

LARVAL FISH ASSEMBLAGES OF THE CALIFORNIA CURRENT REGION AND THEIR HORIZONTAL AND VERTICAL DISTRIBUTIONS ACROSS A FRONT

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ABSTRACT

Cruises of the California Cooperative Oceanic Fisheries Investigations occupied 31,214 survey stations in a one million km² area off California and Baja California during 1951 to 1984. Recurrent group analysis of 249 larval fish taxa placed 36 taxa in 12 recurrent groups. These groups reflect the oceanographic complexity of the region with Subarctic-Transitional, Eastern Tropical Pacific (ETP), and Central Water Mass components. The major shorefish recurrent group is associated with the large shelf area of Sebastian Viscaino Bay off central Baja California. Cluster analysis using correlation coefficients of abundance as the measure of distance and principal component analysis produced groupings that agreed in general with groups formed by presence-absence analysis. Environmental effects on these groups were studied by examining changes in horizontal and vertical distribution across a frontal region. Plankton samples from the FRONTS 85 cruise conducted in July, 1985, southwest of the Southern California Bight, allowed us to investigate the fine scale distribution of assemblages across a semi-permanent frontal zone separating cold eutrophic water to the north from relatively warm, oligotrophic water to the south. Ichthyoplankton samples from a 120-n. mi. transect across the front, including 42 oblique bongo tows and 8 MOCNESS tows to 1,000 m, demonstrated: 1) the transition between Subarctic-Transitional and ETP/Central Water Mass species, and 2) distinctly different patterns of vertical distribution for the same species at the north and south sides of the front.

Research on larval fish assemblages has increased over the past several decades in concert with increasing interest in plankton ecology and dynamics. Ichthyoplankton surveys have produced a growing fund of information on assemblages from major ocean regions [e.g., Eastern Atlantic—Doyle and Ryan (1989), Olivar (1990), Sabatés (1990); Western Atlantic—de Ciechowski et al. (1991), Ditty et al. (1988), Morse et al. (1987), Richards (1984), Richards et al. (1989); Eastern Pacific—Ahlstrom (1972a), Kendall and Clark (1982), Kendall and Dunn (1985), Leis and Miller (1976), Loeb (1980), Loeb and Rojas (1988), Richardson et al. (1980), Santander and Flores (1983), Savage (1989); Western Pacific—Leis and Goldman (1987), Young et al. (1986); Indian Ocean—Nellen (1973); Antarctic—Kellerman and Kock (1988)].

Ichthyoplankton studies in the California Current region were initiated in response to the collapse of the Pacific sardine, *Sardinops sagax*, over a 22-year period from about 1925 to 1947. In 1949 the California Cooperative Oceanic Fisheries Investigations (CalCOFI) began conducting annual biological/oceanographic surveys over a >1 million km² grid extending from northern California to Cape San Lucas, Baja California (Fig. 1). The fact that the CalCOFI sampling grid overlays three coastal zoogeographic provinces, a coastal upwelling zone, and three oceanic water masses has allowed us to examine structure and variation in adjacent ichthyoplankton assemblages for portions of the CalCOFI time series (Loeb et al., 1983; Moser et al., 1987) and for the entire time series in this paper.

An extensive oceanographic literature exists for the California Current region (Reid, 1988) and considerable attention has been directed to the fronts that separate the major water masses (Lynn, 1986). The development of satellite remote sensors and other technological advances has resulted in much recent interest in fine scale oceanographic features (Simpson et al., 1984; Haury, 1984; Pelaez and

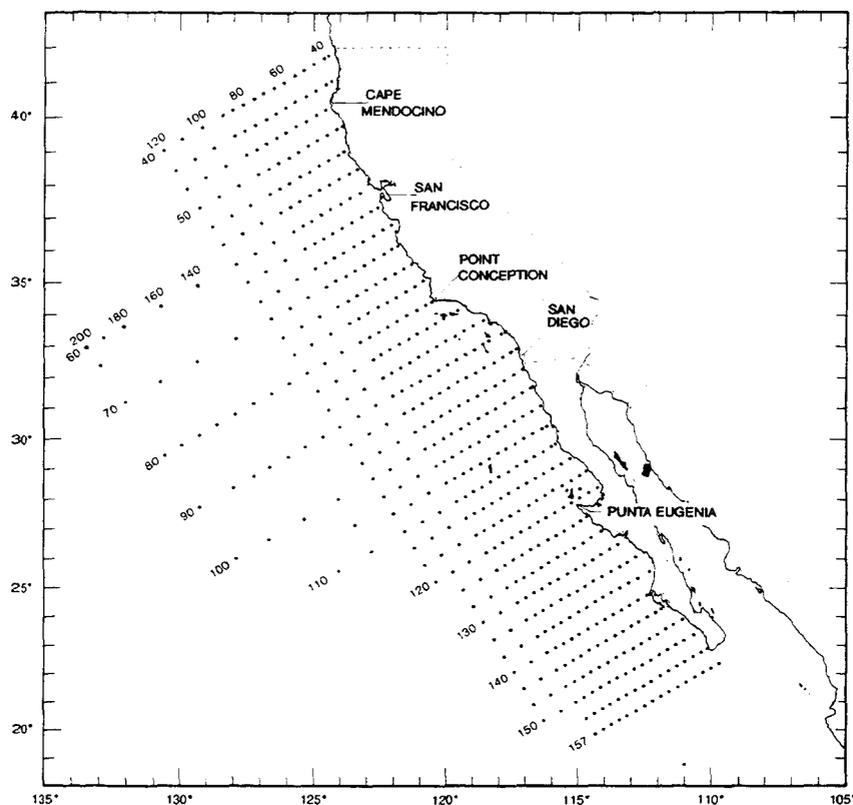


Figure 1. Station pattern for California Cooperative Oceanic Fisheries Investigations survey area. Numbers on the left of the pattern are CalCOFI survey line numbers; numbers above the pattern are station numbers.

McGowan, 1986; Lynn and Simpson, 1987; Niiler et al., 1989; Strub et al., 1991). Of particular interest is the frontal structure formed where the California Current flows shoreward at about 32°N, separating relatively cold, fresh, eutrophic water to the north from warmer, oligotrophic, more saline water to the south. Haury et al. (1993) refer to this semi-permanent feature as the Ensenada Front. The physical, chemical, and biological properties of this front were sampled intensively on the FRONTS 85 cruise (Niiler et al., 1989; Haury et al., 1986). Ichthyoplankton samples from this cruise are the basis for our study of the horizontal and vertical distribution of larval fish assemblages across the front in relation to the abiotic and biotic environment.

We describe the composition and structure of the CalCOFI ichthyoplankton assemblages from recurrent group analysis of the entire 40-year time series. These assemblages are compared with groupings from analyses based on taxon abundance using clustering and ordination techniques. We use presence-absence and abundance analyses to define assemblages because data on taxa "are often very far from being randomly and normally distributed and linearly correlated" (Hubalek, 1982). Results of theoretical work on alternative assembly methods (Hubalek, 1982) and empirical testing (MacDonald, 1975; Hubalek, 1982; Magurran,

1988) generally support Fager and McGowan's (1963) proposal that, for extensive surveys covering several habitats, it is preferable to use presence-absence techniques where joint absences are disregarded. Recurrent group techniques are particularly useful when attempting to describe the interaction of groups of species in which competition or predation, for example, could influence the very quantities used in describing the interaction (Fager, 1957).

Following our summarization of the assemblages, we describe the fine scale vertical and horizontal distribution of certain assemblage groups along a transect across the Ensenada Front. Our purpose is to determine whether assemblage distributions are affected by the abrupt hydrographic changes associated with the front. Specifically, do incidence and abundance of taxa change along the transect and are their vertical distributions different at the north and south ends of the transect on each side of the front? Are shifts in distribution and abundance of taxa across the front coherent within assemblages? Do assemblages differ in the way they react to the front? Can these distributional shifts be linked to specific environmental factors? If so, do these linkages suggest causal factors that may delimit larval fish distributions and form the bases for assemblages? Finally, we examine the fine scale horizontal and vertical distributions of larval fish taxa and assemblages from the FRONTS 85 cruise in relation to the CalCOFI time series and discuss how this new information may affect interpretation of the CalCOFI data.

METHODS AND MATERIALS

CalCOFI.—The description of larval fish assemblages in the CalCOFI region is based on 31,214 plankton-net tows taken on CalCOFI surveys from 1951 to 1984; these tows yielded circa 12.4 million fish larvae distributed in 249 taxa. The overall survey area extended from the Oregon-California border to the southern tip of Baja California, Mexico and offshore to 280 to 360 n. mi. However, most annual surveys covered a smaller area from San Francisco, California to San Jaunico Bay, Baja California and seaward to 160 to 250 n. mi. (Fig. 1). The survey lines, arranged perpendicular to the coastline, are 40 n. mi. apart and principal stations are placed at 40-n.-mi. intervals on the lines. Usually stations were occupied at 20-n.-mi. intervals on the inner half of the pattern and at closer intervals near the coast and islands to accommodate these features. Surveys were made each year from 1951 to 1969, and thereafter every third year until 1984. The sampling pattern was occupied monthly from 1951 to 1960, quarterly from 1961 to 1965, and on a monthly basis from 1966 to 1984. During 1972–1984 there were six or seven monthly cruises per year.

At each station a double oblique plankton-net tow was made to a standard depth (to 140 m during 1951 to 1968 and to 210 m thereafter). Details of CalCOFI sampling methods and laboratory procedures are described in Smith (1971), Kramer et al. (1972), and in a series of 24 data reports that lists the ichthyoplankton and associated station data for each CalCOFI survey conducted from 1951 to 1984 (Ambrose et al., 1987; Stevens et al., 1990).

For presence-absence analysis of the assemblages we employed Fager's (1957) recurrent group technique, as in an earlier study of a portion of the data base (Moser et al., 1987). All 249 taxa identified from the net tows taken on CalCOFI surveys during 1951 to 1984 were used in this analysis. An affinity index was calculated for each pair of taxa that ever co-occurred in a plankton sample. From these indices recurrent groups of taxa were formed by the REGROUP program using a minimum index value of 0.3. Taxa were recognized as group "associates" when they had significant affinity indices (≥ 0.3) with one or more but not all group members in one or more groups. A group "affiliate" had its highest affinity index (always < 0.3) with a particular group. Each recurrent group was given a name based on a prominent member taxon as in Moser et al. (1987).

Analyses using larval fish abundance were performed on the 25 most abundant taxa from 1954 to 1960 in the region of most consistent spatio-temporal coverage extending from CalCOFI line 80 (Point Conception, California) to line 127 (just south of Point Eugenia, Baja California) and seaward to station 90 on each line (200 to 300 n. mi. offshore). The area was divided into rectangular sub-areas (Smith, 1971), each typically 40×120 n. mi. representing an area of circa 4,800 n. mi.². Standardized counts of taxa were pooled by month for each sub-area for the years 1954 to 1960 and transformed by the formula, $\log(10 \cdot x + 1)$, where x is taxon abundance (number of larvae per 10 m² surface area). Linear correlation coefficients were computed and expressed as "distance" (distance = 1 - correlation

coefficient). At each step, the distance was computed between all possible pairs of taxa and the two taxa with the shortest distance between them were classified into one cluster. After defining a cluster, a centroid linkage algorithm was used to form a new centroid (pseudo-taxon) by taking the average of the abundance of taxa within the cluster. The distances and linkage procedures were then summarized in a dendrogram (Kendall et al., 1983; Dixon, 1988). The logarithm-transformed data were also used to compute principal components; in this analysis a set of principal components was extracted from a variance-covariance matrix of the data set and the coefficients of the first and second principal components associated with each species were plotted on X-Y coordinates, as a means of summarizing variation in abundance of component taxa (Morrison, 1990).

FRONTS 85 Cruise.—Data on fine scale vertical and horizontal distribution of larval fishes were obtained from samples taken on Leg II of the FRONTS 85 cruise conducted by Scripps Institution of Oceanography aboard the R/V NEW HORIZON, July 1 to 23, 1985, southwest of the Southern California Bight, in an area characterized by a semi-permanent frontal zone (Haury et al., 1986, 1993). Leg I (July 1 to 11) was an intensive physical oceanographic survey of the frontal structure detected by AVHRR satellite images (Niiler et al., 1989) and Leg II (July 12 to 23) was a biological/oceanographic survey that occupied 37 stations on a south-north and a west-east transect crossing the front (Fig. 2). Stations on the west-east transect had single bongo tows and are not included in this paper. The south-north transect was 120 n. mi. in length, consisted of nine station sites (Stations 2 to 10, Fig. 2), each occupied three times on sequential traverses during July 13 to 21. Stations were circa 13 n. mi. apart, except the terminal stations were 20 n. mi. from their neighboring station. A total of 42 oblique plankton-net tows to 210 m depth was taken on the transect using a 71-cm paired bongo net with 0.505-mm mesh. At each terminal station, two day/night pairs of discrete, vertically stratified tows were made at 2-d intervals with a MOCNESS 1-D (1-m² mouth opening) equipped with 0.333-mm mesh nets (Wiebe et al., 1985). Sequential samples were taken at the following 16 depth strata on each tow: 1,000–850 m; 850–700 m; 700–550 m; 550–400 m; 400–300 m; 300–250 m; 250–225 m; 225–200 m; 200–175 m; 175–150 m; 150–125 m; 125–100 m; 100–75 m; 75–50 m; 50–25 m; 25–0 m.

Hydrographic casts to a maximum depth of 1,000 m, made at each station, consisted of 20 Nansen bottles from which temperature, salinity, oxygen, and nutrients were determined from all depths sampled. A total of eight primary productivity casts was made on the south-north transect. Light penetration was estimated by Secchi depth and by an irradiance meter. Examples of these data, collected in association with productivity measurements, are presented to provide a general comparison of light penetration on each side of the front. Plankton biomass for each sample was determined in the laboratory by measuring the wet displacement volume after removal of large (>5 ml) organisms (Haury et al., 1986, 1993).

Fish eggs and larvae were sorted from the samples at the NMFS Laboratory, La Jolla, California, and identified to the lowest taxon possible. Counts of larvae from the bongo net tows were multiplied by a standard haul factor (Smith and Richardson, 1977) and expressed as number per 10 m² of sea surface. Counts from the MOCNESS tows were expressed as number per 1,000 m³ of water filtered.

Environmental parameters associated with the vertical distributions of larval fish taxa from the MOCNESS samples were evaluated by calculating larva-weighted means for each parameter. Values for temperature, salinity, density (sigma-theta), dissolved oxygen, nitrate, and chlorophyll-*a* were obtained from Nansen bottle casts associated with each MOCNESS cast. Parameters were estimated by linear interpolation of values at "standard" depths (Haury et al., 1986) when they did not coincide with strata sampled by the plankton nets. Larva-weighted mean environmental parameters (\bar{st}) were calculated using the formula:

$$\bar{st} = \frac{\sum f_i v_i st_i}{\sum f_i v_i}$$

where: f_i is the number of fish larvae of taxon i from a net sample; v_i is 1,000 divided by the actual volume of water filtered estimated for each depth stratum for each tow; and, st_i is the mean of the interpolated environmental values for the nominal depth at opening and closing of each net.

RESULTS

CalCOFI Time Series

Recurrent Groups.—The number of taxa per standard CalCOFI tow ranged from 0 to 29 with a mode of six taxa per tow (Fig. 3). Recurrent group analysis of the pooled 1951–1984 data set placed 32 taxa in 10 groups that were connected directly or indirectly with each other or through ties with five associate taxa (Fig. 4,

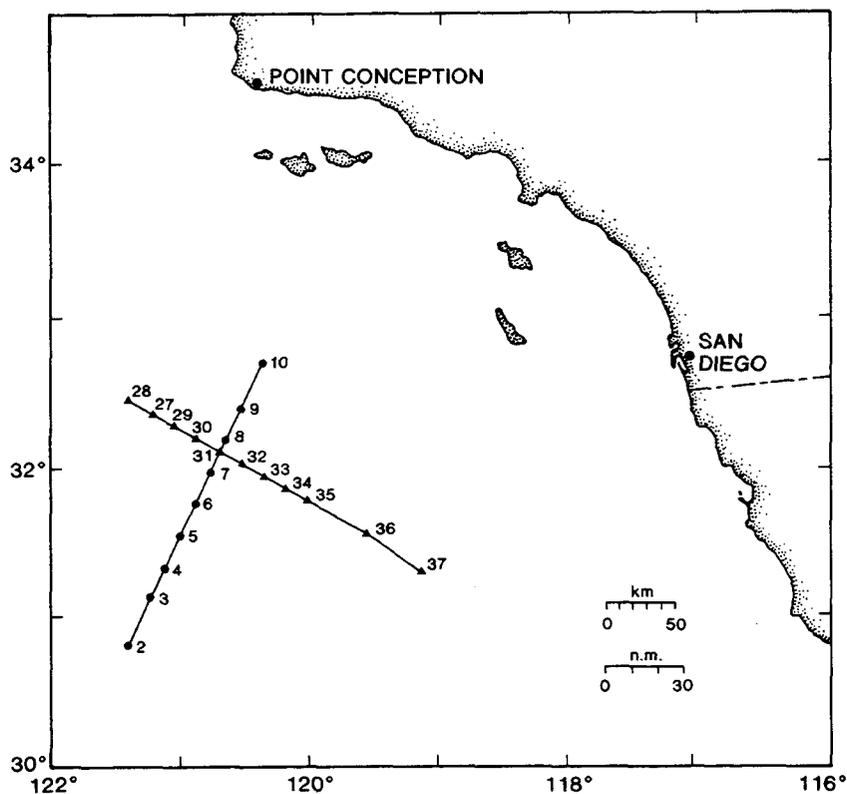


Figure 2. Stations occupied by RV NEW HORIZON on Leg II of the FRONTS 85 cruise, 12 to 23 July, 1985. Modified from Haury et al. (1986).

Appendix). Within this network, intergroup affinities formed two large complexes: 1) a Northern Complex consisting of a five-member group (LEUROGLOSSUS) and four taxon pairs (TARLETONBEANIA, PARALICHTHYS, SARDINOPS, CITHARICHTHYS) and 2) a Southern Complex consisting of a six-member group (SYMBOLOPHORUS), a four-member group (VINCIGUERRIA), and two taxon pairs (CERATOSCOPELUS, TRIPHOTURUS). One group of five shore-fish taxa (SYNODUS) formed no inter-group connections but had three associate taxa; we refer to this recurrent group and its associates as the Southern Shelf Complex. Five pairs of taxa formed isolated groups with no connections to other groups or associate taxa (Appendix). Two of these pairs were based on multiple co-occurrences (*Citharichthys fragilis*-*Citharichthys xanthostigma*, *Cubiceps pauciradiatus*-*Psenes sio*) and three were based on single co-occurrences (Balistidae-Fistulariidae, *Cyclosetta* spp.-Microdesmidae, *Chaetodipterus zonatus*-Sparidae).

