LARVAL FISH ASSEMBLAGES IN THE CALIFORNIA CURRENT REGION, 1954–1960, A PERIOD OF DYNAMIC ENVIRONMENTAL CHANGE

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ABSTRACT

Analysis of nearly 200 taxa of fish larvae from CalCOFI surveys in 1954–60 placed 30 taxa into nine recurrent groups. Two complexes of four recurrent groups each were formed by extensive interlinking among the groups. A "northern" complex represents the subarctic-transitional fauna and the coastal pelagic fauna and its associates. A "southern" complex incorporates transitional, warm-water cosmopolite and eastern tropical Pacific taxa. One recurrent group was associated with the extensive continental shelf area of Bahía Sebastián Viscaíno and the Punta Abreojos-Cabo San Lázaro Bight. Oceanographic changes between the cold 1955–56 period and the warm 1958–59 period changed the boundary between the two pelagic complexes and altered the onshore-offshore distribution of the fauna. There was much variability in the constitution of the recurrent groups within the complexes and some change in the degree of overlapping species distributions among the complexes over the seven-year period from 1954 to 1960. The northern-southern complex structure was similar to that described in a previous analysis of data from 1975.

RESUMEN

El análisis de casi 200 taxa de larvas de peces colectados por CalCOFI durante los años 1954–60 ubicó 30 taxa en nueve grupos recurrentes. Extensas interrelaciones entre los grupos recurrentes dieron como resultado dos complejos con cuatro grupos recurrentes cada uno. Un complejo "norteño" representa la fauna subártica-transicional y la fauna pelágica costera y sus asociados. Un complejo "sureño" incorpora taxa cosmopolitas transicionales de aguas cálidas y taxa del este del Pacífico tropical. Un grupo recurrente está asociado con la extensa plataforma continental en el área de las bahías Sebastián Vizcaíno y Punta Abreojos-Cabo San Lázaro. Los cambios oceanográficos ocurridos entre el período frío de 1955–56 y el período cálido de 1958–59 modificaron el límite entre los dos complejos pelágicos y alteraron la distribución perpendicular a la costa de la fauna. Durante un período de siete años, 1954–60, la formación de los grupos recurrentes dentro de los complejos presentó gran variabilidad; a la vez, se observó algunos cambios en el grado de superposición de las distribuciones de especies entre los complejos. La estructura norte-sur de los complejos es similar a aquella descrita en un previo análisis de datos.

INTRODUCTION

A principal task of ecologists is to define the boundaries of communities. In pelagic ecology the task is made difficult by fluid boundaries controlled by meteorological, bathymetric, and oceanographic factors. The composition and structure of planktonic and nektonic communities of the California Current and adjoining regions have been studied extensively over the past 50 years. Broadscale community analyses (Fager and McGowan 1963; McGowan 1971) and distributional studies (Brinton 1962; Ebeling 1962; Alvariño 1964; Reid et al. 1978) showed that water masses in the North Pacific have highly characteristic faunas, confirming the findings of earlier workers (see Sverdrup et al. 1942; Ekman 1953). Subsequent distributional and community studies provided additional faunal definitions of these water masses: central—McGowan and Walker (1979), Venrick (1979), Loeb (1979, 1980), Barnett (1983, 1984); eastern tropical Pacific—Ahlstrom (1971, 1972a), Brinton (1979); subarctic—Parin (1961), Richardson and Pearcy (1977), Richardson et al. (1980), Kendall and Clark (1982), Willis (1984).

The transitional nature of the California Current region is reflected in its fauna, which is a mixture of species that occur in adjacent water masses, and some endemic species (Figure 1). The fish fauna has been studied intensively, leading to community analyses of the nearshore environment (Horn and Allen 1978; Allen 1985); the Southern California Bight region (Gruber et al. 1982); the coastal demersal habitat (Mearns 1974; Allen 1982); and the offshore mesopelagic zone (Ebeling et al. 1970). Loeb et al. (1983) examined the composition and structure of the ichthyoplankton occurring in the

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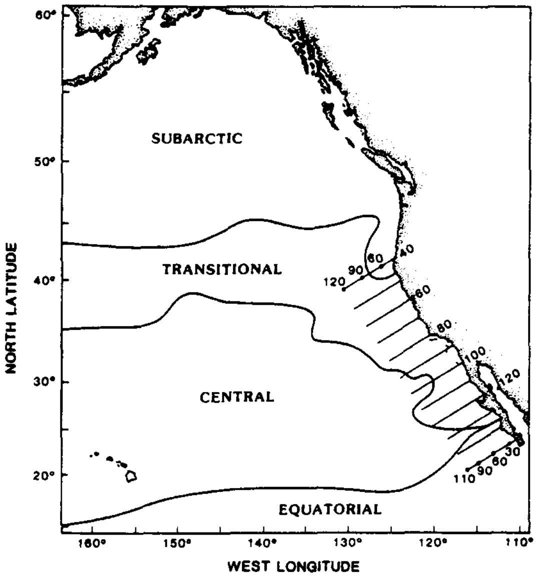

Figure 1. Four major zoogeographic zones in the northeast Pacific as defined by Brinton (1962). The boundaries represent the 50% margins of incidence of the euphausiid shrimp species that characterize these faunal zones. Cardinal lines and selected stations of the basic CalCOFI sampling pattern are shown.

California Cooperative Oceanic Fisheries Investigations (CalCOFI) sampling area during 1975.

This paper is the first step in analyzing community dynamics over the entire CalCOFI time series, from 1949 to the present. Recent progress in establishing a computer data base for CalCOFI ichthyoplankton time series has allowed us to study the seven-year period from 1954–60, which was characterized by maximum areal and seasonal sampling coverage during a seqnence of anomalously cold and warm oceanographic regimes. In this paper we describe the ichthyoplankton assemblages of the California Current region represented by the 1954–60 data base and examine the changes in these assemblages in relation to major oceanographic changes during that period.

Interannual and seasonal oceanographic changes in the California Current region have been studied extensively (Reid 1960; Chelton 1981; Lynn and Simpson, in press), and much attention has been directed to how these changes affect the distribution and abundance of organisms (Bakun 1985; Bakun and Parrish 1982; Chelton et al. 1982; Fiedler et al. 1986; Lasker 1978; Mullin and Brooks 1970; Smith 1985; Smith and Eppley 1982; Smith and Lasker 1978). For our analysis we assembled the CalCOFI oceanographic data from the 1954–60 period into unique sets of files. This allowed us to describe oceanographic changes in relation to changes in larval fish assemblages and their component taxa.

MATERIALS AND METHODS

This study was based on 907,000 fish larvae from 11,500 plankton net tows taken on annual CalCOFI surveys during the seven-year period from 1954 to 1960. Larvae were identified to species or the lowest taxon possible. Of 191 taxa there were 97 species and 39 generic, 51 familial, and 9 ordinal categories. The distribution of taxonomic categories differs from the original set because identifications were improved during the editing and verification of the data base (Ambrose et al., in press a, b; Sandknop et al., in press; Stevens et al. in press a, b; Sumida et al., in press a, b).

Detailed descriptions of the field and laboratory methods employed in sampling the fish larvae used in this study were described in Kramer et al. (1972). Almost all samples can be associated with 10-m temperature and salinity data taken from the same ship within the hour and within hundreds of meters. (Anon. 1963) Geostrophic flow has been analyzed from most of these cruises from approximately a third of the stations (Wyllie 1966).

In this study, larval fish assemblages were described by recurrent group analysis (Fager 1957, 1963; Fager and McGowan 1963). This analysis determines groups of taxa that occur together relatively frequently and are consistently part of each other's environment. Two major procedures are involved in the analysis—the calculation of an index of affinity (program name AFFINITY) for each pair of taxa that ever occur together in a plankton sample, and the formation of groups of taxa (program name REGROUP) based on a chosen minimum index value (0.3 for this work)[1]. The category "group member" is supplemented by the term "associate" for taxa that have significant affinity indices with one or more but not all group members in one or more groups, and "affiliate" for any remaining taxon that is related to a group by having its highest affinity index (always < 0.3) with a group member. To gain a hierarchical view of the relationships of the principal taxa, the REGROUP procedure was applied to the combined 1954–60 data set at three higher critical affinity levels (0.4, 0.5, and 0.6).

The equation for the affinity index is:

$$I = \frac{N_j}{\sqrt{N_a \cdot N_b}} - \frac{1}{2 \cdot \sqrt{N_b}}$$

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[1] Programs, written in Turbo-Pascal, are available from the authors.

where I is the affinity index,

N_j is the number of joint occurences;

N_a is the number of occurrences of taxon a, the less common taxon, and

N_b is the number of occurrences of taxon b, the more common taxon.

The second term in the equation is a correction factor, which adjusts the affinity index according to the sample size. The correction factor is small for the more common taxa. The first term is the geometric mean coincidence. The consequence of the correction factor is that a pair of organisms would have to coincide 52% of the time to have an affinity index of 0.3 if number of occurrences of the commoner taxon were 5; 37% of the time if the number of occurrences of the commoner taxon were 50; but only 31% of the time if the number of occurrences of the commoner taxon were 5,000.

The oceanographic data used in this study are a compilation of physical and chemical observations made in conjunction with the plankton net tows on CalCOFI survey cruises. The data were processed by the Scripps Institution of Oceanography and published in a series of data reports (cited in Eber and Wiley 1982). For the purpose of documenting the changes in oceanic conditions that occurred during the 1957–59 El Niño, the CalCOFI oceanographic data were separated into two periods: 1955–56 (13 cruises) and 1958–59 (24 cruises).

Over much of the region, the largest differences between the two periods did not occur at the surface, but at depths varying from 30 to 100 meters. Therefore, rather than selecting discrete depths for this overview, we computed averages of oceanographic parameters for the upper 100 meters using data from five standard depths: 10, 30, 50, 75, and 100 meters. For mapping the parameters, we rejected stations at locations where depth to bottom was less than 100 meters to avoid bias associated with vertical gradients. We used harmonic coefficients to compute mean values for oceanographic parameters at each CalCOFI station. These coefficients, based on data from all CalCOFI cruises from 1950 to 1978, were computed for each CalCOFI station by the method of least squares fit to a mean annual cycle.

Anomalies of oceanographic parameters for standard depths on individual CalCOFI cruises were determined by computing deviations from the harmonic means. Anomalies of temperature and salinity were obtained in this way for cruises in each of the selected periods. We analyzed each group of anomalies on a two-dimensional grid fitted to the CalCOFI station pattern. We then subtracted the grid, or matrix, of 1955–56 anomalies from that for the 1958–59 anomalies to obtain charts of differences between the periods.

We examined the association between species distribution and oceanographic characteristics in two adjacent offshore areas of the CalCOFI survey region, between Point Conception, California, and Punta Eugenia, Baja California. These areas include that portion of the CalCOFI station pattern between lines 80 and 120, separated by line 100. The northern area is in the southern fringe of the habitat of two subarctic-transition species, *Stenobrachius leucopsarus* and *Tarletonbeania crenularis*. The southern area is in the northern fringe of the habitat of two eastern tropical Pacific species, *Vinciguerria lucetia* and *Diogenichthys laternatus* (Moser and Ahlstrom 1970; Ahlstrom 1972b). CalCOFI net-tow data from cruises conducted during 1954–56 and 1958–60 were scanned for occurrences of these species in the respective areas.

The data for each of the four species were separated into two categories, one representing samples containing no larvae of the targeted species and the other representing samples containing larvae in excess of a fixed threshold number for each species. The threshold (positive) counts were 10 for *S. leucopsarus* and *V. lucetia*, and 3 for *T. crenularis* and *D. laternatus*. The CalCOFI station codes and cruise dates for each category were then used to separate the oceanographic data into two corresponding groups for each species.

The purpose of this exercise was to test whether the presence or absence of these species provided sufficient criteria to partition the oceanographic data into distinctively different groups. Accordingly, all of the data collected at each station within each area were combined into two temperature-salinity profiles for each species, corresponding to the two categories of larval occurrence (zero or positive). After discarding those stations not represented by both categories (for each species), to avoid geographical bias, we combined the station profiles into a single pair of area profiles for each species.

OCEANOGRAPHY

General Description

The California Current region is bordered by three water masses: subarctic to the north, Pacific central to the west, and equatorial to the south (Tsuchiya 1982). The California Current begins as

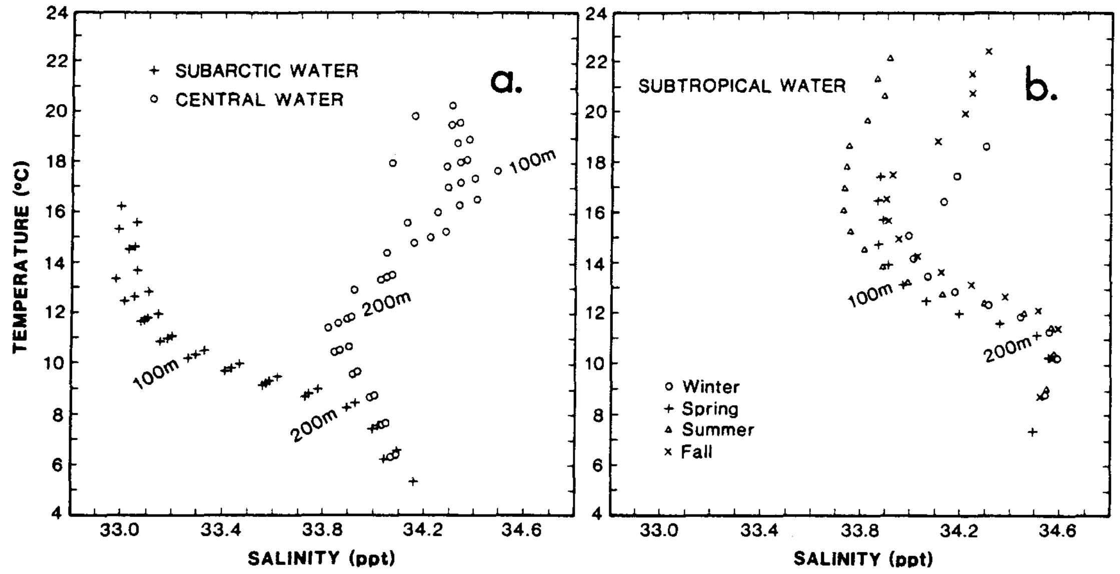

Figure 2. Mean seasonal temperature-salinity plots for modified subarctic water and Pacific central water (*a*) and subtropical water (*b*) in the California Current region. The symbols are plotted for discrete values of sigma-t at intervals of 0.2 g/l.

the southward-turning branch of the transpacific West Wind Drift, with characteristics of subarctic water. As the current proceeds southeastward, these characteristics are modified by excess heating, evaporation, and by intrusion of water from the west and south (Hickey 1979). Further modification is caused by entrainment of mesoscale eddies of upwelled water from coastal areas (Lynn and Simpson, in press).

