



# Mesopelagic fish larval assemblages during El Niño-southern oscillation (1997–2001) in the southern part of the California Current

RENÉ FUNES-RODRÍGUEZ, \* ALEJANDRO ZÁRATE-VILAFRANCO, ALEJANDRO HINOJOSA-MEDINA, ROGELIO GONZÁLEZ-ARMAS AND SERGIO HERNÁNDEZ-TRUJILLO

Centro Interdisciplinario de Ciencias Marinas-Instituto Politécnico Nacional (CICIMAR), Apto. Postal 592, La Paz 23000, B.C.S., Mexico

## ABSTRACT

Mesopelagic species are the principal constituents of larval fish assemblages inhabiting the southerly California Current region. Seasonal larval abundance is influenced by circulation of the California Current and subtropical Countercurrent, including regional changes of the physical, chemical, and biological characteristics during the El Niño-Southern Oscillation. This study examines the mesopelagic fish larvae distribution and abundance patterns between seasons and years, with the aim of describing the mesopelagic larval assemblages during dynamic environmental changes induced by El Niño (1997–1998) and the rapid transition to La Niña (1998–2000) along the west coast of the Baja California Peninsula (25–31°N). Despite large oceanographic variability, larval assemblages varied principally on a seasonal basis, related to reproductive periods and the north–south gradient influenced by the seasonal pattern of the California Current. An increased diversity, number of species, and abundance of tropical species was noticeable during the northward expansion of warm-water taxa during El Niño, principally in the northern areas (Ensenada and Punta Baja). After El Niño, population adjustments and rapid recovery occurred during La Niña conditions, which reflected seasonal differences in the mesopelagic community structure that are closely related to the seasonal pattern of oceanic currents.

**Key words:** Baja California Peninsula, California Current, El Niño, fish larvae assemblages, La Niña, mesopelagic

## INTRODUCTION

Environmental changes during periods of El Niño have a large impact on local ecosystems, including changes in the amount and northward extension of distributions and spawning of tropical fish species (Bailey and Incze, 1985; Moser *et al.*, 1987). Latitudinal shifts and changes in the temporal distribution of plankton and nekton during strong El Niños have been noted by many authors (Smith, 1985; McGowan *et al.*, 1998; Lluch-Belda *et al.*, 2005). Abundances of copepods decline and salps, chaetognaths, and heteropods increase off the coast of the Baja California Peninsula (Lavaniegos *et al.*, 2002), and warm-water copepods become common off Oregon (Peterson *et al.*, 2002). Euphausiid populations are depressed and the usually dominant species are replaced by southern taxa (Marinovic *et al.*, 2002). Equatorial fish larvae ranged northward, whereas temperate taxa contracted northward during the 1958–1959 and 1982–1983 El Niños (Moser *et al.*, 1987; Funes-Rodríguez *et al.*, 2002, 2006; Jiménez-Rosenberg *et al.*, 2007), and increased numbers of fishes of Panamic affinity were present during El Niño 1997–1998 (Lea and Rosenblatt, 2000). La Niña events and associated faunal intrusions into subtropical waters have not been as well studied.

Several mesopelagic fish species spend their larval stages in the productive epipelagic zone, and their distributions reflect surface water masses (Ahlstrom, 1969; Moser *et al.*, 1987; Moser and Smith, 1993; Watanabe and Kawaguchi, 2003; Sassa *et al.*, 2004). Mesopelagic species are present in several major ecological assemblages in the eastern North Pacific water masses, including subarctic–transitional, transitional, central North Pacific, and eastern tropical (Moser *et al.*, 1987; Moser and Smith, 1993). The mix of diverse ecological assemblages is particularly pronounced at the southern extreme of the California Current, where taxa of temperate and warm water

\*Correspondence. e-mail: rfunes@ipn.mx

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converge (Moser and Smith, 1993; Etnoyer *et al.*, 2004; Funes-Rodríguez *et al.*, 2002, 2006).

The west coast of the Baja California Peninsula is a dynamic region with persistent subtropical frontal features generated by dissimilar water masses (Etnoyer *et al.*, 2004) related to the seasonal shifts of the cool southward California Current and the warmer poleward inshore subtropical countercurrent (Reid *et al.*, 1958; Lynn and Simpson, 1987; Soto-Mardones *et al.*, 2004; Kessler, 2006). Interannual fluctuations related to El Niño (1997–1998) and La Niña (1998–2001) produced pronounced regional effects on the physical, chemical, and biological oceanography (Chavez *et al.*, 2002). The major annual variations associated with El Niño were reduced mesoscale flow of the California Current, high subsurface temperature and salinity anomalies (McGowan *et al.*, 1998; Durazo and Baumgartner, 2002), and negative sea level pressure and cyclonic wind anomalies (Schwing *et al.*, 2002). Reversals during La Niña include anomalies of opposite sign (McGowan *et al.*, 1998), strengthening of the southward flow, and increasing meandering and mesoscale activity (Durazo and Baumgartner, 2002; Schwing *et al.*, 2002).

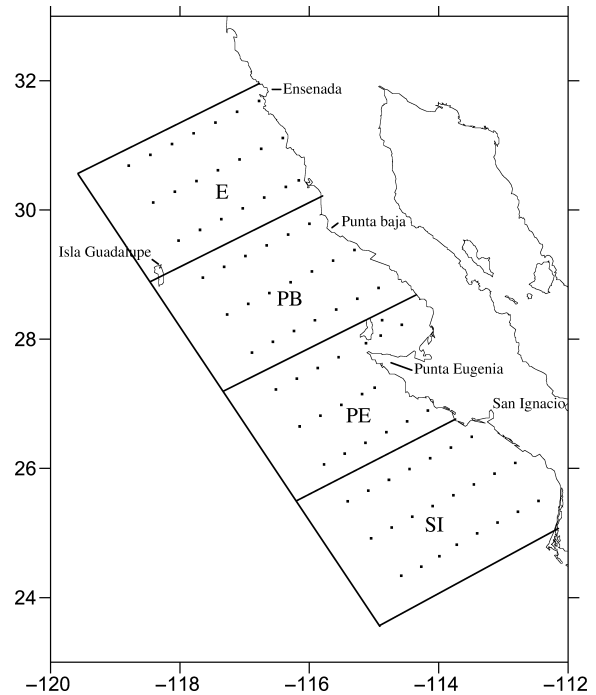
Larval fish assemblages have a predominantly tropical affinity in the southern part of the California Current but exhibit seasonal variability (Loeb *et al.*, 1983; Moser *et al.*, 1993; Jiménez-Rosenberg *et al.*, 2007) related to shifts in oceanic currents and interannual variability related to the intensity of El Niño or La Niña events (Moser *et al.*, 1987; Moser and Smith, 1993; Funes-Rodríguez *et al.*, 2006). Monitoring of the 1997–1998 El Niño and 1999–2001 La Niña on the west coast of Baja California provided the opportunity to test hypotheses of seasonal to interannual changes in the regional mesopelagic larval fish assemblage.

This study examines and compares, between seasons and years, the distribution and abundance patterns of mesopelagic fish larvae to identify and describe their assemblages along the west coast of the Baja California Peninsula (25–31°N). We suggest that the nature and possible origins of these assemblages are related to their faunal associations and environmental changes induced during El Niño (1997–1998) and La Niña (1999–2001).

## MATERIALS AND METHODS

Samples were collected during the Mexican Investigations of the California Current (IMECOCAL) program from near the United States–Mexico border to south of Punta Eugenia (25–31°N). The sampling grid is based on the original California Cooperative

**Figure 1.** Study area and station plan off the west coast of the Baja California Peninsula, Mexico.



Oceanic and Fisheries Investigations (CalCOFI) station plan, lines 100–137 (Fig. 1). The survey lines are perpendicular to the coast, spaced 40 nautical miles (NM) apart, and extend seaward ~108 NM, with a distance between stations on each line of 20 NM. Between October 1997 and January 2001, 13 surveys were made: four in winter (January 1998, 1999, 2000 and 2001), two in spring (April 1999 and 2000), four in summer (September 1997, July 1998, August 1999 and July 2000), and three in autumn (October 1998, 1999, and 2000). For comparisons, the region was divided into four areas following the CalCOFI station plan in Mexican waters (Fig. 1): Ensenada lines (100–107), Punta Baja lines (110–117), Punta Eugenia lines (120–127), and San Ignacio lines (130–137). The Ensenada and San Ignacio areas were not sampled in September 1997, and the San Ignacio area was not sampled in October 1998 and January 1999. Samples from 849 stations were collected during the 13 surveys. Temperature and salinity data (at 50 and 100 m depths) were taken from the IMECOCAL database and the Multivariate ENSO Index (MEI) from the NOAA Earth System Research Laboratory (<http://www.esrl.noaa.gov/psd/data/correlation/mei.data>). Water mass characteristics, dynamic heights (0–500 dbar), temperature and salinity between September 1997 and July 1999 are discussed by Durazo and Baumgartner (2002), and

geostrophic velocities from January 2000 through July 2002 by Soto-Mardones *et al.* (2004).

Plankton was collected in bongo nets (0.6-m mouth diameter, 505- $\mu\text{m}$  mesh) towed obliquely through the water from near the bottom to the surface. A flow meter in the mouth of each net was used to calculate the volume of filtered water. Plankton was preserved with 4% sodium borate-buffered formalin. Fish larvae and eggs were sorted from the samples and fish larvae of mesopelagic taxa were identified according to Moser (1996). Counts of fish larvae were converted to larvae per 10 m<sup>2</sup> of sea surface (Smith and Richardson, 1977).

Abundance of larvae by taxa (85) and stations (849) was organized in a matrix with species as rows and stations as columns. To measure species diversity, the Shannon–Wiener diversity index ( $H'$ ) and Berger–Parker dominance ( $D'$ ) were calculated.

One-way ANOVA was used for discriminating between surveys in each area for the diversity and dominance indices, number of species, abundance, and temperature at 50 and 100 m depths. Confidence limits were set at 95%. Spearman rank order correlations ( $P < 0.05$ ) and critical values for  $P$ , based on Fisher's transformation  $z$  (Zar, 1996), were used to examine the relationships between abundance of larvae and temperature at 100 m.

