RECURRENT GROUPS OF LARVAL FISH SPECIES IN THE CALIFORNIA CURRENT AREA

VALERIE J. LOEB[1]
San Diego Natural History Museum
P.O. Box 1390
San Diego, California 92112

PAUL E. SMITH AND H. GEOFFREY MOSER
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

Recurrent group analysis was performed on larval fish species collected during the 1975 CalCOFI survey. We arranged 27 species in 11 groups based on frequencies of co-occurrence in samples; 5 other species had "high" affinities with some members of the groups. The 2 largest groups (5 and 4 species, respectively) and their 5 associated species pair groups represented 2 major ichthyoplankton assemblages in the CalCOFI area.

Species of each group were frequently taken together in CalCOFI samples, shared generally similar geographical and seasonal distributions, and appeared to be relatively constant parts of one another's environments. However, based on existing vertical distribution information, most group members and associated group species appear to inhabit different depths within the upper water column. This probably indicates limited interspecific contacts (e.g., competition for food). Within-group differences in timing of peak abundances and, in one case, regions of maximum abundance, also reduce the probability of such interactions. As a result, direct interactions at the larval stage may be negligible in controlling the larval abundances and distributions of these species. More detailed vertical distribution information is needed to verify this observation.

RESUMEN

Se efectuaron análisis de grupos recurrentes con varias especies de larvas de peces recolectadas en 1975 durante las exploraciones del programa CalCOFI. 27 especies se distribuyeron en 11 grupos, tomando como base la frecuencia en que aparecían juntas en las muestras, y otras 5 especies presentaban afinidad elevada con alguno de los integrantes del grupo. Los dos grupos mayores, con 5 y 4 especies respectivamente, así como el grupo incluyendo 5 pares de especies asociadas, representaban dos amplias agregaciones de ictioplancton en la zona explorada.

Especies de cada grupo aparecían juntas frecuentemente en las muestras de CalCOFI, presentando distribuciones similares, tanto en espacio como en época del año, apareciendo como partes constantes de ambos ambientes marinos. Sin embargo, tomando como base la información que existe sobre la distribución batimétrica de las especies, la mayor parte de los integrantes del grupo y las especies asociadas, habitaban al parecer diferentes profundidades en la columna de agua atravesada durante el arrastre de la red. Esto indica que, probablemente existen contactos limitados interespecíficos, por ejemplo, competición por alimento. Diferencias dentro del grupo en cuanto a la època de máxima abundancia y regiones de abundancia máxima, reducen también la probabilidad de tales interrelaciones. Las interacciones a nivel de fase larval pudieran resultar de valor directo insignificante, en cuanto al control de la abundancia de larvas y la distribución de estas especies. No obstante, se precisa obtener más información detallada sobre la distribución batimétrica de las especies para poder comprobar estas observaciones.

INTRODUCTION

The ichthyoplankton of the California Current system contains many disparate members, including the larvae of (1) demersal fishes that spawn on the continental shelf and slope, (2) mesopelagic species whose spawning distributions extend across the Pacific, (3) migratory species that feed in rich boreal and northern temperate waters but enter the area to spawn, (4) subarctic and temperate/tropical species whose spawning ranges extend into the northern and southern regions of the area, and (5) species whose distributions are limited to offshore California Current waters.

In addition to the broad geographic sources of the ichthyoplankton, there is a finer-scale structure to larval fish distribution, on the order of meters to tens of kilometers. Although population breadth prevents delimitation of many species, fine-scale structure may also obscure descriptions of coincidence and possible interaction among species. The fundamental CalCOFI sample is of an oblique column of water 800 m long and only a few meters wide from a depth of 210 m. Consequently, species occurring horizontally within several tens of meters of each other and which could be interacting may not be found in the same samples. Conversely, species coming from widely different depths and which may have minimal interaction may be found in the same integrated sample.

[1]Current address: Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, CA 95039.

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There are sufficient differences in the biota at different water-column depths to minimize the problem of oblique integrated samples (Gruber et al. 1982). To overcome the problem of using small samples to represent wider, possibly more relevant community units, it is necessary to consider "recurrent groups" of species in many samples. Aggregation (patchiness) of larval fishes appears to be the rule rather than the exception (Loeb et al. 1983a). Thus it is necessary when forming useful recurrent groups to initially disregard the numbers of fishes and consider instead only species presence/absence in each sample. To do otherwise would grant the occasional coincidence of large numbers of two or more species greater importance than its frequency would warrant. Thus interrelationships among group species are not dominated by localized situations favoring the abundance of some or all members. Once groups are established based on significant frequency of co-occurence of all member species in samples, one may consider abundances of individual species. In doing this, one may categorize abundance relationships indicating predator-prey or no apparent interactions, and may explore aspects of concordance among member species as to optimal environmental conditions.

The study of definitive interactions between any two fish species or among any number of species can only be guided by the results of analysis we report here. The sampling grid is too large; the water volume filtered by each sample is too small; and the number of individuals of the proposed interacting species are too few to offer conclusive findings at this stage of analysis. It is the purpose of this paper, therefore, to explore an existing set of CalCOFI data sufficiently that future specific sampling and surveys may be conducted to delineate species interactions in recurrent groups and make substantive inferences about the nature of their interactions.

METHODS

The recurrent group analysis was based on larval fish species presence/absence data from 1,531 standard CalCOFI samples taken on seven cruises between December 1974 and November 1975 (Loeb et al. 1983a). Subsequent analyses of species abundance relations are based on pooled data representing 11 basic CalCOFI regions. Regional and seasonal sampling information is presented in Table 1. Samples were collected using a net of 1 m mouth diameter, fitted with 505-μm mesh, and fished obliquely to ~ 210 m (Kramer et al. 1972).

Recurrent groups analysis was per Fager (1957, 1963). In this analysis an index of affinity (A) is calculated between all possible species pairs. This index may range from 0.0 (species pair never caught together) to 1.0 (species pair co-occurred in every sample). It is difficult to assign probability levels to affinity values because the distribution of the affinity values is a function of both the number of occurrences of individual species and the frequency of co-occurrences of paired species. The investigator specifies a significant affinity level (a) to be used in developing groups: an a level near 1.0 represents a more stringent grouping criterion than does a lower value. A recurrent group is defined as a set of species each of which has a significant affinity level value (i.e., $A \geq a$) with every other member of the set. Each group species has affinity values with every nongroup species; some of those values may also be significant. Additionally, a member of one group can have significant affinity values with members of other groups. Selection of a "significant" affinity level is subjective; the subsequent grouping procedure is en-

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

tirely objective. The criterion for selection of a significant affinity value is interpretability of results. In the present study an affinity value $a \geq 0.30$ was used; this is lower than used in many other studies (e.g., Fager and McGowan 1963, $a \geq 0.50$; McGowan and Walker 1979, $a \geq 0.50$; Venrick 1982, $a \geq 0.50$, ≥ 0.65, and ≥ 0.80) primarily because of the low numbers of larval fish taxa taken per sample (Loeb et al. 1983a) and the resulting low numbers of co-occurrences. Intergroup connections are reported as the fraction of possible significant affinities between group member species which actually occurred (i.e., the number of affinities $\geq a/MN$) where M is the number of species in one group and N is the number of species in a second group.