The peripheral water masses' influence on California Current water can be seen in mean temperature-salinity (T-S) relationships in the upper few hundred meters at different locations (Figure 2). The symbols on the T-S curves were plotted at constant intervals of sigma-t (0.2 g/l). Each symbol represents a seasonal mean, so that their spread along constant sigma-t lines is a measure of seasonal variation. This variation is particularly large in the upper 100 m of modified subtropical water and shows the reciprocating influences of the California Current in summer, and of intrusion from the south in winter. The core of the California Current in the northern portion, 330–370 km off San Francisco on CalCOFI line 60, reflects subarctic water, with cool temperatures and low salinities near the surface. Below 100 m the salinity increases rapidly with depth. The effect of mixing with central water is evident farther west, 1,040–1,180 km seaward from the Southern California Bight along lines 80 and 90. This area reflects the warm temperatures and high salinities of central water in the upper 100 m, with salinities decreasing with depth to a minimum at about 200 m. Equatorial water moving northward along the Baja California coast also mixes into the California Current and is most evident in the southern portion, about 300 km offshore, along lines 133 and 137. Like central water, equatorial water is warm near the surface, but in the layers below 100 m, salinities increase rapidly with depth.

The southern boundary of the subarctic water mass is called the subarctic front. It is found at 40°–43° north, west of 150° west. To the east of that longitude it turns southeast and forms the western boundary of the California Current, where it has been called the California front. The northern boundary of the North Pacific central water is called the subtropical front. It is found at about 31° north, west of 140° west, and also bends southeast at its eastern end. In the transition zone between these fronts is another front, described by Lynn (1986) as the northern subtropical front. At their southern extremes, these fronts become diffuse, and the extension of the California Current turns westward and joins the North Equatorial Current.

It is important to note that the positions of these boundaries may fluctuate. During the period of this study, in particular, the position of the subarctic front at the North American coastline shifted from 40° north before 1957 to 53° north in 1957–58. Moreover, the waters of the California Current and adjacent zones may contain eddies of tens to hundreds of kilometers in extent. Thus there is a considerable amount of exchange and mixing that must be considered in describing a planktonic fauna in terms of water-mass characteristics and boundaries.

Changes during 1955–60

Long-term annual means in the upper 100 m range from 11° to 18°C for temperature and from 33 to 34 ppt salinity. (Figure 3a, b). The temperature pattern shows the expected warming from north to south and also from inshore to offshore. Salinity increases from north to south and, in the northern part of the pattern, decreases from inshore to offshore out to the core of the California Current. The latter appears as a trough in the salinity field about 330 km from the coast.

A chart of temperature anomaly differences (Figure 3c) reveals that the 1958–59 period was warmer than the 1955–56 period throughout the region. The differences were greatest (exceeding 3°C) in the southern portion and, except for an area south of Punta Eugenia, were greater offshore than inshore. The corresponding chart for salinity anomaly shows that salinities were higher in 1958–59 in the southern portion of the region, with positive differences exceeding 0.4 ppt in the farthest offshore area (Figure 3d). The northern portion, however, had higher salinities in 1955–56 in inshore areas and out to nearly 200 km from the coast.

These charts reflect a northward shift of the contours from 1955–56 to 1958–59, particularly in the temperature field. The displacements of the 12°, 14°, and 16° contours between these periods were approximately 220 km (Figure 4). This shift is reflected by changes of temperature and salinity anomalies along CalCOFI line 100 (off Ensenada, Baja California) during the two periods (Figure 5).

It has been suggested that the lower temperatures in 1955–56 might be associated with stronger northwest winds that would contribute to increased upwelling inshore, and to southward transport offshore in the California Current. We attempted to compare southward transports in the 1955–56 and 1958–59 periods by mapping dynamic height anomalies for the sea surface, relative to 500 m, as a representation of geostrophic flow. The principal differences between the two periods were found in the values of dynamic height; those representing the 1958–59 period were larger by up to 0.08 dynamic meters over much of the region. However, a comparison of gradients of dynamic height anomalies (as indices of transport) along CalCOFI lines 60 to 110 was inconclusive.

RECURRENT GROUPS

Recurrent group analysis was applied to the entire data set of 192 taxa for the seven-year period from 1954 to 1960 and also to each of the seven years (Figures 6 and 7). From the recurrent group analysis of the composite seven-year set, 30 taxa formed 9 groups (2 groups with 5 taxa each, 2 with 4, 2 with 3, and 3 with 2), and 8 other taxa formed associate relationships with taxa in 1 or more of the 9 groups (Figure 6).[2] Intergroup affinities formed 2 large complexes, each consisting of 4 recurrent groups, and 1 isolated southern shelf recurrent group (SYNODUS). We refer to these as the northern and southern complexes, since their member taxa had predominately cold- or warm-water distributions, or affinity indices linking them to cold- or warm-water taxa. The SYNODUS group was the primary constituent of a southern shelf complex, which was more fully characterized in analyses of individual years. There were 12 recurrent group members in the northern complex, 14 in the southern complex, and 4 in the isolated SYNODUS recurrent group (Table 1). There were 2 unique associates in the northern complex, 5 unique associates in the southern group, and 1 unique associate in the SYNODUS group. There were 53 affiliated taxa in the northern group, 68 affiliates in the southern complex, and 33 in the SYNODUS recurrent group (Appendix). The significant affinity index between *Engraulis mordax* and *Triphoturus mexicanus* was the only link between the northern and southern complexes.

Northern Complex

In the northern complex the LEUROGLOSSUS group had 5 taxa, CITHARICHTHYS had 3 taxa, and TARLETONBEANIA and SARDINOPS had 2 taxa each (Figure 8). Members of the northern complex over the seven-year period can be found through the survey area in the north-south plane but were more likely to be found nearshore when in the southern reaches. The LEUROGLOSSUS and TARLETONBEANIA groups

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[2] Two additional pairs of taxa formed two isolated groups. One of these, comprising Serranidae and Carangidae, was based on relatively few (43) occurrences; the other, comprising Balistidae and Fistulariidae, was formed by a single co-occurrence.

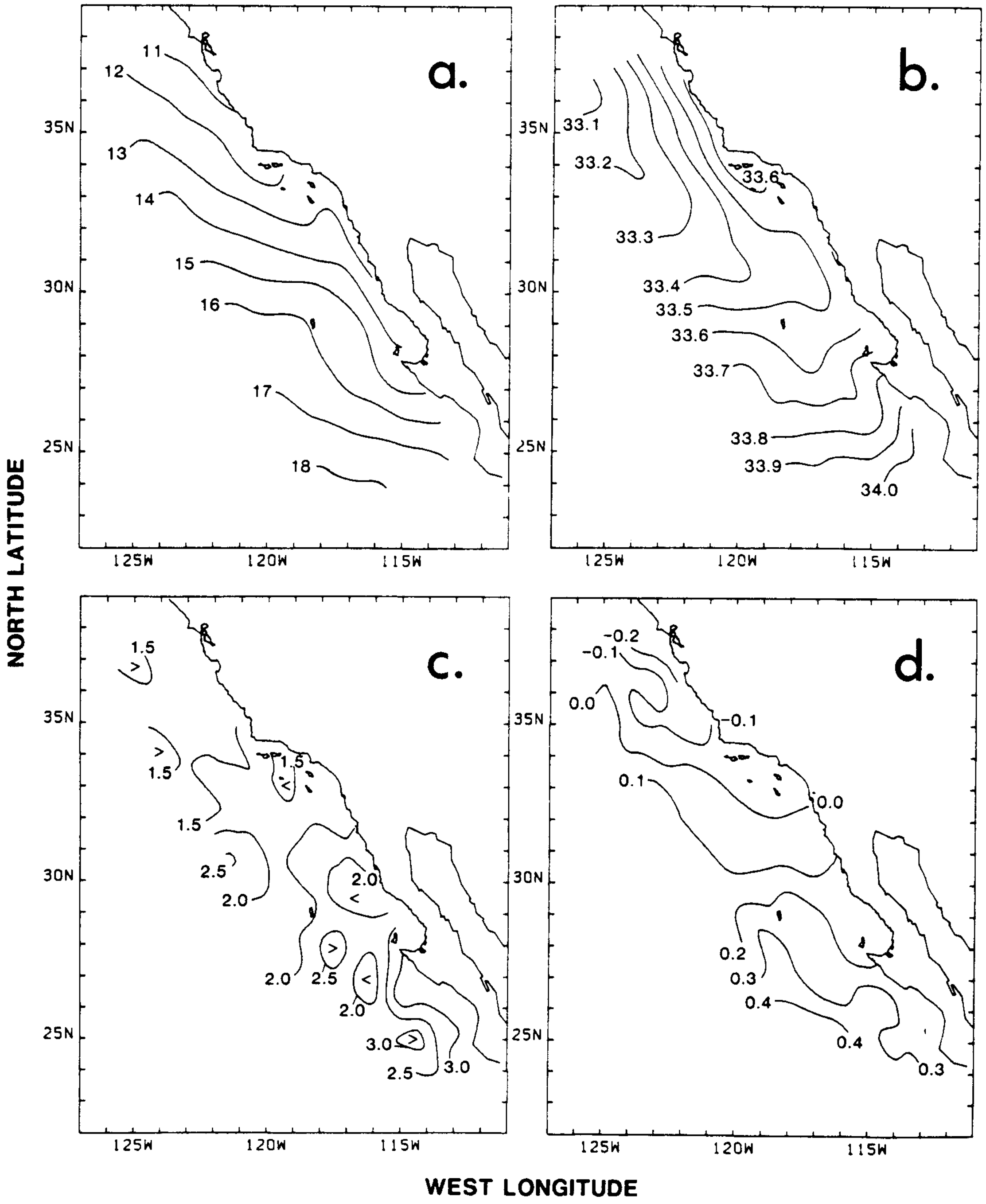

Figure 3. Mean annual temperature (*a*) and salinity (*b*) of the upper 100 meters computed at 5 standard depths (10 m, 30 m, 50 m, 75 m, and 100 m) from harmonic coefficients based on data from CalCOFI cruises from 1950 through 1978. Change, or difference, in the deviations of temperatures (*c*) and salinities (*d*) in the upper 100 meters from the harmonic means, between the periods 1955–56 and 1958–59.

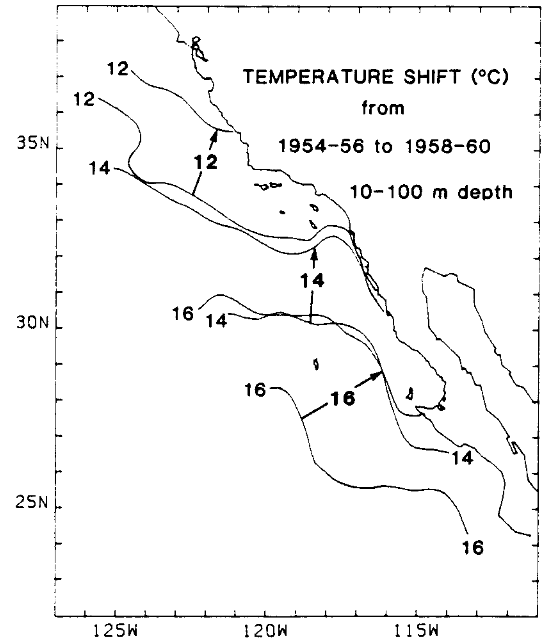

Figure 4. Temperature change in the upper 100 meters between 1955–56 and 1958–59 as depicted by the displacements of the 12°, 14°, and 16°C isotherms between the two periods.

were separated in part by the tendency of the former group to spawn in summer (Table 2). There were significant affinities between *Tarletonbeania crenularis* and 3 of the 5 members of the LEUROGLOSSUS group. Although the distribution of the TARLETONBEANIA group leads one to believe that it was somewhat more northerly than the LEUROGLOSSUS group, this may be because the cruises proceeded farther north in summer, when this group was spawning.

LEUROGLOSSUS recurrent group. This group is made up of 2 mesopelagic argentinoid smelts (*Bathylagus ochotensis* and *Leuroglossus stilbius*), a vertically migrating mesopelagic myctophid (*Stenobrachius leucopsarus*), a schooling gadoid (*Merluccius productus*), and the scorpaenid genus (*Sebastes* spp.), which includes about 60 species in the survey area (Table 2). Faunal associations of the 4 species are subarctic-transitional or transitional; their spawning is highly seasonal, with winter or spring maxima (Table 2). The fifth taxon, the rockfishes of the genus *Sebastes*, is broadly distributed from boreal to transitional waters and has a composite fall-to-spring spawning season with a February peak in the survey area (Table 2).

The distribution for the LEUROGLOSSUS group in the survey area was centered in the Southern California Bight region (Figure 9), reflecting the geographic distribution of *L. stilbius* larvae (Table 3). Populations of *B. ochotensis* and *S. leucopsarus* have more northerly distributions, extending across the subarctic Pacific; their larvae were found predominately in the northern part of the survey pattern, off northern and central California (Table 3). Larvae of *L. stilbius* and *S. leucopsarus* have a more shoreward distribution than *B. ochotensis* larvae. Adults of *M. productus* have a broad distribution from the boreal region to Baja

TABLE 1
Numbers of Larval Fish Taxa That Are Members, Associates, or Affiliates of Recurrent Groups in an Analysis of Pooled Data from CalCOFI Surveys, 1954–60

Complex	Group name	Members	Associates	Unique associates	Affiliates
Northern					
	LEUROGLOSSUS	5	4	0	19
	CITHARICHTHYS	3	7	1	21
	SARDINOPS	2	3	0	5
	TARLETONBEANIA	2	3	0	8
	Subtotal	12	*	1	53
Southern					
	SYMBOLOPHORUS	5	7	1	16
	VINCIGUERRIA	4	6	2	32
	TRIPHOTURUS	3	10	0	9
	CERATOSCOPELUS	2	4	0	10
	Subtotal	14	*	3	66
Southern shelf					
	SYNODUS	4	0	1	32
Total		30	*	5	151

*Not unique sets

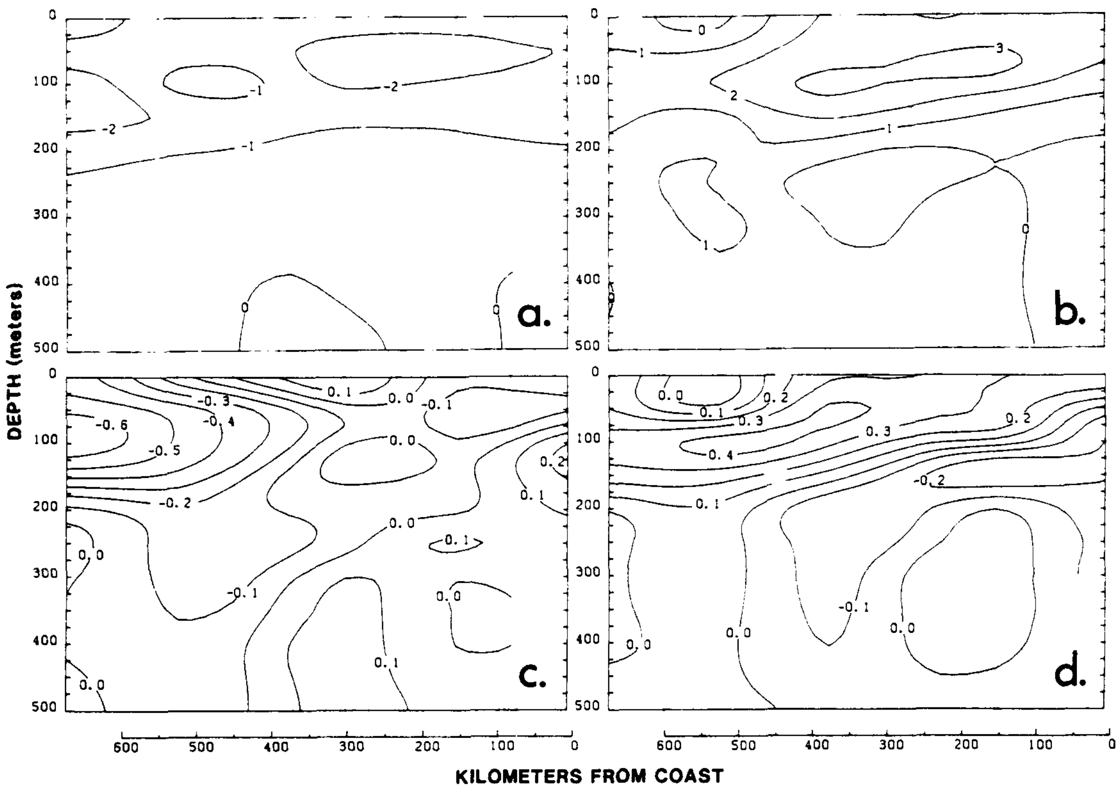

Figure 5. Mean temperature anomaly pattern along CalCOFI line 100 in the upper 500 meters, 1955–56 (*a*), and 1958–59 (*b*). Mean salinity anomaly pattern (computed in the same way) for 1955–56 (*c*) and 1958–59 (*d*). The isopleths represent deviations from harmonic means based on the period 1950–78.

