COMMUNITY STRUCTURE OF EUPHAUSIIDS IN THE SOUTHERN PART OF THE CALIFORNIA CURRENT DURING OCTOBER 1997 (EL NIÑO) AND OCTOBER 1999 (LA NIÑA)

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ABSTRACT

Zooplankton samples collected during October 1997 (El Niño) and October 1999 (La Niña) were used to study the effects of warm and cold events on the community structure of euphausiids from Punta Abreojos (26.7°N) to Punta Baja (30°N), Baja California, México. A total of 24 species (7 genera) were found. Total abundance was 16% higher during the warm event than during the cold conditions, mainly because of a higher contribution of larvae. The most abundant species in both periods was *Nyctiphanes simplex*. Other species showed low abundance, and their presence is presumed to be attributable to the particular oceanographic conditions associated with El Niño and La Niña. Differences in abundances of life stages indicated more intense reproductive activity in October 1997 or better larval-survival strategy than during the cold period. Species with tropical and equatorial affinity were more abundant in October 1997, whereas species with subarctic and temperate affinity were more abundant during October 1999.

INTRODUCTION

Marine ecosystems of the eastern Pacific are strongly affected by El Niño events (Barber and Chavez 1983; Chavez et al. 2002). The response of planktonic communities differs among taxa. The changes noticed are in biomass, abundance, specific distribution patterns, and recruitment rates of some planktonic larvae phases (Tegner and Dayton 1987; Connolly and Roughgarden 1999). Euphausiids, as with other planktonic invertebrates, are subject to environmental changes. These changes may occur seasonally or on longer temporal scales, such as during warmer and cooler years (Brinton 1960, 1962, 1981; Brodeur 1986; Brinton and Willie 1976; Brinton and Reid 1986; Gómez-Gutiérrez et al. 1995a; Marinovic et al. 2002). In the California Current, interannual events such as El Niño produce changes in the composition and distribution patterns of the euphausiid community, causing shifts in species assemblages and range extensions (Brinton 1960, 1981; Brodeur 1986; Brinton and Willie 1976; Brinton and Reid 1986; Gómez-Gutiérrez et al. 1995a).

The beginning of El Niño 1997–98 was marked by a warming of surface waters in the central tropical Pacific in March 1997. Although of shorter duration, this warming episode was comparable in magnitude to El Niño 1983–84. It is the strongest episode recorded in recent years (Webster and Palmer 1997; McPhaden 1999a,b) and has been referred as "the climate event of the century" (Webster and Palmer 1997; McPhaden 1999a,b). In April–July 1998, there was a dramatic transition from strong El Niño conditions to cool-water conditions in the central and eastern tropical Pacific. By late 1998, anticyclonic wind anomalies in the northeastern Pacific were associated with an intense center of high pressure. These anomalies contributed to stronger-than-usual trade winds in the eastern tropical Pacific that favored strong upwelling and colder-than-normal waters along the coast of the northeastern Pacific characteristic of La Niña conditions. This colder-than-usual state prevailed until early 2001 (Hayward et al. 1999; Schwing et al. 2002).

The California Current System (CCS), as an eastern boundary system, is known to be highly vulnerable to the changes in temperature, salinity, and circulation patterns associated with basinwide events (Simpson 1984; Lynn et al. 1998; Hayward et al. 1999). In the CCS, El Niño 1997–98 was recorded on July 1997 due to an expansion of the coastal countercurrent that transported warmer and saltier waters northward in the upper 100 m depth (Lynn et al. 1998). Off the west coast of Baja California (28°N), conditions were warmer (8.7°C) and saltier (0.8) than normal in the upper 600 m; there was also diminished mesoscale activity in the California Current during October 1997 (Durazo and Baumgartner 2002). Similar dynamics were observed to the north (32°N) (Lynn and Bograd 2002) and south (~20°N) (Filonov and Tereshchenko 2000) of this region, though temperature and salinity anomalies were smaller. The anomalous conditions in Baja California waters are attributable mainly to subtropical surface water fed from the southwest as a narrow, poleward flowing coastal jet. Other effects included a westward displacement of the core of the California Current (Lynn and Bograd 2002),

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as well as a volume expansion of waters originating in the eastern tropical Pacific and forming the California Undercurrent. During late 1998 and 1999, the atmospheric pattern of La Niña in the CCS, particularly along the Baja California coast, caused a decrease in sea level, a rise in the thermocline, an increase of baroclinic instability, increased meandering and mesoscale activity, stronger upwelling, and a strengthening of the equatorward flow of the California Current (Hayward et al. 1999; Bograd et al. 2000; Durazo and Baumgartner 2002).

Within the CCS, most of the euphausiid-related studies have been conducted using data from the CalCOFI seasonal-monitoring program. In Mexican waters of the eastern Pacific, particularly along the Baja California peninsula, several investigations have focused on this group (Gómez-Gutiérrez 1995; Lavaniegos-Espejo 1993, 1994; Gómez-Gutiérrez and Robinson-Mendoza 1997; Gómez-Gutiérrez et al. 1995a, b, 1999). Since 1997, the IMECOCAL program (Investigaciones Mexicanas de la Corriente de California, designed to provide quantitative descriptions of the physical, chemical, and biological processes of the coastal waters in this region) has generated useful information to increase understanding of the pelagic ecosystem of the southern California Current. In this context, this study analyzes zooplankton data from IMECOCAL samples collected off Baja California, México, during two contrasting episodes. The goal of this work is to compare the euphausiid patterns of abundance, composition, and distribution from two major climatic events of the twentieth century, El Niño 1997–98 and La Niña 1999–2001. Comparative studies of the effects of warm and cold events on community structure of euphausiid in the southern part of the CCS are of special importance because in general the structure of zooplankton can be used as an indicator of the ecological state of the pelagic system.