Seventy-eight species were included in the present analysis; higher taxonomic categories and rare species (captured in ≤ 5 samples total) were excluded. We emphasize the largest groups determined and their associated groups; independently distributed species groups and individual group associate species receive only cursory attention. Groups are numbered according to intergroup affinities rather than according to the conventional size-dependent grouping order. Water-mass or hydrographic affiliations are assigned to many of the grouped species. These affiliations are based on the works of Ahlstrom (1965, 1969), Paxton (1967), Moser and Ahlstrom (1970), and Moser et al. (1977).

Three nonparametric statistical tests—Kendall's concordance and tau tests, and rank difference correlation coefficients (Tate and Clelland 1957)—are used to examine regional and seasonal abundance relationships of the grouped species. Kendall's concordance test is a nonparametric analysis of variance used here to examine regional and seasonal abundance ranking across several data sets. The tau and rank difference tests each provide a corre'ation coefficient that measures the similarity between the order of species abundance rankings within two data sets.

Depth-vs-abundance information for many of the grouped species has been provided by Ahlstrom (1959). Differences between these reported species depth-vs-abundance distributions are tested here using Kolmogorov-Smirnov (K-S) tests (Conover 1971). These tests are based on the maximum differences between cumulative percent curves (here cumulative percent of each species total abundance vs depth curves) for two sets of data.

RESULTS

Species Groupings

Twenty-seven species formed 11 groups (Figure 1); these included one group of five species (Group I) with three associated species pairs (Groups II, III, and IV); one group of four species (Group V) with one associated species pair (Group VI); and five other species pairs (Groups VII, VIII, IX, X, and XI). Five individual species had affinities ≥ 0.30 with group members. No other species had any affinities ≥ 0.30. The grouped species and group associate species are presented along with their water-mass affiliations in Table 2; within- and between-group affinities are illustrated in Figures 2 and 3.

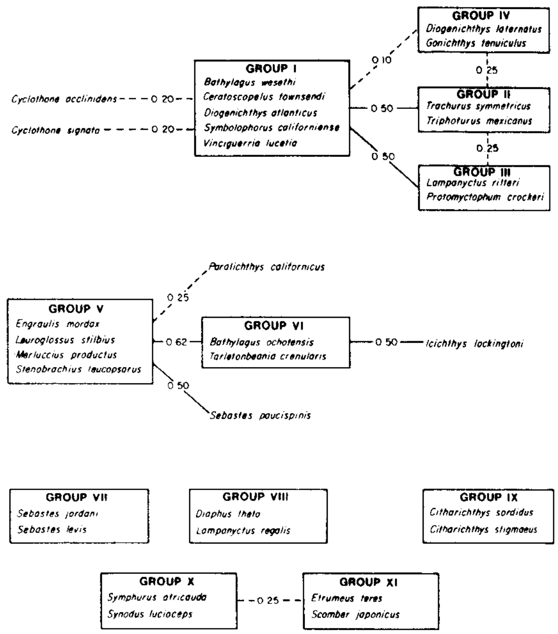

Figure 1. Composition and intergroup affinities of 11 recurrent groups of larval fish species, 1975 CalCOFI survey. Dashed lines denote nonsignificant (< 0.30) intergroup affinity values.

Group I consisted of five mesopelagic species of mixed hydrographic affiliations: one southern bathylagid; one eastern tropical Pacific gonostomatid; and one each warm-water cosmopolite, restricted California Current, and transition-zone myctophid (Table 2). The four species of Group V included one subarctic-transition zone myctophid, one California Current bathylagid, and the two dominant pelagic species—anchovy (*Engraulis mordax*) and hake (*Merluccius productus*). The nine other groups included three pairs of mesopelagic species (5 myctophids, 1 bathylagid) with northern, subarctic-transition zone, and restricted California Current affiliations (Groups III, VI, and VIII); a California Current myctophid and a pelagic species, jack mackerel (*Trachurus symmetricus*) (Group II); a pair of eastern tropical Pacific myctophids (Group IV); a pair of northern rockfishes (VII); a pair of

TABLE 2
Species Composition of Recurrent Groups and the Water Mass or Habitat Affiliations of Member Species

Group no.	Species name	Affiliation	Group associate species	Affiliation
I	*Diogenichthys atlanticus*	C		
	Bathylagus wesethi	S		
	Symbolophorus californiense	T		
	Vinciguerria lucetia	ETP	*Cyclothone acclinidens*	S
	Ceratoscopelus townsendi	CA	*Cyclothone signata*	S
II	*Triphoturus mexicanus*	CA		
	Trachurus symmetricus	PL		
III	*Protomyctophum crockeri*	CA		
	Lampanyctus ritteri	S-T		
IV	*Diogenichthys laternatus*	ETP		
	Gonichthys tenuiculus	ETP		
V	*Leuroglossus stilbius*	N	*Sebastes paucispinis*	N
	Stenobrachius leucopsarus	S-T		
	Engraulis mordax	PL	*Paralichthys californicus*	M
	Merluccius productus	PL		
VI	*Tarletonbeania crenularis*	S-T	*Icichthys lockingtoni*	M
	Bathylagus ochotensis	N		
VII	*Sebastes jordani*	N		
	S. levis	N		
VIII	*Lampanyctus regalis*	S-T		
	Diaphus theta	S-T		
IX	*Citharichthys sordidus*	N		
	C. stigmaeus	N		
X	*Symphurus atricauda*	M		
	Synodus lucioceps	M		
XI	*Etrumeus teres*	M		
	Scomber japonicus	M		

S-T, subarctic-transition zone; T, transition zone; C, warm-water cosmopolite; ETP, eastern tropical Pacific; N, northern or cold water; S, southern or warm water; CA, restricted California Current; PL, pelagic; M, multiple affiliations. Affiliations based on Ahlstrom (1965), Moser and Ahlstrom (1970), Moser et al. (1977), and Paxton (1967).

northern flatfishes (IX); and two pairs of the comparatively rare larvae of southern coastal and pelagic species (X and XI) (Table 2).