California, with a postulated migration to spawning grounds off southern California and northern Baja California. The high mean abundance off southern Baja California may represent a few anomalously large collections in winter (Table 3). Larvae of *Sebastes* spp. were concentrated in the shoreward regions off California and northern Baja California.

The LEUROGLOSSUS group was strongly connected with other groups of the northern complex. Four of the group taxa had strong affinities with *Engraulis mordax*; 3 had affinities with *Sardinops sagax*; and 3 had affinities with *Tarletonbeania crenularis* (Figures 6 and 8).

TARLETONBEANIA recurrent group. This group comprises a vertically migrating mesopelagic myctophid (*Tarletonbeania crenularis*) and an epipelagic oceanic stromateoid (*Icichthys lockingtoni*). Adults of *T. crenularis* range from British Columbia to central Baja California. The range for *I. lockingtoni* is similar in the south, but extends westward to the Gulf of Alaska and Japan. These two species have well-defined spawning seasonality, with summer maxima (Table 2).

The distribution of the group was coincident with the LEUROGLOSSUS group (Figure 9), and members of the 2 groups would have higher affinity indices if the spawning seasons were coincident. Larval distributions for the 2 species in the TARLETONBEANIA groups were concentrated heavily in northern and central California, with a strong peak in northern California for larvae of *T. crenularis* (Table 3).

CITHARICHTHYS recurrent group. This group comprises a coastal pelagic anchovy (*Engraulis mordax*) and 2 shallow-water paralichthyid flatfishes (*Citharichthys fragilis* and *C. xanthostigma*). *E. mordax* has a broad coastal distribution from

TABLE 2
Taxonomic Composition of Recurrent Groups, Number of Observations (1954–60) and Distribution and Spawning Seasons of Members

Recurrent group taxa	Number	Faunal association	Adult habitat	Spawning season /peak month
Northern Complex				
LEUROGLOSSUS group				
Bathylagus ochotensis	1172	S-T	MP (49–901 m)	Win-Spr/May
Leuroglossus stilbius	3011	T	MP (to 690 m)	Spr/Mar
Stenobrachius leucopsarus	2440	S-T	MP (MEP)	Spr/Feb-May
Sebastes spp.	4486	S-T,T	D (to 732 m)	Fall-Spr/Feb-Mar
Merluccius productus	3027	S-T	D (to 914 m)	Win-Spr/Feb-Mar
TARLETONBEANIA group				
Tarletonbeania crenularis	1044	S-T	MP (MEP)	Spr-Sum/May-Jul
Icichthys lockingtoni	634	S-T	EP (to 91+ m)	Sum/Jun-Jul
CITHARICHTHYS group				
Engraulis mordax	5098	T	CP (to 219 m)	Ext/Feb-Mar
Citharichthys fragilis	819	T,SbTr	D (18–347 m)	Bim/Aug,Feb
Citharichthys xanthostigma	980	TtoTr	D (2–200 m)	Bim/Aug,Feb
SARDINOPS group				
Sardinops sagax	1479	T	CP	Ext/Jan-Mar, Aug-Sep
Scomber japonicus	513	T,SbTr	CP	Sum/Aug
Southern Complex				
SYMBOLOPHORUS group				
Bathylagus wesethi	1913	T	MP (40–1,001 m)	Spr-Sum/May
Cyclothone spp.	1784	WWC	MP	Sum-Fall/Aug
Diogenichthys atlanticus	734	WWC	MP (MEP)	Bim/May,Sep-Oct
Lampanyctus ritteri	2288	S-T	MP (MEP)	Spr/May
Symbolophorus californiensis	966	T	MP (MEP)	Spr/May
TRIPHOTURUS group				
Triphoturus mexicanus	4648	SbTr	MP (MEP)	Sum/Aug
Protomyctophum crockeri	2303	T	MP	Spr/May
Trachurus symmetricus	2096	T	EP (to 183 m)	Spr-Sum/May,Jun
CERATOSCOPELUS group				
Ceratoscopelus townsendi	988	T	MP (MEP)	Sum/Aug
Lampadena urophaos	307	SbTr	MP (MEP)	Sum/Aug
VINCIGUERRIA group				
Vinciguerria lucetia	4288	ETP	MP (MEP)	Ext/Aug
Diogenichthys laternatus	2203	ETP	MP (MEP)	Ext/Jan-Feb,Aug-Oct
Gonichthys tenuiculus	537	ETP	MP (MEP)	Ext/Feb
Hygophum atratum	444	ETP	MP (MEP)	Bim/Jan,Aug
Southern Coastal Complex				
SYNODUS group				
Synodus spp.	402	SbTr,Tr	D (to 50 m)	Fall/Sep-Dec
Prionotus spp.	132	SbTr,Tr	D (15–110 m)	Sum-Fall/Aug-Sep
Ophidion scrippsae	192	T,SbTr	D (3–70 m)	Sum-Fall/Aug-Sep
Symphurus spp.	351	T,Tr	D (1–201 m)	Sum-Fall/Aug-Sep

Abbreviations:

S = subarctic, T = transition, SbTr = subtropical, Tr = tropical, WWC = warm-water cosmopolite, ETP = eastern tropical Pacific, MP = mesopelagic, MEP = migrates to epipelagic, EP = epipelagic, D = demersal, CP = coastal pelagic, Bim = bimodal, Ext = extended.

Information on the distribution of adult fishes summarized from Miller and Lea (1972), Eschmeyer et al. (1983), Wisner (1976), and original data.

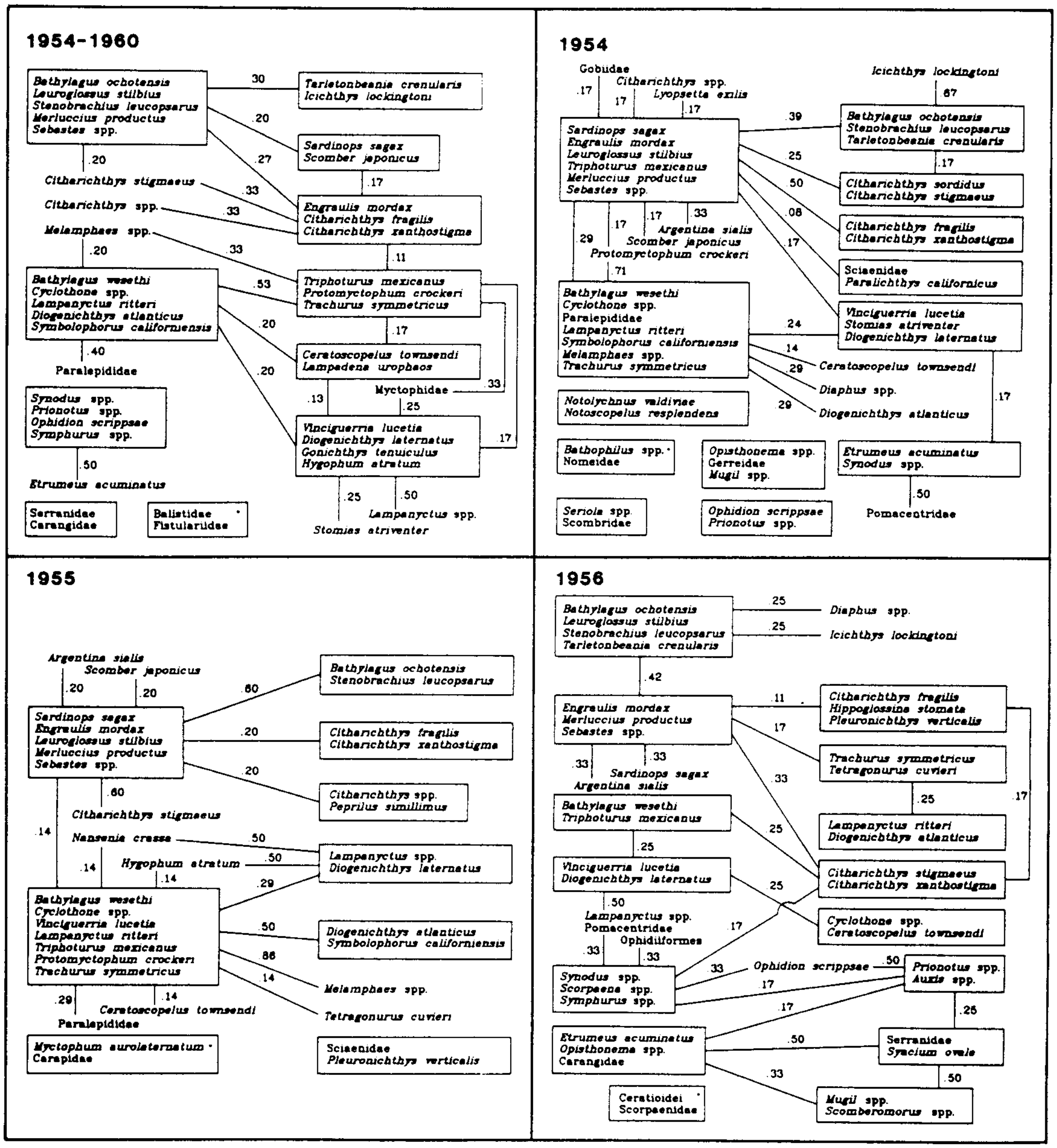

Figure 6. The composition and interrelationships of recurrent groups and their associates in the CalCOFI survey area for pooled 1954–60 data and for three individual years. A line between two recurrent groups indicates that there are intergroup pairs with significant affinity indices (≥ 0.3). The number represents the fraction of significant affinity pairs divided by the possible number of pairs. Recurrent groups represented by a single co-occurrence are indicated by an asterisk.

British Columbia to southern Baja California; however, there are apparently three subpopulations—a northern population extending from central California northward, a central population distributed from central California to central Baja California, and a southern stock from central Baja

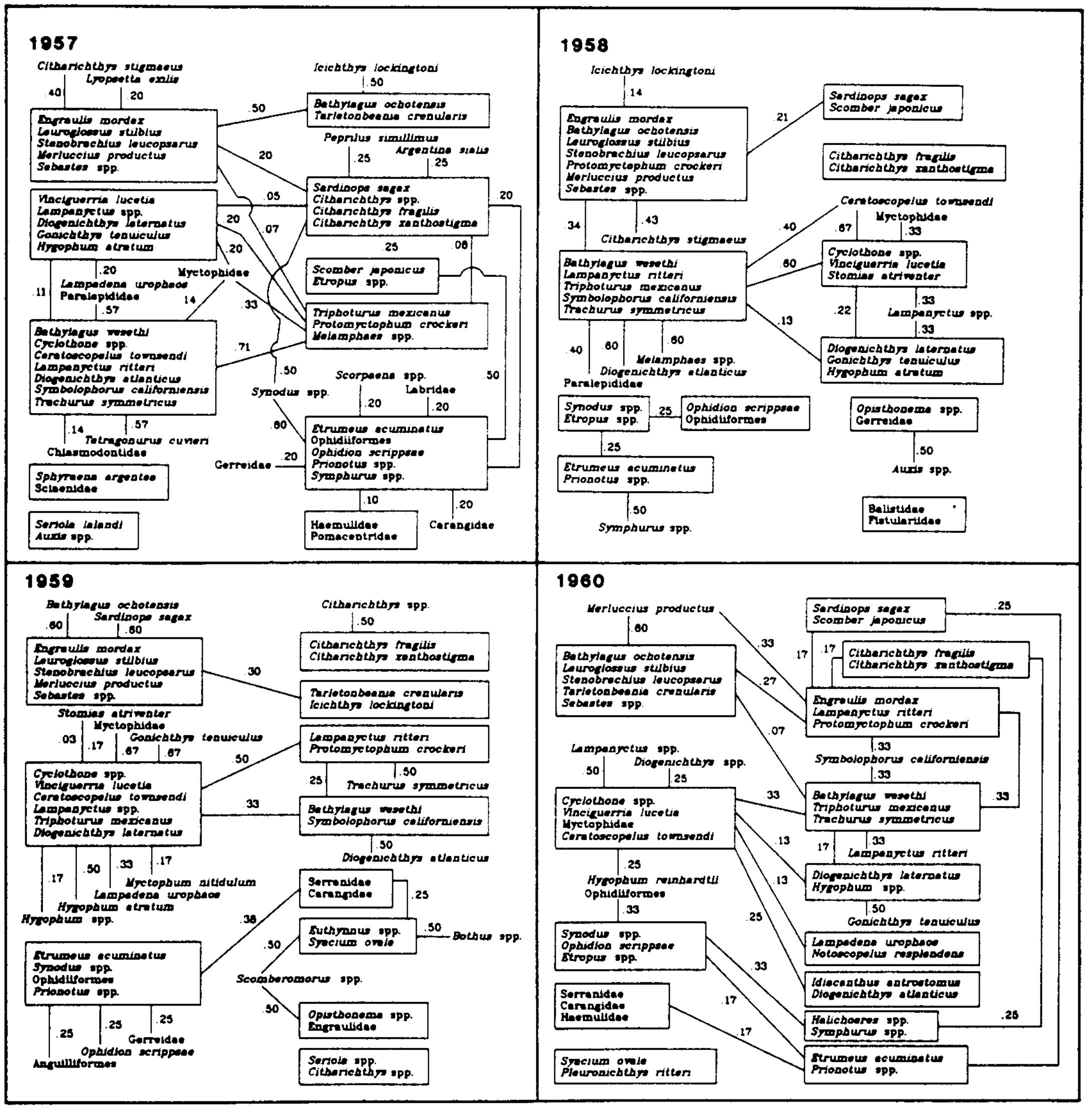

Figure 7. The composition and interrelationships of recurrent groups and their associates in the CalCOFI survey for 1957–60. A line between two recurrent groups indicates that there are intergroup pairs with significant affinity indices (≥ 0.3). The number represents the fraction of significant affinity pairs divided by the possible number of pairs. Recurrent groups represented by a single co-occurrence are indicated by an asterisk.

