Hyperiid amphipod community in the Eastern Tropical Pacific before, during, and after El Niño 1997–1998

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ABSTRACT: To evaluate the hyperiid community's response to the influence of oceanographic conditions related to 'El Niño' (EN) in the Mexican Tropical Pacific area, zooplankton samples collected over 27 mo between December 1995 and December 1998 were analyzed. The most abundant of the 80 species recorded were *Hyperioides sibaginis* and *Lestrigonus bengalensis*. Two different climatic yearly periods were revealed, including one from February to June, related to the strongest flow of the California Current (CC), with cooler (<25°C) and saltier (>34.5 psu) waters. In this period, hyperiids were more species-rich and diverse, with greater evenness, but had lower abundances. From July to December, the North Equatorial Countercurrent (NECC) was predominant, with warmer waters (>25°C) and lower salinity (<34.5 psu). *H. sibaginis* and *L. bengalensis* were dominant, particularly in the aftermath of EN (after June 1998). The influence of the Equatorial water during EN favored a greater abundance of warm-water hyperiid families and a greater evenness, particularly during 1998. During EN, higher hyperiid abundance and diversity but also a 30% increase of species richness and a greater abundance of the dominant species were observed. After the end of EN and for the rest of the sampling period, the oceanographic conditions returned to normality in the area, but the hyperiid community still showed relatively low diversity and high abundance values.

KEY WORDS: Zooplankton ecology · Pelagic crustaceans · Diversity

INTRODUCTION

Hyperiid amphipods are planktonic crustaceans represented by >250 species in the world ocean. Attempts have been made to relate the occurrence of hyperiid species with water masses or oceanographic conditions (Bary 1959a,b, Kane 1962, Shulenberger 1977, Siegel-Causey 1982, Gasca 2004, Lavaniegos & Hereu 2009). Lavaniegos & Ohman (1999) provided data suggesting that hyperiids are sensitive to large-scale climate changes. There are still large neritic and oceanic areas in which basic aspects of this group have not been surveyed; this is true for part of

the North and Central Pacific (Vinogradov 1999). Information about the hyperiids from the Eastern Pacific region has been mainly taxonomic (Brusca & Hendrickx 2005, Gasca 2009a, Gasca et al. 2010), and none of the ecological contributions (Brusca 1967, Gasca & Haddock 2004, Lavaniegos & Hereu 2009) have been related to EN conditions.

It has been documented that EN has important effects on the zooplankton communities of the Pacific Ocean (Fiedler 2002, Badán-Dangón 2003). The influence of EN 1997–98 on the marine biota has been studied in different sectors of the California Current (CC), such as off California (Marinovic et al.

2002, Peterson & Keister 2002) and Baja California (Lavaniegos et al. 2002, 2003, Palomares-García et al. 2003, Hereu et al. 2006), but its influence on the hyperiid community of the Eastern Tropical Pacific remains unstudied.

We analyze the inter-annual variability of the hyperiid community of the Mexican Pacific central coast based on zooplankton samples collected during 27 mo between December 1995 and December 1998, a period including the influence of EN 1997–98.

The study area is located off the central Mexican coast in the Eastern Tropical Pacific (ETP) region (Fig. 1). It is part of the Central American Coastal Province (Longhurst 2006) and bounded by the north and south equatorial fronts. The continental shelf along this coast is relatively narrow (7 to 10 km) (Filonov & Tereshchenko 2000).

The latitudinal position of the transition zone, where the CC joins the North Equatorial Counter-current (NECC) off the surveyed area, varies depending on the strength of winds and currents (Kessler 2006). In winter, when the CC is more intense, the transitional area is located farther south, whereas in the summer, when the NECC is more intense, the transition zone moves to the north. Hence, 2 distinct climatic periods (CPs) can be defined, one influenced by cooler waters of the CC and the second influenced by the NECC. In winter and spring (February to June), the local conditions are characterized by the absence of the NECC and the influence of the CC. The water is relatively cooler (>25°C) and with low salinity (34.5 psu); it has a south-southeast flow far from the coast north of 23°N (Aguirre-Gómez et al. 2003). The direct influence of the CC in the surveyed area has not been proven, but the regional oceanographic dynamics are characterized by the CC-NECC system, so we used this regional frame as our main reference (Kessler 2006, Trasviña & Barton 2008).

Typical ETP surface waters (50–75 m) show 2 seasonal conditions: from June to December, Pacific Tropical Surface Water (PTSW) occurs with salinities <34 psu and temperatures >25°C, whereas Pacific Equatorial Surface Water (PESW) with salinities >34 psu and temperatures <25°C occurs from January to May and June. Under this layer (75–200 m) lies the Pacific Equatorial Water (PEW)

(Trasviña et al. 1999, Filonov & Tereshchenko 2010) (Fig. 2).

In September, large volumes of equatorial water affected the zone, and by December 1997, they comprised the upper 70 m. The maximum intensity of EN occurred in January 1998 when equatorial waters occupied the upper 80 m layer (27.5°C, 34 psu). By May 1998, the hydrographic structure began to return to the conditions that existed in 1996 (Fig. 2) (Trasviña et al. 1999, Filonov & Tereshchenko 2010).

MATERIALS AND METHODS

The hydrographic data used in this work, including local profiles of temperature and salinity during the study period, were described and analyzed by Filonov & Tereshchenko (2000, 2010). The 269 zooplankton samples analyzed were obtained at 12 sites sampled monthly between December 1995 and December 1998 (27 mo). The sampling transects are located on the continental shelf and separated from the coastline by a distance of 3 km (inshore transect) and 4.5 km (offshore transect) (Fig. 1).

The sampling was performed on board the R/V 'BIP-V', following Smith & Richardson (1977); all samples were obtained at nighttime using oblique and semicircular trawls at depths between 30 and 115 m to the surface, depending on the bottom depth. A bongo net (0.6 m mouth diameter, 0.505 mm mesh opening, with a digital flowmeter) was used to obtain the zooplankton samples, which were fixed and preserved with 4% formalde-
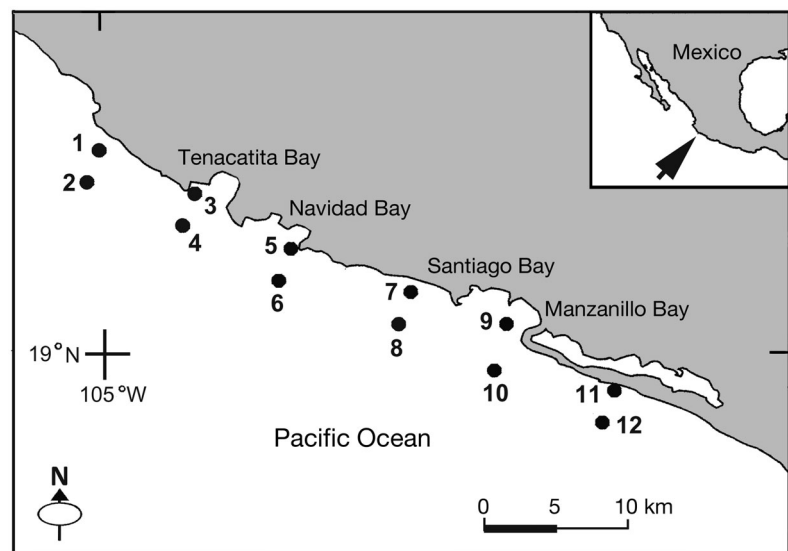

Fig. 1. Study area and sampling stations off the central coast of the Mexican Pacific
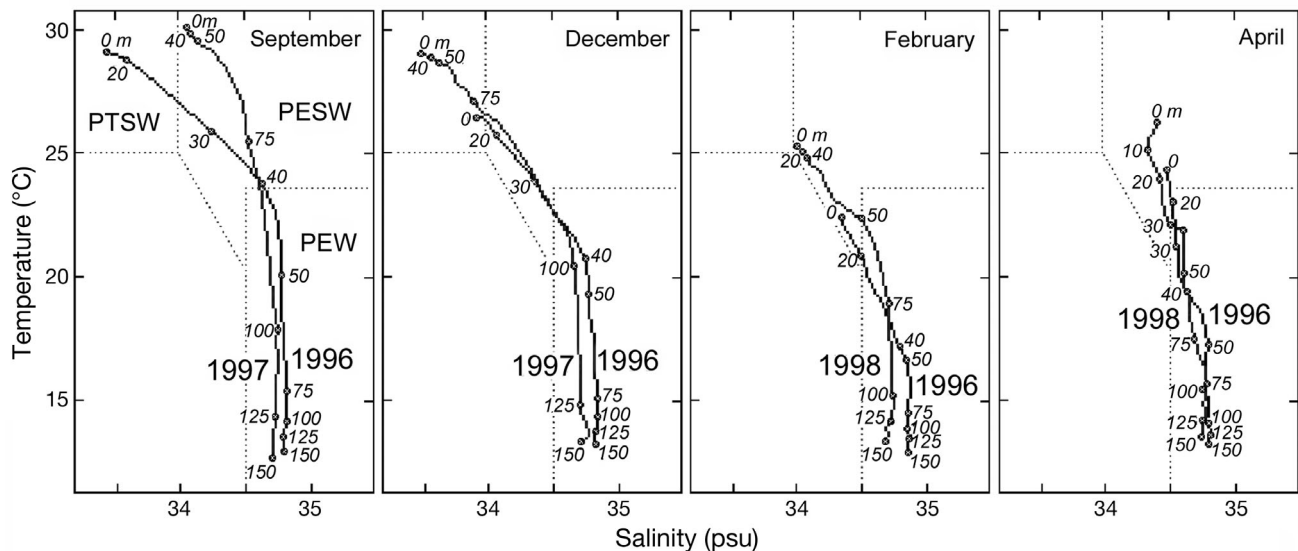
Fig. 2. Monthly average temperature and salinity. Dotted lines outline main water masses. PTSW: Pacific Tropical Surface Water, PESW: Pacific Equatorial Surface Water, PEW: Pacific Equatorial Water (after Filonov & Tereshchenko 2010)

hyde buffered with sodium borate. Hyperiid amphipods were sorted from the original samples and transferred to a solution of distilled water (95%) with propylene glycol (4.5%) and propylene phenoxetol (0.5%) for long-term storage.