The two largest groups (I and V) had connections with several of the smaller groups (Figure 1). Some of the Group I species had high affinities with members of Groups II and III. Three other mesopelagic species (two individual group associate species and one species from Group IV) each had affinities > 0.30 with one of the Group I species (Figure 1). Group II was also weakly associated (one of four possible significant affinities) with both Groups III and IV. Some of the four Group V member species had high affinities with both Group VI species. One and two of the Group V species were also associated with one flatfish and one rockfish species, respectively. Group VI also had a single-species associate. Only two of the five other species pairs had intergroup affiliations; these were weakly associated (intergroup connection = 0.25) Groups X and XI.

Within Group I, affinity levels ranged from 0.323 to 0.478; highest values (0.439-0.478) occurred between *Diogenichthys atlanticus*, *Symbolophorus califor-*

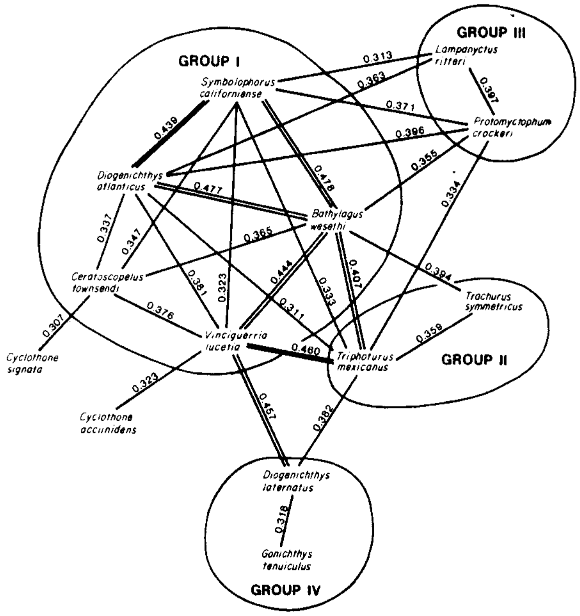

Figure 2. Within- and between-group species affinity values for recurrent Group I and associated Groups II, III, and IV, CalCOFI survey, 1975. Double lines denote species affinity values 0.40-0.49; single lines, affinity values 0.30-0.39.

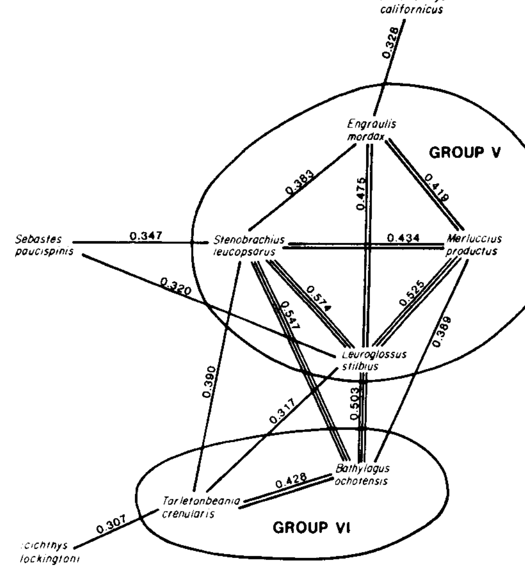

Figure 3. Within- and between-group species affinity values for recurrent Group V and associated Group VI, CalCOFI survey, 1975. Triple lines denote species affinity values ≥ 0.50; double lines, affinity values 0.40-0.49; single lines, affinity values 0.30-0.39.

niense, and *Bathylagus wesethi* and between *Bathylagus wesethi* and *Vinciguerria lucetia* (Figure 2). These four species all had affinities > 0.30 with *Triphoturus mexicanus* of Group II; three of the four (*D. atlanticus*, *S. californiense*, and *B. wesethi*) also had significant affinities (0.313-0.396) with *Lampanyctus ritteri* and/or *Protomyctophum crockeri* of Group III. Additionally, *V. lucetia* had a high affinity (0.457) with Group IV species *Diogenichthys laternatus*. The fifth Group I species, *Ceratoscopelus townsendi*, had relatively low affinities (0.337-0.376) with the other member species, and affinities < 0.30 with members of the three associated groups. Group II species *T. mexicanus*, in addition to its associations with Group I members, also had significant affinities with *D. laternatus* (Group IV) and *P. crockeri* (Group III).

The affinity values between the four Group V species (0.383-0.574) were generally higher than between the Group I species (Figure 3). Highest values occurred between *Leuroglossus stilbius* and hake (*Merluccius productus*) (0.525) and between *L. stilbius* and *Stenobrachius leucopsarus* (0.574). *Leuroglossus stilbius* and *S. leucopsarus* also had high affinity values with Group VI species *Bathylagus ochotensis* (0.503-0.547) and *Tarletonbeania crenularis* (0.317-0.390); hake had an affinity > 0.30 only with *B. ochotensis*, and anchovy (*Engraulis mordax*) had affinities < 0.30 with both species. Both *S. leucopsarus* and *L. stilbius* were also associated with *Sebastes paucispinis*.

Group Distribution and Abundance Relationships

The five Group I species were widely distributed within the CalCOFI area; each was captured in all regions except 4 and 7 (inshore central and southern California) and during all cruises. Co-occurrence in samples by all five species was restricted, however, to offshore and seaward regions 9, 13, and 14 of southern California and northern Baja California; four of the five species also co-occurred in samples within offshore central California and central Baja California regions 5 and 17 (Figure 4). Highest frequencies of co-occurrence were in northern Baja California seaward region 14, where the five species were caught together in 17.7% of all samples; four of five species were caught together in an additional 30.6% of the samples within this region (Table 3). Members of Group I had abundance peaks in the same regions (Kendall's concordance, $P < 0.01$). The regions of maximum abundance (9, 13, and 14) were those of maximum frequency of occurrence of the individual species (rank difference correlation coefficient = 0.85-0.95; $P < 0.01$ in all cases) and of maximum frequency of co-occurrence of the five species (Tables 3, 4). Within regions 9, 13, and 14 there was significant agreement of species rank order of abundance throughout the year (i.e., similar species rankings across all cruises within each region; Kendall's concordance, $P < 0.05$). However, species rankings differed between regions (Table 5), and there was no overall agreement of regional rank order of abundance (Ken-

TABLE 3
Regional Distribution of Six Main Recurrent Groups of Larval Fish Species Based on Frequency of Co-occurrence in Samples by Group Member Species