Cluster analysis was used to describe normal and inverse classifications of the species and survey-area complexes based on the summed abundance of each taxon by each survey in each area (Ensenada, Punta Baja, Punta Eugenia and San Ignacio). Only those species which contributed significantly to the overall spatial patterns were included in this analysis. Taxa occurring in less than 10% of the survey areas for a particular data set were removed. All abundance data were  $\log_{10}(x + 1)$ -transformed prior to analysis. From this matrix (47 taxa and 49 survey areas), a similarity index was calculated (Bray and Curtis, 1957).

Dendrograms were obtained using the farthest neighbor (complete linkage). Similarity levels (cut-off limits) were defined by comparisons with distribution (faunal association) and information on spawning season (Moser, 1996; Fishbase, <http://www.fishbase.org>). Groups of species and survey areas were selected based on the arrangement of entities in the dendrograms and their distinctiveness in terms of species occurrences and levels of abundance, and geographical distribution. In this manner, the survey areas were characterized according to the occurrences and abundances of groups of species. The original abundance data were rearranged according to the order that species and survey-area groups appeared in the dendrograms.

Mean temperature and salinity at 50 and 100 m depth, and the data set based on the matrix of abundance of mesopelagic fish larvae (47 taxa and 49 survey areas) were used to perform canonical correspondence analysis (CCA) with PC-ORD v.4 software (McCune and Mefford, 1999). The CCA is a powerful technique used to understand how multiple species respond simultaneously to environmental factors, extracting significant gradients from ecological matrices (Ter Braak, 1986). Significant environmental parameters were selected with the Monte Carlo permutation test (999 permutations).

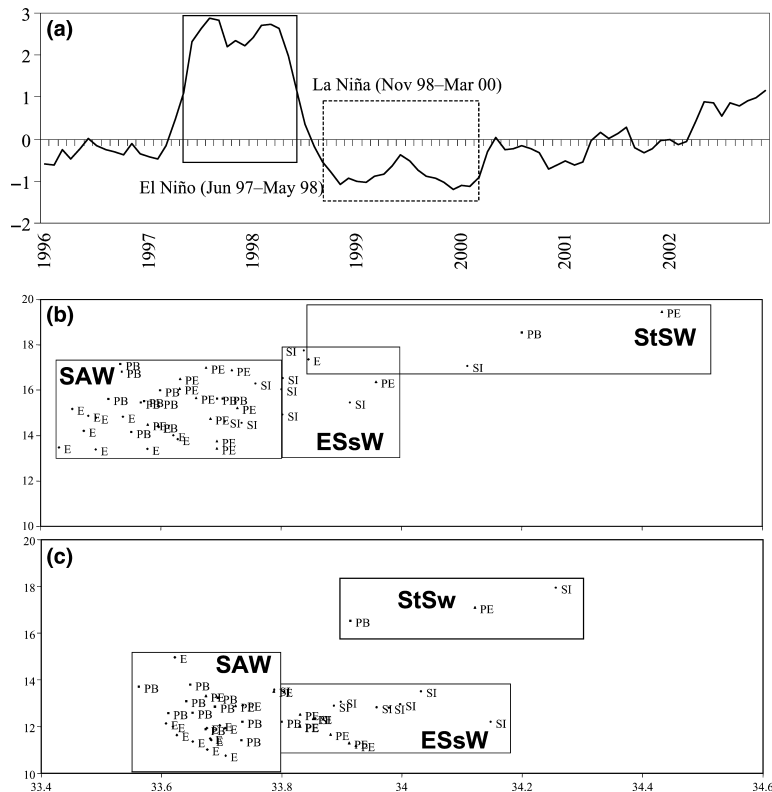
## RESULTS

The 1997–2002 period was a particularly dynamic time, with positive anomalies in the MEI from April 1997 through July 1998, with a peak of about 14 months ( $\sim 2.0$ ; June 1997–May 1998), followed by La Niña (1998–2000) with significant negative values for about 16 months ( $\leq -1.0$ ; November 1998–March 2000). After La Niña, negative anomalies approached the mean (Fig. 2a).

Temperature and salinity indicated particular water masses off the Baja California Peninsula. The subarctic water (SAW; 13–17°C and salinity  $< 33.8$ ) advected southward in the California Current was measured at 50 m depth from Ensenada to Punta Eugenia, with southward extensions at the southernmost area off San Ignacio during La Niña (July 1998, October 1999, April 2000) (Fig. 2b). At 100 m depth, this water mass principally influenced the northern areas, with some intrusions as far south as the Punta Eugenia area (October 1998, August 1999, January 1999; Fig. 2c). The equatorial subsurface water (ESsW), with high salinity ( $> 34.0$ ) indicating the California Undercurrent (poleward flow), was measured at 50 m depth off San Ignacio and as far north as Punta Eugenia at 100 m depth. High temperatures and salinities (16–19°C and salinity  $> 34$ ) at 50 and 100 m depth were related to subtropical surface water (StSW) during El Niño (Fig. 2b,c). Differences in temperatures and salinities were significant between El Niño and La Niña surveys and between northern and southern areas (ANOVA,  $P < 0.05$ ).

Mesopelagic fish larvae belonging to 85 taxa in 21 families were observed. Myctophidae was the most common family (Table 1). Faunal distributions include temperate taxa (subarctic, transitional) and warm-water taxa (subtropical, tropical, and cosmopolitans of warm waters). Only three species, *Vinciguerria lucetia*, *Triphoturus mexicanus*, and *Diogenichthys laternatus*, occurred in  $> 50\%$  of the samples in at least

**Figure 2.** (a) Multivariate El Niño Index, (b) 50 m depth composite temperature–salinity diagram showing the three main water masses off the west coast of the Baja California Peninsula, 1997–2001, (c) same as (b), but for 100 m depth. Data for each cruise correspond to mean temperatures and salinities (ANOVA,  $P > 0.05$ ) off Ensenada (E), Punta Baja (PB), Punta Eugenia (PE) and San Ignacio (SI). SAW (subarctic water; EsSW (equatorial subsurface water); StSW (subtropical surface water).



one of the four regions; *V. lucetia* and *T. mexicanus* were associated with warm water, and occurred in >50% of the samples in all areas, while *Diogenichthys laternatus* occurred principally in the southern areas (Table 1). Species associated with temperate water masses (S and T, Subarctic and Transitional) were principally found in the northern areas, and species with subtropical affinity and distribution were found in warm waters (SBTR and TR, Subtropical and Tropical). Some species with tropical distribution occurred principally in the Punta Eugenia and San Ignacio areas (*Hygophum atratum*, *Nannobranchium idostigma*, and *Lampanyctus parvicauda*; Table 1).

During the ENSO shifts of 1997–2001, the same three most common species were abundant. *Vinciguerria lucetia* composed ~51% of the mesopelagic larval abundance, followed by *D. laternatus* (6.3%) and *T. mexicanus* (4.6%); other species were much less abundant (<2.5%). *Vinciguerria lucetia* ranked first in abundance in all four areas (~50%), whereas the species in second position changed in each area: *Bathylagus wesethi* (synonym of *Bathylagoides wesethi*)

(7.3%) off Ensenada, *T. mexicanus* off Punta Baja (24.7%) and Punta Eugenia (18.9%), and *D. laternatus* (20.9%) off San Ignacio (Table 1). *Vinciguerria lucetia*, *D. laternatus*, and *T. mexicanus* larvae were widespread along the peninsula, with relatively higher abundances during El Niño (September 1997 to July 1998) (Fig. 3). Under post-El Niño conditions, *V. lucetia* larvae were largely confined to the Punta Eugenia area and offshore waters during winter and spring cruises, with increases and wider distribution, principally in oceanic waters, during summer and autumn cruises (Figs 3 and 4). *Diogenichthys laternatus* declined in abundance and occurred mostly in southern areas during La Niña. *Triphoturus mexicanus* larvae were widely distributed but densities remained relatively low except for an increase in July 2000. All three species had coastal–offshore abundance gradients, with higher densities mainly in oceanic waters, whereas distributions during El Niño were closer to the coast, as occurred during summer and autumn, specifically off Punta Baja and Punta Eugenia (Figs 3 and 4).

**Table 1.** Taxonomic composition, faunal association, proportion of larval occurrence and abundance (O%, A%) off Ensenada, Punta Baja, Punta Eugenia, and San Ignacio areas and the percentage of positive tows and abundance of the total mesopelagic fish larvae from September 1997 through January 2001.

