Seasonal and interannual variability of the calanoid copepod community structure in shelf waters of the Eastern Tropical Pacific

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ABSTRACT: The response of the calanoid copepod community structure and diversity to the variability of the oceanographic conditions was analyzed from January 1996 to December 1998 in the central Mexican Pacific. Interannual variability in the water column was marked by the influence of the 1997-98 El Niño (EN). However, seasonal variability was principally linked to the periodicity of coastal upwelling processes. Two species, *Subeucalanus subcrassus* and *Centropages furcatus*, contributed 62% to the copepod abundance over the 3 yr period, with 16 species making up 95% of the copepod community. Most species were subtropical-tropical (88%), but equatorial (8%) and cosmopolitan (2%) species were also present. Up to 17 species were recorded in 50% or more of samples, of which 10 were coastal or neritic forms. The calanoid copepod community structure varied seasonally, with increased abundance and reduced species richness during upwelling conditions. During upwelling relaxation, the abundance declined but the species richness increased. Additional community variations were related to the EN event, when copepod abundances were significantly lower than during non-El Niño (NEN) periods ($F = 20.387$, $p < 0.05$), but seasonal changes were still detectable. There was no increase of species richness in the area related to the influence of EN. These data suggest that the response of this tropical neritic copepod community diverges from that of other zooplankters and that the community is more stable than expected, keeping a seasonal pattern even during the influence of a strong EN.

KEY WORDS: Calanoid copepods · Species assemblages · El Niño · Mexican central Pacific

INTRODUCTION

Calanoid copepods are deemed valuable indicators of environmental variability because they are frequently the most abundant group in the marine zooplankton and their abundance and distribution is strongly influenced by hydrographic conditions (Ashjian & Wishner 1993, Beaugrand & Ibanez 2004). On the central Mexican Pacific coast in the Eastern Tropical Pacific, the knowledge of copepod responses to changes of environmental conditions at shelf and outer areas is limited. The only previous survey in the area (Suárez-Morales et al. 2000) described the structure of the copepod community of near-shore waters during September 2009. Those authors reported relatively high copepod abundances and high levels of across-shelf mixing. Studies of the variability of the zooplankton biomass and the community structure of other zooplankters (including fish larvae, hyperiid amphipods, and euphausiids) in the region has shown that these groups have distinctive responses to the seasonal hydro-climatic regime and interannual variability such as the 1997-98 EN (Franco-Gordo et al. 2002, 2004, Ambriz-Arreola et al. 2012, Gasca et al. 2012).

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Although the central Mexican Pacific is deficient concerning copepod community studies, the general responses of these pelagic crustaceans to seasonal events such as upwelling/downwelling and El Niño (EN) interannual anomalies have been well documented in other regions of the eastern Pacific (Hidalgo & Escribano 2001, Hopcroft et al. 2002). Two major upwelling systems are often the focus of research efforts along the eastern Pacific coast: the California and the Humboldt Current Systems. Seasonal conditions prevail in the northern section of the California system, whereas south of Baja California, there is a weak year-round upwelling. The Humboldt system off southern Chile has a highly productive summer upwelling, which shifts to a low-moderate 'upwelling shadow' off northern Chile and southern Peru, and a highly productive year-round system off central/northern Peru (Chavez & Messié 2009). Usually, the copepod species that dominate each region differ, yet there are some similarities in the general structure. For example, *Acartia* spp. and *Calanus* spp. are abundant in both upwelling systems (Peterson et al. 1979, Rebstock 2001, Jiménez-Pérez & Lavaniegos 2004).

The documented responses of the copepod communities in the eastern Pacific Ocean to the 1997-98 EN, one of the strongest on record (McPhaden 1999), showed distinct regional patterns. In northern Chile the copepod abundance decreased during EN while the number of species increased, with slight diversity variations between non-EN (NEN) and EN conditions (Hidalgo & Escribano 2001). Off Baja California, tropical and equatorial species dominated; subarctic copepod species previously recorded in the area were scarcer (Jiménez-Pérez & Lavaniegos 2004). In contrast to Chile, the abundance of copepod communities off northern California and Oregon remained stable between EN and La Niña periods, while the species composition changed dramatically, with warm water species dominating during EN (Peterson & Keister 2002). There are no previous data of these community aspects in a tropical neritic community of the Eastern Pacific.

The central Pacific coast of Mexico in the Eastern Tropical Pacific (ETP) has a narrow continental shelf, only 7 to 10 km wide (Filonov & Tereshchenko 2000). This is a highly dynamic area affected by local seasonal events, mesoscale features, and a complex mixing of currents not clearly defined (Kessler 2006, Godínez et al. 2010). Upwelling events occur from February to May and favor local increases of the primary production; these are followed by a transition period in late spring/early summer to a stratification of the water column and low productivity from July to December (López-Sandoval et al. 2009a,b). Surface dynamics are affected by the continuous presence of mesoscale features such as eddies and thermal fronts, which account for close to 30% of the local variance (Torres-Orozco et al. 2005, Zamudio et al. 2007, Godínez et al. 2010). The shallow upper boundary of the oxygen minimum zone (OMZ) (9 µmol O_2 l^{-1}), which is characteristic of the ETP, can rise to depths of 60 m in this coastal region during March (upwelling), and drops again in August (upwelling relaxation) (Cepeda-Morales et al. 2013). The OMZ is located between the Tropical Surface Water (<30 m), which has relatively high temperatures (>25°C) and low salinity (<34), and the Subtropical Subsurface Water, characterized by lower temperatures (<18°C) (Wyrtki 1967, Filonov & Tereshchenko 2000). The ocean circulation in the region is influenced by the northward Mexican Coastal Current, which develops in early summer, and an offshore geostrophic branch of the California Current water active during spring (Wyrtki 1967, Kessler 2006, Lavín et al. 2006). The interannual variability in the ETP is influenced by the effects of the El Niño/Southern Oscillation (ENSO) cycle (Lavín et al. 2006, Godínez et al. 2010).

These features allowed us to study the effects of both the local coastal upwelling activity and the interannual EN-related events in a tropical copepod assemblage. We analyzed monthly zooplankton samples from a 1996 to 1998 time series (Franco-Gordo et al. 2002, 2004) in order to describe the interannual response of the adult calanoid copepod community to the prevailing environmental conditions. The community assemblage was examined for its composition, abundance, and diversity over the course of this 3 yr period during which a strong EN event occurred. According to Filonov & Tereshchenko (2000), the EN event locally influenced the Mexican Pacific shelf from July 1997 and ended by fall 1998. We investigated the effect of the 1997-98 EN on the structure of the calanoid copepod community by comparing the non-anomalous 1996 and early 1997 seasons to the correlative EN-influenced seasons.

MATERIALS AND METHODS

Field methods

Zooplankton and hydrographic data were obtained along the Mexican Pacific coast (19° N, 105° W) during a monthly time series carried out from January

1996 to December 1998 at twelve oceanographic stations (Fig. 1). All zooplankton samples were taken at night (20:00 to 07:00 h), hauling 61 cm diameter Bongo nets fitted with 505 μm mesh at a speed of 0.4 to 0.5 m s⁻¹ from 120 m or (at shallow stations) 10 m above the sea bottom to the surface. Calibrated digital flowmeters were attached to the mouth of the nets in order to estimate the amount of seawater filtered (Smith & Richardson 1977). Samples were preserved in a 4% formalin solution buffered with sodium borate (Griffiths et al. 1976). Vertical profiles of temperature and salinity were recorded with a SBE-19 CTD profiler prior to each tow. Due to adverse weather conditions (hurricane season) or logistical issues, the months of August and September in 1996; April, June, October, and November in 1997; and February, October, and November in 1998 were not sampled.