Area	Central California		Southern California			Northern Baja California				Southern Baja California	
Region	4 (inshore)	5 (offshore)	7 (inshore)	8 (offshore)	9 (seaward)	11 (inshore)	12 (bay)	13 (offshore)	14 (seaward)	16 (inshore)	17 (offshore)
Group I											
5 spp	—	—	—	—	2.0%	—	—	4.0%	17.7%	—	—
					(3)			(2)	(1)		
4/5 spp	—	1.6%	—	—	7.8%	—	—	6.8%	30.6%	—	1.8%
	—	(5)	—	—	(2)	—	—	(3)	(1)	—	(4)
Group II											
2 spp	—	—	0.2%	3.8%	5.9%	11.2%	0.6%	25.7%	40.3%	2.4%	5.4%
	—	—	(9)	(6)	(4)	(3)	(8)	(2)	(1)	(7)	(5)
Group III											
2 spp	1.5%	10.9%	0.8%	11.3%	25.5%	7.9%	3.8%	17.6%	32.2%	0.6%	—
	(8)	(5)	(9)	(4)	(2)	(6)	(7)	(3)	(1)	(10)	—
Group IV											
2 spp	—	—	—	—	—	0.6%	—	—	—	2.4%	23.2%
	—	—	—	—	—	(3)	—	—	—	(2)	(1)
Group V											
4 spp	2.9%	0.2%	13.4%	13.2%	9.8%	2.6%	—	—	1.6%	—	—
	(4)	(7)	(1)	(2)	(3)	(5)	—	—	(6)	—	—
Group VI											
2 spp	24.8%	35.9%	2.5%	17.0%	28.4%	—	—	—	—	—	—
	(3)	(1)	(5)	(4)	(2)	—	—	—	—	—	—

Frequency of co-occurrence presented as the percentage of all samples taken within each CalCOFI region containing all member species. For Group I frequency of co-occurrence is also provided for 4 of the 5 member species. Regional values are ranked for each group (in parentheses).

TABLE 4
CalCOFI Regions Ranked by Abundance for Member Species of Six Main Recurrent Groups of Larval Fish Species

Area	Central California		Southern California			Northern Baja California				Southern Baja California	
Region	4 (inshore)	5 (offshore)	7 (inshore)	8 (offshore)	9 (seaward)	11 (inshore)	12 (bay)	13 (offshore)	14 (seaward)	16 (inshore)	17 (offshore)
Group I											
Bathylagus wesethi	—	9	10	4	3	7	8	2	1	6	5
Ceratoscopelus townsendi	—	8	9	4	3	7	10	2	1	5	6
Diogenichthys atlanticus	11	5	10	8	2	7	6	3	1	9	4
Symbolophorus californiense	—	6	10	5	2	4	7	3	1	9	8
Vinciguerria lucetia	—	9	—	8	7	5	6	3	1	4	2
Group II											
Trachurus symmetricus	—	9	10	3	4	6	8	2	1	7	5
Triphoturus mexicanus	—	—	9	7	8	5	6	3	1	4	2
Group III											
Lampanyctus ritteri	9	6	10	5	3	2	7	4	1	11	8
Protomyctophum crockeri	7	5	9	3	4	6	8	2	1	11	10
Group IV											
Diogenichthys laternatus	—	—	7	—	—	6	4	5	3	2	1
Gonichthys tenuiculus	—	—	—	—	—	—	4	3	—	2	1
Group V											
Engraulis mordax	10	11	4	1	8	3	2	6	9	5	7
Leuroglossus stilbius	3	6	1	2	5	4	9	8	10	7	11
Merluccius productus	8	9	6	2	1	3	7	4	5	10	11
Stenobrachius leucopsarus	1	2	3	5	4	7	—	—	6	8	—
Group VI											
Bathylagus ochotensis	1	2	5	3	4	7	9	6	8	—	—
Turletonbeania crenularis	1	2	5	3	4	7	—	—	6	—	—

Regional abundance estimates (mean abundances, pooled cruises) from Loeb et al. (1983b).

TABLE 5
Relative Abundances of Group Member Species Within Regions of Species Co-occurrence in Samples, for Six Main Recurrent Groups of Larval Fish

Area	Central California		Southern California			Northern Baja California				Southern Baja California	
Region	4 (inshore)	5 (offshore)	7 (inshore)	8 (offshore)	9 (seaward)	11 (inshore)	12 (bay)	13 (offshore)	14 (seaward)	16 (inshore)	17 (offshore)
Group I											
Bathylagus wesethi	—	3	—	—	1	—	—	2	2	—	2
Ceratoscopelus townsendi	—	4	—	—	4	—	—	5	5	—	4
Diogenichthys atlanticus	—	1	—	—	2	—	—	3	3	—	3
Symbolophorus californiense	—	2	—	—	3	—	—	4	4	—	5
Vinciguerria lucetia	—	5	—	—	5	—	—	1	1	—	1
Group II											
Trachurus symmetricus	—	—	2	1	1	2	2	2	1	2	2
Triphoturus mexicanus	—	—	1	2	2	1	1	1	2	1	1
Group III											
Lampanyctus ritteri	2	2	2	2	2	2	2	2	2	2	—
Protomyctophum crockeri	1	1	1	1	1	1	1	1	1	1	—
Group IV											
Diogenichthys laternatus	—	—	—	—	—	—	1	—	—	1	1
Gonichthys tenuiculus	—	—	—	—	—	—	2	—	—	2	2
Group V											
Engraulis mordax	4	4	1	1	2	1	—	—	2	—	—
Leuroglossus stilbius	2	2	2	3	4	3	—	—	4	—	—
Merluccius productus	3	3	3	2	1	2	—	—	1	—	—
Stenobrachius leucopsarus	1	1	4	4	3	4	—	—	3	—	—
Group VI											
Bathylagus ochotensis	1	1	1	1	1	—	—	—	—	—	—
Turletonbeania crenularis	2	2	2	2	2	—	—	—	—	—	—

Ranked abundances based on pooled samples (all cruises) within each region (from Loeb et al. 1983b).