California to Cabo San Lucas. The 2 flatfishes have warm-water faunal affinities, with ranges extending from southern California south to the Gulf of California, and were included in the northern complex because of their strong affinity indices with *E. mordax*. Two other flatfish taxa form associate relationships with *E. mordax*—the genus *Citharichthys* as a unique associate and *Citharichthys stigmaeus* as an associate shared with *Sebastes* spp. in the LEUROGLOSSUS group[3]. *C. stigmaeus* is more temperate than its group congeners, with a range extending from Alaska to southern Baja California. A third associate relationship is with the

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[3] The category *Citharichthys* spp. consists of small, damaged specimens of the four common species of this genus present in the CalCOFI region, and is of limited significance in this analysis.

TABLE 3
Geographic Distribution (Percent of Total Abundance) of Recurrent Group Larval Fish Taxa in Eleven Areas of the CalCOFI Sampling Pattern, 1954–60

	CCal		SCal		NBCal			CBCal		SBCal	
Taxon	In	Off	In	Off	In	SVB	Off	In	Off	In	Off
Northern Complex											
LEUROGLOSSUS group											
Bathylagus ochotensis	17	43	8	25	2	1	4	T	0	0	0
Leuroglossus stilbius	12	6	38	22	5	3	5	4	4	T	T
Stenobrachius leucopsarus	20	32	22	24	1	0	2	T	0	0	0
Sebastes spp.	27	7	32	10	6	7	2	5	2	1	T
Merluccius productus	6	11	8	26	6	4	15	4	2	19	T
TARLETONBEANIA group											
Tarletonbeania crenularis	22	57	3	17	T	T	T	0	0	0	0
Icichthys lockingtoni	19	48	3	26	T	T	3	T	T	T	0
CITHARICHTHYS group											
Engraulis mordax	4	2	26	7	9	17	5	17	7	6	T
Citharichthys fragilis	0	0	T	0	2	68	1	17	10	1	T
Citharichthys xanthostigma	T	0	T	T	2	38	4	29	22	2	T
SARDINOPS group											
Sardinops sagax	T	T	10	6	3	24	9	21	4	21	1
Scomber japonicus	0	T	6	3	3	30	9	14	4	29	2
Southern Complex											
SYMBOLOPHORUS group											
Bathylagus wesethi	T	3	T	22	3	3	47	1	18	T	2
Cyclothone spp.	T	1	T	12	T	T	43	2	39	T	T
Diogenichthys atlanticus	T	10	1	27	2	1	44	T	13	0	0
Lampanyctus ritteri	3	16	2	26	2	2	32	T	15	T	1
Symbolophorus californiensis	1	11	1	31	3	1	44	T	6	0	0
TRIPHOTURUS group											
Triphoturus mexicanus	T	T	1	5	5	5	32	7	41	T	3
Protomyctophum crockeri	4	21	3	25	3	2	26	2	13	0	T
Trachurus symmetricus	7	16	2	41	2	1	27	T	4	0	T
CERATOSCOPELUS group											
Ceratoscopelus townsendi	T	2	T	7	T	T	45	T	42	T	2
Lampadena urophaos	0	0	0	5	T	1	38	5	45	T	4
VINCIGUERRIA group											
Vinciguerria lucetia	T	T	T	4	T	T	24	2	38	6	26
Diogenichthys laternatus	0	0	T	T	T	T	7	6	36	12	38
Gonichthys tenuiculus	0	0	T	T	T	T	10	4	42	10	33
Hygophum atratum	0	0	0	0	T	T	3	2	23	11	61
Southern Coastal Complex											
SYNODUS group											
Synodus spp.	0	0	T	0	2	30	T	32	2	32	2
Prionotus spp.	0	0	0	0	0	1	0	64	T	20	T
Ophidion scrippsae	1	T	3	T	T	28	T	42	6	16	T
Symphurus spp.	T	0	3	T	T	23	3	28	24	4	13

Abbreviations:
CCal = Central California (CalCOFI lines 60–77)
SCal = Southern California (CalCOFI lines 80–97)
NBCal = Northern Baja California (CalCOFI lines 100–117)
CBCal = Central Baja California (CalCOFI lines 120–137)
SBCal = Southern Baja California (CalCOFI lines 140–157)
In = Inshore portion of section (usually less than 100 km)
Off = Offshore portion of section (about 100–400 km)
SVB = Bahía Sebastián Viscaíno
T = Trace amounts of larvae (less than 0.5%)

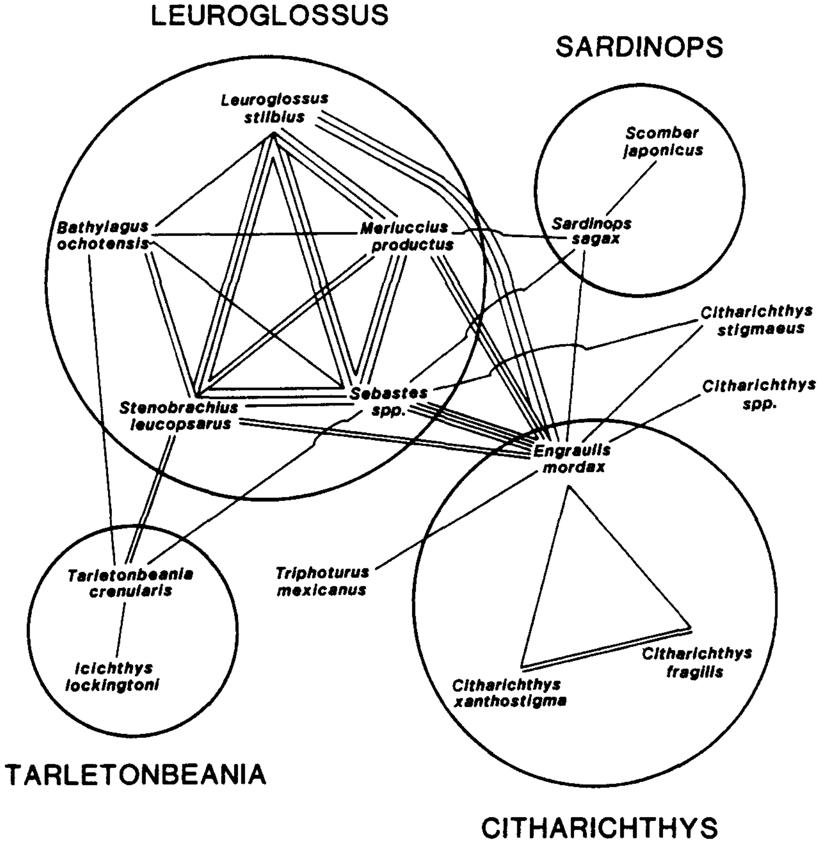

Figure 8. The northern complex of recurrent groups and associates from pooled (1954–60) CalCOFI data. The number of connecting lines indicates the approximate affinity index value. A single line represents an affinity index from 0.30 to 0.39; a double line is 0.40 to 0.49; a triple line is 0.50 to 0.59; and four lines represent an affinity index of 0.60 or greater.

myctophid *Triphoturus mexicanus* in the southern complex. *Engraulis mordax* has a protracted spawning season with a February-March maximum, and the 2 species of *Citharichthys* in the group have bimodal spawning seasons with February and August peaks (Table 3).

The group distribution was centered off coastal northern and central Baja California (Figure 9). Larvae of *E. mordax* were broadly distributed along the coast of the entire survey area, with highest abundance from southern California to central Baja California. Larvae of the two *Citharichthys* species were essentially confined to Baja California, with peak abundance in Bahía Sebastián Vizcaíno and the adjoining region to the south.

SARDINOPS recurrent group. The group comprises 2 coastal pelagic species—a clupeid (*Sardinops sagax*) and a scombrid (*Scomber japonicus*). The Pacific sardine, *S. sagax*, is primarily distributed off California and Baja California and in the Gulf of California. In the southern hemisphere another subspecies occurs off Chile and Peru. The chub mackerel, *S. japonicus*, has a worldwide distribution in temperate and tropical waters, particularly in boundary-current regions. *S. sagax* formed associate relationships with *Sebastes* spp. and *M. productus* in the LEUROGLOSSUS group and with *E. mordax* in the CITHARICHTHYS group. *S. sagax* has a protracted, almost year-round spawning season, with apparent peaks in late winter and late summer; *S. japonicus* has a restricted summer spawning season (Table 3).

The SARDINOPS group has a broad coastal distribution from Point Conception, California, to Cabo San Lucas, Baja California (Figure 9). Larvae of the two species had their highest mean abundance in Bahía Sebastián Vizcaíno and along the coast south to Cabo San Lucas (Table 3).

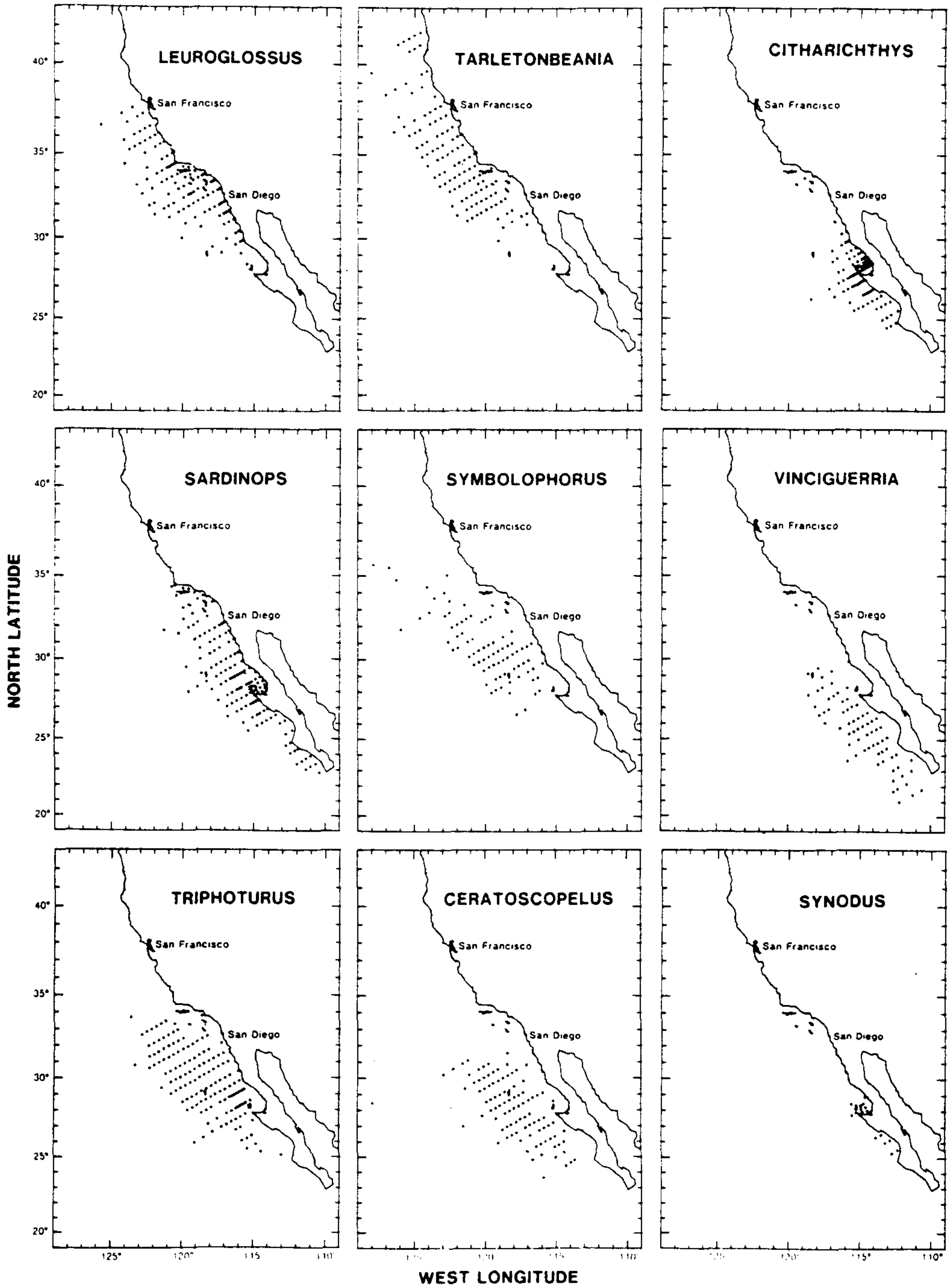

Figure 9. Geographic distribution of recurrent groups of larval fishes in the CalCOFI survey area. The general area for each recurrent group has been approximated by the dots, which represent station positions in which at least one sample in seven years (1954–60) had all recurrent group members present.

Southern Complex

The southern complex was made up of 4 recurrent groups: SYMBOLOPHORUS, TRIPHOTURUS, VINCIGUERRIA, and CERATOSCOPELUS (Figure 10). As in the northern complex, the largest group was connected by shared associates in all the other groups. SYMBOLOPHORUS had 5 member taxa, 7 associates in other recurrent groups, and 1 unique associate. VINCIGUERRIA had 4 member taxa, 6 associates in other recurrent groups, and 2 unique associates. TRIPHOTURUS had 3 member taxa, 8 associates in other groups, and 2 unique associates. CERATOSCOPELUS had 2 members, 4 associates in other groups, and no unique associates.

SYMBOLOPHORUS recurrent group. The group comprises 5 mesopelagic taxa—an argentinoid smelt (*Bathylagus wesethi*), 3 vertically migrating myctophids (*Diogenichthys atlanticus, Symbolophorus californiensis, Lampanyctus ritteri*), and the stomiiform genus *Cyclothone* (Table 2). *B. wesethi* and *S. californiensis* are transitional species characteristic of the California Current region, with distributions extending from the subarctic boundary to central Baja California. *L. ritteri* has a broader subarctic-transitional distribution that includes the Gulf of Alaska. *D. atlanticus* is a warm-water cosmopolite that enters the California Current region off southern California and northern Baja California. Seven species of *Cyclothone* are known from the California Current region. Adult samples are dominated by 2 species, *C. signata* and *C. acclinidens*, and preliminary identifications indicate that this is also true for ichthyoplankton samples. Both species have primarily equatorial distributions in the Pacific; these extend northeastward into the California Current region. Members of the SYMBOLOPHORUS group express a strong spawning seasonality, with *B. wesethi, L. ritteri,* and *S. californiensis* peaking in May and *Cyclothone* in August. *D. atlanticus* is bimodal, with peaks in May and September-October.

Group members form a strong affinity network with all other recurrent groups in the southern complex, which includes 7 groups and 2 individual associates (Figure 10). *L. ritteri* and *B. wesethi* were associates of the mesopelagic genus *Melamphaes,* which was also associated with *Trachurus symmetricus* in the TRIPHOTURUS group. Two species are common in the California Current region: *M. parvus,* which is restricted to this region, and *M. lugubris*, a subarctic-transitional form that ranges westward across the North Pacific. Spawning in *Melamphaes* is highly seasonal, with a peak in May. Paralepididae, a family of mesopelagic predators, was an associate with *B. wesethi.* One paralepidid species, *Lestidiops ringens*, predominates in the adult and larval samples from the California Current region.

The SYMBOLOPHORUS group had an offshore distribution in the central portion of the survey area, impinging on the coast of northern Baja California (Figure 9). Except for *L. ritteri*, all species had their highest larval abundances in the southern California-northern Baja California offshore region (Table 3). *L. ritteri* larvae were slightly more abundant in the northern Baja California offshore region (Table 3).