METHODS

Zooplankton samples were collected onboard the research vessel *Francisco de Ulloa* during IMECOCAL cruises 9709/10 and 9910, between Punta Abreojos (26.7°N) and Punta Baja (30°N), Baja California, México, along 39 stations of the CalCOFI program (fig. 1).

Samples were obtained using a bongo net of 500 μm mesh, 61 cm diameter in October 1997 and 71 cm diameter in October 1999. Oblique tows were conducted from 200 m to the surface. Flowmeters were attached to each net entrance. Samples were preserved and stored in 4% formaldehyde in seawater and buffered with sodium borate. In the laboratory, euphausiid species and larval stages (calyptopes, furcilia, juvenile, and adult) were identified. Samples containing high densities of euphausiid ($n > 100$) were subsampled using a Folsom splitter. The number of each species was standardized to 1,000 m^3 of water.

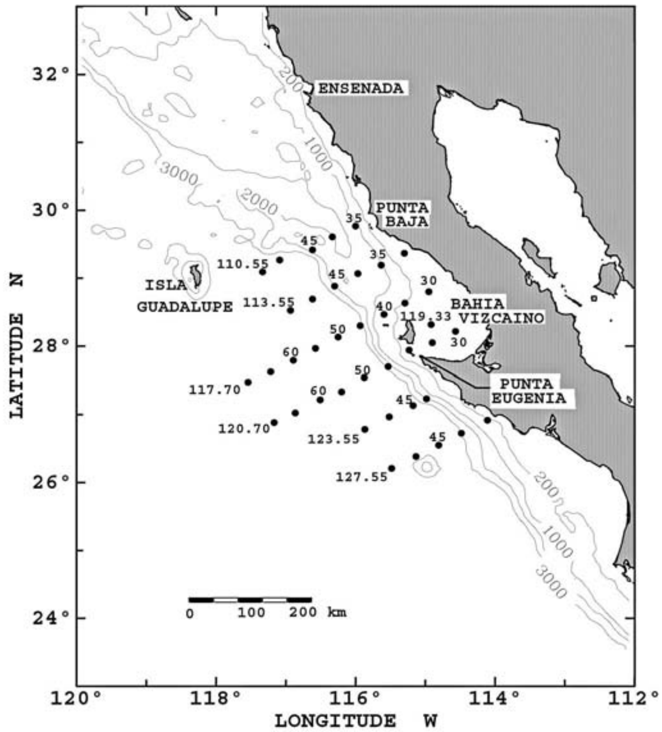

Figure 1. Study area indicating stations (*solid circles*) where zooplankton was sampled during October 1997 and October 1999. The system of numbering lines (110, 113, 117...) and stations (30, 35, 40 ...) follows the CalCOFI practice. Depth contours are given in meters.

Owing to their indistinctly differing morphologies and overlapping occurrences along the warm terminal part of the California Current, larval stages of *Euphausia diomedeae*, *E. eximia*, *E. mutica*, and *E. recurva* were grouped according to the identification key of Brinton (1975). Statistical analysis, particularly nonparametric Mann-Whitney U, were performed to test for significant differences between El Niño and La Niña conditions in total abundances, development stages of euphausiid, biogeographic groups, and the most common and abundant species.

RESULTS

Composition and Abundance

Taxonomic analysis of euphausiids for both periods yielded 24 species belonging to 7 genera. October 1997 samples contained 22 species; October 1999 samples had only 18 species. Table 1 shows the total abundance of each euphausiid species during each period according to its biogeographic affinity (Brinton 1996). The most abundant species during El Niño 1997 was *N. simplex* (83%), followed by *Euphausia eximia* (3%) and *Stylocheiron affine* (2%). The presence of tropical and subtropical species was notable during this period. During La Niña 1999, *N. simplex* was again the most abundant species (67%), while the abundance of *N. difficilis* increased sig-

TABLE 1
Total Abundances of Euphausiid Species Sampled During El Niño (October 1997) and La Niña (October 1999) Conditions (Individuals/1,000 m³), Following Brinton 1996.

Biogeographic group as observed within study area	Species	Period Oct. 1997	Period Oct. 1999
California Current (Baja California)	*Euphausia gibboides*	2,118	4,958
	E. pacifica	0	949
	Nematoscelis difficilis	1,008	34,066
	Nyctiphanes simplex	193,514	111,614
	Thysanoessa gregaria	1,218	5,687
Subtropical Oceanic	*E. eximia*	5,936	364
	E. hemigibba	279	176
	E. mutica	77	8
	E. recurva	1,013	438
	Nematobrachion flexipes	594	116
	N. tenella	290	238
	Stylocheiron longicorne	566	752
	S. maximum	90	85
	Thysanopoda astylata	149	270
	T. monocantha	6	0
	T. obtusifrons	8	87
	T. orientalis	0	7
Eastern Tropical Pacific (ETP)	*E. diomedeae*	396	8
	E. distinguenda	895	0
	E. lamelligera	20	0
	E. tenera	140	0
	N. gracilis	128	0
Subtropical + ETP	*S. affine*	5,663	4,268
	S. carinatum	15	0
	IA group[a]	17,790	3,481
Total		231,910	167,570

[a]Composed of *Euphausia diomedeae*, *E. eximia*, *E. mutica*, and *E. recurva* larvae (Brinton 1975).

nificantly (20%), followed by *Euphausia gibboides* (3%) and *Thysanoessa gregaria* (3%), species typically associated with oceanic waters of the California Current. The IA Group, consisting of species with tropical and subtropical affinity, was more abundant in October 1997 (8%) than in October 1999 (3%). The rest of the species showed low abundance in both periods, their presence in the region being indicative of the anomalous environmental conditions; examples are the warm-water species *Euphausia distinguenda*, *E. lamelligera*, *E. tenera*, *Nematoscelis gracilis*, and *Stylocheiron carinatum* observed only during October 1997; cold-water species, notably *E. pacifica*, were present only during La Niña.