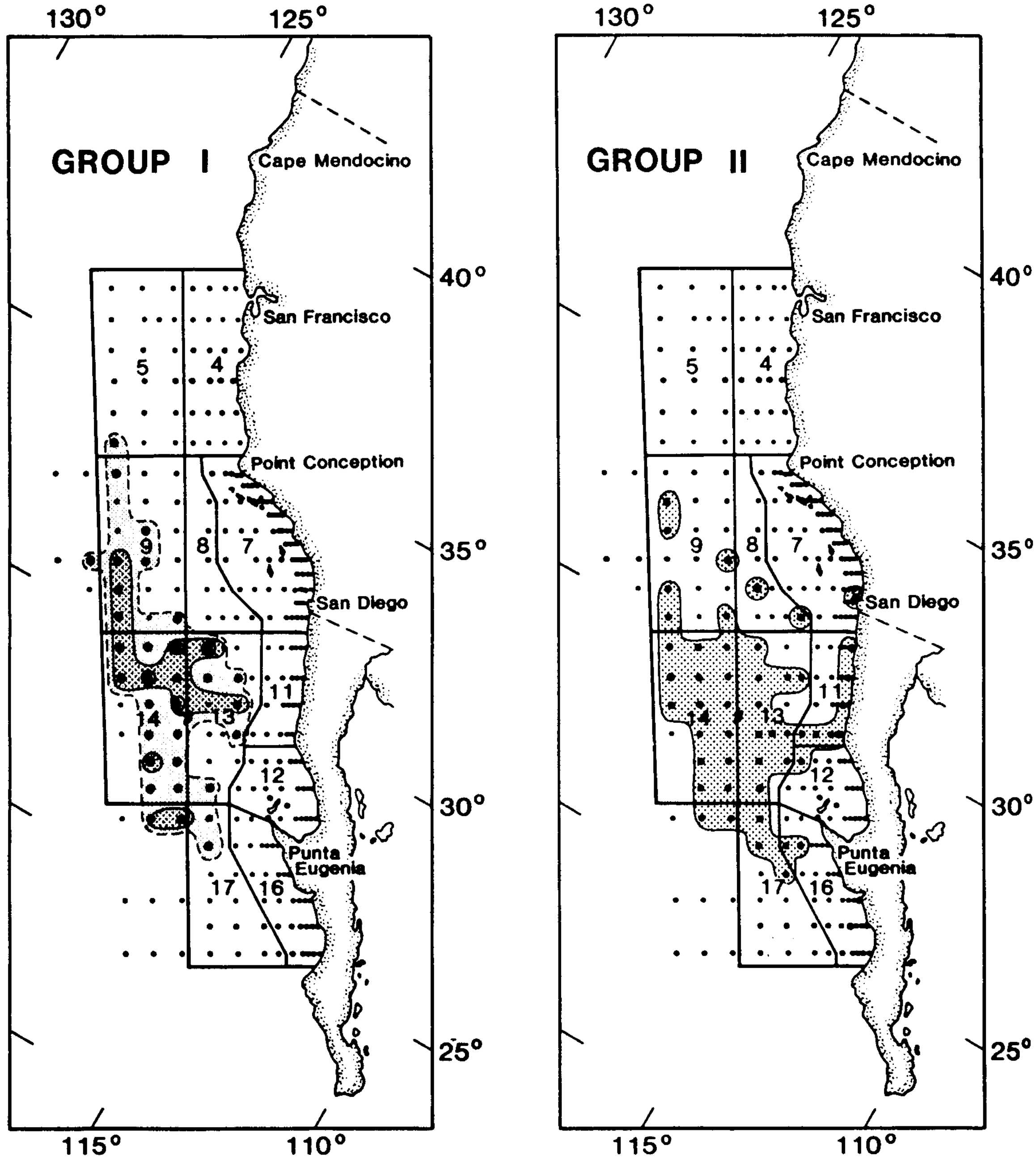

Figure 4. Geographical distributions of recurrent Group I and recurrent Group II in 1975 CalCOFI survey. Station locations are provided for co-occurrences of all five (dark stippling) and four of five (light stippling) Group I species and for both Group II species.

dall's concordance, $P < 0.05$). This is directly due to *Vinciguerria lucetia*'s dominance in southern regions 13, 14, and 17 and its rarity in northern regions 5 and 9; significant agreement of rank order of abundance ($P < 0.01$) exists among the four other species. There was no agreement on season of maximum abundance among the member species (Kendall's concordance, $P > 0.05$). *Diogenichthys atlanticus*, *Bathylagus*

TABLE 6
Cruises Ranked According to Abundances of Member Species of Six Main Recurrent Groups of Larval Fish Species

	Cruise					
	7412	7501	7503	7505	7507	7510
Group I						
Bathylagus wesethi	6	5	1	3	2	4
Ceratoscopelus townsendi	5	4	3	6	2	1
Diogenichthys atlanticus	3	2	1	5	6	4
Symbolophorus californiense	6	3	1	4	2	5
Vinciguerria lucetia	3	4	6	5	1	2
Group II						
Trachurus symmetricus	6	5	1	3	2	4
Triphoturus mexicanus	6	5	4	2	1	3
Group III						
Lampanyctus ritteri	5	1	2	4	3	6
Protomyctophum crockeri	3	1	2	4	5	6
Group IV						
Diogenichthys laternatus	4	3	1	6	2	5
Gonichthys tenuiculus	1	3	5.5	5.5	2	4
Group V						
Engraulis mordax	4	1	2	3	6	5
Leuroglossus stilbius	3	1	2	4	5	6
Merluccius productus	4	1	2	3	5	6
Stenobrachius leucopsarus	4	2	1	3	5	6
Group VI						
Bathylagus ochotensis	4	1	2	3	5	6
Tarletonbeania crenularis	6	5	4	2	3	1

Ranks based on cruise abundance estimates (pooled regions) presented in Loeb et al. (1983b).

wesethi, and *Symbolophorus californiense* had March abundance peaks; *Vinciguerria lucetia* and *Ceratoscopelus townsendi* were most abundant in July and October (Table 6).

The Group III member species (*Protomyctophum crockeri* and *Lampanyctus ritteri*) co-occurred throughout the CalCOFI area (Figure 5; Table 3), but their association throughout the year (all 6 cruises) was limited to offshore and seaward southern California and northern Baja California regions 9, 13, and 14. Maximum frequencies of co-occurrence were in northern Baja California region 14 (32% of all samples) and southern California region 9 (25% of all samples) (Table 3). The two species had significant concordance of abundance across regions (Kendall's tau test, $P < 0.01$), and both were most abundant in region 14 (Table 4). Both species had January-March abundance peaks (Table 6). In most regions and cruises *P. crockeri* was more abundant than *L. ritteri* (Table 5).

Group II species (*Trachurus symmetricus* and *Triphoturus mexicanus*) had a more restricted geographical and seasonal distribution than did Group III. There were few co-occurrences of the two species north of Baja California (Figure 4; Table 3); *T. symmetricus* was absent from December samples and was very rare in January samples (Table 6). The two species co-occurred most frequently from March to July in northern Baja California regions 11, 13, and 14 (Table 3), with maximum co-occurrences in seaward region 14 during April (83% of all samples) and July (93% of samples). They showed significant agreement as to regions of maximum abundance (13 and 14; Kendall's tau, $P < 0.01$). Peak abundances of *T. symmetricus* were in March, of *T. mexicanus*, in July (Table 6). Their relative abundances varied with region (Table 5) and cruise.