VINCIGUERRIA recurrent group. This group comprises 4 mesopelagic vertical migrators—the stomiiform lightfish *Vinciguerria lucetia* and 3 myctophine lanternfishes, *Diogenichthys laternatus, Gonichthys tenuiculus,* and *Hygophum atratum* (Table 2). All are eastern tropical Pacific species that range northward to the Gulf of California and the outer coast of Baja California. All have extended spawning seasons: *V. lucetia* peaks in August; *D. laternatus* and *H. atratum* have winter and summer maxima; and *G. tenuiculus* peaks in February (Table 2).

Group members form a strong affinity network with all other groups in the southern complex, including 5 group associates and 3 individual associates (Figure 10). *V. lucetia* and *D. laternatus* are associates of the myctophid genus *Lampanyctus,* which includes at least a dozen species from the California Current region: the unidentified Myctophidae is an associate shared with *T. mexicanus* of the TRIPHOTURUS group. Unidentified larval Myctophidae in our collections are either small or disintegrated specimens that represent a spectrum of the 40 or more species reported from this region. *Stomias atriventer*, a mesopelagic predator, is a unique associate of *V. lucetia. S. atriventer* is found from central California to mid-Mexico and has an extended spawning season with a winter-spring maximum.

The VINCIGUERRIA group is distributed principally in the offshore central Baja California and inshore-offshore southern Baja California regions (Figure 9). Only *V. lucetia* occurs in appreciable numbers in offshore northern Baja California waters (Table 3).

TRIPHOTURUS recurrent group. This group comprises 2 mesopelagic lanternfishes (*Protomyctophum crockeri* and *Triphoturus mexicanus*) and

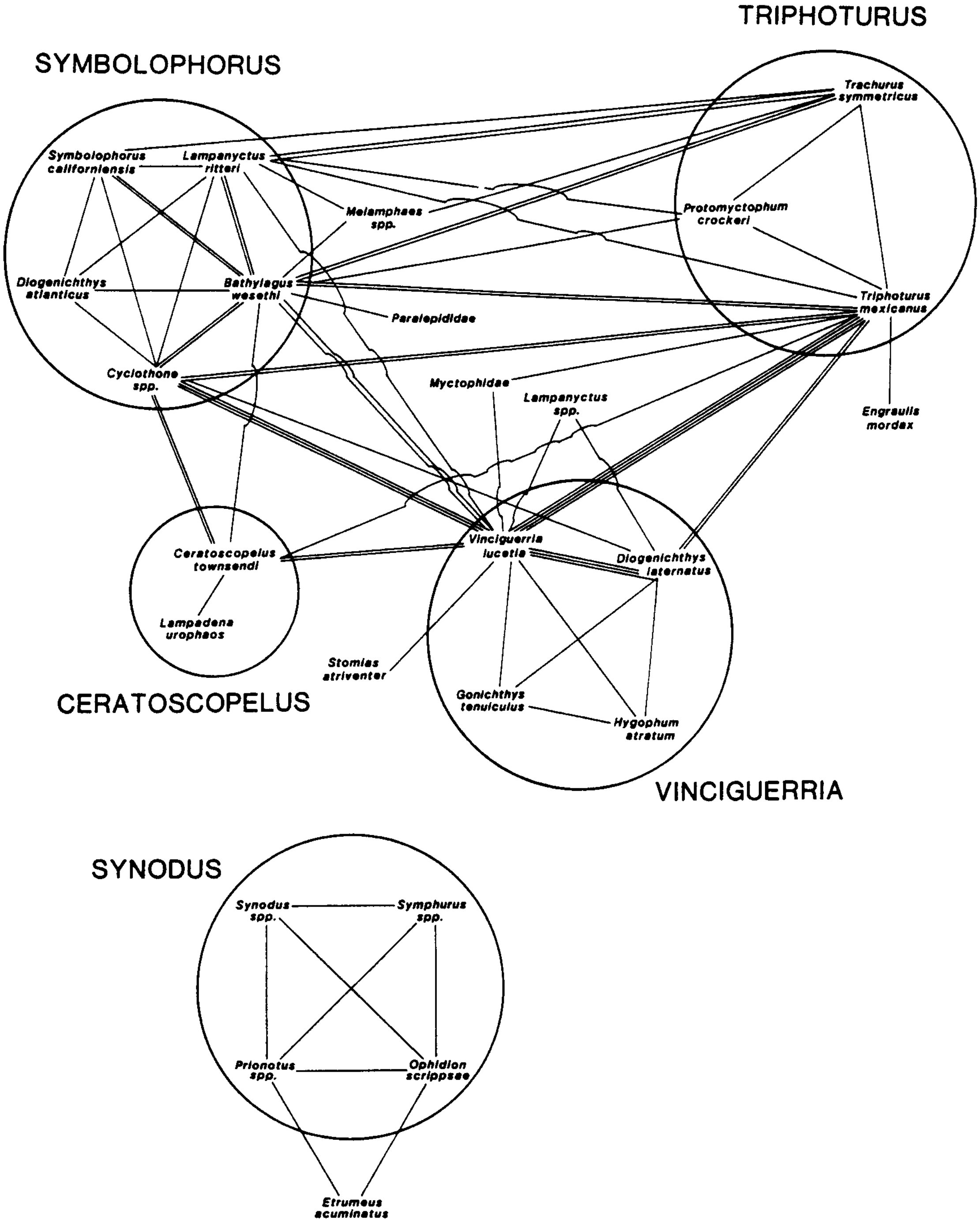

Figure 10. The southern complex and southern coastal complex of recurrent groups and associates from pooled (1954–60) CalCOFI data.

an epipelagic carangid (*Trachurus symmetricus*). *P. crockeri* is a transitional species ranging from central Baja California northward to the coast of Washington and westward to Japan. *T. mexicanus* occurs between 38° and 20°N in the California Current region and in the Gulf of California, with disjunct populations across the tropics (Hulley 1986). The jack mackerel, *T. symmetricus*, occurs from the Gulf of Alaska southward to Cabo San Lucas, Baja California, and has a principal distribution from southern California to central Baja California. Older year classes are noted for their offshore distribution, which can extend 2,400 kilometers seaward. *P. crockeri* has a bimodal spawning pattern with peaks in May and November; *T. mexicanus* peaks in August; and *T. symmetricus* in May–June (Table 2).

The TRIPHOTURUS group was strongly connected with the 2 larger recurrent groups of the southern complex and weakly connected to the CERATOSCOPELUS group (Figure 10). Associations were formed with 7 members of these groups and with 2 individual taxa. The association between *T. mexicanus* and *E. mordax* linked the northern and southern complexes (Figures 6 and 10).

The group had a broad inshore-offshore distribution in the survey area, extending from central California to central Baja California; this reflected the broad distributions of larvae of these species (Figure 9; Table 3).

CERATOSCOPELUS recurrent group. This group comprises 2 vertically migrating myctophids, *Ceratoscopelus townsendi* and *Lampadena urophaos. C. townsendi* is a resident of the California Current region, between 45° and 20°N latitude; *L. urophaos* has a more subtropical distribution that extends westward to Hawaii. Both are highly seasonal spawners, with summer maxima (Table 2).

Affinities exist with all other groups in the southern complex, although only weakly with TRIPHOTURUS (Figure 10). The group's distribution was centered off northern and central Baja California and distinctly offshore, reflecting the areal abundance patterns of both species (Figure 9; Table 3).

Southern Shelf Complex

Four shallow demersal taxa from 4 separate orders form the SYNODUS group—the myctophiform genus *Synodus*, the scorpaeniform genus *Prionotus*, the pleuronectiform genus *Symphurus*, and the ophidiiform species, *Ophidion scrippsae* (Figure 6). In our survey area adult collections of the 3 generic taxa are dominated by 3 species: *Synodus lucioceps*, *Prionotus stephanophrys*, and *Symphurus atricauda*. *S. lucioceps* and *O. scrippsae* are temperate-subtropical species ranging from central California to the Gulf of California. *P. stephanophrys* has a broad distribution that extends from the Columbia River (rarely north of Mexico) to Chile, and *S. atricauda* ranges from Oregon (rarely north of southern California) to Panama. The taxa have well-defined summer-fall spawning seasons, peaking in August-September. Spawning in *Synodus* spp. appears to be bimodal, with peaks in September and December (Table 2).

Although this group borders on all groups of the southern complex, no associate affinities were formed with any other recurrent group; the group had one unique associate, *Etrumeus acuminatus*, a coastal pelagic clupeid (Figure 6). This species ranges from central California to Chile and spawns during the summer.

Coincident samples for this group were found only in the widest continental shelf region in the survey area, Bahía Sebastián Viscaíno and southerly along the Punta Abreojos-Cabo San Lázaro Bight (Figure 9). Mean larval abundances were high in both these regions, except for *Prionotus*, which had a low abundance in Bahía Sebastián Viscaíno (Table 3).

The application of the REGROUP procedure to the combined 1954–60 data set at three higher affinity levels (0.4, 0.5, 0.6) provided a hierarchical view of the relationships of the principal larval fish taxa. At a critical level of 0.4, two large groups representing the northern and southern complexes were formed. The northern group included *E. mordax*, *L. stilbius*, *S. leucopsarus*, *M. productus*, and *Sebastes* spp., with *B. ochotensis* as an associate. The southern group consisted of *B. wesethi*, *Cyclothone* spp., *V. lucetia*, and *T. mexicanus*, with *C. townsendi*, *D. laternatus*, and *S. californiensis* as associates. This group was linked to a group pair, *L. ritteri-T. symmetricus*, by 3 out of 8 possible intergroup pairings. *Citharichthys fragilis* and *C. xanthostigma* formed an isolated group pair.

At a critical affinity index value of 0.5, the groups were reduced and fragmented. The northern complex consisted of 2 small groups—*E. mordax-L. stilbius-M. productus* and *S. leucopsarus-Sebastes* spp.—linked by 4 of 6 possible intergroup pairings. The southern complex was represented by a group pair—*V. lucetia-T. mexicanus*—with *Cyclothone* spp. and *D. laternatus* as associates. At a critical level of 0.6 only 2 group pairs remained: *E. mordax-Sebastes* spp. and *V. lucetia-T. mexi-*

canus, representing the northern and southern complexes, respectively.

INTERANNUAL VARIATION IN RECURRENT GROUPS

A total of 76 taxa were either group members or associates during the individual years over the seven-year period (Figures 6 and 7). The numbers of recurrent groups ranged from 8 in 1955 to 14 in 1956 and 1960. Number of taxa per group ranged from 2–4 in 1956 to 2–7 in 1954, 1955, 1957, and 1958. The average number of taxa per group was lowest in 1955 (2.4 taxa/group) and highest in 1957 (3.5/group). The total number of taxa contributing to recurrent groups ranged from 24 in 1955 to 39 in 1957. Associate taxa ranged from 8 in 1956 and 1960 to 14 in 1957. There were 2 shared associate taxa (those which form associate links with 2 or more groups) in 1957 and 1 in each of the other years.

There was considerable rearrangement of recurrent groups and group components during the seven-year period; however, the northern and southern complexes, as described in the preceding analysis of the composite seven-year data set, were generally conserved (Figures 6 and 7). In four of the years, group members of one complex became group members of another complex. In 1954 the southern complex species, *Triphoturus mexicanus*, formed a group with 5 northern complex taxa, and in 1958 another southern complex species, *Protomyctophum crockeri*, combined with a similar group of 6 northern taxa. In 1960, *Engraulis mordax* formed a group with 2 southern complex species, *P. crockeri* and *Lampanyctus ritteri*. In 1957 the northern complex and southern coastal complexes were linked by the recurrent group pairing of *Scomber japonicus* and the paralichthyid flatfish, *Etropus* spp. (Figures 6 and 7).

The complexes were also linked when significant affinity indices were formed between northern and southern taxa. In 1954 the high proportion (0.29) of associate linkages between the largest northern and southern groups resulted from the inclusion of *T. mexicanus* in the northern group (Figure 6). This species was an associate of all taxa except Paralepididae in the 7-member southern group. Other pairs contributing to this intergroup connection were *Sebastes* spp.-*T. symmetricus*, *M. productus*-*T. symmetricus*, *B. wesethi*-*M. productus*, *S. sagax*-*L. ritteri*, and *S. sagax*-*T. symmetricus*. The inclusion of *T. mexicanus* in the northern group was also responsible for the other northern-southern linkages, since it was an associate of *P. crockeri* and formed associate relationships with each member of the group formed by *V. lucetia*, *S. atriventer*, and *D. laternatus* (Figure 6). In 1955, *T. symmetricus* in the 7-member southern group was largely responsible for the north-south linkage, since it formed associate relationships with *S. sagax*, *L. stilbius*, and *Sebastes* spp. of the 5-member northern group. The northern species *L. stilbius* also formed associations with *T. mexicanus* and *P. crockeri* of the southern group (Figure 6).

In 1956 the northern-southern connections were keyed to the group formed by the sanddabs *C. stigmaeus* and *C. xanthostigma*, and also involved the southern coastal complex. The two species formed associate relationships with *T. mexicanus* in the *T. mexicanus*-*B. wesethi* group and with *Symphurus* spp. in the 3-member southern coastal group. Another northern-southern linkage was between *T. symmetricus* of the *T. symmetricus*-*Tetragonurus cuvieri* group and *M. productus* of the *E. mordax*-*M. productus*-*Sebastes* spp. group (Figure 6).

In 1957, northern-southern linkages also involved a group predominated by sanddab taxa (*Citharichthys* spp.-*C. fragilis*-*C. xanthostigma*-*S. sagax*) and a 5-member southern coastal group (Figure 7). *Symphurus* spp. of the latter group formed associate ties with all but *C. fragilis* in the northern group, and *O. scrippsae* of the southern group was an associate of *Citharichthys* spp. The shared associate, *Synodus* spp., further linked the two groups; it had significant affinities with all but *E. acuminatus* in the southern coastal group and also with *S. sagax* and *C. xanthostigma* in the northern group. The intercomplex group formed by *Scomber japonicus* and *Etropus* spp. was strongly linked with the large southern coastal group; *S. japonicus* was an associate of *E. acuminatus*, *O. scrippsae*, and *Symphurus* spp.; *Etropus* spp. had associate ties with the latter two. The *S. japonicus*-*Etropus* spp. group was connected to the sardine-sanddab group through the pairings of *S. japonicus* with *S. sagax* and *Citharichthys* spp. The sardine-sanddab group was linked to two other southern groups through intergroup associateships involving *C. xanthostigma*. This species was an associate of *T. mexicanus* in a 3-member southern group and also with *D. laternatus* in a 5-member group. The remaining northern-southern link was formed between a 5-member northern group and a 3-member southern group through the associate relationship of *E. mordax* and *T. mexicanus* (Figure 7).

In 1958 the northern and southern complexes were linked by associate relationships formed between a 7-member northern group and a 5-member southern group (Figure 7). The relatively high proportion (0.34) of intergroup associates resulted largely from the inclusion of the southern complex species *P. crockeri* in the northern group. It had significant affinities with all taxa except *T. mexicanus* of the southern group. Also, *T. symmetricus* of the southern group formed associate relationships with *E. mordax*, *S. leucopsarus*, and *M. productus* of the northern group. The myctophid *L. ritteri* also had associate links with these 3 species and with *B. ochotensis*. The two groups were further linked by the associate pairing of *E. mordax* and *T. mexicanus* (Figure 7).