Species	Distribution	Northern areas				Southern areas				%Positive tows	%Total abundance
		Ensenada		P. Baja		P. Eugenia		S. Ignacio			
		%O	%A	%O	%A	%O	%A	%O	%A		
Derichthyidae											
<i>Derichthys serpentinus</i>	CGL					0.45	0.01			0.118	0.004
Bathylagidae											
<i>Bathylagus pacificus</i>	S-T	1.69	0.21							0.471	0.029
<i>Bathylagus nigrigenys</i>	TR					0.45	0.01			0.118	0.003
<i>Bathylagus wesethi</i>	T-SBTR	<b>36.44</b>	<b>7.35</b>	<b>37.09</b>	<b>2.45</b>	<b>21.08</b>	<b>1.41</b>	<b>24.35</b>	<b>0.74</b>	<b>20.377</b>	<b>2.475</b>
<i>Bathylagus stilbius</i>	T	13.14	4.43	12.36	1.81	10.76	2.12	18.26	0.98	12.956	1.255
<i>Lipolagus ochotensis</i>	S-T	10.59	1.73	6.18	0.20	1.35	0.05			5.300	0.325
Microstomatidae											
<i>Nansenia candida</i>	S-T	0.85	0.01	0.36	0.01	0.90	0.02	2.61	0.07	0.942	0.014
<i>Nansenia crassa</i>	SBTR			2.18	0.07	1.79	0.03	3.48	0.09	1.649	0.053
<i>Nansenia pelagica</i>	TR	0.42	0.03	0.36	0.01	0.45	0.01	4.35	0.13	0.942	0.038
<i>Nansenia</i> sp. 1						0.45	0.01			0.118	0.003
<i>Microstoma</i> sp. 1		1.27	0.09			0.90	0.02			0.589	0.019
Gonostomatidae											
<i>Cyclothone acclimdens</i>	WWC	11.86	1.52	22.91	1.33	15.25	0.62	23.48	0.82	17.903	0.894
<i>Cyclothone signata</i>	SBTR-TR	25.00	0.04	28.00	1.47	18.39	1.14	28.70	1.39	24.735	0.870
<i>Cyclothone</i> sp. 1		0.42	0.02							0.118	0.003
<i>Diplophos taenia</i>	WWC			1.09	0.05	0.90	0.03	0.87	0.01	0.707	0.033
Sternoptychidae											
<i>Argyropelecus affinis</i>	SBTR-TR	0.42	0.02							0.118	0.003
<i>Argyropelecus lychnus</i>	T-SBTR	1.27	0.09	1.45	0.06	0.45	0.03	0.87	0.01	1.060	0.044
<i>Argyropelecus sladeni</i>	SBTR-TR	0.42	0.04	0.73	0.03	1.35	0.04			0.707	0.026
<i>Danaphos oculatus</i>	SBRT	0.42	0.04							0.118	0.006
<i>Sternoptyx</i> sp. 1		0.85	0.06	0.36	0.01					0.236	0.013
type 1		0.42	0.03							0.236	0.005
Phosichthyidae											
<i>Ichthyococcus irregularis</i>	SBRT	3.39	0.22	11.27	0.28	6.28	0.16	12.17	0.25	7.892	0.233
<i>Vinciguerria lucetia</i>	SBRT-TR	<b>56.78</b>	<b>56.58</b>	<b>67.27</b>	<b>46.84</b>	<b>72.20</b>	<b>52.74</b>	<b>84.35</b>	<b>52.12</b>	<b>27.208</b>	<b>50.960</b>
Stomiidae											
<i>Astronesthes</i> sp. 1		0.42	0.02	0.36	0.01	0.45	0.01			0.353	0.010
<i>Bathophilus filifer</i>	SBRT-TR	0.42	0.02							0.118	0.003
<i>Idiacanthus antrostomus</i>	SBTR-TR	5.08	0.34	2.55	0.11			0.87	0.02	2.356	0.056
<i>Stomias atriventer</i>	SBTR-TR	18.22	2.31	14.55	0.90	11.66	0.59	2.61	0.73	5.536	0.674
Scopelarchidae											
<i>Rosenblattichthys volucris</i>	SBRT-TR	1.27	0.07	1.45	0.06	0.90	0.02	0.87	0.03	0.707	0.043
<i>Scopelarchoides nicholsi</i>	SBTR-TR	0.42	0.04	0.36	0.01			0.00	0.00	0.824	0.009
<i>Scopelarchus analis</i>	WWC	0.42	0.03	1.09	0.04			0.87	0.04	0.353	0.014
<i>Scopelarchus guentheri</i>	WWC	2.97	0.27	5.82	0.24	8.52	0.20	2.61	0.06	1.531	0.197
Paralepididae											
<i>Arctozenus risso</i>	S-T	0.85	0.06	2.55	0.07					1.060	0.011
<i>Lestidiops pacificum</i>	SBRT-TR	2.54	0.15	1.82	0.09	2.24	0.09			1.885	0.079
<i>Lestidiops neles</i>	SBTR	3.39	0.27	1.82	0.09			0.87	0.02	1.649	0.074
<i>Lestidiops ringens</i>	S-T	1.27	1.06	11.27	0.37	3.14	0.15	0.87	0.01	4.947	0.328
<i>Stemonosudis macrura</i>	SBRT-TR	0.85	0.04	0.36	0.01	1.35	0.02	1.74	0.03	1.178	0.017
Evermannellidae											
<i>Evermannella ahlstromi</i>	SBTR-TR					1.79	0.08	0.87	0.01	0.589	0.025



Table 1. (Continued)

Species	Distribution	Northern areas				Southern areas				%Positive tows	%Total abundance
		Ensenada		P. Baja		P. Eugenia		S. Ignacio			
		%O	%A	%O	%A	%O	%A	%O	%A		
Myctrophidae											
<i>Bolinichthys longipes</i>	SBTR-TR					0.45	0.01			0.118	0.004
<i>Ceratoscopelus townsendi</i>	WWC	<b>18.64</b>	<b>0.44</b>	<b>23.64</b>	<b>3.72</b>	<b>13.00</b>	<b>0.68</b>	<b>13.04</b>	<b>0.50</b>	<b>18.021</b>	<b>1.542</b>
<i>Diaphus pacificus</i>	SBTR-TR	1.69	0.17	0.36	0.01	0.45	0.01			0.707	0.031
<i>Diaphus theta</i>	T	5.51	0.80			0.45	0.02			1.649	0.114
<i>Diogenichthys atlanticus</i>	WWC	<b>25.85</b>	<b>3.72</b>	<b>27.64</b>	<b>1.51</b>	<b>5.38</b>	<b>0.26</b>	<b>4.35</b>	<b>0.26</b>	<b>18.139</b>	<b>1.200</b>
<i>Gonichthys tenuiculus</i>	TR	2.97	0.68	12.00	0.39	17.94	0.74	2.61	1.05	5.536	0.472
<i>Hygophum atratum</i>	TR	5.08	0.58	7.27	0.54	17.04	0.62	23.48	1.68	9.305	0.317
<i>Hygophum reinhardtii</i>	T-SBRT	5.08	0.35	6.91	0.40	4.48	0.27	6.09	0.14	4.594	0.302
<i>Lampadena urophaos</i> <i>urophaos</i>	T-SBRT	2.54	0.16	6.18	0.30	6.73	0.37	7.83	0.18	5.536	0.279
<i>Lampanyctus parvicauda</i>	TR	0.85	0.12	1.09	0.04	5.38	0.15	6.96	0.22	2.945	0.108
<i>Lampanyctus steinbecki</i>	SBTR-TR	0.42	0.03							0.118	0.004
<i>Loweina rara</i>	SBRT-TR	1.27	0.18	2.18	0.06	4.48	0.15	6.09	0.16	2.002	0.124
<i>Myctophum nitidulum</i>	SBTR-TR	6.78	0.70	10.91	0.26	6.73	0.24	1.74	0.04	4.240	0.210
<i>Nannobranchium bristori</i>	SBTR-TR	2.54	0.16	1.09	0.02	0.45	0.01			1.178	0.032
<i>Nannobranchium idostigma</i>	TR	2.97	0.02	7.27	0.21	13.45	0.51	33.04	1.85	5.889	0.537
<i>Nannobranchium regale</i>	S-T	1.27	0.11	1.45	0.07	0.90	0.03			1.060	0.026
<i>Nannobranchium ritteri</i>	S-T	<b>31.36</b>	<b>3.87</b>	<b>25.09</b>	<b>1.45</b>	<b>7.62</b>	<b>0.19</b>	<b>5.22</b>	<b>0.07</b>	<b>19.552</b>	<b>1.140</b>
<i>Nannobranchium</i> sp. 1		0.42	0.06	0.36	0.01	0.45	0.02			0.353	0.017
<i>Notolychnus valdiviae</i>	SBTR-TR	0.42	0.04	2.55	0.05	1.35	0.04			1.296	0.036
<i>Notoscopelus resplendens</i>	WWC	5.08	0.36	12.00	0.74	9.42	0.39	13.04	0.53	9.541	0.542
<i>Parvilux ingens</i>	T-SBRT	0.85	0.12	2.18	0.05	0.45	0.01			1.060	0.039
<i>Protomyctophum crockeri</i>	T	30.08	0.39	26.55	1.29	19.28	0.77	20.00	0.92	11.779	0.940
<i>Stenobrachius leucopsarus</i>	S-T	3.81	0.74	0.36	0.01					1.531	0.107
<i>Symbolophorus californiensis</i>	T	30.08	0.56	23.27	1.56	4.93	0.20	0.87	0.02	12.014	0.715
<i>Symbolophorus evermanni</i>	SBTR-TR	2.54	0.03	1.09	0.03					9.541	0.016
<i>Tarletonbeania crenularis</i>	S-T	6.78	0.09	1.82	0.05	0.45	0.02	1.74	0.05	2.473	0.044
<i>Tarletonbeania</i> sp. 1								0.87	0.02	0.824	0.004
<i>Triphoturus mexicanus</i>	SBTR	<b>58.05</b>	<b>3.73</b>	<b>53.82</b>	<b>24.70</b>	<b>66.82</b>	<b>18.87</b>	<b>58.26</b>	<b>12.60</b>	<b>25.559</b>	<b>4.584</b>
<i>Triphoturus nigrescens</i>	SBTR-TR							0.87	0.03	0.118	0.006
Oneirodidae											
<i>Dolopichthys</i> sp. 1				0.36	0.01					0.118	0.003
<i>Oneirodes</i> sp. 1		0.85	0.04	0.73	0.03	0.45	0.01			0.589	0.018
Ceratiidae											
<i>Cerantias holboelli</i>	CGL					0.45	0.01			0.118	0.002
Bythitidae											
<i>Cataetyx rubrirostris</i>	SBTR			0.36	0.01					0.118	0.003
Melanocetidae											
<i>Melanocetus johnsoni</i>	T-TR			0.73	0.02	0.45	0.02			0.353	0.011
Gigantactinidae											
<i>Gigantactis</i> sp. 1				0.73	0.03					0.236	0.012
Melamphaidae											
<i>Melamphaes lugubris</i>	S-T	17.37	1.58	20.36	0.66	14.35	0.57	13.04	0.30	16.961	0.688
<i>Melamphaes parvus</i>	T			0.36	0.01					0.118	0.004
<i>Melamphaes</i> sp. 1		1.27	0.16	0.36	0.01	0.45	0.02			0.589	0.031
<i>Poromitra crassiceps</i>	CGL	1.69	0.12	2.18	0.07			1.74	0.04	0.942	0.050
<i>Scopelogadus mizolepis</i> <i>bispinosus</i>	SBRT-TR			1.82	0.06	0.45	0.01	0.87	0.02	0.118	0.029
<i>Scopeloberyx robustus</i>	CGL	0.42	0.02							4.240	0.003

Table 1. (Continued)

Species	Distribution	Northern areas				Southern areas				%Positive tows	%Total abundance
		Ensenada		P. Baja		P. Eugenia		S. Ignacio			
		%O	%A	%O	%A	%O	%A	%O	%A		
Chiasmodontidae											
<i>Chiasmodon subniger</i>	SBTR–TR	5.51	0.34	12.73	0.51	12.11	0.34	20.87	0.74	11.661	0.317
Caristiidae											
<i>Paracaristius maderensis</i>	SBRT–TR	0.85	0.01	0.73	0.04	1.35	0.04	0.87	0.01	0.942	0.029
Howelliidae											
<i>Howella</i> sp. 1				0.36	0.01					0.118	0.004
Tetragonuridae											
<i>Tetragonurus cuvieri</i>	S–T	8.90	1.00	4.00	0.22	0.90	0.02	1.74	0.03	2.709	0.227
Regional and total abundance		21 199	56 838			44 031		31 562		153 631	
Stations occupied and totals		236	275			223		115			849

Faunal association: S, subarctic; T, transitional; SBTR, subtropical; TR, tropical; CGL, circunglobal; WWC, cosmopolite warm waters.

