

## GEOGRAPHICAL AND SEASONAL PATTERNS OF LARVAL FISH SPECIES STRUCTURE IN THE CALIFORNIA CURRENT AREA, 1975

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### ABSTRACT

Analysis of 1,504 plankton tows from the 1975 CalCOFI cruise year yielded information on geographical and temporal patterns among 204 larval fish taxa. These taxa represented the spawn of fishes from a variety of habitats and water-mass affiliations. The larvae of certain commercially valuable pelagic spawning fishes (anchovy, hake, sardine, jack mackerel, and Pacific mackerel) dominated (75.5% of total larvae); these species are treated separately from the less abundant taxa (further separated into continental shelf, oceanic, and mesopelagic categories and taxa) to permit description of underlying hydrographically related distribution patterns within the California Current area.

The composition and species abundance relations of the ichthyoplankton were similar to those reported from 1955-58. Exceptions were decreased relative abundance of sardine and increased proportions of anchovy larvae in 1975 vs 1955-58.

Anchovy, hake, and jack mackerel larvae were most abundant south of Point Conception. Abundances of rockfishes and bathylagids decreased, while those of flatfishes, myctophids, and gonostomatids increased, from north to south and inshore to offshore. Absolute ichthyoplankton abundance varied by a factor of 10 between January-March (maximum) and September-December (minimum). Anchovy, hake, jack mackerel, rockfishes, sciaenids, myctophids, and bathylagids had January-March abundance peaks; myctophids and gonostomatids had July abundance peaks; flatfishes were most abundant from October-December. Regional ichthyoplankton abundance fluctuations and compositions were related to hydrographic regimes.

The area off northern Baja California marked a transition between predominantly cold-water or subarctic-transition zone species with January-March abundance peaks and predominantly eastern tropical Pacific or warm-water species with summer and fall abundance peaks. This transition zone coincides with a persistent lobe of negative wind stress curl (surface-layer convergence) extending to the coast from offshore waters;

this zone may separate biological regimes of California and southern Baja California.

### RESUMEN

Los análisis de 1504 colecciones de plancton correspondientes al crucero CalCOFI de 1975, proporcionan información sobre la distribución en espacio y tiempo de 204 taxones de larvas de peces. La puesta de peces procedentes de una variedad de habitats y masas de agua aparece representada en la diversidad taxonómica larval. Las larvas de peces de importancia comercial y de puesta pelágica, *Engraulis mordax* (anchoa), *Merluccius productus* (merluza), *Sardinops caerulea* (sardina), *Trachurus symmetricus* (jurel), eran dominantes, alcanzando el 75.5% del total. Estas especies se estudian en particular y se separan de las especies menos abundantes, clasificadas bajo características taxonómicas y del habitat (plataforma continental, oceánicas y mesopelágicas), para permitir así la descripción de los tipos de distribución en relación con las características hidrográficas dentro de la región de la Corriente de California.

La composición y abundancia de especies del ictioplancton aparecían similares a las presentadas durante el período 1955-58, excepto que en 1975 disminuye la abundancia de larvas de sardina y aumenta proporcionalmente la cantidad de larvas de anchoa.

Larvas de anchoa, merluza y jurel aparecían menos abundantes al sur de Punta Concepción. La abundancia de Scorpenidae y Bathylagidae disminuía, mientras que los peces planos, Myctophidae y Gonostomidae aumentaban de norte a sur y de la costa hacia mar abierto. La abundancia absoluta de ictioplancton fluctuaba en un factor de 10 entre los períodos de Enero-Marzo (máximo) y Septiembre-Diciembre (mínimo). Anchoa, merluza y jurel, Scorpenidae, Sciaenidae, Myctophidae y Gonostomidae aparecían con máximos de abundancia en Julio, y los peces planos eran más abundantes en el período de Octubre-Diciembre. Fluctuaciones en la abundancia regional y la composición del ictioplancton aparecían relacionadas con el régimen hidrográfico.

La zona frente al norte de Baja California marcaba una transición entre aguas predominantemente frías o de la zona subártica-transición, con máximos de abundancia en el período de Enero-Marzo, y especies

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de aguas cálidas, principalmente del Pacífico tropical oriental, muestran máximos de abundancia en verano y otoño. Esta zona de transición coincide con un lóbulo de remolino persistente de presión eólica negativa (convergencia en el lecho superficial), extendiéndose desde mar afuera hacia la costa. Esta zona puede separar regímenes biológicos de California y la zona sur de Baja California.

## INTRODUCTION

The California Current system is a typical eastern boundary current regime (Wooster and Reid 1963; Hickey 1979). The main current is slow, meandering, broad, and indistinct. Embedded in this current are dynamic mesoscale eddies of uncertain origin (Owen 1980), and the current includes water-mass mixtures of diverse origin. The mixed layer can include waters from the (1) North Pacific central water mass, (2) subarctic water mass, (3) Columbia River Plume, (4) subtropical water mass, (5) Davidson Current (a wintertime surface manifestation of the California Undercurrent), and (6) upwelling processes.

The biota of the area also is complex (McGowan and Miller 1980). Invertebrate "holoplankton" species can often be far from their water-mass centers of distribution because of long-range transport; older holoplankton individuals can be far from the reproductive locus of the population. The ichthyoplankton represents a brief phase in a generally longer life cycle, which is in most cases nektonic. Because larval fishes from pelagic spawn are localized at or near the spawning areas of the adults, the analysis of ichthyoplankton in the California Current area can achieve more advanced and precise localization of communities or biological regimes than can analysis of the holoplankton.

To date, most of the descriptive work from the vast set of stations included in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) has concentrated on regional and seasonal characteristics of single oceanographic properties such as current flow, temperature, salinity, and zooplankton volume. The ichthyoplankton has been described only as single species (anchovy, sardine, jack mackerel, hake, individual mesopelagic fish, flatfish, and rockfish species) on distribution charts covering a variety of years. Aside from one paper on the co-occurrence of anchovy and sardine (Ahlstrom 1967) there have been no attempts to characterize the California Current system biota by means of larval fish assemblages.

In this paper we investigate seasonal and geographical distributions within the diverse larval fish assemblage sampled during 1975. We compare the overall composition of this assemblage with that re-

ported from 1955-58. We then divide the ichthyoplankton into various categories based on adult habitats and analyze seasonal abundance relations of these categories (and of their dominant species) within and between pre-established and arbitrary regional divisions.

We emphasize various nonparametric analytical procedures (outlined in Fager 1963) to describe and compare regional ichthyoplankton assemblages. The procedures and results from this study will serve as a basis for subsequent analyses of and comparisons between data sets from other years in the 1951-81 CalCOFI survey. From such analyses we eventually hope to (1) compare variations in larval fish assemblages with variations of reproductive success of commercially valuable fish species; (2) establish the use of changing ichthyoplankton assemblages as indices of general, sustained, and widespread environmental change; and (3) establish the existence of functional relationships between abundances of major fish species and their invertebrate planktonic prey.

## METHODS

The present data came from the same 1,504 samples used to describe geographical and seasonal patterns of ichthyoplankton and zooplankton distributions in Loeb et al. 1983a. These samples were from standard CalCOFI plankton tows taken with a 1-m diameter net (mesh size, 505  $\mu\text{m}$ ) fished from 0-210 m at basic CalCOFI stations and additional inshore stations. Larval fishes were sorted out, identified to the lowest taxon possible, and counted.

Data were formatted by cruise and standard CalCOFI regions. In 1975, 11 regions were "adequately" sampled; "adequate" means that a region was sampled during at least six one-month cruises and was generally represented by  $> 10$  samples per cruise. All regions were sampled in December, January, March, May, and July, and most were sampled in 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 (Loeb et al. 1983a). Regional data were combined into four latitudinal areas (central California, southern California, northern Baja California, and central Baja California) for broader overviews of patterns of species structure. For region and area locations see Loeb et al. (1983a).

We divide the total ichthyoplankton ("TL") into "PL" (the commercially important pelagic schooling species: anchovy, hake, sardine, jack mackerel, and Pacific mackerel) and "OL" (other larval fish) fractions. These two fractions are treated separately be-

cause abundances of the PL (especially anchovy and hake) mask abundance relations of the 200+ other larval fish taxa. The OL taxa are herein further divided into continental shelf ("shelf"), open-ocean epipelagic ("oceanic"), and "mesopelagic" categories for considerations of the major ichthyoplankton components. The shelf category is further divided into "rockfish" (*Sebastes* spp), "flatfish" (Pleuronectiformes), and "other" categories for consideration of regional and seasonal abundance variations.

Larval fish abundances are presented as mean numbers per 10 m<sup>2</sup> sea-surface area (Kramer et al. 1972) and as estimated absolute abundances for each region (mean numbers per 1 m<sup>2</sup> sea surface multiplied by sea-surface area). These latter estimates are summed to provide the total estimated abundances within the CalCOFI survey area by cruise and for all six cruises. As some categories were excluded (e.g., unidentified larvae) the total larval abundances presented here vary slightly from those in Loeb et al. 1983a. Species lists and abundance information for the total CalCOFI area and for each of the 11 regions during 1975 are on file at the Southwest Fisheries Center, La Jolla, California.

We describe species structure using several nonparametric tests. (A) Between-area and between-region comparisons of species percentage composition are made using the Percent Similarity Index (PSI; Whitaker 1975). PSI values compare two species lists based on the relative proportions of individual species within each list. PSI values may range from 0 (no species in common) to 100 (all species in common, and their proportions identical). PSIs are strongly influenced by abundant species. We define as "high" all PSI values > 60, and as "low" values < 40. (B) Comparisons of rank order of abundance of species between sets of data are made using Kendall's tau and concordance tests (Tate and Clelland 1957). Kendall's tau provides a correlation coefficient that is a measure of the similarity between the order of rankings within two data sets. The concordance test is a nonparametric analysis of variance performed on several sets of species' rankings; it is used to test for similarity (nonrandomness) of species' rankings across data sets.

These techniques are used to show similarities in species structure between geographical regions and between seasons. Similarities may occur in the proportions of individual taxa relative to the total ichthyoplankton and in ranks of abundance of individual taxa.

### **Taxonomic Problems**

The 1975 data include 204 ichthyoplankton taxonomic categories: 104 species and 100 higher-level identifications. While many of the abundant larvae (espe-

cially the myctophids and bathylagids) have been identified to species, many of the coastal larvae have not. Problems are greatest with the scorpaenids (> 50 species are lumped into the *Sebastes* spp category), the *Citharichthys* category (5 species), the sciaenids (> 10 species), and some subtropical forms. Such multispecies groupings, especially within dominant taxa, impose limitations on analysis of species structure, and geographical or seasonal changes in the actual species constituting these groupings may be obscured. This is a relatively minor problem in offshore regions dominated by identifiable mesopelagic species; it is a much greater problem in inshore regions where groupings (primarily *Sebastes* spp, *Citharichthys* spp, and Sciaenidae) are among the dominant taxa. These groupings have increased apparent similarities between and within the inshore and southern regions.