In 1959 the northern and southern complexes were connected by the single associate pairing of *E. mordax* and *T. mexicanus;* however, in 1960 a group formed by the northern species *E. mordax* and two southern complex species (*L. ritteri* and *P. crockeri*) was responsible for extensive intercomplex linkage (Figure 7). *E. mordax* formed associate relationships with *Sebastes* spp., *S. leucopsarus*, *L. stilbius*, *M. productus*, *S. sagax*, and *C. fragilis* from 3 northern complex groups and with a 3-member southern group through an associate tie with *T. mexicanus*. The latter species also had a significant affinity with *P. crockeri*. The pairing of *L. ritteri* and *T. symmetricus* further linked the 3-member southern group and the *E. mordax-L. ritteri-P. crockeri* group. Other intercomplex links were through the associate pairs *L. stilbius-P. crockeri* and *L. stilbius-T. mexicanus*. Connections between two northern complex groups and two southern coastal complex groups were formed by associate pairings of *C. xanthostigma-Symphurus* spp. and *S. sagax-E. acuminatus*.

Interannual variability of the constituents and structure of the recurrent groups was more variable than that found in the complexes. In the northern complex, recurrent group analysis of the combined 1954–60 data (Figure 6) produced 4 groups. The largest group contained *B. ochotensis*, *L. stilbius*, *S. leucopsarus*, *M. productus*, and *Sebastes* spp. *Engraulis mordax* formed a group with *C. fragilis* and *C. xanthostigma; S. sagax* formed a group with *S. japonicus;* and *T. crenularis* formed a group pair with *I. lockingtoni* (Figure 6). The group diagrams for individual years showed that *E. mordax* and *S. sagax* were closely allied with the 5 members of the LEUROGLOSSUS group and that these 7 taxa were present in each year. In most of the years these taxa formed one or two groups with one or more of the taxa arranged as associates. *T. crenularis* was either included in one of these groups or was absent from the diagram. An exception was in 1959 when it paired with *I. lockingtoni* to form a group, as it did in the combined data set. The sanddabs *C. fragilis* and *C. xanthostigma* were retained as a group for most of the years. Exceptions were in 1956 when they separated to become members of two other flatfish groups and in 1957 when they combined with *S. sagax* and *Citharichthys* spp. to form a 4-member group (Figures 6 and 7).

The 7 principal taxa of the northern complex co-occurred consistently during the seven-year period. The following pairs had significant affinity indices (>0.30) for each of the seven years as well as for the combined data set: *S. sagax-E. mordax*, *E. mordax-L. stilbius*, *E. mordax-Sebastes* spp., *E. mordax-M. productus*, *B. ochotensis-L. stilbius*, *B. ochotensis-S. leucopsarus*, *L. stilbius-S. leucopsarus*, *L. stilbius-Sebastes* spp., *L. stilbius-M. productus*, *S. leucopsarus-Sebastes* spp., *Sebastes* spp.-*M. productus*. Two other pairs, *E. mordax-S. leucopsarus* and *S. leucopsarus-M. productus*, had significant affinity indices in all but one year, when the index fell just short of 0.30.

The high degree of co-occurrence in the 13 pairs listed above was shown by their high affinity indices. For the seven-year series 71% of the indices were above 0.40, 47% were above 0.50, and 8% exceeded 0.60. Affinity indices exceeded 0.40 for each of the seven years in *E. mordax-L. stilbius*, *E. mordax-M. productus*, *L. stilbius-S. leucopsarus*, *L. stilbius-Sebastes* spp., *L. stilbius-M. productus*, *S. leucopsarus-Sebastes* spp., and *Sebastes* spp.-*M. productus*. In *E. mordax-Sebastes* spp. the index exceeded 0.50 for all years. The other pair of the northern complex that had significant affinity indices for all seven years was *C. fragilis-C. xanthostigma*.

Interannual variability in recurrent group structure was greater in the southern complex than in the northern complex. Recurrent group analysis of the combined seven-year data set produced 5 groups from 18 midwater taxa and *T. symmetricus*. Five other midwater taxa were associates of these groups. Most of these taxa were present in recurrent group analyses of individual years, although group composition and arrangement were highly variable (Figures 6 and 7). In 1954, 1955, and 1959 there were one large group of 5–7 taxa and two smaller groups of 2–3 taxa. In 1957 there were two large groups of 5 and 7 taxa and a 3-member group. The largest group in 1960 contained 4 taxa with connecting links to 4 smaller groups. Group structure in 1956 was the most divergent and was limited to 5 paired taxa; moreover, only 11 of the 19 southern complex taxa from the 1954–60 combined data set contributed to these groups (Figure 6).

Only the following 6 southern complex pairs had significant indices (> 0.30) for all years: *B. wesethi-T. mexicanus*, *Cyclothone* spp.-*V. lucetia*, *Cyclothone* spp.-*C. townsendi*, *V. lucetia-D. laternatus*, *V. lucetia-T. mexicanus*, and *L. ritteri-T. symmetricus*. Of these pairs, only *V. lucetia-D. laternatus* had affinity indices higher than 0.40 for all years. Seven other pairs had affinity indices greater than 0.30 for six of the seven years (*B. wesethi-V. lucetia*, *B. wesethi-S. californiensis*, *Cyclothone* spp.-*T. mexicanus*, *V. lucetia-Lampanyctus* spp., *D. laternatus-T. mexicanus*, *L. ritteri-P. crockeri*, and *L. ritteri-S. californiensis*). In all but one of these pairs the nonsignificant affinity index occurred in 1956. Low affinity indices occurred throughout the southern complex in 1956; in a list of 67 taxon pairs, more than half had their lowest index in 1956. Of the mixed northern-southern complex pairs only *E. mordax-T. mexicanus* had consistently high affinity indices, ranging from 0.26 to 0.50 for the seven years.

The southern coastal complex was highly variable in the structure and composition of its recurrent groups and associate taxa. In the combined seven-year data set, 4 demersal taxa from 4 different orders formed an isolated group with one associate from a fifth order. Two family taxa, Serranidae and Carangidae (all jacks except *Trachurus* and *Seriola*) formed a second isolated group (Figure 6). Four of the taxa from the large group (*Synodus* spp., *Prionotus* spp., *Ophidion scrippsae*, and *Etrumeus acuminatus*) were persistent annually, occurring as group members or associates in six of the seven years (Figures 6 and 7). The fifth taxon, *Symphurus* spp., was present in only four of the seven years. Another key taxon, Ophidiiformes (all cusk-eels except *O. scrippsae* and *Chilara taylori*, and all brotulas except *Brosmophysis marginata*), was present as a group member or associate in five of the seven years. The Carangidae-Serranidae group was less prominent. These taxa occurred as a group in 1959 and 1960 and in separate recurrent groups in 1956. The thread herrings, *Opisthonema* spp., occurred in recurrent groups in four of the seven years. Gerreidae, the mojarras, appeared in four of the seven years: as a group member with *Opisthonema* spp. in 1954 and 1958 and as an associate in two other years. Pomacentridae (damselfishes other than *Chromis*), *Auxis* spp., and *Syacium ovale* occurred as group members or associates in three of the seven years, and 19 other taxa occurred once or twice during the seven-year period.

Group structure changed markedly from year to year. In 1954, 9 taxa were arranged in 4 groups with one of these (*E. acuminatus-Synodus* spp.) connected to the southern complex through an associate linkage between *Synodus* spp. and *Vinciguerria lucetia* (Figure 8). Incidence of southern coastal taxa was anomalously low in 1955, and they did not appear in the recurrent group analysis for that year. The isolated pair, Sciaenidae-*Pleuronichthys verticalis*, had a more northerly coastal distribution. In 1956, 13 taxa formed 5 highly interconnected groups (Figure 6). One of the 3 associate taxa, *O. scrippsae*, was shared by 2 of the groups, and the *Synodus-Scorpaena-Symphurus* group was linked to the northern complex through a *Symphurus* spp.-*Citharichthys xanthostigma* associateship. In 1957, 5 of the key southern coastal taxa formed a group linked to 5 associates and a 2-member group (Figure 7). The extensive associate linkages of this group to the northern complex were described earlier in this section. In 1958, 8 taxa formed 4 group pairs; 3 of these were interconnected, but there was no associate linkage with the northern or southern complexes. Similarly, in 1959, 12 species formed a cluster of 4 linked groups and an isolated group, with no associate connections to the northern or southern complexes (Figure 7). In 1960, 12 species formed a cluster of 4 interconnected groups and one isolated pair (Figure 7). Two groups within the cluster were connected to the northern complex through associate pairings (*C. xanthostigma-Symphurus* spp., *S. sagax-E. acuminatus*) with members of two northern complex groups.

The highly variable nature of incidence and co-occurrence of southern coastal taxa was shown in the list of annual affinity indices for selected pairs. Only 3 pairs had significant affinity indices for four of the seven years: *E. acuminatus-Synodus* spp., *Prionotus* spp.-Carangidae, and *Prionotus* spp.-*O. scrippsae*. Ranges of indices for the seven-year period were wide, and there was no obvious interannual trend except that values for 1955 were either zero or extremely low for selected pairs.

ENVIRONMENTAL CHANGE AND THE DISTRIBUTION OF RECURRENT GROUPS

The dynamic environmental changes that occurred during 1954–60 in the CalCOFI region markedly affected the distribution of larval fishes. These geographic shifts, in concert with changes in the amount and seasonal extent of spawning, re-

TABLE 4

Percent Change of Incidence of Taxa in the Central Part of the CalCOFI Survey Area between 1955–56 and 1958–59

	SCal		NBCal		
	In	Off	In	SVB	Off
Northern complex					
LEUROGLOSSUS group					
Bathylagus ochotensis	−8	−16	−2	−2	−4
Leuroglossus stilbius	−16	−24	−33	−20	−21
Stenobrachius leucopsarus	−23	−20	−18	0	−9
Sebastes spp.	−15	−28	−17	−22	−14
Merluccius productus	11	−3	−25	−28	−25
TARLETONBEANIA group					
Tarletonbeania crenularis	−14	−28	−4	0	−3
Icichthys lockingtoni	−4	−12	−4	−1	−3
CITHARICHTHYS group					
Engraulis mordax	2	12	−4	−9	−4
Citharichthys fragilis	0	0	−4	−3	−1
Citharichthys xanthostigma	0	1	−8	−15	−1
SARDINOPS group					
Sardinops sagax	17	−7	−9	−3	−17
Scomber japonicus	6	1	2	−4	−4
Southern complex					
SYMBOLOPHORUS group					
Bathylagus wesethi	3	19	10	−3	−6
Cyclothone spp.	2	23	6	7	24
Diogenichthys atlanticus	0	0	6	15	17
Lampanyctus ritteri	4	23	−2	−1	−16
Symbolophorus californiensis	3	22	2	0	−2
TRIPHOTURUS group					
Triphoturus mexicanus	15	30	23	23	17
Protomyctophum crockeri	0	4	2	−2	−17
Trachurus symmetricus	5	7	−3	−14	−26
CERATOSCOPELUS group					
Ceratoscopelus townsendi	1	10	7	4	23
Lampadena urophaos	*	2	1	2	8
VINCIGUERRIA group					
Vinciguerria lucetia	9	52	37	29	54
Diogenichthys laternatus	0	0	6	15	17
Gonichthys tenuiculus	*	0	1	3	11
Hygophum atratum	*	*	0	2	5
Southern coastal complex					
SYNODUS group					
Synodus spp.	*	*	0	−5	0
Prionotus spp.	*	*	*	2	*
Ophidion scrippsae	0	*	1	3	0
Symphurus spp.	2	0	1	−1	0

Abbreviations:
SCal = Southern California (CalCOFI lines 80–97)
NBCal = Northern Baja California (CalCOFI lines 100–117)
In = Inshore (usually < 100 km)
Off = Offshore (about 100–400 km)
SVB = Bahía Sebastián Viscaíno
* = No specimens found in region in any year

sulted in changes in the structure and composition of recurrent groups. Distributional shifts for recurrent group taxa are shown in Table 4, which lists the percent change in incidence of larvae between 1955–56 and 1958–59 in five subareas of the CalCOFI survey region. These areas off southern California (SCal) and northern Baja California (NBCal) had the most consistent and equitable monthly sampling effort and greatest environmental effect during the period.

In general, taxa of the northern complex declined, and their southern distributional limits contracted northward during El Niño, while taxa of the southern complex showed a relative increase and a concomitant northward expansion of their northern distributional limits. Members of the LEUROGLOSSUS group, with the exception of *M. productus*, decreased in all five subareas during this period (Table 4). Of the three midwater species, *B. ochotensis* had the smallest decline, with a maximum decrease of 16% in the SCal offshore area. *L. stilbius* decreased in all subareas, and *S. leucopsarus* showed a 43% decrease off SCal. *Sebastes* spp. decreased in all subareas, most notably in the SCal offshore area. *M. productus* decreased consistently in all subareas of NBCal, only slightly in offshore SCal, and showed a substantial increase in the SCal inshore area.

The two taxa of the TARLETONBEANIA group were poorly represented off NBCal and showed only slight decreases there during El Niño (Table 4). They were well represented in the SCal area, particularly offshore, and the decrease there reflected a northward contraction of spawning in these subarctic-transitional species during this period.

Members of the CITHARICHTHYS group decreased in all subareas off NBCal (Table 4). This is particularly noteworthy for the two warm-water sanddab species, whose distributions are concentrated in Bahía Sebastián Viscaíno (SVB) and more southerly shelf areas. *E. mordax* also decreased off NBCal but increased off SCal, particularly in the offshore region, reflecting a northward and seaward expansion of spawning distribution during El Niño.

The two species of the SARDINOPS group have coastal distributions that peak in the SVB area. Both decreased slightly in this area during El Niño (Table 4). *S. sagax* decreased in other areas, particularly in offshore NBCal, but showed a distinct increase in the SCal inshore area. The decrease of *S. sagax* in the four subareas could be attributed to the general decline of the stock during this period, as well as to El Niño effects. *S. japonicus* also increased slightly in SCal and inshore NBCal.

In the southern complex, the members of the SYMBOLOPHORUS group are midwater taxa that occur principally in offshore areas (Table 3). The two warm-water cosmopolite taxa, *D. atlanticus* and *Cyclothone* spp., increased markedly in the NBCal area, particularly offshore, and the latter taxon showed a strong increase in the SCal offshore region; this indicates a shoreward and northerly expansion of its spawning range (Table 4). The two transitional species *B. wesethi* and *S. californiensis* increased substantially in the SCal offshore area, increased to a lesser degree in the SCal and NBCal inshore areas, and decreased slightly in the NBCal offshore area. *L. ritteri* has a broad subarctic-transitional distribution; it increased in the SCal area, particularly offshore, and decreased off NBCal.

