

# Influences of El Niño on assemblages of mesopelagic fish larvae along the Pacific coast of Baja California Sur

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## ABSTRACT

Seasonal assemblages of mesopelagic fish larvae and changes related with environmental factors (plankton biomass, sea surface temperature anomaly, upwelling, and the multivariate El Niño index) were investigated. From 1982 to 1987, 16 oceanographic cruises were carried out along the Pacific coast of Baja California Sur, Mexico. Larvae of 42 mesopelagic fish taxa were collected. Larval abundance was highly variable during the studied period, but summer months coincided with higher abundance (>200 larvae under 10 m<sup>2</sup>). Larval assemblages were dominated by three of the most common species of tropical (*Vinciguerria lucetia*, *Diogenichthys laternatus*) and subtropical affinity (*Triphoturus mexicanus*). A group of species of tropical affinity (*Diplophos proximus*, *Diaphus pacificus*, *Benthosema panamense*) was useful for distinguishing the 1982–84 El Niño event, and an assemblage of larvae of temperate affinity (*Symbolophorus californiensis*, *Melamphaes lugubris*, *Bathylagus ochotensis*, *Leuroglossus stilbius*, *Protomyctophum crockeri*) characterized 'normal' years (mid-1984 to mid-1987).

**Key words:** Baja California coast, California Current, El Niño, fish larvae assemblages, mesopelagic

## INTRODUCTION

Mesopelagic fish are perhaps the most ubiquitous and speciose of all fish in oceanic waters (Ahlstrom *et al.*, 1976; Wisner, 1976). Adults of some species migrate vertically to surface waters at night (Paxton, 1967; Watanabe and Kawaguchi, 2003), and some lanternfish species (e.g. *Benthosema panamense*) form compact aggregations at the surface during daylight (Moser and Ahlstrom, 1970). Diurnal migrations are thought to play an important role in the vertical transport of biomass (biological convection). Mesopelagic fish contribute a considerable portion of the diets of commercially important fish, cephalopods, and marine mammals (Alverson, 1961; Gaskett *et al.*, 2001). Their abundance and ecological role in the marine food chain are recognized in studies of marine ecology, but also in fisheries sciences, as a potential fishing resource (Kawaguchi and Shimizu, 1978).

Larvae of mesopelagic fish are mainly distributed in the upper 100 m (Loeb and Nichols, 1984; Moser and Smith, 1993) and are common in open-ocean plankton tows. For example, seven mesopelagic species ranked in the 13 principal taxa identified by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys from 1951 to 1984 (Moser *et al.*, 1993). Early life history descriptions and spatial and seasonal distributions of early life stages are summarized in the literature (e.g. Moser *et al.*, 1993, 1994; Moser, 1996). Mesopelagic species are the principal constituents of larval fish assemblages that inhabit offshore waters of the southerly California Current (Loeb *et al.*, 1983a; Moser and Smith, 1993; Funes-Rodríguez *et al.*, 2002).

This region is characterized by marked seasonal shifts in cooling and heating. The main source of seasonal variation is related to the coastal circulation pattern, with the south-flowing California Current as the dominant flow during spring and summer, the poleward-flowing inshore countercurrent dominant during fall and winter, and the California undercurrent with subsurface poleward flow present throughout the year (Hickey, 1979; Lynn and Simpson, 1987).

The major variation in the typical annual oceanographic pattern is associated with the El Niño

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(ENSO), reflected in a warm water influx that progresses northward along the North American Pacific coast (Philander, 1990; Durazo and Baumgartner, 2002). El Niño events in 1982–83 and 1987–88 are detected along the Baja California coast as positive sea surface temperature (SST) anomalies (Gómez-Gutiérrez *et al.*, 1995; Hernández-Trujillo, 1999). Environmental changes associated with El Niño events may have a large impact on ecosystems, including expansion in the range of some adult fish populations and consequent expansion of their spawning area (Bailey and Incze, 1985; Moser *et al.*, 1987; MacCall and Prager, 1988). During El Niño 1958–59, the distribution of fish larvae of tropical affinity expanded northward beyond their typical range in the California Current (Moser *et al.*, 1987). During El Niño 1982–83 invertebrate zooplankton and micronekton and fish larvae off Baja California Sur were predominantly of tropical and subtropical affinity, while temperate species, although infrequent in the region, had more restricted geographical distributions during El Niño

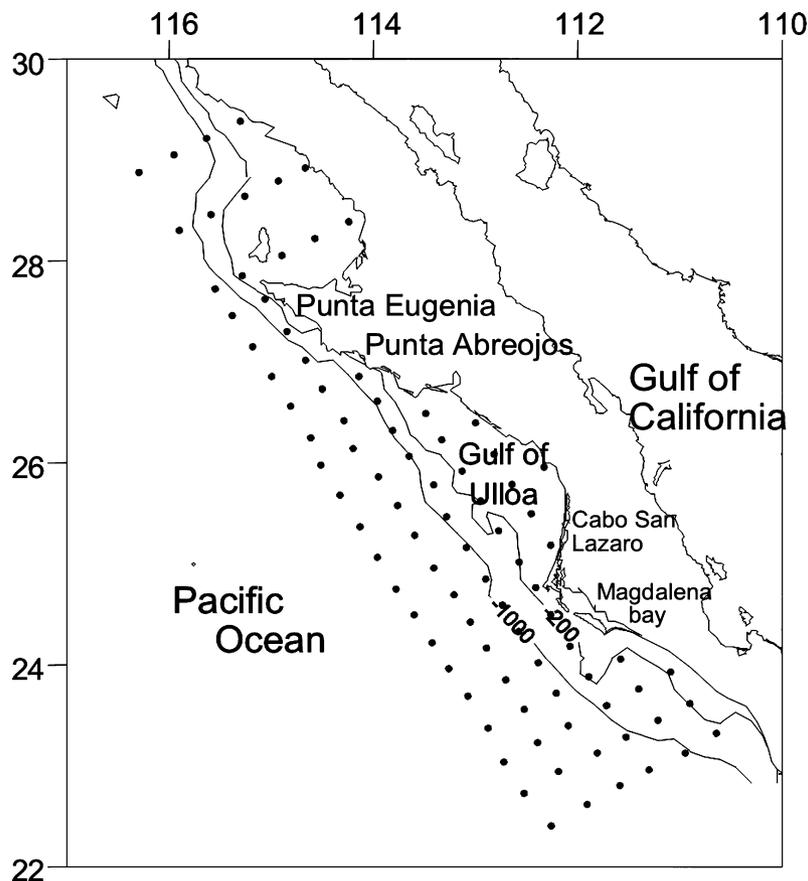
(Funes-Rodríguez *et al.*, 1995, 2002; Gómez-Gutiérrez *et al.*, 1995; Hernández-Trujillo, 1999).