## **RESULTS**

### **Total CalCOFI Area Ichthyoplankton Composition**

The PL contributed 75.5% of the total larval fish captured in 1975. The most abundant PL species were the northern anchovy (*Engraulis mordax*; 58.9%), Pacific hake (*Merluccius productus*; 14.5%), and jack mackerel (*Trachurus symmetricus*; 2.0%) (Table 1). The OL were dominated by mesopelagic fishes (89 taxonomic categories; 16.7% of the area total). Nine species made up over two-thirds of this fraction and 12.1% of the total larvae. These included one gonostomatid (*Vinciguerria lucetia*), three bathylagids (*Leuroglossus stilbius*, *Bathylagus wesethi*, and *B. ochotensis*), and five myctophids (*Triphoturus mexicanus*, *Stenobranchius leucopsarus*, *Protomyctophum crockeri*, *Diogenichthys laternatus* and *Tarletonbeania crenularis*). Continental shelf fishes (92 taxa) made up only 7% of the total; flatfishes (Pleuronectiformes; 3.4%), rockfishes (*Sebastes* spp; 3.1%), and croakers (Sciaenidae; 0.5%) predominated.

### **Geographical Differences in Species Composition**

There were large geographical differences in ichthyoplankton composition. Latitudinal and inshore-offshore differences occurred in the relative abundances of the PL, mesopelagic, shelf, and oceanic fractions, and in the species making up these fractions. The greatest difference was the dominance of the PL south of Point Conception (36.1-92.0% regional totals) versus its relatively low abundance off central California (≤5%) (Table 2). This dominance was due primarily to anchovy and hake, and secondarily to jack mackerel, all of which were rare off central California and had greatest abundances off southern Cali-

TABLE 1  
 Comparison of Relative Abundances of Larval Fishes Taken during 1975 with Those Taken during Annual  
 CalCOFI Surveys 1955-58

	1975		1955		1956		1957		1958	
	% of total	Rank*	% of total	Rank**	% of total	Rank**	% of total	Rank**	% of total	Rank**
<i>Engraulis mordax</i>	58.92	1	39.03	1	33.05	1	29.70	1	45.21	1
<i>Merluccius productus</i>	14.46	2	16.73	2	23.10	2	15.86	2	12.84	2
<i>Sebastes</i> spp	3.12	3	8.17	3	7.14	3	7.39	4	5.27	4
<i>Citharichthys</i> spp	2.79	5	5.68	4	5.79	4	3.20	9	1.46	11
<i>Leuroglossus stilbius</i>	1.46	8	4.21	5	4.56	5	5.98	5	1.07	12
<i>Sardinops sagax</i>	0.13	26	3.93	6	3.80	6	1.99	11	2.51	7
<i>Trachurus symmetricus</i>	2.03	7	3.69	7	1.97	10	4.05	6	1.41	10
<i>Triphoturus mexicanus</i>	2.84	4	3.67	8	2.65	8	3.28	8	3.63	5
<i>Vinciguerria lucetia</i>	2.17	6	3.52	9	2.41	9	11.17	3	12.27	3
<i>Stenobranchius leucopsarus</i>	1.40	9	2.08	10	3.71	7	3.70	7	2.62	6
<i>Diogenichthys laternatus</i>	0.77	13	1.33	11	0.77	13	2.35	10	1.55	8
<i>Bathylagus wesethi</i>	1.05	10	0.90	12	0.52	17	1.29	12	1.54	9
<i>Lampanyctus ritteri</i>	0.40	19	0.55	13	0.47	18	0.56	14	0.68	13
<i>Scomber japonicus</i>	0.005	—	0.54	14	0.37	20	0.38	18	0.28	20
<i>Protomyctophum crockeri</i>	0.78	12	0.51	15	0.45	19	0.29	22	0.39	15
<i>Bathylagus ochotensis</i>	0.98	11	0.36	18	0.55	15	0.22	25	0.34	16
<i>Melamphaes</i> spp	0.24	22	0.22	25	0.26	24	0.27	24	0.28	21
<i>Cyclothone</i> spp	0.63	14	0.43	16	0.20	—	0.58	13	0.62	14
<i>Tarletonbeania crenularis</i>	0.61	15	0.28	21	0.82	12	0.32	21	0.12	—
<i>Argentina sialis</i>	0.05	—	0.23	24	0.32	22	0.28	23	0.06	—
<i>Prionotus</i> spp	0.006	—	—	—	0.60	14	0.55	15	0.29	19
<i>Synodus</i> spp	0.03	—	0.18	—	0.23	25	0.47	17	0.27	23
<i>Pleuronichthys</i> spp	0.06	—	0.29	19	0.27	23	0.12	—	0.04	—
<i>Diaphus theta</i>	0.11	29	0.28	20	0.87	11	0.14	—	0.13	—
Sciaenidae	0.53	16	0.24	23	0.02	—	0.06	—	0.30	18
<i>Symphurus</i> spp	0.05	—	0.02	—	0.34	21	0.32	20	0.05	—
<i>Ceratoscopelus townsendi</i>	0.13	26	0.12	—	0.05	—	0.53	16	0.31	17
<i>Symbolophorus californiense</i>	0.29	20	0.18	—	0.11	—	0.33	19	0.27	22
<i>Icichthys lockingtoni</i>	0.09	30	0.39	17	0.22	—	0.16	—	0.10	—
<i>Peprilus simillimus</i>	0.05	—	0.26	22	0.15	—	0.16	—	0.02	—
<i>Tetragonurus</i> spp	0.03	—	0.14	—	0.53	16	0.14	—	0.01	—
<i>Stomias</i> spp	0.13	26	0.11	—	0.02	—	0.05	—	0.26	24
<i>Hygophum</i> spp	0.03	—	0.11	—	0.05	—	0.16	—	0.22	25
<i>Diogenichthys atlanticus</i>	0.49	17	0.20	—	0.19	—	0.16	—	0.14	—
Other larvae	3.14		1.42		3.41		4.10		3.44	

\*Ranks provided for first 30

\*\*Ranks provided for first 25

1955-58 data from Ahlstrom (1965); and Moser and Ahlstrom (1970) based on total numbers of larvae caught (pooled cruises) each year, 1975 data based on summed regional abundances (mean abundances corrected for region area) from six cruises; taxonomic categories adjusted (i.e., species lumped) to conform with earlier data sets.

fornia and northern Baja California (Tables 2, 3). The other PL species (sardine and Pacific mackerel) were caught in a few regions off Baja California and were comparatively rare (< 2% PL in each region).

As expected, both abundances and relative proportions of PL and shelf forms decreased, and those of mesopelagic and oceanic forms increased, with distance from shore. Within the PL, relative proportions of anchovy larvae generally decreased, while those of hake and jack mackerel increased, from inshore to offshore and seaward regions (Table 3).

Within the OL, major contributors to the shelf and mesopelagic categories had marked geographical differences (Table 2). Among the shelf forms, abundances of rockfishes decreased, and flatfishes increased, from north to south; both decreased offshore. Rockfishes dominated the OL of California inshore regions 4 and 7 (41.7-46.7% total OL) and were relatively abundant in northern Baja California region 11 (26.6%); they were relatively rare ( $\leq$  3.9%) in other Baja California regions. Flatfish larvae were most abundant off Baja California in Viscaïno Bay

TABLE 2  
**Percentage Contribution of Major Taxonomic Categories to the Total Ichthyoplankton Collected in Each of 11 CalCOFI Regions and to the Total (Pooled Regions) 1975 CalCOFI Survey Area**

Taxonomic Category	Area: Region:	Central California		Southern California			Northern Baja California				Central Baja California		Total
		4 (Inshore)	5 (Offshore)	7 (Inshore)	8 (Offshore)	9 (Seaward)	11 (Inshore)	12 (Bay)	13 (Offshore)	14 (Seaward)	16 (Inshore)	17 (Offshore)	
PL		5.01	4.09	82.72	91.94	83.15	91.06	81.49	82.84	36.11	85.47	59.12	75.56
Mesopelagic taxa		42.01	81.05	7.04	5.84	15.12	4.31	2.15	16.49	60.91	6.91	33.80	16.67
Myctophidae		22.42	46.40	2.10	2.55	8.42	2.46	1.57	9.37	25.91	4.85	20.18	8.66
Bathylagidae		18.44	23.60	4.62	2.45	3.45	0.96	0.18	2.30	9.70	0.50	0.89	3.65
Gonostomatidae		0.22	1.37	0.03	0.20	0.98	0.28	0.14	3.00	19.44	1.12	10.83	2.97
Others		0.93	9.68	0.29	0.64	2.27	0.61	0.26	1.82	5.86	0.44	1.90	1.49
Shelf taxa		52.85	14.45	10.23	2.20	1.50	4.60	16.35	0.53	2.77	7.55	7.03	7.58
Rockfishes		44.32	7.41	7.21	1.61	0.57	2.38	0.72	0.09	0.06	0.57	0.36	3.13
Flatfishes		3.71	6.37	0.80	0.34	0.51	0.92	14.39	0.37	2.47	3.95	5.51	3.14
Sciaenids		2.36	—	1.57	0.02	—	0.66	0.50	—	—	0.57	0.65	0.52
Others		2.46	0.67	0.65	0.23	0.42	0.64	0.74	0.07	0.24	2.46	0.51	0.79
Oceanic taxa		0.13	0.41	0.006	0.03	0.23	0.03	0.01	0.14	0.21	0.07	0.05	0.10
Total larval abundance (x 10 <sup>13</sup> )		0.68	0.55	3.78	3.16	2.81	2.23	2.64	2.68	1.90	2.40	1.92	24.76

Estimated total abundances derived from summation of mean regional abundances adjusted for region area.

TABLE 3  
**The 18 Most Abundant Larval Fish Taxa (Including the 10 Most Abundant Species Identifications) in Order of Ranked Abundance, and Their Percentage Contribution to the Total Ichthyoplankton within Each of 11 CalCOFI Regions, 1975**

Central California		Region 4 (inshore)		Region 5 (offshore)		
Rank		no/10m <sup>2</sup>	%	no/10m <sup>2</sup>	%	
1	<i>Sebastes</i> spp	441.6	40.2	<i>Stenobranchius leucopsarus</i>	97.5	17.5
2	<i>Stenobranchius leucopsarus</i>	142.2	12.9	<i>Bathylagus ochotensis</i>	87.2	15.6
3	<i>Leuroglossus stilbius</i>	93.6	8.5	<i>Tarletonbeania crenularis</i>	67.3	12.1
4	<i>Bathylagus ochotensis</i>	92.7	8.4	<i>Sebastes</i> spp	30.7	5.5
5	<i>Tarletonbeania crenularis</i>	74.4	6.8	<i>Protomyctophum crockeri</i>	30.5	5.5
6	<i>Merluccius productus</i>	34.7	3.2	<i>Leuroglossus stilbius</i>	28.1	5.0
7	<i>Sebastes jordani</i>	32.7	3.0	<i>Diaphus</i> spp	22.8	4.1
8	Sciaenidae	25.9	2.4	<i>Melamphaes</i> spp	19.2	3.4
9	<i>Engraulis mordax</i>	20.4	1.9	<i>Citharichthys stigmaeus</i>	16.5	3.0
10	<i>Citharichthys stigmaeus</i>	15.3	1.4	<i>Citharichthys sordidus</i>	13.5	2.4
11	<i>Protomyctophum crockeri</i>	13.3	1.2	<i>Merluccius productus</i>	12.3	2.2
12	<i>Sebastes paucispinis</i>	10.9	1.0	<i>Chauliodus macouni</i>	10.1	1.8
13	<i>Bathylagus pacificus</i>	10.1	0.9	<i>Sebastes paucispinis</i>	10.0	1.8
14	<i>Parophrys vetulus</i>	8.3	0.8	<i>Lampanyctus ritteri</i>	9.5	1.7
15	<i>Icichthys lockingtoni</i>	5.8	0.5	<i>Engraulis mordax</i>	9.0	1.6
16	<i>Citharichthys sordidus</i>	5.7	0.5	<i>Diogenichthys atlanticus</i>	7.5	1.3
17	<i>Citharichthys</i> spp	5.7	0.5	<i>Lampanyctus</i> spp	7.5	1.3
18	<i>Diaphus theta</i>	5.5	0.5	<i>Icichthys lockingtoni</i>	7.2	1.3
	94.6% of total larvae			87.1% of total larvae		

Ranks based on summed mean abundances (numbers per 10 m<sup>2</sup> sea-surface area) of each taxon from six cruises within each region.