Data collection

A total of 139 zooplankton samples were analyzed, using 6 of the original 12 stations sampled in each monthly cruise. In the laboratory, samples were fractioned using a Folsom plankton splitter until 300 to 500 copepods were present in each subsample. Adult calanoid copepods were identified to species level following literature on the taxonomy of copepods found in the Eastern Tropical Pacific (ETP) and global distribution (Fleminger 1967, Palomares et al. 1998, Razouls et al. 2014). Abundance was standard-ized to ind. m⁻³. Species were arranged by biogeographic affinity according to previous records in the ETP (Brinton et al. 1986, Jiménez-Pérez & Lavaniegos 2004, Razouls et al. 2013). Copepod prosomes of selected species were measured for comparison purposes and correlation with environmental variables. Due to potential shrinkage resulting from storage in ethanol, biomass estimates using length-weight relations were not calculated.

Data analysis

The hydrographic and biological data were classified *a priori* following the known climatic periods in the area, as described by Ambriz-Arreola et al. (2012). Conditions were defined as mixed (upwelling), semi-mixed (transitional), and stratified (downwelling). Data were further separated into NEN (January 1996 to June 1997) and EN periods (July 1997 to May 1998). The standardized copepod abundance data were log(x + 1)-transformed in order to decrease the variance of the data set before performing the statistical or multivariate analyses. Analyses of variance (ANOVA) were used to test for statistical differences between groups. In the case of significant differences, exploratory post-hoc analyses using the Tukey method allowed us to define the differences. The coastal upwelling index (CUI) was calculated from the location 21° N, 107° W, and used to classify upwelling and upwelling relaxation conditions during each sampled period (www.pfel. noaa.gov/products/products.html).

Relationships between species assemblages and environmental characteristics were analyzed using redundancy analysis (RDA). Rare species, defined as those appearing in <5% of samples, were not included in the multivariate analyses. Environmental (explanatory) variables consisted of temperature at 10 m, salinity at 10 m, station depth, CUI, and the multivariate ENSO index (MEI) (www.esrl.noaa.gov/psd/enso/ mei/). To test for the significance of the first ordination axis and all canonical axes together, a Monte Carlo permutation test (499 permutations) was applied. Attribute plots of relative abundances of species were presented using the RDA environmental variables over the climatic periods. All multivariate analyses were performed using the CANOCO v. 4.5 software (Ter Braak & Šmilauer 2002). Similarity tests (ANOSIM) were
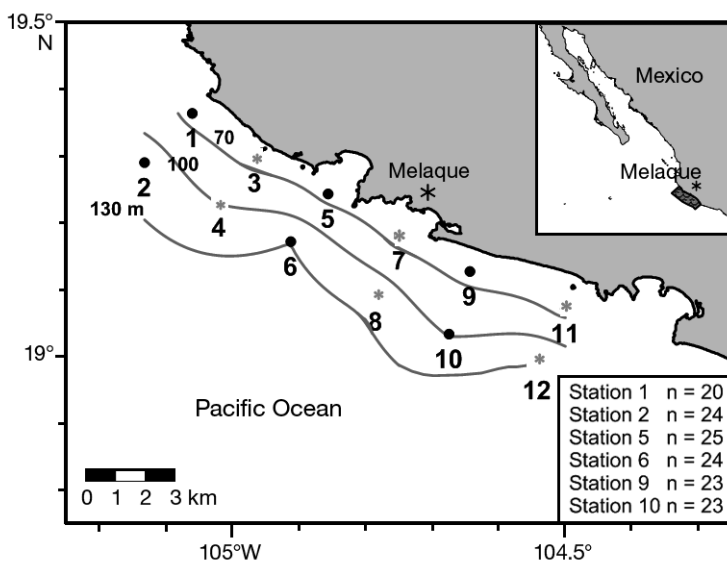

Fig. 1. Study area off the central coast of the Mexican Pacific. Solid circles are sampled stations used for analyses in the present study; asterisks are stations originally sampled but not used

performed to statistically evaluate differences between climatic periods. ANOSIM calculates an *R* statistic which reflects rank similarities between sites, and uses a permutation test to analyze whether *R* is significantly different from zero. An *R* value of zero represents the null hypothesis of no difference among a set of samples. If the species composition of 2 groups of sampling sites is different, then the dissimilarities between the sites will be greater than those within the sites and *R* will be greater than zero (Clarke & Warwick 2001). The similarity percentage (SIMPER) was used to identify the species that contribute to 50% of similarities within sites. Analyses were performed with the PRIMER 6 software, using untransformed data with the Bray Curtis index (Clarke & Gorley 2006).
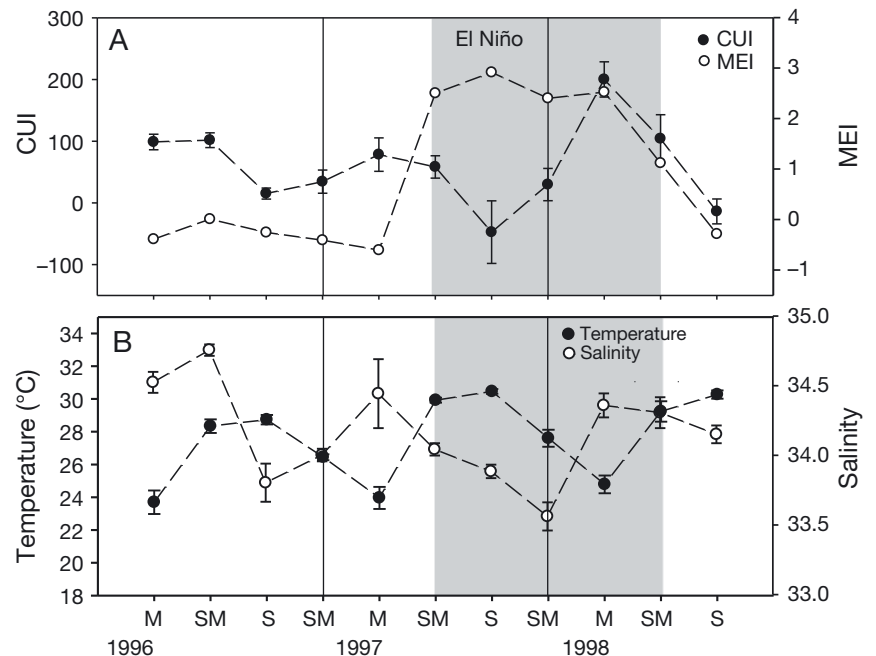

Fig. 2. Environmental conditions per climatic period recorded from 1996 to 1998 in the central Mexican Pacific. (A) Mean daily coastal upwelling index (CUI, $m^3 s^{-1}$ per 100 m coastline, 21° N, 107° W; NOAA) (bars are 95% confidence intervals) and multivariate ENSO index (MEI) (NOAA, www.esrl.noaa.gov/psd/enso/mei/), (B) mean temperature and salinity of 6 oceanographic stations sampled along the coast of Jalisco and Colima, Mexico; bars are 95% confidence intervals. M: mixed period; SM: semi-mixed; S: stratified. Gray area represents an El Niño event