Euphausiid abundances were 16% higher during the El Niño cruise than during the La Niña cruise, owing largely to the higher contribution of larvae—furciliae and calyptopes stages (fig. 2)—although no significant differences were detected between the periods (Mann-Whitney U test, $p = 0.42896$). The furciliae stages represented over half the euphausiid community during the warm-water conditions. There were significant differences in postlarval stages from 1997 to 1999 (Mann-Whitney U test, $p = 0.02198$), and juveniles of cold-water species were more abundant during October 1999 (fig. 2). Indeed, there were significant differences in juvenile abundances between the two periods (Mann-Whitney U test, $p = 0.017497$).

Due to its high abundance, *N. simplex* was excluded, and the developmental stages of the species—larval (calyptopes and furciliae) and postlarval (juveniles and adults)—were similarly grouped according to biogeographic affinity. Significant differences between El Niño and La Niña periods were found (fig. 3; tab. 2). Tropical

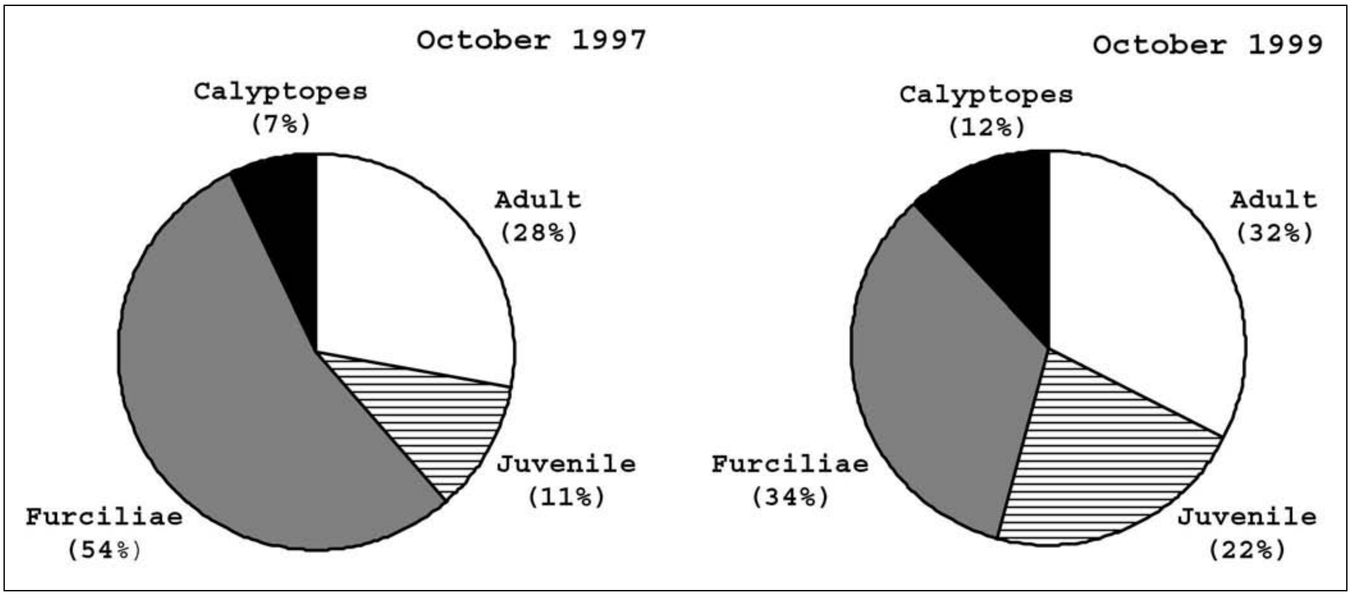

Figure 2. Developmental stages of euphausiids (calyptopes, furciliae, juveniles, and adults) recorded during October 1997 and October 1999.