Continued on next page

TABLE 3 (continued)

Southern California						
Region 7 (inshore)			Region 8 (offshore)			
Rank		no/10m <sup>2</sup>	%		no/10m <sup>2</sup>	%
1	<i>Engraulis mordax</i>	4333.1	79.5	<i>Engraulis mordax</i>	6016.0	78.3
2	<i>Sebastes</i> spp	349.7	6.4	<i>Merluccius productus</i>	997.7	13.0
3	<i>Leuroglossus stilbius</i>	226.3	4.1	<i>Sebastes</i> spp	119.9	1.6
4	<i>Merluccius productus</i>	177.0	3.2	<i>Leuroglossus stilbius</i>	117.3	1.5
5	<i>Stenobranchius leucopsarus</i>	87.8	1.6	<i>Stenobranchius leucopsarus</i>	59.0	0.8
6	Sciaenidae	81.0	1.5	<i>Bathylagus ochotensis</i>	58.8	0.8
7	<i>Bathylagus ochotensis</i>	24.7	0.4	<i>Trachurus symmetricus</i>	49.3	0.6
8	<i>Sebastes jordani</i>	20.5	0.4	<i>Protomyctophum crockeri</i>	37.0	0.5
9	<i>Sebastes paucispinis</i>	16.8	0.3	<i>Tarletonbeania crenularis</i>	28.2	0.4
10	<i>Citharichthys stigmatæus</i>	13.1	0.2	<i>Citharichthys stigmatæus</i>	17.7	0.2
11	Gobiidae	9.2	0.2	<i>Lampanyctus ritteri</i>	15.2	0.2
12	<i>Argyrolepecus</i> spp	8.8	0.2	<i>Argyrolepecus</i> spp	14.6	0.2
13	<i>Citharichthys stigmatæus</i>	8.0	0.1	<i>Lampanyctus</i> spp	14.0	0.2
14	<i>Tarletonbeania crenularis</i>	7.8	0.1	<i>Triphoturus mexicanus</i>	13.5	0.2
15	<i>Protomyctophum crockeri</i>	6.7	0.1	<i>Bathylagus wesethi</i>	12.5	0.2
16	<i>Sebastes levis</i>	6.0	0.1	<i>Chauliodus macouni</i>	12.2	0.2
17	<i>Parophrys vetulus</i>	5.6	0.1	<i>Cyclothone</i> spp	8.0	0.1
18	<i>Pleuronichthys verticalis</i>	5.5	0.1	<i>Diaphus theta</i>	6.3	0.1
	98.6% of total larvae			99.1% of total larvae		
Southern California						
Region 9 (seaward)						
Rank		no/10m <sup>2</sup>	%			
1	<i>Merluccius productus</i>	2119.6	74.9			
2	<i>Engraulis mordax</i>	206.8	7.3			
3	<i>Stenobranchius leucopsarus</i>	62.3	2.2			
4	<i>Bathylagus ochotensis</i>	36.7	1.3			
5	<i>Protomyctophum crockeri</i>	36.6	1.3			
6	<i>Leuroglossus stilbius</i>	30.7	1.1			
7	<i>Bathylagus wesethi</i>	27.0	1.0			
8	<i>Trachurus symmetricus</i>	26.7	0.9			
9	<i>Diogenichthys atlanticus</i>	23.3	0.8			
10	<i>Tarletonbeania crenularis</i>	21.3	0.8			
11	<i>Lampanyctus ritteri</i>	20.5	0.7			
12	<i>Symbolophorus californiense</i>	17.8	0.6			
13	<i>Sebastes</i> spp	14.8	0.5			
14	<i>Diaphus</i> spp	13.2	0.5			
15	<i>Argyrolepecus</i> spp	11.3	0.4			
16	<i>Melamphaes</i> spp	10.7	0.4			
17	<i>Cyclothone</i> spp	10.6	0.4			
18	<i>Chauliodus macouni</i>	10.1	0.4			
	95.5% of total larvae					
Northern Baja California						
Region 11 (inshore)			Region 12 (inshore-Viscaino Bay)			
Rank		no/10m <sup>2</sup>	%		no/10m <sup>2</sup>	%
1	<i>Engraulis mordax</i>	5749.8	81.8	<i>Engraulis mordax</i>	5826.8	80.5
2	<i>Merluccius productus</i>	643.2	9.1	<i>Citharichthys</i> spp	709.6	9.8
3	<i>Sebastes</i> spp	163.8	2.3	<i>Citharichthys xanthostigma</i>	194.2	2.7
4	<i>Triphoturus mexicanus</i>	88.8	1.3	<i>Triphoturus mexicanus</i>	73.0	1.0
5	<i>Leuroglossus stilbius</i>	49.7	0.7	<i>Citharichthys stigmatæus</i>	55.2	0.8
6	Sciaenidae	44.1	0.6	<i>Sebastes</i> spp	45.7	0.6
7	<i>Citharichthys</i> spp	30.9	0.4	<i>Merluccius productus</i>	39.4	0.5
8	<i>Protomyctophum crockeri</i>	27.9	0.4	<i>Citharichthys sordidus</i>	35.9	0.5
9	<i>Lampanyctus ritteri</i>	20.6	0.3	Sciaenidae	34.7	0.5
10	<i>Argyrolepecus</i> spp	20.0	0.3	<i>Sardinops sagax</i>	32.2	0.4
11	Clinidae	16.5	0.2	<i>Peprilus simillimus</i>	20.6	0.3
12	<i>Trachurus symmetricus</i>	13.1	0.2	<i>Paralichthys californicus</i>	18.6	0.3
13	Gobiidae	11.5	0.2	<i>Pleuronichthys verticalis</i>	9.6	0.1
14	<i>Lampanyctus</i> spp	10.7	0.2	<i>Protomyctophum crockeri</i>	9.3	0.1
15	<i>Vinciguerria lucetia</i>	10.1	0.1	<i>Lampanyctus ritteri</i>	9.0	0.1
16	<i>Bathylagus ochotensis</i>	9.9	0.1	<i>Leuroglossus stilbius</i>	8.7	0.1
17	<i>Citharichthys stigmatæus</i>	9.0	0.1	<i>Argentina sialis</i>	8.2	0.1
18	Cottidae	7.9	0.1	<i>Diogenichthys atlanticus</i>	7.7	0.1
	98.4% of total larvae			98.5% of total larvae		

Continued on next page

TABLE 3 (continued)  
**The 18 Most Abundant Larval Fish Taxa (Including the 10 Most Abundant Species Identifications) in Order of Ranked Abundance, and Their Percentage Contribution to the Total Ichthyoplankton within Each of 11 CalCOFI Regions, 1975**

Northern Baja California						
Region 13 (offshore)			Region 14 (seaward)			
Rank		no/10m <sup>2</sup>	%		no/10m <sup>2</sup>	%
1	<i>Engraulis mordax</i>	2454.4	65.5	<i>Trachurus symmetricus</i>	361.7	19.0
2	<i>Merluccius productus</i>	535.8	14.3	<i>Merluccius productus</i>	297.9	15.6
3	<i>Triphoturus mexicanus</i>	199.6	5.3	<i>Vinciguerria lucetia</i>	269.1	14.1
4	<i>Trachurus symmetricus</i>	110.6	3.0	<i>Triphoturus mexicanus</i>	234.5	12.3
5	<i>Vinciguerria lucetia</i>	77.7	2.1	<i>Bathylagus wesethi</i>	171.6	9.0
6	<i>Bathylagus wesethi</i>	54.8	1.5	<i>Cyclothone</i> spp	68.2	3.6
7	<i>Protomyctophum crockeri</i>	46.9	1.2	<i>Diogenichthys atlanticus</i>	60.0	3.1
8	<i>Argyropelecus</i> spp	20.7	0.6	<i>Protomyctophum crockeri</i>	47.9	2.5
9	<i>Diogenichthys atlanticus</i>	20.6	0.6	<i>Citharichthys xanthostigma</i>	38.7	2.0
10	<i>Lampanyctus ritteri</i>	19.6	0.5	<i>Symbolophorus californiense</i>	34.6	1.8
11	<i>Cyclothone</i> spp	16.3	0.4	<i>Argyropelecus</i> spp	32.6	1.7
12	<i>Bathylagus ochotensis</i>	16.0	0.4	<i>Lampanyctus ritteri</i>	31.9	1.7
13	<i>Symbolophorus californiense</i>	14.6	0.4	<i>Engraulis mordax</i>	28.4	1.5
14	<i>Lampanyctus</i> spp	14.1	0.4	<i>Ceratoscopelus townsendi</i>	19.4	1.0
15	<i>Melamphaes</i> spp	12.7	0.3	<i>Stomias</i> spp	15.7	0.8
16	<i>Leuroglossus stilbius</i>	11.6	0.3	<i>Melamphaes</i> spp	14.8	0.8
17	<i>Citharichthys sigmaeus</i>	9.4	0.2	<i>Diogenichthys laternatus</i>	13.6	0.7
18	<i>Ceratoscopelus townsendi</i>	8.1	0.2	<i>Lampanyctus</i> spp	12.3	0.6
	97.2% of total larvae			91.8% of total larvae		
Central Baja California						
Region 16 (inshore)			Region 17 (offshore)			
Rank		no/10m <sup>2</sup>	%		no/10m <sup>2</sup>	%
1	<i>Engraulis mordax</i>	4079.9	83.9	<i>Engraulis mordax</i>	1439.5	58.3
2	<i>Triphoturus mexicanus</i>	166.0	3.4	<i>Vinciguerria lucetia</i>	239.0	9.7
3	<i>Citharichthys</i> spp	135.0	2.8	<i>Triphoturus mexicanus</i>	225.9	9.2
4	<i>Diogenichthys laternatus</i>	53.3	1.1	<i>Diogenichthys laternatus</i>	187.9	7.6
5	<i>Vinciguerria lucetia</i>	43.2	0.9	<i>Citharichthys</i> spp	118.0	4.8
6	<i>Sardinops sagax</i>	41.6	0.9	<i>Argyropelecus</i> spp	26.8	1.1
7	Sciaenidae	27.8	0.6	<i>Lampanyctus</i> spp	21.6	0.9
8	<i>Sebastes</i> spp	22.1	0.4	<i>Cyclothone</i> spp	19.1	0.8
9	<i>Leuroglossus stilbius</i>	18.7	0.4	<i>Ceratoscopelus</i> spp	16.0	0.6
10	<i>Sarda chiliensis</i>	17.5	0.4	Sciaenidae	16.0	0.6
11	<i>Hypsoblennius</i> spp	16.1	0.3	<i>Trachurus symmetricus</i>	13.4	0.5
12	<i>Chromis punctipinnis</i>	15.5	0.3	<i>Bathylagus wesethi</i>	12.4	0.5
13	Serranidae	14.9	0.3	<i>Diogenichthys atlanticus</i>	9.7	0.4
14	<i>Etropus</i> spp	12.8	0.3	<i>Gonichthys tenuiculus</i>	9.3	0.4
15	<i>Citharichthys xanthostigma</i>	12.5	0.3	<i>Stomias</i> spp	9.1	0.4
16	<i>Merluccius productus</i>	11.9	0.2	<i>Sebastes</i> spp	8.9	0.4
17	<i>Symphurus</i> spp	11.2	0.2	<i>Hippoglossina stomata</i>	8.9	0.4
18	<i>Argyropelecus</i> spp	10.2	0.2	<i>Bathylagus pacificus</i>	8.0	0.3
	96.9% of total larvae			96.9% of total larvae		