This paper describes assemblages of mesopelagic fish larvae and associated changes in particular environmental factors (plankton biomass, SST anomaly, upwelling, and the multivariate El Niño Index, MEI) from 1982 through 1987 along the west coast of Baja California Sur.

## MATERIALS AND METHODS

The study area encompassed the Pacific coast of Baja California Sur from Punta Eugenia in the north to the tip of the peninsula in the south (from 23° to 28°N; approximately 1000 km) in a zone extending seaward to 37–185 km west of the coast. A wide continental shelf occurs from Punta Abrejos to Cabo San Lázaro (83 km) but narrows off Bahía Magdalena and Punta Eugenia, where bottom depths >200 m occur close to the shore (Fig. 1). Environmental time series representing conditions along the

Figure 1. Study area and station plan along the Pacific Coast of Baja California Sur, Mexico.



Pacific coast off Baja California Sur were derived from different sources: the MEI was obtained from the NOAA Climate Diagnostic Center (<http://www.cdc.noaa.gov/>); SST data were provided from CICIMAR-IPN cruises; SST anomalies for latitudes 24°–27°N were obtained from NOAA's CDRM NODC-01 Pacific Ocean for 1980–90 (Gómez-Gutiérrez *et al.*, 1995); and the mean upwelling index (at 24°N, 113°W in m<sup>3</sup> per second per 100 m coastline) from NOAA Pacific Fisheries Environmental Laboratory (<http://www.pfeg.noaa.gov/>).

From August 1982 to October 1987, 16 surveys were carried out in the study area: two in winter, five in spring, six in summer, and three in autumn. Survey lines were perpendicular to the coast, extending seaward 37–185 km (20–100 nautical miles, n miles), and stations were placed at 37-km intervals (20 n miles) on the survey lines (Fig. 1). In total 614 plankton net tows were made. Plankton samples were collected with a bongo net (333- and 505- $\mu$ m mesh) with a 0.5-m mouth diameter that were towed obliquely between the surface and approximately 200 m maximum depth in open water, and to near-bottom depth in shallower water (Smith and Richardson, 1977). A flow meter in the mouth of each net was used to calculate the volume of water strained. Plankton samples were preserved with 4% formalin buffered with sodium borate. Plankton biomass (mL per 1000 m<sup>3</sup>) was determined using the displaced volume technique (Beers, 1976). Fish larvae and eggs were sorted from the 505- $\mu$ m mesh samples. Mesopelagic fish larvae were identified from chapters in Moser (1996) as principal sources. Counts of fish larvae were converted to number under 10 m<sup>2</sup> sea surface (Smith and Richardson, 1977).

To measure species diversity, the Shannon–Wiener diversity index ( $H'$ ) and its evenness ( $J'$ ) were calculated (Clarke and Warwick, 2001) as:

$$H' = - \sum_i p_i \log(p_i),$$

$$J' = \frac{H'}{H'_{\max}} = \frac{H'}{\log S},$$

where  $p_i$  is the proportion of total count arising from the  $i$ th species; and  $H'_{\max}$  is the maximum possible value of Shannon diversity, i.e. that which would be achieved if all  $S$  (=species) were equally abundant (namely,  $\log S$ ). Abundance was converted to the log of base 2 prior to applying the Shannon–Wiener index.

Cluster analysis based on the frequency of species occurrence (Fager and McGowan, 1963; Postel *et al.*, 2000; Clarke and Warwick, 2001) was performed to describe seasonal assemblages of taxa (R mode) and

surveys (Q mode). The database for cluster analyses was the percentage of positive data from sampling stations in each survey. Data from species occurring in less than two surveys were not used. A similarity index was calculated for species and surveys using the Bray–Curtis dissimilarity measure (Bray and Curtis, 1957; Clarke and Warwick, 2001). The index was calculated as:

$$\delta_{jk} = 100 \frac{\sum_{i=1}^p |y_{ij} - y_{ik}|}{\sum_{i=1}^p (y_{ij} + y_{ik})},$$

where  $y_{ij}$  = score for the  $i$ th species in the  $j$ th sample;  $y_{ik}$  = score for the  $i$ th species in the  $k$ th sample;  $\delta_{jk}$  = dissimilarity between the  $j$ th and  $k$ th samples summed over all  $p$  species.  $\delta_{jk} = 0$  (no dissimilarity) and  $\delta_{jk} = 100$  (total dissimilarity).

Dendrograms were obtained with the complete linkage technique in R and Q modes (Clifford and Stephenson, 1975). Similarity levels (cutoff limits) were defined by comparisons with faunal association and spawning season data. After classification of species and stations for a particular data set, the original percentage occurrence of each species (positive tows) was rearranged according to the order in which sampling periods and species appeared in the dendrograms. Measurements of similarity and classification were analyzed with the community analysis package 2.13 (Herderson and Seaby, 2002). Spearman's  $\rho$  rank-order correlation analysis was used to explore the relationships between abundance of mesopelagic larvae with SST, plankton biomass, upwelling strength, and MEI. Significance levels were set at  $P < 0.05$ .