Bold face: Common and abundant species.

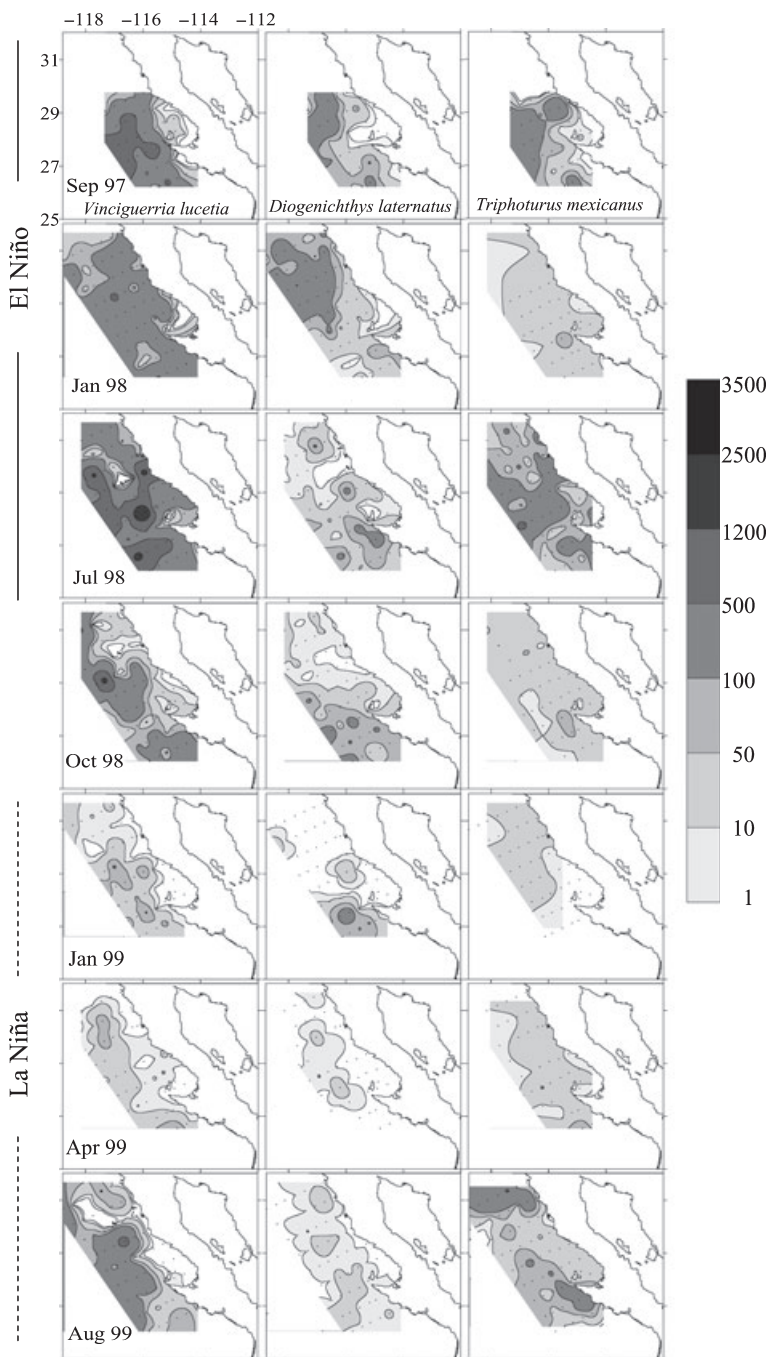
Mean abundances of *V. lucetia* and *T. mexicanus* varied seasonally and annually along the west coast of the Baja California Peninsula (Fig. 5). Both increased in abundance during summer periods from San Ignacio to Punta Baja, especially *V. lucetia*, which peaked during El Niño (280–500 larvae under 10 m<sup>2</sup>), except in the Ensenada area. Both species became scarce with the shift to La Niña conditions (October 1998 through April 2000). These warm-water species increased after La Niña (July 2000) in the Punta Baja and Punta Eugenia areas. *Diogenichthys laternatus* larval abundance was comparatively low in the two northern areas, with slight increases during El Niño and very low counts during La Niña, except in the San Ignacio and Punta Eugenia areas. Temperate species declined in abundance southward during El Niño (*Nannobranchium ritteri*, *B. wesethi*) but were extensive and present in all areas after El Niño. *Symbolophorus californiensis* also diminished during El Niño in the northern areas; however, this species was relatively rare in the Punta Eugenia area and was largely absent from the San Ignacio area (Fig. 6).

Correlations between abundances and temperature at 100 m depth allowed a more detailed description between northern and southern areas. Warm-water species were significantly correlated with temperature from Ensenada to Punta Eugenia (*D. laternatus*, *Gonichthys tenuiculus*, *H. atratum*, *V. lucetia*, *Cyclothone acclinidens*, *Stomias atriventer*). In contrast, the temperate-water species [*Bathylagus stilbius* (synonym

of *Leuroglossus stilbius*), *Protomyctophum crockeri*, *S. californiensis*] were not significantly correlated with temperature in the southern areas, suggesting a possible hydrographic boundary off Punta Eugenia (Fig. 7).

The diversity index principally increased during spring to ~1.5 and decreased during summer and autumn (~1.0) between the Ensenada and Punta Baja areas, definitively influenced by increased abundance of species identified as the most important (usually *V. lucetia*, *D. laternatus*, *T. mexicanus*). During El Niño, increased diversity was associated with more species of tropical affinity spreading to the northern areas (Ensenada, January 1998; Punta Baja, September 1997 and January 1998). Significant differences in diversity in the ENSO period were observed principally in the Ensenada area (ANOVA,  $P < 0.05$ ). Diversity was relatively low in the southern areas, increasing (~1.5) at the beginning of La Niña (January to April 1999) but remaining low until January 2001. The southernmost area did not show striking patterns for any of the indices, except during April 1999 (Fig. 8).

Cluster and ordination analysis of densities showed three groups of spatial–seasonal assemblages separated by ~25% similarity (Fig. 9, Table 2). Group 1 was designated ‘Summer–Autumn’ and mostly includes surveys conducted from Ensenada to Punta Baja, between summer and autumn in different years (1997–2000). Group 2 was designated ‘Winter–Spring’ from



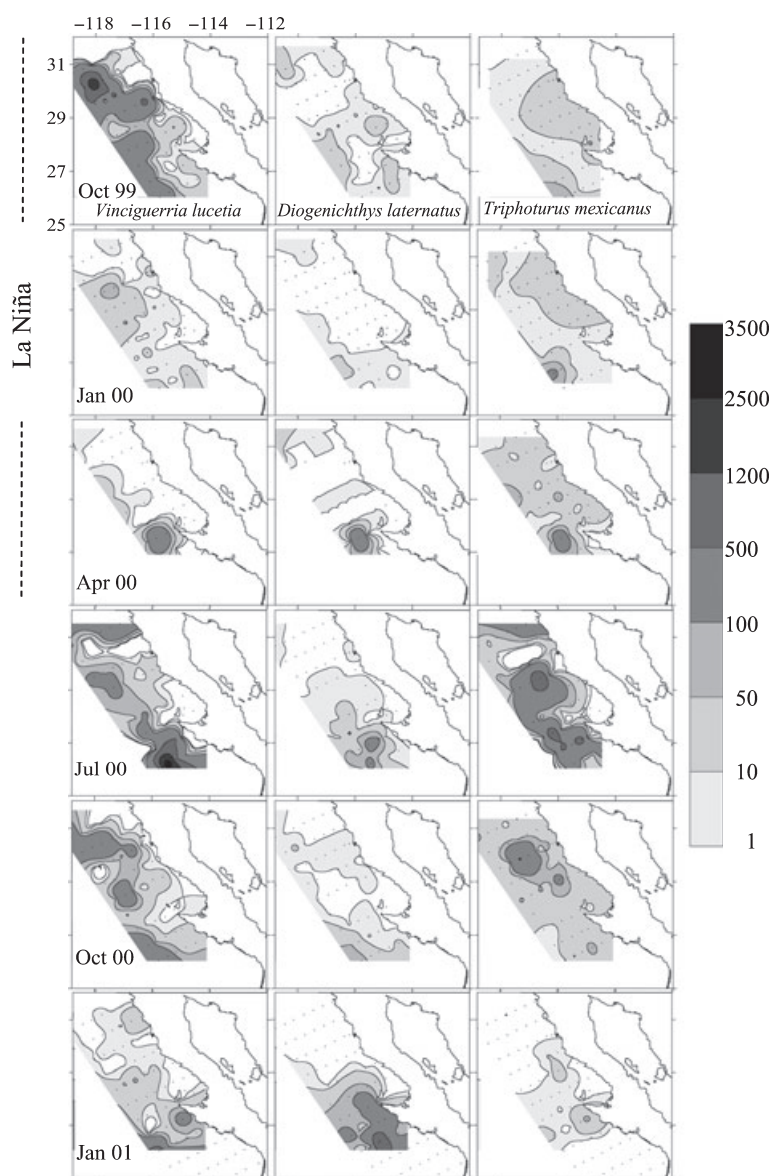
**Figure 3.** Distribution of the most frequent and abundant mesopelagic fish larvae (*Vinciguerria lucetia*, *Diogenichthys laternatus*, *Triphoturus mexicanus*) abundance (per 10 m<sup>2</sup>) off the west coast of the Baja California Peninsula, September 1997 through August 1999.

surveys conducted during winter and spring in the same area. This group was associated with cold environmental conditions during La Niña (1999–2000). Group 3, designated ‘Autumn–Winter’, was principally found in the southern areas, from Punta Eugenia to San Ignacio, during surveys conducted mainly in autumn and winter (1997–2001). *Vinciguerria lucetia* and *T. mexicanus* were the principal constituents of the Summer–Autumn and Winter–

Spring groups, accounting for about 75 and 47% of the abundance, respectively, whereas *V. lucetia* and *D. laternatus* accounted for ~79% of the Autumn–Winter group.

