	112.4	105.9
	σ	—	—	86.4	34.5	—	211.0	132.0	23.2	27.6	93.5	108.0
Total larvae	$\bar{x}$	—	—	684.9	53.5	—	101.5	357.1	79.9	182.4	334.8	182.7
	σ	—	—	448.0	61.0	—	88.9	463.0	33.4	140.0	376.0	202.0
Anchovy	$\bar{x}$	—	—	293.1	30.8	—	23.0	136.3	—	0.8	104.9	27.7
	σ	—	—	219.0	61.5	—	44.7	297.0	—	2.6	229.0	96.6
Hake	$\bar{x}$	—	—	—	—	—	—	0.2	0.2	—	—	—
	σ	—	—	—	—	—	—	0.9	0.9	—	—	—
Jack mackerel	$\bar{x}$	—	—	—	1.2	—	0.5	0.1	—	—	—	—
	σ	—	—	—	2.5	—	1.5	0.4	—	—	—	—
Sardine	$\bar{x}$	—	—	—	—	—	0.7	17.5	—	—	5.0	—
	σ	—	—	—	—	—	2.8	27.1	—	—	13.3	—
Pacific mackerel	$\bar{x}$	—	—	—	—	—	—	1.2	—	—	1.5	—
	σ	—	—	—	—	—	—	4.5	—	—	5.2	—
Other larvae	$\bar{x}$	—	—	391.7	21.5	—	77.4	201.9	79.7	181.6	223.3	154.9
	σ	—	—	311.0	13.2	—	66.3	304.0	33.6	138.0	223.0	189.0
No. tows		—	—	7	4	—	28	29	12	15	37	13

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TABLE 2 (Cont.)

Mean and Standard Deviations of Zooplankton Displacement Volume (cc/1000m^3) and Ichthyoplankton Abundance (no./10^2 sea-surface area) by Region and Cruise for 1975

Cruise 7511		Region 4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	254.2	105.4	107.6	74.2	91.6						
	σ	252.0	59.0	96.5	44.1	88.3						
Total larvae	χ	78.8	32.1	337.5	63.0	68.0						
	σ	55.5	15.8	339.0	35.1	64.8						
Anchovy	χ	0.1	—	292.7	—	1.5						
	σ	0.4	—	335.0	—	2.8						
Hake	χ	—	—	1.6	—	—						
	σ	—	—	4.8	—	—						
Jack mackerel	χ	—	—	0.03	—	—						
	σ	—	—	0.23	—	—						
Sardine	χ	—	—	0.04	—	—						
	σ	—	—	0.35	—	—						
Other larvae	χ	78.8	32.1	43.1	63.0	66.5						
	σ	55.5	15.8	34.6	35.1	64.7						
No. tows		25	11	74	4	14						

Ichthyoplankton abundances given for total larvae, 5 species constituting the PL, and other larvae (OL).

TABLE 3

Mean and Standard Deviations of Zooplankton Displacement Volume (cc/1000m^3) and Ichthyoplankton Abundance (no./10m^2 sea-surface area) for All Samples Taken Within Each of 11 CalCOFI Regions (6 Cruises Total) during 1975

		Region 4	5	7	8	9	11	12	13	14	16	17
Zooplankton	χ	247.2	184.7	179.1	183.6	139.7	225.5	174.1	89.8	60.9	100.6	70.0
	σ	203.0	164.0	245.0	282.0	119.0	372.0	207.0	63.2	30.6	116.0	68.9
Total larvae	χ	193.1	95.0	932.3	1241.2	486.5	1084.5	1146.8	621.3	271.1	617.3	282.3
	σ	246.0	85.7	1653.0	2290.0	1922.0	2404.0	2816.0	1515.0	329.0	1102.0	457.0
Anchovy	χ	3.5	1.4	736.6	966.4	363.8	898.0	908.5	418.5	5.2	475.3	117.6
	σ	12.2	7.6	1528.0	2089.0	1840.0	2310.0	2638.0	1494.0	18.0	1096.0	437.0
Hake	χ	6.3	1.9	30.0	164.0	4.5	81.6	4.7	72.7	19.3	2.0	0.3
	σ	26.4	7.5	193.0	550.0	13.7	388.0	22.5	371.0	141.0	6.2	1.8
Jack mackerel	χ	—	0.3	0.1	8.6	—	2.0	0.2	18.5	27.8	0.5	1.0
	σ	—	1.9	1.8	53.6	—	7.0	1.5	53.9	123.0	2.7	5.9
Sardine	χ	—	—	0.02	—	—	0.13	5.8	—	—	9.1	—
	σ	—	—	0.31	—	—	1.19	21.2	—	—	40.0	—
Pacific mackerel	χ	—	—	—	—	—	—	0.21	—	—	0.34	—
	σ	—	—	—	—	—	—	1.95	—	—	2.45	—
PL	χ	9.8	3.6	766.8	1139.0	404.4	981.8	919.3	509.7	52.3	487.2	119.0
	σ	32.3	10.7	1563.0	2265.5	1904.0	2372.0	2640.0	1522.0	259.0	1098.0	439.0
OL	χ	183.3	91.4	165.5	102.1	82.1	102.7	227.5	111.5	218.7	130.0	163.3
	σ	235.0	82.1	277.0	111.0	67.0	97.3	478.0	137.0	176.0	181.0	188.0
No. tows		137	64	472	53	102	152	159	74	62	170	56
Ranked regional abundance												
Total larvae		10	11	4	1	7	3	2	5	9	6	8
PL		10	11	4	1	7	2	3	5	9	6	8
OL		3	10	4	9	11	8	1	7	2	6	5

Ichthyoplankton abundances given for total larvae, 5 species constituting the PL, and other larvae (OL). Regional ranks provided for total, PL, and OL abundances.

TABLE 4
Index of Dispersion Values for (A) Zooplankton Biomass and (B) Total Larval Fish (TL) and OL Abundances Within 11 CalCOFI Regions by Cruise

		Region										
		Central California			Southern California			Northern Baja California			Central Baja California	
		4	5	7	8	9	11	12	13	14	16	17
A. Zooplankton												
Cruise												
7412		52.5	66.2	(28.3)	44.0	129.3	59.1	16.5	21.6	(2.5)	(18.8)	31.8
7501		111.8	13.6	(29.1)	14.1	40.5	189.8	53.2	(6.9)	(14.5)	(32.7)	(12.8)
7503		34.6	102.0	152.3	25.6	32.9	595.2	309.6	22.1	24.0	155.0	(5.9)
7505		465.3	117.0	663.9	630.1	126.0	784.4	78.3	48.4	(8.8)	10.2	—
7507		135.9	229.1	239.6	85.7	76.6	475.5	169.9	(16.2)	(7.5)	123.6	70.4
7510 (11)		249.8	33.0	(86.5)	26.2	85.1	353.3	147.5	(11.8)	(17.4)	77.8	110.1
B. Total larvae and OL												
Cruise												
7412	TL	460.8	62.9	189.0	119.9	(21.3)	314.1	151.6	26.6	151.4	1150.5	107.8
	OL	471.8	42.8	205.2	96.9	(21.3)	73.1	(38.6)	30.8	151.4	57.0	107.8
7501	TL	278.4	116.7	2389.8	1610.2	9563.6	8631.5	7258.4	4493.6	44.1	3330.0	434.2
	OL	280.0	116.7	479.9	93.1	35.5	112.1	148.3	(17.8)	54.6	86.1	58.9
7503	TL	132.5	68.9	2318.8	2609.8	1877.2	1304.7	6638.1	1139.5	1272.7	2205.0	1220.2
	OL	134.2	68.3	277.7	165.9	85.9	61.6	585.7	24.2	314.1	61.0	228.5
7505	TL	67.4	48.1	572.2	42.5	49.4	4574.0	8336.9	153.3	71.8	47.7	—
	OL	62.8	35.2	(47.3)	47.2	48.3	55.7	957.1	33.2	73.2	120.8	—
7507	TL	(31.0)	32.9	397.0	129.0	43.7	1161.9	1547.6	389.9	158.0	408.7	249.8
	OL	(29.9)	31.7	(33.6)	(12.4)	41.5	62.4	1558.8	452.5	173.9	349.5	198.8
7510(11)	TL	39.1	(7.8)	340.5	19.6	61.8	77.9	600.3	(14.0)	107.5	422.3	223.3
	OL	39.1	(7.8)	(27.8)	19.6	62.9	56.8	457.7	(14.2)	104.9	222.7	230.6

Values within parentheses indicate nonsignificant departures ($P > 0.05$) from random distribution.

Larval fish diversity is presented in Table 5 as (A) mean numbers of taxa per tow and (B) total numbers of taxa in 60 tows within each region. Mean numbers of larval fish taxa per tow varied much less than larval abundance values (standard deviations 0.3-0.7 times mean values) and reflect relatively constant regional diversities within each cruise. Between-cruise mean diversity values generally varied ≤ than a factor of 2 within each region. The two overall diversity measurements indicate similar regional trends and have a rank difference correlation coefficient (Tate and Clelland 1957), calculated across all regions, of 0.714 ($P < 0.05$).

Day-Night Differences in Abundance and Diversity

Day-night catch differences may bias abundance and diversity estimates. Bridger (1956) and Ahlstrom (1959) reported night:day ratios of ~ 3:1 for total (mixed taxa) larval fish abundances, and attributed these differences to daytime net avoidance. Consistent catch differences of this magnitude could introduce large errors in abundance estimates based on combined day and night data. Z tests were performed on mean day and mean night abundance values of each larval fish category by region and cruise and for the combined total of regions and cruises (Table 6). Only 33 of 183 day-night abundance comparisons were significantly different; in 6 cases day catches were larger, and in 27 cases night catches were larger. Twenty-three percent of the comparisons in the total larvae and OL categories yielded significant differences. Nine of the 13 significant night:day catch differences of total larvae were associated with significant catch differences of OL rather than PL categories. Significant day-night catch differences in the combined regional data occurred only within the total larvae and OL categories (Table 6). The ratio of night:day catches of zooplankton and ichthyoplankton varied widely within each region (Table 6). For most categories night catches were generally (but not significantly) larger than day catches. Night:day ratios were: total larvae, anchovy, and OL all 1.3:1; hake, 2.2:1; jack mackerel, 2.4:1. Zooplankton had a 1:1 night:day ratio. Night tows also generally yielded more larval fish taxa per tow (overall night:day ratio = 1.3:1); 11 of 61 comparisons were significant, and all 11 showed greater night than day catches.