## RESULTS

The west coast of Baja California Sur has marked seasonal SST variations; monthly mean values are relatively cold during winter and spring (15–19°C) and warm in summer (23–28°C), with a maximum recorded in summer 1983 (28°C) (Table 1). Two El Niño events, July 1982 to August 1984 (26 months) and October–December 1987 (3 months) had positive SST anomalies. It is important to note that the 1986–87 El Niño event in the Eastern Pacific basin was not for the most part matched by SST positive anomalies off Baja California. September 1984 to September 1987 (37 months; Fig. 2a) were considered 'normal'. Plankton biomass was much more variable during the El Niño period than during normal period, but showed no other clear differences between periods (Fig. 2b). Both maximum (480 mL per 1000 m<sup>3</sup>) and minimum

**Table 1.** Temporal changes in composition of the mesopelagic fish larva community: mean SST; number of mesopelagic species; total mesopelagic larval abundance; Shannon–Wiener's diversity index ( $H'$ ); and evenness ( $J'$ ).

| Month                         | Mean SST | Species number | Total larval abundance | Mean larval abundance | Diversity $H'$ | Evenness $J'$ |
|-------------------------------|----------|----------------|------------------------|-----------------------|----------------|---------------|
| El Niño 1982–83 (warm period) |          |                |                        |                       |                |               |
| July 1982                     | 20.35    | 12             | 1553                   | 129                   | 1.43           | 0.40          |
| August 1982                   | 25.62    | 8              | 1725                   | 216                   | 0.82           | 0.27          |
| December 1982                 | 21.67    | 6              | 546                    | 91                    | 2.20           | 0.85          |
| February 1983                 | 21.07    | 12             | 1501                   | 125                   | 1.66           | 0.46          |
| May 1983                      | 18.90    | 7              | 1725                   | 246                   | 1.58           | 0.56          |
| September 1983                | 27.91    | 13             | 8248                   | 634                   | 1.53           | 0.41          |
| January 1984                  | 19.14    | 9              | 2684                   | 298                   | 1.74           | 0.55          |
| May 1984                      | 17.89    | 16             | 3267                   | 204                   | 2.12           | 0.53          |
| 1985–87 (normal period)       |          |                |                        |                       |                |               |
| May 1985                      | 15.00    | 9              | 619                    | 68                    | 1.83           | 0.58          |
| August 1985                   | 25.25    | 14             | 4581                   | 327                   | 2.11           | 0.56          |
| May 1986                      | 17.83    | 22             | 3566                   | 162                   | 2.21           | 0.50          |
| June 1986                     | 18.93    | 7              | 673                    | 96                    | 1.78           | 0.63          |
| August 1986                   | 23.57    | 7              | 754                    | 108                   | 1.86           | 0.66          |
| November 1986                 | 23.01    | 11             | 813                    | 74                    | 1.13           | 0.33          |
| July 1987                     | 20.16    | 7              | 1810                   | 258                   | 1.71           | 0.61          |
| October 1987                  | 26.00    | 16             | 4998                   | 312                   | 1.84           | 0.46          |

(75 mL per 1000 m<sup>3</sup>) biomass are recorded during 1982–84; biomass was usually higher than 200 mL per 1000 m<sup>3</sup> during the normal period (1985–87). High biomass (>300 mL per 1000 m<sup>3</sup>) principally occurred in spring and was positively related with upwelling activity (60–80 m<sup>3</sup> s<sup>-1</sup>) (Fig. 2b).

Total larval abundance of all mesopelagic fish species collected from 1982 to 1987 was 39 062 larvae under 10 m<sup>2</sup> representing 42 taxa in 13 families (Table 2). Myctophidae was the most diverse family with 15 taxa, compared with others with 1–4 taxa each. Three species accounted for 88% of the larvae (*Vinciguerria lucetia*, *Diogenichthys laternatus* and *Triphoturus mexicanus*); the remaining taxa were uncommon (Table 2). *Vinciguerria lucetia* was dominant in abundance (49.6%) and occurrence (54.9% positive tows), followed by *D. laternatus* (18.7%; 34.9%) and *T. mexicanus* (16.8%; 29.5%). Larvae were principally of tropical and subtropical affinities, accounting for about 40% of the species and 97% of the mesopelagic fish larval abundance. The remaining taxa from subarctic-transitional affinities and warm water cosmopolites occurred in smaller numbers (24% of the species, and 1.2–1.5% of the abundance; Table 2).

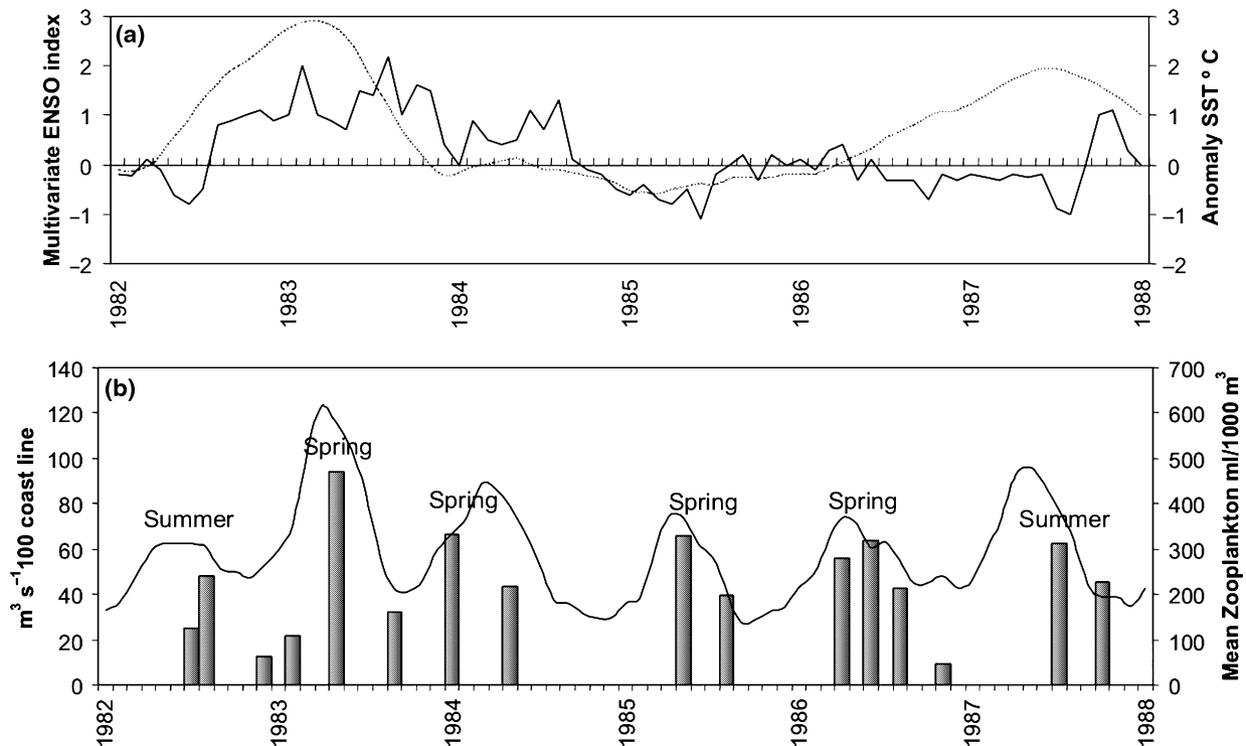
Monthly mean abundance of larvae varied between 68 and 634 (under 10 m<sup>2</sup>). Higher abundances were found principally during summer months (>200 larvae under 10 m<sup>2</sup>), except summer 1986 (Table 1). The Shannon–Wiener diversity values ( $H'$ ) varied between