RESULTS

Oceanographic conditions

Monthly profiles of temperature, salinity, CUI, thermal stratification, and classification of the water column conditions obtained during the 1996 to 1998 cruises were presented in Franco-Gordo et al. (2004) and Ambriz-Arreola et al. (2012). Therefore, the most relevant hydrographic features are summarized here, emphasizing the conditions prevailing during the surveyed period. Over the 3 yr period, seasonal and interannual patterns in oceanographic conditions were clearly defined (Fig. 2). During NEN, seasons were based on the conditions of the water column and defined as mixed (M), semi-mixed (SM), and stratified (S). The M period (February, March, April and May) was characterized by upwelling conditions and mixed water column, relatively low average temperatures (*T*) at 10 m (*T* < 25°C) and high average salinities (*S* ≈ 34.5). During the S period (July, August, September, October and November), upwelling conditions relaxed, the water column appeared stratified, average temperatures increased (*T* > 28°C), and salinity decreased (*S* < 34.0) coinciding with the rainy season. The pattern of upwelling and relaxation was also supported by the CUI, which showed increased upwelling during the M period, and depressed upwelling conditions during the S period. In the transitional SM periods, intermediate between S and M

conditions (December, January and June), the water column had intermediate salinity and temperature values. The MEI positive anomalies allowed detection of an EN event in the region from July 1997 to May 1998. Filonov & Tereshchenko (2000) reported that such sea surface anomalies became positive in July 1997 in the area off the central Mexican coast and continued to increase until reaching a peak in January 1998. After January, the positive anomalies decreased rapidly, decaying to almost zero in June 1998. Seasons during EN event were defined as EN mixed (ENM), EN semi-mixed (ENSM) and EN stratified (ENS); months were the same as the NEN seasons. Seasonal temperature and salinity at 10 m during both EN and NEN periods showed a similar seasonal pattern. However, temperature did increase significantly during ENS and ENSM conditions (*F* = 89.49, p < 0.05). The ENM period mean upwelling increased from average NEN conditions. During the ENS period, CUI was suppressed below average at NEN conditions. There were no significant differences in temperature or salinity between stations at 3 and 5 km from the coast over the sampling period (temp: *F* = 0.01, p > 0.05; salinity: *F* = 0.53, p > 0.05).

Copepod species composition and abundance

A total of 60 calanoid copepod species belonging to 14 families and 31 genera were identified during the surveyed period (Table 1). The neritic species *Subeucalanus subcrassus* and *Centropages furcatus* contributed 48% to the relative abundance over the 3 yr period, with 16 species making up 95% of the total copepod abundance. Ecological affinities of the species recorded included the following categories: mesopelagic (5%), oceanic (59%), coastal (5%), neritic (27%), and estuarine-coastal (3%). Most species were subtropical/tropical (88%), with few equatorial (8%) or cosmopolitan (2%) varieties. Seventeen species were recorded in 50% or more samples; 10 of them were of coastal or neritic affinity. Four species with no previous report in the region were recorded exclusively during EN: *Labidocera detruncata, Labidocera diandra, Neocalanus robustior* and *Pontella agassizi. Scolecithricella nicobarica* was found dur-

ing and after EN, while *Euchaeta magniloba* was seen exclusively after EN. These latter 6 species registered very low abundances (Table 1).

Monthly abundances over the sampling period indicated a seasonal variability of the copepod community (Fig. 3). Abundances were significantly different between water column periods (F = 21.41, $p < 0.05$), with maximum abundances during the M period and lowest in the S period. During the EN event, abundances were significantly lower than in the NEN periods (F = 20.39, $p < 0.05$), although there were still seasonal variations (Fig. 4). During the NEN period, a gradient of decreasing abundance was observed offshore (3 to 5 km from the coast). This gradient was lost during EN, when there was no significant difference in abundance in the same distance range from the coast (F = 4.99, $p < 0.05$) (Fig. 5).

The low abundances of certain oceanic species (i.e. *Cosmocalanus darwini, Euchaeta rimana, Candacia*

Table 1. Adult calanoid copepod species identified over the 1996 to 1998 period of study. Affinity categories are neritic (N), coastal (C), oceanic (O), estuarine-coastal (E-C), mesopelagic (M), tropical-suptropical (Trop), equatorial (Equat), cosmopolitan (Cos). % Abu: percentage of total abundance over the sampled period; GM: geometric mean; %F: percentage of encounters in all samples

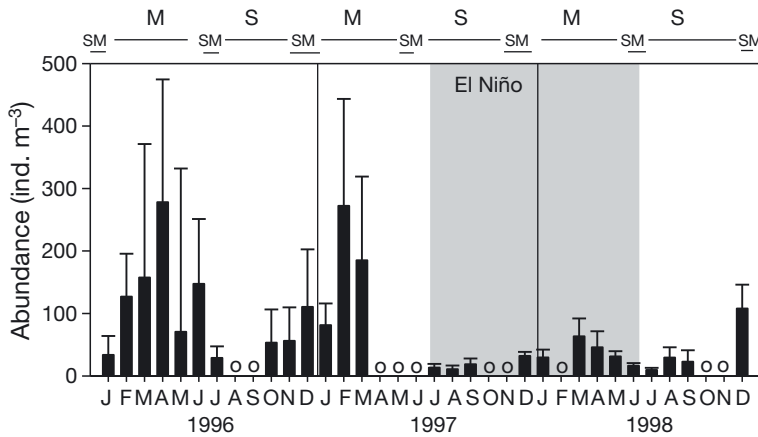| Species	Affinity		% Abu	GM	%F	Species	Affinity		% Abu	GM	%F
Subeucalanus subcrassus	N	Trop	25.80	7.96	99	*Aetideus bradyi*	N	Trop	0.20	0.06	23
Centropages furcatus	N	Trop	23.53	7.26	100	*Mesocalanus tenuicornis*	O	Trop	0.20	0.06	17
Canthocalanus pauper	C	Trop	9.67	2.99	97	*Pleuromamma piseki*	O	Trop	0.15	0.05	16
Temora discaudata	N	Trop	7.67	2.36	96	*Scolecithrix danae*	O	Trop	0.11	0.03	17
Subeucalanus subtenuis	O	Trop	4.84	1.50	83	*Pleuromamma johnsoni*	O	Trop	0.11	0.03	12
Euchaeta indica	O	Trop	4.45	1.37	76	*Clausocalanus farrani*	O	Trop	0.10	0.03	10
Labidocera acuta	N	Trop	2.48	0.77	77	*Pontellopsis lubbockii*	N	Equat	0.10	0.03	14
Undinula vulgaris	N	Trop	2.37	0.73	69	*Eucalanus inermis*	M	Equat	0.09	0.03	11
Subeucalanus crassus	N	Trop	2.31	0.71	87	*Scolecithricella abyssalis*	O	Trop	0.08	0.03	14
Acrocalanus andersoni	N	Trop	2.29	0.71	73	*Calocalanus pavo*	O	Trop	0.07	0.02	4
Candacia catula	N	Trop	1.99	0.61	63	*Scolecithricella nicobarica*	O	Trop	0.06	0.02	10
Euchaeta longicornis	M	Trop	1.81	0.56	71	*Euchirella venusta*	M	Trop	0.05	0.01	5
Scolecitrichopsis ctenopus	O	Trop	1.13	0.35	60	*Pleuromamma gracilis*	O	Trop	0.04	0.01	4
Euchaeta rimana	O	Trop	1.03	0.32	63	*Candacia curta*	N	Trop	0.04	0.01	6
Nannocalanus minor	O	Trop	0.97	0.30	54	*Rhincalanus rostrifrons*	O	Trop	0.03	0.01	7
Cosmocalanus darwini	O	Trop	0.95	0.29	50	*Clausocalanus furcatus*	O	Trop	0.02	0.01	4
Candacia truncata	N	Trop	0.65	0.20	57	*Aetideus armatus*	N	Trop	0.02	0.01	5
Acrocalanus gracilis	N	Trop	0.60	0.18	47	*Rhincalanus nasutus*	N	Cos	0.02	<0.01	4
Pontellina sobrina	O	Equat	0.53	0.16	47	*Pseudodiaptomus culebrensis*	E-C	Trop	0.01	<0.01	1
Scolecithricella marginata	O	Trop	0.46	0.14	16	*Pontellopsis perspicax*	O	Trop	0.01	<0.01	1
Scolecithrix bradyi	O	Trop	0.45	0.14	40	*Candacia pachydactyla*	O	Trop	0.01	<0.01	3
Clausocalanus minor	O	Trop	0.38	0.12	17	*Labidocera diandra*	C	Equat	<0.01	<0.01	1
Acartia tonsa	E-C	Trop	0.34	0.11	17	*Calocalanus plumulosus*	O	Trop	<0.01	<0.01	1
Pareucalanus sewelli	O	Trop	0.29	0.09	38	*Neocalanus robustior*	O	Trop	<0.01	<0.01	1
Paracalanus aculeatus	O	Trop	0.29	0.09	12	*Euchaeta magniloba*	O	Trop	<0.01	<0.01	1
Lucicutia gaussae	O	Trop	0.27	0.08	23	*Clausocalanus mastigophorus*	O	Trop	<0.01	<0.01	1
Clausocalanus jobei	N	Trop	0.26	0.08	14	*Pontella agassizi*	O	Equat	<0.01	<0.01	1
Acartia danae	O	Trop	0.26	0.08	21	*Pontellopsis regalis*	O	Trop	<0.01	<0.01	1
Acartia liljeborgi	C	Trop	0.22	0.07	15	*Pontellina plumata*	O	Trop	<0.01	<0.01	1
Centropages gracilis	O	Trop	0.21	0.07	36	*Labidocera detruncata*	O	Trop	<0.01	<0.01	1