NORTHERN COMPLEX. The LEUROGLOSSUS group, consisting of five taxa, is the largest group in the Northern Complex (Fig. 4, Table 1). Group members have primarily subarctic-transitional associations with highest abundances in winter to spring. Incidence and abundance are high in coastal regions for all taxa, particularly *Merluccius productus*, *Sebastes* spp., and *Leuroglossus stilbius*. The

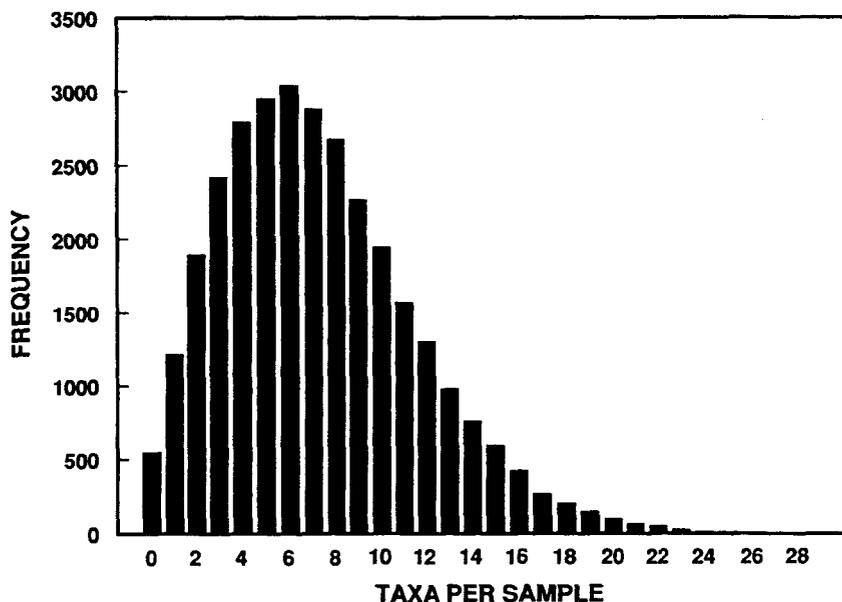


Figure 3. Numbers of larval fish taxa per sample in 31,214 CalCOFI tows taken during 1951 to 1984.

distribution of larvae for the latter is centered in the Southern California Bight. *Bathylagus ochotensis* and *Stenobranchius leucopsarus* have more northerly distributions than other group members and extend farther offshore than the others (Ahlstrom, 1972b).

TARLETONBEANIA (Fig. 4, Table 1) is composed of two subarctic-transitional species with summer maxima in abundance (Moser and Ahlstrom, 1970; Ahlstrom et al., 1976). *Tarletonbeania crenularis* has significant affinities with all but *M. productus* in the LEUROGLOSSUS group and *Icichthys lockingtoni* has significant affinities with *B. ochotensis* and *S. leucopsarus*, the more offshore members of the LEUROGLOSSUS group.

CITHARICHTHYS is composed of an abundant coastal pelagic species, *Engraulis mordax*, and the flatfish genus *Citharichthys*. The genus *Citharichthys* is represented principally by four species in the CalCOFI area. These species have broadly overlapping ranges; however, *C. sordidus* and *C. stigmaeus* have more northerly distributions than *C. fragilis* and *C. xanthostigma* whose ranges are centered off Baja California (Ahlstrom and Moser, 1975; original data). Since larvae of *Citharichthys* were identified to species only during the years 1954 to 1960, the relationships of the component taxa are obscured in the pooled 1951–1984 data. *Engraulis mordax* had significant affinities with all members of the LEUROGLOSSUS group except *B. ochotensis*. *Citharichthys* spp. and *Sebastes* spp. shared a significant affinity index, while *C. fragilis* and *C. xanthostigma* formed a recurrent group with no significant affinities to other groups (Fig. 4, Table 1, Appendix).

CITHARICHTHYS is linked with two other groups in the Northern Complex, each formed by taxon pairs: SARDINOPS, consisting of the coastal pelagics *Sardinops sagax* and *Scomber japonicus*; and PARALICHTHYS, formed by the

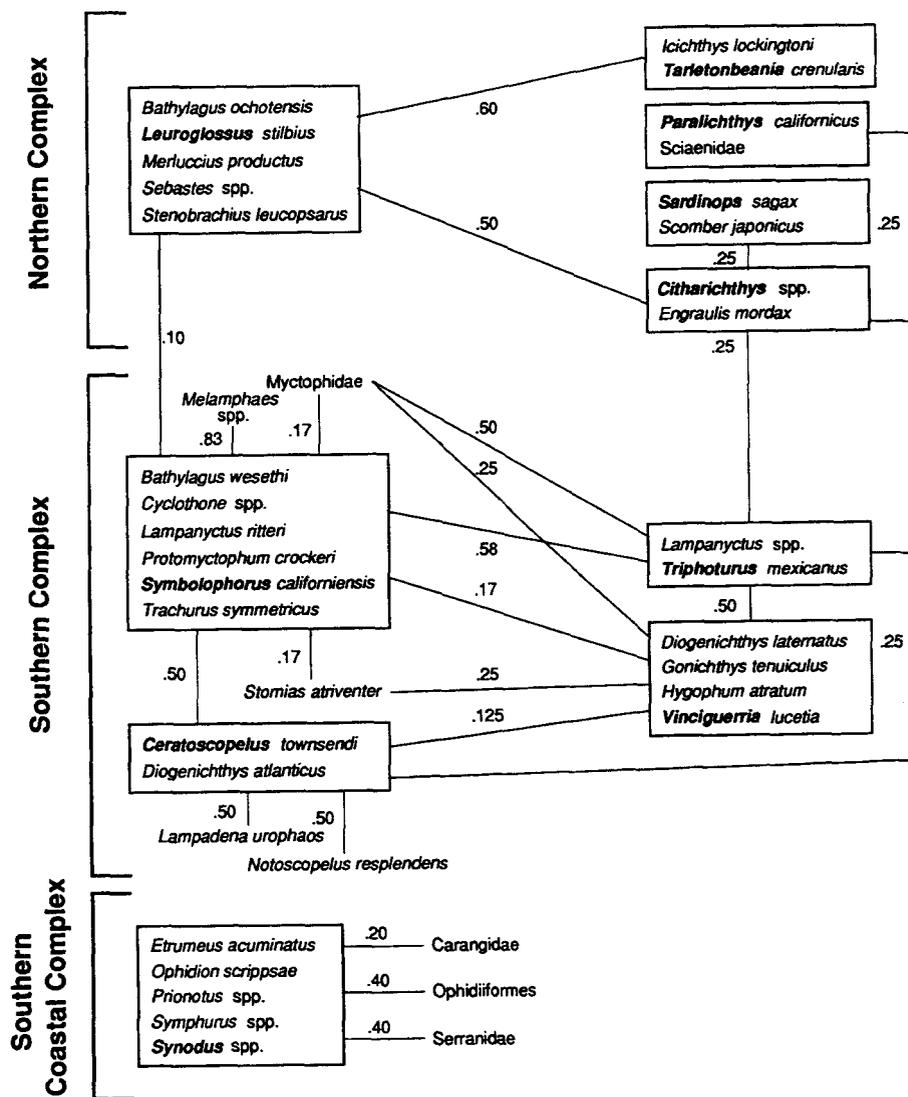


Figure 4. Composition and interrelationships of recurrent groups of larval fishes (in boxes) and their associates (not enclosed) in the CalCOFI area, 1951 to 1984, from an analysis of 31,214 samples. A line connecting recurrent groups to other recurrent groups or to associate taxa indicates there are intergroup pairs with significant affinity indices (≥ 0.3). The value associated with each line represents the number of significant intergroup affinity pairs divided by the total possible pairs. The name for each recurrent group (e.g., LEUROGLOSSUS) is based on the generic name indicated in bold letters.

flatfish *Paralichthys californicus* and the demersal shorefish family Sciaenidae (Fig. 4, Table 1). SARDINOPS is linked with CITHARICHTHYS through a significant affinity index between *S. sagax* and *E. mordax*. Both members of the SARDINOPS group are characterized by dynamic fluctuations in population size

Table 1. Taxonomic composition of recurrent groups of larval fishes in CalCOFI surveys from 1951 to 1984, number of occurrences and months of high abundance (peak month in parentheses), and zoogeographic and depth distribution of adults. Information on the distribution of adult fishes summarized from Brodeur (1988), Eschmeyer et al. (1983), Matarese et al. (1989), Matsuda et al. (1984), Miller and Lea (1972), Moser et al. (1987), Willis et al. (1988), Wisner (1976), and original data (CP = coastal pelagic, D = demersal, EP = epipelagic, ETP = eastern tropical Pacific, MEP = migrates to epipelagic, MP = mesopelagic, NT = no trend, S-T = subarctic-transitional, SbT = subtropical, T = transitional, Tr = tropical, WWC = warm water cosmopolitan)

Recurrent group	Family	Occurrence	Peak abundance	Distribution	Adult habitat
Northern Complex					
LEUROGLOSSUS group					
<i>Bathylagus ochotensis</i>	Bathylagidae	4,555	Jan-Mar (Mar)	S-T	MP (49-901 m)
<i>Leuroglossus stibius</i>	Bathylagidae	8,509	Jan-Apr (Mar)	T	MP (to 690 m)
<i>Merluccius productus</i>	Merlucciidae	7,372	Jan-Mar (Feb)	S-T	D (to 914 m)
<i>Sebastes</i> spp.	Scorpaenidae	12,322	Jan-Apr (Jan)	S-T, T	D (to 732 m)
<i>Stenobrachius leucopsaris</i>	Myctophidae	7,258	Jan-Apr (Mar)	S-T	MP (MEP)
TARLETONBEANIA group					
<i>Ichthyos loekingtoni</i>	Stromateidae	1,992	Jun-Jul (Jun)	S-T	EP (to 91+ m)
<i>Tarletonbeania crenularis</i>	Myctophidae	4,041	NT (Jun)	S-T	MP (MEP)
CITHARICHTHYS group					
<i>Citharichthys</i> spp.	Paralichthyidae	6,322	Jun-Oct (Aug)	S-T to Tr	D (to 549 m)
<i>Engraulis mordax</i>	Engraulidae	14,486	Jan-Apr (Mar)	T	CP (to 210 m)
PARALICHTHYS group					
<i>Paralichthys californicus</i>	Paralichthyidae	1,105	Feb-Mar (Feb)	T to SbT	D (to 183 m)
Sciaenidae	Sciaenidae	1,973	Jul-Aug (Aug) Dec-Mar (Jan) Jul-Aug (Aug)	T to Tr	D (to 183 m)
SARDINOPS group					
<i>Sardinops sagax</i>	Clupeidae	2,999	Feb-Sep (Aug)	T	CP
<i>Scomber japonicus</i>	Scomberidae	1,211	May-Aug (Aug)	T to SbT	CP
Southern Complex					
SYMBOLOPHORUS group					
<i>Bathylagus wesethi</i>	Bathylagidae	5,593	May-Sep (Jun)	T	MP (40-1,001 m)
<i>Cyclhone</i> spp.	Gonostomatidae	5,869	Aug-Oct (Aug)	WWC	MP
<i>Lampanyctus ritteri</i>	Myctophidae	4,707	Jan-Jul (May)	S-T to T	MP (MEP)
<i>Protomyxophum crockeri</i>	Myctophidae	8,048	Dec-Apr (Mar)	T	MP (MEP)
<i>Symblophorus californiensis</i>	Myctophidae	3,219	Apr-Jun (May)	T	MP (MEP)
<i>Trachurus symmetricus</i>	Carangidae	5,612	Mar-Jun (Jun)	T	EP (to 183 m)

Table 1. Continued

Recurrent group	Family	Occurrence	Peak abundance	Distribution	Adult habitat
TRIPHOTURUS group					
<i>Lampanyctus</i> spp.	Myctophidae	5,481	Feb-Aug (Apr)	S-T to Tr	MP to BP
<i>Triphoturus mexicanus</i>	Myctophidae	11,968	Jul-Sep (Aug)	SbT	MP (MEP)
CERATOSCOPELUS group					
<i>Ceratocopelus townsendi</i>	Myctophidae	3,058	Jun-Sep (Aug)	WWC	MP (MEP)
<i>Diogenichthys atlanticus</i>	Myctophidae	2,706	Apr-May (Apr)	WWC	MP (MEP)
VINCIGUERRIA group					
<i>Diogenichthys laternatus</i>	Myctophidae	5,043	NT (Aug)	ETP	MP (MEP)
<i>Gonichthys tenuiculus</i>	Myctophidae	1,234	Feb-Mar (Feb)	ETP	MP (MEP)
<i>Hygophum atratum</i>	Myctophidae	1,309	NT (Nov)	ETP	MP (MEP)
<i>Vinciguerria lucetta</i>	Phosichthyidae	10,510	Jul-Oct (Aug)	ETP	MP (MEP)
Southern Coastal Complex					
SYNODUS group					
<i>Etrumeus teres</i>	Clupeidae	502	Aug-Oct (Aug)	SbT to Tr	EP
<i>Ophidion scrippsae</i>	Ophidiidae	502	Aug-Oct (Sep)	SbT to Tr	D (3-70 m)
<i>Prionotus</i> spp.	Triglidae	363	Aug-Oct (Sep)	SbT to Tr	D (15-110 m)
<i>Symphurus</i> spp.	Cynoglossidae	1,038	Aug-Oct (Aug)	SbT to Tr	D (1-201 m)
<i>Synodus</i> spp.	Synodontidae	1,008	Aug-Oct (Sep)	SbT to Tr	D (to 50 m)

and range. During the 34-year period represented by the CalCOFI time series, the extensive population of *S. sagax* north of Point Conception nearly disappeared and the remainder was centered off coastal Baja California and in the Gulf of California (Ahlstrom, 1966; Smith and Moser, 1988). PARALICHTHYS is linked to CITHARICHTHYS through a significant affinity index between Sciaenidae and *E. mordax*. *P. californicus* inhabits shelf waters from central California to southern Baja California and spawns year-round with late winter and late summer peaks (Moser and Watson, 1990). Two species, *Genyonemus lineatus* and *Seriphus politus*, comprise most of the sciaenid larvae in CalCOFI samples (original data). They are nearshore species, ranging principally from central California to central Baja California and spawn at opposite times of the year with a winter peak for the former and a summer peak for the latter (Watson, 1982; Walker et al., 1987). As a composite, spawning range and seasonality for the two sciaenid species is similar to that of *P. californicus*.

SOUTHERN COMPLEX. The largest group of the Southern Complex, SYMBOLOPHORUS, consists of five mesopelagic taxa (*Symbolophorus californiensis*, *Lampanyctus ritteri*, *Protomyctophum crockeri*, *Bathylagus wesethi*, and *Cyclothone* spp.) and an epipelagic species, *Trachurus symmetricus* (Fig. 4, Table 1). Three mesopelagic taxa were associates of the group: *Melamphaes* spp. (linked with all group members except *L. ritteri*) and two taxa linked to *Cyclothone* spp., *Stomias atriventer* and the family Myctophidae (Fig. 4, Appendix). "Myctophidae" represents all myctophid larvae not identified to species because of their poor condition or small size. SYMBOLOPHORUS can be considered the core group of the California Current. *Bathylagus wesethi* is indigenous to the California Current. *Symbolophorus californiensis*, *P. crockeri*, *L. ritteri*, and *T. symmetricus* inhabit the California Current and range westward in the north Pacific transitional zone (Ahlstrom, 1969, 1972b; Moser and Ahlstrom, 1970; Wisner, 1976; Brodeur, 1988; Willis et al., 1988). *Symbolophorus californiensis* and *P. crockeri* reported from the western Pacific may be discontinuous with eastern Pacific populations (Willis et al., 1988). *Cyclothone* is primarily an equatorial-subtropical genus represented by at least seven species in the CalCOFI survey area, two of which (*C. signata* and *C. acclinidens*) are abundant in the California Current (Mukacheva, 1964). These two species constitute the bulk of the larvae taken in CalCOFI tows (original data). Abundance of larvae is highest in the spring or summer for members and associates of SYMBOLOPHORUS (Table 1). The Northern and Southern Complexes are linked only by the significant affinity index between *P. crockeri* (SYMBOLOPHORUS) and *S. leucopsarus* (LEUROGLOSSUS).

SYMBOLOPHORUS is connected directly and indirectly to the three other groups in the Southern Complex: TRIPHOTURUS, CERATOSCOPELUS, and VINCIGUERRIA (Fig. 4, Table 1). Both TRIPHOTURUS taxa (*Triphoturus mexicanus* and *Lampanyctus* spp.) have significant affinities with *Cyclothone* spp., *B. wesethi*, and *P. crockeri* of SYMBOLOPHORUS; *T. mexicanus* also has a significant link to *T. symmetricus* in the latter group. *T. mexicanus* is a subtropical species with greatest abundance in the southern extent of the California Current (Wisner, 1976). It spawns year-round with a peak in spring-summer (Ahlstrom, 1972b). *Lampanyctus* spp. includes larvae of more than a dozen species in the CalCOFI survey area that were not identified to species and also includes small (<5 mm) larvae of *L. ritteri*.