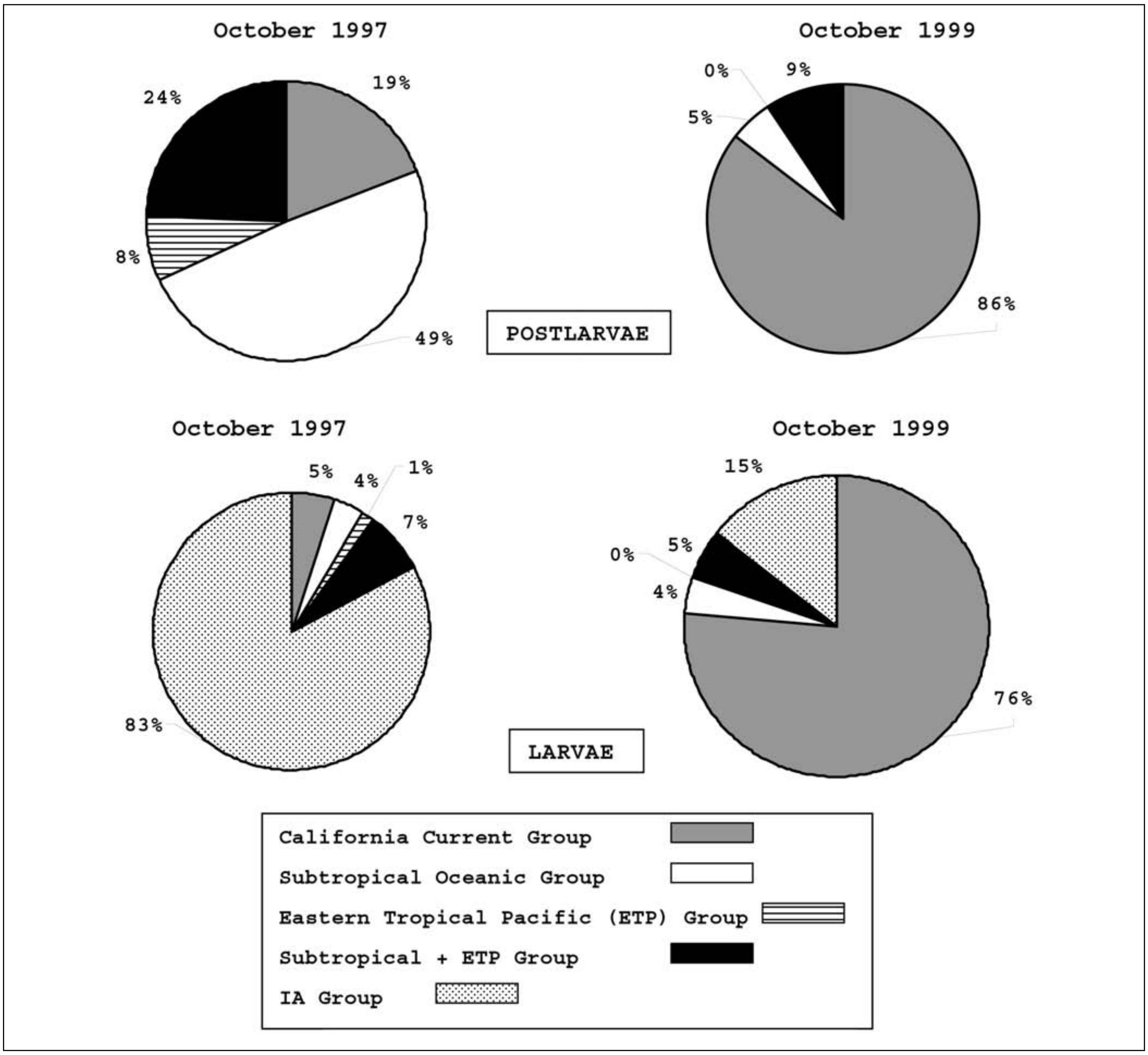

Figure 3. Euphausiids grouped according to biogeographic affinity described by Brinton (1996) during October 1997 and October 1999. Note that percentages exclude *Nyctiphanes simplex* abundance.

TABLE 2
Mann-Whitney U Tests Comparing Total Euphausiid Abundance Between October 1997 and October 1999. Species Grouped According to Their Biogeographic Affinity (Brinton 1996).

Biogeographic Group	Rank Sum Oct. 1997	Rank Sum Oct. 1999	U	*p*-level
California Current[a]	930	1,996	189	**0.0000**
Subtropical Oceanic	1,707	1,219	478	**0.0108**
Eastern Tropical Pacific (ETP)	2,005	922	181	**0.0000**
Subtropical +ETP	1,592	1,334	593	0.1830
IA group[b]	1,927	999	258	**0.0000**

Note: Boldface indicates significant tests ($p < 0.05$).
[a] *N. simplex* abundance was not considered.
[b] Composed of *E. diomedeae*, *E. eximia*, *E. mutica*, and *E. recurva* larvae (Brinton 1975).