region 12 (77.8% OL), inshore region 16 (27.7%), and offshore region 17 (13.5%); they were relatively rare ( $\leq 10\%$  OL) in northern regions. Sciaenid larvae were most abundant (7.4-9.1% OL) in southern California and northern Baja California inshore regions 7 and 11. Among the mesopelagic forms, abundances of Bathylagidae decreased, while those of Myctophidae and Gonostomatidae increased, from north to south and inshore to offshore regions (Table 2). Bathylagid larvae were relatively abundant off central and southern California (19.4-30.4% OL) and rare off Baja California (1.0-15.2%); gonostomatids were rare (0.2-5.8% OL) in all California regions and inshore Baja Califor-

nia regions 11, 12, and 16 but were relatively abundant (17.4-49.4%) in Baja California offshore and seaward regions 13, 14, and 17.

Geographical differences in ichthyoplankton composition were tested using PSI comparisons of total species lists (six cruises combined) from each area and region. We found a high degree of similarity in species percentage composition of the total ichthyoplankton between areas and regions south of Point Conception (Table 4A). High PSI values (ranging from 60.0 to 90.0) resulted from overall comparisons of the southern California and northern and central Baja California areas and from comparisons of the regions

TABLE 4  
 Percent Similarity Index (PSI) Values for Between-Area and Between-Region Comparisons: (A) Total Ichthyoplankton and (B) Other Larvae (OL)

(A) Total ichthyoplankton PSI values				Region											
	Area				CC	SC			NBC				CBC		
	SC	NBC	CBC		5	7	8	9	11	12	13	14	16	17	
CC	17.97	12.05	6.63	CC	4	52.15	21.54	12.16	15.53	11.51	6.11	9.01	9.19	4.72	5.27
SC		74.29	62.15		5		16.88	11.71	18.50	9.33	4.97	10.68	16.10	3.79	6.29
NBC			77.08	SC	7			86.92	15.46	88.44	82.68	70.50	6.80	82.40	60.46
					8				27.16	92.13	80.84	82.42	18.72	80.60	61.20
					9					20.82	10.16	30.47	27.95	10.12	12.19
				NBC	11						85.11	78.94	14.69	86.48	63.12
					12							68.71	6.53	87.96	66.33
					13								34.99	71.96	70.33
					14									8.84	27.56
				CBC	16										69.31

(B) Other larvae PSI values				Region											
	Area				CC	SC			NBC				CBC		
	SC	NBC	CBC		5	7	8	9	11	12	13	14	16	17	
CC	69.02	20.69	10.22	CC	4	50.76	70.36	59.44	43.05	47.81	11.73	10.69	5.62	11.58	6.36
SC		34.88	19.45		5		29.26	57.44	62.54	29.17	13.46	23.98	16.25	9.94	8.02
NBC			62.28	SC	7			56.97	28.56	55.54	14.79	9.68	6.02	17.15	7.60
					8				62.78	53.30	14.80	31.57	23.14	15.78	14.86
					9					37.40	13.08	46.40	37.94	16.13	16.85
				NBC	11						27.33	42.17	36.16	39.45	34.20
					12							14.10	14.71	42.19	25.12
					13								69.71	40.13	49.53
					14									36.34	55.67
				CBC	16										58.66

Based on pooled (6 cruises) species lists for each area and region, 1975. CC = central California; SC = southern California; NBC = northern Baja California; CBC = central Baja California.

within each of these areas (Table 4A). Low PSI values (< 25) resulted from comparisons of the total species lists of regions and areas north and south of Point Conception and reflect the dominance of the PL species south of Point Conception. When PL species were excluded and comparisons were made between the relative proportions of the OL, high PSI values (62.3-69.0) were found for comparisons between the central and southern California areas and between the northern and central Baja California areas; low PSI values (10.2-34.9) were found for comparisons between the California and Baja California areas (Table 4B). Aside from dominance by the PL, the species proportions of the southern California ichthyoplankton were dissimilar to those of the northern and central Baja California areas, but were fairly similar to those of central California. Highest between-region OL PSI values occurred between inshore regions 4-7 (70.4) and offshore and seaward regions 5-9 (62.5) and 8-9 (62.8) of central and southern California and between offshore and seaward regions 13-14 (69.7) of northern Baja California (Table 4B). These high PSI values reflect similarities in proportions of the dominant shelf and mesopelagic taxa (Table 3) in these regions.

Geographical differences in taxonomic composition and relative abundance were tested using Kendall's tau test comparisons of the rank order of abundances

of the 10 most abundant taxa (six cruises pooled) within each area and region (Table 3). All comparisons that included the PL in the rankings supported ( $P > 0.10$ ) the null hypothesis of no agreement of species rank order of abundance. When the PL were excluded, significant agreement ( $P < 0.05$ ) of rank order of abundance among the 10 most abundant OL taxa occurred between regions 4-7, 4-8, 5-8, and 5-9 off central and southern California and between regions 13-14 off northern Baja California.

### Seasonal Differences in Ichthyoplankton Species Structure

The ichthyoplankton underwent large seasonal abundance fluctuations because of seasonal spawning of the main PL species (Figure 1). Maximum areawide abundances of anchovy, hake, and jack mackerel occurred in January and March, during which time the PL made up 84% of the total larvae (TL). PL also dominated the ichthyoplankton during May (67% TL). Shelf forms were most abundant during January and March because of peak abundances of rockfish larvae, but because of PL dominance they made up only 4% (rockfishes 3%) of the total. Sciaenids had a January abundance peak (0.5% TL). Lower, relatively constant numbers of shelf forms occurred from May to October-November, and flatfishes predominated (8-



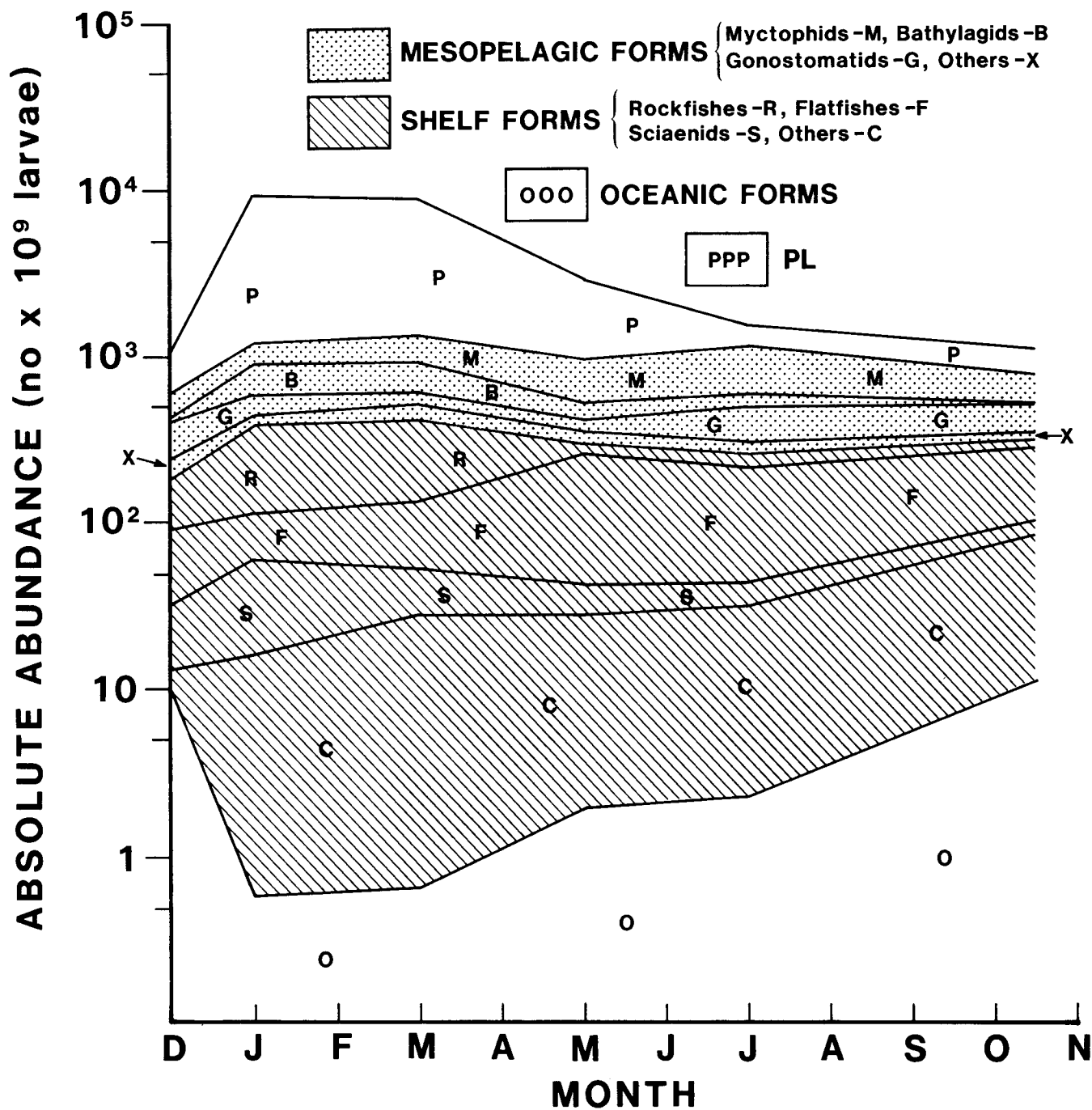


Figure 1. Seasonal abundance fluctuations of major ichthyoplankton categories in the CalCOFI area (all regions combined) during 1975. Categories include PL (anchovy, hake, jack mackerel, sardine, Pacific mackerel); mesopelagic forms (myctophids, bathylagids, gonostomatids, others); shelf forms (rockfishes, flatfishes, sciaenids, others); and oceanic forms. Abundances expressed as estimated absolute numbers  $\times 10^9$  of larvae in the survey area during each cruise. Log scale is used to depict simultaneous abundance fluctuations of forms representing a wide range of relative abundances.

16% TL). Other shelf taxa were most abundant during October (7% TL). Mesopelagic forms had two abundance peaks caused by increased spawning of myctophids and bathylagids during January and March, and of myctophids and gonostomatids during July. Because of decreased PL abundances, mesopelagic

species dominated the ichthyoplankton in July and October-November (57% and 40% TL), and were about equal to the PL in December (mesopelagics 39%; PL 43%). Oceanic species were most abundant (1% TL) during October-November and December.