CERATOSCOPELUS is formed by two warm-water cosmopolites, *Diogenichthys atlanticus* and *Ceratospelus townsendi*. Both have significant affinities with *Cyclothone* spp. and *B. wesethi* of SYMBOLOPHORUS and *D. atlanticus* also has significant links to *P. crockeri* and *S. californiensis*. CERATOSCOPELUS is also connected to the TRIPHOTURUS group through a *C. townsendi*-*T. mex-*

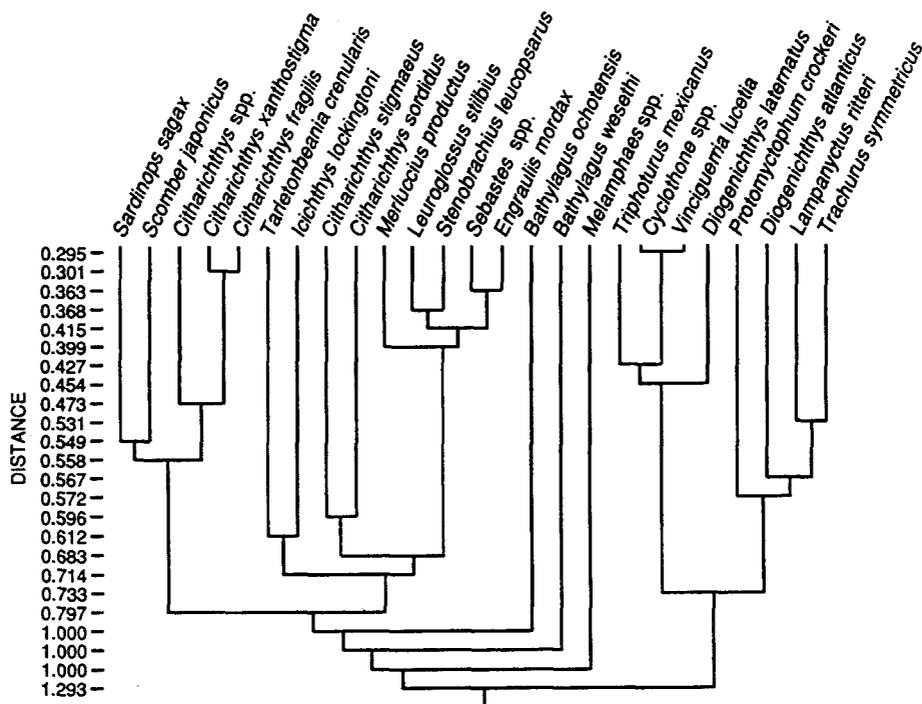


Figure 5. Cluster diagram showing results of an analysis of linear correlation of log-transformed abundances of the 25 most abundant larval fish taxa in the consistently sampled CalCOFI area during 1951 to 1984. Distances are expressed as 1 minus the correlation coefficient.

icanus linkage. Two other warm water cosmopolite myctophid species, *Lampadena urophaos* and *Notoscopelus resplendens*, are associates of CERATOSCOPELUS, through significant linkages with *C. townsendi* (Fig. 4, Table 1, Appendix).

VINCIGUERRIA consists of four eastern tropical Pacific (ETP) mesopelagic species: *Vinciguerria lucetia*, *Diogenichthys laternatus*, *Gonichthys tenuiculus*, and *Hygophum atratum*. The mesopelagic predator *Stomias atriventer* and Myctophidae are associates through links with *V. lucetia*. *Vinciguerria lucetia* and *D. laternatus* have significant affinities with both members of TRIPHOTURUS. VINCIGUERRIA is linked to SYMBOLOPHORUS through *V. lucetia-B. wesethi*, *V. lucetia-Cyclothone* spp., *V. lucetia-P. crockeri*, and *D. laternatus-Cyclothone* spp. and to CERATOSCOPELUS through *V. lucetia-C. townsendi* (Fig. 4, Table 1, Appendix).

SOUTHERN SHELF COMPLEX. This consists of the five-member recurrent group SYNODUS and three associate taxa (Fig. 4, Table 1). SYNODUS is composed of the epipelagic species, *Etrumeus teres*, and four demersal taxa (*Synodus* spp., *Prionotus* spp., *Symphurus* spp., and *Ophidion scrippsae*). Two percoid families, Carangidae and Serranidae, and the order Ophidiiformes (taxa other than *O. scrippsae* and *Chilara tayori*) are associates of the group. All had significantly affinity indices with *Prionotus* spp.; Ophidiiformes also was linked with *Synodus* spp. and Serranidae was linked with *Symphurus* spp. The member and associate taxa have broad tropical-subtropical distributions. Coincident samples of the group occurred only on the broad continental shelf region of central Baja California (Moser et al., 1987).

Cluster Analysis.—Cluster analysis produced two large groups, one composed of eight predominantly offshore taxa and the other composed of 14 taxa primarily with inshore distributions (Fig. 5). Three taxa (*Bathylagus ochotensis*, *B. wesethi*, and *Melamphaes* spp.) were uncorrelated.

The inshore grouping has two major subgroups: 1) a group of five taxa with distributions of larvae associated with the extensive shelf regions of southern California and Baja California, and 2) a group of nine taxa with more northerly distributions in coastal waters or seaward to the core of the California Current. In the shelf subgroup, *Sardinops sagax* and *Scomber japonicus* (the SARDINOPS group) are separated from a cluster of three paralichthyid taxa (*Citharichthys* spp., *C. fragilis*, and *C. xanthostigma*). The latter two species are the second most highly correlated pair in the entire dendrogram. The nine-taxon subgroup contains two species pairs and a highly correlated grouping of five taxa. One species pair is formed by *T. crenularis* and *I. lockingtoni* (the TARLETONBEANIA group), and the other consists of two sanddab species, *C. sordidus* and *C. stigmaeus*, with primarily cold water affinities. The five-species cluster is essentially the LEUROGLOSSUS recurrent group with *E. mordax* replacing *B. ochotensis*.

The offshore grouping consists of two four-member subgroups composed of taxa from the TRIPHOTURUS, VINCIGUERRIA, and SYMBOLOPHORUS recurrent groups of the Southern Complex. The first subgroup contains the pair, *Cyclothone* spp. and *V. lucetia*, the most highly correlated pair of taxa in the analysis. Although the taxa in this cluster represent three different recurrent groups (*T. mexicanus*, TRIPHOTURUS; *Cyclothone* spp., SYMBOLOPHORUS; *V. lucetia* and *D. laternatus*, VINCIGUERRIA), all taxon pairs in the cluster had significant affinity indices in the recurrent group analysis and all species have tropical or equatorial distributions. The other subgroup is composed of three taxa from SYMBOLOPHORUS (*P. crockeri*, *L. ritteri*, *T. symmetricus*) and one from the CERATOSCOPELUS group (*D. atlanticus*). The first three are primarily California Current species and *D. atlanticus* is a warm water cosmopolite that extends eastward into the California Current in the central region of the CalCOFI survey. Interestingly, *D. atlanticus* had a significant affinity index with *P. crockeri* in the recurrent group analysis but not with *L. ritteri* or *T. symmetricus*. In the cluster analysis *D. atlanticus* was more closely correlated with the latter two species.

Principal Component Analysis.—The first and second principal components explained 36% of the variation in the data (20.7 and 15.5%, respectively). The analysis revealed four distinct groups and several subgroups that identify north-south (ordinate) and inshore-offshore (abscissa) components as important variables (Fig. 6). Taxa comprising the Northern Complex of the recurrent group analysis have positive values on the ordinate while Southern Complex taxa have negative values. The upper right quadrant contains coastal demersal and pelagic taxa. All five of the sanddab taxa included in the analysis lie within that quadrant. *Citharichthys* spp. and the *C. fragilis*-*C. xanthostigma* pair lie to the extreme right, consonant with distributions concentrated over southern shelf areas. The more northern and offshore distributions of the other sanddab pair, *C. sordidus*-*C. stigmaeus*, are reflected in the plot. The *S. sagax*-*S. japonicus* pair lies in a similar position. A more northerly distribution is indicated for *E. mordax*.

The upper left quadrant contains the subarctic-transitional taxa that constitute LEUROGLOSSUS, the large recurrent group of the Northern Complex, and its closely connected species-pair group, TARLETONBEANIA. In the former, the two demersal taxa (*Sebastes* spp. and *M. productus*) have the lowest offshore position and *B. ochotensis* has the highest. *Stenobranchius leucopsarus* and *L.*

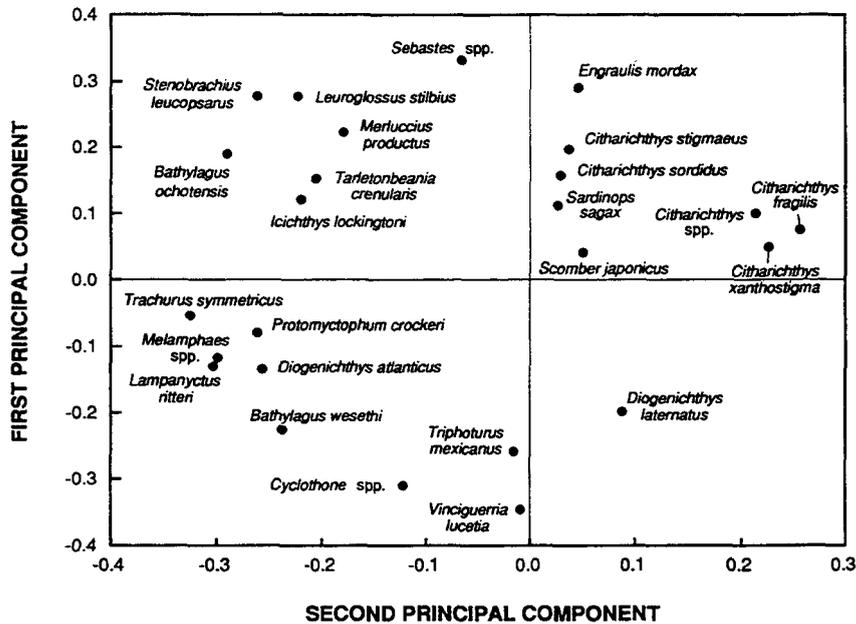


Figure 6. Plot of first and second principal component coefficients from an analysis of the 25 most abundant larval fish taxa in the consistently sampled CalCOFI area during 1954 to 1960.

stilbius, closely paired in recurrent group and cluster analyses, have an intermediate northerly location in the quadrant. *Tarletonbeania crenularis* and *I. lockingtoni* (TARLETONBEANIA), have a more southerly position in the quadrant.

The lower left quadrant contains members of the four Southern Complex recurrent groups. A grouping of six taxa with offshore and relatively more northerly positions includes *T. symmetricus*, *P. crockeri*, *L. ritteri*, and *B. wesethi* of SYMBOLOPHORUS with the group associate *Melamphaes* spp. Also included in the grouping is *D. atlanticus* of the CERATOSCOPELUS group. The remaining taxa in the quadrant, *T. mexicanus*, *Cyclothone* spp., and *V. lucetia*, have more southerly positions and, with *D. laternatus* (the only taxon in the lower right quadrant), constitute a grouping that was also distinct in the cluster analysis.

FRONTS 85 Cruise

Horizontal Distribution.—BONGO NET SAMPLES. A total of 1,376 fish larvae representing 41 taxa was taken in 42 bongo-net tows on the south-north transect (Table 2). Taxa of the Northern Complex occurred infrequently and in low mean abundance. No LEUROGLOSSUS group member occurred in samples south of Station 5 and most were taken north of Station 6, the midpoint of the transect (Table 2). *Merluccius productus* was absent from the samples, since it has a restricted winter-spring spawning season (Table 1). *Tarletonbeania crenularis* larvae (TARLETONBEANIA group) declined markedly in abundance from north to south and were absent south of Station 6 (Fig. 7A). This distribution is consonant with historical data, since the southern extent of *T. crenularis* larvae in the CalCOFI time series is just south of the FRONTS 85 transect (Fig. 7B). *Diaphus* spp., an affiliate of TARLETONBEANIA (Appendix), occurred on all

Table 2. Total occurrences and mean number (per 10 m² surface area, positive tows) of larval taxa in bongo tows at 9 stations on the south-north transect of the FRONTS 85 cruise

Taxon	Stations									
	2	3	4	5	6	7	8	9	10	
<i>Trachurus symmetricus</i>	36	37.6	11.7	19.0	18.0	23.8	4.9	8.0	16.3	
<i>Tripnoturus mexicanus</i>	34	79.9	12.0	15.1	5.2	6.2	21.9	38.0	6.9	
<i>Diaphus</i> spp.	33	4.7	5.0	14.4	11.9	16.3	7.3	18.6	35.7	
<i>Symblophorus californiensis</i>	33	13.4	14.1	7.2	8.0	5.1	9.8	12.1	5.5	
<i>Lampanyctus</i> spp.	30	9.5	12.9	16.6	11.4	10.3	10.9	10.3	17.1	
<i>Bathylagus weselhi</i>	28	9.6	41.7	9.7	18.0	36.1	9.8	16.3	15.9	
<i>Cyclothone</i> spp.	27	6.7	30.7	9.4	15.1	5.2	4.9	7.9	7.1	
<i>Protomyctophum crockeri</i>	26	8.2	10.3	7.2	12.6	10.3	9.9	7.9	12.8	
<i>Ceratospilus townsendi</i>	24	9.6	34.1	11.7	12.6	10.2	4.7	6.4	4.6	
<i>Vinciguerra lucetia</i>	24	30.1	69.8	102.1	80.1	—	5.0	4.5	—	
<i>Tarletonbeania crenularis</i>	18	—	—	—	—	5.1	7.2	7.2	9.6	
<i>Melanphaes</i> spp.	18	5.1	4.7	4.9	7.4	6.1	7.2	7.2	9.6	
<i>Lampanyctus regalis</i>	17	4.5	9.6	—	—	7.4	9.8	6.6	4.8	
<i>Lestidiops ringens</i>	13	7.3	7.8	9.7	5.2	4.8	9.4	4.3	11.3	
<i>Microstoma microstoma</i>	10	7.0	—	4.9	—	4.8	4.9	8.9	—	
<i>Oxyjulis californica</i>	10	—	—	—	—	10.2	14.1	4.4	4.8	
<i>Stomias atriventer</i>	9	4.8	5.4	4.7	4.9	—	4.7	—	9.6	
<i>Engraulis mordax</i>	8	—	—	—	—	—	—	—	—	
<i>Chautilodius macouni</i>	8	4.7	5.7	—	4.9	5.0	—	4.2	6.5	
<i>Diogenichthys atlanticus</i>	7	6.1	11.5	—	—	—	4.9	—	8.2	
<i>Scomber japonicus</i>	6	—	—	—	—	5.0	4.7	4.6	4.6	
<i>Argyropelecus</i> spp.	5	4.7	8.9	—	—	—	—	4.2	9.8	
<i>Bathylagus ochotensis</i>	4	—	—	—	—	—	—	—	5.0	
<i>Sebastes</i> spp.	4	—	—	—	4.9	5.0	9.8	—	4.8	
<i>Danaphos oculatus</i>	2	—	—	—	—	4.9	—	4.5	—	
<i>Idiacanthus antrostomus</i>	2	—	—	—	—	—	—	4.4	—	
<i>Stenobrachius leucopsarus</i>	2	—	—	—	5.1	—	—	—	—	
<i>Etrumeus acuminatus</i>	1	—	—	—	—	5.0	—	—	—	
<i>Nansenia candida</i>	1	—	—	—	—	—	—	—	4.7	
<i>Leuroglossus stilbius</i>	1	—	—	—	—	5.3	—	—	—	
<i>Sternoptyx</i> spp.	1	—	—	4.9	—	5.3	—	—	—	

Table 2. Continued

Taxon	Stations									
	2	3	4	5	6	7	8	9	10	
<i>Stomiiformes</i>	4.9	—	—	—	—	—	—	—	—	—
<i>Bathophilus flemingi</i>	4.9	—	—	—	—	—	—	—	—	—
<i>Notolepis risso</i>	—	—	—	—	—	—	—	—	—	—
<i>Benthalbella dentata</i>	—	4.9	—	—	—	—	—	—	—	4.2
<i>Rosenblattichthys volucris</i>	—	4.4	—	—	—	—	—	—	—	—
<i>Scopelosaurus harryi</i>	—	—	—	—	—	4.9	—	—	—	—
<i>Lowena rara</i>	—	—	—	5.2	—	—	—	—	—	—
<i>Cololabis saira</i>	—	—	—	—	—	5.3	—	—	—	—
<i>Trachipterus</i> spp.	—	—	—	—	—	—	—	—	—	4.5
<i>Icichthys lockingtoni</i>	—	—	—	—	—	4.9	—	—	—	—
Total larvae	94.7	339.5	214.2	206.5	105.4	112.7	103.6	146.4	133.7	

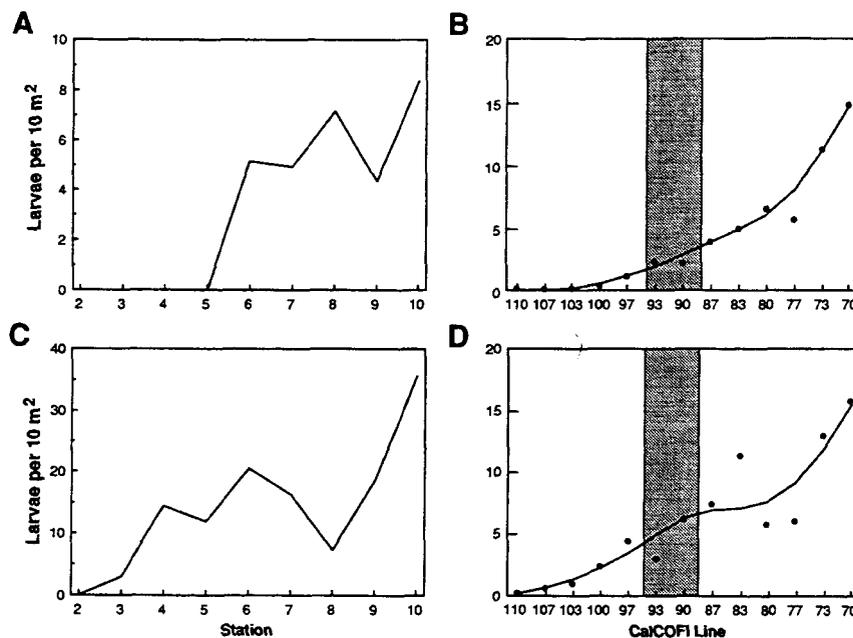


Figure 7. Change in mean abundance of two larval fish taxa representative of the Northern Complex from bongo-net tows at stations on the south-north FRONTS 85 transect (A, C) compared with long term latitudinal trends for the same taxa in 1,555 CalCOFI samples from that region (B, D). *Tarletonbeania crenularis* (A, B); *Diaphus* spp. (C, D). CalCOFI data points are arithmetic means of all stations in July and August between Stations 60 and 80 on 13 survey lines (Fig. 1). The line connects the results of a non-parametric smoother (Velleman, 1980). FRONTS 85 region is indicated by the shaded area on the CalCOFI graphs.

stations of the transect with a trend of decreasing abundance from north to south (Table 2, Fig. 7C.) In historical samples, *Diaphus* spp. larvae extend farther south than *T. crenularis* and long term mean abundance for *Diaphus* spp. in the FRONTS 85 sampling region is about twice that for *T. crenularis* (Fig. 7D). *Diaphus theta*, an abundant species of the subarctic-transitional north Pacific, was the principal, and perhaps only, species of the genus represented in the FRONTS 85 samples. Other taxa of the Northern Complex were too poorly represented to show any trend across the transect. *Scomber japonicus* (SARDINOPS group) had six occurrences, all in the northern half of the transect and *E. mordax* (CITHARICHTHYS group) had eight occurrences, all at the northernmost station (Table 2).