Overview of Abundance and Diversity in the CalCOFI Area

Zooplankton abundance decreased from north to south and from inshore to offshore (Table 7; Figure 2). Mean zooplankton abundance off central California was significantly higher, and off central Baja California significantly lower, than in the other two areas ($P < 0.01$, Z test). Maximum mean and absolute

TABLE 5
Larval Fish Diversity Expressed as (A) Mean and Standard Deviations of Numbers of Larval Taxa per Tow by Region and Cruise and as (B) the Total Numbers of Larval Taxa Taken in 60 Samples Within Each Region

Cruise		Region										
A.		4	5	7	8	9	11	12	13	14	16	17
7412	x	4.3	3.6	4.6	6.6	6.0	5.3	3.6	6.8	10.0	5.6	4.5
	σ	2.4	1.6	2.4	3.6	3.6	2.9	1.7	3.3	5.7	2.6	3.1
No. tows		27	10	80	10	18	26	28	13	4	38	13
7501	x	7.3	6.0	6.7	7.9	10.9	7.6	6.3	7.3	14.9	5.6	6.9
	σ	2.8	4.1	2.2	4.0	4.0	2.3	2.1	3.4	3.0	2.9	1.9
No. tows		26	4	81	8	18	26	28	13	12	38	12
7503	x	6.7	8.3	7.8	8.3	11.8	8.6	5.1	7.0	15.2	4.9	7.5
	σ	2.9	4.7	2.8	3.8	5.0	3.0	3.6	1.5	9.0	1.8	3.7
No. tows		23	18	81	9	16	19	17	10	4	18	4
7505	x	5.1	7.0	4.1	4.9	10.3	4.5	5.4	7.0	12.8	5.5	9.0
	σ	2.3	4.8	2.5	3.5	5.3	2.2	2.6	2.8	3.4	3.5	—
No. tows		13	9	79	9	18	27	28	13	12	2	1
7507	x	2.5	4.5	3.9	7.0	9.8	5.1	6.3	6.7	14.7	6.0	9.3
	σ	1.8	2.0	2.4	4.6	5.7	2.2	2.2	3.8	4.5	3.8	4.8
No. tows		24	12	77	9	18	26	28	13	15	37	13
7510	x	—	—	6.9	5.2	7.0	6.9	7.6	8.7	12.2	10.6	6.8
	σ	—	—	3.1	1.5	3.0	3.7	4.2	4.9	4.6	5.3	4.8
No. tows		—	—	7	4	3	28	29	12	15	37	13
7511	x	3.1	2.9	5.1	6.8	8.9	—	—	—	—	—	—
	σ	1.4	1.9	2.8	5.2	5.5	—	—	—	—	—	—
No. tows		25	11	74	4	14	—	—	—	—	—	—
Total	x	**4.8**	**5.6**	**5.4**	**6.7**	**9.5**	**6.2**	**5.8**	**7.2**	**13.5**	**6.6**	**7.0**
	σ	**2.9**	**4.0**	**2.9**	**3.9**	**5.1**	**3.1**	**3.0**	**3.4**	**4.6**	**4.1**	**4.0**
No. tows		**137**	**64**	**472**	**53**	**105**	**152**	**159**	**74**	**62**	**170**	**56**
Region rank (total means)		**11**	**9**	**10**	**5**	**2**	**7**	**8**	**3**	**1**	**6**	**4**

	Region										
B.	**4**	**5**	**7**	**8**	**9**	**11**	**12**	**13**	**14**	**16**	**17**
No. taxa in 60 tows (* denotes < 60 tows)	**49**	**62**	**51**	**62***	**80**	**74**	**77**	**67**	**99**	**77**	**73***
Region rank	**11**	**8.5**	**10**	**8.5**	**2**	**5**	**3.5**	**7**	**1**	**3.5**	**6**

ichthyoplankton abundances occurred in the areas off southern California and northern Baja California; about 39% of the total estimated larval abundance was from each of these areas, whereas the central Baja California area yielded about 17% of the total, and only 5% of the total larvae occurred north of Point Conception. Mean larval fish abundances decreased from inshore to offshore and seaward areas (Table 7; Figure 3). Mean numbers of larval fish taxa/tow increased from north to south, reaching maximum levels off northern Baja California (Table 7; Figure 4). Unlike abundance, diversity increased with distance from shore, perhaps partly because of better identification ability for larvae of offshore fish species.

Règions differed in total larval fish abundance and in the relative abundances of the PL and OL fractions. Total larval abundances were highest in regions 7, 11, and 12 of southern California and northern Baja California and region 8 of southern California because of large numbers of PL (Figures 3 and 5). Here the PL (primarily anchovy) made up ≥ 80% of the regional totals (Table 3). Anchovy-dominated PL also constituted > 80% of the relatively moderate larval fish abundances of central Baja California region 16 and regions 9 and 13 of southern California and northern Baja California (Figures 3 and 5; Table 3). Total larval abundances were relatively low (Figure 3), and the proportions of PL and OL more similar, in regions 14 and 17 of northern and central Baja California. The PL of region 17 was primarily anchovy, whereas that of region 14 was mostly jack mackerel and hake (Table 3). Central California regions 4 and 5 had the lowest

TABLE 6

Results of Comparisons of Day and Night Catches of Zooplankton, Total Larvae, 5 Species of PL, and the Other Larvae (OL), and the Ratio of Night:Day Abundances of These Categories for (A) Individual Region and Cruise Data (239 Comparisons) and (B) Combined Region and Cruise Data (850 Day Samples, 636 Night Samples)

	Regional data							
	Zooplankton volume	Total larvae	Anchovy	Hake	Jack mackerel	Sardine	Pacific mackerel	Other larvae
No. signif. differences	9	13	2	2	1	2	0	13
No. comparisons	56	56	37	21	9	3	1	56
No. signif. larger day values	1	2	1	2	—	1	—	—
No. signif. larger night values	8	11	1	—	1	1	—	13
	Ratio of night:day abundance values							
Range	0.7-1.5	0.7-2.5	0.6-20	0.3-4.4	0.8-5.5	0.4-7.7	0.5	0.7-2.0
Mean	1.1:1	1.4:1	1.1:1	1.7:1	2.6:1	4.0:1	0.5:1	1.4:1
B.	Combined region and cruise data							
Probability level for signif. differences	$P = 0.63$	$P = 0.03$*	$P = 0.16$	$P = 0.19$	$P = 0.15$	$P = 0.55$	$P = 0.39$	$P = 0.003$*
Ratio night:day	1.0:1	1.3:1	1.3:1	2.2:1	2.4:1	0.8:1	0.4:1	1.3:1

Significance of abundance differences are based on the Z test ($P < 0.05$; 2 tailed); asterisk denotes significant comparisons.

TABLE 7

Areal Summary of Means and Standard Deviations of Zooplankton and Ichthyoplankton Abundances and of Ichthyoplankton Diversity Within the 1975 CalCOFI Survey Area

CalCOFI area	Zooplankton abundance (cc/1000m^3)	Ichthyoplankton abundance (no./10m^2)	Percentage of total CalCOFI area ichthyoplankton	Larval fish diversity (mean no. taxa/tow)
I: Central California (regions 4, 5; 46,599 nmi^2) 201 samples	227 ± 193	162 ± 214	4.98%	5.2
II: Southern California (regions 7, 8, 9; 60,906 nmi^2) 626 samples	173 ± 233	885 ± 1767	39.40%	7.2
III: Northern Baja California (regions 11, 12, 13, 14; 69,394 nmi^2) 447 samples	162 ± 258	917 ± 2293	38.16%	8.2
IV: Central Baja California (regions 16, 17; 36,653 nmi^2) 226 samples	93 ± 107	534 ± 994	17.46%	6.8
Inshore (regions 4, 7, 11, 12, 16; 72,024 nmi^2) 1,090 samples	181 ± 246	843 ± 1848	47.36%	5.8
Offshore (regions, 5, 8, 13, 17; 83,964 nmi^2) 246 samples	130 ± 168	538 ± 1415	33.62%	6.4
Seaward (regions 9, 14; 57,564 nmi^2) 164 samples	110 ± 103	405 ± 1530	19.02%	11.5

Areal estimates based on combined (6 cruises) regional sample data (regions are noted for each area considered). Zooplankton abundance as mean displacement volume (cc/1000m^3); ichthyoplankton abundance as mean numbers of larvae/10 m^2 sea-surface area and as the percentage of the total estimated numbers of larvae represented by each area; and larval fish diversity as mean numbers of larval taxa/tow. Regional areas given as numbers of square nautical miles.

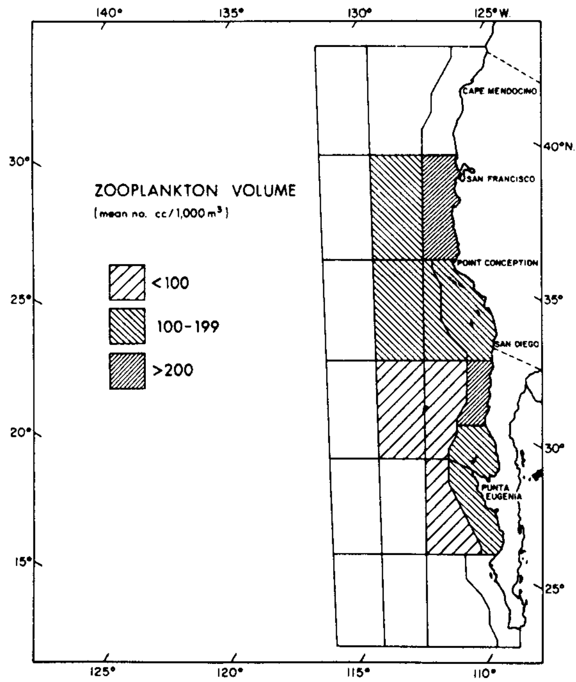

Figure 2. Mean zooplankton volume in 11 CalCOFI regions sampled during 1975.