0.82 and 2.21; most were higher than 1.5 (Table 1). There was some tendency for diversity to be higher, as well as evenness ( $J'$ ) to be slightly higher, during the 1985–87 'normal conditions', than during the 1982–84 El Niño conditions and November 1986, indicating increased dominance by some species, usually *V. lucetia*, during El Niño (Table 1).

The relationships between mean abundance of mesopelagic larvae and SST anomalies were noticeably variable during the study period (Fig. 3). Species of tropical affinity, *V. lucetia* and *Hygophum atratum*, showed mostly high abundance values during 1982–83, and diminished once the strongest El Niño positive anomalies ended (Fig. 3). Abundance of *V. lucetia* was positively correlated with SST ( $\rho = 0.532$ ;  $P < 0.05$ ), but *D. laternatus*, and *H. atratum* were not correlated with SST, plankton biomass, or upwelling. *Triphoturus mexicanus*, with subtropical affinity, showed high abundance values during the normal period (1985–87; Fig. 3), and was negatively correlated with MEI ( $\rho = \text{minus}; 0.591$ ;  $P < 0.05$ ), but did not show a relationship with SST, plankton biomass, and upwelling. Although *H. atratum* relationships with the cited variables cannot be statistically detected with the current data, high abundance values in coincidence with El Niño period suggest the possibility of a relationship.

Using cluster analysis, two principal groups of months (1 and 2) were separated by about 20%

**Figure 2.** (a) Multivariate El Niño-Southern Oscillation Index (dashed line) and SST anomalies (solid line) along the Pacific Coast of Baja California Sur, Mexico 1982–88 (from Gómez-Gutiérrez *et al.*, 1995; Hernández-Trujillo, 1999). (b) Monthly average zooplankton biomass (bars), and upwelling (line;  $\text{m}^3 \text{s}^{-1}$  per 100 m coastline).



similarity (Fig. 4). Group 1 consisted mainly of months with 'normal' or slightly negative SST anomalies from mid-1984 to 1986, and October 1987 which had a moderately large positive anomaly, while group 2 occurred mainly during the months associated with positive SST anomalies, the 1982 to mid-1984 El Niño months.

Three groups of taxa (A, B, and C) were separated in the species dendrogram by more than 8.5% similarity (Fig. 4). Species group A principally contained taxa that were relatively uncommon in the area and have transitional affinity (*Melamphaes lugubris*, *Bathylagus ochotensis*, *Leuroglossus stilbius* and *Protomyctophum crockeri*). These species were present principally in the 'normal period' (group 1). Species group B principally contained tropical and subtropical species, present in both month groups. Species group B was dominated by the three commonest species: *V. lucetia*, *T. mexicanus*, and *D. laternatus*. All three occurred in both month groups, but *T. mexicanus* and *D. laternatus* were more common during 'normal' months (group 1), and *V. lucetia* was slightly more common during El Niño months (group 2). Species in group C were exclusively of tropical affinity that occurred mainly during El Niño months in group 2 (*Diplophos proximus*, *Diaphus pacifi-*

*cus*, and *Benthoosema panamense*). Their non-group 2 occurrence was by *Diaphus pacificus* in 1987, an El Niño month in group 1 (Fig. 4).

Species of transitional affinity such as *P. crockeri* (species group A) occurred to the north (Fig. 5a), or did not occur (*L. stilbius*) during El Niño, but were extensively present once the 1982–83 El Niño anomaly passed (Fig. 5b,c). Conversely, species exclusively of tropical affinity, such as *B. panamense* and *Diaphus pacificus* (species group C), occurred principally during the strong El Niño event (Fig. 5d,e). Finally, species of extensive occurrence during the study period, such as *V. lucetia* and *T. mexicanus* (species group B), were abundant in different periods. The tropical *V. lucetia* was abundant principally during the strongest warm water anomalies (Fig. 5g), while the subtropical *T. mexicanus* occurred principally during normal years (Fig. 5k). Both species extended farther toward shore in September 1983.