The bongo-net samples were dominated by larvae of the Southern Complex. Of the eight most frequently occurring taxa, five were SYMBOLOPHORUS group members (Table 2). Although most of the SYMBOLOPHORUS member taxa had their highest mean abundances at Station 3 in the southern half of the transect, only *B. wesethi* and *Cyclothone* spp. showed a clear trend of decreasing abundance from south to north (Table 2, Fig. 8). The historical data for *T. symmetricus* suggest a local peak in mean abundance in the FRONTS 85 region with a trend of increasing abundance to the north of the region (Fig. 8B). Historical data show that *B. wesethi* larvae decrease sharply in the FRONTS 85 region while *Cyclothone* abundance decreased abruptly south of the FRONTS 85 region (Fig. 8D, F).

Vinciguerria lucetia (VINCIGUERRIA group) had the greatest change in mean abundance of any species sampled, from 102 larvae per 10 m² at Station 4 to 0

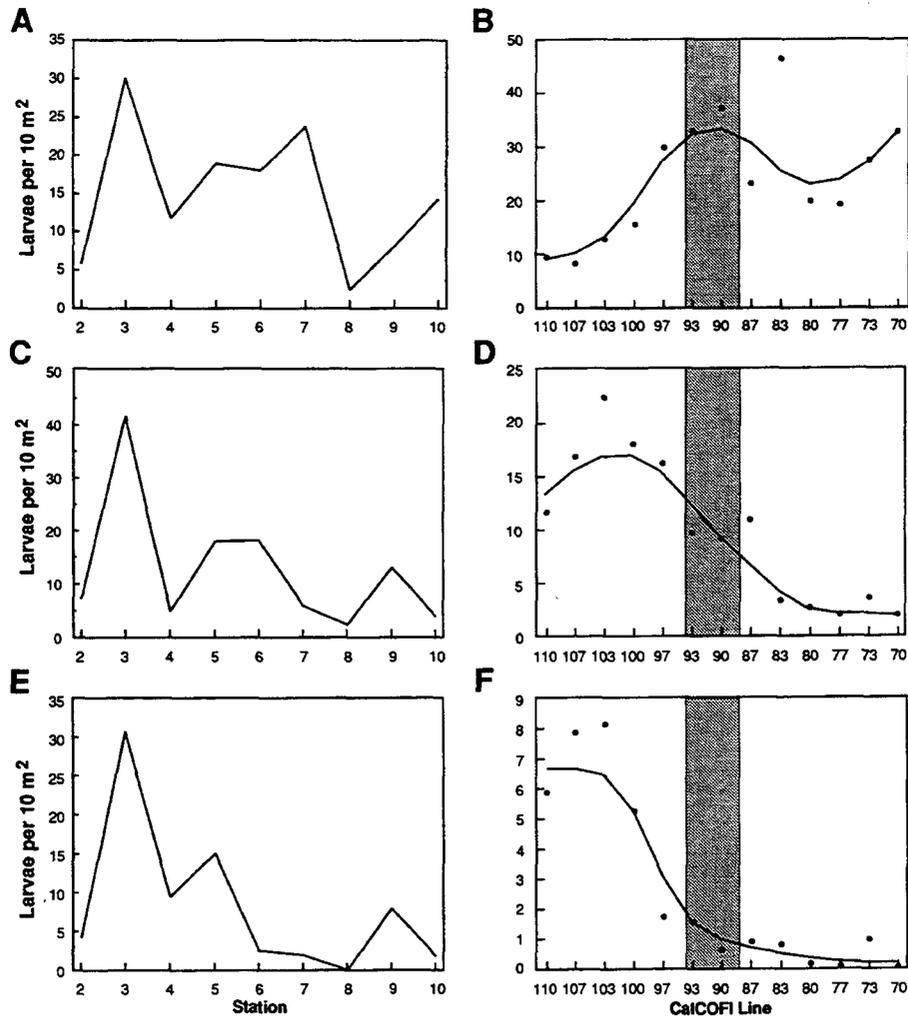


Figure 8. Change in mean abundance of three larval fish taxa representative of the Southern Complex from bongo-net tows at stations on the south-north FRONTS 85 transect (A, C, E) compared with long term latitudinal trends for the same taxa in 1,555 CalCOFI samples from that region (B, D, E). *Trachurus symmetricus* (A, B); *Bathylagus wesethi* (C, D); and *Cyclothone* spp. (E, F). Explanation as in Figure 7.

at mid-transect, and <5.0 per 10 m^2 at all other stations in the northern half of the transect (Table 2, Fig. 9A). Historical data show the FRONTS 85 region to be the northern terminus for larvae of this species (Fig. 9B). Similar but less dramatic trends were apparent for taxa in other Southern Complex groups. *Ceratoscopelus townsendi* (CERATOSCOPELUS) peaked at Station 3, declined sharply at Station 4, then continued its decline more gradually to the north (Table 2, Fig. 9C), while *T. mexicanus* (TRIPHOTURUS) showed a lesser peak at Station 9 in the northern part of the transect (Fig. 9E). Long term CalCOFI data for these species show an abrupt decline south of the FRONTS 85 region (Fig. 9D, F).

Measurements of environmental features along the transect reveal the frontal

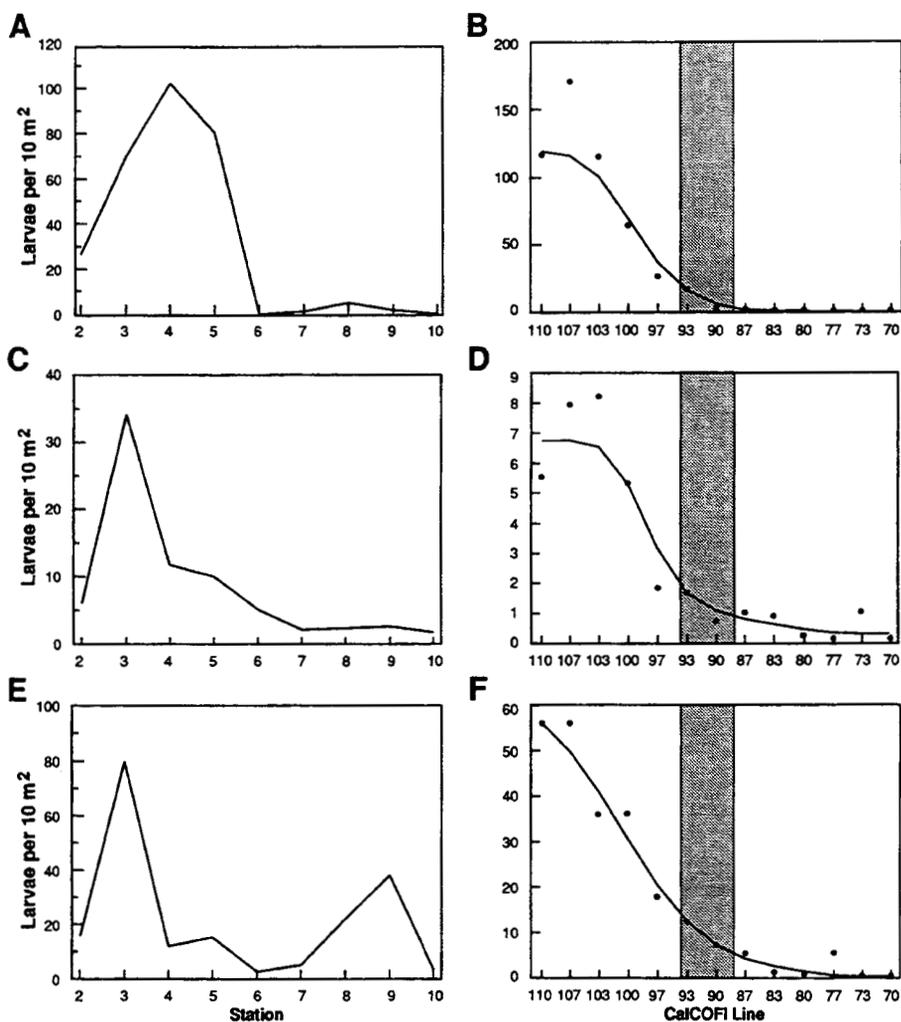


Figure 9. Change in mean abundance of three larval fish taxa representative of the Southern Complex from bongo-net tows at stations on the south-north FRONTS 85 transect (A, C, E) compared with long term latitudinal trends for the same taxa in 1,555 CalCOFI samples from that region (B, D, E). *Vinciguerria lucetia* (A, B); *Ceratoscopelus townsendi* (C, D); and *Triphoturus mexicanus* (E, F). Explanation as in Figure 7.

structure (Fig. 10). Sections of temperature, salinity, density, nitrate, oxygen saturation, and chlorophyll-*a* in the upper 250 m along the south-north transect show the shoaling of isopleths from south to north with rather sharp gradients at Stations 5 and 6 at the mid-transect. Niiler et al. (1989) and Haury et al. (1993) suggest that the tongue of low salinity water at 50–100 m in the southern half of the transect indicates subduction of northern water across the front (Fig. 10).

Vertical Distribution.—A total of 3,013 fish larvae representing 46 taxa was taken in 16 discrete depth strata on the 8 MOCNESS tows at both northern and southern

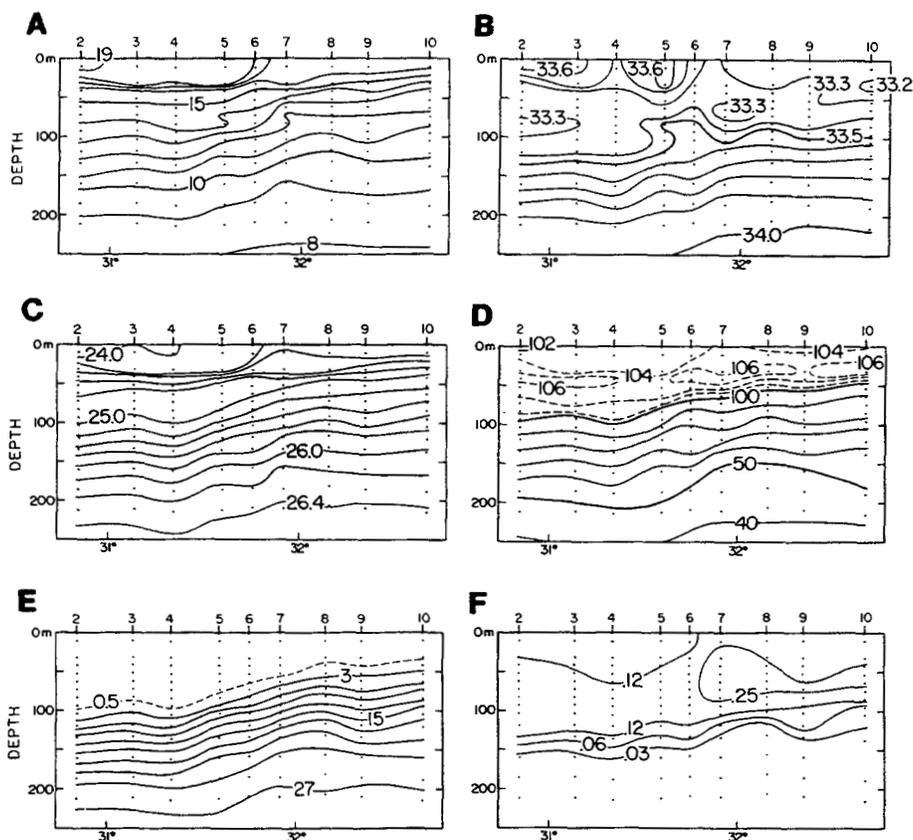


Figure 10. Sections to 250 m on the south-north transect of FRONTS 85 from Station 2 to Station 10: A, temperature ($^{\circ}\text{C}$); B, salinity (‰); C, density ($\text{kg}\cdot\text{m}^{-3}$); D, oxygen concentration (% saturation); E, nitrate ($\mu\text{m}\cdot\text{liter}^{-1}$); F, chlorophyll-*a* ($\text{mg}\cdot\text{m}^{-3}$). Modified from Haury et al. (1986).

stations. Taxa of the Southern Complex accounted for 91% of the total occurrences at the southern station and for 42% at the northern station (Table 3). At the northern station, mean concentration of total larvae was highest at 25–75 m, whereas highest concentration was spread over a broader zone (25–100 m) at the southern station. Peak concentration at the northern station (25–50 m) was almost double that of the peak stratum (75–100 m) at the southern station, although mean abundance (number of larvae per 10 m^2 surface area) for all strata combined was only slightly higher in the north (Table 4).

NORTHERN COMPLEX. Taxa of the LEUROGLOSSUS recurrent group occurred only in samples from the northern station (Table 3, Fig. 11). All had low mean concentration, as would be expected of winter-spring spawners. They occurred moderately deep in the water column (*Sebastes* spp., 75–150 m; *S. leucopsarus*, 75–200 m; *L. stilbius*, 200–300 m; *B. ochotensis*, 75–400 m). The fifth member of the group, *M. productus* (not present in the samples), also deep living, occurs in or below the thermocline (Ahlstrom, 1959). *Tarletonbaenia crenularis* (TARLETONBEANIA) was relatively abundant at the northern station but absent from southern station samples; it occurred between 75 and 400 m, with peak concen-

Table 3. Total occurrences and mean number (per 1,000 m³, positive tows) of 46 larval fish taxa in MOCNESS tows at the north and south ends of the FRONTS 85 cruise transect

Taxon	Total occurrences	South		North	
		Occurrences	Mean number	Occurrences	Mean number
<i>Lampanyctus</i> spp.	36	20	7.7	16	41.0
<i>Symbolophorus californiensis</i>	32	22	10.7	10	14.2
<i>Triphoturus mexicanus</i>	29	23	54.1	6	32.7
<i>Cyclothone</i> spp.	25	24	18.0	1	7.7
<i>Diaphus</i> spp.	25	8	7.1	17	103.1
<i>Bathylagus wesethi</i>	24	19	27.3	5	22.0
<i>Tarletonbeania crenularis</i>	21	—	—	21	21.1
<i>Trachurus symmetricus</i>	21	11	37.7	10	50.2
<i>Vinciguerria lucetia</i>	20	20	62.1	—	—
<i>Protomyctophum crockeri</i>	19	6	6.7	13	13.7
<i>Melamphaes</i> spp.	18	9	7.7	9	8.4
<i>Ceratoscopelus townsendi</i>	17	17	20.6	—	—
<i>Lampanyctus regalis</i>	17	1	5.7	16	37.3
<i>Microstoma microstoma</i>	14	7	3.3	7	4.3
<i>Lestidiops ringens</i>	13	8	17.7	5	8.5
<i>Argyropelecus</i> spp.	11	1	1.1	10	3.4
<i>Diogenichthys atlanticus</i>	11	9	8.4	2	6.2
<i>Chauliodus macouni</i>	9	4	4.6	5	8.8
<i>Oxyjulis californica</i>	7	—	—	7	36.1
<i>Sebastolobus altivelis</i>	6	—	—	6	4.9
<i>Danaphos oculatus</i>	5	1	1.6	4	5.1
<i>Stomias atriventer</i>	5	5	6.0	—	—
<i>Sebastes</i> spp.	5	—	—	5	10.2
<i>Scomber japonicus</i>	5	—	—	5	10.7
<i>Engraulis mordax</i>	4	1	4.5	3	53.4
<i>Bathylagus ochotensis</i>	4	—	—	4	5.0
<i>Leuroglossus stilbius</i>	3	—	—	3	5.4
<i>Sternoptyx</i> spp.	3	2	5.0	1	1.7
<i>Scopelosaurus harrisi</i>	3	2	4.2	1	9.0
<i>Stenobrachius leucopsarus</i>	3	—	—	3	6.7
<i>Trachipterus</i> spp.	3	—	—	3	7.0
<i>Idiacanthus antrostomus</i>	2	1	2.3	1	7.7
<i>Scopelarchus</i> sp.	2	2	5.5	—	—
<i>Citharichthys stigmaeus</i>	2	—	—	2	6.4
<i>Nansenia candida</i>	1	—	—	1	6.2
<i>Tactostoma macropus</i>	1	1	5.7	—	—
Melanostomiidae	1	1	7.1	—	—
<i>Chilara taylora</i>	1	—	—	1	18.0
<i>Poromitra</i> spp.	1	—	—	1	5.6
<i>Scopelogadus bispinosus</i>	1	1	7.7	—	—
<i>Sebastolobus alascanus</i>	1	—	—	1	2.7
<i>Paralabrax</i> spp.	1	—	—	1	7.1
Chiasmodontidae	1	1	6.4	—	—
Gobiidae	1	—	—	1	9.0
<i>Tetragonurus cuvieri</i>	1	1	11.8	—	—
<i>Citharichthys sordidus</i>	1	—	—	1	9.0

tration in strata between 75 and 150 m (Table 3, Fig. 12A). An affiliate, *Diaphus* spp., had a shallower distribution with the highest mean concentration (103 larvae per 1,000 m³) of any taxon in the MOCNESS samples (Fig. 12B, Table 3). *Scomber japonicus* (SARDINOPS) occurred in low abundance in the upper 100 m of the northern samples, with highest concentration at 25–50 m (Fig. 12C). *Engraulis mordax* (CITHARICHTHYS) occurred in one sample at the southern station and in three samples in the north, with a peak at 25–50 m (Fig. 12D).

Table 4. Mean volume (m^3) of water filtered and mean number (per 1,000 m^3) of total fish larvae in 16 strata sampled by 8 MOCNESS tows (4 north, 4 south) on the FRONTS 85 cruise. For the entire water column, total fish larvae divided by total water filtered is expressed as number per 1,000 m^3 ; total larvae per 10 m^2 of surface areas is in parentheses.