Group IV (*Diogenichthys laternatus* and *Gonichthys tenuiculus*) was the most geographically restricted group (Figure 5; Table 3). Co-occurrence was limited to southern regions, primarily central Baja California regions 16 and 17. Maximum frequency of co-occurrence and maximum abundances of both species were in region 17 during December and July; these maxima may be artifacts caused by undersampling of regions 16 and 17 during March and May (Table 1). *Diogenichthys laternatus* was consistently more abundant than *G. tenuiculus* (Table 5).

Co-occurrence of all four Group V species was primarily within the regions of central and southern California (Figure 6) and was limited to winter and spring. Highest frequencies of co-occurrence were within southern California regions 7, 8, and 9 during January and March, when all four species were captured together in from 25%-56% of the samples. The four species had different regions of maximum abundance and of frequency of occurrence (Kendall's concordance, $P > 0.05$ in both cases). *Engraulis mordax* (anchovy) was most abundant and frequent in offshore southern California region 8 and inshore northern Baja California regions 11 and 12; *Merluccius productus* (hake) in southern California offshore and seaward regions 8 and 9; *Stenobrachius leucopsarus* in southern California inshore and offshore regions 7 and 8; and *Leuroglossus stilbius* in central California inshore and offshore regions 4 and 5 (Table 4). Although species rank order of abundances within each region were somewhat consistent between cruises, there was no overall between-region agreement (Kendall's concordance, $P > 0.05$; Table 5). All four species had abundance peaks during January-March, and minimum abundances in July and October/November (Kendall's concordance, $P < 0.01$; Table 6).

Group VI was distributed within the five regions of central and southern California (Figure 6). In contrast to associated Group V, the member species of Group VI co-occurred throughout the year in their regions of maximum abundance (4, 5, and 8) (Table 4). *Bathylagus ochotensis* was overall the more abundant species (Table 5), but because of differing periods of peak abundance (Table 5; January-March for *B. ochotensis*, July-November for *Tarletonbeania crenularis*), species abundance relations within regions changed seasonally.

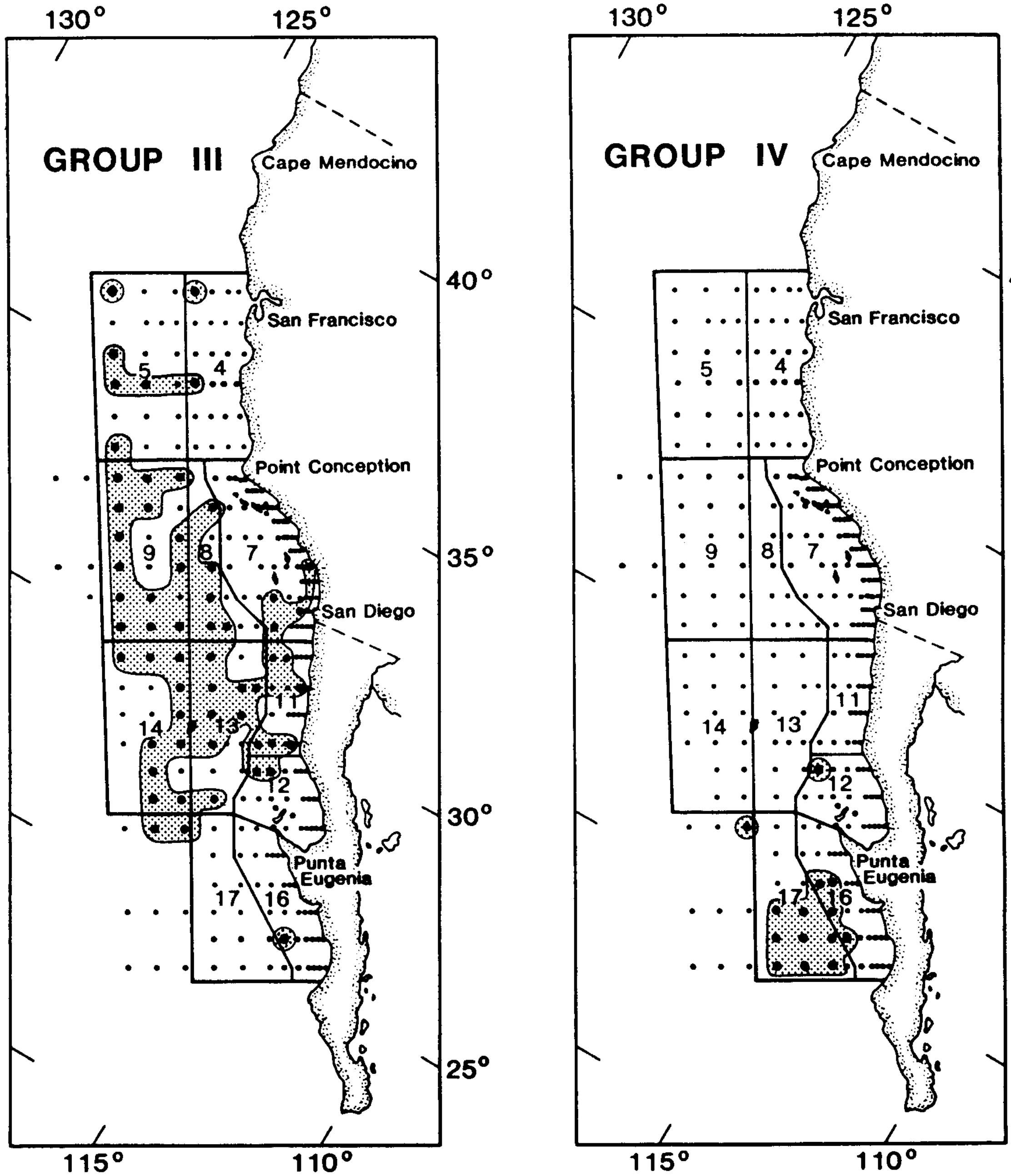

Figure 5. Geographical distributions of recurrent Group III and recurrent Group IV in 1975 CalCOFI survey. Station locations are provided for co-occurrences of both Group III species and both Group IV species.