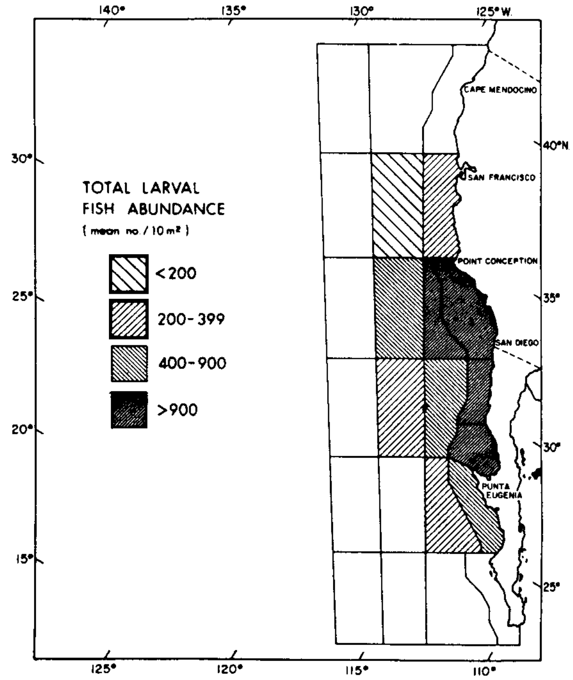

Figure 3. Mean larval fish abundance (total) in 11 CalCOFI regions sampled during 1975.

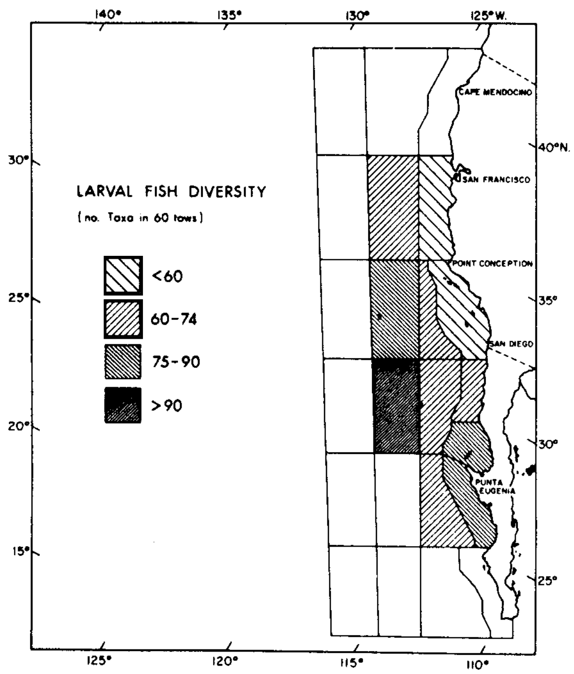

Figure 4. Larval fish diversity in 11 CalCOFI regions sampled during 1975. Diversity expressed as numbers of larval taxa taken in 60 samples within each region.

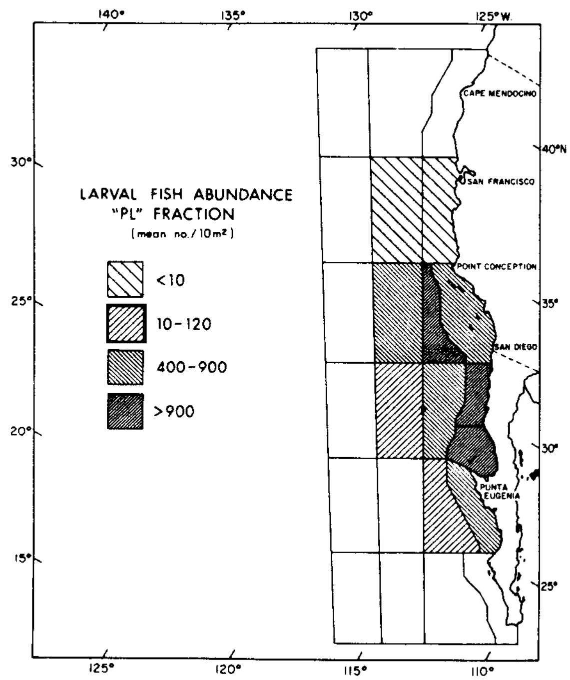

Figure 5. Mean larval fish abundance (PL fraction) in 11 CalCOFI regions sampled during 1975.

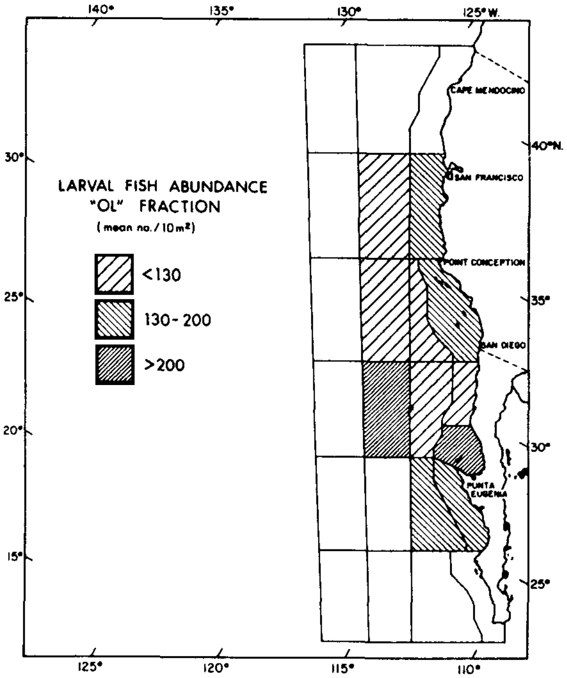

Figure 6. Mean larval fish abundance (OL fraction) in 11 CalCOFI regions sampled during 1975.

concentrations of larvae; absolute abundances here were an order of magnitude lower than in the south, and the PL made up only a small proportion (< 5%) of the total larvae.

Largest mean OL abundances occurred off northern Baja California in Viscaino Bay region 12 (because of flatfishes) and in seaward region 14 (because of mesopelagic fishes) (Figure 6). Absolute OL abundances were highest in northern and central Baja California regions 14 and 17 (19% and 15% of the total CalCOFI OL, respectively). Inshore southern California region 7, although dominated by PL, also contributed 12% of the total OL (Appendix). Although regions 4 and 5 were dominated by OL species, they contributed only 10% and 8% to the total OL.

Maximum larval fish diversity (both numbers of taxa per tow and numbers of taxa per 60 tows within a region) occurred off northern Baja California in seaward region 14 (Table 5, Figure 4) in association with maximum OL abundance. Southern California seaward region 9 ranked second in diversity, but had only moderate OL abundances. The mean numbers of larval fish taxa per tow in these two regions were significantly higher than in all other regions ($P << 0.01$). Minimal diversity values occurred off central and southern California in regions 4, 5, and 7.

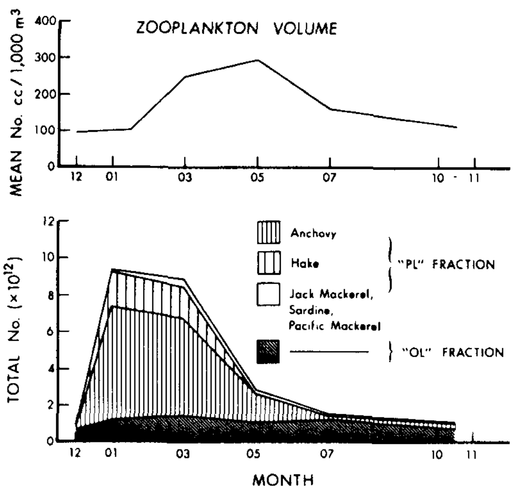

Figure 7. Seasonal variation in zooplankton volume and abundance of major ichthyoplankton components in CalCOFI area during 1975.

Seasonal Changes in Abundance: Areal Overview

Ichthyoplankton and zooplankton abundances underwent large seasonal fluctuations (Figure 7). Maximum larval fish abundances were found during January and March cruises, which captured > 60% of the total (summed six cruises) estimated numbers of larvae. This was due to peak abundances of two PL species—anchovy and hake (Figure 7). This larval abundance peak preceded maximum zooplankton abundance (March and May). The OL abundances from January through July were about twice the October-November and December values. Although the OL made up only a small proportion (≤ 16%) of the total absolute larval abundance during the January-March PL abundance peak, the proportion increased from May to November (May, 39%; July 75%; October-November, 68%) because of decreased PL abundances.

There were north-south differences in seasonal abundance peaks of zooplankton and larval fish (Figure 8). Northern zooplankton peaks occurred later, and northern ichthyoplankton peaks earlier, than their southern counterparts. Off central California, maximum zooplankton abundances were in May and July; off southern California, during May; off northern and central Baja California, during March. Central California peak larval abundances (almost entirely due to OL) occurred during January and March. Southern California peak OL and PL abundances were also in January and March, but the PL dominated. The northern Baja California area had a longer (January-May) period of elevated PL abundance, and a much later (July) OL abundance peak, than did the southern Cali-