Hyperiids were identified following Vinogradov et al. (1996), Harbison & Madin (1976), Shih (1991), and Zeidler (2003, 2004a,b, 2006). Abundance was standardized to ind. 1000 m^{-3}. June and December were removed from the CP analyses of both the CC (January to May) and NECC (July to November) periods. An analysis of variance (ANOVA) was performed with the total hyperiid abundance ($\log_{10}[x + 1]$) considering (1) the CP surveyed, (2) inshore and offshore stations, (3) data collection pre-EN (before July 1997), during EN (July 1997 to April 1998) and post-EN (the remaining stations), and (4) EN and non-EN conditions (EN1: July 1997 to April 1998, EN0: the remaining samples). These analyses were performed using the Brodgar multivariate analysis and multivariate time series analysis (version 2). When necessary, we conducted a post-hoc test for multiple comparisons (Tukey-Kramer method) to determine if averages were statistically different (Sokal & Rohlf 1995).

The hyperiid diversity analysis by CP was performed in terms of species richness, evenness, and diversity (Shannon index). Rarefaction curves (Gotelli & Graves 1996) were produced for each of these parameters and were estimated using the probability of interspecific encounter (PIE) (Hurlbert 1971). This procedure provides comparative estimates, regard-

less of differences in the sample sizes of the groups compared. Abundance levels for simulation were established using the sample with the lowest values of abundance to allow comparisons of sample groups. The ECOSIM program was used to calculate diversity indices (Gotelli & Entsminger 2009), which uses the Monte Carlo method and 1000 replicates in the simulation for each estimate. Samples are randomly selected without replacement, and this procedure is repeated 1000 times to estimate an average value and 95% confidence interval for various levels of abundance.

To determine the response of the hyperiid community associations to the intra-annual (CP) and interannual (EN) temporal and spatial (distance from shore) variation, we performed a similarity analysis (ANOSIM) to statistically evaluate the differences among the groups examined (Clarke & Warwick 2001). A similarity percentage analysis (SIMPER) (Clarke 1993) allowed the detection of groups of species that typify both the similarity (within groups) and the dissimilarity (between groups). Analyses were performed using the PRIMER 6 software, using the Bray Curtis index with untransformed data (Clarke & Gorley 2006).

A non-metric multidimensional scaling (NMDS), based on the standardized abundances of all species, and the Bray Curtis similarity index with zero adjustment (Clarke et al. 2006) was used to explore the hypothesis that seasonality, EN, and distance from coast shape the local hyperiid associations. We also performed a direct gradient redundancy analysis.

This method is the canonical version of a principal component analysis (Leps & Smilauer 2007) and considers a $\log_{10}$ transformed data matrix of the total abundance of species/samples and the multivariate El Niño index (MEI) (Wolter & Timlin 1998). We performed a significance analysis of management models using a permutation test (Monte Carlo method) to evaluate the independence between the matrices of species abundance and environmental variables (Leps & Smilauer 2007). The redundancy analysis was performed using CONOCO (ter Braak & Smilauer 1998).

RESULTS

Species composition

From the taxonomic analysis of the 269 hyperiid samples examined, 80 species were identified, representing 38 genera, 16 families, and 2 suborders. The list of species along with the sequence in which each of them appeared per semester is shown in Table 1. Up to 24 (30%) of the 80 species occurred after July 1997, and 19 occurred in the last year of sampling, during conditions associated with EN.

Table 1. Hyperiid species recorded. First occurrence (FO) by sampling semester I (December 1995 to June 1996), II (July to December 1996), III (January to June 1997), IV (July to December 1997), V (January to June 1998), and VI (July to December 1998); overall numerical abundance (Total Σ; total number of individuals in all samples), average abundance (ind. 1000 m^{-3} over all samples), frequency (F; % of samples in which species occurred), and geometric mean (GM) of species abundance in all samples

	FO	Total Σ	Average	F (%)	GM		FO	Total Σ	Average	F (%)	GM
Hyperioides sibaginis	I	187 757	697.98	83.33	106.66	*Lycaea bovalloides*	I	193	0.72	4.07	1.12
Lestrigonus bengalensis	I	41 167	153.04	76.30	30.68	*Amphithyrus muratus*	III	190	0.70	5.19	1.14
Lestrigonus schizogeneios	I	16 068	59.73	42.96	4.03	*Lycaea serrata*	I	173	0.64	2.22	1.06
Tetrathyrus forcipatus	I	4887	18.17	42.96	3.89	*Lycaea pachypoda*	II	163	0.61	2.22	1.07
Lestrigonus shoemakeri	I	3886	14.45	40.37	3.64	*Dairella californica*	I	155	0.57	3.70	1.1
Parascelus edwardsi	I	3685	13.70	49.63	4.54	*Themistella fusca*	I	135	0.50	4.44	1.11
Lycaeopsis zamboangae	I	2965	11.02	44.07	3.72	*Platyscelus crustulatus*	I	131	0.49	4.44	1.11
Paralycaea hoylei	I	2225	8.27	27.04	2.33	*Oxycepalus latirostris*	V	113	0.42	3.70	1.09
Euthamneus rostratus	I	2210	8.22	11.85	1.46	*Phronima bowmani*	I	105	0.39	3.33	1.09
Hyperia vosseleri	I	2003	7.45	20.00	1.84	*Vibilia chuni*	I	103	0.38	3.70	1.09
Oxycephalus clausi	I	1810	6.73	28.52	2.31	*Paraphronima gracilis*	III	98	0.37	2.59	1.07
Lestrigonus macrophthalmus	III	1722	6.40	20.00	1.93	*Hyperietta luzoni*	III	93	0.35	2.22	1.06
Brachyscelus crusculum	I	1719	6.39	32.59	2.49	*Vibilia viatrix*	V	92	0.34	1.85	1.05
Vibilia longicarpus	III	1694	6.30	5.93	1.28	*Streetsia mindanaonis*	I	62	0.23	1.85	1.05
Simorhynchotus antennarius	I	1634	6.07	37.41	2.77	*Lestrigonus crucipes*	III	59	0.22	1.85	1.05
Lycaea vincentii	I	944	3.51	13.70	1.25	*Phronima dunbari*	I	58	0.22	1.48	1.04
Lycaea pulex	I	867	3.22	17.04	1.61	*Leptocotis tenuirostris*	I	43	0.16	1.48	1.04
Lycaeopsis themistoides	I	845	3.14	17.41	1.63	*Paralycaea gracilis*	IV	39	0.15	1.11	1.03
Anchylomera blossevillei	IV	836	3.11	11.48	1.42	*Phronima bucephala*	III	38	0.14	1.48	1.04
Amphithyrus sculpturatus	I	614	2.28	17.41	1.56	*Phronima sedentaria*	V	37	0.14	1.48	1.03
Phronima atlantica	III	572	2.13	11.11	1.37	*Thyropus sphaeroma*	IV	34	0.13	1.11	1.03
Platyscelus serratulus	I	550	2.05	14.44	1.45	*Eupronoe maculata*	V	32	0.12	0.74	1.02
Eupronoe armata	IV	523	1.94	12.22	1.38	*Vibilia borealis*	II	31	0.12	0.74	1.02
Lestrigonus latissimus	I	467	1.74	10.00	1.31	*Lycaea lilia*	V	30	0.11	0.37	1.01
Amphithyrus bispinosus	I	451	1.68	12.22	1.35	*Primno evansi*	V	28	0.10	1.11	1.03
Hyperoche martinezi	V	413	1.54	2.59	1.1	*Eupronoe minuta*	V	25	0.09	1.11	1.03
Phronimella elongata	IV	381	1.42	5.56	1.18	*Primno brevidens*	V	25	0.09	0.74	1.02
Vibilia armata	I	380	1.41	5.93	1.18	*Amphithyrus glaber*	V	20	0.07	0.74	1.02
Phrosina semilunata	III	368	1.37	8.15	1.25	*Tryphana malmi*	V	19	0.07	0.74	1.02
Phronimopsis spinifera	I	351	1.30	6.67	1.2	*Rhabdosoma minor*	I	18	0.07	0.74	1.02
Lycaea bajensis	I	328	1.22	4.44	1.15	*Hyperioides longipes*	VI	18	0.07	0.74	1.02
Lycaea bovalli	I	273	1.01	5.93	1.18	*Phronima solitaria*	V	16	0.06	0.74	1.02
Brachyscelus rapacoides	I	269	1.00	5.19	1.15	*Eupronoe laticarpa*	V	14	0.05	0.37	1.01
Glossocephalus milneedwardsi	I	245	0.91	6.67	1.19	*Platyscelus ovoides*	V	12	0.05	0.37	1.01
Brachyscelus globiceps	I	243	0.91	4.07	1.12	*Streetsia porcella*	IV	12	0.05	0.37	1.01
Vibilia propinqua	I	231	0.86	2.59	1.08	*Cranocephalus scleroticus*	I	12	0.04	0.37	1.01
Scina marginata	I	230	0.86	1.48	1.06	*Oxycephalus piscator*	V	11	0.04	0.37	1.01
Hyperietta stephenseni	III	225	0.84	4.44	1.13	*Paratyphis parvus*	I	9	0.03	0.37	1.01
Rhabdosoma whitei	I	221	0.82	6.67	1.18	*Hemityphis tenuimanus*	V	7	0.03	0.37	1.01
Parapronoe parva	I	208	0.77	7.04	1.19	*Schizoscelus ornatus*	V	7	0.03	0.37	1.01