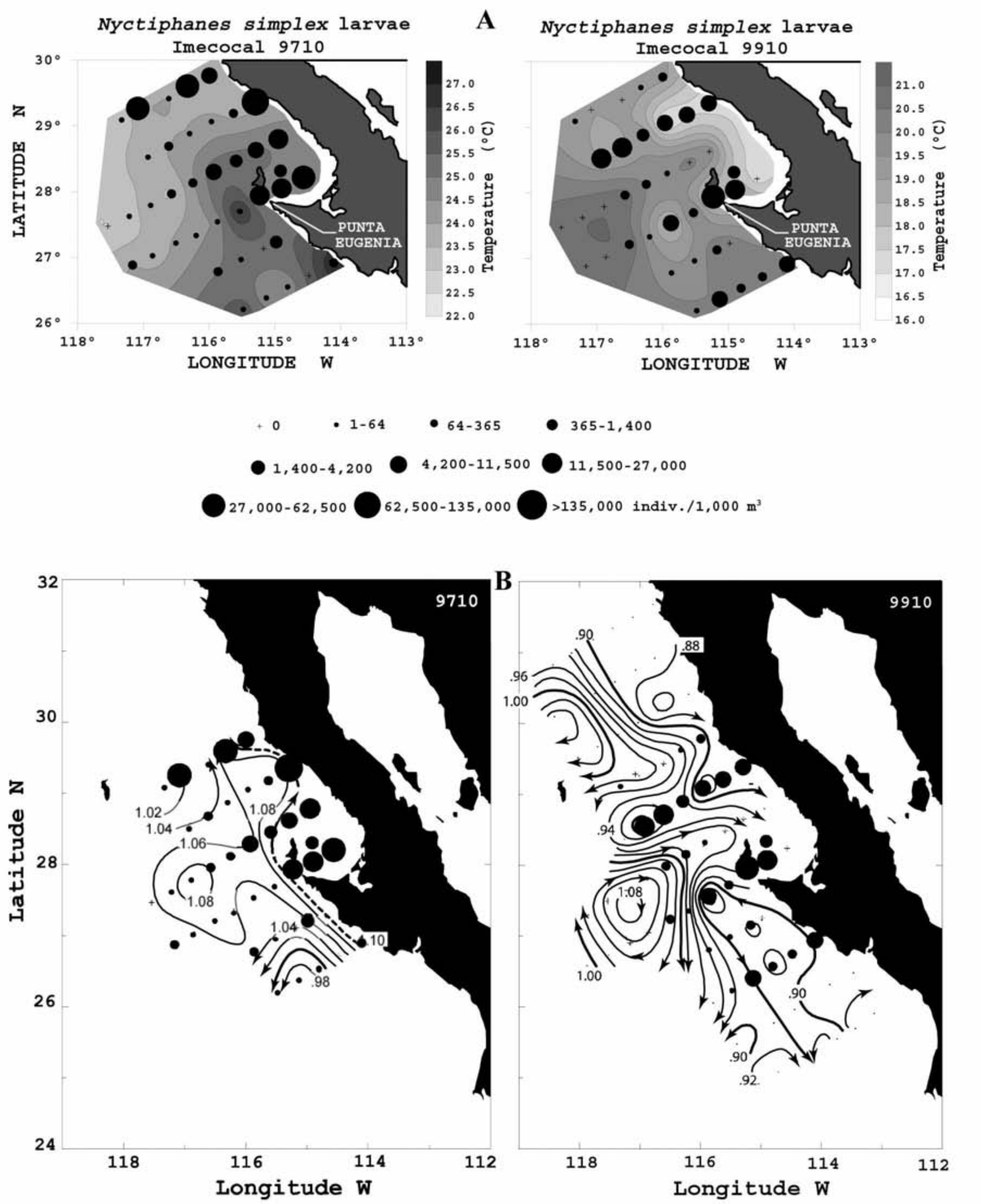

Figure 4. Distribution pattern of *Nyctiphanes simplex* larvae off southern Baja California during October 1997 (El Niño cruise) and October 1999 (La Niña cruise) related to (*A*) 10 m temperature and (*B*) dynamic height anomaly (dynamic meters, 0/500 db). Abundance values were classified in a metric scale $\log^2$. Note that the two temperature scales in *A* are different.

and subtropical species were most abundant during El Niño, October 1997. For the larval stages, the IA Group of species was dominant. During the cold 1999 La Niña, California Current species were more abundant than during the warmer 1997 El Niño.

Spatial Distribution

To illustrate the spatial distribution during both periods, the larval stages of the most abundant species were chosen: *N. simplex*, *N. difficilis*, and IA Group species. The presence of these species during each period was