Each region had seasonal changes in abundance and

relative proportions of major taxa (Figures 2, 3) and species. Maximum PL abundances within all regions occurred between January and May because of peak spawning of anchovy, hake, and jack mackerel; these larvae dominated the ichthyoplankton of all regions south of Point Conception for part or all of this period. Dominance was greatest in inshore regions where the PL made up 80-96% of the total larvae caught from January to May (and July in southern California region 7). PL dominance in offshore regions was restricted to January and March in southern California regions 8 and 9 and northern Baja California region 13 (84-97% TL), and to March in northern and central Baja California regions 14 and 17 (72-84% TL). Seasonal abundance fluctuations of the PL are treated in greater detail in Loeb et al. (1983a).

Seasonal and regional patterns of OL composition and abundance relations were complex. However, four general patterns can be established based on regional similarities of overall dominant taxa. These occur between (1) inshore central and southern California and northern Baja California regions 4, 7, and 11; (2) offshore central and southern California regions 5, 8, and 9; (3) Viscaïno Bay and central Baja California inshore regions 12 and 16; and (4) offshore Baja California regions 13, 14, and 17 (Figures 2, 3).

*California and northern Baja California inshore regions 4, 7, and 11.* OL abundances in the California and northern Baja California inshore regions were elevated from December to March and then (except in region 7 during October) decreased to low and relatively constant levels for the rest of the year. Maximum spring abundances occurred during January and March and were due to large numbers of rockfish, bathylagid, and myctophid larvae (64.6-94.7% OL within each region). Major contributing taxa were *Sebastes* spp, the bathylagids *Leuroglossus stilbius* and *Bathylagus ochotensis*, and myctophids *Stenobranchius leucopsarus* (regions 4 and 7) and *Protomyctophum crockeri* (regions 7 and 11). Abundances of all major categories (except myctophids in region 11) decreased in May and, except for flatfishes, remained low for the rest of the year. In region 11 myctophids had a July abundance maximum dominated by *Triphoturus mexicanus*. Large regional differences occurred in the composition and proportions of major taxa from May to November. Flatfish abundance peaks occurred during October-November in all three regions and were primarily due to large numbers of *Citharichthys* spp, *C. stigmaeus*, *C. sordidus*, and (in region 4) *Parophrys vetulus*. Flatfish abundance was most extreme in region 7 during October, when maximum OL abundance (81% because of flatfishes) occurred. Flat-

fishes made up 25.5% of the October OL in region 11 and 19.6% and 34.6% of the November OL in regions 4 and 7, respectively.

*Central and southern California offshore and seaward regions 5, 8, and 9.* OL abundances in California offshore and seaward regions were elevated during January and March (and May in regions 5 and 9) primarily because of peak spawning of myctophids and bathylagids. Five species—*Leuroglossus stilbius* and *Bathylagus ochotensis* (Bathylagidae) and *Stenobranchius leucopsarus*, *Protomyctophum crockeri*, and *Tarletonbeania crenularis* (Myctophidae)—were consistently abundant and made up 37.8%-70.5% of the OL in each region during this period. Rockfish larvae were also abundant during January and March in regions 5 and 8 (9.0-26.8% OL) and during May in region 9 (6.3%). OL abundances in all three regions decreased from May to October-November, and species composition and relative proportions varied with region and cruise. Flatfishes (*Citharichthys* spp, *C. stigmaeus*, and *C. sordidus*) were most abundant during November (region 8, 24.0%) and December (regions 5 and 9, 25.6% and 12.2% OL, respectively). Oceanic forms were most abundant in region 8 during December (2.3% OL) and in region 9 during November and December (3.6-4.0%).

*Viscaïno Bay and central Baja California inshore regions 12 and 16.* Flatfishes dominated region 12 OL throughout the year (51.6-83.9% within each cruise). Flatfishes dominated region 16 OL during December (48.5%) and were major contributors (31.9-43.0%) during May and October; myctophids dominated during January, May, and July (40.3-52.7%); other shelf forms dominated in October (39.8%). In contrast to the northern inshore regions, January and March OL abundances were relatively low; maximum numbers of rockfishes, bathylagids (primarily *Leuroglossus stilbius*), and sciaenids (in region 12) occurred during this time. Greatest OL abundances occurred during May and July in region 12, and July and October in region 16 because of maximum numbers of flatfishes (primarily *Citharichthys* spp, *C. xanthostigma*, *C. sordidus*, *C. stigmaeus*, *Paralichthys californicus*, and *Symphurus* sp); myctophids (primarily *Triphoturus mexicanus* in region 12, *T. mexicanus* and *Diogenichthys laternatus* in region 16); gonostomatids (in region 16, *Vinciguerria lucetia*); sciaenids (region 16); and other shelf taxa (*Peprilus simillimus* in region 12, *Chromis punctipinnis*, Serranidae, *Etropus* sp, and *Chloroscombrus* sp in region 16). The peak July OL abundances in Viscaïno Bay were the highest for the entire CalCOFI area during 1975; the July and October abundances of other shelf taxa in region 16 were greater than in any other region during the year.

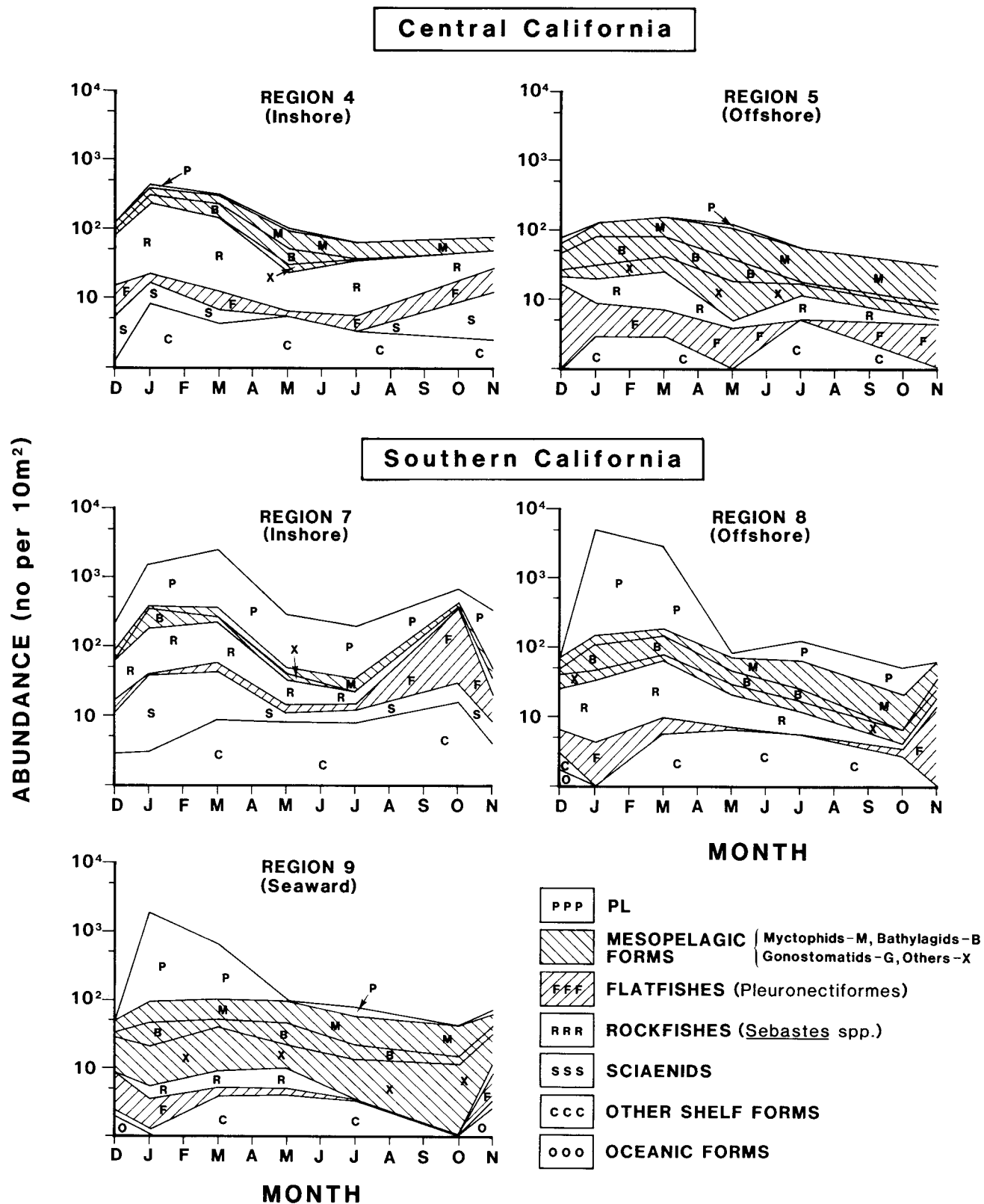


Figure 2. Seasonal abundance fluctuations of major ichthyoplankton categories within CalCOFI regions 4, 5, 7, 8, and 9 during 1975. Categories include PL (anchovy, hake, jack mackerel, sardine, Pacific mackerel); mesopelagic forms (myctophids, bathylagids, gonostomatids, others); shelf forms (rockfishes, flatfishes, sciaenids, others); and oceanic forms. Abundances are expressed as mean numbers of larvae per 10 m<sup>2</sup> sea-surface area during each cruise. Log scale is used to depict simultaneous fluctuations of forms representing a wide range of relative abundances.