Depth (m)	North		South	
	Mean volume filtered	Mean total larvae	Mean volume filtered	Mean total larvae
0-25	142	30.6	151	50.6
25-50	134	490.4	169	230.5
50-75	141	423.5	174	260.0
75-100	123	284.2	169	268.3
100-125	112	147.4	208	184.2
125-150	168	62.1	185	88.4
150-175	149	32.9	238	93.9
175-200	142	8.8	206	73.2
200-225	203	46.2	177	22.8
225-250	112	24.1	153	27.2
250-300	237	32.1	249	15.7
300-400	412	13.0	394	13.7
400-550	595	8.3	631	1.8
550-700	531	1.7	533	0.9
700-850	483	2.8	522	1.5
850-1,000	551	5.1	592	1.4
0-1,000		50.2		51.2
		(431)		(349)

SOUTHERN COMPLEX. All taxa of the SYMBOLOPHORUS recurrent group, except *L. ritteri*, were identified in samples from northern and southern localities and ranked among the 10 most frequently occurring taxa overall (Table 3). SYMBOLOPHORUS taxa had diverse vertical distribution patterns. Occurrences of *T. symmetricus* larvae were about equal at both localities and were restricted to the upper 100 m with a marked peak at 25-50 m, where mean concentration was twice as great in the north compared with the south (Fig. 13A). *Symbolophorus californiensis* had twice as many occurrences in the south as in the north and occupied a broad depth range (25-300 m) at both stations; however mean concentration was greater in deep strata at the southern station compared with the northern station (Fig. 13B). This shift in depth distribution at the two localities was even more apparent in *B. wesethi* (Fig. 13C). Occurrences of *B. wesethi* were four times greater in the south, where larvae ranged from 75 to 250 m depth with a concentration peak at 150-175 m. In the north they ranged from 50 to 125 m with a peak at 75-100 m. *Protomyctophum crockeri* larvae occurred twice as frequently in the north compared with the south and had a markedly deeper distribution than other SYMBOLOPHORUS group members (Table 3, Fig. 13D). In the north they ranged from 175 to 550 m with a peak at 200-225 m, while in the south they ranged from 225 to 550 m with a peak at 300-400 m. *Cyclothone* spp. was fourth in overall incidence with all but one occurrence at the southern site (Table 3). All larvae were taken in the upper 200 m with a distinct peak at 75-100 m (Fig. 14A).

Shoaling of vertical distributions at the northern station was also apparent for associates of SYMBOLOPHORUS. *Melamphaes* spp. occurred in low abundance with a peak at 75-100 m in the north and at 150-175 m in the south (Table 3, Fig. 14B). The paralepidid *Lestidiops ringens*, a SYMBOLOPHORUS affiliate (Appendix), had non-overlapping vertical ranges at the two sites with peak concentration at 50-75 m in the north and at 175-200 m in the south (Fig. 14C).

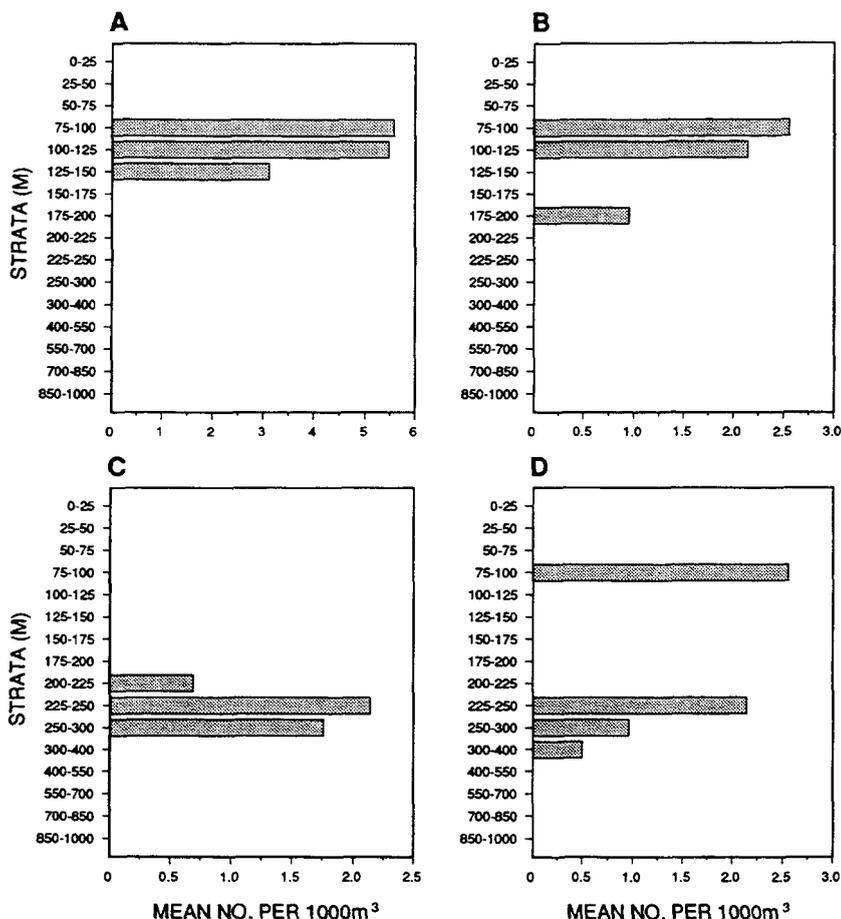


Figure 11. Depth distribution of larvae of four members of the Northern Complex recurrent group LEUROGLOSSUS from MOCNESS samples taken on northern end of the FRONTS 85 transect. A, *Sebastes* spp.; B, *Stenobranchius leucopsarus*; C, *Leuroglossus stilbius*; D, *Bathylagus ochotensis*.

Another affiliate, *Microstoma microstoma*, occurred deep in the water column at each site with concentration maxima at 200–225 m in north and at 300–400 m in the south (Fig. 14D).

Vinciguerrua lucetia (VINCIGUERRIA) occurred only at the southern locality and in high frequency and relative abundance (Table 3). Except for a few late stage specimens, the larvae were restricted to the upper 150 m with a sharp peak at 50–75 m (Fig. 15A). Other VINCIGUERRIA members (*D. laternatus*, *G. tenuiculus*, *H. atratum*) not present in FRONTS 85 samples are known to have comparatively deep distributions (Loeb and Nichols, 1984). *Stomias atriventer*, an associate of the group, occurred in 5 samples in the upper 200 m at the southern site (Table 3, Fig. 15B).

Both members of the CERATOSCOPELUS group were present in the MOCNESS samples. *Ceratoscopelus townsendi* occurred only at the southern station in the upper 175 m, with a peak at 25–50 m (Table 3, Fig. 15C). Captures of *D.*

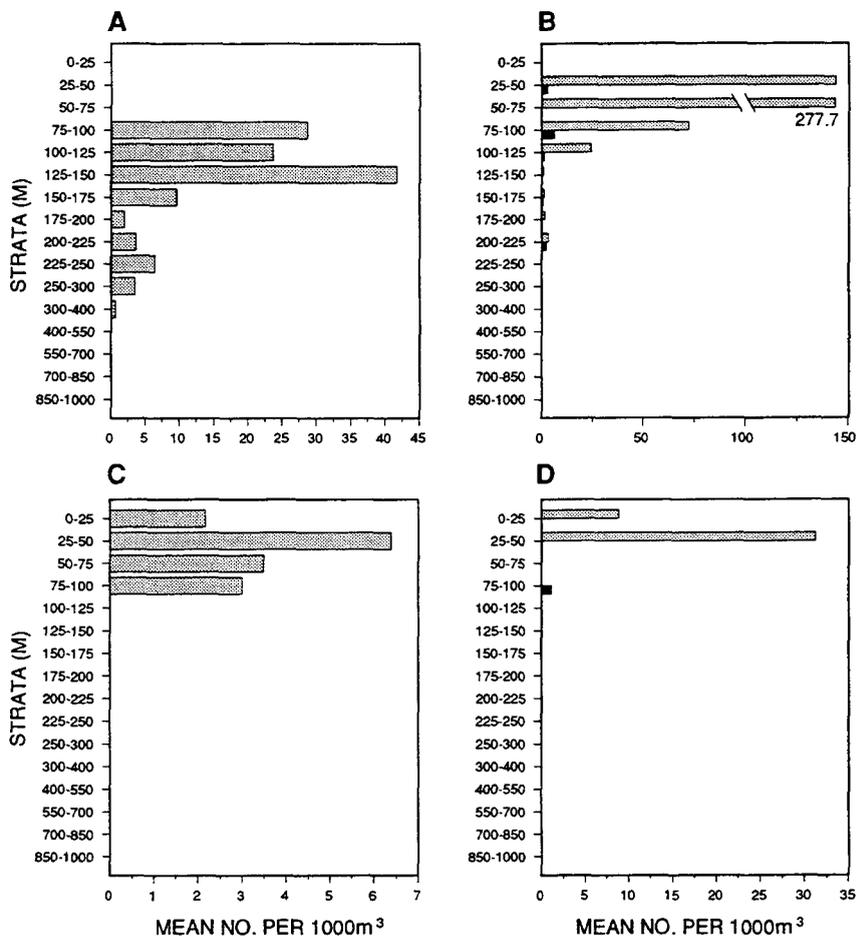


Figure 12. Depth distribution of larvae of four taxa of the Northern Complex from MOCNESS samples taken on FRONTS 85. A, *Tarletonbeania crenularis*; B, *Diaphus* spp.; C, *Scomber japonicus*; D, *Engraulis mordax*. Mean larval fish abundances versus depth are shown for tows at the northern end of the transect (light bars) and for the southern end (dark bars).

atlanticus were mostly at the southern station in a broader and deeper depth band (50 to 300 m) compared with *C. townsendi*, with no apparent peak (Fig. 15D).

At the southern station, *T. mexicanus* (TRIPHOTURUS) had a distribution similar to that of *V. lucetia* with a peak at 50–75 m. Incidence and abundance were markedly lower at the northern station and the distribution was shifted upward with a peak in the 25–50-m stratum (Fig. 16A). The other TRIPHOTURUS member, *Lampanyctus* spp., had the highest number of occurrences of any taxon in the MOCNESS samples (Table 2). Occurrence was slightly higher in the south; however, mean abundance was higher in the north. Larvae occurred over a broad depth range (25 to 300 m), with low concentrations in strata > 125 m in the north and in all strata in the south (Fig. 16B).

Larvae of two mesopelagic predators, *Chauliodus macouini* and *Scopelosaurus harryi*, occurred at both north and south localities and had broad, disjointed

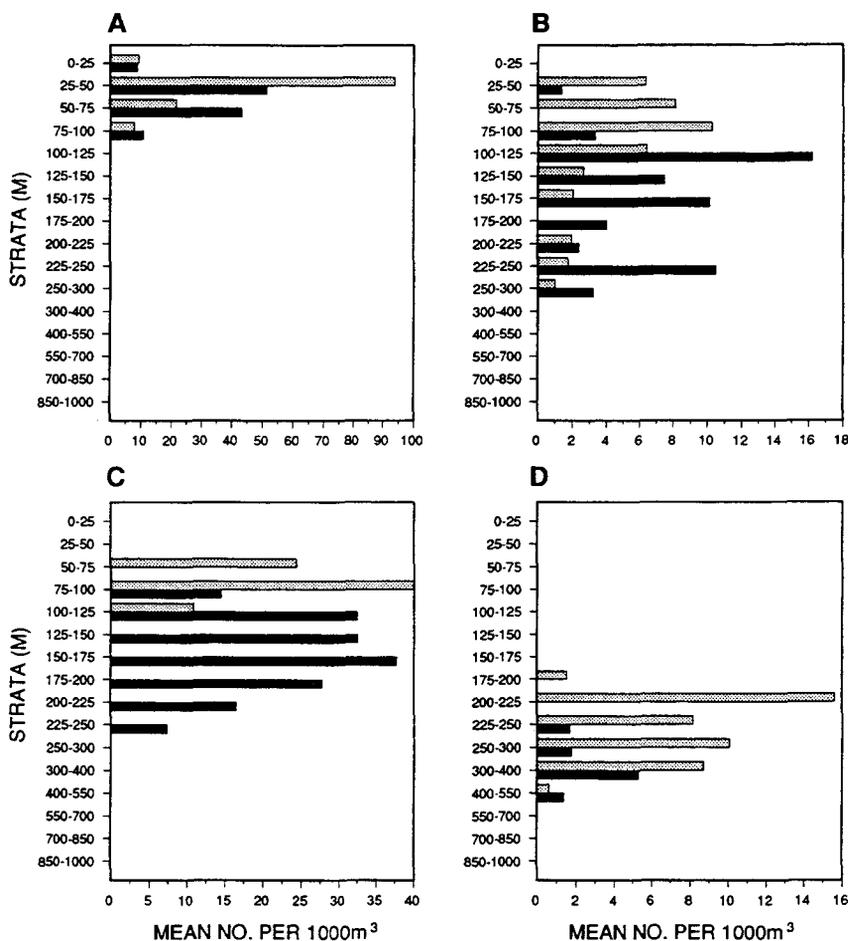


Figure 13. Depth distribution of larvae of four members of the Southern Complex recurrent group SYMBOLOPHORUS from MOCNESS samples taken on FRONTS 85. A, *Trachurus symmetricus*; B, *Symbolophorus californiensis*; C, *Bathylagus wesethi*; D, *Protomyctophum crockeri*. Symbols as in Figure 12.

vertical distributions (Fig. 16C, D). *Chauliodus macouni*, an affiliate of TARLETONBEANIA (Appendix), occurred in two widely separated groups of strata, with no captures in the 100 to 200 m range (Fig. 16D). *Scopelosaurus harryi*, a CERATOSCOPELUS affiliate (Appendix), occurred in only three samples but in widely separated strata at the north and south sites (Fig. 16D). Two sternoptychid taxa affiliated with SYMBOLOPHORUS, *Danaphos oculatus* and *Argyropelecus* spp., had the deepest distributions encountered in the MOCNESS samples. *D. oculatus* was distributed between 400 and 1,000 m with a peak at 400–550 m (Fig. 17A) and *Argyropelecus* spp. was found between 300 and 1,000 m with a peak at 850–1,000 m (Fig. 17B).

ENVIRONMENTAL OBSERVATIONS. Hydrographic conditions differed markedly at the two MOCNESS stations indicative of the separate water masses. Surface temperature was 16.2°C at Station 10 in the north and 19.0°C at Station 2 in the

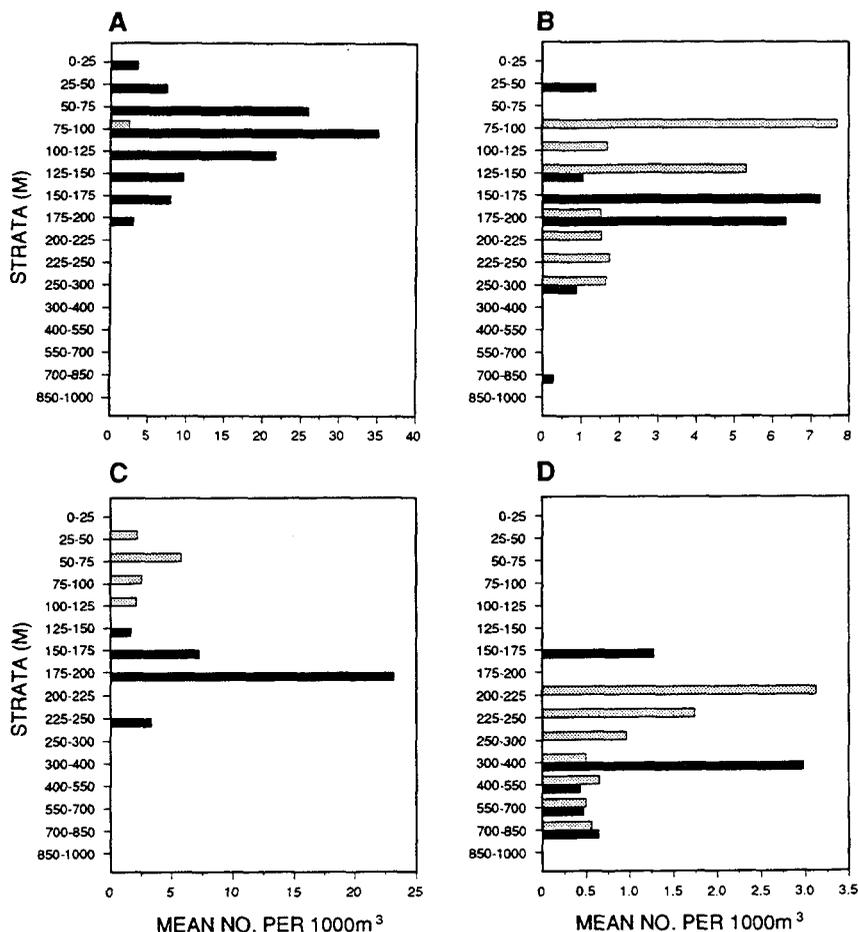


Figure 14. Depth distribution of larvae of group members (A), associates (B), and affiliates (C, D) of the Southern Complex recurrent group SYMBOLOPHORUS from MOCNESS samples taken on FRONTS 85. A, *Cyclothone* spp.; B, *Melamphaes* spp.; C, *Lestidiops ringens*; D, *Microstoma microstoma*. Symbols as in Figure 12.

south. A differential of 3–4°C was maintained down to circa 100 m (Fig. 18A). Surface salinity was 0.3‰ higher at the southern station, then became lower by circa 0.2‰ at the southern station between 60 and 200 m, possibly indicating subduction of water from the north (Fig. 18B). Dissolved oxygen was slightly higher at the surface in the north but below circa 50 m was consistently lower at the northern station (Fig. 18C). The temperature-salinity relationship indicates the colder less saline nature of the shallow water at the northern station compared with the southern station (Fig. 18D).