Fig. 3. Mean abundance of adult calanoid copepods collected monthly from 1996 to 1998 in the central Mexican Pacific (o: months not sampled); bars are 95% confidence intervals. M: mixed period; SM: semi-mixed; S: stratified
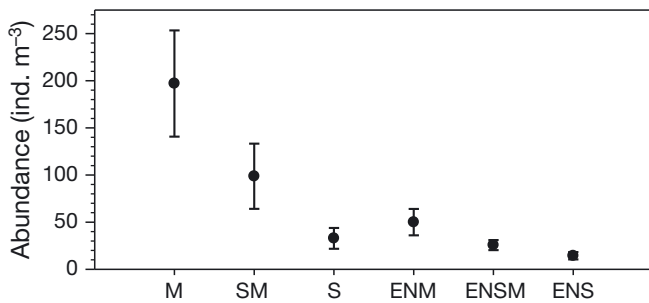

Fig. 4. Mean abundance of adult calanoid copepods per climatic period; bars are 95% confidence intervals. M: mixed period; SM: semi-mixed; S: stratified; ENM: El Niño mixed; ENSM: El Niño semi-mixed; ENS: El Niño stratified
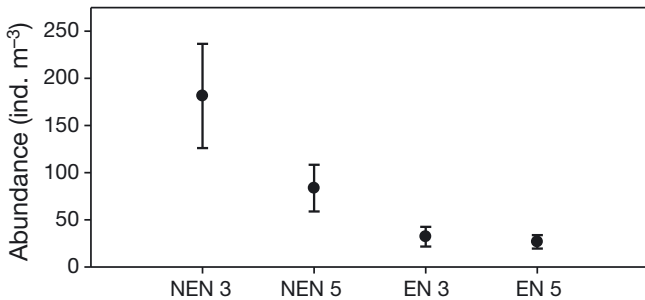

Fig. 5. Mean abundance of adult calanoid copepods per distance from the coast (3 and 5 km, respectively) during non-El Niño (NEN) and El Niño (EN) periods; bars are 95% confidence intervals

catula and *Pontellina sobrina*) observed during NEN contrasted markedly with the increase of these oceanic forms during ENSM and ENS periods. *Subeucalanus subcrassus* was the most abundant species in both M and S periods. The relative abundance of *C. catula* increased from 2.2% in the S period to 24.7% in ENS (Table 2).

Correlation with environmental variables

The RDA displayed an interannual and seasonal copepod abundance related to variability of environmental conditions in the water column, with the 6 *a priori* defined periods clearly evident (Fig. 6). The 4 canonical axes explained 42.2% of the cumulative species variance, with significant correlations in axis 1 ($F = 46.87$, p < 0.05) and across all axes ($F = 14.93$, p < 0.05). The first axis was associated with positive MEI and temperature values, and negative salinity and CUI. The second axis was positively correlated with CUI, and negatively with temperature (Table 3). The distribution of the samples along the first 2 axes indicates the effect of EN on the copepod assemblage. However, the seasonal variability (M, SM, or S) remained the principal factor that determined the change in copepod assemblages.
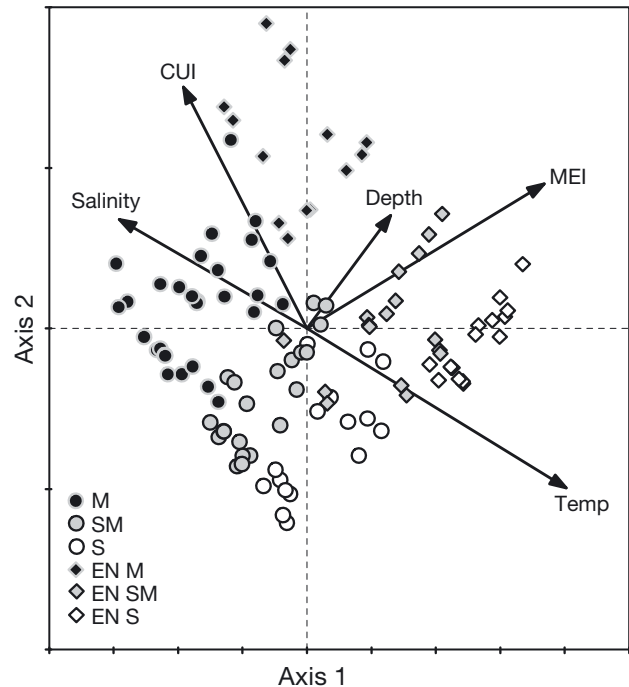

Fig. 6. Redundancy analysis biplot showing the correlation between environmental variables (black lines) and oceanographic stations, classified by water column conditions. Vector length indicates the magnitude of explained variability. Environmental variables are salinity (10 m), temperature (temp) (10 m), coastal upwelling index (CUI) and multivariate ENSO index (MEI). M: mixed period; SM: semi-mixed; S: stratified; ENM: El Niño mixed; ENSM: El Niño semi-mixed; ENS: El Niño stratified

Table 2. Relative abundances of the adult calanoid copepod species contributing at least 90% of the total abundance of each climatic period. M: mixed period; SM: semi-mixed; S: stratified; ENM: El Niño mixed; ENSM: El Niño semi-mixed; ENS: El Niño stratified

Species	M	SM	S	ENM	ENSM	ENS
Subeucalanus subcrassus	50.8	18.1	27.3	35.3	7.4	10.2
Centropages furcatus	26.8	27.1	14.9	48.9	10.0	5.1
Temora discaudata	5.7	6.4	10.6	3.1	6.1	2.4
Canthocalanus pauper	3.8	17.9	16.5		7.5	9.9
Subeucalanus subtenuis	3.4	3.3	5.6	3.1	12.0	
Euchaeta indica		6.9	4.6		15.9	10.7
Acrocalanus andersoni		4.1			2.0	
Labidocera acuta		3.0	3.0			2.7
Subeucalanus crassus		1.9	2.5			3.9
Clausocalanus minor		1.3				
Undinula vulgaris			3.1		9.1	13.3
Candacia catula			2.2		6.1	24.7
Cosmocalanus darwini					6.7	2.0
Euchaeta rimana					4.9	
Candacia truncata					2.2	2.8
Pontellina sobrina						3.7
Total	90.5	90.0	90.3	90.6	89.9	91.3
(no. of species)	(5)	(10)	(10)	(4)	(12)	(12)

Table 3. Summary of the redundancy analysis (RDA), using 5 environmental variables and abundances of adult calanoid copepod species appearing in >5% of 139 samples collected from 1996 to 1998. MEI: multivariate ENSO index; CUI: coastal upwelling index

	1	2	3	4
Eigenvalues	0.310	0.068	0.028	0.016
Species–environment correlations	0.841	0.721	0.681	0.546
Cumulative variance (%)				
Species	31.0	37.8	40.6	42.2
Species–environment relation	72.2	88.1	94.6	98.4
Inter-set correlations of environmental variables with species axes				
Temperature 10 m	0.677	−0.358	0.217	0.010
Salinity 10 m	−0.499	0.245	0.377	0.187
MEI	0.619	0.325	0.052	−0.258
CUI (monthly)	−0.323	0.542	0.261	−0.143
Depth of sampling station	0.218	0.254	−0.128	0.443

Attribute plots displaying the relative abundance of selected species showed differing patterns of abundance in the multivariate space. Species associated with shallow station depths and the M period, which had low temperatures, high salinity and coastal upwelling, included the coastal *Centropages furcatus* and *Subeucalanus subcrassus*. The oceanic *Euchaeta indica* was associated with transitional salinity and temperature values and with greater depths. Those species which were more closely associated with S periods tended to have higher abun-

dances during EN conditions, such as *Undinula vulgaris* and *Candacia catula*. These species were correlated with high temperatures, low salinity, low upwelling, and increased MEI index (Fig. 7).