Analysis of abundance

The most abundant species were *Hyperioides siba-*
ginis, (65.1%), *Lestrigonus bengalensis* (14.27%),
L. schizogeneios (5.57%), *Tetrathyrus forcipatus*
(1.69%), *L. shoemakeri* (1.35%), *Parascelus edwardsi*
(1.28%), *Lycaeopsis zamboangae* (1.03%), *Eutham-*
neus rostratus (0.77%), *Paralycaea hoylei* (0.77%),
Hyperietta vosseleri (0.7%), and *Oxycephalus clausi*
(0.63%) (Table 1). Eight species were found in >100
of the 269 samples: *H. sibaginis* (in 225 samples), *L.*
bengalensis (206), *P. edwardsi* (134), *L. zamboangae*
(119), *L. schizogeneios* (116), *T. forcipatus* (116), *L.*
shoemakeri (109), and *Simorhynchotus antennarius*
(101). Of the 21 species that appeared in ≤3 stations,
only 4 (*Cranocephalus scleroticus, Paratyphis parvus,*
Rhabdosoma minor, and *Vibilia borealis*) occurred
before July 1997, whereas the other 17 species were
collected after this month. The most abundant spe-
cies at inshore stations were *H. sibaginis, L. ben-*
galensis, L. schizogeneios, T. forcipatus, E. rostratus,
and *P. hoylei*.

The overall average abundance of hyperiids was
1070 individuals (ind.) 1000 m^{-3}. Monthly abun-
dances ($\log_{10}[x + 1]$) were highly variable and distinct
from one another ($F = 88.19$, p < 0.001). The abun-
dance values were >1700 ind. 1000 m^{-3} in July 1996,
February, July, and December 1997, and January,

Table 2. Results from the ANOVA for (a) the studied climate
periods; (b) inshore and offshore stations; (c) data from pre-
EN (before July 1997), during EN, and post-EN; (d) during
EN1 (July 1997 to April 1998) and EN0 (remaining data)

Abundance ($\log_{10}$)	df	F	p	SS (resid)
(a) CP	205	26.210	<0.001	59.179
(b) Inshore/offshore	267	12.092	<0.001	116.257
(c) Pre-, post-, during EN	267	52	<0.001	87.319
(d) EN0, EN1	267	22.382	<0.001	112.123

June, July, and September 1998. Abundances <200
ind. 1000 m^{-3} were recorded in February, April, May,
November, and December 1996. The average annual
abundance progressively increased from 502 ind.
1000 m^{-3} during 1995 and 1996 to 1176 in 1997 and
1502 ind. 1000 m^{-3} in 1998.

The average abundance also increased throughout
the CP in each year (1995 to 1998), being 86 ind.
1000 m^{-3} in 96CC, 320 ind. 1000 m^{-3} in 96NE, 823 in
97CC, 1142 in 97NE, 1319 in 98CC, and 1664 in
98NE. In general, the differences among the CP were
significant (Table 2, Fig. 3a). Hyperiids were more
abundant inshore (1432 ind. 1000 m^{-3}) than offshore
(736 ind. 1000 m^{-3}) (Table 2, Fig. 3b). They were
more abundant in the post-EN (1524 ind. 1000 m^{-3})
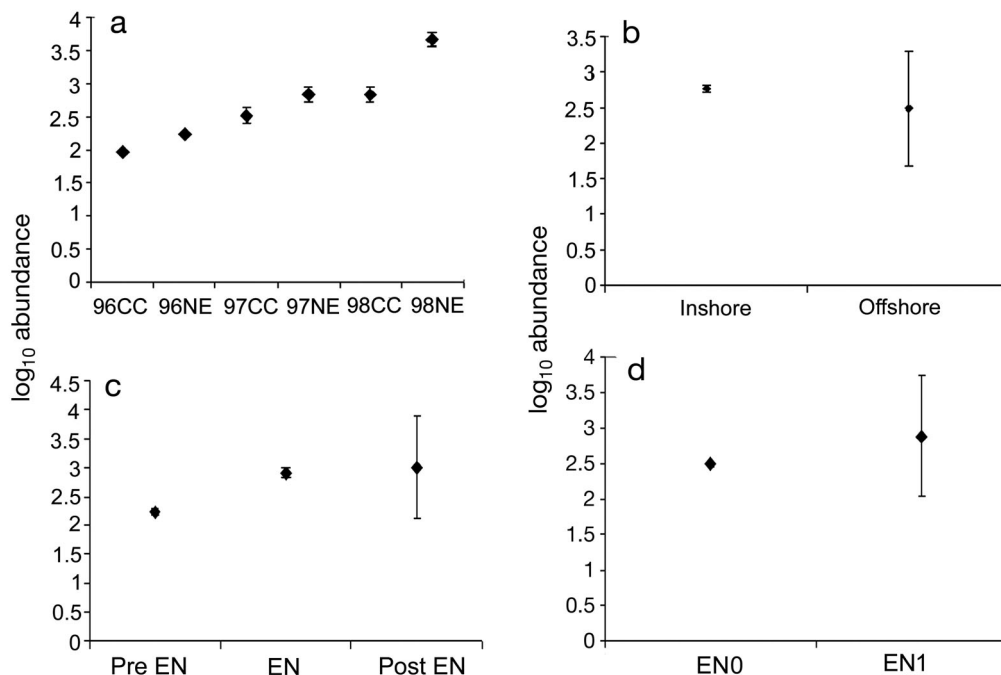
Fig. 3. Total hyperiid abundances ($\log_{10}[x + 1]$) obtained for (a) the surveyed climatic periods (CPs), (b) inshore and offshore
stations, (c) data from pre-EN (before July 1997), EN, and post-EN and (d) during EN1 (July 1997 to April 1998) and EN0 (re-
maining data). Data are averages (dots) and confidence intervals 95% (bars). CPs are named by year and current (e.g. 96CC is
the period of 1996 dominated by the California Current)
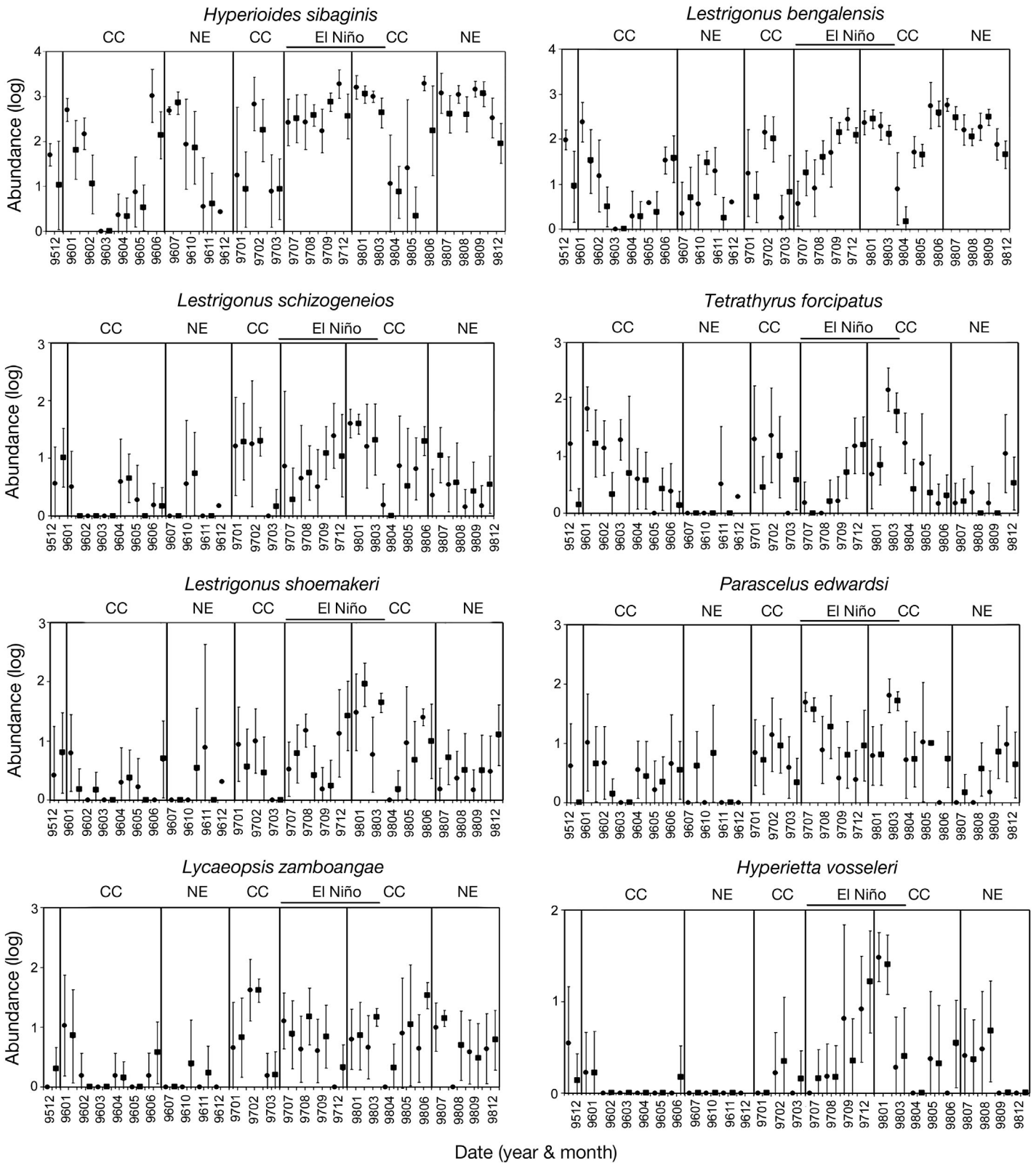
Fig. 4. Monthly average abundances ($\log_{10}[x + 1]$) and 95% confidence interval of total numbers of *Hyperioides sibaginis*, *Lestrigonus bengalensis*, *Lestrigonus schizogeneios*, *Tetrathyrus forcipatus*, *Lestrigonus shoemakeri*, *Parascelus edwardsi*, *Lycaeopsis zamboangae*, and *Hyperietta vosseleri* in the studied area. ●: inshore stations, ■: offshore stations