## DISCUSSION

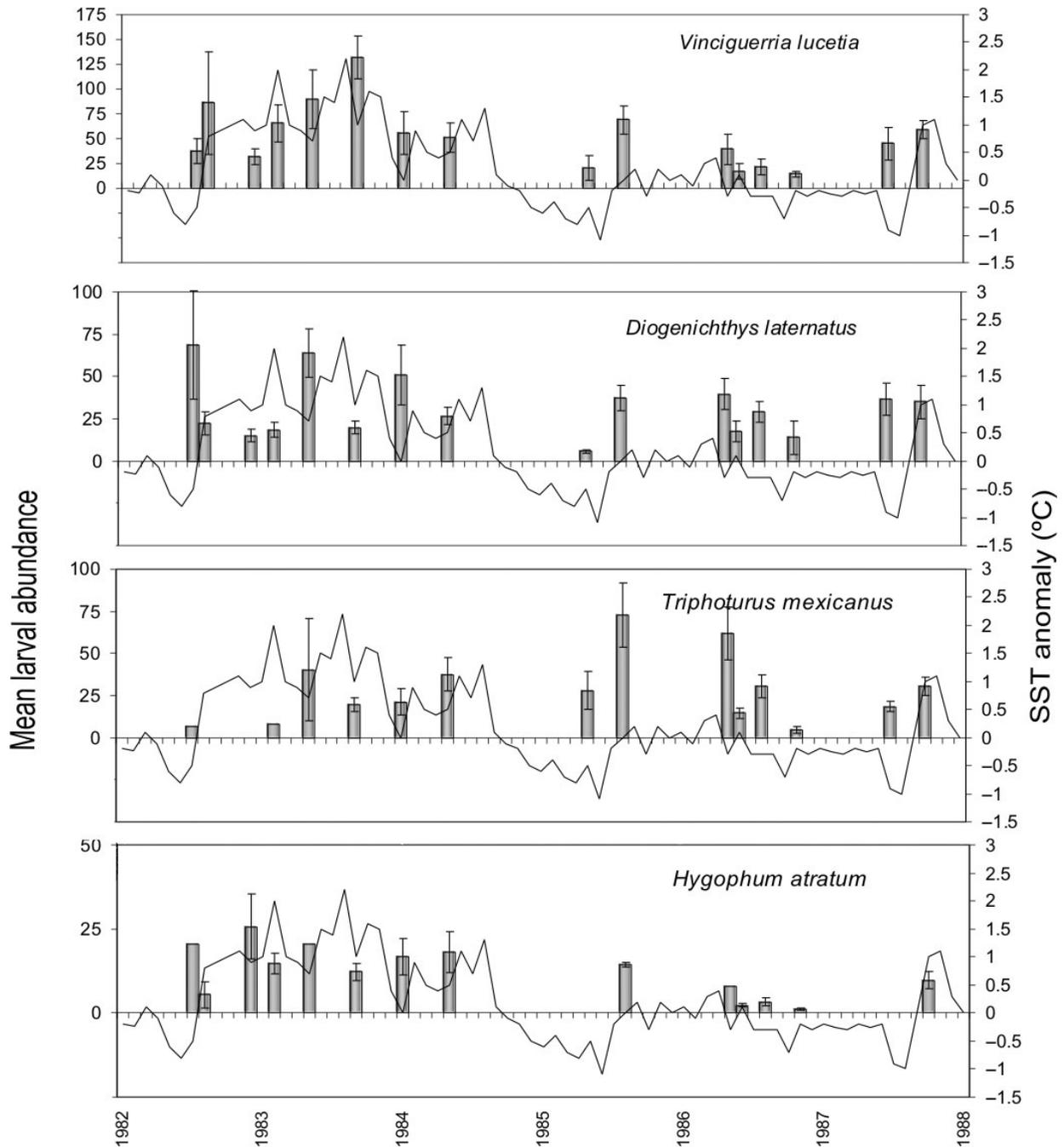
Along the west coast of Baja California Sur from 1982 to 1987, the most abundant and frequently occurring

**Table 2.** Taxonomic composition, faunal association, spawning season, total abundance of all cruises (larvae under 10 m<sup>2</sup>), proportion of larval abundance, proportion of positive tows, and proportion of positive cruises of mesopelagic larval fish along the west coast of Baja California Sur, 1982–87.