**Northern Baja California**

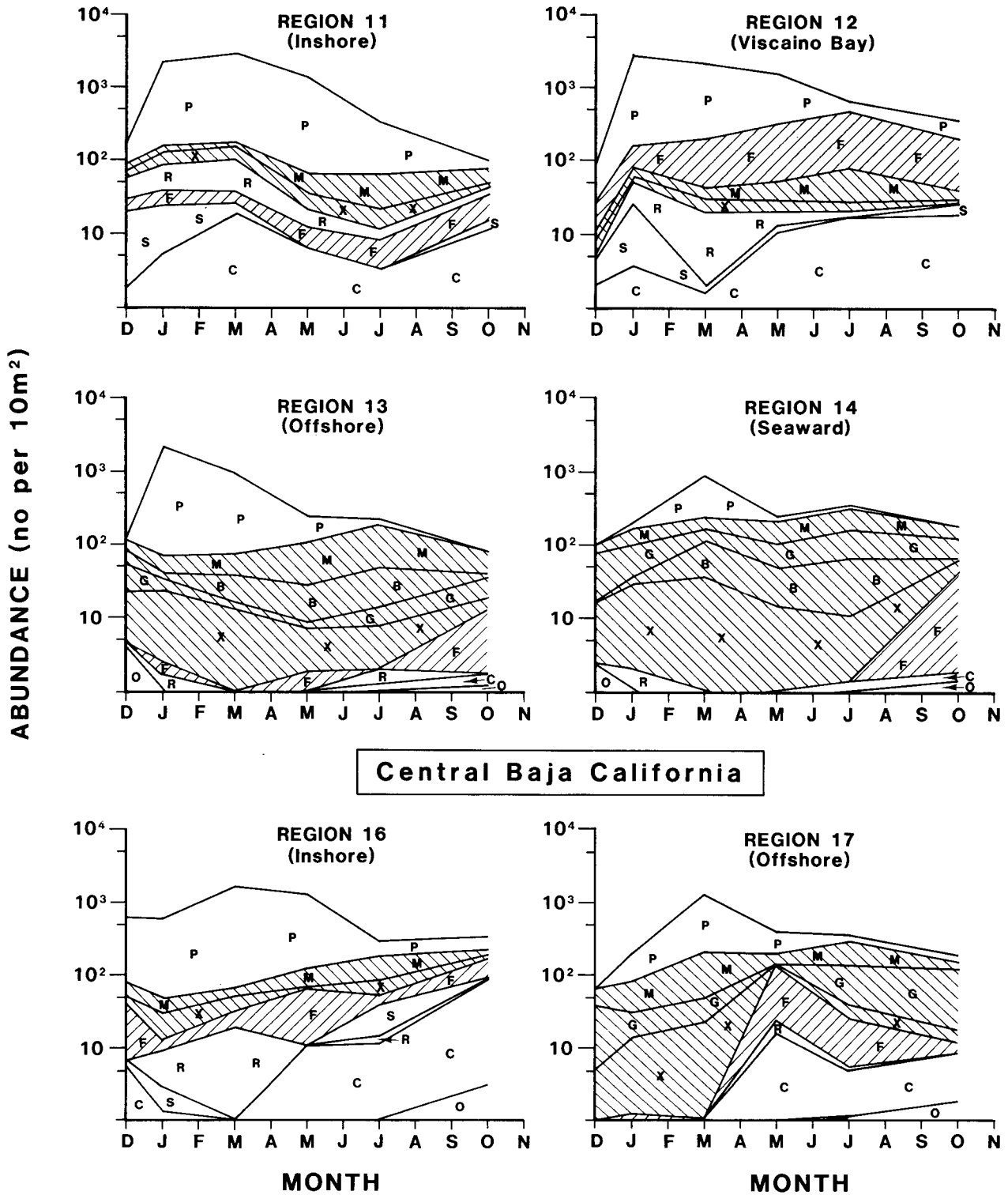


Figure 3. Seasonal abundance fluctuations of major ichthyoplankton categories within CalCOFI regions 11-14, 16, and 17 during 1975. Categories include PL (anchovy, hake, jack mackerel, sardine, Pacific mackerel); mesopelagic forms (myctophids, bathylagids, gonostomatids, others); shelf forms (rockfishes, flatfishes, sciaenids, others); and oceanic forms. Abundances are expressed as mean numbers of larvae per 10 m<sup>2</sup> sea-surface area during each cruise. Log scale is used to depict simultaneous fluctuations of forms representing a wide range of relative abundances.

Northern central Baja California offshore and seaward regions 13, 14, and 17. OL abundances in the Baja California offshore and seaward regions increased from relatively low December-January values to July maxima because of peak abundances of myctophids (mostly *Triphoturus mexicanus*: 38.0-62.9% OL) and, in regions 14 and 17, high gonostomatid abundances (21.4-27.0%; primarily *Vinciguerria lucetia*). Bathylagids (primarily *Bathylagus wesethi*) were most abundant in regions 13 and 14 from March to July (13.0-32.4%); flatfishes were rare or absent in these two regions except during October (13.9% region 13 OL, primarily *Citharichthys stigmaeus* and *C. sordidus*; 26.0% region 14 OL, primarily *C. xanthostigma* and *Symphurus* sp). Because region 17 was undersampled during March and May (5 samples total) little can be determined about the OL during that time. Flatfishes, rockfishes, and sciaenids were abundant in the one May sample; relatively large numbers of flatfishes (6.7% OL, primarily *Citharichthys* spp) were also collected during July. Oceanic forms were most abundant in regions 13 and 14 during December (2.1-3.3%) and in region 17 during October (1.2%).

#### Within- and Between-Region Comparisons of Ichthyoplankton Species Structure

Seasonal changes in ichthyoplankton composition and abundance relations are reflected by PSI values resulting from between-cruise comparisons of species lists. PSI values from comparisons of the total ichthyoplankton and of the OL fraction (all regions combined) were highest (91 and 73, respectively) for January and March cruise comparisons, and lowest (30-41) for January and March vs July and October-November comparisons. These indicate a marked shift in relative proportions of both PL and OL species between spring and summer/fall. These changes were primarily due to decreased abundances of the main PL species (anchovy, hake, and jack mackerel), rockfishes (*Sebastes* spp), *Leuroglossus stilbius* and *Bathylagus ochotensis* (Bathylagidae), and *Stenobrachius leucopsarus* (Myctophidae), and increased abundances of *Triphoturus mexicanus* (Myctophidae), *Vinciguerria lucetia* (Gonostomatidae), and flatfishes (primarily *Citharichthys* spp) during July and October-November. Kendall's concordance test of the rank order of abundance of the 10 most abundant species taken during each cruise showed significant agreement ( $P < 0.01$ ) of rank order of abundance throughout the year. This indicates that despite marked seasonal changes in relative proportions, the same abundant taxa tended to dominate the ichthyoplankton throughout the year.

Within each region, marked seasonal shifts in rela-

TABLE 5  
 Range and Mean of Percent Similarity Index (PSI) Values from Between-Cruise Comparisons of the Total Ichthyoplankton and of the Other Larval Fraction (OL) in 11 CalCOFI Regions, 1975

Region	Total ichthyoplankton		Other larvae	
	Range	Mean	Range	Mean
Central California				
4	31.81-70.50	51.62	33.50-74.46	52.06
5	26.25-59.40	40.61	27.54-64.00	46.68
Southern California				
7	69.17-93.84	83.12	41.23-72.46	56.57
8	1.80-85.16	23.51	20.75-75.89	43.69
9	4.07-87.06	25.88	29.47-67.98	42.64
Northern Baja California				
11	28.32-93.52	58.97	27.14-68.90	43.91
12	29.54-93.38	59.81	26.47-82.66	51.88
13	2.36-50.68	23.87	21.22-73.16	37.44
14	15.52-86.73	39.76	26.70-86.20	48.06
Central Baja California				
16	31.26-93.57	54.40	23.90-60.33	37.33
17	13.93-70.94	40.89	30.57-61.89	48.47

Comparisons based on species lists from each of 6 cruises.

tive proportions of larval fish species are reflected by low between-cruise PSI values (Table 5). The ranges of between-cruise PSI values were smallest in central California regions 4 and 5 (which had little seasonal input of PL) and southern California inshore region 7 (which was dominated by anchovy larvae during all cruises). The other eight regions had large proportions of their total ichthyoplankton contributed by one or more of the PL species during at least two cruises during the year. Because of more equitable abundances among the OL, OL PSI values (except in regions 4, 5, and 14) were lower, and varied less than those for the total ichthyoplankton (Table 5). High ( $\geq 60$ ) total ichthyoplankton PSI values were associated with periods of maximum PL abundance in all regions except 4 and 5 (central California) and 13 and 14 (northern Baja California); in these four regions, highest values were associated with periods of peak OL abundances. Maximum OL PSI values were also generally associated with periods of peak OL abundances; exceptions were in central Baja California regions 16 and 17, where maximum January-March PSI values preceded July peak OL abundance, and in northern Baja California region 11, where maximum May-July PSI values followed January-March peak abundances.

As with area-wide comparisons, low total and OL regional PSI values generally resulted from comparisons of October-November species lists with those of other months. This indicates that, within all regions, the species composition and abundance relations dur-

TABLE 6  
 Percent Similarity Index (PSI) Values from Between-Region Comparisons of the Other Larvae (OL) Category of Ichthyoplankton Taken in CalCOFI Cruises, 1975

Areas	Regions	Cruise					
		7412	7501	7503	7505	7507	7510(11)
CC-CC	4-5	36.77	40.92	56.73	53.11	56.19	46.21
CC-SC	4-7	67.20*	62.63*	70.45*	47.53	41.76	57.92
CC-SC	4-8	48.54	53.64	66.51*	63.88*	44.47	29.26
CC-SC	4-9	22.27	40.83	51.76	49.00	31.26	20.44
CC-SC	5-7	25.04	26.56	34.18	25.46	31.68	25.23
CC-SC	5-8	40.56	42.61	50.66	58.13	51.40	45.31
CC-SC	5-9	28.72	57.47	71.12*	61.16*	47.31	26.80
SC-SC	7-8	53.04	66.14*	56.73	42.71	34.04	38.01
SC-SC	7-9	17.83	29.54	34.84	33.39	25.15	24.43
SC-SC	8-9	49.25	54.34	50.04	55.32	66.19*	50.36
SC-NBC	7-11	50.91	57.59	67.71*	41.79	28.37	49.92
SC-NBC	7-12	26.28	26.80	17.29	13.83	11.26	42.98
SC-NBC	7-13	7.24	9.87	8.96	15.18	18.08	50.36
SC-NBC	7-14	6.84	4.72	10.24	9.47	13.13	41.52
SC-NBC	8-11	47.85	46.86	53.73	28.21	31.63	41.52
SC-NBC	8-12	16.46	20.25	14.63	4.82	10.77	29.76
SC-NBC	8-13	27.15	24.29	20.83	18.01	33.96	41.18
SC-NBC	8-14	29.47	15.59	20.17	10.67	26.56	24.86
SC-NBC	9-11	28.11	42.58	34.42	23.74	30.71	33.57
SC-NBC	9-12	14.12	45.71	11.78	6.98	11.49	15.04
SC-NBC	9-13	37.64	13.76	33.67	33.90	34.43	51.51
SC-NBC	9-14	41.24	33.94	33.87	27.85	30.27	33.22
NBC-NBC	11-12	32.43	41.26	22.21	17.74	18.89	35.25
NBC-NBC	11-13	26.15	34.54	27.58	57.80	65.81*	43.32
NBC-NBC	11-14	21.07	30.47	23.68	45.26	48.46	29.06
NBC-NBC	12-13	9.93	17.09	11.48	10.22	12.23	21.38
NBC-NBC	12-14	9.39	14.67	7.50	9.54	12.42	28.08
NBC-NBC	13-14	68.31*	46.26	53.85	63.89*	63.60*	57.78
NBC-CBC	11-16	27.14	44.36	44.21	40.99	51.33	35.23
NBC-CBC	11-17	21.02	17.69	13.23	24.93	48.23	17.84
NBC-CBC	12-16	60.97*	38.59	35.82	47.57	20.95	36.99
NBC-CBC	12-17	14.74	10.20	6.45	60.97*	17.41	9.03
NBC-CBC	13-16	13.15	28.80	18.77	38.47	51.85	27.39
NBC-CBC	13-17	59.32	24.72	24.70	16.42	50.58	32.71
NBC-CBC	14-16	11.27	26.37	12.42	40.79	55.55	33.78
NBC-CBC	14-17	53.55	45.69	24.64	16.20	67.45*	48.03
CBC-CBC	16-17	35.18	49.72	26.09	65.70*	67.68*	27.20

Comparisons are between regions of the same area and between regions of adjacent areas.

Asterisk denotes high values (i.e.,  $\geq 60$ ).

CC = central California; SC = southern California; NBC = northern Baja California; CBC = central Baja California.

ing fall were markedly different from those during the rest of the year.