period than before (594 ind. 1000 m^{-3}) or during the EN (1432 ind. 1000 m^{-3}) (Table 2, Fig. 3c). Furthermore, they were also more abundant during the influence of EN than in all other samples (914 ind. 1000 m^{-3}) (Table 2, Fig. 3d).

The most abundant species were more abundant inshore than offshore. *Hyperioides sibaginis* had an average of 948 ind. 1000 m^{-3} inshore and 457 ind. 1000 m^{-3} at offshore stations; the same pattern was observed in *Lestrigonus bengalensis* (191 vs. 117 ind. 1000 m^{-3}), *L. schizogeneios* (107 vs. 13), *Tetrathyrus forcipatus* (26 vs. 11), and *Parascelus edwardsi* (15 vs. 12).

A significant correlation ($F = 4.117$, p < 0.1) was obtained between the monthly geometric mean (GM) of hyperiid abundance and Niño Index 3.4 (SST index for the Niño 3.4 Region; Trenberth 1997). We also observed a significant relationship between the monthly GM of *Hyperioides sibaginis* and the same EN index ($F = 2.094$, p = 0.163) but not for the GM of the other most abundant species, *Lestrigonus bengalensis*, ($F = 0.177$, p = 0.6775). The monthly abundances of hyperiid species with average densities >10 ind. 1000 m^{-3} were plotted to observe the temporal variations (Fig. 4).

Analysis of diversity

Species richness

The number of species recorded ranged from 3 (March and December 1996) to 48 (January 1998). We observed fewer species in the first 2 yr of sampling (Fig. 5). Results from the rarefaction curves revealed that the largest expected number of species corresponded to the CC periods of each year, with no differences among them. During NECC periods, the expected number of species was consistently lower than in the CC (cold) periods (Fig. 6a).

The expected number of species was higher offshore than inshore (Fig. 6b). It tended to be higher during EN, followed by the pre-EN and post-EN periods (Fig. 6c); no differences were found between EN1 and the rest of the samples (EN0) (Fig. 6d). Up to 68 species were recorded at inshore stations vs. 77 offshore. Only *Platyscelus ovoides*, *Oxycephalus piscator*, and *Cranocephalus scleroticus* were not recorded at inshore stations.

Shannon diversity

The rarefaction curve analysis of diversity (Shannon) revealed that CC periods were more diverse than the NE periods; the 1997 NE CP was intermediate between the warm and cold CP (Fig. 7a). Diversity at inshore stations was higher than offshore (Fig. 7b); diversity was higher during EN, followed by pre-EN and by post-EN periods, with a very low diversity (Fig. 7c). Diversity was higher during EN1 than in the rest of the samples (EN0) (Fig. 7d).

Evenness

A higher number of samples exhibited evenness values >0.5 (171 vs. 98), i.e. there were no markedly dominant species. Evenness values diverged from the pattern observed for diversity and richness
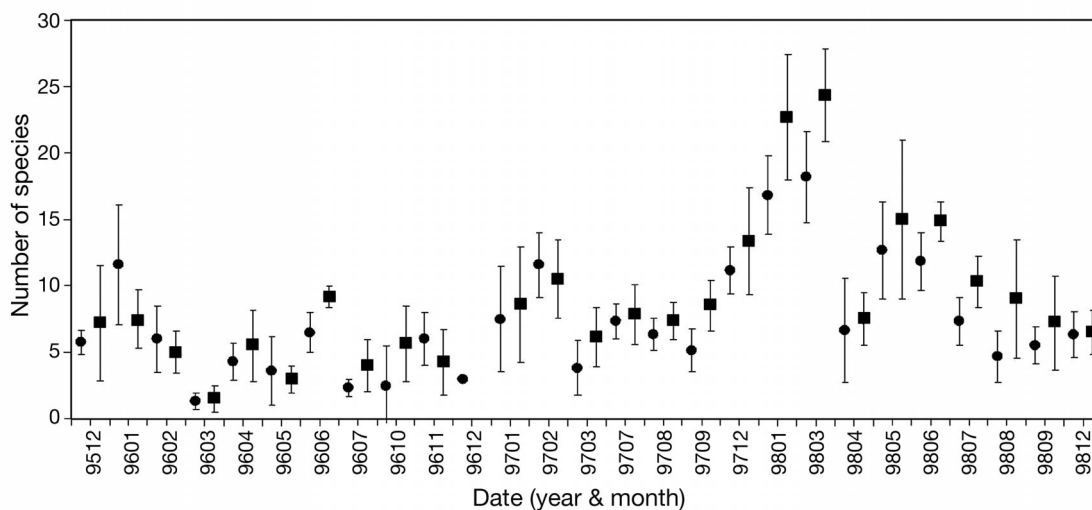

Fig. 5. Average number of species (95 % confidence interval) in the Mexican Central Pacific from 1995 to 1998 at inshore (●) and offshore (■) stations

Fig. 6. Species richness based on rarefaction curves. (a) Surveyed CPs; (b) inshore and offshore stations; (c) data from pre-EN (before July 1997), EN, and post-EN; (d) during EN 1 (July 1997 to April 1998) and EN 0 (remaining data)

(Fig. 8a). Higher values of evenness were found during the influence of EN and were similar to those of 96CC. Extreme values of this index were observed in 1996. A reverse tendency occurred in 1997: during the NE, values were higher than during the CC, and

evenness was uniform between 97CC and 98NE. Dominance was lower offshore (Fig. 8b), and greater evenness values occurred during the pre-EN than in the post-EN period (Fig. 8c). A high evenness was found during EN1 than during EN0 (Fig. 8d).