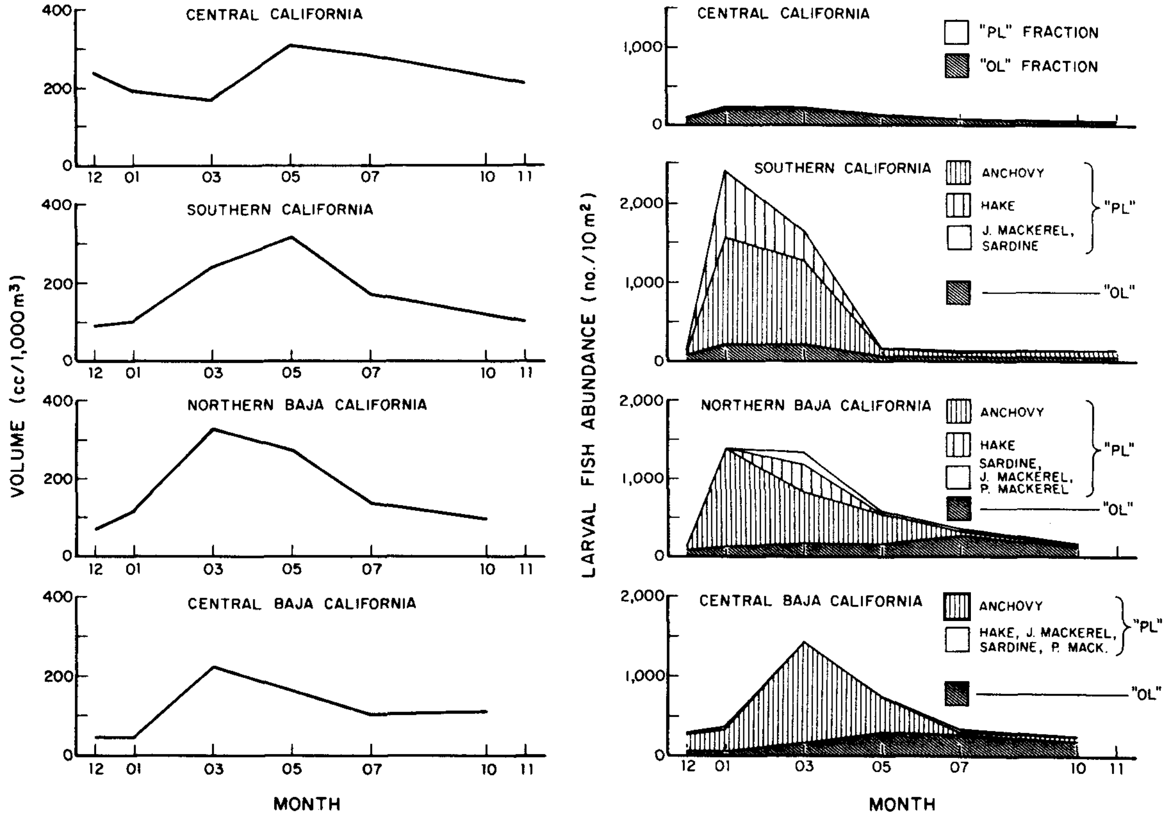

Figure 8. Seasonal variation in zooplankton volume and abundance of major ichthyoplankton components in four latitudinal portions of the CalCOFI area during 1975. Zooplankton abundance (mean displacement volume) based on combined regional sample data for each cruise; ichthyoplankton abundance as estimated total numbers of larvae of each component within each area (summed regional abundance estimates corrected for region surface area) by cruise.

fornia area. Off central Baja California, peak abundances of PL occurred during March, of OL during May and July. Seasonal ichthyoplankton and zooplankton abundance peaks within each area occurred during different months in all but the central Baja California area (Figure 8). Off southern California and northern Baja California, PL abundance peaks occurred before zooplankton abundance peaks. Peak OL abundances off central and southern California preceded, and off northern Baja California followed, peak zooplankton abundances. Off central Baja California, PL and zooplankton abundance peaks coincided; these preceded the OL abundance peak.

Seasonal Changes in Abundance and Diversity

Central California: regions 4 and 5. Central California regions 4 and 5 had similar abundance patterns (Figure 9), although zooplankton and ichthyoplankton abundance peaks in offshore region 5 occurred later than those of inshore region 4. The OL dominated the ichthyoplankton throughout the year in both regions. Significant peak larval abundances ($P < 0.01$; Z test) occurred in region 4 during January and March. Elevated, but significantly lower, abundance values occurred in region 5 at this time and extended through May. In both regions highest larval fish diversity values were associated with the months of maximum larval abundance. Zooplankton abundance within region 4 remained at fairly high levels throughout the year. Within region 5, May and July zooplankton abundances were significantly higher than during other months.

Southern California: regions 7, 8, and 9. The three southern California regions had peak PL and OL abundances during January and March (Figure 10). Inshore region 7 differed from the others by having a second (similar in value) OL peak in November and by having PL (primarily anchovy) dominate the ichthyoplankton throughout the year. Here the PL made up > 58%, and during most months >80%, of the total larvae. In contrast, the PL of offshore and

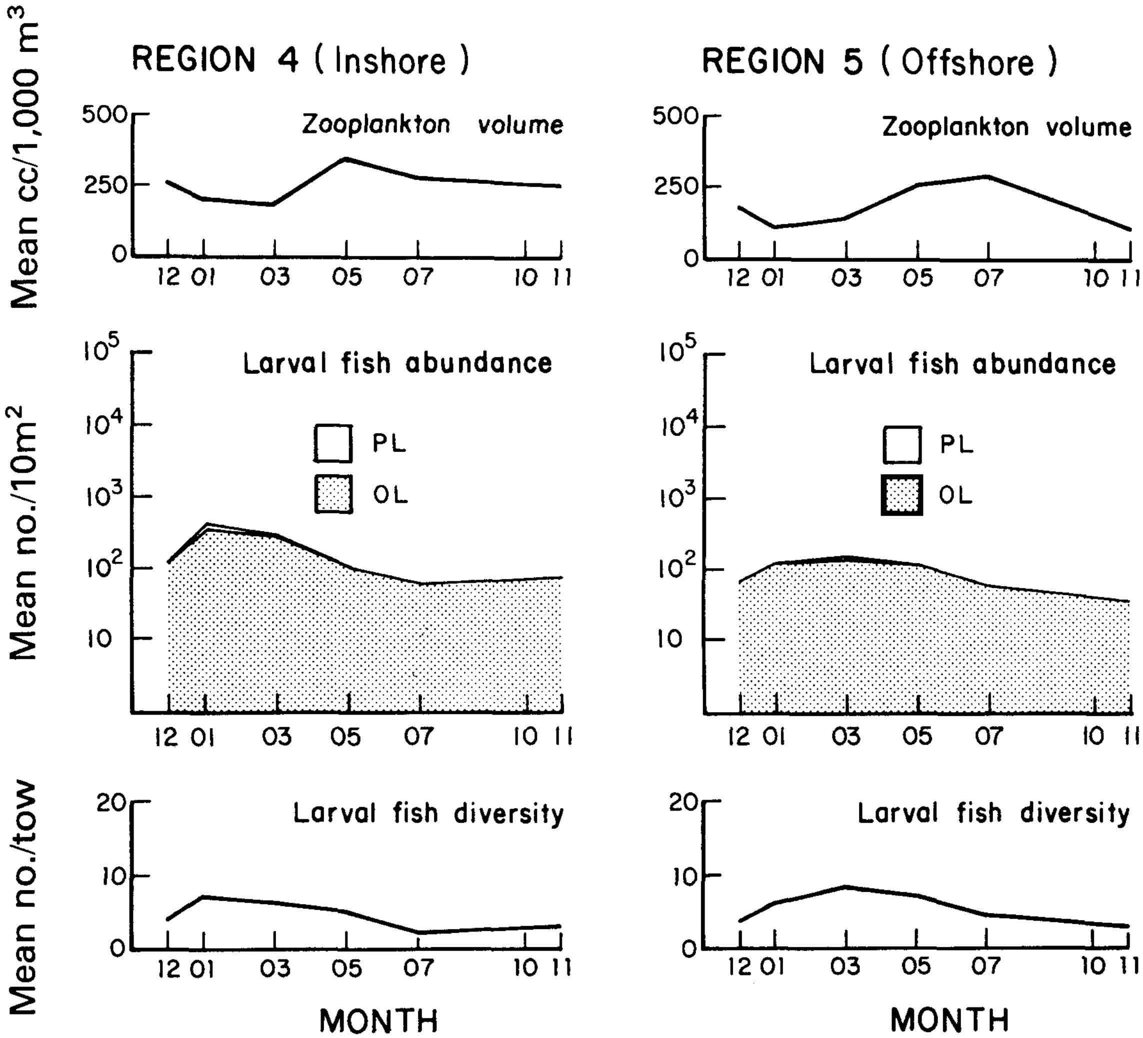

Figure 9. Seasonal variation in zooplankton volume, abundance of fish larvae, and diversity of fish larvae in CalCOFI central California regions 4 and 5 during 1975. Zooplankton biomass expressed as mean displacement volume; abundance of total fish larvae, PL fraction, and OL fraction expressed as mean numbers/10 m² sea surface; and larval fish diversity expressed as mean numbers of taxa/cruise. Note use of log scale for larval fish abundance.

seaward regions 8 and 9 dominated from January to May, after which the OL made up > 50% of the total. The large January PL abundance of region 8 was due mostly to anchovy and was the highest for the entire CalCOFI area during 1975. Hake larvae made up most of the PL of region 9. In all three regions, larval diversity increased with OL abundance. Significant maximum zooplankton values occurred during March and May in region 7, and May in region 8.

Northern Baja California: regions 11, 12, 13, and 14. The inshore and Viscaino Bay regions 11 and 12 of northern Baja California demonstrated different patterns of seasonal abundance and diversity (Figure 11). Although both regions had January-May periods of maximum PL abundance (anchovy and hake in region 11; primarily anchovy in region 12), maximum OL abundance and diversity occurred during January and March in region 11 and during July in region 12. Overall, the OL in Viscaino Bay region 12 (dominated by flatfishes) made up a larger proportion of the ichthyoplankton (18.6% vs 9%) than in region 11 (primarily rockfishes and mesopelagic fishes). Maximum zoo-

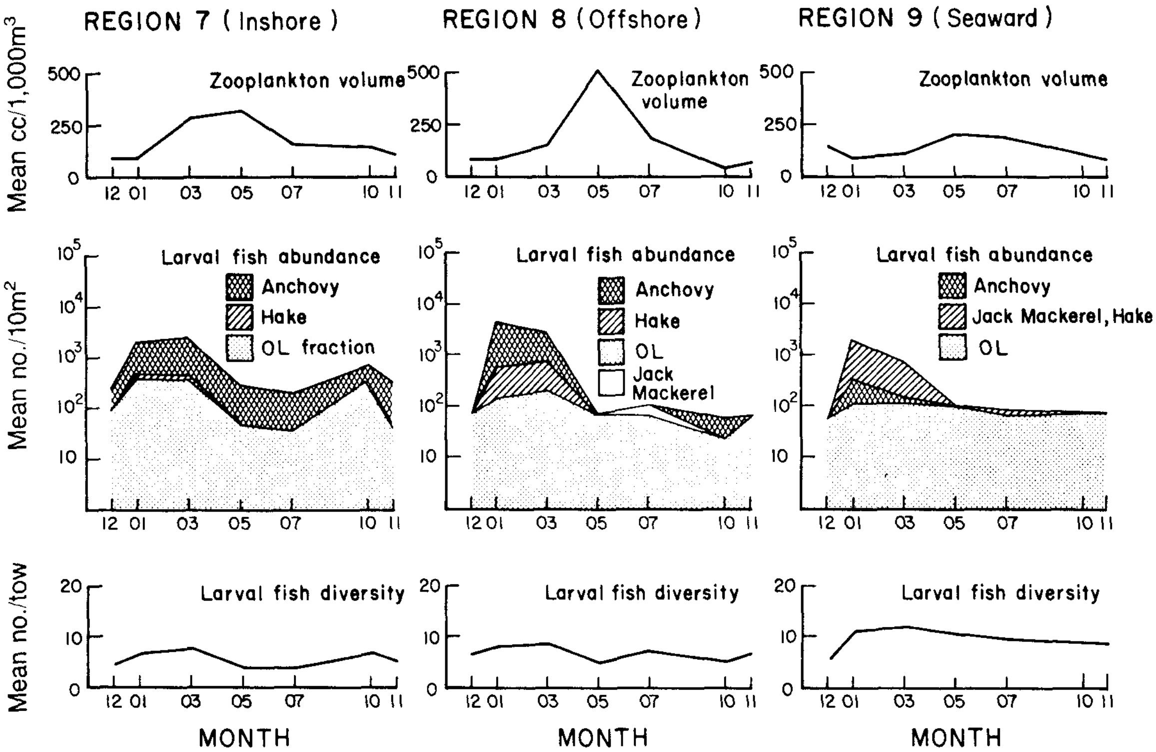

Figure 10. Seasonal variation in zooplankton volume, abundance of fish larvae, and diversity of fish larvae in CalCOFI southern California regions 7, 8, and 9 during 1975. Values as in Figure 9.

plankton biomass values occurred earlier (March) in region 12 than in region 11 (May).