Two major groups of taxa were separated in the species dendrogram by ~25% similarity (Fig. 10, Table 2). Group A (20 taxa) was composed mainly of species of subtropical–tropical affinity, including a few taxa of subarctic–transitional affinity. Subtropical–





**Figure 4.** Distribution of the most frequent and abundant mesopelagic fish larvae (*Vinciguerria lucetia*, *Diogenichthys laternatus*, *Triphoturus mexicanus*) abundance (per 10 m<sup>2</sup>) off the west coast of the Baja California Peninsula, October 1999 through January 2001.

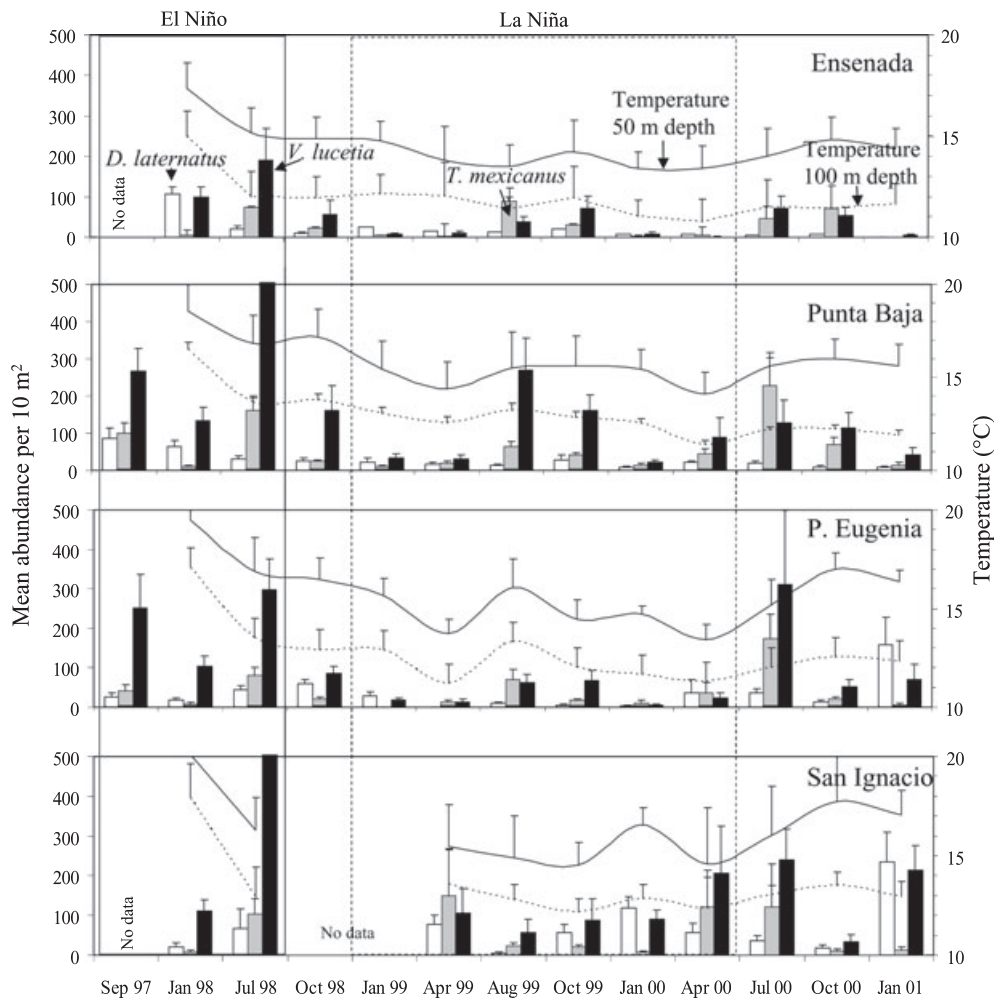
tropical species peaked in abundance in the Summer–Autumn group and taxa with subarctic–transitional affinity of group A peaked in abundance in the Winter–Spring group (Table 2).

The second group split (at ~35% similarity) into subgroups B and C. Species from subgroup B (14 taxa) are principally subarctic–transitional and cosmopolitan warm-water taxa, and principally occur in the Summer–Autumn group, including three taxa of subtropical–tropical affinities. Other subarctic–transitional taxa belonging to subgroup B peaked in the Winter–Spring group (Fig. 10, Table 2). Species from subgroup C (13 taxa) are mainly warm-water species with maximum abundance in the Summer–Autumn

group. Other subgroup C taxa of tropical affinity were associated with the Autumn–Winter group in the two southern areas (*G. tenuiculus*, *H. atratum*, *N. idostigma*, *Lowenia rara*, and *L. parvicauda*) (Fig. 10, Table 2).

Canonical correspondence analysis with sites and environmental variables indicated that Autumn–Winter (group 3) is largely related to warmer temperatures and higher salinities (Fig. 9b), indicating the influence of subtropical waters in the southern areas. The relative positions with respect to temperature and salinity vectors of the Summer–Autumn and Winter–Spring (Groups 1 and 2) indicate their relationship with the cooler and fresher California Current water

**Figure 5.** Mean abundance and SD (larvae per 10 m<sup>2</sup>) of some mesopelagic fish larvae of warm waters (*Vinciguerria lucetia*, *Diogenichthys laternatus*, *Triphoturus mexicanus*) and temperatures at 50 and 100 m depth off the Ensenada, Punta Baja, Punta Eugenia and San Ignacio areas of the Baja California Peninsula, 1997–2001 (ANOVA,  $P > 0.05$ ).



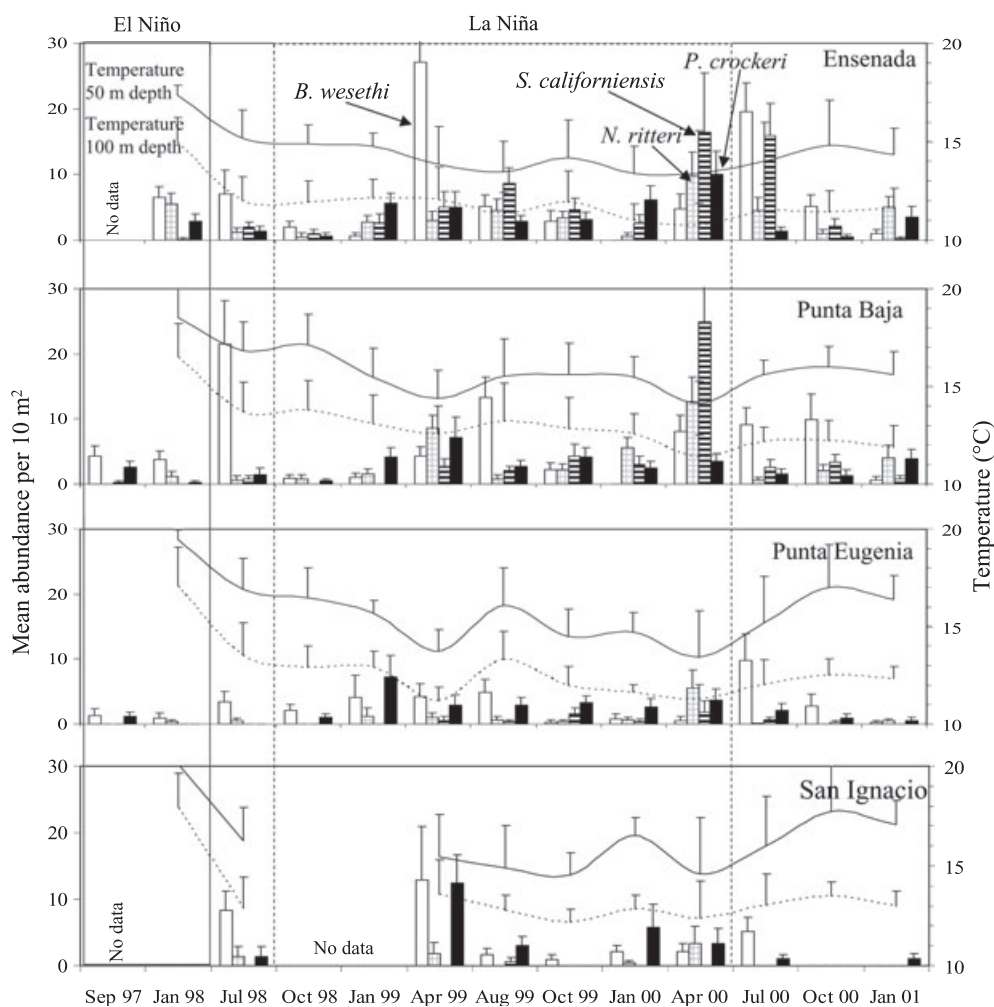
advected along the west coast of Baja California in the different regions (survey areas). Species, distribution, and environmental variables also showed segregation of the groups of taxa (Fig. 10b). The analysis indicates that warm-water species from subgroup C were positively associated with temperature and salinity, as were some common warm-water species from subgroup B (*V. lucetia*, *D. laternatus*, *T. mexicanus*, *C. signata*). Axis 1 eigenvalues were significant ( $P = 0.001$ ) and explained 13.9% of the total variance (Table 3) between species and variables along the survey areas on the west coast of Baja California.

## DISCUSSION

The 1997–2001 period was particularly dynamic, with positive signals in the Multivariate ENSO In-

dex peaking from June 1997 through May 1998, followed by a rapid decline and significant negative values from November 1998 through March 2000. During El Niño 1997–1998, reduced mesoscale activity of the California Current and high subsurface temperature and salinity were well documented during the peak in October 1997 and January 1998, including the strong poleward flow within the survey region (Durazo and Baumgartner, 2002). The poleward subsurface California Undercurrent is common throughout the year (Lynn and Simpson, 1987; Kessler, 2006), but the surface and near-surface poleward flows during El Niño were interpreted as a surfacing of the California Undercurrent to favor the development of the poleward countercurrents (Durazo and Baumgartner, 2002). This was supported by high salinity at 50 and 100 m depth

**Figure 6.** Mean abundance and SD (larvae per 10 m<sup>2</sup>) of some mesopelagic fish larvae of temperate waters (*Bathylagus wesethi*, *Symbolophorus californiensis*, *Nannobranchium ritteri*, *Protomyctophum crockeri*) and temperatures at 50 and 100 m depth off the Ensenada, Punta Baja, Punta Eugenia, and San Ignacio areas of the Baja California Peninsula, 1997–2001 (ANOVA,  $P > 0.05$ ).