| Family                              | Species                          | Faunal association | Spawning season/<br>peak month | Total abundance<br>all cruises | Proportion<br>abundance | Proportion<br>positive<br>tows | Proportion<br>positive<br>cruises |
|-------------------------------------|----------------------------------|--------------------|--------------------------------|--------------------------------|-------------------------|--------------------------------|-----------------------------------|
| Bathylagidae                        | <i>Bathylagus ochotensis</i>     | S-T                | Win–Spr/Feb–Mar                | 12                             | 0.03                    | 0.33                           | 12.50                             |
|                                     | <i>Bathylagus wesethi</i>        | T                  | Spr–Sum/May–Aug                | 100                            | 0.26                    | 1.95                           | 37.50                             |
|                                     | <i>Leuroglossus stilbius</i>     | T                  | Win–Spr/Jan–Apr                | 285                            | 0.73                    | 3.75                           | 31.25                             |
| Microstomatidae                     | <i>Nansenia candida</i>          | S–T                | Ext/Feb                        | 4                              | 0.01                    | 0.16                           | 6.25                              |
|                                     | <i>Nansenia crassa</i>           | SbTr               | Ext/Jan–Mar                    | 6                              | 0.02                    | 0.16                           | 6.25                              |
| Gonostomatidae                      | <i>Diplophos proximus</i>        | ETP                | Aut–Win/Oct–Feb                | 70                             | 0.18                    | 0.81                           | 18.75                             |
|                                     | <i>Diplophos taenia</i>          | WWC                | Ext/Oct–Nov                    | 3                              | 0.01                    | 0.16                           | 6.25                              |
|                                     | <i>Cyclothone acclinidens</i>    | WWC                | Sum–Aut                        | 52                             | 0.13                    | 0.98                           | 25.00                             |
| Sternoptychidae                     | <i>Cyclothone signata</i>        | WWC                | Sum–Aut                        | 187                            | 0.48                    | 4.07                           | 37.50                             |
|                                     | <i>Argyropelecus affinis</i>     | WWC                | Ext/Aut–Spr                    | 6                              | 0.02                    | 0.16                           | 6.25                              |
|                                     | <i>Argyropelecus sladeni</i>     | WWC                | Ext/Aut–Spr                    | 67                             | 0.17                    | 1.47                           | 25.00                             |
| Phosichthyidae                      | <i>Sternopyx</i> sp.             |                    | Ext/Win                        | 11                             | 0.03                    | 0.33                           | 6.25                              |
|                                     | <i>Ichthyococcus irregularis</i> | T                  | Ext                            | 7                              | 0.02                    | 0.16                           | 6.25                              |
| Stomiidae                           | <i>Vinciguerria lucetia</i>      | ETP                | Ext/Sep–Oct                    | 19 378                         | 49.61                   | 54.89                          | 100.00                            |
|                                     | <i>Stomias</i> sp.               |                    |                                | 3                              | 0.01                    | 0.16                           | 6.25                              |
| Scopelarchidae                      | <i>Stomias atriventer</i>        | T–SbTr             | Ext/Feb–Sep                    | 74                             | 0.19                    | 1.63                           | 37.50                             |
|                                     | <i>Scopelarchus guentheri</i>    | WWC                | Ext                            | 72                             | 0.18                    | 0.49                           | 18.75                             |
| Paralepididae                       | <i>Scopelarchoides nicholsi</i>  | Tr–SbTr            | Ext                            | 7                              | 0.02                    | 0.16                           | 6.25                              |
|                                     | <i>Lestidiops neles</i>          | Tr–SbTr            | Jan–Oct                        | 20                             | 0.05                    | 0.16                           | 6.25                              |
| Myctophidae                         | <i>Lestidiops ringens</i>        | S–T                | Ext                            | 7                              | 0.02                    | 0.16                           | 6.25                              |
|                                     | <i>Bolinichthys longipes</i>     | T–Sbtr–Tr          | Ext                            | 8                              | 0.02                    | 0.16                           | 6.25                              |
|                                     | <i>Benthoosema panamense</i>     | ETP                | Ext                            | 2443                           | 6.25                    | 3.09                           | 12.50                             |
|                                     | <i>Ceratoscopelus townsendi</i>  | WWC                | Ext/Aug                        | 55                             | 0.14                    | 0.98                           | 25.00                             |
|                                     | <i>Diaphus pacificus</i>         | ETP                | Ext                            | 195                            | 0.50                    | 1.79                           | 25.00                             |
|                                     | <i>Diogenichthys laternatus</i>  | ETP                | Ext/Feb–Apr<br>and Aug         | 7316                           | 18.73                   | 34.85                          | 100.00                            |
|                                     | <i>Gonichthys tenuiculus</i>     | ETP                | Ext/Dec–May                    | 268                            | 0.69                    | 5.70                           | 75.00                             |
|                                     | <i>Hygophum atratum</i>          | ETP                | Ext/Nov                        | 1005                           | 2.57                    | 12.70                          | 87.50                             |
|                                     | <i>Lampadena urophaos</i>        | T                  | Ext/Sum–Aut                    | 6                              | 0.02                    | 0.16                           | 6.25                              |
|                                     | <i>Lampanyctus parvicauda</i>    | ETP                | Ext                            | 223                            | 0.57                    | 3.58                           | 62.50                             |
|                                     | <i>Myctophum aurolaternatum</i>  | Tr–SbTr            | Jan–Apr<br>and Sep–Nov         | 14                             | 0.04                    | 0.33                           | 12.50                             |
|                                     | <i>Nannobranchium idostigma</i>  | Tr–SbTr            | Ext                            | 301                            | 0.77                    | 5.21                           | 68.75                             |
|                                     | <i>Nannobranchium ritteri</i>    | S–T                | Ext/Spr–Win/Mar                | 12                             | 0.03                    | 0.16                           | 6.25                              |
|                                     | <i>Protomyctophum crockeri</i>   | T                  | Ext/Dec                        | 100                            | 0.26                    | 1.63                           | 18.75                             |
| <i>Symbolophorus californiensis</i> | T                                | Ext/Spr–Win        | 25                             | 0.06                           | 0.65                    | 18.75                          |                                   |
| <i>Triphoturus mexicanus</i>        | Sbtr                             | Ext/Aug–Sep        | 6567                           | 16.81                          | 29.48                   | 87.50                          |                                   |
| Gigantactinidae                     | <i>Gigantactis</i> sp.           | WWC                | Sum                            | 6                              | 0.02                    | 0.16                           | 6.25                              |
| Melamphaidae                        | <i>Melamphaes</i> sp.            |                    |                                | 37                             | 0.09                    | 0.65                           | 25.00                             |
|                                     | <i>Melamphaes lugubris</i>       | S–T                | Ext/Mar–Jun                    | 30                             | 0.08                    | 0.65                           | 25.00                             |
| Chiasmodontidae                     | <i>Chiasmodon niger</i>          | Tr–Sbtr            | Ext/Abr–May<br>and Aug–Sep     | 35                             | 0.09                    | 0.65                           | 6.25                              |
| Gempylidae                          | Type 1                           |                    |                                | 6                              | 0.02                    | 0.16                           | 6.25                              |
|                                     | <i>Gempylus serpens</i>          | WWC                | Ext/Feb–Nov                    | 17                             | 0.04                    | 0.33                           | 6.25                              |
|                                     | <i>Nealotus tripes</i>           | WWC                | ?                              | 22                             | 0.06                    | 0.16                           | 6.25                              |
| Total abundance                     |                                  |                    |                                | 39 062                         |                         |                                |                                   |

Total of 39 062 mesopelagic fish larvae of all cruises; sampling effort 614 tows; and 16 cruises. S = subarctic; T = transitional; SbTr = subtropical; Tr = tropical; WWC = warm water cosmopolite; ETP = eastern tropical Pacific; Ext = extended spawning season. Faunal association and spawning season information principally from Moser (1996).

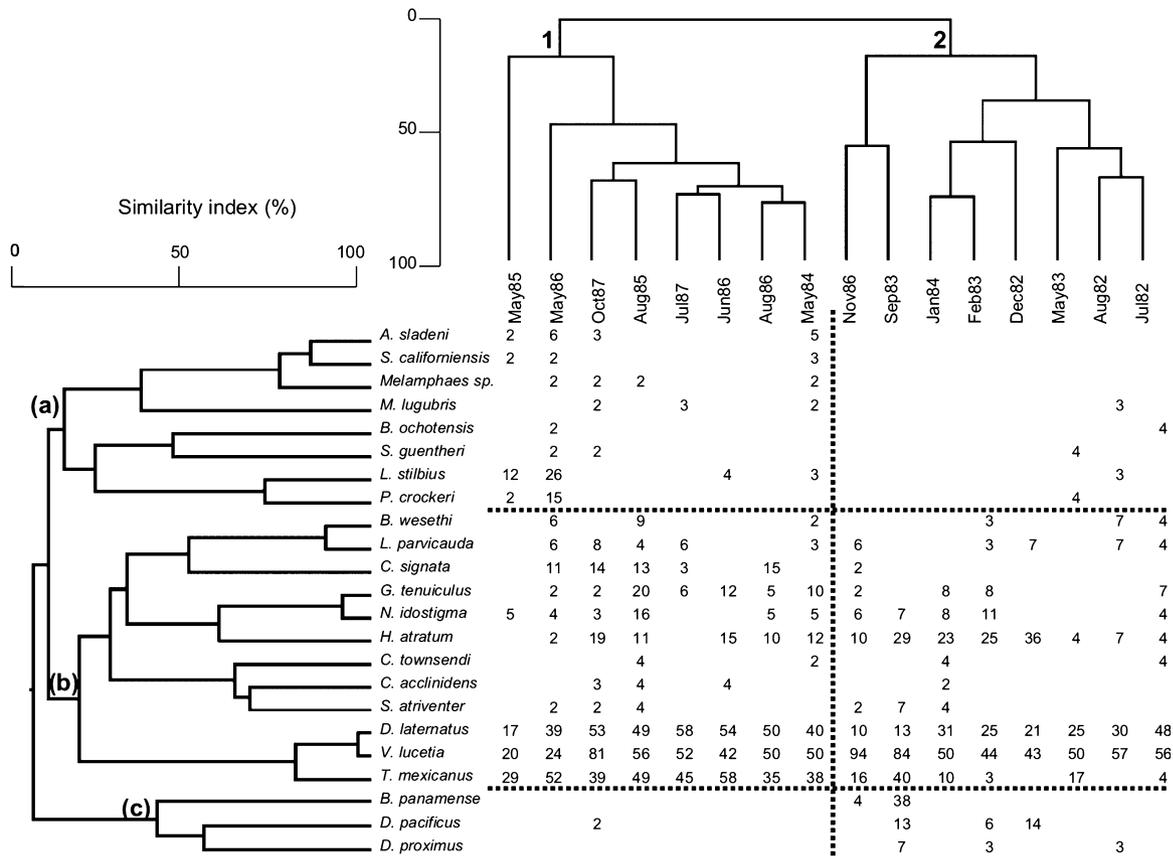
**Figure 3.** Mean abundance (bars) and the standard error of the mean of mesopelagic fish larvae, and SST anomalies (line) along the Pacific Coast of Baja California Sur, 1982–87.