In regions 13 and 14, the PL abundance maximum was shorter (January-March in 13; only March in 14) and less marked than inshore. The January to May PL abundances in both regions were significantly lower than those of regions 11 and 12. Anchovy dominated the January abundance maximum in region 13 (96% of total larvae), but hake and jack mackerel contributed most of the larvae during March (58%); hake and jack mackerel dominated the March peak (67%) in region 14 (Figure 11). OL abundances in region 13 were relatively constant throughout the year. The OL dominated the ichthyoplankton of region 14 during all months but March; lowest abundances occurred in December. Diversity values within region 14 were the highest for the entire CalCOFI area and were relatively constant throughout the year. Zooplankton abundances in both regions were low; a small but significant maximum occurred in region 13 during May.

Central Baja California: regions 16 and 17. Inshore region 16 was unique in having significantly larger numbers of PL during December than any other region (Figure 12); this was primarily due to anchovy (88% of total). Anchovy and PL abundance remained high in January and increased significantly during March. OL abundance was low from December to March and increased significantly in July and October, while PL abundance decreased; the OL made up > 67% of the total ichthyoplankton during July and October. Larval diversity increased in October in conjunction with increased OL abundance. Zooplankton had a significant March abundance peak.

Little can be determined about March and May abundances in offshore region 17 because only five samples represented these months. Based on existing data, this region resembled adjacent region 14, which had peak PL and OL abundances in March and July, respectively (Figure 12). Zooplankton abundances were elevated during March and October.

Chelton (1981) reports that maximum zooplankton biomass values occur in the central Baja California area (regions 16 and 17) during late summer and fall (August-October); this peak is not evidenced here because we lack sample data covering this period.

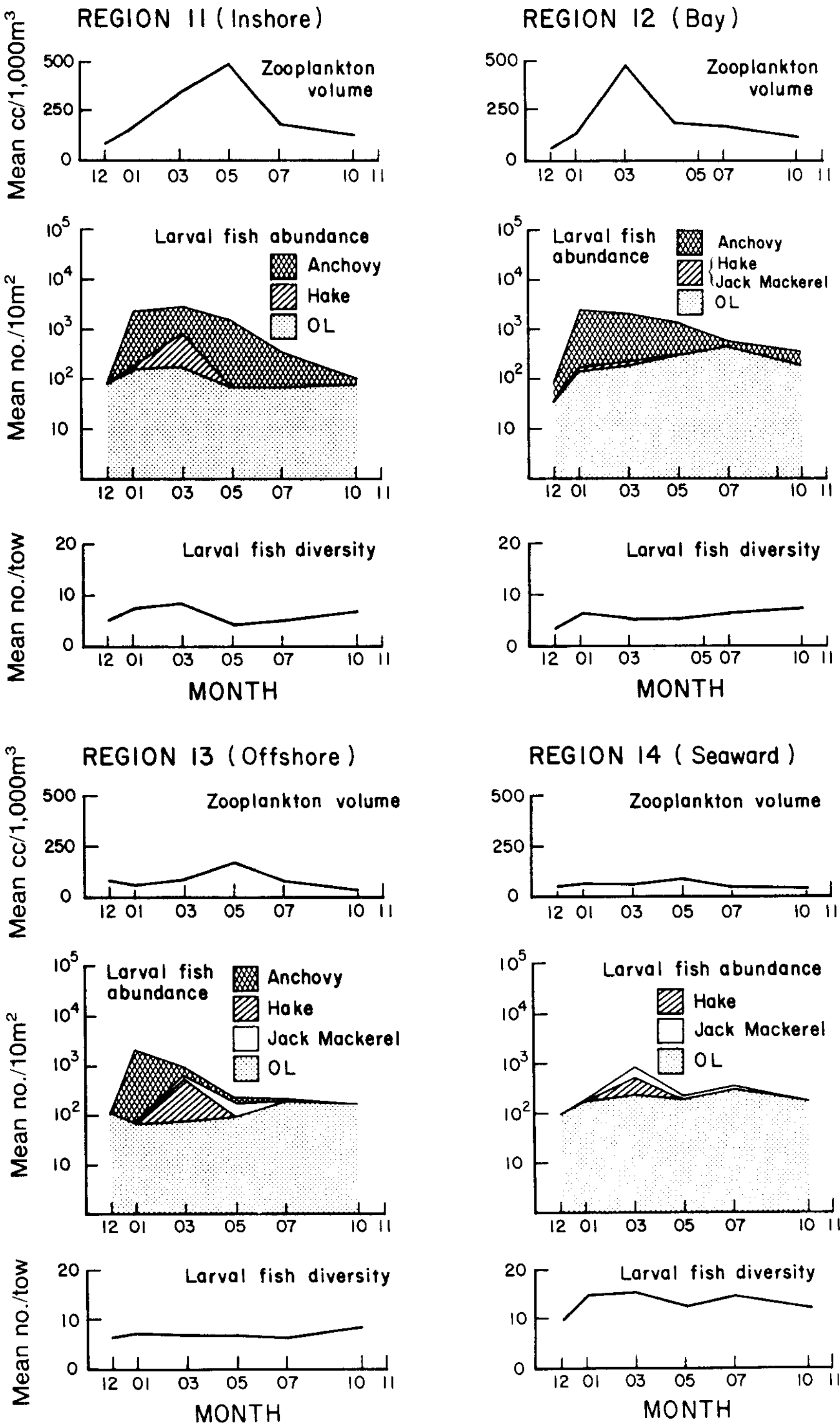

Figure 11. Seasonal variation in zooplankton volume, abundance of fish larvae, and diversity of fish larvae in CalCOFI northern Baja California regions 11, 12, 13, and 14 during 1975. Values as in Figure 9.

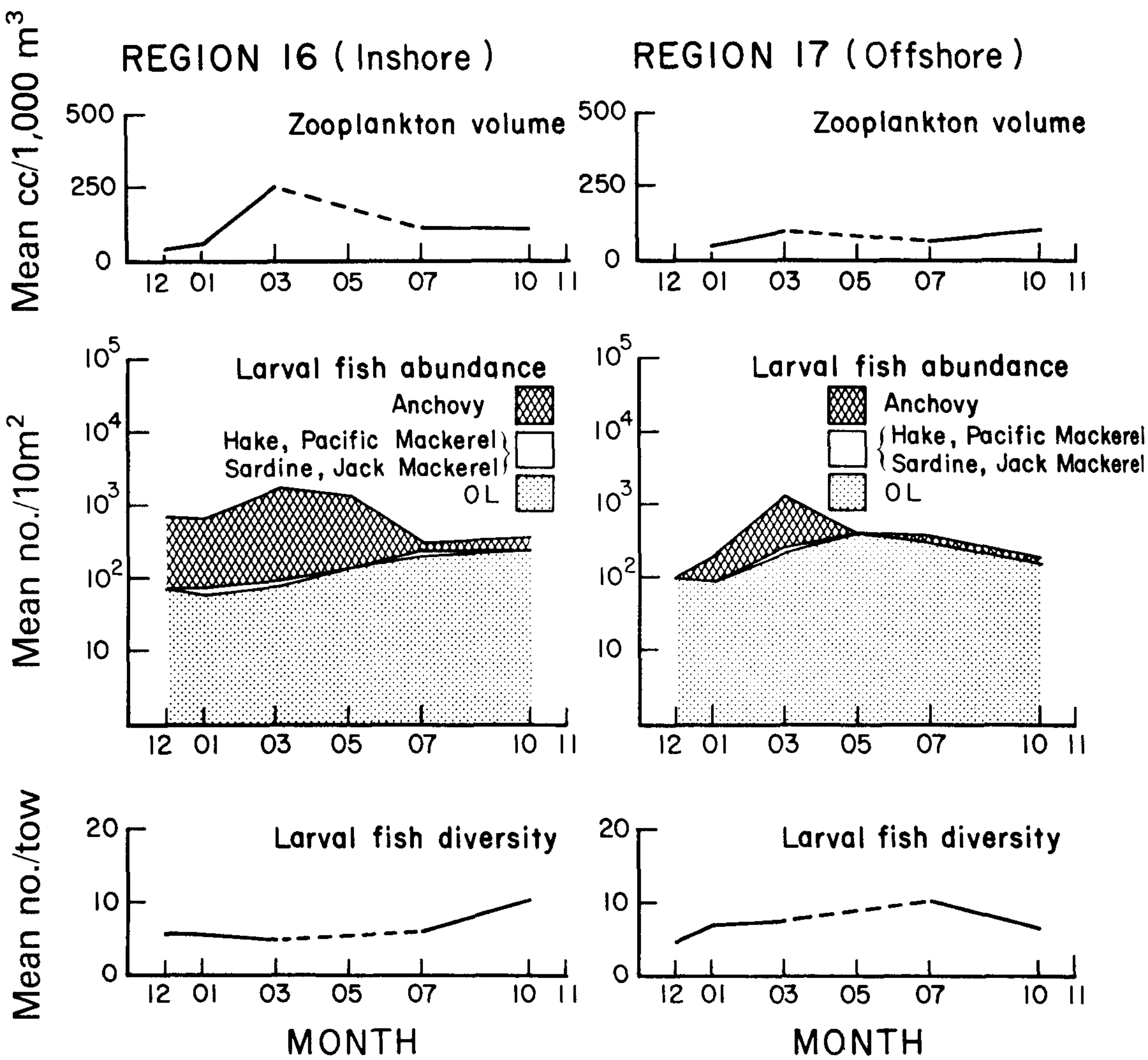

Figure 12. Seasonal variation in zooplankton volume, abundance of fish larvae, and diversity of fish larvae in CalCOFI central Baja California regions 16 and 17 during 1975. Values as in Figure 9.