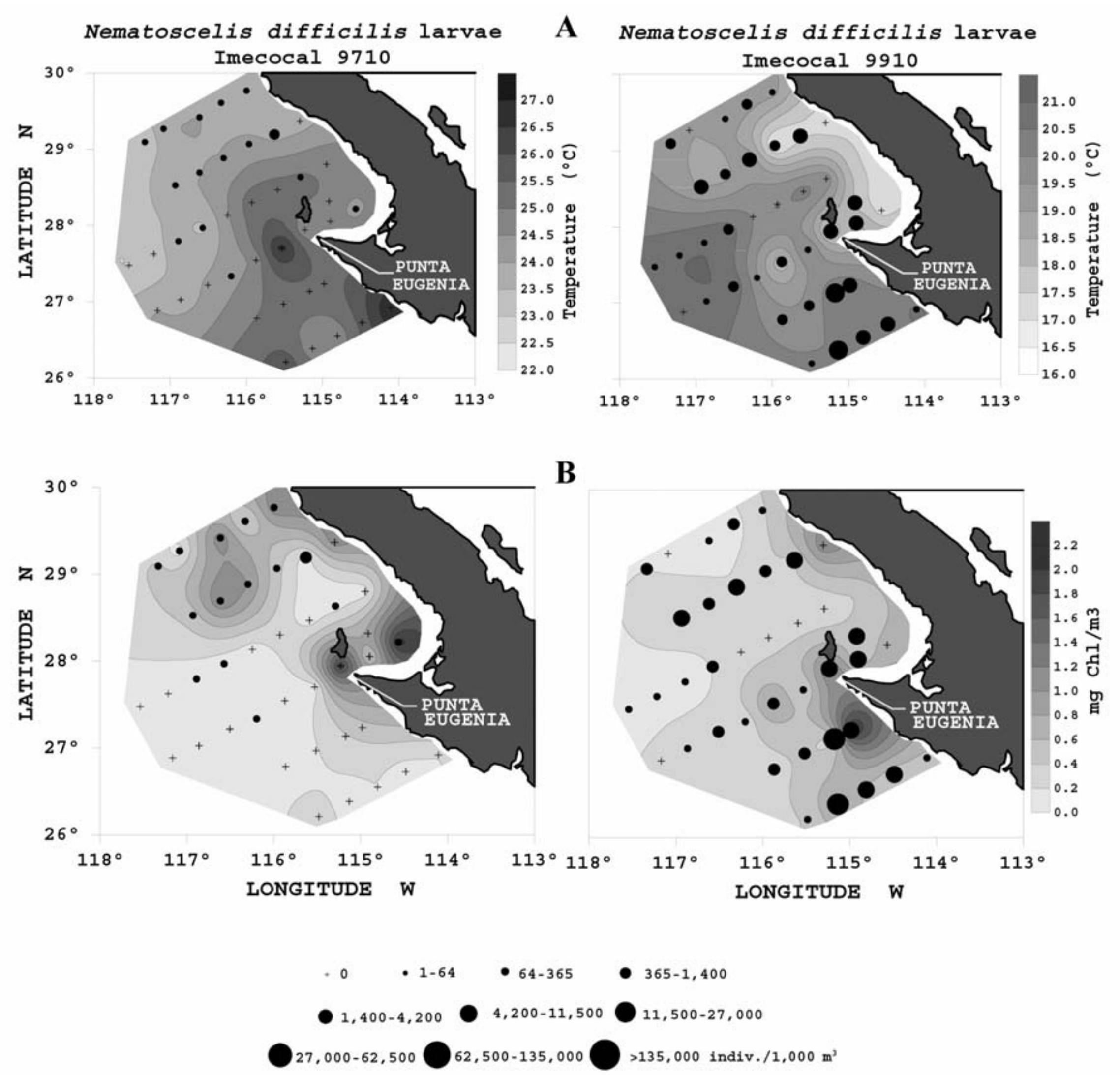

Figure 5. Distribution pattern of *Nematoscelis difficilis* larvae off southern Baja California during October 1997 (El Niño cruise) and October 1999 (La Niña cruise) related to (*A*) 10 m temperature and (*B*) surface chlorophyll *a*. Abundance values were classified in a metric scale log^2. Note that the two temperature scales in *A* are different.

found to be associated with certain environmental parameters: temperature, chlorophyll *a*, and circulation. The most abundant species during the El Niño period, *N. simplex*, displayed striking differences in its larval distributions, though the differences were not significantly different between the two periods (Mann-Whitney U test, $p = 0.38783$). This is possibly associated with the circulation pattern and sea-surface temperature distribution in the study area (fig. 4). It is likely that *N. simplex* larvae were transported by northward (southward) flows to regions of relatively low temperatures during October 1997 (October 1999).

Contrasting patterns in the distribution of the temperate species *N. difficilis* are shown in Figure 5. Unlike *N. simplex*, the abundance and presence of *N. difficilis* during El Niño was relatively low and restricted to the northern part of the study area, while during La Niña large densities were recorded throughout the region. This pattern appears to be associated with low temperatures and food availability (chlorophyll-a). *N. difficilis* larval abundance were significantly different between two periods (Mann-Whitney U test, $p = 0.00000$).

The opposite trend was observed with the larvae of species with tropical-subtropical affinity (fig. 6). The IA Group was most abundant and frequent during the October 1997 cruise associated with the anomalous warm waters of El Niño. At this time, the group was uniformly distributed throughout the region, but during October 1999 the group was at a low level, particularly in coastal and cold regions.

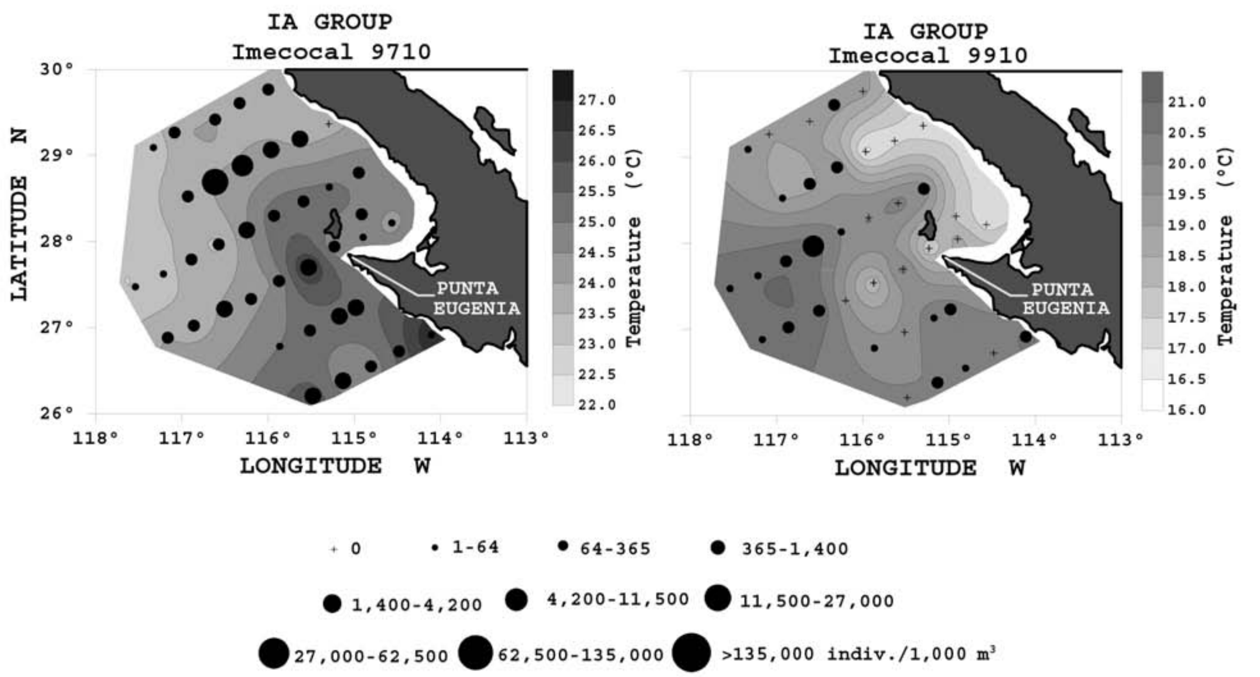

Figure 6. Distribution pattern of IA Group larvae off southern Baja California during October 1997 (El Niño cruise) and October 1999 (La Niña cruise) related to 10 m temperature. Abundance values were classified in a metric scale log². Note that the two temperature scales are different.