In the TRIPHOTURUS group, the warm-water myctophid *T. mexicanus* occurs relatively infrequently north of Baja California. During El Niño it expanded northward throughout the Southern California Bight, where its incidence increased by 15%–30%; it also increased substantially in the other four areas (Table 4). The two transitional species *P. crockeri* and *T. symmetricus* had less striking changes during El Niño. *T. symmetricus* increased slightly off SCal, but decreased off NBCal, particularly in the offshore region. *P. crockeri* experienced little change off SCal and inshore areas of NBCal, but decreased in the NBCal offshore area. The two members of the CERATOSCOPELUS group are myctophids with offshore distributions, centered off Baja California. During El Niño their incidence increased markedly in the NBCal offshore area, reflecting a shoreward and slight northerly expansion of their spawning distribution (Table 4).

In the VINCIGUERRIA group, *V. lucetia* had the greatest distributional change of all recurrent group taxa during El Niño. It is an abundant eastern tropical Pacific mesopelagic with a usual northern limit of about CalCOFI line 100 (Figure 1) off Ensenada, Baja California. During El Niño it expanded to north of Point Conception, California, showing increases greater than 50% in the offshore areas of SCal and NBCal (Table 4). Although it increased substantially in the inshore areas of NBCal, it increased only slightly in the inshore area of SCal and appeared to be excluded from that area. The other three species are eastern tropical Pacific myctophids with more southerly northern limits; *D. laternus* occurs infrequently north of Isla Guadalupe, Mexico, and *H. atratum* and *G. tenuiculus* are rarely found north of Punta Eugenia. During El Niño, *D. laternatus* and *G. tenuiculus* increased off NBCal, largely in the offshore area (Table 4). *H. atratum* increased in SVB and in the NBCal offshore area.

Larvae of the SYNODUS group in the southern coastal complex occurred in the shelf regions of SVB and the Punta Abreojos-Cabo San Lázaro Bight to the south. *Symphurus* spp., *O. scrippsae*, and *Synodus* spp. occurred in small numbers on the SCal shelf; only *Symphurus* spp. showed a slight increase in this area during El Niño (Table 4). *Prionotus* spp. and *O. scrippsae* increased slightly in SVB during this period, while *Synodus* spp. and *Symphurus* spp. decreased.

The fine-scale association of selected larval fish taxa and their environment was examined by identifying the temperature-salinity (T-S) characteristics correlated with the presence and absence of these species in a region of mixed water types. The study area for two subarctic-transitional species, *S. leucopsaris* and *T. crenularis*, was bounded by CalCOFI lines 83 to 100, and the area for the two eastern tropical Pacific species, *V. lucetia* and *D. laternatus*, was bounded by lines 100 to 120.

The T-S profiles (Figure 11) represent stations that were either positive or negative for the four species during a period of highly variable oceanographic conditions (1954–60, excluding 1957). These profiles showed a positive correlation between the presence of larvae of the two northern species and cooler, less saline water. Presence of the southern species was correlated with warmer, more saline water in their area. The depth at which the "positive" and "negative" curves were separated was about 150 m, except for *D. laternatus*, where the curves were separated throughout the water column (Figure 11).

The differences in temperature-salinity characteristics associated with the presence or absence of these species reflect the differences in oceanographic conditions before and after the onset of El Niño in 1957. More than two-thirds of all the samples with positive counts for the two subarctic species (*S. leucopsarus* and *T. crenularis*) were taken during 1954–56. Conversely, more than two-thirds of the samples with zero counts for these species were taken in 1958–60.

In the southern area, more than seven-eighths of the samples with positive counts for *V. lucetia* were taken in 1958–60, whereas three-fourths of the samples with zero counts were taken in 1954–56. The data for the other subtropical species, *D. later-*

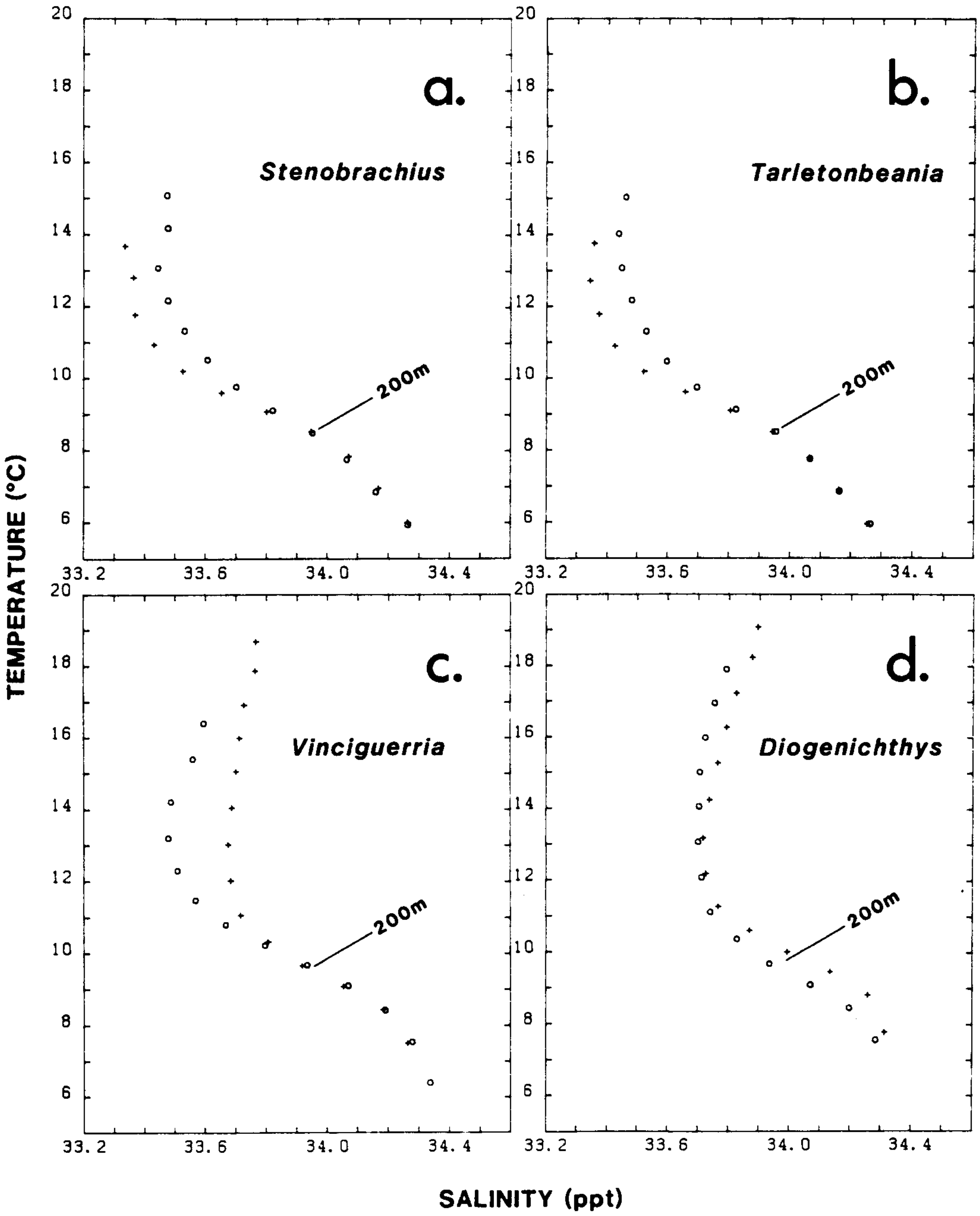

Figure 11. *a*. Mean temperature-salinity curves depicting differences in watermass characteristics associated with the absence (○) or presence (+) of *Stenobrachius leucopsarus* larvae in CalCOFI net tows. The plots represent combined data from 16 offshore stations on lines 83–100 (see Figure 1) occupied during 1954–60. *b*. Same as *a* for *Tarletonbeania crenulans* larvae. The data represented in the figure are from 14 offshore stations on lines 83–100. *c*. Same as *a*, for *Vinciguerria lucetia* larvae. The data represented in this figure are from 21 offshore stations on lines 100–120. *d*. Same as *a*, for *Diogenichthys laternatus* larvae. The data represented in this figure are from 17 offshore stations on lines 103–120.

natus, show less distinction between the pre- and post-1957 periods. Although four-fifths of the samples with positive counts were taken in 1958–60, more than two-thirds of those with zero counts were also taken in that period. Consequently, the T-S curves for both positive and zero counts of *D. laternatus* reflect mainly 1958–60 conditions. The curious separation of these curves below 200 meters is an unexplained feature.

DISCUSSION

The CalCOFI surveys were designed to encompass the areal and temporal limits of the Pacific sardine and its principal ecological associates. The fact that this was accomplished by a monthly sampling program sensitive to mesoscale oceanographic and biological events makes this time series unique. The seven-year period from 1954 to 1960, analyzed in this paper, was of special interest because it contained a major El Niño that was immediately preceded by an anomalously cold period. The recent efforts to reidentify much of the larval fish material from these years and establish a computer data base for it gave us the opportunity to study the structure of fish assemblages in the California Current region during a period of great environmental change.

Recurrent group analysis establishes the co-occurrence of taxa in time and space. When such analysis is applied to an oceanic plankton survey like the CalCOFI sampling program, co-occurrences of larval stages reflect all life-history stages of epipelagic taxa, from egg to adult. Co-occurring taxa experience similar biotic and abiotic environmental conditions and are themselves part of each other's environment. Knowledge of the degree of co-occurrence is a basis for studying trophic relations and competitive interactions between taxa. We view this analysis as a first step in studying the population ecology of these taxa from the standpoint of early life-history stages. Analysis of fluctuations in abundance of these taxa (Smith, Moser, Eber, in prep.) will provide insight into how environment and species interactions affect the populations. Some of these data have been used to estimate population trends of fishery stocks for the past 50 years. These analyses can now be broadened to the ecosystem scale to further define the role of environment, species interaction, and fisheries on the fish stocks of the California Current region.

How well does recurrent group analysis define the larval fish assemblages of the California Current region? Analysis of the pooled data set for 1954–60 identified three major faunal complexes that reflect the transitional nature of the ocean and its zoogeographic components in this region. In the northern complex the CalCOFI surveys define the southern and seaward spawning boundaries of the subarctic-transitional and transitional taxa that make up LEUROGLOSSUS and TARLETONBEANIA, two groups separated by displaced spawning seasons. The pattern also circumscribes the northern spawning limit for *Merluccius productus* in the LEUROGLOSSUS group[4]. Seaward and latitudinal spawning boundaries for the two major clupeoids (*Engraulis mordax* and *Sardinops sagax*) were also defined by the CalCOFI pattern[5]. Larvae of *E. mordax* were pervasive in the CalCOFI sampling region; this in combination with an extended spawning season ensures that larvae of most common species in the CalCOFI region co-occur with anchovy larvae at some time during the year. Indeed, affinity indices with members of the LEUROGLOSSUS group were consistently high, and *E. mordax* was included as a group member with those species in all but one of the single-year analyses during the seven-year period. This same pervasive areal and temporal distribution pattern appears to have characterized *S. sagax* before the collapse of the stock; however, sardine spawning was centered off central Baja California during 1954–60. In the analysis of the pooled 1954–60 data set, *E. mordax* was grouped with two warm-water sanddab species, and *S. sagax* was paired with *Scomber japonicus*. The sanddab species *Citharichthys fragilis* and *C. xanthostigma* are clearly not "northern" species; however, they were linked to the northern complex through their consistently strong affinities with *E. mordax, S. sagax*, and *Sebastes* spp. Likewise, *S. japonicus* is not a "northern" species but was linked to the northern complex through its strong affinity with *S. sagax*.

In contrast to the northern and coastal character of the northern complex, the principal constituents of the southern complex are mesopelagics that inhabit more southerly and offshore waters. Although the taxa were partitioned into 4 groups in the pooled analysis, the various taxa mixed freely and combined to form a variety of groups in analyses of individual years. The 5-member SYMBOLOPHORUS group is faunistically diverse. *Bathylagus wesethi* and *Symbolophorus californiensis* are

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[4] Subpopulations of *M. productus* spawn in the Straits of Georgia, British Columbia, and in Puget Sound, Washington.

[5] The degree of genetic interchange between Gulf of California and outer coast stocks of these two species is unknown.

inhabitants of the California Current region, with distributions centered off Point Conception to Punta Eugenia; their latitudinal and inshore-offshore spawning limits are essentially defined by the CalCOFI pattern. The warm-water cosmopolite *Diogenichthys atlanticus* extends into the CalCOFI area between Point Conception and Punta Eugenia, where its latitudinal limits are well defined. *Cyclothone* spp. has a similar distribution in the CalCOFI area; however, it is primarily equatorial, and only its northern spawning limits are defined by the CalCOFI survey pattern. *Ceratoscopelus townsendi* and *Lampadena urophaos* have distributions similar to *D. atlanticus* and *Cyclothone* spp. in the CalCOFI region. They pair to form a separate group because of the extremely close areal overlap and spawning seasonality, with a sharp peak in August.

TRIPHOTURUS is the most zoogeographically disparate group in the southern complex. *Trachurus symmetricus* and *Protomyctophum crockeri* are transitional species with distributions extending to the western Pacific, and are clearly not "southern" species. In the CalCOFI region their larval distributions have broad temporal and spatial overlap with that of the warm-water myctophid *Triphoturus mexicanus*, particularly in the region between Point Conception and Punta Eugenia. *T. mexicanus* also overlaps broadly with *E. mordax*, with whom it forms consistently high intercomplex affinity indices. It may be viewed as a kind of latitudinal mirror image of *E. mordax* in the southern part of the CalCOFI region. The transitional nature of the TRIPHOTURUS group was shown by the strong affinities its members had with taxa of the northern complex and by the inclusion of *T. mexicanus* and *P. crockeri* in northern complex recurrent groups in 1954 and 1958 (Figures 6 and 7).

VINCIGUERRIA is the most faunistically coherent group in the southern complex. The northern spawning boundaries of its 4 eastern tropical Pacific species are clearly defined by the CalCOFI pattern. *V. lucetia* is abundant and widespread off the entire Baja California coast. *D. laternatus* is widespread but less abundant. *Hygophum atratum* and *Gonichthys tenuiculus* are even less abundant, and chiefly south of Punta Eugenia.

The presence of a southern coastal complex in the CalCOFI data set results from the interplay of coastal bathymetry and the survey pattern. Bahía Sebastián Viscaíno and the Punta Abreojos-Cabo San Lázaro Bight are the only large shelf areas in the station pattern. Taxa in this southern coastal complex are the northern representatives of the shorefish fauna of the tropical-subtropical eastern Pacific. Their northern distributions are sharply curtailed by the narrow shelf of northern Baja California and by the depressed water temperatures of this region that result from coastal upwelling. This complex was isolated from the other complexes in the pooled analysis but formed linkages with the southern and northern complexes in some of the annual analyses.

The descriptions of larval fish assemblages of the CalCOFI region are both informative and conservative. The analysis of pooled data of the northern complex shows the relationship between the subarctic-transitional core group and the pervasive coastal pelagic species with southerly linkages. Likewise the offshore, the California Current region endemic, and the eastern tropical Pacific components of the southern complex are well demonstrated, along with the taxa that bridge the two major complexes. Some of the groupings (e.g., SARDINOPS, CITHARICHTHYS, and TRIPHOTURUS) are not intuitively obvious. Taxa of these groups bind together the divergent fish assemblages of the region by extensive co-occurrence. Annual variation in group composition and in intergroup and associate linkages generally supports the overall scheme described by the pooled data set. Forthcoming analyses of additional yearly surveys and a larger pooled data set will allow further refinement.