Fig. 7. Shannon diversity based on rarefaction curves. (a) Surveyed CPs; (b) inshore and offshore stations; (c) data from pre-EN (before July 1997), EN, and post-EN; (d) during EN 1 (July 1997 to April 1998) and EN 0 (remaining data)
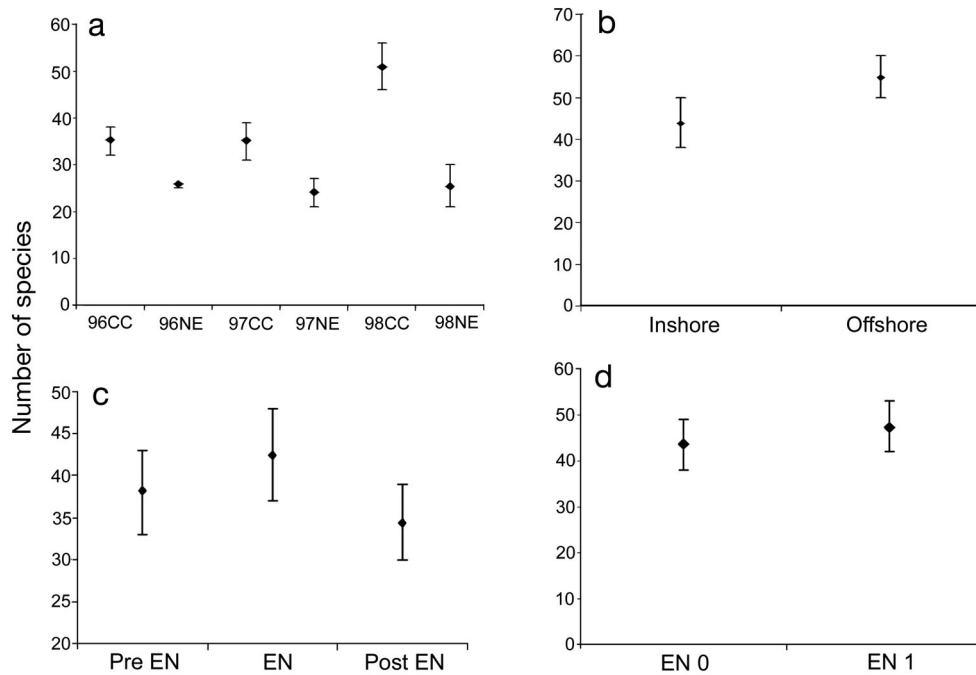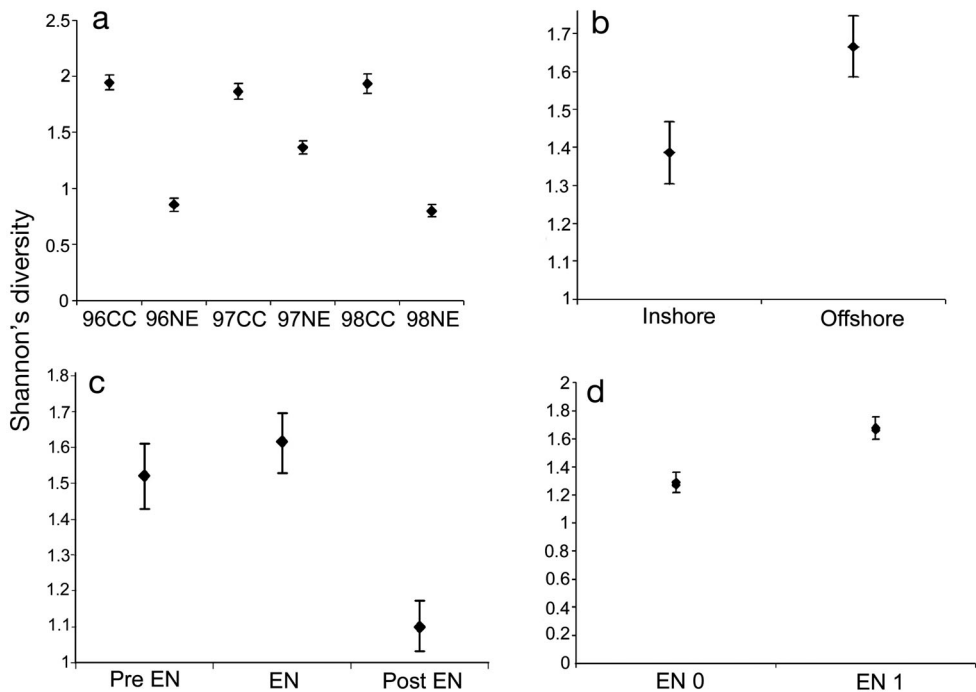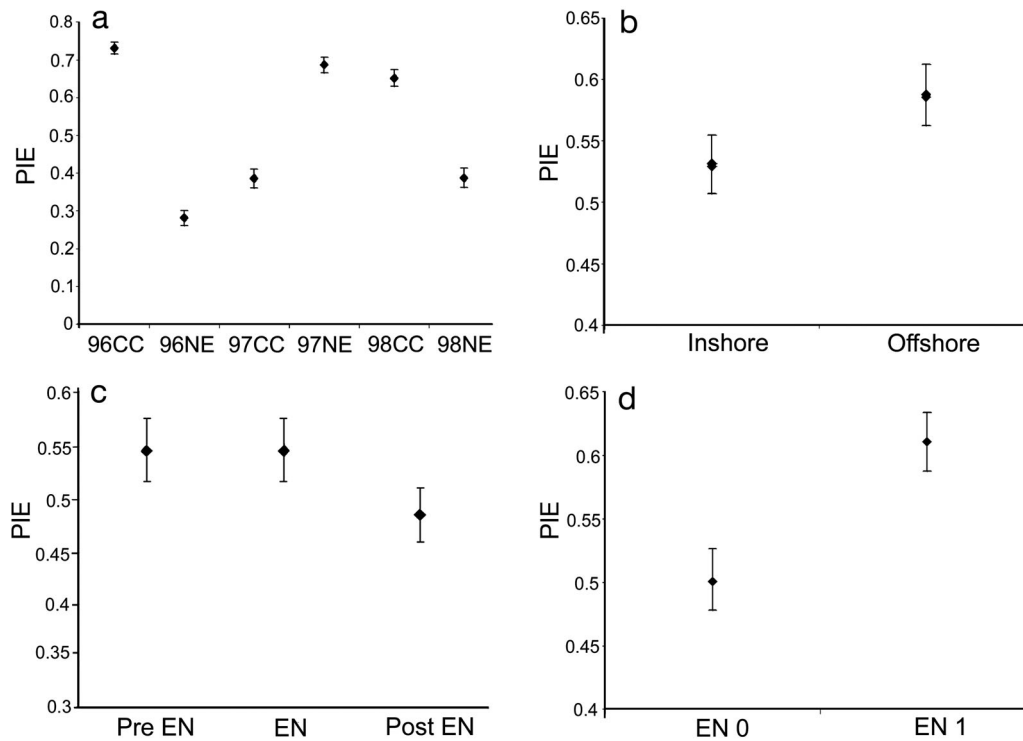
Fig. 8. Evenness based on rarefaction curves. (a) Surveyed CPs; (b) inshore and offshore stations; (c) data from pre-EN (before July 1997), EN, and post-EN; (d) during EN 1 (July 1997 to April 1998) and EN 0 (remaining data). PIE: probability of inter-specific encounter

Community analysis

The nMDS applied to CPs, distance to coast, and EN showed an acceptable fit (stress = 0.14) (Clarke & Gorley 2006); however, the large number of samples in a single graphic hampered the visual detection of spatial and temporal patterns (Fig. 9a–d). The arrangement of the CP (Fig. 9a) shows dispersion of the samples during the EN influence period. The CP CC group shows a greater similarity. The 98CC period reflects the full effect of EN in the area and was the most compact group. No inshore-offshore pattern was observed (Fig. 9b), but the pre-EN, EN, and post-EN periods were well defined (Fig. 9c).

The ANOSIM analysis showed significant differences between the CPs (R = 0.226, p < 0.001), among the pre-EN, EN, and post-EN samples (R = 0.069, p < 0.001), and also based on the distance from the coast (R = 0.03, p < 0.001). The ANOSIM between EN1 (July 1997 to March 1998) and the rest of samples did not show significant differences (R = −0.102, p = 1.00). For all paired analyses of CP, the differences were significant at p < 0.001 (except for 96CC and 96NE, for which p = 0.019, and for the pair 97CC and 96NE with p = 0.012) (Tables 3 to 6).

The SIMPER analysis shows that during the CC periods there are more species with low contribution than in the NE period. During the NE period, *Hyperioides sibaginis* and *Lestrigonus bengalensis* represented >90% of the similarity within groups (Table 3). Also, *H. sibaginis* and *L. bengalensis* dominated in all of the studied groups. Other species, such as *Tetrathyrus forcipatus*, *Oxycephalus clausi*, *Parascelus edwardsi*, and *L. schizogeneios*, contributed mainly to the communities of CC periods (Table 4).

Fewer species contributed to the NE than to the CC community. The last 3 CPs were similar, with high abundance, although their composition differed. The main feature of CP 98NE, the most dissimilar of the CPs, is that *Hyperioides sibaginis* and *Lestrigonus bengalensis* contributed 74.5 and 23.0%, respectively, to their community, and together they dominated, forming >97% of the assemblage during that period. *L. bengalensis* contributed more in this period than in the other NE periods.