Species richness

During upwelling conditions, the composition of species remained identical except for the absence of *Canthocalanus pauper* in the ENM period (Table 2). The differences between NEN and EN periods of SM and S conditions were sharper. Before EN, the SM period had 10 species, but the number increased to 12 in the ENSM. Only 7 species were present in both periods. The same increase (from 10 to 12 species) was observed in the S period, accounting for 90% of total abundance.

Species richness by season showed that the semi-mixed and stratified water column conditions had the highest species richness within each interannual period (SM, S, ENSM and ENS). The M and ENM periods had a significantly lower species richness than all other periods ($F = 9.75$, p < 0.05). The richness of coastal/neritic forms was generally higher than oceanic species, especially during NEN semi-mixed and stratified periods. During ENM and ENSM there was a nearly equal number of both forms, although ENS also showed a higher number of coastal as opposed to oceanic species (Fig. 8).

Community analysis

The ANOSIM confirmed significant differences of the taxonomic composition of copepods between climatic periods (global *R*: 0.539, p < 0.05). Pair-wise comparisons indicated significant differences between each pair as well (*R*: 0.158 to 0.996, p < 0.05 in all cases). Based on the SIMPER analysis, dissimilarities ranged from 57.94 to 92.44. The highest dissimilarities generally occurred in comparisons of ENS
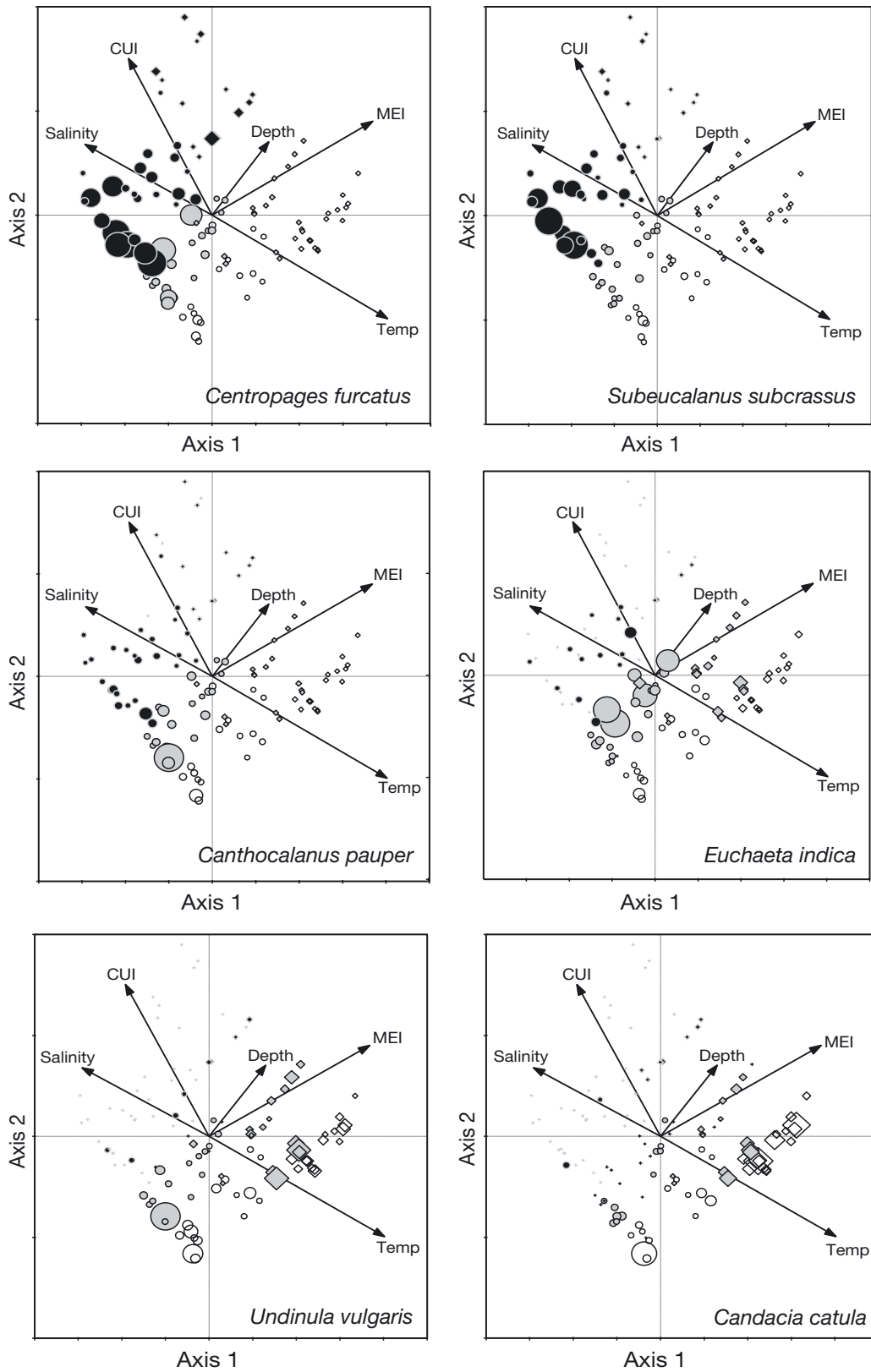
Fig. 7. Attribute plots of relative abundance of adult calanoid copepods during the 6 climatic periods. Defined periods are: mixed (●); semi-mixed (◐); stratified (○); El Niño mixed (◆); El Niño semi-mixed (◈); El Niño stratified (◇). Environmental variables are salinity (10 m), temperature (temp) (10 m), coastal upwelling index (CUI) and multivariate ENSO index (MEI)
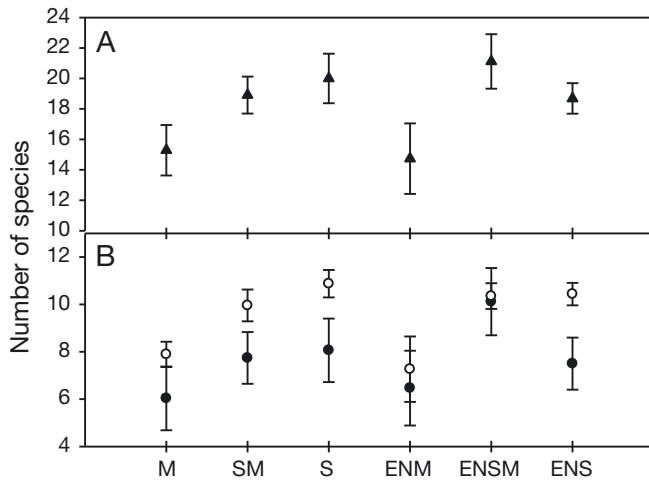
Fig. 8. Species richness of adult calanoid copepods per climatic period. (A) Mean species richness, (B) richness of oceanic species (●) and coastal/neritic species (○); bars are 95% confidence intervals. M: mixed period; SM: semi-mixed; S: stratified; ENM: El Niño mixed; ENSM: El Niño semi-mixed; ENS: El Niño stratified

with other periods. SIMPER taxonomic similarities within climatic periods were between 40 and 60%. At a cut-off of 50% contribution to similarity within the group, *S. subcrassus* dominated the NEN climatic periods (Table 4).