Sampling Variability, Patchiness, and Abundance Estimates

The large tow-to-tow variability of abundance and resulting large index-of-dispersion values (Table 4) indicate a high degree of zooplankton and ichthyoplankton patchiness throughout the area. Zooplankton biomass index-of-dispersion values during 1975 (range of monthly means 42.8-324.7) were typical for the CalCOFI area and resembled those from years of moderate intensity, coarse-scale (30 × 30 km) patchiness (Haury et al. 1978).

The intensity of zooplankton and ichthyoplankton patchiness varied geographically and seasonally. Within each cruise, zooplankton, total larval, and OL index-of-dispersion values were generally positively correlated with regional abundance values (rank difference correlation coefficients 0.49-0.98; $P \leq 0.05$ in 15/18 cases). However, during all but the December cruise maximum zooplankton index-of-dispersion values (1.2-2 times larger than next highest values) occurred in northern Baja California inshore region 11 and were never associated with maximum regional biomass values. Maximum indices of dispersion for total larvae and OL occurred in northern Baja California Viscaino Bay region 12 during all but the December and January cruises; these were associated with maximum regional abundances of total larvae during May, July, and October and of OL during May and July. These high index-of-dispersion values indicate generally greater intensities of both zooplankton and ichthyoplankton patchiness and suggest that throughout much of the year the coastal northern Baja California regions were subject to greater physically induced and/or inherent biological heterogeneity than were the other regions in the survey area.

Within each region, maximum zooplankton and OL patch intensities were generally associated with periods of maximum abundance. Greatest PL patch intensities, however, were associated with periods of maximum abundance only in offshore and seaward regions 9, 13, 14, and 17; most intense patchiness preceded maximum PL abundance in inshore regions 7, 11, and 16 by 2 months and followed maximum abundance in offshore region 8 and Viscaino Bay region 12 by 2 and 4 months, respectively. In all cases this was due to anchovy larvae, which exhibited most extreme patch intensity during the onset of spring spawning activity in the inshore regions and at the end of maximum spawning activity in regions 8 and 12. This suggests more localized or erratic anchovy spawning activity prior to or following peak spawning in inshore regions as compared to those offshore.

Despite sampling variability, both seasonal and geographical differences in abundance and diversity were apparent and statistically significant. In contrast, day-night differences in ichthyoplankton abundance estimates were generally nonsignificant statistically and were less than expected (Bridger 1956; Ahlstrom 1959). As a consequence, we combined day and night samples (day and night data are equally represented) for comparisons of relative abundances within and between regions. Absolute abundance estimates based on combined data will be ~ 15% lower than if based on mean night values alone.

Geographical Abundance and Diversity Patterns

The pattern of decreasing zooplankton abundance from north to south and from inshore to offshore regions (Figure 2) has also been reported by Reid et al. (1958), Smith (1971), and Bernal (1980). The pattern of total larval abundance (Figure 3) is heavily influenced by the PL fraction (Figure 5), and resembles distributions of the more abundant pelagic schooling species: anchovy, hake, and jack mackerel (Kramer and Smith 1970a, b; 1971). The southern California and northern Baja California areas of maximum larval abundance coincide with areas of decreased zooplankton abundance and maximum zooplankton diversity (McGowan and Miller 1980). The OL abundance pattern (Figure 6) is complex and includes (1) decreasing abundance from inshore to offshore regions off California, (2) markedly increased abundances in northern Baja California Viscaino Bay and seaward regions, and (3) moderately high inshore and offshore abundances off central Baja California. This complexity is in part due to the large number of species represented in the OL (shelf, benthic, mesopelagic, and oceanic forms with differing hydrographic affiliations and fecundities). These are treated in Loeb et al. (1983a).

The overall zooplankton, PL, and OL abundance patterns differed markedly. There were no significant area-wide correlations between zooplankton biomass and ichthyoplankton abundances (Kendall's tau test; $P > 0.05$ in all comparisons of 6-month mean zooplankton biomass values and abundances of total larvae, PL, and OL). Additionally, no significant correlation was found between 6-month mean PL and OL abundances within regions. This suggests that overall regional patterns of zooplankton, PL, and OL abundances within the CalCOFI area are independent of one another (i.e., that zooplankton, PL, and OL are most abundant within different regions in the CalCOFI area).

The independence of zooplankton, PL, and OL abundances seen between regions on a 6-month basis is also seen within each region (between cruises) on a seasonal scale, and within each cruise on regional scales (30 × 30 km, samples only hours to days apart). Significant within-region differences occur in the timing of abundance fluctuations of the zooplankton, PL, and OL, as indicated by a lack of significant correlations between the ranked mean abundances of these three categories by cruise within each region (Kendall's tau, $P > 0.20$ in all cases). Additionally, there are few significant correlations between zooplankton biomass and ichthyoplankton abundance in samples by region and cruise (product-moment correlation coefficients; Table 8), and there is no overall trend in correlations between regions. This latter strongly suggests independently distributed patches of zooplankton and of larval fish taxa.

In seven regions, periods of peak OL abundances were associated with maximum larval diversity. However, OL abundance and diversity (by cruise) were significantly correlated ($P < 0.05$; Kendall's tau) throughout the year only within regions 4, 5, and 9. In no region was there a significant correlation between diversity and either PL or zooplankton abundance.

TABLE 8
Number of Significant Correlations ($P \leq 0.05$) Out of the Total Number of Within-Region Cruise Comparisons of Zooplankton Biomass (cc/1000m^3) and Abundances (no./10m^2 sea surface) of Four PL Species and the OL Category

Region	Zooplankton vs anchovy	Zooplankton vs hake	Zooplankton vs jack mackerel	Zooplankton vs sardine	Zooplankton vs OL	OL vs anchovy	OL vs hake	OL vs jack mackerel	OL vs sardine
4	0/6	0/4	—	—	2+/6	0/6	0/4	—	—
5	0/2	0/2	0/2	—	1+/6	0/2	0/2	0/2	—
7	0/6	1−/5	0/3	0/2	2+/6	0/6	1+/5	0/3	0/2
8	1+/6	1+/2	0/2	—	2+/6	1+/6 1−/6	0/3	0/2	—
9	3+/4	1+/3	1−/2	—	2+/6 1−/6	0/4	0/2	—	—
11	1+/3	1−/3	0/4	0/1	0/6	3+/4	1+/3	1+/4	0/1
12	1+/3	0/4	1−/3	1+/4 1−/4	1+/6	4+/6	1+/4	0/3	1+/3
13	1+/5	0/4	0/3	—	0/6	1+/5	1−/4	0/3	—
14	0/5	0/2	0/3	—	1+/6	0/5	0/2	1+/3	—
16	1+/5 2−/5	1−/4	0/2	2+/4	3+/5	1+/5	0/4	0/2	0/4
17	2+/4	0/2	0/2	—	1+/5 1−/5	0/4	1−/2	0/2	—
Sum: Positive correlations	10+/49 (20.0%)	2+/35 (5.7%)	—	3+/11 (27.3%)	15+/64 (23.4%)	10+/55 (18.2%)	3+/35 (8.6%)	2+/24 (8.3%)	1+/10 (10.0%)
Negative correlations	2−/49 (4.1%)	3−/35 (8.6%)	2−/26 (7.7%)	1−/11 (9.1%)	2−/64 (3.1%)	1−/55 (1.8%)	2−/35 (5.7%)	—	—

Significance is based on product-moment correlation coefficients derived from $\log_{10}$ abundances of each category within samples by region and cruise.

Seasonal Abundance and Diversity Patterns

Latitudinal differences in timing of peak zooplankton, PL, and OL abundances were tested using Kolmogorov-Smirnov (K-S) tests on cumulative percent curves constructed using summed mean cruise values of the three categories for each area (Figure 13). The cumulative percent curve for zooplankton biomass vs month for the central California area was significantly different ($P < 0.05$) from those of all other areas; that of southern California was significantly different from the northern Baja California (but not central Baja California) area curves; northern and central Baja California area curves did not differ significantly. Maximum differences among those curves occurred between March and May and indicate earlier seasonal zooplankton abundance peaks in the southern areas. Less than 50% of the total central California area zooplankton was captured between January and May, but over 60% of the southern California and central Baja California area zooplankton, and over 70% of the northern Baja California area zooplankton, was captured during this period. Adequate seasonal coverage of the reported (Chelton 1981) late-summer central Baja California zooplankton biomass peak, however, may distinguish this area from the others by establishing the existence of a significantly later zooplankton peak south of Punta Eugenia.

The cumulative percent curves of PL and OL abundance by cruise also showed significant latitudinal differences ($P < 0.05$) except between the OL of the central and southern California areas. For both PL and OL, maximum increases in cumulative percent abundance within southern areas occurred later in the year than in the northern areas (Figure 13). For the PL, the largest differences occurred between January and March; for the OL, the largest differences occurred between March and May. Additionally, within all four areas the cumulative percent curves for zooplankton, PL, and OL abundances were significantly different from one another ($P << 0.01$). This picture of significant differences in timing of zooplankton, PL, and OL abundance peaks is corroborated by lack of significant agreement of ranked abundance (by cruise) of these three categories (Table 9). Only in the northern Baja California area was there significant agreement (Kendall concordance test, $P < 0.05$) among the zooplankton, PL, and OL; abundances were highest in March-July and lowest in October-December.