DISCUSSION

The species forming the major groups (I and V) and their associated groups (II, III, IV, and VI) were the more abundant and widespread species in the CalCOFI area (Loeb et al. 1983b). The species composition of Groups I and V and their associated groups is in general agreement with the two subjectively determined species assemblages described in Loeb et al. 1983b

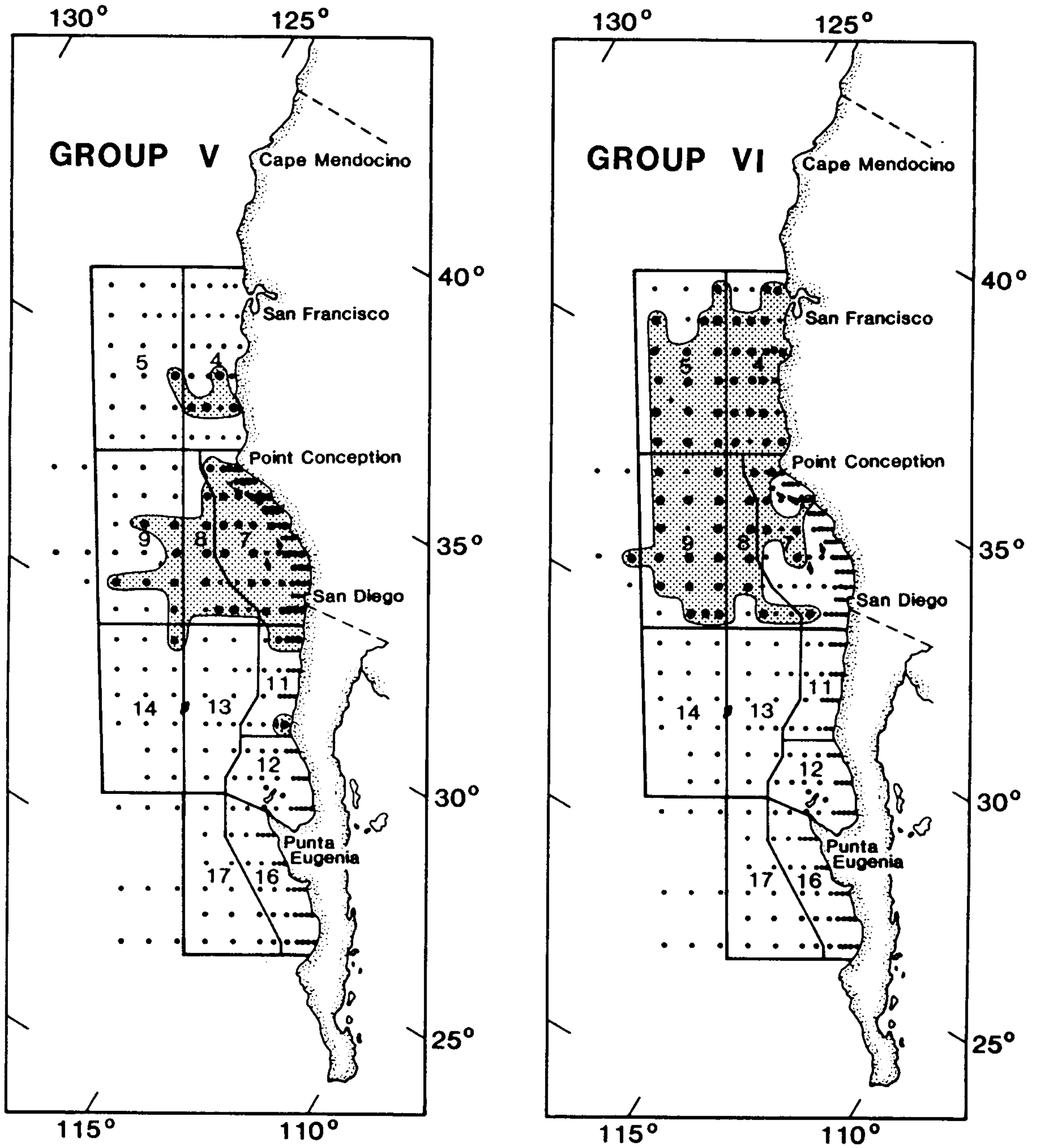

Figure 6. Geographical distributions of recurrent Group V and recurrent Group VI in 1975 CalCOFI survey. Station locations are provided for co-occurrences of all four Group V species and both Group VI species.

(i.e., species with mixed but predominantly warm-water affiliations and highest abundances in northern and central Baja California areas, and species with sub-arctic-transition zone or northern cold-water affiliations and highest abundances in central and southern California areas). This is probably due to the fact that in all cases the frequency of occurrence of group member species was significantly correlated with their abundance (rank difference correlation coefficients = 0.72-0.96; $P \leq 0.05$ in all cases). However, the objectively formed species groups (based on frequency of co-occurrence rather than on agreement of mean regional abundances) had more restricted geographical distributions (Figures 4-6) than did the subjectively determined assemblages. Group I and associated Group II and III members (predominantly warm-water mesopelagic species) were most frequent in the offshore and seaward regions of southern California and northern Baja California; associated Group IV species (eastern tropical Pacific forms) were restricted to central Baja California regions. Group V (anchovy, hake, and cold-water mesopelagic species) co-occurred most frequently in the southern California regions, and is quite similar to Southern California Bight Group I reported by Gruber et al. (1982); associated Group VI (cold-water mesopelagic species) was most frequent in the regions of central California and the offshore region of southern California.

The groups differed in constancy of species rank order of abundance. Although the members of Group III had widespread distributions, they had similar species rank order of abundance within their regions of maximum frequency of occurrence and between all regions within their distributional range. Group VI was less widely distributed, but also demonstrated between-region constancy. In contrast, Groups I and V had within-region similarity of species rank order of abundance across cruises but had significant between-region differences; Group II had significant differences in species abundance relations both within and between regions. The variability of rank order of abundance within Groups II and V may be related to seasonal and geographical differences in abundances of pelagic schooling species (anchovy and hake in Group V; jack mackerel in Group II). Marked between- and within-region differences in the relative abundances of the two Group V mesopelagic species, however, indicates that variability within this group was not restricted to the pelagic species. Group V variability may be partially due to greater heterogeneity and range of environmental conditions (i.e., coastal vs offshore differences) within the group's range. The geographical variability of rank order of abundance of Group I is primarily due to the northern distributional limit of one member species (*Vinciguerria lucetia*); the other four species have relatively constant abundance relations.

Environments of the Recurrent Groups

Recurrent group analysis identifies groups of species, based on co-occurrence in samples, which are likely to be frequent parts of one another's environment. Groups might then be investigated with respect to interspecific relationships of possible importance in controlling the distribution and abundances of the component species. Interspecific relations such as competition for limited food resources may be extremely important in the survival of larval fishes and their ultimate recruitment to adult populations. The groups identified here were based on geographical and seasonal co-occurrence. Because the data were derived from open oblique plankton tows in the upper ~ 200 m, we do not know if the group member larvae were in fact frequent parts of one another's immediate environments or were separated either vertically or horizontally. Larval depth vs abundance distributions of some of the species of the six major groups are available (Ahlstrom 1959), and are presented here as cumulative percent vs depth curves.