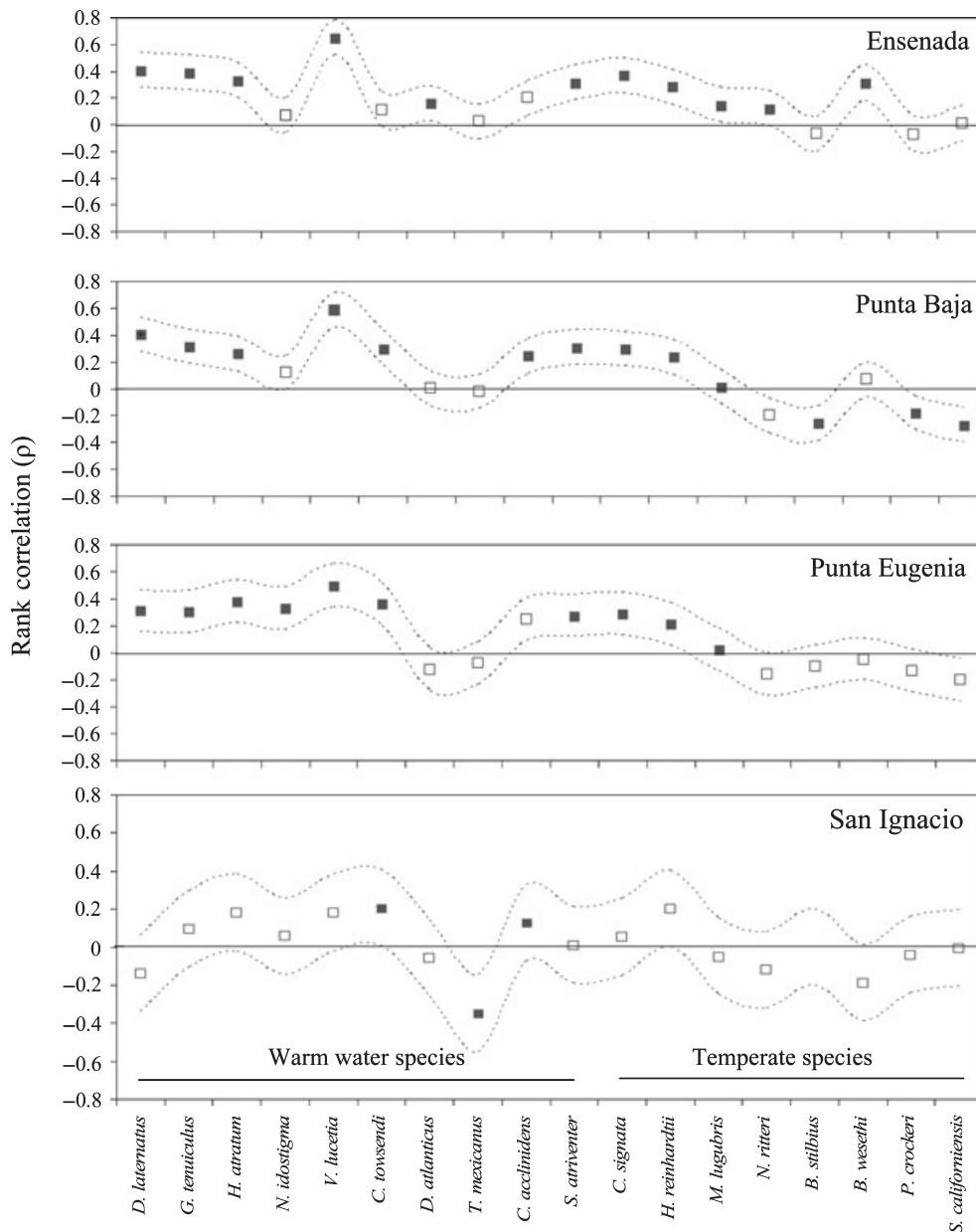
(>33.8) as far north as Ensenada during the peak of El Niño.

Although mesopelagic fauna may be distributed as a continuum, local shifts in diversity and abundance are almost certainly a result of mixing of water masses from different areas with their associated fauna. Northward or southward expansions of fish larvae result from displacement of adults beyond their normal spawning area or advection of eggs or larvae by anomalous or episodic currents (Bailey and Incze, 1985). Species that are characteristic of tropical waters increased and were widely distributed along the peninsula during the peak of El Niño (*V. lucetia*, *D. laternatus*, *T. mexicanus*) as far north as Ensenada and Punta Baja. Nevertheless, *V. lucetia* and *T. mexicanus* were widely distributed along the peninsula (common, including La Niña), at

least during summer and fall. All three species ranged well north of the Ensenada area, to at least southern California (and to the north of Point Conception for *V. lucetia* and *T. mexicanus*) in 1998 (Ambrose *et al.*, 2002a), but not in 1999 (*D. laternatus*), or in much lower numbers and not as far north in 1999 (*V. lucetia* and *T. mexicanus*) (Ambrose *et al.*, 2002b).

Dominance related to high abundances and broad distribution of some tropical species (principally, *V. lucetia*) increased at all latitudes and affected diversity. Conversely, temperate species decreased in abundance (*N. ritteri*, *B. wesethi*, *P. crockeri*), but were extensive and present in all areas after El Niño, or were not found (*S. californiensis*) in the southern areas. The apparent reorganization of the ecosystem and its associated species during La Niña were similar to

**Figure 7.** Rank correlations (Spearman's  $P$ ) between mesopelagic larval abundance (per  $10\text{ m}^2$ ) and temperature at 100 m depth off Ensenada, Punta Baja, Punta Eugenia, and San Ignacio areas of the Baja California Peninsula, 1997–2001. Dashed lines indicate approximate critical values for  $P$  (95% confidence) based on the Fisher  $z$  transformation (Zar, 1996). Black squares are statistically significant and open squares non-significant.

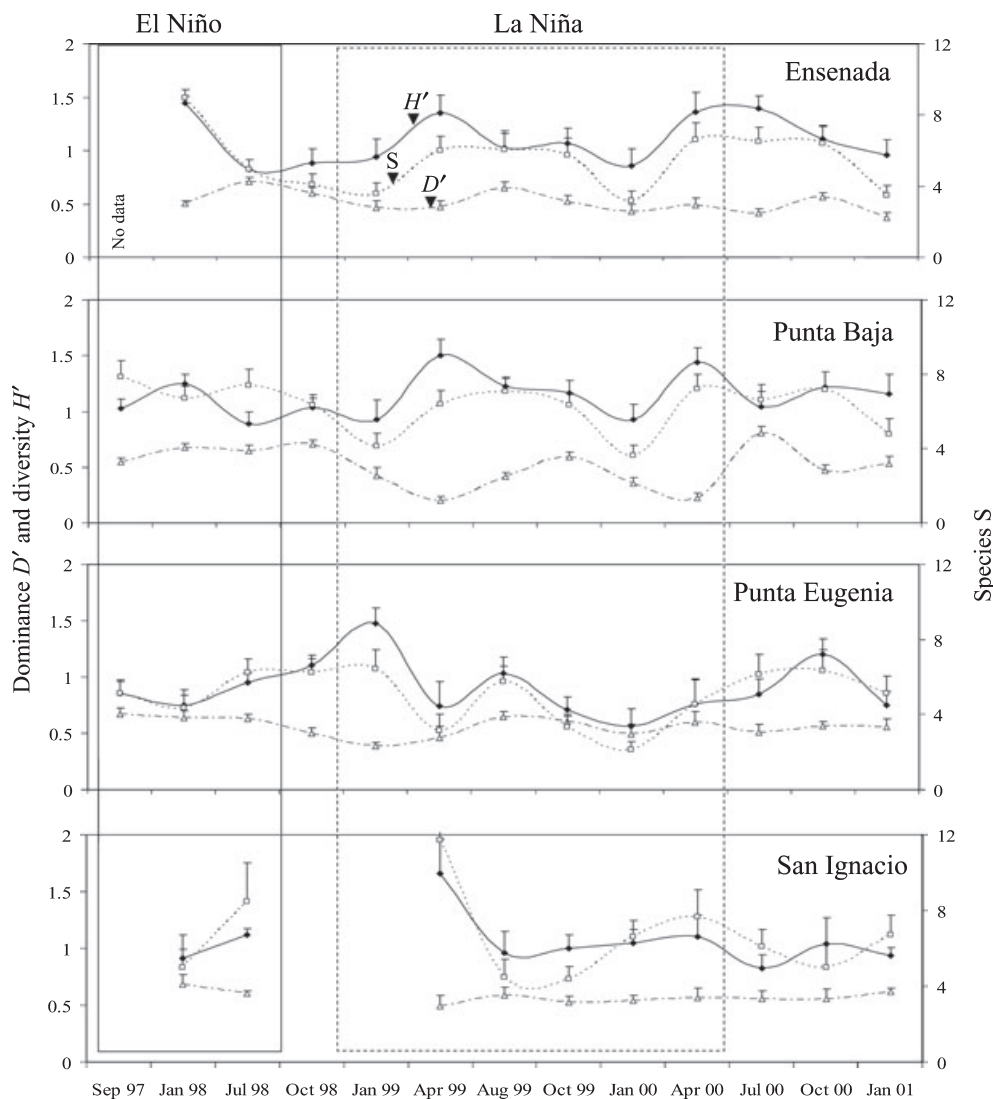


typical seasonal fluctuations in diversity and dominance. In the southernmost area of San Ignacio, variations in seasonal dominance and diversity were not marked, as expected with year-around dominance of tropical species.

During El Niño, a northern presence of tropical coastal pelagic species and oceanic taxa around Punta Eugenia (*Opisthonema* sp., *Etrumeus teres*, *Chloros-*

*combrus orqueta*, *D. laternatus*) was notable (Jiménez-Rosenberg *et al.*, 2007). Larvae of mesopelagic temperate fish species declined along the peninsula, especially in the southernmost area. During El Niño, *V. lucetia*, an abundant eastern tropical Pacific mesopelagic fish which ranges northward to Ensenada, expanded north of Point Conception, California (34.5°N). Tropical species (*D. laternatus*, *H. atratum*,

**Figure 8.** Temporal changes in the assemblage structure of mesopelagic fish larvae: diversity ( $H'$ ); dominance ( $D'$ ); number of species ( $S$ ) of the Ensenada, Punta Baja, Punta Eugenia and San Ignacio areas of the Baja California Peninsula, 1997–2001.