Significant inshore-offshore differences also occur in the months of PL and OL peak abundances (Figure 14). K-S tests indicate that the timing of PL and OL abundance peaks was similar in the offshore and seaward regions within each area, but (except for the central California area) maximum PL abundances (pri-

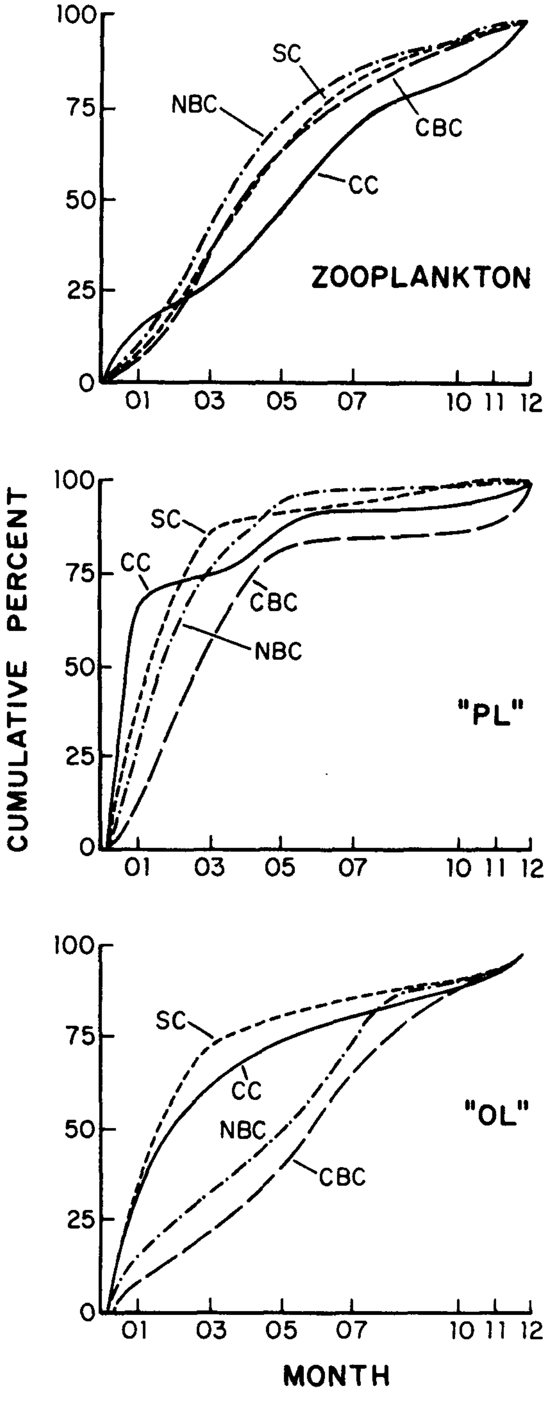

Figure 13. Cumulative percent curves of zooplankton biomass (cc/1000 m^3), PL, and OL abundance (mean no./10 m^2 sea surface) by cruise for four latitudinal CalCOFI areas. CC = Central California; SC = Southern California; NBC = Northern Baja California; CBC = Central Baja California.

TABLE 9
Kendall Concordance Test of Abundances of Zooplankton Biomass, PL, and Other Larvae (OL) Ranked by Cruise for Each of Four Latitudinal CalCOFI Areas

	Zoo-plankton	PL	OL	
Central California				
7412	3	3	3	
7501	5	1	1	
7503	6	4	2	
7505	1	2	4	
7507	2	5	6	
7510(11)	4	6	5	$W=0.35$ $X_5^2 = 5.29$ $p > 0.05$
Southern California				
7412	6	6	3	
7501	5	2	1	
7503	2	1	2	
7505	1	4	4	
7507	3	5	6	
7510(11)	4	3	5	$W=0.47$ $X_5^2 = 7.0$ $p > 0.05$
Northern Baja California				
7412	6	5	6	
7501	4	2	4	
7503	1	1	2	
7505	2	3	2	
7507	3	4	1	
7510(11)	5	6	5	$W=0.77$* $X_5^2 = 11.57$ $p = 0.05$
Central Baja California				
7412	6	4	5	
7501	5	3	6	
7503	1	1	4	
7505	2	2	3	
7507	4	6	1	
7510(11)	3	5	2	$W=0.41$ $X_5^2 = 6.24$ $p > 0.05$

W is Kendall concordance coefficient value; probabilities are based on X_5^2 values at (n-1) degrees of freedom. Asterisk denotes significant correlation.

marily anchovy) in these regions occurred earlier ($P \leq 0.05$) than in the inshore regions. Zooplankton abundances in offshore and seaward regions lagged (nonsignificantly) behind those of inshore regions.

DISCUSSION

Ichthyoplankton is treated here as an element of the macrozooplankton. Larval fishes are a persistent, albeit relatively rare (McGowan and Miller 1980) zooplankton component, present in varying abundances throughout the year and area. Individuals are, however, only temporary members of the plankton; their residency lasts from hatching to metamorphosis, a period of weeks to months. The importance of larval fishes is not their abundance or competition/predation relations with the macrozooplankton, but how their distribution and abundance relate to adult fish populations, which do have a large collective impact on secondary and fish production in the water column. Fishes are most easily caught in their larval stages. Ichthyoplankton collections from the upper ~200m represent the offspring of a wide variety of fishes

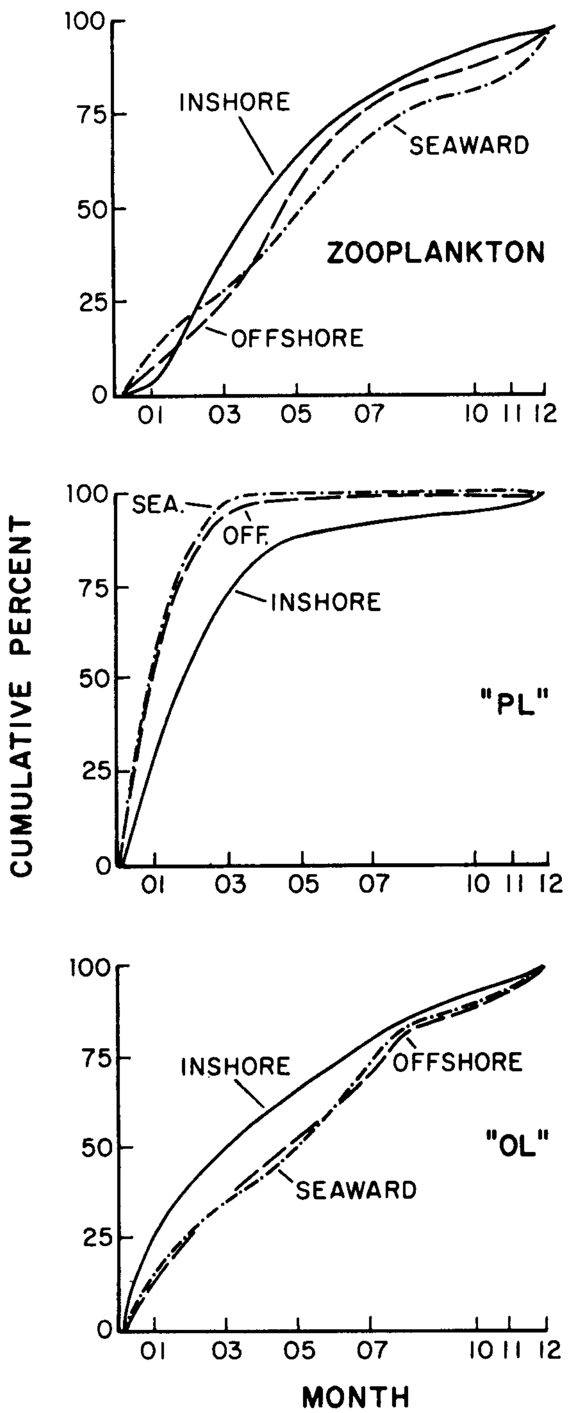

Figure 14. Cumulative percent curves of zooplankton biomass (cc/1000 m^3), PL, and OL abundance (mean no./10 m^2 sea surface) by cruise for inshore, offshore, and seaward CalCOFI zones during 1975.

occurring throughout the water column. Presumably, ichthyoplankton abundance is greatest when and where optimal physical and biological conditions occur for larval survival and ultimate recruitment. Conditions favorable for ichthyoplankton and holoplanktonic invertebrate zooplankton may differ radically, as may conditions favorable for different ichthyoplankton taxa within an area or ichthyoplankton taxa in different areas. These differences should be reflected by different patterns of distribution and abundance between the ichthyoplankton and zooplankton and within the ichthyoplankton.

The geographical and seasonal patterns of zooplankton and ichthyoplankton distribution and abundance described here appear to be related to the physical dynamics of the California Current system. These patterns reflect inshore-offshore and north-south differences in advection and mixing of water from the subarctic, central, and equatorial water masses, and also reflect surface-layer divergence (upwelling) and convergence (downwelling) systems (Reid et al. 1958; Parrish et al. 1981). The differences in distributional patterns and abundance fluctuations of the ichthyoplankton and zooplankton, as well as those of the PL and OL ichthyoplankton categories, suggest that physical processes are influencing these assemblages in different ways. Various patterns of zooplankton and PL distribution and abundance relative to physical processes are discussed below. Patterns within the complex multispecies OL fraction are treated in Loeb et al. (1983a).

The overall pattern of zooplankton abundance (Figure 2) is related to the distribution of surface nutrient levels; maximum abundances are in areas of increased nutrient levels because of advection of subarctic water and coastal upwelled water (Reid et al. 1958). High zooplankton volumes off California are associated with the influence of subarctic water and intense upwelling along the central coastal area extending to Point Conception; high volumes off Baja California are associated with coastal upwelling, especially in the vicinity of Punta Baja and Punta Eugenia (Parrish et al. 1981).

In coastal southern California waters (and presumably elsewhere) the seasonal zooplankton abundance cycle is closely associated with that of primary productivity (Smith and Eppley 1982); both primary productivity and zooplankton biomass increase with the seasonal onset of upwelling in early spring, and reach maximum values during peak upwelling (Smith and Lasker 1978; Smith and Eppley 1982). The zooplankton cycles along the coast (at least from Punta Eugenia northward) appear to follow the northward seasonal progression of coastal upwelling. Off Baja California, upwelling continues throughout the year, with maximum intensities during spring. Off southern and central California, upwelling begins in spring and reaches maximum intensities during summer; upwelling intensities off central California are stronger, and the peak occurs later than off southern California. Chelton (1981) found no significant correlations between zooplankton abundance and upwelling in the four latitudinal CalCOFI areas except off northern Baja California. However, this general lack of correlation may in part result from his use of 30-year averages of monthly biomass and upwelling values; these could obscure existing intra-annual correlations.