mesopelagic taxa were the tropical *V. lucetia* and *D. laternatus* and subtropical *T. mexicanus*, whether the regime was warm or not. These species occurred mainly in the southern region of the California Current, and their larvae ranked third, eleventh, and sixth, respectively, among ichthyoplankton taxa

identified from CalCOFI survey cruises from 1951 to 1984 (Moser *et al.*, 1993). They occurred throughout the year; abundance of *V. lucetia* and *T. mexicanus* larvae peaked in summer and *D. laternatus* larvae peaked during late winter and again in summer (Moser *et al.*, 1993). The current data set did not support the

**Figure 4.** Time and species dendrograms based on percentage occurrences of mesopelagic fish larvae during each survey along the Pacific Coast of Baja California Sur, 1982–87.



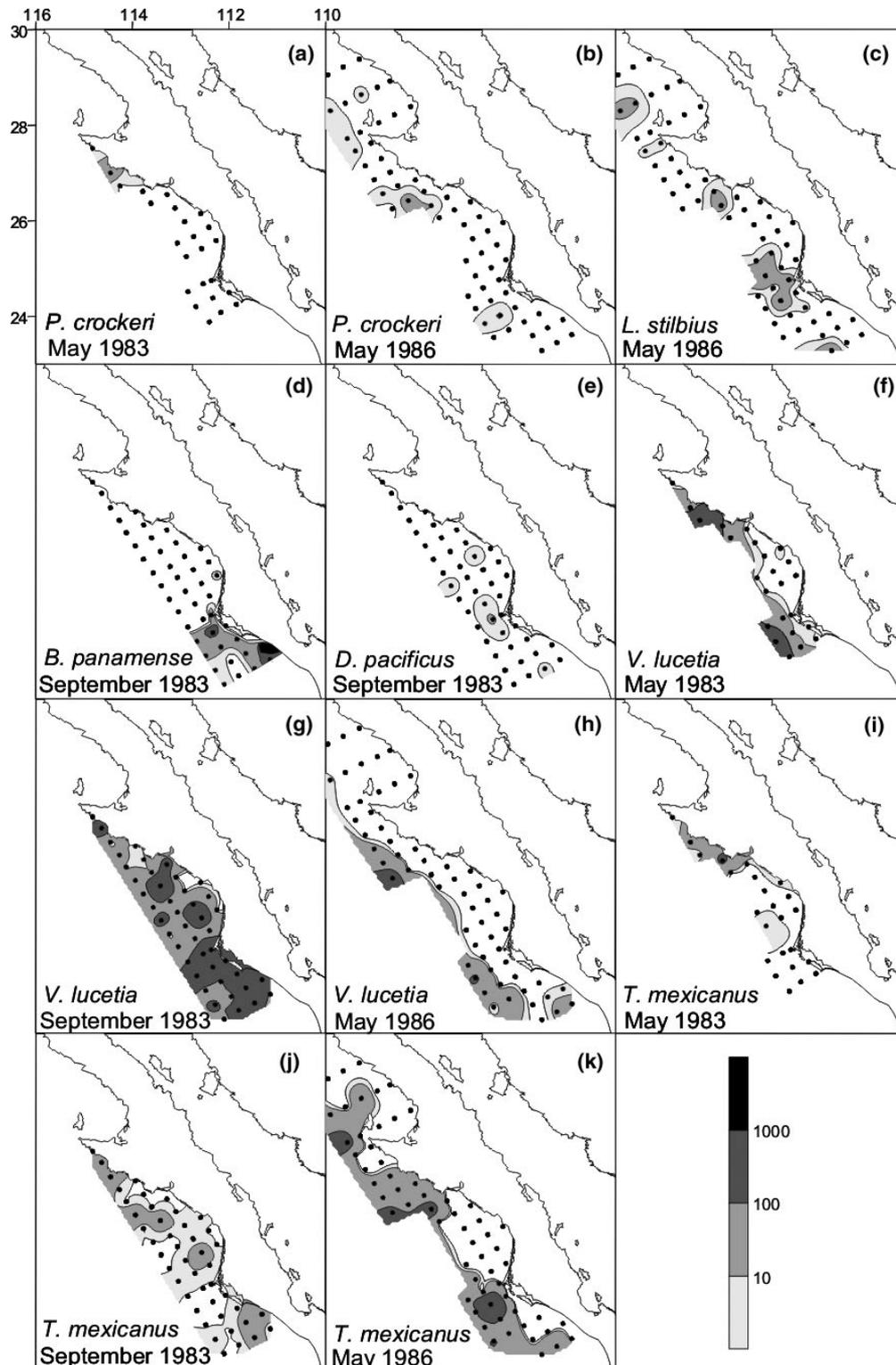
view that mesopelagic fish larvae had a marked seasonal trend in abundance and occurrence during the studied period. However, tropical species such as *V. lucetia*, and *H. atratum* peaked mostly during periods with a positive SST anomaly, principally during 1982–83, but *D. latematus* appears to be more frequent when SST anomalies were smaller and varied between positive and negative, while the highest abundances and occurrences of *T. mexicanus* were principally during ‘normal years’ (1985–86). Historical data showed that *T. mexicanus* ranked second in abundance off central Baja California during the cool year 1975, followed by *D. latematus* and *V. lucetia* (Loeb *et al.*, 1983a), similar to the findings registered during ‘normal years’ (1985–86).