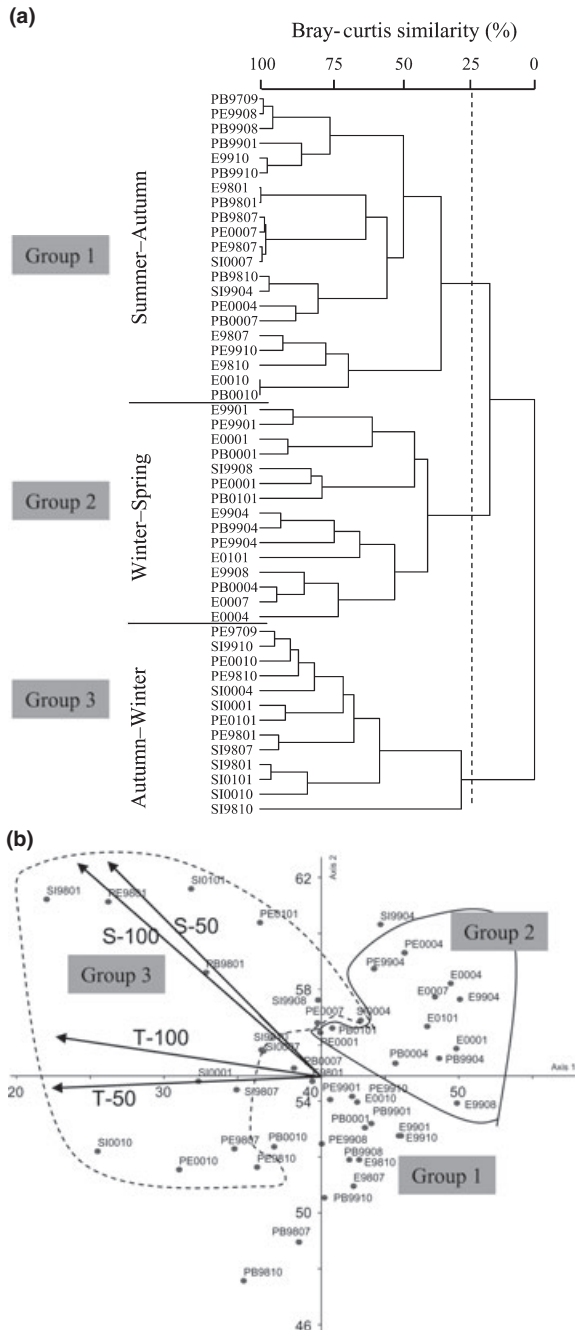
*G. tenuiculus*) also spread to the northern area of the Baja California Peninsula (Moser *et al.*, 1987). Coincident with the strong 1983 El Niño off the southern Baja California Peninsula were shelf and tropical mesopelagic taxa, primarily *Benthosema panamense*, which is commonly captured at the southern end of the peninsula, as well as greater numbers of other mesopelagic tropical species (Funes-Rodríguez *et al.*, 2002, 2006).

Dynamic heights and positive anomalies of temperature not related to El Niño during summer and autumn suggest that warmer waters were carried onshore from the outer margin of the California Current and penetrated eastward around Isla Gua-

dalupe and often formed a large meander in the equatorward flow (Soto-Mardones *et al.*, 2004). These observations explain the eventual increase of temperature around Punta Baja; in the southern regions, this mesoscale mechanism would account for onshore transport of mesopelagic fish larvae. In spring, the circulation is more homogeneous, with no distinctive eddy formation (Soto-Mardones *et al.*, 2004). However, during El Niño, mesopelagic fish larvae were widespread, including at stations close to the coastal shelf, specifically off Punta Baja and Punta Eugenia (September 1997 to July 1998). This was probably related to recirculation associated with westerly and poleward winds that produced anoma-



**Figure 9.** (a) Dendrogram of the clustering of the three spatial–seasonal groups (mode Q), based on the summed abundance of each taxa in each survey area (47 taxa and 49 survey areas) and (b) CCA ordination diagram using the same similarity matrix for 1997–2001. Temperatures and salinities at 50 and 100 m depth: T-50, T-100 and S-50 and S100 (arrows). Clusters 1, 2, and 3 from the dendrogram are indicated in the ordination. E (Ensenada); PB (Punta Baja); PE (Punta Eugenia); SI (San Ignacio).



lous horizontal convergence in surface Ekman transport (Durazo and Baumgartner, 2002; Schwing *et al.*, 2002).

The transition to La Niña in July 1998 and its firm establishment by October 1998 was indicated by the presence of a predominant southward flow, and the presence of high temperature and salinity water only south of Punta Eugenia (Durazo and Baumgartner, 2002). Pacific subarctic water enters the California Current system with low temperature and salinity from the surface to 100 m depth off California (Lynn and Simpson, 1987). Stronger southward flow of the California Current occurs in the first half of the year (Lynn and Simpson, 1987; Kessler, 2006), with more homogeneous flow during spring off the Baja California Peninsula (Soto-Mardones *et al.*, 2004). A reduced core of subarctic water (<21°C and salinity <34) occurs as far south as the tip of the peninsula, implying that the width of the California Current near the surface progressively narrows until it reaches the southern tip of the peninsula, as a result of mixing with warmer and more saline waters along its southerly path (Reid *et al.*, 1958; Durazo and Baumgartner, 2002).

During the ENSO shifts of 1997–2001, widespread and notable changes of larval mesopelagic fishes occurred between the northern and southern offshore areas of the west coast of the Baja California Peninsula. The conjunction of diverse ecological assemblages was particularly pronounced in the northern areas (Ensenada and Punta Baja) in contrast to the southern areas (Punta Eugenia and San Ignacio), where the ichthyoplankton was composed principally of warm-water species. Mesopelagic species occurrences were higher in the Punta Baja area, a result of mixing of taxa of different affinities. During the La Niña period, both abundance and the number of temperate taxa increased rapidly in the two northern areas, but shifted only gradually in the two southern areas. Some temperate species (*B. stilbius*, *P. crockeri*, and *S. californiensis*) were negatively correlated with temperature at 100 m depth off Punta Baja, and reductions in larval abundances of temperate species south of this area suggest a hydrographic boundary. This occurred because most fish larvae, including myctophids, reside in the productive epipelagic zone within 200 m of the surface and their distributions reflect surface water masses (Moser and Smith, 1993; Sassa *et al.*, 2004). During La Niña, warm water masses do not extend north of the tip of Punta Eugenia (Durazo

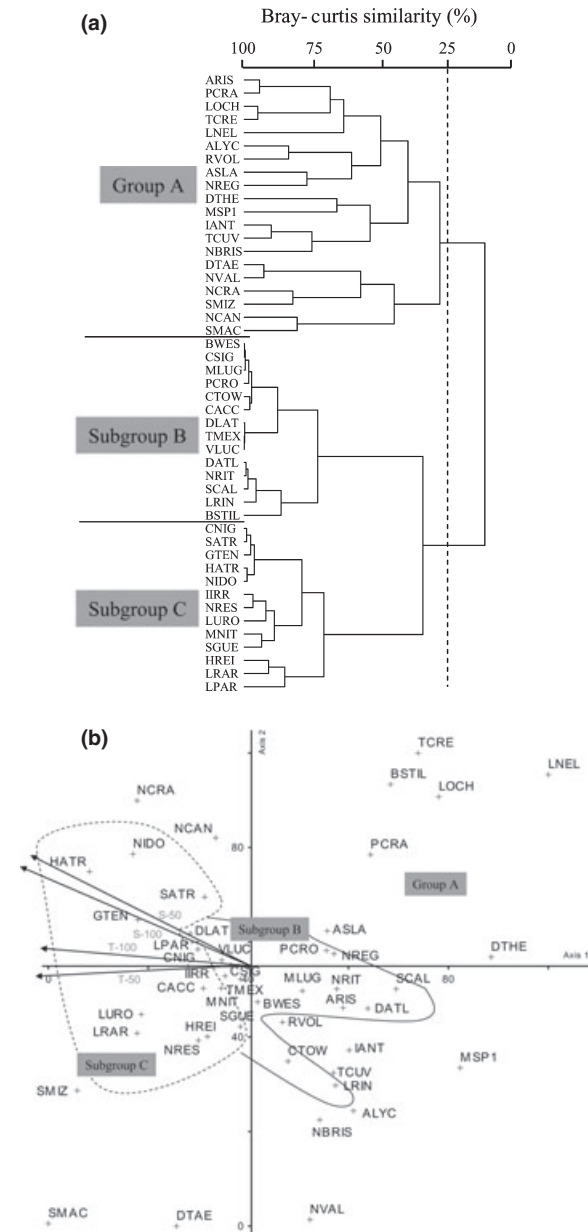
**Table 2.** Species and survey-area groups derived from classification diagrams (modes R and Q) off the west coast of Baja California Peninsula, 1997–2001. Abundances per 10 m<sup>2</sup>.