Nutrient and pigment concentrations differed markedly north (Station 10) and south (Station 2) of the front. Phosphate concentration was higher at comparable depths in the north, with the greatest difference in the upper 200 m (Fig. 19A). Similarly, nitrate concentrations were different at the two stations down to approximately 400 m (Fig. 19B). The chlorophyll maximum was at 50 m in the

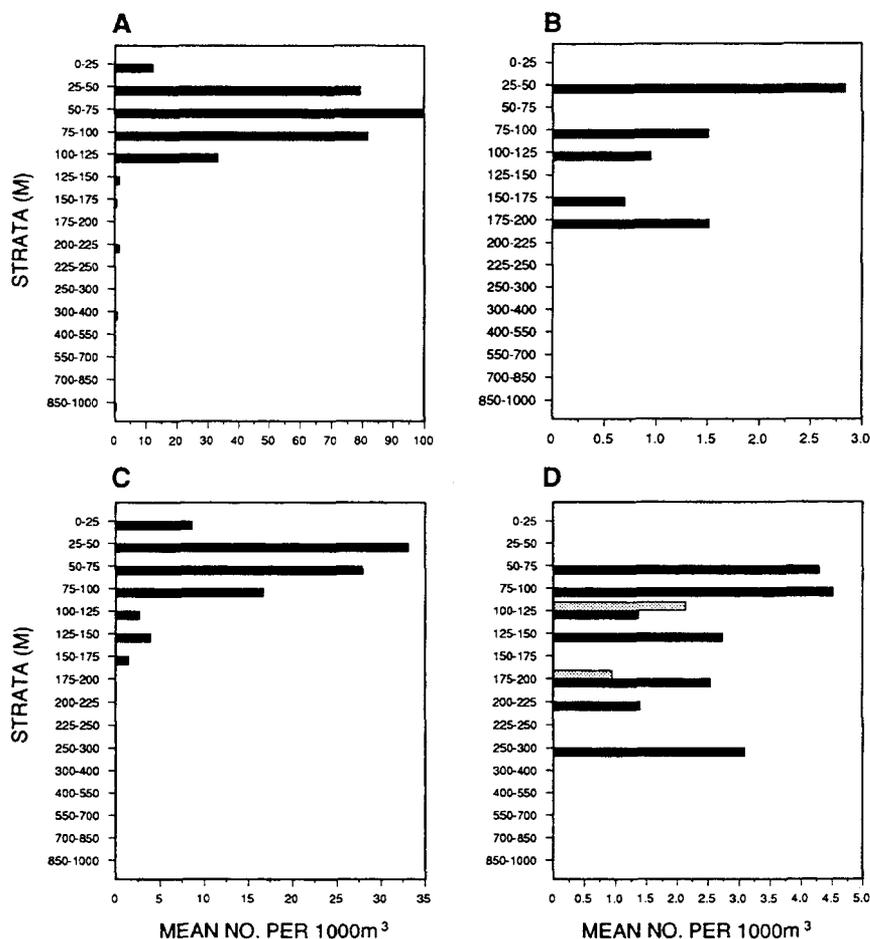


Figure 15. Depth distribution of larvae of a member (A) and an associate (B) of the Southern Complex recurrent group VINCIGUERRIA and two members of the Southern Complex recurrent group CERATOSCOPELUS (C, D) from MOCNESS samples taken on FRONTS 85. A, *Vinciguerria lucetia*; B, *Stomias atriventer*; C, *Ceratoscopelus townsendi*; D, *Diogenichthys atlanticus*. Symbols as in Figure 12.

north and at 100 m in the south (Fig. 19D). The depth curve for phaeophytin showed a similar contrast between the two stations (Fig. 19D). Primary production was circa 3.5 times greater in the north compared with the south, reaching a maximum uptake rate of almost $7 \text{ mg carbon} \cdot \text{m}^{-3} \cdot \text{half-day}^{-1}$ experiment at 25 m in the north (Fig. 20). Standing crop of macrozooplankton was higher throughout the water column in the north (Fig. 21). In the south, displacement volume varied between 100 and $200 \text{ cm}^3 \cdot 1,000 \text{ m}^{-3}$ at strata from the surface to 250 m and was $< 100 \text{ cm}^3 \cdot 1,000 \text{ m}^{-3}$ at deeper strata. In the north, displacement volume was 600 to $800 \text{ cm}^3 \cdot 1,000 \text{ m}^{-3}$ in the upper 50 m, four to six times greater than at that depth range in the south. Light penetration differed greatly north and south of the front; the 1% level of surface light was 20 to 25 m deeper at the southern station, 85 to 86 m in the south vs. 61 to 65 m in the north (Fig. 22).

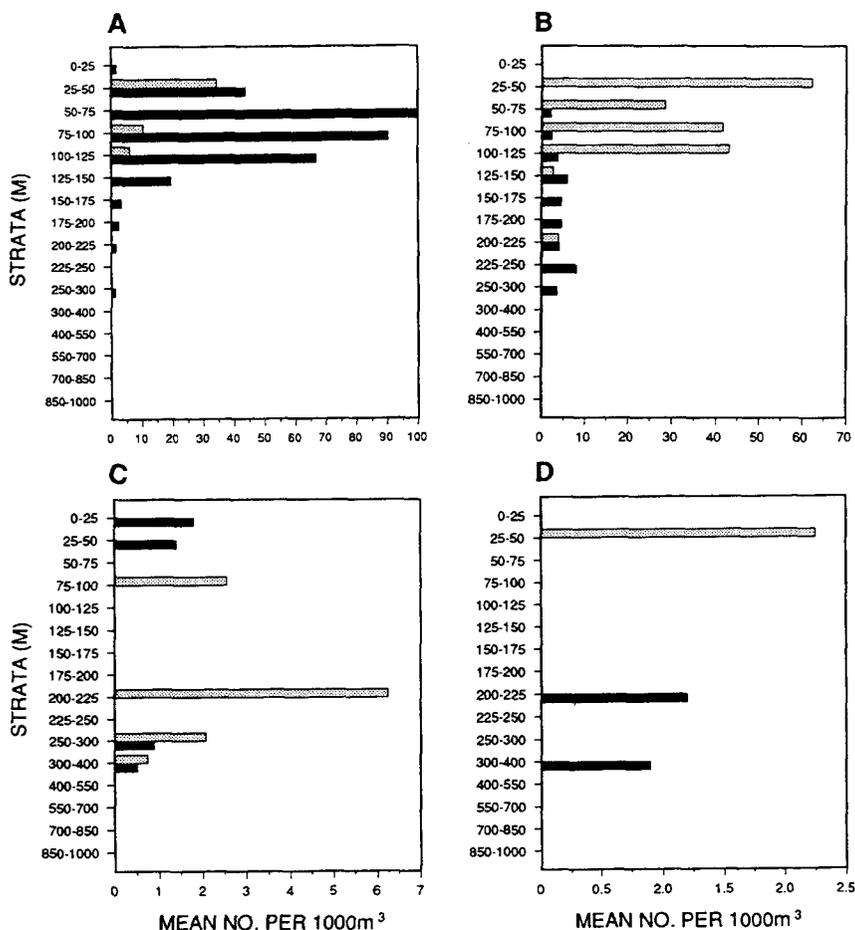


Figure 16. Depth distribution of larvae of two members of the Southern Complex recurrent group TRIPHOTURUS (A, B) and of two taxa of mesopelagic predators (C, D) from MOCNESS samples taken on FRONTS 85. A, *Triphoturus mexicanus*; B, *Lampanyctus* spp.; C, *Chauliodus macouni*; D, *Scopelosaurus harryi*. Symbols as in Figure 12.

The environmental changes experienced by taxa that occurred on both sides of the front are shown by larva-weighted mean values for depth and associated hydrographic and biological parameters (Table 5). The shallow living *T. symmetricus* and *T. mexicanus* changed the least, and generally, the difference between the two localities increased in deeper living taxa. Larva-weighted mean temperature decreased substantially in *T. symmetricus* and *T. mexicanus* in the north while, in most other taxa, it increased at the northern station because they occurred at shallower depths north of the front. Larva-weighted density values increased in *T. symmetricus* and *T. mexicanus* at the northern station while they decreased from south to north in the deeper living taxa because of the shoaling of their distributions. Larva-weighted salinity was slightly lower in the north for most species. In *T. symmetricus* and *T. mexicanus* this is due to the lower salinities in the upper 75 m at the northern station. The deeper living taxa experienced lower

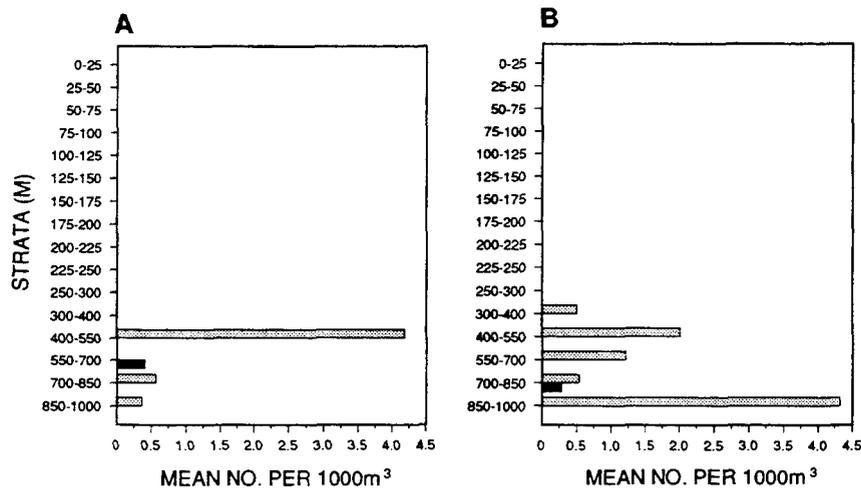


Figure 17. Depth distribution of larvae of two sternoptychid taxa from MOCNESS samples taken on FRONTS 85. A, *Danaphos oculatus*; B, *Argyropelecus* spp. Symbols as in Figure 12.

salinities at their shallower habitat in the north (Table 5, Fig. 18B). In *T. symmetricus*, the slight increase in the larva-weighted mean for dissolved oxygen at the northern station was related to higher levels in surface waters there (Fig. 18C). Higher values for the other taxa at the northern station resulted from the change in oxygen concentration with depth (Fig. 18C) and shoaling of their distributions north of the front (Table 5).

Larva-weighted mean chlorophyll-*a* concentrations were higher north of the front for all taxa, despite the highly disparate chlorophyll-*a* profiles at the two sites (Table 5, Fig. 19C). The shift was smallest for *T. mexicanus* whose mean depth distributions were near the chlorophyll maxima at each site. *Lestidiops ringens* experienced a 1,900% increase from south to north, since its mean depth was well below the euphotic zone south of the front but near the chlorophyll-*a* maximum at the northern site (Table 5, Fig. 19C). Likewise, larva-weighted zooplankton displacement volumes were markedly higher north of the front for all taxa, with increases ranging from 114% in *Microstoma microstoma*, the deepest living taxon, to 400% in the shallow living *T. symmetricus*. *Lestidiops ringens* had the largest shift (427%) because of its extreme change in vertical distribution (Table 5, Fig. 21).

DISCUSSION AND CONCLUSIONS

Recurrent group analysis of the entire CalCOFI time series identified an assemblage of larval fish groups whose composition and structure were generally consistent with those derived from portions of the time series and with groupings based on principal component and cluster analyses of abundance data. These groups reflect the major water masses and boundary regions present in the California Current region.

The California Current, generated from the West Wind Drift off Washington and Oregon, carries subarctic-transitional water southward. Larval fish assemblages off Washington and Oregon are dominated by the myctophids *S. leucopsarus*, *T. crenularis*, and *D. theta*, the bathylagid *B. ochotensis*, and the scorpaenid

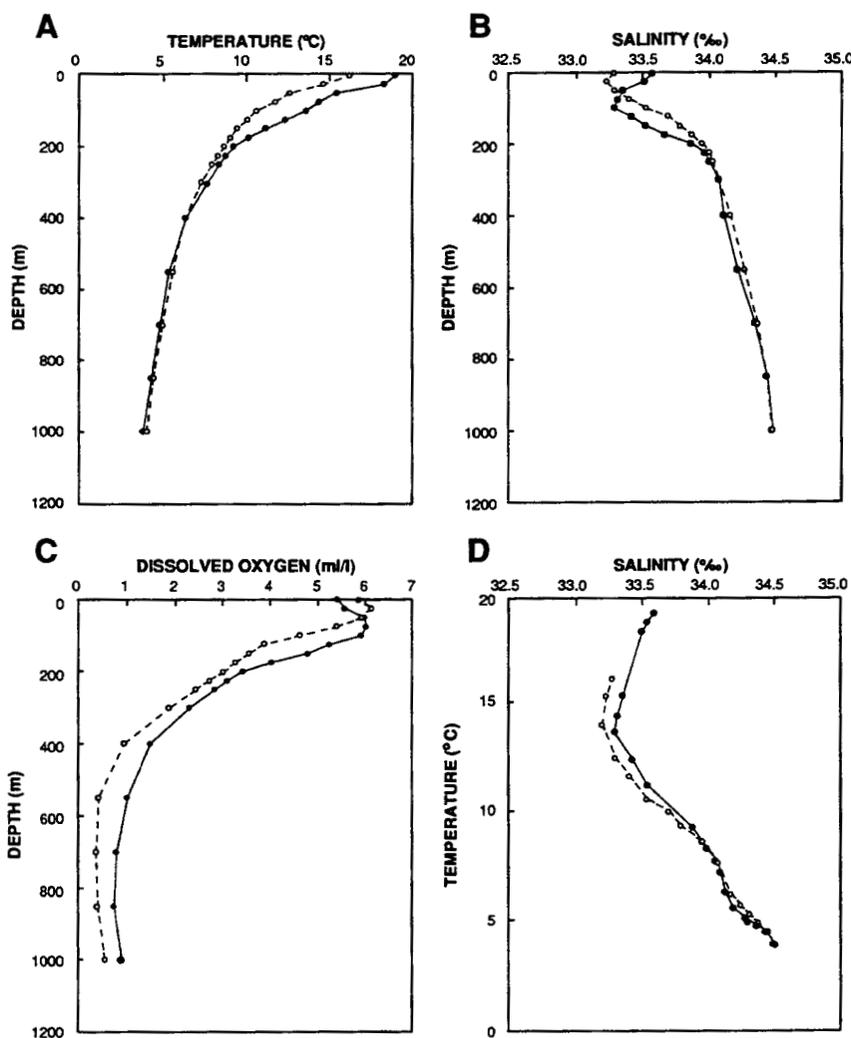


Figure 18. Temperature (A), salinity (B), and dissolved oxygen (C) depth profiles and T-S diagrams (D) for Station 2, Cast 8 at the southern end of the FRONTS 85 transect (closed circles) and for Station 10, Cast 1 at the northern end (open circles). Data from Haury et al. (1986).

genus *Sebastes* (Doyle et al., this volume). These taxa are prominent members of the Northern Complex of recurrent larval fish groups in the CalCOFI survey area; *S. leucopsarus*, *B. ochotensis*, and *Sebastes*, with *M. productus* and another bathylagid (*L. stilbius*), form LEUROGLOSSUS, the major recurrent group of the Northern Complex.

South of Point Conception, the California Current bends shoreward; part of the flow heads north to form the Southern California Eddy and part continues south along Baja California. Off northern Baja California, central and ETP water impinge on the California Current from the west and south, respectively. Mesopelagic taxa dominate the larval fish assemblages of these water masses (Loeb,

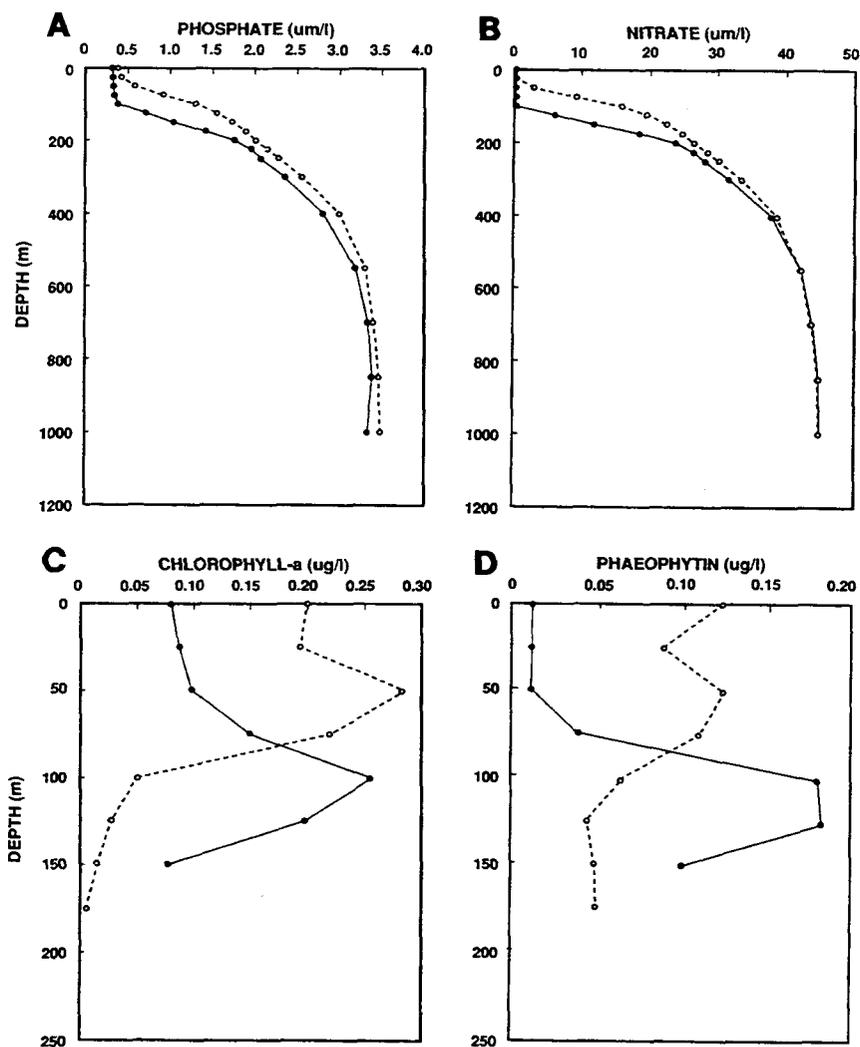


Figure 19. Depth profiles of concentrations of phosphate (A), nitrate (B), chlorophyll-a (C), and phaeophytin (D) for Station 2, Cast 8 at the southern end of the FRONTS 85 transect (closed circles) and for Station 10, Cast 1 at the northern end (open circles). Data from Haury et al. (1986).

1980; Ahlstrom, 1972a) and some of these taxa are important constituents of the Southern Complex of assemblages in the CalCOFI survey area. The myctophids *C. townsendi* and *D. atlanticus* ranked third and sixth in total abundance in Loeb's (1980) Central Water Mass study and formed the Southern Complex recurrent group DIOGENICHTHYS in the CalCOFI area. The myctophid *D. laternatus* and the phosichthyid *V. lucetia* ranked first and second in abundance in Ahlstrom's (1972a) ETP study and, with two myctophids, formed the Southern Complex recurrent group VINCIGUERRIA in our study.