Unlike other CC periods, the 98CC period had a minor relative contribution of *Hyperioides sibaginis*; a group of species including *Brachyscelus crusculum*, *Tetrathyrus forcipatus*, *Parascelus edwardsi*, *Paralycaea hoylei*, *Phronima atlantica*, and *Vibilia armata*
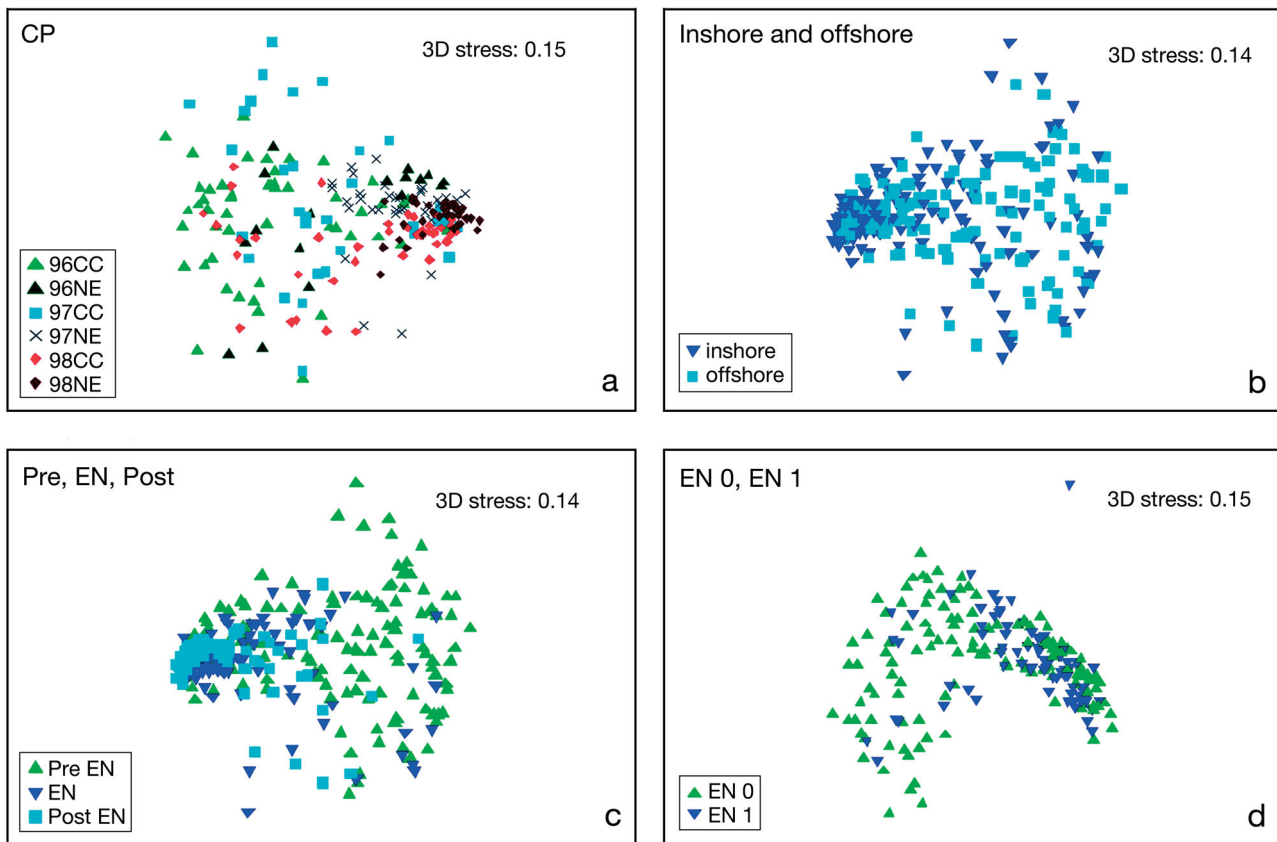
Fig. 9. NMDS graphical analysis of samples collected in the surveyed area (not during June or December). (a) The various climate periods studied; (b) inshore/offshore stations; (c) data pre-EN (before July 1997), during, and post-EN; (d) EN1 (July 1997 to April 1998) and EN0 (all others)

Table 3. SIMPER analysis (similarity) of the hyperiid abundances during the climate periods. CC: period dominated by California Current, NE: period dominated by North Equatorial Countercurrent, SP: mean similarity percentage in the group, Av: average abundance (ind. 1000 m^{-3}) in the group, %: mean contribution percentage to similarity. Table shows the group of species contributing >90% to similarity in each period

	Climatic period											
	96CC		96NE		97CC		97NE		98CC		98NE	
SP:	15.04		22.56		16.61		39.7		27.35		54.04	
Species	Av	%	Av	%	Av	%	Av	%	Av	%	Av	%
Hyperioides sibaginis	132	36.16	271	85.04	442	31.41	605	87.78	758	50.48	1261	74.49
Lestrigonus bengalensis	61	11.26	11	7.15	94	12.78	76	7.21	157	14.15	324	23.01
Tetrathyrus forcipatus	20	20.82	1		31	4.08	3		49	3.79	31	
Oxycephalus clausi	13	10.34	4						9			
Brachyscelus crusculum	5	5.72	1		8		5		19	4.84	20	
Lestrigonus schizogeneios	4		2		39	6.35	342		28	2.00	39	
Parascelus edwardsi	9	3.49	3		11	6.36	27	5.33	26	3.78	3	
Lestrigonus shoemakeri	4		6		8		8		41	2.42	41	
Vibilia longicarpus	0				44	17.97			1		44	
Lycaeopsis zamboangae	8		1		26	7.70	14		10		26	
Simorhynchotus antennarius	4	4.65	1		3		5		13	1.41	8	
Euthamneus rostratus	3				55	4.26			0		55	
Paralycaea hoylei	3		1		4		12		24	2.84	2	
Phronima atlantica	0		0		1				13	2.65	1	
Lestrigonus macrophthalmus	0		0		1		0		22	1.72	1	
Total		92.42		92.19		90.9		93.32		90.09		97.49

Table 4. SIMPER analysis (dissimilarity) of the hyperiid species abundances during the climate periods. DP: mean dissimilarity percentage for each group, R: results of the ANOSIM test of paired comparisons, p: associated probability, %: mean contribution percentage to dissimilarity. CC: period dominated by California Current, NE: period dominated by North Equatorial Countercurrent

Species	96CC & 96NE	96CC & 97CC	96CC & 97NE	96CC & 98CC	96CC & 98NE	96NE & 97CC	96NE & 97NE	96NE & 98CC	96NE & 98NE	97CC & 97NE	97CC & 98CC	97CC & 98NE	97NE & 98CC	97NE & 98NE	98CC & 98NE
DP:	86.92	88.23	84.93	87.37	87.09	86.91	72.32	82.69	75.11	81.19	83.89	81.51	73.14	60.69	67.16
R:	0.126	0.170	0.278	0.249	0.443	0.139	0.225	0.241	0.484	0.263	0.192	0.425	0.126	0.174	0.129
p:	0.019	0.001	0.001	0.001	0.001	0.012	0.006	0.003	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
Hyperioides sibaginis	49.95	28.79	58	39.64	66.23	43.75	60.85	46.34	66.02	52.27	39.41	61.41	50.46	60.33	58.26
Lestrigonus bengalensis	9.19	10.33	9.76	10.84	21.1	7.24	8.08	9.46	22.97	8.22	9.33	17.97	9.36	19.53	16.14
Lestrigonus schizogeneios	1.78	4.88	6.98	2.18		3.75	7.43	1.85		7.53	3.04	1.84	6.66	6.4	1.53
Tetrathyrus forcipatus	4.8	6.04	2.17	4.72	1.25	3.56		3.82		2.3	4.3	1.52	2.94		2.4
Vibilia longicarpus		12.22				10.07	1.1			6.27	5.74	3.55			
Parascelus edwardsi	2.31	2.99	4.75	3.02		2.1	4.76	2.62		3.27			2.87	2.26	1.47
Lestrigonus shoemakeri	3.75	2.31	1.62	2.76		2.91	2.24	3.34		1.49	2.64		2.51		2.01
Lycaeopsis zamboangae	1.34	4.47	2.39	1.85		3.51	2.15	1.39		2.45	2.37	1.46	1.38		0.79
Brachyscelus crusculum	1.93	2.62		5.26		1.8		4.43			3.49		2.45		1.66
Paralycaea hoylei			1.59	3.74			1.58	3.41		1.35	2.92		2.66		1.77
Euthamneus rostratus	1.27	5.36				4.23				2.8	2.72	2.06			
Oxycephalus clausi	4.44	3.17	1.93	2.25		0.96		0.93							
Hyperietta vosse			2.21				2.33			2.08	0.85		2.1	1.9	0.82
Lestrigonus macrophthalmus				1.43	1.43			1.42	1.52		1.26	1.23	1.24		1.6
Lycaea pulex	2.55	1.15		1.15		1.68		1.41			1.2		0.81		
Vibilia armata	1.55			2.36				2.24			1.56		1.11		
Simorhynchotus antennarius	2.03	1.44		1.41				1.11			0.96		0.94		
Phronima atlantica				2.15				1.87			1.5		1.22		0.89
Lycaea vincentii	1.44	1.35		0.91		1.38		1.02			1.05				
Lycaeopsis themistoides				1.52				1.58			1.22		1.06		
Platyscelus serratulus				1.12				0.89			0.74		0.75		0.78
Scina marginata		1.64				1.3					0.78				
Rhabdosoma whitei	1.37										2.16				
Lycaea pachypoda		1.19				1.48									
Vibilia propinqua			0.9					0.99			0.7				
Lycaea serrata		1.19				0.96									
Amphithyrus sculpturatus				0.96							0.74				
Vibilia borealis	1.17														
	90.87	91.13	91.38	90.18	90.02	90.67	90.53	90.1	90.51	90.03	90.68	91.04	90.53	90.43	90.13