The analysis of the average abundance, changes in prosome length, and sex ratio of the 6 species respon-

sible for the 50% contribution to similarities in the SIMPER analysis provides an overview of their seasonal variability. Each of the species deemed representative of the NEN periods had a different pattern of peak abundances, in either M or SM periods. However, all had a significant decrease of their numbers during EN (Fig. 9). Each of the 3 species contributing to a higher similarity during EN conditions also had a different seasonal variability pattern; however, they shared an extremely reduced abundance in both M and ENM conditions (Fig. 10).

Sex ratio, prosome length, and specific abundance

The patterns of prosome length varied somewhat among seasons between species and sexes, but females of all species measured were larger than their male counterparts. Among the NEN-representative species, females of *Centropages furcatus* and *Subeucalanus subcrassus* had significantly smaller prosome lengths during the ENM period than during all other climatic periods, while the minimum male prosome size for both species was observed during the ENS period (Fig. 9). This pattern was also observed in *Undinula vulgaris* (Fig. 10). The other 3 species showed similar changes in prosome size among male and female across climatic periods.

Table 4. (A) Analysis of similarity (ANOSIM) indicating the dissimilarity between groups. *R*: results of the paired comparisons; DS: mean dissimilarity percentage for each paired group (both above the diagonal); p%: percentage result of test for significant differences between pairs (below diagonal). Significant differences in **bold**. (B) Similarity percentage (SIMPER) shows the group of adult calanoid copepod species contributing >50% similarity to each period. Av: average abundance (ind. m⁻³) in the group; %: mean contribution percentage to similarity. M: mixed period; SM: semi-mixed; S: stratified; ENM: El Niño mixed; ENSM: El Niño semi-mixed; ENS: El Niño stratified

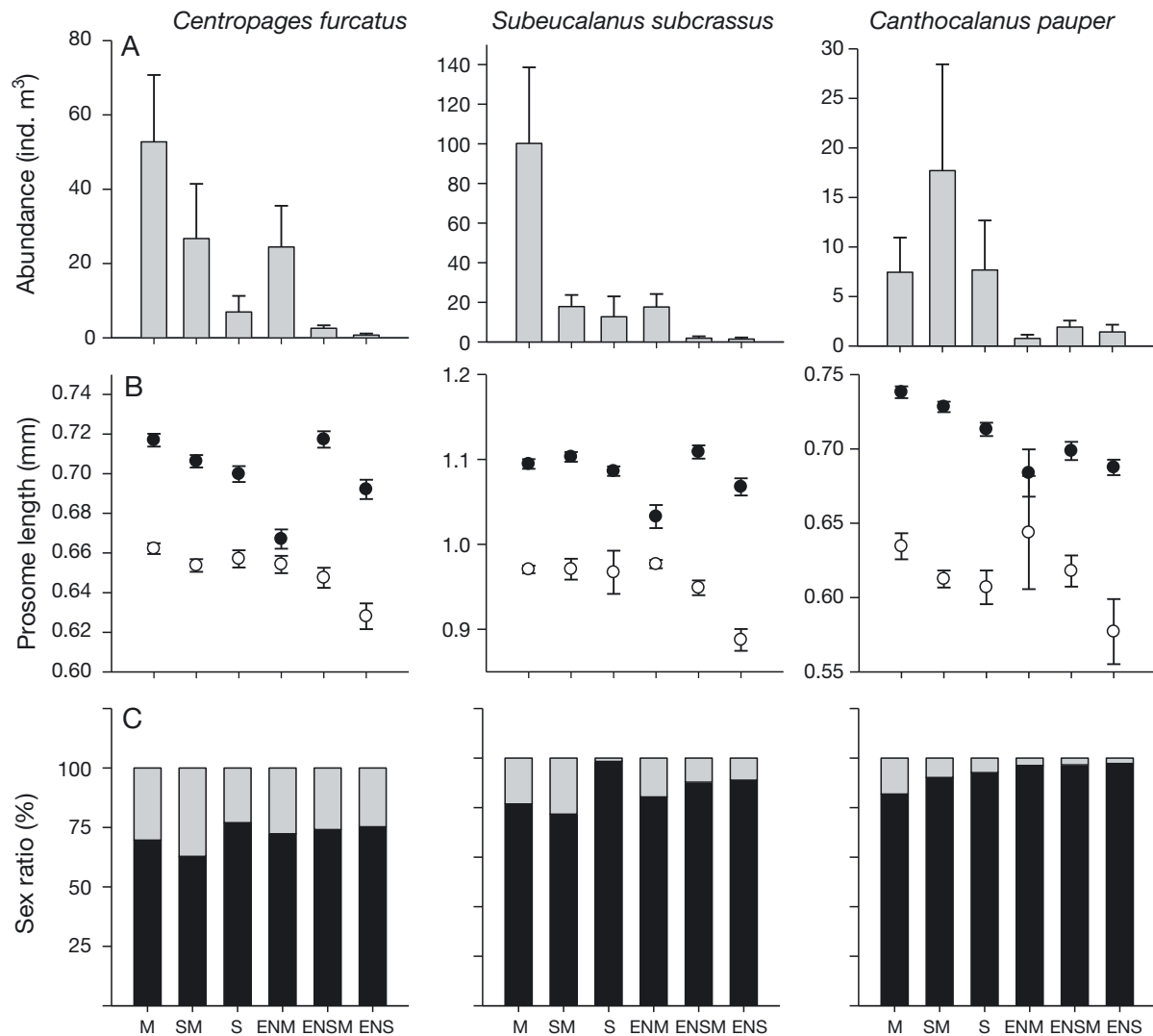|		M		SM		S		ENM		ENSM		ENS	
(A) ANOSIM				*R*	DS	*R*	DS	*R*	DS	*R*	DS	*R*	DS
M				0.281	66.41	0.463	75.20	0.725	64.24	0.810	87.14	0.894	92.44
SM	p%	**0.1**				0.158	61.97	0.271	57.94	0.640	72.74	0.862	82.72
S	p%	**0.1**		0.9				0.460	65.81	0.360	65.23	0.577	70.98
ENM	p%	**0.1**		**0.1**		**0.1**				0.888	78.18	0.996	86.82
ENSM	p%	**0.1**		**0.1**		**0.1**		**0.1**				0.489	61.51
ENS	p%	**0.1**		**0.1**		**0.1**		**0.1**		**0.1**			
(B) SIMPER													
Average similarity:		41.36		44.84		40.04		59.21		47.73		52.32	
Species		Av	%	Av	%	Av	%	Av	%	Av	%	Av	%
Subeucalanus subcrassus		99.98	52.26	17.83	27.93	12.70	20.34	17.64	42.89	1.90	8.30		
Centropages furcatus				26.71	23.97	6.95	13.98	24.45	46.91	2.56	15.03		
Canthocalanus pauper						7.67	20.60			1.92	10.20		
Euchaeta indica										4.08	20.56	1.54	13.77
Undinula vulgaris												1.90	17.80
Candacia catula												3.54	29.69
Total		52.26		51.9		54.92		89.8		54.09		61.26	

Fig. 9. Seasonal changes in adult non-El Niño representative species *Centropages furcatus, Subeucalanus subcrassus,* and *Canthocalanus pauper* of (A) mean abundance, (B) mean prosome length and (C) percentage of female (black) to male (gray); bars are 95 confidence intervals. Note different *y*-axis scales in (A) and (B). M: mixed period; SM: semi-mixed; S: stratified; ENM: El Niño mixed; ENSM: El Niño semi-mixed; ENS: El Niño stratified

The female:male sex ratio of most species showed a higher ratio of females to males, with some variations between climatic periods. The 2 exceptions to this pattern were *Candacia catula* and *Undinula vulgaris*, which apart from the M period when specific abundances were extremely low, had a uniform 1:1 sex ratio.