In addition to those recurrent groups that are clearly associated with distinct

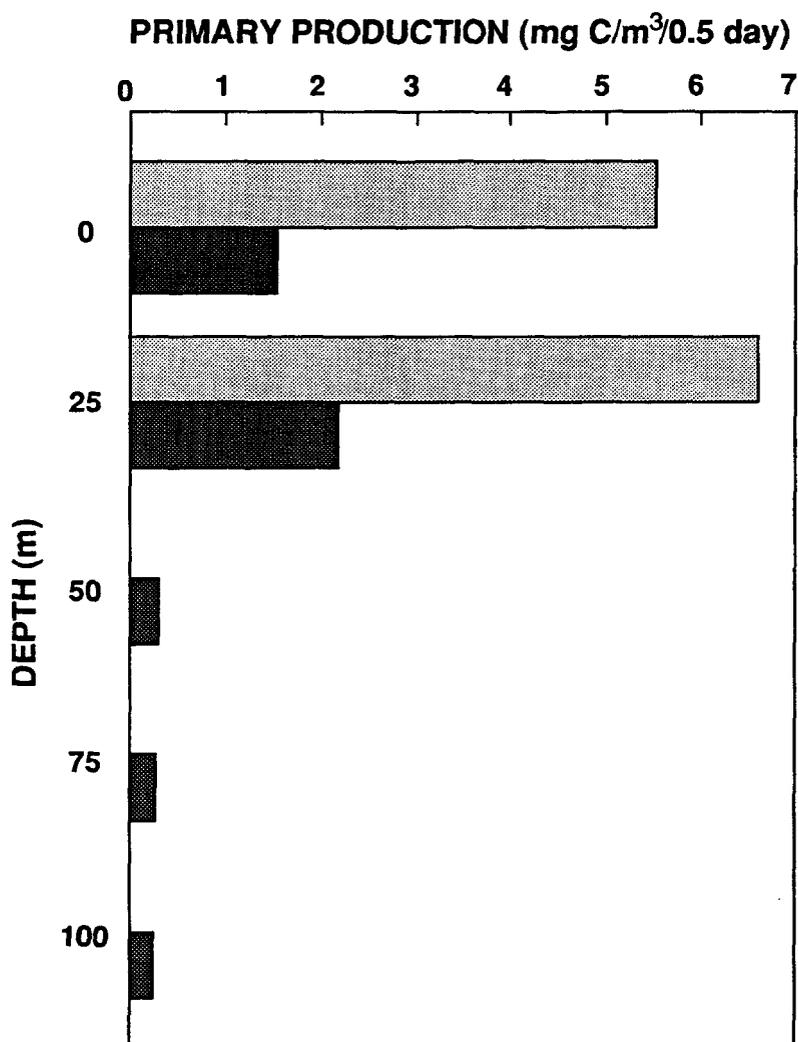


Figure 20. Primary production vs. depth derived from noon-to-dusk incubations at Station 2 at the southern end of the FRONTS 85 transect on June 13, 1985 (dark bars) and at Station 10 at the northern end on June 16, 1984 (light bars). Data from Haury et al. (1986).

water masses, our analysis identified SYMBOLOPHORUS, the major group of the Southern Complex. All of its member taxa, except *Cyclothone* spp., have distributions of larvae that are centered in the California Current and extend southward to the warmer waters off central Baja California. The two species of *Cyclothone* that are well represented in CalCOFI, *C. acclinidens* and *C. signata*, are distributed across the equatorial Pacific and penetrate eastward into the southern half of the CalCOFI pattern. Their larvae have not been routinely identified in CalCOFI samples.

The CalCOFI survey area overlies two coastal faunal provinces, the Oregonian

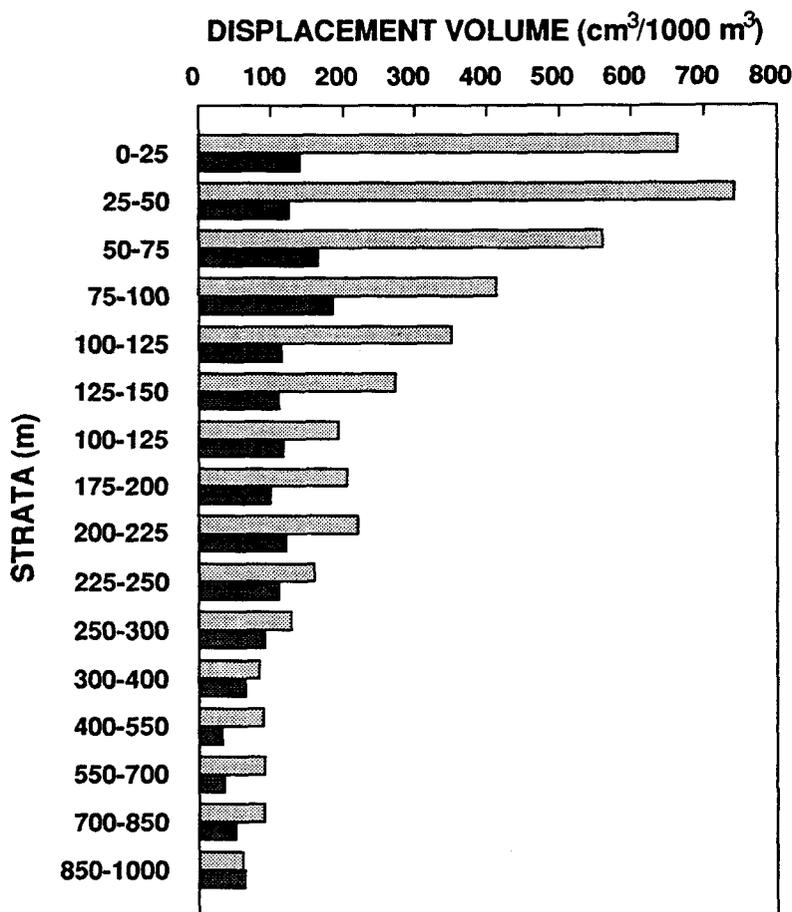


Figure 21. Mean zooplankton displacement volumes for stations at the southern end of the FRONTS 85 transect (dark bars) and for stations at the northern end (light bars). Data from Haury et al. (1986).

Province north of Point Conception and the San Diegan Province from Point Conception south to Magdalena Bay, Baja California (Allen and Smith, 1988). The Panamic Tropical Province south of Magdalena Bay was sampled on relatively few CalCOFI surveys during the 1950's. Annual and seasonal coverage off northern California was sporadic in the 1951-1984 period and the shelf was poorly sampled. Accordingly, our analysis did not identify the distinct coastal, shelf transition, and oceanic larval fish assemblages as described by Richardson et al. (1980) for Oregon and by Doyle et al. (this volume) for the Washington-Oregon-Northern California region.

The coastal environment off southern California is characterized by a narrow shelf, a circulation pattern dominated by the Southern California Eddy, and the topographically complex Southern California Borderland. Larvae of coastal taxa occur far offshore, especially coastal pelagics, while mesopelagic species occupy the borderland basins and impinge on the narrow shelf region. Despite this com-

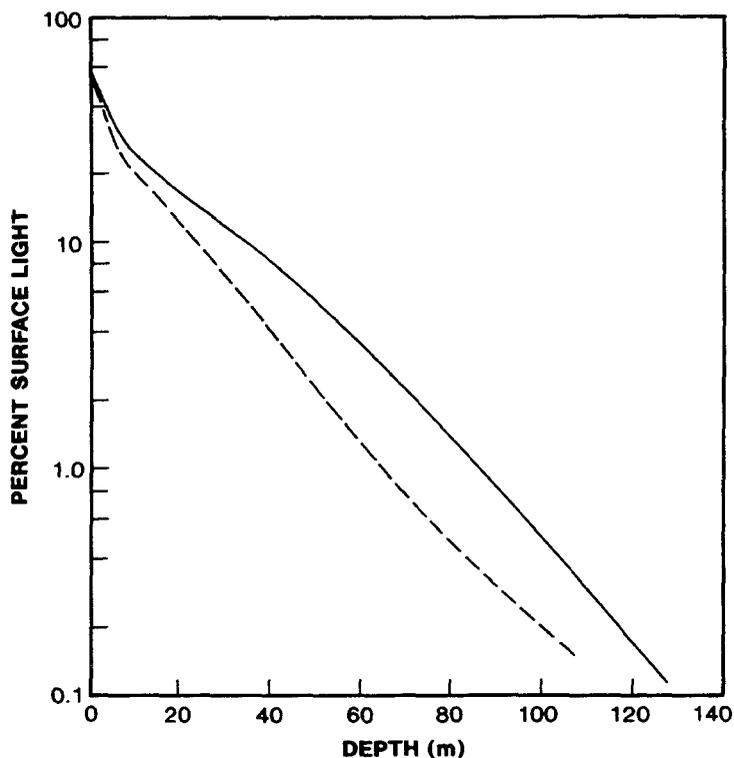


Figure 22. Light penetration (percent of surface light) at Station 2 at the southern end of the FRONTS 85 transect (solid line) and at Station 10 at the northern end (broken line). Data provided by L. R. Haury (Scripps Institution of Oceanography).

plexity, there is considerable overlap among larval fish assemblages described in regional studies of the Southern California Bight and those described for the more extensive CalCOFI survey area. The major recurrent group of Gruber et al. (1982) included three of the five members of our LEUROGLOSSUS group, with the other two members as associates. Another group identified by Gruber et al. (1982) was essentially the same as our PARALICHTHYS and a third group consisted of summer-spawning shelf taxa. A major assemblage in McGowen's (this volume) analysis of nearshore ichthyoplankton included three of our LEUROGLOSSUS taxa. Also, three of the five taxa of our SYNODUS recurrent group formed a distinct sub-unit in his large summer-spawning assemblage.

The only extensive shelf areas sampled thoroughly on CalCOFI surveys were Sebastian Viscaïno Bay and the area between Point Eugenia and Cape San Lazaro, within the southern part of the San Diegan faunal province (Allen and Smith, 1988). SYNODUS, the only large nearshore recurrent group identified by the analysis, was centered in this area. Taxa in this group were not abundant enough to be included in the cluster or principal component analysis. Distributions of group members ranged northward to the Southern California Bight with minima along the cold, upwelling region of northern Baja California, characterized by its narrow shelf. The robust nature of the group is evident from its presence in the

Table 5. Larva-weighted mean values for depth, temperature, salinity, density, dissolved oxygen, chlorophyll-*a*, and zooplankton displacement volume for 10 larval fish taxa occurring in MOCNESS tows at the south and north ends of the FRONTS 85 transect

	Depth (m)		Temperature (°C)		Salinity (ppt)		Density (kg m ⁻³)		Dissolved O ₂ (ml liter ⁻¹)		Chlorophyll- <i>a</i> (mg m ⁻³)		Zooplankton (cm ³ · 1,000 m ⁻³)	
	S	N	S	N	S	N	S	N	S	N	S	N	S	N
Northern Complex														
TARLETONBEANIA														
<i>Diaphus</i> spp.	109	62	12.91	12.21	33.47	33.39	25.20	25.29	5.18	5.36	0.14	0.24	168	572
Southern Complex														
SYMBOLOPHORUS														
<i>Trachurus symmetricus</i>	48	41	15.92	13.59	33.39	33.29	24.51	24.94	5.87	5.98	0.12	0.26	142	710
<i>Bathylagus weselhi</i>	151	82	11.01	11.32	33.59	33.46	25.67	25.52	4.46	5.09	0.09	0.17	107	417
<i>Symbiolophorus californiensis</i>	161	99	10.79	11.09	33.64	33.54	25.74	25.61	4.24	4.78	0.09	0.15	119	458
<i>Metamphaes</i> spp.	175	148	10.31	9.63	33.73	33.75	25.89	26.03	3.83	3.77	0.03	0.05	107	240
<i>Lestidiops ringens</i>	185	72	9.50	11.85	33.80	33.42	26.10	25.39	3.48	5.32	0.01	0.20	106	559
<i>Protomyctophum crockeri</i>	335	253	7.19	7.72	34.07	34.02	26.66	26.54	1.91	2.45	—	—	66	180
<i>Microstoma microstoma</i>	387	323	7.20	7.28	34.05	34.09	26.63	26.67	1.98	2.01	—	—	78	167
TRIPHOTURUS														
<i>Triphoturus mexicanus</i>	85	58	13.87	12.79	33.37	33.36	24.94	25.15	5.67	5.62	0.16	0.22	157	673
<i>Lamppanyctus</i> spp.	179	75	10.24	11.79	33.72	33.46	25.90	25.41	3.91	5.16	0.06	0.18	112	532

analysis of the 1954–1960 subset of the CalCOFI time series and in individual years in that subset (Moser et al., 1987). The strong northward flowing counter-current located off the shelf edge along Baja California probably plays an important role in supplying larvae of these warm water taxa to the Southern California Bight.

The spacing of the CalCOFI sampling grid is adequate to define distributions of larval fish taxa and the structure of assemblages; however, definition of distributions at frontal boundaries requires fine scale, three-dimensional sampling in conjunction with satellite imaging. This is clearly shown by the new information reported here on larval fish distributions at the Ensenada Front. Although the south-north transect of the cruise was only 120 n. mi. long, the change from the southern to the northern CalCOFI larval fish complexes was apparent. This was most clearly demonstrated for the Northern Complex by *T. crenularis* (TARLETONBEANIA recurrent group) whose larvae were absent from MOCNESS tows at the southern station and from bongo tows on all stations south of mid-transect. *Diaphus* spp., an affiliate of TARLETONBEANIA, was 15 times more abundant in MOCNESS tows at the northern MOCNESS station compared with the south. LEUROGLOSSUS, the major Northern Complex group, was poorly represented on the FRONTS 85 cruise because its members are primarily winter-spring spawners; however, those that were present on FRONTS 85 (*B. ochotensis*, *L. stilbius*, *S. leucopsarus*, *Sebastes* spp.) occurred only in northern MOCNESS samples and in bongo samples from the northern part of the transect. Definitive information on the distribution these species at the front awaits sampling of the front during winter or spring; thus far, all cruises have been in the summer when the front is most strongly developed (Niiler et al., 1989).

Distributional boundaries of most Southern Complex taxa were less clearly defined than those of the Northern Complex on the FRONTS 85 cruise; however, taxa with affinities to equatorial or central gyre water showed a clear pattern. *V. lucetia* (VINCIGUERRIA) and *C. townsendi* (CERATOSCOPELUS) were present only in tows from the southern MOCNESS station and showed a marked decline in mean abundance in bongo tows in the northern part of the transect. *Cyclothone* spp. (SYMBOLOPHORUS) had a similar pattern except for a single occurrence in a MOCNESS sample from the northern station. Most members of SYMBOLOPHORUS had greater numbers of occurrences at the southern MOCNESS station compared with the northern station even though abundance showed no clear south-north pattern. In bongo tows, some SYMBOLOPHORUS taxa (*B. wesethi*, *P. crockeri*, *T. symmetricus*) showed abundance peaks at mid-transect stations where gradients of physical properties were greatest, while *S. californiensis* had lower mean abundance at mid-transect stations.

The MOCNESS samples showed that vertical distributions of larval fish taxa on the north side of the front were shallower than on the south side. This is true for *Diaphus* spp., the only taxon of the Northern Complex occurring at both north and south MOCNESS stations in sufficient abundance to show a pattern. Members of SYMBOLOPHORUS shoaled to varying degrees at the northern station. For some species (*T. symmetricus* and *S. californiensis*) the overall vertical ranges did not change but the modal peak shifted. In other taxa (*B. wesethi* and *P. crockeri*) the upward shift of distributions at the northern station was more pronounced and there was only partial overlap of the distributions at the two stations. The most striking difference occurred in a SYMBOLOPHORUS affiliate, *L. ringens*, whose larvae had non-overlapping distributions at the two stations with peaks separated by a depth interval of 100 m. In another affiliate of the group, *M. microstoma*, the northern and southern peaks were at 200–225 m and 300–400 m, respectively, showing that the shoaling effect occurred deep in the water col-

umn. Shoaling at the northern station also occurred in TRIPHOTURUS, the other Southern Complex group whose member taxa (*T. mexicanus* and *Lampanyctus* spp.) occurred at the northern and southern stations.

Typically, major recurrent groups are composed of taxa whose larvae occupy a variety of depth strata. For example, LEUROGLOSSUS contains some taxa with relatively shallow distributions, *Sebastes* spp. and *S. leucopsarus*, and some with deeper depth profiles, *L. stilbius*, *B. ochotensis* and *M. productus* (Fig. 11; Ahlstrom, 1959; Moser and Boehlert, 1991). In SYMBOLOPHORUS, larvae of *T. symmetricus* are shallow living, *Cyclothone* spp. and *L. ritteri* have moderately shallow distributions, larvae of *B. wesethi* and *P. crockeri* are moderately deep, and *S. californiensis* are widely distributed in the water column (Figs. 13, 14; Ahlstrom, 1959). In VINCIGUERRIA, *V. lucetia* larvae are shallow living, while those of *D. laternatus*, *G. tenuiculus*, and *H. atratum* are moderately deep (Fig. 15; Loeb and Nichols, 1984). The two members of CERATOSCOPELUS have contrasting vertical distributions; *C. townsendi* is moderately shallow and *D. atlanticus* moderately deep (Fig. 15). This diversity in vertical distribution within groups may reflect adaptation of larvae of these taxa to environmental variables in different depth strata and is, at least, suggestive that vertical habitat diversity and resource partitioning may play a role in the structure of larval fish assemblages. Concentrations of larval fish prey vary with depth and are generally higher in the surface waters. For example, Beers and Stewart (1969, 1971) found maximum concentrations of 0.035- to 0.202-mm zooplankters in the upper 70 m of the water column at a variety of locales in the tropical and temperate eastern Pacific. The vertical ranges of larvae of the highly abundant coastal pelagic (*E. mordax*, *S. sagax*, *T. symmetricus*, *S. japonicus*) and mesopelagic (*V. lucetia*, *Cyclothone* spp.) fishes of this region also occupy this stratum (Figs. 12-15; Ahlstrom, 1959). The same or closely related coastal pelagic species occur in all eastern boundary currents (Bakun, 1985) and their larvae are a dominant fraction of the ichthyoplankton of these regions (Santander and Flores, 1983; Loeb and Rojas, 1988; Olivar and Shelton, this volume). It is likely that shallow distributions, centered in the zone of highest primary production and zooplankton biomass, are a requirement for their high larval production. There, survival may be enhanced by higher light intensity leading to more visible prey and by higher temperatures and concomitant higher metabolic and growth rates. This is balanced by increased mortality from probable increased predation rates. We suggest that species with lower production of larvae, living in deeper strata, experience conditions opposite to those listed above. Lower production of larvae is balanced by physiological and behavioral adaptations to diminished prey concentrations and by reduced predation pressure.