Mesopelagic fish larvae off Baja California Sur fall into several major ecological assemblages, including subarctic-transitional, transitional, central north Pacific, and eastern tropical Pacific, in agreement with Moser *et al.* (1987). The conjunction of diverse ecological assemblages is particularly pronounced at the southern extreme of the California Current where cold

and warm water collide, creating rich ‘meadows’ (Malakoff, 2004). Our data on taxonomic composition confirms this. Subtropical and tropical species were the primary constituents (75%) of mesopelagic fish larvae off Baja California. Consequently, larval fish assemblages reflect the transitional nature of this part of the California Current region and its zoogeographic components (Moser *et al.*, 1987). This is similar to hydrographic structures in the Kuroshio Current region and myctophid larvae assemblages related to it (Sassa *et al.*, 2004). Other studies of plankton populations off Baja California Sur showed that the number of tropical species was relatively constant (Gómez-Gutiérrez *et al.*, 1995; Hernández-Trujillo, 1999). Nevertheless, there is high inter-annual variation in species composition that could be related to changes in the California Current system and environmental shifts like El Niño. Such a shift between years was reported during the 1957–58 El Niño (Moser *et al.*, 1987).

Marked seasonal shifts in SST, with low temperature from January to June (15–19°C) and high tem-

**Figure 5.** Distribution patterns of some mesopelagic fish larvae (larvae under  $10\text{ m}^2$ ) belonging to transitional (*Protomyctophum crockeri*, *Leuroglossus stilbius*), tropical (*Benthoosema panamense*, *Diaphus pacificus*, *Vinciguerria lucetia*), and subtropical affinity communities (*Triphoturus mexicanus*), along the Pacific Coast of Baja California Sur during El Niño (May and September 1983) and normal years (May 1986).



perature from August to October (20–28°C), reflect the local coastal circulation pattern. The cool California Current is the predominant influence in the area during the first half of the year and the warm California Countercurrent predominates near shore in summer and autumn (Hickey, 1979; Lynn and Simpson, 1987). During El Niño events poleward flow is intensified and during 1982–83 northward excursions of high SSTs were exceptional (Norton *et al.*, 1985). The 1982–83 El Niño event produced maximum positive anomalies along the Pacific Coast of Baja California, compared with a positive anomaly of about 1°C during the weak El Niño 1986–87 (Gómez-Gutiérrez *et al.*, 1995; Hernández-Trujillo, 1999). However, its duration of about 26 months was exceptionally large during El Niño 1982–83 off the southern Baja California coast.

Responses of plankton to equatorward advection of nutrients in synchrony with seasonal coastal upwelling (Roesler and Chelton, 1987) as well as late summer/autumn local blooms have been observed (Loeb *et al.*, 1983b). We found that density of plankton increased principally during intense upwelling (60–80 m<sup>3</sup> s<sup>-1</sup>) in spring, and a secondary (summer autumn) peak in plankton density appears to be associated with periods of weak southward advection of the California Current, in agreement with the findings of Loeb *et al.* (1983b). Mesopelagic fish larvae were scarce during spring plankton blooms, except during the 1983–84 El Niño conditions. Subarctic-transitional species tended to occur although scarce in late winter and spring when the California Current is strongest, but these species were relatively uncommon or restricted to the north during spring 1983. Seasonal changes in abundance of mesopelagic fish larvae appear to be primarily controlled by reproductive activity of species with warm water affinity (>200 larvae under 10 m<sup>2</sup> of sea surface), coinciding with the inshore countercurrent as the domain flow and favorable warm water conditions during summer.

Various authors have observed increased abundances of equatorial fish larvae and northward expansion of their distributions, coupled with declining abundance of temperate taxa and a northward retreat during El Niño (Moser *et al.*, 1987; Funes-Rodríguez *et al.*, 1995), resulting from displacement of adults outside their normal spawning area or advection of eggs or larvae by anomalous currents (Bailey and Incze, 1985). Species that are characteristic of the southern part of the California Current increase during El Niño conditions (*V. lucetia*, *D. laternatus*, *H. atratum*), and uncommon species (subarctic and transitional) may be affected by changes in flow regime resulting in seasonal or interannual

expansion or contraction of spawning ranges. This also occurs in the euphausiid and copepod assemblages off Baja California with an increase in tropical species during El Niño conditions (Hernández-Trujillo *et al.*, 1987; Gómez-Gutiérrez *et al.*, 1995; Hernández-Trujillo, 1999).

Cluster analysis clearly distinguished two groups of months: one primarily during El Niño conditions (1982 to early 1984), except November 1986, separated from the group composed predominantly of 'normal' or generally prevailing conditions (1985–87), except October 1987. Both groups (1 and 2) contained three of the most common species of tropical and subtropical affinity: *V. lucetia*, *D. laternatus*, and *T. mexicanus* (species group B). However, frequencies of occurrence of tropical affinity species (species group C) during El Niño conditions were useful to distinguish them from 'normal' months, when subarctic-transitional taxa occurred relatively more frequently (species group A). *Triphoturus mexicanus* that is characteristic of the southern half of the California Current region may be less affected by changes in the flow regime off Baja California Sur, compared with species at or near their range limits which are probably at their southernmost occurrence in the California Current region. *Triphoturus mexicanus* was primarily associated with tropical, subtropical, and warm water cosmopolitan species (species group B), but occurs principally during 'normal' months, possibly related to the transitional nature of the *Triphoturus* group strongly connected with two larger recurrent groups of the southern complex (*Vinciguerria* and *Symbolophorus*; Moser *et al.*, 1987).

## CONCLUSIONS

Species of tropical affinity were highly variable during the studied period, but only *V. lucetia* and *H. atratum* increased in abundance during warm water conditions. Although tropical mesopelagic larvae showed a seasonal trend in abundance, their maximum values occurred mostly during the El Niño. Our study supports the conclusion that environmental changes associated with the 1982–83 El Niño event influenced the mesopelagic larvae assemblages of transitional and tropical species.

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