DISCUSSION

Most of the species identified in the current investigation have been previously reported in the study area by Brinton (1962), Gómez-Gutiérrez (1995), Lavaniegos-Espejo (1993, 1994), Gómez-Gutiérrez et al. (1995a, b, 1999), and Gómez-Gutiérrez and Robinson-Mendoza (1997). There were distinct differences between the species reported for "ordinary years" and those reported here in the Baja California region. Species present in October 1997 with tropical and subtropical affinities, such as *E. diomedeae*, *E. lamelligera*, *N. gracilis*, *S. carinatum*, *Thysanopoda monocantha*, and *T. obtusifrons*, have not all been reported for other periods, for example, October 1966 (Lavaniegos-Espejo 1993) and October 1994 (Gómez-Gutiérrez et al. 1999), years that can be considered normal or neither El Niño or La Niña periods. These previous works also recorded examples of species with subtropical (*Nematoscelis atlantica*, *Stylocheiron suhmii*, *S. elongatum*, *S. abbreviatum*) and temperate (*Thysanoessa spinifera*) affinities, species that were not recorded either in October 1997 or October 1999. Likewise, these oceanic species were not reported by Gómez-Gutiérrez et al. (1995a) in the same region during October 1987, a period characterized by weak El Niño conditions. However, Gómez-Gutiérrez et al. (1995a) recorded a subarctic affinity species, *E. pacifica*, typical of the California Current, found in the current investigation only during the La Niña cruise. This suggests that species' responses vary differentially, depending on environmental conditions modulated by interannual events that vary in strength and duration.

Euphausiid development stages varied in both periods (fig. 2). The large percentage of larvae during October 1997, mostly furciliae stages, was associated with the introduction of subtropical waters from the southwest to the coastal zone causing positive temperature anomalies of ~8.7°C (Durazo and Baumgartner 2002). While this water displaced California Current waters offshore, it is likely to have also displaced temperate species. However, the sampling region covered only the coastal zone (200 km), not enough area to discern whether these temperate species had indeed been displaced offshore or just remained off the study area. It is also possible that a transient development of an equatorial environment to the north enabled individuals to reproduce there and augment the larval stages of species that normally inhabit warmer, more southern waters. This is suggested by the high temperatures recorded in the region and the high proportion of developmental stages in the euphausiid community during October 1997. Brinton (1960) suggested this for during the warm period of 1957–58, when he found species with equatorial affinities, such as *E. distinguenda*, in the mid-Baja California region. The pattern was also recorded near Punta Eugenia (28°N) by Gómez-Gutiérrez et al. (1995a) during the weak El Niño of 1986–87, when the populations of tropical species, such as *E. distinguenda*, *E. lamelligera*, and *E. diomedeae*, contained adults in the reproductive phase. The significant differences in postlarval stage abundances between the two periods may be related to an increase in juveniles of temperate species during October 1999 (fig. 2), mainly *N. difficilis* and *E. pacifica*. This incremental difference in postlarval stages could be associated with an increased offshore advection of early developmental stages of euphausiid (calyptopes and furciliae), owing to stronger-than-usual upwelling recorded in the area during La Niña conditions (Hayward et al. 1999; Bograd et al. 2000; Durazo and Baumgartner 2002).

Composition and abundance of euphausiid, and consequently their spatial distribution pattern, appears to be strongly modulated during El Niño/La Niña, favoring the presence/absence and the increase/decrease of species according to the prevailing conditions. Differences found in the biogeographic groups between the two periods seem to be a consequence of advective processes that influenced the groups' abundances—that is, poleward flows during El Niño favored the transport of eastern tropical Pacific and subtropical oceanic species, whereas anomalously strong equatorward winds during La Niña favored the southward transport of cold-water species, characteristic of the California Current, toward the study area.

Advection appears to play an important role on the latitudinal limits of some species, even for those as abundant in these regions as *N. simplex*. A distinctive spatial distribution of larval stages of *N. simplex* was observed for both periods (fig. 4) and appears to be regulated by the circulation observed during 1997 and 1999, as Bograd et al. (2000) and Durazo and Baumgartner (2002) have described. Even though this warm-temperate, typically coastal species has a close association to the California Current, its maximum abundances were during the warm period (tab. 1), showing a distribution through most of the sampling grid. This distribution and nearshore abundance during El Niño could be associated with high concentrations of chlorophyll *a* north of Punta Eugenia (fig. 5b) as a consequence of an entrainment of California Current waters from offshore, as is suggested by the clockwise gyre in the dynamic height contours of Figure 4b. Therefore, the strong poleward flow during this period could be causing the larvae to be transported to the north, where cooler waters were recorded (fig. 4a). The effect of warm episodes on the abundance and distribution of *N. simplex* in the California Current along central and northern California waters has been reported for El Niño years. Northward extensions beyond its usual Baja California maximal distribution range were recorded during El Niño events in 1957–59, 1977–78, 1982–83, and 1997–98. Northern species, such as *E. pacifica* and *T. spinifera*, retracted northward, and *N. simplex* was abundant well into California waters (Brinton 1960, 1981; Broudeur 1986; Brinton and Willie 1976; Brinton and Reid 1986; Marinovic et al. 2002). Similar patterns were recorded during El Niño 1986–87 along the Baja California coast. The high-concentration centers of *N. simplex* were displaced progressively from Bahía Magdalena (24.5°N) to the north, attributable to a northward movement of the tropical countercurrent during July and October 1987 in response to seasonal variation of the CCS, possibly intensified during years of warming of the California Current (Gómez-Gutiérrez et al. 1995a).