Geographical and seasonal differences in taxonomic composition are shown by within-cruise PSI comparisons between the OL of adjacent regions (Table 6). Most of the PSIs were low ( $< 40$ ), indicating a great degree of geographical heterogeneity throughout the year. High PSI values were generally associated with comparisons between north-south adjacent regions for the central and southern California areas and with comparisons between inshore-offshore adjacent regions within the northern and central Baja California areas. High between-region similarities were sea-

sonally restricted. Highest PSI values in the California and northern Baja California inshore regions (62.6-70.4) occurred between regions 4-7 during December, January, and March and between regions 7-11 during March. Highest inshore-offshore and offshore-seaward values off California occurred between regions 4-8 and 5-9 during March and May, regions 7-8 in January, and regions 8-9 in July. Except for the last, these high PSI values reflect similar proportions of dominant rockfish, bathylagid, and myctophid species (*Sebastes* spp, *Leuroglossus stilbius*, *Bathylagus ochotensis*, *Stenobranchius leucopsarus*, *Tarletonbeania crenularis*, and *Protomyctophum crockeri*)

during periods of elevated and peak OL abundances. High July values between regions 8-9 reflect similar proportions of a variety of myctophid and bathylagid species during a time of relatively low OL abundance. High PSI values in the Baja California areas (63.9-68.3) occurred between offshore and seaward regions 13-14 during December, May, and July because of similar proportions of dominant myctophid, gonostomatid, and bathylagid species (primarily *Triphoturus mexicanus*, *Vinciguerria lucetia*, and *Bathylagus wesethi*); high values also occurred between regions 11-13, 14-17, and 16-17 during July, and reflect shared dominance by *T. mexicanus* and (in all but region 11) *V. lucetia* during peak OL abundance.

## DISCUSSION

### *Total Ichthyoplankton, 1975*

Despite the large interannual variability in flow and biology of the California Current system (Reid et al. 1958; Sette and Isaacs 1960; Colebrook 1977; Bernal 1980), the 1975 ichthyoplankton resembled that taken on CalCOFI cruises between 1955 and 1958 (Table 1). Ahlstrom (1965) found that 12 kinds of larvae consistently contributed between 90% and 93% of the total CalCOFI ichthyoplankton. Eleven of the 12 are among the 13 most abundant taxa taken during 1975 (species were lumped into higher taxonomic categories in 1975 data to conform to the 1955-58 data; Table 1). The one major exception was the sardine (adjusted rank 26 during 1975 vs rank 6-11 in 1955-58).

The 12 most abundant taxa taken during 1975 included 91% of the total ichthyoplankton. The rank order of abundance within these 12 taxa was quite similar to that of 1955-58 (Kendall's tau tests,  $P < 0.01$ ). However, while the proportion of hake larvae (14.5% of the total ichthyoplankton) in 1975 was similar to 1955-58 values, the proportion of anchovy larvae (58.9%) was 1.3 to 2 times higher, and the proportions of the other 10 taxa were reduced (and more similar to each other) in 1975 as compared to 1955-58 (Table 1). Caution must be used in making such direct rank and proportion comparisons between the two sets of data (especially between the less abundant taxa) because the 1955-58 values are based on actual total numbers of larvae caught and not on abundances adjusted for the area sampled (used here). Also, because the 1955-58 data were not standardized, direct comparisons of numerical abundances between 1975 and the earlier years cannot yet be made.

The large-scale CalCOFI sampling plan covers the spawning areas of the major pelagic fishes (sardine, anchovy, hake, jack mackerel) off California and Baja California (Ahlstrom 1965), and the sampled ichthyo-

plankton is dominated by these abundant and fecund species and by other offshore (mesopelagic) species. Shelf species other than *Sebastes* spp and *Citharichthys* spp (which have long larval periods) make limited contributions.

Geographical differences in larval fish species distributions within the CalCOFI area are to some extent obscured by the widespread distributions of anchovy, hake, and jack mackerel. However, there are distinct underlying patterns of distribution among the other larvae. Some of these species are associated with major Pacific Ocean water masses, or with cold-water (northern) or warm-water (southern) conditions, and year-to-year variations in these species' distributions and abundances have been related to changes in flow within the California Current system (Ahlstrom 1965, 1969; Paxton 1967; Moser and Ahlstrom 1970; Moser et al. 1977). Regional mean abundances of the dominant OL species during 1975 reflected their documented water-mass affiliations (Table 7). Two of three subarctic-transition zone myctophids (*Stenobrachius leucopsarus* and *Tarletonbeania crenularis*; Paxton 1967) and the two "northern" *Sebastes* species (*S. paucipinis* and *S. jordani*; Moser et al. 1977) occurred in greatest abundance off central and southern California. The warm-water cosmopolite *Diogenichthys atlanticus* (Ahlstrom 1965) was most abundant off northern Baja California, and the restricted California Current species (*Protomyctophum crockeri*; Ahlstrom 1965) and eastern tropical Pacific species (*Triphoturus mexicanus*, *Vinciguerria lucetia*, and *Diogenichthys laternatus*; Ahlstrom 1965; Paxton 1967) were most numerous off of northern and central Baja California.

Within the central and southern California areas, maximum abundances of mesopelagic species occurred in inshore region 4, while offshore and seaward regions 8 and 9 were locations of maximum anchovy (region 8) and hake (region 9) abundances (Table 7). In contrast, within the northern and central Baja California areas, mesopelagic species were most abundant in seaward region 14, while inshore regions 11 and 12 had maximum anchovy (region 12) and hake (region 11) abundances (Table 7). These shifts suggest inshore-offshore differences in adult distributions and spawning activities and possible differences in net larval transport between the areas off California and Baja California.

The northern Baja California area was one of faunal transition with marked north-south shifts in regional dominance by rockfishes and bathylagids to dominance by gonostomatids, flatfishes, and other shelf taxa. It also marked shifts in dominance by subarctic, cold-water, and northern species to eastern tropical

TABLE 7  
 Regional Ranks of Abundance of the 22 Most Abundant Larval Fish Species in the CalCOFI Area, 1975

	Affil- iation	Region										
		Central California		Southern California			Northern Baja California				Central Baja California	
		4	5	7	8	9	11	12	13	14	16	17
<i>Stenobranchius leucopsarus</i>	S-T	1	2	3	5	4	7	—	—	6	8	—
<i>Bathylagus ochotensis</i>	N	1	2	5	3	4	7	9	6	8	—	—
<i>Tarletonbeania crenularis</i>	S-T	1	2	5	3	4	7	—	—	6	—	—
<i>Sebastes jordani</i>	N	1	5	2	3	6	4	—	—	—	—	—
<i>Sebastes paucispinis</i>	N	2	3	1	6	5	4	—	—	—	—	—
<i>Leuroglossus stilbius</i>	M	3	6	1	2	5	4	9	8	10	7	11
<i>Engraulis mordax</i>	M	10	11	4	1	8	3	2	6	9	5	7
<i>Merluccius productus</i>	M	8	9	6	2	1	3	7	4	5	10	11
<i>Citharichthys sordidus</i>	N	4	2	10	6	7	5	1	8	—	3	9
<i>Citharichthys stigmaeus</i>	N	4	3	7	2	8	6	1	5	10	9	11
<i>Symbolophorus californiense</i>	T	—	6	10	5	2	4	7	3	1	9	8
<i>Diogenichthys atlanticus</i>	C	11	5	10	8	2	7	6	3	1	9	4
<i>Lampanyctus ritteri</i>	S-T	9	6	10	5	3	2	7	4	1	11	8
<i>Protomyctophum crockeri</i>	CA	7	5	9	3	4	6	8	2	1	11	10
<i>Trachurus symmetricus</i>	M	—	9	10	3	4	6	8	2	1	7	5
<i>Ceratoscopelus townsendi</i>	CA	—	8	9	4	3	7	10	2	1	5	6
<i>Bathylagus wesethi</i>	S	—	9	10	4	3	7	8	2	1	6	5
<i>Citharichthys xanhostigma</i>	S	—	—	—	—	—	—	1	5	2	3	4
<i>Sardinops sagax</i>	M	—	—	4	—	—	3	1	—	2	—	—
<i>Triphoturus mexicanus</i>	ETP	—	—	9	7	8	5	6	3	1	4	2
<i>Vinciguerria lucetia</i>	ETP	—	9	—	8	7	5	6	3	1	4	2
<i>Diogenichthys laternatus</i>	ETP	—	—	7	—	—	6	4	5	3	2	1

Ranks based on total mean numbers of larvae (6 cruises, summed) in each region. Water mass or habitat affiliations assigned to each species: S-T, subarctic-transition zone; T, transition zone; C, warm-water cosmopolite; ETP, eastern tropical Pacific; N, northern/cold water; S, southern/warm water; CA, restricted to California Current; M, multiple affiliations. Affiliations from Ahlstrom (1965), Paxton (1967), Moser and Ahlstrom (1970), and Moser et al. (1977).

Pacific, warm-water, and southern species. Offshore and seaward regions 13 and 14 contained mixtures of species from all three water-mass source areas plus restricted California Current species; dominant OL of inshore regions 11 and 12 included subarctic and eastern tropical Pacific species. The transitional nature of the northern Baja California area is reflected by the relatively low OL PSI values resulting from comparisons of its regions with north-south adjacent regions (Table 4B). Despite its transitional nature, the northern Baja California area had relatively large numbers of larval fishes (Loeb et al. 1983a): PL abundance was extremely high in inshore regions 11 and 12, and maximum areawide OL abundances occurred in regions 12 (primarily flatfishes) and 14 (mesopelagic taxa).

Seasonal changes were evident in both larval fish abundance (Loeb et al. 1983a) and relative abundance of species. However, within each region there was a general dominance by a limited suite of taxa throughout the year. Seasonal differences were probably due to differences in the timing of peak spawning activity among these few abundant taxa. Highest area-wide abundances occurred during the peak January-May PL spawning period. Highest OL abundances occurred during January and March in the central and southern California areas and in inshore region 11 of northern

Baja California; this was primarily due to peak spawning of *Sebastes* spp and four mesopelagic species with subarctic-transition zone, northern/cold-water, or restricted affiliations (*Stenobranchius leucopsarus*, *Protomyctophum crockeri*, *Leuroglossus stilbius*, and *Bathylagus ochotensis*; Table 8). Low OL abundances prevailed within all of these regions (except region 7) from May to December because of minor summer/fall spawning input; within region 7, the October OL abundance peak was attributed to *Citharichthys* spp. Within the central Baja California regions and regions 12, 13, and 14 of northern Baja California, maximum OL abundances occurred between May and October primarily because of peak summer or fall spawning of flatfish and southern shelf species and three eastern tropical Pacific or warm-water mesopelagic species (*Triphoturus mexicanus*, *Vinciguerria lucetia*, and *Bathylagus wesethi*; Table 8).