Table 5. SIMPER analysis (similarity and dissimilarity) of the hyperiid species abundances during pre-EN (before July 1997), EN (July 1997 to April 1998), and post-EN periods. Av: average abundance of group, SA: similarity average, DA: dissimilarity average, R: ANOSIM test of paired comparisons, p: associated probability, %: contribution to group

	Similarity						Dissimilarity		
	Pre-EN		EN		Post-EN		Pre- & EN	Pre- & post-EN	EN & post-EN
SA/DA:	15.01		32.72		38.54		82.1	82.12	65.9
R:							0.09	0.109	0.017
p:							0.001	0.002	0.014
Species	Av	(%)	Av	(%)	Av	(%)			
Hyperioides sibaginis	394	51.26	880	74.4	1041	67.24	52.54	55.37	55.44
Lestrigonus bengalensis	70	15.49	139	11.33	342	25.81	10.36	19.5	16.52
Tetrathyrus forcipatus	18	7.81	28		7		3.11	1.83	1.92
Oxycephalus clausi	9	4.65	8		0		1.47	0.95	
Brachyscelus crusculum	5	3.44	11		3		2.54		1.29
Lestrigonus schizogeneios	13	2.59	167	1.53	9		4.4	1.52	3.78
Parascelus edwardsi	10	3.73	25	3.91	7		3.12	1.37	1.98
Lestrigonus shoemakeri	6		29	1.66	11		2.5	1.67	2.07
Vibilia longicarpus	12		3		0		1.8	1.2	
Lycaeopsis zamboangae	11		10		13		1.63	1.86	1.21
Simorhynchotus antennarius	3		9		8		0.91		0.78
Euthamneus rostratus	17	1.91			2		1.06	1.44	
Paralycaea hoylei			*11*		*15*		1.27	1.95	1.83
Lestrigonus macrophthalmus			10		13			1.4	1.35
Hyperietta vosseleri			19		4		1.7		1.42
Total		90.87		90.87		93.05	88.4	90.05	89.59

was related to the peak of EN influence (ca. January 1998) (Table 4).

Hyperioides sibaginis and *Lestrigonus bengalensis* contributed up to 93% of the similarity during the post-EN period (Table 5). In the pre-EN group, besides *H. sibaginis*, other species (*Tetrathyrus forcipatus*, *Oxycephalus clausi*, *Parascelus edwardsi*, *Brachyscelus crusculum*, *Lestrigonus schizogeneios*, and *Euthamneus rostratus*) marked the group. During EN, *P. edwardsi*, *L. shoemakeri*, and *L. schizogeneios*, in addition to the 2 most abundant species, contributed >90% to the group. The EN and post-EN groups were the least dissimilar, but the greater dominance of *H. sibaginis* and *L. bengalensis* and a higher number of species in the post-EN group were the main differences (Table 5).

Up to 90% of the group at the inshore stations was represented by *Hyperioides sibaginis*, *Lestrigonus bengalensis*, and *Tetrathyrus forcipatus*; the offshore group included the first 2 species as well (Table 6). The dissimilarity analysis showed that the main inshore-offshore difference is that these species are less abundant off the coast.

The redundancy analysis showed 2 almost orthogonal axes representing the temporal variation defined by the multivariable El Niño Index (MEI) and the spatial variation defined by the distance of the stations on the coast (Fig. 10). Zooplankton biomass showed a high correlation with the axis of distance from shore. The species associated with EN (high MEI values) were *Eupronoe armata*, *Lycaeopsis themistoides*, *Amphithyrus sculpturatus*, *Lestrigonus shoemakeri*, *Phronimella elongata*, *Hyperietta vosseleri*, and *Phronima atlantica.* The species related to low MEI values were *Lycaea pachypoda*, *Cranocephalus scleroticus*, and *Rhabdosoma minor*. Both of the patterns of variability, the inter-annual related to the EN event and the seasonal one, were detected (Fig. 10). The group of stations during the EN period was more compact than in the pre-EN period. The greater dispersion of stations on the vertical axis shown during CC periods suggests a warm-cold periodic variability, which was weak but detectable during 98CC (EN). The Monte Carlo method indicates a significant relationship with environmental variables (Table 6).

DISCUSSION

The search for understanding of the functional structure of the pelagic ecosystem is currently at the core of modern oceanography. This structure is de-

termined by physical forces and the associated biological responses (Platt & Sathyendranath 1999). Our analysis provides evidence showing that the local hyperiid community structure has distinctive features according to distinct hydrographic patterns. It also reveals that these patterns are different from those observed in surrounding areas and diverge from those known for other zooplanktonic taxa.

Species composition

Previous studies of the hyperiids of Mexico's central Pacific are scarce (Gasca & Franco-Gordo 2008). It was expected that the monthly collection of samples for 2 yr (1996 to July 1997) would provide a complete account of species in the area. We did not expect the additional increase of species observed after July 1997 in the surveyed area. The addition of almost 30% of the previous species richness indicates that hyperiids, like other zooplankton, show a sharp increase of tropical-equatorial forms during EN, as was observed for copepods (Lavaniegos et al. 2003, Palomares-García et al. 2003, López-Ibarra & Palomares-García 2006) and salps (Hereu et

al. 2006). Furthermore, considering the 56 species known before the onset of EN and the 24 recorded after July 1997, the increase was 43% (Table 2) (Gasca 2009a, Gasca et al. 2010).

The 84 species recognized in tropical areas of the Pacific coast of Mexico, south of Baja California, i.e. 80 in this study plus *Vibilia pyripes*, *V. australis*, *V. cultripes*, and *V. stebbingi*, recorded by Shih & Hendrycks (2003), represent ~50% of all known species in the tropical Pacific (Vinogradov 1991). This figure is comparable to that of other subregions of the Pacific (Vinogradov 1991: 119 species; Shulenberger 1977: 83 species). However, >200 species have been found to occur in the Pacific Ocean (Shih & Cheng 1995, Vinogradov et al. 1996), and regional lists should grow when deeper waters are sampled (Gasca 2009b).

Table 6. SIMPER analysis (similarity and dissimilarity) of the hyperiid species abundances at inshore and offshore stations during the surveyed period. Av: average abundance of group, %: contribution to group, SA: similarity average, DA: dissimilarity average

| | Similarity | | | | Dissimilarity |
	Inshore		Offshore		Inshore vs. offshore
SA/DA (%)	24.43		21.11		78.21
	Av	%	Av	%	
Hyperioides sibaginis	948	73.39	458	58.14	51.75
Lestrigonus bengalensis	191	14.66	117	19.94	13.79
Tetrathyrus forcipatus	26	3.06	11		3.26
Oxycephalus clausi	9		5		1.78
Brachyscelus crusculum	7		6	2.09	1.8
Lestrigonus schizogeneios	108		13	2.49	3.51
Parascelus edwardsi	15		13	3.44	2.31
Lestrigonus shoemakeri	12		17	2.17	2.21
Vibilia longicarpus	7		5		2.12
Lycaeopsis zamboangae	10		12	2.68	1.73
Euthamneus rostratus	13		3		1.55
Total		91.11		90.95	85.81