DISCUSSION

The local tropical coastal calanoid copepod species composition was fairly stable over the sampled period, although it showed a seasonal signal that was detectable even during the 1997-98 EN. Most of the species collected in the study area have been hitherto reported from waters of the Eastern Tropical Pacific (Palomares et al. 1998, Fleminger 1964, 1967, Razouls et al. 2014), but up to 35 species were recognized as new records. The total number of calanoid copepod species reported in the study area increased from 28 to 63 species (see Suárez-Morales et al. 2000). According to Razouls et al. (2014), up to 372 species of marine calanoid copepods have been known to occur in the ETP; thus only ~17% of this figure has been recorded in the surveyed area. More species would likely be recorded with the use of smaller mesh nets, greater sampling depths, and increased distances from the coast (Hopcroft et al. 2001).
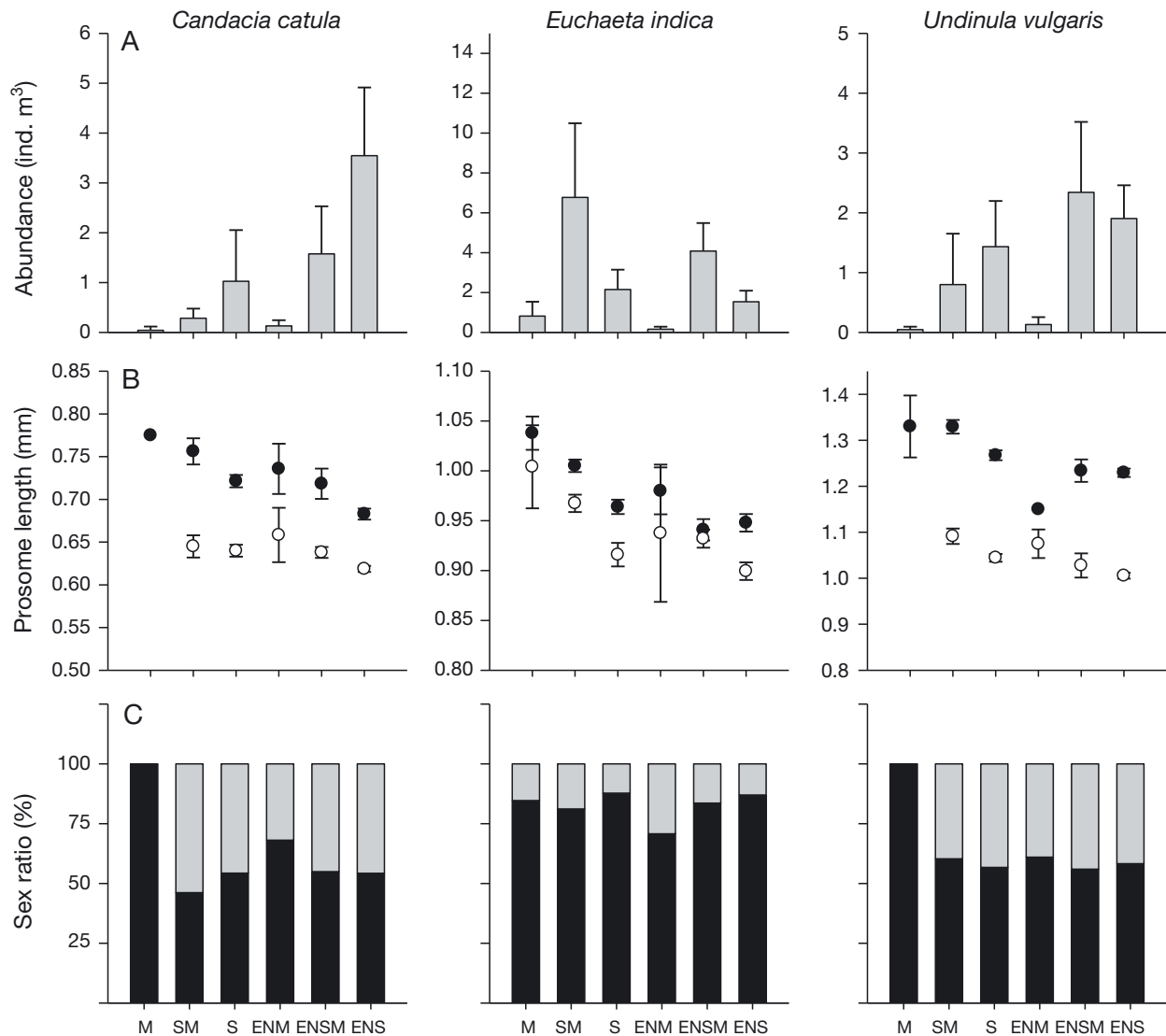
Fig. 10. Seasonal changes in adult El Niño representative species *Candacia catula, Euchaeta indica,* and *Undinula vulgaris* of (A) mean abundance, (B) mean prosome length and (C) percentage of female (black) to male (gray); bars are 95% confidence intervals. Note different *y*-axis scales in (A) and (B). M: mixed period; SM: semi-mixed; S: stratified; ENM: El Niño mixed; ENSM: El Niño semi-mixed; ENS: El Niño stratified

Non-El Niño

During the NEN period, we were able to characterize a complete 'normal' seasonal cycle, and the effects of hydrographic conditions on the calanoid copepod assemblage. The local copepod community reflected the seasonal signal through variations in its abundance and richness; this was also detectable at different conditions in the water column.

Mixed conditions (M)

Similar to that reported from temperate coastal ecosystems (Peterson 1998), during local upwelling

events only 4 to 5 species dominated the community, although the general species composition reflected the tropical character of the region. Hidalgo & Escribano (2001) suggested that in coastal zones with a shallow OMZ, the copepod diversity and abundance should increase during upwelling conditions. In our study, an increased abundance was observed during M conditions, but the richness was reduced as compared to other periods (SM and S). The local increase of the abundance was likely due to the greater availability of resources, similar to that reported from Bahía Magdalena, Baja California, with high copepod abundances and low species richness during upwelling conditions (Gómez-Gutiérrez et al. 2001). However, the upwelling period in Bahía Magdalena

was marked by the dominance of *Calanus pacificus* resulting from the influence of the California Current, whereas the fully tropical surveyed area was dominated by *Subeucalanus subcrassus.*

Gusmão & McKinnon (2009) and Gusmão et al. (2013) suggested that skewed sex ratios result from a variety of factors, including differential adult longevity, temperature, and food availability. Hirst et al. (2010) postulated that adult mortality in the form of sex-specific predation and differential longevity are the main drivers of skewed sex ratios. Realistically, it seems unlikely that one factor would principally contribute to the sex ratio across all copepods. Different seasonal patterns appeared among all of the species studied here, indicating that differences in sex ratios are likely due to a combination of elements from the above hypotheses. It would be ideal to research drivers of the sex ratio in various species of copepods that show differing patterns of the ratio, so as to understand more completely the different mechanisms affecting copepod sexes.

Semi-mixed (SM)

As might be expected, abundances during the transitional SM periods fell between those of M and S conditions. However, it is remarkable that these transitional periods are more than just a shift between M and S conditions. The RDA showed a well-defined transitional period, featuring erratic variations in temperature, salinity and upwelling conditions. Dur et al. (2007) found that a transitional period between monsoon seasons around Taiwan had a distinct community composition, resulting from mixing of temperate with tropical waters. In this study, species richness increased from M period levels, which could be correlated with the intrusion of oceanic water into the coast during periods of upwelling relaxation, bringing oceanic species into the surveyed area. However, there was no difference in the number of oceanic species between the NEN periods. There were significantly more coastal species during the SM period as compared to the M, indicating that the coastal species have more dynamic populations than those with oceanic affinities in the surveyed region. In addition, coastal species were responsible for the increase in species richness. This was probably an effect of the Mexican Coastal Current, which flows poleward along the coast in the summer, bringing new members of tropical neritic communities into the region.