#### *Ichthyoplankton Distribution and Seasonal Abundance Patterns in Relation to California Current Flow*

The dominant OL taxa of the central and southern California areas are subarctic-transition zone, northern, and cold-water forms, and reflect the northern sources of the California Current. These species,



TABLE 8  
 Cruise Ranks of Abundance of the 22 Most Abundant Larval Fish Species in the CalCOFI Area, 1975

	Affil- iation	Cruise					
		7412	7501	7503	7505	7507	7510(11)
<i>Stenobranchius leucopsarus</i>	S-T	4	2	1	3	5	6
<i>Bathylagus ochotensis</i>	N	4	1	2	3	5	6
<i>Tarletonbeania crenularis</i>	S-T	6	5	4	2	3	1
<i>Sebastes jordani</i>	N	—	—	1	—	—	—
<i>Sebastes paucispinis</i>	N	3	1	2	4	—	5
<i>Leuroglossus stilbius</i>	M	3	1	2	4	5	6
<i>Engraulis mordax</i>	M	4	1	2	3	6	5
<i>Merluccius productus</i>	M	4	1	2	3	5	6
<i>Citharichthys sordidus</i>	N	2	3	5	6	4	1
<i>Citharichthys stigmaeus</i>	N	2	4	3	6	5	1
<i>Symbolophorus californiense</i>	T	6	3	1	4	2	5
<i>Diogenichthys atlanticus</i>	C	3	2	1	5	6	4
<i>Lampanyctus ritteri</i>	S-T	5	1	2	4	3	6
<i>Protomyctophum crockeri</i>	CA	3	1	2	4	5	6
<i>Trachurus symmetricus</i>	M	—	5	1	3	2	4
<i>Ceratoscopelus townsendi</i>	CA	5	4	3	6	2	1
<i>Bathylagus wesethi</i>	S	6	5	1	3	2	4
<i>Citharichthys xanhostigma</i>	S	—	—	—	3	2	1
<i>Sardinops sagax</i>	M	4	3	6	5	1	2
<i>Triphoturus mexicanus</i>	ETP	6	5	4	2	1	3
<i>Vinciguerrria lucetta</i>	ETP	3	4	6	5	1	2
<i>Diogenichthys laternatus</i>	ETP	4	3	1	6	2	5

Ranks based on summed adjusted abundances of larvae from 11 CalCOFI regions for each cruise. Water mass or habitat affiliations assigned to each species: S-T, subarctic-transition zone; T, transition zone; C, warm-water cosmopolite; ETP, eastern tropical Pacific; N, northern/cold water; S, southern/warm water; CA, restricted to California Current; M, multiple affiliations. Affiliations from Ahlstrom (1965), Paxton (1967), Moser and Ahlstrom (1970), and Moser et al. (1977).

although present and generally dominant throughout the year, were most abundant in January-March, during reduced surface countercurrent flow and the onset of upwelling. During 1975 the upwelling period in the central and southern California areas extended from March to late September; maximum intensities occurred from May to July (Parrish et al. 1981). Decreased and relatively constant OL abundances prevailed here during most of this upwelling period and throughout most of the surface countercurrent period. The OL species proportions of the inshore regions of the central and southern California areas and inshore region 11 of northern Baja California were most similar from December or January to March (Table 6), possibly because these regions experienced similar environmental conditions at the onset of increased spawning activity by shared dominant taxa. Except for regions 7 and 8, greatest similarity of species proportions between inshore-offshore regions occurred later (March to May or July) than for the inshore regions; this corresponds to the period of maximum offshore advection of surface water associated with upwelling (Bakun and Nelson 1977) and may implicate larval drift. Regions 7 and 8 were most similar during December, January, and March (Table 6), perhaps because of similar wintertime conditions prevailing within the Los Angeles bight area (Lasker 1978). Between-region PSI values were relatively low during summer and fall, suggest-

ing greater environmental heterogeneity (on regional scales) during the period of surface countercurrent flow and reduced upwelling.

The dominant OL taxa of the central Baja California area, and to a lesser degree of the northern Baja California area, are eastern tropical Pacific, southern, and warm-water forms. In these southern regions (except region 11) highest OL abundances occurred during summer and fall. This is a period of decreased upwelling, weakened southward flow, increased surface temperatures, and surface countercurrent flow off Baja California. Throughout the year 67% of all between-region PSI values in these areas were < 40.0 as compared to the regions of central and southern California, where only 33% of all comparisons were < 40.0 (Table 6). This suggests a greater degree of between-region heterogeneity in species composition in the south, because of the transitional nature of the northern Baja California area. Greatest similarity of species proportions between inshore-offshore regions generally occurred during the May-July period of maximum OL abundance (Table 6) and reflect dominance by a few summer-spawning species.

Among the 11 regions, only offshore and seaward regions 13 and 14 of northern Baja California did not have significant seasonal OL abundance peaks (Loeb et al. 1983a). These were the only regions that, despite marked seasonal changes in species proportions

(i.e., low within-region PSI values; Table 5), had generally high between-region similarities of species proportions throughout the year. They also had similar ranked abundances of their dominant species. These facts imply that more homogeneous environmental conditions existed offshore of northern Baja California than elsewhere in the CalCOFI area during 1975, and probably reflect decreased influence by coastal processes in this locale.

Among the PL species, anchovy and hake most resembled the northern OL species, whereas jack mackerel and sardine were more like the southern OL species, in their distributions and seasonal abundance peaks (Tables 7 and 8). These associations are corroborated by the results of recurrent group analysis on the 1975 ichthyoplankton data (Loeb et al. 1983b). During January-March peak spawning, anchovy and hake in the southern California area had maximum abundances in offshore and seaward regions, while off northern Baja California they were most abundant in inshore regions. These differences were apparently not directly related to coastal upwelling timing or intensity, because the February onset and subsequent spring upwelling intensities were similar in both areas (Bakun and Nelson 1977; Lasker 1978). They may, however, reflect differences in spawning stocks. Apparently, central and southern spawning stocks of the northern anchovy and hake (as well as subpopulations of sardine and jack mackerel) are separated near the northern Baja California coast (Nelson 1977; Vrooman and Paloma 1977; Bakun and Parrish 1980; Hewitt 1981; Parrish et al. 1981).

The northern Baja California area is a transition zone for subarctic/cold-water and eastern tropical Pacific/warm-water fishes, as well as for copepods and euphausiids, and marks a separation of spawning stocks of the major pelagic fish species (Hewitt 1981). It separates areas that have significantly different periods of both zooplankton and OL seasonal abundance peaks (Loeb et al. 1983a). Its inshore regions have concentrations of characteristically offshore zooplankton species plus extreme zooplankton patchiness throughout the year (Arthur 1977; Loeb et al. 1983a). These features may be related to the unique hydrography of the area.

In general, wind-driven surface-layer (Ekman) transport along the coast is directed offshore (positive wind stress curl), creating a coastal divergence or upwelling zone, the extent of which varies seasonally and annually with changes in wind field and intensity. Offshore, surface convergence or downwelling (negative wind stress curl) predominates throughout the year. The boundary between convergence and divergence zones parallels the coast 100-300 km offshore

except off northern Baja California (Figure 4; Bakun and Nelson 1977; Parrish et al. 1981). Here a lobe of surface convergence (negative wind stress curl) extends shoreward and impinges on the coast in the Baja California maximum upwelling area between Punta Baja and Punta Eugenia (regions 11 and 12). This feature persists throughout the year and separates the cyclonic eddy of the Southern California Bight and a seasonal coastal eddy south of Punta Eugenia. As indicated by the results presented in this study and in Loeb et al. (1983a), this feature also appears to separate both coastal and offshore biological regimes within the California Current area.

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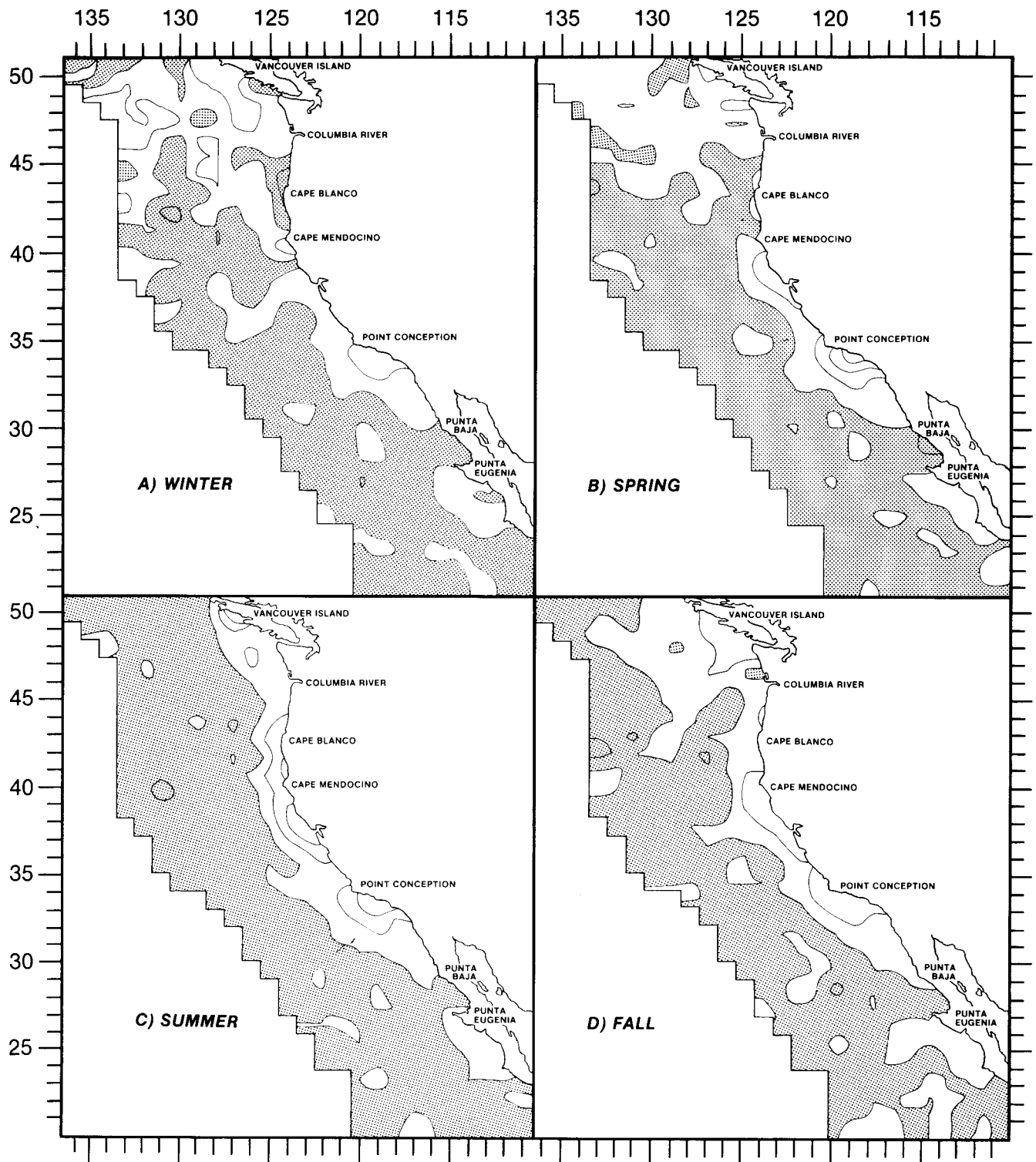


Figure 4. Patterns of wind stress curl, and divergence and convergence zones off California and Baja California, reproduced from Parrish, Nelson, and Bakun (1981). Monthly composite fields of wind stress curl were computed from surface wind stress fields for (A) winter (December-February), (B) spring (March-May), (C) summer (June-August), and (D) fall (September-November). The contour interval is  $0.25 \text{ dyne/cm}^2 \cdot 100 \text{ km}$ . Negative values are shaded and indicate surface Ekman convergence. Unshaded areas indicate surface Ekman divergence.

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