Maximum ichthyoplankton abundance (Figure 3) occurs in the coastal regions of southern California and northern Baja California (the Southern California Bight) and is due to large spawning stocks of migratory PL species. This area is characterized by minimal offshore surface water transport relative to the rest of the Pacific coast; Parrish et al. (1981) suggest that PL spawning here may be a reproductive strategy to minimize loss of egg and larval stages to less favorable seaward environments. Anchovy and hake abundances here peak in late winter (January-March), prior to the onset of spring upwelling. For anchovy (and possibly for hake), relatively stable water column conditions at this time may provide well-defined layers and aggregations of larval fish food, and this may favor successful feeding of the early stages (Lasker 1978). Later larval stages grow and develop during periods of upwelling and increasing zooplankton abundance, and actively feeding juvenile stages are contemporary with the May zooplankton abundance peak. The other PL species (jack mackerel, sardine, and Pacific mackerel) have peak spawning during periods of maximum upwelling and increasing zooplankton abundance (March-May); at this time the larval food stocks (copepod nauplii; Arthur 1977) are at their highest.

The persistent high intensity of zooplankton patchiness in northern Baja California region 11 is associated with a persistent zone of surface-layer convergence extending from offshore areas and impinging on the coast between Punta Baja and Punta Eugenia (Nelson 1977; Bakun and Nelson 1977; Parrish et al. 1981). This coastal area is characterized by strong upwelling, and Bakun and Nelson (1977) predicted that surface-layer convergence here may result in the formation of fronts and convergent patches of recently upwelled water. Convergence may also concentrate near-surface zooplankton in fronts or patches (Parrish et al. 1981). The extreme zooplankton patchiness, plus concentrations of characteristically offshore zooplankton species in the inshore northern Baja California region (Arthur 1977) appear to confirm the physical nature of these predictions.

The northern Baja California area of convergence and maximum upwelling separates the cyclonic eddy of the Southern California Bight and a seasonal eddy south of Punta Eugenia (Parrish et al. 1981). It also separates subpopulations of various pelagic fishes (anchovy, hake, sardine, jack mackerel, and Pacific mackerel; Nelson 1977; Hewitt 1981; Parrish et al. 1981) as well as coastal zones of high (northern Baja California) and low (central and southern Baja California) zooplankton diversity (McGowan and Miller 1980). Additionally, the reported late summer/fall zooplankton peak off of central Baja California (south of Punta Eugenia) distinguishes this area from the three northern areas. This late seasonal peak may result from surface expression of the nutrient-rich inshore countercurrent (Reid et al. 1958) and the onset of gyral circulation off the central and southern Baja California coast during the period of relaxed upwelling. These features suggest that the coastal region south of Punta Eugenia represents a separate biological regime (i.e., one with its own species composition and regulating influences).

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APPENDIX

Estimated absolute abundances (as numbers x 10^{11}) of total larvae, PL, and OL fractions of the total, and of the 5 species constituting the PL, by region and cruise. Abundances of total larvae, PL, and OL are ranked by cruise and by region (pooled cruises).

Cruise	Region 4	5	7	8	9	11	12	13	14	16	17	Total	Percentage of area total	Cruise rank
7412														
Total	8.08	7.48	14.75	3.44	5.26	5.62	3.40	9.12	10.51	33.21	5.40	106.27	3.70%	6
PL	0.19	0.84	8.62	0.39	—	2.80	2.26	0.32	—	29.62	—	45.04	2.46%	4
OL	7.89	6.64	6.13	3.05	5.26	2.82	1.14	8.80	10.51	3.59	5.40	61.23	9.56%	6
Anchovy	0.13	0.84	8.50	0.39	—	2.80	2.26	0.32	—	29.22	—	44.46		
Hake	0.05	—	0.12	—	—	—	—	—	—	0.03	—	0.20		
Sardine	—	—	—	—	—	—	-	—	—	0.37	—	0.37		
7501														
Total	25.92	12.60	134.09	190.69	186.43	69.21	92.42	151.88	19.13	30.58	15.50	928.45	32.37%	1
PL	2.48	—	107.13	184.42	176.14	64.13	86.75	147.03	2.39	27.81	8.46	806.75	43.89%	1
OL	23.44	12.60	26.96	6.27	10.28	5.08	5.67	4.85	16.74	2.77	7.04	121.70	19.08%	3
Anchovy	0.72	—	100.98	165.91	18.76	63.31	86.43	146.64	2.39	27.12	8.38	620.64		
Hake	1.76	—	6.14	18.51	157.39	0.82	0.05	0.39	—	0.27	0.08	185.41		
Jack mackerel	—	—	0.01	—	—	—		—	—	—	—	0.01		
Sardine	—	—	...	—	—	—	0.27	—	—	0.42	—	0.69		
7503														
Total	18.98	14.92	172.11	112.12	65.20	90.60	76.91	67.06	86.49	80.99	100.40	885.78	30.88%	2
PL	0.24	0.17	147.00	103.89	54.20	84.81	69.93	61.54	62.56	77.12	83.24	744.69	40.51%	2
OL	18.74	14.75	25.12	8.23	11.00	5.79	6.98	5.52	23.93	3.87	17.16	141.09	22.11%	1
Anchovy	0.12	0.04	141.27	81.30	1.51	65.11	68.56	22.30	0.25	76.73	82.06	539.25		
Hake	0.12	0.11	5.72	22.59	51.87	19.56	1.32	37.67	29.39	0.28	0.13	168.76		
Jack mackerel	—	0.02	—	—	0.82	0.14	0.05	1.57	32.92	0.12	1.04	36.68		
Sardine	—	—	0.05	—	—	—	—	—	—	—	—	0.05		

Cruise	4	5	7	8	9	Region 11	12	13	14	16	17	Total	Percentage of area total	*Cruise rank
7505														
Total	6.30	11.77	20.27	3.15	9.62	44.26	54.99	17.66	21.84	64.52	30.72	285.10	9.94%	3
PL	0.34	1.11	16.77	0.11	0.16	42.16	44.31	9.76	1.11	58.00	—	173.83	9.46%	3
OL	5.96	10.66	3.50	3.04	9.46	2.10	10.68	7.90	20.73	6.52	30.72	111.27	17.44%	4
Anchovy	0.18	—	16.77	0.11	—	41.98	44.05	4.28	0.05	58.00	—	165.42		
Hake	0.16	1.11	0.003	—	0.16	0.01	—	0.07	—	—	—	1.51		
Jack mackerel	—	—	—	—	—	0.17	0.01	5.41	1.06	—	—	6.65		
Sardine	—	—	—	-	—	—	0.25	-	—	-	.	0.25		
7507														
Total	3.81	5.54	13.72	4.91	7.90	10.52	23.33	16.30	33.90	13.91	26.40	160.23	5.59%	4
PL	0.09	0.12	11.33	2.18	1.83	8.43	5.90	2.14	1.75	4.38	2.62	40.77	1.73%	6
OL	3.72	5.41	2.39	2.73	6.07	2.09	17.43	14.16	32.15	9.53	23.77	119.46	20.12%	2
Anchovy	0.09	—	11.29	0.15	0.02	8.34	5.83	1.24	0.01	3.32	2.61	32.90		
Hake	—	—	—	—	—	—	0.06	—	0.02	0.005	—	0.085		
Jack mackerel	—	0.12	0.05	2.03	1.81	0.09	—	0.90	1.72	0.05	0.01	6.78		
Sardine	—	—	—	—	—	—	0.01	—	—	0.99	—	1.00		
7510-11														
Total	4.81	3.17	23.29	2.20	6.72	3.22	13.00	5.69	18.00	16.37	14.03	110.50	3.85%	5
PL	0.005	—	20.31	1.31	0.15	0.76	5.65	0.02	0.08	5.45	2.13	35.87	1.95%	5
OL	4.81	3.17	2.97	0.89	6.57	2.46	7.35	5.67	17.92	10.92	11.90	74.63	11.70%	5
Anchovy	0.005	—	20.20	1.26	0.15	0.73	4.96	-	0.08	5.13	2.13	34.64		
Hake	—	—	0.11	—	—	-	0.006	0.02	—	—	—	0.14		
Jack mackerel	—	—	0.002	0.05	—	0.01	0.002	—	—	—	—	0.06		
Sardine	—	—	0.003	—	—	0.02	0.64	—	—	0.25	—	0.91		
Pac. mackerel	—	—	—	—	—	—	0.04	—	—	0.08	—	0.12		

Cruise	4	5	7	8	9	Region 11	12	13	14	16	17	Total	
Grand total for 6 1-month cruises	67.90	55.48	378.23	316.51	281.13	223.43	264.05	267.71	189.87	239.58	192.45	2,476.33 x 10^{11}	larvae
Percentage (total)	2.74%	2.24%	15.27%	12.78%	11.35%	9.02%	10.66%	10.81%	7.67%	9.67%	7.77%		
Regional rank	10	11	1	2	3	7	5	4	9	6	8		
Total PL	3.34	2.24	311.16	292.30	232.49	203.09	214.80	220.80	67.88	202.38	96.46	1,846.94 x 10^{11}	PL
Anchovy	1.24	0.88	299.01	249.12	20.44	182.27	212.09	174.77	2.77	199.52	95.18	1,437.31 x 10^{11}	anchovy
Hake	2.10	1.22	12.13	41.10	209.42	20.39	1.44	38.15	29.41	0.59	0.21	356.16 x 10^{11}	hake
Jack mackerel	—	0.14	0.01	2.08	2.63	0.41	0.06	7.87	35.70	0.17	1.05	50.13 x 10^{11}	jack mackerel
Sardine	—	—	0.008	—	—	0.02	1.17	—	—	0.25	—	3.22 x 10^{11}	sardine
Pac. mackerel	—	—	—	—	—	—	0.04	—	—	0.08	—	0.12 x 10^{11}	Pacific mackerel
Total OL	64.56	53.24	67.07	24.21	48.64	20.34	49.25	46.91	121.97	37.20	95.99	629.39 x 10^{11}	OL
Region:													
Percent PL	4.92%	4.03%	79.90%	92.35%	82.70%	91.01%	81.35%	82.48%	35.75%	84.47%	50.12%	Percent PL	74.23%
Percent OL	95.08%	95.97%	20.10%	7.65%	17.30%	8.99%	18.65%	17.52%	64.25%	15.53%	49.88%	Percent OL	25.77%
Regional contribution to													
Total PL	0.18%	0.12%	16.44%	15.90%	12.65%	11.06%	11.68%	12.01%	3.69%	11.01%	5.25%		
Total OL	10.12%	8.34%	11.91%	3.79%	7.62%	3.15%	7.72%	7.35%	19.12%	5.83%	15.04%		
Regional ranked abundance:													
PL	10	11	1	2	3	6	5	4	9	7	8		
OL	4	5	3	10	7	11	6	8	1	9	2		