Stratified (S)

Stratified (S) conditions were defined by a relaxation of the upwelling, a deeper thermocline, and an increased sea surface temperature. Tropical water, with a lower salinity and higher temperature than seen during upwelling periods, was brought into the region by the Mexican Coastal Current. Under these conditions, the copepod community showed an increased richness and reduced abundance. Despite the seasonal changes between periods, NEN conditions were not accompanied by a reorganization of the dominant copepod species as reported in other temperate or tropical areas (Raymont 1983, Fernández-Álamo et al. 2000). *Subeucalanus subcrassus* retained the highest abundance, although greatly reduced from M conditions. In Bahía Magdalena, high abundance and low species richness during upwelling conditions also shifted to a more diverse community, with lower biomass during upwelling relaxation and stratification of the water column (Gómez-Gutiérrez et al. 2001). This process also included a shift in the local dominance of species: temperate forms were dominant during upwelling, whereas tropical species dominated during upwelling relaxation conditions as warm waters invaded the region. This response was not observed in our study, as tropical/equatorial species remained dominant throughout the entire study period.

El Niño

It was expected that many calanoid copepod species would be incorporated into the local zooplankton community as a result of the increased influence of tropical-equatorial waters resulting from the EN event (see Lavaniegos et al. 2003, Palomares-García et al. 2003, Gasca et al. 2012), but this was not the case. Only 6 species with no prior record in the region were registered during and/or after the EN event, and all had very low abundance. Considering that there were 35 total new records in the region, it seems unlikely that many of those species were responding to the effects of EN. The possible exception is *Euchaeta magniloba,* which was present after EN and had not been previously recorded in the Mexican Pacific. While there was a moderate change in the composition among seasons as well as between the NEN and EN periods, the same 5 species were present across almost all defined climatic periods. The overall copepod abundance declined during EN, but the general seasonal pattern observed, i.e. with

highest abundances during mixed periods and lowest during stratified conditions, remained during the EN event. Overall, the local copepod community appears to be one of the more stable among the different zooplankton groups studied in the area, many of which are deeply affected by EN events (Franco-Gordo et al. 2004, Gasca et al. 2012).

Mixed (ENM)

When compared to the M period, the ENM period showed lower abundances, which is explained by the lower abundance of the dominant species during that period. A brief depression in abundance was observed off Monterey Bay, California, after the peak of EN, affecting larger-bodied copepods more than smaller forms (Hopcroft et al. 2002). Off southern Chile, total copepod abundance also declined during EN (Hidalgo & Escribano 2001). In addition, a decline of the abundance of zooplankton and ichthyoplankton taxa has been reported (Franco-Gordo et al. 2004); hence, a local decrease of the copepod abundance was also expected. An increase in species richness would be expected during the ENM period as well, based on the increase reported for hyperiid amphipods in the region (Gasca et al. 2012). However, this was not the case and species richness remained low, as seen in the M period.

Semi-mixed (ENSM)

The transitional periods from NEN to EN conditions had pronounced changes in the composition of dominant species. This period had the highest influx of oceanic species, and was the only period with a significant difference in the average number of oceanic species ($F = 5.04$, $p < 0.05$). The increase in oceanic species during the ENSM period could be an effect of the EN, bringing a more diverse population into the area of study. It appears ENSM periods are more dynamic transitions than the NEN transitional periods, with the effects of EN converging with the normal conditions of variability in the water column during this period.

Copepods are smaller at higher temperatures; however, it is worth noting here the female prosome size of several species deviated from this pattern during the ENM period. Although the temperatures were cooler than in ENS, *Centropages furcatus*, *Subeucalanus subcrassus*, and *Undinula vulgaris* all had significantly smaller prosomes during the ENM.

These species are herbivorous/omnivorous copepods; their smaller body size during this period could be a result of the observed decrease of food availability. Interestingly, males did not follow the same pattern, maintaining a similar prosome length to previous periods. This could be an expression of a differential growth response to resource availability based on diverging reproductive requirements between sexes.

Stratified (ENS)

The ENS period had the most distinct changes of all the climatic periods. Both S and ENS were the only 2 correlative seasonal periods with completely different taxonomic groups at the 50% total copepod abundance level. The onset of the EN coincided with the local period of stratified water column conditions. The first half of EN was the strongest, with high temperature anomalies (Filonov & Tereshchenko 2000), and possibly for this reason, the effects were more notable on the local copepod community. During EN, copepod communities off Baja California showed a marked increase (75%) of tropical species. A similar response of increased diversity and lower abundance in the surveyed region during November 1997 was also reported (Jiménez-Pérez & Lavaniegos 2004, López-Ibarra & Palomares-García 2006).

There is a bias in the sampled data, given that the mesh of the plankton net was much coarser than generally recommended for planktonic copepods. Many smaller species were likely under-sampled, as well as the copepodite stages of larger ones. For this reason we chose to identify and enumerate adult calanoid copepods, which tend to be larger than other orders and make an important contribution to the abundance and biomass in the copepod community. This is not completely without antecedent in copepod studies. Rebstock (2001, 2002) used samples taken by CalCOFI with a 505 µm mesh net to analyze calanoid copepods. Other investigations nearer to the region of study used similar sized mesh nets (Jiménez-Pérez & Lavaniegos 2004, IMECOCAL, Fernández-Álamo et al. 2000). Although taxonomic groups with smaller copepods such as *Oithona* were left out of the analysis, this study still provides a valuable insight into the effects of El Niño and seasonal changes in an under-studied coastal tropical plankton community.

Overall, the variability of the local calanoid copepod community can be explained by (1) seasonal patterns of upwelling and non-upwelling periods, (2) the stable tropical-equatorial profile of the local fauna, and (3) the effect of EN on the abundance and rich-

ness. The seasonal transitions appear to have the strongest impact on the community. Nonetheless, the structure of the community in this region was relatively stable, without the radical changes in composition that are typical of a transitional oceanic region. The occurrence of oceanic species along the surveyed area could be related to the narrowness of the continental shelf, as this intergradation has been observed in other tropical communities from a narrow shelf region (Suárez-Morales & Gasca 1997, 2000). The neritic conditions of the surveyed area could explain part of this stability; future surveys from fully oceanic areas are likely to provide useful information to understand the effect of the shelf in the local oceanographic dynamics. Studies on the reproduction, feeding habits and vertical distribution of these tropical species would be valuable.

This work provides a more detailed insight of the biological–physical coupling of the most abundant group of the zooplankton community, and it is interesting to note the contrasting responses of different zooplankton taxa to the same set of hydrographic conditions (Gasca et al. 2012, Ambriz-Arreola et al. 2012). The response of a given zooplankton taxon to seasonal and interannual conditions in the region should be studied separately and cannot be extrapolated to other taxonomic groups. It is likely that some of these changes are responses to local processes of competition and/or predation. The low abundance of copepods during EN conditions could have been intensified as a result of competition with euphausiids or other pelagic herbivores. Adults of tropical euphausiids are opportunistic omnivores, whereas larval stages feed primarily on phytoplankton and microzooplankton (Mauchline & Fisher 1969). Levels of phytoplankton in the eastern Pacific were reduced during EN, including regions close to the area of study (Strutton & Chavez 2000, Kahru et al. 2004). Ambriz-Arreola et al. (2012) found little change in euphausiid abundances during EN. This could indicate an increased predation by euphausiids on copepods in response to reduced food availability, as has been seen in other interactions between the groups (Atkinson & Snÿder 1997). The reduced food availability together with increased competition and predation would directly affect abundances of herbivorous and omnivorous copepods. Previous surveys in the area during the 1997-98 EN (Franco-Gordo et al. 2002, 2004) described a clear impoverishment of the zooplankton biomass and fish larvae during EN. Given the high level of predation on copepods (>80%) by the abundant fish larvae in the area (Siordia-Cermeño et al. 2006), it is to be expected that lower abundances of copepods would be reflected in a decrease of larval abundances as well.

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