The apparent interaction of trophic dynamics and larval vertical distribution is particularly striking in the Myctophidae. The lanternfish subfamily Myctophinae (e.g., *T. crenularis*, *S. californiensis*, *P. crockeri*, *D. atlanticus*) have deeper distributions than larvae of the other major subfamily, the Lampanyctinae (e.g., *S. leucopsarus*, *Diaphus* spp., *C. townsendi*, *Lampanyctus* spp., *T. mexicanus*). The opposite is true for the adults of the two subfamilies, since adult myctophines are comparatively shallow living strong vertical migrators, while adult lampanyctines are deeper living and may or may not undergo diurnal vertical migrations (Clarke, 1973; Wisner, 1976; Loeb, 1986). Thus, the larval and adult stages of each subfamily are effectively separated vertically as Ahlstrom (1959) and Loeb (1980, 1986) have pointed out. We suggest that this pattern of vertical separation would limit the encounters between larvae and adults of the same species and may have evolved through selection for reduced mortality from cannibalism.

The shift to shallower distributions for larvae in the north is mirrored by environmental features. Isoleths of temperature, salinity, density, dissolved oxygen, and nutrients shoal from south to north along the transect. The abrupt change of isotherms and isohalines at the middle of the transect indicates a strong frontal feature. At the northernmost station, primary productivity is more than double that at the southernmost station and zooplankton standing stock is three times larger at the northern station. As with physical properties, the change in productivity and zooplankton biomass is greatest at mid-transect (Haurly et al., 1993). Depth of the chlorophyll maximum is at 50 m in the north and at 100 m in the south. Changes in vertical distribution of larval fish taxa may be related to one or more of these parameters; however, larva-weighted mean values of physical properties at the northern and southern station indicated that larvae did not maintain a constant environment by changing their depth distribution. It is unlikely that deeper distributions at the southern station are related to subduction of northern surface waters south of the front, since changes in vertical distribution occurred in all species regardless of their position in the water column. Lack of vertically discrete samples from other than the terminal stations on the transect precluded further examination of this hypothesis. We suggest that changes in vertical distribution of larvae are most likely related to changes in trophic conditions and larval shoaling may involve an interplay of the vertical shift of maximum prey densities and specific feeding behaviors that are light-level dependent. Diel changes in the vertical distribution of herring (*Clupea harengus*) larvae provide inferential support for this hypothesis (Munk et al., 1989). In the daytime, herring larvae occupied depths where light was sufficient for feeding and vertical adjustments in that zone were apparently a compromise between optimal light conditions for feeding and optimal prey densities. Extension of these findings to explain changes in vertical distribution of larval fish assemblages across the Ensenada Front will require synoptic vertical profiling of fish larvae, microzooplankton, and irradiance.

The discovery that many California Current species have deep living larvae has important implications in the interpretation of CalCOFI data. Some of these larval fish distributions are below the 210-m depth for standard tows and many are below 140 m, the standard tow depth on surveys during 1951 to 1968. Calculations of abundance based on numbers of larvae per unit surface area would be variously underestimated for many species. Indeed, one wonders how some of the very deep living taxa (e.g., *M. microstoma*, *Argyropelecus* spp., *D. oculatus*) ever occur in CalCOFI tows. Standard tow depths encompass the vertical ranges of larvae of the principal CalCOFI target species (clupeioids and other coastal pelagics); however, studies of community dynamics would require deeper tows to sample the entire larval ichthyofauna quantitatively.

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Appendix. Composition of larval fish recurrent groups and their associate and affiliate taxa from CalCOFI survey data, 1951 to 1984. Associates listed under each recurrent group may include members or associates of other recurrent groups

Taxon	Incidence (of 31,214)	Associate group
Northern Complex		
LEUROGLOSSUS		
<i>Sebastes</i> spp.	12,322	
<i>Leuroglossus stilbius</i>	8,509	
<i>Merluccius productus</i>	7,372	
<i>Stenobrachius leucopsarus</i>	7,258	
<i>Bathylagus ochotensis</i>	4,555	
Associates		
<i>Engraulis mordax</i>	14,486	CITHARICHTHYS
<i>Protomyctophum crockeri</i>	8,048	SYMBOLOPHORUS
<i>Citharichthys</i> spp.	6,322	CITHARICHTHYS
<i>Tarletonbeania crenularis</i>	4,041	TARLETONBEANIA
<i>Icichthys lockingtoni</i>	1,992	TARLETONBEANIA
Affiliates		
<i>Argentina sialis</i>	1,294	
<i>Tetragomurus cuvieri</i>	1,031	
Chiasmodontidae	726	
<i>Bathylagus</i> spp.	676	
<i>Bathylagus pacificus</i>	536	
<i>Sebastolobus</i> spp.	462	
<i>Sebastes paucispinis</i>	372	
<i>Sebastes jordani</i>	209	
<i>Brosmophycis marginata</i>	208	
<i>Zaniolepis</i> spp.	207	
<i>Scorpaenichthys marmoratus</i>	206	
<i>Brama</i> spp.	166	
<i>Medialuna californiensis</i>	152	
<i>Oxylebius pictus</i>	147	
Macrouridae	137	
<i>Bathylagus milleri</i>	106	
Gempylidae	101	
<i>Sebastes aurora</i>	91	
<i>Sebastes levis</i>	44	
<i>Icosteus aenigmaticus</i>	40	
Hexagrammidae	37	
Carapidae	19	
Osmeridae	13	
<i>Ophiodon elongatus</i>	13	
Uranoscopidae	7	
<i>Anoplopoma fimbria</i>	5	
Merlucciidae	1	

Appendix. Continued

Taxon	Incidence (of 31,214)	Associate group
TARLETONBEANIA		
<i>Tarletonbeania crenularis</i>	4,041	
<i>Icichthys lockingtoni</i>	1,992	
Associates		
<i>Sebastes</i> spp.	12,322	LEUROGLOSSUS
<i>Leuroglossus stilbius</i>	8,509	LEUROGLOSSUS
<i>Stenobranchius leucopsarus</i>	7,258	LEUROGLOSSUS
<i>Bathylagus ochotensis</i>	4,555	LEUROGLOSSUS
Affiliates		
<i>Diaphus</i> spp.	2,118	
<i>Chauliodus macouni</i>	1,701	
Trachipteridae	650	
<i>Protomyctophum thompsoni</i>	23	
<i>Leuroglossus schmidti</i>	3	
<i>Parvilux ingens</i>	3	
<i>Dolichopteryx longipes</i>	1	
SARDINOPS		
<i>Sardinops sagax</i>	2,999	
<i>Scomber japonicus</i>	1,211	
Associates		
<i>Engraulis mordax</i>	14,486	CITHARICHTHYS
Affiliates		
<i>Sphyraena argentea</i>	301	
<i>Euthynnus</i> spp.	4	
CITHARICHTHYS		
<i>Engraulis mordax</i>	14,486	
<i>Citharichthys</i> spp.	6,322	
Associates		
<i>Sebastes</i> spp.	12,322	LEUROGLOSSUS
<i>Triphoturus mexicanus</i>	11,968	TRIPHOTURUS
<i>Leuroglossus stilbius</i>	8,509	LEUROGLOSSUS
<i>Merluccius productus</i>	7,732	LEUROGLOSSUS
<i>Stenobranchius leucopsarus</i>	7,258	LEUROGLOSSUS
<i>Sardinops sagax</i>	2,999	SARDINOPS
Sciaenidae	1,973	PARALICHTHYS
Affiliates		
Gobiidae	1,991	
<i>Peprilus simillimus</i>	713	
<i>Oxyjulis californica</i>	467	
Pleuronectiformes	217	
Cyclopteridae	203	
<i>Sygnathus</i> spp.	154	
<i>Sarda chiliensis</i>	123	
<i>Girella nigricans</i>	73	
<i>Macroramphosus gracilis</i>	71	
<i>Sebastes macdonaldi</i>	63	
Blennioidei	62	
Gobiesocidae	60	
<i>Physiculus</i> spp.	42	
<i>Lepidopus xantusi</i>	39	
<i>Hypsypops rubicundus</i>	16	
<i>Cubiceps pauciradiatus</i>	12	

Appendix. Continued

Taxon	Incidence (of 31,214)	Associate group
<i>Porichthys</i> spp.	12	
<i>Microgadus proximus</i>	9	
Alepocephalidae	3	
<i>Gadus macrocephalus</i>	1	
CITHARICHTHYS A		
<i>Citharichthys xanthostigma</i>	984	
<i>Citharichthys fragilis</i>	821	
Affiliates		
<i>Citharichthys stigmaeus</i>	2,710	
<i>Citharichthys sordidus</i>	450	
<i>Caulolatilus princeps</i>	89	
<i>Seriola</i> spp.	3	
<i>Anotopterus pharao</i>	3	
PARALICHTHYS		
Sciaenidae	1,973	
<i>Paralichthys californicus</i>	1,105	
Associates		
<i>Engraulis mordax</i>	14,486	CITHARICHTHYS
Affiliates		
Cottidae	722	
Clinidae	600	
Agonidae	247	
Atherinidae	125	
<i>Genyonemus lineatus</i>	104	
<i>Seriphus politus</i>	31	
Acanthuridae	1	
Southern Complex		
SYMBOLOPHORUS		
<i>Protomyctophum crockeri</i>	8,048	
<i>Cyclothone</i> spp.	5,869	
<i>Trachurus symmetricus</i>	5,612	
<i>Bathylagus wesethi</i>	5,593	
<i>Lampanyctus ritteri</i>	4,707	
<i>Symbolophorus californiensis</i>	3,219	
Associates		
<i>Triphoturus mexicanus</i>	11,968	TRIPHOTURUS
<i>Vinciguerria lucetia</i>	10,510	VINCIGUERRIA
<i>Leuroglossus stilbius</i>	8,509	LEUROGLOSSUS
<i>Stenobranchius leucopsarus</i>	7,258	LEUROGLOSSUS
<i>Lampanyctus</i> spp.	5,841	TRIPHOTURUS
<i>Diogenichthys laternatus</i>	5,043	VINCIGUERRIA
<i>Bathylagus ochotensis</i>	4,555	LEUROGLOSSUS
<i>Melamphaes</i> spp.	4,065	
Myctophidae	3,806	VINCIGUERRIA
<i>Ceratospinelus townsendi</i>	3,058	CERATOSCOPELUS
<i>Diogenichthys atlanticus</i>	2,706	CERATOSCOPELUS
<i>Stomias atriventer</i>	2,548	VINCIGUERRIA
Affiliates		
Sternoptychidae	2,934	
Paralepididae	1,334	
<i>Lestidiops ringens</i>	1,210	
Scopelarchidae	944	

Appendix. Continued

Taxon	Incidence (of 31,214)	Associate group
<i>Microstoma microstoma</i>	681	
<i>Cololabis saira</i>	513	
<i>Lampanyctus regalis</i>	455	
<i>Poromitra</i> spp.	452	
<i>Scopelogadus bispinosus</i>	434	
<i>Nansenia candida</i>	431	
<i>Danaphos oculatus</i>	218	
<i>Notolepis risso</i>	136	
<i>Tactostoma macropus</i>	121	
<i>Electrona rissoi</i>	115	
<i>Scopelarchus</i> spp.	102	
<i>Rosenblattichthys volucris</i>	88	
<i>Stemonosudus macrura</i>	28	
<i>Scopeloberyx robustus</i>	27	
<i>Benthalbella dentata</i>	27	
Evermannellidae	19	
<i>Sudis atrox</i>	17	
Apogonidae	16	
Eutaeniophoridae	9	
<i>Triphoturus nigrescens</i>	7	
Myctophiformes	4	
<i>Gonostoma</i> spp.	3	
<i>Hygophum proximum</i>	2	
<i>Bathylchnops exilis</i>	1	
VINCIGUERRIA		
<i>Vinciguerria lucetia</i>	10,510	
<i>Diogenichthys laternatus</i>	5,043	
<i>Hygophum atratum</i>	1,309	
<i>Gomichthys tenuiculus</i>	1,234	
Associates		
<i>Triphoturus mexicanus</i>	11,968	TRIPHOTURUS
<i>Protomyctophum crockeri</i>	8,048	SYMBOLOPHORUS
<i>Cyclothone</i> spp.	5,869	SYMBOLOPHORUS
<i>Lampanyctus</i> spp.	5,841	TRIPHOTURUS
<i>Bathylagus wesethi</i>	5,593	SYMBOLOPHORUS
Myctophidae	3,806	SYMBOLOPHORUS
<i>Ceratospopelus townsendi</i>	3,058	CERATOSCOPELUS
<i>Stomias atriventer</i>	2,548	SYMBOLOPHORUS
Affiliates		
<i>Nansenia crassa</i>	836	
<i>Ichthyococcus</i> spp.	426	
Astronesthidae	3	
<i>Macropinna microstoma</i>	3	
<i>Oxyporhamphus micropterus</i>	1	
TRIPHOTURUS		
<i>Triphoturus mexicanus</i>	11,968	
<i>Lampanyctus</i> spp.	5,481	
Associates		
<i>Engraulis mordax</i>	14,486	CITHARICHTHYS
<i>Vinciguerria lucetia</i>	10,510	VINCIGUERRIA
<i>Protomyctophum crockeri</i>	8,048	SYMBOLOPHORUS
<i>Cyclothone</i> spp.	5,869	SYMBOLOPHORUS
<i>Trachurus symmetricus</i>	5,612	SYMBOLOPHORUS
<i>Bathylagus wesethi</i>	5,593	SYMBOLOPHORUS
<i>Diogenichthys laternatus</i>	5,043	VINCIGUERRIA

Appendix. Continued

Taxon	Incidence (of 31,214)	Associate group
Myctophidae	3,806	SYMBOLOPHORUS
<i>Ceratoscopelus townsendi</i>	3,058	CERATOSCOPELUS
Affiliates		
<i>Diogenichthys</i> spp.	909	
<i>Hygophum</i> spp.	408	
Gonostomatidae	271	
<i>Loweina rara</i>	224	
Stomiiformes	143	
Exocoetidae	73	
CERATOSCOPELUS		
<i>Ceratoscopelus townsendi</i>	3,058	
<i>Diogenichthys atlanticus</i>	2,706	
Associates		
<i>Vinciguerria lucetia</i>	10,510	VINCIGUERRIA
<i>Protomyctophum crockeri</i>	8,048	SYMBOLOPHORUS
<i>Cyclothone</i> spp.	5,869	SYMBOLOPHORUS
<i>Bathylagus wesethi</i>	5,593	SYMBOLOPHORUS
<i>Symbolophorus californiensis</i>	3,219	SYMBOLOPHORUS
<i>Lampadena urophaos</i>	722	
<i>Notoscopelus resplendens</i>	674	
Affiliates		
<i>Idiacanthus antrostomus</i>	843	
<i>Myctophum nitidulum</i>	795	
<i>Lampadena urophaos</i>	722	
<i>Hygophum reinhardtii</i>	414	
<i>Notolychnus valdiviae</i>	238	
<i>Scopelosaurus</i> spp.	236	
<i>Aristostomias scintillans</i>	196	
<i>Bathophilus</i> spp.	104	
<i>Vinciguerria poweriae</i>	63	
<i>Photonectes</i> spp.	34	
<i>Centrobranchus</i> spp.	26	
<i>Valenciennellus stellatus</i>	16	
<i>Eustomias</i> spp.	7	
<i>Bathylagus longirostris</i>	6	
<i>Woodsia nonsuchae</i>	1	
<i>Taaningichthys minimus</i>	1	
<i>Lobianchia</i> spp.	1	
Southern Coastal Complex		
SYNODUS		
<i>Symphurus</i> spp.	1,038	
<i>Synodus</i> spp.	1,008	
<i>Ophidion scrippsae</i>	502	
<i>Etrumeus teres</i>	437	
<i>Prionotus</i> spp.	363	
Associates		
Ophidiiformes	847	
Serranidae	759	
Carangidae	211	
Affiliates		
<i>Lyopsetta exilis</i>	1,206	
<i>Parophrys vetulus</i>	953	
Labridae	931	

Appendix. Continued

Taxon	Incidence (of 31,214)	Associate group
<i>Hypsoblennius</i> spp.	910	
<i>Pleuronichthys verticalis</i>	893	
<i>Hippoglossina stomata</i>	756	
Trichiuridae	547	
<i>Chromis punctipinnis</i>	537	
<i>Microstomus pacificus</i>	479	
Anguilliformes	386	
<i>Chilara taylori</i>	306	
<i>Scorpaena</i> spp.	305	
<i>Glyptocephalus zachirus</i>	276	
<i>Halichoeres</i> spp.	266	
<i>Seriola lalandi</i>	233	
<i>Xystreurus liolepis</i>	202	
<i>Pleuronichthys</i> spp.	181	
<i>Pleuronichthys ritteri</i>	165	
<i>Pleuronichthys coenosus</i>	157	
Haemulidae	134	
<i>Semicossyphus pulcher</i>	129	
<i>Coryphaena hippurus</i>	120	
Gerreidae	106	
Pomacentridae	104	
<i>Bregmaceros</i> spp.	101	
<i>Auxis</i> spp.	89	
<i>Pleuronichthys decurrens</i>	85	
Scombridae	84	
<i>Etropus</i> spp.	70	
<i>Hypsopsetta guttulata</i>	63	
<i>Syacium ovale</i>	48	
<i>Bothus</i> spp.	38	
<i>Mugil</i> spp.	29	
<i>Opisthonema</i> spp.	25	
Nomeidae	25	
<i>Scomberomorus</i> spp.	19	
<i>Thunnus albacares</i>	12	
Hemiramphidae	11	
<i>Psenes pellucidus</i>	11	
Mullidae	8	
Tetraodontidae	6	
<i>Albula vulpes</i>	5	
Engraulidae	5	
<i>Hippoglossina</i> spp.	3	
Bothidae	2	
<i>Paralichthys</i> spp.	2	
Polynemidae	2	
<i>Cheilotrema saturnum</i>	2	
Priacanthidae	1	
<i>Roncador stearnsii</i>	1	
MICRODESMIDAE		
Microdesmidae	1	
<i>Cyclopsetta</i> spp.	1	
Affiliates		
Scorpaenidae	34	
<i>Benthoosema pterota</i>	12	
<i>Aulopus</i> spp.	11	
PSENES		
<i>Cubiceps pauciradiatus</i>	12	
<i>Psenes sio</i>	5	

Appendix. Continued

Taxon	Incidence (of 31,214)	Associate group
Affiliates		
<i>Diplophos taenia</i>	192	
<i>Myctophum aurolaternatum</i>	57	
<i>Scopelarchoides nicholsi</i>	19	
SPARIDAE		
Sparidae	1	
<i>Chaetodipterus zonatus</i>	1	
BALISTIDAE		
Balistidae	2	
Fistulariidae	1	