Abundance

A group of species including *Phronima atlantica*, *Phronimella elongata*, *Phrosina semilunata*, and some species of *Primno* was proposed by Vinogradov (1999) as being among the
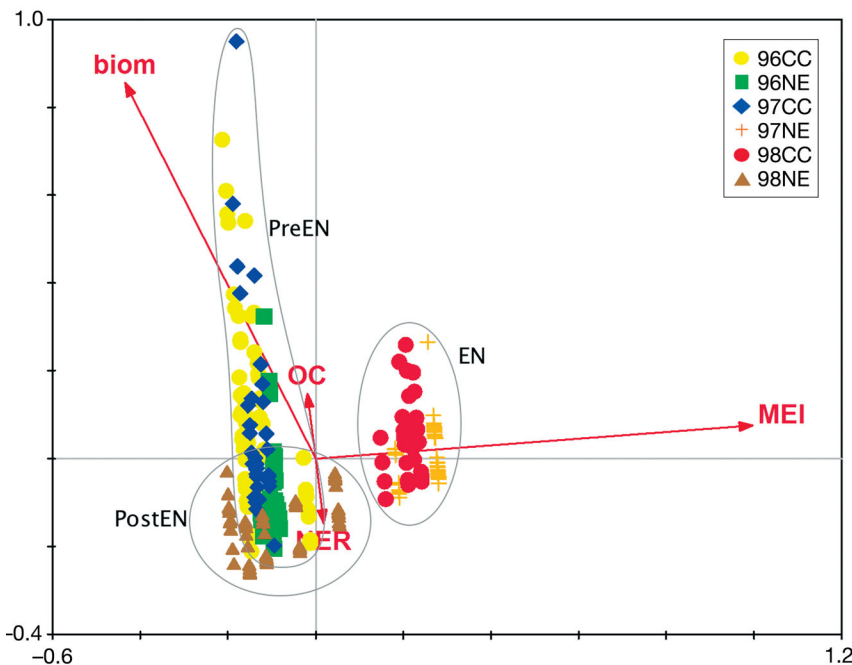

Fig. 10. Ordination pattern of temporal variation from the redundancy analysis

most abundant species in the Pacific. However, data from different regions, such as the eastern South Pacific Gyre (Vinogradov 1991), the Gulf of California (Siegel-Causey 1982) and the CC area off Baja California (Lavaniegos & Hereu 2009), suggest a different trend. In the study area and in other tropical Pacific regions, *Hyperioides sibaginis* and *Lestrigonus bengalensis* were the most abundant (Gasca & Franco-Gordo 2008, Zeidler 1984, Valencia & Giraldo 2009). In general, each area of the Eastern Pacific with different oceanographic features can be characterized by a defined group of most abundant species.

The hyperiid fauna of the Mexican tropical Pacific resembles that of the Gulf of California but clearly differs from that of the CC. None of the 4 most common species in the surveyed area are among the predominant forms in the California region (Brusca 1981, Lavaniegos & Ohman 1999). This suggests that the presumed CC influence was not detected in the local hyperiid fauna even during the CC periods. However, the increase in the number of species in the CC periods shows the arrival of species from other subregions.

The overall average abundance of hyperiids in the study area (1070 ind. 1000 m^{-3}) was similar to that found in the adjacent Banderas Bay (1167 ind. 1000 m^{-3} in September) (Gasca & Franco-Gordo 2008) and is comparable to values reported in other areas, like the North Pacific Central Gyre (1 to 3695 ind. 400 m^{-3}) or adjacent areas of the Atlantic such as the Gulf of Mexico (1437 ind. 1000 m^{-3}) (Gasca 2004), but is higher than those found in oligotrophic waters of the Caribbean (240 ind. 1000 m^{-3}) (Gasca & Suárez-Morales 2004).

Hyperiid abundance was relatively low during 1996, and the local community structure was characterized by the dominance of *Hyperioides sibaginis* and *Lestrigonus bengalensis*. The progressive increase in the abundance of hyperiids from the beginning to the end of the sampling period, as shown by the average of the different CP (Fig. 2a), was unexpected. It is possible that it resulted from the addition of populations of different origins or the influence of EN. The influence of the cold (CC) and warm (NE) conditions in the area was clear, with lower abundances during the cold periods than in the warm ones, a pattern that remained even during the EN year. The only CPs in which no differences in abundance occurred were 97NE and 98CC, both during EN. Hence, the hyperiid abundance could be considered as a local indicator of EN. Furthermore, even greater abundances were recorded in the following months, suggesting that EN may trigger or favor higher reproductive rates of the dominant species for a longer period.

Quite unexpectedly, hyperiids were more abundant during the EN than during the previous years. EN has been commonly associated with a relatively low zooplankton productivity and abundance (Barber & Chavez 1983, Roemmich & McGowan 1995, Franco-Gordo et al. 2001a,b, 2004). Locally, this effect could be explained by an increase in the reproduction of the dominant hyperiid species and possibly by the addition of populations of different origins resulting from the local convergence of distinct water masses.

The 4 most abundant species in this study (*Hyperioides sibaginis*, *Lestrigonus bengalensis*, *L. schizogeneios*, and *Tetrathyrus forcipatus*) were the same throughout the study period. The other species showed 2 patterns: (1) occurring or being more frequent during EN (e.g. *Paralycaea gracilis*, *Eupronoe armata*, *Anchylomera blossevillei*, and *Phronimella elongata*) and (2) absent or decreasing in frequency during EN (e.g. *Scina marginata*, *T. forcipatus*, *Cranocephalus scleroticus*, *Rhabdosoma minor*, and *Lycaea pachypoda*); these species were also absent when warm waters prevailed in the area.

Diversity

Sequential changes in richness were evident and related to the arrival of warmer waters (PESW) resulting from the influence of EN. The number of species was significantly lower during the first half of the study than in the second (Fig. 5). During the study period, the temporal monitoring of the species richness allowed the detection of changes that may be associated with variations of the hydrographic conditions. Unexpectedly, richness values in the CC CPs were higher than during the warm (NE) periods, but an even greater richness value was recorded in CC 1998; this could be due to the addition of the PEW fauna arriving with EN. Lavaniegos & Ohman (1999) observed a different pattern in the CC off southern California; they observed that the years with fewer species were 1995 and 1997, although in 1972 (another EN year), they also recorded more species. The finding of greater richness during EN (vs. pre- and post-EN) and EN-related CPs indicates the strong influences of this event on the expected number of species.

Greater diversity values in CC than in NECC periods are explained by the combination of the following factors: (1) the high number of species found in CP CC, (2) their low dominance, (3) the arrival of

water from the north and east adding to the local fauna, and (4) reduced dominance of the 2 most abundant species in the area. The greater diversity observed in the 97NE period resulted from a higher evenness value. The high diversity found in EN1 is related to the higher number of species found in that period. In contrast, the post-EN low diversity results from the high dominance of *Hyperioides sibaginis* and *Lestrigonus bengalensis* in that period; these species were favored by the warm conditions associated with EN.

Evenness

The mixing of water masses during the CC and EN periods was favorable for higher values of evenness and characterized the convergence of waters in the area. The arrival of warm water fauna weakened the dominance of some species, as observed in other NECC periods. That is, at the onset of EN, the NECC hyperiid community is more similar to that influenced by the CC influence (with higher diversity and lower dominance).

Analysis of the hyperiid community

The ANOSIM revealed CP- and EN-related communities and also inshore and offshore communities in an area where the continental shelf is very narrow. There is a defined community structure related to EN (EN1: July 1997 to March 1998). The SIMPER analysis allowed us to define the structure of each of the communities tested (Tables 3 to 6).

As found in our survey, the known biological consequences of EN in the zooplankton include changes in species composition (Gómez-Gutiérrez et al. 1995, González et al. 2000, Lavaniegos & Ohman 1999). Also, biomass may increase (Brodeur & Ware 1992), decrease (Roemmich & McGowan 1995), or remain stable (Lavaniegos & Ohman 1999), depending on the area and the group surveyed (Fiedler 2002). The impoverishment of the pelagic environment as an effect of EN has also been described for zooplankton and ichthyoplankton taxa in the eastern Pacific (Chavez et al. 1999, Franco-Gordo et al. 2004); however, the local hyperiid community showed a reverse pattern (e.g. higher abundances and diversity). This may be related to the biology of some of the species that use other organisms (gelatinous zooplankton) for their sustainment and thus do not depend entirely on the availability of food in the environment.

Franco-Gordo et al. (2004) found local inter-annual variations of the zooplankton biomass and the ichthyoplankton related to EN (e.g. less abundance and diversity). They also detected a response of the fish larvae community to seasonal cycles related to hydrographic and climatic conditions. As reported herein, hyperiids showed a seasonal variation resulting from the influence of EN, but with an opposite pattern. Under the influence of the CC, fish larvae and biomass showed a greater abundance and a reduced diversity and evenness, whereas during EN, the abundance and diversity were lower.

During the onset of EN, the biological production and dynamics changed in coastal areas of the CC system and other areas of the Eastern Tropical Pacific (Morales-Ramírez & Brugnoli-Olivera 2001, Lavaniegos et al. 2002). Conditions returned to normality in the aftermath. A similar response, with a delay of 1 to 2 mo, was observed in the tropical Pacific (Chavez et al. 1998, 1999), suggesting that the influence of EN in the regional biota is detectable at the initial but not at the final stages. This is true for the local hyperiid community, whose return to pre-EN conditions was not observed. Our results suggest that the residual effects of EN on the hyperiid community continued for several months after the oceanographic end of EN. This inertial response has not been described previously and is evidence of the wide variety of potential responses that different zooplankton taxa may present as part of this complex pelagic community. It is necessary to study the biological-physical coupling of different zooplankton groups in the area during EN to fully understand the effects of this event in the community.

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