The curves for 8 of the 11 species of Group I and associated Groups II, III, and IV (Figure 7A) and for 5 of the 6 species of Group V and associated Group VI (Figure 7B) show a wide variety of depth-abundance distributions. Within Group I, two species (*D. atlanticus* and *S. californiense*) had similar distributions (K-S test, $P > 0.05$); most of these larvae occurred below those of *V. lucetia* and above those of *B. wesethi* ($P < 0.01$ in all four curve comparisons). The depth vs abundance distributions of the two Group II species also differed significantly ($P < 0.01$); most of the *T. symmetricus* larvae occurred above the *T. mexicanus* larvae. Additionally, only four of the total 21 intergroup comparisons showed similar species distributions. *Trachurus symmetricus* (Group II) had the shallowest distribution of the eight species considered (Figure 7A); this distribution resembled only that of *V. lucetia* (Group I) ($P > 0.05$). The distributions of *T. mexicanus* (Group II) and *L. ritteri* (Group III) were also relatively shallow and similar to each other and to *V. lucetia* (Group I) ($P > 0.05$ in all cases), but significantly different from those of the other four species. The species with deepest distributions—*D. laternatus* (Group IV) and *B. wesethi* (Group I)—were significantly different from each other and from all other species in the Group I and associated group assemblage ($P < 0.01$ in all cases).

The vertical distributions of the four Group V species (Figure 7B) differed significantly ($P < 0.05$). Associated Group VI species *T. crenularis* had a relatively shallow distribution similar to that of Group V species *S. leucopsarus* ($P > 0.05$); most *T. crenularis* larvae were significantly deeper than those of *E. mordax* (anchovy; $P < 0.01$) and shallower than those of *M. productus* (hake) and *L. stilbius* ($P < 0.01$).

It appears likely that although group members were frequently collected within the same locales and seasons they were probably not constant members of each

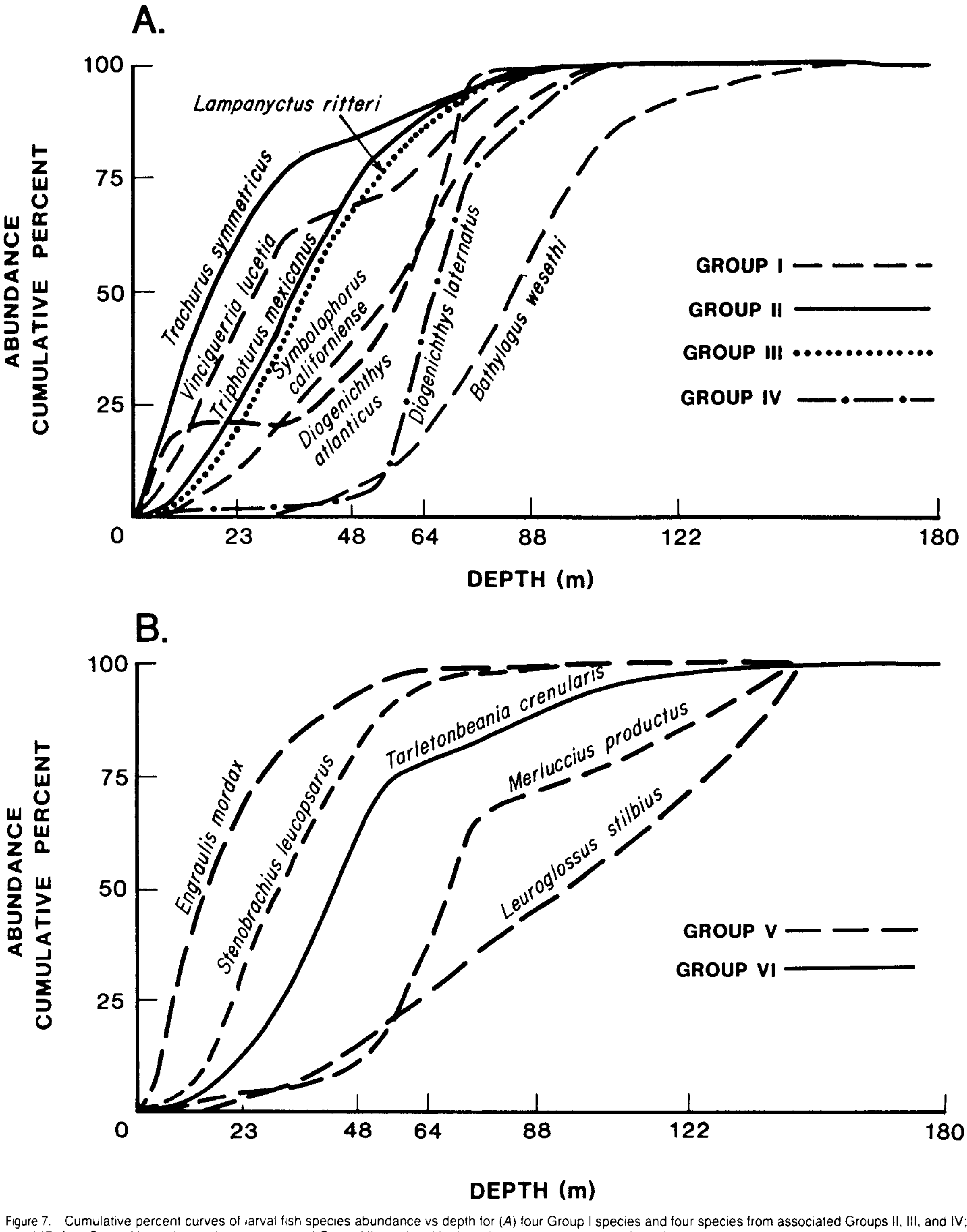

Figure 7. Cumulative percent curves of larval fish species abundance vs depth for (*A*) four Group I species and four species from associated Groups II, III, and IV; and (*B*) four Group V species and one associated Group VI species. Vertical abundance distributions from Ahlstrom (1959).

other's immediate environment (except for *D. atlanticus* and *S. californiense* of Group I) because of significantly different depth distributions. Also the group member species generally were not frequent parts of the immediate environments of species from associated groups.

In addition to vertical separation, there were seasonal abundance differences to further reduce the potential impact of interspecific relations within a group. The periods of peak abundances of two of the five Group I species differed from the others; peak abundance periods of both species within the Group II, IV, and VI species pairs differed significantly from each other; and timing of peak abundance of one of the four Group V species differed from the rest. Within Group V, the regions of maximum abundance of the member species differed, thereby further reducing the potential for interspecies impacts.

Because of within-group differences of seasonal, vertical, and (for Group V) geographical distributions, it is probable that, within each group, ecologically important interactions such as direct competition for limited food resources are minimal. This indicates that (based on the present data) within the CalCOFI area such interspecific processes during the larval stages are likely to be negligible in controlling fish species abundances and distributions. However, more detailed vertical distribution information is definitely needed to verify this observation.

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