	Species	Species code	Distribution	Spawning season/peak month abundance	Summer–Autumn Group 1 Abundance	Winter–Spring Group 2 Abundance	Autumn–Winter Group 3 Abundance	
Group A	ARIS	<i>Arctozenus risso</i>	S–T	Y-R	<b>29</b>	24		
	PCRA	<i>Poromitra crassiceps</i>	CGL	Y-R; Spr–Sum	27	<b>45</b>	5	
	LOCH	<i>Lipolagus ochotensis</i>	S–T	Win–Spr/Mar	16	<b>412</b>		
	TCRE	<i>Tarletonbeania crenularis</i>	S–T	Spr–Sum/May–Jul	29	<b>111</b>		
	LNEL	<i>Lestidiops neles</i>	SBTR	Jan and Oct	6	<b>108</b>		
	ALYC	<i>Argyropelecus lychnus</i>	T–SBTR	Y-R/Aut–Spr	<b>50</b>	15	4	
	RVOL	<i>Rosenblattichthys volucris</i>	SBTR–TR	Y-R/Aug–Jan	<b>33</b>	23	9	
	ASLA	<i>Argyropelecus sladeni</i>	SBTR–TR	Y-R; Aut–Spr	22	8	11	
	NREG	<i>Nannobranchium regale</i>	S–T	Y-R; Spr–Sum/Jul	<b>38</b>	37		
	DTHE	<i>Diaphus theta</i>	T	Y-R; Spr–Sum/Jul	11	<b>164</b>		
	MSP1	<i>Microstoma</i> sp. 1			5	<b>17</b>	7	
	IANT	<i>Idiacanthus antrostomus</i>	SBTR–TR	Sum–Aut/Aug–Nov	<b>91</b>	43	7	
	TCUV	<i>Tetragonurus cuvieri</i>	S–T	Y-R; Aut	<b>178</b>	65	6	
	NBRIS	<i>Nannobranchium bristori</i>	SBTR–TR	Y-R; Sum	<b>28</b>	13		
	DTAE	<i>Diplophos taenia</i>	WWC	Y-R/Oct–Nov	<b>41</b>		9	
	NVAL	<i>Notolychnus valdiviae</i>	SBTR–TR	Y-R; Spr–Sum/Aug	<b>24</b>	13	17	
	NCRA	<i>Nansenia crassa</i>	SBTR	Y-R/Jan–Mar	22	26	<b>33</b>	
	SMIZ	<i>Scopelogadus m. bispinosus</i>	SBTR–TR	Y-R/Jul–Nov	<b>35</b>		10	
	NCAN	<i>Nansenia candida</i>	S–T	Y-R/Feb	5	18	<b>25</b>	
	SMAC	<i>Stemonosudis macrura</i>	SBTR–TR	Y-R	15		<b>19</b>	
Subgroup B	BWES	<i>Bathylagus wesethi</i>	T–SBTR	Spr–Sum/May–Aug	<b>1965</b>	562	240	
	CSIG	<i>Cyclothone signata</i>	SBTR–TR	Y-R; Sum–Aut	<b>1581</b>	473	525	
	MLUG	<i>Melamphaes lugubris</i>	S–T	Y-R/Mar–Jun	<b>556</b>	356	144	
	PCRO	<i>Protomyctophum crocked</i>	T	Win–Spr/Mar	772	<b>1164</b>	184	
	CTOW	<i>Ceratoscopelus townsendi</i>	WWC	Y-R; Sum/Aug	<b>2575</b>	414	118	
	CACC	<i>Cyclothone acclinidens</i>	WWC	Sum–Aut	<b>1045</b>	154	318	
	DLAT	<i>Diogenichthys laternatus</i>	SBTR–TR	Y-R/Feb–Apr; Aug	7776	831	<b>9202</b>	
	TMEX	<i>Triphoturus mexicanus</i>	SBTR	Y-R; Spr–Aut/Aug–Sep	<b>25 025</b>	4481	2638	
	VLUC	<i>Vinciguerria lucetia</i>	TR	Y-R; Sum–Aut/Sep–Oct	<b>50 500</b>	5995	18 647	
	DATL	<i>Diogenichthys atlanticus</i>	WWC	Y-R; Spr/Apr	<b>997</b>	777	7	
	NRIT	<i>Nannobranchium ritteri</i>	S–T	Y-R; Win–Spr/May	505	<b>989</b>	24	
	SCAL	<i>Symbolophorus californiensis</i>	T	Y-R; Spr–Sum/Apr–May	420	<b>1726</b>	5	
	LRIN	<i>Lestidiops ringens</i>	S–T	Y-R	<b>318</b>	179	7	
	BSTI	<i>Bathylagus stibius</i>	T	Win–Spr/Jan–Apr	771	<b>1775</b>	129	
	Subgroup C	CNIG	<i>Chiasmodon subniger</i>	SBTR–TR	Y-R/Apr–May; Aug–Sep	<b>393</b>	114	242
		SATR	<i>Stomias atriventer</i>	SBTR–TR	Y-R/Feb; Sep	<b>817</b>	276	339
GTEN		<i>Gonichthys tenuiculus</i>	TR	Win/Feb	455	57	<b>509</b>	
HATR		<i>Hygophum atratum</i>	TR	Y-R/Nov	507	58	<b>668</b>	
NIDO		<i>Nannobranchium idostigma</i>	TR	Y-R	284	105	<b>580</b>	
IIRR		<i>Lchthyococcus irregularis</i>	SBTR	Y-R	<b>232</b>	71	56	
NRES		<i>Notoscopelus resplendens</i>	WWC	Sum–Aut/Aug	<b>757</b>	35	41	
LURO		<i>Lampadena u. urophaos</i>	T–SBTR	Y-R; Sum–Aut/Aug	<b>333</b>	37	58	
MNIT		<i>Myctophum nitidulum</i>	SBTR–TR	Y-R; Sum–Aut/Aug	<b>314</b>	61	38	
SGUE		<i>Scopelarchus guentheri</i>	WWC	Y-R	<b>235</b>	31	36	
HREI		<i>Hygophum reinhardtii</i>	T–SBTR	Y-R; Sum–Aut/Aug; Nov	<b>337</b>	68	59	
LRAR		<i>Loweina rara</i>	SBTR–TR	Y-R/Mar	55	62	<b>74</b>	
LPAR	<i>Lampanyctus parvicauda</i>	TR	Y-R	60	38	<b>84</b>		
Abundance					100 289	22 029	35 135	

Faunal association: S, subarctic; T, transitional; SBTR, subtropical; TR, tropical; WWC, cosmopolite warm waters; CGL, circunglobal; Y-R, year-round.

Bold face: maximum value.

**Figure 10.** (a) Dendrogram of the inverse analysis (mode R) to describe species assemblages based on the summed abundance of each taxa in each survey area (47 taxa and 49 survey areas) and (b) CCA ordination diagram using the same similarity matrix for 1997–2001. Temperatures and salinities at 50 and 100 m depth: T-50 and T-100; S-50 and S-100 (arrows). Clusters A, B, and C from the dendrogram are indicated in the ordination.



and Baumgartner, 2002) and abundances of the most common warm-water species declined at all latitudes (*V. lucetia*, *D. laternatus*, and *T. mexicanus*), except during their summer and autumn spawning period.

**Table 3.** Axis eigenvalues and explained variance (%) from a canonical correspondence analysis using the 47 taxa and 49 survey areas matrix for the period 1997–2001.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.133	0.045	0.028
Explained variance (%)	13.9	4.7	2.9
Accumulated variance (%)	13.9	18.6	21.5
Correlation values			
T-50	-0.892	-0.043	-0.442
S-50	-0.683	0.662	-0.298
T-100	-0.678	0.089	-0.692
S-100	-0.652	0.563	0.333

Local shifts in species assemblages are related to the confluence of oceanic currents and mixing of water masses from different sources with their associated faunas (Moser *et al.*, 1987; Moser and Smith, 1993; Etnoyer *et al.*, 2004; Sassa *et al.*, 2004; Funes-Rodríguez *et al.*, 2002, 2006). Here, mesopelagic fish larvae assemblages were defined mostly by the seasonal variation in the strength of the California Current southward flow along the west coast of the Baja California Peninsula. Winter and spring during La Niña were included in the Winter–Spring assemblage, and summer and autumn during El Niño were included in the Summer–Autumn group. These groups principally occurred from Ensenada to Punta Eugenia. The disparate Autumn–Winter group, composed principally of tropical species, occurred in the southern areas (Punta Eugenia and San Ignacio).

Larval assemblages (Winter–Spring group from Ensenada to Punta Eugenia) showed increases in abundance of subarctic–transitional species during La Niña (*B. stilbius*, *S. californiensis*, *P. crockeri*, *N. ritteri*, *L. ochotensis*, and *Tarletonbeania crenularis*), the same northern complex species of Moser *et al.* (1987), whose highest abundance is in winter and spring (Moser *et al.*, 1987; Moser and Smith, 1993). This suggests that the maximum shift of temperate taxa observed during 1999–2001 was attributable to La Niña.

The equatorward flow of the California Current is primarily well offshore (200 km) during the second half of the year (Lynn and Simpson, 1987), while along the coast, a surface countercurrent occurs as far north as Punta Eugenia (Reid *et al.*, 1958; Lynn and Simpson, 1987; Durazo and Baumgartner, 2002; Soto-Mardones *et al.*, 2004). At this time, dominance of some topical and subtropical species occurs at all latitudes along the Baja California Peninsula. The Summer–Autumn group is composed principally of warm-water taxa, including the more common species

(*V. lucetia*, *T. mexicanus*, *D. laternatus*, *Ceratoscopelus townsendi*, *Cyclothone signata*). All these taxa, including others associated with species group B, were present in the southern complex of Moser *et al.* (1987), although they are clearly associated with different water masses within the CalCOFI area (Moser *et al.*, 1987; Moser and Smith, 1993). Finally, the group in the southern areas of Punta Eugenia and San Ignacio (Autumn–Winter) was composed principally of representatives with more southerly northern limits, distributed principally in the central Baja California and southern Baja California areas (Moser *et al.*, 1987).

Our results support the hypothesis that mesopelagic fish larvae have widespread spatial distributions. Nevertheless, the Winter–Spring and Summer–Autumn assemblages of larval mesopelagic fishes responded to the spatial and temporal differences of the environmental factors (temperature, salinity, and current meandering), indicating that larval distributions are closely related to reproductive periods and the seasonal pattern of the oceanic currents. The most characteristic group occurred in the southern areas and was associated with temperature and salinity. However, along the entire peninsula, differences between El Niño and La Niña were observed principally as changes in diversity and abundance. Species that are characteristic of tropical waters increased and were widely distributed along the peninsula during the peak of El Niño, whereas temperate species decreased in abundance as their distributions contracted northward. The temperate species were extensive and present during La Niña in all four areas along the peninsula. Although the diversity of larval mesopelagic fish remained at similar levels in every survey during El Niño, both the proportion and abundance of tropical species increased remarkably compared to the La Niña period.

## CONCLUSIONS

Assemblage structure of mesopelagic fish larvae in offshore areas along the west coast of the Baja California Peninsula underwent major modifications as the strength of the southerly flow of the California Current changed. Despite wide oceanographic differences during El Niño and La Niña, mesopelagic fish larval assemblages were principally characterized as seasonal differences. This result implies that the high seasonal variability in mesopelagic larval abundance is primarily related to reproductive periods and, secondarily, with the north–south gradient influenced by the seasonal pattern of the California Current. Nevertheless, increased diversity, number of species, and abundance of larvae of some species was notable, particularly the

northward expansion of tropical taxa into the northern areas (Ensenada and Punta Baja) during El Niño, whereas larvae of temperate taxa declined along the peninsula, especially in the southernmost area. Rapid recovery during the following La Niña once again resulted in the seasonal differences in larval community structure related to reproductive periods and the usual coastal patterns of the oceanic currents.

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