The conservative quality of the faunal assemblages is shown by examining the effect of El Niño on recurrent group structure. The cooling trend, which peaked in 1956, resulted in lowered affinity indices among southern-complex species and produced depauperate southern-complex groups. Only about half of the group taxa present in the seven-year pooled analysis were present in 1956. With the onset of the warming trend in 1957 these taxa regained their prominence; northern-complex taxa, however, did not show an analogous decrease in representation as the El Niño peaked in 1958 and 1959, despite lowering of affinity indices for some northern-complex pairs. Neither was there major intermixing of northern and southern recurrent groups resulting from northward and shoreward expansion of spawning of the latter. Taxa of the TRIPHOTURUS group (*T. mexicanus*, *Trachurus symmetricus*, *Protomyctophum crockeri*) were the central figures in intercomplex linkages throughout the seven-year period, because of their inclusion in northern recurrent groups or their extensive associate pairings with northern group members. Intercomplex connections were also caused by *E. mordax* and *S. sagax*, particularly through affinities of the former with *T. mexicanus*.

The interconnections of northern and southern complexes made through the sanddab *C. xanthostigma* in 1957 and 1960 were an expression of the warm-water distribution of this species and the absence of its indirect connection to the northern complex through *E. mordax*. The same was true for *S. japonicus*, which paired with the flatfish *Etropus* spp. instead of *S. sagax* in 1957. Interestingly, the sanddab recurrent group, *C. xanthostigma* and *C. fragilis*, was isolated from all other groups in the peak El Niño years 1958 and 1959. This was apparently related to the marked reduction of their numbers during this period, the opposite of what one would expect for warm-water species. Perhaps increased larval mortality associated with reduced productivity was the cause.

We anticipated that species assemblages arising from presence-absence techniques like the Fager recurrent group analysis (Fager 1963) would be more robust than those techniques which use the estimates of the quantities of organisms (MacDonald 1975). This is so because within the habitats of these species, spawning products are patchy and the chance co-occurrence of large numbers of two patchy organisms would assume greater importance than may be warranted. Fager (1957) also pointed out that, in analyses based on abundance, inverse quantities of organisms resulting from predation or competition could be misinterpreted by quantitative analysis so as to displace one of the organisms from an assemblage.

One possible disadvantage of the Fager recurrent group analysis relates to the method of resolving ties in the assembly of large groups. It appears that the more ubiquitous of two alternate group members may tend to be eliminated because it could eventually form a larger group than the less ubiquitous alternate. One example was *E. mordax*. Within the LEUROGLOSSUS group *E. mordax* had high affinities with every group member but *Bathylagus ochotensis*. If *E. mordax* had been selected as the member, *B. ochotensis* would have been displaced and made a member of the TARLETONBEANIA recurrent group; *Icichthys lockingtoni* of that group would have been displaced to an associate of that group; CITHARICHTHYS would have been diminished to two group members; and all of the associates of CITHARICHTHYS would have been transferred to LEUROGLOSSUS. Only in 1958 were *E. mordax* and *B. ochotensis* in the same recurrent group.

The northern and southern complexes were preserved when recurrent group analysis was applied to the combined 1954–60 data set, using a series of high critical affinity values (0.4, 0.5, 0.6). One can observe in the northern complex diagram (Figure 8) that the removal of the 0.3 links (single lines) leaves only a group of five taxa with an associate and an isolated pair. The southern complex (Figure 10) dissolved similarly into one group of four taxa with several associates. Almost all the diversity is gone when both 0.3 and 0.4 (double) lines are removed, and only two isolated pairs remain when the 0.5 line (triple) is also removed. It appears that in this analysis of larval stages of fish taxa, the critical values of 0.3 maintained the structure of the common fish assemblages and permitted the description of associations like the southern coastal complex, SYNODUS, near the sampling threshold.

Considering the possibilities for chaos with several faunal groups contributing to the California Current region, it appears that the structure of the system is clear when several years are pooled. These seven years were selected because they had two cold years, 1955 and 1956; had two warm years, 1958 and 1959; were bounded by two relatively "normal" years, 1954 and 1960; and were separated by one transitional year, 1957. The recurrent group analysis of 1975 clearly separated the same northern and southern complexes as this set (Loeb et al. 1983). It remains to be seen whether the 1954–60 set can be considered to be representative or whether new forms of assemblages will arise from the other 16 years yet to be analyzed. It is probable that another complex, representative of the central water mass, will be defined from analysis of extended cruises in 1972. Also, it may be possible that more intensive coastal sampling of the recent decade (Barnett et al. 1984; Lavenberg et al. 1986) may define a "northern coastal complex" similar to that found by Gruber et al. (1982) in the Southern California Bight.

Lastly, the distinctions among the complexes are exceedingly clear, considering that the system is embedded in a current which is moving several thousand kilometers each year and mixing with coastal temperate, subarctic, and subtropical waters. There is much to be learned from the study of the necessary physiological, behavioral, and oceanographic mechanisms that maintain these groups of populations in one locale.

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APPENDIX

Larval Fish Taxa That Constitute Recurrent Groups, Associates, and Affiliates, from Pooled CalCOFI Survey Data, 1954–60

Taxon	Incidence (11,551 total)	Associate group
Northern Complex		
LEUROGLOSSUS recurrent group		
Leuroglossus stilbius	3,010	
Bathylagus ochotensis	1,172	
Stenobrachius leucopsarus	2,439	
Sebastes spp.	4,485	
Merluccius productus	3,027	
Associates (members or associates of other recurrent groups)		
Engraulis mordax	5,097	CITHARICHTHYS
Citharichthys stigmaeus	1,322	CITHARICHTHYS
Sardinops sagax	1,477	SARDINOPS
Tarletonbeania crenularis	1,044	TARLETONBEANIA
Affiliates		
Osmeridae	4	
Nansenia spp.	3	
Bathylagus milleri	7	
Bathylagus pacificus	54	
Valenciennellus stellatus	1	
Macrouridae	40	
Brosmophycis marginata	80	
Hexagrammidae	4	
Oxylebius pictus	38	
Cottidae	250	
Scorpaenichthys marmoratus	53	
Agonidae	78	
Cyclopteridae	41	
Lyopsetta exilis	485	
Microstomus pacificus	147	
Parophrys vetulus	297	
Pleuronichthys coenosus	51	
Pleuronichthys decurrens	22	
Psettichthys melanostictus	22	
TARLETONBEANIA recurrent group		
Tarletonbeania crenularis	1,044	
Icichthys lockingtoni	633	
Associates (members or associates of other recurrent groups)		
Bathylagus ochotensis	1,172	LEUROGLOSSUS
Stenobrachius leucopsarus	2,439	LEUROGLOSSUS
Sebastes spp.	4,485	LEUROGLOSSUS
Affiliates		
Leuroglossus schmidti	3	
Danaphos oculatus	1	
Chauliodus macouni	421	
Diaphus spp.	628	
Bathymasteridae	1	
Pholididae	1	
Icosteus aenigmaticus	6	
Glyptocephalus zachirus	62	

Taxon	Incidence	Associate group
CITHARICHTHYS recurrent group		
Engraulis mordax	5,097	
Citharichthys fragilis	821	
Citharichthys xanthostigma	980	
Associates (members or associates of other recurrent groups)		
Leuroglossus stilbius	3,010	LEUROGLOSSUS
Stenobrachius leucopsarus	2,439	LEUROGLOSSUS
Sebastes spp.	4,485	LEUROGLOSSUS
Merluccius productus	3,027	LEUROGLOSSUS
Citharichthys stigmaeus	1,322	LEUROGLOSSUS
Sardinops sagax	1,477	SARDINOPS
Triphoturus mexicanus	4,648	TRIPHOTURUS
Associates (unique)		
Citharichthys spp.	904	
Affiliates		
Argentina sialis	438	
Gobiesocidae	4	
Atherinidae	18	
Syngnathus spp.	29	
Ophiodon elongatus	7	
Zaniolepis spp.	39	
Caulolatilus princeps	55	
Sciaenidae	499	
Clinidae	118	
Gobiidae	592	
Sarda chiliensis	18	
Peprilus simillimus	216	
Blennioidei	5	
Pleuronectiformes	109	
Citharichthys sordidus	424	
Paralichthys californicus	244	
Hippoglossina stomata	258	
Pleuronichthys spp.	100	
Pleuronichthys ritteri	19	
Pleuronichthys verticalis	178	
Hypsopsetta guttulata	5	
SARDINOPS recurrent group		
Sardinops sagax	1,477	
Scomber japonicus	513	
Associates (members or associates of other recurrent groups)		
Sebastes spp.	4,485	LEUROGLOSSUS
Merluccius productus	3,027	LEUROGLOSSUS
Engraulis mordax	5,097	CITHARICHTHYS
Affiliates		
Girella nigricans	17	
Hypsypops rubicundus	2	
Sphyraena argentea	107	
Semicossyphus pulchrum	5	

(*continued*)

APPENDIX (*continued*)

Larval Fish Taxa That Constitute Recurrent Groups, Associates, and Affiliates, from Pooled CalCOFI Survey Data, 1954–60

Taxon	Incidence	Associate group
Southern Complex		
SYMBOLOPHORUS recurrent group		
Bathylagus wesethi	1,935	
Cyclothone spp.	1,784	
Diogenichthys atlanticus	734	
Lampanyctus ritteri	2,288	
Symbolophorus californiensis	966	
Associates (members or associates of other recurrent groups)		
Protomyctophum crockeri	2,303	TRIPHOTURUS
Triphoturus mexicanus	4,648	TRIPHOTURUS
Melamphaes spp.	1,309	TRIPHOTURUS
Trachurus symmetricus	2,095	TRIPHOTURUS
Vinciguerria lucetia	4,288	VINCIGUERRIA
Diogenichthys laternatus	2,204	VINCIGUERRIA
Ceratoscopelus townsendi	988	CERATOSCOPELUS
Associates (unique)		
Paralepididae	772	
Affiliates		
Microstoma microstoma	176	
Tactostoma macropus	31	
Aristostomias scintillans	45	
Idiacanthus antrostomus	161	
Alepocephalidae	1	
Scopelarchidae	327	
Scopelosaurus spp.	36	
Myctophum nitidulum	268	
Centrobranchus spp.	1	
Electrona rissoi	4	
Poromitra spp.	111	
Trachipteridae	145	
Sebastolobus spp.	45	
Apogonidae	11	
Chiasmodontidae	294	
Isopsetta isolepsis	1	
VINCIGUERRIA recurrent group		
Vinciguerria lucetia	4,288	
Diogenichthys laternatus	2,204	
Gonichthys tenuiculus	537	
Hygophum atratum	444	
Associates (members or associates of other recurrent groups)		
Bathylagus wesethi	1,935	SYMBOLOPHORUS
Cyclothone spp.	1,784	SYMBOLOPHORUS
Lampanyctus ritteri	2,288	SYMBOLOPHORUS
Myctophidae	1,078	TRIPHOTURUS
Triphoturus mexicanus	4,648	TRIPHOTURUS
Ceratoscopelus townsendi	988	CERATOSCOPELUS
Associates (unique)		
Lampanyctus spp.	966	
Stomias atriventer	803	
Affiliates		
Anguilliformes	163	
Stomiiformes	50	
Nansenia crassa	326	
Bathylagus spp.	29	
Bathylagus nigrigenys	9	
Gonostomatidae	3	
Diplophos taenia	93	
Ichthyococcus spp.	165	
Sternoptychidae	428	
Bathophilus spp.	34	
Myctophiformes	2	
Evermannellidae	10	
Diogenichthys spp.	250	
Hygophum spp.	248	
Loweina rara	82	
Myctophum aurolaternatum	30	
Antennariidae	1	
Moridae	5	
Physiculus spp.	20	
Bregmaceros spp.	60	
Carapidae	11	
Macroramphosus gracilis	6	
Fistularidae	1	
Scorpaenidae	6	
Seriola spp.	3	
Uranoscopidae	5	
Gempylidae	20	
Thunnus albacares	10	
Nomeidae	20	
Citharichthys platophrys	1	
Bothus spp.	24	
Balistidae	1	
TRIPHOTURUS recurrent group		
Protomyctophum crockeri	2,303	
Triphoturus mexicanus	4,648	
Trachurus symmetricus	2,095	
Associates (members or associates of other recurrent groups)		
Bathylagus wesethi	1,935	SYMBOLOPHORUS
Cyclothone spp.	1,784	SYMBOLOPHORUS
Lampanyctus ritteri	2,288	SYMBOLOPHORUS
Symbolophorus californiensis	966	SYMBOLOPHORUS
Melamphaes spp.	1,309	SYMBOLOPHORUS
Vinciguerria lucetia	4,288	VINCIGUERRIA
Diogenichthys laternatus	2,204	VINCIGUERRIA
Myctophidae	1,078	VINCIGUERRIA
Ceratoscopelus townsendi	988	CERATOSCOPELUS
Engraulis mordax	5,097	CITHARICHTHYS

(*continued*)

APPENDIX (*continued*)

Larval Fish Taxa That Constitute Recurrent Groups, Associates, and Affiliates, from Pooled CalCOFI Survey Data, 1954–60

Taxon	Incidence	Associate group
Affiliates		
Nansenia candida	104	
Aulopus spp.	1	
Lampanyctus regalis	164	
Exocoetidae	18	
Cololabis saira	177	
Medialuna californiensis	47	
Oxyjulis californica	23	
Scombridae	57	
Tetragonurus cuvieri	417	
CERATOSCOPELUS recurrent group		
Ceratoscopelus townsendi	988	
Lampadena urophaos	307	
Associates (members or associates of other recurrent groups)		
Bathylagus wesethi	1,935	SYMBOLOPHORUS
Cyclothone spp.	1,784	SYMBOLOPHORUS
Vinciguerria lucetia	4,288	VINCIGUERRIA
Triphoturus mexicanus	4,648	TRIPHOTURUS
Affiliates		
Notoscopelus resplendens	227	
Hygophum reinhardtii	111	
Hygophum proximum	2	
Notolychnus valdiviae	21	
Ceratioidei	105	
Scopeloberyx robustus	3	
Scopelogadus mizolepis	165	
Howella brodiei	1	
Brama spp.	39	
Southern Coastal Complex		
SYNODUS recurrent group		
Synodus spp.	402	
Prionotus spp.	132	
Ophidion scrippsae	195	
Symphurus spp.	353	
Associates (unique)		
Etrumeus acuminatus	172	
Affiliates		
Albula vulpes	1	
Opisthonema spp.	13	
Engraulidae	5	
Anotopterus pharao	1	
Porichthys spp.	1	
Lophiidae	1	
Ophidiiformes	318	
Chilara taylori	62	
Hemiramphidae	2	
Scorpaena spp.	111	
Serranidae	190	
Priacanthidae	1	
Carangidae	81	
Seriola lalandi	118	
Coryphaena hippurus	77	
Gerreidae	34	
Haemulidae	48	
Mullidae	6	
Pomacentridae	75	
Chromis punctipinnis	125	
Mugil spp.	16	
Labridae	549	
Halichoeres spp.	24	
Hypsoblennius spp.	235	
Trichiuridae	266	
Euthynnus spp.	3	
Scomberomorus spp.	7	
Auxis spp.	56	
Etropus spp.	70	
Syacium ovale	22	
Xystreurys liolepis	32	
Tetraodontidae	1	