During October 1999, the abundance and distribution of *N. simplex* larvae (fig. 4b) was closely associated with the circulation pattern and coastal upwelling regions. Isopicnal shoaling near the coast at sections 113 and 120 (not shown) brought to the surface cold, nutrient-rich waters that were trapped into offshore-displacing meanders and gyres. This dynamic promotes the formation of retention sites of nutrients and high densities of *N. simplex* larvae, as was observed off Punta Baja and Punta Eugenia. The proliferation of *N. simplex* in or adjacent to upwelling regions has been frequently recorded, apparently a general feature of the genus observed in other regions for *Nyctiphanes couchii* (Le Roux 1973) and *N. australis* (Bradford and Chapman 1988). The more offshore distribution of *N. simplex* recorded during La Niña period, in contrast to October 1997 (fig. 4), seems to be a consequence of increased westward advection (Ekman transport) related to a high upwelling index anomaly during September 1999 (70 m^3/s per 100 m coastline), a large value compared with -44 m^3/s per 100 m coastline computed in September 1997 for the region (www.pfeg.noaa.gov).

Nematoscelis difficilis inhabits a subarctic to subtropical transition zone of the California Current (Brinton 1960, 1962) and is a temperate species that displayed significant differences between the two periods described here. Its presence, restricted to the northernmost sections and significant low abundance during El Niño, was associated with the advection of warmer-than-normal waters from the southwest into the region, displacing the low-temperature and fresh waters of the California Current offshore (~275 km) (Durazo and Baumgartner 2002; Lynn and Bograd 2002). Thus, the centers of high chlorophyll *a* concentrations and smaller temperatures were located north of Punta Eugenia, where this species was largely present (fig. 5b). Low larval survival of *N. difficilis* at high temperatures (> 24°C) is closely tied to unfavorable tropical conditions, as has previously been reported in the zone by Gómez-Gutiérrez et al. (1995a).

A significantly different pattern in the larval distribution of *N. difficilis* was recorded during October 1999. Its high abundances appeared to be related to a more intense than normal California Current. During La Niña, the California Current core was shallow (~30–60 m) and closer to shore (~100–150 km). The salinity minimum depicting this core follows closely the 0.94–0.96 dynamic meter isolines, limiting the California Current meridionally (fig. 4b, 9910). The meandering equatorward flow favored local retention sites for nutrients, chlorophyll *a*, and species (fig. 5b, 9910). Thus, the highest abundances of *N. simplex* and *N. difficilis* were located eastward of the California Current core, which constrained productive, low-temperature upwelled waters, as well as an important portion of the euphausiid community, to a narrow region near the coast during the La Niña cruise. Similarly, Marinovic et al. (2002) found a high abundance of *N. difficilis* within Monterey Bay associated with the inshore intrusion of the California Current in central California waters during spring and summer of 1998. Seasonal changes in abundance of this species in the study zone have been noted (e.g., Brinton 1960, 1981; Gómez-Gutiérrez et al. 1995a) when the influence of the California Current was more intense.

Compared with the pattern of *N. difficilis* described above, the IA Group had significantly different changes in its abundance and distribution between periods (fig. 6 and tab. 2). It appears that the wide range of 10 m temperatures during the two cruises (22–27°C during 9710 and 16–21°C during 9910) was the main reason for the differences observed in their distribution. The latter is based in the tropical-subtropical affinity of the larvae. Indeed, the presence of warmer-than-usual waters during El Niño 1997 due to the intrusion of subtropical surface water (Durazo and Baumgartner 2002, their fig. 12) probably aided proliferation of this group once it entered the region. Moreover, during La Niña, a stronger-than-usual California Current limited the distribution range of this group to open ocean waters typical of the central Pacific. Bograd et al. (2000) described the development of a clockwise gyre off Punta Eugenia in October 1999, shown here in the dynamic height field in Figure 4b. The eddy brings central Pacific waters inshore and acts as a retention mechanism. This may be responsible for the high abundance spots of the IA Group at stations well off Punta Eugenia during La Niña cruise (fig. 6).

Although larvae in this group were not identified to species level, it is likely that *E. eximia* represented a large percentage of the population because of the high density of adults compared to other species in the group (tab. 1). *E. eximia* is known as an endemic species of eastern tropical Pacific waters and usually inhabits oceanic waters off southern Baja California (Brinton 1960; Gómez-Gutiérrez et al. 1999). Therefore, the large occurrence of the IA group during El Niño cruise could be favored because of a better survival of larval stages, mainly *E. eximia*.

El Niño/La Niña events play a substantial role in the circulation dynamics and ecosystem structure of the CCS. The results shown here largely reflect advective processes associated with variable flow of California Current waters and intrusion of water masses of different characteristics that modified the abundance and distribution patterns of euphausiid species between October 1997 and October 1999. This study shows that basinwide events, such as El Niño 1997–98 and La Niña 1999–2001, have strongly influenced the community structure of euphausiid in central Baja California waters.

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